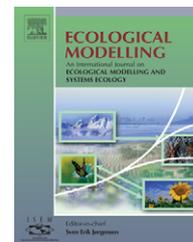


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The structure of food webs with adaptive behaviour

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ABSTRACT

We investigate mainly analytically the influence of the implementation of population dynamics and of adaptive behaviour on the number of links in a food web and on the stability of species with a small population size. By comparing models with Lotka–Volterra and Holling type II functional responses, models with and without predator avoidance, models with linear and nonlinear constraints on the foraging efforts, and diet selection models versus patch choice models, we find that adaptive foraging always has a stabilizing effect on small populations and that nonlinear functional responses and in particular nonlinear constraints on the foraging efforts lead to more realistic link numbers in the food web.

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1. Introduction

Many species show adaptive behaviour in the way they forage for prey or avoid predators. Such adaptive behaviour must affect the population dynamics and the food web structure in several ways, and in recent years various publications were devoted to this topic. Thus, analytical and numerical investigations of models of predator–prey systems have shown that adaptive behaviour can promote the coexistence of competing consumers (Křivan, 2003) as well as of competing prey (Křivan and Eisner, 2003). Furthermore, adaptive behaviour was shown to affect the link–species relationship (Matsuda and Namba, 1991; Matsuda et al., 1994, 1996) and to promote the persistence of species (van Baalen et al., 2001) and the stability of food webs (Genkai-Kato and Yamamura, 1999, 2000; Kondoh, 2003).

Adaptive behaviour of individuals allows a species to increase its growth rate by assigning more time or effort to searching for the more profitable prey or to avoiding dangerous predators (Alexander, 1996; McNamara et al., 2001; Sih

and Christensen, 2001). As the total time or energy available to a species is limited, the adaptive dynamics happens under the constraint that the total time or energy invested in the different activities remains constant. This is usually modelled by introducing a parameter, which we call “effort” in this paper, that is associated with each link of a species. It represents the fraction of time or energy devoted to this link, and it is therefore normalized to one for each species. The effort into links that yield more gain per unit effort is increased. For fixed populations sizes, this usually leads to a fixed point of the adaptive dynamics, which is a Nash equilibrium in the language of game theory (Hofbauer and Sigmund, 1998). If the time scale of the population dynamics is not much slower than that of adaptive dynamics, complex dynamical behaviour may arise. This was pointed out by Abrams and Matsuda (2004), who realized the importance of the time lag in the response of predator preference to changes in prey density.

A predator searching for one prey may at the same time encounter another prey that requires a similar search strategy.

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For this reason, the condition that the different efforts of one species add up to one is not always realistic. This is usually taken into account by grouping species that are searched for simultaneously into “prey trophic species” (Matsuda and Namba, 1991), as if they constituted a single food item. Alternative approaches that also consider the intermediate case of partial overlap between search strategies for different predators have not been suggested so far.

Adaptive behaviour has been implemented in different ways. It has been used in combination with Lotka-Volterra and Holling type II functional responses, and with growth terms that are linear or nonlinear in the prey consumption rate. Different prey species may be well mixed in space, or confined to different patches. Predator avoidance can be predator-specific, unspecific or not included at all. In the case of Holling type II functional response, the effort is by some authors multiplied with the functional response, and by other authors it is multiplied with the encounter rate. All these variations will affect the possible number of links that can be realized at fixed points of the dynamics. This has been shown for the case of nonspecific predator avoidance versus specific predator avoidance by Matsuda et al. (1994). However, there exists not yet a systematic study of the effect of these different variations.

In this paper, we fill the mentioned gaps by investigating mainly analytically the influence of the precise implementation of population dynamics and of adaptive behaviour on the number of links in a food web and on the stability of species with a small population size. In contrast to most other authors, we perform analytical calculations on larger food webs consisting of several trophic levels. Where such calculations are not possible, we perform computer simulations on small networks. We study systems with Lotka-Volterra and Holling type II functional response, without and with predator avoidance, without and with prey being distributed in different patches, and with linear and nonlinear constraints on efforts. We find that for Lotka-Volterra population dynamics and linear constraints on the efforts, the possible link numbers are very restricted, while we do not find such constraints in nonlinear equation systems. Nonlinear terms are also necessary if nontrivial predator avoidance behaviour shall emerge. Since nonlinear terms appear to be more realistic, this finding fits well together with the empirically found large link numbers in large food webs.

We also find that for any type of adaptive foraging, species with small population sizes can survive irrespective of the number and strength of their predators, as long as they have enough food to compensate for the natural death rate and as they are not the only prey of their predator. This finding is satisfactory as adaptive behaviour has been shown to stabilize food web dynamics in various ways.

The outline of this paper is as follows: in the next section, we will introduce the basic models for population dynamics and adaptive foraging. These models include also patch choice models and nonlinear constraints on the foraging efforts. In Section 3, we investigate the stabilizing effect of adaptive foraging on small populations, and we use analytical calculations and computer simulations to find the possible number of links in the different models. Finally, in Section 4, we will compare the properties of food webs with the different versions of adaptive behaviour, and we will discuss the consequences of our

findings. Appendix contains several calculations not included in the main text, and a discussion of the effects of predator avoidance.

2. Population dynamics and adaptive behaviour

In this section, we present and discuss the different types of dynamical equations used in the literature to describe population dynamics without and with adaptive foraging. The consequences for the possible link numbers and the stability of the networks described by these equations will be investigated in the next section.

2.1. Population dynamics

We consider food web models with L trophic levels. Species in level l feed on species in level $l - 1$. The classical population dynamics is then

$$\frac{dN_j^{(l)}(t)}{dt} = G_j^{(l)}(N(t))N_j^{(l)}(t), \quad (l = 1, \dots, L; j = 1, \dots, S^{(l)}), \quad (1)$$

where $S^{(l)}$ is the number of species included in level l and $N_j^{(l)}$ is the population of the j th species in level l . The function $G_j^{(l)}(N(t))$ depends on the population sizes of level l and the two neighboring levels, and on the functional response considered. For Lotka-Volterra functional response and in the absence of adaptive behaviour, $G_j^{(l)}(N(t))$ is of the form

$$G_j^{(l)} = \sum_{i=1}^{S^{(l-1)}} \lambda_{ji} a_{ji} N_i^{(l-1)} - \sum_{k=1}^{S^{(l+1)}} a_{kj} N_k^{(l+1)} - \alpha - \beta N_j^{(l)}, \quad (2)$$

where λ_{ji} is the nutritional value of an individual i for its predator j , a_{ji} the coupling strength between j and i , which can in the Lotka-Volterra model be interpreted as foraging rate, α a death rate and β measures the strength of competition within a species for necessities other than food. We will also consider variations of this model with no direct competition term (which is a good model if predation and food limitation determine the population size), and with interspecific competition. We assume that the external resources on which the basal species feed, are replenished at a sufficiently large rate, such that they can be modelled as species with constant population size. Thus, for basal species the first and third term on the right-hand side of Eq. (1) add up to a constant and positive growth term.

The Holling (type II) model is (Arditi and Michalski, 1996)

$$G_j^{(l)} = \sum_{i=1}^{S^{(l-1)}} \frac{\lambda_{ji} a_{ji} N_i^{(l-1)}}{1 + \sum_{i'=1}^{S^{(l-1)}} h_{ji'} a_{ji'} N_{i'}^{(l-1)}} - \sum_{k=1}^{S^{(l+1)}} \frac{a_{kj} N_k^{(l+1)}}{1 + \sum_{j'=1}^{S^{(l)}} h_{kj'} a_{kj'} N_{j'}^{(l)}} - \alpha - \beta N_j^{(l)}, \quad (3)$$

which is an extension to several prey of the form originally proposed by Holling (1959b). Here, h_{ji} is the handling time that species j takes to deal with an item of prey i . The coupling a_{ji} is most naturally interpreted as an encounter rate. The Holling type II functional response is the one most widely used in the modelling of food webs, since it has a mechanistic basis (Holling, 1959a; Real, 1977).

Generalization of all these equations to include omnivory is straightforward. Our investigations in the next section will mainly use the layered model, for which is easier to obtain analytical results. This is already a big progress compared to existing calculations of that type, which are confined to small systems or to systems with only two trophic levels. However, we will also briefly discuss the effect of omnivory on our results.

