

SPECIES DIVERSITY IN A TROPICAL CAVE ECOSYSTEM

by

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ABSTRACT

Caves in the Gunung Mulu National Park, Sarawak, contain at least four types of living-spaces, or habitats, each of which is consistently used by a particular group of animal species. The structure of each group of animals carries information about the adaptations of individual species, the history of the group as a whole, and the character of the habitat. This information can be measured in terms of the 'species diversity' of the group. In this study the species diversities of several groups were compared with the stability, predictability, food supply and complexity of their habitats. The aim was to test a model which predicted that species diversity is promoted by high habitat stability, predictability, heterogeneity and an abundant supply of food. Only habitat predictability was shown to affect species diversity. Low species diversity was correlated with unpredictable floods which disturb or destroy the structure of the group.

INTRODUCTION

In an earlier paper (Chapman, 1982), I presented evidence that cave-dwelling invertebrates in the Gunung Mulu National Park, Sarawak, tend to distinguish a small number of component habitats within the cave environment, each categorized by a typical assemblage of species. There appeared to be four easily identified associations of component habitat-communities, which I termed SCAT, SHALLOW, SWIFTLET and BAT. The most widespread of these, and in many ways the most interesting, is the SCAT association, consisting of up to 23 species of cave-evolved troglobites and troglaphiles. Members of the SCAT association are found where there are scattered faeces of *Collocalia* swiftlets to eat, but not on large patches or beds of swiftlet guano, from which they are excluded by the guano specialists of the SWIFTLET association. Individual species of the SCAT association vary greatly in their tolerance to drying air currents (the smaller animals tend to be less tolerant), so that cave topography and microclimate determines which species are found in particular patches of habitat with a suitable food supply. By contrast, the guano specialists of the SWIFTLET association occur wherever swiftlet guano is plentiful, even in areas subject to a high rate of evaporation, but are absent from the very damp situations favoured by SCAT members. The BAT association was found only in a single cave, on guano beds beneath enormous roosts of the freetailed bat *Tadarida plicata plicata*. Perhaps surprisingly, only two of the twelve identified species sampled on the BAT site occur on swiftlet guano. The SHALLOW association may be characteristic of caves developed in isolated tower karst outliers on the alluvial plain, which is where the only such community I studied was located. It consists of a few of the larger, more mobile troglaphiles found in other Mulu caves, plus several forest



Plate 12. An undescribed cave-specialized cricket (*Caconemobius* sp.) patrols the glassy wall of Kazumura Cave, a lava tube on Kilauea Volcano, Hawai'i. This picture was taken by U.B.S.S. member Phil Chapman during a recent biospelaological expedition sponsored by the University of Bristol.

floor species, and is therefore more accurately considered a hybrid community or ecotone between cave and forest habitats. Another such hybrid community was present on a damp bed of mixed guano of the bentwinged bat *Miniopterus australis witekampi* and the swiftlet *Collocalia salangana*. The fauna here contained a few species from the SWIFTLET and SHALLOW associations, plus a large number of species not found in other cave habitats in Mulu. An idealized distribution of these various associations in Mulu caves is shown in Fig. 52.

None of the associations described above can be termed an ecosystem in the strict sense, as the energy base of each 'component community' is guano or other detritus imported from the surrounding forest ecosystem by swiftlets, bats, or floods. Nevertheless, the SCAT, SWIFTLET and BAT invertebrate associations are sufficiently distinct and well-established to be considered as co-evolved ecological systems, within which energy is channelled along more-or-less predictable pathways. The routes along which food-energy travels in each system have been refined over many thousands of years of evolutionary selection. Each component community contains a vast store of information, coded in the genetic constitution of individual species and in the evolved structure of the community itself. This information forms a cybernetic system which influences the future, or bridges time, because the genotype of each species and the organization of the community are self-regulating systems.

