

# Zoogeography of *Bombus* and *Psithyrus* in northwestern Europe (Hymenoptera, Apidae)

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The distribution of bumblebees (*Bombus*) and cuckoo bumblebees (*Psithyrus*) in the British Isles and Fennoscandia was plotted on 100 km squares. A relatively low decrease of species number is seen from the south to the north and about 20 (or more) species have been recorded in many areas of the northern boreal zone. The areal distribution of different bumblebee species and the similarity of the bumblebee fauna in different squares was studied by cluster analysis, two-way indicator species analysis and detrended correspondence analysis. Eleven distribution clusters of bumblebees were separated. Distributions of various *Bombus* species and their inquiline *Psithyrus* species show an incomplete overlap. Numbers of species recorded from various islands were correlated with the size and distance of the islands from the nearest continent. In Fennoscandia, the areal distribution groups obtained follow fairly closely the bioclimatic vegetation zones, which are largely correlated by effective temperature sums during the vegetative period. Also, in the British Isles the effective temperature sums are important determinants of the distribution groups obtained. Zonations observed in other insects, birds and mammals in northwestern Europe are compared with those of bumblebees. The distributional history of bumblebee species in northern Europe is discussed in the light of their present distribution patterns.

## 1. Introduction

The geographical distribution of bumblebee species is well established in northwestern Europe (e.g. the British Isles: IBRA 1980; Norway and Sweden: Löken 1973, 1984; Finland: Pekkarinen et al. 1981). About 32 *Bombus* species and nine *Psithyrus* (cuckoo bumblebee) species have been

recorded from the area. These numbers are fairly high compared with the corresponding numbers in the whole of Europe (53 and 10, respectively, Reinig 1981), indicating a rich bumblebee fauna in this largely boreal area.

Bumblebees are eusocial insects with annual colonies and solitary hibernating queens. Bumblebee communities may contain several common

or fairly common species. Cuckoo bumblebees live asinquilines (social parasites) in bumblebee nests. The active season of bumblebees, lasting from early spring to the beginning of autumn, is longer than that of the majority of solitary insects. In their environment, bumblebees are dependent on numerous nectar and pollen plants flowering at different times of the season. Regarding the autecology of bumblebees, their distribution areas presumably closely correspond to the different types of vegetation and further to vegetational zonations which, in turn, are basically determined by climatic patterns.

Only a few attempts have been made to analyze the zoogeography of certain groups of insects on the basis of their distribution in northwestern Europe, the studies made by Lomholdt

(1974) on sphecids wasps, by Baroni Urbani & Collingwood (1977) on ants and by Väisänen et al. (1992) on Saltatoria, Sesiidae, Buprestidae and Cerambycidae being the most noteworthy. The aim of the present study is to investigate (1) distribution patterns, (2) zoogeographical zonations and (3) distributional history of the bumblebee fauna in northwestern Europe in the light of their present distribution.

## 2. Material and methods

### 2.1. Bumblebee species

The bumblebee species recorded in northwestern Europe are presented in Table 1. The nomenclature

Table 1. Bumblebee species observed in the study area; abbreviations used in figures; number of squares in which the species have been observed (BI = the British Isles, 62 squares; Fe = Fennoscandia and Denmark, 162 squares); and distribution types (DT) and zonal distribution (ZD) based mainly on the classification of Gorodkov (1984). Ca = circumareal, Tp = Transpalearctic, Eu = European, Es = Eurosiberian, Si = Siberian, Ar = arctic, Aa = arcto-alpine, Ab = arcto-boreal, At = arcto-temperate, Bo = boreal, Bm = boreo-montane, Te = temperate, Sb = subboreal.

		BI	Fe	DT	ZD			BI	Fe	DT	ZD
<i>Bombus (Alpigenobombus)</i>						<i>B. (Thoracobombus)</i>					
<i>wurlenii</i> Radoszkowski	wu	0	50	Eu	Bm	<i>humilis</i> Illiger	hu	27	63	Es	Sb
<i>B. (Kallobombus)</i>						<i>muscorum muscorum</i> (Linnaeus)	mm	58	37	Es	Te
<i>soroensis</i> (Fabricius)	so	35	129	Es	Te	<i>m. "smithianus"</i>	ms	7	21		
<i>B. (Bombus)</i>						<i>pascuorum</i> (Scopoli)	pa	58	154	Es	Te
<i>lucorum</i> (Linnaeus)	lu	62	159	Tr	At	<i>runderarius</i> (Müller)	ru	50	80	Es	Te
<i>patagiatus</i> Nylander	pt	0	1	Si	Bo	<i>sylvarum</i> (Linnaeus)	sy	31	60	Eu	Sb
<i>sporadicus</i> Nylander	sp	0	92	Si	Bo	<i>veteranus</i> (Fabricius)	ve	0	47	Es	Te
<i>terrestris</i> (Linnaeus)	te	53	37	Eu	Sb	<i>B. (Subterraneobombus)</i>					
<i>B. (Cullumanobombus)</i>						<i>distinguendus</i> Morawitz	di	54	105	Tp	Te
<i>cullumanus</i> (Kirby)	cu	7	7	Es	Sb	<i>subterraneus</i> (Linnaeus)	su	20	46	Es	Sb
<i>semenoviellus</i> Skorikov	se	0	1	Si	Bo	<i>B. (Rhodobombus)</i>					
<i>B. (Pyrobombus)</i>						<i>pomorum</i> (Panzer)	pm	1	0	Tp	Sb
<i>cingulatus</i> Wahlberg	ci	0	77	Si	Bo	<i>Psithyrus (Ashtonipsithyrus)</i>					
<i>hypnorum</i> (Linnaeus)	hy	0	149	Tp	Te	<i>bohemicus</i> Seidl	bo	55	137	Tp	At
<i>jonellus</i> (Kirby)	jo	58	159	Tp	At	<i>vestalis</i> (Geoffroy in Fourcroy)	vs	28	1	Eu	Sb
<i>lapponicus</i> (Fabricius)	lp	0	75	Es	Ab	<i>P. (Psithyrus)</i>					
<i>monticola</i> (Smith)	mo	28	38	Eu	Bm	<i>rupestris</i> (Fabricius)	rp	39	65	Tp	Te
<i>pratorum</i> (Linnaeus)	pr	52	157	Es	At	<i>P. (Metapsithyrus)</i>					
<i>B. (Melanobombus)</i>						<i>campestris</i> (Panzer)	ca	49	65	Tp	Te
<i>lapidarius</i> (Linnaeus)	la	59	100	Eu	Te	<i>P. (Allopsithyrus)</i>					
<i>B. (Alpinobombus)</i>						<i>barbutellus</i> (Kirby)	br	51	42	Es	Te
<i>alpinus</i> (Linnaeus)	al	0	28	Eu	Aa	<i>P. (Fernaldaepsithyrus)</i>					
<i>polaris</i> Curtis	po	0	31	Ca	Ar	<i>flavidus</i> Eversmann	fl	0	82	Tp	Bm
<i>balteatus</i> Dahlbom	ba	0	50	Ca	Ab	<i>quadricolor globosus</i> Eversmann	qu	0	64	Es	Te
<i>hyperboreus</i> Schönherr	hb	0	15	Ca	Ar	<i>norvegicus</i> Sparre Schneider	no	0	89	Tp	Te
<i>B. (Megabombus)</i>						<i>sylvestris</i> (Lepeletier)	sv	44	125	Tp	Te
<i>consobrinus</i> Dahlbom	co	0	48	Tp	Te						
<i>hortorum</i> (Linnaeus)	ho	62	143	Tp	Te						
<i>rudratus</i> (Fabricius)	rt	23	19	Eu	Sb						

ture of *Bombus* species follows Löken (1973) and Svensson (1979), and that of *Psithyrus* species follows Löken (1984).

