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Jonathan W. Silvertown

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THE DISTRIBUTION OF PLANTS IN LIMESTONE PAVEMENT: TESTS OF SPECIES INTERACTION AND NICHE SEPARATION AGAINST NULL HYPOTHESES

JONATHAN W. SILVERTOWN

Department of Biology, Open University, Walton Hall, Milton Keynes MK7 6AA

SUMMARY

(1) The concept of the niche and the competitive exclusion principle have proved difficult to apply to plant communities because it has been difficult to decide what variables should be measured. The vascular plants of limestone pavements occur in discrete compartments (grikes) which give clear limits to possible niches.

(2) Tests of species distribution against null models show that some significant deviations from random distribution do occur.

(3) A comparison of niche overlap, an analysis of species association and an analysis of sympatric *v.* allopatric plant distribution all suggest that competitive exclusion and niche separation are not important phenomena in this habitat.

INTRODUCTION

The concept of the niche and the principle of competitive exclusion are both key components of contemporary and evolutionary theory. Under equilibrium conditions there are theoretical limits to the degree by which co-occurring species may share the same niche (MacArthur & Levins 1967). If these limits to niche overlap are exceeded, one or more species will be excluded from the community by the competitive effects of others which draw upon the same limiting resources. Alternatively, a niche shift may occur in the zone of overlap between competing species, so reducing the effects of competition.

Circumstantial evidence for the occurrence of niche shifts and of competitive exclusion has been claimed for many communities in which certain combinations of ecologically similar species appear to be rare or absent. The proper interpretation of this kind of distributional data requires that observed patterns of co-occurrence between species should be compared with a null model of the community. Such models are artificial communities, which contain the same number of species (and often the same number of individuals) as the real community but in which they are distributed at random so that the influence of interspecific competition on distribution is, as far as possible, eliminated (Harvey *et al.* 1983).

A common problem in niche studies with plants, particularly when confined to a single habitat, is the quantitative delimitation of a plant's realized niche (Hutchinson 1957). Such measures are essential if observations of plant distribution are to be tested against a null hypothesis or a null model of community organization. This paper reports the results of measurements of plant distribution for the vascular flora of several limestone pavements, a habitat in which many of the problems of measuring the relative distribution of different species are obviated.

The vascular flora of limestone pavements

Limestone pavements occur in several upland regions of Britain (Ward & Evans 1976) on plateaux denuded of soil and surface vegetation, to expose a regular pattern of vertical fissures (grikes) in the rock from 5 cm to 1 m wide and up to 30 m long. Grikes are generally orientated and parallel to each other in two major directions. The intersection of grikes, orientated along different axes, divides the surface of the pavement into approximately rectangular blocks called clints.

Grikes are approximately rectangular compartments with vertical sides and vary in width, depth and length. A fine mull or rendzina soil is found at the bottom of most grikes and in crannies and solution hollows formed in the side walls. The grikes of most limestone pavements contain a vascular flora of plants typical of woodland, with some species which are characteristic colonizers of exposed rocks and walls (Ward & Evans 1976; Ratcliffe 1977). Limestone pavements in the Craven plateau where my study sites were situated have probably been treeless since the Iron age (Pigott & Pigott 1959). The woodland flora found in them may be a relict of former woodland.

The distribution of individual species within the pavements in the area appears to be influenced by two main factors: the depth of individual grikes and grazing by sheep. Temperature, humidity, light and the diurnal fluctuation of these factors are all related to grike depth and width (Heslop-Harrison 1960; Dickinson, Pearson & Webb 1964; Silvertown 1982). Grazing effects also depend upon grike dimensions since sheep are unable to graze any grike below a depth equal to the grike width, unless it is wide enough to allow them to enter it bodily (Ward & Evans 1976). These correlations suggest that grike dimensions themselves may be used as an integrated measure of local growing conditions experienced by plants. In both a physical and a metaphorical sense a grike is a measurable niche.

