Trophic Levels and Trophic Dynamics:⁼ A Consensus Emerging?

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There are three clearly different views on trophic levels. The systemsecological tradition sees trophic levels as relatively discrete and welldefined units whose interactions cannot be derived from interactions between constituent populations. The reductionist population-ecological tradition sees trophic levels as inappropriate abstractions that cannot be used in formulating predictive theories. The tradition of trophic dynamics sees the first three trophic levels of autotroph-based ecosystems as reasonable abstractions, useful in formulating predictive theories, but devoid of properties that could not be directly extrapolated from those of constituent populations. Recent literature suggests that the first two schools are converging towards the viewpoints of the third, though the latter has also been modified by the interaction.

Different schools of scientific thought develop as a consequence of different tacit premises shared by various groups of the scientific community. As these premises may range from specific scientific assumptions to philosophical viewpoints and differences in the usage of shared terminology, communication between schools tends to be imperfect, such that genuine scientific differences are difficult to distinguish from semantic ones.

These phenomena are visible in the current debate on trophic levels and trophic interactions¹⁻⁹. Traditionally, two questions have divided ecologists working on biotic communities: whether or not the darwinian approach is sufficient for understanding community-level phenomena, and whether trophic levels can be regarded as reasonable abstractions. The Odum school of systems ecology^{1,2,6-9} maintains that nature must not only be viewed with microscopes and binoculars but also with 'macroscopes' that eliminate excessive details and reveal the grand design of ecosystems. In the field of the 'macroscope', trophic levels are supposed to emerge as central entities that interact in ways that could not be predicted from interactions between constituent populations. Instead of struggling with each other, trophic

Lauri Oksanen is at the Dept of Ecological Botany, University of Umeå, S-901 87 Umeå, Sweden. levels supposedly cooperate because those energy circuits with maximal ability to reinforce themselves become prevalent in the ecosystem^{7–9}.

In a language tangible for an evolutionary ecologist, the above reasoning translates to group selection between energy circuits. Even much less extreme forms of group selection are normally regarded as grossly unrealistic, so it is hardly surprising that the Odum view of ecosystem organization has little support amongst evolutionary ecologists. The majority of evolutionary ecologists, accustomed to working with individuals and populations, tend to favor a more reductionistic view of nature. They may discuss issues like community structure; however, their communities are normally just extended guilds, consisting only of taxonomically and ecologically related species (e.g. field-layer plant communities, passerine bird communities). Even when looking at broader sets of interacting organisms (e.g. marine intertidal communities), evolutionary ecologists usually try to work on individual populations, as far as time and taxonomic ability allow.

In 1960, three prominent evolutionary ecologists - Nelson Hairston, Frederick Smith and Lawrence Slobodkin (HSS)¹⁰ – initiated what can be called the trophic-dynamic tradition by adopting the macroscopic view of communities and by using the concepts of plant, herbivore and carnivore trophic levels. However, interactions between these trophic levels were derived from the standard darwinian perspective of the struggle for existence: that each individual tries to maximize its shortterm fitness, regardless of the population- and community-level consequences of its actions. It was proposed that carnivores regulate herbivores to a relatively low level (i.e. they overexploit their prey), such that plants experience little grazing and have their communities structured mainly by resource competition^{10,11}

In later extensions of the theory^{12–18}, it has been proposed that large, continuous tracts of barren land (tundras, steppes, semideserts) have two-link trophic dynamics (resourcelimited grazers and grazingcontrolled vegetation), whereas the three-link dynamics of HSS are supposedly typical for relatively productive terrestrial ecosystems and for oligotrophic and eutrophic pelagic ecosystems. Mesotrophic pelagic ecosystems in turn are proposed to have four-link trophic dynamics (resource-limited piscivores, predation-controlled planktivores, resource-limited zooplankton and predation-controlled phytoplankton)¹⁸. Aquatic ecologists have been particularly successful in establishing these ideas and have also introduced the catchword 'cascading trophic interactions'¹⁹ as a label for the HSS principle of top-down population regulation.

Real and imagined problems of the trophicdynamic approach

Predictably, the trophic-dynamic approach of HSS was vigorously challenged by reductionistic population ecologists^{20,21} who argued that (1) trophic levels are not state variables but abstractions, (2) no predictive theories can be built on such abstractions, and (3) herbivores may not be able to control the abundance of plants. The first argument is rather peculiar: state variables only exist in models and they are always abstractions of the material reality. The second argument is guestionable both logically¹¹ and empirically^{22,23}, and the third argument is in conflict with a vast body of experience on the impact of domesticated grazers on terrestrial vegetation^{24,25}. Also, in aquatic ecosystems, top-down effects reach all the way to plants^{18,19,26}.

