An Overview of Organismal Interactions in Ecosystems in Evolutionary and Ecological Time

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ABSTRACT

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The argument is developed that, in terms of development of terrestrial food webs, ecology recapitulates phylogeny. This is because food webs are based on bacteria, protozoa and fungi, and plants and animals are nested within links among these taxa. For most of evolutionary time, the only substrates for colonization were soil, water and submerged sediments. The development of new evolutionary lines built directly from the bacteria, through mutualistic associations, to form eukaryotes, including plants. As larger organisms evolved, micro-organisms were utilized as mutualists, providing complex biosynthetic pathways, facilitating extensive adaptive radiation. Thus, present food webs reflect ancient associations; the oldest taxa form the base of the terrestrial food web, feeding on organic debris, with progressively more macroscopic forms at higher trophic levels.

INTRODUCTION

Many members of the general public, including biologists, are convinced that large plants and animals are the most important organisms on earth. The organisms we relate to most easily, being the shrubs, trees, birds and mammals, are translated subliminally into those which are most significant. I will call this view "Noah's Ark Ecology" because it has a long tradition. This perspective has been influential in the development of concepts in general ecology and evolutionary biology.

In actual fact, birds and mammals illustrate only diminutive radiations compared with many other taxa of smaller organisms, such as nematodes, mites, insects, protozoa and bacteria. And a better perspective, in my view, is obtained by considering the evolution of life on earth and the evolutionary time over which adaptive radiations have proceeded. This view forces an appreciation of micro-organisms as the dominant forms of life for the vast majority of time since life began. The bacteria (Monera) evolved some 3.5–3.9 billion years ago

(Woese, 1984), and were the only organisms on this earth for perhaps, all but the last billion years. The protozoa (Protista) and fungi evolved about 1 billion years ago (Margulis, 1981). But the Kingdom Animalia began perhaps only 0.75 billion years ago, and the Kingdom Plantae only 0.45 billion years ago (Margulis, 1981). So, micro-organisms were the exclusive occupants of the biosphere for about 3 billion years, while larger organisms such as animals and plants have existed for less than a billion years.

Remembering these points forces a perspective different from the Noah's Ark Ecology: (1) most of evolutionary time was spent with soil, water and submerged sediments as the only substrates; (2) the development of new evolutionary lines built directly from the bacteria through mutualistic associations — Urkaryotes + Eubacteria (now mitochondria) = Eukaryotes; Eukaryotes + Cyanobacteria (now chloroplasts) = Plants (Woese, 1984). These were two of the greatest evolutionary innovations ever to occur in the biosphere; (3) as larger life forms evolved they were colonized by micro-organisms, and the evolutionary capacity of micro-organisms and their biosynthetic abilities, including "genetic engineering", were exploited fully by larger forms of life, or the latter were fully exploited by micro-organisms; (4) in sum, the evolution of animals and plants depended entirely on micro-organisms, and the tight link between the taxa has hardly ever been broken (Malloch et al., 1980; Margulis, 1981; Boucher et al., 1982). One of the themes in this chapter is that mutualism facilitates adaptive radiation.

In a very general sense, I would argue that ecology recapitulates phylogeny. At the level of Kingdoms, food webs have been built along phylogenetic lines with the oldest taxa at the base of the web feeding on organic debris, and progressively more macroscopic forms at higher trophic levels. Just as 1% of "snow" on our television screens is caused by remnants of the "big bang", making the beginning of time over 15 billion years ago a tangible event, so present food webs reflect ancient relationships. This is another theme of the chapter.

ECOLOGY RECAPITULATES PHYLOGENY

Whittaker's (1969) five-kingdom system for classifying life on earth established a scheme for understanding the evolution of food chains and food webs in the biosphere. Food webs have built up in an additive way; so that more derived taxa depended fully on earlier forms of life, as sources of food, as mutualists, for biosynthetic pathways, for acquisition of new genetic material and so on.

