

Food chain dynamics: the central theory of ecology?

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The analysis of ecosystems is experiencing a revolution in both perspective and method. The perspective of basically food or habitat limited populations is giving way to a more balanced perspective including varying levels of predation. The heavily descriptive, detailed methods of the traditional naturalist and the modern system analyst are being complimented with models of Hutchinsonian simplicity, where idealized, easily understandable models are offered as an approximation to reality. The analysis of Hairston, Smith, and Slobodkin is presented as the major turning point in this revolution, where some key assumptions about trophic levels and population regulation are first used as a basis for analysis. Modeling by Rosenzweig put these assumptions on solid ground, and introduced a key variable, primary productivity. Fretwell and Oksanen and his colleagues generalized and extended the kind of logic used in these pioneering studies, to provide a theory that could be central to all of ecology. This theory is reviewed in the present study, is extended to include the field of community ecology, and arguments are offered defending the position that this research program, called Food Chain Dynamics, could be regarded as the central theory of ecology, at least as important as the theory of evolution.

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Introduction

In 1960, the result of an intensive seminar at the University of Michigan was published, authored by three of the most critical and careful thinkers working then in ecology. The seminar, called "Etude", had met for an entire semester, had carefully discussed the central issues in ecology and had arrived at a remarkably general conclusion. The authors were Nelson Hairston, Frederick Smith, and Lawrence Slobodkin, and their paper published in the *American Naturalist* was titled: Community Structure, Population Control, and Competition. It crystallized a scientific revolution that began with Elton's 1927 classic *Animal Ecology*, and had reached widespread attention with Lindeman's great classic: *The trophic-dynamic aspect of ecology* (1942). This revolution is still in progress. My goal in this paper is to review the progress of that revolution, and to perhaps hasten that progress to producing the kind of scientific fruit that has made our generation so prosperous.

The revolution, briefly, is shifting the ecological thinking of both population and ecosystem ecologists.

Although common knowledge among hunters and farmers explained population size in terms of both predators and food, one existing dogma in ecology, as exemplified by both David Lack's, and Andrewartha and Birch's seminal books on population regulation, was to view natural populations as primarily limited from below by resources, habitats or food. To cite some prominent examples, until very recently limnologists have largely treated eutrophication, a major distinguishing characteristic of aquatic systems, as resource determined; biogeographic botanists have usually reached the same conclusion about the distribution of plants. This view still has its proponents (White 1978), and has found application in the fields of range and wildlife management in the United States which are heavily committed to the provision of habitat. The revolution which was brought into focus by Hairston et. al. (1960, hereafter referred to as HSS) placed this rather restricted point of view in a larger perspective where predation or grazing play roles equal in importance to that of resources or habitat. In their analysis, predation plays the key role for some populations, and resources for others.

This was, at the time, a new perspective. Its emphasis on regulation, balance of nature, and control of populations was considered naive by some ecologists. Moreover, it treated hypothetically whole ecosystems in a way that simplified the more complex descriptions of Gene and Howard Odum (E. P. Odum 1959, H. T. Odum 1957). As expected by the philosophers of science, HSS was honored with quick resistance in print (e.g., Ehrlich and Birch 1967, Murdoch 1966), and immediate status as a classic in the field. It has been continually if tentatively cited since then (about ten times a year since its publication, according to Science Citation Index, with the highest rates in more recent years) and has spawned, sometimes indirectly, a significant research programme (Lakatos 1972) that I submit is earning for it the role: The central theory of ecology.

Development of the theory

Lindemann, building on the definitions of Elton (1927) offered (1942) an initial synthesis of ecosystems and trophic levels that allowed, as Hutchinson said in a postscript to Lindeman's paper, a "productive abstract analysis". What HSS accomplished was to use Lindemann's abstractions as building blocks for a specific hypothesis. They began with the observation that excessive or widespread destruction of vegetation by grazers is rare and that there seemed to be an abundant, under-exploited food resource available to animals on the second trophic level. HSS deduced from the abundance of vegetation that the grazer trophic level was not food limited and was therefore predator limited. This required the assumption that trophic levels, as a whole, could be limited by food or predation, and that either food or predation, but not both limited these levels. They further argued that the limitation of grazers by predation was what kept grazers from limiting their plant food resource. Although it is clear that not all plants can be eaten by all grazers, HSS implied that every plant can be sufficiently grazed by some grazer to be substantially reduced in or even eliminated from the producer trophic level. Thus, they implicitly rejected the hypothesis that plant defences account for the abundance of vegetation.

HSS argued that since grazers must be predator limited, their predators must be food limited, and so generally free of higher level predation. Thus, they arrived at the assumption of a three link food chain.

