A Numerical Analysis of the Distribution of British Formicidae[1]) (Hymenoptera, Aculeata)

by

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With 11 Figures

The ant fauna of the British Isles is one of the best known of all insect groups. Donisthorpe (1927) published all vice-county records of the less common species known to him. The vice-county distribution was brought up to date by Collingwood and Barrett (1965) with emendations and additions (Collingwood and Barrett 1966). In addition a list of recorded species for the Channel Islands and a few unpublished records have been included in the present analysis. We are confident that such an analysis has reasonable accuracy despite the low numbers of species involved and will also have considerable interest because of the good knowledge we have of the British fauna.

Methods

For the purpose of the present study the vice-county distribution is considered more appropriate than the 10 km grid distribution prepared by Barrett (1976) for the Provisional Atlas of Insects of the British Isles. The advantages of the Watson-Praeger system over the standard grid employed by the European Invertebrate Survey have already been discussed by Ragge (1965). Although not all the arguments reported fit with the case represented by the ant population, we have at least two fundamental reasons to avoid the use of the 10 km side square units. First our knowledge of the ant fauna is not good enough and several squares will be blank because of lack of appropriate collecting. Second, such a small unit, even if properly collected, will inevitably carry different sources of error in a purely objective computer analysis. For instance, a common wood inhabiting species will never be recorded from a 100 km^2 unit without wood although within its natural range; moreover, unnatural discontinuities due to human disturbance such as cultivations, big cities, etc., will appear in a very high similarity between squares comprising industrial areas and the naturally faunistically poorest parts of the country, like the Shetlands, Achill island, a.o.

[1]) The illustrations for this paper have been made possible by a grant of the National Science Foundation of Switzerland, request No. 3.785.72.

The vice-counties, although not perfect, provide a reasonable approach being units of convenient size, largely based on natural partitions.

In the literature, we have now a discrete number of papers using binary coefficients in bioassociational analyses but the two best known to the zoogeographer are probably the so called Simpson coefficient, first proposed by SZYMKIEWICZ (1926) and used by SIMPSON (1943, 1960), KOSTROWICKI (1965), JACZEWSKI and KOSTROWICKI (1971), etc. and the resemblance equation (PRESTON 1962) used, between the others, by HAGMEIER and STULTS (1964), HOLLOWAY and JARDINE (1968), HOLLOWAY (1969), etc. The Simpson coefficient is the simplest one. The similarity in it is given by n_{JK}/n_J where n_{JK} is the number of species in common between the two units to be compared and n_J is the number of species in the smallest unit. Its use has been criticized by HAZEL (1970, 1972) because it overemphasizes similarity, although the results obtained by it in the previously mentioned papers seem to be quite reasonable. We also obtained good enough results by using this coefficient both with the ants of the British Isles and of other regions having units very different in size (BARONI URBANI, unpublished observations). Of course, one would a priori expect to have better results by some index taking into account more information.

The resemblance equation is written as $[n_{Jk}/(n - n_{jk})]^{1/z} + [n_{jK}/(n - n_{jk})]^{1/z} = 1$, in which n_{Jk} = number of species present in the first and not in the second unit, n_{jK} = number of species present in the second unit and not in the first, n_{jk} = number of species absent in both units compared but present in the rest of the studied area, and n = total number of species. The use of this equation has been criticized among others by WILLIAMS (1949) on theoretical grounds, and by BULLOCK (1971) after application to actual data. It has in any case the big disadvantage of being not applicable to situations in which one unit has more than twice the number of species than the second and this property automatically excludes it for the study of the ant fauna of the British Isles.

In the rest of zoogeographical literature we often find the use of different indices and each of them, of course, is formally correct but implies a quantitatively different evaluation of similarity.

For the present study we used the FORTRAN IV programme CLUSTER for the UNIVAC 1108 computer of the Sandoz Computing Center, through the terminal of the Universitätsrechenzentrum in Basle. This program has been specially written to allow the calculation of all the 22 coefficients listed in the paper by CHEETHAM and HAZEL (1969) printing out the corresponding distance matrix. It provides, moreover, a cluster analysis for each matrix by the unweighted pair-group method (UPGM) and a print out of the corresponding phenogram. The UPGMA of cluster analysis has been selected because it implies less distortion (SOKAL and ROHLF 1962; FARRIS 1969; HAZEL 1970).

By comparing the different dendrograms obtained working on the ants of the British Isles, we find some clearly absurd outputs, although most appeared very similar, sharing in common most of the characteristic patterns. Despite that, consistent differences have been found between them or groups of them. The dendrogram best fitting our own idea of the ant population of the British Isles and even demonstrating some patterns we did not recognize before but that would be supported by evidence from distributional data, is the one based on the coefficient of HAMANN

(1961). As far as we know, this coefficient has been employed only in Hamann's paper on the classification of Monocotyledons, although it has been obviously discussed in the book by SOKAL and SNEATH (1963).

Similarity is defined by Hamann as $[(n_{JK} + n_{jk}) - (n_{Jk} + n_{jK})] \cdot n^{-1}$, where n_{JK}, n_{jk}, n_{Jk}, n_{jK} and n are defined as for the Simpson coefficient and for the resemblance equation. Although the results we obtained by other methods are often very similar, the dendrogram based on the calculation of the coefficient of Hamann offers slight but consistent advantages at some of the crucial nodal partitions and we refer only to it in the following pages.

Finally, more recently, stereograms have been proposed in numerical taxonomy (ROHLF 1968) and multivariate analysis has been used in both taxonomy and zoogeography (see e.g. FISHER 1968, etc.), but we have still preferred cluster analysis in our research for purely practical reasons.We do not think the advantages of factor analysis very relevant in a situation like that we are dealing with, while cluster analysis shows the advantage of ending up in a single result with an extremely high didactic value. There is no doubt that the relationships between 157 OTU's (the number of vice-counties in the British Isles) are much more easy to understand and to visualize in a dendrogram than in a three-dimensional stereogram or in a series of plots of different axes taken two at a time.

Biogeographical areas from the coefficient of similarity based on ant distribution

The dendrogram print out is reproduced in Figure 1 and area groupings extracted from this are mapped in Figures 2–4.

The first major partition occurs at the 30% difference level and divides the territory clearly into three main areas corresponding to Britain north of the South Midlands and including Ireland, the rest of South England and the Channel Islands. The Channel Islands have the species *Leptothorax unifasciatus* LATR., *Plagiolepsis vindobonensis* LOMNICKI and *Lasius emarginatus* OL. which are absent from the rest of Britain together with an absence of some of the commoner mainland British species and form a clearly distinct faunal area. South England within the area partitioned off at this level includes 17 species not found in the larger area of the north. The only apparent anomalies according to the ant distribution are Huntingdon with a very low number of species records compared with surrounding counties and South Somerset where 5 of the commoner species are lacking.

In order to examine a further division of biogeographical areas, a map has been drawn showing the vice-county groupings appearing on the same branch by arbitrarily cutting the dendrogram at the 20% difference level (Fig. 3) which falls between the 11th an 12th nodal partition so that 12 biogeographical areas only are shown on the map. These divisions are discussed in sequence.

1. W. Cornwall is differentiated first from the rest of South Britain probably by the relative poor fauna recorded from the exposed Atlantic seabord and also by the inclusion of the Scilly Isles where *Formica rufibarbis* FAB. occurs. This, together with Surrey, represents the only record for this species in the British Isles.

2. S. Devon, Dorset, S. Hants and Wight include most of the rarer species found in Britain such as *Strongylognathus testaceus* SCHENCK, *Anergates atratulus* SCHENK,

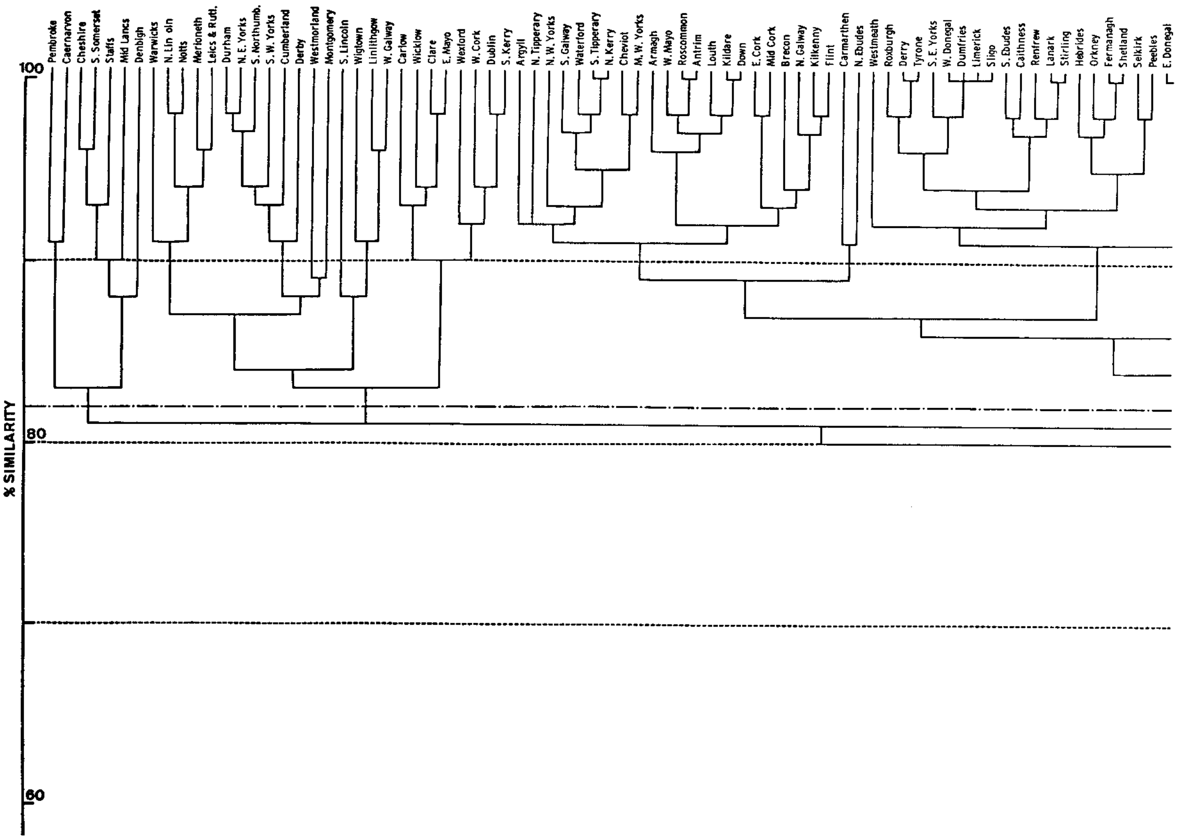
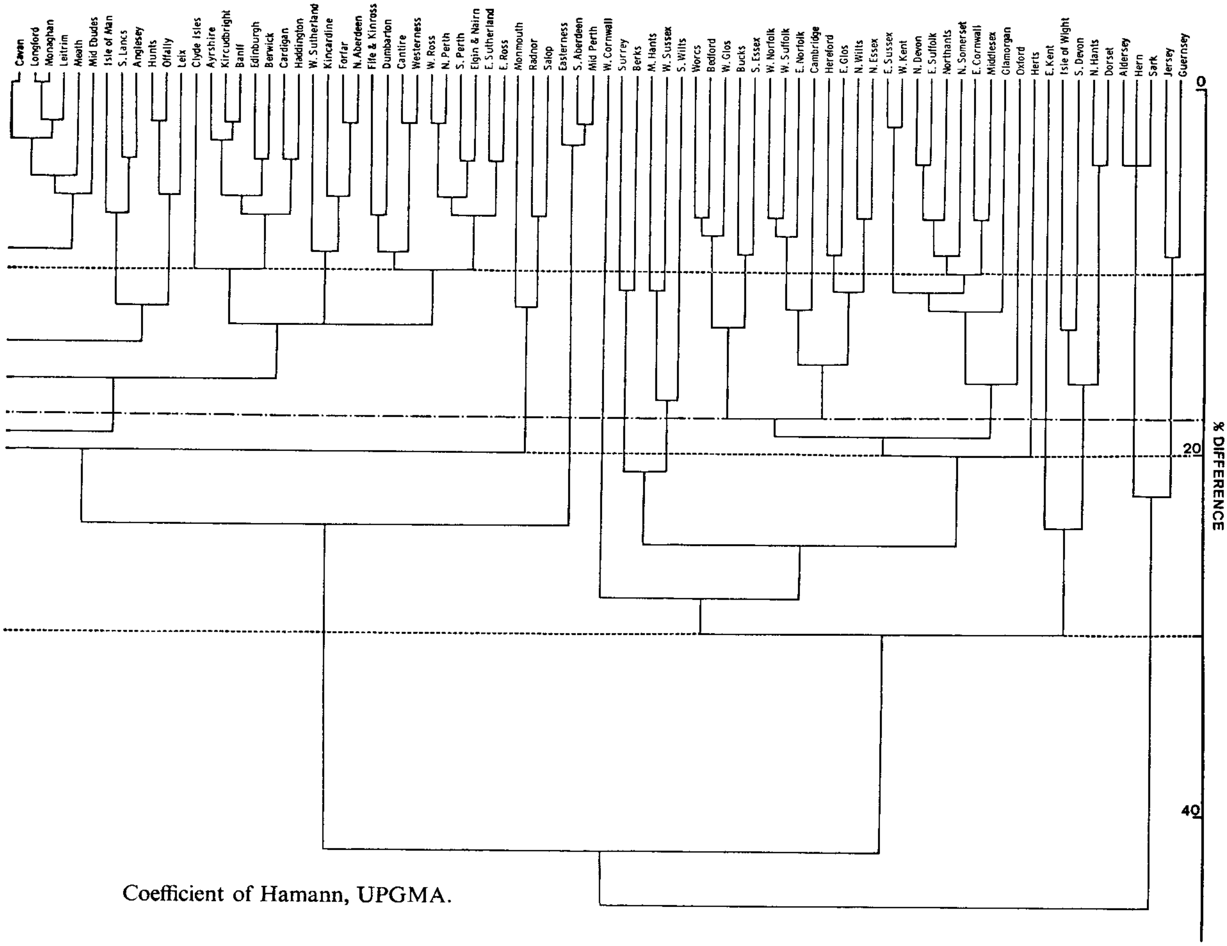


Fig. 1. Dendrogram obtained from the Q mode analysis of the British ants distribution data.

