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THE DISTRIBUTION AND DECLINE OF BRITISH BUMBLE BEES (*BOMBUS* LATR.)

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Summary

The suggested recent decrease in the distributional ranges of certain species of bumble bees was investigated in the data collected by the Bumblebee Distribution Maps Scheme, using a numerical classificatory approach. Three major biogeographic elements and four biogeographic regions are defined, and changes in their composition and distribution described. Large reductions in the distributional ranges recorded after 1960 were found for two of the biogeographic elements (especially for the Southern Local Species: *Bombus subterraneus* (L.), *B. sylvarum* (L.), *B. ruderatus* (F.) and *B. humilis* Ill.), which have resulted in the emergence of a new Central Impoverished Region covering 23 vice-counties in Central England.

Introduction

It has been 'commonly supposed that the bumblebee population has declined in recent years' in Britain (Free & Butler, 1959; see also Manning, 1974), as was previously suggested for Manitoba in Canada (Stephen, 1955). The British authors did not specify whether the change was primarily in abundance, distribution (range or continuity), or which species were involved. However Alford (1975) believed that although *Bombus ruderatus* (Fabricius) in particular was 'formerly considered to be a very common species in England [presumably after Sladen, 1912], at least in the southern counties, this certainly does not apply at the present time, and [*B.*] *ruderatus*, although not necessarily rare, must be regarded as one of our less common species'. The object of the present investigation is to determine whether only certain species have suffered reduced distributional ranges in recent years and, if so, to identify such species and the particular geographical areas where there has been the greatest change.

Method

Rationale

The Bumblebee Distribution Maps Scheme results were published as a final 'Atlas of the bumblebees of the British Isles' in 1980, which incorporated records for Ireland and 2317 of the British National Grid 10-km grid squares in England, Wales and Scotland, received from collectors and museums between 1970 and 1976. The bumble bees of Ireland are not dealt with here, because it is considered that there are not enough records to allow valid comparisons. In this investigation the BDMS 10-km grid square records are blocked into 113 Watsonian vice-country species' lists. These are still sufficiently numerous to enable major biogeographical regions to be identified, and this procedure reduces the problems arising from uneven recorder coverage between the many 10-km grid squares.

The BDMS records had been mapped under two date-classes: 'pre 1960' and '1960 onwards'. 'Pre 1960' records are indicated for 10-km grid squares only where no records were received for that species post-1960; i.e., where a '1960 onwards' record is shown there is no information on the maps—or on most 10-km grid square record cards—as to whether or not that species was present before 1960. But if it were to be assumed that a '1960 onwards' record suggests the probable existence of a species at that locality before 1960, then that species' pre-1960 distributional status could be approximated by combining the 'pre 1960' and '1960 onwards' data, although these data cannot show any expansions in distributional ranges between pre- and post-1960. However, it is believed that distributional expansions by *Bombus* species to new areas within England, Wales and Scotland were relatively few compared with the range contractions hypothesized for certain species (Professor O. W. Richards, pers. comm.), and the blocking procedure renders irrevelant any small extensions or contractions in species' distributions within each vice-county. The post-1960 BDMS data are based upon only

16 years of recording, whereas there has been approximately a century of discontinuous recording pre-1960. This discrepancy in recording periods is likely to have been compensated for, in terms of sample size, by the extra collecting activity stimulated by the BDMS between 1970 and 1976.

The null hypothesis, that the distributions of all the species of *Bombus* had decreased by the same proportion between the pre-1960 and post-1960 BDMS vice-county data, was rejected ($\chi^2 = 61{\cdot}96$, df = 16, $P<<0{\cdot}001$): more species' distributions were found to have decreased by a large proportion and more by a small proportion than might be expected at random. It might have been possible to classify the species by the post-1960 reductions in their distributions after subtracting the numbers of post-1960 vice-county records from those of pre-1960), but this eliminates information on species' current distributions. However such information can be retained for the study of their habitat requirements and is likely to be useful in elucidating the mechanisms of change. Therefore it was decided to compare separate biogeographic analyses of the pre-1960 and post-1960 BDMS data for the assessment of any changes.