I would modify Whittaker's view only slightly, to ensure that we recognize the role of Monera, Protista and Fungi in the further radiations of the Kingdoms Plantae and Animalia (Fig. 1). Land plants may well have evolved from the mutualistic association of a green alga and an aquatic fungus (Pirozynski and Malloch, 1975), and are still associated mainly with fungi in the form of
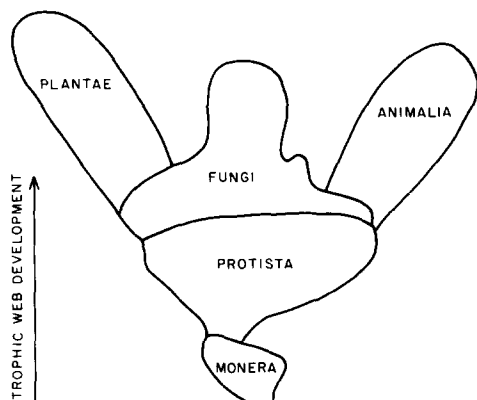
Fig. 1. Whittaker's (1969) five-Kingdom classification of life on earth, altered slightly, to emphasize that the Kingdoms act as building blocks in food-web development. The alteration broadens the base of the fungi, to illustrate their essential role in the radiation of plants and many animal groups.

mycorrhizae (Malloch et al., 1980), and other fungal endophytes (e.g. Bernstein and Carroll, 1977; Clay et al., 1985a,b). These associations have been very important in the evolution of food-web interactions. Animals also depend on mutualists of many kinds: bacteria as fermenters of plant food for ruminants; bacteria and protozoa as fermenters of plant food for termites; and fungi as converters of cellulose to sugars for almost all "wood-feeding" animals (cerambycid beetles, ambrosia beetles, bark beetles, wood wasps and other primitive insects taxa listed by Hamilton (1978). In addition, earthworms may well be associated mutualistically with bacteria and fungi, and bacteria associated with nematodes act as pathogens on the hosts the nematodes invade.

It is no leap of faith to declare that micro-organisms have dominated the biosphere and still do. As was emphasized earlier, they have had 3 billion years alone on this earth to evolve their intricate relationships and biosynthetic pathways. Burkholder (1952) illustrated that all 9 possible types of coaction between weak and strong organisms could be illustrated in the bacteria, protozoa and fungi. Micro-organisms are small, with large populations and short generation times, so their evolutionary capacity is enormous, and their niche space is huge. In contrast, the large organisms have a relatively brief fossil record and rather limited evolutionary potential, with consequent relatively minor adaptive radiation on this earth. Before the development of an oxygenated atmosphere, bacteria had evolved with the major biosynthetic pathways in an anaerobic world (Margulis, 1981). When the Eubacteria evolved the capacity to photosynthesize, aerobic processes were added to the anaerobic in biogeochemical cycles. So, the easy answer for the evolution of larger orga-

nisms was simply to acquire micro-organisms, pre-adapted with complex enzyme systems for acting as mutualists.

I am convinced that the evolution of life on earth tells us a great deal about the development of food webs, but there is much more to discover on this theme. Trophic relationships developed in nested fashion (Fig. 2) with each Kingdom nested within, and dependent upon, the Kingdoms which evolved before. This view differs radically from the Noah's Ark perspective: (1) micro-organisms provide the food and mutualists for almost all higher forms of life, being at the base of food webs; (2) their evolutionary history and evolutionary potential is so much more extensive than larger organisms, that their capacity to solve biological problems is infinitely greater, and this capacity has been exploited during the adaptive radiation of animals and plants; (3) most of the basic links in terrestrial food webs are in the soil, for this is the medium of primaeval importance, and most organisms in terrestrial ecosystems still live there; (4) obviously, all efforts at a comprehensive understanding of trophic systems should begin and end with the soil biota; (5) this almost unassailable set of
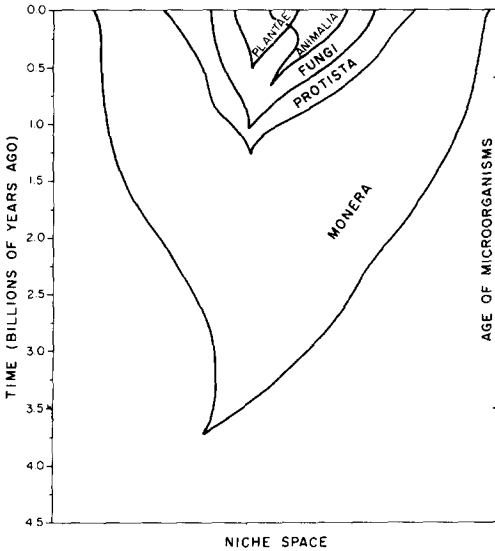