The species previously known as *B. lucorum* has been reported to comprise two or even three species in northern Europe, namely *B. lucorum* (Linnaeus, 1761), *B. cryptarum* (Fabricius, 1775) and *B. magnus* Vogt, 1911 (Rasmont 1981, 1984, Rasmont et al. 1986, Scholl & Obrecht 1983, Pamilo et al. 1984). Two of these (possibly *B. lucorum* and *B. cryptarum*) are widely distributed in Fennoscandia. *B. magnus* is separated from *B. lucorum* in the British Isles (IBRA 1980) and in Sweden and Norway (Löken 1973), but Pekkarinen et al. (1981) do not separate these species in eastern Fennoscandia. Therefore, at the present, we have insufficient distribution records on these three taxa and we have treated them collectively as *B. lucorum*.

*B. muscorum* "smithianus" is recorded separately from *B. muscorum muscorum* (L.), otherwise taxons at subspecies level are not separated. Löken (1973) described the subspecies *B. m. liepetterseni* from Norway. The subspecies belongs to the "smithianus" group, but we have treated the group covering all the dark forms of *B. muscorum* collectively.

The records of the British Isles are according to IBRA (1980, records until 1976). The distribution of *Bombus* species in Sweden and Norway is recorded according to Löken (1973, with the additions presented in Löken 1978), and that of *Psithyrus* species according to Löken (1984). Danish records are according to Hammer & Holm (1970) and Löken (1973, 1984); the information is given only generally for different parts of the country and therefore the detailed plotting of the records in the mainland study squares was uncertain. The Finnish records are according to Pekkarinen et al. (1981), but we have added records which have been supplied to us later.

The records cover a long period starting about the middle of the 19th century. Moreover, there are only a few records at our disposal from Karelia and the Kola Peninsula after 1944. In England, an extensive decline or retreat of several *Bombus* species has been recorded (IBRA 1980), possibly caused by intensification of agriculture (Williams 1986). Also, some species may have retreated in Finland (Pekkarinen et al. 1987) and probably in other areas studied, too. Thus the

present study is based on "maximal" distribution of species during the last few decades.

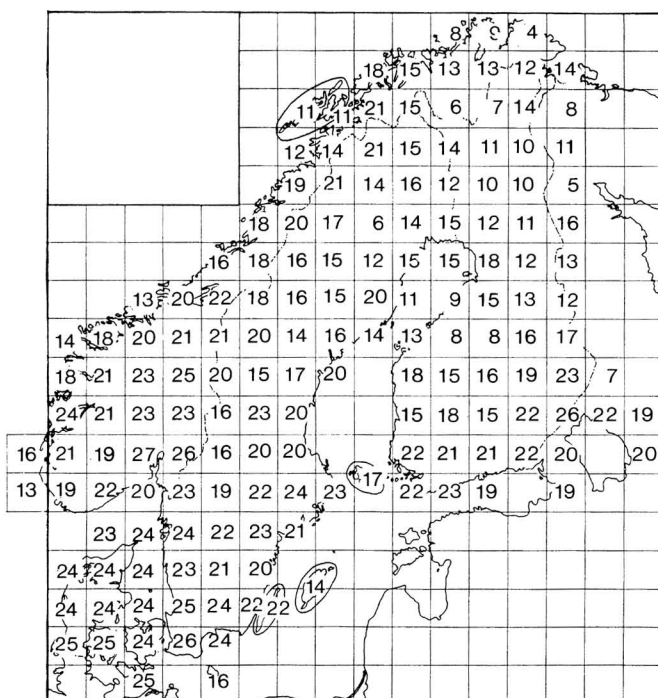
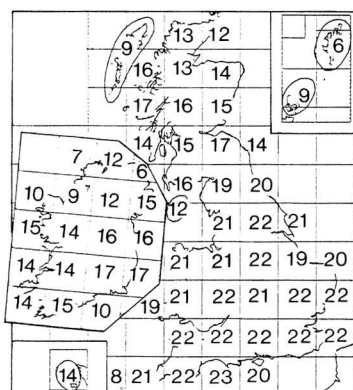
## 2.2. Mapping

Records are given in 100 × 100 km squares. The squares in the British Isles are taken directly from IBRA (1980). The squares in Fennoscandia and Denmark are based on the Finnish uniform grid system (Heikinheimo & Raatikainen 1971) which has been extended to cover the whole area (the N-S axis coincides with the meridian 27°E) as presented by Järvinen & Väisänen (1978; see also Ranta 1982). 100 km squares are too coarse for expressing detailed distributions in the area. On the other hand, markedly smaller squares would give a falsely accurate picture of distributions in certain relatively poorly studied areas (mainly in northern Fennoscandia). In Fennoscandia and Denmark, so-called biogeographical provinces have often been used when presenting (rough) species distributions (e.g. Baroni Urbani & Collingwood 1977, Väisänen et al. 1992), but in the British Isles vice-counties are used instead. Therefore, for the sake of uniformity, we prefer 100 km squares.

There are 240 squares altogether in the study area, but a) island squares are lumped together, b) one square which happened to contain areas from both Ireland and Wales is split into two squares, one belonging to Ireland and the other to Wales, and c) those squares which have less than 3% of land area (excepting islands), are omitted. In the Kola Peninsula and Karelia, only the squares near the present Finnish border are included plus the thoroughly studied squares (numbers 221–224) around the north end of Lake Ladoga (the majority of this area belonged to Finland before the Second World War). The number of study squares thus reduces to 224, which are used in the analyses.

Collecting activity is not evenly distributed over the study area and the distribution records in some squares are presumably lacking due to insufficient collecting (for instance, in Ostrobothnia media in Finland and Pite and Lule Lappmark in Sweden). However, only certified records have been included in the analyses. Records of the presence or absence of the species in different squares are presented in the Appendix.

Fig. 1. The numbers of bumble-bee species in 224 study squares in northwestern Europe.



### 2.3. Clustering

In all cases, binary data (species present or absent) were used to calculate the similarity matrices. The similarity between species  $s_1$  and  $s_2$  was calculated using Jaccard's dichotomy coefficient ( $r_j$ ), the formula of which is:

$$r_j = a/(a+b+c),$$

where  $a$  = number of squares where both  $s_1$  and  $s_2$  are found,  $b$  = number of squares where  $s_1$  is found but not  $s_2$ , and  $c$  = number of squares where  $s_2$  is found but not  $s_1$ . Janson & Vegelius (1981) consider Jaccard's coefficient as one of the most suitable coefficients for measuring ecological coexistence.

The cluster analysis of species distribution was made using the SYSTAT package for microcomputers. The similarity matrix produced by Jaccard's coefficient was clustered using the complete linkage method (CLM), in which the between-cluster distances are computed taking the most distant pair of objects in two clusters (Wilkinson 1988).

The squares were grouped using two-way indicator species analysis (TWINSPAN), in which the program divides the samples into groups by repeated dichotomization and then does the same for the species (Hill 1979a). The number of indicators was five and the maximum level of divisions was four, otherwise default values were used. The indicator species in the first division were *B. ruderarius*, *B. lapponicus*, *B. cingulatus*, *P. campestris* and *P. barbutellus*.

Both the species and the squares were also analyzed by detrended correspondence analysis (DCA, Hill 1979b), in which detrending by segments was used. The length of the gradient was 2.886 SD.