While the topic of Hairston, Smith and Slobodkins' seminal paper grew out of a tradition begun by ecologists who brought the concept of trophic level to maturity, it was also heavily influenced in methods by G. E. Hutchinson, who in response to Harold Jefferies's book, *Scientific Inference* (1931) had begun to introduce a method or approach to ecology which was to allow the growth and development of modelling techniques. A. J. Lotka, V. Volterra, and others (see Kingsland 1985) had already introduced the logistic and pred-

ator-prey models into ecology in an effort to describe nature with mathematical precision. But, these models had a mixed reception, and were generally distrusted by most ecologists, who approached the science with a heavy descriptive bias. Hutchinson combined these models with a philosophical attitude that sought simplifying, even qualitative understanding of patterns in nature. Hutchinson's approach to ecology was demonstrated by HSS (both Smith and Slobodkin were Hutchinson's students). MacArthur (1958) had already demonstrated its usefulness as an approach for population level problems, and the research strategy was eventually to gain wide acceptance and much success in that arena. It still is little used in approaching whole ecosystems, however, being eclipsed by the more complex systems approach. I suggest that ecosystem analysis is significantly hindered by this fact.

In 1963, Rosenzweig and MacArthur began to construct (or revive) predation models of population regulation, which gave more precise meaning to the concept "limited by predation". Rosenzweig (1968, 1969, 1971, 1973a) then made two extremely critical advances in the theory. First, he modelled a three link food chain and so brought clarity and objectivity to the HSS arguments. Second, he showed that primary productivity was extraordinarily variable in terrestrial ecosystems, and was a critically important variable that could be easily incorporated into the models he and MacArthur had been developing.

The application of the assumptions of HSS to more than three trophic levels, while not a new idea (see Varley, 1959, for an early foreshadowing), was independently suggested, first by Smith (1967) and later by Wiegert and Owen (1971). Recall that HSS concluded that:

- 1) "Producers, carnivores and decomposers are limited by their respective resources in the classical density-dependent fashion.
- 2) Interspecific competition must necessarily exist among the members of each of these three trophic groups.
- 3) Herbivores are seldom food-limited, appear most often to be predator limited, and therefore are not likely to compete for common resources".

This argument considered a three link food chain, with the top link being limited by food, and exerting regulatory pressure on the second link, the grazers. They argued that because of predation pressure, grazers are unable to regulate their food resources. Thus, the producers are left to compete for resources: sun, water, or nutrients. My own efforts to generalize (1977) this argument sought a wide application of the hypothesis, to grasslands, deserts, and aquatic systems where producers seemed to be relatively scanty. I argued that deserts were basically one link systems, grasslands two links, forests three links, and marshes four links. I made much (probably too much) of the fact that this ter-

restrial productivity cline shows a cycle of woody, grassy, woody, and grassy vegetation (desert shrubs, prairie grasses, forest trees, and marsh grasses). Even-linked food chains (2, 4, 6, etc.), by the arguments of HSS, should be based on grazer limited producers, which I interpreted to mean grasses. Conversely, odd linked chains should be supported by resource limited plants, which to me meant woody vegetation. Thus, increasing food chains means alternating odd-even lengths, which "explained" the alternating woody-grassy plant forms. By supposing that food chains got longer as productivity increased, I offered a tidy, if naive, theory of ecosystems. This attracted a thorough development by Oksanen et al. (1981).

Oksanen's contributions (1981, Oksanen et al. 1983) basically tried to place my own analysis in the mainstream established by Rosenzweig. Rosenzweig had modelled two and three link ecosystems and had explored the impact of variable productivity on two link systems. He had not explored the impact of variable productivity on three or four link systems. Moreover, Rosenzweig had derived predictions about stability and productivity and about equilibrial biomass and productivity, but for two-link food chains only. Oksanen extended the analysis to three-link food chains and, more importantly, found data from nature to test some of the predictions on biomass. These predictions were dramatically confirmed, establishing this development and approach as a viable way to the understanding of ecosystems.

My own verbal arguments had recognized the role increasing productivity might play in adding trophic levels to food chains, and had wrestled with the problem that while trophic levels have to exist as discrete integers, productivity varies continuously. How increasing energy flow might cause a food chain to go from three to four levels was not clear, but one possibility was to define non-integer food chain lengths that could vary continuously from one integer to another. The 2.5 link food chain, for example, was defined as containing a producer community, a grazer community, and a predator community; but the predator community was so inefficient that the predators had only a modest impact on the grazers. Thus, predator removal would result in a small increase in the abundance of grazers, but grazer populations should even normally be so close to the carrying capacity set by plant productivity that competition between grazers should be important even in the presence of predators.

The models of Oksanen et al. (1981) gave a clear way to define the concept of non-integer food chains, and provided the necessary link to justify a Hutchinsonian approach to ecosystem analysis. We followed Rosenzweig's definition of predator or consumer efficiency as the minimum standing biomass of resource population needed for positive growth in the consumer population. Thus, more efficient predators have positive r values on lower prey populations. This value was assumed to be

fixed and can be compared directly to the predator-free resource determined carrying capacity (K) of the prey. Thus, the importance of the predator is relative, varying according to the productivity of the system, since increased productivity of the resources increases the prey's carrying capacity, but does not affect the predator's efficiency. Low productivity could cause the prey K to be below that of the predator's efficiency, in which case predator growth rate, r , would be below zero, and the predator could not persist in the system. Increasing productivity might increase the prey K to a value 10 times as high as the predator's efficiency. In the latter case, the predator-prey equilibrium should keep prey populations at one-tenth the level set by the prey's resources, and the predator should be a dominant part of the system.