MacArthur (1955) proposed that cybernetics, or information theory (Shannon, 1949), could be used to quantify the information contained in the structure of a community. MacArthur and MacArthur (1961) and Watt (1964) have used the Shannon-Wiener function to express the information content of a community in terms of the proportions of its component species. More recent authors have expressed species diversity in other ways, and Hurlbert (1971), reviewing some of these approaches, comments that: "It has not been shown that information theoretic indices have any greater biological relevance than do the infinite number of other potential indices which have a minimum value when $S = 1$ and a maximum value when $S = N$ " (N being the number of individuals in a community containing S species). Nevertheless I have to choose one method or another by which to compute species diversity and I shall use the Shannon-Wiener function because this is the method used in other studies of species diversity in caves, by Poulson and Culver (1969) and Culver and Poulson (1970).

In practice, it is very difficult to gain an accurate picture of the diversity of most ecosystems, because an enormous sample is required in order to include a fair proportion of all component habitats, or because individual species' abundances fluctuate seasonally so that samples must be taken over a long period of time. Many cave biologists have suggested that cave ecosystems are ideally suited to quantitative ecological studies because they are spatially well-defined, stable in time and contain few species (e.g. Barr, 1967; Culver, 1982). Having identified these desirable characteristics of the cave environment, biologists have nevertheless tended to conduct their studies in those cave eco-