Data analysis

The method employed follows the procedures of continental phytosociology (see Shimwell, 1971). This is a widely used technique developed for describing vegetation from different areas by simplifying the complex patterns of plant species' distributions. It seeks to define both (*a*) groups of species with similar distributions amongst the samples collected, and (*b*) groups of samples with similar assemblages of species. Two-way tabular re-arrangement is then used to display this data structure. Such a two-way classificatory approach can be applied to biogeographical data (Birks, 1976) : only the scale of such data distinguishes them from phytosociological data. The groups of species so defined are now biogeographic elements, and the groups of samples become biogeographic regions.

Two separate analyses were conducted, on (1) the pre-1960 (from the combine 'pre 1960' and '1960 onwards') and (2) the post-1960 ('1960 onwards') BDMS records, as proposed in the Rationale. The samples used in these analyses are the 113 Watsonian vice-counties in England, Wales and Scotland (see Alford, 1975). The nomenclature for the 17 species of *Bombus* included follows Fitton et al. (1978). *B. pomorum* (Panzer) was excluded because it was considered to be 'very doubtfully British' (Yarrow, in Free & Butler, 1959).

The FORTRAN IV program CLUSTER (see Birks, 1976), written by H. J. B. Birks and B. Huntley, was employed to implement the classifications. In the first stage it calculates a matrix of dissimilarity coefficients between all pairs of data individuals based on their variables (e.g. species by distribution between vice-counties), using the Jaccard index of similarity converted to a dissimilarity by subtraction from 1. This index ignores negative matches between individuals, a desirable characteristic when there are only a few records for many of the species, as in the post-1960 BDMS data. The second stage of CLUSTER is a polythetic agglomerative algorithm for minimum variance clustering, which seeks to group the individuals by the coefficients in the dissimilarity matrix so as to minimize the total within-group error sum-of-squares. The results are represented as dendrograms, showing the level and order of fusion of individuals into groups. To classify species and vice-counties for both pre- and post-1960 analyses required four separate runs, which were executed on the University of Cambridge IBM 370/165 computer.

A GENSTAT program, written by N. W. Galwey, was used to sort the pre-1960 and post-1960 BDMS data matrices into their respective differentiated tables by the species' and vice-county sequences given in the CLUSTER dendrograms. Major divisions within these dendrograms were then used to delimit biogeographic elements and regions on the differentiated tables. The information in these tables can be summarized by mapping the biogeographic regions.

Results

The dendrograms produced using CLUSTER are available for consultation in the Library of the International Bee Research Association. The differentiated tables resulting from the pre-1960 and post-1960 BDMS data analyses are presented in Fig. 1 and Fig. 2. The biogeographic elements, and their corporate regional ranges as biogeographic regions, are

indicated by boxes delimiting areas within Fig. 1 and Fig. 2. The biogeographic regions are also mapped in Fig. 3 and Fig. 4, respectively. The general similarity between Fig. 1 and Fig. 2 suggests the non-random, broad-scale biogeographic patterns in the data. The major differences are believed to reflect real changes that have occurred in species' distributions at the regional level.

I. Biogeographical elements

The dendrogram from the clustering of species in the post-1960 BDMS data analysis distinguishes 3 groups of species, and *B. distinguendus* Morawitz at the 38% level of average within-group sum-of-squares. These 3 major biogeographic elements are labelled (from their distributions in Fig. 2) as the Southern Local Species, the Mainland Ubiquitous Species, and the Widespread Local Species. At the same level in the clustering of the pre-1960 BDMS data analysis, only 2 groups of species and *B. cullumanus* (Kirby) are distinguished : the smaller group is closely similar to the Southern Local Species of the post-1960 analysis, and the larger group can be split at the 9·5% level into 2 species' groups similar to the Mainland Ubiquitous Species and the Widespread Local Species of the post-1960 analysis (*B. distinguendus* and *B. monticola* Smith are also separated individually at this level). Therefore 3 recurring patterns of regional distribution are described below.

