ACTA ZOOLOGICA FENNICA

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Cesare Baroni Urbani and **Cedric A. Collingwood**
The zoogeography of ants (Hymenoptera, Formicidae)
in Northern Europe

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THE ZOOGEOGRAPHY OF ANTS (HYMENOPTERA, FORMICIDAE) IN NORTHERN EUROPE

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Abstract

BARONI URBANI, CESARE & COLLINGWOOD, CEDRIC A.: The zoogeography of ants (Hymenoptera, Formicidae) in Northern Europe. 1. — Acta Zool. Fennica 152:1—34. 1977.

Results from a numerical analysis of 67 indigenous ant species mapped on 103 area units to include the British Isles, Denmark and Fennoscandia are discussed. 12 sets of species groups clustering at a similarity level $\geq$ 0.5 represent the major distribution patterns of North European ants.

Multiple regressions calculated between species number per area unit and 11 environmental variables showed that main determinants included bright sunshine, July temperatures, relative oceanicity and length of growing season; these showed correlations in decreasing order with the distribution type having the largest number of species (40 %) representing the numerically dominant component of every area unit.

Presence/absence analysis separated 21 biogeographical areas clustering at the 0.75 similarity level. The British Isles, as the largest homogenous area, separates out mainly from the absence of particular species, especially members of the world-wide genus *Camponotus*. Some characteristic island faunae may be explained by the competitive advantage of post-glacial first colonisers. No support for postulating pre-glacial relict species was found.

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Contents

I. INTRODUCTION

The ants of North Europe, both taxonomically and in their geographical distribution, are among the better known faunas of the world. Minor changes and additions to present day knowledge are to be expected in the future; in particular some areas in Central Fennoscandia are under recorded. However we consider that the general picture of the population as presented here is not likely to change to an extent that would modify our main conclusions. Therefore an attempt to describe and interpret the distributional phenomena observed together with a statement of conclusions of general interest appear to be justified at this time.
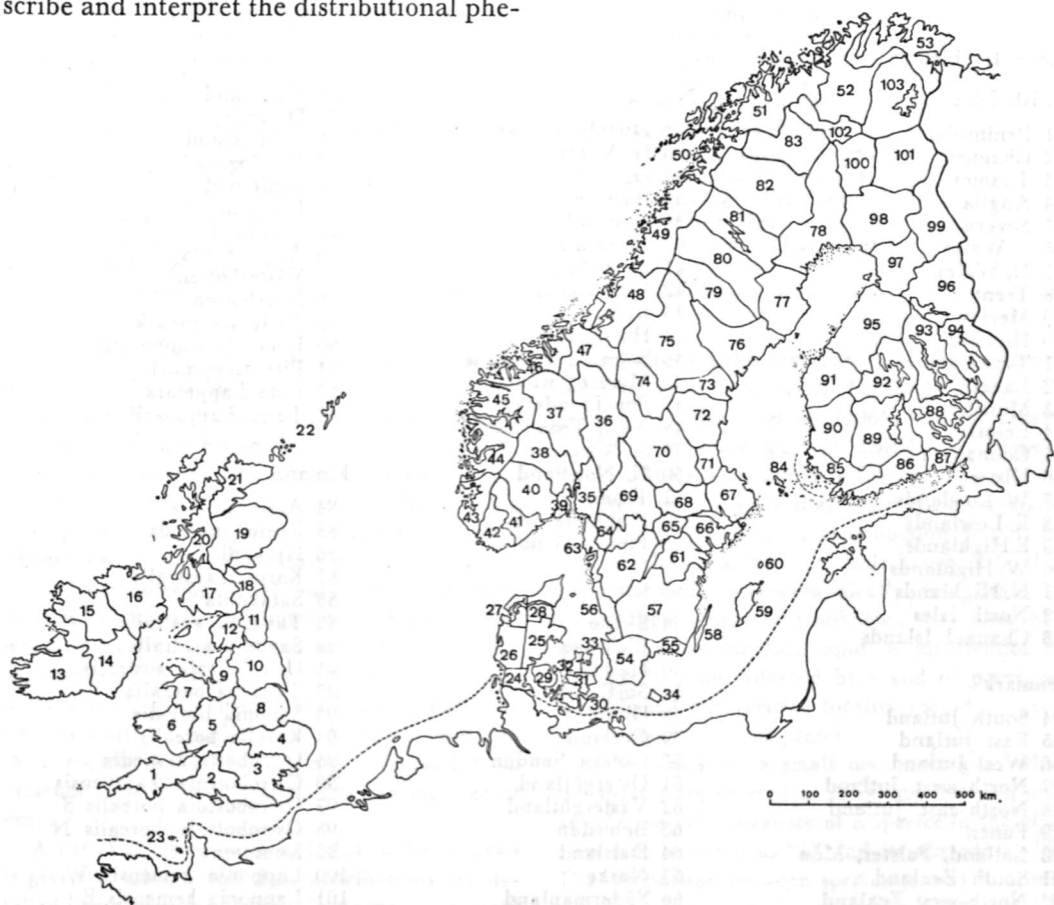
FIG. 1. The area units used for Fennoscandia, Denmark and the British Isles. For explanation see Table 1.

II. MATERIALS AND METHODS

The limits of the region studied do not correspond exactly with the geographical limits of Northern Europe but have been dictated for practical reasons to include those areas best known in detail from a myrmecological point of view. In this paper the British Isles, Channel Islands, Denmark and the whole of Fennoscandia with their related islands up to the political boundary between Finland and Russia are included. The Baltic countries, North Germany, Belgium, Holland, North France are excluded for practical reasons because of the lack of detailed information available from certain areas while the northernmost lands such as the Faroes, Iceland and Spitzbergen are known to have no indigenous ants at all.

The next decision to be made was the size and shape of the area units on which the presence/ absence of ants species were to be mapped. We have already suggested (Baroni Urbani & Collingwood 1975) that the use of geometrical grid maps, as recommended by the European Invertebrate Survey, could lead to misleading results in a biogeographical analysis because of lack of detailed information on the one hand and the presence of unnatural discontinuities due to human disturbance on the other. Therefore we adopted as a practical solution the use of area units often stemming from a compromise between geographical and administrative barriers. The 103 area units are mapped in Figure 1 and listed in table 1 and although they have probably never been used together in the same paper, and in the same way as in the present study, they have been widely employed in the literature and are well known

Table 1. List of Area units

British Isles	Norway	69 Värmland
		70 Dalarna
1 Peninsula	35 Østfold & Akershus	71 Gästrikland
2 Channel	36 Hedmark	72 Hälsingland
3 Thames	37 Opland	73 Medelpad
4 Anglia	38 Buskerud	74 Härjedalen
5 Severn	39 Vestfold	75 Jämtland
6 S. Wales	40 Telemark	76 Ångermanland
7 N. Wales	41 Aust-Agder	77 Västerbotten
8 Trent	42 Vest-Agder	78 Norrbotten
9 Mersey	43 Rogaland	79 Åsele Lappmark
10 Humber	44 Hordaland	80 Lycksele Lappmark
11 Tyne	45 Sogn og Fjordane	81 Pite Lappmark
12 Lakes	46 Møre og Romsdal	82 Lule Lappmark
13 Munster	47 Sør-Trøndelag	83 Torne Lappmark
14 Leinster	48 Nord-Trøndelag	
15 Connaught	49 S. Nordland	
16 Ulster	50 N. Nordland	Finland
17 W. Lowlands	51 Troms	
18 E. Lowlands	52 Finnmark wi	84 Alandia
19 E.Highlands	53 Finnmark ne	85 Regio aboensis
20 W. Highlands		86 Nylandia
21 N. Highlands		87 Karelia australis
22 North Isles	Sweden	88 Satakunta
23 Channel Islands		89 Tavastia australis
	54 Skåne	90 Savonia australis
	55 Blekinge	91 Ostrobottnia australis
Denmark	56 Halland	92 Tavastia borealis
	57 Småland	93 Savonia borealis
24 South Jutland	58 Öland	94 Karelia borealis
25 East Jutland	59 Gotland	95 Ostrobottnia media
26 West Jutland	60 Gotska Sandön	96 Ostrobottnia kajanensis
27 North-west Jutland	61 Östergötland	97 Ostrobottnia borealis S
28 North-east Jutland	62 Västergötland	98 Ostrobottnia borealis N
29 Funen	63 Bohuslän	99 Kuusamo
30 Lolland, Falster, Mön	64 Dalsland	100 Lapponia kemensis W
31 South Zealand	65 Närke	101 Lapponia kemensis E
32 North-west Zealand	66 Södermanland	102 Lapponia enontekiensis
33 North-east Zealand	67 Uppland	103 Lapponia inarensis
34 Bornholm	68 Västmanland	

TABLE 2. List of species.

Hypoponera punctatissima (Roger)
Ponera coarctata (Latreille)
Stenamma westwoodii (Westwood)
Myrmica rubra (Linnaeus)
Myrmica ruginodis (Nylander)
Myrmica sulcinodis (Nylander)
Myrmica rugulosa Nylander
Myrmica gallieni Bondroit
Myrmica specioides Bondroit
Myrmica sabuleti Meinert
Myrmica scabrinodis Nylander
Myrmica schencki Emery
Myrmica lobicornis Nylander
Sifolinia karavajevi (Arnol'di)
Diplorhoptrum fugax (Latreille)
Formicoxenus nitidulus (Nylander)
Harpagoxenus sublaevis (Nylander)
Leptothorax acervorum (Fabricius)
Leptothorax muscorum (Nylander)
Leptothorax nylanderi (Förster)
Leptothorax corticalis (Schenck)
Leptothorax tuberum (Fabricius)
Leptothorax interruptus (Schenck)
Leptothorax unifasciatus (Latreille)
Myrmecina graminicola (Latreille)
Anergates atratulus (Schenck)
Tetramorium caespitum (Linnaeus)
Strongylognathus testaceus (Schenck)
Tapinoma erraticum (Latreille)
Camponotus herculeanus (Linnaeus)
Camponotus ligniperda (Latreille)
Camponotus vagus (Scopoli)
Camponotus fallax Nylander
Plagiolepis vindobonensis Lomnicki

Lasius niger (Linnaeus)
Lasius emarginatus (Olivier)
Lasius alienus (Förster)
Lasius brunneus (Latreille)
Lasius flavus (Fabricius)
Lasius mixtus (Nylander)
Lasius umbratus (Nylander)
Lasius rabaudi (Bondroit)
Lasius bicornis (Förster)
Lasius carniolicus Mayr
Lasius fuliginosus (Latreille)
Formica exsecta Nylander
Formica pressilabris Nylander
Formica foreli Emery
Formica forsslundi Lohmander
Formica suecica Adlerz
Formica truncorum Fabricius
Formica rufa Linnaeus
Formica polyctena Forster
Formica aquilonia Yarrow
Formica lugubris Zetterstedt
Formica pratensis Retzius
Formica nigricans Emery
Formica sanguinea Latreille
Formica uralensis Ruzsky
Formica fusca Linnaeus
Formica lemani Bondroit
Formica gagatoides Ruzsky
Formica transkaucasica Nassonow
Formica cunicularia Latreille
Formica rufibarbis Fabricius
Formica cinerea Mayr
Polyergus rufescens (Latreille)

to most North European naturalists. Indeed the area units for Denmark and Fennoscandia are precisely those used in the current series of volumes of the Fauna Entomologica Scandinavica.

A large part of the information on the ant distribution used here is already published and a few papers dealing with individual countries (FORSSLUND 1957; COLLINGWOOD & BARRETT 1964; COLLINGWOOD 1974) but in addition many records for the other territories have been assembled through the help of local naturalists including in particular C. Bisgaard and C. Skøtt for Denmark and H. Wuorenrinne for Finland and from various scattered publications. All the species and their records have been carefully checked from museum and private collections during recent years.

A list of all the species included in the analysis is given in table 2 and their distributions are detailed in a sequence of maps. These maps represent the data input for our analyses and provide an easily understandable presentation of our updated

information on the distribution of the indigenous species known to occur in Northern Europe. Papers by GÖSSWALD et al. (1965) and by GASPAR (1971) also show general distribution maps of some of the species but in a few cases give a very different picture from that presented here, mainly through the non critical reproduction of old literature references. Some records however in these papers appear biogeographically acceptable but where their sources are unknown they have been excluded from our data input. A justification for the classification adopted here and of previously unpublished but verified locality records is given in COLLINGWOOD (in press).

Data consist of a small mxn matrix in which the species are entered as rows and the area units as columns. The presence of a species in the given area unit is coded as "1" and its absence as "0". The comparison between species (rows) is termed the R analysis and the comparison between biogeographical units (columns), Q analysis. According to the type of analysis performed, each row

or each column represents an Operational Taxonomic Unit (OTU).

The Q and R analyses of the original data matrix were carried out by the programme CLUSTERTREE available at the computing centre at the University of Basle. The similarity matrix was calculated by the S_{**} coefficient of BARONI URBANI & BUSER (1976): similarity between two OTU's given by

$$S_{**} = \frac{\sqrt{ad} + a}{\sqrt{ad} + a + b + c}$$

where, a = number of attributes (presences) in common, b = number of attributes present in the first OTU and absent in the second, c = number of attributes absent in the first OTU and not in the second, d = number of attributes absent in both OTU's compared but present in others. The calculation of the similarity coefficient gives a symmetrical m×m (or n×n) similarity matrix on which the similarity between every possible pair of OTU's can be found. From the numerous techniques that would allow a graphic representation of the results with a minimum distortion of the similarity matrix, we used the clustering by single linkage in which each OTU joins the most similar one in the matrix at a distance corresponding to its similarity; once one OTU is ascribed to a given set, it remains there until the end of clustering.

