166

NEWS AND VIEWS

ECOLOGY

Just proportions in food webs

Joel E. Cohen

In food webs of natural communities with varying numbers of species, the number of green plants and other species that consume no prey in the web (basal species) is nearly proportional, on average, to the number of species that have both predators and prey in the web (intermediate species), according to studies reported over the past dozen years[1-4]. Empirical rules[5,6] of that type describe structural or anatomical properties of food webs. An important question in community ecology is whether parallel regularities exist in the way in which food webs function[7,8]. On page 142 of this issue[9], McNaughton *et al.* report remarkable regularities in measures of food web function. Their findings indicate the existence of a physiology of food webs that generalizes across natural communities. Their report opens up the distant, but highly attractive, prospect of linking the previously known structural regularities

with new functional patterns.

McNaughton *et al.* show that the biomass, consumption and net secondary productivity (NSP) of herbivores are all related to the net above-ground primary productivity (NAP) of a natural habitat by simple power laws. Particularly striking is that the exponent of the power law that relates NSP to NAP is not significantly different from 1: to a first approximation, NSP and NAP are directly proportional. In effect, the energy converted into herbivores per square metre of surface area per year is, on average, about one-thousandth of the energy that is converted into plants per square metre of surface area per year. The ecological energy pyramid has a much larger base than second storey.

This proportionality would be a triviality if secondary productivity were passively controlled and limited by primary productivity. But this trickle-down view of

NATURE · VOL 341 · 14 SEPTEMBER 1989

community structure ignores evidence that herbivores not only depend on, but strongly influence, the plants they eat. In *The Origin of Species*, Darwin reported that, on a small cleared plot, he "marked all the seedlings of our native weeds as they came up, and out of 357 no less than 295 were destroyed, chiefly by slugs and insects." More recent studies show clearly that the feedback effects of herbivores on plant populations are both negative[10] and positive[11]. In the light of these studies, it is far from an expected finding that the complex interplays between plants and herbivores should yield a simple proportionality between NAP and NSP. Moreover, the constant of proportionality, one-thousandth, is far less than might have been guessed from widely quoted ecological efficiencies of the order of 10–20 per cent. Nor would the trickle-down theory explain why consumption by herbivores rises as the square of net foliage production, as McNaughton *et al.* find.

If studies of food-web structure demonstrate a rough proportionality between the numbers of basal and intermediate species (trophic species, really, since biological species with identical predator species and identical prey species are counted as a single unit), and if future studies of food-web function confirm the finding of McNaughton *et al.* that NSP and NAP are proportional, the next problem, and

opportunity, is to relate the two proportionalities. In the 35 studies where NSP and NAP were both measured directly, are the numbers of basal trophic species proportional to the numbers of herbivore trophic species? What is the relation between primary or secondary productivity and the diversity of biological and trophic species in these studies? Stay tuned!

But as Mark Twain advised a young reporter: first get your facts straight, then you can distort 'em. McNaughton *et al.* acknowledge that their findings would be considerably strengthened by more data from tropical forests and other structurally complex systems. At present, their results rely heavily on structurally simple vegetation such as grassland and tundra. Moreover, the wide scatter of the assembled data with respect to the log–log linear regression proposed to describe them brings to mind the statistical maxim that, on log–log coordinates, even an elephant looks like a straight line. The report of McNaughton *et al.* does not have all the answers, but it has some and, better still, it raises important new questions.

Both the structural and the functional proportionalities found in food webs are purely descriptive. Though a model exists that explains much of food-web structure[5,12], it too is phenomenological; and there is no hint of a mechanistic explanation for the observed patterns in the report of McNaughton *et al.*. But ecology is a

NEWS AND VIEWS

very young science. A backward glance to the early stages of other, now maturer, sciences shows the tremendous power of empirical proportionalities. Joseph Louis Proust proved that elements combine in definite proportions by weight when they form chemical compounds (the law of definite composition), laying a cornerstone of the empirical support for the atomic theory[13]. Gregor Mendel found fixed proportions of different phenotypes in offspring in his experiments on plant breeding; his explanation in terms of genes was phenomenological. Erwin

Chargaff's discovery that the concentration of adenine equals that of thymine and that the concentration of guanine equals that of cytosine in DNA from various sources was one of the chief clues to Watson and Crick's solution of DNA structure. Time will reveal the scientific consequences of the new proportionalities in food-web structure and function. The possibilities are exciting. □

Joel E. Cohen is Professor of Populations at The Rockefeller University, New York, New York, 10021-6399, USA.

1. Cohen, J. *Nature* 270, 165–166 (1977).
2. Briand, F. & Cohen, J. *Nature* 307, 264–267 (1984).
3. Jeffries, M.J. & Lawton, J.H. *Freshwater Biology* 15, 105–112 (1985).
4. Sugihara, G., Schoenly, K. & Trombla, A. *Science* 245, 48–52 (1989).
5. Cohen, J.E., Briand, F. & Newman, C.M. *Community Food Webs: Data and Theory* Biomathematics Vol. 20 (Springer, Heidelberg, 1989).
6. Lawton, J.H. & Warren, P.H. *Trends Ecol. Evol.* 3, 242–245 (1988).
7. Pimm, S. *Food Webs* (Chapman and Hall, London, 1982).
8. Cole, J.J., Findlay, S.E.G. & Lovett, G.M. (eds) *Comparative Analyses of Ecosystems: Patterns, Mechanisms and Theories* (Springer, New York, 1990).
9. McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. *Nature* 341, 142–144 (1989).
10. Dirzo, R. in *Perspectives on Plant Population Ecology* (eds Dirzo, R. & Sarukhán, J.) 141–165 (Sinauer, Sunderland, Massachusetts, 1984).
11. Bianchi, T.S., Jones, C.G. & Shachak, M. *Trends Ecol. Evol.* 4, 234–238 (1989).
12. Cohen, J.E. & Newman, C.M. *Proc. R. Soc.* B224, 421–448 (1985).
13. Jaffe, B. *Crucibles: The Story of Chemistry* (Fawcett, New York, 1957).