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SPECULATIONS ON THE FUTURE OF FOOD WEBS

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PREFACE

Food webs should be more closely integrated with other descriptions of community ecology. Recent technology should be exploited to observe food webs better. The effects of human interventions on food webs should be more carefully studied and better understood.

INTRODUCTION

A food web describes only feeding relations in an ecological community. Food webs are therefore partial descriptions of biological communities. Present practice in constructing and reporting food webs could be improved in many ways (Cohen et al. 1993a). Here I speculate on future opportunities to link food webs with the rest of biology and with human concerns. I suggest that food webs should be more closely integrated with other descriptions of community ecology; recent technology should be exploited to observe food webs better; and the effects of human interventions on food webs should be more carefully studied and better understood.

These speculations are not the first on this topic (e.g., Fretwell 1987; Pianka 1987; Cohen 1991; Matson et al. 1992). As past sages knew, it is very difficult to predict, especially the future. You read further at your own risk.

INTEGRATING FOOD WEBS INTO COMMUNITY ECOLOGY

A major future direction lies in integrating food webs with other descriptions of ecological communities. Other descriptions, not all of them independent, include: species area relations; species abundance distributions; particle size (or body size) distributions; parasitism, competition, and mutualism; physical forms of growth; persistence in the face of perturbations; trophic pyramids and trophic levels; guilds; energy fluxes; material fluxes and balances in terms of chemical species and compounds (e.g., DeAngelis 1992); succession; phenology; life cycles of species; environmental variability, especially climatic; and so on. All these descriptions may depend on the physical and temporal scales selected for observation.

I pick out two specific examples for illustration: chemical fluxes and body size. One tends to think of the gross flows of carbon, nitrogen, phosphorus and other major constituents of living beings as directed by the feeding relations among organisms. In some cases, the direction of causality may be reversed: chemical fluxes may strongly shape the details of a food web. For example (Eisner and Meinwald 1987, p. 257), a Florida moth *Utetheisa ornatrix* feeds as a larva on a certain legume of the genus *Crotalaria* that contains pyrrolizidine alkaloids (PAs). The presence of PAs in the adult moth makes the moth unpalatable to a predatory spider *Nephila clavipes*. If the spider finds this moth in its web, and the moth has eaten the plant with the unpalatable chemical, the spider cuts the moth out of its web and the moth flies away. If the moth has been raised on a plant that lacks the unpalatable PAs, the spider eats the moth. Treating other insects normally eaten by the spider by topical addition of PAs makes the spider reject them. The chemicals in the moth's food determine which predators prey on the moth. It may be common for autotrophs, including algae, to produce toxic chemicals that influence which herbivores feed on the autotrophs, but in the example just given the PAs produced by the plant influence the spider predator of the moth herbivore. Anderson and White (1992) describe related examples in marine biology. How generally do specific chemical metabolites control food web structure? How often is such control exercised directly through the consumers of a given organism, and how often indirectly through the consumers of the consumers or even more remotely?

Body size also strongly influences the organization of food webs. About 90% of trophic links between pairs of animal species in natural communities go from a smaller prey to a larger predator (Cohen et al. 1993b). Body size of animals is also strongly associated with numerical abundance; roughly, smaller animals are more abundant. This implies an association, through body size, between the trophic position and the numerical abundance of animal species; roughly, animals that are higher in a food chain would be expected to be rarer than animals that are lower in the same food chain. Body size, species abundance, and food webs are all fundamental aspects of community organization; for the most part, these aspects have been studied as if they were independent. Now the relations among animal body size, abundance and food web structure need to be studied directly and quantitatively to gain a more unified view of natural communities.

What about plants, fungi, and other microbes that are neither plants nor animals? I know of no quantitative, non-anecdotal data on size and abundance for links from non-animal resources to animal consumers in natural communities.

USE OF NEW TECHNOLOGIES

A second major future direction for food webs lies in refining and extending the description and analysis of food webs through the use of new technologies. The first task is to identify what organisms are out there. Where microbes are important, as in marine biology and the soil, new molecular techniques hold great promise as means of characterizing organisms that have resisted traditional techniques of laboratory culture (DeLong and Ward 1992). To identify individual trophic links, many powerful physical and biochemical techniques are only beginning to be exploited. An enzyme immunoassay has been used to identify protein antigens of prey larvae in predatory larvae (Schoof, Palchick and Tempelis 1986). Scanning electron microscopy applied to the teeth of a fossil ape showed that it ate grasses and fruits (Ciochon, Piperno and Thompson 1990). Stable isotope ratios of sulphur, carbon and nitrogen can be used to identify feeding links (Peterson, Howarth and Garritt 1985, Rounick and Winterbourn 1986, Fry 1991). Although I have seen no applications to food webs, polymerase chain reaction (PCR) technology could, in principle, identify very small quantities of DNA in stomach contents, provided the DNA could be obtained before it was digested.

New platforms can extend the scope of observation of entire food webs. For example, manned submersibles have added significantly to knowledge of marine food webs (Youngbluth, Bailey and Jacoby 1990), and promise further additions (Myers and Anderson 1992). Unmanned submersibles, being cheaper and expendable, are likely to discover still more. Ecological remote sensing from aircraft and satellite (e.g., Greegor 1986; Rock et al. 1986; Waring et al. 1986) could be used to assess the functioning of food webs, in conjunction with ground truth supplied by down-to-earth field studies. A great frontier for high-technology studies of food webs is the dirt beneath our feet. Satellites can't see through soil, so far.