I(A) *The Southern Local Species*

This category includes 5 species before 1960 : *B. subterraneus* (Linnaeus), *B. ruderatus*, *B. sylvarum* (Linnaeus), *B. humilis* Illiger, *B. ruderarius* (Muller). All have patchy southern distributions with few records in Scotland and Central Wales. Post-1960 sees a reduction in the range of the 4 former species by almost one half, from a mean of 51·8 (standard deviation 5·6) to 26·3 (sd 8·9) vice-counties per species; this results in the relatively constant *B. ruderarius* being classified under the Mainland Ubiquitous Species.

B. cullumanus had a distribution similar to the Southern Local Species pre-1960, in that it was recorded from chalkland localities in 9 vice-counties of south-eastern England, but it has not been recorded in Britain post-1960. *B. distinguendus* more closely resembled the Widespread Local Species with its scattered distribution throughout Britain and the Outer Scottish isles before 1960, but it suffered a large reduction, from 66 vice-county records to 19 post-1960, causing it to be clustered next to the Southern Local Species, because of this small number.

I(B) *The Mainland Ubiquitous Species*

This group consists of 6 species before 1960 : *B. pascuorum* (Scopoli), *B. lucorum* (Linnaeus), *B. hortorum* (Linnaeus), *B. pratorum* (Linnaeus), *B. terrestris* (Linnaeus), *B. lapidarius* (Linnaeus). The group forms a broad central column in both Fig. 1 and Fig. 2. Only *B. hortorum* is recorded from every vice-county, and the remaining species are recorded in most vice-counties except the Outer Scottish Isles, although there are few records for *B. lapidarius* and *B. terrestris* in Northern Scotland and for *B. pratorum* on islands. The Mainland Ubiquitous Species are also usually recorded in a larger proportion of the 10-km grid squares within each vice-county than are the species of the other elements. For this group there is only a relatively small decrease in the mean number of vice-county records per species after 1960, from 105·2 (sd 7·0) to 97·4 (sd 16·0).

I(C) *The Widespread Local Species*

This category contains 4 species according to the results of the post-1960 analysis : *B. muscorum* (Linnaeus), *B. jonellus* (Kirby), *B. soroeensis* (Fabricius), *B. monticola*. Before 1960 *B. monticola* is separated in the dendrogram because of its unique upland distribution. These species were widespread between regions within Britain before 1960, but their distributions were less continuous (i.e., more local) than those of the Mainland Ubiquitous Species. After 1960 there is a 26% reduction in the mean number of vice-county records per species, from 85·7 (sd 4·0) to 63·8 (sd 13·4).

II. Biogeographic Regions

Four major regions are distinguished in the vice-county clustering of the post-1960 BDMS data analysis by their different combinations of the above biogeographic elements. Only 3 of

