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Competition in di- and tri-trophic food web modules

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HIGHLIGHTS

- Competition in many species in di- and tri-trophic food webs is studied.
- The top species have either fixed or adaptive preferences for their prey.
- It is shown that prey switching strongly promotes species coexistence.
- In food-web modules studied, prey switching leads to food-web dynamics that are similar to linear-food chains.

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ABSTRACT

Competition in di- and tri-trophic food web modules with many competing species is studied. The food web modules considered are apparent competition between n species sharing a single predator and a diamond-like food web with a single resource, a single top predator and many competing middle species. The predators have either fixed preferences for their prey, or they switch between available prey in a way that maximizes their fitness. Dependence of these food web dynamics on environmental carrying capacity and food web connectance is studied. The results predict that optimal flexible foraging strongly weakens apparent competition and promotes species coexistence. Food web robustness (defined here as the proportion of surviving species) does not decrease with increased connectance in these food-webs. Moreover, it is shown that flexible prey switching leads to the same population equilibria as in corresponding food webs with highly specialized predators. The results show that flexible foraging behavior by predators can have very strong impact on species richness, as well as the response of communities to changes in resource enrichment and food-web connectance when compared to the same food-web topology with inflexible top predators. Several results on global stability using Lyapunov functions are provided.

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1. Introduction

Understanding coexistence of competing species on a limited number of resources has been one of the most challenging tasks for ecologists. The "competitive exclusion principle" states that two complete competitors cannot coexist at an equilibrium when feeding on a single resource (e.g., Gause, 1934; Hardin, 1960). More generally, n competing species cannot coexist at a population equilibrium if they are limited by less than n limiting factors (Levin, 1970). How is it then possible that many species do survive in nature? One such example is the large number of phytoplankton species surviving on just a few common resources. This puzzling discrepancy between empirical observations and theoretical predictions has been termed "the paradox of phytoplankton" (Hutchinson, 1961). Since that time, several possible mechanisms explaining competing species coexistence were proposed. Hutchinson (1961) proposed that species coexistence can be achieved due to fluctuating environment that prevents population densities to settle at an equilibrium and favors different species at different times. Similarly, intrinsic oscillations in species abundances can promote species coexistence (e.g., Armstrong and McGehee, 1980; Huisman and Weissing, 1999). Predation is another mechanism that can relax competition among competitors. This was experimentally verified by Slobodkin (1964) with his hydra experiments and on a larger spatial scale by Paine (1969) who showed that removal of starfish *Pisaster ochraceus* resulted in the competitive exclusion of most barnacle species on which the starfish normally feeds. Thus, barnacle co-existence was facilitated by the common predator.

As specialized predators act as limiting factors, it is not surprising that in food-webs where each competitor is limited

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by its own predator, coexistence is possible. The question is when a single predator species can enhance survival of several competing species. Leibold (1996) and Holt et al. (1994) showed that two competing species can coexist in a diamond-like food web where they both compete for a common resource and are consumed by a common generalist predator. These predictions do not violate the competitive exclusion principle because in the diamond-like food web with two competing middle species there are exactly two limiting factors: the common resource and the predator. However, Křivan (2003) showed that even with two competitors coexistence is limited to a narrow range of demographic parameters. The situation dramatically changed when top predators were flexible foragers with foraging preferences that maximized their fitness. In this case, the set of parameters for which the two species coexisted was much larger when compared to the same system with fixed predator preferences. Similar results were obtained by several authors who studied two-consumer–one-predator food webs with optimally foraging predators (e.g., Abrams, 1982; Holt, 1983; Fryxell and Lundberg, 1993, 1994; Holt et al., 1994; Křivan, 1996, 1997; Fryxell and Lundberg, 1997; Abrams, 2010). These works focused mostly on simple food-web modules (sensu Holt, 1997) such as exploitative or apparent competition (Holt, 1977, 1984) between consumers. While analyses of these modules are instrumental in our understanding of basic mechanisms of species coexistence, it is much more difficult to extrapolate these results to complex food-webs.

