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Biogeography of northern European insects: province records in multivariate analyses (Saltatoria; Lepidoptera: Sesiidae; Coleoptera: Buprestidae, Cerambycidae)

Rauno Väisänen, Kari Heliövaara & Auli Immonen

Väisänen, R., Water and Environment Research Institute, P.O. Box 250, SF-00101, Finland
Heliövaara, K. & Immonen, A., Finnish Forest Research Institute, P.O. Box 18, SF-01301 Vantaa, Finland

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Species lists of Saltatoria, Sesiidae, Buprestidae and Cerambycidae from 101 provinces in Fennoscandia and Denmark were classified by two-way indicator species analysis and ordinated by detrended correspondence analysis and canonical correspondence analysis. The distributional patterns obtained agreed roughly with the vegetation zones presented earlier, especially in Finland and Sweden, but the extension of southern vegetation zones northwards along the Atlantic coast can hardly be discerned in the present results. Group-specific differences in details were apparent. The most important determinants of the biogeographical variation were temperature variables associated with latitude; in comparison with these annual precipitation and longitude were poor determinants. The application of multivariate analyses to province records of insects showed that even the limited species lists now existing can be used in quantitative biogeography. This approach is also discussed in relation to global climatic change.

1. Introduction

Organisms often show biogeographical patterns, which can be associated with the climate, vegetation and history of the area. In particular, the numbers of species have been recognized to increase from high to low latitudes (Fisher 1960). In northern Europe, biogeographical zonation has been studied chiefly in plants (Ahti et al. 1968) and birds (e.g. Järvinen & Väisänen 1978). A clear transition from southern to northern floristic elements can be seen even within the borders of Finland (Lahti et al. 1988). In insects, these patterns have usually been studied by visual examination of distribution maps or by simple comparisons with vegetational zones. Direct application of botanical zones to entomological data seems unwarranted, but *a posteriori* comparisons may be interesting.

Multivariate analysis techniques, such as canonical correspondence analysis (CCA), have recently been developed to relate community composition directly to the known variation in the environment (Ter Braak 1985b, 1986, Ter Braak & Prentice 1988). Techniques such as detrended correspondence analysis (DCA) have also been used to extract the dominant pattern of variation in community composition by ordination of the species data (Hill & Gauch 1980). An attempt has then been made to relate this pattern indirectly to the environmental variables (Gauch 1982). These approaches are called direct and indirect gradient analyses. Gradient analyses have also been applied to biogeographical data (Peet 1978, Luff et al. 1989, Eyre et al. 1990). Two-way indicator species analysis (TWINSPAN) has been used to classify insect communities (Eyre & Foster 1989, Eyre et al. 1989).

Here, we test the suitability of these techniques with province records of northern European insects. Data on the distributions of individual species are readily available in tables and figures, including those in the comprehensive series of entomological handbooks, Fauna Entomologica Scandinavica. This series covers Fennoscandia (i.e. Norway, Sweden, Finland and some northwestern parts of the U.S.S.R) and Denmark. Since quantitative biogeographical analyses are usually missing, we selected four volumes of this series for a preliminary examination. The distribution of these terrestrial insect groups is fairly well known in northern Europe. The numbers of species in the groups ranges from 17 to 120 and three of them are predominantly associated with woody plants, while the fourth (Saltatoria) is a group of open ground. The purpose of the present study is to ordinate and classify species and provinces on the basis of these data and relate them to some environmental variables. Although many biogeographical data have been gathered on insects, they have largely been left untreated.

2. Material and methods

The distribution of the Saltatoria, Sesiidae, Buprestidae and Cerambycidae were used in the analyses. The numbers of species in these groups were 42, 17, 43 and 120, excluding the imported species. The province records were obtained from Holst (1986), Fibiger & Kristensen (1974), Bílý (1982) and Bílý & Mehl (1989), respectively. The biological data used in interpreting the patterns that emerged came from the same sources.

A list of the abbreviations and full names for the provinces and maps of the study area are given, for instance, in every volume of Fauna Entomologica Scandinavica. The study area consisted of 101 provinces (Fig. 1), which mostly correspond to the so-called biogeographical provinces. The most significant differences concern the provinces of the U.S.S.R. (for details, see Leikola 1985).

The nomenclature follows the above-mentioned references. The species names are given in full in Tables 1, 3, 5 and 7. In the figures, abbreviations are used, consisting of four letters of the generic name and four of the species name. There is one exception in Cerambycidae: *Pogo hisp* = *Pogonocherus hispidus*, and *Pogo hisl* = *Pogonocherus hispidulus*.

The statistical programs used in the analyses were TWINSPAN (Hill 1979a), DECORANA (Hill 1979b) and CANOCO (Ter Braak 1985a). Although these methods are sensitive to deviating samples, no samples have been omitted, because they may have biogeographic significance. In the two-way indicator species analyses, the number of indicators was 7 for Saltatoria, 4 for Sesiidae, 3 for Buprestidae and 10 for Cerambycidae (6 for both species trees of Coleoptera). The maximum level of divisions was 5 for Cerambycidae and 4 for the others (5 for buprestid species tree). In the DCAs, detrending by segments was used, while in the CCAs detrending by second order polynomials was used. In the weighted averaging methods (DCA, CCA), the eigenvalue is a measure of 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), reduced to sea level in 1921–1950, and *effective temperature sum* of vegetative period (in ddu) (ETS) when absolute altitude has been taken into account (Laaksonen 1979);

Annual precipitation (PRE) using the scale: 1 = <500 mm, 2 = 500–600, 3 = 600–1000, 4 = 1000–2000 and 5 = >2000 mm (Hultén 1950); 0.5 was added to the lower value in borderline cases;

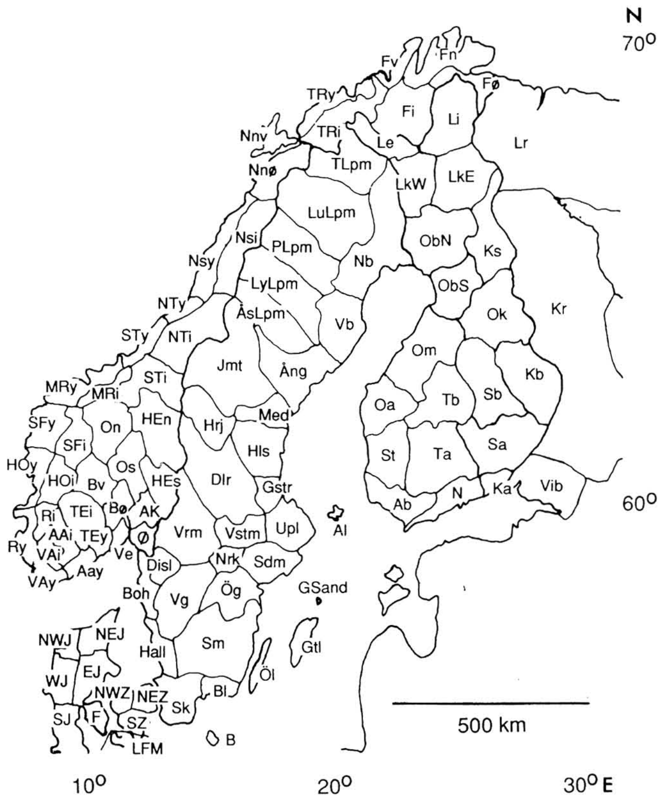

Fig. 1. A map of the study area with the abbreviations of the provinces.

Vegetation zones (VEG): 1. atlantic, 2. subatlantic, 3. hemiboreal, 4. southern boreal, 5. middle boreal, 6. northern boreal and 7. arctic-alpine (Kalliola 1973);

Distribution of Picea abies (L.) Karst. (PIC) and *Pinus sylvestris* L. (PIN) using the scale: 0 = absent, 1 = scattered, 2 = intermediate and 3 = continuous (Hultén 1950).

Values for the variables PIC and PIN were determined according to the general distribution of these trees in a given province, while the values of other variables represent the areal midpoint. The arrow lengths in the CCA ordination diagrams give an idea of the significance of the environmental variables. The arrow points roughly in the direction of maximum variation in the value of the variable. The Monte Carlo permutation tests of CCA were carried out by randomly permuting 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 CCA are the coefficients of a weighted multiple regression of the sample scores on the standardized environmental variables. Student's *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 value, the variable does not greatly increase the contribution of the other variables in the analysis to the fit of the species data. The variable thus does not have an effect that is uniquely attributable to it and it can therefore be deleted without strongly affecting the canonical eigenvalues.

The inter-set correlations of 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 correlated with each other. The fraction of total variance in the stand-

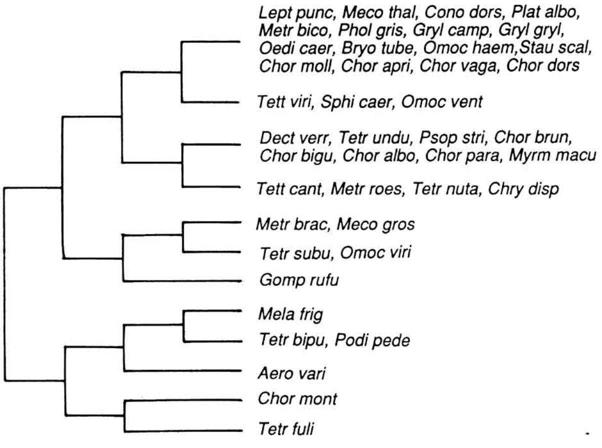

Fig. 2. A dendrogram of a two-way indicator species analysis (TWINSPAN) using the Saltatoria data.

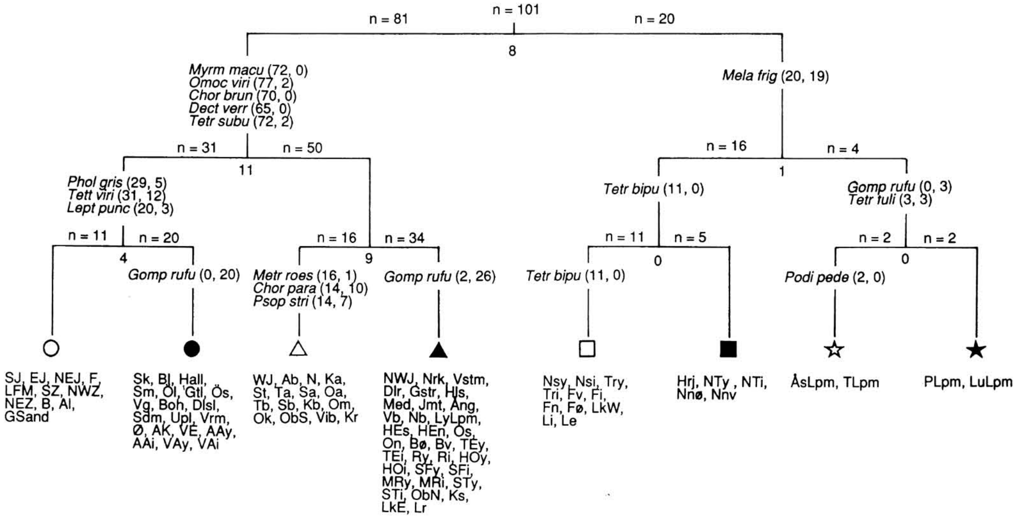

Fig. 3. A province dendrogram of the TWINSPAN using the Saltatoria data. Numbers in parentheses are the frequencies of each indicator species in the left- and right-hand cluster. The number of borderline and misclassified plots is indicated at each division.

ardized 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 makes no unique contribution to the regression equation. Its canonical coefficient is consequently unstable and does not merit interpretation (Ter Braak 1986).