2.2. Adaptive foraging

Now, let us include adaptive behaviour. The adaptive behaviour of the individuals of a population has the effect that coupling terms in the population dynamics equations become time dependent. The functional response $G_j^{(l)}$ in Eq. (1) depends then not only on the population sizes, but also on time-dependent parameters $\{f_{ji}^{(l)}(t)\}$, which we call “efforts”. We focus here on adaptive foraging and discuss the effect of predator avoidance mainly in Appendix D.

2.2.1. Linear constraints on the efforts

Usually, it is assumed that the sum of all foraging efforts that a predator j invests in its prey species i is unity,

$$\sum_{i=1}^{S^{(l-1)}} f_{ji} = 1. \tag{4}$$

This is a linear constraint on the efforts, and the simplest interpretation of this rule is that predators divide their time among the different prey species, f_{ji} being the proportion of time devoted to prey i .

Lotka-Volterra population dynamics, Eq. (2) then becomes (Matsuda and Namba, 1991)

$$G_j^{(l)} = \sum_{i=1}^{S^{(l-1)}} \lambda_{ji} a_{ji} f_{ji} N_i^{(l-1)} - \sum_{k=1}^{S^{(l+1)}} a_{kj} f_{kj} N_k^{(l+1)} - \alpha - \beta N_j^{(l)}. \tag{5}$$

The time dependence of the efforts is usually described by an equation of the form

$$\frac{df_{ji}(t)}{dt} = \kappa f_{ji}(t) \left(\frac{\partial G_j^{(l)}}{\partial f_{ji}} - \left\langle \frac{\partial G_j^{(l)}}{\partial f_{ji}} \right\rangle \right), \tag{6}$$

where κ is the ratio between the time scales of adaptive foraging and of population dynamics, and $\langle \partial G_j^{(l)} / \partial f_{ji} \rangle = \sum_{i=1}^{S^{(l-1)}} f_{ji} \partial G_j^{(l)} / \partial f_{ji}$ is the mean change in predator growth rate due to a change of the efforts (Weibull, 1996; Hofbauer and Sigmund, 1998). The efforts are changed such that the growth rate increases. At the fixed point, the efforts into prey species

i for which the inequality

$$\left. \frac{\partial G_j^{(l)}}{\partial f_{ji}} \right|_{f_{ji}=0} < \left\langle \frac{\partial G_j^{(l)}}{\partial f_{ji}} \right\rangle \tag{7}$$

holds, vanishes.

If there was no population dynamics, a predator would according to these rules put all its effort into the most profitable prey, and all other efforts would become zero. Of course, this does not remain so under population dynamics. If a predator feeds only on its most profitable prey, the population size of this prey decreases, until it becomes equally profitable to feed on a different prey. The combined population dynamics and adaptive dynamics lead therefore to fixed points where efforts can be different from unity or zero (Matsuda et al., 1994, 1996).

2.2.2. Nonlinear constraints on the efforts

If the prey of a predator occur in different sub-habitats, adaptive foraging implies that the predator will focus its searching activities on the sub-habitat with the more profitable prey (Murdoch et al., 1975). In this case, searching for specific prey species is mutually exclusive and switching to a specific prey implies that the encounter rates are reduced for all other prey. In contrast, in spatially homogeneous habitats adaptive foraging does not change the encounter rates between a predator and its various prey (Siddon and Witman, 2004). Nevertheless, predators tend to focus on their more profitable prey. In both situations, there are several reasons rendering it unlikely that a predator puts all its effort exclusively into the most profitable prey as suggested by the linear constraint (4). First, few habitat subdivisions are strict and even in structured habitats predators still encounter alternative prey while searching for specific prey (Murdoch et al., 1975). Efforts into different activities are therefore not completely mutually exclusive. Second, predators may not be capable to confine their search completely to the most profitable prey. This would possibly prevent them from noticing increasing abundances of different prey. Third, a broader variety of food might be important in order to obtain all needed nutrients, and therefore it might be better to adjust foraging behavior only to some extent to food abundances. Indeed, empirical data suggest that a predator does not put all its effort in its most profitable prey (Murdoch et al., 1975; Siddon and Witman, 2004), but that the ratio of the rates of consumption of two prey is given by

$$\frac{a_{j1} f_{j1} N_1^{(l-1)}}{a_{j2} f_{j2} N_2^{(l-1)}} \propto \left(\frac{a_{j1} N_1^{(l-1)}}{a_{j2} N_2^{(l-1)}} \right)^b \tag{8}$$

with an exponent b that is larger than 1 if adaptive foraging takes place (Greenwood and Elton, 1979; Elliott, 2004).

Such a law is obtained if we impose nonlinear constraints on the efforts,

$$\sum_i f_{ji}^x = 1. \tag{9}$$

Maximizing the consumption rate

$$a_{j1} f_{j1} N_1^{(l-1)} + a_{j2} f_{j2} N_2^{(l-1)}$$

with respect to the efforts then leads to Eq. (8) with $b = x/(x - 1)$.

In the limit $x = 1$, we obtain again linear constraints. We would then have $b \rightarrow \infty$, implying that the predator focusses completely on the most profitable prey. In the opposite limit $x \rightarrow \infty$, there is no adaptive foraging, and $b \rightarrow 1$. By choosing an appropriate value of x , one can adjust the extent of adaptive foraging.

In Appendix A, we motivate nonlinear constraints on the efforts in more detail. There, we also show that the appropriate dynamical equation for the efforts is (30)

$$\frac{df_{ji}(t)}{dt} = \kappa f_{ji}(t) \left(f_{ji}^{1-x} \frac{\partial G_j^{(l)}}{\partial f_{ji}} - \sum_k f_{jk} \frac{\partial G_j^{(l)}}{\partial f_{jk}} \right).$$

Whether linear or nonlinear constraints are more appropriate, should also depend on the extent to which species in the food web are aggregated. The higher the level of aggregation, the more do “species” differ from each other, because similar species are grouped together. It is thus easier for predators to discriminate between prey, and the strategies required for searching for different prey are more distinct. One might expect that for higher levels of aggregation the exponent x should be closer to 1.

In Appendix D, we will also discuss the effect of predator avoidance. The usual way of modelling predator avoidance consists in assigning efforts to the avoidance behavior. Here, it is even more evident that linear constraints on the efforts might not be realistic. They would imply that a prey cannot feed while hiding from the predator. In contrast, empirical evidence suggests that predator avoidance behavior reduces only partially the capability of consuming food by forcing prey species to feed less or to exploit less profitable resources (Loose and Dawidowicz, 1994; Peckarsky, 1996; Turner et al., 2000; Amarasekare, 2006). As seen in Appendix D, linear constraints on the efforts do not allow for any predator avoidance behavior if the type of population dynamics discussed in this paper is used. This is one more reason to use nonlinear constraints.

2.2.3. Diet choice and patch choice

For Holling type II functional response, finding appropriate equations describing adaptive dynamics becomes more complicated. A classical result by Stephens and Krebs (1986) is the “all or none” rule that a prey should always or never be taken upon encounter, leading to a growth term of the form

$$\frac{\lambda_{ji} a_{ji} p_{ji} N_i^{(l-1)}}{S^{(l-1)} + \sum_{i'=1} h_{ji'} a_{ji'} p_{ji'} N_{i'}^{(l-1)}}. \tag{10}$$

The parameters p_{ji} are determined by the so called prey algorithm and take only the value 0 or 1 (Charnov, 1976; Stephens and Krebs, 1986). This result is based on the assumptions that different resources can be substituted for each other, and that the adaptive behaviour of predators does not affect encounter rates, but only the decision to attack a prey item when encountered. We will focus on the case that the encounter rates themselves are affected by the adaptive behaviour. In the literature, there can be found two versions of

