

Chapter 8

The Role of Stochastic Simulations to Extend Food Web Analyses

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ABSTRACT

Food webs are schematic representations of who eats whom in ecosystems. They are widely used in linking process to pattern (e.g., degree distribution and vulnerability) and investigating the roles played by particular species within the interaction web (e.g., centrality indices and trophic position). First, I present the dominator tree, a topological structure reducing food web complexity into linear pathways that are essential for energy delivery. Then, I describe how the dominance relations based on dominator trees extracted from binary food webs may be modified by including interaction strength. Consequences related to the skewed distribution of weak links towards the trophic chain are discussed to explain higher risks of secondary extinction that characterize top predators dominated by basal species. Finally, stochastic simulations are introduced to suggest an alternative approach to static analyses based on food web topology. Ranking species importance using stochastic-based simulations partially contradicts the predictions based on network analyses.

INTRODUCTION

Within ecosystems, species interact in various ways (e.g., predator-prey, plant-seed disperser, host parasite, plant-pollinator, and plant-ant). Types and strengths of interaction change through

time and space, varying between individuals that are subject to the rules of natural selection and genetic drift (Case & Taper, 2000; Fussmann *et al.*, 2007; Bascompte & Jordano, 2007).

In community ecology, food relations are certainly the most investigated. Dealing with the whole set of trophic interactions is possible by

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graph theory, and ecosystems can be represented as sets of nodes (species or trophospecies) connected by edges (trophic relations). From this idea, two types of tools have come about: food webs (Yodzis, 1989; Cohen *et al.*, 1990; Polis & Winemiller, 1995) and ecological networks (Ulanowicz, 2004; Fath & Patten, 2004). The former describes feeding relations among species in a qualitative way (presence/absence); the latter includes also the magnitude of the interactions, in terms of amount of matter (or energy) that is exchanged in a given time period, over a reference area (*e.g.*, kcal m⁻² year⁻¹; gC cm⁻² month⁻¹). Food webs and ecological networks are widely used in linking process to pattern (*e.g.*, degree distribution and vulnerability) and investigating the roles played by particular species within the interaction web (*e.g.*, centrality indices and trophic position).

A central issue in ecology is understanding the processes that shape food webs. This is of key importance as the topology (*i.e.*, static graph configuration associated to trophic links between species) of these networks is one of the major determinants of ecosystem dynamics and is ultimately responsible for response to human impact. For this reason, discovering patterns in food web topology has long been a prominent topic in ecology (Cohen, 1978). To unveil mechanisms lying behind community structure we are asked to identify general rules governing such architectures. Progress towards this knowledge would help advances on applied issues such as understanding the potentially catastrophic consequences of species loss on cascades of further extinctions (Pimm, 1980; Allesina & Bodini, 2004), and predicting the direct and indirect impact of invasive species (Woodward & Hildrew, 2001).

The existence of empirical patterns has stimulated analyses to identify which mechanisms are responsible for shaping the structure of food webs. It has been shown unambiguously that real food webs are topologically distinct from randomly connected networks (Solow & Beet, 1998) and several simple models predict in detail many regu-

larities of food web topology (Cohen & Newman, 1985; Williams & Martinez, 2000; Cattin *et al.*, 2004; Stouffer *et al.*, 2006; Allesina *et al.*, 2008).

Newly developed algorithms aim to identify the role of species by quantifying the effect of their loss on ecosystem structure. Key species are those possessing the greatest strategic value and, from a network perspective, their conservation promotes the persistence of other species (Jordán & Scheuring, 2002; Jordán *et al.*, 2006; Jordán, 2009). A promising issue concerns the forecasting of secondary extinctions (*i.e.*, the possibility that species loss may lead to cascades of further extinctions) based on food web structure. In particular, studies on simulated food web models have focused on the relation between connectance and secondary extinctions, showing how the loss of random species is likely to result only in a few extinctions, whereas there are structurally dominant taxa whose loss is responsible for stronger impact (Dunne *et al.*, 2002a,b, 2004). Other works have shown the potential of the dominator tree (a structure describing the dominance relationship between nodes in a hierarchical digraph) to assess secondary losses caused by species exclusion, and to identify which nodes are likely to cause the greatest impact if removed (Allesina & Bodini, 2004; Bodini *et al.*, 2009).

Models capturing the non-random topology of food webs, and the majority of techniques estimating the robustness of networks, are based on binary (*i.e.*, unweighted) data. Food webs are often considered to have rigid architectures, with links connecting prey to predators summarizing the observed diet. This inflexible structure represents a limit, since it does not describe what really happens in nature. Although binary food webs have been deeply analyzed in recent years, many ecologists claimed the need of using weighted trophic links to unveil important dynamics, such as the role of skewed interaction strength distribution (*e.g.*, many weak and few strong links; Paine, 1992; McCann *et al.*, 1998), or effects of species with

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