Limestone pavement comprises an array of rectangular boxes of assorted sizes. A null model of the community is equivalent to tossing plants randomly into these boxes so that each species is represented in each size of box only in proportion to the number of boxes of that size in the pavement. In practice the real distribution of species is tested against the null model by comparing the frequency distribution for the occurrence of species in grikes of different size with the frequency distribution of size for all available grikes.

Both experimental and quantitative survey methods were used in this study to assess some aspects of the niche relationships between vascular plants in limestone pavements. The objectives of the study were to determine the extent to which plant distribution and survival were determined by grike dimensions and by interspecific effects.

METHODS

Relative plant survival

In July 1980 an experiment was set up to determine the survival of plants of two common limestone pavement species *Geranium robertianum** and *Mercurialis perennis* in relation to grike depth and grazing. Shoots of *M. perennis* were dug up from an area of woodland near Malham, Yorkshire (National Grid reference SD 895673) and planted singly in 9-cm diameter plastic pots filled with a 50:50 mixture of John Innes No. 1 and Levingtons soilless compost. Young seedlings of *Geranium robertianum* obtained from a

* Plant names follow Clapham, Tutin, & Warburg (1962).

nearby limestone pavement were similarly planted in another set of pots. Each seedling was ringed with a section cut from a plastic drinking straw to aid later identification.

One week later the pots were transferred to an area of limestone pavement at Highfolds (National Grid reference SD 895676). Any plants damaged in transit were discarded. Seventy-five pairs of pots, each consisting of one of each species, were placed at the bottom of E. to W. orientated grikes in a pavement protected from grazing. The grikes were selected so as to give approximately equal numbers of pairs of pots at depths above and below 60 cm. Grike width varied little compared with depth in the sample of grikes and so was ignored as a variable. This set of treatments was repeated in an adjacent area of pavement grazed by sheep. Few grikes deeper than 70 cm were found in this area so that only fifty pairs of pots could be sited, in equal numbers above and below 55 cm depth.

The location of each pair was mapped and was marked with paint on the surface of the pavement. Pots took 2 days to place in position, concluding on 30 July 1980. The plants were not watered or attended in any other way after being placed in position. On 15 and 17 May 1981 all the pots were relocated and the surviving plants noted.

Results from the seventy-five pairs of pots in the ungrazed treatment and the fifty pairs in the grazed treatment were then ranked according to the depth at which they had been placed and subdivided into equal numbers of pairs above and below the median depth of placement. These are referred to as the upper and lower samples. Data were then tabulated in contingency tables which incorporated the variables: species \times depth \times grazing \times survival. Each variable has two conditions which are respectively: *Geranium* or *Mercurialis*; upper sample or lower sample; grazed or ungrazed; alive or dead. Two-by-two contingency tables incorporating two variables at a time were analysed by a two-way *G*-test and tested by chi-square (Sokal & Rohlf 1969). In the event, grazing by sheep over the grazed treatment was light due to a change in tenancy of the land.

Association between species

There are various problems in sampling the vegetation of limestone pavements for a test of association due to the compartmentation of the habitat. Grikes tend to be regularly spaced which rules out the use of straightforward random sampling. Grikes may vary in depth along their length and some species may root in grike walls as well as on the floor. The linear shape of grikes encourages the spread of rhizomatous plants along their length and occasionally into parallel grikes via transverse fissures and, even in a relatively large pavement, the actual area of vegetation present may be quite small. Thus, low density random sampling produces only small sample sizes and high density random sampling tends to re-sample interconnected sections of grike at an unacceptably high frequency. Such over-intensive sampling would be likely to produce spuriously high values of association between species.