The R analysis of the data matrix and the successive clustering were used to identify the basic distribution types in the selected area. From the reasonable symmetry properties of S_{**} and of the low distortion of the original similarity matrix during clustering by single link, distributions clustering at a level of ≥ 0.5 were interpreted as being similar and representing the major generalised distribution patterns. Clustering with $S_{**} < 0.5$ should connect true differences and are not considered here.

In addition we attempted a stepwise multiple regression between the number of species per area unit of each distributional type and a set of environmental variates, translating the original data into meristic values. These were abstracted from source works on climatology by LANDSBERG et al. (1965) and WALLÉN (1970). The following parameters were used: Average annual rainfall (6 categories), July mean temperature (4 categories), Average bright sunshine hours per year (5 categories), Average annual atmospheric pressure (6 categories), Average length of growing season (6 categories), Inland versus island climate (3 categories), Latitude (6 categories), Longitude (4 categories), January mean temperature (5 categories), Boreal versus oceanic climate (5 categories), Mean altitude (2 categories). A constant proportion of the sum of squares > 1 % was used to limit the number of variables in the regression.

III. THE BASIC DISTRIBUTION TYPES OF THE ANTS OF NORTH EUROPE

The dendrogram based on the similarity between species distributions is presented in Figure 2. By cutting this dendrogran at the 50 % similarity level, we obtained 12 basic distribution types as described below.

Distribution Type A

The sole species in this distribution type is *Formica foreli* Emery. This is a local species with a scattered distribution in Central and Eastern Europe (DLUSSKY 1967). The only 2 records for North Europe are from North Zealand and North

East Jutland in Denmark. No correlations with environmental variables were shown by the analysis.

Distribution Type B

This is presented in Figure 3 and includes the species *Hypoponera punctatissima* (Roger), *Sifolinia karavajevi* (Arnol'di), *Myrmica specioides* Bondroit and *Leptothorax interruptus* (Schenck) (Figures 4—7). They have in common their regular presence on Thames and scattered records in the southern part of the studied area. The regression analysis for
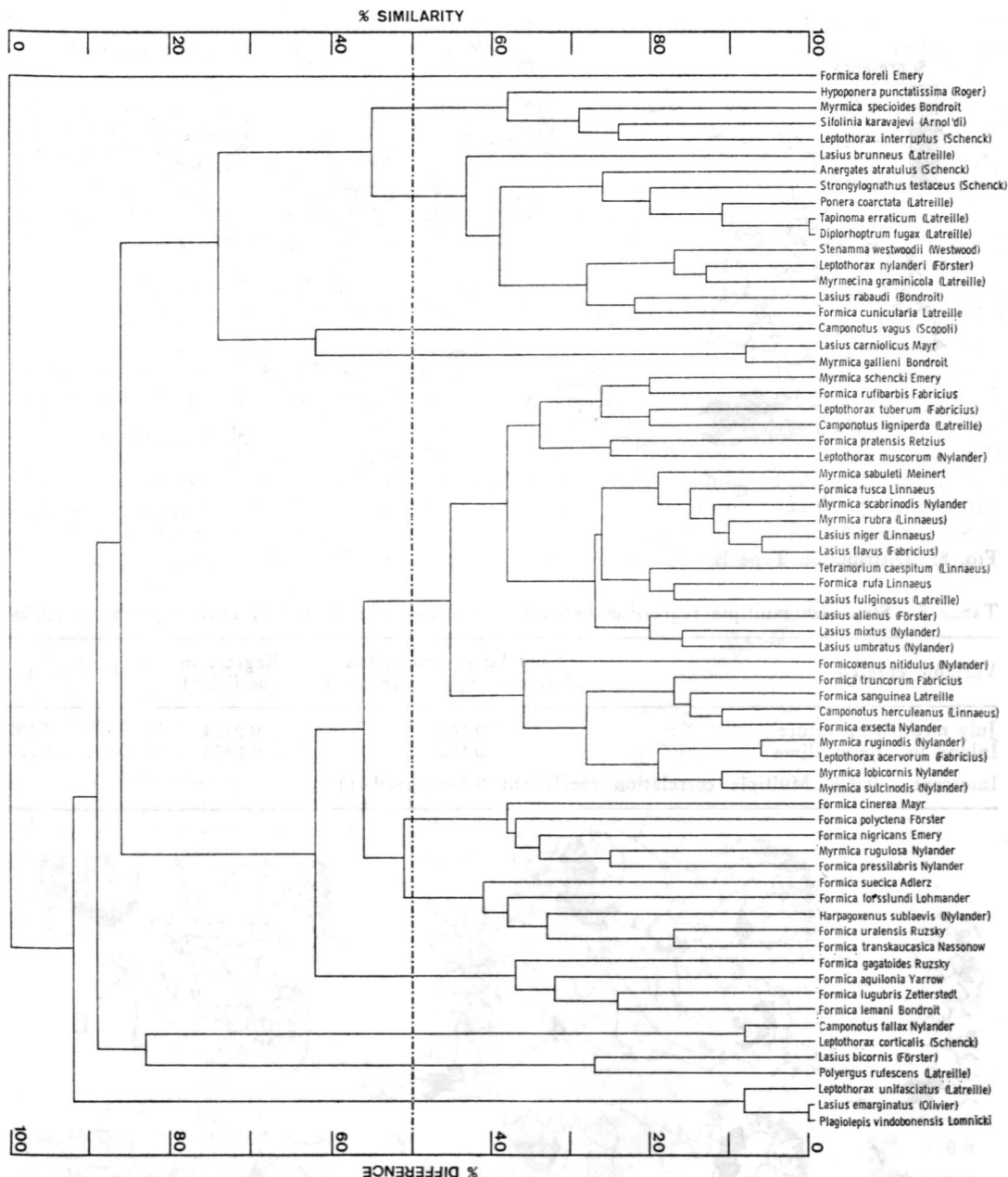
% SIMILARITY

FIG. 2. Dendrogram of species distribution similarity.

this distribution type (Table 3) suggests a double and antithetical influence of 2 factors: a positive influence of the July mean temperature which should account for the southern pattern within a wide longitudinal range and a negative influence of inland climate. However these 2 factors contribute only 13 % of the observed variation although coupled with a high R value and additional environmental data are needed for a full interpretation. *H. punctatissima* is a cosmopolitan species long established in Europe where it colonises outside rubbish tips,
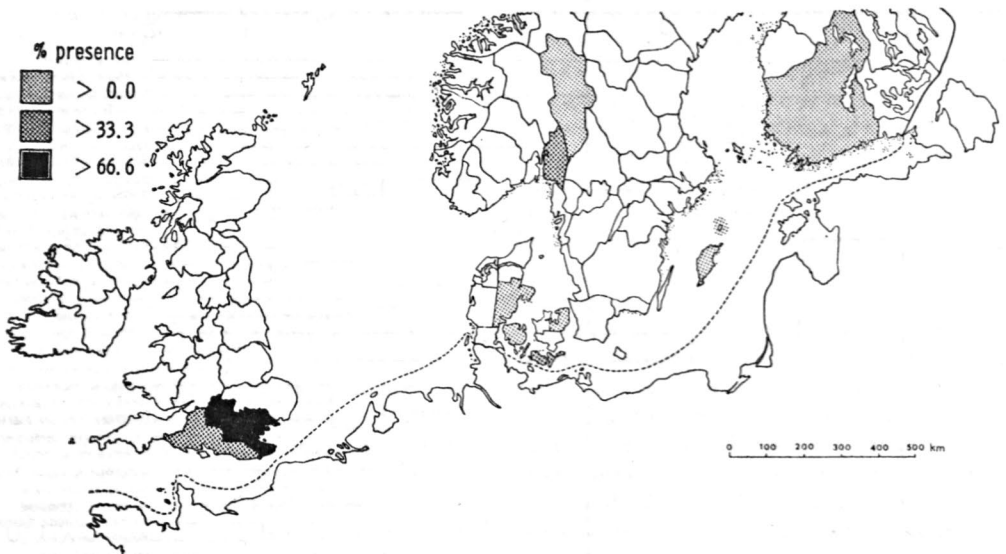
FIG. 3. Distribution Type B.

TABLE 3. Step-wise multiple regression between distribution type B and 11 environmental variables.

Variable entered	Cumulative proportion of sum of squares reduced	Regression coefficient	t
July mean temperature	0.107	0.2314	3.199
Inland vs. island clima	0.130	—0.1453	—1.627

Intercept —0.098. Multiple correlation coefficient 0.348 (p<0.01).
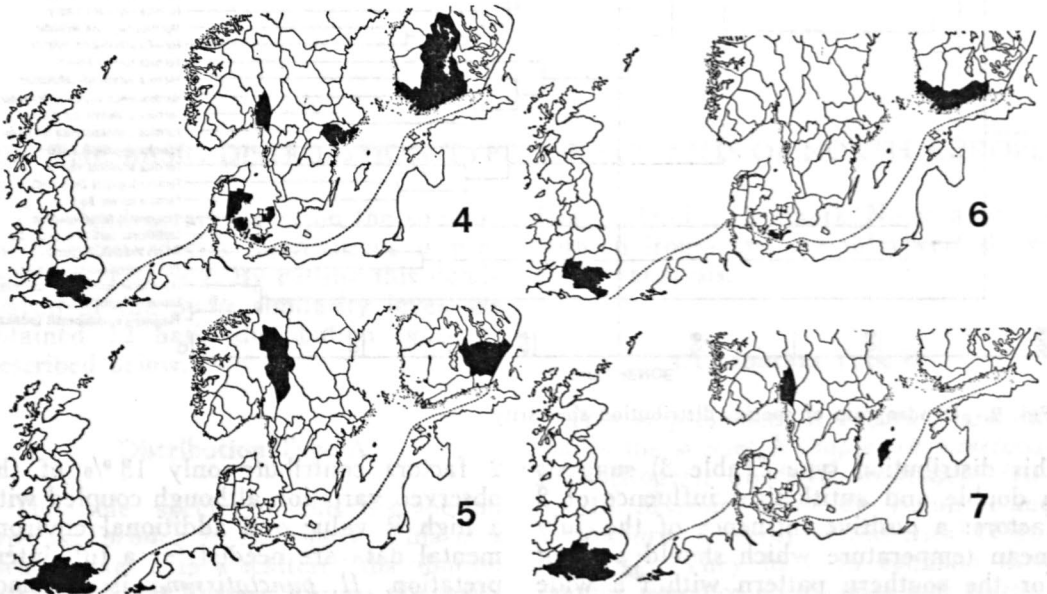
FIG. 4. *Hypoponera punctatissima* (Roger), FIG. 5. *Sifolinia karavajevi* (Arnol'di), FIG. 6. *Myrmica specioides* Bondroit, FIG. 7. *Leptothorax interruptus* (Schenck).

sawdust heaps, mines in addition to heated premises. For the purposes of this paper its distribution relates only to recorded locations away from buildings. *S. karavajevi* is parasitic on *Myrmica. M. specioides* and *L. interruptus* are widely but sparsely distributed through Central Europe and in the north are found on coastal sand or dry lowland heath.

Distribution Type C

This distribution type (Figure 8) includes a group of species with a wide range in Central and Southern Europe: *Formica cunicularia* Latr., *Lasius rabaudi* Bondroit, *L. brunneus* (Latr.), *Tapinoma erraticum* (Latr.), *Myrmecina graminicola* (Latr.), *Stenamma westwoodii* Westwood, *Diplorhoptrum fugax* (Latr.), *Strongylognathus testaceus* (Schenck), *Anergates atratulus* (Schenck), *Leptothorax nylanderi* (Foerster) and *Ponera coarctata* (Latr.) (Figures 9—19). *Lasius brunneus, Leptothorax nylanderi Stenamma westwoodii* and *Myrmecina graminicola* are species usually associated with deciduous woodland mainly *Quercus robur.* This reaches its northern distribution in Central Sweden; there are no records for these species from Finland where pedunculate oak is restricted to the southwest extremity of the country. In England remnants of this type of woodland occur in the south up to a broad band extending across the English Midlands to the Eastern Counties and in several localities there is a characteristic association of *Lasius brunneus* and *Leptothorax nylanderi* in old oaks throughout this area, with *S. westwoodii* also usually present on the woodland floor. Such associations occur throughout Belgium and the oakwoods of Northern and Central France. However, in Norway *L. brunneus* occurs in similar remnants of old oak woodland in restricted areas round Oslofjord without *L. nylanderi* while in Central Sweden *L. brunneus* is also not uncommon in old oaks but not apparently associated with *L. nylanderi* which is found more frequently in the southwest of the country. Similarly in Zealand *L. brunneus* occurs locally in oak without *L. nylanderi.*