Since the prey's carrying capacity could be any number of times as large as the predator's efficiency, there is a problem of deciding when exactly a new link has been completely added. There are two possible solutions suggested by the models. The increasing carrying capacity and productivity of the prey results in increased numbers of the predator which could in turn attract (or support) some sort of limitation on its population, by a new predator, by disease, by cannibalism, or some self-regulation such as territoriality. Then, further increases in the prey's productivity would not be consumed and the prey populations, which had up to this point not been increasing even though becoming more productive, would themselves start to increase again with any increased productivity. We could define a predator as completely present if and only if it becomes so numerous that it is itself on the verge of being so limited.

A second possibility would have the resource population become saturated with its own increasing resource as its potential carrying capacity increases. Thus, as overall, or potential productivity increases, the resource or prey population which is held at a constant level by predators may find itself unable to consume all the increase. A plant population held down by grazers would be unable to photosynthesize as fast as water and nutrients might allow, and so the increase in evapotranspiration that might have meant increased energy flow in the system is simply lost. A grazer community held down by predators may not be able to consume all the plant material produced, and so organic matter is accumulated or is lost as detritus instead of flowing into the grazing food chain and increasing its length. The point at which productivity of the prey ceases to be resource dependent, because prey biomass is held down by predation, is another place where its predator could be defined as being fully present. At our present stage of knowledge, it is difficult to choose between these approaches, but it suffices for my proposal to know that some way exists.

There thus are two points – a low productivity, low prey carrying capacity point where the predator is only present as a visitor or scavenger; and a high productivity

point where the predator is "fully present". Between these two, there should be a continuous gradient of systems, where decimal values of food chain length could be easily defined, allowing us to measure the food chain length of systems in a precise and meaningful manner.

These more general models had a more general application, extending HSS's already sweeping statements about forests to aquatic and to non-forest terrestrial ecosystems. They allowed the basic assumptions of HSS to make sense of ecosystems where most plant material seems indeed to be grazed (many aquatic systems, with inverted trophic pyramids - See Wiegert and Owen 1971; grasslands). They also accounted for the curious distribution of woody and non-woody plants, for the immense variations in body size of individuals at all trophic levels, and for patterns in the occurrence or non-occurrence of competition.

Meanwhile, empirically oriented ecologists paralleled this development with advances that questioned the idea that food or habitat alone need be considered when making predictions about or managing ecosystems. Paine (1980), drawing heavily from the food web ideas of Elton (1927) found that predation pressure was critical in determining the outcome of competition within a community. Limnologists have now successfully overturned the idea that nutrient input or organic pollution is the sole cause of eutrophic waters. Classic studies by Brooks and Dodson (1965) and by Hrbacek (reviewed in Benndorf et al. 1984) have been followed by a host of experimental or observational studies (e.g., Hall et al. 1970, Zaret and Paine 1973, Spodniewska and Hillbricht-Ilkowska 1973, Stenson et al. 1978, Gliwicz et al. 1978, Shapiro and Wright 1984, Spencer and King 1984) all of which prove beyond reasonable doubt that the presence or absence of primary or secondary predation frequently is a main determinant of both phytoplankton biomass and productivity, through food-chain dynamics of the sort proposed by HSS and by Oksanen et al. (1981). These studies frequently do the experiment suggested by Oksanen's models, removing a top predator (often a fourth link) and watching their prey (link three) increase in population up to a resource determined carrying capacity. This, in turn, allowed the link three prey to reduce *their* prey (often second level zooplankton grazers) to the level determined by their efficiency, preventing these zooplankters from holding down the plant biomass. The result is an algal bloom, increased turbidity, and incidentally increased productivity. These are exactly the patterns predicted by Oksanen's models.

Finally, study of the ecology of grazing ecosystems (grasslands grazed by large mammals) has implied that the large grazers have a major impact on the form and abundance of the vegetation (e.g., review by McNaughton 1984) as predicted by the theory. The unproductive grasslands presumably have such a low grazer carrying capacity that predators are relatively inefficient and so unable to have much impact on the

grazers. The grazers, though limited themselves to modest levels by low plant productivity still are able to limit plant biomass below the grazer free equilibrium biomass. This is thus at least a two-link system. If an increase in productivity results in an increase in grazers with no increase in plant biomass (e.g., the desert grassland-short grass prairie transition), we can regard the system as varying from two-to-three links. When grazers are finally held down by predators, so that increased plant productivity produces an increase in plant biomass, then the three-link system begins (3.0, 3.1, 3.2 and so on).

Food chains and community structure

In the 1981 models of Oksanen et al., we essentially modelled a system of one plant species, one grazer species, and one predator species. We supposed that the trophic levels could be treated as species; and, to a degree, this assumption is valid (at least, the observed producer biomass-productivity patterns behave as if this were true). However, this assumption also predicts the complete absence of predators in 1 to (but not including) 3-link systems. Grazers should be absent in 1 to 2-link systems (deserts). This is not the case (Pimm and Lawton 1977), although in terms of biomass and energy flow, grazers in deserts take only a small part (1-3%) of the productivity and predators are energetically almost negligible there and also in desert grasslands. In order to accommodate this contradiction to the prediction, I therefore propose to modify the assumptions of the 1981 models, preserving the major assumptions of HSS, but hopefully refining the model so that a research programme in the sense of Lakatos (1972) can continue.

