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Habitat use by bumble bees (*Bombus* spp.)

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ABSTRACT. 1. Analysis of surveys of bumble bee distribution among 2 km grid-squares in Kent revealed that some species are nearly ubiquitous among localities and abundant within each. For these ubiquitous species, Kent is near the middle of their latitudinal ranges.

2. The other species have very restricted distributions among localities and are less abundant where they occur. For each of these local species, Kent is near the margin of its latitudinal range.

3. The areas to which the local species are restricted are characterized by only a few of the many kinds of vegetation represented in Kent (shingle, sand dune, saltmarsh or old meadow). The ubiquitous species are also more abundant in areas with these kinds of vegetation.

4. A random model (Gause, 1936) and the core/satellite hypothesis (Hanski, 1982a) were proposed to explain similar patterns of distribution. I conclude that their assumptions are not well supported by the results of the present analysis.

5. A marginal mosaic model (after Andrewartha & Birch, 1954; Hengeveld & Haeck, 1981; Brown, 1984) is used to account for these patterns. This model depends on environmental factors (including resource levels and climate) affecting the economics of energy and, consequently, local persistence.

6. It follows from the marginal mosaic model that if the level of limiting resources in a habitat declines, then it is the species closest to their distribution limits that are most likely to face local extinction. These selective extinctions would result in a form of 'community structure'.

Key words. Distribution, habitat mosaic, suitability, climate, energy economics, community structure, *Bombus*.

Introduction

Some species are considerably more widespread than others. Regional differences in the distributions of British bumble bees were summarized in an earlier analysis (Williams, 1982) of records from a national survey (Alford, 1980). This analysis revealed three groups of species (Table 1) that differ in their representation among three regions of Britain. The first group, the Mainland Ubiquitous Species, remains well represented throughout mainland Britain, both before and after 1960. These species generally do not reach

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TABLE 1. Species composition of the three principal biogeographic elements in Britain (excluding the very rare *B.distinguendus* Morawitz, abbreviated to 'di' in Fig. 2, and *B.cullumanus* (Kirby) and *B.pomorum* (Panzer), which are apparently extinct in Britain), as defined by a classification of the Bumblebee Distribution Maps Scheme (B.D.M.S.) post-1960 vice-county records (Williams, 1982). Since 1960 most records for the 'Widespread' Local Species have been from the north and west of Britain. Nomenclatural changes arising from problems outlined by Løken (1973) and Day (1979) are incorporated. *B.magnus, B.monticola* and *B.ruderatus* are all names that have been applied to regional colour forms that occur in Britain, but it has not been established definitely that they do not interbreed with forms referable to the older names, *B.terrestris, B.lapponicus* and *B.argillaceus* respectively as parts of just three, more widespread, biological species.

Biogeographic element	Abbreviation	Species of *Bombus* Latreille included
Mainland Ubiquitous Species	te	*terrestris* (L.)=*lucorum* (L.)=? *magnus* Vogt
	pa	*pascuorum* (Scopoli)
	ho	*hortorum* (L.)
	pr	*pratorum* (L.)
	au	*audax* (Harris)=*terrestris* of earlier authors
	la	*lapidarius* (L.)
	re	*ruderarius* (Müller)
Widespread Local Species	mo	*monticola* Smith=? *lapponicus* (F.)
	so	*soroeensis* (F.)
	jo	*jonellus* (Kirby)
	le	*laevis* Vogt=*muscorum* of earlier authors
Southern Local Species	sy	*sylvarum* (L.)
	mu	*muscorum* (L.)=*humilis* (Illiger)
	rt	*ruderatus* (F.)=? *argillaceus* (Scopoli)
	su	*subterraneus* (L.)

the limits of their latitudinal distributions within Britain (Løken, 1973; Pekkarinen *et al.*, 1981; collection of the British Museum (Natural History)). In contrast, after 1960 the second group, the 'Widespread' Local Species, have become more restricted in their distributions. Most recent records have come from the north and west of Britain, although some of the species also occur near the southern coasts. This group of species is strongly represented in the north of Scandinavia (*op. cit.*). They do occur further south in Europe, but mainly at higher altitudes and especially in the Alps. The third group, the Southern Local Species, has also become more restricted in Britain after 1960, but has retreated in the opposite direction, to the far south. These species clearly reach their northern limits within Britain and southern Scandinavia (*op. cit.*). Thus the resulting pattern of faunal regions in mainland Britain after 1960 (Williams, 1982: Fig. 4) consists of (a) a Northern Region with the Widespread Local Species and Mainland Ubiquitous Species; (b) a Central Impoverished Region, where the Mainland Ubiquitous Species persist alone; and (c) a narrow Southern Region that is the only part of Britain to retain a strong representation of all three biogeographic elements.

Here I explore the distributions of bumble bees among many localities in Kent, which lies within the Southern Region. This provides a link between the regional patterns described above and the many previous studies that have dealt with foraging, interspecific competition and the composition of species' assemblages at just a very few localities (e.g. Inouye, 1977; Ranta *et al.*, 1981; Ranta & Tiainen, 1982; Prŷs-Jones, 1982; Barrow, 1983). In particular, I examine the relationships between local distribution, abundance, habitat vegetation and position within the world distribution of each species.

Possible explanations for the separation into ubiquitous and local species are described in a random model (Gause, 1936) and in the core/satellite hypothesis (Hanski, 1982a, c). Their assumptions of random distributions and of no differences between species in their habitat requirements are not supported by results from the present analyses. A third, marginal mosaic model is developed from existing ideas (Andrewartha & Birch, 1954; Hengeveld & Haeck, 1981; Brown, 1984) to account for these and other, similar patterns in the distributions of many species of organisms (e.g. Hengeveld & Haeck, 1981, 1982; Brown, 1984).

