Competition in di- and tri-trophic food web modules

Vlastimil Křivan [a,b,*]

[a] Institute of Entomology, Biology Center, Academy of Sciences of the Czech Republic, Czech Republic
[b] Department of Mathematics and Biomathematics, Faculty of Science, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic

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.

ARTICLE INFO

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.

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

* Correspondence address: Institute of Entomology, Biology Center, Academy of Sciences of the Czech Republic, Czech Republic. Tel.: +420 38 7775365.
E-mail address: vlastimil.krivan@gmail.com

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
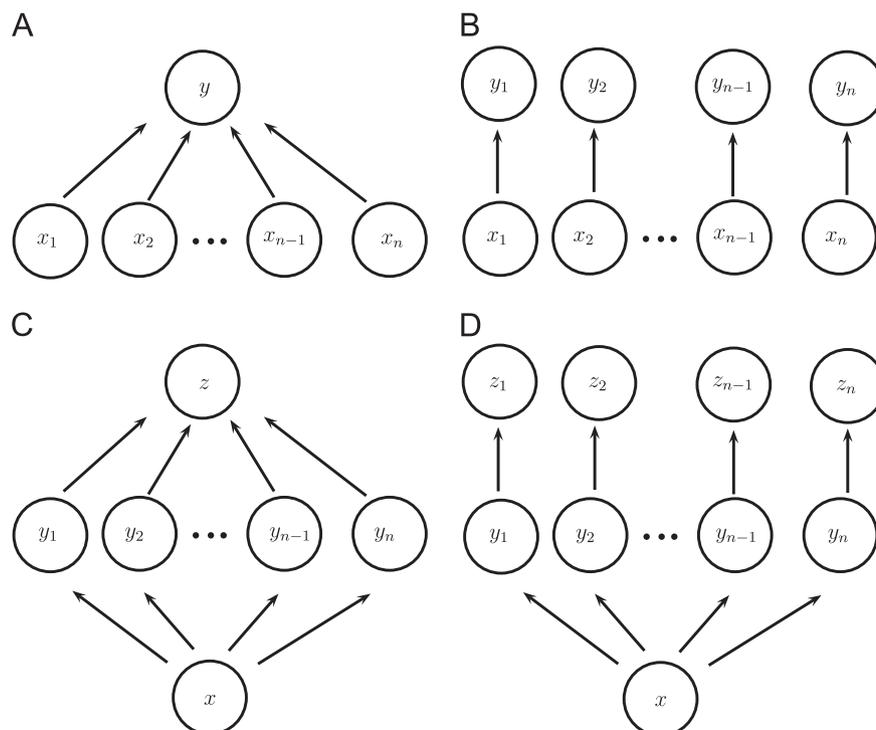

Fig. 1. Top panels show di-trophic food webs where predators are either generalists (A) or specialists (B). Bottom panels (C and D) show the corresponding tri-trophic food webs.

(Fig. 1, panels B and D). The situation is strikingly different for inflexible generalist predators.

2. Di-trophic food webs

In this section I will study a di-trophic food web consisting of several resources $(x_1, \ldots, x_n)$ and their common generalist consumer (y, Fig. 1A). Such a food web can model mobile consumers feeding on patchily distributed immobile resources. Corresponding population dynamics can be conceptualized by the Lotka–Volterra model of apparent competition (Holt, 1977, 1984):

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) - \lambda_i u_i x_i y, \quad i = 1, \ldots, n$$

$$\frac{dy}{dt} = y \sum_{i=1}^{n} u_i (e_i \lambda_i x_i - m_i), \tag{1}$$

where $0 \le u_i \le 1$ describes consumer preference for the i-th resource. In particular, u_i can be interpreted as a fraction of time an average consumer spends by foraging on the i-th resource type. Resources grow logistically with the per capita population growth rate r_i and environmental carrying capacity K_i. Parameter λ_i stands for the consumer specific search rate for resource i, e_i is the efficiency rate with which resources are converted to new consumers, and m_i is the consumer mortality rate.

2.1. Non-flexible consumers

I start with an assumption that consumer preferences for resources (u_i) are fixed and independent of prey population densities. In other words this means that the interaction strength is fixed, which is the usual assumption in predator–prey models. Under these assumptions model (1) was analyzed in detail by Holt (1984). The interior equilibrium of model (1) is

$$x_i^* = \frac{K_i}{r_i}(r_i - \lambda_i u_i y^*), \quad i = 1, \ldots, n$$

$$y^* = \frac{\sum_{i=1}^{n} u_i (e_i \lambda_i K_i - m_i)}{\sum_{i=1}^{n} \frac{e_i K_i \lambda_i^2 u_i^2}{r_i}}. \tag{2}$$

Appendix A shows that interior equilibrium (2) is globally asymptotically stable, whenever it exists (i.e., whenever all population densities are positive). However, the equilibrium can exists only for intermediate environmental carrying capacities. When K's are too small (i.e., for each $i = 1, \ldots, n$, $K_i < m_i/(e_i\lambda_i)$) consumers will not survive in the system because of scarcity of resources. When K's are too large, consumers will be too abundant and due to strong apparent competition (Holt, 1977, 1984; Bonsall and Hassell, 1997; Abrams et al., 1998; Abrams, 1998) some resources will be outcompeted. This is documented in Fig. 2, left panels. As the mean environmental productivity $\overline{K}$ increases, both the resource (Fig. 2B) and consumer (Fig. 2C) abundance increase, causing the number of coexisting resources (i.e., robustness) to decrease (Fig. 2A). As the mean environmental capacity increases to infinity (i.e., when resource growth rate is density independent and resources grow exponentially), at most one resource can survive due to the principle of competitive exclusion (Gause, 1934; Levin, 1970). Dependence of robustness on food web connectance (calculated as $n/(n+1)^2$ for the food web topology shown in Fig. 1A) is shown in Figure 2D. Here robustness increases with increasing connectance. Because connectance is inversely proportional to the initial number of species in the food web, this also shows that robustness decreases with increasing number of resources in the food web. Details of simulations are given in Appendix B.

Model (1), in common with most of the traditional population models, assumes fixed predators' foraging preferences (u_i), i.e., fixed interaction strength. However, many foragers adjust their feeding preferences according to the frequency of prey types in the environment (e.g., Murdoch, 1969; Oaten and Murdoch, 1975; Stephens and Krebs, 1986). In the next section I will consider model (1) with resource switching.

2.2. Flexible consumers

Predator foraging behavior under which an increase in the proportion of a particular prey in predator's diet increases with increased prey proportion in the environment faster than linearly is called switching (Oaten and Murdoch, 1975). Resource switching leads to flexible foraging where generalist consumers allocate more effort to those prey that provide them with a higher fitness (measured here as the per capita predator population growth rate $e_i\lambda_i x_i - m_i$). I start analysis of model (1) with prey switching by assuming that consumers adjust their feeding preferences instantaneously to current population densities. In other words, switching is very fast when compared to population dynamics, and consumers feed on the most profitable resource(s) at the current population densities. In particular, at each population densities, feeding on any resource included in consumers diet must provide the consumer with the same fitness. Such distribution of foraging activities corresponds to the Ideal Free Distribution (Fretwell and Lucas, 1969). Under the IFD, for every resource i currently in consumers diet

$$e_i \lambda_i x_i(t) - m_i = c(t) \ge e_j \lambda_j x_j(t) - m_j$$

for any other resource j not included in the diet. Thus, at the population equilibrium, feeding on any resource included in predator's diet provides zero fitness (i.e., $e_i\lambda_i x_i - m_i = 0$) while feeding on resources not included in the diet provides a non-positive fitness (i.e., the resources not included in consumers' diet are at their environmental carrying capacities and $e_j\lambda_j K_j - m_j \le 0$). In other words, all resources that can maintain a positive consumer population density (i.e., those which satisfy $K_i > m_i/(e_i\lambda_i)$) will be included in consumers' diet at the population equilibrium (Holt, 1984). Appendix C shows that the interior equilibrium of model (1) with resource switching

$$x_i^* = \frac{m_i}{e_i \lambda_i}, \quad i = 1, \ldots, n,$$

$$y^* = \sum_{i=1}^{n} \frac{r_i}{\lambda_i} \left(1 - \frac{m_i}{e_i \lambda_i K_i} \right),$$

$$u_i^* = \frac{r_i}{\lambda_i y^*} \left(1 - \frac{x_i^*}{K_i} \right), \quad i = 1, \ldots, n \tag{3}$$

is globally asymptotically stable.