% presence

▨ > 0.0
▦ > 33.3
■ > 66.6
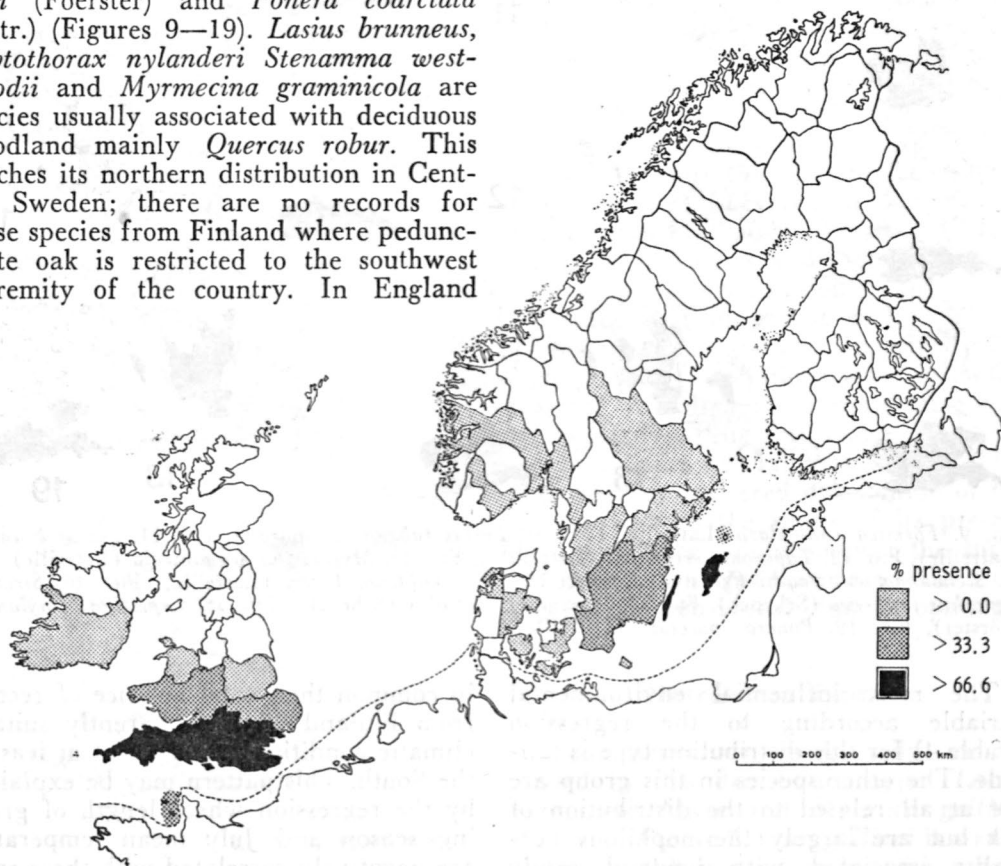
FIG. 8. Distribution Type C.
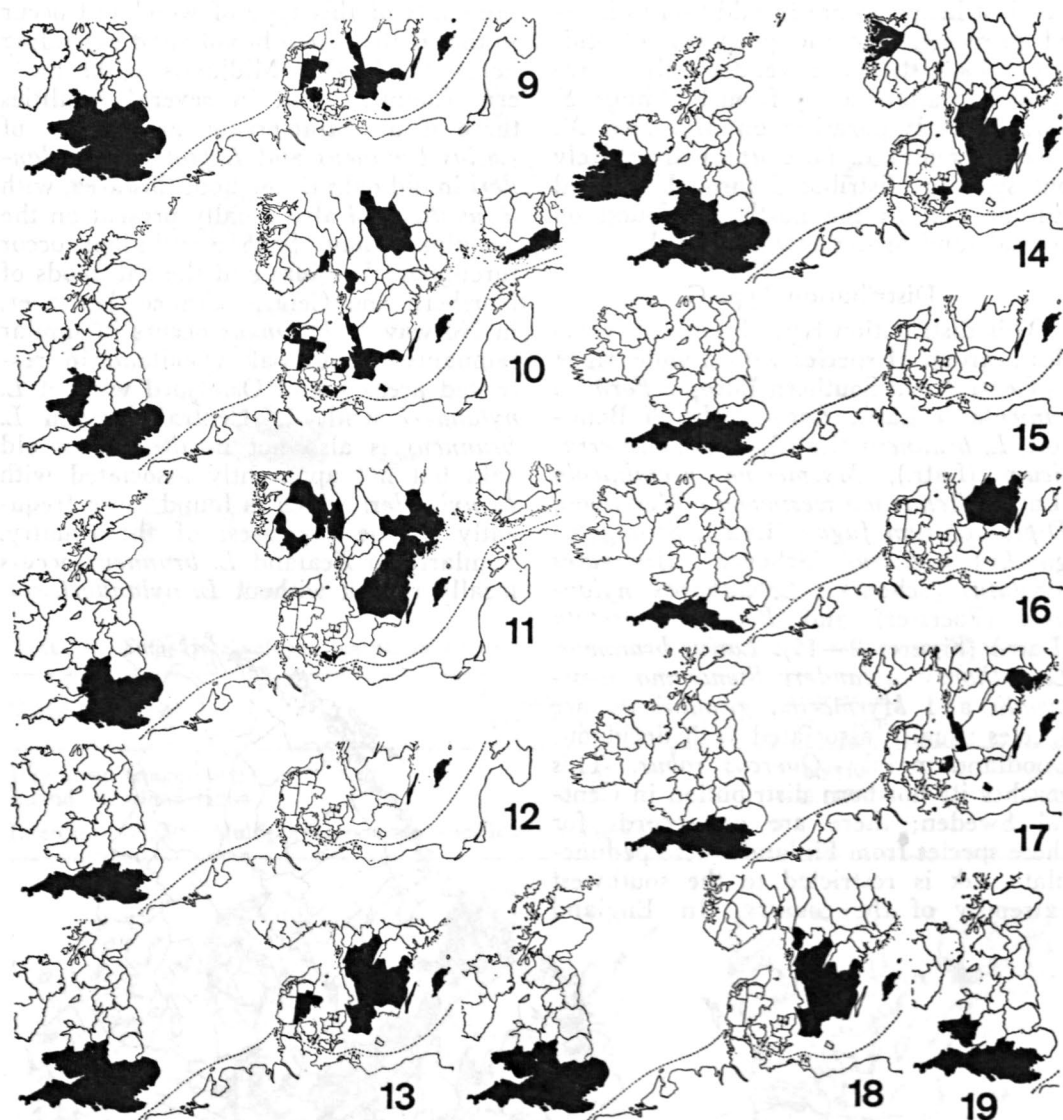
Fig. 9. *Formica cunicularia* Latreille, Fig. 10. *Lasius rabaudi* (Bondroit), Fig. 11. *Lasius brunneus* (Latreille), Fig. 12. *Tapinoma erraticum* (Latreillle), Fig. 13. *Myrmecina graminicola* (Latreille), Fig. 14. *Stenamma westwoodii* (Westwood), Fig. 15. *Diplorhoptrum fugax* (Latreille), Fig. 16. *Strongylognathus testaceus* (Schenck), Fig. 17. *Anergates atratulus* (Schenck), Fig. 18. *Leptothorax nylanderi* (Förster), Fig. 19. *Ponera coarctata* (Latreille).

The most influential environmental variable according to the regression (Table 4) for this distribution type is latitude. The other species in this group are not at all related to the distribution of oak but are largely thermophilous normally associated with lowland sandy heath. Except for *L. rabaudi* they have in common their total absence of records from Finland where apparently suitable climatic conditions are present at least in the South. This pattern may be explained by the regression where length of growing season and July mean temperature are negatively correlated with these species within the set of variables considered,

so that although they are of generally southern distribution, notably *Formica cunicularia, Diplorhoptrum fugax, Tapinoma erraticum* and *Ponera coarctata,* they are not positively correlated with temperature. A possible hypothesis would be the influence of a historical factor in Southern England where an older fauna directly derived from continental Europe would be well established. In Southern Scandinavia this might have given way to later invading species from Eastern Europe except in such island refugia as Öland and Gotland which were not reached by the later invaders.

One apparent anomaly is *Stenamma westwoodii* in the Bergen district of Norway but the record (COLLINGWOOD 1974) is based on specimens collected in a botanic garden which may well have been introduced on imported plant material. However, areas of coastal Norway in the southwest are climatically not dissimilar from parts of Southern Ireland where this species is indigenous.

Anergates atratulus and *Strongylognatus testaceus* are satellite or parasite species dependant on their host *Tetramorium caespitum* (L.) and have an evidently restricted range within the larger range of that species.

Distribution Type D

The sole species segregated in this distribution type is *Camponotus vagus* Sco-

FIG. 20. Distribution Type D: *Camponotus vagus* (Scopoli).
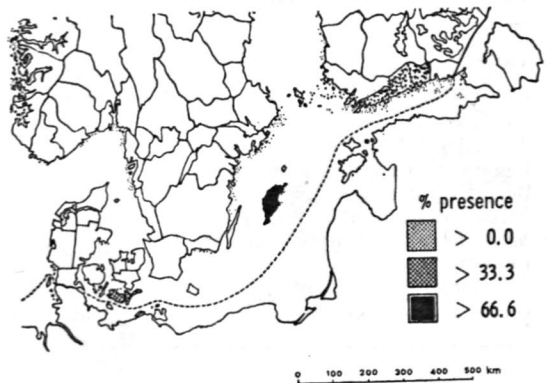
FIG. 21. Distribution Type E: *Lasius carniolicus* Mayr and *Myrmica gallienei* Bondroit.

poli (Figure 20). This is a South European species abundant in the Mediterranean area but sparse and discontinuous north of latitude 47°. It has been recorded very locally in Central and Southern Poland (PISARSKI 1975). Old records from Gotland and Öland and South Finland were doubted by FORSSLUND, 1947 but are supported by specimens in the Lund University Museum and the species has recently been rediscovered in the extreme southwest of Finland by MERISUO and KÄPYLÄ, 1975. This is a distinctly thermophilous species even in South Europe and evidently able to persist still in North Europe on sun exposed, climatically favoured sites. Correlations with the broad regional and climatic environmental variables analysed in this paper including sunshine hours and latitude are low. This and the very scattered distribution of the species well to the north of its present day abundance would support the suggestion that *C. vagus* may be a relict from the warmer sub-boreal climatic optimum.

Distribution Type E

Two arenicolous species only are included in this distribution type: *Lasius carniolicus* Mayr and *Myrmica gallieni* Bondroit (Figure 21). *M. gallieni* is a sand dune and salt marsh species with a concentration of records in the coastal Baltic

TABLE 4. Step-wise multiple regression between distribution type C and 11 environmental variables.

Variable entered	Cumulative proportion of sum of squares reduced	Regression coefficient	t
Latitude	0.300	—1.2385	—2.688
Annual rainfall	0.362	—0.4168	—2.120
Length of the growing season	0.400	—0.8017	—3.226
Boreal vs. oceanic clima	0.424	0.0334	1.264
Bright sunshine hours	0.443	0.7827	2.884
Mean annual atmosph. pressure	0.494	1.2085	3.738
Longitude	0.511	1.0104	2.236
July mean temperature	0.526	—0.7061	—1.738

Intercept 2.774. Multiple correlation coefficient 0.725 ($p \ll 0.01$).

recorded under its synonym *M. jacobsoni* Kutter (KUTTER 1972) but occurring more locally in other parts of Europe. *L. carniolicus* by contrast is probably a true relict recorded only from Gotland with a known distribution in Europe restricted to South Switzerland, Austria, the Balcans, South Italy and the Pyrenées Orientales. According to the regression analysis the only significant variable for this distribution is a negative correlation with inland climate.

% presence
> 0.0
> 33.3
> 66.6
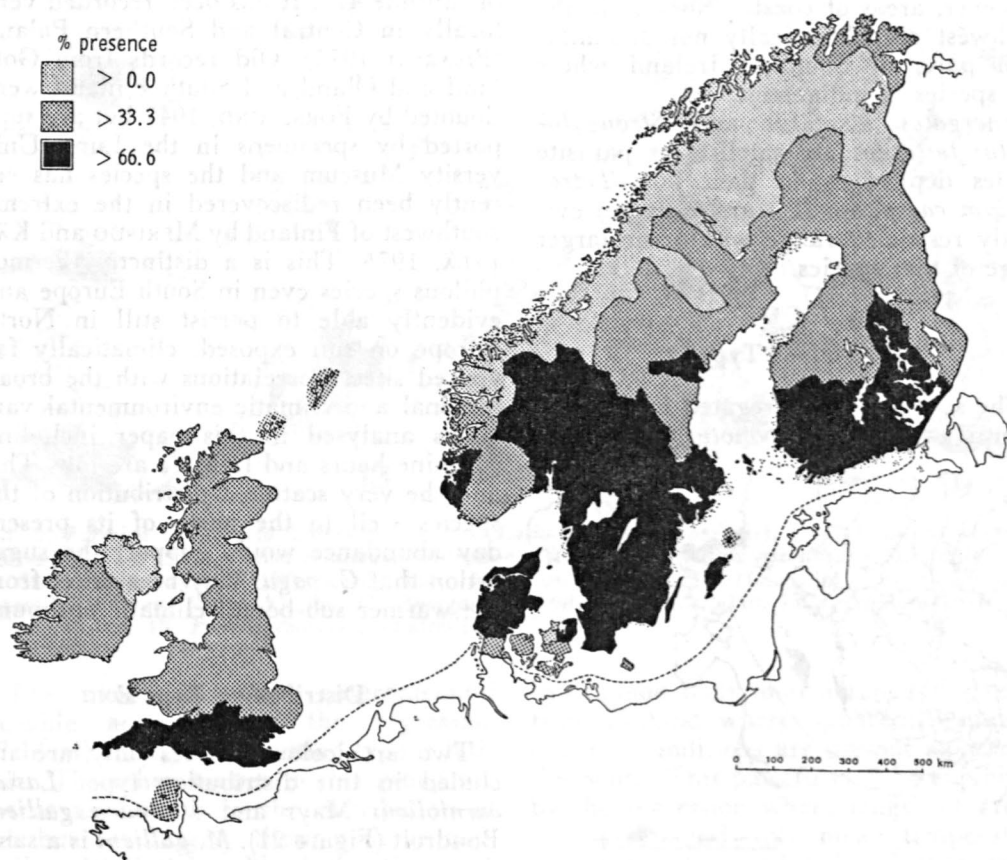
FIG. 22. Distribution Type F.