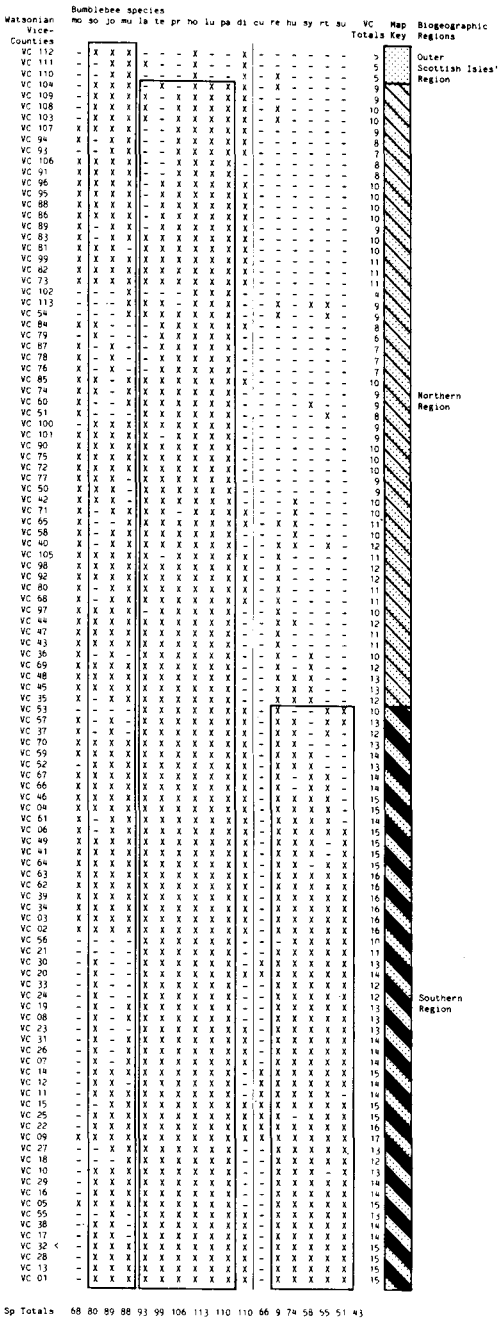

FIG. 1. Differentiated table of the pre-1960 (combined 'pre-1960' and '1960 onwards') BDMS data classified by CLUSTER.

Vice-county numbers follow Alford (1975); bumble bee species name abbreviations are: mo *Bombus monticola*; so *B. soröeensis*; jo *B. jonellus*; mu *B. muscorum*; la *B. lapidarius*; te *B. terrestris*; pr *pratorum*; ho *B. hortorum*; lu *B. lucorum*; pa *B. pascuorum*; di *B. distinguendus*; cu *B. cullumanus*; re *B. ruderarius*; hu *B. humilis*; sy *B. sylvarum*; rt *B. ruderatus*; su *B. subterraneus*. The boxes enclose (from left to right) records of: Widespread Local Species; Mainland Ubiquitous Species; Southern Local Species.

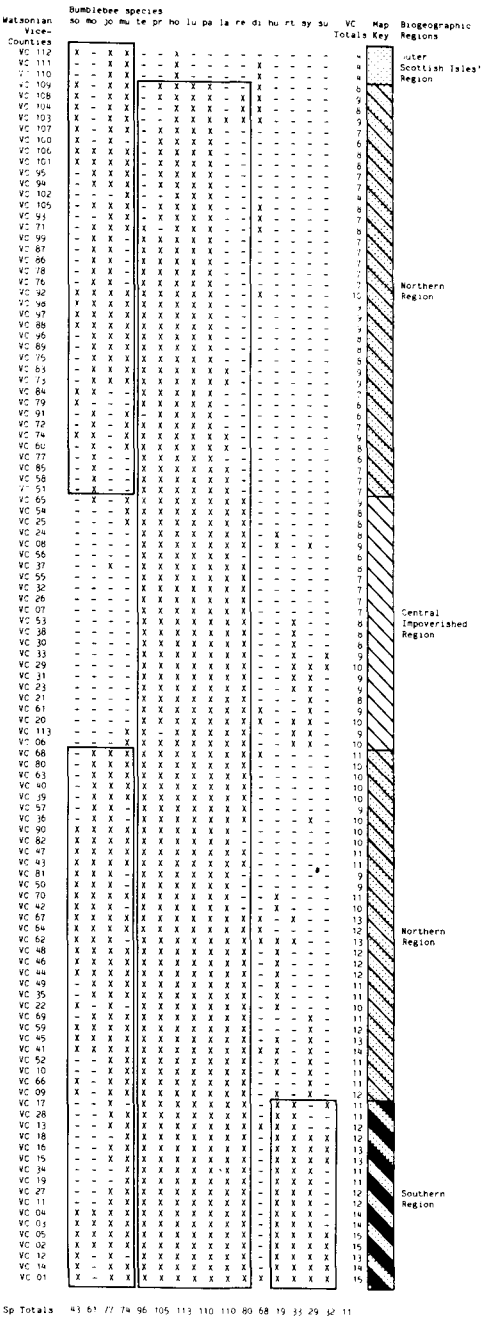

FIG. 2. Differentiated table of the post-1960 ('1960 onwards') BDMS data classified by CLUSTER.