Fig. 2. The nesting of Kingdoms of organisms in relation to niche space exploited by each Kingdom and the time over which these Kingdoms occupied the earth. Each Kingdom after the Monera, was dependent on all earlier Kingdoms for food and mutualists. Note that radiation of plants and animals was also facilitated by mutualistic association in pollination and seed dispersal (Regal, 1977), illustrated by the overlap of their niche spaces in the figure. Niche space occupied by each Kingdom is used only to illustrate the relative sizes of adaptive radiations, related to the size of the organisms and their evolutionary potential. Times of origins of Kingdoms are based on Margulis (1981). The ability to develop in the aerial biosphere has been achieved only recently by plants and animals, but all other Kingdoms have colonized with members of these groups.

conclusions is certainly not consistent with the world view of most ecologists, or most ecological research.

CONTEMPORARY FOOD WEBS

Most food webs illustrated in ecology text books, including my own (Price, 1984) miss more than half the organisms involved in the real transfer of energy and nutrients. They emphasize macroscopic organisms and omit soil bacteria, mycorrhizae, endosymbionts in herbivores and so on. A big animal such as a giraffe has evolved only because it can support a microcosm of bacteria which are still doing roughly what the methanogens did before oxygen developed in the atmosphere from 2.2 to 1.8 billion years ago (as indicated by the banded iron formations when iron oxides were deposited in sediments — Walker et al. (1983) give a wider spread of ages). Moreover a big animal can get enough food only because big plants are supported by a microcosm in the soil, particularly mycorrhizae, fungi and nitrogen-fixing nodulating bacteria. Big organisms are very dependent upon small organisms, without the reverse being true (as suggested in Figs. 1 and 2).

The situation of termites feeding on plant tissue, which may be considered as a two-species interaction, actually illustrates the union of Kingdoms in trophic webs very well. The plant depends heavily on interactions in the soil and a bottom-heavy food web in terms of both number of species and population sizes, and possibly even biomass (Fig. 3). The plant may have to be colo-
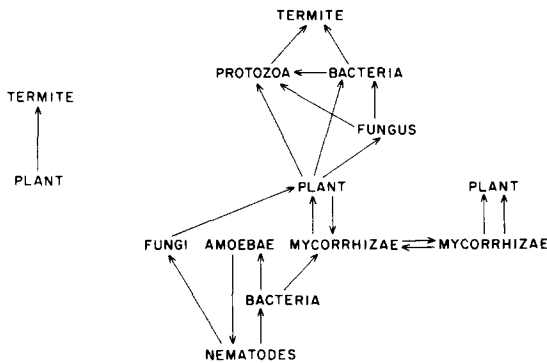

Fig. 3. A conventional illustration of a food chain between a termite species and dead plant material (left), and a more accurate, but simplified food web of the same association (right), which recognizes that the plant is part of a network of interactions in the soil and the termite is a microcosm of interactions, derived from ancient associations in rotting plant material. In some cases fungi may detoxify plant chemicals that would otherwise kill protozoa in the termite paunch, as in use by termites of Bald Cypress. Arrows indicate direction of movement of energy and nutrients. Based on information in Breznak (1975), Nordbring-Hertz and Jansson (1984) and Chiariello et al. (1982).

nized by a fungus which breaks down toxins (as with *Coptotermes* on Bald Cypress), before the protozoa can persist in the paunch of the termite (see also Martin, 1979; Waller and La Fage, 1987), and the bacteria are methanogens and nitrogen fixers essential to the protozoa (Breznak, 1975). Indeed, the large organisms, plant and termite, act as substrates, on and in which micro-organisms still do their work. The terrestrial food web is founded in the soil, and only marginally has it emerged from the soil. Never has it divorced itself from the soil. Large organisms are still very much tied to the life of small organisms; this can never be any different (see also Kurihara and Kikkawa, 1986). The small organisms have the upper hand evolutionarily, and if we are looking for rapid evolutionary change, subtlety, finesse and biochemical and genetic wizardry, we should study the small organisms, most of which are in the soil.

It is clear that the smaller an organism, the greater the organism number of species (May, 1978) and the size of the population (Peters, 1983). Therefore, ecological interactions become much richer, and more complex, between small organisms. Also, because of the great age of many taxa of micro-organisms, interactions between them are highly evolved. For example, nematode-trapping fungi are beyond the intuitive perception of most biologists (e.g. Nordbring-Hertz and Jansson, 1984).