Resource switching, as modeled above, assumes omniscient consumers that track resource densities and instantaneously switch to the resource that provides maximum fitness. This leads to a step-like switching when the i-th resource is included in consumer diet ($u_i = 1$) if $e_i\lambda_i x_i - m_i \ge e_j\lambda_j x_j - m_j$ for all other resources j and is instantaneously excluded from the diet ($u_i = 0$) if $e_i\lambda_i x_i - m_i < e_j\lambda_j x_j - m_j$ for some consumer j. Such instantaneous switching, while instrumental for mathematical analysis of the model, is unrealistic for non-omniscient consumers. For numerical simulations I use a more realistic, sigmoidal approximation of the switching function:

$$u_i = \frac{e^{\mu(e_i\lambda_i x_i - m_i)}}{e^{\mu(e_1\lambda_1 x_1 - m_1)} + \cdots + e^{\mu(e_n\lambda_n x_n - m_n)}} \tag{4}$$

where parameter $\mu \ge 0$ models the accuracy of switching (Fryxell and Lundberg, 1993). When $\mu = 0$ predators do not switch and they equally prefer all competitors ($u_i = 1/n$). When $\mu > 0$
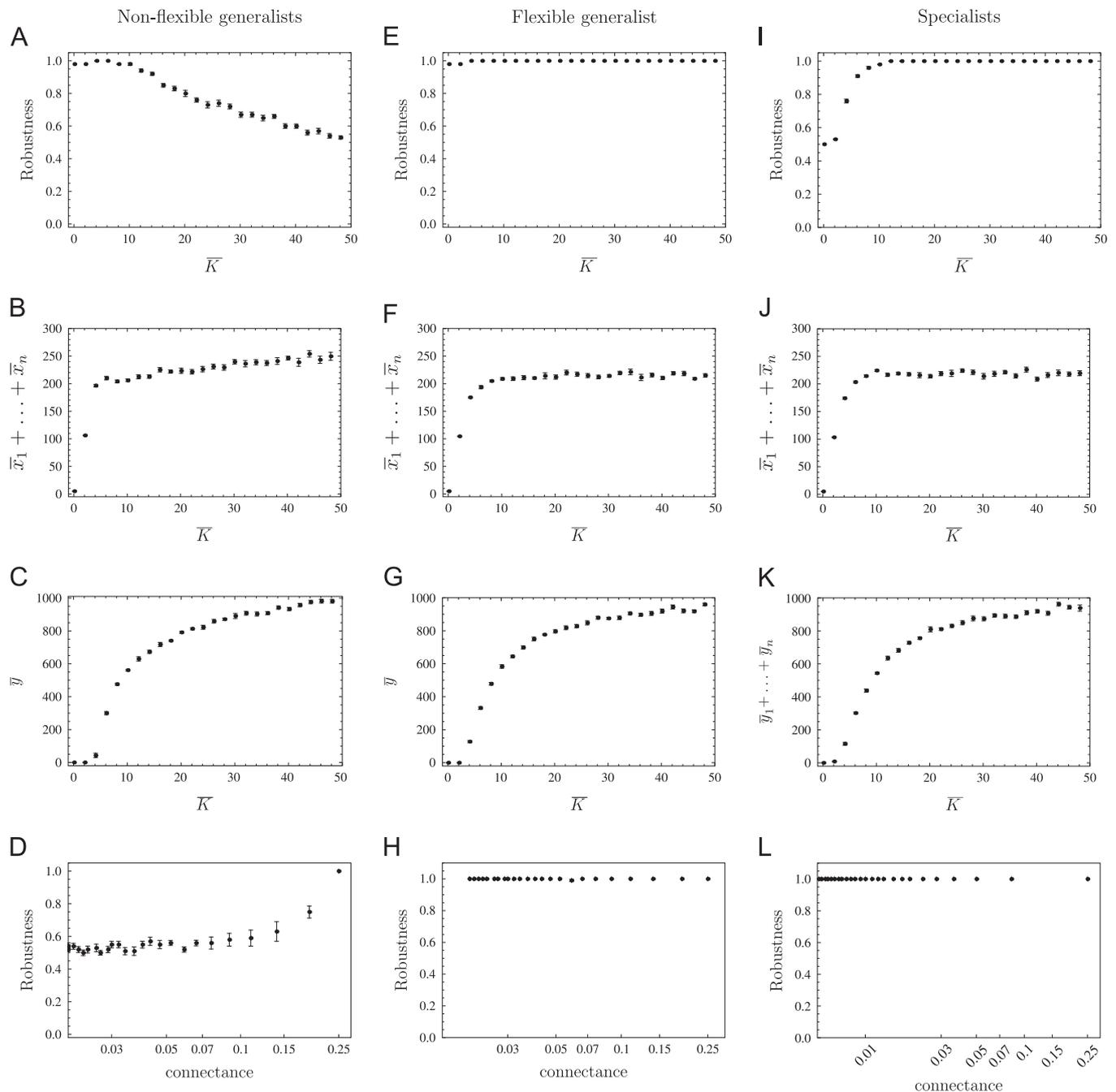
Fig. 2. Simulations of di-trophic food-webs. The left panels show results for the food web with non-flexible generalist predators (model 1, Fig. 1A) and uniform predator preferences for resources ($u_i = 1/n$), the middle panels show results for flexible generalist predators ($\mu = 10$ in (4)), and the right panels for the food web shown in Fig. 1B for specialized predators modeled by (5). Panels show mean values over 10 simulations. The whiskers denote $\pm$ standard errors. Panels in the first three rows show in sequel robustness, mean resource density, and mean consumer density as a function of the mean environmental carrying capacity. Panels in the bottom row show dependence of food-web robustness on food web connectance at the mean environmental carrying capacity $\overline{K} = 50$. Parameters were generated at random from the normal distribution $N(\nu, \sigma)$ with mean ν and standard deviation σ: $r = N(2, 0.4)$, $\lambda = N(0.1, 0.02)$, $e = N(0.5, 0.1)$, $m = N(0.2, 0.04)$, and $K = N(\overline{K}, 0.2\overline{K})$.

consumers feed on resources disproportionally to their relative profitability. At large values of μ, consumers become very selective and they feed on the most profitable resource only (i.e., on the resource that provides them with the highest fitness $e_i \lambda_i x_i - m_i$). Thus, as μ increases, (4) converges to the instantaneous step-like resource switching.

