

8.4 | SPATIAL ASPECTS OF FOOD WEBS

*Ulrich Brose, Mitchell Pavao-Zuckerman,
Anna Eklöf, Janne Bengtsson, Matty P. Berg,
Steven H. Cousins, Christian Mulder,
Herman A. Verhoef, and Volkmar Wolters*

Aspects of spatial scale have until recently been largely ignored in empirical and theoretical food web studies (Cohen and Briand, 1984; Martinez, 1992; but see Bengtsson et al., 2002; Bengtsson and Berg, Chapter 5.1). Most ecologists tend to conceptualize and represent food webs as static representations of communities, depicting a community assemblage as sampled at a particular point in time, or highly aggregated trophic group composites over broader scales of time and space (Polis et al., 1996a). Moreover, most researchers depict potential food webs, which contain all species sampled and all potential trophic links based on literature reviews, several sampling events, or laboratory feeding trials. In reality, however, not all these potential feeding links are realized as not all species co-occur, and not all samples in space or time can contain all species (Schoenly and Cohen, 1991), hence, yielding a variance of food web architecture in space (Brose et al., 2004). In recent years, food web ecologists have recognized that food webs are open systems—that are influenced by processes in adjacent systems—and spatially heterogeneous (Polis et al., 1996a). This influence of adjacent systems can be bottom-up, due to allochthonous inputs of resources (Polis and Strong, 1996; Huxel and McCann, 1998; Mulder and De Zwart, 2003), or top-down due to the regular or irregular presence of top predators (Post et al., 2000a; Scheu, 2001). However, without a clear understanding of the size of a system and a definition of its boundaries it is not possible to judge if flows are internal or driven by adjacent systems. Similarly, the importance of

allochthony is only assessable when the balance of inputs and outputs are known relative to the scale and throughputs within the system itself. At the largest scale of the food web—the home range of a predator such as wolf, lion, shark, or eagle of roughly 50 to 300 square kilometers—the balance of inputs and outputs caused by wind and movement of water may be small compared to the total trophic flows within the home range of the large predator (Cousins, 1990).

Acknowledging these issues of space, Polis et al. (1996a) argued that progress toward the next phase of food web studies would require addressing spatial and temporal processes. Here, we present a conceptual framework with some nuclei about the role of space in food web ecology. Although we primarily address spatial aspects, this framework is linked to a more general concept of spatio-temporal scales of ecological research.

DEFINING SPATIAL SCALES

Given that not every species occurs everywhere, spatial distributions of trophic interactions define (1) the spatial heterogeneity of food webs and (2) differences between local and macroecological food webs (Brose et al., 2004). More specifically, even food webs within the same metacommunity differ to some extent when studied at different locations. In such local community food webs, all species co-occur and all potential trophic links—based on the physiological feeding capacities of the species—are realized. This concept of co-occurrence has to be given up when larger spatial scales are considered that integrate different local community food webs into a metacommunity food web. In the following sections, we will give two examples for this. First, some large-bodied predators are too low in numerical abundance to invade all local community food webs simultaneously. Second, not all potential resource species in a metacommunity can persist under strong top-down pressure by their consumer species and thus avoid co-existence in the same local communities. Therefore, in macroecological metacommunity food webs not all species co-occur and not all potential links are realized due to spatial and temporal separation (Brose et al., 2004). The variance in local food web structure and the difference between food webs studied within local communities versus metacommunities are important challenges for future research. In the following, we will discuss some consequences of these spatial considerations for theory on food web structure and dynamics.

SPECIES OPERATE AT DIFFERENT SPATIAL SCALES

Food webs consist of organisms that vary in their taxonomic identity, body size, trophic interactions, and their trophic position and thus might have very different spatial scales of interactions. In general, species' home ranges increase with their body sizes (see Kelt and Van Vuren, 2001, for detailed explanations), and in many food webs, mean body size increases with trophic level (Warren and Lawton, 1987; Cohen et al., 1993a; Cohen et al., 2003). However, frequent exceptions to this pattern such as parasitoid food webs with constant predator–prey body size ratios (Memmott et al., 2000) and food webs with mobile prey but sessile consumers (Östman et al., 2001) suggest a cautious use of this relationship. In general, mean body size is inversely related to numerical abundance (Brown et al., 2000; Gaston and Blackburn, 2000; Cohen et al., 2003) and positively related to territory size (cf. Ghilarov, 1944; Hendriks, 1999; Jennings and Mackinson, 2003). Accordingly, a metacommunity is likely to contain small and abundant species that occur more frequently in local community food webs than larger and less abundant species. These differently sized species operate at different spatial scales. As a consequence, large predators of low abundance are likely to be distributed unevenly within the metacommunity thus having a spatio-temporally heterogeneous impact on other species in local communities. Furthermore, in consequence of the abiotic heterogeneity of most habitats not all small species at the base of the food web occur everywhere in the metacommunity.