Holling type II functional response with adaptive behaviour. The first one is based on the assumption that a predator j invests the proportion f_{ji} of its time to search exclusively for prey i . This happens if different prey live in different patches, or if predators form a search image for a specific prey and look only for this prey during a given time. The population dynamics then becomes

$$G_j^{(l)} = \sum_{i=1}^{S^{(l-1)}} f_{ji} \frac{\lambda_{ji} a_{ji} N_i^{(l-1)}}{1 + h_{ji} a_{ji} N_i^{(l-1)}} - \sum_{k=1}^{S^{(l+1)}} f_{kj} \frac{a_{kj} N_k^{(l+1)}}{1 + h_{kj} a_{kj} N_j^{(l)}} - \alpha - \beta N_j^{(l)}. \tag{11}$$

The second version is based on the assumption that different prey species may be encountered at the same time, but that there is somehow a payoff between the different encounter rates. This leads to the expression

$$G_j^{(l)} = \sum_{i=1}^{S^{(l-1)}} \frac{\lambda_{ji} a_{ji} f_{ji} N_i^{(l-1)}}{1 + \sum_{i'=1} h_{ji'} a_{ji'} f_{ji'} N_{i'}^{(l-1)}} - \sum_{k=1}^{S^{(l+1)}} \frac{a_{kj} f_{kj} N_k^{(l+1)}}{1 + \sum_{j'=1} h_{kj'} a_{kj'} f_{kj'} N_{j'}^{(l)}}, \tag{12}$$

which is used, for instance, in Abrams and Matsuda (2004) and Brose et al. (2003), together with linear constraints (4). The difference between the two versions of adaptive foraging is irrelevant for the Lotka-Volterra model, since both versions lead to the same equations.

For the second version, there is no reason why there should be linear constraints on the efforts. Eq. (12) cannot be interpreted at all in terms of a search time. This equation takes into account a payoff between the encounter rates of predator j with its different prey, and there is in fact no reason to assume that the payoff between encounter rates is such that efforts have to add up to a constant.

In fact, nonlinear constraints on the efforts in (11) and (12) lead to a relation similar to (8), which is important as a Type II functional response is considered more realistic. More precisely, we obtain exactly (8) if we start from (11) with nonlinear constraints on the efforts. If we start from (12), we get $F_1/F_2 = ((A_1/A_2)^x)/(x - 1)((1 + (h_2 - h_1)F_2)/(1 + (h_1 - h_2)F_1))^{1/(x-1)}$, where $F_i = a_i f_i N_i$, $A_i = a_i N_i$. If the handling times are not too different from each other, this can be well approximated by (8).

Since there are so many reasons to allow for nonlinear constraints on the efforts, we will study below model networks with nonlinear constraints as well as with linear constraints.

3. Food web stability and food web structure

Let us now explore the consequences of using one or the other type of population dynamics or adaptive dynamics on the structure and stability of networks. We will first investigate the stability of small populations and find that adaptive

foraging has always a stabilizing effect. Then, we will derive constraints on the number of links in the food web for the different types of models.

3.1. Stability of small populations due to adaptive foraging

First, we show that adaptive foraging has a stabilizing effect on food webs because it protects species with small population sizes. With linear constraints on the efforts, we obtained the result that the effort into all prey i for which the inequality (7) holds vanishes. For Lotka-Volterra dynamics, we have $\partial G_j^{(l)} / \partial f_{ji} = a_{ji} N_i^{(l-1)}$, and therefore the effort into a prey vanishes when its population size becomes very small (as long as other prey with larger population sizes are present). This means that species in a food web have a higher chance of survival in the presence of adaptive dynamics. If the population of a species becomes very small, its population dynamics Eq. (5) reduces to

$$G_j^{(l)} \simeq \sum_{i=1}^{S^{(l-1)}} \lambda_{ji} a_{ji} f_{ji} N_i^{(l-1)} - \alpha, \tag{13}$$

which means that a species can survive if only there is enough food for it to compensate for the death rate α . This conclusion breaks down if species j is the only prey of one of its predators, or if all other prey of one of its predators have also a small population size.

Of course, small populations are at a high extinction risk, since accidents, genetics or demography, may also kill them (MacArthur and Wilson, 1967; Soule and Simberloff, 1986; Wilcox, 1986; Raup, 1991), an effect which is contained in our deterministic modelling only through a fixed extinction threshold. Even though we neglect stochastic effects, we expect that the main conclusion remains valid that the risk of extinction of a small population is smaller if there is adaptive foraging.

That predators can indeed drive their prey extinct has been documented, for instance, in biological control experiments (Simberloff and Stiling, 1996). Some of the predators that were introduced to control a pest have become important predators of other native species and eventually caused their extinction. A prominent example is given by the introduction of the Indian mongoose (*Herpestes auro-punctatus*) to Hawaii and the islands of the West Indies that drove some native reptiles extinct (Lever, 1985).

In the same way, as we did for Lotka-Volterra dynamics, we can also show for Holling type II dynamics that adaptive foraging of its predators allows a species to survive if only enough food is available for it, irrespective of the number and strength of predators, provided that the predators have other prey with larger population size. We have from Eqs. (11) and (12) again

$$\frac{\partial G_j^{(l)}}{\partial f_{ji}} \propto N_i^{(l-1)},$$

and therefore the effort into prey species vanishes the population size of which is so small that

$$\frac{\partial G_j^{(l)}}{\partial f_{ji}} < \left\langle \frac{\partial G_j^{(l)}}{\partial f_{ji}} \right\rangle.$$

We can therefore approximate the growth rates (11) and (12) for small population sizes by

$$G_j^{(l)} \simeq \sum_{i=1}^{S^{(l-1)}} f_{ji} \frac{\lambda_{ji} a_{ji} N_i^{(l-1)}}{1 + h_{ji} a_{ji} N_i^{(l-1)}} - \alpha$$

and

$$G_j^{(l)} \simeq \sum_{i=1}^{S^{(l-1)}} \frac{\lambda_{ji} a_{ji} f_{ji} N_i^{(l-1)}}{S^{(l-1)} + \sum_{i'=1} h_{ji'} a_{ji'} f_{ji'} N_{i'}^{(l-1)}} - \alpha.$$

If only there is enough food available for the species to compensate for the death rate, a species can exist.

Now, let us consider the situation of nonlinear constraints on the efforts. According to (30), when $x > 1$ an effort always increases if it becomes too small. This means that at a fixed point all efforts are nonzero! This is no surprise if we remember that we have assumed that a predator can still pursue other activities while searching for a specific prey. Nevertheless, the effort into a prey with a small population size becomes very small, as we can immediately conclude from Eq. (27), where the left-hand side is proportional to $N_i^{(l-1)}$ when $N_i^{(l-1)}$ is very small for Lotka-Volterra dynamics as well as for Holling type II dynamics. The effort f_{ji} therefore also becomes very small unless species i is the only prey of species j or all prey of species j have a very small population size, in which case γ_j becomes very small. We can therefore repeat the reasoning that we did for the case of linear constraints to obtain the result that a very small population size always increases if only there is enough food for the species to compensate for the death rate α , irrespective of the number and population size of predators, provided that adaptive dynamics of the predators is fast enough and the species is not the only prey of a predator.

3.2. Link structure of Lotka-Volterra models

We first consider Eq. (5) with the constraint (4) and the adaptive dynamics (6) and focus on fixed points of the combined adaptive and population dynamics.

In Matsuda and Namba (1991), Matsuda et al. (1994, 1996), it was found that for Lotka-Volterra systems with several trophic levels the resulting webs must be so sparse that the number of links with nonzero effort is smaller than twice the number of existing species. This is due to the linear dependence of the functional $G_j^{(l)}$ on the prey population sizes and the efforts. We will see that this constraint cannot be derived for nonlinear functional response of Holling type II, which indicates that the property is dependent of the functional response.