There is an additional justification for this refinement. To treat trophic levels as a single species population ignores the whole of community ecology, where intra-trophic level interactions shape both species populations and the trophic level itself (e.g., MacArthur 1972). For the food chain dynamics model to qualify as a central theory, it must create a perspective that facilitates understanding at the community level.

To begin, consider the theoretical possibility of competitors which, in the absence of predation, replace one another on a unit-biomass per unit-biomass basis. Thus, I imagine a series of tree species making up forests that are all similar in overall biomass even though species composition from forest to forest may vary. I imagine a group of mammalian grazers which make up herds similar in over-all biomass irrespective of which species are in the herds. This ideal is, of course, not to be found in nature, but natural communities may approximate it. Thus, I continue to build a Hutchinsonian model.

Next, I borrow an idea from Paine's illuminating work in the intertidal (1966), and suppose these competitors are differentially vulnerable to predators, and are differentially competitive. I further assume that their vulnerability is positively related to their competi-

itive ability. Thus, in the absence of predation, a good competitor will prevail; but, in the presence of predation, the good competitor will be eliminated (or reduced) to be replaced by a weaker competitor, a species less vulnerable to predation.

Finally, I define a "donor-controlled predator" as a predator which only impacts the population size of its prey by removing individuals that have high probabilities of dying from starvation or exposure. A population of prey that is food-limited still might over-shoot, or be above, its carrying capacity, perhaps due to seasonal or other fluctuations in resources. Then, the population enters a decline and stressed individuals appear, mostly poorly established seedlings or juveniles. These individuals are unable to maintain a positive energy balance, and are at least slowly starving. Their energy situation makes them uniquely vulnerable to inefficient predators, which catch and remove them. The prey population declines more rapidly to the lowered carrying capacity; but, once there, all individuals potentially have a balanced energy budget, and become able to avoid the inefficient predators that had been removing their population excess. These predators must then switch to other prey.

Removing a donor-controlled predator does not result in higher prey populations, and may result in lower ones. Population declines take longer, but overgrazing or over-exploitation of the prey's food supply during the decline could result in a lower carrying capacity. In the case of removed donor-controlled grazers, the reduced rate of nutrient cycling may cause a decline in plant production and biomass.

This concept of donor-controlled predator is taken from the studies of Errington (1963), on muskrats (*Ondatra zibethica*) and mink (*Mustela vison*), where the muskrat population is apparently controlled by food supply, and minks only prey on individuals rejected from the food rich environments by social behavior. Provided that Errington is right, removal of minks would not influence the number of muskrats in marshes at all, and would only result in the population of starving muskrats in peripheral habitats lasting a bit longer.

Armed with these definitions, we can envision an increase in food chain length along a productivity gradient. Before doing this, we need to note Pimm's discovery (1979) that stability is as or more critical to food chain length than productivity. In terrestrial systems, productivity and stability are correlated, so a productivity gradient might well behave as the models predict even though stability is really very important. This important question does not, therefore, prevent us from describing such a gradient in terms of the model, and the new assumptions described above.

We begin with a completely barren habitat with food chain length zero. As soon as a single plant can survive there, we define the ecosystem as having food chain length slightly above zero. As productivity and plant biomass increase, the food chain can be operationally

defined as being longer (0.1, 0.2, 0.3, and so on) food chains, until a grazer appears. At this point, the grazer may be donor-controlled, or may be able to control some but not all the species of plants present. The food chain is defined as having length one at the point of appearance of the first grazer. Further increases in plant productivity result in increased plant biomass through the increase of grazer free plants, or of plants with only donor-controlled grazers (e.g., a grazer that eats only floral parts, or seeds, but not so many that the establishment of new individuals would be curtailed). The grazers may well limit highly competitive but grazer vulnerable species, and most biomass increase may come from grazer resistant species. Thus, grazer biomass increases very slowly with additional productivity. Plant diversity also increases, due to grazers limiting competitive species, in the way Paine (1966) has shown in other ecosystems. Food chain length increases from one up to two links. Theoretically, I predict that the productivity-biomass graph would show a simple linear trend from barren to two-link ecosystems. Any predators in these ecosystems would be donor-controlled or limiting only to a few of the grazers.

At food chain length two, grazers will have increased in abundance and diversity to the point that they are finally able to control the total plant biomass. Predators will certainly be present, and probably even some 2nd degree predators, but these are either restricted to certain species, or are all donor-controlled. In any case, further increases in productivity result in no increase in plant biomass, but in accelerated increase in grazers, which now can eat every plant that is involved in the increase in production. Predators influence grazers here in the same way grazers had influenced the plants in the one to two link systems. Individual grazer species are limited, but other grazers increase and take up the slack, so to speak, so that grazer biomass and diversity increases. Plant diversity drops here as only grazer-resistant species can survive.