These problems were overcome by regular sampling. It is legitimate to test the null hypothesis of no association between species using regular samples, but no measure of the degree of association may be obtained (Greig-Smith 1964). A frequency distribution of the lengths of 100 grikes at each site was drawn up. Transects were spaced at intervals calculated to reduce the probability of sampling the same grike on two adjacent transects to below 0.05. A 25-cm length of grike was sampled at every point where a grike intersected, at right angles, a series of transects across the pavement. Grikes which were wider than they were deep were ignored because the intense grazing in them removes all but grassland plants. Two pavements were exhaustively sampled by this method: Ings car (National Grid reference SD 915648) with 375 samples and Gordale (SD 894745) with

483 samples. Grike depth and width, the identity of each species found within the 25-cm sample length and its rooted depth (on the grike floor or side) were recorded. Only data on species presence and absence within samples were employed in the initial analysis of association. A contingency table for all species in each pavement was compiled and chi-square values computed. Statistical significance was determined against the null hypothesis of random association between species.

Species distribution in relation to grike depth

Data on grike depths within each pavement were used to draw up a frequency distribution of grike depths. Plants randomly distributed in the grikes in a pavement should have depth–frequency distributions not significantly different from the distribution of grike depths. The frequency distribution of grike depths was therefore used as a null model of species distribution and actual frequencies of plant occurrence in grikes of different depths were compared with it. The frequency distributions of grike depths and of rooted depth for each species were compared by a chi-square test.

The frequency distributions of depths for different species sampled in the same pavement may also be compared with each other and tested in an analogous fashion. In these cases, tests are against the null hypothesis that the frequency distributions of species–depths were the same as each other. Grike width was not used in this analysis because a two-dimensional division of data would have reduced some already small sample sizes to unusable proportions for several species. An analysis incorporating width as a variable would be unlikely to produce different results since grike width varied rather little by comparison with grike depth.

Analysis of species interaction

Negative associations between species may be due to interaction between species or may be the result of niche differences unrelated to interactions. A species which occupies only deep grikes and one which occupies only shallow ones will never interact but will still appear negatively associated. Likewise, differences between species in depth distribution may be due to interaction between them but might not be revealed by the association analysis if such interactions result only in the vertical displacement of species within shared grikes.

A way of checking for species interactions which are not revealed in the association analysis is to divide the data for a pair of species into samples where they occur together (sympatric samples) and samples where they occur apart (allopatric samples). Interaction is implied if a species occurs at a different depth to a companion whenever they are sympatric in a grike but at about the same height as the companion when the distribution of allopatric samples are compared. Conversely, no interaction is demonstrated if the depth distributions of two species are more similar in sympatric than allopatric samples.

RESULTS

Relative plant survival

Comparisons of mortality within grazing treatments

In ungrazed pavement, *Mercurialis perennis* experienced the same mortality in upper and lower samples, but in grazed pavement its mortality was significantly higher in upper samples than lower ones ($G = 5.01$, $P < 0.05$) (Table 1). More *Geranium robertianum*

TABLE 1. Mortality of *Geranium robertianum* and *Mercurialis perennis* grown in pots placed in grikes in limestone pavement at Highfolds, Yorkshire, in areas accessible to or fenced from sheep grazing. Grikes are divided into two depth classes (upper and lower) and the values are the proportions of the original populations found dead after 10 months. Mortalities sharing any superscript are not significantly different from each other at $P = 0.05$. See text for further details of the statistical comparisons made

	Grazing treatment	
	Ungrazed	Grazed
<i>Geranium robertianum</i>		
Upper	0.34 ^{ce}	0.33 ^{bde}
Lower	0.67	0.55 ^b
<i>Mercurialis perennis</i>		
Upper	0.32 ^{acf}	0.48 ^{df}
Lower	0.35 ^a	0.18

plants died in lower samples than upper ones in ungrazed pavement ($G = 6.07$, $P < 0.02$) but no significant difference in mortality was found between sampling depths in grazed pavement.

There were no differences in mortality of the two species in the upper samples of the ungrazed treatment but in the ungrazed lower sample *Geranium robertianum* showed substantially greater mortality than *Mercurialis perennis* ($G = 111$, $P \ll 0.001$). The same patterns of relative mortality in each species occurred in the grazed pavement though the difference between them in the lower samples was less significant ($G = 6.50$, $P < 0.02$). This is not surprising since fewer very deep grikes were present in the grazed area than in the ungrazed area.