The fixed point of the adaptive dynamics (6) is given by

$$\frac{\partial G_j^{(l)}}{\partial f_{ji}} = \frac{\partial G_j^{(l)}}{\partial f_{ji'}}, \quad (f_{ji} \neq 0, f_{ji'} \neq 0), \tag{14}$$

$$\lambda_{ji} a_{ji} N_i^{(l-1)} = \lambda_{ji'} a_{ji'} N_i^{(l-1)} =: \bar{g}_j. \tag{15}$$

Now we denote by $C_j^{(l)}$ the number of prey species that species j in level l actually feeds on, that is, the number of variables f_{ji} that do not vanish. Then we see from Eq. (14) that there are $C_j^{(l)}$ homogeneous linear equations for the free variables $N_i^{(l-1)}$. This relation must hold for all j . Therefore, in order that the system of equations has a nontrivial solution, the following condition must hold:

$$\sum_{j=1}^{S^{(l)}} (C_j^{(l)} - 1) \equiv C^{(l)} - S^{(l)} < S^{(l-1)}, C^{(l)} < S^{(l-1)} + S^{(l)}. \tag{16}$$

This shows that the number of viable links from level l to level $l - 1$ must be smaller than the sum of the number of species in levels $l - 1$ and l . On the other hand, the number of links between these two levels must be at least $S^{(l)}$ because each predator must have at least one prey, otherwise a predator has no resource and becomes extinct. Up to $S^{(l-1)} - 1$ additional links can exist between these two layers. Moreover, if we consider only a part of the food web, the same conditions must hold for this part.

In addition to the $(C^{(l)} - S^{(l)})$ conditions resulting from Eq. (14), there are $S^{(l)}$ conditions resulting from Eq. (4) and $S^{(l)}$ conditions resulting from the condition that population dynamics is at a fixed point, i.e., that $G_j^{(l)}$ in Eq. (5) vanishes for each species in layer l . If we take the sum over all levels, we have in total

$$\sum_l (C^{(l)} + S^{(l)}) \equiv C + S$$

conditions for C efforts and S population sizes, as it must be.

If the network contains omnivores, we still have inequalities limiting the number of possible links. The most general expression for the restriction on the link number is $C^{(P,r)} < S^{(P)} + S^{(r)}$, where P is a set of species, r is a subset of the prey

set R of P (i.e., $R = \bigcup_{j \in P} R_j$, R_j is the set of prey of j). Therefore, inequality (16) must hold even if there are omnivores regardless of the definitions of trophic levels.

With nonlinear constraints on the efforts, all efforts remain nonzero at the fixed point. If $x = 2$, the efforts can be calculated analytically, as is shown in Appendix A. The result is (36)

$$f_{ji} = \frac{\lambda_{ji} a_{ji} N_i^{(l-1)}}{\sqrt{\sum_i (\lambda_{ji} a_{ji} N_i^{(l-1)})^2}}. \tag{17}$$

This means that the effective connectance is identical to the potential connectance.

3.3. Holling type II dynamics: diet selection

The inequality (16) followed from the linear dependence of $G_j^{(l)}$ on the efforts. We therefore find a different result for Holling functional response. In this subsection, we only report on results for model (12), and we keep model (11) for the next subsection.

As is shown in Appendix C, a constraint of the type (16) cannot be derived for Holling type II dynamics. For this reason, we performed simulations of small systems. We generated small food webs consisting of two predators, two prey and one resource using random values for the couplings chosen from the interval $[0, 1]$. We simulated the combined population and foraging dynamics with $\kappa = 2$. We chose $\lambda = 0.23$ which can be found, for example, in Krebs (2002) and found that for this value of λ the dynamics always reaches a fixed point. For larger values of λ , more complicated dynamics can arise. We fixed the initial population densities at 0.2 and 0.3 for predators and 0.8 and 0.6 for prey. Initial efforts are also fixed at 1/2. We considered species as being extinct when the population density dropped below 0.001 (Matsuda et al., 1996), and if a species died out, we generated a new system. If no species died out, we noted the link structure at the fixed point. Table 1 indicates how often each of the four possible link structures at

Table 1 – Frequency of different link structures obtained with different population and foraging dynamics for a system of two predators, two prey and one resource, in the case where all four species survive

Link structure ^a	 2a	 2b	 3	 4
1 Diet choice, L-V ^b , linear	55	499	446	0
2 Diet choice, H ^b , linear	48	643	309	0
3 Diet choice, L-V, nonlinear	0	0	0	1000
4 Diet choice, H, nonlinear	0	0	0	1000
5 Patch choice, L-V	41	480	473	6
6 Patch choice, H	31	483	481	5
7 Patch choice (id. death rates), H	43	385	572	0
8 Patch choice (same habitat)	289	97	488	126

^a Link structure 2a indicates that the two predators finally feed on the same prey. Number 2b means that one predator feeds on one prey and the other predator feeds on the other prey. In both cases, there are in total 2 links between predators and preys. In the cases 3 and 4, there are three and four links.

^b L-V and H are abbreviations for Lotka-Volterra and Holling functional responses, respectively.

the fixed point was obtained out of 1000 times. The handling times were chosen at random from the interval [0, 0.02] for each simulation.

The result for the Holling model is shown in the second row in Table 1. Comparing to the results of Matsuda et al. (1994) found for a Lotka-Volterra system (also shown in the first row in Table 1), we see that these results are similar in that the first link pattern (where both predators feed on the same and only one prey) is not frequently achieved. In the above parameter range, we were not able to numerically find the case of four links. Considering that the limit $h_{ji} \rightarrow 0$ leads to Lotka-Volterra systems, we expect that it should be more likely to find systems with four links when handling times are larger. Indeed, for larger values of handling times, we found systems with four links, however, the parameter range where they occur appears to be very small.

With nonlinear constraints on the efforts, all potential links are realized, just as for the Lotka-Volterra systems. Our simulation of small systems confirms this conclusion.

Empirically, the number of links per species increases with the number of species in natural food webs. In most food webs, this linkage density is much higher than two as predicted by the Lotka-Volterra model with linear constraints (Martinez, 1992; Schmid-Araya et al., 2002; Brose et al., 2005; Dunne, 2006). These empirical findings are more consistent with the results presented here under a model with nonlinear constraints.

3.4. Holling type II dynamics: patch choice models

The models for adaptive foraging considered so far could all be interpreted in terms of search images formed by predators, so that they search for a certain part of the time only for a certain type of prey. Part of them can also be interpreted as the predator spending a certain part of the time in a certain patch, where a certain prey is found. Here, we pursue the patch choice models further. We want to study systems with more than two trophic levels. This means that we have to specify the search behaviour of a predator whose prey chooses between different patches. We can define two types of such multilevel patch choice models: in the first model, each species in each level is searched by its predator only in a given patch. This model is discussed briefly in the next subsection, and it resembles formally a lot the diet choice model. The main difference is that the death rate can be dependent on the patch, and therefore the death term becomes dependent on the efforts.

Clearly, this model has its limitations. A species is supposed to divide its time between different patches, where it finds different prey. However, the predators of this species are assumed to search for it in only one area. Even if we assume that this area is so large that it comprises all the patches the species moves through, the model would need some modifications in order to be more realistic. It should probably include larger overlaps (or larger exponents x in the constraint) for prey in higher trophic levels, and the predator success should depend on the foraging behaviour of the prey. Alternatively, we discuss another patch choice model in the subsection after the next one. We divide space into patches according to the resources for the species at the lowest level. Predators on higher levels searching in one patch encounter a given prey with a probability proportional to the effort this prey puts into

this patch. We will see that under certain conditions the populations in the different patches can be treated formally as independent species. This means that there are weaker constraints on link numbers than in the first model.

3.4.1. Each species has its own habitat

We first discuss the situation considered in Křivan (1996, 2003); Křivan and Schmitz (2003), Křivan and Sikder (1999), van Baalen et al. (2001), Křivan and Eisner (2003) and Křivan and Diehl (2005), where each prey species has its specific habitat (or patch) Brose (2003); Tews et al. (2004). Each predator tries to maximize its energy intake by assigning time (effort) in the optimum way to the habitats of their prey species (Amarasekare, 2006). The model consequently resembles the diet choice model, with the only difference that death rates differ in different habitats.

The functional response is in this case

$$G_j^{(l)} = \sum_{i=1}^{S^{(l-1)}} (\lambda_{ji} a_{ji} N_i^{(l-1)} - \alpha_{ji}) f_{ji} - \sum_{k=1}^{S^{(l+1)}} a_{kj} f_{kj} N_k^{(l+1)} - \beta N_j^{(l)}. \quad (18)$$

Compared to the diet choice model, α is replaced with $\sum_{i=1}^{S^{(l-1)}} \alpha_{ji} f_{ji}$. The functional response $G_j^{(l)}$ will now be maximized when

$$\lambda_{ji} a_{ji} N_i^{(l-1)} - \alpha_{ji} =: \bar{g}_j \quad (19)$$

holds for all prey i of j for which $f_{ji} \neq 0$. This set of equations is inhomogenous, leading to the condition

$$C^{(l)} \leq S^{(l-1)} + S^{(l)} \quad (20)$$

instead of (16). Simulations of the two-predator two-prey model show that now four links can occur at the fixed point, see Table 1. For $\beta = 0$, we obtain Eq. (41), as for the diet choice model.