### 3. Number of species, distributional groups and zonation

The numbers of species in various squares are relatively constant (about 20) in large areas of northwestern Europe (Fig. 1, see also Appendix). There is only a minor decrease in the number



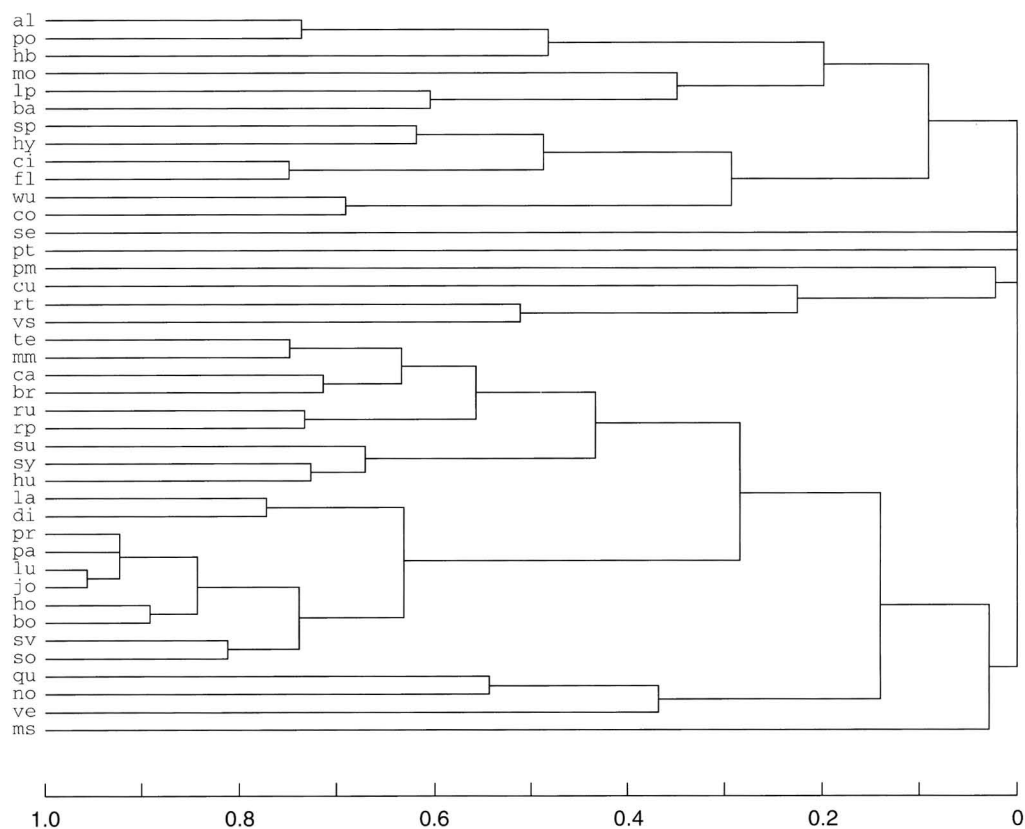


Fig. 2. The dendrogram of bumblebee species (complete linkage method, CLM) based on distribution in north-western Europe. The abbreviations of the species names are given in Table 1.

of *Bombus* species from the south to the north while the corresponding decrease is more pronounced in the case of *Psithyrus* species. The highest numbers of species are found in the southernmost squares and in several squares located in the Scandinavian mountain area. Even in northernmost Sweden and Norway, more than twenty species have been recorded in some squares indicating an important role of bumblebees in mountain and northern boreal communities. The numbers of species recorded on most of the islands (Åland, Gotland, Bornholm, Lofoten, Channel Islands, Scilly, Isle of Man, Outer Hebrides, Orkney, Shetland) are clearly lower than those observed in the nearest continental areas.

The clusters of species were quite similar in the CLM dendrogram (Fig. 2) and in the DCA ordination (Fig. 3). The main differences were as follows:

- 1) *B. wurflenii* and *B. consobrinus* clustered (fairly loosely) with the *B. sporadicus* – *P. flavidus* group in CLM, but with the *B. alpinus* – *lapponicus* group in DCA.
- 2) *B. monticola* clustered with the last named species group in CLM, but with *B. muscorum* “*smithianus*” in DCA (in CLM *B. m.* “*smithianus*” clustered loosely with all other species).

On the basis of the clusters in Figs. 2–3, the following distributional groups of species have been obtained in northwestern Europe:

- 1) Northern – montane: *B. alpinus*, *hyperboreus*, *polaris*, *balteatus*, *lapponicus*, *wurflenii* and *consobrinus*.
- 2) Boreobritish: *B. monticola* and *muscorum* “*smithianus*”.

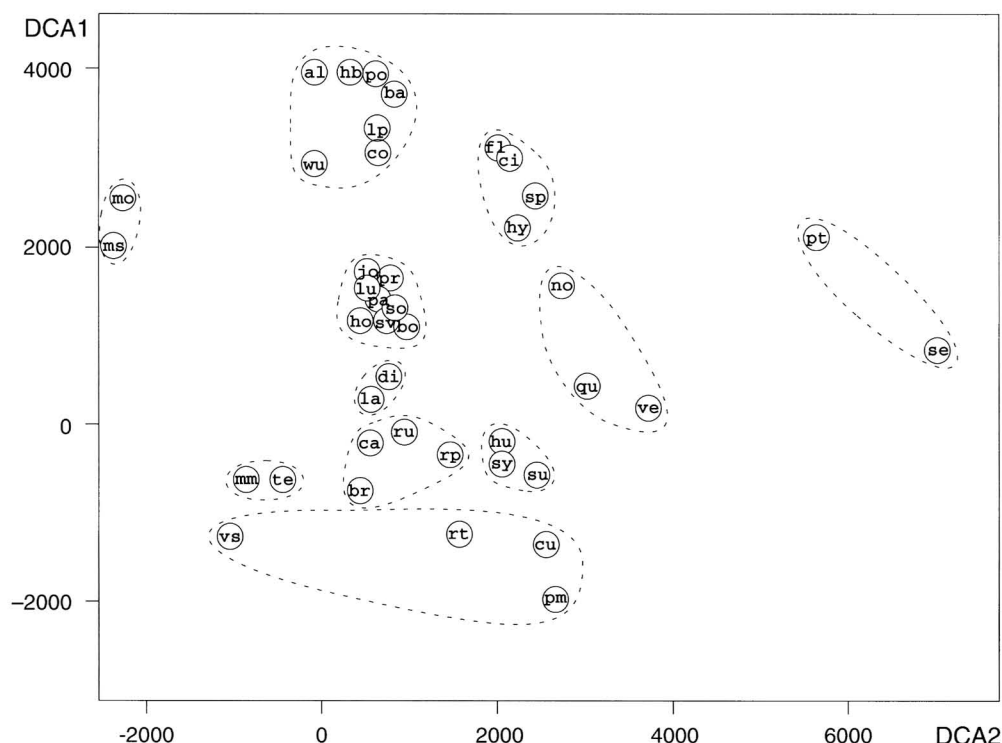


Fig. 3. The bumblebee species in northwestern Europe plotted on the 1st and 2nd axes (eigenvalues are 0.367 and 0.098, respectively) of detrended correspondence analysis (DCA). Abbreviations of the species names, see Table 1. The encircled clusters correspond to separated distributional groups.

- 3) Eastern not in the British Isles: *B. sporadicus*, *cingulatus*, *hypnorum* and *P. flavidus*.
- 4) Extremely eastern, only in easternmost Fennoscandia: *B. patagiatus* and *semenoviellus*.
- 5) Widely distributed, a) practically over the whole area: *B. jonellus*, *pratorum*, *lucorum*, *pascuorum*, *soroeensis*, *hortorum*, *P. bohemicus* and *sylvestris*; b) not in northernmost Fennoscandia: *B. distinguendus* and *lapidarius*.
- 6) Southern not in the British Isles: *P. norvegicus*, *quadricolor* and *B. veteranus*.
- 7) Southern with limited distribution in the British Isles: *B. humilis*, *sylvarum* and *subterraneus*.
- 8) Southern with wide distribution in the British Isles: *B. ruderarius*, *P. campestris*, *barbutellus* and *rupestris*.
- 9) Southern not in eastern Fennoscandia: *B. terrestris* and *muscorum muscorum*.
- 10) Extremely southern: *B. cullumanus*, *ruderatus*, *pomorum* and *P. vestalis*.