Distribution Type F

This includes most of the commoner species found in the region (Figure 22). The 27 species partitioned off in this group are *Myrmica schencki* Emery, *M. sabuleti* Meinert, *M. rubra* (L.), *M. scabrinodis* Nylander, *M. sulcinodis* Nylander, *M. lobicornis* Nylander, *M. ruginodis* Nylander, *Leptothorax tuberum* (Fabricius), *L. muscorum* Nylander, *L. acervorum* Fabricius, *Formicoxenus nitidulus* Nylander, *Tetramorium caespitum* (L.), *Camponotus ligniperda* Latreille, *C. herculeanus* (L.), *Lasius alienus* (Foerster), *L. umbratus* (Nylander), *L. mixtus* (Nylan-

FIG. 26.　*Myrmica scabrinodis* Nylander.

FIG. 23.　*Myrmica schencki* Emery.

FIG. 24.　*Myrmica sabuleti* Meinert

FIG. 27.　*Myrmica sulcinodis* Nylander.

FIG. 25.　*Myrmica rubra* (Linnaeus)

der), *L. fuliginosus* (Latreille), *L. niger* (L.), *L. flavus* (Fabricius), *Formica rufibarbis* Fabricius, *F. pratensis* Retzius, *F. rufa* L., *F. truncorum* Fabricius, *F. sanguinea* Latreille, *F. fusca* L. and *F. exsecta* Nylander (Figures 23—49).

It is noteworthy that although all are common European species *F. truncorum*, *Camponotus ligniperda*, *C. herculeanus* and *L. muscorum* are not represented in the British Isles. This is evidently of less importance than the general association with bright sunshine which the regression shows (Table 5) accounts for over 50 % of the environmental variables and is

TABLE 5. Step-wise multiple regression between distribution type F and 11 environmental variables.

Variable entered	Cumulative proportion of sum of squares reduced	Regression coefficient	t
Bright sunshine hours	0.504	3.2372	5.785
July mean temperature	0.543	1.5531	1.692
Inland versus island clima	0.568	2.5808	3.235
Length of the growing season	0.591	0.7837	2.305

Intercept —6.788. Multiple correlation coefficient 0.760 (p<<0.01).

FIG. 28. *Myrmica lobicornis* Nylander.

FIG. 29. *Myrmica ruginodis* Nylander.

FIG. 30. *Leptothorax tuberum* (Fabricius)

FIG. 31. *Leptothorax muscorum* (Nylander).

FIG. 32. *Leptothorax acervorum* (Fabricius)

highly significant for this distribution group. The implication of this particular segregation from the analysis is that the distribution type selects out the species that could be present according to the climatic possibility as well as the species

actually present. Finland in this analysis is a discriminant area where the British Isles and even Ireland with its reduced fauna are not. The British Isles in fact are the only area in the world within the climatic ranges of the genus *Camponotus* where species of this genus have never been recorded. The Scandinavian species have differing ecological valencies but *C. herculeanus* at least should be able to establish in plantations in Northeast Britain

FIG. 33.   *Formicoxenus nitidulus* (Nylander)

FIG. 36.   *Camponotus herculeanus* (Linnaeus).

FIG. 35.   *Tetramorium caespitum* (Linnaeus)

FIG. 37.   *Lasius alienus* (Förster)
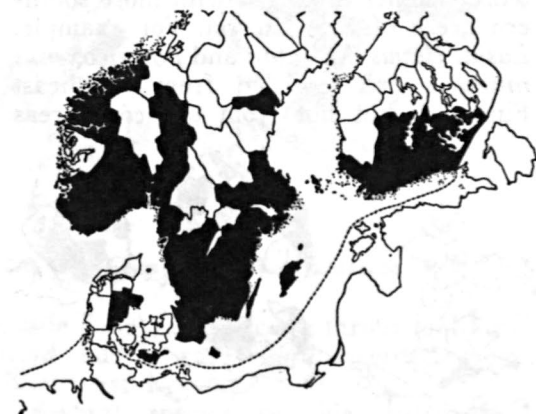
FIG. 35.   *Camponotus ligniperda* (Latreille).

FIG. 38.   *Lasius umbratus* (Nylander).

Fig. 39.   *Lasius mixtus* (Nylander).

Fig. 42.   *Lasius flavus* (Fabricius).

through to the more local *L. muscorum*, *M. schencki* and *C. ligniperda*. The inclusion of Northeast Finnmark is probab-

Fig. 40.   *Lasius fuliginosus* (Latreille).

Fig. 43.   *Formica rufibarbis* Fabricius

ly related to the relatively higher number of species recorded there than from immediately adjacent area units through its geographical situation, sheltered from exposure to western gales and the more intense summer linking it with more southern areas of Scandinavia. For example, *Lasius flavus*, *M. rubra* and *Formicoxenus nitidulus* are recorded from Northeast Finnmark but not from adjacent areas

Fig. 41.   *Lasius niger* (Linnaeus)

and is sometimes imported into the country in timber from Eastern Europe.

The lower density of species to the north in this group is clearly related to the positive association with summer climate and the species included range from the universally distributed *Myrmica ruginodis* and *Leptothorax acervorum*

Fig. 44.   *Formica pratensis* Retzius.

FIG. 45. *Formica rufa* Linnaeus.

FIG. 46. *Formica truncorum* Fabricius.

FIG. 47. *Formica sanguinea* Latreille.

M. *scabrinodis, C. herculeanus, L. niger,
L. flavus* and *F. sanguinea* have been re-
cognised from sub-fossil deposits ranging
in age between 600 and 4.850 years in
South Finland (KOPONEN & NUORTEVA,
1973).

Distribution Type G

This is rather similar to the previous
distribution but excludes the British Isles
entirely (Figure 50). The five species in-
clude *Formica nigricans* Emery, *F. polyc-
tena* Foerster, *F. cinerea* Mayr, *F. pressi-
labris* Nylander and *Myrmica rugulosa*

FIG. 48. *Formica fusca* Linnaeus.

FIG. 49. *Formica exsecta* Nylander.

while *F. sanguinea* occurs throughout Fin-
land but is rare or unrecorded from
Northwest Norway.

Several species in this distribution
group including *M. rubra, M. ruginodis,*

TABLE 6. Step-wise multiple regression between distribution type G and 11 environmental variables.

Variable entered	Cumulative proportion of sum of squares reduced	Regression coefficient	t
Bright sunshine hours	0.357	0.4592	3.208
Mean annual atmosph. pressure	0.368	—0.7013	—3.957
Latitude	0.422	—0.5605	—2.450
Boreal vs. oceanic clima	0.442	0.0397	2.356
Inland vs. island clima	0.458	0.3405	1.661

Intercept 1.620. Multiple correlation coefficient 0.660 (p≪0.01).
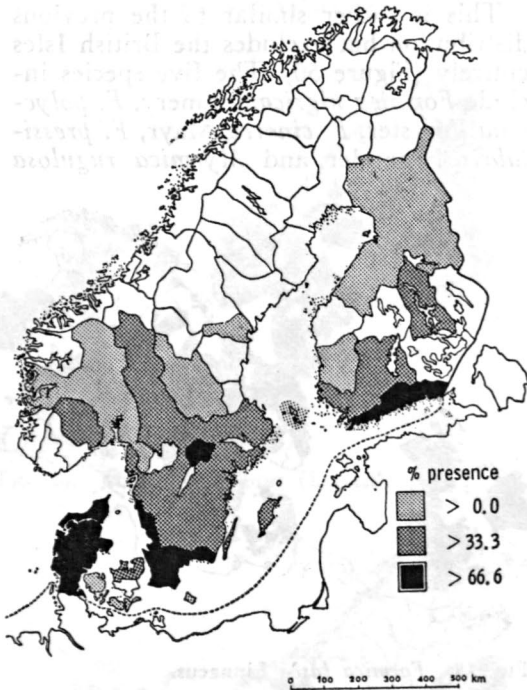
FIG. 50. Distribution Type G.

% presence
> 0.0
> 33.3
> 66.6
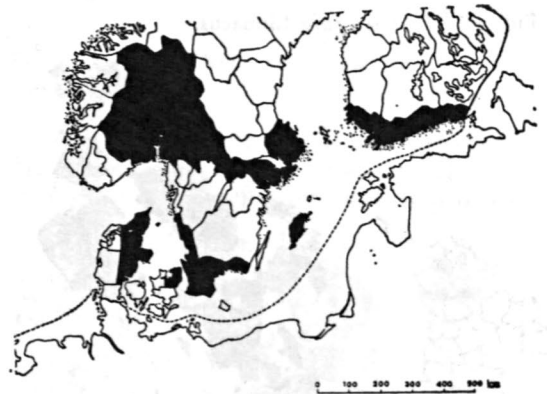
FIG. 52. *Formica polyctena* Förster.

FIG. 51. *Formica nigricans* Emery.

FIG. 53. *Formica cinerea* Mayr.
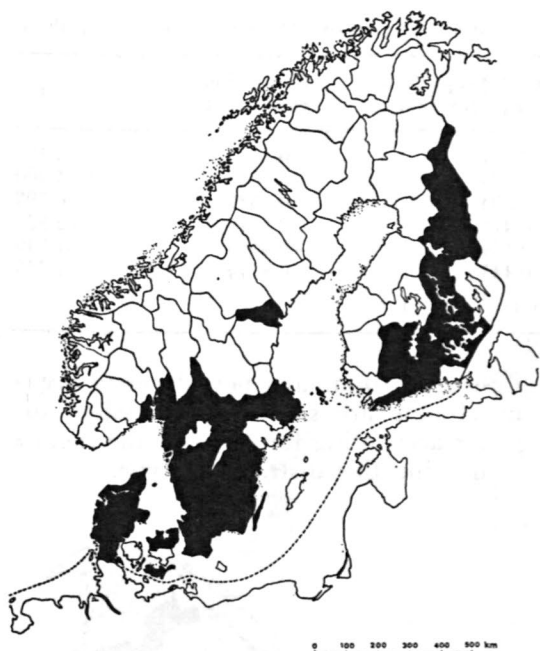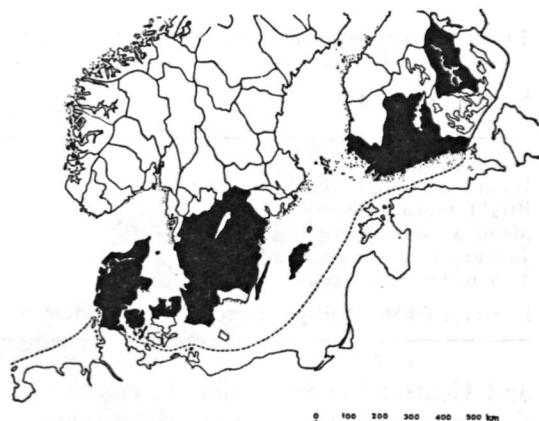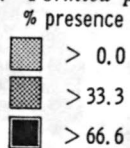
FIG. 55. *Myrmica rugulosa* Nylander.

Nylander (Figures 51—55). These all have a high concentration in Denmark but are rather more scattered in Southern

↓ FIG. 56. Distribution Type H.

FIG. 54. *Formica pressilabris* Nylander.

% presence

> 0.0
> 33.3
> 66.6

TABLE 7. Step-wise multiple regression between distribution type H and 11 environmental variables.

