

Omnivory can both enhance and dampen perturbations in food webs

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Abstract We investigate how perturbations propagate up and down a food chain with and without self-interaction and omnivory. A source of perturbation is a shift in death rate of a trophic level, and the measure of perturbation is the difference between the perturbed and unperturbed steady-state populations. For Lotka–Volterra food chains with linear functional response, we show analytically that both intraspecific competition and intraguild predation can either dampen or enhance the propagation of perturbations, thus stabilizing or destabilizing the food web. The direction of the effect depends on the position of the source of perturbation, as well as on the position of the additional competitive and predatory links. These conclusions are confirmed numerically for a food chain with more realistic type II functional response. Our results extend and confirm previous numerical results for short food chains and support positions on both sides in the long-standing debate on the effect of intraspecific competition and omnivory on the stability of trophic systems.

Keywords Omnivory · Stability · Competition · Food webs · Lotka–Volterra

Introduction

Food web stability is a topic with a tremendous scientific and practical significance (Bascompte et al. 2005; Dunne et al. 2002; Dunne 2006; Fowler and Lindström 2002; Herendeen 2004; Pimm 2002; Pimm and Lawton 1977; Quince et al. 2005). A large number of both theoretical and experimental studies have addressed the question of how the stability of a food web depends on its structure and, specifically, on the presence of omnivory (see e.g., Diehl and Feibel 1999; Fagan 1997; Holt and Polis 1997; Holyoak and Sachdev 1998; McCann and Hastings 1997; Pimm and Lawton 1977; Rudolf 2007; Vandermeer 2006, just to mention a few). Omnivory, defined broadly as feeding on more than one trophic level, which generally includes cannibalism, is a common phenomenon in natural communities (Rosenheim 2007; Rudolf 2007). However, a consensus on the effect of omnivory on food web stability is still lacking. Thus, according to some results from mathematical food web theory, omnivory destabilizes ecological communities (Holt and Polis 1997; Pimm and Lawton 1977), whereas other models and experiments suggest that omnivory should be a strongly stabilizing factor in food webs (Fagan 1997, HilleRisLambers et al. 2006; Holyoak and Sachdev 1998; McCann and Hastings 1997). In Vandermeer (2006), it was observed that, depending on the parameters of the model, omnivory can either promote or prevent extinction of species in a three-species model and hence can have both stabilizing and destabilizing effects. In general, in the context of food webs, the notion of “stability” itself is broadly understood: The most common examples include a scarcity of secondary extinction events in response to removal or a shift in birth or death rate

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of a species (Fowler and Lindström 2002), temporal characteristics of a return to a new equilibrium following such removal (Fagan 1997), the mere existence of locally stable steady states (McCann and Hastings 1997; Vandermeer 2006), and a global permanency of food web dynamics (Law and Blackford 1992; McCann and Hastings 1997).

In addition to this apparent lack of consensus on how food web structure affects stability, it seems that there still exist fundamental questions related to the effect of omnivory on food web stability which have remained unanswered and, even more, not specifically formulated. For example, in many practical situations, a population at a certain position in a food web is harvested on a fairly permanent basis (for example, by fishing). Alternatively, reproductive rates or death rates of some species may shift due to environmental changes, endemics, etc. Such long-term removal (or possibly, addition, Diehl and Feibel 1999) of a resource from a certain trophic level naturally affects populations of the other levels in the food web. Generally, such removal may lead to extinction of certain species and to destabilization of initially steady-state population dynamics in the food web. However, if the initial or unperturbed network is sufficiently stable, a continuous harvesting within certain limits may often result, after some transient behavior, in constant shifts in population of other trophic levels, bringing the whole food web to a new steady state. The susceptibility of the steady state food web populations, or the difference between the new and old, unperturbed steady states, is another characteristic of the stability of food webs with respect to shifts in death or birth rates or harvesting. This new characteristic has an evident practical significance. For example, it is interesting and important to determine “sustainable” levels of harvesting that produce a limited effect on the rest of the food web and on the harvested level itself. Intuitively, it is clear that such a susceptibility-based definition of stability is related to previously used definitions because a food web that is less susceptible to harvesting is less likely to leave a basin of attraction of a fixed point, a permanence domain, or suffer an extinction.

As with other definitions of stability, susceptibility of a food web to long-term removal of resource from a certain trophic level depends on the position of this level in the web, predation strengths, and natural death rates. The induced population shifts also depend on the structure (topology) of the food web and, specifically, on the presence, position, and strength of omnivory interactions. This leads to the formulation of the main question we address in this paper: How is the effect of the steady removal of a population of a certain level

on the rest of the foodweb mediated by the presence of omnivory and self-interaction? In other words, we compare the steady-state response of two model food webs, with and without omnivory trophic relations, to a shift of a death rate of a certain trophic level. When the response of the food web in the presence of omnivory is less pronounced than without it, omnivory is considered to be a stabilizing factor. Conversely, when the induced changes in population densities are greater with omnivory than without, omnivory is considered destabilizing. To analyze this question in its most isolated and fundamental form, we focus on the topologically simplest form of a food web, a linear food chain. Also, our principle analysis deals with the most basic form of predator–prey interactions, i.e., with Lotka–Volterra models with linear functional responses, which turn out to be analytically tractable. Harvesting of a certain species is modeled as an introduction of a certain per capita rate of removal, which effectively modifies the death rate of the corresponding species in the food web. We consider two possible forms of omnivory added to linear food chains. First, we consider competition, or a negative self-interaction, at a certain trophic level, which is modeled as an additional per capita death rate term proportional to the population density at this level. This can be thought of as omnivory because it is mathematically equivalent to cannibalism with a linear functional response. Second, we consider intraguild predation, which we define as a “shortcut” trophic link introducing an additional predator–prey interaction between two nonadjacent trophic levels.

Our conclusions confirm both existing viewpoints regarding stability and food web structure (and hence support neither as an overarching principle): Both intraspecific competition and intraguild predation can either stabilize or destabilize a food chain. Our observations also confirm and extend the results of Vandermeer (2006), who showed that omnivory can both promote and prevent extinction of a food web level. Whether stabilization or destabilization occurs depends on the relative position of the level at which the food web is perturbed on the one hand and where the additional interaction links are introduced on the other hand. We also show numerically that both stabilizing and destabilizing effects of omnivory, derived analytically for Lotka–Volterra systems, qualitatively hold for food chains with more realistic, nonlinear functional responses.

The paper is organized as follows: In the next section, we define the framework of our food web study, which is based on systems of coupled Lotka–Volterra equations, and find the steady state solution for the population densities at all levels of the food chain. Next, we

consider the effect on the steady state induced by a shift of a death rate of a given trophic level and determine how this perturbation spreads over the food chain. We then derive how competition, or self-interaction, at a certain trophic level, modify the steady state of a food chain, and consider the effect of such self-interaction on the spread of perturbation induced by a shift in a death rate. We show that depending on the position of self-interacting and death-rate modified levels, self-interaction may inhibit or enhance such propagation. Then the same analysis is repeated for omnivory links, and we present two examples of how such a link inhibits and enhances spread of perturbation. In the discussion, we present examples of quantitative similarities between the effects of omnivory and self-interactions in food chains with type II functional responses food chain and our results for the Lotka–Volterra systems. We also illustrate how our results can be applied to more topologically complex food webs. The “Appendix 1” contain the description of a model with type II functional responses in the presence of omnivory links.