UNDERSTANDING THE EFFECTS OF HUMAN INTERVENTIONS

A third major direction for the future of food webs lies in understanding the effects of human interventions. Studies such as those of Vitousek et al. (1986) on the fraction of net primary productivity used by people could be verified, refined in detail, and extended to other measures of ecosystem function and other aspects of food web structure. Webs in which man is a minor actor (e.g., in foraging societies) and webs in which man is a major actor (e.g., in agricultural fields, fish ponds, and managed forests and wetlands) need to be compared with webs, if such can be found, in which man is an insignificant actor. Paradoxical phenomena in model food webs (e.g., Abrams 1992, 1993) and other paradoxical network effects analogous to Braess's paradox in

traffic networks (Cohen 1988) need to be better understood theoretically and empirically and better recognized in management.

An important precondition for the future study of natural food webs is the conservation of a diversity of natural habitats. In fact, human interactions with food webs are a two-way street: humans affect food webs, and food webs affect people. The notion of an endangered food web will gain political immediacy when it is recognized that a few of these webs feed billions of human beings, some of whom vote.

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REFERENCES

Abrams, P. (1992). Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *American Naturalist*, 140(4), 573-600.

Abrams, P. (1993). Effect of increased productivity on the abundances of trophic levels. *American Naturalist*, 141(3), 351-371.

Anderson, D. A. and White, A. W. (1992). Marine biotoxins at the top of the food chain. *Oceanus*, 35(3), 55-61.

Ciochon, R. L., Piperno, D. R., and Thompson, R. G. (1990). Opal phytoliths found on the teeth of the extinct ape Gigantopithecus blacki: Implications for paleodietary studies. *Proceedings of the National Academy of Sciences U.S.A.* **87**, 8120-8124.

Cohen, J. E. (1988). The counterintuitive in conflict and cooperation. *American Scientist*, 76, 576-583.

Cohen, J. E. (1991). Food webs as a focus for unifying ecological theory. *Ecology International*, **19**, 1-13.

Cohen, J. E., R. Beaver, S. Cousins, D. DeAngelis, L. Goldwasser, K. L. Heong, R. Holt, A. Kohn, J. Lawton, N. Martinez, R. O'Malley, L. Page, B. Patten, S. Pimm, G. Polis, M. Rejm nek, T. Schoener, K. Schoenly, W. G. Sprules, J. Teal, R. Ulanowicz, P. Warren, H. Wilbur, & P. Yodzis. (1993a). Improving food webs. *Ecology*, **74** (1), 252-258.

Cohen, J. E., Pimm, S. L., Yodzis, P. and Salda, J. (1993b). Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, **62**, 67-78.

DeAngelis, D. L. (1992). *Dynamics of Nutrient Cycling and Food Webs*. Chapman and Hall, London.

DeLong, E. F. and Ward, B. B. (1992). Biological oceanography from a molecular perspective. *Oceanus*, **35** (3), 47-54.

Eisner, T. and Meinwald, J. (1987). Alkaloid-derived pheromones and sexual selection in Lepidoptera. In: *Pheromone Biochemistry*, eds. G. D. Prestwich and G. J. Blomquist. Florida: Academic Press, 251-269.

Fretwell, S. D. (1987). Food chain dynamics: the central theory of ecology? *Oikos* , **50**, 291-301.

Fry, B. (1991). Stable isotope diagrams of freshwater food webs. *Ecology*, **72**, 2293-2297.

Greegor, D. H. (1986). Ecology from space. *BioScience* , **36**, 429-432.

Matson, P. A., Hunter, M. D., Price, P. W., Power, M. E., Strong, D. R., and Menge, B. A. (1992). Top-down and bottom-up forces in population and community ecology (special feature). *Ecology*, **73** (3), 723-765.

Myers, F. S. and Anderson, A. (1992). Microbes from 20,000 feet under the sea. *Science*, **255**, 28-29.

Peterson, B. J., Howarth, R. W. and Garritt, R. H. (1985). Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* **227**, 1361-1363.

Pianka, E. R. (1987). The subtlety, complexity and importance of population interactions when more than two species are involved. *Revista Chilena de Historia Natural*, **60**, 351-361.

Rock, B. N., Vogelmann, J. E., Williams, D. L., Vogelmann, A. F., and Hoshizaki, T. (1986). Remote detection of forest damage. *BioScience*, **36**, 439-445.

Rounick, J. S. and Winterbourn, M. J. (1986). Stable carbon isotopes and carbon flow in ecosystems. *BioScience*, **36**, 171-177.

Schoof, D. D., Palchick, S., and Tempelis, C. H. (1986). Evaluation of predator-prey relationships using an enzyme immunoassay. *Annals of the Entomological Society of America*, **79**, 91-95.

Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. H., and Matson, P. A. (1986). Human appropriation of the products of photosynthesis. *BioScience*, **36**, 368-373.

Waring, R. H., Aber, J. D., Melillo, J. M., and Moore, B. (1986). Precursors of change in terrestrial ecosystems. *BioScience*, **36**, 433-438.

Youngbluth, M. J., Bailey, T. G., and Jacoby, C. A. (1990). Biological explorations in the mid-ocean realm: food webs, particle flux, and technological advancements. In: Y. C. Lin and K. K. Shida (eds.), *Man in the Sea* vol. **2**, 191-208. San Pedro, CA: Best Publishing.