Variable entered	Cumulative proportion of sum of squares reduced	Regression coefficient	t
Longitude	0.271	0.1533	0.465
Inland vs. island clima	0.339	1.1010	4.300
Bright sunshine hours	0.394	0.1536	0.793
Mean annual atmosph. pressure	0.416	—0.6649	—2.823
January mean temperature	0.434	—0.4983	—1.746
July mean temperature	0.445	0.3749	1.375

Intercept 0.686. Multiple correlation coefficient 0.645 $(p \ll 0.01)$.

and Central Fennoscandia. *F. cinerea* in this region is largely a sand dune species. According to the regression analysis (Table 6) bright sunshine, atmospheric pressure, latitude and boreal versus oceanic climate are significant variables together accounting for 44 % of the factors influencing this distribution type.
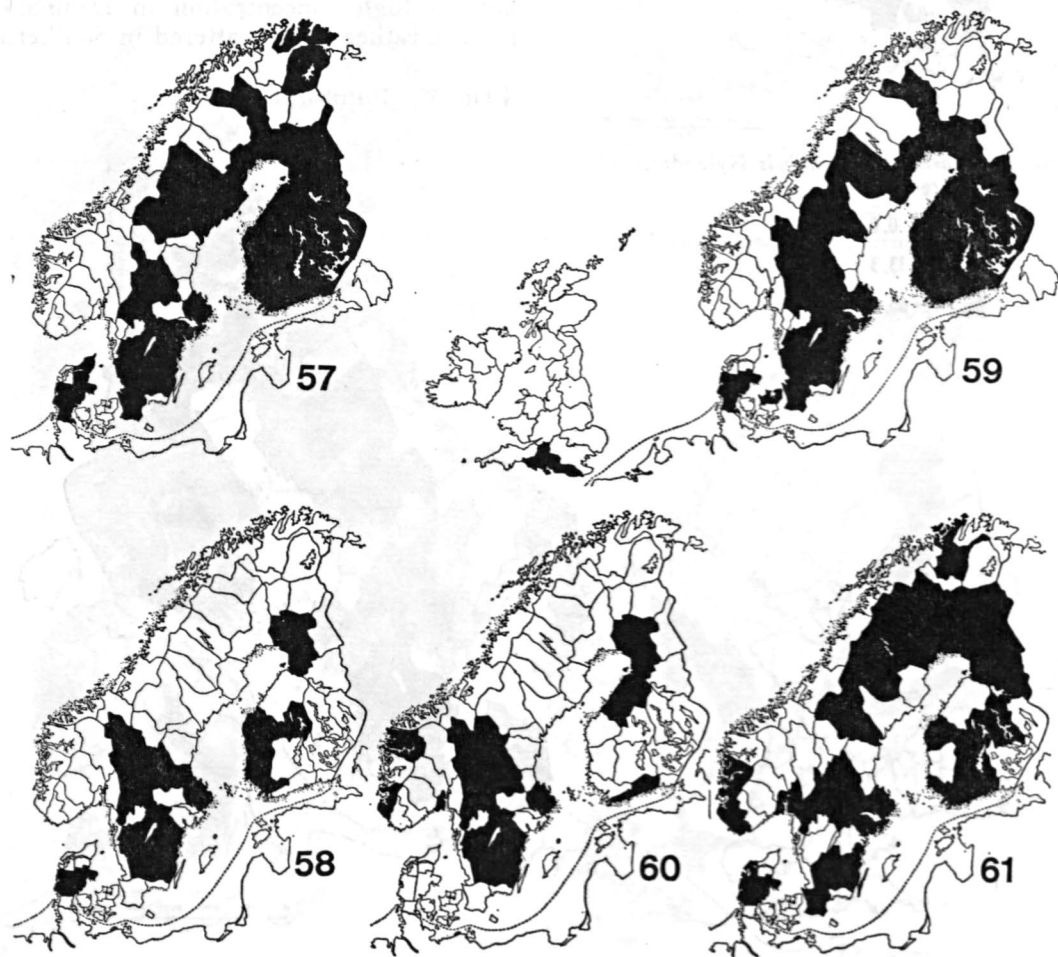
FIG. 57. *Formica uralensis* Ruzsky, FIG. 58. *Formica forsslundi* Lohmander, Fig. 59. *Formica transkaucasica* Nassonow, FIG. 60. *Formica suecica* Adlerz, FIG. 61. *Harpagoxenus sublaevis* (Nylander).

% presence
> 0.0
> 33.3
> 66.6
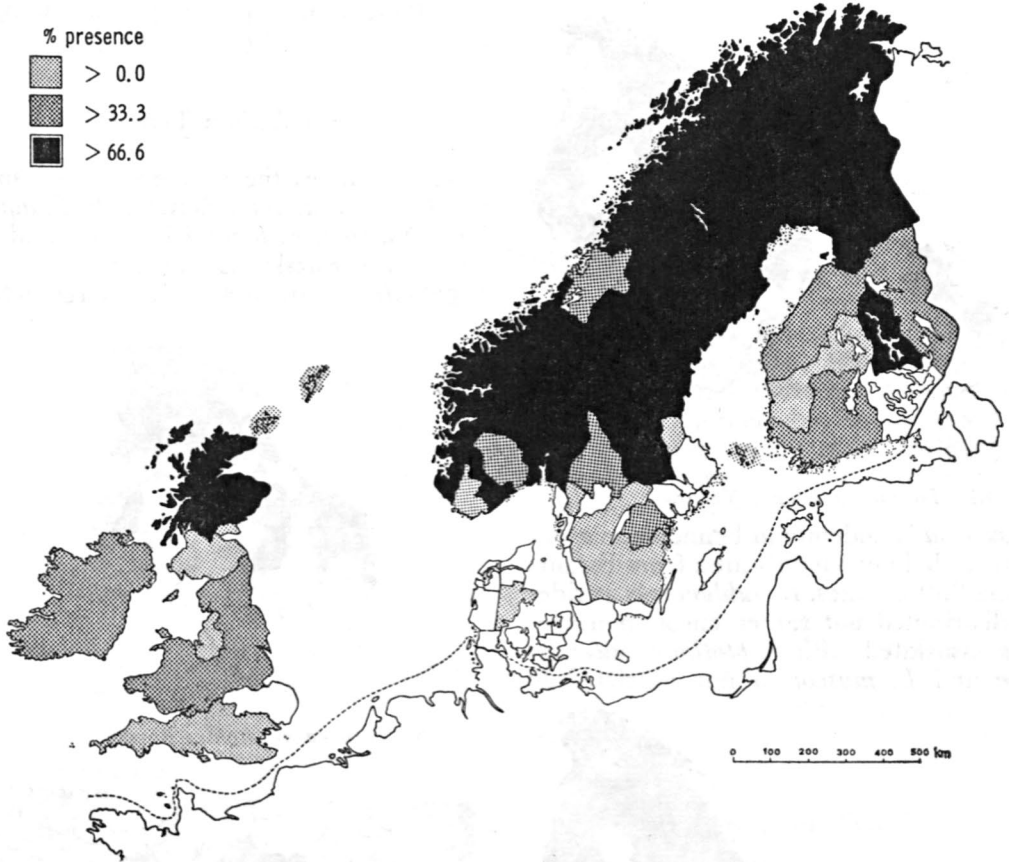
FIG. 62. Distribution Type I.

Distribution Type H

This distribution type (Figure 56) includes *Formica uralensis* Ruzsky, *F. forsslundi* Lohmander, *F. transkaucasica* Nassonov (= *F. picea* Nyl.) *F. suecica* Adlerz and *Harpagoxenus sublaevis* (Nylander) (Figures 57—61). The main variables according to the regression analysis are longitude, implying a mainly eastern continental distribution, inland versus island climate and hours of bright sunshine which together account for over 39 % of the factors influencing the distribution of this group (Table 7). Only *F. transkaucasica* occurs locally in the British Isles and this species together with *F. forsslundi* and *F. uralensis* are characteristic of lowland forest bog in Northern Europe. ROSENGREN (1969) demonstrated that *F. uralensis* is a weak competitor, easily displaced by more aggressive species which may account for its restriction to bogland habitats in North Europe contrasting with its recorded habits in the Urals, South Siberia and Mongolia where it is a dryland steppe species.

FIG. 63. *Formica lugubris* Zetterstedt.

Scandinavia but found in the higher mountain areas of Central Europe.

Distribution Type I

This includes the northern boreal species *Formica lugubris* Zetterstedt, *F. aquilonia* Yarrow, *F. lemani* Bondroit and *F. gagatoides* Ruzsky (Figures 62—66). *F. gagatoides* is an arctic species restricted
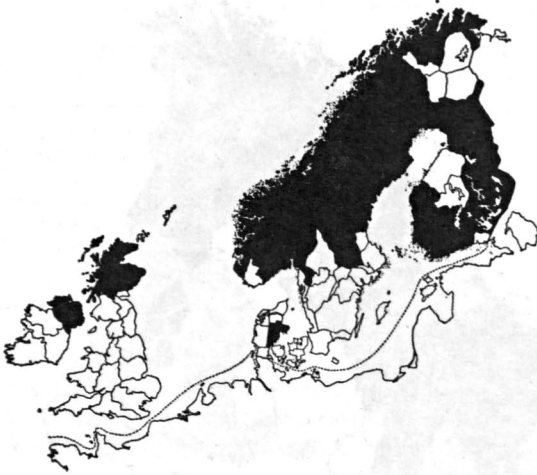
FIG. 64.   *Formica aquilonia* Yarrow

F. suecica is endemic to Fennoscandia only recorded outside this area from Estonia in the Baltic States. *H. sublaevis* is a widely distributed but rather uncommon species associated with *Leptothorax acervorum* and *L. muscorum* not restricted to

FIG. 66.   *Formica gagatoides* Ruzsky.

FIG. 65.   *Formica lemani* Bondroit.

% presence
> 0.0
> 33.3
> 66.6
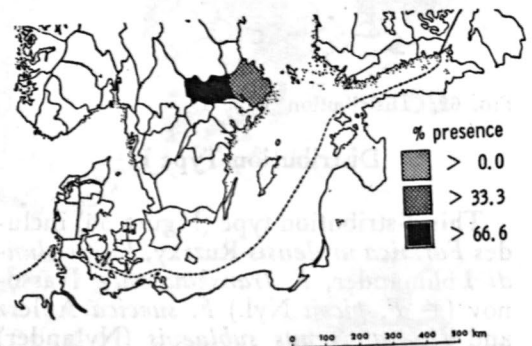
FIG. 67.   Distribution Type J: *Leptothorax corticalis* (Schenck) and *Camponotus fallax* (Nylander).

TABLE 8.   Step-wise multiple regression between distribution type I and 11 environmental variables.

Variable entered	Cumulative proportion of sum of squares reduced	Regression coefficient	t
Mean altitude	0.396	0.7332	3.314
Latitude	0.541	0.6719	4.021
Bright sunshine hours	0.617	—0.1707	—1.398
Inland versus island clima	0.648	0.5088	3.296
Longitude	0.664	—0.3979	—2.138

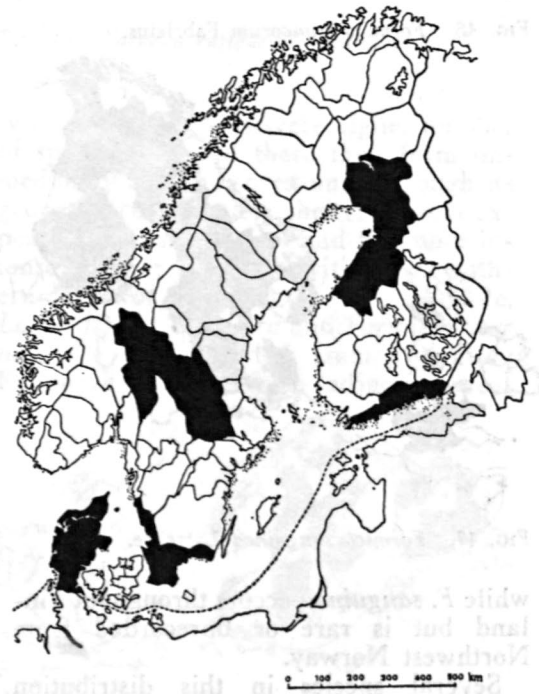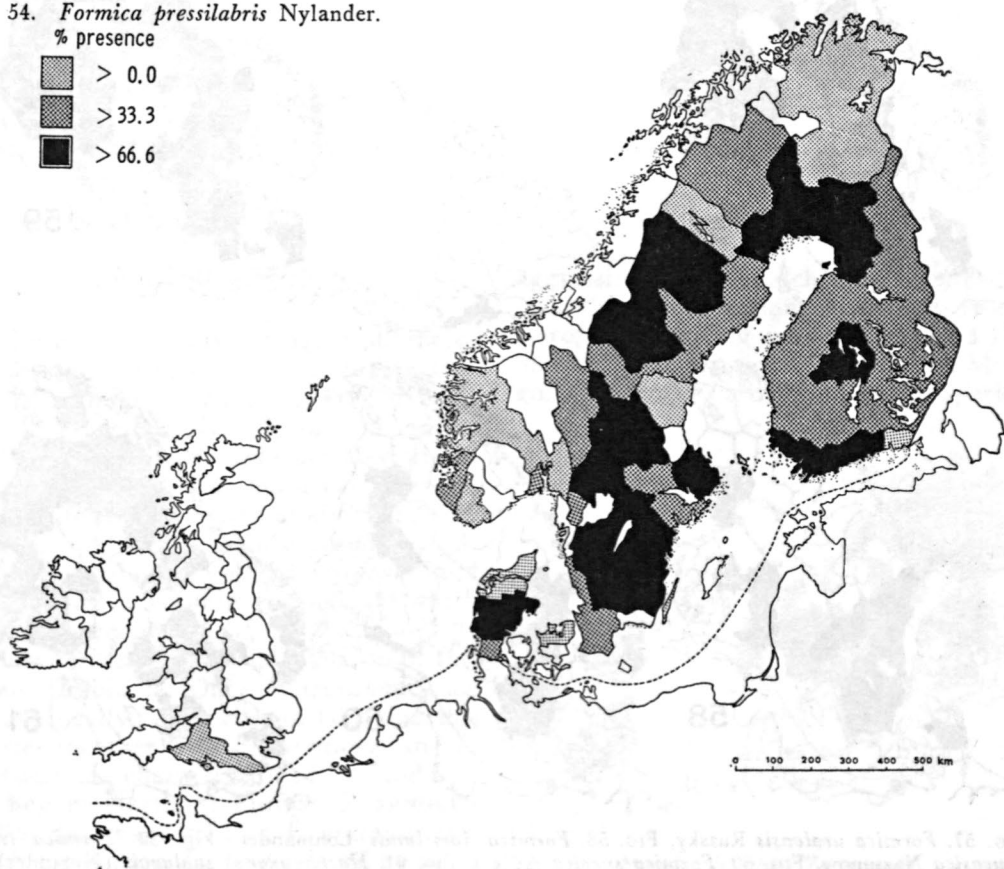Intercept —1.173. Multiple correlation coefficient 0.806 ($p \ll 0.01$).