LARGE PREDATORS INTEGRATE LOCAL WEBS

We illustrate a metacommunity example of seven species that are not evenly distributed in space (Figure 1A) and trophically linked in a potential food web module (see Figure 1B). The top predator has the largest home range, whereas the other species with smaller home ranges occur locally (see Figure 1A, species 1–6). This yields a turnover of species and trophic interactions across space (see Figure 1C), and hence a beta-diversity. Exemplary samples at different locations yield a three species food chain (see Figure 1C, *I*), a four-species module (see Figure 1C, *II*), or a four-species food chain (see Figure 1C, *III*). Although species and trophic interactions vary, this exemplary food web module is linked by the predator with the largest home range that occurs in all three samples. Documenting the coupling of the local webs by the largest predator

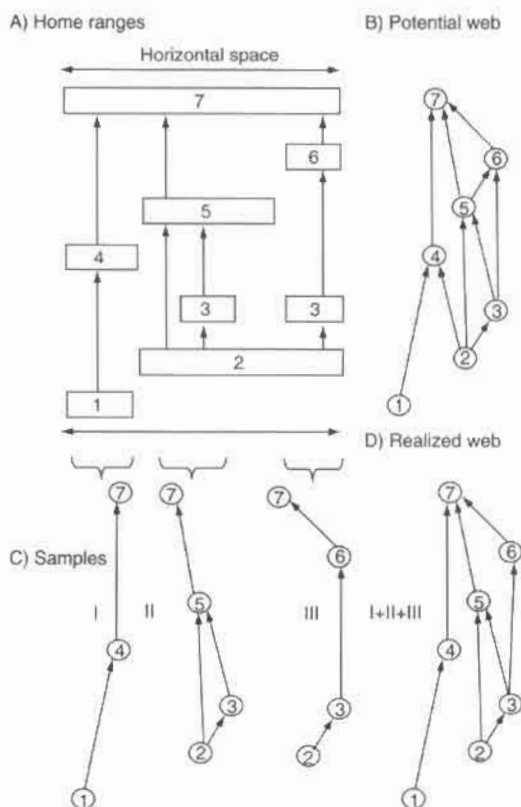


FIGURE 1 | A spatially explicit food web of seven species (1–7) that is connected by a single top predator. **A**, Distribution of the seven species' home ranges (boxes) in horizontal space. **B**, The potential food web showing physiologically possible feeding interactions (arrows) between the seven species (nodes). **C**, Three exemplary samples at different points in space with different local food webs. **D**, Realized food web showing the feeding interactions that are realized in the spatial food web.

requires studies on a time scale long enough for the predator to visit all sites in its home range. Thus, large predators may couple local webs, but the extent to which they do so depends on time. This example illustrates the impact of spatio-temporal scaling on food web studies: the more local webs are sampled and combined, and the more samples in time, the more the food web architecture approaches the metacommunity food web configuration (see Figure 1C, D). Empirical examples for this spatio-temporal concept are nested microbial compartments that are integrated by the predation activities of larger soil fauna (Pokarzhevskii et al., 2003).

as beta-diversity—it is most likely that the number of realized links does not equal the number of potential links (compare Figure 1B,D). For any given species-area relationship, the difference between potential and realized webs depends on the area studied and the efficiency of predators tracking their prey species (Holt et al., 1999; Brose et al., 2004).