In Křivan (1997), patch choice with Holling type II functional response is considered. This is model (11), with α being replaced with $\sum_{i=1}^{S^{(l-1)}} \alpha_{ji} f_{ji}$. The energy intake is maximized if

$$\frac{\lambda_{ji} a_{ji} N_i^{(l-1)}}{1 + h_{ji} a_{ji} N_i^{(l-1)}} - \alpha_{ji} =: \bar{g}_j \quad (21)$$

is satisfied for all prey i of j for which $f_{ji} \neq 0$. We see that the simulation result shown in Table 1(6th row) is similar to that of 5th row. Even when all death rates are equal (7th row), we cannot rule out the occurrence of four links, however, this was not observed for the parameter ranges used in the simulations.

3.4.2. Common habitats

Now let us assume that there are in total M patches, between which all species in the community move. Each species j tries to maximize its growth rate by spending the appropriate proportion of time in each patch m . We will see that in the absence of a competition term the populations in the different patches decouple, and the community in each patch can be considered independently. We will also find that if the death rate does not

depend on the patch the species in the second level from above spend the same time in each of those patches where they can be found.

We consider here a three-level system of plants (indexed by $i = 1, \dots, I$), herbivores (indexed by $j = 1, \dots, J$) and carnivores (indexed by $k = 1, \dots, K$), and suppose that there are M useful patches (indexed by $m = 1, \dots, M$). Each species optimizes its energy intake through its optimal habitat choice. We denote the population of each consumer species by $N_s (s = j, k)$, and the proportion of (or fraction of time spent by) species N_k, N_j in patch m by y_{km}, x_{jm} , respectively, and the population of each plant in patch m by N_{im} , and its growth term by E_{im} . Thus, we have $\sum_m y_{km} = 1$ and $\sum_m x_{jm} = 1$. Then the population dynamics with Lotka-Volterra functional response is

$$\begin{aligned} \frac{dN_k}{dt} &= N_k \left(\sum_{j=1}^J \lambda_{kj} a_{kj} \sum_m y_{km} (x_{jm} N_j) - \sum_m \alpha_{km} y_{km} - \beta N_k \right), \\ \frac{dN_j}{dt} &= N_j \left(\sum_{i=1}^I \lambda_{ji} a_{ji} \sum_m x_{jm} N_{im} - \sum_{k=1}^K a_{kj} \sum_m x_{jm} (y_{km} N_k) - \sum_m \alpha_{jm} x_{jm} - \beta N_j \right), \\ \frac{dN_{im}}{dt} &= N_{im} \left(E_{im} - \sum_{j=1}^J a_{ji} (x_{jm} N_j) - \beta N_{im} \right). \end{aligned} \tag{22}$$

If the competition for resources other than food does not affect population dynamics, the last term in the first two equations can be dropped. Introducing $N_{km} = y_{km} N_k$ and $N_{jm} = x_{jm} N_j$, we then obtain for the first two equations

$$\begin{aligned} \frac{dN_k}{dt} &= \sum_m N_{km} \left(\sum_{j=1}^J \lambda_{kj} a_{kj} N_{kj} - \alpha_{km} \right), \\ \frac{dN_j}{dt} &= \sum_m N_{jm} \left(\sum_{i=1}^I \lambda_{ji} a_{ji} N_{im} - \sum_{k=1}^K a_{kj} N_{km} - \alpha_{jm} \right), \end{aligned} \tag{23}$$

which shows that the growth rate of a species is the sum of the growth rates of its populations in the different patches. The food web is identical to a set of independent food webs in different patches, without adaptive foraging. Independent population dynamics in each patch leads to exactly the same fixed points as adaptive foraging between different patches.

Let us now assume $\beta \neq 0$ and explore the consequences of adaptive dynamics. Maximizing the growth rate of carnivores and herbivores gives the conditions

$$\begin{aligned} \sum_{j=1}^J \lambda_{kj} a_{kj} x_{jm} N_j - \alpha_{km} &=: \gamma_k \\ \sum_i \lambda_{ji} a_{ji} N_{im} - \sum_{k=1}^K a_{kj} y_{km} N_k - \alpha_{jm} &=: \gamma_j \end{aligned} \tag{24}$$

for all those patches m where the species k (first equation) or j (second equation) are found. If the death rate is independent of the patch, the x_{jm} is the only m -dependent quantity in the first set of equations. As we will show in the next paragraph, the

population sizes are determined independently of the efforts, leaving the x_{jm} as the only variables in the first equation. For $J \geq K$, the solution $x_{jm} = x_{jm'}$ is the only one for all patches m, m' where species j is found. Predation leads to an equal distribution of the species in the second level from above between the different patches if there are at least as many carnivore species as herbivore species. This is plausible, since a predator will put more effort into a patch with more prey, until the prey population size is equal in all patches. If the carnivore death rates depend on the patch, Eq. (24) still determines the x_{jm} , which are however no longer identical.

Let us now determine the conditions for the population sizes. Inserting conditions (24) into the population dynamics

(22) for carnivores and herbivores, we obtain

$$\begin{aligned} \frac{dN_k}{dt} &= N_k (\gamma_k - \beta N_k), \\ \frac{dN_j}{dt} &= N_j (\gamma_j - \beta N_j), \end{aligned} \tag{25}$$

giving $\gamma_k = \beta N_k$ and $\gamma_j = \beta N_j$ at the fixed point. Inserting this result into Eqs. (24) and performing the sum over m , we obtain $J + K$ equations for the $J + K$ population sizes of carnivores and herbivores, which are independent of the efforts x_{jm} and y_{km} . This fixes the population sizes, and Eqs. (24) can be understood as equations for the efforts alone.

The link statistics for systems with two patches with one plant species each, two herbivores and two carnivores is shown in the last row of Table 1 for the case of equal death rates. Four links between carnivores and herbivores are achieved only in 10% of the systems.

Our results imply that using efforts into patches instead of efforts into prey leads to less restrictions on link numbers, even if constraints are linear. The model presented in this subsection allows that predators still encounter other prey while searching for a given prey. This is what motivated our introduction of nonlinear constraints on the foraging efforts. It now appears that efforts into patches with linear constraints can achieve the same goal.

4. Conclusion

We have investigated mainly analytically the link structure and the survival chances of prey species of food webs with different types of population dynamics and different types of adaptive dynamics. The results depend strongly on the type

of population dynamics and the model of adaptive behaviour used.

A general finding is that models with equations that are linear in the efforts allow less links than nonlinear models. Thus we have for Lotka-Volterra dynamics the restriction that the sum of links of two neighboring levels cannot be larger than the sum of species in these two levels. The high number of trophic links found in natural food webs (Martinez, 1992; Schmid-Araya et al., 2002; Brose et al., 2005; Dunne, 2006) is more consistent with the predictions of the nonlinear model. In the absence of a competition term (where population dynamics becomes linear also in the considered population size), there is an additional constraint which becomes most relevant for the two top levels, where each prey can at most be taken by one top predator. Such constraints cannot be derived for Holling type II dynamics. Nevertheless, computer simulations of small model food webs show similar results for the link numbers of the Holling and the Lotka-Volterra systems, indicating that larger link numbers are achieved only for a small part of parameter space.

We also explored the consequences of abandoning the linearity of the constraints for the efforts. We found that for nonlinear constraints all possible links are present, even if very weak for very small prey population size. Nevertheless, nonlinear constraints for the efforts still allow small prey populations to survive as long as they have enough food and as long as their predators have other, more abundant prey. The stabilizing effect found for linear constraints therefore exists also for nonlinear constraints on the efforts.

