Food Webs at the Landscape Level

Edited by Gary A. Polis, Mary E. Power, and Gary R. Huxel

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Preface

On 27 March 2000, Gary Polis, Michael Rose, Shigeru Nakano, Masahiko Higashi, and Tayuka Abe perished when their boat capsized in a violent, unexpected storm offshore from Bahía de Los Angeles in the Sea of Cortez. Gary had been leading an expedition to the islands in the Gulf of California off the central Baja coast, where he had studied desert food webs and their interaction with the marine ecosystem for 11 years. The scientists lost in the Sea of Cortez accident will be terribly missed by many people all over the world. They leave important legacies to the study of food webs. This book, which Gary began as an outgrowth of a session on food webs and landscapes at the 1998 INTECOL conference in Florence, Italy, attempts to capture some of the momentum and excitement in this field, to which Gary contributed so much energy and insight. In this preface, we attempt to set this contribution into the context of Gary's unfolding career in food web ecology.

Gary grew up in southern California, and did his Ph.D. at the University of California, Riverside, where he was supervised by a physiologist, not an ecologist. His self-instruction in ecology began in deserts, where he immersed himself in intense study of natural history, particularly of arachnids. His early papers and a book focus on the interactions of spiders, scorpions, and solpugids, which compete for prey and frequently eat one another. These interactions motivated his development of the intraguild predation concept, and its theoretical extension, in collaboration with Bob Holt, to analysis of the ecological dynamics and evolutionary implications of this widespread interaction.

His deep grounding in natural history prepared Gary to take a leadership role in directing the field of food web ecology away from previously entrenched theory that had been derived from the study of books, not nature (to paraphrase Agassiz). The food web papers that dominated the pages of *Nature* and *Science* through the 1970s and 1980s were largely contributed by theoreticians seeking to test May's (1973) prediction that food webs should persist, or recover quickly from perturbations, only if their richness (*S*), connectance (*C*, the number of nonzero interactions) and average interaction strengths (β) were constrained, so that $\beta(SC)^{1/2} < 1$. The theoreticians most interested in this idea emphasized richness and connectance, recognizing that interaction strength was difficult to measure. Empirical evidence, from published data on food webs collected for reasons other than to test May's theory, indicated that connectance and richness were often inversely correlated. Many publications interpreted these trends as support for May's theory. A skeptic pointed out, however, that the literature reported on food webs that were arbitrarily delimited and inconsistently described, and that more effort devoted to a large system encompassing many species meant that less could be allocated to detailed diet analyses (Paine 1988). Food web theoreticians at this time also asserted that omnivory, cannibalism, and loops (A eats B eats C eats A) were rare in nature, as they expected, because these features destabilized this generation of models. These assertions were deeply irritating to field biologists working in diverse systems, who saw such interactions everywhere in nature.

Gary Polis galvanized these grumblings in a talk he gave at the 1990 INTECOL meetings in Yokahama, Japan, where he first met Nakano and other Japanese colleagues. The content of the talk was later published as his 1991 *American Naturalist* paper. Here, he forcefully pointed out that omnivory, cannibalism, and loops were not rare, but rampant in nature, that many predators that compete for food eat one another when possible (intraguild predation), and that literature-based descriptions were not adequate for deriving or testing food web theory. The paper's effectiveness may, in part, derive from its positive, almost exuberant tone—in it, Gary celebrates the complexity of the Coachella Valley desert food web, which he and other field biologists had richly documented. This work by Gary led theoretical ecologists to revisit the relationship between the complexity and stability of communities. For example, McCann and Hastings (1997) developed a model in which omnivory stabilized food webs, in contrast to earlier models (e.g., Pimm and Lawton 1977).

While the 1991 paper steered food web studies toward a more realistic view of nature, it also was somewhat deconstructionist. Gary commented at this time that he didn't want to be just a "nay-sayer" (personal communication to MEP). He was evolving his own view of the larger picture, which fused food web dynamics with spatial or landscape ecology. As early as 1979, he and David Spiller, also a spider ecologist, had shared their common observation that there were extraordinary densities of spiders on beaches (Spiller, personal communication to MEP). This was true on the Baja islands, among other places, and especially true on the smaller islands. Gary entertained three hypotheses to explain this pattern: a lack of predation, including intraguild predation on island spiders; highly suitable habitats for webs, possibly related to island vegetation; and food subsidies from the ocean. The last hypothesis was the one best supported by field evidence. Beach wrack washed up on the Baja shores was teeming with kelp flies and amphipods, which in turn fed the spiders. These spiders attained extraordinarily high densities, and as a consequence, protected desert vegetation from herbivory, although terrestrial primary production was not sustaining them energetically. Gary coined the term "apparent trophic cascades" in analogy to apparent competition (Holt 1977) to describe this interaction.