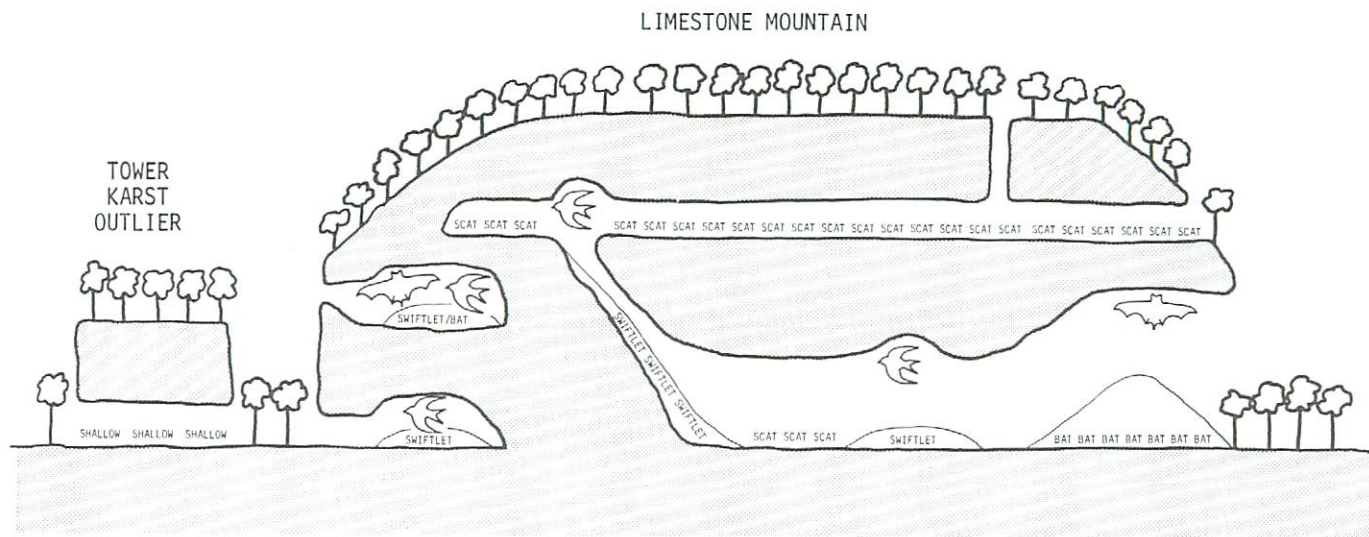


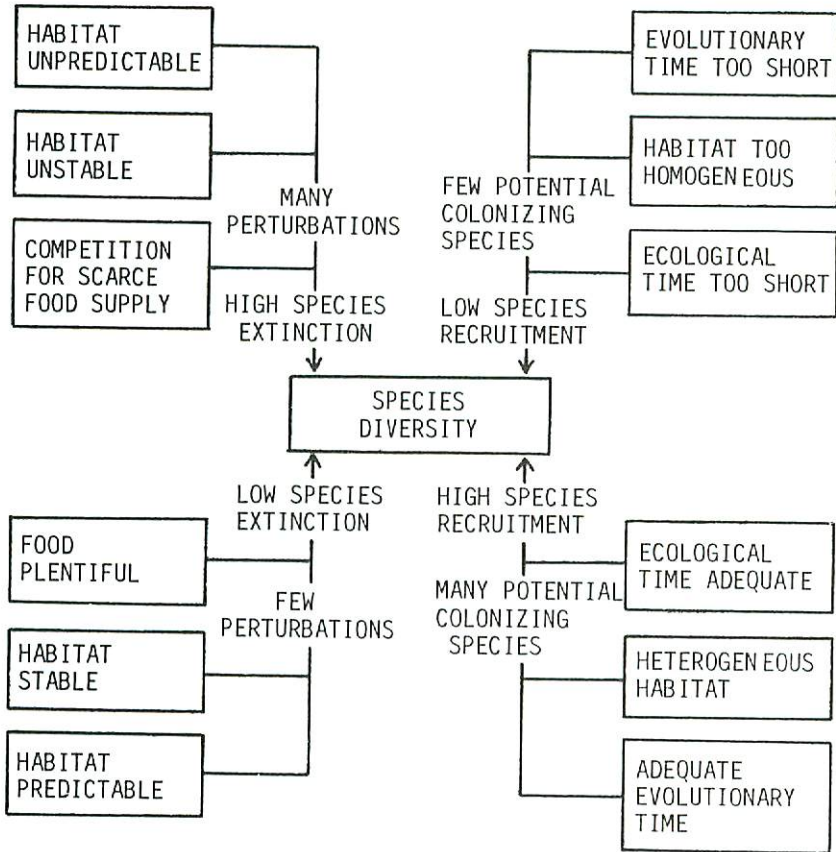
Fig. 52. An idealized cross section through the Mulu karst, showing the distribution of the various faunal associations found in the caves. Explanation: The outline diagrams of bats and swiftlets indicate their respective roosting places. The BAT association lives on beds of bat guano. The SWIFTLET association lives on beds of swiftlet guano. the SCAT association lives on the floor of passages along which swiftlets fly, but avoids guano beds. The SHALLOW association lives in caves in isolated tower karst outliers. Hybrid communities occur where swiftlets and bats roost together, and where SCAT habitats are reached by daylight from entrances.

systems which are the least well-defined in space and least stable in time—the detritus-based communities of temperate caves. Recent evidence (Juberthie et al., 1980; Juberthie and Delay, 1981) has shown that many small cave-limited detritivores and their predators may actually be more plentiful in sub-soil cracks in karst and even non-karstic rocks than they are in caves. Exchange of individuals between the cave and connecting cracks (which cannot be sampled) may be considerable (Chapman, unpublished), so that it is not clear exactly what proportion of the subterranean community is being sampled, or to what extent the numerically small cave-dwelling population is typical of the whole hypogean community. The food supply of temperate caves may be strongly seasonal, or the result of unpredictable floods (Barr, 1968; Chapman, 1983). By contrast, guano-based ecosystems in the tropics are more predictable and spatially more discrete. The food supply varies over each 24 hour period, but is more-or-less constant over longer time spans, and guano specialists are confined to cave passages which contain troglodite roosts, or flightways between roosts and entrances. This paper deals with the diversity of component communities which occupy clearly defined areas within such predictable guano-based ecosystems.

