Community ecology

Patterns in three dimensions

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MUCH of the best in ecology comes from recognizing and correctly interpreting patterns of community structure. Occasionally, the interpretation of one pattern can throw light on another, even in an apparently disparate area of the science. Just such a claim is made by Brown and Maurer on page 248 of this issue¹. They find that within a group of species that exploit the same class of environmental resources in a similar way, larger-bodied species seem to use up a disproportionate amount of the resources available. They go on to argue that, if their results are correct, a mixture of individual and species selection could provide an explanation for Cope's rule—the finding that members of taxonomic groups typically become larger sized over evolutionary time².

Brown and Maurer's analyses concern the relationship between population density and body size in assemblages of birds, fishes, rodents and plants. Larger bodied species are found at lower population densities. Damuth earlier pointed out that population density among African ungulates decreases with approximately the -0.75 power of body size³. Because mammalian basal metabolic needs increase with the 0.75 power of body size⁴, it seemed to follow that populations of large and small species were using about the same amount of energy. Peters⁵ subsequently claimed that the exponents relating population density to increases in body size over a wider range of animal groups are less than -0.75 , probably nearer -1.0 , indicating that smaller bodied species use more resources. In contrast, the latest analyses by Brown and Maurer suggest that across species exploiting similar resources in a similar way within communities, exponents are appreciably shallower than -0.75 . Hence, large species seem to use more energy per population than do small species.

Population density and body size can be considered with a third community variable, the number of species. Each of the three pairs of variables—population density and body size^{3,5}; population density and number of species^{6,8}; and body size and number of species⁹—are generally considered independently of each other. But knowledge of any two of these relationships automatically provides information about the third (J.H.L. & S.C. Pimm, in preparation). Indeed, if we understand the ecological and evolutionary determinants of any two of the patterns, then the third follows as a necessary consequence. With one exception⁹, theories that have been developed to explain each separate

relationship in this three-dimensional space have not recognized their interdependence. Even if the energy flow per species is lower in small organisms, because there are almost always more small species than large species in communities¹⁰, the proportion of total community energy flow through small species may nevertheless exceed community energy flow through large species.

The problem then is to explain why energy, or resources in general, are partitioned by many small, or a few large species, and how shares are allocated¹¹. Brown and Maurer's observations on population energy use are an important step in this direction. Ecologists need to pay much more attention to establishing reliable empirical relationships between body size, population abundance and number of species in plant and animal communities, as well as to their theoretical interrelationships.

An example comes from the study of species abundance curves that describe the relationship between population density and the number of species. For many years it has been recognized that frequency histograms of the relative abundances (population densities) of the different species exploiting similar resources, when plotted with the abundance on a logarithmic scale, are normally distributed. The distribution is said to be log normal. Furthermore, the number of species in the sample often seems to bear a particular

relationship to the variance of the distribution¹⁰. Log normal distributions with this property are termed 'canonical'. Models of the ways resources might be partitioned among the different species have been produced, the most notable being MacArthur's broken stick¹¹ and Sugihara's sequential niche division⁸ models. The latter actually predicts a species abundance distribution very similar to that observed (it is both log normal and canonical). But such models rest on the assumption that individuals of the different species have identical resource requirements. As Brown and Maurer and others have shown, this assumption does not hold and, furthermore, there is usually an inverse relationship between individual resource requirements and population density. One consequence of the distribution of relative species abundances is that energy may be partitioned among species according to a log normal distribution, but that distribution will not be canonical¹². It may be that, for once, ecologists have less to explain than they originally thought. □

1. Brown, J.H. & Maurer, B.A. *Nature* **324**, 248 (1986).
2. Stanley, S.M. *Evolution* **27**, 1 (1973).
3. Damuth, J. *Nature* **290**, 699 (1981).
4. Kleiber, M. *The Fire of Life* (Wiley, New York, 1961).
5. Peters, R.H. *The Ecological Implications of Body Size* (Cambridge University Press, 1983).
6. Preston, F.W. *Ecology* **29**, 254 (1948).
7. May, R.M. in *Ecology and Evolution of Communities* (eds Cody, M.L. & Diamond, J.M.) 81 (Harvard University Press, 1975).
8. Sugihara, G. *Am. Nat.* **116**, 770 (1980).
9. May, R.M. in *Diversity of Insect Faunas* (eds Mound, L.A. & Waloff, N.) 188 (Blackwell, Oxford, 1978).
10. Preston, F.W. *Ecology* **43**, 185; 410 (1962).
11. MacArthur, R.H. *Am. Nat.* **94**, 25 (1960).
12. Harvey, P.H. & Godfray, H.C.J. *Am. Nat.* (in the press).

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A new nebula

A COLOUR-ENHANCED image of the Circinus X-1 region of the galactic plane obtained with the Sydney University Molonglo Observatory telescope at 843 MHz, with Circinus X-1 itself in the upper region of the image.

Circinus X-1 may well be one of the more peculiar cosmic objects. It appears to be a binary system, one part of which is so compact it may be a neutron star or a black hole.

As discussed by R.F. Haynes *et al.* on page 233 of this issue, the association of Circinus X-1 with with newly discovered radio nebula is in contrast to most X-ray emitting binary stars. Circinus X-1 is in some ways similar to Cygnus X-1, but no analogous extended radio component has been discovered associated with Cygnus X-1. Comparison is also made with SS433 and the Crab nebula. It is suggested that the nebula results from accumulated energetic particles emitted during flaring activity.