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Hot-spots of insect diversity in northern Europe

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Threatened species have received a lot of attention in northern Europe, while little is known about the biogeography of biodiversity. We investigated the species diversity of Saltatoria, Sesiidae, Buprestidae and Cerambycidae to try to discover hot-spots for conservation among the 101 biogeographical provinces of Denmark, Norway, Sweden, Finland and the adjacent parts of Russia using presence/absence data from the literature. In each insect group examined the number of species was generally highest in the southern provinces, declining to the north and northwest. Critical fauna analysis showed that 70–80% of the species were recorded from the most species-rich province and 3–11 provinces covered the whole fauna. The use of different rarity indices to compensate biases caused by unequal collecting gave variable results and indicated that there are considerable differences between insect groups. No relation was found between species richness and the geographical size of the province. The rarity values were more or less indifferent as regards longitude and even the relation with latitude was relatively indistinct. There was a clear difference between the ranking of provinces on the basis of the number of threatened species and the indices based on species richness or (biogeographical) rarity.

1. Introduction

Recently, many conservation-oriented studies have tried to find mega-diversity countries or ecological hot-spots of global biodiversity, i.e. areas of exceptional species richness (Mittermeier & Werner 1990, Myers 1990, WCMC 1992). It is not an uncommon observation that a few species-rich areas may sometimes encompass a large share of a region's total biodiversity (e.g. Minns 1987, Baz 1991, Harrison et al. 1992, Heliövaara et al. 1992). Although most efforts have so far been concentrated on discovering the hot spots on a global scale, more detailed analyses (e.g. Margules & Usher 1981, Dony & Denholm 1985, Minns 1987, Dinerstein & Wikramanayake 1993) are also needed as a basis for regional and national policies of environmental protection and the use of natural resources. However, even in the best censused regions the accurate geographical distribution of most taxonomic groups of organisms is poorly and unevenly known (Udvardy 1969, Gaston 1990). Consequently, more emphasis is needed both on increasing the available biological information (e.g. taxonomic research) and on developing techniques for the assessment of data-poor areas.

The conservation of biodiversity is also complicated by conceptual difficulties in the formulation of conservation goals (Haila & Kouki 1994). Species richness is the oldest and most fundamental meaning of biodiversity (McIntosh 1967, Peet 1974, Baltanás 1992). Depending on the viewpoint, however, the conservation of biodiversity may also focus on endemic, rare or endangered species, or taxonomic diversity (Williams et al. 1991). The apportioning of taxa objectively among categories of rarity or endangerment has proved to be difficult (e.g. Rabinowitz et al. 1986, Mace et al. 1992, Wilcove et al. 1993).

We investigated the distribution of the species diversity of four insect families in the biogeographical or natural provinces of northern Europe and along the S-N gradient. There is no single natural scale at which ecological phenomena should be studied (Levin 1992). We chose to adopt the biogeographical provinces for the study, since a large body of entomological information has been gathered on a provincial basis in northern Europe. Of course, many factors contribute towards biasing of the data based on accumulated records (e.g. collecting period and intensity). On the other hand, although the collecting effort has not been standardized, the existence of the provinces in the entomological literature has served as a comprehensive mapping programme, emphasizing species records new to a province. It is likely that this has improved the quality of the data compared with random recording (Väisänen et al. 1992).

First, we used the data on species richness to locate the regional hot-spots of insect species diversity. Second, we investigated the smallest possible combination of provinces containing the whole fauna of the study area (see Collins & Morris 1985, Margules et al. 1988). Third, we have tried to compensate the bias in the species richness caused by unequal collecting efficiency in different provinces by using different rarity indices, which take into account species' commonness in ranking the provinces. We use the term rarity only in the sense of narrow geographical distribution not referring to habitat specificity, local population size (cf. Rabinowitz et al. 1986, McCoy & Mushinsky 1992), range composition or range affinity (Kudrna 1986). Fourth, we have compared our results with national red data lists for the Cerambycidae in order to develop more objective and scientifically based methods of including species on such lists, the criteria of which have recently been under discussion (Mace et al. 1992).