General distributional types and the zonal distribution of the bumblebee species are given in Table 1. Only three arctic species have holarctic (circumareal) distribution. 17 species from this area do not occur in the British Isles. These species have mostly either arctic (-alpine) or eastern distribution. The ranges of *B. hypnorum*, *B. veteranus*, *P. norvegicus* and *P. quadricolor* extend to or near the continental coast of the English Channel (see e.g. Rasmont 1988), but there are no records from the British Isles.

The squares were classified into sixteen groups according to their fauna by TWINSpan. Distribution of the squares in the TWINSpan groups is seen in Fig. 4 and the squares in DCA ordination in Fig. 5. Both analyses gave quite similar pictures and the groups of squares corresponded well with

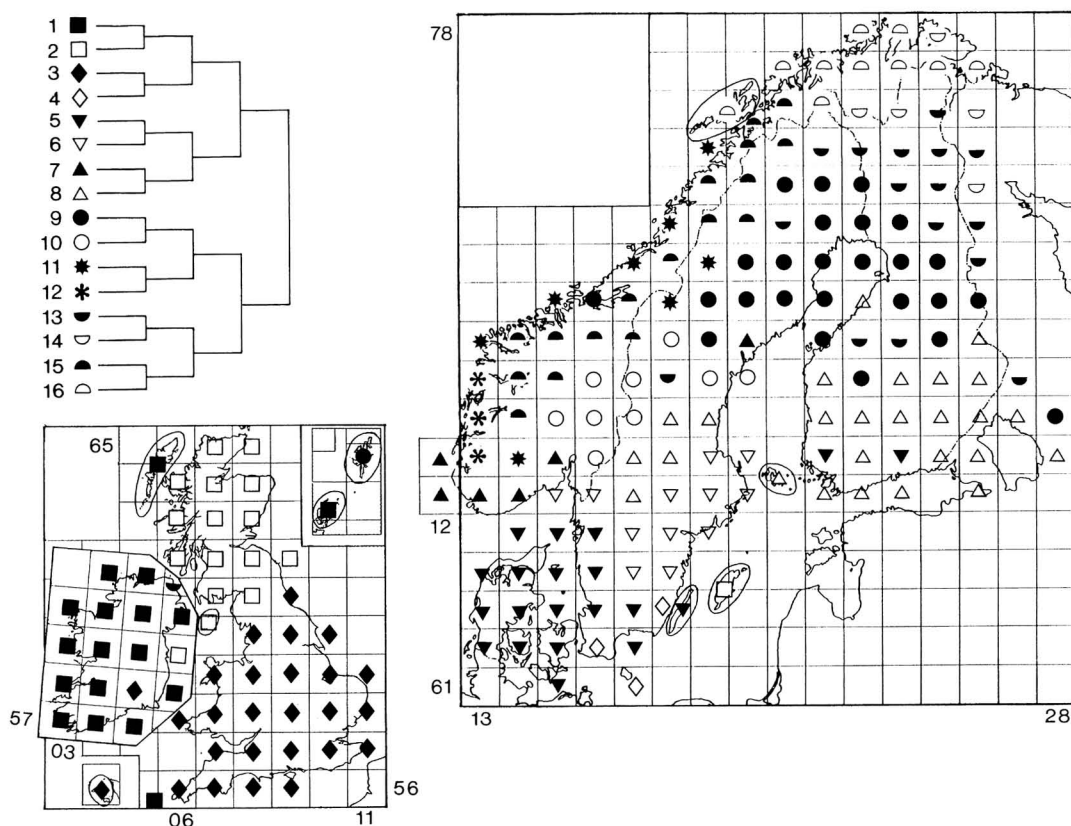


Fig. 4. Distribution of the study squares in the groups interpreted from TWINSpan analysis. The numbers in the margins of the maps refer to the coding system of the squares presented in the Appendix.

each other in the two analyses. Sporadic or markedly deviating squares are possibly caused by insufficient records. The groups in common in the two analyses can be summarized as follows:

- 1) Scotland, Ireland, Wales and England (TWINSpan branches 1, 2 and 3). The Isle of Man, Outer Hebrides, Orkney Isles and Gotland in the Baltic were also clustered with this group (the Shetland Islands, the Isles of Scilly and the Channel Islands are distinctly separate from this group in DCA ordination).
- 2) Denmark and six squares in southwestern and southern Sweden (TWINSpan branch 5) (two squares in southern Finland were clustered with this group in TWINSpan).
- 3) Most of southern Sweden (TWINSpan branch 6).
- 4) An area through central Sweden and southern Finland (TWINSpan branch 8).
- 5) Large area in central and northern Scandinavia and northern Finland around the Gulf of Bothnia (TWINSpan branches 9 and 10).
- 6) Main part of Norway, part of northwestern Sweden and northern Finland (TWINSpan branches 11–16). Relatively great heterogeneity is characterized by this area, especially in DCA ordination, which is possibly caused by an insufficient number of records in several squares.

The number of species in different islands varies from 1 to 22 (Table 2). The number was lowest in small isolated islands (for instance, in Fair Isle, Foula and Gotska Sandön) and highest in large islands lying near the mainland (especially in Öland). Because the number of mainland species varies slightly according to the latitude, we used the percentage of the species