TABLE 9. Step-wise multiple regression between distribution type K and 11 environmental variables.

Variable entered	Cumulative proportion of sum of squares reduced	Regression coefficient	t
Bright sunshine hours	0.071	0.0631	2.776

Intercept —0.146. Correlation coefficient 0.266 (p<0.01).

FIG. 68. Distribution Type K: *Lasius bicornis* (Förster) and *Polyergus rufescens* (Latreille).

to Northeastern Europe and Siberia north of latitude 60° (DLUSSKY, 1967) and not found in the British Isles or Central Europe. The other species are characteristic of woodland and upland areas of North Britain, the mountains of Central Europe and are also widely and abundantly distributed throughout the northern coniferous forest belt from Norway to Kamchatka. According to the regression analysis, the distribution of these species is positively correlated with altitude and latitude and also with bright sunshine with increasing latitude (Table 8).

Distribution Type J

This includes two species only, *Leptothorax corticalis* (Schenck) and *Camponotus fallax* (Nylander) (Figure 67). None of the variables examined are important in influencing their distribution. Both species are very local in Central Europe, mainly associated with old deciduous woodland and are probably relict species with a discontinuous or mosaic distribution north of latitude 50°. *C. fallax* becomes much more common in South Europe and the Mediterranean area including North Africa but *L. corticalis* is sparsely distributed in Europe and is one of the least known of the European *Leptothorax* species.

Distribution Type K

This includes *Polyergus rufescens* (Latreille) and *Lasius bicornis* (Foerster) (Figure 68). The only significant variable for this group is hours of bright sunshine which however only accounts for 7.1 % of the observed variation according to the regression analysis (Table 9) suggesting that these also are relict species in North Europe with little relationship to the present environment. *P. rufescens* is not un-

TABLE 10. Step-wise multiple regression between distribution type L and 11 environmental variables.

Variable entered	Cumulative proportion of sum of squares reduced	Regression coefficient	t
Latitude	0.063	—0.1392	—1.978
Length of the growing season	0.109	—0.1039	—2.443
Inland versus island clima	0.156	—0.1486	—2.765
Boreal versus oceanic clima	0.192	—0.0104	—2.344
Mean annual atmosph. pressure	0.206	0.0810	1.769
Bright sunshine hours	0.218	0.0444	1.196

Intercept 1.319. Multiple correlation coefficient 0.421 (p<0.01).

common in South Europe but *L. bicornis,* as with *Leptothorax corticalis* above, is sparsely distributed and one of the least known *Lasius* species in Central and South Europe. Its Scandinavian distribution rests with one locality record only in Smaland whereas *P. rufescens* has a wider distribution with several records in South Sweden.

Distribution Type L

This distribution type includes *Lepto-thorax unifasciatus* (Latreille), *Plagiolepis vindobonensis* Lomnicki and *Lasius emarginatus* (Olivier). These all occur in the Channel Islands but *L. unifasciatus* has recently been found also in Öland in Sweden. The main variables selected by the analysis include negative correlations with latitude, length of growing season, inland versus island climate and boreal versus oceanic climate (Table 10). All three species are abundantly distributed in South Europe with main ranges extending into Northern France and Central Poland.

IV. THE BIOGEOGRAPHICAL AREAS

The interrelations between the area units on the basis of their ant distributions were studied by using principal component analysis. An arrangement of the area units according to the three major axes is represented in a three dimensional model, Figure 69. This allows the identification of grouping corresponding with the major geographical regions such as the British Isles, Denmark and Fennoscandia. It is to be noted that all the Fennoscandian localities show little variation according to Factor III (14.9 % contribution) while all the British area units are strongly positively correlated with it. All the units at the top of the model correspond to areas within the British Isles with the sole exception of the faunistically poor North Isles. The Danish areas appear relatively close one with another and are characterised by their common positive correlation with Factor I (44.1 % contribution) and a negative correlation with Factor II (27.2 % contribution). However no general criteria for isolating these groupings in a standard way was found and despite the implied loss of information we preferred the single link cluster analysis for a clearer representation of the most characteristic groupings of the area units. These are shown by the dendrogram illustrated in Figure 70. Two levels of similarity have arbitrarily been selected for our purpose: the 50 % and 75 % similarity levels.

At the 50 % similarity level, the studied area divides straightforwardly into north and south on the basis of numbers of species present. At this partition, the southern zone includes the whole of the British Isles exclusive of the Northern Islands, Denmark, South Norway up to and including Hedmark, Opland, Buskerud and Hordaland, South Sweden up to and including Medelpad, Hälsingland and Dalarna, and South Finland including Karelia borealis, Savonia borealis and Ostrobottnia media, Figure 71.

In this southern zone most of the characteristic species of distribution type F are present, notably *F. rufa, F. fusca, L. fuliginosus, L. mixtus, L. umbratus, L. niger, L. alienus, M. sabuleti, L. muscorum, L. tuberum* and *T. caespitum.* With a few exceptions these are all absent from the northern zone and all are widely distributed in Denmark and Southern Fennoscandia and with the exception of *L. muscorum* are also present in the British Isles. This division corresponds approximately with that between middle boreal and south boreal climates as defin-
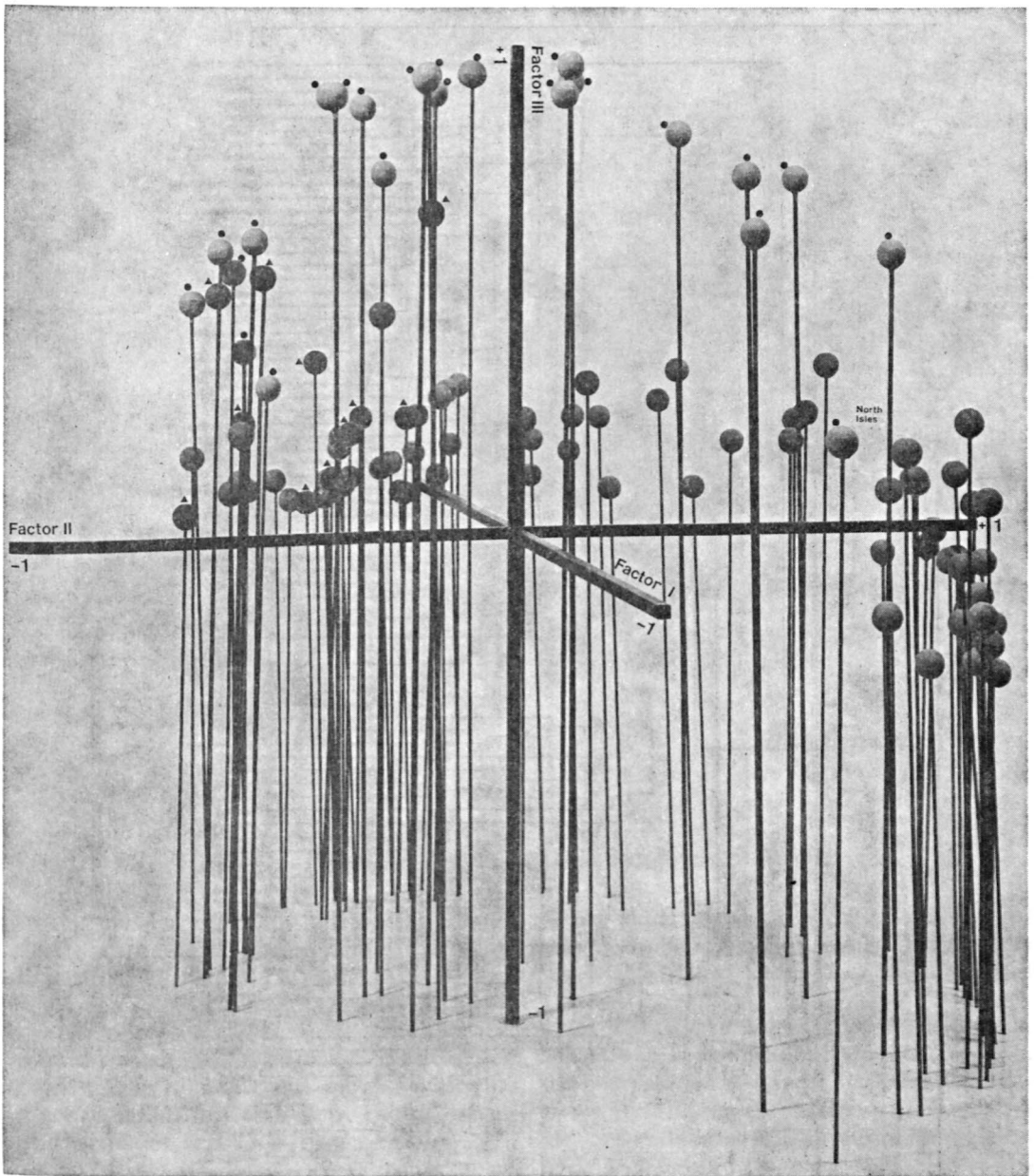
FIG. 69. Arrangement of 103 area units along 3 axes from similarity matrix analysis of ant fauna. British areas marked by dot, Danish by triangle, Fennoscandian areas unmarked.

ed by KALLIOLA (1973) on the basis of vegetation types. In Finland this is near the northern limit of *Formica rufa* and *F. pratensis* and of the southern pine zone (WUORENRINNE 1975).

In the northern zone, the north boreal species represented in distribution type I including *F. aquilonia, F. lugubris, F. le-* *mani* and *F. gagatoides* are characteristic and present with the more generally distributed *M. ruginodis, M. sulcinodis* and *L. acervorum*. No species however is entirely restricted to this zone and even the arctic *F. gagatoides* overlaps the two zones in the mountains of Opland and Hordaland in Norway, although the distribution

% SIMILARITY

Channel Islands
Peninsula
Thames
Channel
Severn
S. Wales
Anglia
Gotland
Öland
North West Jutland
West Jutland
South Jutland
Blekinge
Halland
East Jutland
Skåne
Södermanland
Uppland
Östergötland
Närke
Regio aboensis
Nylandia
Tavastia australis
Västergötland
Småland
Alandia
Bohuslän
Savonia australis
North East Jutland
Karelia australis
Hordaland
Rogaland
Ostrobottnia media
Hälsingland
Savonia borealis
Ostrobottnia australis
Tavastia borealis
Karelia borealis
Satakunta
Buskerud
Opland
Vestfold
Østfold + Akershus
Dalsland
Värmland
Västmanland
Dalarna
Hedmark
Medelpad
North West Zealand
Funen
North East Zealand
Telemark
Gästrikland
Vest-Agder
Aust-Agder
Bornholm
Golska Sandön
N. Wales
Trent
Humber
Lakes
E. Lowlands
Mersay
W. Lowlands
Connaught
Munster
Leister
Ulster
Tyne
E. Highlands
W. Highlands
N. Highlands
Lolland, Falster, Mon
South Zealand
Ostrobottnia kajanensis
Jämtland
Norrbotten
Ostrobottnia borealis, N part
Ostrobottnia borealis, S part
Härjedalen
Västerbotten
Ångermanland
Lycksele Lappmark
Åsele Lappmark
Kuusamo
eastern northern Finnmark
Lule Lappland
Torne Lappland
Pite Lappland
Lapponia kemensis, E part
Lapponia kemensis, W part
Lapponia enotekensis
Lapponia inarensis
western inner Finnmark
Troms
southern Nordland
northern Nordland
Møre og Romsdal
Sogn og Fjordane
Sør-Trøndelag
Nord-Trøndelag
North Isles

Fig. 70. Dendrogram of area unit groups.

% DIFFERENCE

Fig. 71.   Map of area units. Partitioned at 50 % similarity level.

of this species is mainly within the boundaries of the north boreal climatic area as illustrated by KALLIOLA (1973).

At the 75 % similarity level a total of twenty-one biogeographical areas are separated as shown in Figure 72. These include the following areas each of which is more or less characterised by the presence or absence of certain key species.