2. Material and methods

2.1. Species richness in biogeographical provinces

The distribution of the Saltatoria, Sesiidae, Buprestidae and Cerambycidae was used in the analyses. The number of species in these groups were 42, 17, 43 and 120, excluding the imported species. The provincial distribution data were obtained from Holst (1986), Fibiger & Kristensen (1974), Bílý (1982) and Bílý & Mehl (1989), respectively. The frequency distribution of species per province is given for each taxon in Fig. 1. The groups examined were selected to represent different types of frequency distribution. The Sesiidae, Buprestidae and Cerambycidae are predominantly associated with forests and woody plants, whereas the Saltatoria is a group of open ground.

The study area consisted of 101 provinces. A list of the abbreviations for the provinces and the map of the study area are given, for instance, in every volume of Fauna Entomologica Scandinavica. These provinces are here called biogeographical provinces.

2.2. Rarity indices, critical fauna analyses and endangered species

We calculated the conservation index (Q) and the importance index (I) as described by Minns

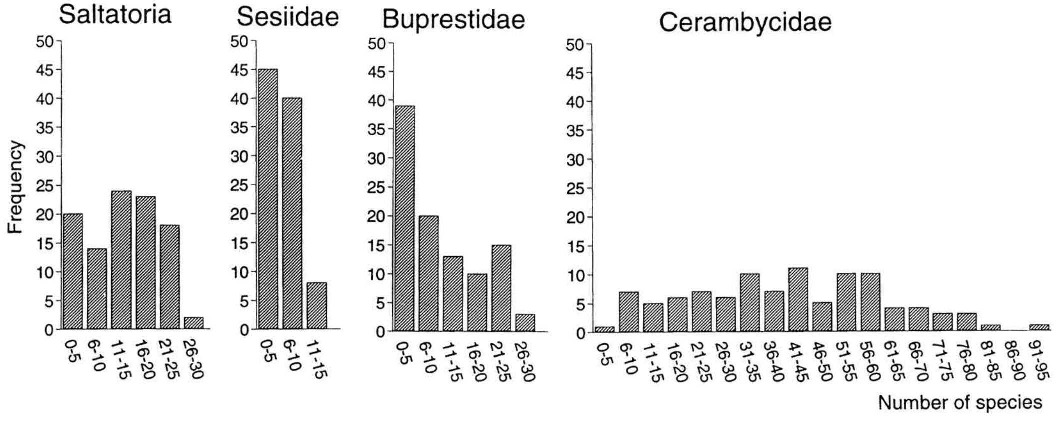

Fig. 1. Frequency distribution of species per province for the Saltatoria, Sesiidae, Buprestidae and Cerambycidae.

(1987). The conservation priority (Q_j) of each species is defined as

$$Q_j = 1 - \sum_{i=1}^{n} S_{ij} / n$$

where n = number of provinces, and S_{ij} = presence (1) or absence (0) of species j at province i. In effect, Q_j is the number of provinces where species j is missing divided by the total number of provinces.

Species which occur in all provinces have a priority (Q_j) of zero while a species only occurring in one province has a $Q_j = (n - 1)/n$. As the distribution of a species diminishes, its conservation priority increases.

The relative importance (I_i) of a province is the sum of priorities of species present divided by the sum of priorities for all the assemblage species,

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

where m = number of species.

To compensate for the species richness of the province an index (Q_i) is calculated. It is the average priority of species present,

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

The importance index (I_i) can vary between 0 and 1, whereas the average priority (Q_i) can vary in the range of species priorities (Q_j) roughly between 0 and 1. For the sake of simplicity we call I_i the importance index (I) and Q_i the conservation index (Q). Provinces with a large proportion of assemblage species present tend to have high I and intermediate Q values.

In order to identify provinces with several rare species we also calculated the rarity association index (R) (see Dony & Denholm 1985, Eyre & Rushton 1989). First, species recorded in 1, 2–3, 4–7, 8–15, 16–31, 32–63, and 64 and more provinces were given geometric scores from 64 to 1, respectively. A province score was the sum of priorities of species present:

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

where m = number of species, S_{ij} = presence (1) or absence (0) of species j in province i, and Q_j = conservation priority of species j; A rarity index (R) for a province was then calculated as PS_i, but accepting only species that scored 2 or more in the geometric scale. The highest species 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.

We applied and modified to the regional level the critical fauna analysis used for the assessment of the distribution of endemic swallowtail butterfly species on the global scale by Collins & Morris (1985). Thus, there are no real endemics but only species with a limited distribution in the study area. In the analysis, the initial step was to find the smallest number of provinces that includes all the species of each insect family examined. The procedure is rather similar to the heuristic algorithm developed by Margules et al. (1988) for finding the minimum set of sites for the conservation of plant species in Australian wetlands.