Eventually, the biomass of predator-resistant grazers reaches a point where predators able to eat them all can persist, and predators begin to limit the over-all grazer biomass. The food chain length now is set at three, and now predators begin to rapidly increase in abundance as productivity increases. Grazers are held down and their diversity decreases, due to elimination of predation vulnerable species. However, plants begin to increase as increased productivity but curtailed grazing pressure allows greater plant biomass. This release of plant biomass and diversity will probably also eventually result in some increase in grazer diversity.

This scenario allows the definition of very precise food chain lengths, according to breaks in the graph where plant and grazer biomass is plotted against productivity. Thus, considerations on food chain dynamics do not become stranded in the immense complexity of real food webs. So, I will from this point on refer to the food chain lengths in the abstract way discussed above and

abbreviate the dynamical food chain length as *dfcl*. This emphasizes the dynamic or regulatory nature of the links I count. Only when grazers regulate plants are grazers counted, and only when predators regulate grazers are they fully counted.

Modelling which includes a predator of predators or a fourth trophic level has not proceeded beyond that presented by Smith (1967), although the arguments of Fretwell (1977) were not limited. In these arguments the inclusion of a fourth link results in a limitation of the third link, the predators of grazers. Then the grazers are freed to limit the producers, which therefore become reduced in biomass.

Looking just at the critical points of the theory – the 1, 2, 3, ... link food chains, we have the following verbal descriptions:

dfcl = 1. A poor, barren plant community with almost no grazers.

dfcl = 2. A fairly rich or dense plant community with light grazing which affects plant form and diversity, but which is insufficient to significantly affect biomass. Competitive plants still dominate, but many antigrazing adaptations are present. A relatively lush desert is a good example.

dfcl = 3. An open, highly grazed plant community, with productivity much higher, and perhaps coverage, but plant biomass the same or smaller in comparison to 2. Shortgrass to mid-grass plains provide a good example.

dfcl = 4. A rich, lightly grazed plant community, again much more productive than 1. or 2., with grazers small in body size and lacking signs of competition, being controlled by predators. A tropical rain forest is a good example.

dfcl = 5. Similar to 3. with grazers larger than the producers and abundant, with predators of grazers scarce and severely predator limited, and with predators of predators abundant. Aquatic systems based on the productivity of small, single cell algae, with rapid turnover and an inverted pyramid of biomass between the producer and grazer trophic levels, and with small and large fish making up to the primary and secondary predators are clear examples.

Oksanen et al. (1981) suggest from the structure of their models that *dfcl* = 3 to 4 links may be an upper limit in terrestrial systems, with no more than *dfcl* = 5 in aquatic systems. Increasing resources for plant productivity may not be used because the plants are limited in biomass by grazers and so are unable to use all the water, light, or nutrients available. Nor are there any clear examples of longer dynamic food chains. However, both kelp beds and coral reefs may be examples worth studying. The luxuriant kelp beds could be up to six links, while the coral reef, with its producers actually existing symbiotically inside a major "grazer", the coral, could be up to seven. In speaking of these different systems, most deserts are between one and two links, and are referred to as odd-linked systems. Most desert

grasslands are between *dfcl* = two and three, and are even-linked. Most forests are three to four levels, and are again odd-linked.

Tests of the theory

The early tests of the more generalized form of the theory by Arruda (1979) and Oksanen (1983) primarily showed that standing biomass patterns of various trophic levels were associated with overall ecosystem productivity (potential production, growth of plants) in the way predicted by the model. Supposedly resource limited trophic levels increased in biomass with productivity while predator or grazer limited levels showed no change. Measures of productivity supposedly reflect the real photosynthesis in the system and varies independently of biomass as turnover rates vary. Both authors also reported preliminary evidence that resource competitive and grazer or predator resistant forms replace one another along productivity clines in the way expected. Elliot et al. (1983) conducted an experiment to specifically test the predictions of Fretwell (1977), confirming them as well. Finally, Jager et al. (1984), discovered that stochastic simulation produced results very similar to those of the deterministic models. Thus, the few efforts made to subject the theory to a falsifiable test have found it corroborated. Of course, this testing cannot be considered completed, and most of our confidence in the theory comes from the inadvertent "tests" that can be compiled from the literature, especially on eutrophication, and on African grasslands (see above). There is enough of this to suggest that the theory may be of as general application as it pretends to be.

Food chain dynamics as the central theory in ecology

My purpose in this section is to argue that there is a value in having a central theory for population ecology, and that the food chain model is a viable candidate for that role. The first point requires that we briefly consider the structure of the science of ecology. The study of natural systems is divided into the study of ecological dynamics and the study of adaptive strategies, and any consideration of a central theory for ecology must proceed from a clear understanding of these two branches. Although deeply interdependent, these fields ask different questions. Population ecology asks how population sizes are determined while evolutionary ecology asks why creatures are formed as they are. They also operate in somewhat different time scales (ecological versus evolutionary time) and have different realms of application (resource management versus developing conceptual insights). The field of evolutionary ecology has a central theory, the concept of natural selection on genetic variation, which has been the basis of an active research program for over a hundred years and which is now well accepted. The value of a central theory in ecology is in fact demonstrated by the success of evolu-

tionary theory in organizing research in the area of adaptive strategies. The field is marked by synthesis after synthesis (e.g., Huxley 1942, Mayr 1963) in contrast to population ecology where unending controversy is the rule. This difference is attributable to the fact that work on the central theory of adaptive strategies began almost 100 years before efforts to produce such a theory for population ecology.