Once macro-organisms evolved, food webs continued to develop along predictable evolutionary pathways, with early taxa such as nematodes, mites, small primitive insects, springtails and segmented worms as the next stage in trophic-web development. An example is from litter decomposition in the Chihuahuan desert, studied by Santos and Whitford (1981), Santos et al. (1981) and Parker et al. (1984) (Fig. 4). As with many other food webs based on decaying organic matter, bacteria, fungi and protozoa form the real link between plant
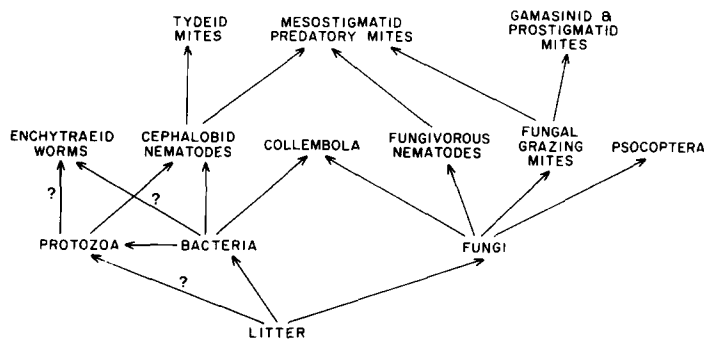

Fig. 4. The food web involved with litter decomposition in the Chihuahuan desert studied by Santos and Whitford (1981), Santos et al. (1981) and Parker et al. (1984). Note that the food web is structured in a sequence similar to the evolution of Kingdoms in Fig. 1; with the basic decomposers of cellulose as bacteria and fungi, and perhaps protozoa, with protozoa predacious on bacteria, and metazoans feeding on these three ancient Kingdoms. Arrows indicate direction of energy and nutrient movement.

matter and the rest of the food web, with the next trophic level composed of ancient groups of microarthropods, nematodes and other worms. This complexity of interactions results in a high probability that indirect effects become important, for there are so many alternative pathways along which interactions may develop. It is also important to note that, even after all these energy transfers, organisms are still not large enough to become what many ecologists regard as "bird food" (i.e. arthropods large enough to become an important component of insectivorous bird diets).

The nesting of small arthropods within the template of Monera, Protista and Fungi was the focus of attention in Hamilton's (1978) original view of evolution in rotting wood. "Many of the major insect groups have diverged there" (p. 155) he said, listing 25 orders of insects which were associated primitively with rotting trees. Many of these orders have remained associated with these habitats, and the micro-organisms that enable utilization of wood as food, or provide a direct source of food: bacteria and protozoa for wood roaches and some termites, fungi for the gardens of leaf cutter ants (e.g. Stradling, 1987) and other termites (e.g. Waller and La Fage, 1987), and the fungi, yeasts and spores eaten by Zoraptera, Psocoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera and Acarina listed by Hamilton.

Other taxa associated primitively with rotting wood have left that site and colonized living plants, or senescent plants, or standing newly dead trees, but they have always taken the micro-organisms with them, which mediate the interaction between plant and herbivore: wood wasps, bark and ambrosia beetles, cecidomyiid flies, thrips, lice and many other groups (Buchner, 1965; Price, 1984).

Now we have reached animals large enough to become important as, what the ornithologists call, "bird food". We enter the realm with which the typical ecologist is familiar. We have followed the trophic web to the point where the "Noah's Ark Ecologist" is at home, and where much of conceptual ecology has developed.

But my argument has helped me to be certain that all terrestrial trophic systems depend upon the soil and decaying matter, both in evolutionary time and ecological time. It is from the soil that trophic systems have emerged to colonize aerial habitats, but still their roots are in the soil, in both senses of the word "roots". The potential is always there, that the soil microcosm will affect all other trophic interactions as matter moves up the food chains and webs. The nesting of taxa in their trophic relations within the confines of formerly evolved groups, and the great species richness of earlier taxa, places most of ecological interactions squarely among small organisms, most of which are in, or closely associated with, the soil. Only after many trophic links and many other interactions do organisms become large enough for the typical "Noah's Ark" and "Bird Food" kinds of ecologist.

So, to the question "What is the importance of interactions between soil

organisms in ecosystem function?" the answer must be that they are funda-
mental to the working of all terrestrial systems, both in evolutionary and eco-
logical time.

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