Comparisons of mortality between grazing treatments

The difference in the number of deep grikes between the grazing treatments limits the number of valid comparisons that may be drawn between them. Despite this difference, median values of grike depth for the two areas were nearly the same (60 cm ungrazed, 55 cm grazed) so that it is valid to compare the mortality in the upper samples of both treatments. This is not the case for lower samples but it does not greatly affect the interpretation of results since grazing effects are only likely to be observed in the upper samples which are in the depth zone accessible to sheep (rarely deeper than 30 cm). No significant difference in mortality between grazing treatments was observed for either *Geranium robertianum* or *Mercurialis perennis*.

Association between species

The species occurring in samples taken at Ingsar and Gordale are listed in Table 2. Most species were relatively rare and consequently the expected values of association between the species were small. No significant negative or positive associations were detected between any species in either pavement.

Species distribution in relation to grike depth

Only the distributions of species occurring in at least ten samples in a pavement were analysed. Fourteen species were analysed for Gordale and nine species for Ingsar. Both seedlings (with cotyledon leaves still present) and mature plants of *Geranium robertianum* were found at Ingsar and the distributions of these two stages were analysed separately.

TABLE 2. Distribution of vascular plant species in limestone pavements at Ingscar and Gordale, Yorkshire, in relation to their expected distribution if at random. Significant departures from randomness are indicated by * $P < 0.05$; ** $P < 0.01$, and *** $P < 0.001$; NS, not significant. U indicates that the species was found less often than expected in the upper (shallower) depths and L in the lower (deeper) depths.

Species	Ingscar				Gordale			
	<i>n</i>	χ^2	d.f.	<i>P</i>	<i>n</i>	χ^2	d.f.	<i>P</i>
Flowering plants								
<i>Allium ursinum</i>	—				61	21.03	14	NS
<i>Anemone nemorosa</i>	3				12			
<i>Chamaenerion angustifolium</i>	1				4			
<i>Cirsium vulgare</i>	—				7			
<i>Epilobium montanum</i>	22	17.71	19	NS	40	10.45	14	NS
<i>Geranium robertianum</i>	222	83.47	20	L***	115	35.72	14	L**
<i>G. robertianum</i> (seedlings)	249	14.02	19	NS	136	15.21	14	NS
<i>Hedera helix</i>	—				22	21.18	14	NS
<i>Heracleum sphondylium</i>	9				11			
<i>Mercurialis perennis</i>	48	21.51	19	NS	147	33.11	14	U**
<i>Mycelis muralis</i>	163	18.13	19	NS	14	18.73	14	NS
<i>Oxalis acetosella</i>	42	7.09	19	NS	32	15.42	14	NS
<i>Sanicula europaea</i>	1				15	13.07	14	NS
<i>Stachys sylvatica</i>	4				76	52.65	14	U***
<i>Thalictrum minus</i>	—				25	83.56	14	L***
<i>Urtica dioica</i>	13				55	25.32	14	L*
Ferns								
<i>Asplenium ruta-muraria</i>	16	280.12	21	L***	22	126.05	15	L***
<i>A. trichomanes</i>	33	94.73	20	L***	44	40.16	14	L***
<i>A. viride</i>	18	84.07	19	L***	27	49.37	14	L***
<i>Cystopteris fragilis</i>	1				13			
<i>Dryopteris filix-mas</i>	1				38	22.37	14	NS
<i>Phyllitis scolopendrium</i>	276	17.98	19	NS	259	29.13	14	U*
<i>Polypodium vulgare</i>	1				1			
<i>Polystichum aculeatum</i>	—				38	7.16	14	NS
Total sample size	375				483			

Significant deviations from a random distribution are indicated for each pavement in Table 2. The distributions of grike depth in the null models and the actual distributions of species are shown in Figs 1 and 2. The distribution of different species within individual pavements may also be compared in these figures. Such differences as occur are clear enough to obviate the need to calculate an index of overlap.