Formica pratensis RETZIUS and *F. transkaucasica* NASSONOV which are unique to that area although none of these have been recorded together so far from all 4 vice-counties. Other rare British species in this area also found elsewhere very locally in S. England include *Sifolinia karavajevi* ARNOL'DI, *Diplorhoptrum fugax* LATR. and *Leptothorax interruptus* FÖRSTER and this grouping of countries furthermore contains 75% of the total British fauna.

3. Eastern Highlands of Scotland including Easterness, S. Aberdeen and Mid Perth have the largest grouping of the genus *Formica* to be found in Scotland including *F. sanguinea* LATR., *F. exsecta* NYL., *F. lugubris* ZETT., *F. aquilonia* YARROW and also the inquiline *Formicoxenus nitidulus* NYL. These species are to be found in some of the other Scottish vice-counties but occur together only in the Eastern Highlands.

4. Hertfordshire is the next division separated by the phenogram and this may be explained by the absence of records for several southern species including *Leptothorax nylanderi* FÖRST., *Lasius alienus* FÖRST. and *Formica cunicularia* LATR. recorded from all adjacent counties.



Coefficient of Hamann, UPGMA.

5. Radnor, Shropshire and Monmouth are grouped at the next partition. Each has some elements of the southern fauna including *Leptothorax nylanderi* but they exclude *Myrmecina graminicola* LATR. found in the other South Midland counties and also contain *Formica lemani* BONDROIT and *F. sanguinea* not present in some of the other vice-countries of the South Midland area.

6. Surrey and Berkshire next go together as counties with a very similar recorded fauna although Surrey uniquely includes *F. rufbarbis* found elsewhere in Britain only on the Scillies and also the parasite *S. karavajevi*. However, these vice-counties have 31 and 25 species each respectively, 25 of which are in common.

7. E. Kent includes *Myrmica specioides* BONDROIT not fount elsewhere in Britain and also other relatively uncommon species such as *Tapinoma erraticum* LATR., *L. interruptus* and *Diplorhoptrum fugax*.

8. The next partition groups most of the remaining S. English counties from E. Anglia and Northamptonshire to Hereford, E. Cornwall and W. Kent. All of these except W. Norfolk and W. Suffolk include *Formica cunicularia* and *F. rufa* L.

Fig. 2. The three main biogeographical areas separate at the 70% similarity level.

Fig. 3. Biogeographical areas separate at the 80% similarity level.

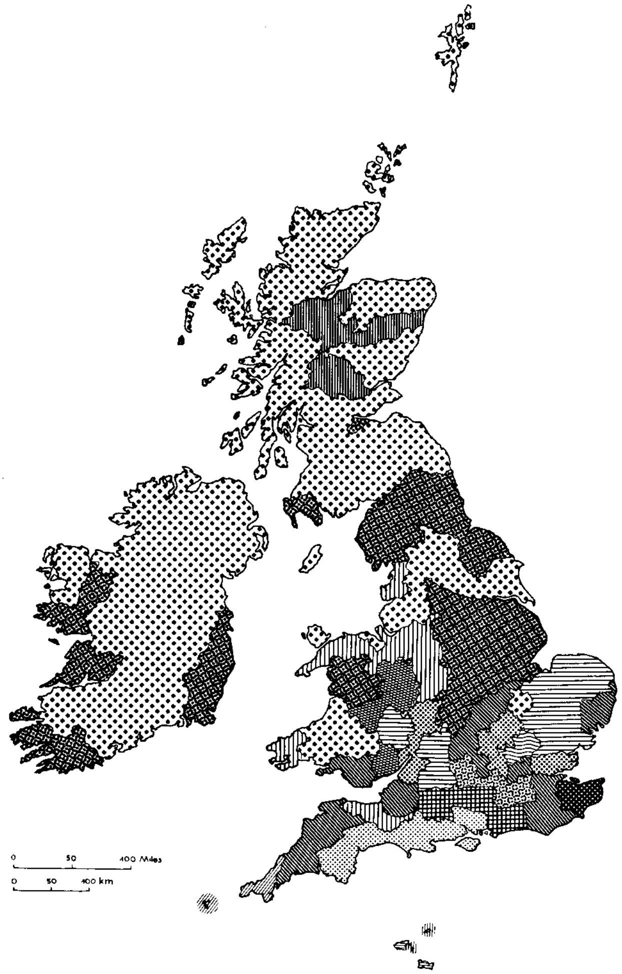


Fig. 4. Biogeographical areas separate at the 82% similarity level.

and most include *Myrmica schencki* EM. and apart from Oxford, W. Gloucestershire, E. Cornwall and N. Devon have no records for *F. lemani*.

9. S. Wiltshire, N. Hampshire and S. Essex form a group within the larger area of South England having many southern species but none of the rarer ants.

10. The rest of the British Isles (Channel islands excluded) still remains as a compact set without biogeographical partitions because of its poor ant fauna almost destitute of characteristic elements.

11. A clear partition between the Channel Islands arises. The first group contains only Jersey and Guernsey which have in common at least 7 common species occurring more or less frequently in Britain but not on the 3 other islands. These 7 species are *Diplorhoptrum fugax* LATR., *Myrmecina graminicola*, *Myrmica scabrinodis* NYL., *Lasius fuliginosus* LATR., *L. niger* L., *Formica pratensis* RETZIUS and *F.fusca*. It is obvious that the main reason for this spilt of the Channel Islands is purely ecological and not biogeographical, being due to the smaller surface of the last three islands.

12. Alderney, Hern and Sark represent the last group. They are characterized by the absence of the 7 species above recorded from Jersey and Guernsey and by the common presence of *Plagiolepsis vindobonensis* LOMNICKI and *Leptothorax unifasciatus* NYLANDER, completely lacking in Britain. Other species such as *Ponera coarctata* LATR., *Diplorhoptrum fugax* LATR., *Myrmica ruginodis* NYL., etc. have a non uniform and discontinuous distribution within the Channel Islands and surely contribute to some extent to the construction of the pattern we described.

To continue the study of the dendrogram at regular intervals as is usually done in numerical taxonomy would imply a cutting at the 10% difference level. At this level we see an enormous increase of the areas separable in S. England because of higher number of species together with a greater uniformity of species incidence north of the Midlands. The main conclusion to be drawn from this is that the ant population of the British Isles follows a rather uniform pattern with a trend to an even decrease in species numbers from South to North. This can be expected from what is known about mainly thermophilous insects which increase in species number towards the tropics.

We prefer to postpone, for the moment, the discussion of the areas separable at the 10% difference level and to try to find a subjectively better difference level allowing further partitions in the Northern areas. Such a situation was found by arbitrarily cutting the dendrogram at the 18th nodal partition corresponding to the 18% difference level (Fig. 4). At this level additional groupings can be shown within Ireland, Scotland and N. England that seem worth further comment.

Most of the counties of the Eastern Midlands, parts of Yorkshire and Lancashire, with North Wales and the eastern and western vicecounties of S. Ireland come together with Wigtown and Linlithgow in Scotland as a main grouping. The main resemblance between these areas appears to be the presence of *L. mixtus* NYL., *L. niger* and *L. flavus* FAB. with, in at least some of the vice-counties, *L. umbratus* NYL., *L. alienus*, *Tetramorium caespitum* L. and *Formica fusca*.

Another grouping split off at this level includes Staffordshire, Cheshire, Mid Lancashire, N. Wales and Pembrokeshire. These share *Myrmica lobicornis* NYL., *L. umbratus* and *F. fusca* as well as *F. lemani* BONDR.

In order to show the reliability and limitations of the method we used, further groupings are shown in Figure 5 by finally cutting the dendrogram at the 90% similarity level. At this level it is clear that even a single species added to any part of the present known vicecounty distribution in Ireland and Scotland could result in a relatively large alteration in the apparent groupings. Moreover the total number of species recorded is evidently too low in these northern areas to produce a consistent biogeographical classification regardless of the method employed. Nevertheless, some comments on special features in this map would appear to be justified as revealing patterns of ant distribution that seem reasonable at the present state of our knowledge.

Here the main grouping includes most of the northern Irish counties, Lowlands of Scotland, the outer Scottish Islands, Caithness and SE Yorkshire which have the lowest numbers of recorded species.

Man, Anglesey and S. Lancashire form another grouping sharing in common such species as *Lasius fuliginosus* LATR., *L. alienus* FÖRST., *L. mixtus* NYL. and *F. fusca* L. Between these two extremes of areas with 6 or fewer species recorded on the one hand and 10 or more species on the other there are a variety of groupings of which

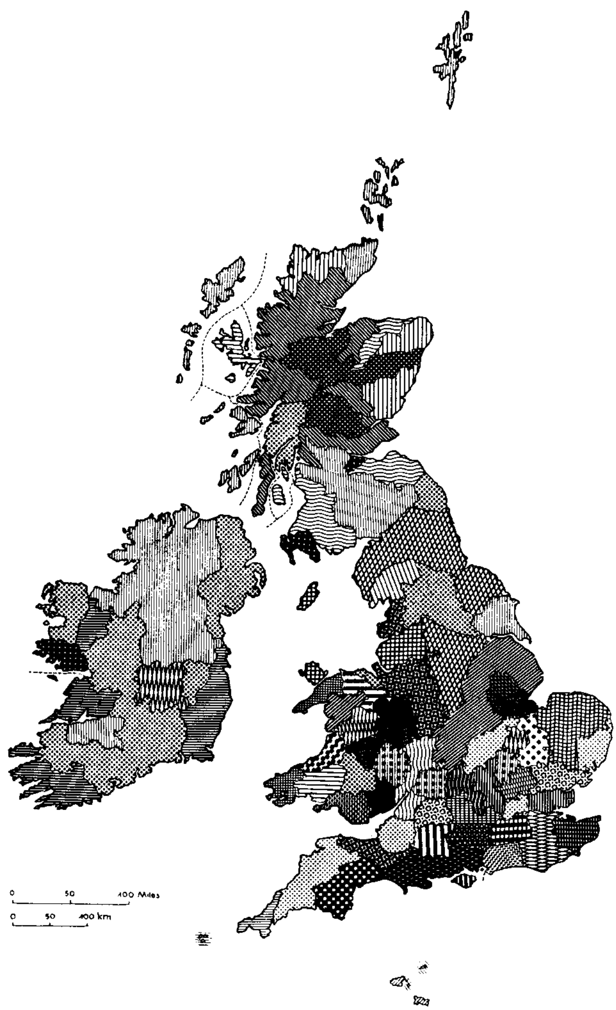


Fig. 5. Biogeographical areas separate at the 90% similarity level.

perhaps the most consistent includes the Northern Highland vice-counties of East Sutherland, Eastern and Western Ross, South and North Perthshire and Elgin which have in common the species *F. aquilonia* YARROW.

Basic distribution patterns of the ants of the British Isles

The importance of an analysis per columns (species) of the original distributional data matrix in zoogeographical studies should be self evident. Its significance is analogous to the R-technique in ecological research, although it has been used very little in zoogeography up to now. Problems and aims in a R-mode analysis are essentially different from those of a Q-mode analysis and the choice of the most appropriate coefficient must be considered again.

We claim that the supposed disadvantage of the Simpson coefficient while analysing faunal resemblance (i.e. overemphasizing similarity) should be a strong argument in favour of its use in the study of distributional patterns at least within relatively small geographical areas like the British Isles. In fact it is evident that every species present in only one or a few vice-counties will end up as representing a separate distribution pattern by using a coefficient taking into account also its absence from other units instead of the common presence only. In our opinion, there are good reasons to consider as non-desirable an output of this type. None of the British ant species known from one or a few vice-counties only is a true endemic, but all of them have a more or less wide geographical distribution outside of the British Isles. It seems more reasonable to consider these species as relicts of a formerly larger distribution similar to the present or past distribution of some of the existing species or as a relatively recent immigrant still expanding its range and following already known and comparable patterns.

Moreover, considering the small number of species involved in our study, it seems to be preferable to have just a few major groupings comprising as many species as possible.

The dendrogram relative to the R-mode matrix of British ants compared by the Simpson coefficient is represented in Figure 6. The problem of having an adequate number of distributional groupings has been arbitrarily solved by considering only the branches accounting for $^1/_2$ or more of the total difference observed. Because the maximum difference level observed in the phenogram was 86%, we cut it at the 43% difference level obtaining 4 basic distribution patterns (see figure). Each pattern has been mapped (Fig. 7–10) by darkening or shading in a different way the areas occupied respectively by more than 66.6%, 33.3% of the species respectively or the areas where at least one species pertaining to the grouping was present, but less than 33.3% of the total.

The distribution type A (Fig. 7) comprises the species *Leptothorax unifasciatus* NYL., *Plagiolepis vindobonensis* LOMNICKI, *Lasius emarginatus* OL., *Tetramorium caespitum* L., *Diplorhoptrum fugax* LATR., *Formica pratensis* RETZIUS and *Tapinoma erraticum* LATR. More than $^2/_3$ of these species are present on the islands of Guernsey, Jersey and Sark that we may call the typical area for this distribution type, while all of them are present on Guernsey. More than $^1/_3$ of the species are moreover concentrated on W. Cornwall, S. Devon, S. Wilts, Dorset, S. Hants and E. Kent. It is also interesting that the atypical pattern shown in Scotland and Ireland is due only to the inclusion in the group of *Tetramorium caespitum.* To explain this pattern we should note that *T. caespitum* is a species very easily imported by man; moreover it may be the only taxonomical problem still requiring solution in the British ant fauna. According to Dr. B. Poldi (personal communication) two species may have been confused under this name and it would be interesting to verify if the geographical discontinuity may be imputable to the presence of a northern and a southern separate species.