Fig. 2 (middle column) shows results of numerical simulations of model (1) with switching function (4) and switching precision $\mu = 10$. Fig. 2E shows that robustness is independent of the mean environmental carrying capacity and maximal. This is in agreement with the fact that habitat partitioning relaxes apparent

competition as predicted by Holt (1984). The mean resource and consumer abundance as functions of the mean environmental carrying capacity are shown in panels F and G, respectively. Fig. 2H just documents that because robustness is maximal, it is independent of food web connectance.

Fig. 3A shows that robustness increases with precision of switching (μ). Thus, all initially present species (50 resources and 1 consumer) survive in the food web when switching precision is high enough. Panels B and C also show that switching slightly reduces mean resource and consumer densities when compared with non-selective consumers (i.e., when $\mu = 0$).
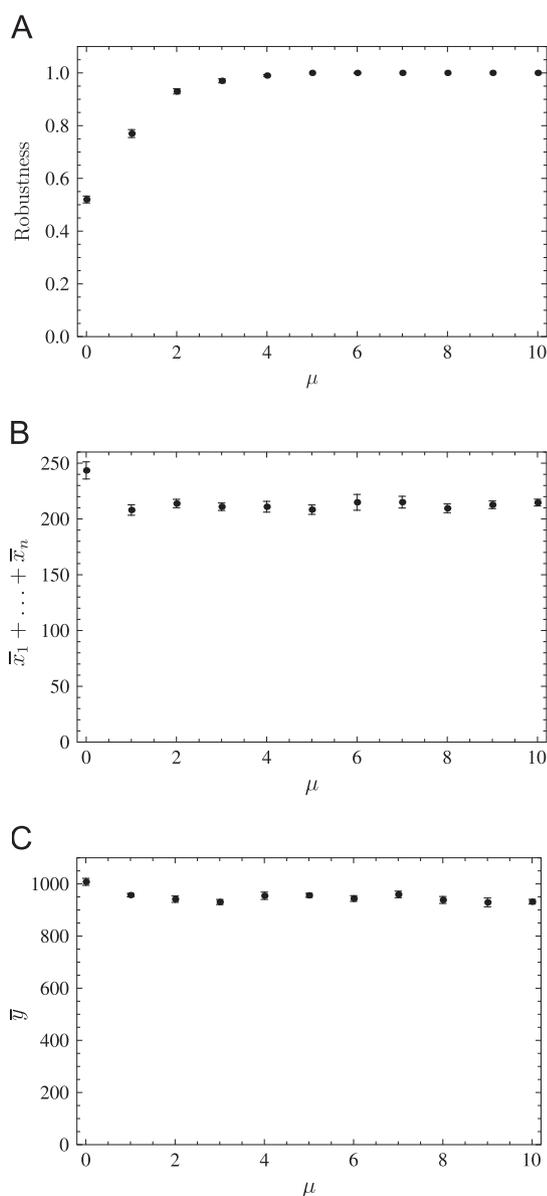
Fig. 3. Dependence of di-trophic food-webs with flexible predators on precision of switching (μ). Panels show mean values $\pm$ standard errors of 10 simulations of model (1) with switching function (4). Parameters: $r = N(2, 0.4)$, $\lambda = N(0.1, 0.02)$, $e = N(0.5, 0.1)$, $m = N(0.2, 0.04)$, and $K = N(50, 10)$.

It is interesting to note that the food-web with flexible generalist consumers has the same population equilibrium as a food web with specialized consumers (Fig. 1, panel B). Indeed such a system can be conceptualized by n-pairs of independent Lotka–Volterra resource-consumer models , i.e.,

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) - \lambda_i x_i y_i, \quad i = 1, \dots, n$$

$$\frac{dy_i}{dt} = (e_i \lambda_i x_i - m_i) y_i, \quad i = 1, \dots, n. \tag{5}$$

Provided the resource environmental carrying capacity is high enough ($K_i > m_i/(e_i \lambda_i)$), the i-th resource–consumer pair coexists at the stable equilibrium:

$$(x_i^*, y_i^*) = \left(\frac{m_i}{e_i \lambda_i}, \frac{r_i(e_i \lambda_i K_i - m_i)}{e_i K_i \lambda_i^2}\right).$$

This is exactly the same equilibrium as in the case of flexible generalist consumers (provided we set $y_i^* = u_i^* y^*$ in (3)).

Robustness of model (5) as a function of the mean environmental carrying capacity ($\overline{K}$) is shown in Fig. 2I. At low environmental carrying capacities (satisfying $K_i < m_i/(e_i \lambda_i)$) only resources will survive and the food web robustness equals to 0.5. As the mean carrying capacity increases, more and more thresholds for the resource–consumer coexistence will be met and the number of surviving resource–consumer pairs will increase. The total mean abundance of resources (Fig. 2J) and consumers (Fig. 2K) increases too, similarly to the case of flexible generalists (Fig. 2, middle column). Fig. 2L shows that robustness of the food web as a function of the food web connectance (calculated as $n/(2n)^2 = 1/(4n)$) is maximal provided the environmental carrying capacity is high enough.

3. Tri-trophic food webs

In this section I consider tri-trophic food-webs consisting of a common resource (x), n consumer species ($y_1, \dots, y_n$) competing for the common resource, and a top predators (z). The corresponding food web topology is shown in Fig. 1C. Similarly to the di-trophic case I consider two situations. Either the top predators are generalists with fixed preferences for their prey, or they are flexible foragers with density dependent preferences that maximize their fitness. The diamond-like food-web topology considered in this section combines two types of competition among the consumer species: exploitative competition for the common resource (Tilman, 1982) and apparent competition (Holt, 1977, 1984) by the shared generalist predator. When compared with the food web topology in Fig. 1A, conditions for species coexistence are much more stringent now, because in addition to the apparent competition between consumer species there is also competition for the shared resource (x). The Lotka–Volterra population dynamics are described by

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \sum_{i=1}^{n} \lambda_i y_i x,$$

$$\frac{dy_i}{dt} = y_i(e_i \lambda_i x - m_i - \Lambda_i u_i z), \quad i = 1, \dots, n,$$

$$\frac{dz}{dt} = z \sum_{i=1}^{n} u_i(E_i \Lambda_i y_i - M_i), \tag{6}$$

where $u_i (u_1 + \dots + u_n = 1)$ is the predator foraging preference for the i-th consumer species, Λ_i stands for the predator specific search rate for consumer i, E_i is the efficiency rate with which consumers are converted to new predators, and M_i is the predator mortality rate. Other parameters have the same meaning as those in model (1).