3. Results and discussion

3.1. Saltatoria

A TWINSPAN dendrogram shows 12 distributional groups of species (Fig. 2). The primary division cannot easily be related to rough habitat preferences or general distribution. However, one branch was formed by the species with Holarctic distribution (*Melanoplus frigidus*, *Chorthippus montanus*, *Tetrix fuliginosa*) and three species with more or less northern distribution. The other main branch included species with western Palaearctic distribution and species preferring dry open habitats such as steppes.

The provinces were classified into eight groups according to their fauna by TWINSPAN (Fig. 3). The left branch of the primary division was characterized by *Myrmeleotettix m. maculatus*, *Omocestus viridulus*, *Chorthippus b. brunneus*, *Decticus verrucivorus* and *Tetrix subulata,* and the right branch by *Melanoplus frigidus*. The southern Scandinavian provinces were characterized by *Pholidoptera griseoaptera*, *Tettigonia viridissima* and *Leptophyes punctatissima* (province groups 1–2). Among these, the Danish provinces lacked *Gomphocerus rufus*. The indicator species of the mainly Finnish group 3 were *Metrioptera roeseli*, *Chorthippus p. parallelus* and *Psophus stridulus*, while the central Scandinavian group 4 was characterized by *Gomphocerus rufus*.

The number of provinces in the TWINSPAN groups varied between 2 and 34 (Fig. 4). Most of Denmark, Gotska Sandön and Aland formed a group with a sister group in southern Sweden and Norway. Large areas of central Norway and Sweden with extensions in NW Jylland, northern Finland and Russian Lapland also formed a group. Its sister group almost entirely covered southern

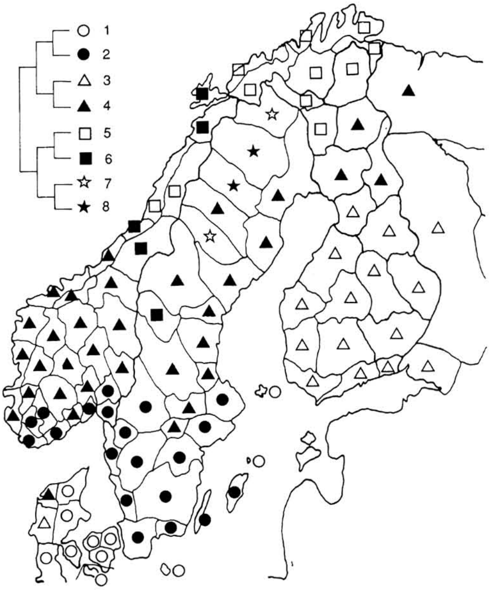

Fig. 4. Distribution of the provinces in the groups interpreted from the TWINSPAN analysis of the Saltatoria data. The numbers refer to Table 1.

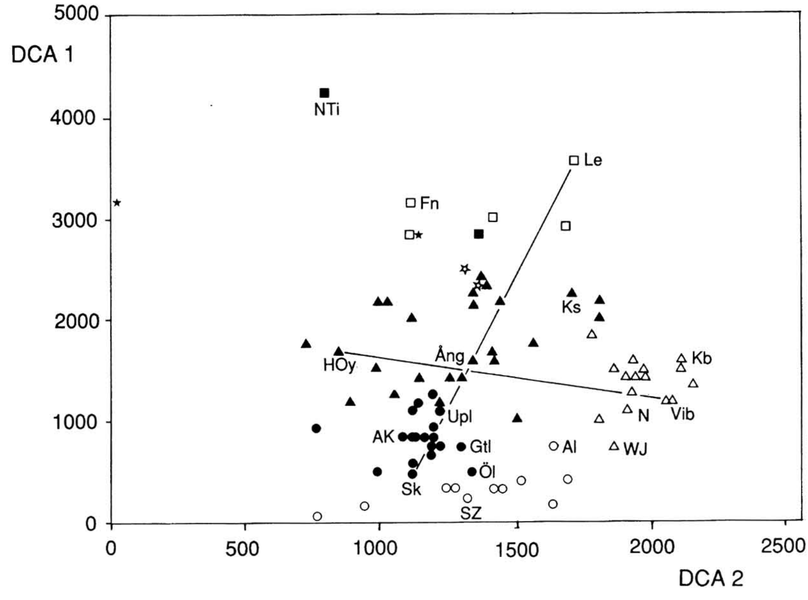

Fig. 5. The provinces plotted on the 1st and 2nd axes (eigenvalues 0.38 and 0.14) of the detrended correspondence analysis ordination (DCA) using the Saltatoria data. Symbols of provinces as in Figs. 3–4. Seventeen provinces are named and to help interpretation lines connect the southern province Sk with northern Le, and western HOy with eastern Vib.

and central Finland with adjacent areas in the U.S.S.R. The rest of the groups contained northern and mountainous provinces.

A DCA ordination gave a very similar picture (Fig. 5) and the clusters of provinces corresponded well with those classified by TWINSPAN.

The northern provinces lay in the upper part of the diagram and the southern ones in the lower part, and similarly, the western provinces on the left and the eastern on the right. The Danish group 1 (e.g. WJ) and the Finnish group 3 seemed to be more connected than their geographical

Table 1. Frequency table showing the percentage occurrence of species of Saltatoria in eight province groups interpreted from the TWINSPAN analysis. Numbers in italics indicate percentages over 70 %. Species order is as given by the TWINSPAN analysis. The number of provinces in each group is given in parentheses.

Province group:	1 (11)	2 (20)	3 (16)	4 (34)	5 (11)	6 (5)	7 (2)	8 (2)
Leptophyes punctatissima (Bosc, 1792)	64	65	–	9	–	–	–	–
Meconema thalassium (DeGeer, 1773)	*73*	45	–	–	–	–	–	–
Platycleis albopunctata (Goeze, 1758)	54	60	–	–	–	–	–	–
Metrioptera bicolor (Philippi, 1830)	–	5	–	–	–	–	–	–
Pholidoptera griseoaptera (DeGeer, 1773)	*100*	*90*	31	–	–	–	–	–
Gryllus campestris Linnaeus, 1758	9	–	–	–	–	–	–	–
Gryllotalpa gryllotalpa (Linnaeus, 1758)	64	30	–	–	–	–	–	–
Oedipola caerulescens (Linnaeus, 1758)	18	5	–	–	–	–	–	–
Omocestus haemorrhoidalis (Charpentier, 1825)	18	20	–	–	–	–	–	–
Stauroderus scalaris (Fischer–Waldheim, 1846)	–	5	–	–	–	–	–	–
Chorthippus apricarius (Linnaeus, 1758)	54	30	–	–	–	–	–	–
Chorthippus vagans (Eversmann, 1848)	9	–	–	–	–	–	–	–
Chorthippus dorsatus (Zetterstedt, 1821)	*73*	30	6	3	–	–	–	–
Conocephalus dorsalis (Latreille, 1804)	*91*	60	37	–	–	–	–	–
Tettigonia viridissima (Linnaeus, 1758)	*100*	*100*	12	29	–	–	–	–
Sphingonotus c. caerulans (Linnaeus, 1767)	–	45	19	6	–	–	–	–
Omocestus ventralis (Zetterstedt, 1821)	–	*85*	6	21	–	–	–	–
Chorthippus m. mollis (Charpentier, 1825)	18	–	6	–	–	–	–	–
Decticus verrucivorus (Linnaeus, 1758)	*91*	*100*	*100*	56	–	–	–	–
Tetrix undulata (Sowerby, 1806)	*91*	*90*	12	50	–	20	–	–
Psophus stridulus (Linnaeus, 1758)	–	*85*	*87*	21	–	–	–	–
Bryodema tuberculata (Fabricius, 1775)	18	5	19	3	–	–	–	–
Chorthippus b. brunneus (Thunberg, 1815)	*91*	*100*	*100*	71	–	–	–	–
Chorthippus b. biguttulus (Linnaeus, 1758)	*91*	*85*	*75*	23	–	–	–	–
Chorthippus a. albomarginatus (DeGeer, 1773)	*91*	*100*	69	32	–	–	–	–
Chorthippus p. parallelus (Zetterstedt, 1821)	*82*	*80*	*87*	29	–	–	–	–
Myrmeleotettix m. maculatus (Thunberg, 1815)	*91*	*100*	*100*	*76*	–	–	–	–
Tettigonia cantans (Fuessly, 1775)	27	–	44	–	–	–	–	–
Metrioptera roeseli (Hagenbach, 1822)	18	–	*100*	3	–	–	–	–
Tetrix nutans (Hagenbach, 1822)	–	–	50	–	–	–	–	–
Chrysochraon d. dispar (Germar, 1831–35)	9	10	56	9	–	–	–	–
Metrioptera brachyptera (Linnaeus, 1761)	54	*95*	*100*	53	–	–	50	50
Mecostethus grossus (Linnaeus, 1758)	*82*	*95*	*100*	59	9	–	*100*	–
Omocestus viridulus (Linnaeus, 1758)	*91*	*100*	*100*	*91*	9	20	–	–
Tetrix subulata (Linnaeus, 1758)	*82*	*90*	*100*	*85*	18	–	–	–
Gomphocerus rufus (Linnaeus, 1758)	–	*100*	12	*76*	–	–	50	*100*
Tetrix fuliginosa (Zetterstedt, 1828)	–	–	19	21	27	–	*100*	50
Melanoplus frigidus (Boheman, 1846)	–	–	19	50	*100*	*100*	50	*100*
Aeropedellus variegatus (Fischer–Waldheim, 1845)	–	–	–	3	9	–	–	–
Tetrix bipunctata (Linnaeus, 1758)	18	*85*	*94*	*100*	*100*	–	–	–
Podisma pedestris (Linnaeus, 1758)	–	*80*	*94*	*85*	*100*	–	*100*	–
Chorthippus montanus (Charpentier, 1825)	–	30	50	41	9	20	–	–

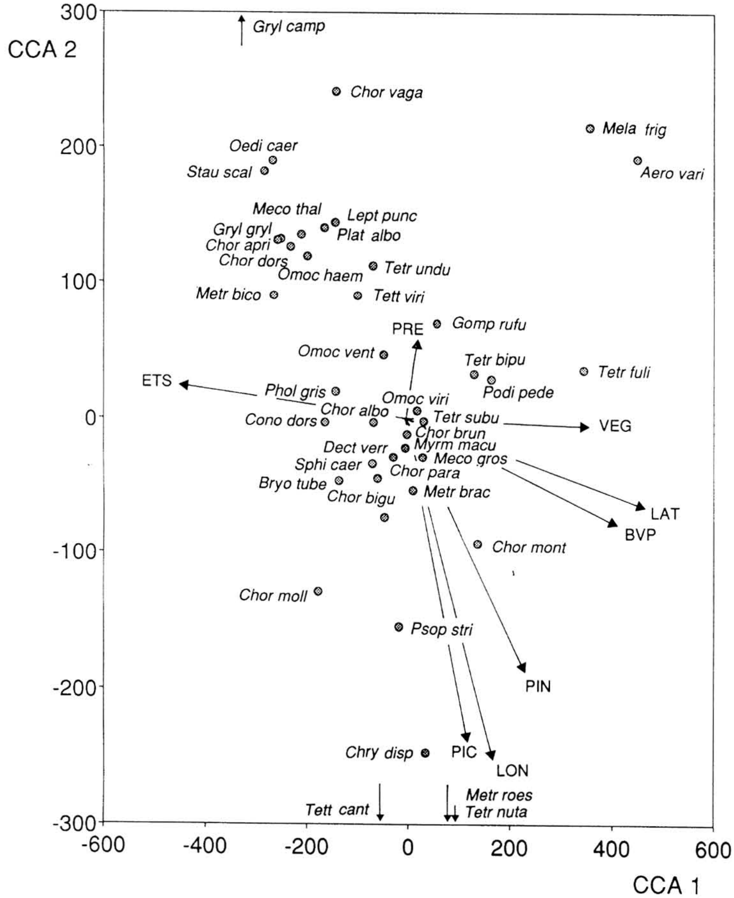

Fig. 6. Ordination diagram based on canonical correspondence analysis (CCA) of the distribution of Saltatoria in northern European provinces with respect to eight environmental variables. The species abbreviations consist of the first four letters of their generic and specific names (see Table 1). The 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).

location would have predicted, while group 3 was separated distinctly from the southern Norwegian and Swedish group 2.