1. Channel Isles — these are clearly separated by the common presence of *P. vindobonensis* and *L. emarginatus* which are entirely absent from the rest of the area studied. This partition corresponds with distribution type L except for *L. unifasciatus* which also occurs on Öland.
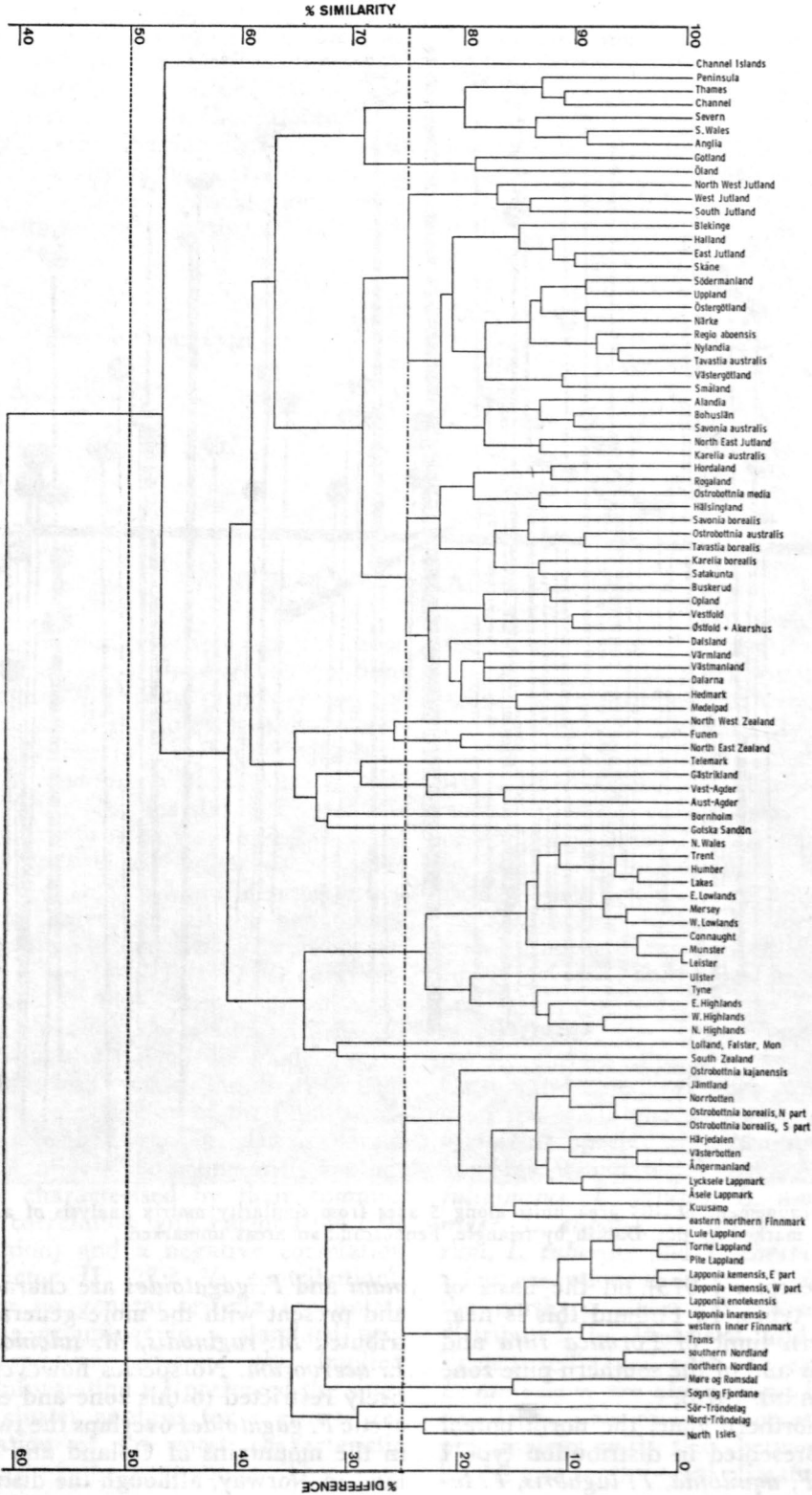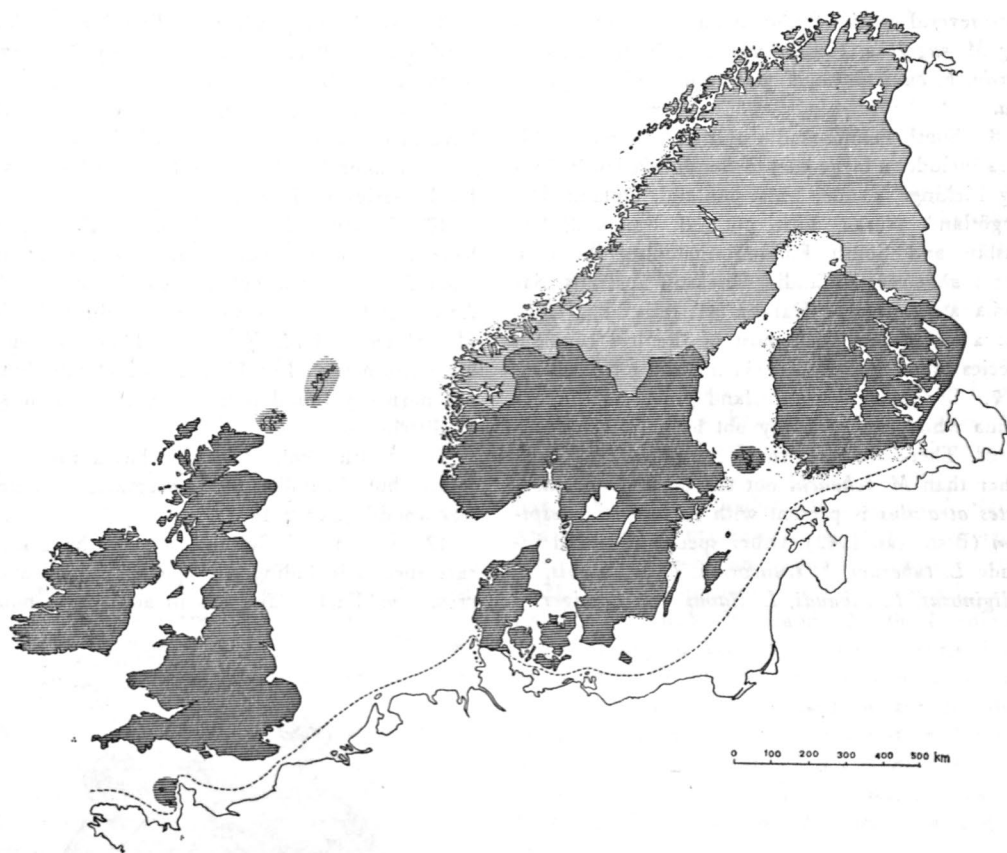
2. South England — this area includes Peninsula, Channel, Thames and Anglia corresponding in part with distribution type C. The area includes *Ponera coarctata* which is not present in Denmark or Fennoscandia and also many other southern species which are more common in South England than in South Scandinavia and are not found in the British Isles to the north of the demarcated area.

3. Rest of the British Isles (excluding the North Isles) — this area corresponds exactly with the first partition of BARONI URBANI & COLLINGWOOD (1975) from their analysis of the British vice-county distribution. The area includes a relatively impoverished fauna and lacks some species that are widely distributed in Northern Fennoscandia including *F. truncorum*, *F. gagatoides* and *C. herculeanus*.

4. The North Iseles and North Trøndelag — these two area units are very poor in number of species with only *L. acervorum* and *F. lemani* recorded from both areas and *C. herculeanus* and *F. aquilonia* present in North Trondelag but absent from the North Isles.

5. Northwest, West and South Jutland — these have a number of species in common but

lack several species found in East Jutland including *M. rugulosa, F. nitidulus, L. mixtus, C. ligniperda, F. cunicularia, F. polyctena* and *F. aquilonia.*

6. South Fennoscandia and E. Jutland — this area includes a large part of South Sweden including Blekinge, Skåne, Södermanland, Upland, Östergötland, Närke, Västergötland, Småland, Bohuslän and South Finland including Alandia, Regio aboensis, Nylandia, Tavastia australis, Savonia australis and Karelia australis. This area has a rich fauna with most of the less common species found in Scandinavia including *F. cinerea.*

7. Bornholm — this island group has a poor fauna which has probably not been fully investigated. There are no records for *Myrmica* species other than *M. schencki* but the uncommon *Anergates atratulus* is present with its host *T. caespitum* (BISGAARD 1942). Other species recorded include *L. tuberum, F. truncorum, F. rufibarbis, L. fuliginosus, L. rabaudi, L. flavus* and *L. niger.*

8. Northwest Zealand — *Formica* and *Lasius* species are well represented but only *M. rugulosa* of the genus *Myrmica* has been recorded.

9. Funen and Northeast Zealand — these have in common the presence of *H. punctatissima* from outdoor locations and *F. nitidulus*, a rather local species in Denmark.

10. Lolland, Falster, Mön — these islands have no representatives of the *F. rufa* group apart from *F. truncorum* but are well represented by *Lasius* and *Myrmica* species including the local *M. gallieni* and *M. specioides.* These two species have also occurred at Täktom in Nylandia but are not normally found together in their main areas of distribution.

11. South Zealand — this has a rather poor fauna but includes the uncommon *Stenamma* westwoodii (SKØTT 1973).

12. Öland and Gotland — these have several rare species including *C. vagus, D. fugax* and *T. erraticum.* Each island has in addition a number
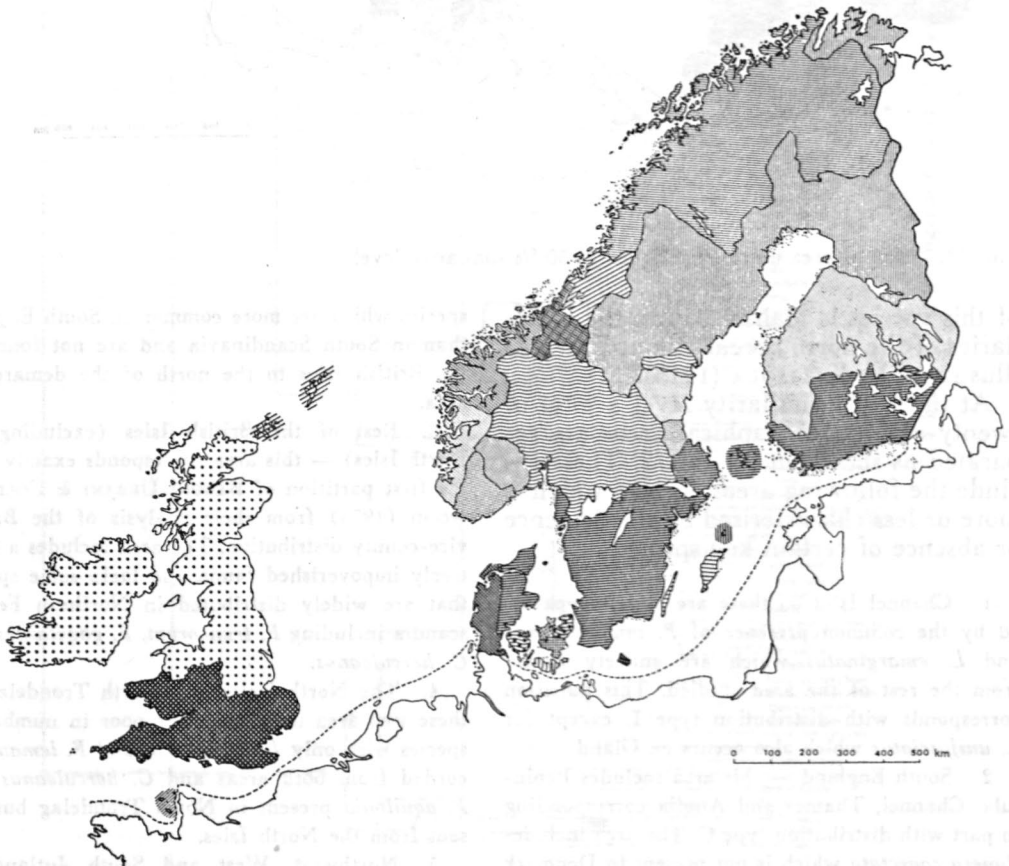

FIG. 72. Map of area units. Partitioned at 75 % Similarity Level.

of uncommon species separately including *M. gallieni, L. interruptus, L. unifasciatus, Strongylognathus testaceus* and *L. carniolicus.*

13. Gotska Sandön — this also has a peculiar fauna with few *Lasius* or *Myrmica* but including the very local *L. interruptus* and *L. nylanderi* in common with Gotland.

14. Gästrikland, Aust-Agder, Vest-Agder — these have *F. rufibarbis* in common but lack *M. schencki* and *L. muscorum* found in adjacent areas.

15. Telemark — this has no records for several common species of *Myrmica* and *Formica* known from adjacent areas.

16. Møre og Romsdal, Sogn og Fjordane — these have both *C. herculeanus* and *C. ligniperda* as well as the north boreal species included in Distribution Type I but are poor in *Myrmica* species.

17. Sør Trøndelag — the common species *M. ruginodis* and *C. herculeanus* are not recorded. This is a poorly represented area with records only for *F. aquilonia, F. gagatoides, F. lemani, L. flavus, M. rubra, M. sulcinodis* and *L. acervorum.*

18. Hordaland, Rogaland, Hälsingland, Savonia borealis, Ostrobottnia australis, Tavastia borealis, Karelia borealis, Satakunta — this is evidently a transitional zone with several northern boreal species such as *F. aquilonia, F. lugubris* and

F. lemani as well as the more southern *F. rufa, F. pratensis* and *F. fusca. Lasius* species are poorly represented with only *L. flavus* and *L. niger* recorded from all area units, *L. mixtus* from Hordaland and Rogaland, and *L. fuliginosus* from the Finnish areas.

19. Vestfold, Opland, Dalsland, Västmanland, Hedmark, Buskerud, Østfjold and Akershus, Värmland, Dalarna, Medelpad — this area has records for most of the more local *Formica* species including *F. suecica, F. pressilabris, F. forsslundi* and *F. uralensis.*

20. Härjedalen, Jämtland, Ångermanland, Västerbotten, Lycksele Lappmark, Åsele Lappmark, Ostrobottnia kajanensis, Ostrobottnia borealis, Kuusamo, E and N Finnmark — most of the commoner *Myrmica* species are recorded in this area, also *F. nitidulus,* either or both *L. flavus* and *L. niger, F. uralensis, F. aquilonia, F. sanguinea* and other common northern *Formica* species.