To distribution type B (Fig. 8) pertain the following seven species: *Sifolinia karavajevi* ARNOL'DI, *Formica sanguinea* LATR., *F. exsecta* NYL., *Leptothorax acervorum* NYL., *Myrmica lobicornis* NYL., *M. sulcinodis* NYL. and *Formicoxenus nitidulus* NYL. The basic pattern of these species comprises two main areas where more than $^2/_3$ of them are present. The first area is in S. England and includes S. Devon, Dorset, S. Hants, Surrey and Berks, i.e. a good part of the myrmecologically richer region of the British Isles. The second area is represented by the three Scottish vice-counties of

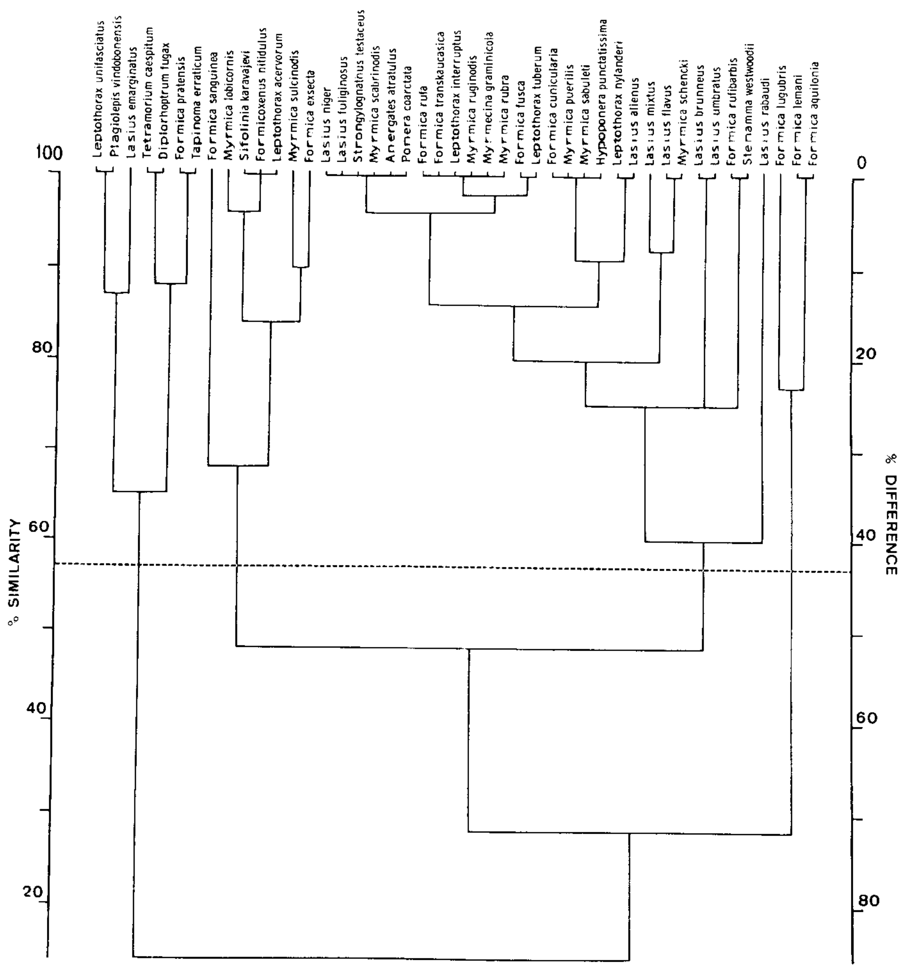


Fig. 6. Dendrogram obtained from the R mode analysis of the British ants distribution data. Coefficient of Simpson, UPGMA.

Mid Perthshire, S. Aberdeen and Easterness. Only one of the previously mentioned species (*S. karavajevi*) shows a strong contraction of this typical distribution being present only in Dorset, S. Hant and Surrey. All the remainder species occupy both the previously mentioned areas, sometimes with a really discontinuous distribution (*Formica exsecta*, *F. sanguinea*), or being present on an increasing number of vice-counties that, in one case (*Leptothorax acervorum*) may represent most of the studied territory. But from Figure 8 one can see also a number of regions that could easily be within the range of these species and from which all of them are regularly absent. The most significant of these regions (in comparison with the other distribution types) seem to be all the Channel Islands, Herts and Mid Lancashire with the isles of Anglesey and Man. The Shetlands, S. Ebudes and some Irish counties also fall within the areas of regular absence for these species, but being very poorly populated

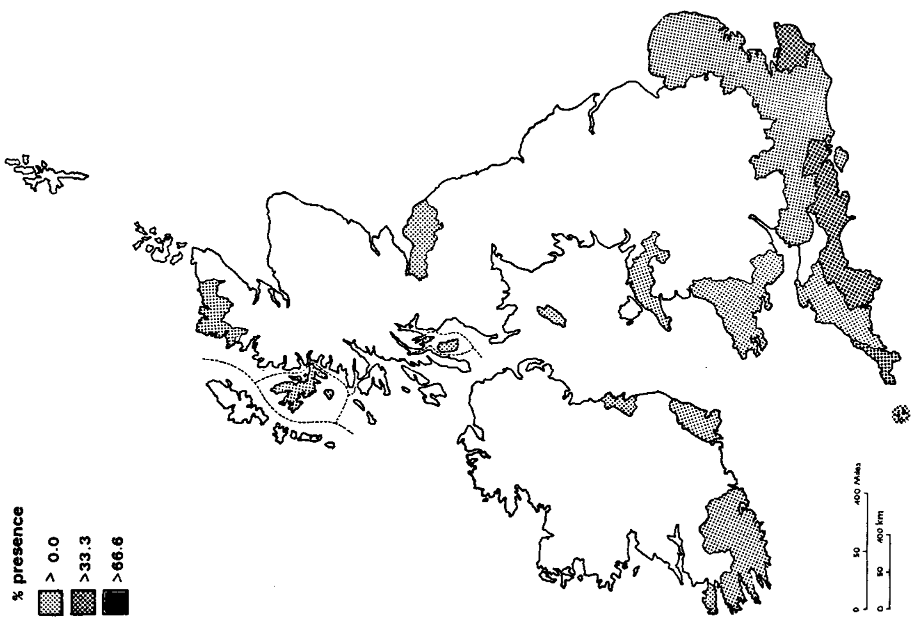


Fig. 7. Ant distribution type A. The different shading shows areas of different species concentration.

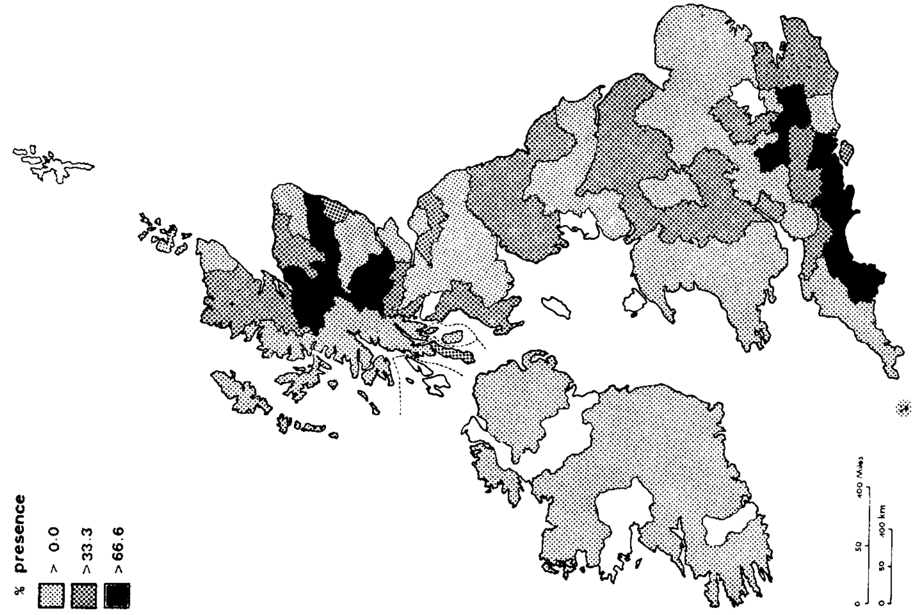


Fig. 8. Ant distribution type B. The different shading shows areas of different species concentration.

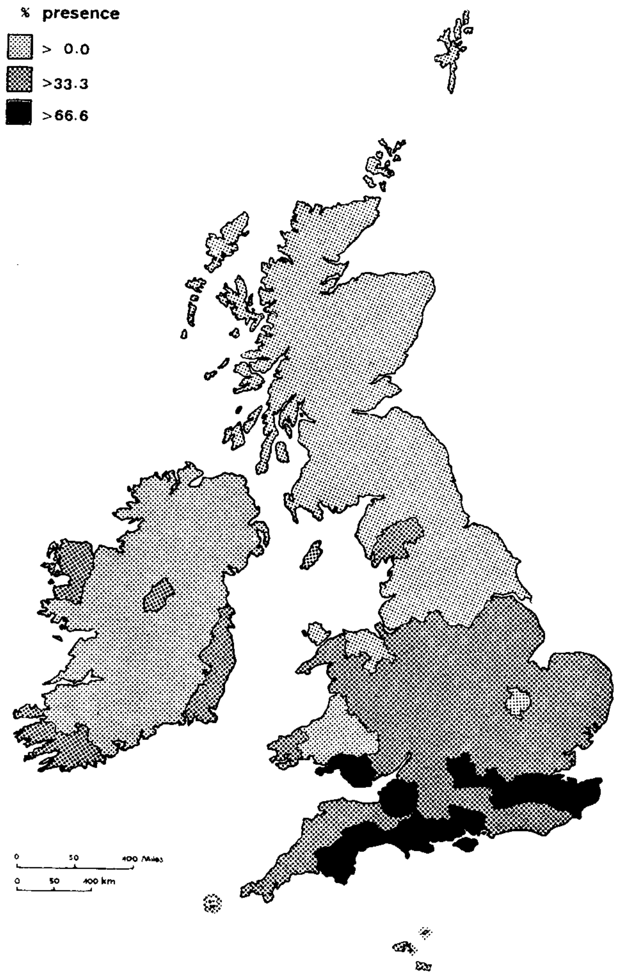


Fig. 9. Ant distribution type C. The different shading shows areas of different species concentration.

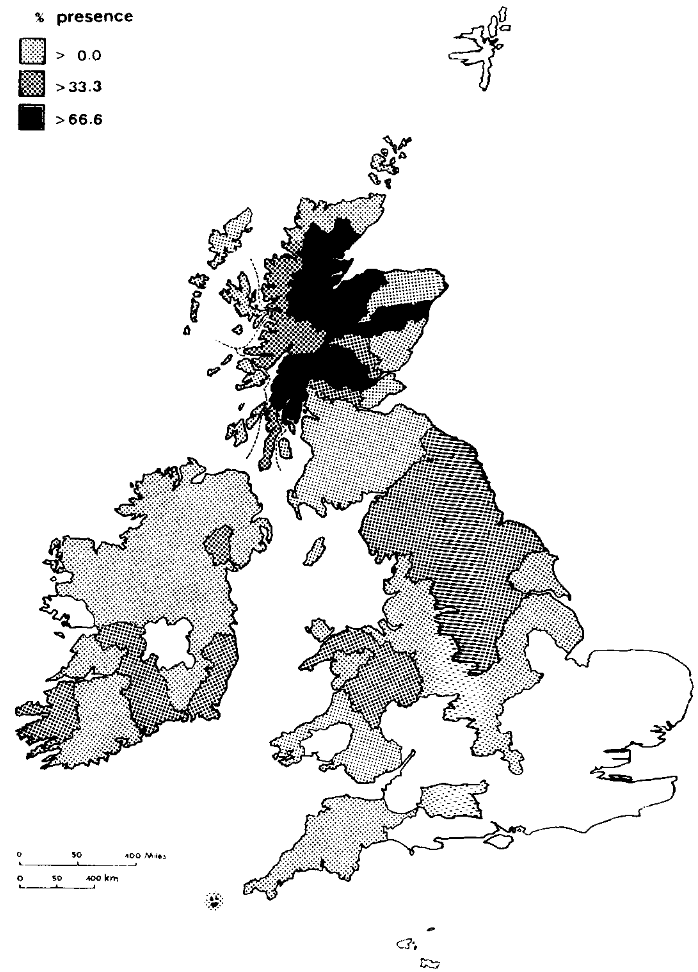


Fig. 10. Ant distribution type D. The different shading shows areas of different species concentration.

and perhaps insufficiently collected regions, we attribute less importance to the phenomenon.

Distribution type C (Fig. 9) comprises the highest number of species (28) and includes also all the commonest species of ants of the British Isles. The species pertaining to this group are the sole potentially distributed on the whole territory from the Channel Islands to the Shetlands (*Myrmica ruginodis* only). But, of course, their maximum concentration occurs in S. England and in a number of vice-counties partly similar to those of distribution type B. In fact more than $^2/_3$ of the species occur in S. Devon, N. Somerset, Isle of Wight, S. Hants, E. and W Kent, Surrey, Berks and Glamorgan. Moreover, their density follows a rather uniform pattern of decrease from South to North. More than $^1/_3$ of the species are present through all S. England with the only exceptions of Hunts, Brecon, Carmarthen, Cardigan, Denbigh, Flint and Anglesey and do not penetrate in N. England and Scotland north of the line represented by Cheshire, Derby, Notts and N. Lincoln. Exceptions are Westmorland and the Isle of Man with 17 and 12 species respectively. Some of these less regular presences may also serve to differentiate this distribution type from the preceding type B. In fact 33–66% of the species are present in Herts, Isle of Man, Jersey and Guernsey where the species pertaining to group B are regularly absent.