Material and Methods

A measure of distribution used here is the degree of 'occupancy' of an area by a species. This is defined as the proportion (p) of samples from different parts of the area in which a species is found to occur (from ubiquitous $p_i=1.0$, to locally restricted, e.g. $p_j=0.05$). For these analyses, I accept the pooled records of queens, workers and males as occupancy data.

An appropriate size of unit for analysis of patterns in species' distributions among regions is the vice-county (Williams, 1982). The Bumblebee Distribution Maps Scheme (B.D.M.S.) provides suitable records from throughout Britain, collected between 1960 and 1976 (Alford, 1980).

Survey of local occupancy in Kent

Distributions of bumble bees within a region are represented by occupancy of contiguous 2 km squares of the National Grid, because these units are of a similar size to the maximum foraging areas of colonies (Teräs, 1979). Dr G. H. L. Dicker and E. G. Philp surveyed the bumble bees of Kent by 2 km grid-squares between 1960 and 1983 (unpublished). The sampling regime was not standardized and the sample sizes were not recorded. Most of the survey effort was concentrated in the period 1972–78, during which 450 of the 1044 2 km grid-squares were sampled (Fig. 1). I accept records from this 1972–78 subset as data (listed in Williams, 1985) for analysis, because they are less likely to have been affected by the pronounced changes in distributions through time (Williams, 1986).

The habitat in each grid-square is described here by the representation (i.e. quality) of the vegetation formations present. Representation,

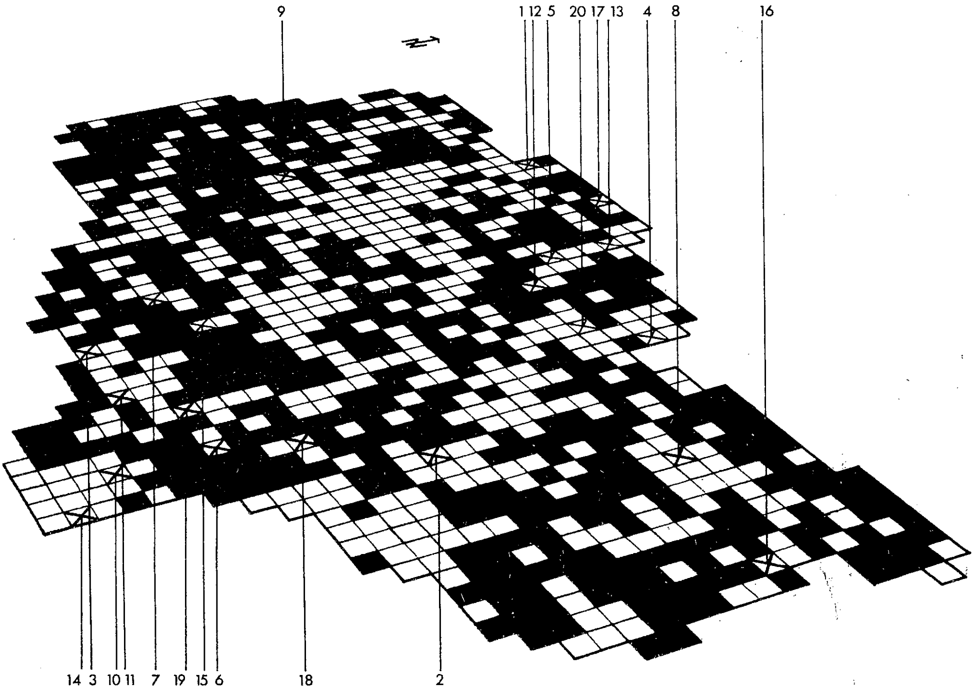

FIG. 1. Kent 2 km National Grid viewed across Folkestone towards London, which lies beneath the north pointer. The light areas show the positions of the 450 grid-squares sampled between 1972 and 1978 during the Kent survey and the crosses indicate the twenty grid-squares that were also sampled during the 1983 Kent census. Details of these numbered sites are given in Table 4.

independent of cover, is calculated for each vegetation formation in turn as the proportion of formation-constant species (from lists in Tansley, 1939) present in the grid-squares under study (distribution records in Philp, 1982).

Census of local density in Kent

The different bumble bee species exhibit different phenological profiles of abundance (Prŷs-Jones, 1982), so that the relative densities of different species change through the season. This limits the period during which reasonably comparable estimates of density can be made in any census. Sampling was therefore restricted and I chose the period between 25 June and 25 July in order to maximize the chance of recording all species present (from phenological data in Williams, 1985). I also divided Kent into quadrants and sites were sampled in each quadrant in turn, with the order of sampling randomized within each quadrant.

In order to select sites for sampling, I ranked the 2 km grid-square data from the Kent survey by their combined numbers of Southern Local Species and Widespread Local Species and chose twenty sites from the top of the list. If sites were to have been selected at random, then only four out of twenty sites would have been expected to support any species from these groups. I also ensured that the centres of chosen sites were more than 5 km apart (Fig. 1) so that samples would be independent.

I carried out sampling during 1983, using a belt transect method (Banaszak, 1980; Teräs, 1983). Each transect was chosen before arriving at the site to follow a nearly circular route that passed through all four of the component 1 km grid-squares. Recording did not begin unless light intensity was above 200 W m^{-2} and air temperature exceeded 16°C while rain and fog were absent (see Lundberg, 1980). The distance walked was measured using a 'Walker Pedo-Meter' (Table 4) in order to calculate the average density of bees of each species in 1 km of transect at each site.

The habitat at each site is described by the cover (i.e. quantity) of the vegetation formations present. These were recorded as a subjective assessment of the vegetation formation dominant within 25 m on either side of the transect belt. This measure, as a proportion of each transect length, is used as the cover estimate in the following analyses (data in Williams, 1985).