Vice-county numbers follow Alford (1975); see Fig. 1 for bumble bee species name abbreviations. The boxes enclose (from left to right) records of: Widespread Local Species (split to the north and south by the Central Impoverished Region); Mainland Ubiquitous Species; Southern Local Species.

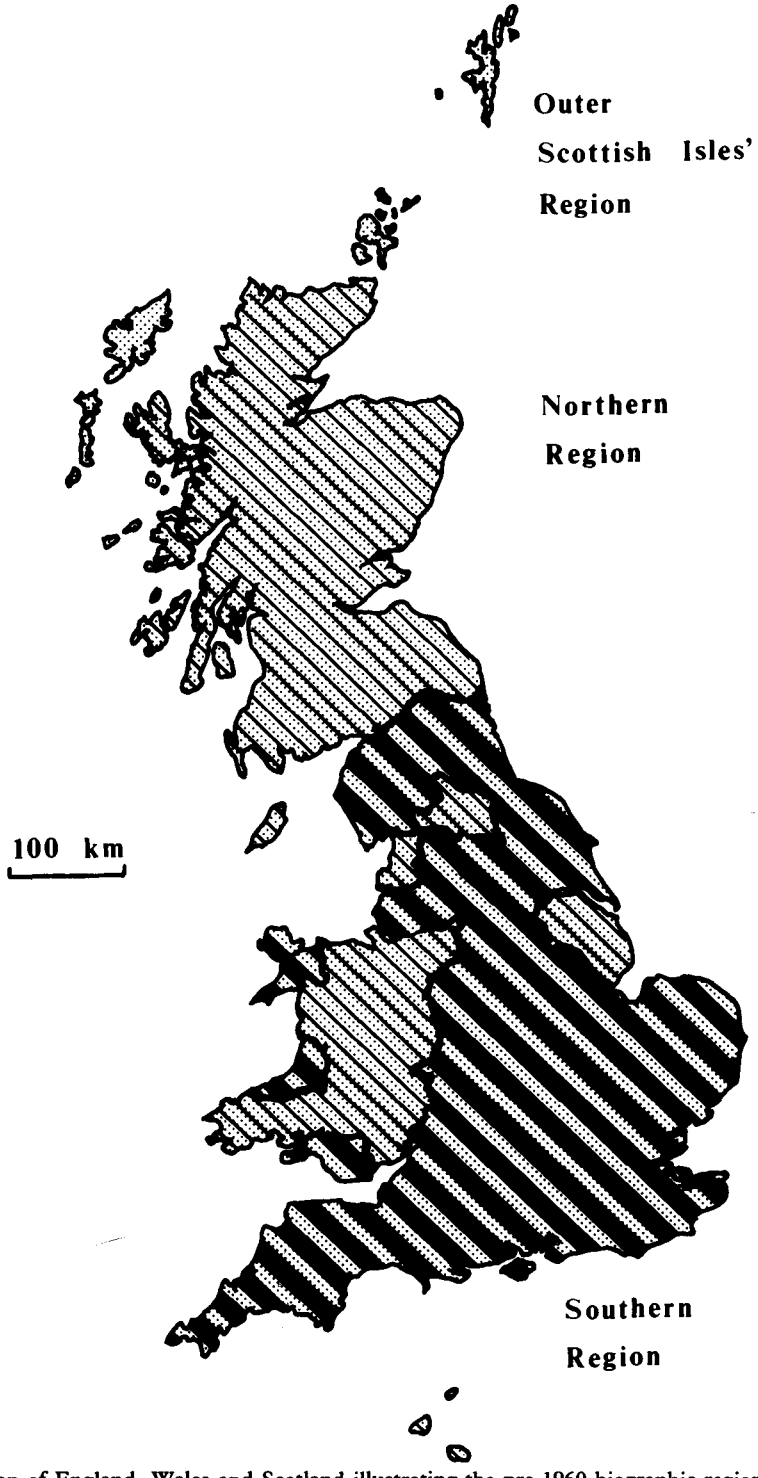

FIG. 3. Map of England, Wales and Scotland illustrating the pre-1960 biographic regions defined in Fig. 1. Dots represent Widespread Local Species; narrow lines Mainland Ubiqutous Species; broad stripes Southern Local Species.