SPATIAL ASPECTS OF FOOD WEB DYNAMICS

Many studies have shown how patch density, patch size, and species' dispersal rates affect metacommunity population dynamics, but surprisingly few studies have considered food web structure (Melian and Bascompte, 2002; Ellner and Fussmann, 2003; Brose et al., 2004). Brose et al. (2004) demonstrated that variances in patch size systematically affect food web diversity and complexity. Accordingly, habitat destruction may yield qualitatively new consequences when considering species that are embedded in a web of ecological relationships (Ellner and Fussmann, 2003). Species' abundances and extinction thresholds vary with food web structure (Melian and Bascompte, 2002). Accordingly, the consequences of habitat loss for a specific species do not only depend on the species' own traits but also on community characteristics such as food web architecture and diversity. Furthermore, depending on food web structure primary extinctions within a local habitat patch can result in a cascade of secondary extinctions (Borrvall et al., 2000). Such cascading extinctions can lead to community closure that prevents re-colonization by the originally lost species (Lundberg et al., 2000). The result of species extinctions—secondary extinctions or re-colonization by the originally lost species—depends on the balance between relaxation time and dispersal rate within the metacommunity. Relaxation time is the time elapsed from initial species loss until the new species composition is reached, and long relaxation times means that there will be time available for dispersal of species between local communities and hence time for rescue effects to operate and re-colonization to take place. Recent evidence suggests that relaxation times are longer in diverse communities than in communities with few species. Together, all these studies indicate that metacommunity dynamics differ substantially depending on community diversity and food web structure. Clearly, it will be an important future task to study metapopulation dynamics and the consequences of habitat loss in more complex and thus more realistic communities under varying food web structure.

DISCUSSION AND CONCLUSIONS

Current food web models generally assume that all species within the food web occur everywhere in the local habitat under study (Cohen and Briand, 1984; Martinez, 1992). This causes all potential links—who is able to eat whom—to be realized links—who eats whom. The above spatial considerations, however, suggest that not all species occur everywhere at any time and that some potential links are not realized at any single point in time. As shown in this chapter, a more thorough consideration of space in food webs extends the simple one-way concept of “spatial subsidies” (Polis and Strong, 1996) considerably. The dynamical links between habitats are more generally two-way rather than one-way. Recognition of the importance of spatial scale in food web studies has several implications for food web theory. In particular, the potential food webs that are frequently described by ecologists will often differ from how food webs are realized in actual space and time. Clearly, choosing the right spatio-temporal scale for a food web study depends on the species studied (e.g., their home ranges and locomotive behavior) and the study objective (e.g., local interaction structure versus metacommunity patterns). Although suggestions on spatio-temporal scales and boundary conditions are hard to generalize, we anticipate that our definitions of local versus metacommunity food webs will foster a healthy debate on how to deal with scaling in empirical food web research. Moreover, integrating spatial processes such as extinction and colonization by dispersal in food web models is an important step towards understanding population dynamics in complex communities, and understanding the consequences of habitat loss for the community structure and food web dynamics. Such important spatial characteristics of food webs need to be treated as such if the merging of food web and landscape ecology that Gary Polis and others envisioned (Cousins, 1993; Polis et al., 1996a; Power and Rainey, 2000; Chust et al., 2003) is to be realized.

References

- Bengtsson, J., & Berg M.P. 2004. Variability in soil food web structure across time and space, this book
- Bengtsson, J., Engelhardt, K., Giller, P., Hobbie, S., Lawrence, D., Levine, J., Vilà, M. & Wolters, V. 2002. Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations. In: Loreau, M., Naeem, S. & Inchausti, P. (eds.) *Biodiversity and ecosystem functioning: synthesis and perspectives*, pp. 209-220. Cambridge University Press.
- Borrvall, C., Ebenman, B. & Jonsson, T. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* 3: 131-136.
- Brose, U., Ostling, A., Harrison, K. & Martinez, N.D. 2004. Unified spatial scaling of species and their trophic interactions. *Nature* 428:167-171.
- Brown, J.H. & West, G.B. 2000. *Scaling in biology*. Oxford University Press.
- Chust, G., Pretus, J.L., Ducrot, D., Bedòs, A., Deharveng, L. 2003. Identification of landscape units from an insect perspective. *Ecography* 26: 257-268.
- Cohen, J.E. & Briand, F. 1984. Trophic links of community food webs. *Proceedings of the National Academy of Science USA* 81: 4105-4109.
- Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. 1993. Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology* 62: 67-78.
- Cohen, J.E., Jonsson, T. & Carpenter, S.R. 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Science USA* 100: 1781-1786.
- Cousins, S.H. 1990. Countable ecosystems deriving from a new food web entity. *Oikos* 57: 270-275