First we selected all provinces with any species which occurred only once. Then we selected from all provinces on which unrepresented species occur, the province contributing the maximum number of additional unrepresented species until all species were represented at least once. Where two or more provinces contributed an equal number of unrepresented species, we gave them as alternative choices.

The lists of threatened cerambycid species in different countries are based on the national red data books of Denmark (Asbirk & Søgaard 1991), Finland (Rassi et al. 1992), Norway (Størkensen 1992) and Sweden (Andersson et al. 1987; note that a revised list was published by Ehnström et al. 1993 after the present analysis). The Russian provinces (Vib, Kr and Lr) were omitted from the analysis of threatened species.

3. Results

3.1. Distribution of species richness

In each insect group examined, the number of species was high in southern Sweden (Fig. 2). The highest numbers of species were found in Öland (Öl) for Saltatoria, in Scania (Sk) for Sesiidae, and in Småland (Sm) both for Buprestidae and Cerambycidae (see Table 2). In the Saltatoria, high numbers of species were also recorded in Eastern Jutland (EJ) and the Isthmus of Carelia (Vib). In the Sesiidae, the species-rich provinces were rather widely distributed but associated with big cities and universities. In the Buprestidae, the highest numbers of species were found in south-southeastern parts of the area. A similar pattern was found in the Cerambycidae.

The area of the provinces varied from 36 km^2 (Gotska Sandön) to 169 000 km^2 (Russian Kr). The total number of species recorded from a province was not correlated with the log-area of the province in any taxa examined. The number of species generally decreased with increasing latitude in each group examined. The tendency was most distinct in Saltatoria whereas in the Sesiidae and the Buprestidae the pattern was more disperse. The relation of the number of species to longitude was obscure.

3.2. Critical faunal areas

In the Saltatoria, as much as 84% of the fauna occurred in two provinces (Öland and Russian Vib or Kr), and a combination of seven provinces (Öl, Vib, Kr, B, NEJ, Sk and ObN or Le) included all the species (Table 1). In the Sesiidae, 77% of the species have been recorded from Scania (Sk), and different combinations of three provinces, including a southern Finnish province and a northern province, covered the whole family. About 70% of the Buprestidae occurred in Småland (Sm) and the whole fauna was covered by seven more or less southern provinces. Similarly, 80% of the Cerambycidae occurred in Småland and the rest of the species were covered by ten other provinces.

3.3. Centres of rarity

In the Saltatoria, both the importance and rarity association indices (*I*, *R*) gave the highest ranking to Öland (Table 2, Fig. 3). The conservation index (*Q*) received its highest value on Gotska Sandön. Large areas in central Sweden and mountainous southern Norway had low values of rarity.

In the Sesiidae, both the importance and rarity association indices (*I*, *R*) gave the highest values to Scania (Table 2, Fig. 3). In general, the indices gave very mosaic-like patterns for the Sesiidae compared to other groups. There were drastic differences in the results obtained using different methods to estimate rarity. The indices which do not take into account species numbers