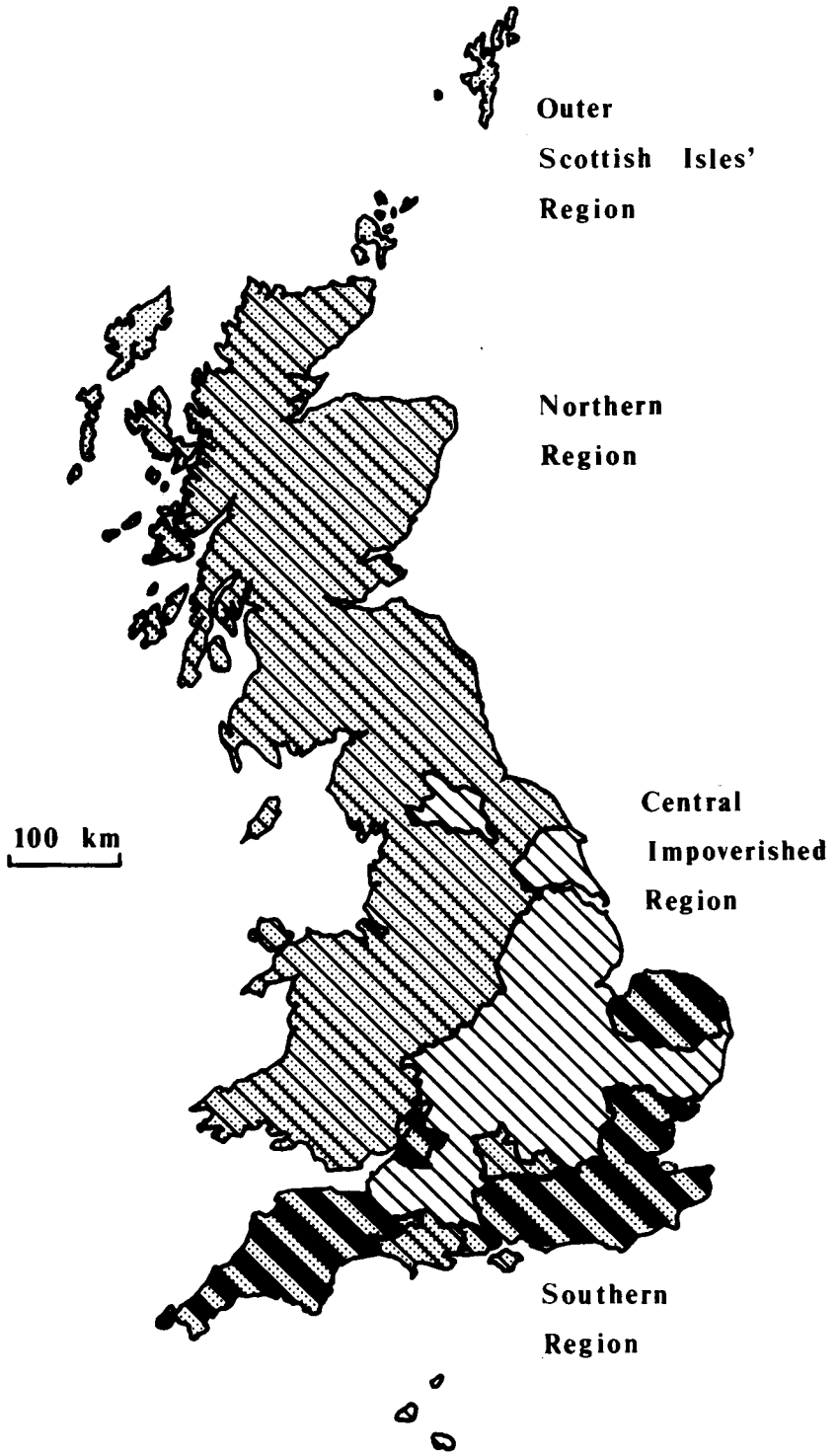

FIG. 4. Map of England, Wales and Scotland illustrating the post-1960 biographic regions defined in Fig. 2. Dots represent Widespread Local Species; narrow lines Mainland Ubiquitous Species; broad stripes Southern Local Species.

these regional combinations of elements are represented in the results of the pre-1960 BDMS analysis.

II(A) *The Outer Scottish Isles Region*

This area includes the Shetland, Orkney and Outer Hebrides Islands, where only the Widespread Local Species are well represented by 3 of the 4 species (*B. monticola* is not recorded from this region). The number of species in each vice-county was 5 in the pre-1960 and 4 in the post-1960 BDMS records.

II(B) *The Northern Region*

This heterogeneous region is defined by the frequent occurrence of the Widespread Local Species and the Mainland Ubiquitous Species in an area with few records for any representatives of the Southern Local Species. Before 1960, 57 vice-counties of both Highland and Lowland Scotland with Central Wales fell within the region, but the post-1960 retreat of the Southern Local Species expanded this area to encompass 70 vice-counties. This was accompanied by only a slight change from a mean of 9·7 (sd 1·7) to 9·1 (sd 2·1) species per vice-county. The anomalous but borderline status of North-West Yorkshire (vice-county 65) may be due to under-recording.

II(C) *The Southern Region*

This area is characterized by many records for the Widespread Local Species, the Mainland Ubiquitous Species and the Southern Local Species. However, the only vice-county in which all 17 species of *Bombus* were ever recorded was Dorset (vice-county 9) before 1960. The region underwent a 68% reduction in area, from 53 to 17 vice-counties, with the retreat of the Southern Local Species in the post-1960 BDMS data, while the mean number of species per vice-county remained relatively constant, 14·0 (sd 1·5) pre-1960 and 12·8 (sd 1·4) post-1960.