Analysis of species interactions

Because no significant negative or positive associations between species were found (see above), the question of testing the relative distribution by depth of such cases does not arise. For each pavement, the depth distributions of allopatric and sympatric samples was found for all possible pairs of the commonest species. Two examples of the results obtained in this analysis are shown in Fig. 3. A comparison of *Geranium robertianum* and *Phyllitis scolopendrium* (Fig. 3(b)) illustrates the general finding that the depth distributions of species in sympatric samples are more alike than the depth distributions of allopatric samples.

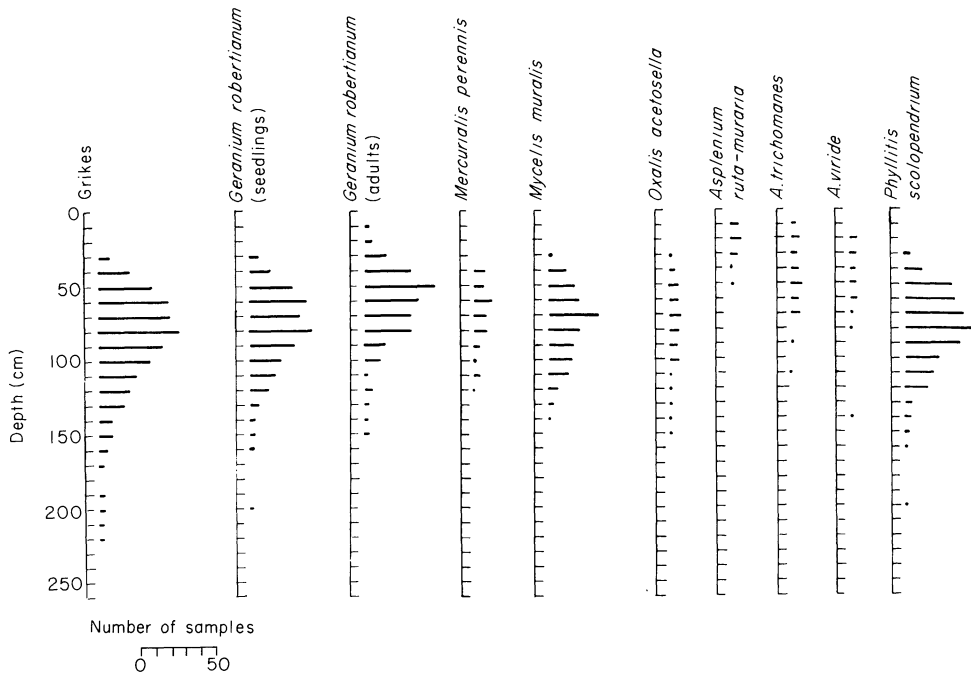


FIG. 1. Frequency distribution of grike depths and of species occurring in the grikes for the most abundant species in limestone pavement at Ingsar, Yorkshire.