Analyses and Results

Distribution at different spatial scales and abundance

Within the Southern Region of Britain, species tend to be either local or nearly ubiquitous (Fig. 2). Distribution within Kent is correlated with distribution among the regions of Britain (Fig. 3: Kendall $\tau=0.53$, $P<0.05$). So

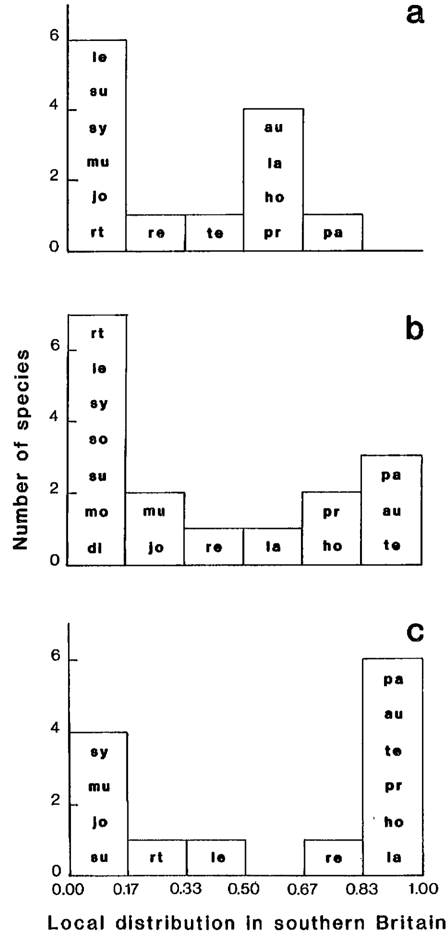

FIG. 2. Histograms of occupancy by bumble bee species within the Southern Region. (a) Data from the Kent survey of 450 2 km grid-squares. (b) Data from the B.D.M.S. survey of 410 10 km grid-squares throughout the Southern Region. (c) Data from the Kent census of twenty 2 km grid-squares. Abbreviations for species' names follow Table 1.

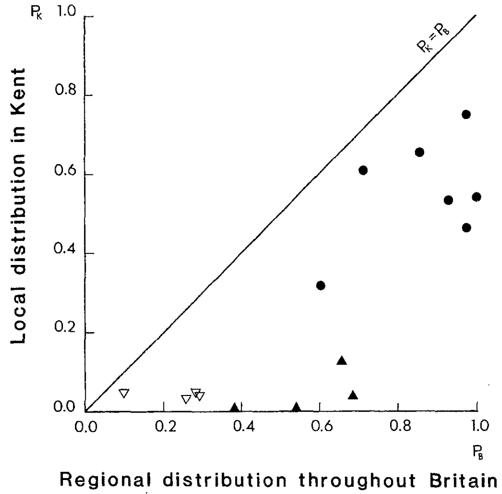

FIG. 3. Plot of intra-regional occupancy in the Kent survey 2 km data against inter-regional occupancy in the B.D.M.S. survey vice-county data. Circles represent the Mainland Ubiquitous Species; dark triangles the Widespread Local Species; and light triangles the Southern Local Species. The diagonal line follows equivalent occupancy at the two spatial scales.

members of the only group of species to remain well represented in all regions of mainland Britain after 1960, the Mainland Ubiquitous Species, are present at almost every locality. The northern and western species, and even the southern species, are not only restricted to particular regions of Britain but are also restricted to very few localities within Kent. Furthermore, the local species tend to be the less abundant species even at the few localities where they do occur (Kendall $\tau=0.54$, $P<0.05$; see also Table 4).

Association and aggregation among local species

Is each bumble bee species responding independently to the local habitat, or are there habitat characteristics that correlate with occupancy and abundance for groups of species? Association between all pairs of the local species was examined using exact tests on the contingency of association in the 2 km grid-square data from the Kent survey. To exclude the very smallest samples (2/450), data were used only if at least one of the Mainland Ubiquitous Species was also present. The results show association between all pairs of local species, because in 81% of the grid-squares sampled, only the ubiquitous species have been recorded.

To remove the effect of the many grid-squares where only the ubiquitous species were recorded, the same tests were then carried out using data from only those samples that included local species other than the pair under test (Table 2). Association persists among the group of Southern Local Species, although most mutual presences occur at Dungeness, reflecting its uniquely species-rich character. When these tests were repeated with the six Dungeness 2 km grid-squares (10 km grid square TR 01) removed from the data, almost all association is lost (Table 3). Thus the local bumble bee species are all restricted to a particular group of favourable localities in Kent, but among this subset they are generally not associated. The distribution of these species-rich localities can be seen in Fig. 4, although only 43% of the grid-squares have been sampled. Fig. 4 shows apparent aggregation of records for local species in the south around Dungeness, and also along the north of Kent, especially around the Swale (this is unlikely to be an artefact of uneven sampling: see Table 4 for the numbers of local bees compared to ubiquitous bees in the census samples and the discussion of the random model).

TABLE 2. Results of exact tests on the contingency of association between pairs of local species in the Kent survey 2 km grid-square data. Data admission conditional on the presence of other local species in the grid-squares (see text). '+' indicates significant ($P<0.05$) positive association, 'ns' no significant association and '−' significant negative association. Abbreviations of species' names follow Table 1.

	jo	le	sy	mu	su	rt
rt	+	ns	+	+	+	
su	+	ns	+	+		
mu	+	ns	+			
sy	+	+				
le	−					
jo						

TABLE 3. As for Table 2, except with the six Dungeness (TR 01) grid-squares removed from the data.

	jo	le	sy	mu	su	rt
rt	ns	ns	ns	ns	+	
su	ns	ns	ns	ns		
mu	ns	ns	ns			
sy	ns	ns				
le	−					
jo						