II(D) *The Central Impoverished Region*

This is a region in Central and Eastern England where only the Mainland Ubiquitous Species are well represented. It appears only in the results of the post-1960 BDMS analysis as a subset of the pre-1960 Southern Region from which the Widespread Local Species and Southern Local Species have become largely absent. Within the 23 vice-counties it now encompasses, the mean number of species per vice-county has fallen from 12·7 (sd 1·8) to 8·3 (sd 1·0). The largest change recorded by the BDMS for Britain in one vice-county list is the loss of 8 species post-1960 from Northamptonshire (vice-county 32, arrowed in Fig. 1 and Fig. 2). The inclusion of the Channel Islands (vice-county 113) is somewhat misleading, in that the number of species recorded, although small, is unchanged.

Discussion and Conclusions

It can be seen from Fig. 1 and Fig. 2 that the vice-county sequences chosen by CLUSTER correspond approximately to north-south gradients: the numbers of species recorded per vice-county decrease northwards through England, Wales and Scotland (although this is partially confounded post-1960 by the decline in the number of species recorded from the Central Impoverished Region). A decreased number of species towards the north has also been described for Scandinavia by Løken (1973). However, whereas only 7 species of *Bombus* have ever been recorded from the relatively isolated Outer Scottish Isles Region, 14 were recorded from Troms and Finnmark 10° farther north in Norway. This suggests the additional involvement of a species/area effect. Similar effects may also be responsible for the depauperate bumble bee fauna of the British Isles, as a whole, when compared to Continental Europe.