The last distribution type, D, is represented in Figure 10 and it is shown by three species only: *Formica lugubris* ZETT., *F. aquilonia* YARROW and *F. lemani* BONDROIT. They show, at least within the British Isles, a typically boreal pattern having a more or less wide distribution in Scotland and Ireland and being entirely absent from S. England (*F. lugubris* and *F. aquilonia*) or from great part of it (*F. lemani*). The Scottish vice-counties in which these species are regularly present include the three already considered as typical for distribution type B (Mid Perthshire, S. Aberdeen and Easterness), plus Argyll, E. Ross and E. Sutherland. But the main difference between these two distribution types is obviously represented by the regular presence or absence in most of the South English vice-counties.

Discussion

One of the first conclusions appearing from the results obtained is that none of the major biogeographical areas we have drawn exactly corresponds to the distribution of a single species. If this may seem a disappointing feature at a first glance, it represents, in our opinion, the greatest advantage of our approach to the problem. In fact to consider the distribution of a single or of a few species as preferentially significant in a biogeographical analysis is an incorrect oversimplification implying the loss of information relative to the other species. It is obvious that a biogeographically significant region is the result of a complex set of environmental factors present and past, each of which plays a different but equally important role relative to every species in the studied area.

The first partition we obtained between Channel Islands, South England and the rest of British Isles, may be easily justified on the basis of climatic factors only. The Channel Islands, in fact, have the highest daily temperature in July and the S. English separate vice-counties are practically all those included in the 62 °F (= 16.7 °C) isotherm of the July mean temperature. Although it is obvious that the summer temperature plays a great role in limiting the geographical distribution of ants, even this appears to be a too simplistic explanation. For this reason we would avoid any further discussion on the other areas that, in our opinion, can be profitably done only by factor analysis of the ant distribution together with the distribution of environmental factors presented in a comparable way (i.e. per vice-counties). And a complete information of this type is not available at present. The partition between S. England and the rest of the British Isles as has been drawn by us, can be used also for a historical interpretation of the data. Our boundary in fact fits well the maximum extent of the ice during quaternary (WRIGHT 1937).

Furthermore, we do not expect very many concordances between our results and the results that can be obtained in an analogous manner working on other groups of animals and plants because each species reacts in a different way to the same environmental pressure and each environmental variable would, by consequence, produce even more significant synecological situations in the mosaic of species competing or associating one with each other. It seems logical to assume that these differences will be even greater between greater taxonomical categories.

Despite this, concordances and analogies evidently exist and some of them must be objectively considered as the demonstration of the presence of a true and wide biological discontinuity. The most evident of these is probably the grouping of some vice-counties in the Scottish Highlands that comes out very clearly both in the Q-mode and in the R-mode analysis of our ant distributional data matrix (see Fig. 3 and 11). This region corresponds very well also to the only area in which the Scots Pine (*Pinus sylvestris* L.) is truly native within the British Isles (PERRING and WALTERS 1962). Other insects peculiar to this region are, for example, the beetles *Elater tristis* L. and *Otiorrhynchus scaber* L. (JOY 1932), and in the same region one can find also the maximum concentration of species of the genus *Carabus* of the British Isles (BREUNING 1932–36). In other cases the correspondence is even more striking, like the punctiform distribution of the ant *Myrmica specioides* BONDR. and of the bumblebee *Bombus pomorum* PANZER (ALFORD 1973) which have both been collected only in a restricted area on the coast of East Kent. But for this second example we cannot evoke a similar reaction to the same ecological factors or palaeogeographical events and we prefer to regard the case as a mere coincidence.

The presence or absence in the following three regions of the British Isles seem to have mostly determined the split of the four distributional types we described in the preceding text: the Scottish Highlands, some S. English counties and the Channel Islands. To these distribution types within the British Isles one can grosso modo adjust also the general geographical distribution of the involved species, although in a discussion of this type there is a considerable risk of error because of our very imperfect knowledge of the fauna of S. Europe and East palaearctic. But we can observe, for instance, that all the species pertaining to distribution type D (regularly present in the Scottish Highlands) have a wide boreal distribution in Scandinavia reaching the northernmost parts of Norway and Finland. On the other hand, most of the species pertaining to distribution type A (regularly present on the Channel Islands) are entirely absent from the whole of Scandinavia or major parts of it. Exceptions are *Tetramorium caespitum* already discussed in the text and *Formica pratensis*. All these considerations seem to emphasize once more the importance of temperature in determining the ant distribution, although it is evident that this sole factor cannot account for all the patterns observed.

Acknowledgments

The list of the recorded species for the Channel Islands was kindly supplied by Mr. C. DAVID. Thanks are also due to Dr. G. BÄCHLI of the Zoological Institute of the University of Zürich for allowing us the use of his NTL1 program for numerical taxonomy. The part relative to cluster analysis by UPGMA has been taken from NTL1 and introduced in the CLUSTER program we used. Its adaptation to the available computer facilities and the rest of the program allowing the explicit print out of the phenogram are entirely due to Mr. M.W. BUSER of the Computing Center of the University of Basel.

SUMMARY

A numerical analysis of the ant distribution data of the British Isles based on the Watson-Praeger vice county system was performed using the 22 coefficients of faunal resemblance available from the literature. After comparing the different dendrograms obtained, the one based on the Hamann coefficient was retained as being more useful for the purpose of a Q mode analysis. By cutting the dendrogram at different levels of similarity, a number of biogeographical areas were demonstrated. The first main break differentiated the three most dis-similar areas: Channel Islands, South England, the rest of British Isles. Further cuts at a higher similarity level separated off several regions within South England together with a constant separation of the Eastern Scottish Highlands that seems to constitute one of the more characteristic biogeographical areas within the British Isles. This area includes most of the old Caledonian pine forest on morainic drift and contains other plant and animal species not found elsewhere in the studied territory. However, in general none of the regions separated by this analysis corresponds exactly to the distribution of a single species because each comparison takes into account the whole information relative to the presence-absence of species in common with other regions.

The Simpson coefficient was preferred for the R mode analysis so as to isolate a few major species groupings showing fundamental distribution types. Distribution type A, with 16% of the species, is characterised by species regularly present on the Channel Islands and not necessarily present in South England although some may occur as far as North Scotland. Distribution type B also includes 16% of the species with a typically discontinuous pattern being present in the Scottish Highlands as well as in some South English counties but not recorded from the Channel Islands. Distribution type C is the more widespread comprising 62% of the British species including several recorded from the Channel Islands and either or both Isle of Man and Anglesey where none of distribution type B have been collected. The last distribution type, D, contains only 6% of the British species including the most boreal elements regularly present in the Scottish Highlands but not found together in most of England, Wales and Ireland, There appears to be some correlation between these four major distribution types within the British Isles and the general geographical distribution of the species concerned. Temperature, especially summer maxima, appears to be one of the most important determinants of the ant distributional type but does not provide an explanation for all the features observed.

ZUSAMMENFASSUNG

Eine numerische Analyse der Verbreitung der Ameisen auf den Britischen Inseln

Als Basiseinheit wurde aus praktischen Überlegungen der Teilung in «vice-counties» nach Watson-Praeger der Vorzug gegeben, gegenüber dem Raster U.T.M. und den 10-km-Quadraten der der Kartographie der Invertebraten Europas. Die Angaben wurden für die 22 binären Ähnlichkeitskoeffizienten ausgearbeitet, die der Literatur zu entnehmen sind. Die für jede Methode erzielten Dendrogramme wurden miteinander verglichen. Für die biogeographische Teilung des untersuchten Gebietes hat der Koeffizient von Hamann die besten Resultate ergeben. Indem das Phänogram auf verschiedenen Ähnlichkeitsebenen geschnitten wurde, konnte eine gewisse Anzahl biogeographischer Regionen aufgezeichnet werden. Die drei Hauptregionen sind die Normannischen Inseln, der Süden

Englands und der ganze Rest der Britischen Inseln. Weitere Aufteilungen auf höheren Ähnlichkeitsebenen ergeben eine rasche Zunahme der Anzahl besonders abgetrennter Regionen im Süden Englands, der myrmekologisch am reichsten ist. Im Gegensatz dazu wird ein Teil des Schottischen Plateaus konstant abgeteilt. Dieser Teil Schottlands beherbergt auch andere Tiere und Pflanzen, die sonst nirgends auf dem untersuchten Gebiet gefunden werden. Im allgemeinen bemerkt man, dass keine der durch die Analyse abgetrennten Regionen genau mit der Verbreitung einer Art überein stimmt, weil jede Region auf Grund der insgesamt verfügbaren Informationen über gemeinsame Ab- oder Anwesenheit aller Arten mit anderen Regionen abgegrenzt ist.

Für eine Klassifikation der Angaben nach Arten hat man absichtlich den Koeffizienten von Simpson gewählt, womit man nur die wichtigsten Gruppierungen der fundamentalen Verbreitungstypen der Arten erzielt hat. Die vier folgenden Typen wurden erkannt: Die Verbreitung des Typus A (16% der Arten) schliesst die zwangsläufig auf den Normannischen Inseln – aber nicht unbedingt in England – anwesenden Arten ein, selbst wenn eine Art Nordschottland erreicht. Zur Verbreitung des Typus B (ebenfalls 16% der Arten) gehören die Arten mit einer typisch diskontinuierlichen Verbreitung, die einen Teil des Schottischen Plateaus und den Süden Englands bewohnen, selbst wenn eine Art gegenwärtig nur auf den Süden Englands beschränkt ist und eine andere über den grössten Teil Englands und Schottlands verbreitet ist. Keine dieser Arten findet sich jedoch auf den Normannischen Inseln. Der Verbreitungstypus C (62% der Arten) umfasst alle häufigsten Arten, welche typisch in einigen südenglischen «vice counties» verbreitet sind (aber nicht genau die gleichen wie für den Typus B); sie können sich jedoch potentiell auf dem ganzen untersuchten Gebiet der Normannischen Inseln bis zu den Shetlandinseln finden. Diese Arten weisen eine weite Verbreitung im Norden auf, und man könnte sie daher mit denjenigen des Typus B verwechseln. Viele dieser Arten finden sich jedoch auf den Normannischen Inseln wieder (wo die Arten des Typus B regelmässig fehlen), und wenn eine dieser Arten vom Schottischen Plateau gemeldet wird, so wird sie es gleichzeitig von der Insel Man oder von beiden Inseln Man und Anglesey, von wo keine der Arten des Typus B gemeldet ist. Zum letzten Typus D (6% der Arten) gehören die typisch borealen Elemente, die regelmässig nur auf dem Schottischen Plateau anzutreffen sind und meistens im übrigen England und Irland fehlen.

Soweit man auf Grund unserer lückenhaften Kenntnisse der myrmekologischen Fauna vieler europäischer Gebiete urteilen kann, ist es oft möglich, diese 4 grundsätzlichen geographischen Verbreitungstypen der britischen Ameisen mit der allgemeinen geographischen Verbreitung dieser Arten in gegenseitige Beziehung zu bringen. Man findet zahlreiche Beispiele, welche zeigen, dass die Temperatur (vor allem die Sommermaxima) eine ausschlaggebende Rolle in der Bestimmung des Typus der geographischen Verbreitung der Ameisen spielt. Natürlich kann man mit diesem Faktor nicht alle beobachteten Verbreitungsphänomene erklären.

RÉSUMÉ

Une analyse numérique de la distribution des fourmis dans les Iles Britanniques

Comme unité de base la partition en «vice-comtées» de Watson-Praeger a été préferée au quadrillage U.T.M. et à la grille de 10 km de côté de la Cartographie des Invertébrés Européens pour des raisons essentiellement pratiques. Les données ont été élaborées par les 22 coefficients binaires de ressemblance réperables dans la littérature et les dendrogrammes obtenus par chaque méthode ont été comparés. Pour la partition biogéographique de la région étudiée le coefficient de Hamann a fourni les résultats les meilleurs et, en coupant le dendrogramme à différents niveaux de similarité, on a pu tracer un certain nombre de régions biogéographiques. Les trois régions principales sont les îles Normandes, le sud de l'Angleterre et tout le reste des îles Britanniques. Des partitions ultérieures à des niveaux de similarité plus poussés montrent une augmentation rapide du nombre de régions distinctes dans le sud de l'Angleterre qui est la partie myrmécologiquement la plus riche du pays et une séparation constante d'une partie du plateau écossais qui réprésente apparemment un des emplacements les plus caractéristiques parmi les îles Britanniques. Cette même partie de l'Ecosse abrite aussi d'autres expèces animales et végétales qui ne se retrouvent pas ailleurs dans le territoire étudié. En général on peut voir que aucune des régions séparées par l'analyse correspond exactement à la distribution d'une espèce puisque chaque région est délimitée sur la base de toute l'information disponible de présence-absence de toutes les espèces en commun avec d'autres régions.

Pour une classification des données par colonnes (espèces), on a intentionnellement choisi le coefficient de Simpson pour avoir seulement les groupements principaux des types de distribution

fondamentaux des espèces. Les quatre types suivants ont été reconnus. Distribution de type A (16% des espèces) comprenant des espèces obligatoirement présentes aux Iles Normandes, mais pas nécessairement en Angleterre, même si une espèce atteint jusqu'au nord de l'Ecosse. A la distribution de type B (16% des espèces également) appartiennent des espèces avec, typiquement, une distribution discontinue, habitant une partie du plateau écossais et du sud de l'Angleterre, même si une espèce est actuellement confinée au sud de l'Angleterre seulement et une autre est répandue dans la plupart de l'Angleterre et de l'Ecosse. Mais aucune de ces espèces se trouve aux îles Normandes. Le type de distribution C (62% des espèces) comprends toutes les espèces les plus communes qui, typiquement, sont distribuées dans quelques comtées du sud de l'Angleterre (mais pas exactement les mêmes que pour le type B), mais peuvent potentiellement se trouver dans tout le territoire étudié des îles Normandes jusqu'aux Shetlands. Lorsque ces espèces ont une ample distribution au nord on pourrait les confondre avec celles du type B, mais beaucoup de ces espèces se retrouvent aux îles Normandes (d'où les espèces du type B manquent régulièrement) et si une de ces espèces est signalée du plateau écossais elle l'est aussi au moins de l'île de Man sinon des deux îles de Man et d'Anglesey où aucune espèce du type B est signalée. Au dernier type, D (6% des espèces), appartiennent les éléments typiquement boréales regulièrement présents seulement sur le plateau écossais et absents dans la plupart de l'Angleterre et de l'Irlande.