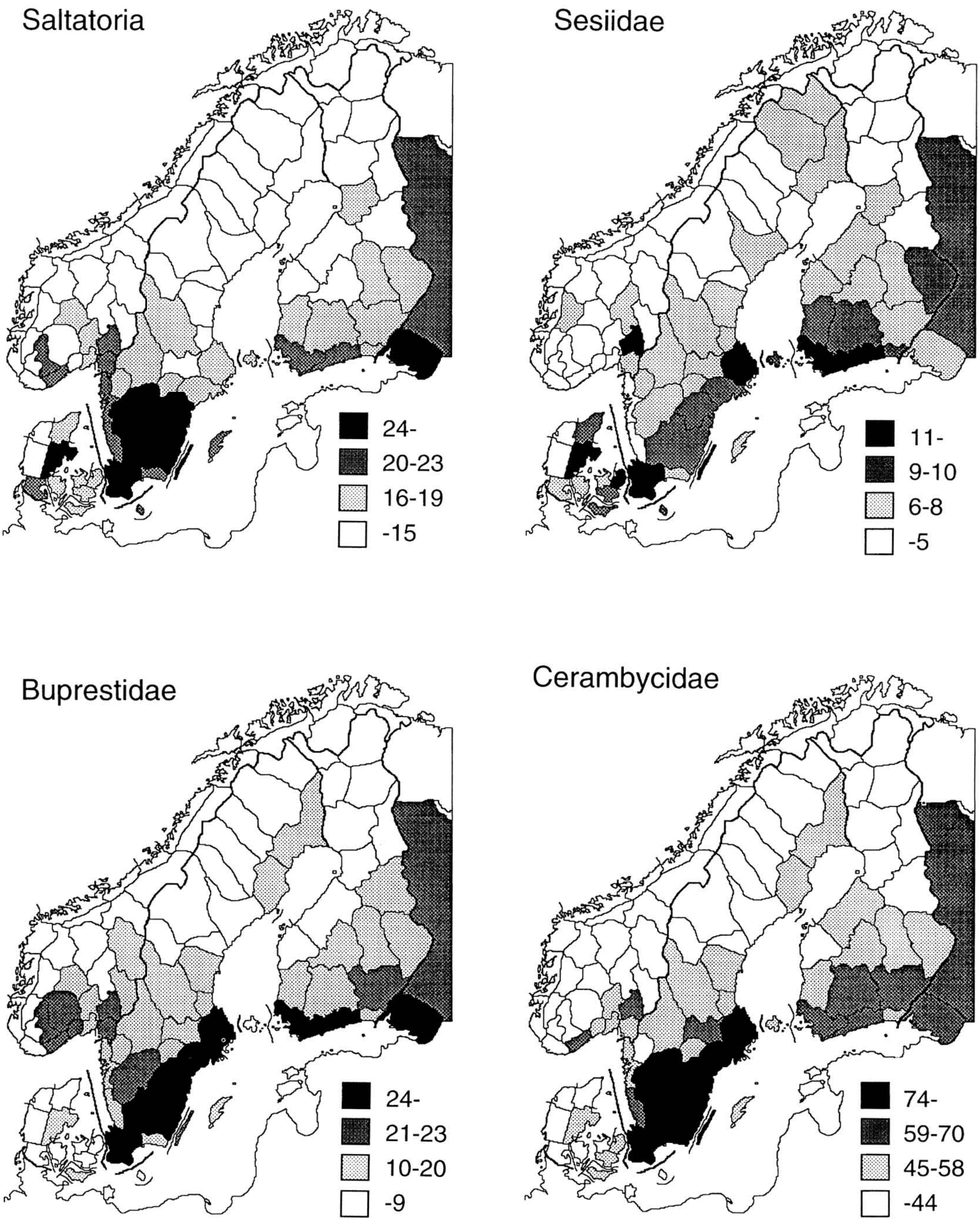

Fig. 2. The number of species per province for the Saltatoria, Sesiidae, Buprestidae and Cerambycidae.

in the provinces had high values in densely populated areas, whereas patterns revealed by the conservation index (*Q*) were more complex.

In the Buprestidae, both the importance and rarity association indices (*I, R*) gave the highest values to Småland (Table 2, Fig. 3). The indices which ignore species number had high values in southern Sweden, southern Finland and adjacent Russia and even in southern Norway. When species number was taken into account (*Q*) some provinces in Denmark also had high values. In general, the values were low in the large area covering the northwestern provinces.

In the Cerambycidae, all the indices gave the highest value to Småland (Table 2, Fig. 3). The Indices ignoring species number emphasized southern Sweden and, to a lesser degree, southern Finland. When relative index was used, some northern and Danish provinces also received high values.

The values of indices generally decreased with increasing latitude but were more or less indifferent as regards longitude. In the Saltatoria, the indices were relatively closely associated with latitude, though the use of relative index slightly obscured the patterns. In the Sesiidae, the relation of indices even to latitude was weak, if any. In the Buprestidae, a slight tendency towards increasing values of indices with decreasing latitude was observed. In the Cerambycidae, the relation between index values and latitude was apparent.

Table 1. Summary of the results of the critical fauna analysis of Saltatoria, Sesiidae, Buprestidae and Cerambycidae in northern European biogeographical provinces. The whole fauna is covered by the provinces listed below.