Linear Lotka–Volterra chain

We consider a linear food chain with nearest neighbor predator–prey interactions of Lotka–Volterra form. We do not limit ourselves to a specific number of levels in the chain and label the basal level by 0 and the highest predator by n . The rate of change of the population density $x_k(t)$ of trophic level k (which will also be called “species” k) is given by

$$\frac{dx_k}{dt} = x_k [\lambda_k a_{k,k-1} x_{k-1} - a_{k+1,k} x_{k+1} - d_k]. \quad (1)$$

Here $a_{i,j}$ determines the strength of predation of species i on species j , λ_k is the conversion efficiency which connects the birth rate of species k to the amount of other it consumes, and d_k is the per capita death rate of species k . Evidently, the top predator, occupying the n th level, does not have any species that prey on it, which could be expressed by setting $x_{n+1} \equiv 0$. In addition, the basal species, occupying the lowest (zeroes) trophic level, is characterized by a logistic growth term, which mimics the finite input of energy into the system, given in the form of a finite carrying capacity K for the basal species. Without loss of generality, the linear death term for the basal species can be absorbed into the linear part of the birth term β , which yields

the following for the rate of change of the population density of the basal species:

$$\frac{dx_0}{dt} = x_0 \left[\beta \left(1 - \frac{x_0}{K} \right) - a_{1,0} x_1 \right]. \quad (2)$$

We look for a steady-state solution of this system, $d\bar{x}^*/dt = 0$, which is defined by the following system of linear equations:

$$x_{k-1}^* = x_{k+1}^* \frac{a_{k+1,k}}{\lambda_k a_{k,k-1}} + \frac{d_k}{\lambda_k a_{k,k-1}} \quad (3)$$

Recurrence relations of the form $x_k^* = F(x_{k+2}^*)$ given by Eq. 3 indicate that in the steady state, the Lotka–Volterra food chain splits into two subsets or partitions: The steady state of even-numbered levels depends only on another even number level and a set of constants, and similarly, odd-number levels are coupled only to odd number levels. To solve the system Eq. 3, one needs to consider the closing equations which describe the steady-state populations of the top and bottom levels. Because the dynamics of the top predator population depends only on x_{n-1} , the first closing equation (or the boundary condition for the recurrence relation Eq. 3) defines the population of the $n - 1$ level,

$$x_{n-1}^* = \frac{d_n}{\lambda_n a_{n,n-1}}. \quad (4)$$

Consequently, sequential application of recurrence Eq. 3 allows one to determine the populations of lower levels of the same parity as $n - 1$, down to level one or zero. The second boundary condition,

$$x_1^* = \frac{\beta}{a_{1,0}} \left(1 - \frac{x_0^*}{K} \right), \quad (5)$$

which follows from the stationarity of the basal population, connects the populations of levels one and zero, thus linking the even and odd partitions. Finally, applying Eq. 3 upstream, or expressing x_{k+1}^* through x_{k-1}^* , we determine the steady-state populations of levels of the same parity as n . Thus, Eqs. 3, 4, and 5 define the stationary solution of the whole Lotka–Volterra food chain: The recurrence starts from the $n - 1$ th level, descends to level one or zero depending on the parity of n , and then ascends to the top predator level n . This is illustrated schematically in Fig. 1.

In the following, we will widely use this natural separation of the food chain into two partitions: The regression in the “descending”, or “ $\{n - 1\}$ ” partition, starts from the $n - 1$ st level and goes down along the indexes of the same parity as $n - 1$ to level one or zero, depending on whether n is even or odd. It is important to note that the steady-state population of a level of the descending partition is determined only by the level

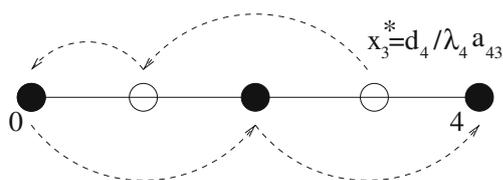


Fig. 1 Direction of recurrence for finding the steady-state populations x_k^* in a five-level (0–4) Lotka–Volterra linear chain. The solution starts with finding the population of the second from the top level, x_3^* , and is propagated downward so that x_1^* is determined via Eq. 3. Then, x_0^* is determined using the Eq. 5, and the recursion is propagated upward to determine x_2^* and x_4^* . Here and below the levels of $\{n\}$ (or ascending) partition are shown as *black circles* and the levels belonging to the $\{n - 1\}$ (or descending) partition are shown as *white circles*

immediately above it in the same partition. Conversely, the regression in the “ascending”, or “ $\{n\}$ ” partition, which spans indexes of the same parity as n , starts from zero or one and goes up to n . The population density of a given level in the ascending partition depends only on the population of its lower nearest neighbor in the same partition.

Assuming for simplicity equality of the predation intensities, $a_{ij} = a$, conversion coefficients, $\lambda_i = \lambda$, and death rates, $d_i = d$, it is possible to express the general solution for the steady-state populations in a compact form. The system of equations for the steady-state populations (Eq. 3) becomes

$$\lambda x_{k-1}^* = x_{k+1}^* + \frac{d}{a}. \tag{6}$$

The notation

$$y_k = x_k^* \lambda^{-k/2} a/d, \tag{7}$$

reduces the recurrence relation Eq. 6 to

$$y_{k-1} = y_{k+1} + \lambda^{-(k+1)/2}.$$

Thus, y_k can be expressed as a sum of a geometric progression, and the general solution for arbitrary i and k reads

$$x_{k+2i}^* = \lambda^i x_k^* - \frac{d}{a} \frac{1 - \lambda^i}{1 - \lambda}. \tag{8}$$

The first boundary condition defines the population of the $n - 1$ level,

$$x_{n-1}^* = \frac{d}{\lambda a}, \tag{9}$$

and, via Eq. 8, the populations of the levels of the $\{n - 1\}$ partition. The second boundary condition links $\{n\}$ to $\{n - 1\}$ partitions,

$$x_1^* = \frac{\beta}{a} \left(1 - \frac{x_0^*}{K} \right), \tag{10}$$

and yields the full explicit form of the stationary-state populations. For example, for odd n ,

$$x_{2k}^* = \frac{d}{a} \frac{\lambda^{k-(n+1)/2} - 1}{1 - \lambda}$$

$$x_{2k+1}^* = \frac{\beta \lambda^k}{a} \left(1 - \frac{x_0^*}{K} \right) - \frac{d}{a} \frac{1 - \lambda^k}{1 - \lambda} \tag{11}$$

In the following, we denote, where possible, the levels of the $\{n - 1\}$ partition as i and levels of the $\{n\}$ partition as j . It also follows from Eq. 11 that for a given set of rate constants, the maximum length of the chain is finite and limited by the requirements that the descending partition does not exceed the carrying capacity even at its maximum, $x_0^* < K$ and the ascending partition does remain positive even at its minimum, $x_n^* > 0$.

Perturbations caused by shifts in the death rate of a single level

Now we consider how changes of conditions at a certain trophic level affect the steady-state populations of all levels of the Lotka–Volterra food chain. We assume the simplest form of a perturbation equivalent to imposing a certain probability per unit time ϵa for each individual inhabiting the level p to be removed from the population. This can be taken into account by modifying the death rate coefficient, $d'_p = d_p + \epsilon a$ (the factor a is introduced for further convenience).