Gary championed the idea that flows of energy, materials, or organisms from one habitat to another could strongly influence the structure and dynamics of food webs, igniting the interest of many other food web ecologists. Similar insights had occurred long ago to the great field ecologist Charles Elton (Summerhayes and Elton 1923), but in the years that followed, food web studies had taken two different tracks, both veering away from landscape scales. Community ecologists who were experimentalists studied the effects of species interactions or physical factors by manipulating conditions or densities of organisms within small (<1–100 m^2) areas within single habitats, for obvious logistical reasons. As river, lake, terrestrial, intertidal, open ocean, or subtidal marine ecologists, we were not focusing on processes affecting communities that operated across landscape boundaries (but see Duggins et al. 1989). The theory that dominated food web ecology in the 1970s and 1980s did not portray much physical or temporal context. Interest in habitat boundaries and fluxes across them was maintained in ecosystem ecology (Likens et al. 1977; Jackson and Fisher 1986) and landscape ecology (e.g., Turner 1989), but among scientists working at large scales without resolving population dynamics or interactions of species in food webs. Polis, struck by the importance of regional oceanic processes for food webs on the small desert islands he studied in the Gulf of Mexico, exhorted community ecologists to "stop looking at our feet." He and his colleagues wrote several highly influential reviews (e.g., Polis, Anderson, and Holt 1997) pointing out that subsidies (fluxes of organisms, energy, or materials from productive to less productive habitats) strongly influenced the structure and dynamics of recipient food webs in a wide range of ecosystems. Theoretical ecologists again responded to his work by examining the potential effect of allochthonous resources or spatial subsidies on food web stability. For example, Huxel and McCann (1998; see also McCann et al. 1998) found that low to moderate levels of allochthonous resources could stabilize communities (see also Schoener 1973; Sommer 1984; Nisbet et al. 1997).

Gary Polis remained deeply grounded in and inspired by natural history throughout his career. He also developed an uncommonly broad vision that over the last several years has been catalyzing useful syntheses of community, ecosystem, and landscape ecology. The Japanese scientists who perished with Gary, Shigeru Nakano, Masahiko Higashi, and Tayuka Abe, shared this vision because of their own deep understanding of the natural history of their systems and of the larger scales over which exchanges and interactions among organisms can occur (Fausch 2000; Power 2001; Fausch et al. 2002). We hope that this book records and communicates some of the energy and excitement that Gary Polis infused into this international endeavor.

The contributed chapters in this book reflect similarly ambitious research efforts of scientists, many of whom are grounded in particular subdisciplines of ecology, but are striving to integrate and expand the spatial and temporal scales of understanding while still resolving process mechanisms and species interactions. These chapters are a sample of a rapidly increasing number of studies of food webs and landscapes in a burgeoning area of ecology. They draw on work in a wide range of ecosystems (in table 1 and in the description that follows, the chapters are ordered by landscape elevation, from marine subtidal to intertidal to terrestrial and freshwater, upstream, and upslope). The influences of marine resources are examined in subtidal ocean food webs where food and propagules are advected by internal waves (Witman et al., chap. 9); in intertidal food webs that respond to resources from regions in the open ocean that vary in productivity (Menge, chap. 5); in the now famous terrestrial food webs of small desert islands in Baja (Anderson and Polis, chap. 6); and in arctic riparian and upland habitats thousands of kilometers upstream from the ocean, to which nutrients and energy are vectored by anadromous salmon (Willson et al., chap. 19). Fluxes flowing downstream are studied by Riley et al. (chap. 16) in their examination of how watersheds affect estuarine food webs; by Caraco and Cole (chap. 20) in their large-scale assessment of the influence of terrestrial carbon on the earth's lakes and rivers, and by DeAngelis and Mulholland (chap. 2), who model how vertical flow separations partition sources and sinks over very small spatial scales, influencing the uptake of nutrients by attached algae. Organisms can sometimes vector resources against the physical flow, as described by Willson et al. (chap. 19) as well as by Winemiller and Jepsen (chap. 8), who examine the trophic effect of prochilodid migrations on fluxes from rich whitewater to poor blackwater habitats in South American rivers; by Vanni and Headworth (chap. 4), who discuss the importance of gizzard shad in resuspending sedimented nutrients into the photic water column of reservoirs; and by Power et al. (chap. 15), who document the importance to terrestrial consumers of river-to-forest fluxes, mediated by emergent aquatic insects. On land, Cadenasso et al. (chap. 10) show that fluxes between forests and meadows vectored by animals such as deer and mice depend on the structure of the forest boundary; Jefferies et al. (chap. 18) document huge, probably irreversible, effects on Arctic marshes of continental-scale agricultural subsidies to snow geese; and Baudry and Burel (chap. 21) describe the largest fluxes of energy and nutrients ever to occur on Earth, mediated by global commerce in industrial agriculture, with future consequences that we can only guess.

These chapters show the generality across scales (microns to thousands of kilometers; seconds to millennia) and ecosystems of the strong effects of fluxes of resources and organisms across traditional habitat boundaries. Holt (chap. 7), pointing out that local systems can be open with respect to some components but closed with respect to others, models the consequences for populations in food webs that receive allochthonous inputs at different trophic positions. Schindler and Lubetkin (chap. 3) review the use of stable isotopes for spatially tracing fluxes and determining the quantitative importance of different sources of elemental constituents to organisms that assimilate them. They preview an exciting modeling breakthrough by Lubetkin that promises to relax the constraint that one cannot determine the relative contributions from more sources than the number of isotopes analyzed.