Taxon	Province	Increase of cumulative species number *n*	%
Saltatoria	Öl	30	69.8
	Vib and Kr	6	14.0
	B	2	4.7
	NEJ and Sk and ObN or Le	1	2.3
Sesiidae	Sk	13	76.5
	Ab or N	3	17.6
	Hrj or Nb or PLpm or LuLpm or TLpm or Os or On or Bv or Ks or Li or Le	1	5.9
Buprestidae	Sm	14	69.8
	Sa	5	11.6
	Ø or AK	3	7.0
	Vib	2	4.7
	SJ or EJ or WJ and Öl or Gtl and Ab or N	1	2.3
Cerambycidae	Sm	96	80.0
	Sa or Kr	8	6.7
	SJ and WJ and LFM	4	3.3
	GSand and Upl and Ab and Ta	2	1.7
	Li or Lr and Le	1	0.8

Table 2. Mean and maximum values for the rarity indices (*I, Q, R*) and the number of species and genera of Saltatoria, Sesiidae, Buprestidae and Cerambycidae in northern European biogeographical provinces.

	Mean ± *SD*	Max.	Province
Saltatoria			
I	0.23 ± 0.14	0.62	Öl
Q	0.49 ± 0.09	0.76	GSand
R	62.00 ± 62.42	288	Öl
Species	13.19 ± 7.01	30	Öl
Genera	9.36 ± 4.47	21	Öl
Sesiidae			
I	0.23 ± 0.16	0.68	Sk
Q	0.44 ± 0.11	0.88	Bv, STy
R	28.68 ± 28.81	134	Sk
Species	5.71 ± 3.30	13	Sk
Genera	2.84 ± 1.39	5	EJ, NEJ, B, Öl, Ög, Vg, Nrk, Sdm, Upl, AK, Al, Ab, N
Buprestidae			
I	0.18 ± 0.17	0.63	Sm
Q	0.49 ± 0.14	0.76	F
R	66.48 ± 75.55	298	Sm
Species	10.16 ± 8.06	30	Sm
Genera	6.19 ± 3.78	12	Sk, Sm, Ø, Ak, N, Sa
Cerambycidae			
I	0.23 ± 0.15	0.72	Sm
Q	0.39 ± 0.11	0.60	Sm
R	177.51 ± 160.62	1048	Sm
Species	40.89 ± 20.40	96	Sm
Genera	34.23 ± 16.08	73	Sm

