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Temporal and Spatial Aspects of Food Web Structure and Dynamics

Robert D. Holt

Ecologists of all persuasions are becoming increasingly aware of the importance of dispersal, patchiness, and spatial heterogeneity (Gilpin and Hanski, 1991; Ricklefs and Schluter, 1993; Kareiva, 1994). The significance of temporal environmental variation is also an increasingly important theme (Pimm, 1991), as is the role of life histories in determining the effects of such variation on communities (Winemiller, Chapter 28). The chapters in this section of the volume are a testament to the importance of spatial, temporal, and life history effects in food web ecology.

One can usefully, if somewhat crudely, cleave food web variation in time or space into two sorts: qualitative variation and quantitative variation. Qualitative variation occurs when the species composition of a community changes, say along a spatial environmental gradient, or seasonally, or because of colonization and local extinction. For instance, Williamson (1981) described temporal variation in the summer bird community of a 16-ha English woodland (Eastern Wood, Surrey). Out of the 44 species which were recorded, only 16 species bred each year. A food web resolved to the species level would necessarily reveal a great deal of churning. Such variation might be obscured by aggregation (e.g., if all birds are lumped into either owls or owl food). Moreover, quantitative variation may exist in the strength (or even existence) of particular interactions, even within a defined, nonvarying species assemblage. Many organisms are quite labile in their food choices, depending upon, e.g., season and relative availabilities of different foodstuffs.

In addition to such sources of variability, food web ecologists need to come to grips with the messy reality that communities and ecosystems usually are made up of species and components with vastly different spatial strategies (Holt, 1993 (in Ricklefs and Schluter (1993)). In most communities, there will be some species which have relatively closed populations, others whose populations are quite open, and yet others for which it is silly to speak of a "population" in the community at all. In the case of Eastern Wood, two persistent resident species (one crow, one woodpecker) had individual home ranges greater than the spatial span of the study. These birds could conceivably each day couple spatially separate communities, dropping in one place little packets of nutrients extracted in another. Such spatial fluxes, generated at one trophic level, may have effects percolating through many others. In like manner, differences in life histories lead to disparate mechanisms for averaging over temporal variability; communities comprise species with sharply different life histories, leading to a whole spectrum of modulated responses to temporal variation.

Disentangling the relative impact of these sources of variation on food web patterns is a challenging task for future work. The papers in this section help highlight several aspects of the rich implications of space, time, and life history for food web ecology.

A time-honored tool in community ecology is analyzing communities along major environmental gradients to infer the causal underpinnings for observed patterns (e.g., Whittaker (1956)). Menge et al. (Chapter 25) demonstrate that replicated experiments along gradients provide a powerful tool for teasing apart the relative importance of different factors in community regulation. They argue that an important driving force in intertidal communities is the magnitude of inputs of marine phytoplankton. This study from the Pacific northwest provides an excellent example of the methodological value of experimental manipulations carried out along gradients, and moreover illustrates the general importance of spatial fluxes in determining patterns in community regulation and food web dynamics.

The theme of spatial fluxes also emerges as a central message in the elegant study by Polis and Hurd (Chapter 26) of marine subsidies for island communities in the Gulf of California and coastal communities in the Kalahari. A general feature of communities highlighted by this chapter is the significance of edges between habitats. The spatial configuration of habitats that is a central concern of landscape ecology is defined by the distribution of edges. The Polis-Hurd study clearly reveals the potential impact of flows across edges as determinants of the strength of food web interactions.

Spatial fluxes often vary enormously through time. The effects of such variation are filtered through organisms' life histories to determine food web effects. Winemiller (Chapter 28) provides a model case study for how one can use an understanding of life history strategies (in the case of his floodplain system, of key fish species) to enrich food web analyses. The dynamics of food webs in floodplains are driven on long timescales by geomorphological processes, and on shorter timescales by temporal variation in the hydrologic cycle. Strong temporal pulses in the magnitude of spatial transfers in productivity are a conspicuous feature of these systems. The food web effects of these pulses are modulated by fish species with distinct life history syndromes (which tend to be correlated with habitat stability and trophic rank). Similar temporal pulses in production propagating through space doubtless characterize many natural landscapes.

Power et al. (Chapter 27) emphasize yet another kind of temporal variability influencing food web dynamics, namely, physical disturbance. Northern California rivers experience regular scouring by floods. This disturbance sets up a kind of riverine succession, in which the initially dominant species are transients, adept at dispersal but vulnerable to predation. As predators become more important following the cessation of disturbance, these species are gradually replaced by predator-resistant species. Such local successional dynamics will often involve spatial dynamics, including colonization. This study nicely complements the chapter by Winemiller, as both illustrate the need for closer analyses of temporal dynamics in food webs, and a characterization of driving forces such as major disturbances (e.g., floods) and temporal pulses in productivity.

Many of the above chapters emphasize the quantitative importance of spatial and temporal variability for food web dynamics. Holt (Chapter 29) explores a rather different, but complementary, qualitative effect that may play out through space and time, namely colonization and extinction dynamics for food webs on islands. He presents several models which, in effect, provides a first step toward an island biogeography of food webs (see also Schoener et al., in press). These models predict that if species are trophic specialists, one should expect more marked species-area and species-distance effects for species of high trophic rank, than for species of low trophic rank. This kind of spatial dynamics may be significant for community assembly, even in situations where spatial fluxes are not great enough in magnitude to dominate in situ dynamics. Holt also cautions that predictions regarding species-area relationships may be much murkier for communities dominated by trophic generalists.

Collectively, the chapters in this section convincingly demonstrate that understanding many food web patterns and their underlying processes will require a recognition of the manifold roles of spatial and temporal heterogeneity in natural communities.

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