The frequency of occurrence of species in the province groups is shown in Table 1. None of the species occurred in all groups. The species richness was much higher in the first four groups, representing the southern provinces, than in the others.

The faunistic data were related to variation in the environment using CCA (Fig. 6). The Monte Carlo permutation test showed that the species are related to the environmental variables (99 random permutations, $P < 0.01$). The same result was obtained for the other insect groups. The canonical coefficient of the latitude (LAT) obtained a very high absolute value on the first axis (Table 2). The beginning of the vegetative period (BVP), the distribution of *Picea abies* (PIC) and the longitude (LON) had negative coefficients but added little to the fit of the species data. The fraction of the total variance in the standardized environmental data extracted by species axis 1 was 48.6 %, that extracted by axis 2 was 20.8 %, and that by axis 3 was 14.5 %. The effective temperature sum (ETS) associated with the latitude, the beginning of the vegetative period and the vegetation zone (VEG) seem to determine the trends in the assemblages of Saltatoria along axis 1. This axis correlates fairly strongly with these variables, positively (latitude, beginning of vegetative period, vegetation zone) or negatively (effective temperature sum) (Table 2). Longitude (LON) and precipitation (PRE) seem important for the faunal composition along axis 2.

Table 2. Canonical coefficients and the inter-set correlations of environmental variables with the first three axes of canonical correspondence analysis (CCA) in Saltatoria. Canonical coefficients with the *t*-value higher than 2.0 in absolute value are indicated by *. VIF = variance inflation factor.

Variable	Canonical coefficients			Correlation coefficients			VIFs
Axis:	1	2	3	1	2	3	
Eigenv.:	0.32	0.14	0.09				
LAT	0.80*	–0.22*	0.15	0.90	–0.16	0.05	17.66
LON	–0.11	–0.54*	0.30*	0.33	–0.63	0.32	4.17
BVP	–0.14	0.55*	–0.15	0.76	–0.20	0.17	19.03
ETS	–0.05	0.01	–0.01	–0.87	0.06	0.07	12.12
PRE	–0.03	–0.11*	–0.07	0.03	0.14	–0.31	2.45
VEG	0.02	–0.01	0.02	0.68	–0.01	–0.17	3.24
PIC	–0.13	–0.21*	–0.15*	0.23	–0.59	–0.41	8.48
PIN	0.07	0.07	–0.23*	0.45	–0.46	–0.49	9.65

The 45 species of Saltatoria native to northern Europe are only a small fraction (6 %) of the number found in the whole of Europe. The large numbers of species found in southern and eastern Europe may be explained by the higher temperatures and greater number of hours of sunshine in summer (Holst 1986). Our results are consistent with this explanation, emphasizing the significance of latitude and associated temperature variables.

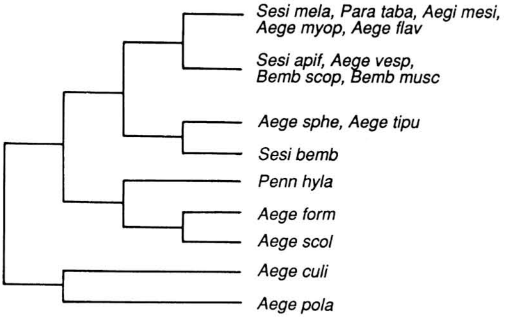

Fig. 7. A dendrogram of a two-way indicator species analysis (TWINSPAN) using the Sesiidae data.

3.2. Lepidoptera: Sesiidae

A TWINSPAN dendrogram shows nine distributional species groups (Fig. 7). Northern *Synanthedon polaris* (*Aege pola*) and the widely distributed *S. culiciformis* (*Aege culi*) formed a sister group to the others, but it is difficult to find a common biological background for the further divisions.

The provinces were classified into 10 groups according to their fauna by the TWINSPAN (Figs. 8–9). Six groups consisted of one or two provinces, and the other four groups belonged to one branch, in which the indicator species were *Sesia apiformis* and *Pennisetia hylaeiformis*. More than half of the provinces belonged to a group characterized by *Paranthrene tabaniformis*, while its sister group was characterized by *Bembecia scopicera* and *B. muscaeformis*. Most of Denmark and southern Sweden form a group, as do also most of central Sweden, southern Norway and southern and central Finland.

A DCA ordination emphasizes provinces with a deviating sesiid fauna (e.g. STy, Bv; Fig. 10), but southwestern (white triangles), central (black triangles) and northern provinces (white quadrats) can still be recognized as groups. The frequency of occurrence of species was highest in provinces with triangle codes (Table 3), while few species live in the other provinces.

A CCA ordination diagram illustrates the Sesiidae fauna in relation to the environmental variables (Fig. 11). The canonical coefficients of the effective temperature sum obtained the highest absolute value on the first axis, and apart from precipitation the other variables made little contribution to the fit of the species data (Table

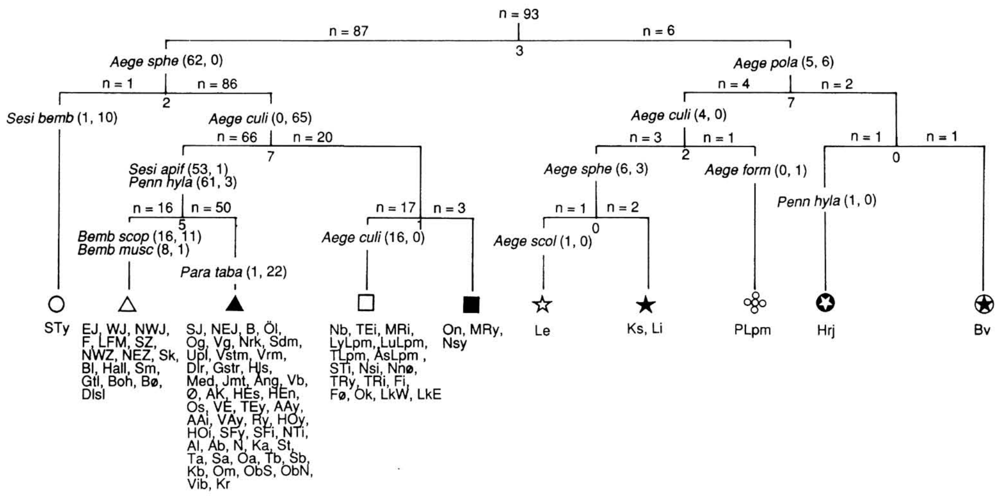

Fig. 8. A province dendrogram of the TWINSPAN using the Sesiidae data. Numbers in parentheses are the frequencies of each indicator species in the left- and right-hand cluster. The number of borderline and misclassified plots is indicated at each division.

4). The second axis was related to the beginning of the vegetative period and the precipitation. However, the canonical coefficient of the beginning of the vegetative period correlated strongly with other environmental variables, as is indicated by the high value of the VIF. The fraction of the total variance in the environmental data extracted by species axis 1 was 21.1 %, while axis 2 extracted 18.6 %, and axis 3 extracted 3.9 %. The effective temperature sum together with the latitude and vegetation zone seems to determine the species composition along axis 1. Axis 2 was related to the distribution of *Pinus sylvestris* (PIN), the distribution of *Picea abies*, and the longitude. Roughly, the southwestern species lay in the upper part of the diagram and the eastern ones on the lower left-hand side, while northern *Synanthedon polaris* lay on the extreme right.

About half of the Scandinavian species occur in all four countries and extend northwards beyond the Arctic Circle. The distributions of individual species have been discussed by Fibiger & Kristensen (1974). They pointed out that the species diversity of sesiids associated with herbaceous plants diminishes much more rapidly towards the north of Europe than does that of the wood-borers. Only two of the 23 herb-feeding European species occur in the study area. Our results show that the composition of the wood-boring species assemblage is largely correlated with temperature variables.

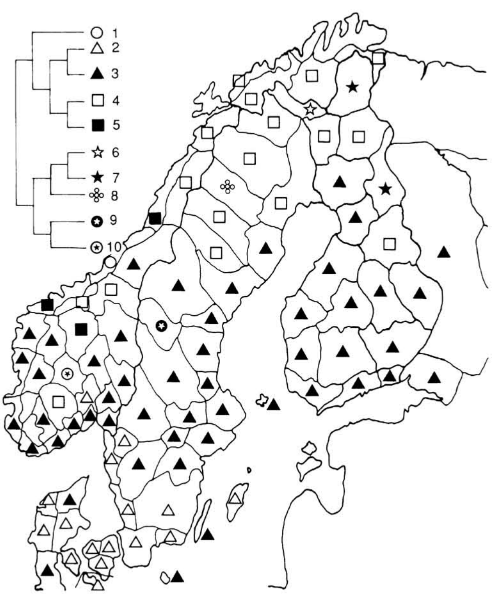

Fig. 9. Distribution of the provinces in the groups interpreted from the TWINSPAN analysis of the Sesiidae data. The numbers refer to Table 3.

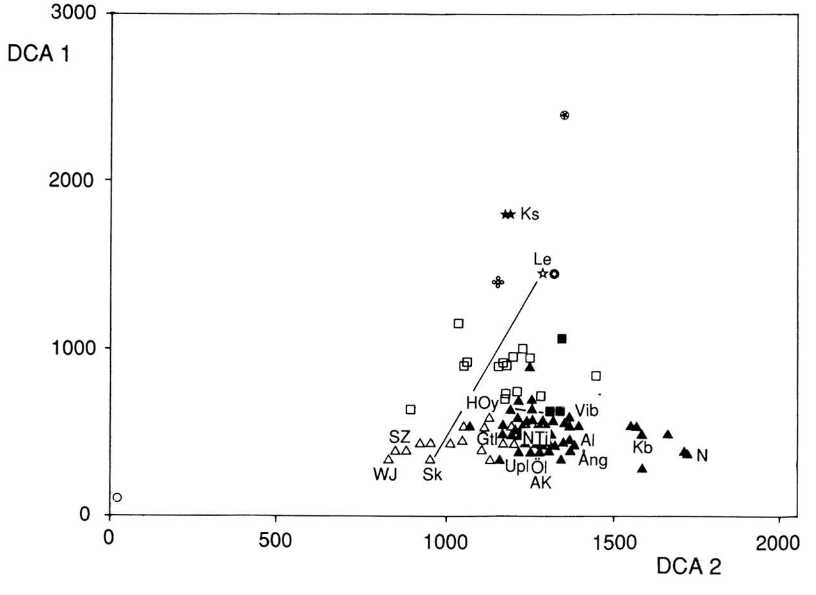

Fig. 10. The provinces plotted on the 1st and 2nd axes (eigenvalues 0.38 and 0.16) of the detrended correspondence analysis ordination (DCA) using the Sesiidae data. Symbols of provinces as in Fig. 8–9, lines as in Fig. 5.

Fig. 11. Ordination diagram based on canonical correspondence analysis (CCA) of the distribution of Sesiidae in northern European provinces with respect to eight environmental variables. Environmental variables as in Fig. 6. For species abbreviations, see Table 3.

Table 3. Frequency table showing the percentage occurrence of species of Sesiidae in 10 province groups interpreted from the TWINSPAN analysis. Numbers in italics indicate percentages over 70 %. Species order is as given by the TWINSPAN analysis. The number of provinces in each group is given in parentheses. The valid genus name for the *Aegeria* species is *Synanthedon* (Varis et al. 1987).