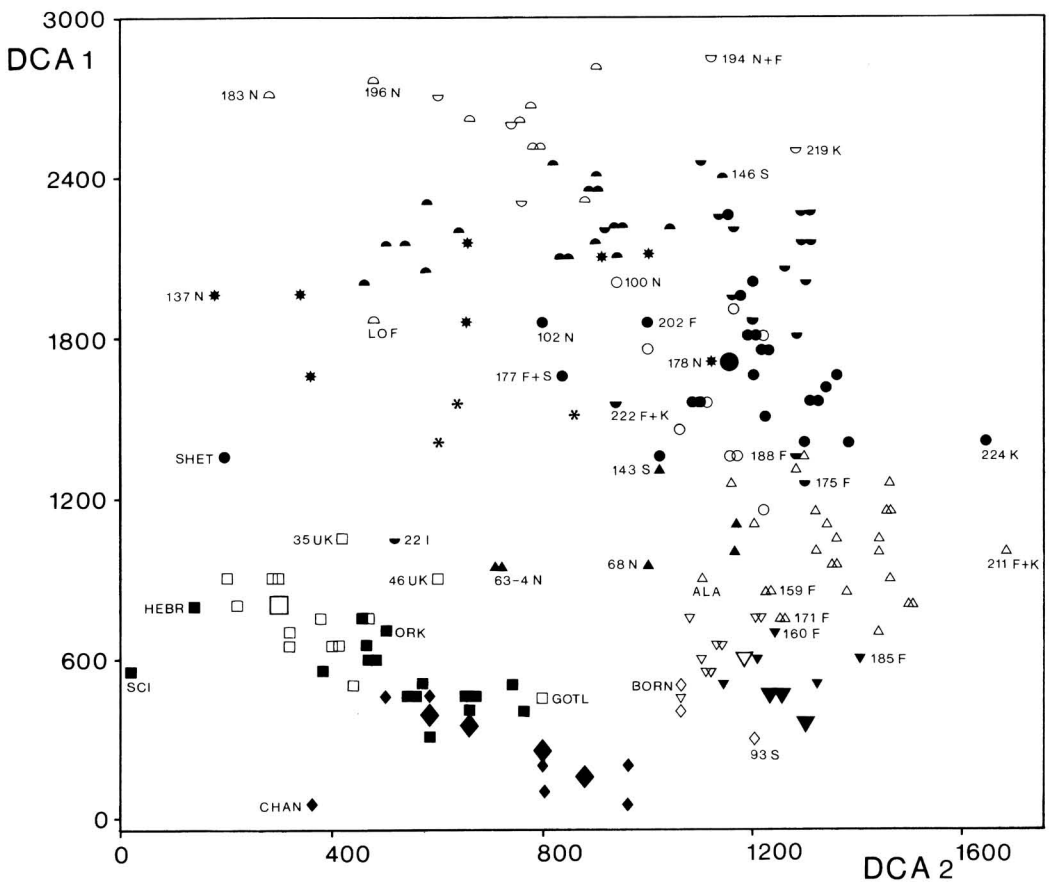


Fig. 5. The study squares in northwestern Europe plotted on the 1st and 2nd axes of detrended correspondence analysis (DCA). For the numbers and the symbols of the squares, see Appendix and Fig. 4. Big symbols refer to 3–6 squares. Some squares lying outside the main area of the cluster (squares with the same symbol) are named.

number of the island compared to the numbers observed in the nearest mainland (m) or the nearest bigger island (i) to study the effect of the island area and distance. The correlations between these percentage values and island areas / distances are as follows:

	correlation probability	
log area / percent (m)	0.571	0.006
log area / percent (i)	0.589	0.004
distance (m) / percent (m)	–0.636	0.001
distance (i) / percent (i)	–0.204	0.363

The percentage of the species number is positively correlated with the island area and the correlation is significant when we use the loga-

rithm of the area. The percentage of species number is negatively correlated with the distance from the mainland, but the correlation is not significant with the distance from the nearest bigger island.

## 4. Discussion

### 4.1. Number of species

In terrestrial animal groups, the number of species usually decreases from the equator towards the poles. However, explanations for this widespread phenomenon vary (e.g. Pianka 1966, Udvardy

1969). The number of bumblebee species is quite stable in large areas of northern temperate and boreal zones of the Holarctic region, as already noted by Ranta (1982). For information on local species numbers see Ranta (1984) and Pekkarinen (1984). Especially high numbers are found in mountain areas and approximately one half of the Palaearctic bumblebee species do live in mountain areas (Skorikov 1922:137).

Comparison between the species numbers of (A) solitary bees (= Apoidea excluding *Apis*, *Bombus* and *Psithyrus*) and (B) bumblebees (= *Bombus* and *Psithyrus*) in five areas of Fennoscandia illustrates the low number of solitary bees in northern habitats (records on solitary bees mainly after Elfving 1968, Erlandsson et al. 1988, Svensson et al. 1990 and Janzon et al. 1991):

	A	B
Southernmost Sweden (Scania, Halland, Blekinge, Öland)	212	26
Southernmost Finland (Alandia, Regio aboensis, Nylandia, Karelia australis)	180	24
Central Finland (Ostrobothnia media and kajanensis)	62	18
Northernmost Sweden (Torne Lappmark)	21	22
Northernmost Finland (Lapponia enontekiensis and inariensis)	14	16

The high success of bumblebees in cool and even cold environments is presumably connected with certain evolutionary adaptations, the most important of which are (1) annual colonies and

Table 2. The island characteristics area (km<sup>2</sup>), distances to the mainland (m) and possibly to a bigger island (i), and the number of bumblebees in the nearest mainland (or bigger island) and in the island itself (B = *Bombus* spp., P = *Psithyrus* spp.).

	Area	Distance		No. of species				Tot.	Ref.
		m	i	m	i	B	P		
British Isles									
Jersey	116	20		21		7	3	10	5
Guernsey	63	45		21		9	4	13	5
Alderney	8	15		21		8	3	11	5
Sark	5	35	10	21	13	4	2	6	5
Scilly	16	40		22		6	2	8	2
Lundy	4	20		21		6	1	7	2
Isle of Wight	381	4		22		13	2	15	2
Isle of Man	588	30		21		10	2	12	2
Aran Islands	47	10		15		7	2	9	2
Cara + Gigha	12	4		14		9	3	12	2
Outer Hebrides	3500	25		16		8	1	9	2
Orkney	975	10		13		6	3	9	2
Shetland	1485	170	80	13	9	6	0	6	2
Foula	10	175	25	13	6	1	0	1	2
Fair Isle	8	125	40	13	6	1	0	1	2
Denmark									
Bornholm	588	35		26		13	3	16	1+3
Norway									
Lofoten	1677	2		18		9	2	11	3+4
Sweden									
Öland	1347	5		22		15	7	22	3+4
Gotland	2959	90	55	22	22	11	3	14	3+4
Gotska Sandön	36	85	40	22	14	3	1	4	3+4
Finland									
Åland Islands	1481	40		23		13	4	17	6
Hailuoto	198	10		19		8	2	10	6

References: 1 = Hammer & Holm 1970, 2 = IBRA 1980, 3 = Löken 1973, 4 = Löken 1984, 5 = Rasmont 1988, 6 = Pekkarinen et al. 1981.

solitarily-hibernating queens, (2) facultative endothermy and (3) coevolution between bumblebees and arctic nectar and pollen plants, especially Fabaceae (= Leguminosae) (e.g. Panfilov et al. 1960). The differences of habitats in various altitudinal vegetation zones is the most natural explanation for rich bumblebee faunas in mountain areas (Pekkarinen 1984).

The reason for the low numbers of bumblebee species on islands may be that a) the island is too far from the mainland or from a bigger island, b) the island is too small, or that c) suitable habitats for certain species are lacking on the island. Although bumblebees are excellent fliers (*B. lucorum* queens have been seen flying in the middle of the Gulf of Finland, Mikkola 1984), they are not good island colonizers. For example, *B. jonellus* is the only original bumblebee species in Iceland (Prýs-Jones et al. 1981). Also, a negative correlation between the species numbers and the distance from the mainland indicates fairly poor colonization ability. Bumblebees do not seem to use bigger islands as "stepping stones" to smaller islands. On the other hand, because bumblebees are strong fliers, they are seldom found in the insect drifts (see Mikkola 1984).

Even on the islands smaller than 10 km<sup>2</sup> there was at least one bumblebee species present, and the number of species on the smallest Island examined (Lundy, 4 km<sup>2</sup>) was as high as seven (Table 2). On large islands the percentage of the species number compared with that of the main-

land was more than 50% (except in Shetland). Usually, the species which have a large distribution area (for example, *B. hortorum* and *B. lucorum*) are found both on large and small islands. On the other hand, *B. jonellus* and *B. muscorum* seem to be present even on the smallest islands (*B. muscorum smithianus* is the only species both on Foula and Fair Isle). The number of *Psithyrus* species is low especially on the smallest islands.

The relatively low numbers of species on many islands near adjacent mainland (Table 2) may partially be caused by the scantiness of suitable forest habitats. The species preferring open terrains (e.g. *B. jonellus* and *B. muscorum*) are recorded on islands more often than species living mainly in forests. For example, *B. pratorum*, which typically prefers forest habitats and has a wide distribution on the mainland, is lacking on most of the islands (see also Pekkarinen 1984). However, it has recently been found on the Isle of Man (Crellin 1992).