3.1. Non-flexible predators

Here I assume that predators are generalists with fixed preferences for consumers. For each consumer species i coexisting in the system at a positive population equilibrium, the following equation must hold

$$e_i \lambda_i x - m_i - \Lambda_i u_i z = 0. \tag{7}$$

Provided predator foraging preferences are fixed (i.e., predators behave as non-flexible foragers with fixed u_i's), there are only two free variables (x, z) and, in general, it is impossible to find a positive solution of Eq. (7) for more than two coexisting competitors. Thus, not more than two competing species can survive at the population equilibrium. This is numerically documented in Fig. 4A where top predators have equal foraging preferences for consumers ($u_i = 1/n$) and most species are outcompeted from the system. Even if species coexistence is
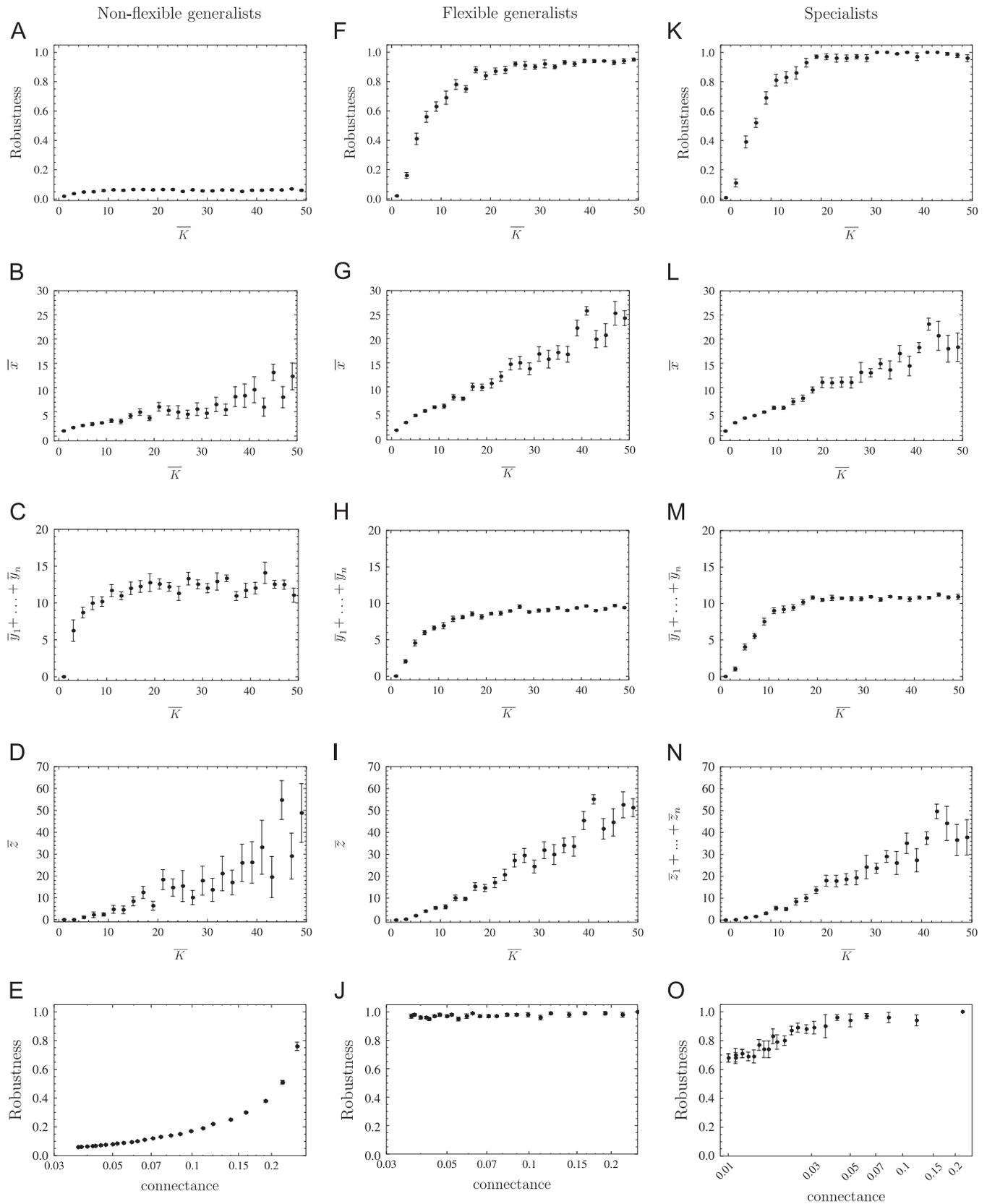
Fig. 4. Simulations of tri-trophic food-webs. The left panels show results for model (6) with non-flexible predators (with fixed preferences $u_i = 1/n$). The middle panels show results for flexible predators with foraging preferences given by (10) (with $\mu = 10$). The right panels show results for model (6) with specialized predators. Means $\pm$ standard errors over 10 simulations are shown. The first four rows show in sequel dependence of robustness, mean resource density, mean consumer density, and mean predator density on the mean environmental carrying capacity. Panels in the bottom row show dependence of food-web robustness on food web connectance. Parameters were generated at random from the normal distribution $N(\nu, \sigma)$ with mean ν and standard deviation σ: $r = N(2, 0.4)$, $\lambda = N(0.1, 0.02)$, $e = N(0.5, 0.1)$, $m = N(0.2, 0.04)$, $M = N(0.1, 0.02)$, $E = N(0.5, 0.1)$, $\Lambda = N(1, 0.2)$, and $K = N(\overline{K}, 0.2\overline{K})$.

considered (not necessarily at an equilibrium), permanence for the Lotka–Volterra type models requires existence of an interior equilibrium (Hofbauer and Sigmund, 1998). It follows that model (6) cannot be permanent for more then two competing species. Conditions for permanence for two competing species were given elsewhere (Leibold, 1996; Holt et al., 1994; Křivan, 2003). Fig. 4E shows that robustness of the food web increases with increasing connectance (calculated for the food-web topology in Fig. 1C as $2n/(n+2)^2$). As connectance is inversely proportional to the initial number of species in the food web, we observe that robustness decreases with the initial number of competitors.

3.2. Flexible predators

Now I consider the situation where predators are omniscient optimal foragers that instantaneously switch to feed on the most profitable consumer(s). It follows that at the population equilibrium feeding on all consumers included in the predator's diet must be equally profitable (and more or equally profitable than would be feeding on consumers not included in predators diet). Appendix D shows that at the population equilibrium where top predators exist, at most one consumer species is excluded from predators' diet. When all competitors do survive, the corresponding interior population equilibrium is (Appendix D)

$$x^* = \frac{K}{r}\left(r - \sum_{i=1}^{n} \frac{\lambda_i M_i}{E_i \Lambda_i}\right),$$

$$y_i^* = \frac{M_i}{E_i \Lambda_i}, \quad i = 1, \ldots, n$$

$$z^* = \sum_{i=1}^{n} \frac{e_i \lambda_i x^* - m_i}{\Lambda_i},$$

$$u_i^* = \frac{e_i \lambda_i x^* - m_i}{\Lambda_i z^*}, \quad i = 1, \ldots, n. \tag{8}$$

Appendix D shows that this equilibrium is globally asymptotically stable. Moreover, population dynamics (6) simplify to

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - x\sum_{j=1}^{n} \frac{\lambda_j}{\Lambda_j E_j}(E_1 \Lambda_1 y_1 - M_1 + M_j)$$

$$\frac{dy_1}{dt} = y_1(e_1 \lambda_1 x - m_1 - \Lambda_1 u_1 z)$$

$$\frac{dz}{dt} = z(E_1 \Lambda_1 y_1 - M_1), \tag{9}$$

where the densities of other competitors $(i = 2, \ldots, n)$ are $y_i = (E_1 \Lambda_1 y_1 - M_1 + M_i)/(E_i \Lambda_i)$. Population dynamics (9) are the same as those for a tri-trophic food-chain.

For numerical simulations I consider gradual switching described by a sigmoidal function

$$u_i = \frac{e^{\mu(E_i \Lambda_i y_i - M_i)}}{e^{\mu(E_1 \Lambda_1 y_1 - M_1)} + \cdots + e^{\mu(E_n \Lambda_n y_n - M_n)}}. \tag{10}$$

Numerical simulations of model (6) with predator preferences (10) as those given in Fig. 5A show that precision of consumer switching (μ) increases food web robustness when compared to the case of no switching (i.e., when $\mu = 0$ in Fig. 5A). For high switching precisions (i.e., large values of μ), all initially present competitors survive in the system. Fig. 5B and D also shows that switching increases the mean resource and top predator densities when compared with the case of no switching (i.e., when $\mu = 0$), while the mean consumer density (Fig. 5C) decreases.