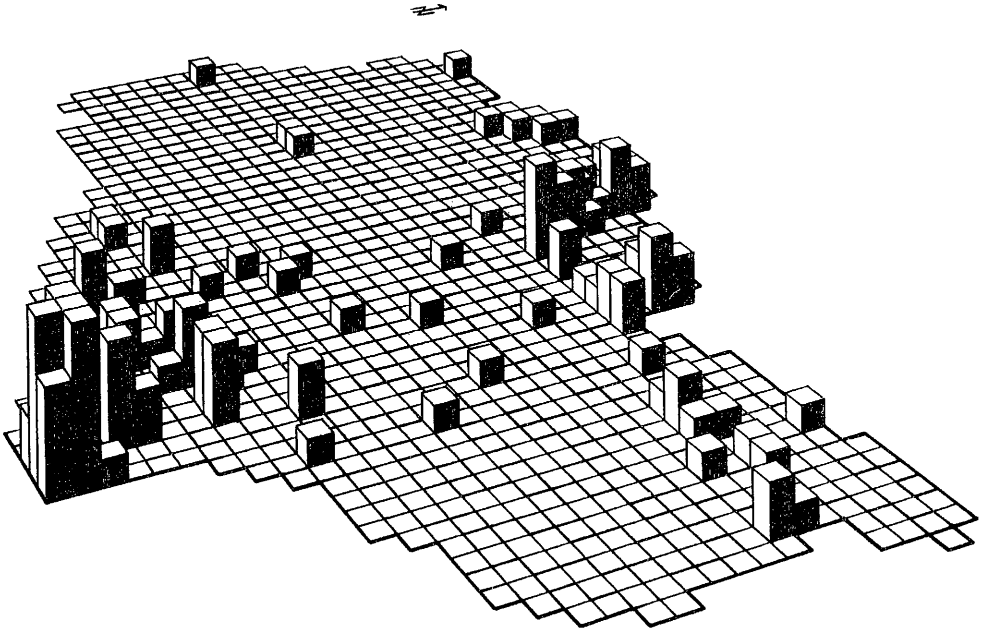

FIG. 4. Histogram of the numbers (up to six) of local bumble bee species recorded during the Kent survey, 1972–78, plotted on the 2 km National Grid, which is viewed across Folkestone towards London. Dungeness on the south coast is to the far left of centre. The Swale marshes around the Isle of Sheppey are on the mid-northern coast, to the right of centre.

Vegetational characteristics of the species-rich localities

To see whether the species-richness of the localities shown in Fig. 4 is associated with characteristics of the local vegetation, the major patterns of variation in the representation of vegetation formations among the twenty Kent census sites were examined using principal components analysis (see Blackith & Reyment, 1971).

The first vegetation component accounts for more than half (57%) of the variance in the original representation variables. It also discriminates completely between ten high-scoring sites, where the local species were re-recorded, and ten low-scoring sites where they could not be found during the 1983 census (Table 4). Only four of the sixteen vegetation formations make positive contributions to the first component (Table 4): saltmarsh, shingle, sand dune and, much more weakly, old meadow. Component 1 is strongly inversely dependent on the various forms of woodland, with a weaker inverse relationship with grasslands.

To assess the validity of this characterization of the species-rich localities from twenty sites as a generalization for the whole of Kent, the representation of saltmarsh, shingle, sand dune and old meadow vegetation was scored for all 1044 of the 2 km grid-squares (data in Philp, 1982). This is plotted in Fig. 5(a), using the same relative weightings that had contributed (as the eigenvectors) to the discrimination of the species-rich localities by vegetation in the first component. If these four vegetation formations are truly linked to the important factors that influence the distributions of the local species of bumble bees, then this extrapolation should indicate the relative quality of the favourable habitat in each grid-square and so reflect the distribution of the species-rich localities throughout the county. When this expectation (Fig. 5a) is compared with the distribution of species-rich localities from the Kent survey in Fig. 4 (allowing that only 43% the grid-squares have been sampled for bumble bees, Fig. 1, and that local species have not been re-recorded in mid Kent, see Williams, 1986), there is a good agreement in so far as aggregations of grid-

TABLE 4. Results of the principal components analysis of representation of vegetation formations for all twenty sites in the Kent census.

Contributions of variables to component 1

Vegetation formation	Loading (eigenvector) on PC1
Saltmarsh	0.567
Shingle	0.262
Sand dune	0.205
Old meadow	0.054
Pine woodland	−0.026
Fen	−0.030
Basic grassland	−0.075
Neutral grassland	−0.096
Old pasture	−0.096
Beech woodland	−0.140
Marsh	−0.170
Acid grassland	−0.184
Heath	−0.229
Scrub/hedgerow	−0.259
Alder woodland	−0.337
Oak woodland	−0.474

Site scores on component 1

Map reference	Site name	Vegetation score	No. of local bumble bee species (and number of individuals)	No. of ubiquitous bumble bee species (and number of individuals)	Sampling effort (transect lengths in km)	Sample order (site number)
TR 06 P	Shell Ness	0.959	2 (24)	7 (282)	3.5	4
TQ 87 X	Grain	0.851	2 (4)	7 (160)	3.9	13
TQ 87 E	St Mary's Marshes	0.720	1 (18)	7 (379)	4.7	17
TQ 86 Z	Iwade	0.718	1 (1)	7 (93)	5.2	5
TR 06 C	Oare	0.704	1 (6)	7 (165)	4.3	20
TQ 77 D	Cliffe	0.632	2 (9)	7 (174)	6.0	1
TR 35 P	Sandwich	0.518	2 (17)	7 (249)	4.2	16
TR 01 Z	Dungeness	0.356	6 (62)	7 (148)	5.2	14
TQ 96 H	Murston	0.106	2 (5)	7 (150)	5.3	12
TR 02 L	Lydd	−0.033	3 (5)	7 (155)	6.1	10
TR 03 K	Newchurch	−0.041	0	7 (101)	7.2	6
TQ 93 V	The Dowels	−0.216	0	7 (320)	5.8	19
TR 03 T	Aldington	−0.295	0	7 (154)	6.1	18
TQ 92 N	Stone	−0.495	0	7 (109)	6.0	11
TR 26 A	Westbere Marshes	−0.505	0	7 (132)	3.5	8
TQ 82 T	Wet Level	−0.532	0	7 (58)	5.8	3
TQ 83 T	Biddenden	−0.775	0	6 (116)	6.9	15
TQ 65 H	Mereworth Woods	−0.778	0	6 (132)	6.0	9
TR 14 H	Maxted Street	−0.882	0	6 (162)	6.3	2
TQ 83 C	Hemsted Forest	−1.013	0	6 (128)	5.5	7

squares with high vegetation scores and most local bee species occur especially around Dungeness, Sandwich and the north Kent coast. The correlation is likely to be enhanced when local cover of the various vegetation formations is included in the weighting. This is because the cover of shingle is nearly 100% around Dungeness, whereas the cover of all four vegetation formations associated with the local species is limited to a narrow shoreline band at many sites along the north Kent coast.