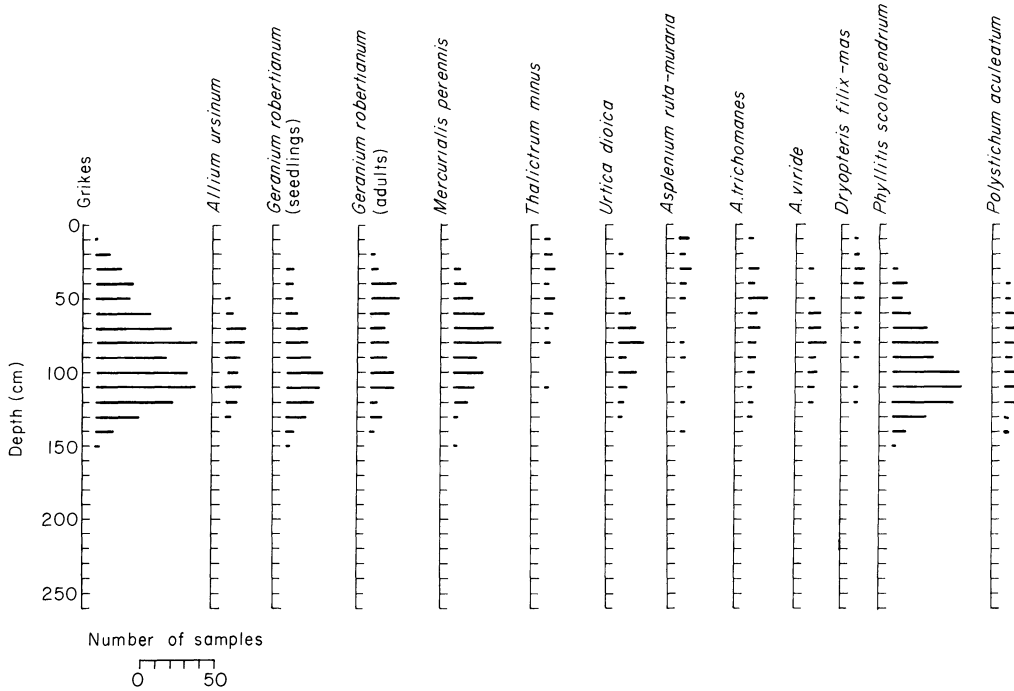


FIG. 2. Frequency distributions of grike depths and of species occurring in them for the most abundant species in limestone pavement at Gordale, Yorkshire.

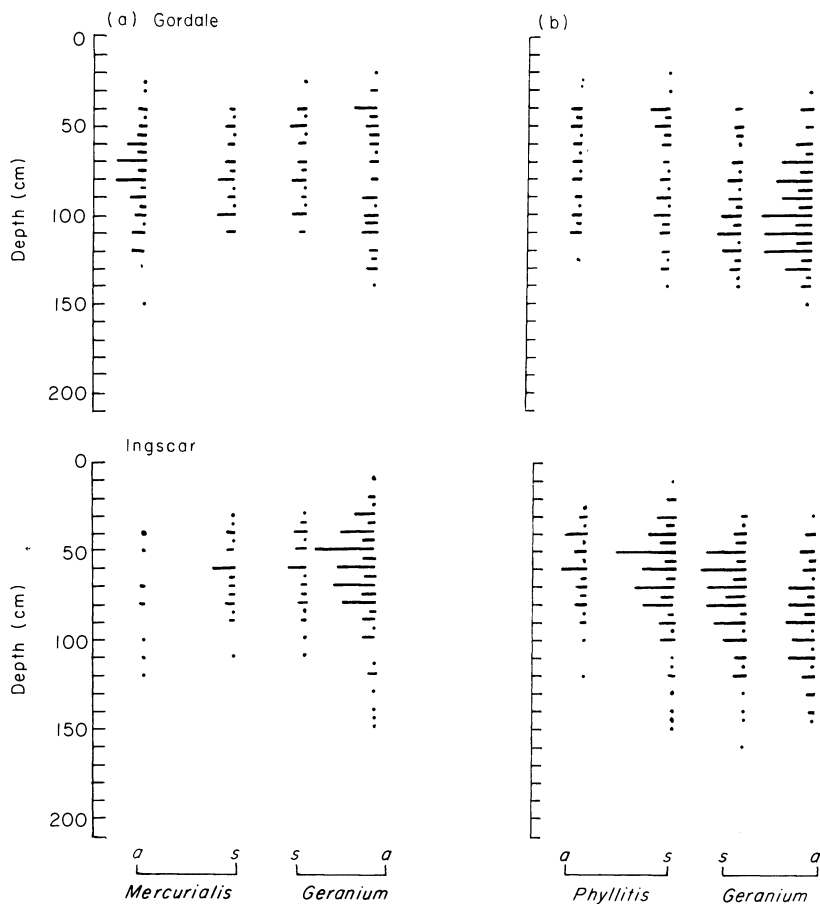


FIG. 3. Pairwise comparisons of frequency distributions of species in (a) allopatric and (s) sympatric samples in pavements at Gordale and at Ingscar. (a) *Geranium robertianum* and *Mercurialis perennis*; (b) *Geranium robertianum* and *Phyllitis scolopendrium*.

