

NOTES AND COMMENTS

DOES FOOD WEB COMPLEXITY ELIMINATE
TROPHIC-LEVEL DYNAMICS?NELSON G. HAIRSTON, JR.,^{1,*} AND NELSON G. HAIRSTON, SR.²¹Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853-2701;²Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599-3280*Submitted June 27, 1996; Revised August 12, 1996; Accepted August 27, 1996*

Investigators are always divided into those who are looking for rules and those who are looking for exceptions. (Hackett 1937, p. 106)

We doubt that it will come as a surprise to the readers of this journal that natural communities are complex. Polis and Strong (1996) recently laid out in detail the multifold ways that ecological complexity pervades nature. Their principal purpose in doing so was to comment on the conclusion that we (Hairston and Hairston 1993) and others (e.g., Fretwell 1977; Oksanen et al. 1981; Oksanen 1991) have drawn that despite complexity, general patterns exist in the abundances, biomasses, and productivities of different broad categories of organisms and in the efficiencies with which material and energy move between these groups. Polis and Strong (1996) believe instead that communities are too complex to show general patterns. In particular, they suggest that the catalog of diverse interactions that they describe must lead inescapably to the view that no natural groupings of organisms into trophic levels is possible because of the fact that many, most, or nearly all consumers (depending on point of view) feed on tissue at a variety of numbers of food-chain links from the primary producers; trophic transfer efficiencies are dictated as much by the defenses of the consumed as by the relative abundances of consumer and consumed; external subsidies of energy and materials frequently override trophic transfers within communities; and the interacting herbivore- and detritus-based food webs negate the possible use of trophic levels.

In our review of trophic structure and interspecific interactions (Hairston and Hairston 1993), we covered in some detail each of these points and asked whether general patterns exist despite the fact that nature is sloppy. Polis and

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Strong (1996) failed to acknowledge our treatment of these complexities, so it is unclear whether they considered any of our interpretations. Our goal was to use the wealth of data on trophic transfer efficiencies collected over the past several decades to investigate what general patterns might or might not exist. We focused on estimates of consumption efficiency (i.e., the percentage of net production at level n that is consumed by level $n + 1$) because this encompasses the questions of whether trophic levels exist; whether defensive compounds, structures, and behaviors completely diffuse the effects of consumers on their food; and whether external subsidies obscure general patterns in trophic transfers. We chose to compare and contrast consumption efficiencies within and between terrestrial and pelagic freshwater communities because existing evidence suggests an interesting difference in the importance of secondary carnivores between these two communities. We found that consumption efficiencies do exhibit general patterns within each of these community types and that these patterns differ in interesting and informative ways between terrestrial and freshwater communities. The patterns appear to make sense in light of the difference in secondary carnivores.

We agree with Polis and Strong that any one or all of the complexities that they document could, in principle, lead to a negation of general patterns among communities provided that these complexities are pervasive. If trophic levels do not exist, if resource species are so well defended as to control the abundance of their consumers independent of their predators, or if external subsidies generally approach or exceed direct trophic transfers through the food chain, then no general patterns in efficiencies should be found either between putative trophic levels within a community or among trophic links between communities. We do not agree with Polis and Strong, however, that the mere existence of complexity necessitates a rejection of general patterns. Indeed, some trophic levels unarguably do exist: primary producers, obligate terrestrial herbivores, and true decomposers. Not all ecosystems can be subsidized; some must provide the subsidies. Polis and Strong (1996) provided no quantification of the importance of the linkages between species in any of the many examples they discussed, and although they clearly stated that some links are more likely to translate into community-wide impacts than others, they rejected the idea that communities may have a sufficient number of dominant pathways in common (e.g., herbivory, primary carnivores eating herbivores) that general ecological patterns emerge.

The studies of trophic transfer efficiencies that we reviewed (Hairston and Hairston 1993) provide data that suggest that general patterns do exist. For example, consumption efficiencies of herbivores on primary producers are much higher in freshwater pelagic communities (32%) than in terrestrial communities (3%). We suggested that this difference lies in the fact that secondary carnivores (piscivorous fish) are an important component of freshwater communities in reducing the numbers of primary carnivores (zooplanktivorous fish), thus allowing grazing zooplankton to become abundant and reduce algal densities. In contrast, we pointed out that in terrestrial communities, secondary carnivores are quantitatively an unimportant part of the mortality of primary carnivores. Thus, preda-

tion is a major source of herbivore mortality in terrestrial communities (e.g., Strong et al. 1984; Feeny 1992), and grazing on plants is held at a lower level than would otherwise be the case. The existence of terrestrial omnivores and true secondary predators may have some effect on transfer efficiencies as we have considered them, but the great majority of energy flow is regulated through the trophic pathways that we described.