At present, there are four candidates for the role of central theory in ecology: The resource-controlled population hypothesis (Lack 1954, White 1978), the Odum and Biever mutualism hypothesis (1984), the self regulation hypothesis of Chitty (1960) and the food chain dynamics hypothesis discussed here. As noted above, the first two hypotheses seem inadequate to account for the clear role predators play in the regulation of some populations, and the second, besides being so new that testing has not really begun, has an unclear relationship to the theory of natural selection. The food chain hypothesis assumes the simplest kind of Darwinian selection. Yet, by providing insights into the factors that regulate populations, food chain dynamics has great potential usefulness to evolutionary ecologists trying to understand, for example, the body sizes or the life-history strategies of species. The self-regulation hypotheses proposed by Chitty (1960), besides being of limited application (mostly vertebrates), is also only weakly supported in its major predictions.

Arguing that a hypothesis can play the role of central theory however requires much more than simply showing that it has more strengths than its competitors. A central theory must be shown to integrate most ongoing studies in the field. Thus, we now turn our attention to the various branches of ecology, asking how food chain dynamics relates to each.

Population regulation and cycles

The questions of population regulation are: "What factor or factors regulate population growth", and "How is population regulation achieved?" The food chain hypothesis clearly sets a context wherein populations may be more or less limited by resources or by grazing or predation or by competitors. The application of the hypothesis to the analysis of particular species requires further study. For example, we suggest that many very barren or dry plant communities ought to consist of species that are limited in population by some resource. Such species ought to increase in abundance with the addition of water or whatever resource is limited, but the scenario described above indicates that grazing may set limits to the abundances of some individual species, even though other species and the community as a whole are resource limited. In most productive desert grasslands, increasing resources should have an impact on species composition, but should not increase overall biomass. Still, the patterns laid out by HSS and later by Fretwell indicate where resource or grazer/predator lim-

ited populations will be found. The modelling of Rosenzweig (1972) suggests how populations will be limited by food and predation in concert, and emphasizes the changes in predators and food supply that actually cause a population to be regulated. The models of Oksanen et al. (1981) make statements about patterns of cyclic behavior that indicate when cycles should and should not occur, and why they occur at all. For example, producer-herbivore-predator cycles are supposed to be characteristic of the more productive desert and other grasslands, while herbivore-predator cycles might occur in forests.

Competition

How do organisms compete? What are the implications of competition for community structure? These questions have attracted much attention and controversy (Cody and Diamond 1972, Simberloff 1984). The use of food chain dynamics as a central theory is particularly obvious here, for the controversy has directly involved entomologists who have worked mostly with the supposedly predator limited grazers of three level systems. It has been argued since 1960 that such species should not compete for resources but for predator escape strategies, if at all (see Ricklefs and O'Rourke 1975). Thus, the objections of these entomologists to the emphasis placed on competition by colleagues studying predatory vertebrates in the same systems is entirely understandable. If indeed the predators are competing for insect prey and limiting their prey's populations, then these grazers cannot also be competing for food.

Diversity and stability

The dynamics of diversity are tightly related to the relative importance of predation and competition for a limited resource, and so the models on food chain dynamics provide a potentially critical overview for interpreting and integrating the presently independent perspectives of, for example Paine (1980), Connell (1975) and MacArthur (1972). The model makes many predictions about patterns of increase and decrease of diversity along clines of changing food chain length. One relevant scenario can be offered for the situation described above involving the increase of plant biomass in zero to one link deserts. In this scenario, I imagine the first plant species to invade an otherwise barren habitat being entirely grazer-free. By virtue of its ability to survive and reproduce under conditions of very low resources, this species ought to be a very able competitor for the limiting resources. Such a species would be alone in the system and would appropriate any increase in resources into its own population increase. This increase would eventually attract a grazer capable of regulating the plant's population growth setting a limit to the number of individual plants in the population and, therefore, to its competitive ability. Further increases in

resources will be left available to support different species of plants, ones that while less competitive, are perhaps resistant to the particular grazer feeding on the established species (e.g. a *Cholla* cactus invading a creosote bush, barrens – the grazers of creosote bush are not likely to be able to consume the cactus). This species in turn would increase as resources increase until it too attracted a grazer adapted to it, which could limit its growth. Then, further resources would allow a third species to invade and the trend would continue. The end result would be a strong correlation between overall productivity and diversity until grazing pressure finally stops all increase in all plant populations. Beyond that point, increasing grazing pressure would result in a decline in plant diversity. Meanwhile, similar arguments applied to grazers along the cline from grasslands to forests might produce similar results, although grazer diversity is likely tied also to plant diversity. Thus, plant diversity and grazer diversity will be positively correlated in deserts but negatively correlated in desert grasslands. Insofar as diversity depends on stability the patterns of cycling predicted by the model will also be relevant.