When adaptive behaviour comprises predator avoidance as well as adaptive foraging, linear (Lotka-Volterra) population dynamics leads to the result that it pays never off to put effort into predator avoidance. Only when the growth term is a nonlinear function of food intake does predator avoidance become profitable. Empirically, predator avoidance behaviour has been documented for many predator-prey interactions in various ecosystem types (Loose and Dawidowicz, 1994; Peckarsky, 1996; Turner et al., 2000). Again, this is more consistent with the findings obtained using the nonlinear model.

Finally, we studied models where space is divided into patches, between which consumers divide their foraging time. Under certain conditions, this leads to an equal distribution between patches of the species in the second layer from above. In the absence of direct competition between consumers, such a system is formally equivalent to a set of independent systems that do not contain adaptive foraging. More interestingly, assigning efforts to patches instead of prey, has a similar effect on link numbers as using nonlinear constraints on efforts into prey.

To conclude, we confirm the hypothesis that adaptive foraging has a stabilizing effect on food web dynamics. However, the standard implementation of adaptive foraging, which uses linear constraints on the efforts, has the drawback that it leads to unrealistically small link numbers in food webs. This can be rigorously shown for Lotka-Volterra models, and appears to be also true for a large part of the parameter space of Holling type II models. We have argued in this paper that using nonlinear constraints on the efforts can be motivated from ecology much better than linear constraints, and that it

allows for the large link numbers found in nature. Using patch choice models where higher-level predators choose patches and not prey, has a similar effect. We therefore suggest that in theoretical investigations where link numbers are important, nonlinear population growth and nonlinear constraints on efforts should be used.

Future extensions of our modelling approach will address the body size structure of natural food webs (Woodward et al., 2005; Brose et al., 2006a) that has important implications for the stability of predator-prey interactions (Weitz and Levin, 2006) and complex food webs (Brose et al., 2006b). Together, adaptive behaviour and body-size structures, may account for much of the stability of complex natural food webs that has been extensively debated for several decades (McCann, 2000; Dunne et al., 2005).

Other extensions of the model could aim at including the dynamics of the external resources, in particular under the influence of limiting factors and temporally fluctuating influences. Here, ideas from completely different approaches to the modelling of ecosystems, such as structurally dynamical modelling (Zhang et al., 2003) could be useful.

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Appendix A. Nonlinear constraints on the efforts

In this Appendix, we motivate in more detail nonlinear constraints on the foraging efforts. We assume that a predator searching for one prey may at the same time encounter another prey that requires a similar search strategy.

Let us now denote the proportion of time predator j searches for prey i with \tilde{f}_{ji} . The sum $\sum_k \tilde{f}_{jk} = 1$ is normalized as before, however, we now assume that predator j may also encounter prey k while searching for prey j . We denote with $\rho_{ik}^{(j)}$ the similarity of prey i and prey k for predator j . Then the encounter rate of predator j with prey i becomes

$$a_{ji}f_{ji} = a_{ji} \sum_k \tilde{f}_{jk} \rho_{ik}^{(j)},$$

where we now have to find the constraint on the effective efforts f_{ji} . A detailed model that specifies the similarity between every pair of species would yield expressions for the $\{f_{ji}\}$, however, we try to find here a generic way of arriving at constraints for the effective efforts. The average size of an effective effort is given by

$$\langle f_{ji} \rangle = \left\langle \sum_k \tilde{f}_{jk} \rho_{ik}^{(j)} \right\rangle \simeq \sum_k \tilde{f}_{jk} \langle \rho_{ik}^{(j)} \rangle = \langle \rho_{ik}^{(j)} \rangle. \tag{26}$$

The step from the first to the second line of this calculation is to be understood as a rough estimate of the order of magnitude of $\langle f_{ji} \rangle$ rather than an exact calculation. Next, we have to estimate the average size $\langle \rho_{ik}^{(j)} \rangle$ of the overlap between two

prey species for predator i . We can expect the overlap between a randomly chosen pair of prey species to be smaller when a predator has more prey and therefore set

$$\langle \rho_{ik}^{(j)} \rangle \propto S_j^{-y}$$

with S_j denoting the number of prey of species j (i.e., the number of species i for which $a_{ji} > 0$), and y is an exponent between 0 and 1. The value of y cannot be larger than 1, since the overlap of prey i with itself must be 1, and therefore $\langle \rho_{ik}^{(j)} \rangle \geq 1/S_j$. We then obtain

$$\sum_i \langle f_{ji} \rangle \simeq S_j \langle f_{ji} \rangle \simeq S_j \langle \rho_{ik}^{(j)} \rangle \propto S_j S_j^{-y} = S_j^{1-y}$$

or, by defining $x = 1/(1 - y)$,

$$\sum_i \langle f_{ji} \rangle^x \propto 1.$$

We therefore introduce the constraint (9)

$$\sum_i f_{ji}^x = 1$$

for the effective efforts. The value of the constant on the right-hand side could be different from 1, however, this can be taken into account by renormalizing other parameters, for instance, the couplings a_{ij} . Because of $0 \leq y < 1$, we have $x \geq 1$.

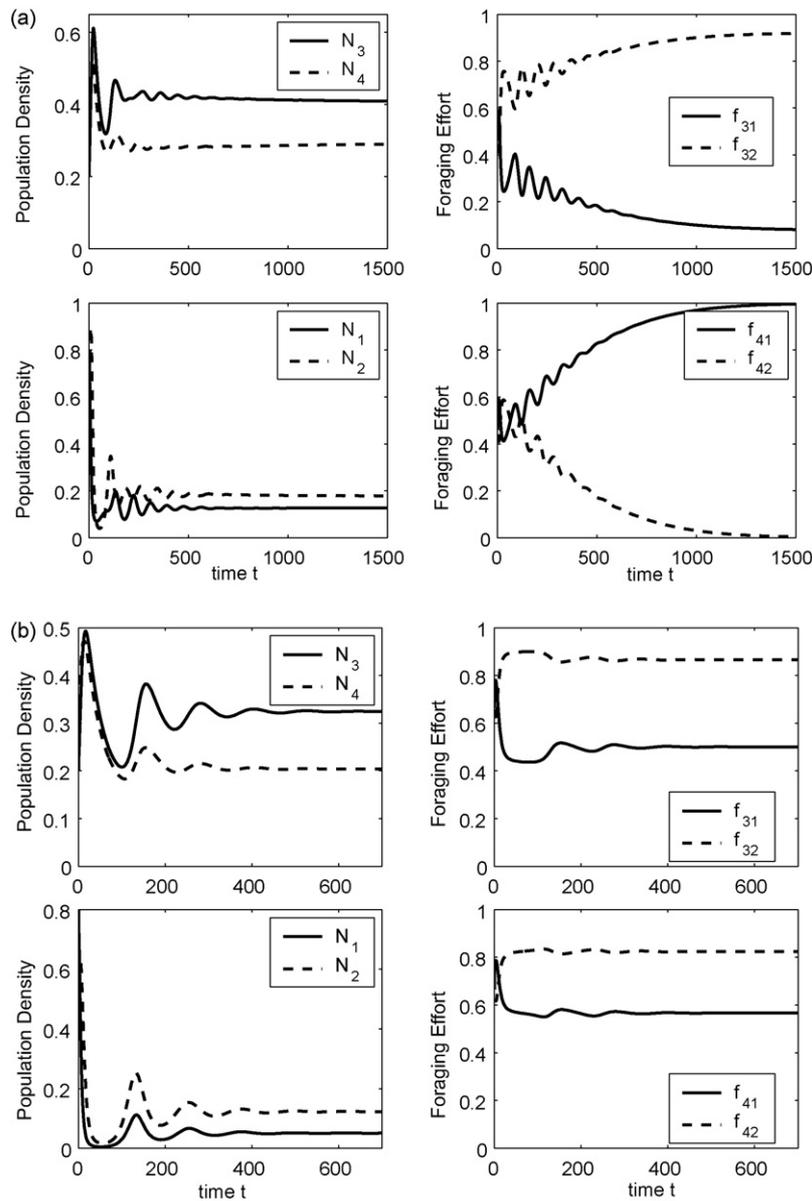


Fig. A.1 – (a) Time series of the four populations (left figures) and foraging efforts (right figures) for the model with Lotka-Volterra functional response with linear constraints on the efforts. N_1 and N_2 are population densities of the bottom species, N_3 and N_4 are those of the top species. f_{ij} denotes the foraging effort species i invests in species j . The values of the couplings between predators and prey are $a_{11} = 0.7$, $a_{12} = 0.3$, $a_{21} = 0.5$, $a_{22} = 0.3$, and between the prey species and the resource, $a_{10} = 0.8$, $a_{20} = 0.9$. All these values were chosen at random. Other parameter values are fixed at $\alpha_1 = 0.01$, $\alpha_2 = 0.0001$, $\beta = 0.05$, $\lambda = 0.23$, $\kappa = 2$. (b) Same as (a), but with nonlinear constraints on the efforts.