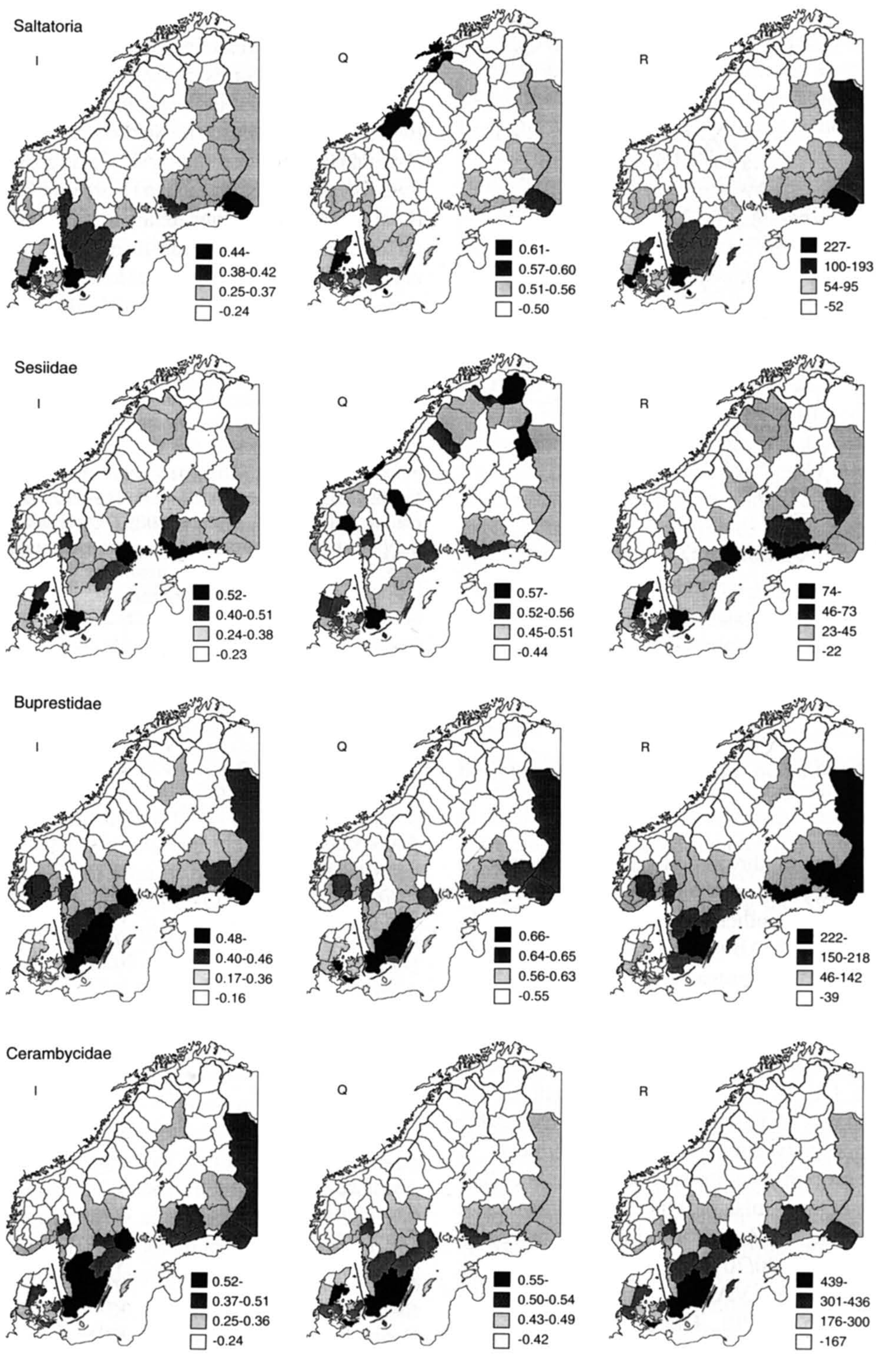

Fig. 3. Rarity indices calculated for Saltatoria, Sesiidae, Buprestidae and Cerambycidae in the northern European provinces.

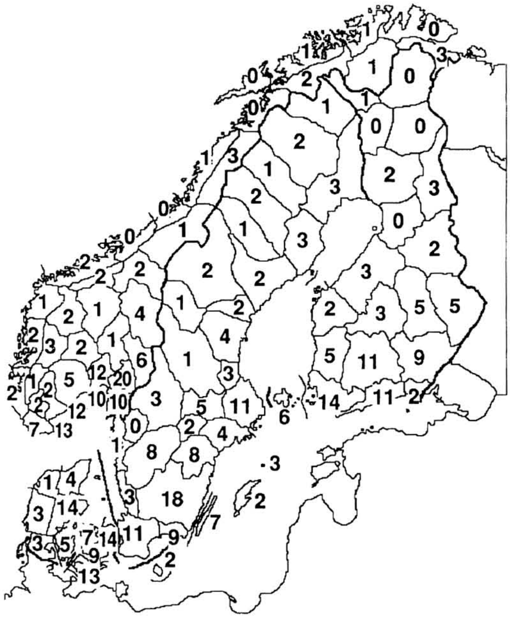

Fig. 4. Number of threatened species of Cerambycidae recorded from the northern European provinces based on national red lists.

3.4. Distribution of threatened cerambycid species

The number of threatened cerambycid species was highest in the southeastern Norwegian province AK (20), southern Swedish Sm (18), southwestern Finnish Ab (14) and Danish NEZ (14) (Fig. 4). The number was very low (0–3) north of latitude 64°N. Except for the southern Norwegian provinces (see below), the number was relatively low in provinces bordering on other countries (e.g. Ka, Gtl, B, SJ, Boh, Dlsl). The pattern that emerged was very fragmented, with considerable differences between neighbouring provinces.

The proportion of threatened species was 20% or more in the Danish provinces EJ (14/54), LFM (13/58) and NEZ (14/56), in the Norwegian provinces AK (20/70), Bø (12/56), TEy (12/56), AAy (13/60) and VAi (2/9), and in the Finnish province Ab (14/70). The proportion was less than 10% e.g. in the Swedish provinces Öl (7/74), Gtl (2/53), Boh (1/54), Nrk (2/53), Sdm (4/74), Vstm (5/66), Vrm (3/55), Dlr (1/57), Gstr (3/51), Hls (4/58) and Nb (3/51), and in the Finnish provinces Ka (2/47), St (5/55) and Kb (5/56). The number of threatened species was not correlated with the log-area of the province.