We now investigate how such a shift in death rate of the level p affects the steady-state population of all levels, or, in other words, how the perturbed steady-state populations x'_k are different from the unperturbed ones x_k^* . For simplicity in the following, we will assume that predation intensities and conversion coefficients are constant for all levels, $a_{ij} = a$ and $\lambda_i = \lambda$. Evidently, the shift in a death rate affects only the levels in the direction of recurrence from the perturbed site p . That is, if a level of the $\{n\}$ partition is perturbed (so that $p \in \{n\}$), the perturbation first manifests itself at the $p - 1$ level, while x_{p+1}^* and populations of higher levels of the $\{n - 1\}$ partition remain unaffected. It follows from Eq. 6 that

$$\lambda x'_{p-1} = x_{p+1}^* + \frac{d_p}{a} + \epsilon, \tag{12}$$

and

$$x'_{p-1} = x_{p-1}^* + \frac{\epsilon}{\lambda}. \tag{13}$$

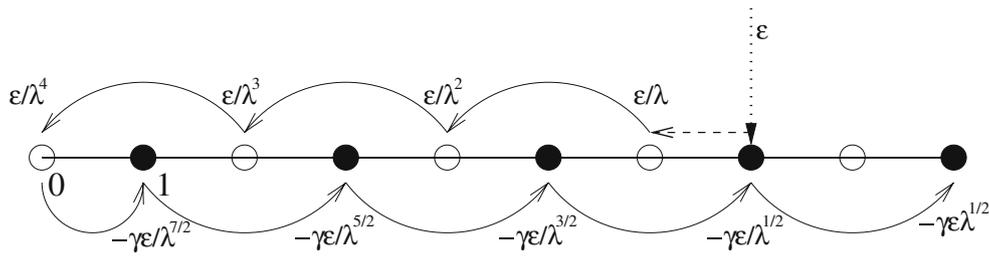


Fig. 2 Propagation of perturbation caused by a shift by ϵa of the death rate of a level belonging to the $\{n\}$ partition; the recurrence relation Eq. 12, perturbed by the shift in death rate, is shown by a dashed arc. The resulting spread of perturbation is shown by

solid line arcs. The numbers above and below vertices indicate the change in the population of the corresponding trophic level induced by the perturbation

Consequently, the perturbation propagates down the food chain to the zeroth level if n is odd and to first level if n is even,

$$x'_i = x_i^*, \quad i > p; \quad x'_i = x_i^* + \frac{\epsilon}{\lambda^{(p+1-i)/2}}, \quad i < p. \quad (14)$$

Then at the basal level, due to the second boundary condition (Eq. 5), the perturbation changes sign,

$$x'_1 = x_1^* - \frac{b}{aK} \frac{\epsilon}{\lambda^{(p+1)/2}} \quad (15)$$

for odd p and n , and

$$x'_0 = x_0^* - \frac{aK}{b} \frac{\epsilon}{\lambda^{p/2}} \quad (16)$$

for even p and n . For the $\{n\}$ partition, the “ascending” regression yields

$$x'_j = x_j^* - \gamma^\psi \frac{\epsilon}{\lambda^{(p-j+1)/2}} \quad (17)$$

Here, we introduced a universal notation for odd and even n ,

$$\gamma \equiv \frac{b}{a\sqrt{\lambda}K}; \quad (18)$$

with $\psi = 1$ for odd n and $\psi = -1$ for even n . Thus, when the death rate of a species in $\{n\}$ partition is increased, the population of the levels of $\{n - 1\}$ partition lying below p increases, while the population of all levels of the $\{n\}$ partition, including the perturbed level p , decreases.

Similarly, when the death rate of the level $p \in \{n - 1\}$ is shifted, the perturbation propagates recurrently upward from $j = p + 1$,

$$x'_i = x_i^*, \quad x'_j = x_j^*, \quad j < p, \quad x'_j = x_j^* - \epsilon \lambda^k, \quad j = p + 1 + 2k. \quad (19)$$

In this case, the $\{n - 1\}$ partition, including the directly affected level p , remains unperturbed, while the population of the levels of $\{n\}$ partition that are above p is decreased.

We illustrate the propagation of perturbations in a linear Lotka–Volterra food chain in Figs. 2 and 3.

Self-interaction

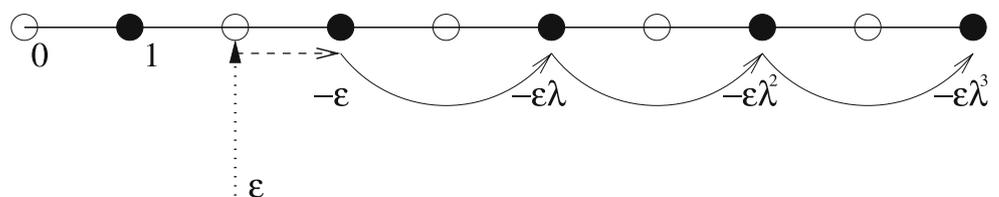
Self-interaction at level s in a linear food chain is taken into account by adding $-\alpha ax_s^2$ to the right-hand side of the rate equation for x_s ,

$$\frac{dx_s}{dt} = x_s [\lambda ax_{s-1} - ax_{s+1} - d - \alpha ax_s]. \quad (20)$$

Here, α defines the intensity of self-interaction, relating it to the intensity of predation a . As mentioned, the self-interaction can be thought of as either competition or cannibalism. As a consequence of self-interaction, the s th equation for the steady-state population is modified to

$$\lambda x_{s-1} = x_{s+1} + \frac{d}{a} + \alpha x_s. \quad (21)$$

Fig. 3 Propagation of perturbation caused by a shift by ϵa of the death rate of a level belonging to the $\{n - 1\}$ partition; notations and symbols are the same as in Fig. 2



Thus, similarly to the case of death rate shift, the self-interaction of a level s of one partition affects the population of those levels of the opposite partition which are recursively downstream from the perturbation site, that is, $s - 1$ if $s \in \{n\}$ and $s + 1$ if $s \in \{n - 1\}$. We denote δx_k the change to the steady-state population induced by a self-interaction, so that the new populations in system with self-interaction are $x_k^* + \delta x_k$. Then, from Eq. 20,

$$\lambda \delta x_{s-1} = \delta x_{s+1} + \alpha(x_s^* + \delta x_s). \tag{22}$$

The unperturbed steady-state populations x_k^* are given by Eq. 11.

There are two principal cases:

- $s \in \{n\}$. Here, self-interaction directly affects the $s - 1$ level,

$$\lambda \delta x_{s-1} = \alpha(x_s^* + \delta x_s), \tag{23}$$

and recursively affects all lower levels $i < s - 1$ of the $\{n - 1\}$ partition,

$$\lambda \delta x_{i-2} = \delta x_i \tag{24}$$

and all levels j of the $\{n\}$ partition,

$$\lambda \delta x_j = \delta x_{j+2} \tag{25}$$

From the boundary condition 10 and regressions 24 and 25, it follows that

$$\delta x_s = -\gamma^\psi \sqrt{\lambda} \delta x_{s-1}. \tag{26}$$

Thus,

$$\delta x_i = \frac{\alpha x_s^*}{(1 + \alpha \gamma^\psi / \sqrt{\lambda}) \lambda^{(s+1-i)/2}} \tag{27}$$

for $i < s$, and

$$\delta x_j = -\gamma^\psi \frac{\alpha x_s^*}{(1 + \alpha^*) \lambda^{(s+1-j)/2}} \tag{28}$$

for any j . We denote by $\alpha^* \equiv \alpha \gamma^\psi / \sqrt{\lambda}$, a frequently occurring group of parameters which is proportional to α .