#### 4.2. *Psithyrus* species and their hosts

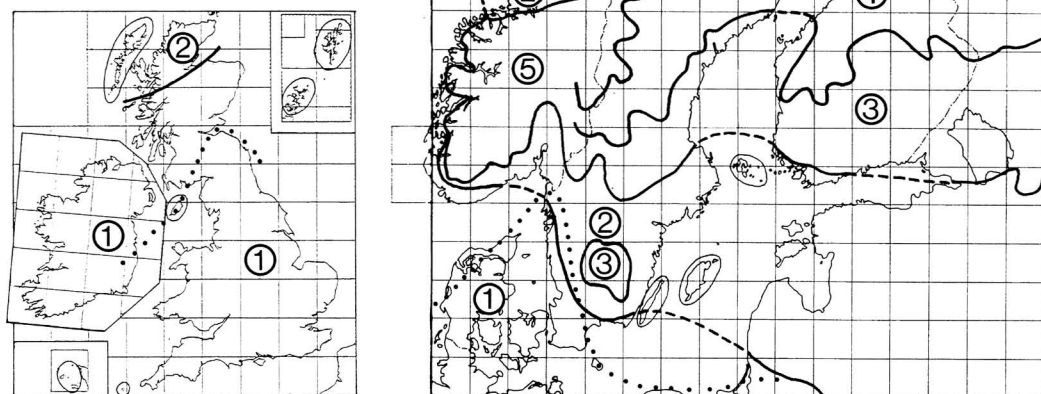
*Psithyrus* species are inquilines of bumblebees and their host specificity is variable (e.g. Pekkarinen et al. 1981, Löken 1984, Rasmont 1988). The most probable inquiline-host relationships in the study area are given in Table 3. Great conformity of distributions was seen both in CLM

Table 3. Possible inquiline-host relationships of bumblebees in northwestern Europe. a = number of squares where both the inquiline and the host are observed, b = number of squares where the inquiline is found but not the host, c = number of squares where the host is found but not the inquiline,  $r_j$  = Jaccard's coefficient.

Inquiline	Possible host	a	b	c	$r_j$
<i>P. bohemicus</i>	<i>B. lucorum</i>	191	1	30	0.86
<i>P. rupestris</i>	<i>B. lapidarius</i>	103	1	56	0.64
<i>P. campestris</i>	<i>B. humilis</i>	74	40	16	0.57
<i>P. campestris</i>	<i>B. pascuorum</i>	114	0	98	0.54
<i>P. barbutellus</i>	<i>B. hortorum</i>	93	0	112	0.45
<i>P. sylvestris</i>	<i>B. pratorum</i>	167	2	42	0.79
<i>P. flavidus</i>	<i>B. jonellus</i>	82	0	135	0.38
<i>P. flavidus</i>	<i>B. cingulatus</i>	68	14	9	0.75
<i>P. norvegicus</i>	<i>B. hypnorum</i>	89	0	60	0.60
<i>P. quadricolor</i>	<i>B. ruderarius</i>	57	7	73	0.42
<i>P. vestalis</i>	<i>B. terrestris</i>	29	0	61	0.32
<i>B. hyperboreus</i>	<i>B. polaris</i>	15	0	16	0.48



Fig. 6. Vegetation zones in north-western Europe mainly according to Ahti et al. (1968), Kalliola (1973), Hämet-Ahti (1981) and Abrahamsen et al. (1982). Dotted line shows the isopleth of effective temperature sum  $50^{\circ}\text{C}$  (threshold  $+5^{\circ}\text{C}$ , in monthly degrees) according to Tuhkanen (1984). — 1 = temperate, 2 = hemiboreal, 3 = southern boreal, 4 = middle boreal, 5 = northern boreal zone.



and DCA (Figs. 2 and 4) and pairwise coexistence (Table 3) was noted between *P. bohemicus* and *B. lucorum*, *P. sylvestris* and *B. pratorum*, and *P. flavidus* and *B. cingulatus*. Reports on the hosts of several *Psithyrus* species found in the study area vary and these species possibly have two or more hosts. *B. jonellus* is a possible host of *P. flavidus* (e.g. Löken 1984). However, the distributions of *P. flavidus* and *B. cingulatus* coincide very well, and they also have a large common distribution area in the eastern Palaearctic region indicating a probable inquiline-host relationship. Yet, *B. cingulatus* does not occur in disjunct distribution areas of *P. flavidus* in the Pyrennees and Alps.

#### 4.3. Fauna areas and vegetation zones

Vegetation zones distinguished by Sjörs (1963) and Ahti et al. (1968) are often cited in connection with biogeographic zonation in northwestern Europe (e.g. Abrahamsen et al. 1982). These two zonations are fairly similar, the greatest differences being in the western coast of Norway. Ahti et al. (1968) evaluated various criteria, such as

climatic, edaphic, topographic, floristic, ecological and phytosociological, for the delimitation of vegetation zones; their zonation can be characterized as bioclimatic. This zonation largely follows certain thermal parameters, such as potential evapotranspiration, temperature sums, and the length of vegetative period (Tuhkanen 1980, see also Laaksonen 1979). In the following, we use mainly the terminology of Ahti et al. (1968) and make comparisons with the zonation of Ahti et al. (1968), Hämet-Ahti (1981) and Abrahamsen et al. (1982) (see Fig. 6).

100 km squares give only an approximate picture of the distribution of various species and fauna areas. Also, the records from several squares are insufficient, and thus a detailed resemblance with more accurate vegetation zonations cannot be expected. Yet, relatively great basic conformity can be seen between fauna areas and vegetation zonation in Fennoscandia, which can be summarized as follows (branches of TWINSPLAN dendrogram refer to Fig. 4):

- 1) Area of branch 5 equates quite well with the temperate zone in Denmark and southern

Sweden. The isle of Bornholm and two squares in southernmost Sweden form the sister branch of branch 3 (Wales and England).

- 2) Area of branch 6 equates well with the hemiboreal zone in southern Sweden. The area does not extend to southern Norway or southwestern Finland, but in DCA ordination (Fig. 5) three squares (159, 160, 171) in the southwestern corner of Finland and in the Åland Islands were clustered with the squares of branch 6.
- 3) Area of branch 8 covers the main part of the southern boreal zone in Central Sweden and southern Finland. The sister branch 7 comprises five squares in the mainly hemiboreal zone of southernmost Norway.
- 4) Area of the sister branches 9 and 10 equates with the main part of the middle boreal zone in Finland and northern Sweden.
- 5) Area of branches 11–16 equates quite well with the large northern boreal zone in Fennoscandia. The area of the sister branches 15 and 16 coincides with the oroarctic area in Ahti et al. (1968) or the alpine zone in Abrahamson et al. (1982). However, the bumblebee fauna in the narrow belt of southern vegetation zones on the western coast of Norway does not coincide with that of the same zones in Sweden and Finland.

In the British Isles, only northern Scotland is classified as the hemiboreal vegetation zone by Hämet-Ahti (1981) while Tuhkanen (1984) regarded the whole of the British Isles as the temperate zone. Yet, the isopleth of the effective temperature sum 50°C (monthly mean) in Scandinavia follows approximately the border between the temperate and hemiboreal zones and in the British Isles the isopleth separates Scotland and the main part of Ireland (areas of the sister branches 1 and 2 in Fig. 4) from Wales and England (area of branch 3) (see Tuhkanen 1984: app. 1, fig. 12). Thus effective temperature sums are also in the British Isles significant determinants of the distribution groups obtained.

The relative isolation of the British Isles from Denmark and Fennoscandia in TWINSpan and DCA analyses is caused by the absence from the British Isles of several bumblebee species otherwise widely distributed in the continent of northern Europe. On the other hand, clustering of Gotland

with Scotland or Ireland in the analyses is caused by the absence of the same species (i.e. *B. veteranus*, *P. quadricolor* and *P. norvegicus*) in these areas.