We investigated the conspicuous contrast between the southeastern Norwegian provinces Østfold (Ø) and Akershus (AK) and the adjacent Swedish provinces Bohuslän (Boh) and Dalsland (Dlsl) (Fig. 4) in more detail to find out if the differences were only due to different national classifications of species (Table 3). The proportion of species recorded from both the neigh-

Table 3. Comparison of the threatened species of Cerambycidae in the Norwegian provinces Ø and AK (Størkensen 1992) and the adjacent Swedish provinces Boh and Dlsl (Andersson et al. 1987). The Nordic status is based on Størkensen (1992). The nomenclature follows Bílý & Mehl (1989). Symbols: E = endangered, V = vulnerable, V+ = care-demanding, R = rare, I = indeterminate, K = insufficiently known, + = non-threatened, – = not recorded.

Species	Ø	AK	Boh	Dlsl	Status
Prionus coriarius (L.)	I	–	–	–	+
Stenocorus meridianus (L.)	V+	V+	+	–	+
Evodinus borealis (Gyll.)	V+	V+	–	–	+
Acmaeops marginata (F.)	–	V+	–	–	+
Dinoptera collaris (L.)	V+	V+	+	+	+
Anoplodera sexguttata (F.)	–	–	V	–	V
Necydalis major L.	–	V+	–	–	+
Nothorhina punctata (F.)	–	R	–	–	+
Hylotrupes bajulus (L.)	V+	V+	–	–	+
Leioderus kollari Redt.	–	V+	–	–	V+
Anaglyptus mysticus (L.)	–	K	+	+	+
Mesosa curculionoides (L.)	V	V	–	–	V
Monochamus urussovii (Fisch.)	K	K	–	–	V
Pityphilus decoratus (Fairm.)	R	R	+	–	+
Oplosia fennica (Payk.)	V+	V+	+	–	+
Acanthocinus griseus (F.)	V+	V+	–	–	V
Exocentrus lusitanus (L.)	–	V+	–	–	+
Tetrops starkii Chevr.	–	K	–	–	V
Anarea similis (Laich.)	–	V+	–	–	+
Saperda perforata (Pall.)	–	V+	–	–	+
Stenostola ferrea (Schrk.)	–	K	+	–	+
Oberea linearis (L.)	–	K	–	–	+
Threatened species	10	20	1	0	
All species recorded	52	70	55	39	
Threatened species (%)	19	29	2	0	

bouring provinces AK and Boh was 29% (6/21) of the threatened (in either province) species and 71% of the non-threatened species. Five of the ten threatened species recorded from Ø were known from Boh and one of them was considered threatened in Sweden. Thus, the differences between the Norwegian and Swedish provinces were not only due to differences in the national classification of species.

4. Discussion

4.1. Hot-spots and conservation of species diversity

The present results show that the most diverse provinces as regards insect species richness and rarity were usually in the southwestern part of the study area. Furthermore, a few southwestern provinces include a very large share of the whole species diversity as shown by the critical fauna analysis.

The previous study on the same insect groups suggested that climatic factors were strongly associated with the variation in the species composition in northern Europe (Väisänen et al. 1992). The present results are generally in agreement with this, although we also found notable deviations from this pattern. This may be partly because of the high variation in the quality of our data, but the results suggest that more specific factors than latitude may also affect insect species diversity. Apparently local research activity (especially in the Sesiidae, see Fig. 2), altitudinal differences, distribution of host plants (e.g. oak and beech) and probably the shape of land masses (or waters as dispersal barriers) are significant modifiers of species richness and composition.

One basic goal of nature conservation is the retention of samples of the full range of species and their natural habitats. Critical fauna analyses will serve to direct attention to faunistically important provinces, though local knowledge is the basis for more detailed conservation planning (Collins & Morris 1985). In the insect groups examined, 70–80% of species were recorded from the most species-rich province. The minimum set of provinces which included all the species typically included southernmost provinces supplemented with a few southeastern-eastern provinces and, excluding the Buprestidae, also one or two northern/mountain provinces. Most of the provinces in the central part of the study area did not contribute significantly to the critical fauna.