The interest in studies of species diversity comes in explaining the results in terms of biologically significant influences on the studied community. In order to cut down data gathering to manageable proportions it is helpful to formulate a model before fieldwork is undertaken and to record only those environmental variables which are of direct relevance to the model. In this case the model was derived from the results of a similar study by Poulson and Culver (1969) conducted in the Flint Ridge-Mammoth Cave system in Kentucky, U.S.A. These authors distinguished five primary-level explanations of diversity: evolutionary time, ecological time, stability of the environment, predictability of the environment, and rigour of the environment. Of these, evolutionary time and ecological time were not considered in this study, because I had no way of measuring or of making an informed guess about either one, without recourse to all kinds of unfounded assumptions, such as that species showing a greater degree of regression in eyes and pigment have experienced a longer period of cave evolution than those retaining pigment and functional eyes. Rigour (or 'stressfulness') of the environment was excluded from this study as it could not be measured or estimated without considerable knowledge of the behaviour and physiology of the cavernicoles under study, which I did not have. In any case, the concept of environmental rigour is of little practical use in explaining distributions of animals in caves, as is well shown by two opposing interpretations of cavernicolous adaptation, advocated by Vandel (1965) and Howarth (1980). Vandel argued that terrestrial troglodites are confined to the humid cave habitat because they cannot cope with the (rigorous) desiccating conditions found outside caves. Howarth argues that for many terrestrial invertebrates which invade caves, a saturated humidity represents a high degree of environmental rigour which has forced troglodites to make a major adaptive change in their water balance mechanisms. It is difficult to measure stability or predictability of the habitat, but an attempt was made to do so. Both of the

secondary-level explanations of diversity proposed by Poulson and Culver: habitat heterogeneity and 'productivity' (or rather food input in the case of caves) were measured or estimated in this study.

The simple model to be tested here, therefore, is that species diversity is enhanced by habitat stability, predictability and heterogeneity, and by rate of food input. One way in which these tested variables may be related with diversity and with the important, but untested, variables: ecological and evolutionary time, is shown in Fig. 53.



Key: ↓ Factors which depress species diversity
 ↑ Factors which promote species diversity

Fig. 53. A model of the inter-relationships of factors affecting diversity in a cave community.

TABLE 1
The composition of the invertebrate faunas of fifteen study sites in Mulu caves.

Species	Site Number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Pink leech															10
<i>Armadillo solumcolus</i>				3											
<i>Paraperiscyphis platyperaeon</i>		1	1			1									
<i>Setaphora parvicaputa</i>							5	5							
Glomeridesmid millipede			1												
White Polydesmid millipede										8					
Pyrgodesmid millipede						1				8					
Cambalopsid millipede														200	
<i>Hyleoglomeris</i> sp.									6						
Scolopendrid centipede									1					1	
Red scutigermorph	1				2			1							
Black/yellow scutigermorph												8			
<i>Oratemnus saigonensis</i>															1050
<i>Lychas</i> sp.	2														
Amblypygid	11				1				26		5	10		20	
Schizomid	50						10	10	320	100			50	100	
<i>Spermophora</i> sp.						3			110				12		
<i>Pholcus</i> sp.	1														
Ochyroceratid spider									370	30					
Nesticid spider	150														
Pacullid spider	10													10	
Ctenid spider			1												
<i>Heteropoda</i> sp.	50				12	10	6	50		10	30			60	
<i>Psechrus</i> sp.															2
'Acarine' opilionid			1		3									20	
Phalangodid opilionid					2	1	2			4					

METHODS AND RESULTS

A variety of methods were used to estimate the numbers of each of 57 invertebrate species on fifteen large study sites in caves in the Gunung Mulu National Park, Sarawak (Chapman, 1982). The results are presented in Table 1.

Cluster analysis (Mather, 1976) led to the identification of several associations of component habitats or communities (Chapman, 1982). These have already been described in the introduction to this paper.

In Table 2, the results of cluster analysis have been used to group the figures presented in Table 1 according to the association represented in each sampled site. Thus, 7 out of 8 sites identified by cluster analysis as representative of the SCAT association are treated as if they comprised a single enormous SCAT site. The eighth site is excluded on the grounds that it was the only SCAT site in the twilight (rather than the dark) zone, and therefore had an atypically reduced SCAT fauna, excluding all but one cave-limited species, but including two species characteristic of the cave threshold. Three sites identified by cluster analysis as representing the SWIFTLET association are treated as a single site. In a similar way, the two SHALLOW sites are considered together, while the distinctive BAT site, and hybrid Deer Water Cave site, are listed separately.