Pour ce qu'on peut juger de notre connaissance imparfaite de la faune myrmécologique de beaucoup de régions européennes, il est souvent possible de faire correspondre ces 4 types fondamentaux de distribution géographique des fourmis britanniques à la distribution géographique générale de ces espèces. On trouve de nombreux cas indiquant que la température (surtout les maxima d'été) joue un rôle prépondérant dans la détérmination du type de distribution géographique des fourmis. Naturellement on ne peut pas expliquer toutes les modalités observées par ce facteur seulement.

Appendix

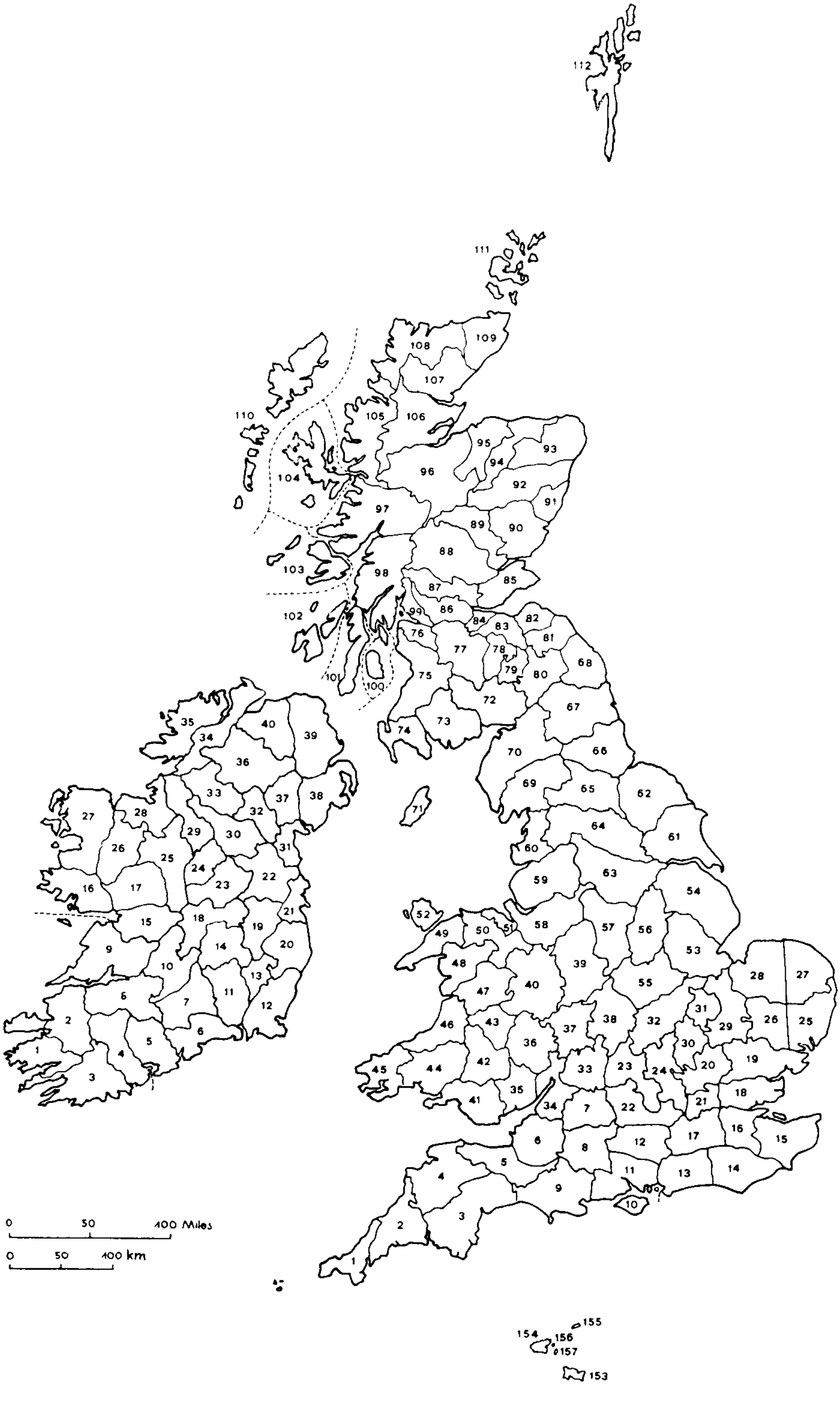
We think useful to reproduce here the vice-county distribution maps for all the British species of ants. No similar maps have been published recently and if on one hand the few previously published maps need considerable additions and corrections, on the other hand the study of those reproduced here will be indispensable for a correct understanding of the preceding text.

Apart from the rarest species which have been grouped together to save space and their distribution represented by dots, all the maps are drawn only on the vice-county basis. Thus a species recorded from W. Cornwall but not from the Scilly Isles will be mapped on both. But similar cases are in a very small minority and we do not think a further partition of the area unit useful for our purpose so that the following maps actually represent a discrete picture of the ant distribution in the British Isles and moreover, exactly the data input used to draw our conclusions.

The Watson-Praeger vice-counties with their identification numbers are represented in Figure 11. The corresponding vice-counties list is as follows.

England and Wales

1. West Cornwall (with Scilly)
2. East Cornwall
3. South Devon
4. North Devon
5. South Somerset
6. North Somerset
7. North Wiltshire
8. South Wiltshire
9. Dorset
10. Isle of Wight
11. South Hampshire
12. North Hampshire
13. West Sussex
14. East Sussex
15. East Kent
16. West Kent
17. Surrey
18. South Essex


0 50 100 Miles
0 50 100 km

19. North Essex
20. Hertfordshire
21. Middlesex
22. Berkshire
23. Oxfordshire
24. Buckinghamshire
25. East Suffolk
26. West Suffolk
27. East Norfolk
28 West Norfolk
29. Cambridgeshire
30. Bedfordshire
31. Huntingdonshire
32. Northamptonshire
33. East Gloucestershire
34. West Gloucestershire
35. Monmouthshire
36. Herefordshire
37. Worcestershire
38. Warwickshire
39. Staffordshire
40. Shropshire (Salop)
41. Glamorgan
42. Breconshire
43. Radnorshire
44. Carmarthenshire
45. Pembrokeshire
46. Cardiganshire
47. Montgomeryshire
48. Merionethshire
49. Caernarvonshire
50. Denbighshire
51. Flintshire
52. Anglesey
53. South Lincolnshire
54. North Lincolnshire
55. Leicestershire (with Rutland)
56. Nottinghamshire
57. Derbyshire
58. Cheshire
59. South Lancashire
60. West Lancashire
61. South-east Yorkshire
62. North-east Yorkshire
63. South-west Yorkshire
64. Mid-west Yorkshire
65. North-west Yorkshire
66. Durham
67. South Northumberland
68. North Northumberland (Cheviot)
69. Westmorland with North Lancashire
70. Cumberland
71. Isle of Man

Scotland

72. Dumfriesshire
73. Kirkcudbrightshire
74. Wigtownshire
75. Ayrshire
76. Renfrewshire
77. Lanarkshire
78. Peeblesshire
79. Selkirkshire
80. Roxburghshire
81. Berwickshire
82. East Lothian (Haddington)
83. Midlothian (Edinburgh)
84. West Lothian (Linlithgow)
85. Fifeshire (with Kinross)
86. Stirlingshire
87. West Perthshire (with Clackmannan)
88. Mid Perthshire
89. East Perthshire
90. Angus (Forfar)
91. Kincardineshire
92. South Aberdeenshire
93. North Aberdeenshire
94. Banffshire
95. Moray (Elgin)
96. East Inverness-shire (with Nairn)
97. West Inverness-shire
98. Argyll Main
99. Dunbartonshire
100. Clyde Isles
101. Kintyre
102. South Ebudes
103. Mid Ebudes
104. North Ebudes
105. West Ross
106. East Ross
107. East Sutherland
108. West Sutherland
109. Caithness
110. Outer Hebrides
111. Orkney Islands
112. Shetland Islands (Zetland)

Ireland

1. South Kerry
2. North Kerry
3. West Cork
4. Mid Cork

5. East Cork
6. Waterford
7. South Tipperary
8. Limerick
9. Clare
10. North Tipperary
11. Kilkenny
12. Wexford
13. Carlow
14. Leix (Queen's County)
15. South-east Galway
16. West Galway
17. North-east Galway
18. Offaly (King's County)
19. Kildare
20. Wicklow
21. Dublin
22. Meath
23. West Meath
24. Longford
25. Roscommon
26. East Mayo
27. West Mayo
28. Sligo
29. Leitrim
30. Cavan
31. Louth
32. Monaghan
33. Fermanagh
34. East Donegal
35. West Donegal
36. Tyrone
37. Armagh
38. Down
39. Antrim
40. Londonderry

Channel Islands

153. Jersey
154. Guernsey
155. Aldersey
156. Sark
157. Hern

For *Hypoponera punctatissima* only the records of Kent have been arbitrarily considered as possibly not due to human introduction.

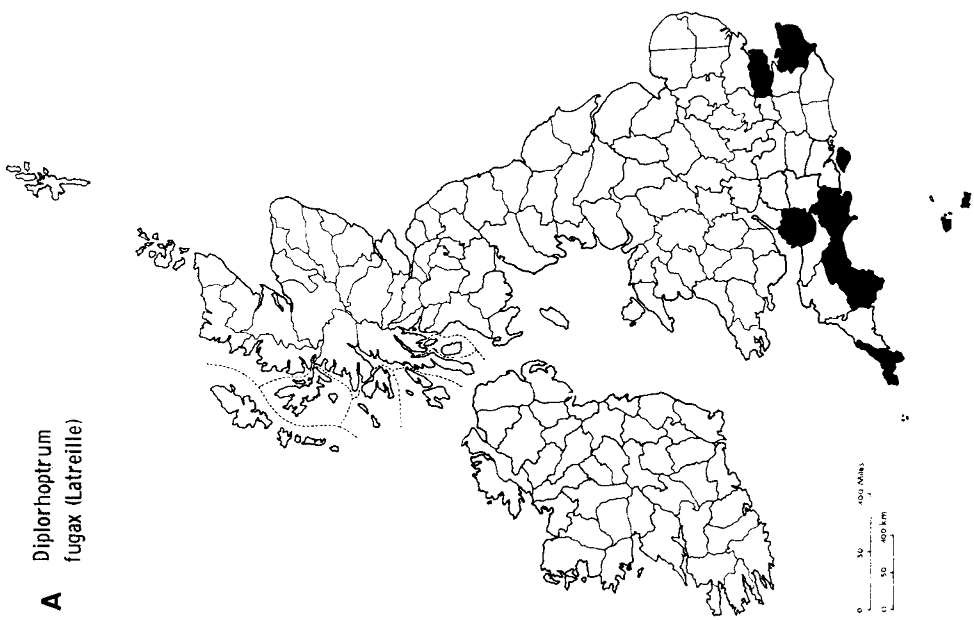

A ● Plagiolepis vindobonensis Lomnicki
B ▲ Sifolinia karavajevi (Arnol'di)
C ■ Anergates atratulus (Schenck)
0 50 100 Miles
0 50 100 km

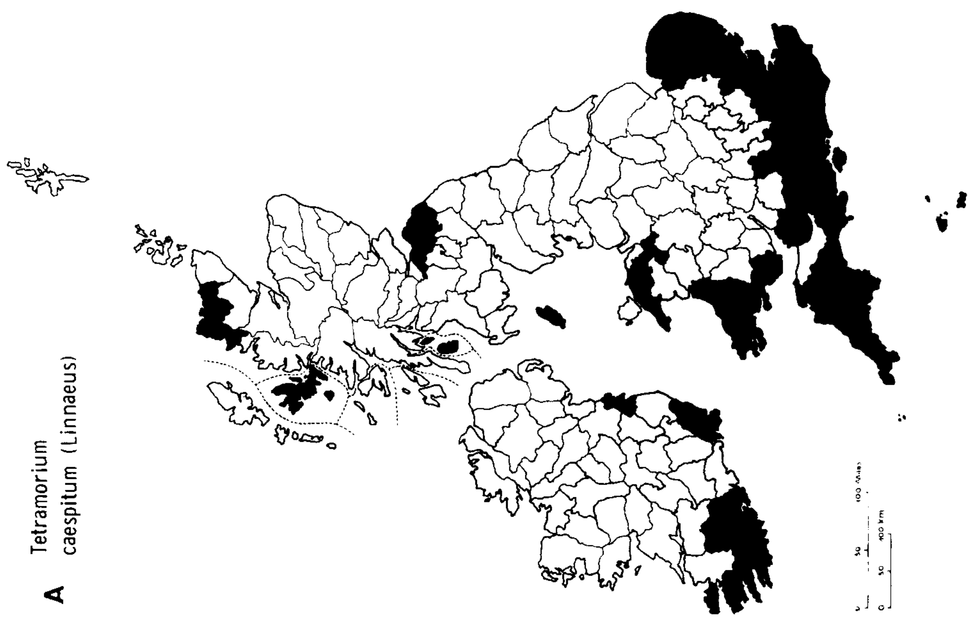

A ● Leptothorax unifasciatus (Latreille)
C ▲ Leptothorax interruptus (Schenck)
C ■ Myrmica puerilis Stärcke
0 50 100 Miles
0 50 100 km


A ● Lasius emarginatus (Olivier)
C ▲ Formica rufibarbis Fabricius
C ■ Formica transkaucasica Nassonow
0 50 100 Miles
0 50 100 km