Nevertheless, arguments (1) and (2) are frequently reiterated. For instance, Cousins³ recently suggested the example of a hypothetical hawk that could be anywhere from the third trophic level to the seventh, depending on what its prey happened to have eaten. The message is that trophic levels are not just convenient abstractions, but abstractions without even approximate material counterparts.

Recall, however, that HSS never discussed trophic levels above the third one. My interpretation of the underlying logic can be summarized as follows. It takes entirely different kinds of adaptations to photosynthesize, to consume fiber-rich vegetative plant organs and to capture mobile prey. Thus, no organism can efficiently combine two of these ways of energy intake. Some animals are omnivores in the sense that they prey on other animals and utilize especially nutritive plant organs. However, such omnivores are inevitably inefficient grazers, unable to reduce the standing crop of perennial vegetation. Thus, they are functionally members of the carnivore trophic level, as stated already by the HSS team¹¹. Another type of omnivory

consists of within-guild predation (predators preying on herbivores and other predators)²⁷. In most food chains, abundance relationships between herbivores and carnivores ensure that such predators will obtain almost all of their energy from herbivores; secondary carnivory can be thus regarded as an extreme form of interference competition between carnivores.

Except for Fretwell's tentative contribution¹² and Pimm's reviews²⁸ (where he, as a matter of methodological principle, accepts the food webs as described in the original sources), proponents of the trophicdynamic approach have restricted the concept of a fourth trophic level to pelagic ecosystems. There, grazers are usually small due to the minute size of the plants. Because of the size difference between zooplankters and fishes, planktivory and piscivory emerge as two distinct feeding niches which require different kinds of adaptations. Indeed, planktivorous fishes freely consume both herbivorous and predaceous zooplankters when given an opportunity. However, predaceous species tend to be larger than their prey, and intense planktivory seems to lead to virtual elimination of all large-sized zooplankters²⁹. Thus, pelagic ecosystems seem to be good examples of 'Pimm's principle'28, according to which a combination of intense and persistent predation and competition by the same species makes life very hard for the victim, and is likely to lead to its extinction and thus to structural simplification of the food web.

The controversy between Cousins and the trophic-dynamic school thus seems to be largely a matter of semantics. Cousins' critique is directed against the Odum school of systems ecology and concerns trophic levels that HSS never dreamed of. Moreover, Cousins admits that the three trophic levels recognized by HSS are often fairly distinct. For him, these trophic levels represent categories defined by taxonomic relations (plants, animals eating plants, and animals eating animals; notice that similar taxonomical redefinition can be extended to the four trophic levels of pelagic ecosystems by splitting the 'animals eating animals' group into 'vertebrates eating invertebrates' and 'vertebrates eating vertebrates'). I prefer to regard the trophic discontinuities as the primary factor and taxonomical categories as consequences of peaks and valleys in the adaptive landscape, and I suppose that this has been the point of departure of the HSS team, too.

Whichever interpretation one likes,

the fact remains that Cousins has endorsed the position of HSS in substance though not in semantics. Moreover, he has made a significant contribution to the HSS approach by proposing a practical way of delimiting ecosystems with HSS-type (topdown) dynamics³⁰.

Indirect effects and mutualism between trophic levels

An even more profound position shift is visible in the recent defense of the systems-ecologists' mutualism hypothesis by Vadas⁴. He explicitly rejects the idea of natural selection between energy circuits. Instead, he argues that indirect impacts of consumers on their resources make the relationships between trophic levels mutualistic (in the sense that consumers enhance the productivity of exploited populations). This point is substantiated by a large number of examples and by the widespread occurrence of omnivory in benthic and littoral aquatic systems³¹, which, by Pimm's principle, is difficult to reconcile with consumer-controlled trophic dynamics. (High degrees of omnivory have also been discovered in the arthropod-dominated food chains of arid deserts³².) Unfortunately, Vadas does not discuss counterexamples (e.g. induced plant defense^{33,34}, antipredator behavior of animal prey35) where the indirect effects of predation reduce the production or availability of adequate food items. The abundance of omnivory in some systems may, in turn, reflect nonequilibrium dynamics (opportunistic exploitation of outbreak species is stabilizing rather than destabilizing) and spatial heterogeneity (constant immigration of species that would be eliminated by local dynamics) rather than mutualistic trophic interactions.