DISCUSSION

Several lines of evidence demonstrate that the depth of a grike is an important dimension of resource use to plants occupying limestone pavement habitats. The survival of *Geranium robertianum* and *Mercurialis perennis* in pots depended upon their depth of placement above or below about 60 cm. The two species responded differently to depth such that grazing mortality, related to grike depth, may selectively remove *M. perennis* from shallow grikes whilst some factor, perhaps related to the shade intolerance of the plant, removes *Geranium robertianum* from deep grikes.

These trends of selective mortality are in agreement with the relative distribution of the two species in the two pavements studied. The distribution of adult *Geranium robertianum* is significantly truncated at lower depths in both pavements whereas the distribution of seedlings of the same species is not (Figs 1 and 2). This pattern strongly suggests selective mortality. The distribution of *Mercurialis perennis* is significantly truncated in upper depths at Gordale but not at Ingscar. This difference is probably related to differences in grazing intensity. Finally, the distribution of several other species differs significantly from

randomness (Table 2). Variables which were not investigated (e.g. soil depth) may influence plant distribution but collectively these findings justify the assumption that grike depth has been correctly identified as a highly significant dimension of resource use for plants in limestone pavement.

Niche theory (e.g. see MacArthur 1972; Vandermeer 1972) would predict that the plants of limestone pavement should partition the habitat among them with respect to grike depth. On the contrary, the evidence shows that despite some differences between plant distribution and the null model there is substantial overlap between species in their depth ranges (Figs 1 and 2). This may be explained partly by the rarity of species and the relative emptiness of the habitat since this will reduce the frequency of interspecific encounters. Niche differences will only be maintained where interspecific competition takes place. But this cannot be the full explanation.

There are many grikes where species do occur together. Yet an analysis of the depths at which species are rooted in these, shows that similarities between species are greater for sympatric than for allopatric samples. If interspecific competition between plants was important in the organization of this community the opposite result would be expected.

If the behaviour of *Geranium robertianum* and *Mercurialis perennis* transplants had been studied in isolation it might have been concluded that their distributional ranges were determined by different limiting factors (grazing and shade, respectively) and that these provided the necessary niche differences to allow the species to coexist. However, the other analyses suggest that competition has no influence on their distribution, even where they do occur together. Hence any 'niche differences' are irrelevant.

Of the four species whose distribution differs significantly from randomness at Ingscar, three are rupestral ferns, all in the genus *Asplenium*. These same ferns comprise three of the nine species at Gordale whose distributions are significantly different from random. All three *Asplenium* species are rare in both pavements so that interspecific encounters between them, or at least between their sporophytes, is extremely infrequent. Nothing is known of their gametophyte distributions.

Two species of the ten which are common to both pavements show differences between their distributions at Ingscar and Gordale in relation to the respective null models. The distributions of both of these, *Mercurialis perennis* and *Phyllitis scolopendrium*, are truncated at the upper end at Gordale but not at Ingscar. The most likely explanation for this is a difference in sheep grazing pressure between the two sites. This difference between the sites does not reduce the substantial overlap in vertical distribution between the species.

Limestone pavement is an ideal habitat in which to quantify niche separation between plants and yet when this opportunity is grasped, the phenomenon of niche partitioning appears to disintegrate. This is not a unique discovery. Pickett (1980) and Watson (1980) have commented on the elusiveness of examples of niche separation amongst plants. Niche separation and the paradigm of competitive exclusion are so well established that one must ask, if it is not applicable, why not?

Connell (1978), Hubbell (1979), Huston (1979) and Pickett (1980) have all pointed out that plant communities are often subject to disturbance and that these conditions may facilitate coexistence and high diversity. The present study has demonstrated the inadequacy of niche theory as an aid to understanding the organization of plants in a rather specialized environment. In fact, this study suggests that to call the disposition of plants in this habitat 'organized' at all is to prejudge the issue. Their very coexistence may depend upon the dynamics of the flora and upon disturbance in the habitat rather than upon any organizing force such as interspecific competition.

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