From the figures presented in Table 2, it is possible to compute the diversity of each of the 6 listed component communities or hybrid communities (ecotones) in terms of the Shannon-Wiener function:

$$H(S) = - \sum_{i=1}^S p_i \log_2 p_i$$

$$\text{or } H(S) = \log N - \frac{1}{N} \sum_{i=1}^S n_i \log_2 n_i$$

where: $H(S)$ = diversity of sample containing S species
 n = numbers found in the i species
 N = total individuals
 p = proportion of total individuals in the i species

The results are shown in Table 3, where they are compared with:

1. *Habitat stability*—rated for each of the 15 study sites on an arbitrary scale 1-4 (4 being most stable), based on standard deviation in humidity and evaporation rate measurements, variations in relative humidity and temperature shown by thermohygrograph traces, nature of food supply and regularity of flooding. In the case of communities represented by more than one sample site, the figures given in Table 3 are the averages from the sites representing that particular community.
2. *Predictability*—rated on an arbitrary scale 1-4 (4 being most predictable), based on food supply and flooding.
3. *Food input*—rated on a rising arbitrary scale 1-5, based on the nature of the food supply and the measured organic content of the sediments.

TABLE 2

The composition and species diversity of the faunal groupings compared in this study
(derived from figures presented in Table 1).

ASSOCIATION / (Sites)

Species	SCAT SWIFTLETSHALLOW		BAT	(Deer Water)	(Sky-light)	
Pink Leech				10		
<i>Armadillo solumcolus</i>	3					
<i>Paraperiscyphis platyperaeon</i>	3					
<i>Setaphora parvicaputa</i>	5				5	
Glomeridesmid millipede	1					
White Polydesmid millipede	8					
Pyrgodesmid millipede	9					
Cambalopsid millipede				200		
<i>Hyleoglomeris</i> sp.		6				
Scolopendrid centipede		1		1		
Red scutigeromorph	2	1			1	
Black/yellow scutigeromorph			8			
<i>Oratemnus saigonensis</i>				1050		
<i>Lychas</i> sp.		2				
Amblypgid	1	37	15	20		
Schizomid	110	420		100	10	
<i>Spermophora</i> sp.	3	122				
<i>Pholcus</i> sp.		1				
Ochyroceratid spider	30	370				
Nesticid spider		150				
Pacullid spider		10		10		
Ctenid spider	1					
<i>Heteropoda</i> sp.	22	100	40	60	6	
<i>Psechrus</i> sp.				2		
'Acarine' opilionid	4			20		
Phalangodid opilionid	9					
<i>Trogloblattella chapmani</i>	171				9	
<i>Symploce cavernicola</i>				7000		
<i>Pycnoscelus indicus</i>				350		
<i>Rhaphidophora oophaga</i>	84	100	96	50	20	
<i>Diestrammena mjobergi</i>	965	10030			2	
<i>Diestrammena sarawakana</i>			92	7600	10	
<i>Diestrammena</i> cf. <i>sarawakana</i>			10			
<i>Nala ornata</i>				10		
Mycetophilid larvae	200			20		
Guanobious Diptera		1500		540		
Trichoptera				55		
<i>Ptomaphagus chapmani</i>	1449	50				
<i>Hister</i> sp.				1400		
<i>Gnathoncus</i> sp.				70		
<i>Trox costatus</i>				2030		
<i>Tenebrio antricolor</i>				560		
<i>Anaulacus</i> sp.					100	
<i>Hyphaeron</i> sp.					40	
<i>Euglenes troglodytes</i>	20	835	6	250	260	
<i>Lithocharis vilis</i>	7					
<i>Anoiylus</i> sp.			20			
Rhapharochromine shieldbug		1000				
<i>Pheidologeton silenus</i>			2500			
<i>Crematogaster</i> sp.			1000			
<i>Monomorium</i> sp.			100			
<i>Pheidole longipes</i>					400	
<i>Stenogaster</i> sp.			20			
Ichneumonid wasps		28				
<i>Tinea antricola</i>	1	1730		3200		
<i>Tinea porphyropa</i>				26300		
<i>Crypsithyroides concolorella</i>				500		
TOTAL NUMBER (N)	3108	16493	3907	45012	9096	463
DIVERSITY	H(23)= 2.17	H(20)= 2.02	H(12)= 1.54	H(13)= 2.11	H(17)= 1.05	H(9)= 0.942