By deriving the mutualistic features of trophic interactions solely from indirect effects, Vadas has in fact left the Odum school of systems ecology and joined the trophic-dynamic tradition. From the Odum school, he has retained the broad operational definition for the concept of 'mutualism', a general recognition of the importance of indirect effects and an appreciation of the complexity of many ecosystems. Similar position shifts can also be seen in other ecologists identified with the Odum school. A fresh contribution of Ulanowicz³⁶ focuses on indirect effects and does not include assumptions of extradarwinian causal mechanisms. In another recent contribution, Ulanowicz37 identifies two major approaches: 'Eltonian' reductionism and the holistic Lindeman–Odum approach which

is defined broadly enough to embrace the trophic-dynamic school.

On the way towards a synthesis?

The original lines of demarcation between the three schools related to darwinism and to the trophic-level concept. In these issues, the three schools seem to have converged. The arguments of Vadas do not include extra-darwinian elements, and these elements are also absent or strongly toned down in the recent contributions of Ulanowicz. Cousins, in turn, accepts *de facto* the first three trophic levels of autotroph-based ecosystems as fair abstractions.

However, the three approaches are still accompanied by genuine biological differences. The systemsecological tradition emphasizes positive indirect interactions, whereas negative indirect interactions are easier to understand from the point of departure of traditional evolutionary ecology. The trophic-dynamic tradition assumes that the attributes of resources relevant for a consumer (digestibility, size) usually correlate well with trophic position, and population-dynamical effects (Pimm's principle) are assumed to further simplify the trophic structure by eliminating omnivorous links with persistent and substantial population-dynamical significance. This view is guite different from the idea of the trophic continuum proposed by Cousins³⁸. which is compatible with the Menge-Sutherland hypothesis of monotonic trends in the importance of predation along food chains³⁹.

In part, the remaining differences may reflect differences between the systems that different ecologists are primarily working on. Indeed, few ecologists would argue that all types of food chain fit into a single model. HSS¹⁰ have already proposed that decomposers as a group are resourcelimited. As the concept of 'decomposers' includes an entire food web, the argument implies that detritusbased food webs lack distinct trophic levels. However, the debate on the importance of omnivory and on the relevance of Pimm's principle in various autotroph-based food chains is only beginning. The fact that detritus-based and grazer-based trophic systems often are interconnected further confounds the issue. Thus the limits of the range of applicability of the trophic continuum and trophic-level approaches are still an open question.

To conclude, the emerging consensus is limited to organizing principles. On the level of specific hypotheses, the three traditions still exist and are quite heterogenous even internally – fortunately, one might say. Differences on the level of specific issues stimulate theoretical analyses, comparative empirical studies and experiments, and thus serve as fuel for scientific progress.

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Implications of 'Supply-side' == Ecology for Environmental Assessment and Management

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Recent work in marine ecology has reaffirmed an insight from fisheries science that knowledge about the production, dissemination and success of propagules can guide our management of populations and assemblages. Understanding the variable nature of recruitment relationships can both aid and hinder attempts at environmental monitoring, rehabilitation and innovative selection of marine reserves. The effects of human impacts in marine environments may be first manifest in alterations to recruitment, which also constitutes the only path by which many populations could recover.

Fisheries science has long been concerned with the recruitment dynamics of fish and shellfish¹. The

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need to study the levels and variability of recruitment of all types of marine organism, as well as the distribution and abundance of adults. has recently been re-emphasized^{2,3}. The stages studied (which I shall call 'propagules') include gametes, fertilized eggs, larvae, spores and presettlement juveniles during their production, dispersal, metamorphosis and recruitment to adult populations. Many propagules are small and undergo a planktonic phase that can be difficult to study² and so are often ignored. Recruitment is necessary to maintain many marine populations, but how recruitment translates to subsequent abundances of adults is not fully understood. The study of such phenomena has been termed 'recruitment processes' in fisheries and, more recently, 'supply-side' ecology^{4,5}.

'Supply-side' ecology has so far included studies of the physical transport of propagules, the role of recruitment limitation or variability in determining population levels and as input to interactions within assemblages², as well as biogeographic scales of dispersal over ecological or evolutionary time scales⁴. The extent of this domain was only vaguely specified by Roughgarden and others⁴, who coined the term, and by Lewin⁵, who popularized it. The term itself has been criticized as a neologism^{2,6} and as representing a bandwagon³.

More substantial criticism^{7.8} has revolved around the fact that papers developing these principles have concentrated on species, such as barnacles, that have very long larval lives and thus much potential variability for in recruitment. Species with shorter periods in the plankton, such as algae and many colonial animals may engage in less dispersal and consequently have much tighter stock-recruitment relationships7.8. Nevertheless, longer larval durations are widespread⁹ amongst marine taxa such as fish, molluscs, crustaceans, echinoderms