Province group:	1	2	3	4	5	6	7	8	9	10
	(1)	(16)	(50)	(17)	(3)	(1)	(2)	(1)	(1)	(1)
Sesia melanocephala Dalman, 1816	–	25	34	–	–	–	–	–	–	–
Paranthrene tabaniformis (Rottemburg, 1775)	–	6	44	–	–	–	–	–	–	–
Aegeria mesiaeformis (Herrich–Schäffer, 1845)	–	–	6	–	–	–	–	–	–	–
Aegeria myopaeformis (Borkhausen, 1789)	–	6	8	–	–	–	–	–	–	–
Aegeria flaviventris (Staudinger, 1883)	–	–	12	–	–	–	–	–	–	–
Sesia apiformis (Clerk, 1759)	–	*87*	*78*	–	33	–	–	–	–	–
Aegeria vespiformis (Linnaeus, 1761)	–	12	4	–	–	–	–	–	–	–
Bembecia scopigera (Scopoli, 1763)	–	*100*	22	–	–	–	–	–	–	–
Bembecia muscaeformis (Esper, 1783)	–	*50*	2	–	–	–	–	–	–	–
Aegeria spheciformis (Denis & Schiffermüller, 1775)	–	69	*84*	35	*100*	–	–	–	–	–
Aegeria tipuliformis (Clerck, 1759)	–	*81*	*86*	23	–	–	–	–	–	–
Sesia bembeciformis (Hübner, 1797)	*100*	31	6	12	–	–	–	–	–	–
Pennisetia hylaeiformis (Laspeyrés, 1801)	–	*94*	*92*	18	–	–	–	–	–	–
Aegeria formicaeformis (Esper, 1779)	–	69	62	41	–	–	–	–	–	–
Aegeria scoliaeformis (Borkhausen, 1789)	–	50	58	*71*	33	*100*	–	–	–	–
Aegeria culiciformis (Linnaeus, 1758)	–	*75*	*74*	*94*	–	*100*	*100*	*100*	–	–
Synanthedon polaris (Staudinger, 1877)	–	–	2	18	33	*100*	*100*	*100*	*100*	*100*

Table 4. Canonical coefficients and the inter-set correlations of environmental variables with the first three axes of canonical correspondence analysis (CCA) in Sesiidae. Canonical coefficients with the *t*-value higher than 2.0 in absolute value are indicated by *. VIF = variance inflation factor.

Variable		Canonical coefficients			Correlation coefficients			VIFs
	Axis	1	2	3	1	2	3	
	Eigenv:	0.20	0.11	0.06				
LAT		–0.14	0.25	–0.15	0.63	–0.32	0.07	25.86
LON		–0.02	–0.03	0.24*	0.16	–0.41	0.43	3.67
BVP		–0.08	–0.36*	0.25	0.57	–0.33	0.21	24.23
ETS		–0.62*	–0.12	0.21	–0.70	0.31	0.03	14.97
PRE		–0.14*	–0.21*	0.04	–0.07	–0.13	–0.24	1.98
VEG		0.16	–0.02	0.14*	0.64	–0.34	0.03	4.04
PIC		–0.15	–0.17	–0.07	0.03	–0.66	–0.05	10.84
PIN		–0.08	–0.15	–0.11	0.19	–0.66	–0.11	12.72

3.3. Coleoptera: Buprestidae

A TWINSPAN dendrogram shows 20 distributional species groups (Fig. 12). All species associated with coniferous trees (*Anthaxia quadripunctata*, *Melanophila acuminata*, *Chrysobothris c. chrysostigma*, *Phaenops cyanea*, *Buprestis n. novemmaculata*, *B. r. rustica*, *B. h. haemorrhoidalis*, *B. splendens*, *B. o. octoguttata*, *Chalcophora m. mariana*, *Anthaxia godeti*, *Anthaxia similis*) were grouped in the upper branch of the first division. The primary division is also associated with the biogeographical ranges of the species; 16 of the 18 species known to belong to the Eurosiberian element occurred in the upper branch (exceptions: *Chrysobothris c. affinis*, *Agrilus v. viridis*).

The provinces were classified into eight groups according to their buprestid fauna by the

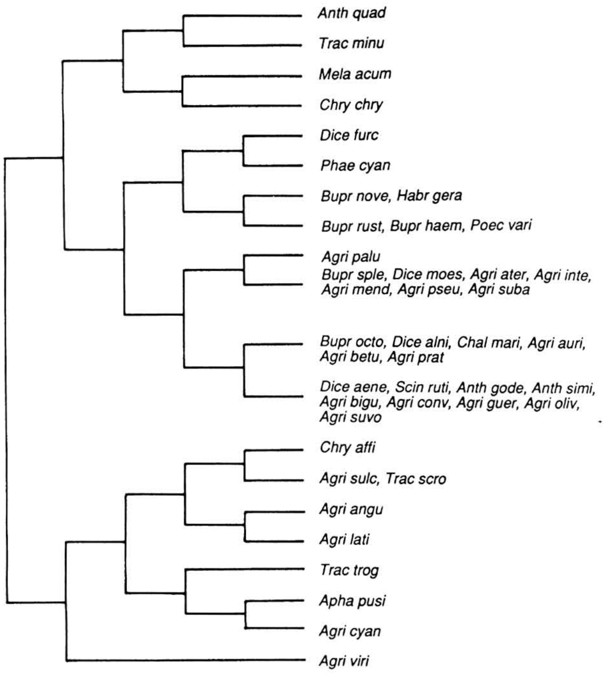

Fig. 12. A dendrogram of a two-way indicator species analysis (TWINSPAN) using the Buprestidae data.

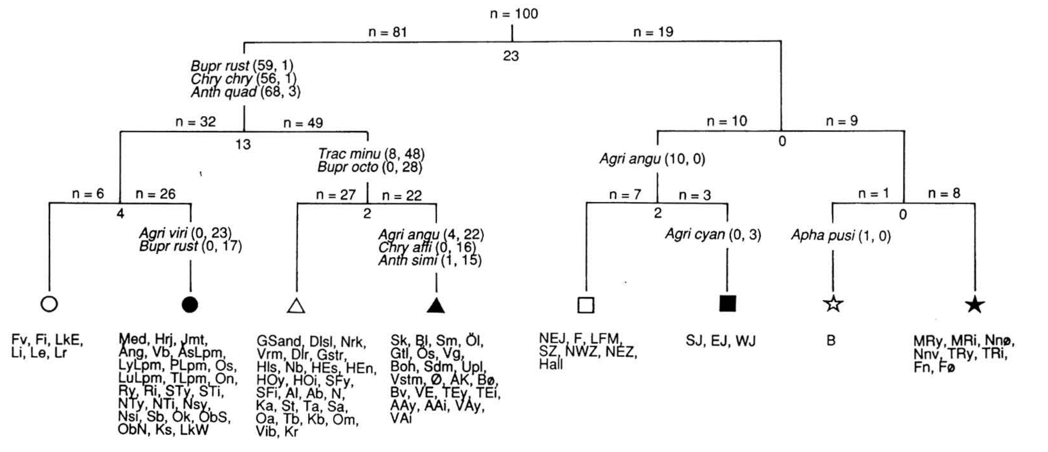

Fig. 13. A province dendrogram of the TWINSPAN using the Buprestidae data. Numbers in parentheses are the frequencies of each indicator species in the left- and right-hand cluster. The number of borderline and misclassified plots is indicated at each division.

TWINSPAN (Fig. 13). The left branch of the primary division, with most of the provinces, was characterized by *Buprestis r. rustica*, *Chrysobothris c. chrysostigma* and *Athaxia quadripunctata*. On the right branch the Danish provinces (quadrats) were characterized by *Agrilus angustulus*. The indicator species of the secondary division on the left were *Trachys m. minutus* and *Buprestis o. octoguttata*.

In the provincial classification by the TWINSPAN (Fig. 14), several provinces in southern Norway and Sweden formed a group (black triangles), with a sister group covering central Norway and Sweden, southern and central Finland, and adjacent areas in the U.S.S.R. (white triangles). The island of Bornholm (white star) was a sister group to the central and northern Norwegian provinces (black stars). Denmark formed a distinct group. The rest of the groups consisted mainly of northern and mountainous provinces.

The groups classified by the TWINSPAN were visible in a DCA ordination (Fig. 15). The Danish provinces, indicated by squares, were widely

Table 5. Frequency table showing the percentage occurrence of species of Buprestidae in eight province groups interpreted from the TWINSPAN analysis. Numbers in italics indicate percentages over 70 %. Species order is as given by the TWINSPAN analysis. The number of provinces in each group is given in parentheses.

Province group:	1 (6)	2 (26)	3 (27)	4 (22)	5 (7)	6 (3)	7 (1)	8 (8)
Melanophila acuminata (DeGeer, 1774)	*100*	*61*	*59*	*73*	*14*	*33*	*100*	*50*
Agrilus v. viridis (Linnaeus, 1758)	–	88	81	100	86	100	100	100
Aphanisticus pusillus (Olivier, 1790)	–	–	–	27	100	67	100	–
Agrilus cyanescens Ratzeburg, 1837	–	–	–	–	–	100	–	–
Trachys troglodytes Gyllenhal, 1817	–	–	4	23	43	33	–	–
Agrilus laticornis (Illiger, 1803)	–	–	4	64	57	67	–	–
Agrilus angustulus (Illiger, 1803)	–	–	15	*100*	*100*	*100*	–	–
Trachys scrobiculatus Kiesenwetter, 1857	–	–	–	18	14	–	–	–
Agrilus sulcicollis Lacordaire, 1835	–	–	26	*77*	57	–	–	–
Chrysobothris a. affinis (Fabricius, 1794)	–	–	–	*73*	57	–	–	–
Trachys m. minutus (Linnaeus, 1758)	–	31	*96*	*100*	29	67	–	–
Habroloma geranii (Silfverberg, 1977)	–	15	55	*86*	–	33	*100*	–
Anthaxia quadripunctata (Linnaeus, 1758)	33	*85*	*85*	*100*	29	33	–	–
Chrysobothris c. chrysostigma (Linnaeus, 1758)	17	65	*74*	*82*	14	–	–	–
Buprestis r. rustica Linnaeus, 1758	–	65	*85*	*91*	14	–	–	–
Agrilus p. pseudocyaneus Kiesenwetter, 1857	–	4	7	–	–	–	–	–
Agrilus aurichalceus paludicola Krogerus, 1922	17	38	33	–	–	–	–	–
Dicerca furcata (Thunberg, 1787)	–	38	52	50	–	–	–	–
Phaenops cyanea (Fabricius, 1775)	–	27	67	*86*	–	–	–	–
Poecilonata v. variolosa (Paykull, 1799)	–	8	63	*82*	14	–	–	–
Buprestis n. novemmaculata Linnaeus, 1767	–	–	26	32	14	–	–	–
Buprestis h. haemorrhoidalis Herbst, 1780	–	19	*74*	*86*	–	33	–	–
Agrilus suvorovi populneus Schaefer, 1946	–	–	4	36	–	–	–	–
Agrilus subauratus Gebler, 1833	–	–	30	18	–	–	–	–
Agrilus p. pratensis (Ratzeburg, 1839)	–	–	37	50	–	–	–	–
Agrilus olivicolor Kiesenwetter, 1857	–	–	4	50	–	–	–	–
Agrilus mendax Mannerheim, 1837	–	–	30	–	–	–	–	–
Agrilus integerrimus (Ratzeburg, 1839)	–	–	15	–	–	–	–	–
Agrilus guerini Lacordaire, 1835	–	–	–	4	–	–	–	–
Agrilus c. convexicollis Redtenbacher, 1849	–	–	–	9	–	–	–	–
Agrilus biguttatus (Fabricius, 1777)	–	–	–	45	–	–	–	–
Agrilus b. betuleti (Ratzeburg, 1837)	–	–	48	54	–	–	–	–
Agrilus a. aurichalceus Redtenbacher, 1849	–	–	4	4	–	–	–	–
Agrilus ater (Linnaeus, 1767)	–	–	7	–	–	–	–	–
Chalcophora m. mariana (Linnaeus, 1758)	–	–	30	59	–	–	–	–
Anthaxia similis Saunders, 1871	–	–	4	68	–	–	–	–
Anthaxia godeti Gory & Laporte de Castelnau, 1841	–	8	7	59	–	–	–	–
Scintillatrix rutilans (Fabricius, 1777)	–	–	7	18	–	–	–	–
Dicerca alni (Fischer, 1823)	–	–	33	32	–	–	–	–
Dicerca a. aenea (Linnaeus, 1761)	–	–	–	14	–	–	–	–
Dicerca moesta (Fabricius, 1793)	–	8	48	41	–	–	–	–
Buprestis o. octoguttata Linnaeus, 1758	–	–	44	73	–	–	–	–
Buprestis splendens Fabricius, 1775	–	–	7	4	–	–	–	–

separated from each other. The southern provinces mostly lay in the upper left corner of the diagram and the northern ones in the opposite corner. The southeastern provinces (e.g. Vib) lay in the lower left corner, while the southwestern province WJ was in the upper right corner. Table 5 shows the frequency of occurrence of buprestid species in the province groups. *Melanophila acuminata* was recorded from all the groups. The species richness was highest in the Danish groups. Only a few species live in the northernmost provinces.