Fig. 4 (middle column) shows dependence of food web dynamics on the mean environmental carrying capacity (panels F–I), and the food web connectance (calculated here as $2n/(n+2)^2$, panel J). Food web robustness increases with the mean
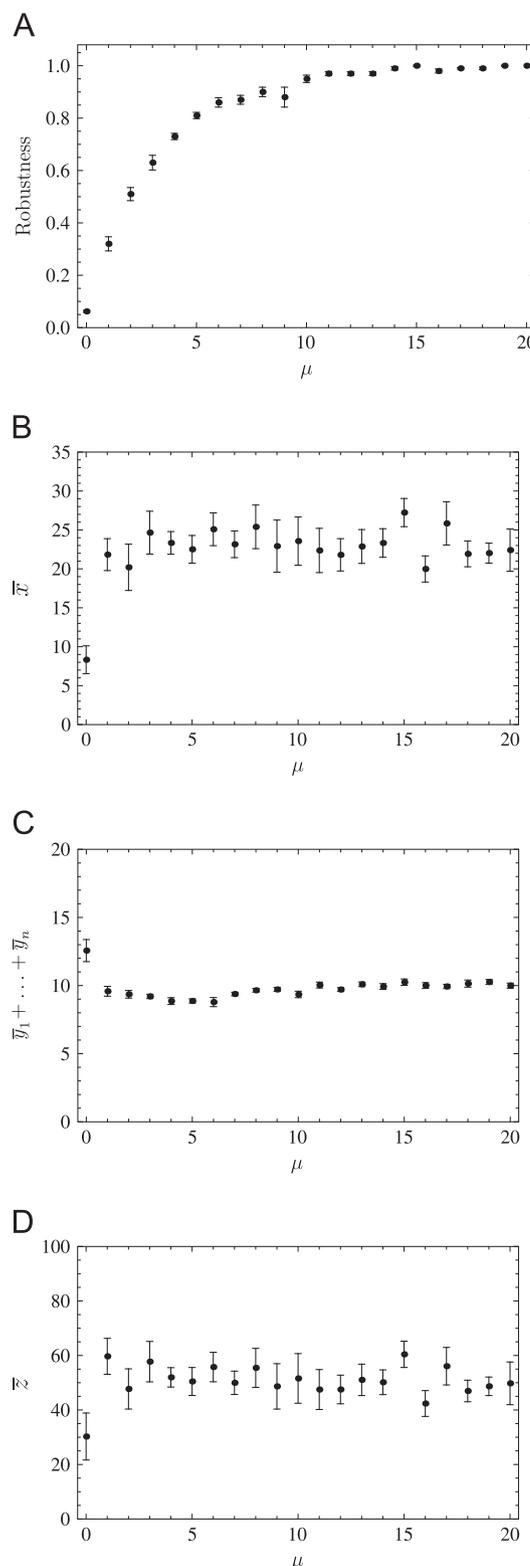

Fig. 5. Dependence of robustness (A), mean resource density (B), mean consumer density (C) and mean predator density (D) in tri-trophic food webs with flexible predators on precision of switching (μ). Panels show mean values of 10 simulations of model (6). The whiskers denote ± standard errors. Parameters were generated at random from the normal distribution $N(\nu, \sigma)$ with mean ν and standard deviation σ: $r = N(2, 0.4)$, $\lambda = N(0.1, 0.02)$, $e = N(0.5, 0.1)$, $m = N(0.2, 0.04)$, $M = N(0.1, 0.02)$, $E = N(0.5, 0.1)$, $\Lambda = N(1, 0.2)$, and $K = N(50, 10)$.

environmental carrying capacity (panel F). When compared to the food web with inflexible predators (panel A), we observe that robustness is much higher here.

We have seen that at the population equilibrium, optimally switching predators have preferences for consumers described by $u_i^* = (e_i\lambda_i x^* - m_i)/(\Lambda_i z^*)$. There are two possible interpretation of this result. Either the predator population is monomorphic and u_i^* shows preferences of each predator, or the predator population becomes polymorphic and u_i^* is the proportion of predators that feed on the i-th consumer. With this second interpretation in mind, the corresponding food web topology would be as shown in Fig. 1D. Therefore, it is interesting to compare population dynamics of the diamond-like food web with top flexible generalist predators with population dynamics with n specialized predators. The corresponding food web dynamics are described by the Lotka–Volterra model

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \sum_{i=1}^{n} \lambda_i y_i x$$
$$\frac{dy_i}{dt} = y_i(e_i\lambda_i x - m_i - \Lambda_i z_i), \quad i = 1, \ldots, n,$$
$$\frac{dz_i}{dt} = z_i(E_i\Lambda_i y_i - M_i), \quad i = 1, \ldots, n, \tag{11}$$

where z_i denotes the predator that specializes on the i-th consumer. The interior equilibrium of (11) is

$$x^* = K\left(1 - \frac{1}{r}\sum_{i=1}^{n} \frac{\lambda_i M_i}{E_i\Lambda_i}\right)$$
$$y_i^* = \frac{M_i}{E_i\Lambda_i}, \quad i = 1, \ldots, n,$$
$$z_i^* = \frac{e_i\lambda_i x^* - m_i}{\Lambda_i}, \quad i = 1, \ldots, n. \tag{12}$$

This is the same equilibrium as in the case of flexible generalist predators (provided we set $z_i^* = u_i^* z^*$). For this interior equilibrium to exist, the resource intrinsic population growth rate (r) must be large enough to support consumers and their predators at positive densities. Otherwise some consumers will die out. The competition exclusion principle does not apply here, because although consumers (y_i) directly compete for the shared resource, they are regulated by n top predators. Appendix E shows that when interior equilibrium (12) exists then it is stable. The resource density converges to x^* and numerical simulations suggest that population dynamics of model (11) converge to equilibrium (12), although the speed of convergence can be very slow. The right panels in Fig. 4 show dependence of the food web dynamics (11) on the mean carrying capacity (panels K–N) and food web connectance (O). These results show that robustness increases with increasing mean environmental carrying capacity. Indeed, for predators to survive, environmental carrying capacity must be high enough. When predators do survive in the food web they act as limiting factors that allow survival of several competing species. It is interesting to note that flexible generalist predators increase abundance of resources and top predators, while the abundance of consumers is slightly decreased (cf. Fig. 4 panels G–I vs. panels L–N). Such pattern seems to be a consequence of exploitative competition, as it does not appear in di-trophic food-web modules (cf. Fig. 2 panels F and G vs. panels J–K). Fig. 4O shows that robustness of the food web increases with increasing connectance (calculated as $2n/(2n+1)^2$).