- $s \in \{n - 1\}$. Here, self-interaction directly affects the $s + 1$ level and recursively affects only the higher levels of the same $\{n\}$ partition. Hence,

$$\delta x_j = -\alpha \lambda^{(j-s-1)/2} x_s^*, \quad j > s \tag{29}$$

Thus, a self-interaction in $\{n\}$ partition increases the population of the lower levels of the $\{n - 1\}$ partition but decreases the population of all levels in $\{n\}$ partition. A self-interaction in $\{n - 1\}$ partition decreases the population of the higher levels of $\{n\}$ partition and does not affect the $\{n - 1\}$ partition.

Death rate shifts with self-interactions

Having established how perturbations induced by a shift in a death rate propagate in the linear Lotka–Volterra chain and how the linear chain is affected by self-interaction, we now consider the first of our two principal questions: How does self-interaction affect the propagation of perturbations? Specifically, we would like to know if self-interaction stabilizes the system by reducing the amplitude of perturbations induced by a shift of death rate, or, on the contrary, whether self-interaction destabilizes the system by increasing this amplitude. We denote by Δx_k the change in the steady-state population of level k resulting from the death rate shift $d'_p = d + \epsilon a$ in a chain with self-interaction of the form given by the Eq. 20 at the level s . We are interested only in the terms that vanish when the death rate shift is zero; thus, Δx_k does not contain ϵ -independent terms proportional to x_s^* . Formally, the recurrent relation for Δx_k follows from Eqs. 12 and 22),

$$\lambda \Delta x_{k-1} = \Delta x_{k+1} + \delta_{k,p} \epsilon + \delta_{k,s} \alpha \Delta x_k, \tag{30}$$

where Kronecker’s delta-symbol $\delta_{i,j} = 1$ for $i = j$ and $\delta_{i,j} = 0$ when $i \neq j$. Since death rate shifts and self-interaction can occur at levels belonging to any of the two partitions, there are four classes of scenarios. It turns out that among these four scenarios there are two examples of a stabilizing effect of a self-interaction, one of a destabilizing effect, and one of an absence of any effect on stability.

- Both the perturbed level p and the self-interaction level s are located in the ascending $\{n\}$ partition, Fig. 4. First consider the case when $p > s$. For $i > s$, the levels experience only the effect of the death rate perturbation and Δx_i is given by Eq. 14. For the $s - 1$ st level, Eq. 30 reads

$$\lambda \Delta x_{s-1} = \Delta x_{s+1} + \alpha \Delta x_s, \tag{31}$$

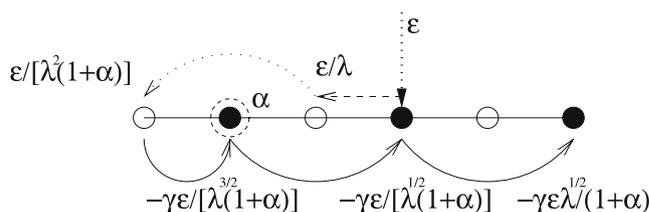


Fig. 4 The effect of self-interaction at level 1 (shown by a large dashed circle) on propagation of perturbation caused by a shift by ϵa of the death rate at level 3; both self-interacting and perturbed levels belong to the $\{n\}$ partition. The recurrence relation modified by self-interaction (Eq. 21) is shown by a dotted arc

where $\Delta x_{s+1} = \epsilon/\lambda^{(p+s)/2}$ from Eq. 14. Similarly to Eqs. 27 and 28, we express Δx_s through Δx_{s-1} and obtain for $i < s$

$$\Delta x_i = \frac{\epsilon}{(1 + \alpha^*)\lambda^{(p+1-i)/2}}, \tag{32}$$

and

$$\Delta x_j = -\gamma^\psi \frac{\epsilon}{(1 + \alpha^*)\lambda^{(p+1-j)/2}} \tag{33}$$

for any j . Now we consider the case when $p < s$. Then self-interaction enters the recurrence relation first,

$$\lambda \Delta x_{s-1} = \alpha \Delta x_s. \tag{34}$$

The equation for the level with a shifted death rate becomes

$$\lambda \Delta x_{p-1} = \frac{\alpha \Delta x_s}{\lambda^{(s-p)/2} + \epsilon} \tag{35}$$

Expressing Δx_s through Δx_{p-1} using the boundary condition at the base of the chain, we obtain

$$\Delta x_{p-1} = \frac{\epsilon}{(1 + \alpha^*)\lambda} \tag{36}$$

Consequently, the results for $i < p$ and all j are given by Eqs. 32 and 33. Thus, we observe that when both the perturbed and self-interaction levels belong to the $\{n\}$ partition, self-interaction weakens the effect of death rate shift on other levels and therefore has a stabilizing effect.

- The perturbed level p belongs to the ascending $\{n\}$ partition and the level of self-interaction s belongs to the descending $\{n-1\}$ partition (Fig. 5). If $p < s$, no joint effect occurs as the self-interacting level remains unperturbed by the death rate shift. However, in the opposite case of $p > s$, $\Delta x_i = \epsilon/\lambda^{(p+1-i)/2}$, $i < p$, see Eq. 14, and $\Delta x_j = -\gamma^\psi \epsilon/\lambda^{(p-j+1)/2}$, $j < s$, see Eq. 17. For $j > s$, the

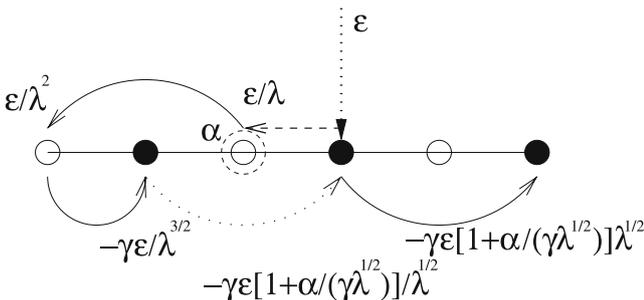


Fig. 5 The effect of self-interaction at level 2 of the $\{n-1\}$ partition with a perturbation caused by a shift of the death rate at level 3 of the $\{n\}$ partition

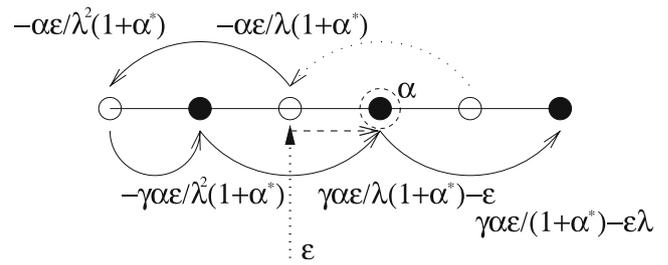


Fig. 6 The effect of self-interaction at level 3 of the $\{n\}$ partition when perturbation is caused by a shift of the death rate at level 2 of the $\{n-1\}$ partition

effect of self-interaction simply adds to the effect of perturbation,

$$\Delta x_j = -\gamma^\psi \frac{\epsilon}{\lambda^{(p-j+1)/2}} \left(1 + \frac{\alpha}{\gamma^\psi \lambda^{1/2}} \right). \tag{37}$$

Here, we observe that self-interaction enhances the effect of perturbation and hence is destabilizing.