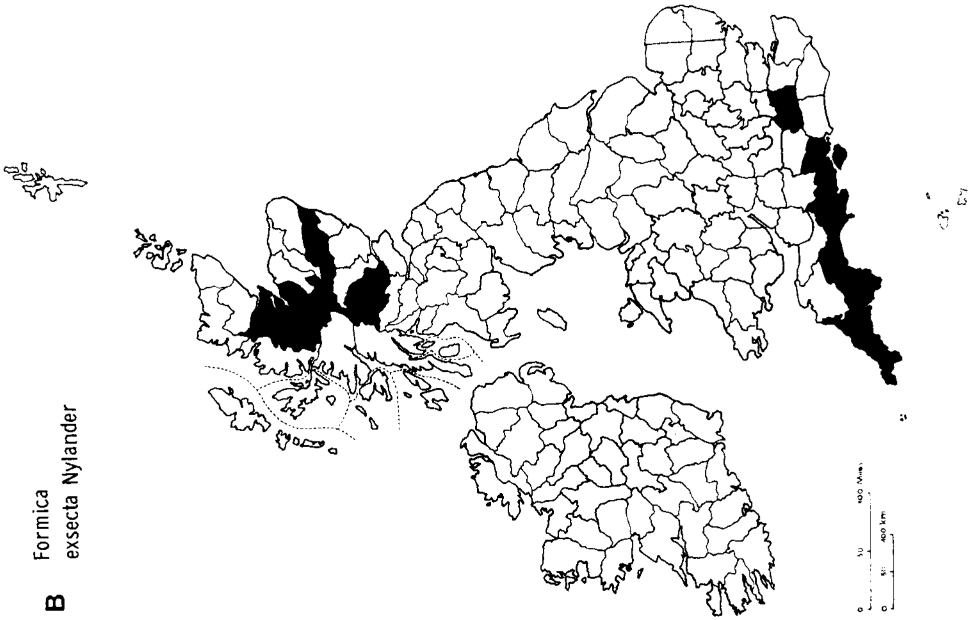

A ● Formica pratensis Retzius
C ▲ Hypoponera punctatissima (Roger)
C ■ Strongylognathus testaceus (Schenck)
0 50 100 Miles
0 50 100 km


A
Tapinoma
erraticum (Latreille)
0 50 400 Miles
0 50 400 km

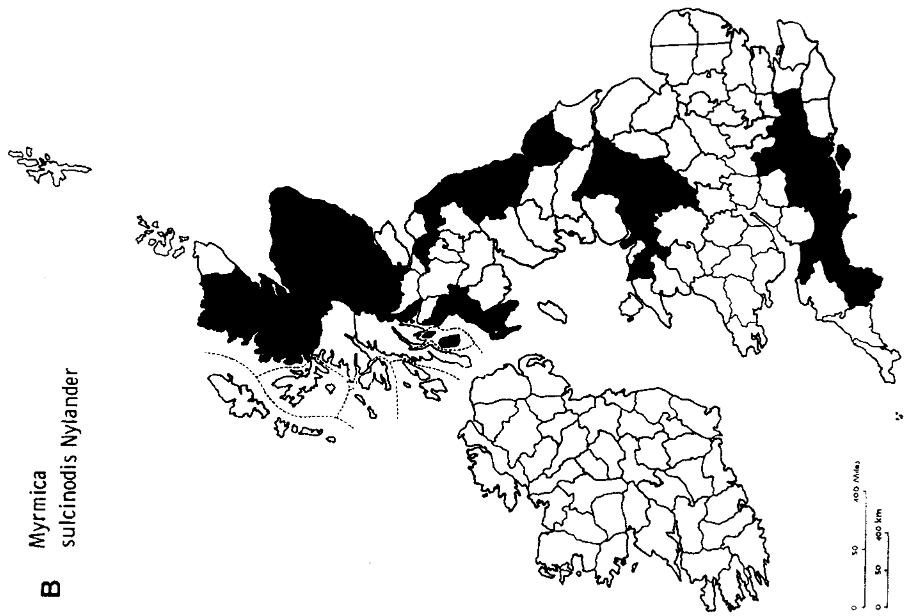

A
Diplorhoptrum
fugax (Latreille)
0 50 400 Miles
0 50 400 km

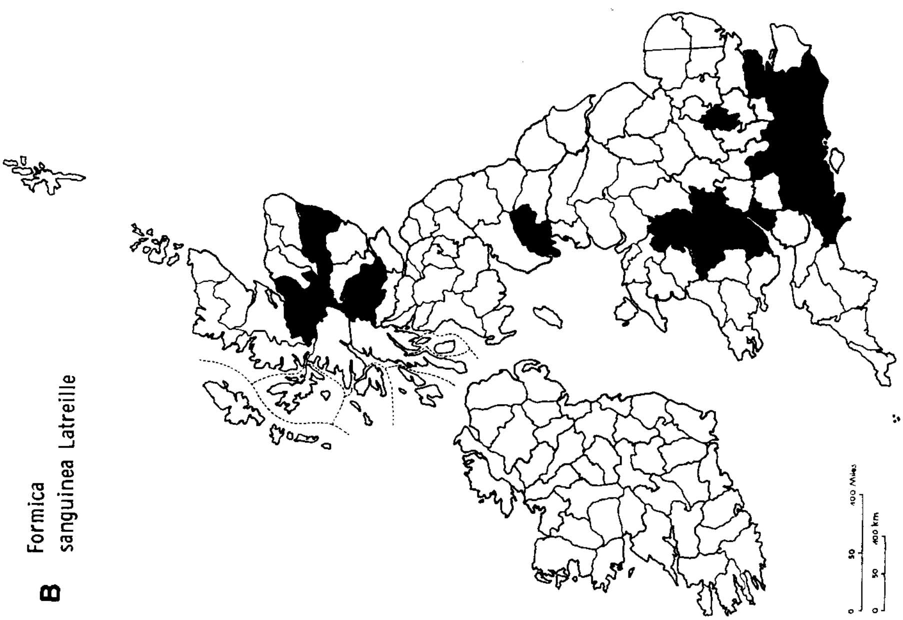


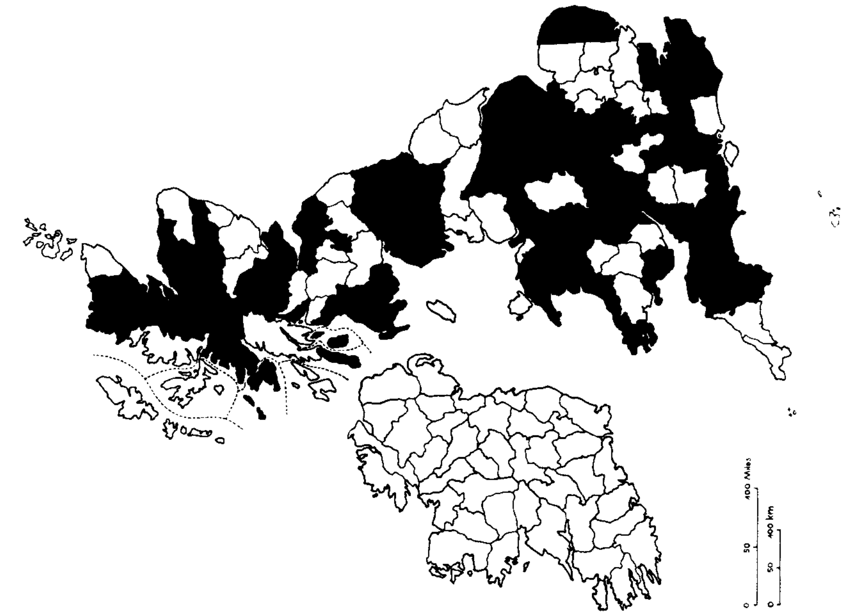
A Tetramorium caespitum (Linnaeus)



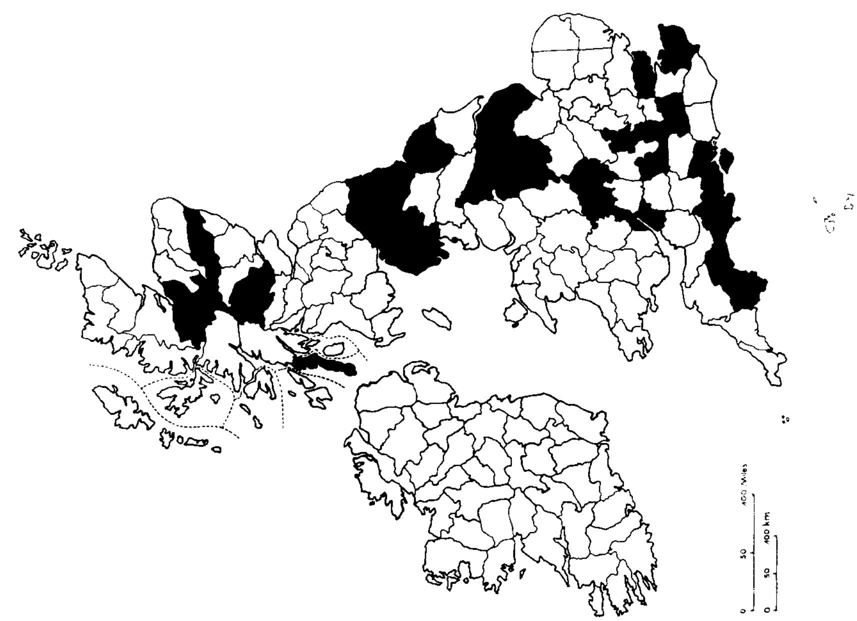
B Formica exsecta Nylander


B
Myrmica
sulcinodis Nylander
0 50 100 Miles
0 50 100 km


B
Formica
sanguinea Latreille
0 50 100 Miles
0 50 100 km

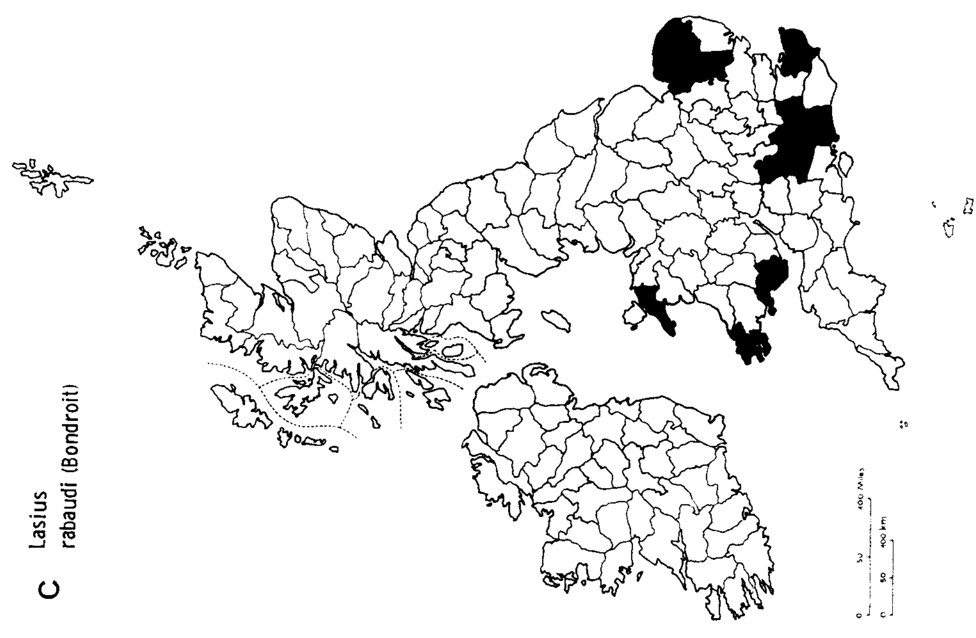


B Myrmica lobicornis Nylander

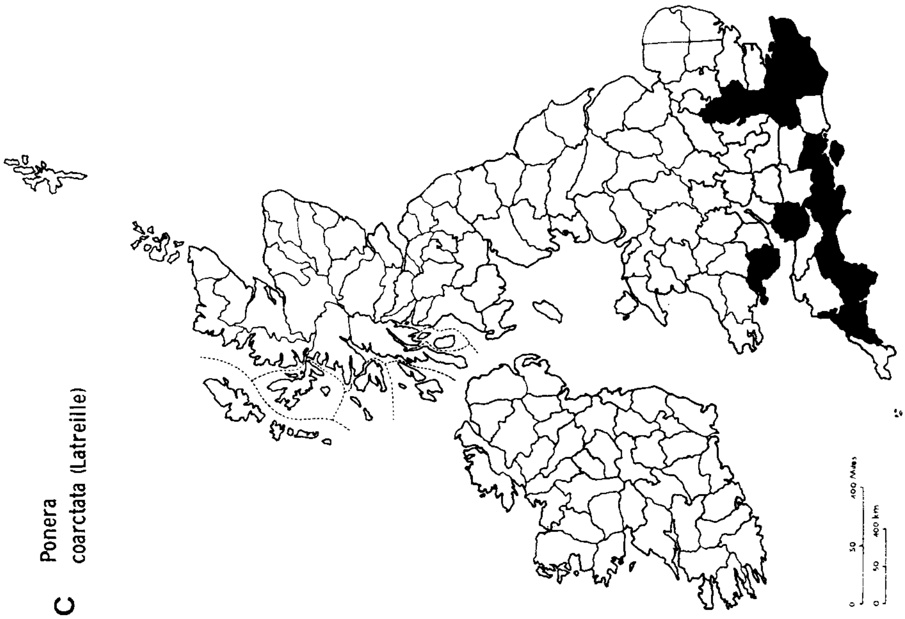


B Formicoxenus nitidulus (Nylander)