In contrast, Fig. 5(b) presents a similar treatment of the other twelve vegetation formations investigated. I infer from the lack of

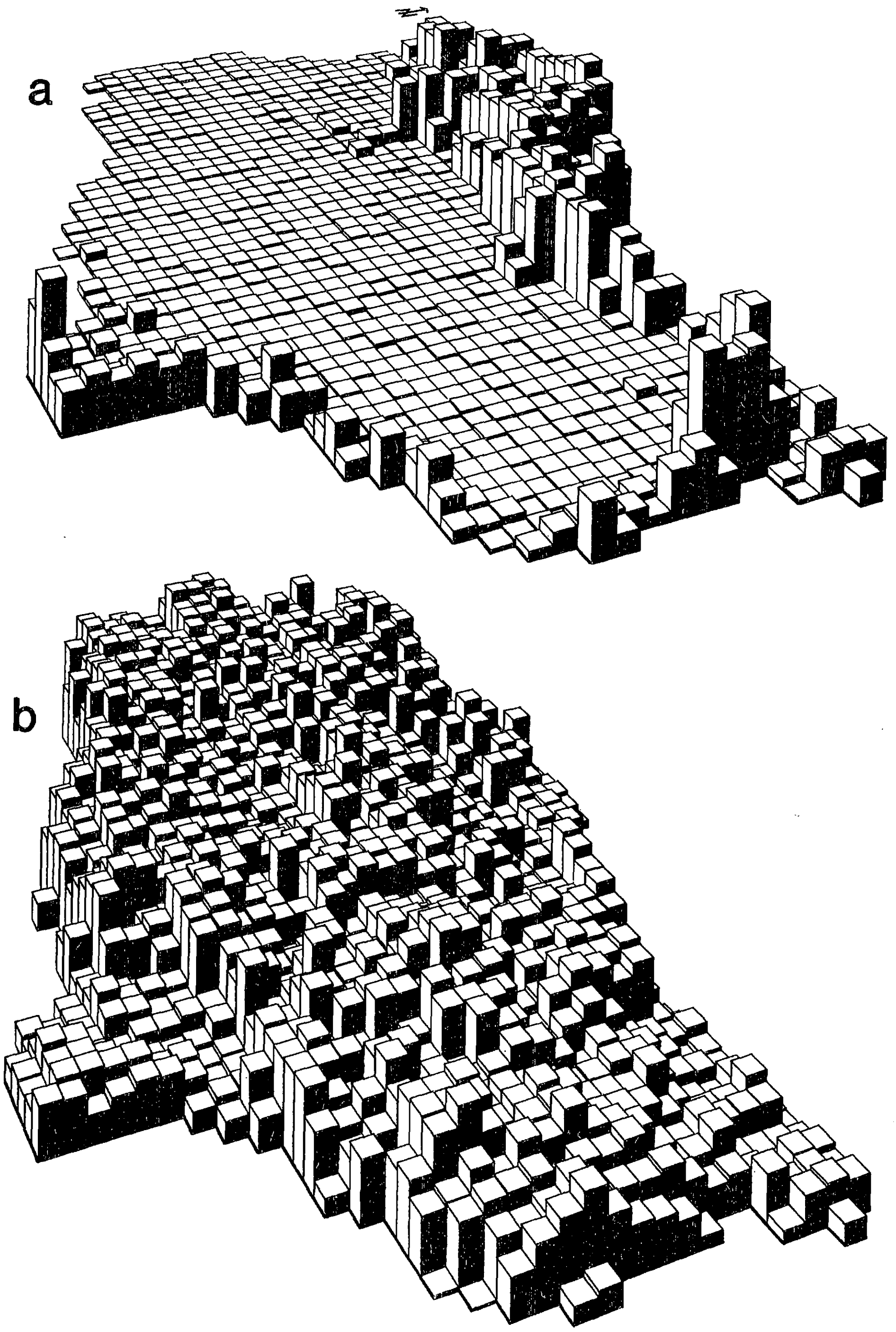

FIG. 5. Histograms of the relative representation (not corrected for local cover) of (a) the four vegetation formations weighted according to their positive loadings on the first principal component (Table 5), and (b) the other twelve vegetation formations weighted according to their negative loadings on the first principal component. Both histograms are plotted on the Kent 2 km National Grid and viewed across Folkestone towards London. Plant species were selected according to Tansley (1939) and distribution data were taken from Philp (1982).

resemblance to the pattern in Fig. 4 that it is unlikely to be vegetational diversity *per se* in the coastal areas that favours the local species of bumble bees.

Variation in assemblages of local species among species-rich localities

None of the local bumble bee species is restricted to any one of the four kinds of vegetation with which they are associated in Kent. However, it is possible to summarize any more subtle variation in composition of the assemblages of local bumble bee species with respect to the quantities of the four associated vegetation formations by using canonical correlation analysis (see Blackith & Reyment, 1971). Data are available from the density estimates for the local bumble bee species from the ten sites where they were recorded during the Kent census, when estimates for cover of the associated vegetation formations were also made.