Evolutionary ecology

Hutchinson (1965) wrote an insightful analysis of the interaction between ecology and evolution, titling his book: *The Ecological Theatre and The Evolutionary Play*. Historically, evolutionary thinking has based its logic on ecological ideas, Darwin responding to the ideas on population growth by Malthus, and even now it seem clear that evolutionary processes are profoundly shaped by ecological dynamics. Predator or grazer limited populations have quite different selective pressures compared with populations limited by resources. Age of first reproduction, adult body size, growth rate, shoot structure of plants, development of toxins, spines, or other predator defenses, or antlers, plumes, or other display features, all of these depend on the predation pressure and competition for resources. Thus, the trophic level of a population, and where on the food chain spectrum its ecosystem lies will be of importance in understanding why it has evolved the way it has.

Succession

Disturbed plant communities often undergo a particular set of changes in which one association of plants is followed in dominance by another association. The impact of grazing pressure on this succession is little studied, and yet we logically expect there to be a succession not only in plants but also in grazers and predators. Grazers ought not to invade until a plant community is established, and predators not until after grazers. Of course, much depends on the time course of such a sequence of invasions, but it is possible that the absence of grazing in the earliest stages of succession might well

influence the kinds of plants that begin a successional sequence. And, the absence of predators in the early stages of grazer invasion might similarly affect the pattern of herbivore invasion. For example, in a potential three-link system, we might expect competitive plant forms early in the succession, followed by grazer resistant forms as grazers invade and again, by competitive forms as predators invade to limit grazers. This might explain why the tall fireweeds are first replaced by relatively small grasses and only later by tall herbs and shrubs and why voles can deplete the vegetation even on productive clear-cuttings (Hansson 1987).

Biogeography

The basic biogeographical unit is the species range, which is a description of where a species occurs and what its pattern of abundance is within that region of occurrence. For a range to be fully described, detailed information about density variation, carrying capacity, population dynamics, and regulatory factors is desirable, but often unavailable. Except for trivial cases, such as spruce trees growing down to the water's edge near some rocky coasts, the factors determining the edge of a species range are not well known either. I submit that widespread use of the food chain model as a central theory in ecology might do much to remedy this situation. For example, the boreal herbaceous plant *Oxalis acetosella* is found in northern (or barren) and luxuriant habitats, but not in habitats of intermediate productivity. Ericson and Oksanen (1987) have shown this species to be highly preferred by voles and likely to be eliminated by grazing thought to be more likely in these 2 to 3 link habitats of intermediate productivity.

The food chain hypothesis sets up clines of productivity or stability, with regions of varying competition and grazing pressure within which species of varying form and nature may exist. A prostrate or otherwise grazing resistant plant species may find itself unable to survive in a region of higher productivity where grazers are limited by predators, and plants grow tall to compete for light. It may also fail in very unproductive environments, again free of intense grazing pressure, where there might be intense competition below ground or for and at the few sites where plant growth is possible. Similarly, a grazer species unable to survive persistent predation or disease associated with high densities may be eliminated from regions of high productivity where abundant food fosters high population size. Thus, specific predictions about range limits emerge from the hypothesis.

Broader questions of biogeography, involving continental differences and ranges for higher taxa are less clearly related to food chain dynamics. While some major groups tend to be predisposed to competitive interactions or grazer/predator resistance, exceptions abound. Grasses, as a group, seem grazer resistant but bamboos and many tall tussock grasses are clearly com-

petitive. Plant communities in areas without vertebrate grazers, such as New Zealand, are frequent sources of such exceptions.

Future tests

Even if we accept the applicability of food chain dynamics to essentially all of ecology and therefore qualify it as a candidate for a central theory (like Darwinian evolution), it remains to show the idea sufficiently plausible before it can be widely accepted. The two questions we must address are 1) are there any plausible alternative hypotheses that, if true, would render the food chain hypothesis basically irrelevant? and 2) what testable, falsifiable predictions can we generate from the hypothesis that would, if confirmed, increase the Bayesian plausibility (Tricker 1965) of the idea.

In the arena for explaining the bulk of plant and grazer populations, the most plausible alternative is the hypothesis of passively harsh environments (White 1978, Rhoades 1985), which argues that all grazer populations are donor-controlled. According to this hypothesis, grazers affect plants largely in evolutionary time through causing the evolution of toxins and other anti-grazing adaptations. Grazers are thought to have little effect in ecological time on the equilibrium plant biomass or population size. Grazers are not supposed to be predator controlled, even in what I regard as three-link systems; instead, grazers are hypothesized to be unable to eat most of the plant material available. Only when environmental or grazer induced stresses limit plant defenses can grazers "break-out" and substantially limit plant abundance.