The special case $x = 1$ corresponds to the traditional linear constraints.

The condition that the growth rate is maximized subject to (9) can be implemented using the method of Lagrange multipliers. Defining $H_j = G_j - \gamma_j (\sum_{i=1}^{S^{(l-1)}} f_{ji}^x - 1)$ with Lagrange-multipliers γ_j , we have

$$\begin{aligned} \frac{\partial H_j}{\partial f_{ji}} &= \frac{\partial G_j}{\partial f_{ji}} - x\gamma_j f_{ji}^{x-1} = 0; \\ \frac{\partial G_j}{\partial f_{ji}} &= x\gamma_j f_{ji}^{x-1}. \end{aligned} \tag{27}$$

This gives

$$\begin{aligned} \gamma_j &= x^{-1} f_{ji}^{1-x} \frac{\partial G_j}{\partial f_{ji}}, \\ \sum_i f_{ji}^x \gamma_j &= x^{-1} \sum_i f_{ji} \frac{\partial G_j}{\partial f_{ji}} = \gamma_j. \end{aligned} \tag{28}$$

For Lotka-Volterra dynamics, we can easily eliminate the efforts from the expression for γ_j by making use of the constraint (9), and we obtain

$$x\gamma_j = \left[\sum_i \left(\frac{\partial G_j}{\partial f_{ji}} \right)^{x/(x-1)} \right]^{1-1/x}. \tag{29}$$

The dynamics of the efforts (6) becomes with nonlinear constraints

$$\frac{df_{ji}(t)}{dt} = \kappa f_{ji}(t) \left(f_{ji}^{1-x} \frac{\partial G_j^{(l)}}{\partial f_{ji}} - \sum_k f_{jk} \frac{\partial G_j^{(l)}}{\partial f_{jk}} \right). \tag{30}$$

Let us from now on consider the case $x = 2$ with Lotka-Volterra dynamics. We now have the constraint

$$\sum_{i=1}^{S^{(l-1)}} f_{ji}^2 = 1, \tag{31}$$

or in vector notation

$$|\vec{f}_j| = 1, \tag{32}$$

where $\vec{f}_j = (f_{j1}, \dots, f_{ji}, \dots, f_{jS^{(l-1)}})$. We can rewrite the population dynamics also in a vector form,

$$G_j^{(l)} = \vec{f}_j \cdot \vec{g}_j - \sum_{k=1}^{S^{(l+1)}} a_{kj} f_{kj} N_k^{(l+1)} - \alpha - \beta N_j^{(l)}, \tag{33}$$

where $\vec{g}_j = (\lambda_{j1} a_{j1} N_1^{(l-1)}, \dots, \lambda_{ji} a_{ji} N_i^{(l-1)}, \dots, \lambda_{jS^{(l-1)}} a_{jS^{(l-1)}} N_{S^{(l-1)}}^{(l-1)})$. The first term satisfies the inequality

$$\vec{f}_j \cdot \vec{g}_j \leq |\vec{f}_j| |\vec{g}_j| = |\vec{g}_j|, \tag{34}$$

and the equality holds only if

$$\vec{f}_j = \frac{\vec{g}_j}{|\vec{g}_j|} \tag{35}$$

or

$$f_{ji} = \frac{\lambda_{ji} a_{ji} N_i^{(l-1)}}{|\vec{g}_j|}. \tag{36}$$

If this is achieved, the growth rate (33) is maximized. Since the effort into a prey with vanishing population size vanishes (if other prey is present), we obtain

$$G_j^{(l)} \rightarrow |\vec{g}_j| - \alpha \tag{37}$$

for $N_j^{(l)} \rightarrow 0$.

In Fig. A.1, we show an example for the dynamics of a small system consisting of two predators, two preys and one resource with nonlinear and linear constraints. Four links are forbidden for the system with linear constraints (Matsuda and Namba, 1991; Matsuda et al., 1994, 1996), and here we obtain four links at the fixed point only in the case of nonlinear constraints. For Holling type II dynamics (12), we find a similar behaviour.

Table 1 shows that for models with nonlinear constraints there result always four links at the fixed point. The predators always feed on all their prey, albeit with a small rate if a prey population size is small.

Appendix B. Lotka-Volterra systems with other forms of competition

In the main body of this paper, we looked at the case where there is direct intraspecific competition but no interspecific competition. If the self competition β is set to be 0, we obtain a second set of inequalities in addition to (16), because the fixed point condition $G_j^{(l)} = 0$ is independent of $N_j^{(l)}$,

$$\sum_{i=1}^{S^{(l-1)}} \lambda_{ji} a_{ji} f_{ji} N_i^{(l-1)} - \sum_{k=1}^{S^{(l+1)}} a_{kj} f_{kj} N_k^{(l+1)} - \alpha = 0. \tag{38}$$

Since, the variables f_{jk} and $N_k^{(l+1)}$ appear only in the combination $f_{kj} N_k^{(l+1)}$ in Eq. (38), we can define new variables $x_{kj} := f_{kj} N_k^{(l+1)}$ and obtain

$$\vec{g}_j \sum_{i=1}^{S^{(l-1)}} f_{ji} - \sum_{k=1}^{S^{(l+1)}} a_{kj} x_{kj} - \alpha = 0, \quad \vec{g}_j - \sum_{k=1}^{S^{(l+1)}} a_{kj} x_{kj} - \alpha = 0 \tag{39}$$

for all prey i of species j . Thus, if we remember $\vec{g}_j = a_{ji} N_i^{(l-1)}$ for any i , we obtain a system of linear equations

$$a_{ji} N_i^{(l-1)} - \alpha - \sum_{k=1}^{S^{(l+1)}} a_{kj} x_{kj} = 0. \tag{40}$$

The variables in these equations are $N_i^{(l-1)}$ and x_{kj} . Hence, there are $S^{(l-1)} + \sum_{k=1}^{S^{(l+1)}} C_k^{(l+1)}$ variables and $\sum_{j=1}^{S^{(l)}} C_j^{(l)}$ linear equations. In order that the system has a nontrivial solution,

$$C^{(l)} \leq S^{(l-1)} + C^{(l+1)} \tag{41}$$

must hold. Especially, $C^{(L)} \leq S^{(L-1)}$ is valid for the top level L . Each species in level $L - 1$ will be eaten by at most one species.

If we replace the term $-\beta N_j^{(l)}$ in (5) with interspecific competition $-\sum_m \beta_{jm} N_m^{(l)}$, the condition (16) for the number of links does not change.