4. Discussion

In this article, two food web modules with many competing species are studied. The first module considers apparent competition between several resources sharing a common consumer. The second module considers a tri-trophic diamond-like food web with a single resource and several consumers that share a common predator. The top predators are assumed to be either non-flexible generalists, or flexible generalists that maximize their fitness through diet choice. Two types of dependencies are studied in detail: effects of the environmental carrying capacity on food web robustness (measured as the proportion of surviving species) and food web dynamics, and effects of food web connectance (measured as the number of realized links over all possible links in the food web) on food web robustness. The article confirms that flexible foraging of top species strongly weakens apparent competition and promotes species coexistence when compared with non-flexible predators (Holt, 1984, cf. Fig. 2 panel A vs. panel E and Fig. 4 panel A vs. panel F). Moreover, it shows that the resulting food-web dynamics for flexible predators closely resemble food web dynamics with specialized predators (cf. Figs. 2 and 4 middle panels vs. right panels). This is interesting in the light of recent research on individual specialized feeding (Araujo et al., 2008; Bolnick et al., 2003) or cryptic species complexes which suggests that some presumed dietary generalists may be complexes of dietary specialists (Bickford et al., 2007). For example, if the top species in food webs in Fig. 1A and C were complexes of specialized predators, the correct food web topology would correspond to that shown in Fig. 1B and D, respectively. Predictions for food web dynamics with top generalists depend very much on whether the top predators are flexible or inflexible foragers. If top predators are non-flexible generalists then this article shows that robustness in food webs with top generalists will be generally lower when compared with top specialists (cf. Fig. 2A vs. I and Fig. 4A vs. K). Therefore, diversity in food webs with top predators consisting of dietary specialists should be higher when compared to the same food web with dietary generalists. However, when top predators are flexible generalists then at high environmental carrying capacities there may be no significant difference in food web robustness when compared with cryptic species complexes (or polymorphic populations) of dietary specialists (cf. Fig. 2E vs. I and Fig. 4F vs. K).

Whether or not flexible animal foraging promotes species stability and persistence was studied both in simple food web modules (e.g., Roughgarden and Feldman, 1975; Comins and Hassell, 1976; Hassell, 1978; Abrams, 1987, 1989; Holt, 1983, 1984; Fryxell and Lundberg, 1993, 1994; Holt et al., 1994; Abrams, 1995; Křivan, 1996, 2000; Fryxell and Lundberg, 1997; Křivan, 1997; Abrams, 1999, 2005; Křivan and Schmitz, 2003; Beckerman, 2005; Abrams, 2010; Visser et al., 2012) as well as in complex food webs (Brose et al., 2003; Kondoh, 2003, 2006; Garcia-Domingo and Saldaña, 2007; Uchida et al., 2007; Uchida and Drossel, 2007; Berec et al., 2010). In the case of simple food webs these findings clearly document that a flexible foraging behavior of top predators strongly promotes coexistence of two competing species. In particular, Holt (1984) showed that under the Ideal Free Distribution of predators among several foraging patches the apparent competition disappears at the population equilibrium. The same mechanism leads to high robustness of models with flexible top predators in this article. In the case of complex systems researchers focused on the relation between food web connectance and species survival or stability. This research followed May (1972) observation that in randomly generated food webs stability is lost as the connectance exceeds a critical threshold. A similar result shows that food web robustness decreases with increasing connectance (Brose et al., 2003). Kondoh (2003) proposed that such a pattern can be partially overturned when consumers in the food web behave as flexible foragers that maximize their fitness. It was shown that this prediction depends crucially on the food web topology (Brose et al., 2003; Uchida and Drossel, 2007) and on the way how optimal foraging is modeled (Berec et al., 2010). While these articles assumed complex food web topologies generated by stochastic graph theoretical models (i.e., random, cascade, niche),

in this article I study food webs with fixed (deterministic) topologies. Variation in food web connectance was achieved by changes in the initial number of species. Quite interestingly, robustness in models considered in this article never decreases with increasing connectance, just the opposite what general food web models predict. Because connectance is inversely proportional to the initial number of species in food webs considered in this article, these results also show that robustness decreases with the number of species in the food web. This prediction agrees with similar observations for food webs generated by the niche model (Uchida and Drossel, 2007).

Acknowledgments

Appendix A. A Lyapunov function for model (1) with fixed predator preferences

Here I prove that the interior population equilibrium (2) of model (1) is globally asymptotically stable whenever it is positive. Let

$$V = \sum_{i=1}^{n} e_i \left(x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*} \right) + \left(y - y^* - y^* \ln \frac{y}{y^*} \right) \quad \text{(A.1)}$$

denote the standard Lotka–Volterra type Lyapunov function. The derivative of V along trajectories of model (1) is

$$\frac{dV}{dt} = - \sum_{i=1}^{n} \frac{e_i r_i}{K_i} (x_i - x_i^*)^2 \leq 0.$$

Thus, the interior equilibrium of model (1) is stable. As the only solution of model (1) that satisfies $x_i = x_i^*$ for $i = 1, ..., n$ is the equilibrium, the LaSalle theorem (LaSalle, 1976; Harrison, 1979) implies asymptotic stability.

Appendix B. Simulation procedure

All numerical simulations were done in Mathematica 8 or 9 using routine `NDSolve` for numerical solution of differential equations. Initial data for resource(s) were set to 1, for consumers to 0.1 and for predators (in the case of tri-trophic food webs) to 0.01. Simulations were done on time interval $(0, 100000)$. Parameters were generated from the normal distribution $N(\mu, \sigma)$ with mean μ and variance $\sigma = 0.2\mu$, using Mathematica commands `Random[NormalDistribution[μ, σ]]` (for parameter values see figure captions). A species was assumed to survive in the system when at the final time T its population density was higher than 0.00001. Population densities and number of surviving species at the final time were recorded. Plots in figures are averages over ten simulations at each focal parameter value (i.e., at each mean environmental carrying capacity $\overline{K}$ in Figs. 2 and 4, and switching precision μ in Figs. 3 and 5. To study robustness as a function of connectance in bottom panels of Figs. 2 and 4, the initial number of consumers in the food web was varied between 1 and 50 to generate a range of initial food web connectance.

In those cases where numerical algorithm failed to generate a trajectory on the whole interval $(0, 100000)$ a new set of parameters was generated until 10 replicates were obtained.

Appendix C. A Lyapunov function for model (1) with instantaneous prey switching

Provided predators switch instantaneously at current population densities and consumers exist at a positive density at an equilibrium, the equilibrium resource and predator densities of (1) must satisfy the following equalities:

$$r_i \left(1 - \frac{x_i}{K_i} \right) - \lambda_i u_i y = 0$$

$$\sum_{i=1}^{n} u_i (e_i \lambda_i x_i - m_i) = 0.$$

Moreover, at this equilibrium feeding on any resource must provide consumers with the same fitness, so that

$$e_i \lambda_i x_i - m_i = c$$

for all consumers that coexist at the population equilibrium. It follows that $c = 0$ at the equilibrium. Thus, if a resource j is not included in predators' diet $e_j \lambda_j K_j - m_j \leq 0$. This shows that only resources with low carrying capacity will not be included in predators' diet. Thus at the population equilibrium population densities of resources that are included in consumers' diet are $x_i^* = m_i / (e_i \lambda_i)$. Substituting this equilibrium in the equation for resources, leads to expression (3). I remark that model (1) can be written in the form:

$$\frac{dx_i}{dt} = \frac{r_i}{K_i} x_i (x_i^* - x_i) - \lambda_i x_i (u_i y - u_i^* y^*)$$

$$\frac{dy}{dt} = y \sum_{i=1}^{n} u_i e_i \lambda_i (x_i - x_i^*) \quad \text{(C.1)}$$

where x_i^*, $i = 1, ..., n$ and y^* are equilibrium population densities (3). I will show that function V given by (A.1) with equilibrium population densities (3) remains a Lyapunov function for model (C.1). The derivative of his function along trajectories is

$$\frac{dV}{dt} = - \sum_{i=1}^{n} \frac{r_i}{K_i} (x_i - x_i^*)^2 + e_i \lambda_i (x_i - x_i^*)(u_i^* - u_i) y^*.$$