Bartlett's test shows that there are significant canonical correlations and that they are explained by the first ($\chi_{24}^2=109$, $P<0.001$) and second ($\chi_{15}^2=46$, $P<0.001$) canonical axes. Redundancy analysis shows that 46% of the variance in local bumble bee species' densities is explained by variation in the cover of the four associated vegetation formations in the first correlation and 7% in the second.

The first vegetation axis is very strongly correlated with shingle (Table 5) but inversely related to the amount of saltmarsh. This axis represents site variation in the direction of increasing aridity, with Dungeness being strongly differentiated. The three more restricted species (*B.muscorum*, *B.ruderatus* and *B.subterraneus*) are all strongly associated with high values on this axis, whereas only *B.laevis* increase in relative density at the wetter sites.

The second vegetation axis is related inversely to the cover of the three vegetation formations, other than shingle, that are characteristic of species-rich localities (Table 5). The order of the site scores corresponds to their combined quantities of these three kinds of vegetation. Associated with this higher cover are higher relative densities of *B.jonellus* and, more weakly, *B.sylvarum*. Thus there is an overall weak tendency for marshier sites to favour *B.laevis* and sandier sites to favour *B.jonellus* (cf. Table 3).

Discussion

This study has shown that, within Kent, local occurrence of different bumble bee species shows a bimodal distribution that correlates with, on the one hand, regional distribution in Britain, and on the other, local abundance. Investigation of associations between species

TABLE 5. Results of the canonical correlation analysis of cover estimates for vegetation formations (predictor variables) and density estimates for bumble bees (response variables) from the sites where local bumble bee species were recorded during the Kent census.

Ranked correlations between original predictor variables and canonical axes derived from predictor variables		Ranked correlations between original response variables and canonical axes derived from predictor variables	
Canonical correlation 1			
Shingle	0.990	*B.muscorum*	0.992
Sand dune	0.071	*B.ruderatus*	0.989
Old meadow	−0.199	*B.subterraneus*	0.749
Saltmarsh	−0.428	*B.jonellus*	0.450
		B.sylvarum	0.192
		B.laevis	−0.161
Canonical correlation 2			
Shingle	−0.055	*B.subterraneus*	0.429
Old meadow	−0.259	*B.ruderatus*	0.054
Saltmarsh	−0.295	*B.muscorum*	0.035
Sand dune	−0.549	*B.laevis*	−0.073
		B.sylvarum	−0.210
		B.jonellus	−0.446

reveals that local bumble bees are all restricted to a particular group of localities, among which they are not closely mutually associated (except around Dungeness). Principal components analysis characterizes the habitat at these species-rich localities by the presence of one or more of the vegetation formations of shingle, sand dune, saltmarsh and old meadow. The weak tendencies of each local species towards any further habitat specialization are described using canonical correlation analysis. A study of foraging by the local bumble bee species at Dungeness has been described in detail elsewhere (Williams, 1985). I discriminated species of plants that are preferred by the local species of bumble bees, but found no association between the distributions of these bees and their preferred food plants among 2 km grid-squares in Kent. What, then, is the explanation for the existence of two sorts of bumble bee, the ubiquitous species and the local species, which seem to show a structure in their distribution patterns over the whole range of spatial scales studied? Three mechanisms that may be governing these patterns are discussed here.

Random model and Raunkiaer's law of frequency

Raunkiaer's law describes a bimodal frequency distribution of occupancy among quadrats (Raunkiaer, 1918, 1934). It is explained by a simple model, whereby the individuals of a species are dispersed randomly (Gause, 1936). This can be applied to several species in one survey area, rather than just one species between several surveys, provided that all species are distributed independently by Poisson processes. The model will then convert the nearly lognormal distribution of abundances among the species (e.g. Sugihara, 1980; Preston, 1981) into a bimodal distribution of frequency for occupancy (Preston, 1948), because the higher classes of occupancy include a wider range of abundances.

The requirement by this model of independent, random distributions does not appear to be met by bumble bees in Kent. The local species are all mutually associated in these data, although this might have been an artefact of sampling, since there could be just a better chance of finding rare species in larger samples. Samples might differ in size even if sampling effort were perfectly uniform, because some localities are likely to have more bees, perhaps because they have more resources. The Kent census provides numbers of individuals of (a) the widespread species and (b) the local species at each of twenty sites by a standardized sampling technique (data in Table 4). The hypothesis that there is no difference between these two groups of bees in their distributions among the twenty samples is very unlikely to be realistic ($\chi_{19}^2=407$, $P\ll0.001$). Furthermore, during 10 years of casual observation at Petts Wood on the western border of Kent, I found the same six or seven widespread species every year, but not a single individual of any of the local species.

Hanski's core/satellite hypothesis

Hanski (1982a) elaborated Levins' (1969) simple model for the dynamics of spatial distribution to derive a spatial analogue to the logistic equation (Lotka, 1925). Hanski's model can yield a bimodal distribution of occupancy over time, depending on large, random variation in the difference between the colonization and extinction parameters (the net spatial growth parameter) relative to the mean of their difference. This model requires that there be no minimum threshold for viable density, so that an increase in a species' net spatial growth parameter can always allow recovery and continuation of the oscillation between high and low values of occupancy. The model can also be applied to assemblages of species at one point in time. This application requires the additional assumption that all species may establish local occupancy of the same localities.

Although Hanski sought to remove some effects of habitat variation before assessing the fit of the theory to patterns in the distributions of plants (1982b), he did not do so when he applied the model to assemblages of bumble bee species (Hanski, 1982c). He included distributions in southern England (B.D.M.S. data in Alford, 1975) where, as has been shown here, the local bumble bee species are associated with particular vegetation formations (reported from elsewhere in Europe by e.g. Reinig, 1972; Pekkarinen, 1984). This cannot be explained simply as an artefact of sampling from localities with higher densities of bees (discussed under the random model). Thus the apparent differences in the habitat requirements of the different species contravenes the uniformity assumption of the core/satellite hypothesis.