One of the community interactions that Polis and Strong suggest should dilute our ability to detect trophic-level patterns is plant defenses against herbivores (and other forms of resource defenses). An alternative view is that for quantitative defenses (*sensu* Feeny 1976), the net effect of plant chemistry is to increase the impact of predators on herbivores. Feeny (1976, 1992) and Price et al. (1980) have concluded that when herbivores' consumption efficiencies are decreased by phytochemicals in their diet, the grazers must spend more time feeding and thus more time exposed to their predators. Thus, a third trophic level in terrestrial communities may be an integral part of the effectiveness of plant defenses. In this scenario, plant chemistry simply enhances the ability of predators to control herbivore densities. The important point here is that consumption efficiency is dictated directly not only by the amount eaten by each grazer (which is influenced by plant chemical defenses) but also by the number of grazers feeding. If predators fail to control the numbers of herbivores, then even plants that are relatively poor food can still be decimated. Polis and Strong suggest that freshwater phytoplankton are less well chemically defended than are terrestrial plants. This is a debatable point since many algae possess demonstrably effective grazer-inhibiting compounds (e.g., Lampert 1987; Gliwicz and Lampert 1990; DeMott and Moxter 1991) and many terrestrial plants are highly edible, as demonstrated by the occurrence of many species of generalist insect herbivores that feed on a large number of different plants. Those insects whose food is confined to one or a few plant species have become specialists to detoxify, sequester, or rapidly excrete a specific toxic compound. The generalists are feeding on nontoxic plants. (See the analysis of Futuyma 1976 and the experiments of Cates and Orians 1975; Otte 1975; Scriber and Feeny 1979.) Indeed, when Ehrlich and Birch (1967) suggested that plant chemical defenses might explain why the world is green, Slobodkin et al. (1967) responded that every plant species has some herbivore that consumes it. What keeps these grazers from decimating their food?

Patterns of consumption efficiency within and among communities do not, however, necessarily imply process. The most effective way to test the importance of trophic structure in ecological communities (say, e.g., the indirect impact of primary carnivores on primary producers) is to carry out an experiment. Polis and Strong also support an experimental approach to understanding ecological community dynamics, but they raise concerns about whole trophic-level manipulations on the grounds that it will be difficult to decide exactly which species or group of species to remove (e.g., where do we place omnivores or intraguild predators?). Complications such as these, however, could plague any experiment in a natural community and cannot be justifiably invoked as a rea-

son, a priori, not to manipulate. Rather, we join with Polis and Strong in advocating careful experimental design based on a thorough knowledge of the natural history of the system to be studied and a judicious use of comparative data.

If natural communities are as complex as Polis and Strong suggest, then removal of primary carnivores will not have any repeatable effect on primary producers because the chain of effect through the herbivores will be dissipated by omnivory, by plant and prey defenses, and by external subsidization. If, on the other hand, effects of carnivore removal are detected in the abundance or productivity of plants, then this should be strong evidence for both the existence of trophic levels and the process of alternation of trophic control (as postulated in Hairston et al. 1960; Fretwell 1977; Oksanen 1991; Hairston and Hairston 1993). The best-known examples of experiments of this type have been carried out in freshwater pelagic communities (e.g., Carpenter et al. 1987; Leibold 1989; Morin et al. 1991; Hambright 1994). Although Polis and Strong argue that consumer-mediated effects have been most readily observed in fresh water because algae are edible (again, a debatable point; see above), we propose that it is rather because the primary carnivore and secondary carnivore trophic levels are dominated by a few species of relatively easily manipulated animals (i.e., zooplanktivorous and piscivorous fish) contained in a habitat with natural boundaries (the lake's edge). Furthermore, in many cases, the primary producers and the principal herbivores are short-lived organisms that can show a rapid response to manipulation. In contrast, in most terrestrial ecosystems, carnivores are distributed more evenly among a much larger array of taxonomically diverse species, and the herbivores and primary producers are often relatively long-lived. Removal of a dominant component of this assemblage is typically much more difficult than in the freshwater pelagic zone, and responses to manipulation will take a long time to develop fully. Few investigators have attempted this experiment, though some examples do exist. The most complete study is that of Spiller and Schoener (1988, 1990). On Staniel Cay in the Bahamas (a habitat with a natural boundary), the dominant predators in this relatively simple terrestrial community are lizards and spiders that consume a variety of herbivorous insects. Lizard-removal experiments caused a significant increase in scar damage by homopterans, corresponding to the frequent occurrence of these insects in the lizards' diet. Gall formation by midges caused more damage with lizards present, corresponding to a threefold increase in spider abundance in areas from which lizards were removed and to the frequent abundance of gall midges caught in spider webs. Scars accounted for most of the leaf damage, and Spiller and Schoener concluded that their results supported the three-trophic-level model and that lizard predation on spiders was much less important than was the effect of lizards on herbivorous insects. Despite the fact that the predators were in part supported by the detritivore food chain (Spiller and Schoener 1995), the biomass of the primary producers was still controlled indirectly through the trophic cascade. Linkages of this kind are a common feature of terrestrial ecosystems, as illustrated in figures 1 and 2 of our earlier work (Hairston and Hairston 1993).