Let us assume that the first k resources are included in the diet at current population densities, i.e.,

$$e_1 \lambda_1 (x_1 - x_1^*) = ... = e_k \lambda_k (x_k - x_k^*) \geq e_i \lambda_i (x_i - x_i^*), \quad i = k+1, ..., n,$$

and $u_i = 0$ for $i = k+1, ..., n$. It follows that

$$\frac{dV}{dt} = - \sum_{i=1}^{n} \frac{r_i}{K_i} (x_i - x_i^*)^2 + \sum_{i=1}^{k} e_i \lambda_i (x_i - x_i^*)(u_i^* - u_i) y^*$$

$$+ \sum_{i=k+1}^{n} e_i \lambda_i (x_i - x_i^*) u_i^* y^*$$

$$= - \sum_{i=1}^{n} \frac{r_i}{K_i} (x_i - x_i^*)^2 + y^* \sum_{i=1}^{n} (e_i \lambda_i (x_i - x_i^*) - e_1 \lambda_1 (x_1 - x_1^*)) u_i^* < 0.$$

It follows that trajectories converge to the set where $dV/dt = 0$ and the only solution of (1) in this set is the equilibrium solution. Thus, the equilibrium is asymptotically stable.

Appendix D. Model (6) with flexible predators

Without loss of generality, I will assume that the first k ($k \leq n$) consumers are included in the predator's diet at the population equilibrium. Because the profitability of these consumers must be the same (and higher or equal than the profitability of other consumers not included in predators' diet)

$$E_1 \Lambda_1 y_1 - M_1 = ... = E_k \Lambda_k y_k - M_k \geq E_i \Lambda_i y_i - M_i, \quad i = k+1, ..., n.$$

$$\text{(D.1)}$$

Moreover, at the population equilibrium where predators are present ($z > 0$)

$$r\left(1-\frac{x}{K}\right) - \sum_{i=1}^{n} \lambda_i y_i = 0,$$

$$e_i \lambda_i x - m_i - \Lambda_i u_i z = 0, \quad i = 1, \ldots, k,$$

$$y_i(e_i \lambda_i x - m_i) = 0, \quad i = k+1, \ldots, n,$$

$$\sum_{i=1}^{k} u_i(E_i \Lambda_i y_i - M_i) = 0. \tag{D.2}$$

It is generically impossible for two or more competitors that are not included in predator's diet to survive at the equilibrium (because for general parameters $e_i \lambda_i x - m_i = 0$ can hold for not more than one index i). Thus, at most one competitor that is not included in the predator's diet can survive at the population equilibrium. I calculate the interior equilibrium now.

First, I will assume that predators feed on all consumers. It follows from (D.1) and (D.2) that at the population equilibrium $E_i \Lambda_i y_i - M_i = 0$, i.e.,

$$y_i^* = \frac{M_i}{E_i \Lambda_i}, \quad i = 1, \ldots, n. \tag{D.3}$$

Consequently,

$$x^* = \frac{K}{r}\left(r - \sum_{i=1}^{n} \frac{\lambda_i M_i}{E_i \Lambda_i}\right),$$

and

$$u_i^* z^* = \frac{e_i \lambda_i x^* - m_i}{\Lambda_i}, \quad i = 1, \ldots, n$$

where u_i^* is predators preference for consumer i at the population equilibrium. As $\sum_{i=1}^{n} u_i^* = 1$, I get

$$z^* = \sum_{i=1}^{n} \frac{e_i \lambda_i x^* - m_i}{\Lambda_i}$$

and

$$u_i^* = \frac{e_i \lambda_i x^* - m_i}{\Lambda_i z^*}.$$

Now I will show that once all consumers are included in predators' diet, model dynamics (6) are those of a food chain. Because under the IFD feeding on any consumer provides predators with the same payoff, $E_i \Lambda_i y_i(t) - M_i = k(t)$ for every $i = 1, \ldots, n$. It follows that

$$E_i \Lambda_i \frac{dy_i}{dt} = \frac{dk}{dt} = c.$$

Substituting dy_i/dt from model (6) leads to

$$u_i = \frac{e_i \lambda_i x - m_i}{\Lambda_i z} - \frac{c}{E_i \Lambda_i^2 y_i z}$$

where

$$c = \frac{\sum_{i=1}^{n} \dfrac{e_i \lambda_i x - m_i}{\Lambda_i z} - 1}{\sum_{i=1}^{n} \dfrac{1}{E_i \Lambda_i^2 y_i z}}.$$

Because

$$y_i = (E_1 \Lambda_1 y_1 - M_1 + M_i)/(E_i \Lambda_i) \tag{D.4}$$

and $\sum_{i=1}^{n} u_i = 1$ model (6) can be rewritten as a food chain:

$$\frac{dx}{dt} = rx\left(1-\frac{x}{K}\right) - x \sum_{j=1}^{n} \frac{\lambda_j}{\Lambda_j E_j}(E_1 \Lambda_1 y_1 - M_1 + M_j)$$

$$\frac{dy_1}{dt} = y_1(e_1 \lambda_1 x - m_1 - \Lambda_1 u_1 z)$$

$$\frac{dz}{dt} = z(E_1 \Lambda_1 y_1 - M_1). \tag{D.5}$$

Because the interior equilibrium of a food chain is globally asymptotically stable (Harrison, 1979), interior equilibrium (8) is also globally asymptotically stable.

Second, I will assume that predators feed on all but one consumer. It follows from (D.1) and (D.2) that at the population equilibrium $E_i \Lambda_i y_i - M_i = 0$, for $i = 1, \ldots, n-1$, i.e.,

$$y_i^* = \frac{M_i}{E_i \Lambda_i}, \quad i = 1, \ldots, n-1. \tag{D.6}$$

Consequently,

$$x^* = \frac{m_n}{e_n \lambda_n}$$

$$u_i^* z^* = \frac{e_i \lambda_i x^* - m_i}{\Lambda_i}, \quad i = 1, \ldots, n-1$$

where u_i^* denotes predators preference for consumer i at the population equilibrium (and $u_n^* = 0$). As $\sum_{i=1}^{n-1} u_i^* = 1$, I get

$$z^* = \sum_{i=1}^{n-1} \frac{e_i \lambda_i x^* - m_i}{\Lambda_i}$$

and

$$u_i^* = \frac{e_i \lambda_i x^* - m_i}{\Lambda_i z^*}, \quad i = 1, \ldots, n-1.$$

In addition

$$y_n^* = \frac{r}{\lambda_n}\left(1-\frac{x^*}{K}\right) - \sum_{i=1}^{n-1} \frac{\lambda_i}{\lambda_n} y_i^* = \frac{r}{\lambda_n}\left(1-\frac{m_n}{e_n \lambda_n K}\right) - \sum_{i=1}^{n-1} \frac{\lambda_i M_i}{\lambda_n E_i \Lambda_i}.$$

For the nth consumer to be excluded from predators diet at the equilibrium, $E_n \Lambda_n y_n^* - M_n$ must be non-positive, which yields the following condition on parameters for which this can happen:

$$E_n \Lambda_n\left(\frac{r}{\lambda_n}\left(1-\frac{m_n}{e_n \lambda_n K}\right) - \sum_{i=1}^{n-1} \frac{\lambda_i M_i}{\lambda_n E_i \Lambda_i}\right) \leq M_n.$$

Appendix E. A Lyapunov function for model (11) with specialized predators

Here I prove that the interior equilibrium (12) of model (11) is globally stable. Let

$$V = x - x^* - x^* \ln \frac{x}{x^*} + \sum_{i=1}^{n} \frac{1}{e_i}\left(y_i - y_i^* - y_i^* \ln \frac{y_i}{y_i^*}\right) + \sum_{i=1}^{n} \frac{1}{e_i E_i}\left(z_i - z_i^* - z_i^* \ln \frac{z_i}{z_i^*}\right). \tag{E.1}$$

Then

$$\frac{dV}{dt} = -\frac{r}{K}(x - x^*)^2$$

along trajectories of model (11) and V is a Lyapunov function. Moreover, it follows that $x(t)$ converges to the equilibrium x^*.