4. *Substrate diversity*—calculated from the Shannon-Wiener formula according to the proportion of the site covered by a number of substrate categories which were judged to provide distinguishable microhabitat categories for the fauna. These categories were:

- (1) Guano, either of bats or swiftlets. It consists of fairly dry insect remains, plus excretory products.
- (2) Bog guano is produced when fresh guano accumulates in drip pockets in bedrock. It has a very high organic and water content, is avoided by most guanobious species and thus merits a separate category.
- (3) Fruit bat guano consists of seed ejecta rather than insect remains.
- (4) Guano-derived mud. An organically-rich water-transported sediment derived from bat or swiftlet guano and usually present as a fine, smooth, chocolate-brown deposit some distance from fresh guano deposits.
- (5) Guano-derived crust. A dark-brown, hard mineral encrustation, rich in gypsum and apatite, on the surface of sediments or bedrock in passages frequented by swiftlets over a long period.
- (6) Mud. Usually of exogenous fluvial origin, and often rich in organic material.
- (7) Cricket Mud. A fine, laminated sediment derived from surface soils by vertical downward percolation.
- (8) Matrix-supported gravel. An unsorted fluvial sediment underlying the Cricket Muds.
- (9) Gravels. A fluviially-sorted (reworked) sediment derived from the above.
- (10) Sand. Either of clastic origin (gypsum crystals spalled from the cave ceiling and walls) or of fluvial origin (allogenic siliceous sand).
- (11) Breakdown (blocks). In draughty passages, these provide shelter from the desiccating environment.
- (12) Bedrock. Provides no such shelter.
- (13) Flowstone.

DISCUSSION

Several investigators have found diversity to be correlated with environmental heterogeneity, one measure of the number of niches available (MacArthur and MacArthur, 1961; Pianka, 1966). Poulson and Culver (1969) took substrate heterogeneity to be the principal contributor to environmental diversity, as I have in formulating the model tested in this study. However, the evidence of this study (Table 3) is that either environmental diversity is not correlated with faunal diversity, or substrate diversity, as calculated in this study, is not the most significant indicator of environmental diversity. Perhaps a homogeneous substrate, such as uninterrupted guano, does not necessarily imply the presence of fewer niches. In a detailed study of the ecology of bat guano in Tamana Cave, Trinidad, Hill (1969) found that decomposition of the guano occurred step by step, each step involving one or more specialized species. Thus the conditioning effect on the food substrate of each species group in turn effectively created a series of niches. Such a series presumably involves progressively more species as niches are finely divided by new additions to the fauna (on an evolutionary timescale) and also as guano beneath a newly-established bat colony is invaded by a succession of guano-specialized species (on an ecological timescale). Decou (1981) states that diversity of guano faunas is greater in tropical than in temperate caves. He attributes this to the mixed species composition of tropical bat roosts which provides a greater number of niches for the guanobious fauna. Perhaps more significantly, he draws attention to the large number of guano-dependent troglobites in Cuban caves,

compared to the few known from temperate caves. This surely is a consequence of the longer, uninterrupted habitation of tropical caves by perennial bat colonies, which has allowed a greater degree of specialization to this resource among tropical cavernicoles. Thus, in the tropics, guano substrates may possess as diverse, or almost as diverse, a fauna as other component habitats in the cave, as seen in the results of this study. The crucial factors in controlling diversity in the SCAT, BAT and SWIFTLET associations in Mulu may well be evolutionary time (uninterrupted time-span since the first bat and swiftlet colonies became resident in the caves) as a primary-level control, with ecological time (span of uninterrupted habitation of an individual bat or swiftlet roost, or use of passage as a flight-path) as a secondary-level control. Measurement of species diversity in caves in different karst regions could well provide clues to the relative ages of their faunas and so to the history of the karst areas themselves.