A marginal mosaic model

For a species distributed across a climatic gradient, density usually decreases gradually on either side of the optimum region of maximum density (e.g. Andrewartha & Birch, 1954; Hengeveld & Haeck, 1982; Brown, 1984). Therefore, a graph of density against latitude is likely to give a bell-shaped curve (see Brown, 1984), at least for data from similar altitudes. For bumble bees, the supply of energy, derived principally from nectar, is probably the factor ultimately limiting colony development (Heinrich, 1979). Increases in thermoregulatory costs, as an effect of less favourable climates away from a physiological optimum, may reduce foraging profits per unit time and so reduce the effective local levels of resources. This would dictate lower local carrying capacities, and consequently decreasing densities of foragers, towards the edges of a species' distribution. These considerations provide a simple 'large-scale optimum-surface model' (Hengeveld & Haeck, 1981) for the density of a species of bumble bee, even if the fundamental level of resources were to remain nearly constant throughout the species' range.

There is evidence that bumble bee species are present at lower local densities nearer to their distribution limits than at the centres of their ranges (comparing numbers of B.D.M.S. vice-county records with densities of foraging bumble bees from the Kent census, Kendall $\tau=0.35$, $P<0.05$). This may result, in part, from the production of smaller colonies nearer to the limit of a species' distribution, at least in the north (Yalden, 1982). Pomeroy & Plowright (1982) concluded that peak colony size influences the number of young queens reared. In Britain, only young queens survive the winter. Ultimately colonies that remain relatively small within the limited annual season available for their development may produce workers and even males, but are unlikely to rear enough young queens to ensure local persistence of the species. Therefore, if (a) colonies must on average exceed a certain peak size in order for the local population to escape extinction, whereas (b) foraging areas are constrained in size by travelling costs in time and energy expenditure, then local persistence could be viewed (for a simple, deterministic version of the model) as depending on (c) an annual peak density of individuals in excess of some (non-trivial) minimum threshold. So even though the effective level of resources may decline only very gradually across the distribution limit (cf. Carter & Prince, 1981), there may be a threshold step in the carrying capacity. Minimum threshold densities for local persistence could also arise from other factors (Andrewartha & Birch, 1960). These thresholds are not necessary for a stochastic version of the model in which probability of local extinction increases at lower local densities (see Hengevald & Haeck, 1981; Hanski, 1982a). Either way, the distribution limits of at least the Southern Local Species in northern Europe do appear to correlate most closely with summer isotherms (Williams, 1986).

Different kinds of habitat have different fundamental levels of resources that will support differing carrying capacities for the same species under identical climatic conditions. But because local densities are more likely to fall below the minimum threshold in a habitat with a lower level of resources, a species could have different latitudinal limits in different kinds of habitat (Fig. 6). A simple hypothetical environment might consist of a uniform mosaic of local patches of either of just two kinds of habitat with two differing resource levels. In the climatically favourable central region of its distribution, a species could occupy all patches of both kinds of habitat. Further from the centre of distribution would be a marginal region, where the species occurred only in those local patches of habitat with the higher fundamental level of resources that could support densities above the threshold (Fig. 6). This model requires only that any change between habitats in the threshold density would not compensate exactly for the difference between density responses at their different levels of resources. The model provides a mechanism by which resource levels and climate could govern regional patterns of 'suitability' for habitats in Fretwell's 'ideal free distribution' (Fretwell & Lucas, 1970; MacArthur, 1972). His model shows the conditions of local density under which a freely dispersing population should colonize progressively less 'suitable' habitats.

Unlike the random and core/satellite models,

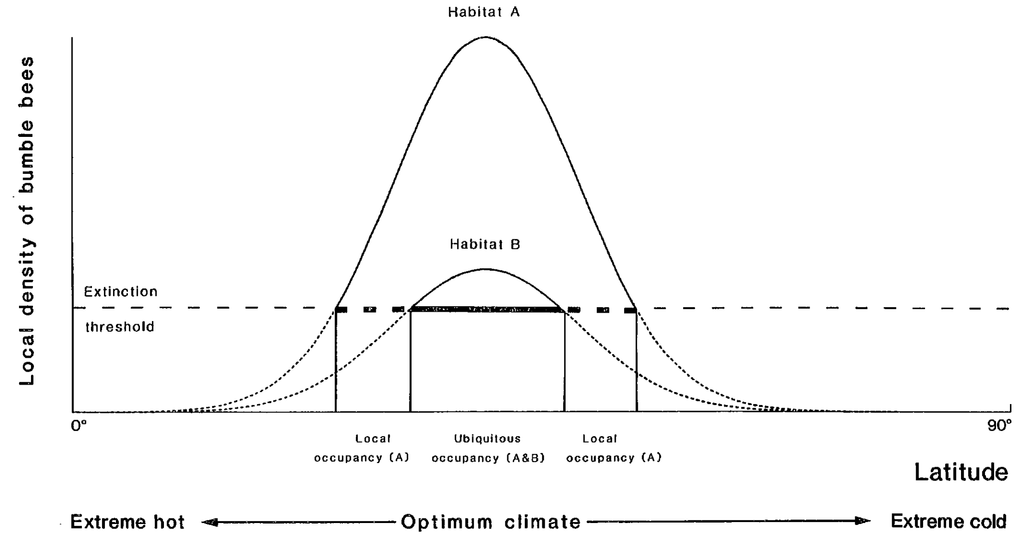

FIG. 6. Diagram illustrating the marginal mosaic model for regional patterns of suitability of habitats for a species. In the simple, idealized case represented above, the environment for a single species is taken to consist of only two distinct kinds of habitat that present uniformly higher (habitat A) and lower (habitat B) levels of resources. The maximum amplitudes of the density responses at the carrying capacities are dependent on these fundamental levels of resources in each kind of habitat. The carrying capacity in each is believed to be further affected (shown by the curves) by local foraging profitability as determined by climate, which is expressed here with respect to latitude. The horizontal line represents a minimum threshold density that must be exceeded in order to escape local extinction within each habitat. The species' latitudinal limits are consequently wider in habitat A than in habitat B because of the different density responses in the two habitats. In a uniform mosaic of these two habitats, the distribution pattern at equilibrium would therefore consist of a central region of ubiquitous occupancy (patches of habitats A and B), surrounded by marginal regions where occupancy would be locally restricted to the higher resource-level habitat (patches of habitat A alone).