Modeling and tracer studies like these are together supporting the efforts of ecologists to answer general questions about the community-level and ecosystem-level consequences of cross-habitat fluxes. What are characteristic temporal and spatial scales for these fluxes? How does the contrast in productivity, or the timing of peak productivity in linked habitats (Sears et al., chap. 23; Nakano and Murakami 2001) influence the interaction? Will allochthonous inputs stabilize or destabilize communities? Theory has suggested that this outcome depends on the amount, quality, and edibility of the resource (Huxel and McCann 1998). Chapters in this book include examples of destabilizing subsidies (seabird guano that results in larger-amplitude fluctuations in plant and arthropod populations on Anderson and Polis's bird islands, chap. 6; shad-stirred phosphorus that can initiate a positive feedback toward eutrophication in Vanni and Headworth's reservoirs, chap. 4), as well as examples in which subsidies may stabilize interactions among recipient predators and their

Table 1 Source and recipient habitats, boundaries, vectors, fluxes, and recipient web members described in the chapters of this volume

Author(s)	Source habitat	Recipient habitat	Boundaries /corridors	Vectors	Flux	Recipient organisms
Witman (chap. 9)	Open ocean	Benthic subtidal		Internal waves	Nutrients, plankton, propagules	Attached benthic invertebrates and algae
Menge (chap. 5)	Open ocean	Benthic intertidal		Surface waves, tides	Nutrients, plankton, propagules	Benthic invertebrates and algae
Anderson and Polis (chap. 6)	Open ocean	Desert islands	Seashore	Seabirds, beach wrack	Nutrients, carrion, plant detritus, feces	Marine and terrestrial arthropods and their vertebrate predators
Willson et al. (chap. 19)	Open ocean	Terrestrial watersheds	Rivers	Migrating anadromous fishes	Marine-derived nutrients and energy in fish bodies	Vertebrate predators and scavengers, terrestrial and riverine plants and invertebrates
Riley et al. (chap. 16)	Rivers and watersheds	Estuaries		River discharge	Nutrients, detritus, terrestrial invertebrates	Seaweeds, macroinvertebrates, and vertebrates
Caraco and Cole (chap. 20)	Terrestrial watersheds	Lakes and rivers	Shorelines	Runoff, groundwater, wind, gravity	Organic carbon	Aquatic microbes, detritivores, and grazers
DeAngelis and Mullholland (chap. 2)	Upstream chemostat Free-flowing upper stream	Downstream Sluggish near-bed storage zone	Vertical flow layers	Diffusion, mixing of layers, leaching from particles	Nutrients	Phytoplankton Periphyton
Winemiller and Jepsen (chap. 8)	Whitewater Neotropical rivers	Blackwater Neotropical rivers		Migrating Semaprochilodus	Migrating Semaprochilodus	Resident predatory Cichla in blackwater rivers
Vanni and Headworth (chap. 4)	Watersheds, bottom sediments	Reservoir planktonic and pelagic zones	Streams, groundwater	Gizzard shad	Dissolved and particulate nutrients (P)	Reservoir plankton and their consumers
Power et al. (chap. 15)	Upland river	Forested watershed	River surface, floating algal mats		Emergent aquatic insects	Insectivorous bats, lizards, and spiders
Cadenasso et al. (chap. 10)	Meadow	Interior forest	Forest edge	Wind, foraging deer and voles	Nutrients (N), detritus, seeds	Forest plants and consumers
Jefferies et al. (chap. 18)	U.S. agricultural fields	Arctic salt marshes	Migratory flyways	Lesser snow geese	Nutrients (N), grazing geese	Arctic graminoids, presently severely overgrazed
Baudry and Burel (chap. 21)	Globally derived agro-chemicals and crops	European agro-ecosystems	Hedgerows, grassy strips, earth banks	Industrial agriculture, world trade, wind, water	Nutrients (N), organic matter, crops	Local farmers, consumers in human and natural local food webs
Schindler and Lubetkin (chap. 3)	Watershed	Fresh water		Water movement	Nutrients	Zooplankton, fish
Rasmussen and Vander Zanden (chap. 11)	Watershed	Fresh water		Water movement	Contaminants	Zooplankton, fish

local prey over time scales of weeks to months (e.g., aquatic insects decrease lizard predation on riparian spiders; Sabo 2000, cited in Power et al., chap. 15).

Other general patterns of theoretical interest should emerge as more works reveal the spatial linkage of trophic interactions across scales and ecosystems. These models, analytical tools, and empirical studies will be critical in assessing how human distortion of patterns and fluxes affects food webs and ecosystems, and what players, processes, and scales of protection or restoration are essential if we are to maintain on Earth the intricate and diverse food webs that Gary Polis so appreciated.

Mary E. Power
Gary R. Huxel

PART I

FLUXES OF NUTRIENT AND DETRITU ACROSS HABITAT