- The perturbed level p belongs to the $\{n-1\}$ partition and the level of self-interaction s belongs to the $\{n\}$ partition (Fig. 6). There is no joint effect when $p > s$. When $p < s$, the correction to the $j > p$ levels of $\{n\}$ partition, including the level s , comes both self-interaction and shift of death rate. Hence, similarly to Eq. 27, we write for the $i < s$ levels of $\{n-1\}$ partition

$$\Delta x_i = -\frac{\alpha\epsilon}{1 + \alpha^*} \lambda^{(i-p)/2-1}, \tag{38}$$

and, similarly to Eq. 28, for $j < p$ levels of $\{n\}$ partition

$$\Delta x_j = \gamma^\psi \frac{\alpha\epsilon}{1 + \alpha^*} \lambda^{(j-p)/2-1}. \tag{39}$$

For $j > p$, a direct correction from the death rate shift is added,

$$\Delta x_j = \gamma^\psi \frac{\alpha\epsilon}{1 + \alpha^*} \lambda^{(j-p)/2-1} - \epsilon \lambda^{(j-p-1)/2}. \tag{40}$$

Thus, the self-interaction dampens the propagation of perturbations and stabilizes the system.

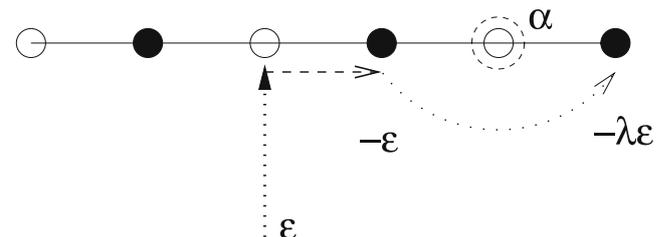


Fig. 7 The effect of self-interaction at level 3 of the $\{n\}$ partition when perturbation is caused by a shift of the death rate at level 2 of the $\{n-1\}$ partition

Table 1 Qualitative summary of the effect of self-interaction

	$s \in \{n\}$	$s \in \{n - 1\}$
$p \in \{n\}$	Dampens	Enhances
$p \in \{n - 1\}$	Dampens	No effect

- Finally, both the perturbed level p and self-interaction level s are located in the descending ($\{n - 1\}$) partition (Fig. 7). In this case, no joint effect of perturbation and self-interaction occurs since the descending partition levels remain unperturbed and do not add any terms depending on ϵ through self-interaction.

A qualitative summary of the effect of self-interaction on propagation of perturbations is presented in the Table 1.

Omnivory shortcuts

Here, we address the second principal question of our study: How does an intraguild trophic relation, or a predator–prey interaction connecting two nonadjacent trophic levels, affect the spread of perturbations in the food chain (where we again consider perturbation induced by shifting the p -level death rate)? A shortcut trophic link connects what we call an upper level u to a lower level w , $u - w \geq 2$. As in the self-interaction case, we would like to know if such an omnivory link stabilizes the system by reducing the perturbations induced by shifts in death rates. The shortcut link modifies the rate equations for the u level by adding a gain term

$$\alpha \chi \alpha x_w x_u$$

and for the w level by adding a loss term

$$-\alpha \alpha x_w x_u.$$

As in the case of self-interaction, the dimensionless factor α defines the intensity of a shortcut relative to regular predation. The gain term has a conversion factor χ which is distinct from λ since preying across several trophic level can have different efficiency in terms of the birth rate of the predator, compared to preying on the next nearest level below. The u th and w th equations for the stationary concentrations are modified accordingly,

$$\begin{aligned} \lambda x_{u-1} &= x_{u+1} + \frac{d}{a} - \chi \alpha x_w, \\ \lambda x_{w-1} &= x_{w+1} + \frac{d}{a} + \alpha x_u \end{aligned} \tag{41}$$

As in the case of self-interactions, it follows that the omnivory link between u and w directly affects the population of the levels that are recursively downstream from u and w . Similarly to the self-interaction case, we denote corrections to the population steady states resulting from the effect of a death rate shift on a food chain with shortcuts by Δx_k . A formal recursion equation for Δx_k , analogous to Eq. 30 reads

$$\lambda \Delta x_{k-1} = \Delta x_{k+1} + \delta_{k,p} \epsilon + \delta_{k,w} \alpha \Delta x_u - \delta_{k,u} \chi \alpha \Delta x_w \tag{42}$$

Since the perturbed level, the upper level of a shortcut, and the lower level of the shortcut can belong to either $\{n\}$ or $\{n - 1\}$ partition, there exist $2^3 = 8$ distinct scenarios. Below we present detailed analysis for two examples of enhancement and dampening of perturbations by a shortcut. The analysis of the remaining six scenarios is straightforward and yields additional stabilizing and destabilizing examples.

Example of destabilization

We consider a case where all three levels p, u, w belong to the $\{n\}$ partition, as illustrated in Fig. 8. Let us first assume that the death rate shift occurred at $p > u$. The corrections to population induced by the omnivory link depend on Δx_u and Δx_w , which, in their turn, could be expressed through x_{w-1} via the relation 26 linking both partitions.

$$\Delta x_w = -\gamma^\psi \sqrt{\lambda} \Delta x_{w-1}; \quad \Delta x_u = \lambda^{(u-w)/2} \Delta x_w. \tag{43}$$

On the other hand, Δx_{w-1} depends on Δx_w directly (see Eq. 42 for $k = w$) and on Δx_{u-1} recurrently through Δx_{w+1} . Δx_{u-1} in turn directly depends on Δx_u via Eq. 42 for $k = u$, and recurrently through Dx_{u+1} , which depends on the death rate shift at p . Putting together

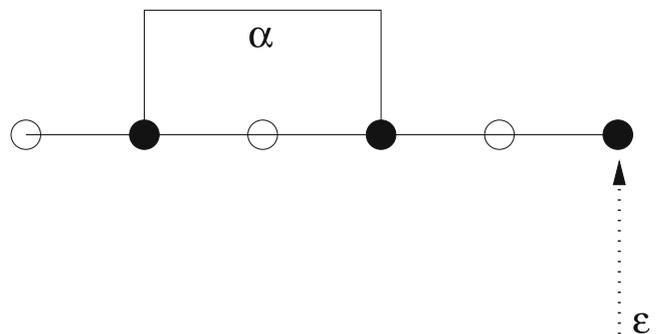


Fig. 8 The effect of omnivory interaction between levels $u = 3$ and $w = 1$ on the propagation of a perturbation caused by a shift by ϵa of the death rate at level $p = 5$; all these three levels $\{u, w, p\}$ are in $\{n\}$ partition

all these dependencies yields an equation for Δx_{w-1} and Δx_w ,

$$\Delta x_{w-1} = \epsilon \lambda^{(w-p-2)/2} + \frac{\Delta x_w \alpha}{\lambda} (\lambda^{(u-w)/2} - \chi \lambda^{(w-u)/2}). \tag{44}$$

Combining Eqs. 43 and 44 produces an expression for the population correction $i < w$,

$$\Delta x_i = \frac{\epsilon \lambda^{(i-p-1)/2}}{1 + \alpha^* (\lambda^{(u-w)/2} - \chi \lambda^{(w-u)/2})}, \tag{45}$$

and, via Eq. 26, for any j ,

$$\Delta x_j = -\gamma^\psi \frac{\epsilon \lambda^{(j-p-1)/2}}{1 + \alpha^* (\lambda^{(u-w)/2} - \chi \lambda^{(w-u)/2})}, \tag{46}$$