One of the fundamental questions of ecology asks how diversity relates to species coexistence. A general early belief was that higher diversity creates greater opportunities for negative regulatory feedbacks in food webs which, in turn, enhance species coexistence and stability (Odum, 1971). The assumption that complexity begets stability was challenged by May (1972) (see also Gardner and Ashby, 1970) who showed that for randomly assembled food webs with fixed interaction strength between species, there is a sharp transition from stability to instability when complexity measured as the food-web connectance (i.e., the number of realized links in the food web divided by the number of all possible links) exceeds a critical threshold. It was also shown that robustness (defined as the proportion of surviving species) decreases with increasing connectance (e.g., Brose et al., 2003; Berec et al., 2010). May's work was challenged by Kondoh (2003) who showed that when predators are flexible foragers (i.e., when interaction strength adaptively changes with changes in population densities), complexity can enhance community persistence. However, some subsequent works revealed that this prediction depends on other factors such as population dynamics (Brose et al., 2003), food web topology (Brose et al., 2003; Kondoh, 2006; Garcia-Domingo and Saldaña, 2007; Uchida and Drossel, 2007), and details of foraging behavior (Berec et al., 2010).

In this article I will focus on four food web modules (Fig. 1) with a fixed topology and many species. The deterministic food webs considered in this article are more complex when compared with simple food-web modules consisting of a few (usually 2–4) species, but they are simpler when compared with stochastic food webs generated e.g. by the cascade or niche model (Williams and Martinez, 2000). Such an intermediate level of complexity can allow one to discern ties to preexisting ecological theory more cleanly than is often the case with models dealing with stochastic complex food webs. In particular, I will study apparent competition (Fig. 1A) and combined apparent and exploitative competition (Fig. 1C) among many species when top predators are generalists. I will also compare these food webs with similar food-web modules with highly specialized top predators (Fig. 1B and D). For generalist predators I consider two possibilities: either predators have fixed foraging preferences for their prey (called non-flexible predators), or they switch between available prey in a way that maximizes their fitness (called flexible predators). Dependence of the number of surviving species and the mean population abundances on the mean environmental carrying capacity and food web connectance is studied. I will show that population dynamics in the two food webs with a single flexible top predator (Fig. 1, panels A and C) are very similar to population dynamics with specialized predators

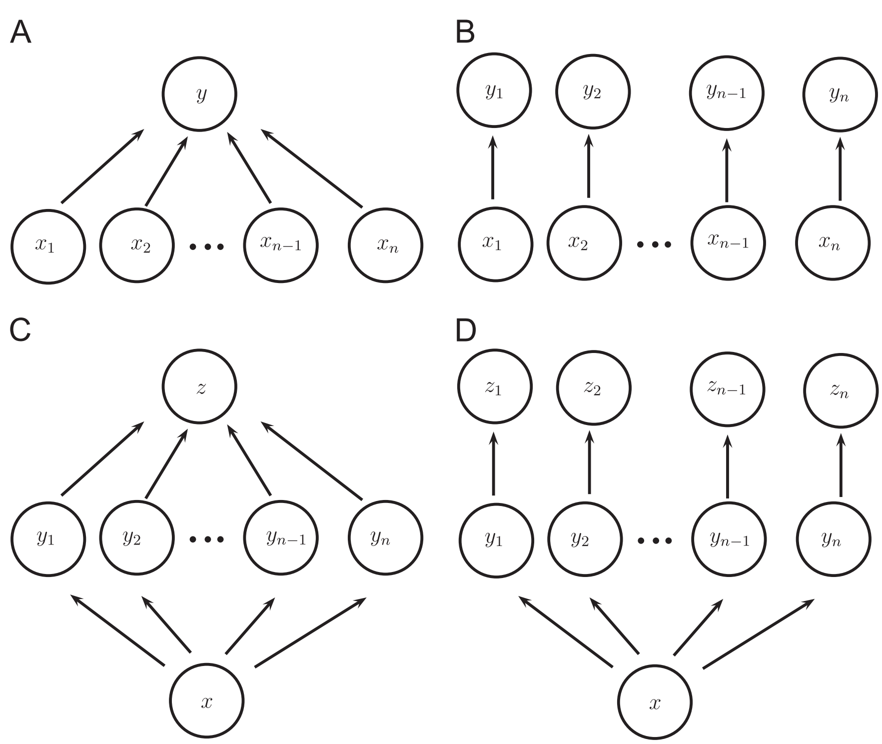

Fig. 1. Top panels show di-trophic food webs where predators are either generalists (A) or specialists (B). Bottom panels (C and D) show the corresponding tri-trophic food webs.

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