In Finland, a large loop on the border between the southern and middle boreal zones (Fig. 6) is clearly seen in Fig. 4. The southward loop runs along the Suomenselkä watershed and is mainly the result of only small differences in the topography. Also, the middle boreal zone is largely modified by topography and southern species are able to disperse northwards along river valleys, for example, where the local climate is often less severe.

Resemblance to vegetation zonations can be clearly seen in the actual distribution of several Fennoscandian bumblebee species or distributional groups of species. Thus extremely southern species are restricted to the temperate zone, the northern limit of many southern species follows the northern border of the hemiboreal zone in Scandinavia, and northern-montane species are restricted mainly to the northern boreal zone. There are no, or only a few, records in accurately plotted maps by Löken (1973, 1984) of several southern species (*B. terrestris*, *humilis*, *muscorum*, *runderarius*, *sylvorum*, *P. barbutellus*, *rupestris* and *campestris*) from the isolated southern boreal area of Småland in southern Sweden. True absence (or scantiness) of these species in this oroboreal upland area is possible, but may partly be an artefact due to low collecting activity.

In Finland, Merikallio (1946) studied the quantitative structure of land bird fauna and placed (two) transitional zones with a rapid stepwise change of avifauna on the northern borders of southern and middle boreal zones. Further, in the area of the southern loop of the middle boreal zone (in Suomenselkä), the density of birds was significantly lower and the proportion of northern species higher than in the area of southern boreal zone (Merikallio 1955). On the basis of species diversity of avifauna, Järvinen & Väisänen (1980) verified the transitional character of the northern border of the middle boreal zone in Finland. Yet, the southern border of the middle boreal zone distinguished by these authors runs through Finland from southeast to northwest without any southward loop.

The narrow area running approximately along the northern border of the middle boreal zone is a transitional zone where the ranges of several closely related allopatric vertebrates meet and the cline of colour polymorphism of red squirrel (*Sciurus vulgaris*) changes stepwise (Voipio 1956). The same area is the northern limit of a secondary intergradation zone of two races of yellow wagtail (*Motacilla flava*) in Finland (Sammalisto 1958).

Baroni Urbani & Collingwood (1977) distinguished fauna areas of ants in northwestern Europe on the basis of a distribution similarity dendrogram. Their areas are quite different to those found by us and the areas do not follow vegetation zonations. However, they used a complicated coefficient of similarity (see Janson & Vegelius 1981) and (biological) provinces as area units which are often too large to reveal real limits of distribution. Moreover, ants are not bound to flowering plants in the same way as bumblebees. The fauna areas of sphecids wasps drawn by Lomholdt (1974) have great similarity to vegetation zonations in northwestern Europe and thus also to the areas of bumblebee distribution. Five of the seven sphecids regions of Lomholdt (1974) correspond quite well with temperate (although including a small area in southernmost Finland), hemi- and southern boreal (together), middle boreal and northern boreal zones in Denmark, Sweden and Finland. Lomholdt concluded, however, that discontinuities do not exist between the regions. Väisänen et al. (1992) studied the province records of Saltatoria, Sesiidae, Buprestidae and Cerambycidae from Fennoscandia and Denmark by TWINSpan, DCA and canonical correspondence analyses. Distribution patterns obtained in this study coincide only roughly with vegetation zones, possibly the greatest similarity being with respect to the Cerambycidae.

The reality of distinct boundaries or transitional zones of biogeographic areas has been a subject of an extended controversy (see e.g. Udvardy 1969:285–288, MacArthur 1972:161). However, since temperature, moisture and topography do not change in a parallel manner, areal changes of climate are gradual but not even. For example, in southern Scandinavia, rigid areal differences in oceanicity cause packing of isopleths

of effective temperature sums (Fig. 14 in Laaksonen 1979) and consequently rapid areal changes in vegetation. Further, packing of isopleths is seen in the border area between middle boreal and northern boreal zones in Finland, previously characterized as a meaningful faunal transitional zone (see also Fig. 12 in Voipio 1956 presenting isotherms of growth periods in Finland).

We suppose that temperature (measured as effective temperature sum) largely determines the northern limits of many bumblebee species. Direct effects of temperature and length of season are significant as well as having an indirect effect on vegetation and food plants of bumblebees. Among environmental variables studied by Väisänen et al. (1992), temperature (including effective temperature) associated with geographic latitude was the most important determinant for distribution of insect species. Temperature sum during the growing period is extraordinarily important for bumblebees owing to the long active season of bumblebee colonies and the great energy consumption of foraging queens and workers. The southern limit of “northern” species may be largely determined by competition in the border area with more southerly species (e.g. MacArthur 1972). A general rise in temperature has been recorded in most of the Fennoscandian area starting in the middle of the last century, and being most pronounced in the spring temperatures ( $>2^{\circ}\text{C}$ , Lindroth 1972, Heino 1978). Extensions of the distribution of the temperate or subboreal species *B. sylvarum* and *B. subterraneus* since the 1930's in Finland (Niemelä 1947, Pekkarinen et al. 1981) and *B. terrestris*, *B. lapidarius* (Löken 1973, 1978) and *P. vestalis* (Andersson 1992) in Scandinavia are possibly due to this warming of the climate.

#### 4.4. Distributional history of bumblebees in Fennoscandia and the British Isles

During the last Pleistocene glaciation (Würm), northern Europe was largely covered with ice, only southern Ireland, southern England and western Jutland being free of ice. Reinig (1939, 1965, 1970) has discussed the distributional history of bumblebees after the last glaciation in Europe and Löken (1973) in Scandinavia. All

species with a European type of distribution have invaded Scandinavia from the south. Most species with a Transpalaeartic distribution have invaded Scandinavia from the south or from both the south and the southeast through Finland (Löken 1973:200). Boreal, arctoboreal and arctic species are the most prominent eastern immigrants in Fennoscandia.

#### 4.4.1. Boreo-montane species

Three Fennoscandian species (*B. wurflenii*, *B. monticola* and *P. flavidus*) have a boreo-montane distribution, but they seem to belong to different branches (Fig. 2) or groups (Fig. 3) in the present analyses. *P. flavidus* is an eastern immigrant and its range in Fennoscandia is connected with the wide Transpalaeartic distribution of this species. *B. wurflenii* and *monticola* have invaded from the south, perhaps following the retreating edge of the ice (Löken 1973:201). In northern Europe, the distribution of *B. wurflenii* is restricted to Scandinavia only (the record from Suomussalmi, eastern Finland, is obviously based on a mislabelled specimen, see Pekkarinen et al. 1981). The Scandinavian subspecies *B. wurflenii brevigena* (Thomson) differs chromatically from Alpine specimens (Reinig & Rasmont 1988).

The specific status of *B. lapponicus* and *B. monticola* was clarified by Svensson (1979). Outside Fennoscandia, *B. monticola* is distributed to several isolated areas in central European mountains and to a quite large area in the British Isles. Svensson (1979) demonstrated that the British and Swedish specimens of *B. monticola* differ distinctly from each other in certain metric and chromatic characters, the Swedish specimens being more similar to specimens from the Alps and the Pyrennees. Populations of mountain species were able to survive during various phases of Würm glaciation by adapting to life on the seacoasts and, on the other hand, some grassland and woodland species adapted to the heath and moorland habitats (Beirne 1952). In Britain, *B. monticola* is restricted to *Vaccinium* moorland habitats (Alford 1975:186, Yalden 1982) while in central European mountain areas it lives in coniferous forests (Reinig 1965) and in Scandinavia only in subalpine/alpine habitats. Thus

metric and bionomic differences between British and Scandinavian populations indicate long-continued isolation and a possible interglacial origin of the range in the British Isles (cf. so-called "boreobritish" Coleoptera, Lindroth 1935).