Appendix C. Fixed point for Holling type II

We write Eq. (12) in the form

$$G_j^{(l)} = \frac{S_j}{1 + T_j} - \sum_{k=1}^{S^{(l+1)}} \frac{a_{kj} f_{kj} N_k^{(l+1)}}{1 + T_k} - \alpha - \beta N_j^{(l)}. \tag{42}$$

where

$$S_j = \sum_{i=1}^{S^{(l-1)}} \lambda_{ji} a_{ji} f_{ji} N_i^{(l-1)} \quad \text{and} \quad T_j = \sum_{i=1}^{S^{(l-1)}} h_{ji} a_{ji} f_{ji} N_i^{(l-1)}.$$

The fixed point condition for adaptive dynamics is again

$$\frac{\partial G_j^{(l)}}{\partial f_{ji}} = \frac{\partial G_j^{(l)}}{\partial f_{j'}}$$
, $(f_{ji} \neq 0, f_{j'} \neq 0).$ (43)

This does not yield linear equations any more, because $G_j^{(l)}$ is nonlinear. By applying the chain rule $\partial G_j^{(l)} / \partial f_{ij} = (\partial G_j^{(l)} / \partial S_j)(\partial S_j / \partial f_{ij}) + (\partial G_j^{(l)} / \partial T_j)(\partial T_j / \partial f_{ij})$, we can explicitly represent Eq. (43) as

$$\left(\lambda_{ji} a_{ji} + \left(\frac{\partial G_j^{(l)} / \partial T_j}{\partial G_j^{(l)} / \partial S_j} \right) h_{ji} a_{ji} \right) N_i^{(l-1)} =: \bar{g}_j. \tag{44}$$

Using

$$\frac{\partial G_j^{(l)} / \partial T_j}{\partial G_j^{(l)} / \partial S_j} = - \frac{S_j}{1 + T_j}, \tag{45}$$

the fixed point condition of the population dynamics (42) gives

$$\frac{\partial G_j^{(l)} / \partial T_j}{\partial G_j^{(l)} / \partial S_j} = - \sum_{k=1}^{S^{(l+1)}} \frac{a_{kj} f_{kj} N_k^{(l+1)}}{1 + T_k} - \alpha - \beta N_j^{(l)}. \tag{46}$$

The right-hand side is a function of the $N_k^{(l+1)}$ and the $N_i^{(l)}$ alone, making Eq. (44) a linear equation in $N_i^{(l-1)}$. However, the population sizes of the higher levels cannot be fixed independently of those at the lower levels, and we obtain no constraint of the type (16). Only if $\beta = 0$ do we obtain a constraint for the top levels: The right-hand side of Eq. (46) is a constant if l is the top level, which leads to a linear set of Eqs. (44) and to the condition (16) for the number of links between the upper two levels.

Appendix D. Models with predator avoidance

D.1. Lotka-Volterra model with linear constraints

Let us now include predator avoidance in the behaviour of each species (Matsuda et al., 1994, 1996; Strauss et al., 2002, 2004; Lass and Spaak, 2002). Each species tries to maximize its growth rate by devoting some effort to reducing the probability of being caught by predators. The growth rate of population j in trophic level l is now

$$G_j^{(l)} = \sum_{i=1}^{S^{(l-1)}} \lambda_{ji} f_{ji} a_{ji} (1 - v_{ji}) N_i^{(l-1)} - \sum_{k=1}^{S^{(l+1)}} (1 - v_{jk}) a_{kj} f_{kj} N_k^{(l+1)} - \alpha - \beta N_j^{(l)}, \tag{47}$$

where v_{jk} represents the fraction of time that species j spends avoiding predator k . So f_{ji} and v_{jk} must be constrained by

$$\sum_{i=1}^{S^{(l-1)}} f_{ji} + \sum_{k=1}^{S^{(l+1)}} v_{jk} = 1. \tag{48}$$

Instead of Eq. (6) for the efforts, we have now combined equations for the foraging and avoidance behaviour,

$$\begin{aligned} \frac{df_{ji}(t)}{dt} &= \kappa f_{ji}(t) \left(\frac{\partial G_j^{(l)}}{\partial f_{ji}} - \left(\sum_i f_{ji} \frac{\partial G_j^{(l)}}{\partial f_{ji}} + \sum_k v_{jk} \frac{\partial G_j^{(l)}}{\partial v_{jk}} \right) \right) \\ \frac{dv_{jk}(t)}{dt} &= \kappa v_{jk}(t) \left(\frac{\partial G_j^{(l)}}{\partial v_{jk}} - \left(\sum_i f_{ji} \frac{\partial G_j^{(l)}}{\partial f_{ji}} + \sum_k v_{jk} \frac{\partial G_j^{(l)}}{\partial v_{jk}} \right) \right). \end{aligned} \tag{49}$$

The condition that the growth rate is maximized is given by

$$\begin{aligned} \frac{\partial G_j^{(l)}}{\partial f_{ji}} &= \frac{\partial G_j^{(l)}}{\partial f_{j'}} = \frac{\partial G_j^{(l)}}{\partial v_{jk}} \\ &= \frac{\partial G_j^{(l)}}{\partial v_{j'k}} =: \Gamma_j^{(l)}, \quad (f_{ji} \neq 0, f_{j'} \neq 0, v_{jk} \neq 0, v_{j'k} \neq 0) \end{aligned} \tag{50}$$

We should notice here that the growth rate $G_j^{(l)}$ is linear in f_{ji} and v_{jk} , leading to a relation between $G_j^{(l)}$ and $\Gamma_j^{(l)}$. Let the index $k = 1, \dots, S_j^{(l-1)}$ count the predators that are avoided by species j , and let m count the predators that are not avoided. Then, we have

$$\begin{aligned} G_j^{(l)} &= \sum_{i=1}^{S^{(l-1)}} f_{ji} \Gamma_j^{(l)} - \sum_{k=1}^{S_j^{(l+1)}} (1 - v_{jk}) \Gamma_j^{(l)} - \sum_{m=S_j^{(l+1)}+1}^{S^{(l+1)}} f_{mj} a_{mj} N_m^{l+1} - \alpha - \beta N_j^{(l)} \\ &= \left(\sum_{i=1}^{S^{(l-1)}} f_{ji} + \sum_{k=1}^{S_j^{(l+1)}} v_{jk} \right) \Gamma_j^{(l)} - \sum_{k=1}^{S_j^{(l+1)}} \Gamma_j^{(l)} \end{aligned}$$

$$\begin{aligned}
 & - \sum_{m=S_j^{(l+1)}+1}^{S^{(l-1)}} f_{mj} a_{mj} N_m^{l+1} - \alpha - \beta N_j^{(l)} = \Gamma_j^{(l)} - S_j^{(l+1)} \Gamma_j^{(l)} \\
 & - \sum_{m=S_j^{(l+1)}+1}^{S^{(l-1)}} f_{mj} a_{mj} N_m^{(l+1)} - \alpha - \beta N_j^{(l)} \tag{51}
 \end{aligned}$$

where $S_j^{(l+1)}$ is the total number of predators avoided by species j . It follows that the growth rate $G_j^{(l)}$ in the population dynamics (1) is always negative, unless no predators are avoided. Consequently, in computer simulations the avoidance variables always go to zero. This means that this simple implementation of predator avoidance does not work. If, however, we assume that foraging contributes to the growth rate in a nonlinear way,

$$\begin{aligned}
 G_j^{(l)} = B & \left(\sum_{i=1}^{S^{(l-1)}} \lambda_{ji} f_{ji} a_{ji} (1 - v_{ji}) N_i^{(l-1)} \right) \\
 & - \sum_{k=1}^{S^{(l+1)}} (1 - v_{jk}) a_{kj} f_{kj} N_k^{(l+1)} - \alpha - \beta N_j^{(l)} \tag{52}
 \end{aligned}$$

with $B(x) > x$, then we can obtain nonzero values of v_{jk} at the fixed point. This was, for instance, found in [Matsuda et al. \(1994\)](#), where a function $B(x) \propto \sqrt{x}$ for $x < 1$ was used.

D.2. Lotka-Volterra model with nonlinear constraints

If we take nonlinear constraints

$$\sum_{i=1}^{S^{(l-1)}} f_{ij}^2 + \sum_{k=1}^{S^{(l+1)}} v_{jk}^2 = 1, \tag{53}$$

then exactly as in the model without predator avoidance behaviour, the vector

$$\left(\dots, \frac{\partial G_j^{(l)}}{\partial f_{ji}}, \dots, \frac{\partial G_j^{(l)}}{\partial v_{jk}}, \dots \right) \tag{54}$$

must be parallel to the unit vector

$$(\dots, f_{ji}, \dots, v_{jk}, \dots). \tag{55}$$

when the growth rate $G_j^{(l)}$ is maximized. This means that each f_{ji} is proportional to $N_i^{(l-1)}$ and each v_{jk} is proportional to $N_k^{(l+1)}$, and we obtain nonvanishing values for the v_{jk} at the fixed point. This analytical result is confirmed in computer simulations.

D.3. Holling model with predator avoidance

Since, the analytical investigation becomes very complicated, we did not perform a thorough analysis of the Holling model with predator avoidance. However, it appears from computer simulations that in the case of linear constraints the avoidance

coefficients decrease to zero, while they can remain nonzero for nonlinear constraints.

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