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From isolation to the matrix: toward a coherent food web theory

McCann, Kevin S. 2012. **Food webs.** Monographs in Population Biology, No. 50. Princeton University Press, Princeton, New Jersey. xii + 241 p. $99.50 (cloth), ISBN: 978-0-691-13417-8 (alk. paper); $45.00 (paper), ISBN: 978-0-691-13418-5 (alk. paper).

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The study of food webs has been one of the most prolific ecological research areas over the last 40 years, with a good dialogue between theoretical developments and empirical studies. However, different perspectives have been undertaken, mainly characterized by the different number of interacting species and level of detail of interacting partners, ranging from very detailed age-structured, predator-prey models to the characterization of the statistical properties and dynamics of large food webs.

Despite this proliferation, we still lack a coherent conceptual synthesis across these different scales of observation. Kevin S. McCann's *Food webs* does it and to a very high standard, using the question of what governs the stability of ecological systems as the backbone of the book.

The book is divided into three sections: "The problem and the approach," "Food web modules: from populations to small food webs," and "Toward whole systems."

The first section constitutes an excellent introduction as both to why this synthesis is needed and to the methodology to be used in the remaining sections. *Food webs* is based on the premise that understanding the stability and collapse of ecosystems is a fundamental societal need. What determines community stability is not only a fascinating academic research area, it is actually the stability of the provision of ecosystem functions and services that determines the sustainability of societies from local to global scales. This is the starting point of the book. The rest of the book aims to understand how complex ecosystems work and determine this stability, using antagonistic predator-prey interactions as the slice of ecosystem complexity considered. For doing so, Chapter 2 is a brief, clear, and not-too-technical introduction to the mathematics of dynamical systems, pivotal to understand predator-prey dynamics. This chapter is very intuitive, making complex mathematical concepts like nonequilibrium steady states and bifurcation plots really accessible for any audience—thanks to nice but concise prose, graphical representations, and illustrative empirical examples.

The second section is a comprehensive summary of dynamical systems theory applied sequentially to single populations, two interacting populations, and three and four interacting species. In all cases, chapters are biased towards extracting general rules from theory into the general biological conditions under which population dynamics are stabilized or destabilized. In Chapter 4, stability conditions are explored as population growth increases using continuous and discrete resource population models. A fundamental conclusion for interpreting food web dynamics is obtained, highlighting the dual effect of increasing growth rates on population stability. While all resource models that beget monotonic dynamics towards equilibrium carrying capacity are stabilized by increased growth rates, those models that beget oscillatory dynamics to the equilibrium are destabilized by increased growth rates. In addition, the inclusion of lags of any form, including discrete and stage-structured models, tends to be dominated by the destabilizing effects of increased population growth rates.

In Chapter 5, consumer-resource dynamics are explored and focus on a particular aspect of consumer-resource theory: how changes in interaction strength affect population stability. Despite the various definitions of interaction strength and their dynamical consequences, McCann shows the importance of the balance between interspecific consumer-resource flux rates and consumer and resource loss rates. In this context, any ecological mechanism that increases interspecific consumer-resource interaction strengths relative to the strength of intraspecific interactions tends to destabilize population dynamics. These theoretical predictions are supported by various empirical data and mesocosm experiments, identifying fundamental differences between aquatic and terrestrial systems. The author suggests that population dynamics in aquatic systems should be less stable, i.e., more variable, than in terrestrial ecosystems because

the rates of flux between resources and consumers are higher in the former. The inclusion of lagged consumer-resource dynamics and stage-structured interactions can alter stability, and this particular aspect is explored in Chapter 6.