References

Abrams, P.A., 1982. Functional responses of optimal foragers. Am. Nat. 120, 382–390.

Abrams, P.A., 1987. The functional responses of adaptive consumers on two resources. Theor. Popul. Biol. 32, 262–288.

Abrams, P.A., 1989. Decreasing functional responses as a result of adaptive consumer behavior. Evol. Ecol. 3, 95–114.

Abrams, P.A., 1995. Dynamics and interaction in food webs with adaptive foragers. In: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns & Dynamics. Chapman & Hall, New York, NY, USA, pp. 396–434.

Abrams, P.A., 1998. High competition with low similarity and low competition with high similarity: exploitative and apparent competition in consumer-resource systems. Am. Nat. 152, 114–128.

Abrams, P.A., 1999. The adaptive dynamics of consumer choice. Am. Nat. 153, 83–97.

Abrams, P.A., 2005. 'Adaptive Dynamics' vs. 'adaptive dynamics'. J. Evol. Biol. 18, 1162–1165.

Abrams, P.A., 2010. Implications of flexible foraging for interspecific interactions: lessons from simple models. Funct. Ecol. 24, 7–17.

Abrams, P.A., Holt, R.D., Roth, J.D., 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. Ecology 79, 201–212.

Araujo, M.S., Guimaraes Jr., P.R., Svanbaeck, R., Pinheiro, A., Guimaraes, P., Dos Reis, S.F., Bolnick, D.I., 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. Ecology 89, 1981–1993.

Armstrong, R.A., McGehee, R., 1980. Competitive exclusion. Am. Nat. 115, 151–170.

Beckerman, A.P., 2005. The shape of things eaten: the functional response of herbivores foraging adaptively. Oikos 110, 591–601.

Berec, L., Eisner, J., Křivan, V., 2010. Adaptive foraging does not always lead to more complex food webs. J. Theor. Biol. 266, 211–218.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K., Meier, R., Winker, K., Ingram, K.K., Das, I., 2007. Cryptic species as a window on diversity and conservation. Trends Ecol. Evol. 22, 148–155.

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., Forister, M.L., 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. 161, 1–28.

Bonsall, M.B., Hassell, M.P., 1997. Apparent competition structures ecological assemblages. Nature 388, 371–373.

Brose, U., Williams, R.J., Martinez, N.D., 2003. Comment on "Foraging adaptation and the relationship between food-web complexity and stability". Science 301, 918.

Comins, H.N., Hassell, M.P., 1976. Predation in multi-species communities. J. Theor. Biol. 62, 93–114.

Fretwell, D.S., Lucas, H.L., 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 19, 16–32.

Fryxell, J.M., Lundberg, P., 1993. Optimal patch use and metapopulation dynamics. Evol. Ecol. 7, 379–393.

Fryxell, J.M., Lundberg, P., 1994. Diet choice and predator-prey dynamics. Evol. Ecol. 8, 407–421.

Fryxell, J.M., Lundberg, P., 1997. Individual Behavior and Community Dynamics. Chapman & Hall, London, UK.

Garcia-Domingo, J.L., Saldaña, J., 2007. Food-web complexity emerging from ecological dynamics on adaptive networks. J. Theor. Biol. 247, 819–826.

Gardner, M.R., Ashby, W.R., 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. Nature 228, 784.

Gause, G.F., 1934. The Struggle for Existence. Williams and Wilkins, Baltimore.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.

Harrison, G.H., 1979. Global stability of food chains. Am. Nat. 114, 455–457.

Hassell, M.P., 1978. The Dynamics of Arthropod Predator-prey Systems. Princeton University Press, Princeton, NJ, USA.

Hofbauer, J., Sigmund, K., 1998. Evolutionary Games and Population Dynamics. Cambridge University Press, Cambridge.

Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. Theor. Popul. Biol. 12, 197–229.

Holt, R.D., 1983. Optimal foraging and the form of the predator isocline. Am. Nat. 122, 521–541.

Holt, R.D., 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. Am. Nat. 124, 377–406.

Holt, R.D., 1997. Community modules. In: Gange, A.C., Brown, V.K. (Eds.), Multi-trophic Interactions in Terrestrial Systems. Blackwell Science Ltd, London, UK, pp. 333–350.

Holt, R.D., Grover, J., Tilman, D., 1994. Simple rules for the interspecific dominance in systems with exploitative and apparent competition. Am. Nat. 144, 741–771.

Huisman, J., Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. Nature 402, 407–410.

Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 137–145.

Kondoh, M., 2003. Foraging adaptation and the relationship between food-web complexity and stability. Science 299, 1388–1391.

Kondoh, M., 2006. Does foraging adaptation create the positive complexity-stability relationship in realistic food-web structure? J. Theor. Biol. 238, 646–651.

Křivan, V., 1996. Optimal foraging and predator-prey dynamics. Theor. Popul. Biol. 49, 265–290.

Křivan, V., 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. Am. Nat. 149, 164–178.

Křivan, V., 2000. Optimal intraguild foraging and population stability. Theor. Popul. Biol. 58, 79–94.

Křivan, V., 2003. Competitive coexistence caused by adaptive predators. Evol. Ecol. Res. 5, 1163–1182.

Křivan, V., Schmitz, O.J., 2003. Adaptive foraging and flexible food web topology. Evol. Ecol. Res. 5, 623–652.

LaSalle, J.P., 1976. The Stability of Dynamical Systems. Society for Industrial and Applied Mathematics, Philadelphia, Penn, USA.

Leibold, M.A., 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. Am. Nat. 147, 784–812.

Levin, S.A., 1970. Community equilibria and stability: an extension of the competitive exclusion principle. Am. Nat. 104, 413–423.

May, R.M., 1972. Limit cycles in predator-prey communities. Science 177, 900–902.

Murdoch, W.W., 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39, 335–354.

Oaten, A., Murdoch, W.W., 1975. Switching, functional response, and stability in predator-prey systems. Am. Nat. 109, 299–318.

Odum, E.P., 1971. Fundamentals of Ecology. Saunders, Philadelphia, USA.

Paine, R.T., 1969. A note on trophic complexity and community stability. Am. Nat. 103, 91–93.

Roughgarden, J., Feldman, M., 1975. Species packing and predation pressure. Ecol. Soc. Am. 56, 489–492.

Slobodkin, L.B., 1964. The strategy of evolution. Am. Sci. 52, 342–357.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton, NJ, USA.

Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ, USA.

Uchida, S., Drossel, B., 2007. Relation between complexity and stability in food webs with adaptive behavior. J. Theor. Biol. 247, 713–722.

Uchida, S., Drossel, B., Brose, U., 2007. The structure of food webs with adaptive behaviour. Ecol. Model. 206, 263–276.

Visser, A.W., Mariani, P., Pigolotti, S., 2012. Adaptive behaviour, tri-trophic food-web stability and damping and chaos. J. R. Soc. Interface 9, 1373–1380.

Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex foodwebs. Nature 404, 180–183.