Species-environment correlations were obtained by CCA. The canonical coefficients of the latitude and the effective temperature sum obtained the highest absolute values (of opposite sign) on the first axis (Table 6); the distribution of *Pinus*, the distribution of *Picea* and the beginning of the vegetative period also had a high negative coefficient. The fraction of the total variance in the environmental data extracted by species axis 1 was 39.9 %, while axis 2 extracted 25.6 %, and axis 3 extracted 16.2 %. The species-environment biplot (Fig. 16) shows that the first species axis was mainly related to the latitude, the beginning of the vegetative period, both with relatively high VIFs, and the effective temperature sum, while the second axis was related mainly to the distribution of the conifers. Species with southwestern distribution (*Agrilus cyanescens, Aphanisticus pusillus, Trachys troglodytes*) lay on the upper right-hand side of the diagram. *Agrilus guerini* is known from a limited area in southern Sweden, while *A. ater* is known only from southern Finland.

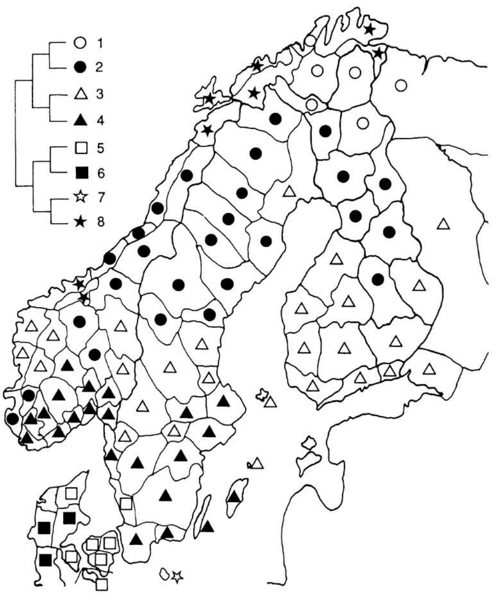

Fig. 14. Distribution of the provinces in the groups interpreted from the TWINSPAN analysis of the Buprestidae data. The numbers refer to Table 5.

Buprestids are poorly represented in the fauna of the study area. According to Bílý (1982), this is explained by the ecological needs of these insects, which are usually extremely xerophilous and heliophilous. Only about 24 % of the European and 3 % of the Palaearctic species occur in Fennoscandia and Denmark. In the present study, the latitude and variables associated with temperature best explained the variation observed in the species assemblages.

Table 6. Canonical coefficients and the inter-set correlations of environmental variables with the first three axes of canonical correspondence analysis (CCA) in Buprestidae. Canonical coefficients with the *t*-value higher than 2.0 in absolute value are indicated by *. VIF = variance inflation factor.

Variable		Canonical coefficients			Correlation coefficients			VIFs
	Axis:	1	2	3	1	2	3	
	Eigenv.:	0.27	0.17	0.06				
LAT		–0.17	0.64*	0.22*	–0.86	0.35	0.02	19.16
LON		–0.06	–0.14*	0.51*	–0.58	–0.14	0.64	3.45
BVP		–0.11	–0.07	–0.41*	–0.83	0.27	0.16	19.45
ETS		0.20*	0.22*	0.05	0.78	–0.30	0.19	11.48
PRE		–0.00	–0.07	–0.06	0.15	0.06	–0.37	1.99
VEG		0.00	–0.02	0.01	–0.59	0.16	–0.25	3.80
PIC		–0.12*	–0.34*	–0.16*	–0.56	–0.62	–0.01	5.37
PIN		–0.13*	–0.08	–0.05	–0.68	–0.49	–0.14	5.51

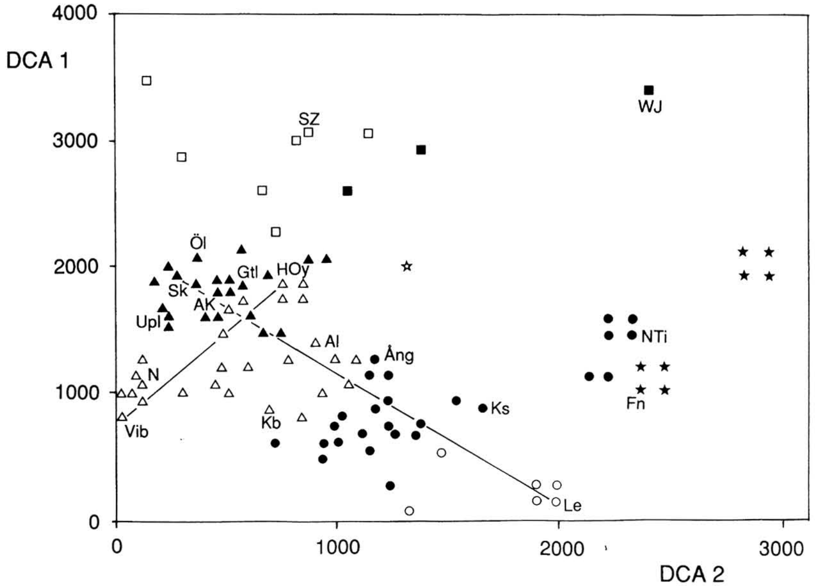

Fig. 15. The provinces plotted on the 1st and 2nd axes (eigenvalues 0.32 and 0.18) of the detrended correspondence analysis ordination (DCA) using the Buprestidae data. Symbols of provinces as in Figs. 13–14, lines as in Fig. 5.

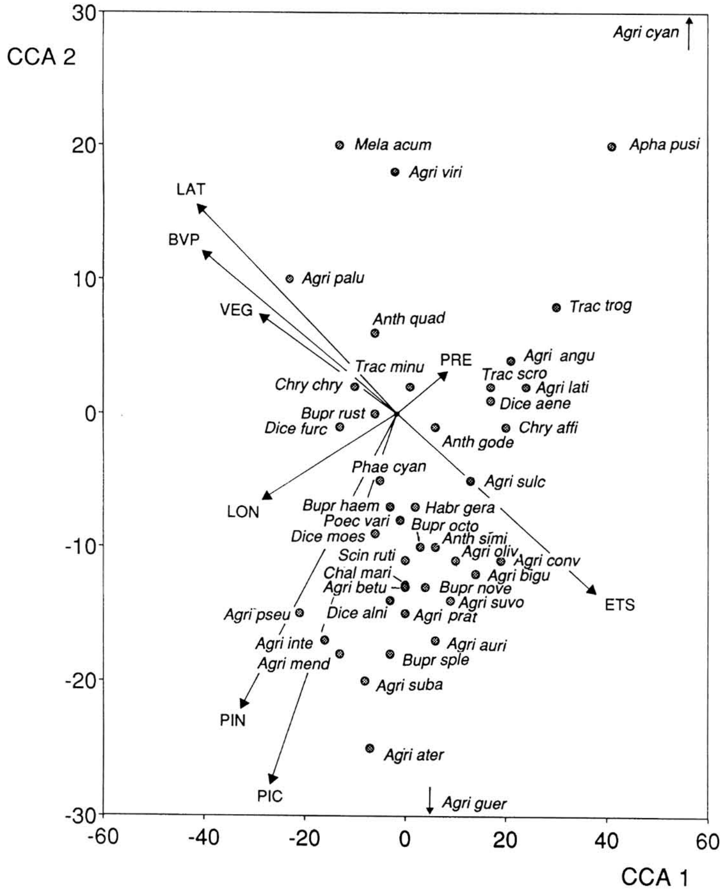

Fig. 16. Ordination diagram based on canonical correspondence analysis (CCA) of the distribution of Buprestidae in northern European provinces with respect to eight environmental variables. Environmental variables as in Fig. 6. For species abbreviations, see Table 5. The lengths of the arrows indicating environmental variables have been divided by 10.

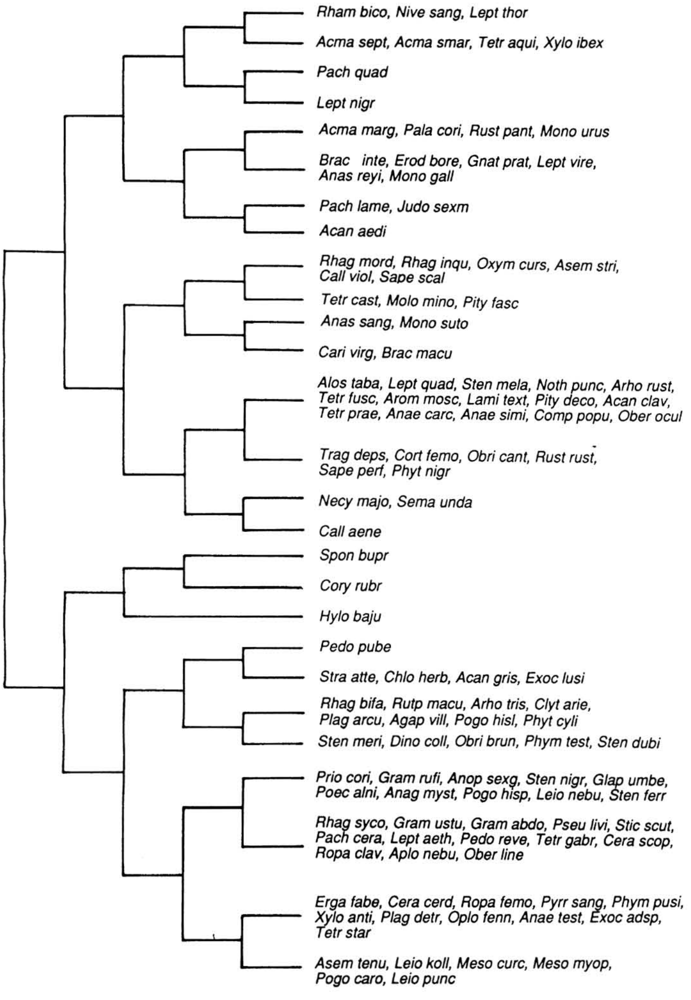

Fig. 17. A dendrogram of a two-way indicator species analysis (TWINSPAN) using the Cerambycidae data.