For $w < i < u$, only the u and p levels affect the population perturbation, so that,

$$\Delta x_i = \frac{\epsilon \lambda^{(i-p-1)/2}}{1 - \alpha^* \chi \lambda^{(w-u)/2}}, \tag{47}$$

and for $i > u$, no effect of the omnivory link is present. These results hold for arbitrary positions of the death rate-shifted level p with respect to u and w : Once $p \in \{n\}$, all $\{n\}$ partition levels, including u and w , are perturbed. The only difference with the above case occurs when $p < i$. In this case, the direct effect of death rate perturbation $\epsilon \lambda^{(i-p-1)/2}$ should be subtracted from Δx_i defined via Eqs. 45 and 47. It follows from Eqs. 45 and 46 that the sign of the effect depends on the values of λ and χ . In a common scenario with $\lambda < 1$ and $\chi \approx \lambda$, the effect of the omnivory link at the $i < w$ and all j levels is destabilizing: The perturbation induced by a shift in death rate is enhanced in the presence of the omnivory link. However, the strongest enhancement or destabilization, which is universal and manifests itself for arbitrary λ and χ , occurs for the $w < i < u$ levels of the $\{n-1\}$ partition, Eq. 47. In the idealized case with $\lambda = \chi = 1$, the two terms in brackets in the denominators of Eqs. 45 and 46 cancel each other, so that the destabilizing effect of the omnivory can be seen only at the levels with $w < i < u$.

Example of stabilization

Here, we consider a case where the omnivory link connects a level u of the $\{n\}$ partition to a level w of the $\{n-1\}$ partition, while the death rate perturbation occurs at a level p of the $\{n\}$ partition, as illustrated in Fig. 9. First consider the case when $p > u$. From Eq. 42, it follows that

$$\Delta x_{u-1} = \epsilon \lambda^{u_j-p-2)/2} - \Delta x_w \alpha \chi / \lambda \tag{48}$$

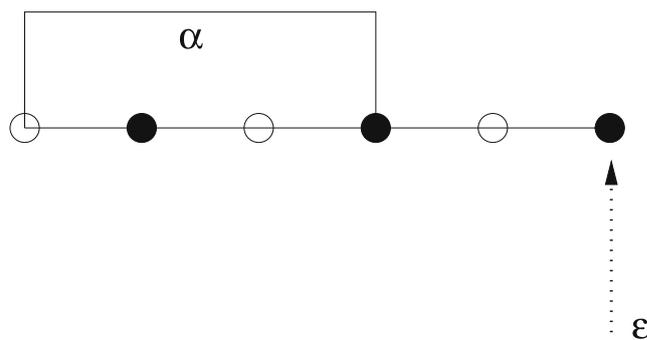


Fig. 9 The effect of the omnivory interaction between levels $u = 3$ of the $\{n\}$ partition and $w = 0$ of the $\{n-1\}$ partition on propagation of perturbation caused by a shift by ϵa of the death rate at level $p = 5$, which belongs to the $\{n\}$ partition

Taking into account that Δx_w is related to Δx_{u-1} via a simple recurrence,

$$\Delta x_w = \Delta x_{u-1} \lambda^{(w-u+1)/2},$$

one obtains for $i < u$

$$\Delta x_i = \frac{\epsilon \lambda^{i-p-1)/2}}{1 + \alpha \chi \lambda^{(w-u-1)/2}} \tag{49}$$

Consequently, for $j < w$, the perturbation is a simple recurrent continuation of Eq. 49,

$$\Delta x_j = -\frac{\epsilon \gamma^\psi \lambda^{j-p-1)/2}}{1 + \alpha \chi \lambda^{(w-u-1)/2}}. \tag{50}$$

For Δx_{w+1} , it follows from Eq. 41 that

$$\lambda \Delta x_{w-1} = \Delta x_{w+1} + \alpha \Delta x_u = \Delta x_{w+1} (1 + \alpha \lambda^{(u-w-1)/2}). \tag{51}$$

Hence, for $j > w$

$$\Delta x_j = -\frac{\epsilon \gamma^\psi \lambda^{j-p-1)/2}}{(1 + \alpha \chi \lambda^{(w-u-1)/2}) (1 + \alpha \lambda^{(u-w-1)/2})}. \tag{52}$$

A similar scenario occurs when $w < p < u$; to get the population corrections, one needs to subtract the direct effect of the death rate shift $\epsilon \lambda^{(i-p-1)/2}$ from the corrections Δx_i given by Eq. 49 for $i > p$. When $p < w$, there is no effect of the shortcut on the propagation of perturbation in the $\{n-1\}$ partition and the lower part, $j < w$, of the $\{n\}$ partition. However, for $j > w$, the shortcut does have an effect on perturbation amplitude, which is expressed by the second term in the denominator of Eq. 52,

$$\Delta x_j = -\frac{\epsilon \gamma^\psi \lambda^{j-p-1)/2}}{1 + \alpha \lambda^{(u-w-1)/2}} \tag{53}$$

Thus, we observe that an omnivory link between $u \in \{n\}$ and $w \in \{n-1\}$ stabilizes the food chain by

reducing the effect of a death rate shift on the population. This conclusion holds for arbitrary λ and χ and for any relative position of the levels linked by omnivory and the level at which the death rate perturbation occurs.

Discussion and conclusions

Using linear Lotka–Volterra food chains, we have investigated how perturbation at one trophic level cascades to other trophic levels and how such perturbation cascades are affected by the introduction of additional links in the food chain, representing either self-interaction (intraspecific competition or cannibalism) or omnivory. Our results show that such additional links can either dampen or enhance the perturbation cascade, depending on the position of the level at which the perturbation occurs, and the levels connected by the additional link. Thus, self-interaction and omnivory can be either stabilizing or destabilizing, depending on the details of the setup.

In establishing these results, we obtained a closed-form solution for the steady-state populations of Lotka–Volterra food chains of arbitrary length, and we derived analytic expressions for the changes in the steady states in response to shifts of death rate, self-interaction, and additional intraguild trophic relations.

Our definition of stability, based on susceptibility of steady-state populations to long-term removal or addition of a population of a certain level, is somewhat different from previously considered ones. These previously considered definitions of stability include the size of cascading extinction events following the removal of randomly chosen species (Fowler and Lindström 2002), permanency, or localization to a certain region of phase space for systems with possibly nonstationary asymptotic behavior (Law and Blackford 1992), time of relaxation to a new equilibrium (Fagan 1997), and the mere convergence to a nontrivial steady state (McCann and Hastings 1997; Vandermeer 2006). Our definition is inspired by practical applications in which the effect of continuous harvesting of a certain species on the whole food web needs to be considered. However, susceptibility to perturbation is intrinsically related to other definitions of stability, such as the existence of steady states and lack of extinction events. In response to a perturbation, a less susceptible (and thus more stable, according to our definition) system deviates less from a steady state than a more susceptible one, thus having a lower probability of leaving the basin of attraction of a stable fixed point, or cross the boundary of a phase region with permanent behavior. This can be

illustrated by considering, for example, the expressions for stabilizing (Eq. 33) and destabilizing (Eq. 37) effects of self-interaction. When $x_j + \Delta x_j$ is negative, a steady state is no longer possible, which means that either the population of the level j (and consequently, all higher levels) becomes extinct or the behavior of the system becomes nonstationary. When the effect of additional links is stabilizing, Eq. 33, this happens for a higher level of harvesting, and when the effect is destabilizing, Eq. 37, the sustainable level of harvesting is lower. In other words, if a system is more stable according to our susceptibility criteria, it would also be more stable according to the traditional definitions. Hence, our conclusions about stabilizing (or dampening) and destabilizing effects of competition and intraguild predations are relevant for other definitions of stability.