Løken (1973) described 6 biogeographic elements in her synopsis of the 29 Scandinavian *Bombus*. These include all the British species, and thereby invite comparison with the results of the present analyses. Of her biogeographic elements, there were 6 'Species Widely Distributed throughout Scandinavia', including *B. lucorum*, *B. pascuorum*, *B. hortorum* and *B. pratorum* of the Mainland Ubiquitous Species as defined for Britain, while *B. jonellus* belongs to the Widespread Local Species. Presumably none of these is near the limits of its potential distribution : collections in the British Museum (Natural History), London, indicate that *B. lucorum* probably has the most extensive holarctic distribution of any species of bumble bee.

The sixth species, *B. hypnorum* (Linnaeus), was believed to be a representative of a North Eurosiberian taiga fauna, and has not been recorded in Britain. The 3 'Eastern Species' were also considered to be part of this taiga fauna, and are similarly absent from Britain. The 'Western Species', *B. wurfleini* Radoszkowski, exhibits a wide distribution in the coniferous forest and the subalpine zones of Scandinavia, as well as disjunct occurrences confined to mountain ranges and adjacent forests in Central and Southern Europe, but not in Britain. Of the 'Arctic and Subarctic Species' only *B. monticola* is found in Britain at present, although *B. alpinus* (Linnaeus) occurs further south in the Alps. Løken confused *B. monticola* with *B. lapponicus* (Fabricius) (Svensson, 1979), but its description as a subarctic/subalpine species is nevertheless valid, and supports its separation from the Widespread Local Species in the pre-1960 BDMS data analysis above. Only *B. ruderatus* out of the 4 'Species with Restricted Southern Distribution' is included in the Southern Local Species defined here, because *B. cullumanus* is differentiated by its rarity in the pre-1960 BDMS data, and *B. pomorum* had been excluded from the British analysis. The largest of the groups described from Scandinavia was the 'Northerly Advanced Southern Species', which contains representatives of all 3 major biogeographical elements defined by the British analyses, i.e.: *B. muscorum* and *B. soröeensis* of the Widespread Local Species; *B. terrestris, B. lapidarius* and *B. ruderarius* of the Mainland Ubiquitous Species; *B. subterraneus, B. sylvarum* and *B. humilis* of the Southern Local Species. Examination of the distribution maps for these species within Scandinavia suggests that this discrepancy, rather than being caused by different factors limiting such species' distributional ranges to differing extents in more distant parts of Europe (as might have to be postulated for *B. terrestris*), may owe more to the different classification methods employed.

Bumble bee distributions may never have been static, but probably changed slowly with variable factors such as climate. However, certain of these distributions, recorded over the last century, assembled by the BDMS and summarized here in comparison with the post-1960 BDMS distributions (Fig. 3 and Fig. 4), have undergone dramatic contractions in range, which have resulted in the creation after 1960 of the Central Impoverished Region of 23 vice-counties in Central England. This suggests profound deleterious changes in habitat 'quality', possibly resulting from changes in land use, throughout this region, which have selectively reduced the Widespread Local Species, and more especially the Southern Local Species. The last record traced for the southern *B. cullumanus* is 'c. 1941' (BMNH collection), and this species could now be extinct in Britain (IBRA & ITE, 1980).

No two species exhibit precisely the same distributional pattern, so a classificatory approach must inevitably result in some distortion of the data. The closeness of the fit for the elements and regions defined here can be assessed by inspection of Fig. 1 and Fig. 2. The analytical method used provides a useful summary of the data from which an overall picture can be mapped, at the same time avoiding the dangers of undue emphasis on subjectively chosen 'typical' distribution patterns. Employed here in the analysis of the BDMS records, it has indicated patterns of change as species and areas of decline, while retaining the information on species' present distributions. These results serve to highlight the value of mapping schemes such as the BDMS and suggest avenues for further study towards conserving these important pollinating insects.

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