3.4. Coleoptera: Cerambycidae

A dendrogram showing the 27 distributional species groups interpreted from the TWINSPAN analysis of the Cerambycidae data is given in Fig. 17. All species associated with *Quercus* (*Strangalia attenuata*, *Plagionotus arcuatus*, *Pogonocherus hispidulus*, *Dinoptera collaris*, *Prionus coriarius*, *Anoplodera sexguttata*, *Poecilium alni*, *Anaglyptus mysticus*, *Pogonocherus hispidus*, *Rhagium sycophanta*, *Grammoptera ustulata*, *G. abdominalis*, *Pseudoalosterna livida*, *Cerambyx scopoli*, *Aplocnemia nebulosa*, *Cerambyx cerdo*, *Ropalus femoratus*, *Pyrrhidium sanguineum*, *Phymatoderus pusillus*, *Xylotrechus antilope*, *Plagionotus detritus*, *Anaesthetis testacea*, *Exocentrus adsperusus*, *Mesosa myops*) were grouped in the lower branch of the first division. In the upper branch, species associated with coniferous trees predominated (at least 27 species). Species with Holarctic distribution (*Gnathacmaeops pratensis*, *Pachyta lamed*, *Judolia sexmaculata*, *Rhagium inquisitor*, *Callidium violaceum*) and 12 of the 14 Eurosiberian species were restricted to the upper branch (exceptions: *Asemum tenuicorne*, *Mesosa myops*). Most of the species with European distribution (27 out of 35) occurred in the lower branch. The developmental time of the species was divided into three categories (1–2 yrs, 2 yrs, and 3 or more yrs), but the dendrogram was not related to this variation.

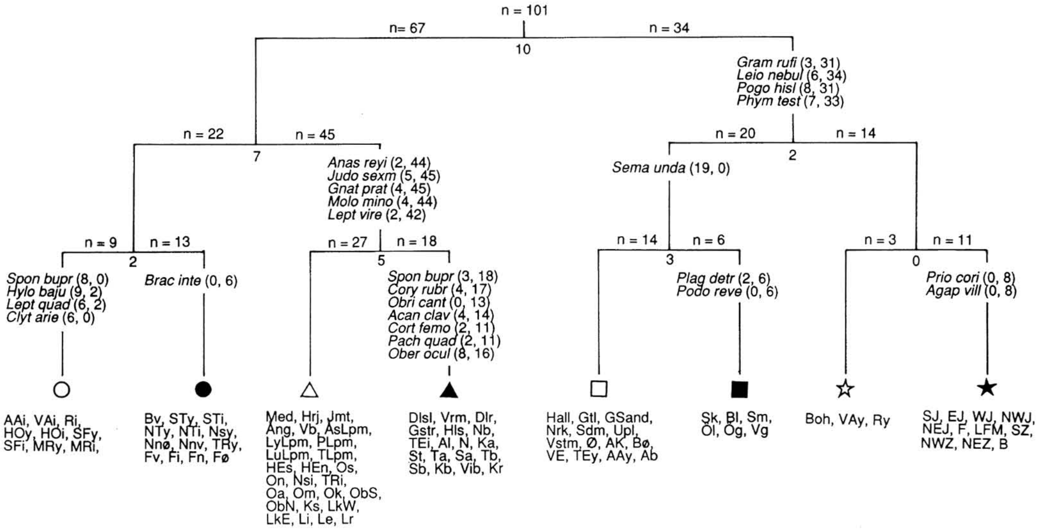

Fig. 18. A province dendrogram of the TWINSPAN using the Cerambycidae data. Numbers in parentheses are the frequencies of each indicator species in the left- and right-hand cluster. The number of borderline and misclassified plots is indicated at each division.

A TWINSPAN classification of the provinces shows eight groups (Fig. 18). The indicator species of the primary division were *Grammoptera ruficornis*, *Leiopus nebulosus*, *Pogonocherus hispidulus* and *Phymatodes testaceus*, which are typical of the southern provinces. The absence of *Semanotus undatus* and the presence of *Prionus coriarius* and *Agapanthes villosoviridescens* characterized the Danish provinces. On the primary left branch, the next division was indicated by *Anastrangalia reyi*, *Judolia sexmaculata*, *Gnathacmaeops pratensis*, *Molorchus minor* and *Lepturobosca virens*. A scarcity of these species characterized two Norwegian province groups.

The number of provinces in the TWINSPAN groups varied between 3 and 27 (Fig. 19). Denmark forms a separate group with a small sister group in southern Norway and Sweden. Another group in southern Norway and Sweden can be recognized. Southern Finland, with adjacent provinces in the U.S.S.R., belongs to a group extending as a narrow belt over central Sweden to Norway. Its sister group covers large areas in northern Finland and Sweden, with an extension in central and northern Norway. Two province groups are entirely restricted to Norway.

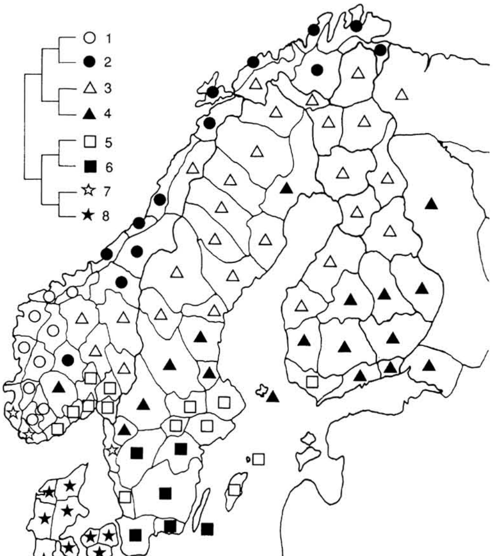

Fig. 19. Distribution of the provinces in the groups interpreted from the TWINSPAN analysis of the Cerambycidae data. The numbers refer to Table 7.

Table 7. Frequency table showing the percentage occurrence of species of Cerambycidae in eight province groups interpreted from the TWINSPAN analysis. Numbers in italics indicate percentages over 70 %. Species order is as given by the TWINSPAN analysis. The number of provinces in each group is given in parentheses.

Province group:	1 (9)	2 (13)	3 (27)	4 (18)	5 (14)	6 (6)	7 (3)	8 (11)
Rhamnusium bicolor (Schrank, 1781)	–	–	–	5	–	–	–	–
Nivellia sanguinosa (Gyllenhal, 1827)	–	–	11	39	–	17	–	–
Acmaeops septentrionis (Thomson, 1866)	–	23	*85*	67	7	17	–	–
Acmaeops smaragdula (Fabricius, 1792)	–	8	67	39	–	–	–	–
Tetropium aquilonium Plavilstshikov, 1940	–	–	7	–	–	–	–	–
Xylotrechus ibex (Gebler, 1825)	–	–	4	–	–	–	–	–
Leptura thoracica Creutzer, 1799	–	–	–	22	–	–	–	–
Pachyta quadrimaculata (Linnaeus, 1758)	–	–	7	61	7	–	–	9
Lepturalia nigripes (DeGeer, 1775)	–	–	48	*72*	14	33	–	–
Acmaeops marginata (Fabricius, 1781)	–	8	37	67	50	17	33	–
Palaeocallidium coriaceum (Paykull, 1800)	–	–	*78*	*83*	*71*	*83*	–	–
Rusticoclytus pantherinus (Savenius, 1825)	–	8	22	61	29	33	–	–
Monochamus urussovii (Fischer, 1806)	–	8	41	67	43	50	–	–
Brachyta interrogationis (Linnaeus, 1758)	–	46	*100*	*83*	29	50	–	–
Erodinus borealis (Gyllenhal, 1827)	–	8	44	50	29	–	–	–
Gnathacmaeops pratensis (Laicharting, 1784)	–	31	*100*	*100*	64	67	33	–
Lepturobosca virens (Linnaeus, 1758)	–	15	*93*	*94*	*71*	67	–	–
Anastrangalia reyi (Heyden,1889)	–	15	*96*	*100*	*71*	*83*	–	–
Monochamus galloprovincialis (Olivier, 1795)	–	15	52	*78*	29	50	33	–
Pachyta lamed (Linnaeus, 1758)	11	46	*100*	*94*	*93*	67	67	9
Judolia sexmaculata (Linnaeus, 1758)	11	31	*100*	*100*	*93*	*100*	33	9
Acanthocinus aedilis (Linnaeus, 1758)	*89*	*77*	*100*	*100*	*100*	*100*	*100*	27
Carilia virginea (Linnaeus, 1758)	11	23	*81*	*100*	*93*	*100*	67	–
Brachyleptura maculicornis (DeGeer, 1775)	44	31	*78*	*100*	*93*	*100*	67	9
Anastrangalia sanguinolenta (Linnaeus,1761)	*78*	46	67	*100*	*100*	*100*	*100*	36
Rhagium mordax (DeGeer, 1775)	67	*85*	*96*	*100*	*93*	*100*	*100*	*100*
Rhagium inquisitor (Linnaeus, 1758)	*89*	*77*	*100*	*100*	*100*	*100*	*100*	54
Oxymirus cursor (Linnaeus, 1758)	*89*	61	*93*	*94*	*86*	*100*	*100*	45
Asemum striatum (Linnaeus, 1758)	67	*85*	*100*	*100*	*93*	*100*	*100*	*100*
Callidium violaceum (Linnaeus, 1758)	67	*85*	*100*	*100*	*100*	*100*	*100*	*100*
Monochamus sutor (Linnaeus, 1758)	44	*77*	*100*	*100*	*100*	*83*	*100*	27
Saperda scalaris (Linnaeus, 1758)	67	*77*	*96*	*100*	*100*	*100*	*100*	*100*
Alosterna tabacicolor (DeGeer, 1775)	33	31	63	*100*	*86*	*100*	67	*100*
Tetropium castaneum (Linnaeus, 1758)	11	38	*96*	*100*	*93*	*100*	67	*100*
Molorchus minor (Linnaeus, 1758)	11	23	*96*	*100*	*93*	*100*	67	*91*
Pityphilus fasciculatus (DeGeer, 1775)	44	46	*96*	*100*	*93*	*100*	*100*	*100*
Leptura quadrifasciata Linnaeus, 1758	67	15	*70*	*100*	*100*	*100*	*100*	*100*
Stenurella melanura (Linnaeus, 1758)	22	8	59	*100*	*93*	*100*	33	*100*
Nothorhina punctata (Fabricius, 1798)	–	–	26	61	*71*	67	–	–
Arhopalus rusticus (Linnaeus, 1758)	44	–	*78*	*100*	*100*	*100*	67	*73*
Tetropium fuscum (Fabricius, 1787)	–	23	*74*	*94*	*93*	*100*	33	*91*
Aromia moschata (Linnaeus,1758)	22	–	37	*89*	*93*	*100*	*100*	64
Rusticoclytus rusticus (Linnaeus, 1758)	22	–	63	*94*	*93*	*100*	67	18
Lamia textor (Linnaeus, 1758)	11	–	48	*94*	*86*	*100*	*100*	64
Pityphilus decoratus (Fairmaire, 1855)	–	8	33	*83*	*86*	*100*	33	18
Tetrops praeusta (Linnaeus, 1758)	22	15	44	*89*	*93*	*100*	67	*100*
Anaerea carcharias (Linnaeus, 1758)	22	23	63	*100*	*93*	*100*	*100*	*82*
Composidia populnea (Linnaeus, 1758)	11	–	*89*	*94*	*86*	*100*	67	*100*
Oberea oculata (Linnaeus, 1758)	11	8	30	*89*	*86*	*83*	67	9
Tragosoma depsarium (Linnaeus, 1767)	–	8	26	*78*	43	67	33	–
Cortodera femorata (Fabricius, 1787)	–	–	7	61	43	*83*	–	–
Obrium cantharinum (Linnaeus, 1767)	–	–	–	*72*	43	67	–	–
Acanthoderus clavipes (Schrank, 1781)	–	–	15	*78*	*71*	*83*	–	18
Anaerea similis (Laicharting, 1748)	–	–	18	61	36	*83*	33	–
Saperda perforata (Pallas, 1773)	–	–	37	*78*	*79*	67	–	–
Phytoecia nigricornis (Fabricius, 1781)	–	–	–	22	–	50	–	–
Necydalis major Linnaeus, 1758	11	–	48	*94*	*71*	*100*	–	–
Semanotus undatus (Linnnaeus, 1758)	–	8	*74*	*89*	*93*	*100*	–	–
Callidostola aenea (DeGeer, 1775)	–	–	63	61	57	*83*	–	–
Corymbia rubra (Linnaeus, 1758)	44	8	15	*94*	*71*	*100*	67	*73*