The lack of any correlation between measured faunal diversity and estimated food input implies that lack of food is not a limiting factor on the number of species inhabiting any of the habitats studied. However, there are extremely food-poor habitats in Mulu caves which appear to be entirely devoid of life, or support only one or two species (Chapman, 1980 p. 147).

The lack of any correlation between measured faunal diversity and estimated habitat stability implies that fluctuation in the cave microclimate (the main contributor to habitat instability of the study sites) does not constitute an appreciable problem to the established faunas of the various habitats studied. This is not to say that unfavourable regimes of cave climate do not limit the distributions of individual cavernicoles. Indeed there is good evidence to suppose that they do (Chapman, 1982, Fig. 7). However, the faunas of the various habitats examined in this study appear to be well-adapted to cope with predictable changes in microclimate. For example, small hygrophilic arthropods take shelter from drying air currents in the permanently humid environment of burrows dug by the large cave cricket, *Rhaphidophora oophaga*, and smaller *Diestrammena mjobergi* crickets migrate to and fro between cave walls and guano beds, presumably in response to microclimate changes (Chapman, 1981). Unpredictable microclimate changes such as floods, on the other hand, may be expected to seriously disrupt the lives of cavernicoles in affected habitats. In extreme cases, flooding will destroy a significant proportion of the fauna, or at least dramatically change the food standing crop, by removing existing food supplies such as guano, and redepositing them, together with freshly introduced organic material at the high water mark. The three sites or associations with lowest diversity in Table 3 are all affected to some extent by floods. Of the three associations with highest diversity in Table 3, sites representing the BAT and SWIFTLET associations are unaffected by floods, whereas 3 of the 7 SCAT sites are liable to flooding (Chapman, 1981). Significantly, the three flood-prone SCAT sites have the lowest species diversities of all the SCAT sites (Chapman, 1981). Flooding probably reduces species diversity because it sets back the successional process

which would eventually produce a maximum species diversity if the community were allowed to develop to a climax.

Christiansen and Bouillon (1978) argue that the deep cave is normally the most stable region of the cave, that stability favours predictability, and that stability plus predictability may lower the extinction rate of small populations, thus bringing about greater biological complexity. Culver and Poulson (1970), however, found the opposite to be the case in Cathedral Cave, Kentucky, where faunal complexity proved to be greatest at the interface of the cave and surface communities, a phenomenon which these authors presume to be characteristic of ecotones in general. The results of this study support neither of these possibilities. The only two deep cave sites studied (numbers 3 and 4, Table 1) had the lowest and fifth lowest number of species present, and the lowest and fourth highest species diversities of the fifteen sites studied. On the other hand, the sites or associations closest to, or actually in cave entrances (BAT, SHALLOW and Skylight site) had the highest, third highest and sixth highest number of species present, but the second, fourth and lowest species diversities listed in Table 3.

TABLE 3

Species diversity compared with factors hypothesized to affect it.

Association or Site	Species Diversity	Stability	Predictability	Food Input	Substrate Diversity rank no.
SCAT	2.17	4	4	2	2.61 1
BAT	2.11	3	4	5	0.13 5
SWIFLET	2.02	4	4	4	2.05 2
SHALLOW	1.54	1½	3	3	0 6
Deer Water Site	1.05	3	3	4	1.41 3
Skylight Site	0.94	3	3	3	0.95 4
Statistical significance:		NS	.01	NS	NS
Test used:		MW	MW	MW	SR
Groupings compared:		1-3vs4	3vs4	2-3vs4-5	

Statistical tests used: SR = Spearman's Rank Correlation; MW = Mann-Whitney Test.

CONCLUSION

In conclusion, the only generalization concerning species diversity which is supported by the results of this study is that diversity is lowered by unpredictable environmental perturbations, such as floods, which suppress the development of a diverse climax community.

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