For our analysis, we considered topologically very simple systems of a linear food chains with a single additional link representing intraspecific competition or omnivory. In addition, we assumed linear functional responses to describe the predator–prey relation between adjacent trophic levels in the food chain. Nevertheless, our results can be generalized in a number of ways.

For example, numerical simulations reveal that our results remain true qualitatively with nonlinear functional responses, as is shown in the “Appendix 1”. In Fig. 10, we present an example of a destabilizing effect of an omnivory link, and in Fig. 11, an example of stabilizing effect of omnivory is shown. It follows from these figures that in systems with type II functional response, the effect of omnivory links on stability is qualitatively similar to the structurally equivalent Lotka–Volterra

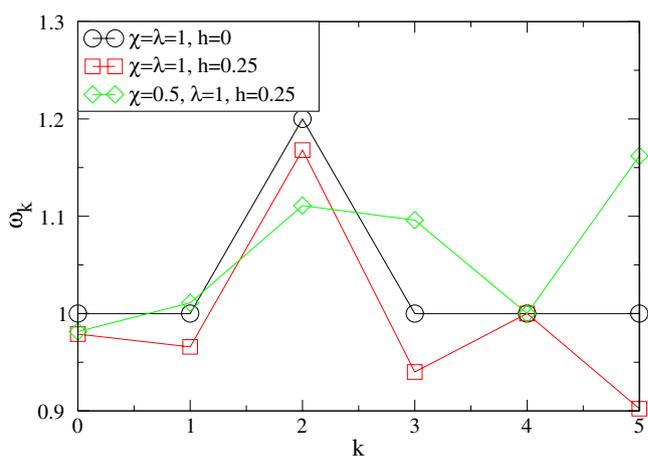


Fig. 10 The ratio $\omega_k \equiv \frac{(x'_k - x_k)_{\text{omn}}}{x_k - x_k}$ of the differences between the perturbed and unperturbed population with ($\alpha = 0.2$) and without ($\alpha = 0$) omnivory, for Lotka–Volterra functional response (circles) and type II functional response with $h = 0.25$ and $\chi = \lambda = 1$ (squares) and $\chi = 0.5$, $\lambda = 1$ (diamonds)

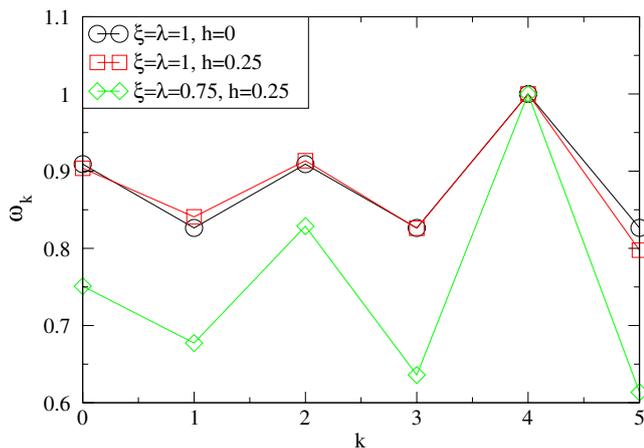


Fig. 11 The ratio $\omega_k \equiv \frac{(x'_k - x_k)_{\text{omn}}}{x'_k - x_k}$ of the differences between the perturbed and unperturbed population with ($\alpha = 0.1$) and without ($\alpha = 0$) omnivory, for Lotka–Volterra functional response (circles) and type II functional response with $h = 0.25$ and $\chi = \lambda = 1$ (squares) and $\chi = l = 0.25$ (diamonds)

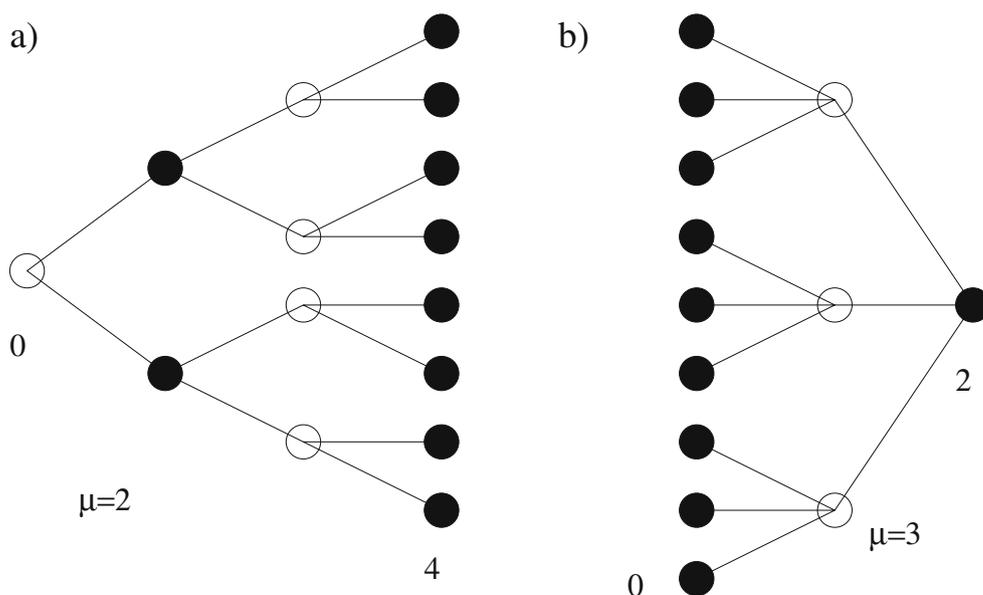
counterparts. Moreover, our results can be generalized to more complicated forms of regular food webs, such as the Cayley trees, as shown in the “Appendix 2” and illustrated in Fig. 12. It is possible to derive results for the effects of self-interaction and omnivory on Cayley tree food web stability that are analogous to the results presented in “Perturbations caused by shifts in the death rate of a single level” and “Omnivory shortcuts” sections (“Appendix 2”). In particular, omnivory and self-interaction can have both stabilizing and destabilizing effects in these more complicated food webs. Extrapolating from this, we conjecture that in more

realistic food webs with more complex topologies and with a multitude of self-interaction and omnivory links, it would be even harder to draw general conclusions about whether a particular link stabilizes or destabilizes the whole food web.

Our results may help to resolve the long-standing controversy on the effect of omnivory and self-interaction on the stability of food webs by essentially showing that general uniform conclusions regarding stabilization (Fagan 1997; HilleRisLambers et al. 2006; Holyoak and Sachdev 1998; McCann and Hastings 1997) or destabilization (Holt and Polis 1997; Pimm and Lawton 1977) cannot be drawn. Rather, whether a particular link in a food web leads to more or less stability very much depends on the details of how this link is embedded in the whole food web. For example, the sign of the effect depends on such features as the relative position of omnivory or self-interaction and the perturbation level from the top of the food web. In our simplified modeling situation, these positions are unambiguously defined. However, in reality, the top predator is often rare (e.g., big carnivores, which may often have low population densities), which will make the determination of positions relative to the top level difficult in real food webs. Nevertheless, it seems feasible that our results could be tested experimentally in simple and well-compartmentalized trophic systems.