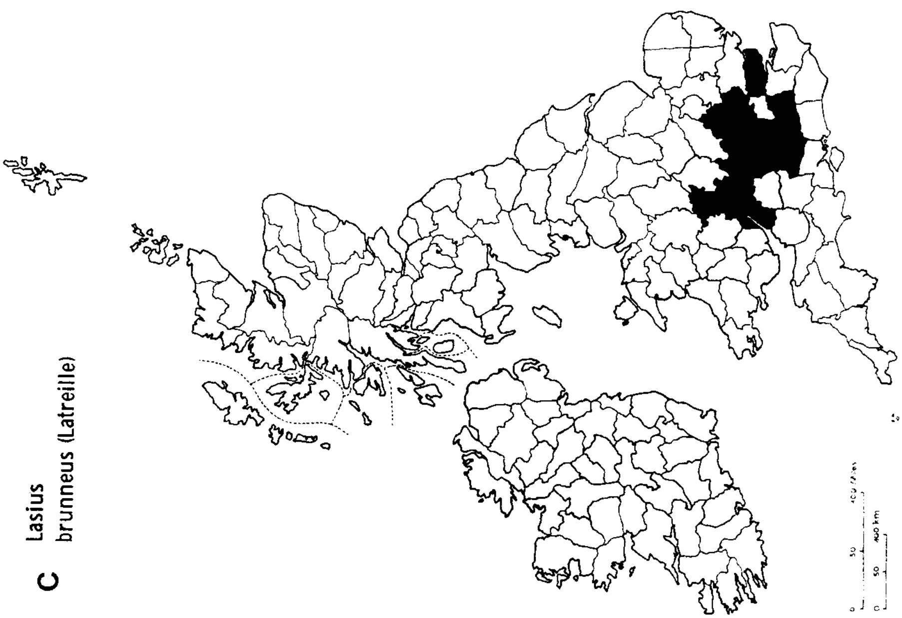
B Leptothorax acervorum (Fabricius)



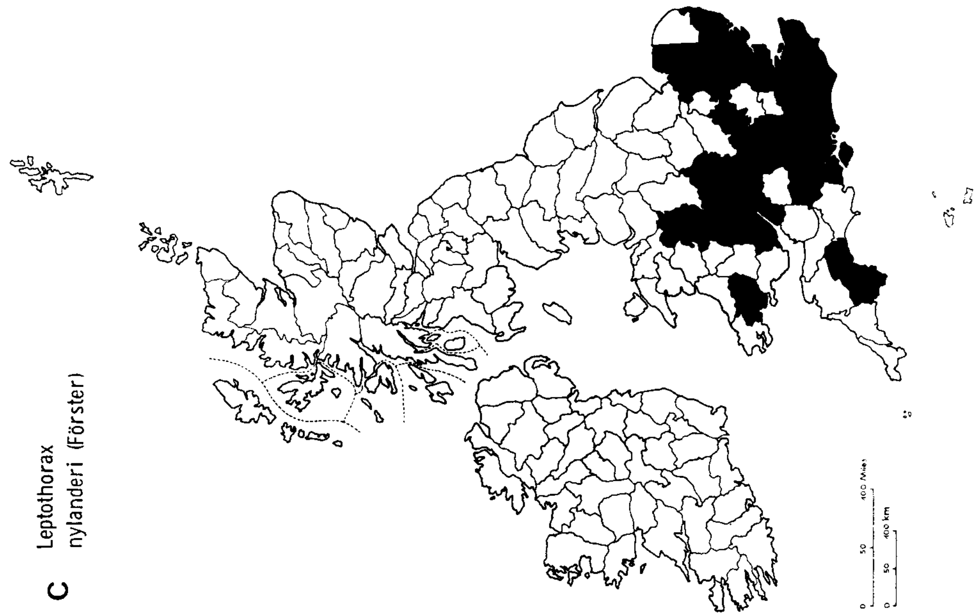
C Lasius rabaudi (Bondroit)



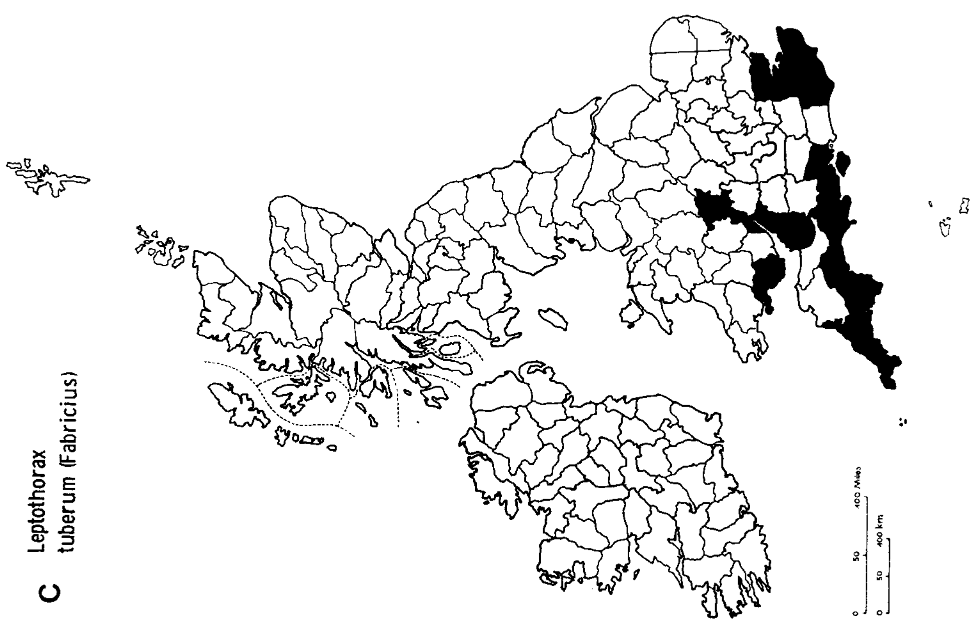
C Ponera coarctata (Latreille)



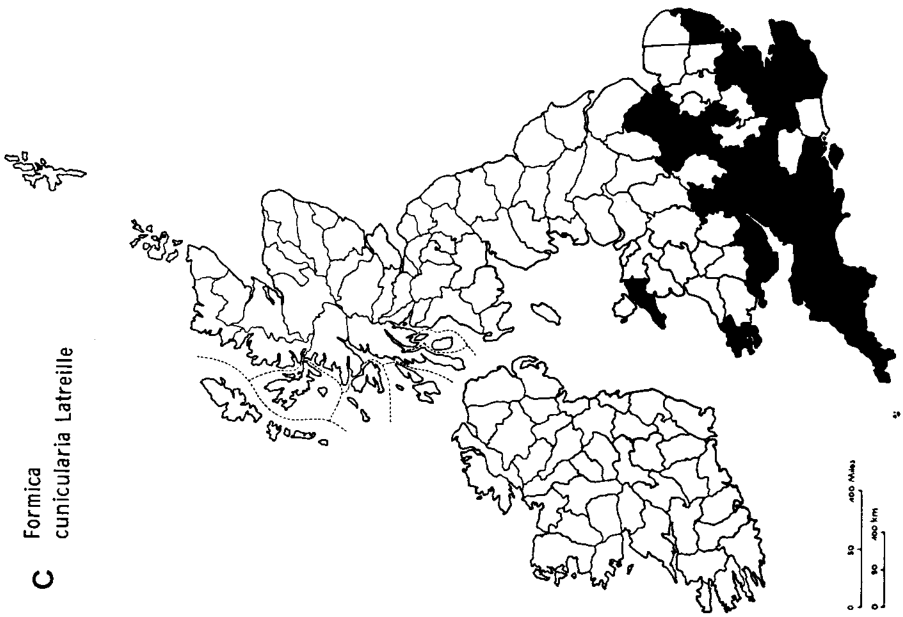
C Lasius brunneus (Latreille)



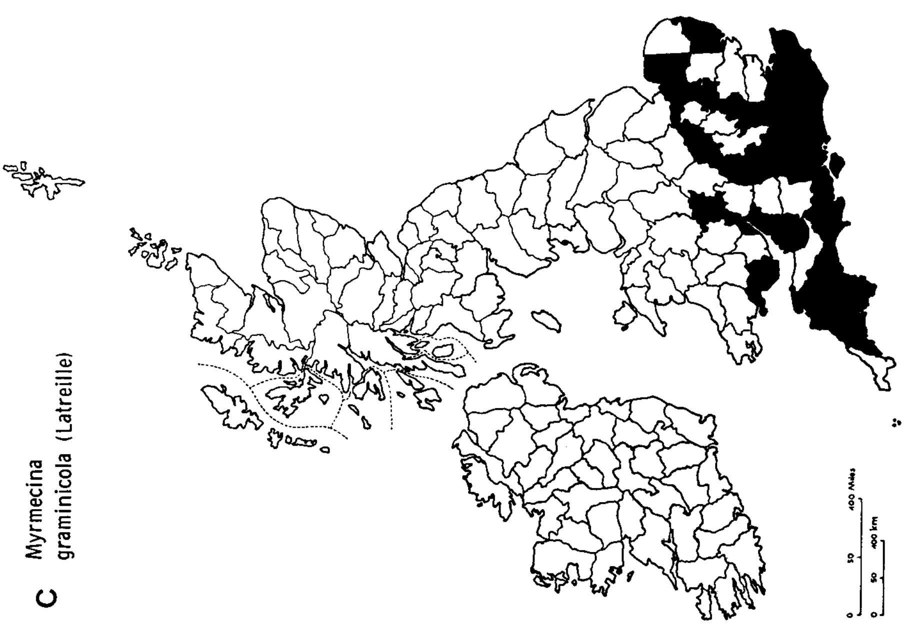
C Leptothorax nylanderi (Förster)



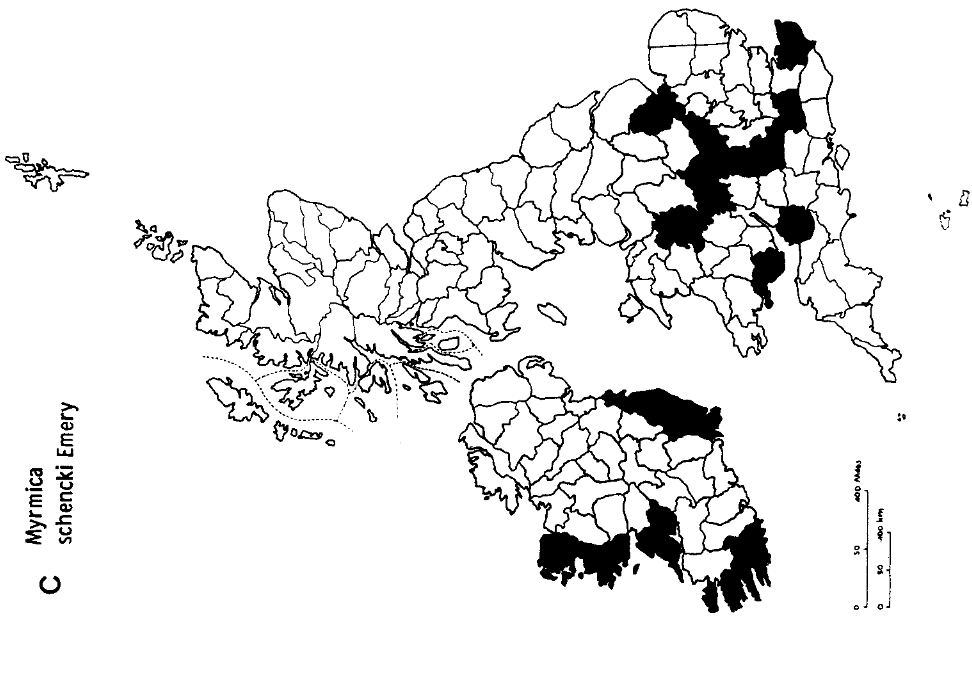
C Leptothorax tuberum (Fabricius)