21. Lule Lappmark, Torne Lappmark, Pite Lappmark, South Nordland, North Nordland, Troms, East and West Lapponia kemensis, Lapponia inarensis, Lapponia enontekiensis — this northern area is characterised by the complete absence of *Lasius* species and a restricted fauna including *M. ruginodis, M. sulcinodis, M. lobicornis, L. acervorum, C. herculeanus, F. lugubris, F. gagatoides, F. lemani, F. truncorum* and *F. exsecta.*

V. DISCUSSION

It is of interest to demonstrate briefly how the distribution types recognised contribute to the fauna of each of the biogeographical areas separated out by our analysis (Figure 73). Since both distribution types and biogeographical areas are derived through two different approaches from the same data matrix, conclusions cannot be rigidly drawn because of the implied circular reasoning. However, the species groupings obtained show some significant correlations with the environmental variables used and it seems reasonable to regard them as natural sets of some biological significance.

First the more peculiar and well known

phenomena relating to the North European ant fauna should be mentioned. The British Isles within the regions inhabited by ants are unique as a relatively large area entirely without indigenous species of the worldwide genus *Camponotus.* However, there is at least one, probably credible, record of a fossil species described from the Oligocene of the Isle of Wight, *C. brodei,* referred to the tropical temperate subgenus *Colobobsis* (DONISTHORPE 1920). The genus *Camponotus* is assumed to have been wiped out of the British Isles and Northern Europe during the Pleistocene glaciations and to have repopulated Northern Europe after the
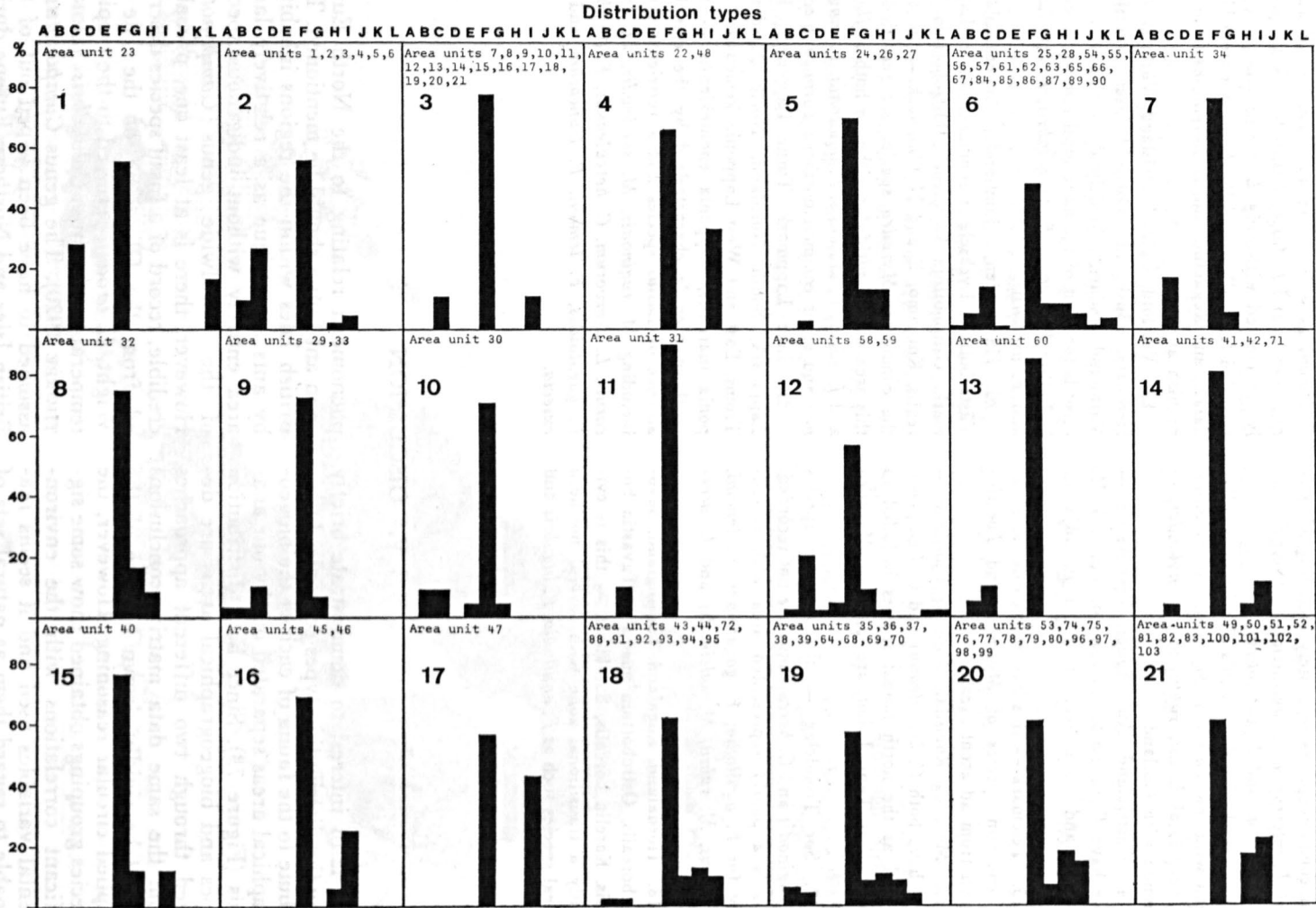
Distribution types

FIG. 73. Diagram of species distribution types showing their contribution to biogeographical areas.

separation of the British Isles from the European continent (EMERY 1920). The last land connection between England and the continent corresponds to the Dogger Bank formation dating back to at least 5 000 years ago (LINDROTH 1935). This fits with the analysis of subfossil insects recovered from deposits at Piilonsuo in South Finland by KOPONEN & NUORTEVA (1973) who found *Camponotus herculeanus* in deposits up to 4 000 years in age but not older, while ant remains older than 5 000 years were not detected. Since at least one very common *Camponotus* species *(C. mengei* Mayr) with over 100 specimens has been described from the Baltic amber of the lower Oligocene (WHEELER 1914) it seems reasonable to conclude that the genus was widespread in North Europe during tertiary times and disappeared during the Pleistocene glaciations, recolonising the area only during the fairly warm sub-Boreal period.

However the most interesting result from our analysis is that the four *Camponotus* species now living in North Europe pertain to three different distribution types. Thus there is not a single "*Camponotus* pattern" which excluded the British Isles from its colonisation range but the genus repopulated North Europe through at least three different paths and there seems no reason to postulate a similar reaction to past or present environmental situations for such ecologically disparate species as *C. herculeanus, C. vagus* and *C. fallax* or for their nearest hypothetical ancestors.

Another result from our analysis is worth comment. Both from the principal component analysis and from the cluster analysis, the British Isles are separated as the largest and most characteristic area within the boundary of our study with the exception of the myrmecologically poorest North Isles. Despite this there is no distribution type peculiar to this area and entirely missing from Scandinavia and only one indigenous species, *Ponera coarctata,* but no endemic species known only from the British Isles. Some of the distribution types separated out such as distribution types C, H and I have a statis-

tically significant E-W pattern implying more or less important correlations with longitude but most of the species of these groups are present also in South England at least. However, distribution type G (Figure 50) shows a purely Scandinavian pattern and includes 7.5 % of the studied species. These species show a typical north-south distribution with factors such as sunshine and latitude contributing to the regression. Yet the absence of the species of this group presents the main peculiarity of the British fauna which is thus characterised more by its absences than by the presence of significant species.

There are at least three well known and documented attempts to explain the presence of some organisms in North Europe by a pre-glacial or inter-glacial origin (LINDROTH 1935, 1953; HOLDHAUS 1954). Probably the best known of these is the work of HOLDHAUS (op. cit.) on the boreoalpine distribution type. This term is applied to many different organisms regularly present in North Europe and on the mountains of Southern Europe, in particular the Alps, and absent from or more local in Central Europe. Such a distribution pattern is shown also by some ant species as *Formica uralensis, F. aquilonia* and *F. lugubris.* This disjunction is supposed to have originated during the Riss glaciation although for some organisms the northern part of the area will also have been recolonised in post glacial times. (DE LATTIN 1966). However to postulate non glaciated refugia in North Europe during Pleistocene glaciations for animals with a high potential dispersal capacity such as ants seems unnecessary. Many such organisms indeed supposed to have had a Pleistocene origin fit at least equally well the contemporary distribution of the alpine climate as mapped by LANDSBERG et al. (1965).

The second distribution type of supposed Pleistocene origin in North Europe has been termed by LINDROTH (1935) as Boreo-British. Such species, of Würm origin, should be restricted now essentially to the British Isles and to Scandinavia but none of the North European ant species

shows clearly enough a pattern of this type.

There is evidence that substantial areas of the Norwegian coast constituted ice free refuges during the Pleistocene glaciations on which several species of plants and animals should have survived (PETERSEN 1947; LINDROTH 1953). However these same regions are still today under the beneficial influence of the Gulf stream, yet none of the studied ants shows a preferential distribution there. Although a relatively high species concentration in Northeast Norway comes out clearly in both the Q and R analysis this is more likely to be an expansion of the richer eastern continental fauna into a relatively favourable area than a relict fauna of Pleistocene origin and no similar pattern is present on the more beneficially exposed west coast. Although it is possible to suppose that the most typically north boreal elements included in our analyses (Distribution type I, Figure 62) could have survived in ice free refugia, there is not enough evidence to prefer this hypothesis to the simpler explanation of a post Pleistocene colonisation from the south.

It should be mentioned here that ant zoogeography has some peculiarities in that the biological unit is not the individual but the colony which is relatively non motile in space and usually restricted to a well defined foraging territory (BRIAN 1965). On the other hand ant dispersal capacity though differing for different species may be relatively great at the time of the nuptial flight and over periods of hundreds of years most species would have a potential to colonise all available free spaces within a region. However, competition, including defence of a territory for food exploitation (DLUSSKY 1965) and predation of mated females, would favour the first colonisers of a given area. Such species would play a dominant role through North Europe where the annual

period of activity and food resources are relatively limited.

We have already suggested that the peculiarities of the ant fauna of Öland and Gotland where climate or other features do not contrast sharply with their nearest continental lands, can be explained by interspecific competition favouring the first chance arrivals on a limited insular surface; a similar explanation may apply to the presence of *F. rufibarbis* on the Scilly Isles contrasting with its total absence from the nearest British mainland where the similar *F. cunicularia* is abundant. The pre-existence of any one number of a species group of a dominant genus such as *Formica* would be prejudicial for the settlement of another member of the same species group.

Moreover the presence of a given species in a given locality clearly implies the existence of contemporary appropriate environmental conditions independently of the origin of that species. There is evidence that the ant geographical picture for the more observable species of the *F. rufa* group is continuously changing in response to man made environmental changes (HUGHES 1975; BREEN 1976). At the same time in the British Isles the more local species appear to have been rather stable over the past 100 years in relatively unaltered biotopes (COLLINGWOOD 1971). The results of our regressions demonstrate the important role played by environmental factors such as sunshine and summer temperature and despite the limitations of the large generalisations on homogeneity within our area units we have been forced to make, this study can be regarded as a first rough approach to evidentiate and explain phenomena of this type. Considering the known continuous variation of environmental factors in time, there seems to be little need to search for explanations for the present day ant population in North Europe beyond a few thousand years.

VI. SUMMARY

A numerical analysis of the 67 indigenous ant species mapped on 103 area units was carried out to describe and to attempt a general interpretation of the population of Northern Europe. Northern Europe is regarded here, for purely practical reasons, as including the British Isles, Denmark and the whole of Fennoscandia up to the political boundary with Russia. Twelve sets of species distributions have been recognized for clustering at a similarity level ≧0.5 and are regarded as representing the major distribution patterns of the North European ants. Multiple regression analyses were calculated between the number of species per area unit of each distribution type and 11 environmental variables coded into major intervals assumed to be uniform within a unit. Some results showed high correlation values with environmental variables such as annual number of bright sunshine hours, July temperature, relative oceanicity and length of the growing season which are regarded as the dominant factors in determining the general picture of ant distribution in Northern Europe. One distribution type (type F) includes 27 species and shows a decreasing correlation with the previously mentioned 4 environmental variables in that same order. This large group of species, 40 % of the total fauna, represents the numerically dominant component of the ant population of every area unit.

The same numerical analysis carried out on the presence-absence of species per area unit permits the recognition of 21 biogeographical areas clustering at the 0.75 similarity level. These results, supported also by principal component analysis of the same similarity matrix, indicate the whole British Isles (with the single exception of the myrmecologically poorest North Isles) as the most peculiar and largest homogeneous biogeographical area within the studied territory. The reasons for this peculiarity are mainly due to absences than to the presence of endemic or of particularly significant species. The best known absence, i.e. that of the world distributed genus *Camponotus*, is explained with different reasons for at least 3 of the 4 known North European species and the hypothesis of a homogeneous *Camponotus* colonization in Northern Europe excluding the British Isles through some common dispersal pattern is rejected.

Some highly characteristic faunae, like those of the isles of Öland and Gotland are explained as probably due to historical factors such as the competitive advantages of the first randomly arrived colonizers on a limited insular surface in post glacial time, but no evidence has been found for postulating pleistocenic relicts in the ant fauna of Northern Europe.

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