Province group:	1 (9)	2 (13)	3 (27)	4 (18)	5 (14)	6 (6)	7 (3)	8 (11)
Spondylis buprestoides (Linnaeus, 1758)	*89*	–	11	*100*	*100*	*100*	*100*	45
Hylotrupes bajulus (Linnaeus, 1758)	*100*	15	–	17	*86*	*100*	67	54
Pedostrangalia pubescens (Fabricius, 1787)	–	–	–	39	36	67	–	–
Strangalia attenuata (Linnaeus, 1758)	33	–	–	11	43	*83*	–	18
Chlorophorus herbstii (Brahm, 1790)	–	–	–	17	21	50	–	–
Acanthocinus griseus (Fabricius, 1792)	–	–	7	17	43	33	–	–
Exocentrus lusitanus (Linnaeus, 1767)	–	–	–	39	50	*83*	–	9
Rhagium bifasciatum Fabricius, 1775	22	–	–	–	7	–	33	64
Rutpela maculata (Poda, 1761)	55	8	–	22	*86*	*100*	*100*	*82*
Arhopalus tristis (Fabricius, 1787)	–	–	–	33	29	67	–	45
Clytus arietis (Linnaeus, 1758)	67	–	4	22	*86*	*100*	67	*100*
Plagionotus arcuatus (Linnaeus, 1758)	11	–	–	39	*71*	*100*	*100*	*82*
Agapanthia villosoviridescens (DeGeer, 1775)	–	–	4	22	14	17	–	*73*
Pogonocherus hispidus (Linnaeus, 1758)	22	–	–	33	*86*	*100*	*100*	*91*
Phytoecia cylindrica (Linnaeus, 1758)	–	–	7	44	50	*100*	67	64
Stenocorus meridianus (Linnaeus, 1758)	–	8	4	28	*71*	*100*	67	64
Dinoptera collaris (Linnaeus, 1758)	–	–	–	22	50	*100*	33	45
Obrium brunneum (Fabricius, 1792)	–	–	–	11	7	50	–	18
Phymatodes testaceus (Linnaeus, 1758)	–	–	4	33	*100*	*100*	67	*100*
Stenostola dubia (Laicharting, 1784)	11	8	7	22	*71*	*100*	33	*82*
Prionus coriarius (Linnaeus, 1758)	11	–	–	22	57	*100*	–	*73*
Grammoptera ruficornis (Fabricius, 1781)	22	8	–	–	*79*	*100*	*100*	*100*
Anoplodera sexguttata (Fabricius, 1775)	–	–	–	5	50	67	67	36
Stenurella nigra (Linnaeus, 1758)	11	–	–	–	57	*100*	67	64
Glaphyra umbellatarum (Schreber, 1759)	–	–	–	–	29	*83*	–	54
Poecilium alni (Linnaeus, 1767)	–	–	–	–	43	*83*	67	27
Anaglyptus mysticus (Linnaeus, 1758)	–	–	–	17	36	*100*	33	*73*
Pogonocherus hispidulus (Piller & Mitterpacher, 1783)	–	–	–	5	*79*	*100*	67	*73*
Leiopus nebulosus (Linnaeus, 1758)	–	–	4	28	*100*	*100*	*100*	*100*
Stenostola ferrea (Schrank, 1776)	–	–	–	11	29	50	67	27
Rhagium sycophanta (Schrank, 1781)	–	–	–	–	21	*100*	33	*82*
Grammoptera ustulata (Schaller, 1783)	–	–	–	–	7	*100*	33	64
Grammoptera abdominalis (Stephens, 1831)	–	–	–	–	–	–	–	27
Pseudoalosterna livida (Fabricius, 1776)	–	–	–	–	–	–	–	9
Stictoleptura scutellata (Fabricius, 1781)	–	–	–	–	7	50	–	36
Pachytodes cerambyciformis (Schrank, 1781)	–	–	–	–	–	–	–	36
Leptura aethiops Poda, 1761	–	–	–	–	–	–	–	45
Pedostrangalia revestita (Linnaeus, 1767)	–	–	–	5	–	*100*	–	36
Tetropium gabrieli Weise, 1905	–	–	–	–	–	–	–	54
Cerambyx scopoli Fuesslin, 1775	–	–	–	–	14	*83*	–	45
Ropalopus clavipes (Fabricius, 1775)	–	–	–	–	–	–	–	18
Aplocnemia nebulosa (Fabricius, 1781)	–	–	–	–	21	*83*	–	64
Oberea linearis (Linnaeus, 1761)	–	–	–	–	14	*100*	–	36
Ergates faber (Linnaeus, 1761)	–	–	–	–	14	50	–	–
Cerambyx cerdo Linnaeus, 1758	–	–	–	–	–	67	–	–
Ropalopus femoratus (Linnaeus, 1758)	–	–	–	–	–	33	–	–
Pyrrhidium sanguineum (Linnaeus, 1758)	–	–	–	5	36	*83*	–	18
Phymatoderus pusillus (Fabricius, 1787)	–	–	–	–	–	17	–	–
Xylotrechus antilope (Schönherr, 1817)	–	–	–	–	14	33	33	–
Plagionotus detritus (Linnaeus, 1758)	–	–	–	5	14	*100*	–	9
Oplosia fennica (Paykull, 1800)	11	–	–	11	*71*	*100*	33	9
Anaesthetis testacea (Fabricius, 1781)	–	–	–	–	–	17	–	–
Exocentrus adspersus Mulsant, 1846	–	–	–	–	–	33	–	–
Tetrops starkii Chevrolat, 1859	–	–	–	–	14	50	–	–
Asemum tenuicorne Kraatz, 1879	–	–	–	–	7	–	–	–
Leioderus kollari Redtenbacher, 1849	–	–	–	–	36	–	–	–
Mesosa curculionoides (Linnaeus, 1761)	–	–	–	–	29	33	–	–
Mesosa myops (Dalman, 1817)	–	–	–	–	7	–	–	–
Pogonocherus caroli Mulsant, 1863	–	–	–	–	14	–	–	–
Leiopus punctulatus (Paykull, 1800)	–	–	–	–	14	–	–	–

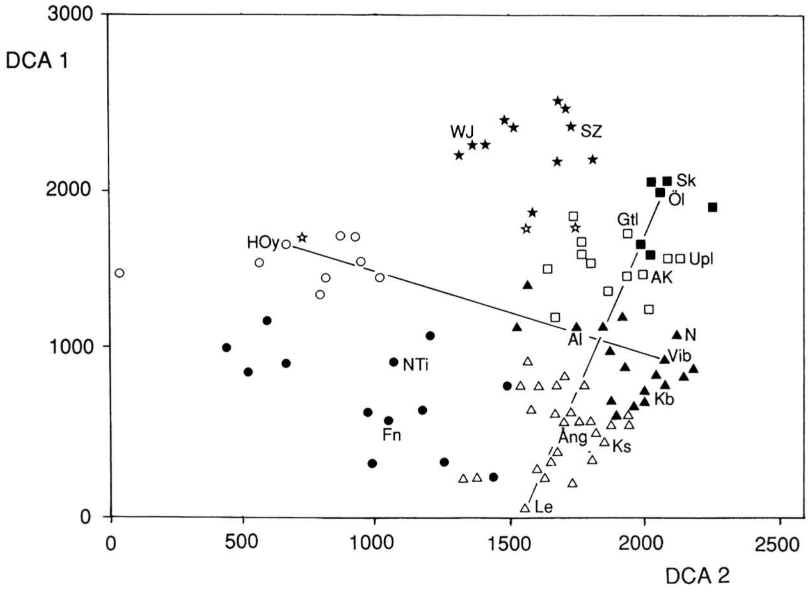

Fig. 20. The provinces plotted on the 1st and 2nd axes (eigenvalues 0.28 and 0.10) of the detrended correspondence analysis ordination (DCA) using the Cerambycidae data. Symbols of provinces as in Figs. 18–19.

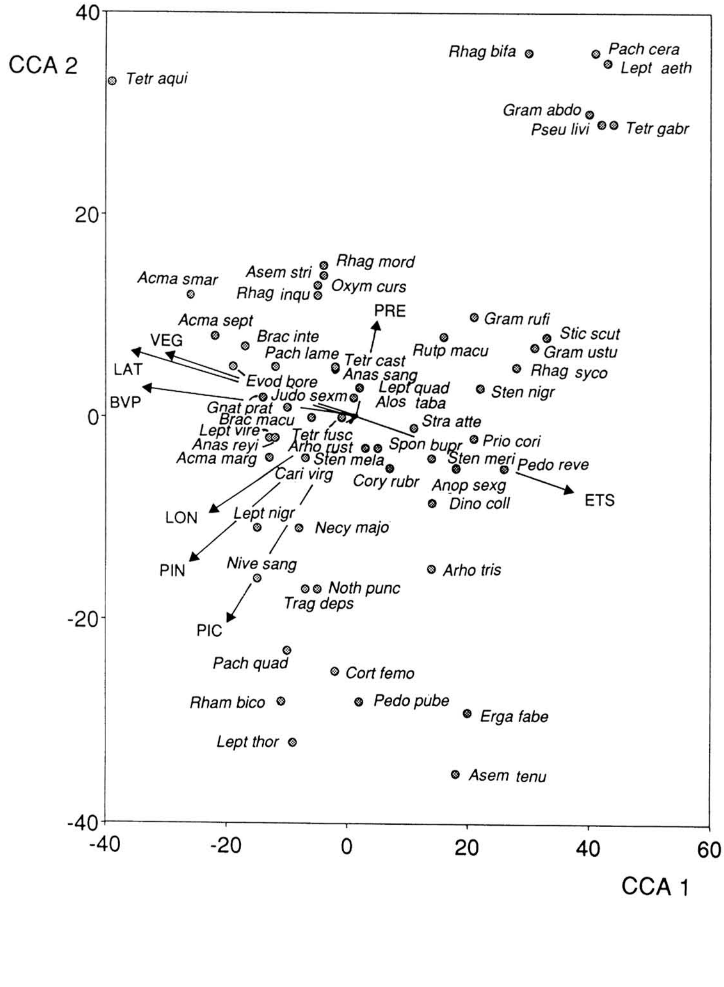

Fig. 21. Ordination diagram based on canonical correspondence analysis (CCA) of the distribution of Cerambycidae in the northern European provinces with respect to eight environmental variables. Environmental variables as in Fig. 6. For species abbreviations, see Table 7. (continues)

A similar division can be seen in the DCA ordination (Fig. 20). The southern provinces lay in the upper part and the northern ones in the lower part of the diagram. The Norwegian provinces (dots and circles) were widely spread, while the white triangles were densely clustered compared to their geographic distribution. Table 7 shows the frequency of occurrence of cerambycid species in the province groups. Twenty-three species occurred in all province groups. Several species reached a frequency of 100 % even in large province groups, indicating continuous distribution and a satisfactory level of recording.

The CCA ordination diagram illustrates the cerambycid fauna in relation to the environmental variables (Fig. 21). On the first axis the canonical coefficients of the latitude and the effective temperature sum obtained the highest absolute values (of opposite sign) (Table 8). The second axis was related to the latitude, the distribution of *Picea* and the effective temperature sum. The canonical coefficient of the latitude is unstable, however, as is indicated by the high value of the VIF. The fraction of the total variance in the environmental data extracted by species axis 1 was 50.7 %, that of axis 2 was 14.2 %, and that of axis 3 was 10.3 %. The species-environment biplot shows that the first species axis was mainly related to the latitude, the effective temperature sum and the beginning of the vegetative period, while the second axis was mainly related to the distribution of the conifers. *Xylotrechus ibex* is known only from Finnish Lapland and *Phymatoderus pusillus*, *Anaesthetis testacea* and *Ropalopus femoratus* only from southern Sweden. Species with Holarctic and Eurosiberian distributions are concentrated on the left-hand side of the diagram.