Our conclusion that omnivory can both stabilize or destabilize food webs confirms and extends the results of Vandermeer (2006), who has used numerical simulations to show both stabilizing and destabilizing effects of omnivory for food chains of lengths 2 and 3 with a type II functional response. Vandermeer (2006) did

Fig. 12 Sketch of branching food webs (Cayley trees) in which $\mu = 2$ predators are feeding on the same prey, **a)** and in which each predator is feeding on $\mu = 3$ preys, **b)**



not consider food webs of arbitrary lengths, and he did not consider the effects of self-interaction. Moreover, Vandermeer (2006) used a different definition of stability, as stability was essentially defined as the absence of extinction of any of the interacting species. This is in contrast to the definition of stability used here, which is based on the magnitude of changes in steady-state population densities induced by perturbations. Nevertheless, taken together, these results apparently confirm the very general observation that while omnivory (and self-interaction) does affect the stability of food webs, the direction of the effect depends on many details and would be hard to predict on general grounds in any natural food web.

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Appendix 1: Type-II functional response

Here, we show that the results derived above for the Lotka–Volterra type of functional response qualitatively hold for a more realistic, type II functional response. We consider a linear food chain with nearest neighbor predator–prey interactions so that a rate of change of population density $x_k(t)$ of the k th trophic level is given by

$$\frac{dx_k}{dt} = x_k \left[\frac{\lambda_k a_{k,k-1} x_{k-1}}{1 + a_{k,k-1} h_k x_{k-1}} - \frac{a_{k+1,k} x_{k+1}}{1 + a_{k+1,k} h_{k+1} x_k} - \delta_k \right]. \quad (54)$$

Here, $a_{i,j}$ are predation strength of species i on species j , λ_k is the conversion efficiency which connects the birth rate for the species k to the amount of other species it consumes, h_k is the handling time for species k , and d_k is the death rate coefficient of the species k . Evidently, the top predator, occupying the n th level, does not have any species that prey on it, which could be expressed by setting $x_{n+1} \equiv 0$. In addition, the basal species, occupying the basal trophic level, is characterized by the logistic growth term, which mimics the finite input of the energy into the system (or finite carrying capacity K). The linear death term d_0 is absorbed into the linear part of the birth term β , which gives for the rate of change of the basal species concentration,

$$\frac{dx_0}{dt} = x_0 \left[\beta \left(1 - \frac{x_0}{K} \right) - \frac{a_{1,0} x_1}{1 + a_{1,0} h_1 x_0} \right]. \quad (55)$$

As in the main text, we consider the effect of “shortcuts”, or omnivory food links, reflecting predation of

the species u not only on its nearest neighbor $u - 1$ below it in the food chain but also on the species w with the intensity α and conversion efficiency χ (which replaces λ). Introduction of such link modifies the rate equations 54 and 55) for the species w ,

$$\frac{dx_w}{dt} \Big|_{\text{omn}} = \frac{dx_w}{dt} - x_w \left[\frac{\alpha a x_u}{1 + h_u (a_{u,u-1} x_{u-1} + \alpha a x_w)} \right], \quad (56)$$

the species $u - 1$

$$\frac{dx_{u-1}}{dt} \Big|_{\text{omn}} = \frac{dx_{u-1}}{dt} + a_{u,u-1} x_u x_{u-1} \times \left[\frac{1}{1 + a_{u,u-1} h_u x_{u-1}} - \frac{1}{1 + h_u (\alpha a x_w + a_{u,u-1} x_{u-1})} \right], \quad (57)$$

and for the species u

$$\frac{dx_u}{dt} \Big|_{\text{omn}} = \frac{dx_u}{dt} + x_u \left[- \frac{a_{u,u-1} \lambda_u x_{u-1}}{1 + a_{u,u-1} h_u x_{u-1}} + \frac{\lambda_u a_{u,u-1} x_{u-1} + \chi \alpha a x_w}{1 + h_u (a_{u,u-1} x_{u-1} + \alpha a x_w)} \right]. \quad (58)$$

We use the following values of the constants, $a_{ij} = a = 1$, $\lambda_i = 0.75$, 1 , $\chi_i = 0.5$, 0.75 , 1 , $K = 1$, $\beta = 1$, $\delta_i = 0.1$, and $h_i = 0.25$ for all i and j . As an example of destabilizing effect of intraguild predation (Fig. 10), we consider a linear food chain with an omnivory link of the intensity $\alpha = .2$ between levels $u = 3$ and $w = 1$. The perturbation is caused by a shift by ϵa , $\epsilon = 0.1$ of the death rate of the level $p = 5$; all these three levels $\{u, w, p\}$ are in $\{n\}$ partition.

As an example of stabilizing effect of intraguild predation (Fig. 11), we consider an omnivory link between levels $u = 3$ of the $\{n\}$ partition and $w = 0$ of the $\{n - 1\}$ partition. The perturbation is caused by a shift by ϵa , $\epsilon = 0.1$ of the death rate of the level $p = 5$, which is in $\{n\}$ partition.

It follows from Figs. 10 and 11 that the conclusions made in “Omnivory shortcuts” section qualitatively hold for foodwebs with type II functional response as well: Depending on the position of the level with a death rate shift and a shortcut link, the omnivory can either stabilize or destabilize the food web. When the omnivory link connects the levels $u = 3$ and $w = 1$ of the $\{n\}$ partition and the death rate shift occurs at the level $p = 5$ also belonging to the $\{n\}$ partition, the perturbation is enhanced, especially at the level(s)

$w < i < u$ of the $\{n - 1\}$ partition. Conversely, when the omnivory link connects the levels $u = 3$ of the $\{n\}$ partition and $w = 0$ which belongs to $\{n - 1\}$ partition and the shift of the death rate occurs at the level $p = 5$ which belongs to the $\{n\}$ partition, the perturbation is dampened.

Appendix 2: Cayley tree food webs

Our results can be generalized to more complicated forms of regular food webs, such as the Cayley trees. In “upward” Cayley trees (Fig. 12a), m predators in the next higher trophic level are feeding on the same prey, and in “downward” Cayley trees (Fig. 12b), a given predator feeds on m prey species on the next lower trophic level, so that for $m = 1$ the linear food chains are recovered.

For upward Cayley trees (Fig. 12a), the population dynamics at the various trophic levels is given by

$$\frac{dx_k}{dt} = x_k (\lambda a x_{k-1} - \mu a x_{k+1} - \delta_k). \quad (59)$$

In this case, the expression 11 for the steady-state populations still holds, but in all subsequent steps of the analysis presented in “[Linear Lotka-Volterra chain](#)” section, λ should be replaced by λ/μ and d by d/μ . In the complimentary scenario of “downward” branching (Fig. 12b), λ in Eq. 11 and subsequent equations should be replaced by $\mu\lambda$. Starting with these expressions, the effects of self-interaction and omnivory on Cayley tree food webs can be analyzed along the lines presented in “[Perturbations caused by shifts in the death rate of a single level](#)” and “[Self-interaction](#)” sections. Thus, omnivory and self-interaction can have both stabilizing and destabilizing effects in these more complicated food webs.

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