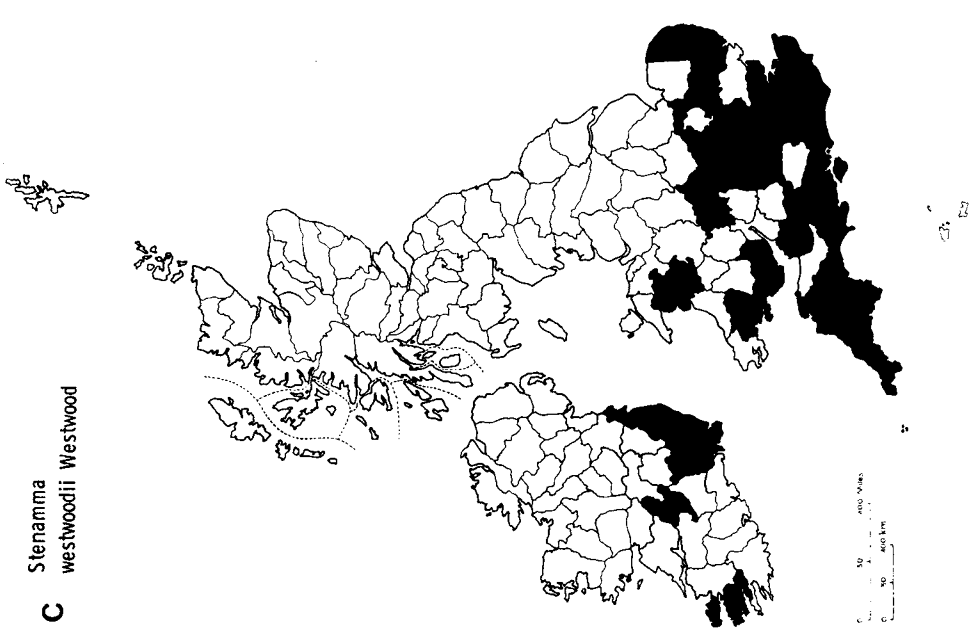


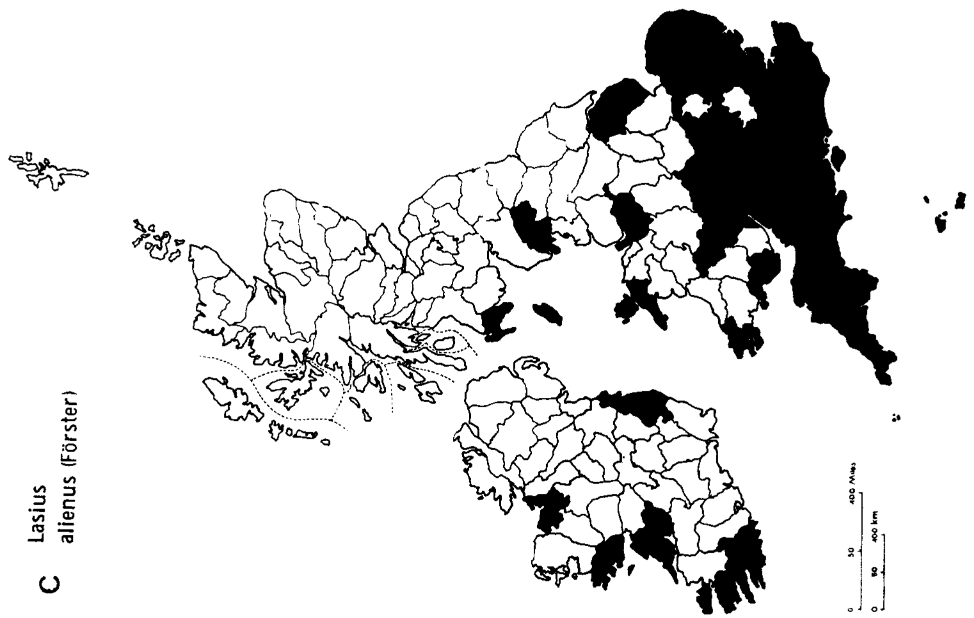
C Formica cunicularia Latreille

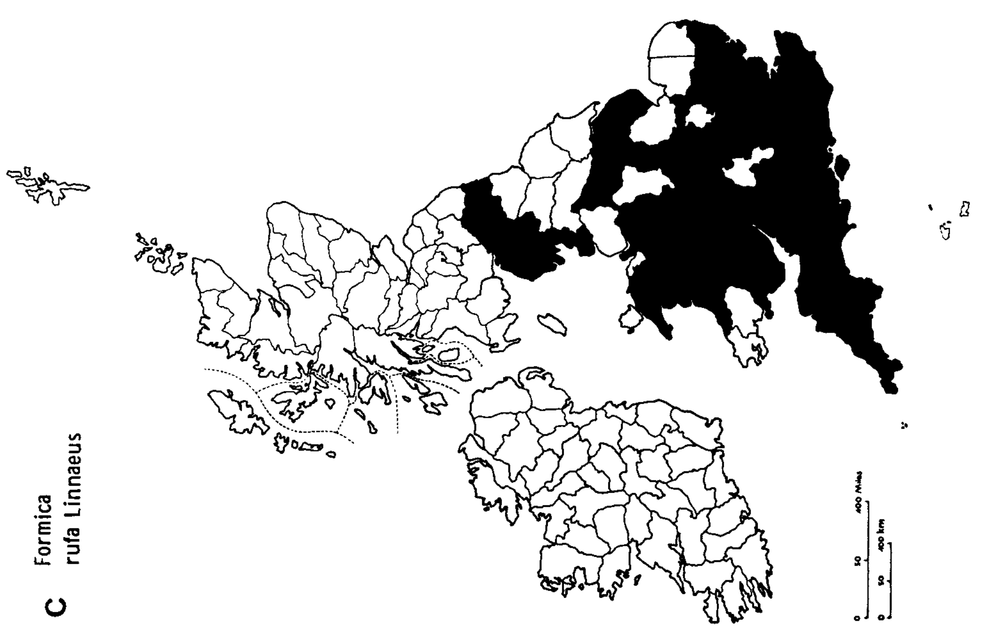


C Myrmecina graminicola (Latreille)

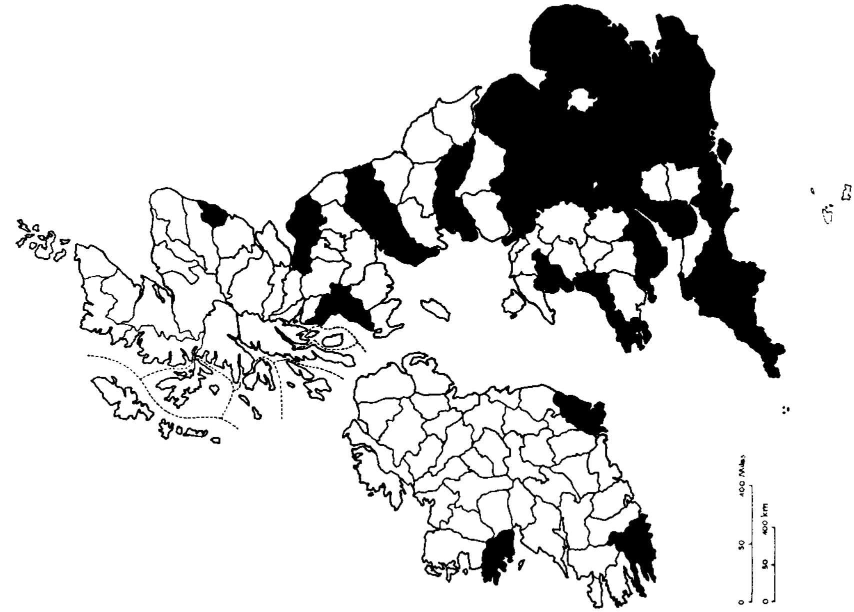

C Myrmica
schencki Emery
0 50 400 Miles
0 50 400 km


C Stenamma
westwoodii Westwood

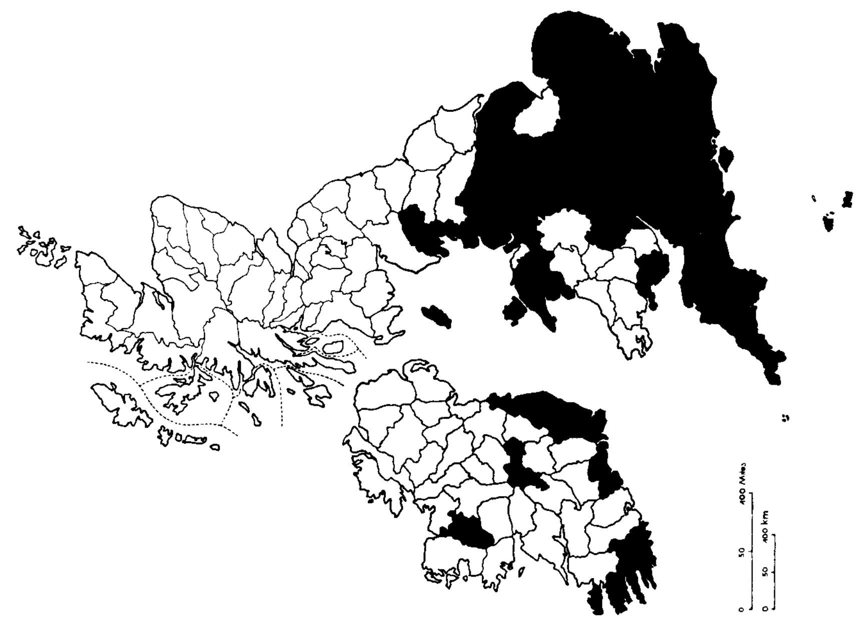

C
Lasius
alienus (Förster)

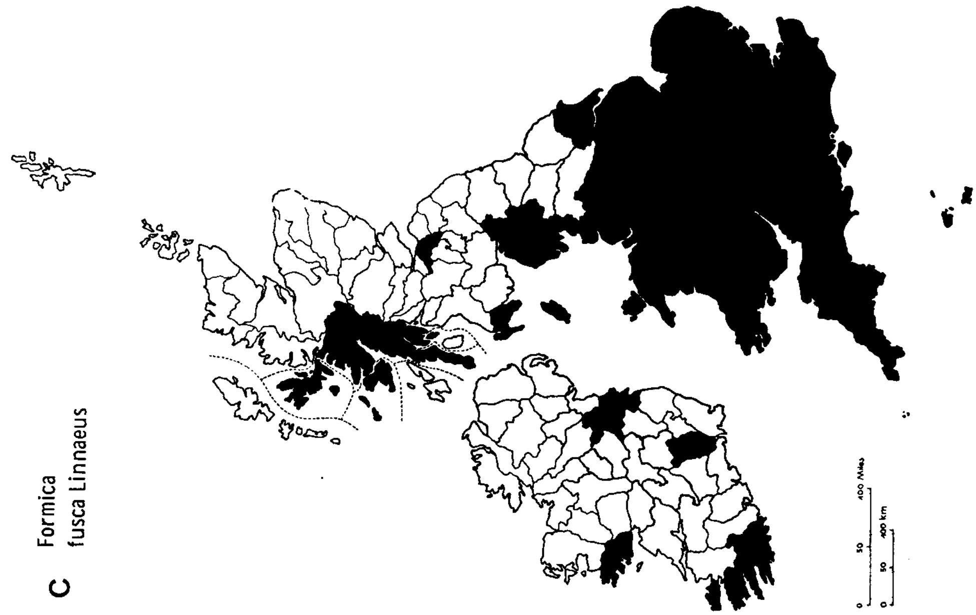

C
Formica
rufa Linnaeus

C Lasius umbratus (Nylander)

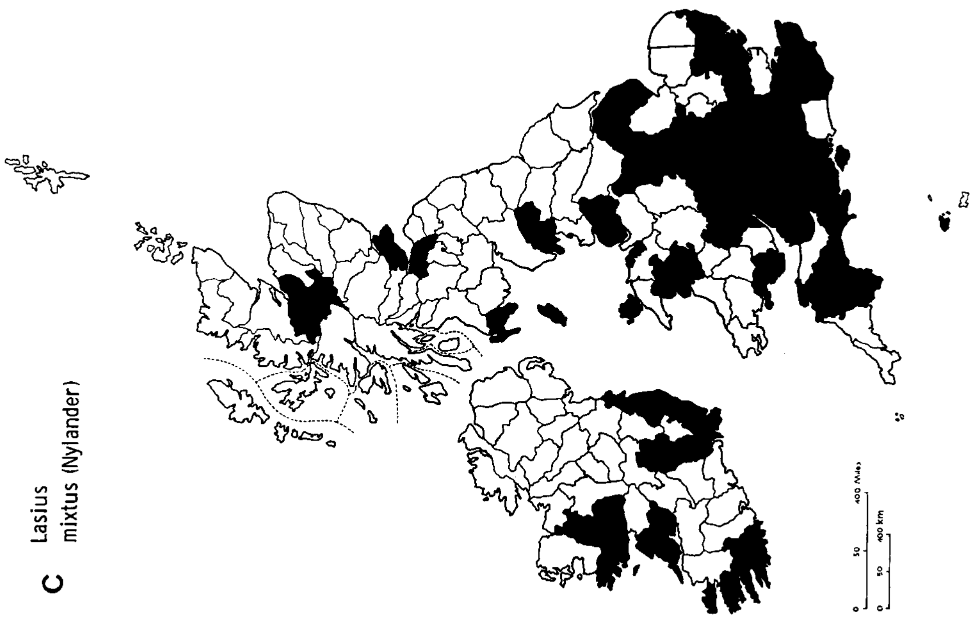


C Lasius fuliginosus (Latreille)





C Formica fusca Linnaeus



C Lasius mixtus (Nylander)


C
Lasius
flavus (Fabricius)
0 50 400 Miles
0 50 400 km

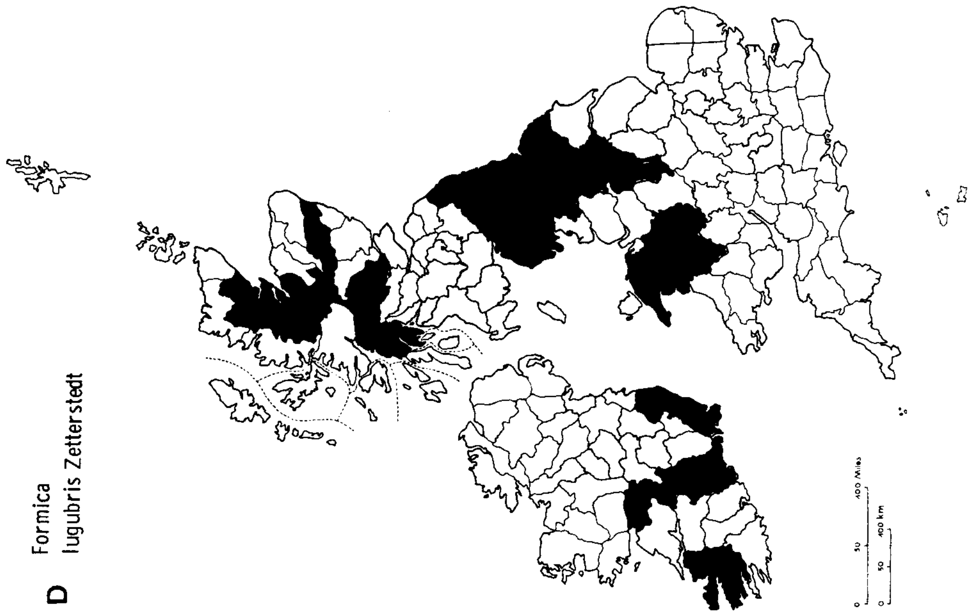

C
Myrmica
sabuleti Meinert
0 50 400 Miles
0 50 400 km


C
Lasius
niger (Linnaeus)


C
Myrmica
rubra (Linnaeus)


C
Myrmica
ruginodis Nylander


C
Myrmica
scabrinodis Nylander


D Formica
lugubris Zetterstedt
0 50 100 Miles
0 50 100 km


D Formica
aquilonia Yarrow
0 50 100 Miles
0 50 100 km

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