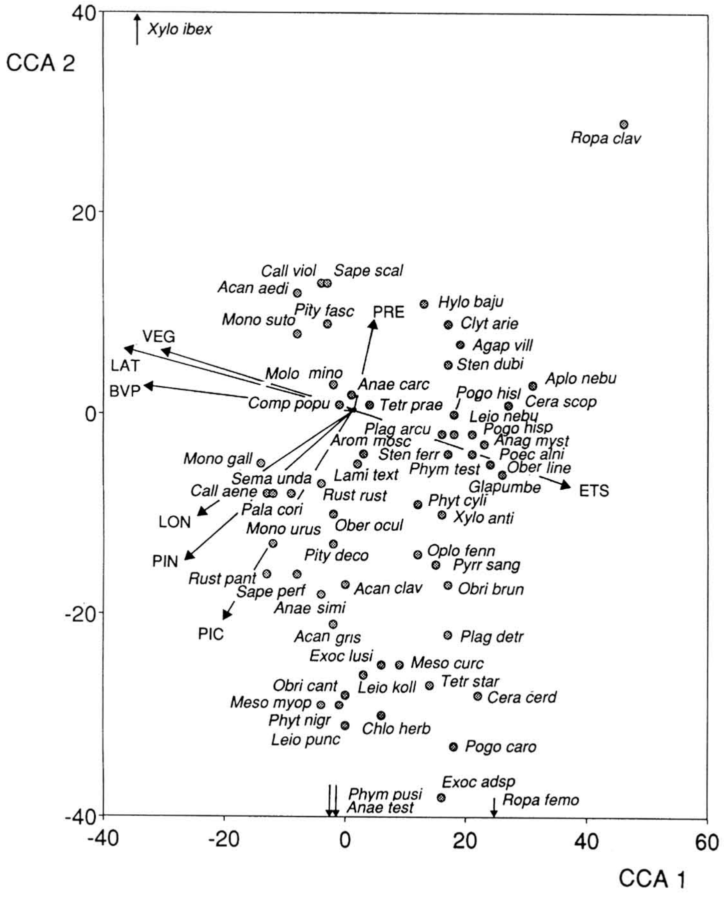

Fig. 21 (continued). The lengths of the arrows indicating environmental variables have been divided by 12. To help the interpretation, the species have been divided into two groups of approximately equal size.

Table 8. Canonical coefficients and the inter-set correlations of environmental variables with the first three axes of canonical correspondence analysis (CCA) in Cerambycidae. Canonical coefficients with the t-value higher than 2.0 in absolute value are indicated by *. VIF = variance inflation factor.

Variable		Canonical coefficients			Correlation coefficients			VIFs
	Axis:	1	2	3	1	2	3	
	Eigenv.:	0.26	0.10	0.05				
LAT		–0.30*	0.47*	–0.36*	–0.92	0.24	0.09	21.57
LON		–0.09*	–0.10*	0.08*	–0.59	–0.33	0.39	3.53
BVP		0.07	–0.12	0.19*	–0.86	0.10	0.31	20.86
ETS		0.21*	0.20*	–0.20*	0.90	–0.23	–0.06	12.83
PRE		–0.02	0.02	–0.15*	0.12	0.32	–0.67	2.05
VEG		–0.04	0.07*	0.00	–0.78	0.22	–0.02	20.86
PIC		–0.11*	–0.25*	–0.12*	–0.51	–0.70	–0.21	7.92
PIN		–0.05	–0.02	–0.02	–0.67	–0.50	–0.25	9.00

After the last glaciation, the main colonization routes of the Cerambycidae in Fennoscandia went through Denmark and Finland and the bulk of the southern species reached southern Sweden and Norway via Denmark. Some eastern species have their westernmost distribution limit in Finland. The northern distribution limit of some species is associated with their host plants (e.g. *Quercus*, *Fagus*), which also have their northern limits here, but the northern limit of other species may be determined by climatic factors. The isolated distribution of eight species in Sweden is attributable to two factors: the primeval oak forests in Småland and on Öland, and a climatic factor — a hot and dry summer period — these conditions fulfilling their requirements for successful reproduction (Bílý & Mehl 1989).

3.5. Regional division of the study area

There are numerous different biogeographical classifications of northern Europe. Zones and their sections distinguished on the basis of the flora or vegetation have most commonly been used (Ahti et al. 1968, Abrahamsen et al. 1977, Tuhkanen 1984). However, several equally valid classifications could be made. Since different organisms are dependent on different environmental factors and constraints, the resulting biogeographical patterns could be group-specific.

In general, the present distributional patterns agree roughly with the vegetation zones presented earlier, especially in Finland and Sweden, though the extension of southern vegetation zones northwards along the Atlantic coast can hardly be seen in the present results. The present TWINSPAN and DCA analyses demonstrate that the fauna of Denmark can be relatively easily distinguished from that of the rest of the area. The Danish sesiid fauna, however, resembles that of southern Sweden. In the beetle families, southern Sweden forms a separate class, while in the Saltatoria this area is extended to southern Norway. In the Saltatoria, the provinces of southern and central Finland can be placed in a separate eastern group, while in the three other insect groups the southern Finnish provinces have a fauna similar to those of central Sweden and Norway. The species-poor northern provinces were usually divided into several groups by TWINSPAN. In the Buprestidae, Norway has its own two classes of provinces along the coast. In spite of their peculiar fauna, Öland, Gotland and Gotska Sandön did not form separate classes as regards the present insect groups. On the whole, the differences in regional division between the groups were not dramatic, though the southern Finnish section of the Saltatoria is distinctive compared with the divisions of the other groups.

In indirect gradient analyses such as DCA, attention is first focused on the major pattern of variation in community composition. These analyses have the advantage that no prior hypothesis is needed about the relevant environmental variables (cf. direct gradient analyses such as CCA). Thus one can use these ordinations in hypothesis generation without being constrained by the environmental variables. The eigenvalues measuring the separation of the species distributions along the first DCA axis varied from 0.28 in the Cerambycidae to 0.38 in the Sesiidae and Saltatoria. The pattern that emerged in each group can easily be interpreted when compared with the maps (see above). In the Sesiidae, the deviating provinces with a poor fauna affected the pattern, which is probably connected with the small number of species in this family.

3.6. Environmental variation and species assemblages

In spite of the differences in ecological characteristics, species richness and the level of information between the insect groups, the relation of the geographic variation of the faunal composition with the environmental variables was fairly similar. Our results indicated not only that latitude and temperature variables associated with it were the most important determinants of the biogeographical variation, but also that annual precipitation and longitude were rather poor determinants in comparison. The canonical coefficients of latitude or the effective temperature sum were the highest in all insect groups. The CCA axis 1 correlated best with latitude except in the case of the Sesiidae. The distribution of the Scots pine was important for the Buprestidae, and that of the Norway spruce for both the Buprestidae and Cerambycidae. Since there are no species of the Saltatoria or Sesiidae living on these conifers, these trees could affect these insects only indirectly, mainly through the structure of the vegetation.

As temperature has been considered the dominant factor controlling insect development and survival, many geographic studies on insects have been based on some measure of temperature as a factor limiting insect distribution. Temperature and other climatic variables have formerly been widely used in forecasting the potential spread of insect pests into unoccupied areas (Messenger 1959). In one type of analysis, the climatic conditions occurring in localities within the known limits of the species have been compared with those of uninfested places, and the similarities and differences so found have been used as a basis for assessing the likelihood of invasion. Another common technique has been to correlate the geographic spread of a biotic association or community with certain indicator species. When the climatic requirements of such an indicator species have been determined, its distribution and abundance can be used as climatic indicators as well (Messenger 1959). Much more precise results can be obtained by the application of multivariate methods. A quantitative biogeographical approach will make it easier to analyse updated information on the significance of different environmental variables. For example, the effects of a global climatic change on the fauna can be examined by these techniques, provided that biogeographical data have been accumulated for different periods by long-term monitoring.

The effects of climatic change, including large-scale shifts in species ranges, changes in the species composition of biotic communities, and extinctions of species, can be expected to be pronounced in temperate and arctic areas, where temperature increases are predicted to be relatively large (Peters 1990). Even without human impact, alternating periods of generally cool and generally warm conditions have been typical of northern Fennoscandian summers through the last millennium (Briffa et al. 1990). This has also affected insects. In recent decades, for example, the southern element of the butterfly and moth fauna of southern Finland has shown a strong tendency to become commoner and to extend its range. The phases of extension and abundance correspond accurately with the periods of warm summers. In other insect orders the extensions of range have been similar to those in the Lepidoptera (Kaisila 1962).

The effects of climatic change depend on relative alterations in temperature and precipitation and also on the habitats of the species, which makes it difficult to assess them accurately on the basis of the present data. Temperature and humidity interact closely when affecting insect activity, development, and survival. For instance, it has been observed that after severe frost when a snow cover is lacking in the autumn or spring, the abundance of the early summer Lepidoptera has been considerably reduced in northern Europe (Nordman 1952). The precipitation conditions affect the abundance of fungal diseases and bacterioses. Furthermore, as the snow cover and frost depth depend on the terrain (Mustonen 1965), the response of insect species also depends on their habitat preferences. Thus, it is not surprising that not all the marginal populations of Lepidoptera have reacted in a similar way to the recent climatic change in northern Europe; some have shown expansion, others have not (Kaisila 1962).

3.7. Applicability of province records

The more comprehensive the faunistic records and the smaller the areal units, the greater is the likelyhood of satisfactory classifications and ordinations. When the insect group is small or its distribution poorly known, the present methods may give somewhat confusing results. This may be seen in the present study in the Sesiidae, the smallest group analysed, in which some deviating provinces were overweighted. This could be avoided by omitting some data from the analyses, as is often recommended (see Ter Braak & Prentice 1988), but since methodological coherence is required, this solution is not suitable in this context. In a large and well-known group, such as the Cerambycidae, the methods give a more reliable picture and reveal the general trends, which are difficult to recognize by simple visual examination of tables or maps.

The biogeographical provinces themselves are largely historical concepts (Leikola 1985). They are large areas of unequal size, in which the species composition is affected by local topographic and climatic variation. Consequently, the mean values of environmental variables are not representative of the whole area. However, the present results show that province records can reveal some major biogeographical patterns. Although the collecting effort has not been standardized, the existence of the provinces in biological literature has for decades served as a comprehensive mapping programme, emphasizing species records new to a province. This factor has apparently improved the quality of the data compared with random recording.

Unfortunately, records of the abundances of insect species are not available for large taxonomic groups in northern Europe. When possible, a rough division of species into different abundance classes could improve the results of the analyses. However, even simple presence/absence data can be used, at least in preliminary analyses and hypothesis generation, though equal weight is given to indigenous and casual species.

We consider that a large body of information present in traditional papers with province records has been overlooked. The analyses can be further developed by selecting and measuring additional or alternative environmental variables of ecological significance to a particular insect group. For example, the use of standard meteorological information is somewhat unrealistic in attempts to relate climate to insect behaviour and survival, since the different climatic factors vary in intensity within limited distances in the natural environment. The use of modern quantitative methods in the biogeographical analysis of insects has the advantage that the analyses can be repeated when additional data have been obtained. This allows an accurate assessment of the significance of new records. Although specialists have had a general picture of the biogeography, it has been qualitative and a matter of dispute. The tests of modern techniques presented here suggest that even the limited provincial species lists can be used successfully in quantitative biogeography.

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