The existence of plant defenses cannot be denied and indeed patterns in the occurrence of various sorts of plant defenses (spines, chemicals, tough tissues, rapid growth) are part of the predictions from the food chain hypothesis (Fretwell 1977). Thus, plant defense ecologists will ultimately be served by the food chain hypothesis as it proves successful. The central question raised by plant defense ecologists is how often (if ever) predation actively limits grazers and prevents their overgrazing a plant community. This is actually an open but very important question in natural systems. Certainly the biological control literature contains some very dramatic examples of predators regulating grazers, but the applicability of these to natural systems is unclear. Thus, the challenge to food chain dynamics is to demonstrate that predator removal causes dramatic increases in at least some grazers and that these grazers have the capacity to dramatically reduce the amount of phytomass. The curious case involving sea otters, man, sea urchins, and the macroalgae, kelp, is a model experiment. Here, man eliminated otters from some Aleutian Islands, with the result that the sea urchins which are the natural prey of the otters exploded in numbers and essentially eliminated the kelp forests (Estes et al. 1978). We await other studies, especially from terres-

trial systems where the predator trophic level would be significantly reduced from a three level system, and defoliation results. Meanwhile, the food chain hypothesis raises a question to ecologists studying plant defense: What role, if any, do plant defenses play in limiting consumption by vertebrates, which may be the ultimate grazers in any system?

One other suggestion competing with food chain dynamics for explaining grazer-plant and predator-grazer interactions is that of Odum and his colleagues, invoking mutualism in these consumer-consumee relationships. This idea, though relatively untested, must have some relevance in that corals have developed symbiotic unions with the algae they graze. Ruminants can also perhaps be viewed as bacterial symbionts, collecting "detritus" for bacterial decomposition from plants before the plants die naturally. (But then, ruminants would be primary consumers in the detrital food chain). However, for most predator-prey interactions, the concept strains Darwinian evolution, and so seems of limited application.

In summary, alternative explanations for predator-prey interactions can be subsumed by the food chain model but not, as far as we know vice versa. There are some critical tests needed before food chain dynamics is established, but it remains a strong candidate for consideration.

Other tests

One of the most disturbing observations to the food chain model is the occurrence of higher trophic levels in ecosystems that are supposed to have short food chains. At first consideration of the theory, it seems that grazers ought to be rare and predators nonexistent in such unproductive ecosystems, and yet they are found there regularly. Pimm and his colleagues (especially Pimm and Lawton 1977) have found no correlation between food chain length computed without regard to species abundance, and productivity or any other variable. My ad hoc explanation for the presence of such higher trophic levels is that they are somehow on the fringe of the dynamics of the system, being either too rare or too restricted in diet to significantly influence the biomass of the level on which they feed. Ad hoc explanations are of course an admission of weakness to any theory, but this one at least has the virtue of being testable. If elimination of spiders from an arid shrubby desert causes defoliation of the desert shrubs, and their eventual replacement by more rapidly reproducing herbs and grasses, much of the development of the theory since the mid-1970's must seriously be questioned, especially as to generality. Oksanen et al. (1981) indeed wondered whether variations in food chain length occurred in arthropod branches.

Testing the above prediction ought to be done in concert with testing a key prediction from the theory.

The model predicts that elimination of predators from both two and three level systems (in both of which predators are supposed to be present and influential to certain species of prey) would cause dramatic changes in both the species composition and the community biomass of both the plants and grazers in only the three level system. In the two level system, just the species composition of the grazers should be affected. Thus, a predator removal study is predicted to have no effect in very unproductive systems dominated by competitive plants, such as shrubby deserts; to only have an effect on the species composition of the grazers in moderately unproductive systems dominated by a mix of competitive and small, grazer resistant plants (desert grasslands); but to have a sweeping effect on the whole ecosystem in productive system dominated by competitive producers (forests).

There are, of course, many possible predictions to explore, all of interest, but not critical in testing the hypothesis. For example, it is unclear whether four level food chains exist in terrestrial systems. While marshes are more productive than forests and have less biomass, there are such great physical differences in the environment that the dynamic food chain length may not be a significant factor. Unlike the shrubby desert-short grass prairie transition where the desert grassland forms an intermediate step, the forest to marsh step is normally abrupt. At present, we have no examples of forests where productivity and biomass are negatively correlated as would be expected by the theory if the three level food chain approached four levels. Still, the gradient of productivity is also very steep between forests and marshes, and there are plenty of forests in subtropical regions that grow in water. The transition between mangrove forests and *Spartina* marshes is interesting in this regard.

Notice that the marshes need not have a distinct fourth trophic level in order to have four link dynamics. It suffices to have predators (minks) that are limited by cannibalism, allowing herbivores (muskrat) to reduce the abundance of reeds and cattails so that grazing-resistant duck weeds can take over (see Danell 1978).

In all these cases, an analysis of the biomass-productivity correlation is critical. The simplest application of the food chain model predicts that the most productive forests might show a negative or zero biomass-productivity correlation, and that marshes would surely have such a trend. It predicts that the elimination of muskrats, geese and other large aquatic grazers would reverse this trend causing a positive correlation, and might result in the invasion of more competitive plant forms.

In conclusion, the further development of ecology as a science would be greatly enhanced by the advent of a theoretical structure comparable in generality to the theory of evolution that can serve as a synthesizing or central theory for the science. The food chain hypothesis is at present a viable contender for that role and thus

deserves intensive study to establish its range of applicability.

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