In the next two chapters, the stability of three and four interacting species modules is explored. These models of intermediate complexity have received considerable attention in the past, and recent network studies have tried to deconstruct food webs into these modules in order to understand food web stability. But what McCann does here is to understand the stability and dynamics of each module using the framework presented in previous chapters. And, as expected, predictions get more complex, but not that much more complicated. The case of omnivory is illustrative here. Since Pimm and Lawton's seminal theoretical explorations in the late 1970s, there has been a lot of work on the role of omnivory in food webs, with contradictory findings as to whether it begets stability or instability. McCann's framework reconciles these contradictions and suggests that weak omnivory tends to be quite stabilizing, while strong omnivory is often destabilizing and in some cases it does not allow for species coexistence. Empirical work reviewed in Chapter 7 supports this theoretical prediction, showing that omnivory is a stabilizing force.

The last four chapters of the book tackle the challenge of scaling toward whole systems. In opposition to the gradualism that characterizes the book so far, now it bifurcates into four different directions, where each chapter is a conclusion on its own. In Chapter 9, the spatial dimension connecting simple food web modules is introduced. As the Spanish ecologist Ramon Margalef once pointed out, and I apply this to food web ecologists, we often ignore space as if ecosystems were dancing on a needle's tip. In this chapter, McCann explores the role of mobile generalist (and/or adaptive) consumers for the stability of coupled food chains in space (e.g., aquatic and terrestrial, pelagic, and littoral). Many interesting and intriguing predictions populate this chapter. One of them is the dual effect of generalist couplers on stability. While they are a strong stabilizing force when they are embedded in a spatially expansive ecosystem, they can be an important destabilizing force within spatially constrained or restricted ecosystems. One of the consequences of this dual effect is that when expansive ecosystems are transformed into restricted ecosystems, as a consequence of habitat loss, for instance, generalist consumers may become detrimental for population stability.

Chapter 10 will probably be one of the most-read parts of this book. Like a Hollywood movie, it goes from Modules to the Matrix, i.e., from simple modules to real food webs. Given the long tradition on the matrix approach in food webs and on stability-related issues as to whether complexity begets stability, the question here is whether results from the modular approach hold in light of the matrix approach. Despite previous confrontations between the more reductionist and the more holistic approaches, McCann shows that the results from both theories make sense in light of each other. One example is the prevalence of the stabilizing effect of weak interaction strengths in small modules to the entire food web. Also intriguing is the theoretical finding that stable modules, when linked to unstable ones, tend to stabilize them. The sum can therefore be more stable than the parts.

Although *Food webs* is a community ecology book, many ecosystem ecology concepts are introduced in several chapters, in particular the relationships between biomass flux and interaction strength. However, it is not until Chapter 11 that the ecosystem is explicitly introduced in the form of two fundamental ecosystem processes mediated by food webs: nutrient cycling and decomposition. And this is done only for very simple modules, not for complex food webs. The addition of even a simple detritus module tends to stabilize consumer-resource dynamics. This chapter, I think, is going to leave many readers unsatisfied, because one of the key research areas in this area is to link food webs and ecosystem dynamics. But this area deserves a book on its own, and the recent book by Michel Loreau (2010. *From populations to ecosystems: theoretical foundations for a new ecological synthesis*. Monographs in Population Biology, No. 46. Princeton University Press, Princeton, New Jersey) is a good expansion of this chapter.

Food webs is an imaginative but very concise book in terms of methodology and selection of concepts. It is extremely coherent, though some may think extremely selective in the models and concepts used. But to build a food web theory across different scales of organization, from single populations to real multispecies interaction networks, this selectivity is needed, and the unifying concept of stability makes it fascinating. The last chapter is a mixture of this imagination and conciseness. Instead of an open-perspective, vague finishing chapter typical of many books, this chapter presents empirical data to support the conclusion that food webs are, ultimately, a (special) class of complex adaptive system. They change and adapt, but they do so in a predictable way. This is beautifully illustrated by Canadian Shield lake ecosystems across several gradients, including ecosystem size and different degrees of habitat coupling. Topological properties of food webs and their stability vary across these gradients. Understanding these sources of variability is the key, especially in an increasingly modified world, if we aim at predicting the adaptability and stability of food webs.

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