Several other terrestrial studies that only involved parts of the ecosystems, did

not use experiments, or removed all insects (both predators and herbivores) with insecticides nevertheless demonstrate the potential for alternation of trophic control. Edson (1985) removed daily by hand aphid predators from the goldenrod *Solidago altissima*. Where the predators had been removed, the increased densities of aphids retarded plant growth and caused obvious damage to the leaves. It is noteworthy that the experiment was on the same plant species that Root (1996) had treated with an insecticide that killed both herbivores and predators and obtained minor results as far as protecting the plants from damage was concerned. Marquis and Whelan (1994) used cages to exclude insectivorous birds from individual oak saplings in a research forest in Missouri. In both of two successive years, herbivorous insects were significantly more abundant within the cages than on control saplings. They also showed that bird enclosure resulted in significantly greater leaf damage than was observed on the controls. Holmes et al. (1979) also established replicate bird enclosures in Hubbard Brook Forest and found significant increases in the numbers of lepidopteran larvae but not other insects. They did not report an effect on plants. Other predator-exclusion experiments by Eickwort (1977), Faeth (1980), and Skinner and Whittaker (1981) resulted in increased abundances of herbivores, but no observations of an effect on plants were reported. More recently, Strong et al. (1996) found much observational evidence that a nematode invades the body of a root-feeding lepidopteran and infects it with its lethal symbiotic bacterium, with the result that the host plant, *Lupinus arboreus*, is protected from the otherwise lethal effect of the caterpillar. These examples serve to show the potential for effects of predators on the health and survival of plants two trophic levels removed in terrestrial communities.

Even in fresh water it is possible to remove an insufficient number of the important zooplanktivorous fish species. Elser et al. (1995) found that when they reduced rainbow trout densities in Castle Lake, California, other zooplanktivorous species (brook trout, golden shiners, and cyclopoid copepods) compensated. In fact, the two remaining planktivorous fish species became much more abundant than the total had been before the exclusion of small rainbow trout. They were shown to consume very large numbers of daphnids, and the result was the opposite of what had been expected. Instead of becoming clearer than it had been in previous years, the lake supported a denser crop of phytoplankton, as shown by the decrease in Secchi disk transparency.

Any attempt to understand broad ecological patterns will be challenged by the complexity of nature. This is why ecologists must ultimately measure interaction strengths, execute controlled and replicated experiments, and carry out statistical analyses of their data. Whereas a knowledge of the nature of the complexities in any given community is critical for forming hypotheses and designing experiments, simply acknowledging that complexity exists is insufficient reason to conclude that general patterns do not emerge. We (Hairston and Hairston 1993) provided an explanation for part of the complexity of nature, an explanation based on quantitative measures of consumption efficiency. It is an explanation that can, at least in principle, be tested experimentally. Polis and Strong (1996) admitted freely that they were unable to provide either quantitative measures or

experimental tests for the food webs they discussed. Perhaps if they had obtained measurements of the interaction strengths between species, for example, in the manner of Paine (1980), or were to manipulate broad categories of consumers (even if trophic position is sometimes ambiguous), they would be able to perceive a pattern.

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