#### 4.4.2. *B. consobrinus*

The history of a disjunct distribution of *B. consobrinus* in Scandinavia is disputable. Reinig (1965) and Löken (1973) considered *B. consobrinus* as a postglacial immigrant in Scandinavia. *B. consobrinus* is nearly monolectic for wolfsbane (*Aconitum septentrionale*) and the ranges of the plant and the bumblebee are practically identical in northwestern Europe (Löken 1973). *Aconitum* has a large range in Scandinavia, but there is a wide gap in Finland and the ranges in Karelia and the Kola peninsula are connected with a large and continuous distribution over northern Eurasia. Fries (1949) suggested, on good grounds, that the disjunct Scandinavian distribution of wolfsbane is due to spreading from one or several glacial refuges. He emphasized that *Aconitum* seeds mainly disperse via running water and the southeasterly direction of watercourses in southeastern Finland would afford a natural explanation for the postglacial history of wolfsbane in Scandinavia and its absence in Finland.

*A. septentrionale* is completely protandrous (Löken 1949) and is thus dependent on bumblebees for its pollination. If *A. septentrionale* occurred in Scandinavian refuges during Würm glaciation, bumblebees must have lived there, too. In this connection we stress that *Aconitum* is often found in subalpine meadows in Scandinavia, and note the differences in flower morphology of *Aconitum* and in enzyme gene alleles of *B. consobrinus* between Scandinavian and Karelian (southeastern Finland) populations (Pekkarinen 1979). Also, the clustering of *B. consobrinus* in the present DCA analysis close to arctic or arctoboreal species indicates the alpine character of the range of this species in Scandinavia. Conspecificity of *B. consobrinus* and central European *B. gerstaeckeri* is uncertain. Similarity in some metric characters measured by Löken (1973) does not indicate a specific difference, neither, necessarily, do differences in en-

zyme gene alleles noted by Rasmont (1988). For the present, it seems the question of whether *B. consobrinus* (or any other arctic or arcto-alpine or boreo-montane bumblebee species) has survived in Scandinavian refuges during Würm glaciation is not settled. The whole theory of glacial refuges in Scandinavia has been questioned by Brinck (1966, but see Lindroth 1969).

#### 4.4.3. Intergradation zones and melanic populations

Two secondary intergradation zones of three areal colour forms of *B. pascuorum* through central and northern Scandinavia may be caused by three separate post-glacial invasions of Scandinavia (Löken 1973). The intergradation zone between two dominant colour forms of *B. pascuorum* in Scandinavia (*B. p. pallidofacies* and *B. p. sparsareanus*) runs through southern Norway and central Sweden along the transitional area of hemiboreal and southern boreal vegetation zones. This area is also a border of the ranges of several bumblebee species classified here as southern or eastern and similarly the area between branches 6 and 8 in the present TWINSPLAN analysis. Moreover, a melanic form of *B. pascuorum* is restricted to Denmark and to Sweden on the extreme west coast of Scania (Löken 1973:168) corresponding closely with the temperate vegetation zone.

The distribution of polymorphic melanic populations of *B. hortorum* and *B. balteatus* in Scandinavia does not seem to follow any biogeographic zonation. Generally, melanic populations of bumblebees are restricted to coastal and mountain areas of southern Scandinavia and we do not suggest that the existence of melanism in *B. hortorum* and *B. balteatus* would have been caused by invasions of melanic and light populations from opposite directions. The adaptive value of melanic colours for bumblebees is an unsettled question but we suggest that the thermal effect of insulation is a meaningful selective factor maintaining melanic colours in oceanic and cold environments (see also Pekkarinen 1979). In southernmost Finland (Hanko Peninsula), the areally-restricted polymorphic melanism of *B. veteranus* (with a high frequency of melanic individuals) has obviously appeared

quite recently (Pekkarinen & Teräs 1986), indicating a rapid change of frequency of melanic phenotypes.

The dark form of *B. muscorum* ("smithianus") is restricted to coastal areas and is unique among bumblebees in northwestern Europe. The intergradation zone between the dark and light forms of *B. muscorum* in southern Norway (see Löken 1973) indicates conspecificity of the forms. The dark form possibly invaded the British Isles during the first interstadial phase of Würm (Beirne 1952, see also Reinig 1970) and adapted to life on the sea coasts during the colder stadial phase. The range of the light form of *B. muscorum* might be due to a more recent invasion and the distributional history of the two forms may be similar in Fennoscandia, too.

In the early post-glacial period, Great Britain was connected to the continent across the Straits of Dover (Beirne 1952) allowing a good south-eastern passage for immigration from the continent. Immigration of bumblebees across the English Channel is still a possible explanation but the absence of *B. hypnorum* and *B. veteranus* in England and their rich occurrence on the continental coast of the Channel (Rasmont 1988) indicate that a relatively narrow sea crossing may be an effective barrier to dispersal.

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Appendix. The presence (+) or absence (–) of bumblebee species in different 100 km study squares in the British Isles and Fennoscandia. Squares are numbered from west to east and from south to north (e.g. 1 = southwest-ernmost Ireland, 224 = northeasternmost Karelia). The first two figures of the code give the west-east position, the last two figures the south-north position of the square. Abbreviations of the areas and islands: ALA = Åland Islands (Finland), BORN = Bornholm (Denmark), CHA = Channel Islands (the British Isles), DK = Denmark, F = Finland, GOTL = Gotland (Sweden), HEBR = Outer Hebrides (the British Isles), I = Ireland (including North Ireland), K = Karelia and Kola Peninsula (Russia), LOF = Lofoten (Norway), MAN = Isle of Man (British Isles), N = Norway, OLA = Öland (Sweden), ORK = Orkney Islands (the British Isles), S = Sweden, SCI = Isles of Scilly (the British Isles), SHET = Shetland Islands (the British Isles), UK = England, Wales and Scotland. Abbreviations of bumblebee species, see Table 1. B/P = total number of *Bombus* species/total number of *Psithyrus* species.

No.	Area	Code	wu so	lu ut	pt	sp	te	se	cw	ci	hy	jv	lp	mz	pj	ta	al	po	bq	hb	co	ho	rj	hu	mm	ms	pa	ru	sy	ve	dj	su	pm	bo	vs	rp	ca	br	fl	qu	no	sv	B/P	
1	I	0357	--	-	+--	+	--	--	+	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	10/4	
2	I	0358	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	10/4	
3	I	0359	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	11/4	
4	I	0360	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	9/1	
5	I	0457	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	11/4	
6	I	0458	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	10/4	
7	I	0459	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	10/4	
8	I	0460	--	-	+	--	--	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	--	+	--	+	--	+	--	+	--	7/2
9	I	0461	--	-	+	--	--	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	--	--	--	--	--	--	--	--	7/0	
10	SCI	0556	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	--	+	--	+	--	+	--	+	--	6/2
11	I	0557	--	-	+	--	--	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	9/1	
12	I	0558	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	12/5	
13	I	0559	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	11/5	
14	I	0560	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	10/2	
15	I	0561	--	-	+	--	+	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	9/3	
16	HEBR	0564	--	-	+	--	--	--	--	--	+	--	+	--	+	--	--	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	+	--	8/1	
17	UK	0656	--	+	+	--	+	--	--	--	+	--	+																															

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No.	Area	Code	w	u	s	o	p	t	s	p	e	s	e	c	u	a	y	i	o	p	m	o	p	r	a	l	d	o	b	a	b	c	o	r	t	h	u	m	m	s	p	a	r	s	y	v	e	d	i	s	u	p	m	b	o	v	s	p	c	a	d	f	l	q	u	n	o	s	y	B/P																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																												
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