this marginal mosaic model can account for the observation made here for bumble bees that it is the species nearer the edges of their distributions, the regionally restricted species, that are the more restricted species at the local scale (Andrewartha & Birch, 1954; Hengeveld & Haeck, 1981; Brown, 1984). This concentric pattern of a restricted local distribution in the marginal region of a species' world distribution, surrounding a more nearly ubiquitous distribution within the species' central region, can also be seen even within Britain for *B. lapidarius* (Map 10 in Alford, 1980; world distribution, Chart 3 in Reinig, 1935). So what is it that is especially favourable about the local 'islands' (Fig. 4) that are occupied in the marginal regions? At these sites in Kent, even the ubiquitous bumble bees occur at higher densities than at the other sites (combined densities of the ubiquitous species alone at the two sets of ten sites from the Kent census, log-transformed data $t_{18}=2.45$, $P<0.025$). These higher densities of the ubiquitous species may reflect generally higher levels of resources in the habitats that support the local species. For instance, densities of all bumble bees were found to be low inside closed-canopy woodlands, where flowers providing suitable food sources are usually sparse in summer. In contrast, the 'islands' of high resources are characterized by four, mainly coastal, vegetation formations (Table 4) that occur in open habitats with a lack of recent and drastic disturbance by man. The largest contribution to the local species' density data was from Dungeness, the only extensive area not to have been ploughed, drained or otherwise 'improved'. Elsewhere in open habitats, such disturbance may have reduced the availability of suitable food (Williams, 1986). The pronounced distinction between ubiquitous and local species within a region (Fig. 2) could simply be due to the restricted distribution of the kind of habitat that still provides these high levels of resources (although the frequency distribution of how widespread the species are, inclusive of their entire distributions, may be unimodal, see Brown, 1984).

The relationship between distribution within and among regions is not symmetrical (Fig. 3): species that are regionally restricted within Britain are rarely even nearly ubiquitous in Kent, although several species that are more widespread in Britain are only very local in Kent. This may be due, in part, to the small samples taken for the Kent survey. However, a species could be local even near the centre of its distribution if the environment contained widely scattered patches of one or more kinds of habitat with very low levels of resources, in which the species' density could nowhere exceed the threshold necessary to escape local extinction. For example, latitudinal distributions are complicated by the effects of altitude on climate (e.g. Carter & Prince, 1985; Prince *et al.*, 1985). Thus *B.monticola* is widespread between regions within Britain, but, as is usual south of the Arctic (e.g. Svensson, 1979), it is restricted to higher altitudes, which are not attained in Kent (association with land above 300 m in England, Wales and Scotland, B.D.M.S. 10 km data, $\chi_1^2=407$, $P \ll 0.001$; with the presence of *Vaccinium myrtillus* L., data in Perring & Walters, 1976, $\chi_1^2=232$, $P \ll 0.001$).

None of the models considered here deals with the history of populations and it is assumed that colonization is not limited by isolation. The roles of various historical factors in modifying bumble bee distributions in Britain, especially in the recent past, are discussed elsewhere (Williams, 1986).

Corollary for community structure

The problem of where a species can persist is discussed above in the context of the species' total distribution. An alternative perspective of the same occupancy problem is to consider which species can persist at a particular locality. The question then becomes: which factors influence the composition of the subset of species from the regional species-pool that actually occur together in a local assemblage?

The number of species at a particular locality is generally believed to be affected by the level of resources in the habitat. At lower levels of limiting resources, the species with lower local profit rates from foraging are more likely to be lost from the local assemblage, because their peak densities are less likely to attain the minimum threshold necessary for local persistence within the foraging season. For instance, most localities in Kent can be considered to be relatively depauperate in that only six or seven bumble bee species have been recorded out of a regional pool of sixteen species.

The relative profit rates of foraging bumble bees have been assessed in previous studies by comparing their respective flower handling times or visitation rates. Handling times, and therefore visitation rates, are dependent on the sizes of bee proboscides relative to the depths of the nectar-rich flowers (Inouye, 1980; Ranta, 1983; Harder, 1983). It has been suggested that under conditions of reduced resource availability, intensified interspecific competition might result in selective extinctions, so that the surviving species would be more regularly spaced in their utilization of the limiting resource axis (e.g. MacArthur, 1972; Inouye, 1977).

The inference of 'community structure' among bumble bees, from patterns in the relative sizes of their proboscides, has rarely been tested. However, results of the few comparisons (using test statistics from Barton & David, 1956) between simulations and actual bumble bee species' assemblages do not support the generality of the expected size patterns (Simberloff & Boecklen, 1981; Williams, 1985: among the widespread species in Kent, constant ratio deviation $P=0.705$ n.s., minimum ratio deviation $P=0.195$ n.s.).

According to the marginal mosaic model, the local profit rate from foraging for each species of bumble bee depends more crucially on the particular conditions of local climate in relation to the species' physiological optimum. So the relative performance of the different species at a particular locality might be predicted very roughly from the proximity of that site to each species' adjacent latitudinal limit. This provides another criterion that can be used to test for a pattern of community structure. A simulation by randomly drawn assemblages of seven species from the regional species-pool can be used to measure the deviation in the total number of British vice-county records (as an index of whether the species reach a latitudinal or altitudinal limit within Britain). The assemblage that occurs most frequently deviates much more strongly ($P<0.001$) from a random model in this form of structure than in proboscis length structure, because it is simply the Mainland Ubiquitous Species (i.e. those furthest from their distribution limits) that occur alone at these 'depauperate' sites.

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