The present results emphasize the clear difference between the concepts of rarity and vulnerability. For example, the highest number of threatened species were found in Akershus, southern Norway, and the highest relative vulnerability scores were found in some Danish and Norwegian provinces and the Finnish province Ab. By contrast, the indices of rarity ranked the Swedish province Småland highest.

The results showed that the differences between the southern Norwegian and adjacent Swedish provinces in the number of threatened species cannot be simply explained by differences in the national listing of species, although this may contribute to the observed differences. The southern Norwegian hot-spot was apparent also in rarity indices including conservation index taking species richness into account. The Oslo Field is one of the most fertile districts in Norway, geologically comprising sedimentary rocks such as slate, limestone and sandstone (Skinnemoen 1964). The differences were apparently also due to the variation in the state of faunistic knowledge, in the threats to the fauna and in the real faunistic composition. The international significance of SE Norway for species conservation clearly deserves further study including the Swedish side of the border.

4.2. Use of indices to describe species diversity

The larger the area examined or the number of insects collected, the more species are found. Sample representativeness is the cornerstone of the process of estimating species richness (Baltanás 1992). Problems related to this may seriously affect regional species richness analysis. However, we approach the problem by noting that it is better that conservation plans are based on the available data rather than on no data at all.

Effects of unequal collecting effort on species richness can be corrected by using different indices. There are several reasons for weighting provinces according to the rarity of species present (or at least recorded). Different indices may be applied in different contexts, and we stress that there are currently no clear criteria for selecting only one of those available. Several of the indices are, however, correlated with each other.

The rarity association index (*R*) tended to be largely determined by the number of species reported from the provinces. Thus, it gave fairly similar results to those given by a simple species list. In general, the importance index (*I*) gave rather similar rankings to those obtained using the rarity association index. The conservation index (*Q*) tries to compensate for the effect of the species richness of the province (Minns 1987). The results on the Sesiidae, especially, indicate that the interpretation of indices should be done with special care when the number of species is small and the quality of the original data passable at most.

4.3. Conclusions

The basic objective of species conservation is the conservation of all species. The main strategies for attaining this objective are to prevent any species from going extinct and to maintain sites that support the greatest species richness. The species with limited distributions, i.e. the rare species of the present paper, or species specifically assessed to be threatened are especially prone to extinction.

Recently, threatened species have received much attention and caused public debate in northern Europe (e.g. Andersson et al. 1987, Asbirk & Søgaard 1991, Rassi et al. 1992, Størkensen 1992, Ehnström et al. 1993). One problem is that criteria for judging species' vulnerabilities may vary in different countries, and for example species occurring only in the margins of particular countries may be over-emphasized. According to our results the number of threatened cerambycid species was relatively low in provinces near national borders even in the south. Thus, in this example the marginal populations did not seem to have played a major role in endangerment assessment (the case of SE Norway is questionable). Yet it is obvious that consideration of rarity and vulnerability always also introduces a problem of scale, i.e. whether rarity should be assessed at provincial, regional, national or international level. Standardization of criteria in different countries is still needed.

The present entomological results suggest that especially the southern Swedish provinces Scania, Småland and Öland were hot-spot areas with their luxuriant deciduous forests and other southern habitats. On the island of Öland the highest number of insects occur in habitats rich in vegetation associated with the wide steppe-like limestone formation, but most of the characteristic species, which have existed there since Late Glacial or Preboreal times, are found in habitats with poor, low-growing vegetation (Coulianos & Sylvén 1983). Southwestern Finland (with oak and other deciduous trees; Ab, N) and southeastern Norway (AK, Ø), as well as some Danish provinces (e.g. EJ), were also important areas for the insects. So far little attention has been paid to the maintenance of hot-spots of species diversity. For instance, the nature reserves are disproportionately distributed mostly over the species-poor northern areas, whereas hot-spot provinces are poor in reserves. Moreover, the establishment and delimitation of nature reserves has been often based on political arguments, while ecological criteria have been ignored or overlooked (e.g. Nilsson & Götmark 1992). A balance between similar proportional representativeness of different biogeographical zones (or e.g. provinces), independent of the number of species in them, in conservation networks is challenged by the unequal need of having more reserves in the species-rich areas. Irrespective of the approach, a very high proportion of biodiversity is concentrated in a small proportion of the area of northern Europe.

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