- Cousins, S.H. 1993. Hierarchy in ecology: its relevance to landscape ecology and geographical information systems. In: Haines-Young, R., Green, D.R. & Cousins, S.H. (eds.) *Landscape ecology and GIS*, pp. 75-86 Taylor & Francis Ltd, London.
- Ellner, S.P. & Fussmann, G. 2003. Effects of successional dynamics on metapopulation persistence. *Ecology* 84: 882-889.
- Elton, C.S. 1927. *Animal Ecology*. Sidgwick and Jackson, London.
- Gaston, K.J. & Blackburn, T.M. 2000. *Pattern and process in macroecology*. Blackwell Science, Oxford.
- Ghilarov, M.S. 1944. Correlations between size and number of soil animals. *Proceedings of the Academy of Science of the USSR* 43: 267-9.
- Hendriks, A.J. 1999. Allometric scaling of rate, age, and density parameters in ecological models. *Oikos* 86: 293-310.
- Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. 1999. Trophic rank and the species-area relationship. *Ecology* 80: 1495-1504.
- Hunt, H.W. & Wall, D.H. 2002. Modelling the effects of soil biodiversity on ecosystem functioning. *Global Change Biology* 8: 33-50.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113: 81-101.
- Huxel, G.R. & McCann, K. 1998. Food web stability: the influence of trophic flows across habitats. *American Naturalist* 152: 460-469.
- Jennings, S. & Mackinson, S. 2003. Abundance-body mass relationships in size-structured food webs. *Ecology Letters* 6: 971-974.
- Kelt, D.A. & Van Vuren, D.H. 2001. The ecology and macroecology of mammalian home range area. *American Naturalist* 157: 637-645.
- Lundberg P., Ranta E. & Kaitala V. 2000. Species loss leads to community closure. *Ecology Letters* 3: 465-468.

- Martinez, N.D. 1992. Constant connectance in community food webs. *American Naturalist* 139: 1208-1218.
- May, R.M. 1974. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, N.J.
- Melian C.J. & Bascompte J. 2002. Food web structure and habitat loss. *Ecology Letters* 5: 37-46.
- Memmott, J., Martinez, N.D. & Cohen, J.E. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology* 69: 1-15.
- Moore, J.C. & Hunt, H.W. 1988. Resource compartmentation and the stability of real ecosystems. *Nature* 333:261-263.
- Mulder, Ch. & De Zwart, D. 2003. Assessing fungal species sensitivity to environmental gradients by the Ellenberg indicator values of above-ground vegetation. *Basic and Applied Ecology* 4: 557-568.
- Mulder, Ch., De Zwart, D., Van Wijnen, H.J., Schouten, A.J. & Breure, A.M. 2003. Observational and simulated evidence of ecological shifts within the soil nematode community of agroecosystems under conventional and organic farming. *Functional Ecology* 17: 516-525.
- Östman, Ö., Ekbom, B. & Bengtsson, J. 2001. Natural enemy impacts on a pest aphid varies with landscape structure and farming practice. *Basic and Applied Ecology* 2: 365-371.
- Pokarzhevskii, A.D., van Straalen, N.M., Zaboev, D.P. & Zaitsev, A.S. 2003. Microbial links and elemental flows in nested detrital food-webs. *Pedobiologia* 47: 213-224
- Polis, G.A. & Strong, D.R. 1996. Food web complexity and community dynamics. *American Naturalist* 147: 813-846.

- Polis, G.A., Holt, R.D., Menge, B.A. & Winemiller, K.O. 1996. Time, space, and life history: influences on food webs. In: Polis, G.A. & Winemiller, K.O. (eds.) *Food webs: integrations of patterns and dynamics*, pp 435-460. Chapman and Hall, New York.
- Post, D.M., Conners, M.E. & Goldberg, D.S. 2000. Prey preference by a top predator and the stability of two linked food chains. *Ecology* 81: 8-14.
- Power, M.E. & Rainey W.E 2000 Food webs and resource sheds: towards spatially delimiting trophic interactions. In: Hutchings, M.J., John E.A. & Stewart, A.J.A.(eds.) *The ecological consequences of environmental heterogeneity*. pp. 291-314. Blackwell Science Ltd, Oxford.
- Scheu, S. 2001. Plants and generalist predators as links between the below-ground and above-ground system. *Basic and Applied Ecology* 2: 3-13.
- Schoenly, K. & Cohen, J.E., 1991. Temporal variation in food web structure: 16 empirical cases. *Ecol. Monogr.* 61: 267-298.
- Warren, P.H. & Lawton, J.H. 1987. Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia* 74: 231-235.