

IDEA AND PERSPECTIVE

Simple rules describe bottom-up and top-down control in food webs with alternative energy pathways

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Abstract

Many human influences on the world's ecosystems have their largest direct impacts at either the top or the bottom of the food web. To predict their ecosystem-wide consequences we must understand how these impacts propagate. A long-standing, but so far elusive, problem in this endeavour is how to reduce food web complexity to a mathematically tractable, but empirically relevant system. Simplification to main energy channels linking primary producers to top consumers has been recently advocated. Following this approach, we propose a general framework for the analysis of bottom-up and top-down forcing of ecosystems by reducing food webs to two energy pathways originating from a limiting resource shared by competing guilds of primary producers (e.g. edible vs. defended plants). Exploring dynamical models of such webs we find that their equilibrium responses to nutrient enrichment and top consumer harvesting are determined by only two easily measurable topological properties: the lengths of the component food chains (odd–odd, odd–even, or even–even) and presence vs. absence of a generalist top consumer reconnecting the two pathways (yielding looped vs. branched webs). Many results generalise to other looped or branched web structures and the model can be easily adapted to include a detrital pathway.

Keywords

Bottom-up control, dynamical model, energy channel, enrichment, food chain length, food web, harvesting, indirect effects, top-down control, topology.

Ecology Letters (2012) 15: 935–946

INTRODUCTION

Many human influences on the world's ecosystems have their largest direct impacts at either the top or the bottom of the food web. For example, hunting, fishing, habitat loss and bioaccumulation of toxicants typically most strongly affect larger-bodied carnivores and apex predators (Connell 1990; Laliberte & Ripple 2004; Schipper *et al.* 2008; Lotze & Worm 2009), whereas land use changes, fertilisation and climate change most immediately impact primary producers (Asner *et al.* 1997; Behrenfeld *et al.* 2006; Haberl *et al.* 2007). These direct impacts frequently cascade up and down the food chain (Chavez *et al.* 2003; Baum & Worm 2009; Beschta & Ripple 2009), the community-wide consequences sometimes being so pervasive that they result in regime shifts (Cury & Shannon 2004; Estes *et al.* 2011). Clearly, to predict the ecosystem-wide consequences of human impacts we must understand how their direct effects propagate through entire food webs. Consequently, better conceptual integration of the interplay of bottom-up and top-down forces within ecosystems has been called for in several areas of applied ecology, e.g. in fisheries, oceanography and climate impact research (Frank *et al.* 2007; Cury *et al.* 2008; Walther 2010).

While substantial progress has been made in the description and theoretical exploration of complex food webs (Pascual & Dunne

2006; Bascompte 2010), food web theory has historically focussed on network properties such as intervality, connectance and interaction strength, but has made few tangible contributions to questions concerning human impacts on ecosystem function (e.g. standing stocks and fluxes of biomass) (Mémott 2009). A critical issue in the exploration of the effects of bottom-up and top-down forces on ecosystems is how to reduce food web complexity to a mathematically tractable, but empirically relevant system (Yodzis 1998; Cury *et al.* 2008). The most simplifying approach lumps species into trophic levels, resulting in a single food chain describing the whole ecosystem (Hairston *et al.* 1960; Oksanen *et al.* 1981). While food chain theory has had some success in describing empirical patterns (e.g. Persson *et al.* 1992; Crete 1999; Aunapuu *et al.* 2008), it has long been criticised for its oversimplification of trophic complexity (Polis & Strong 1996; Leibold *et al.* 1997).

A pervasive issue in the critique of community-wide food chain theory has been the recognition that primary producers differ vastly in size, defendedness and nutritional quality for herbivores (Murdoch 1966). These differences frequently lead to compensatory biomass responses within the primary producer level when productivity or herbivore pressure changes (Leibold 1989; Grover 1994; Hillebrand *et al.* 2007). Primary producers differing in size, defendedness and nutritional quality do, in turn,

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often have their own, distinct suites of consumers. In many systems a size relationship between herbivores and their food is observed, the body mass of herbivores typically increasing with increasing producer size and defendedness and with decreasing producer quality (Armstrong 1994; Hillebrand *et al.* 2009; Olf *et al.* 2009). The resulting food chains originating from different types of primary producers represent parallel pathways of energy flow through an ecosystem. These energy pathways may remain entirely separated, but are frequently connected by consumers at higher trophic levels (Rooney *et al.* 2006; Pringle & Fox-Dobbs 2008; Olf *et al.* 2009).

Simplification of food webs to main energy channels linking producers to top consumers is a recently advocated approach in the analysis of ecosystem dynamics which, in the marine realm, has been termed end-to-end models (Fulton 2010; Shin *et al.* 2010). Contrary to food chain theory this approach can describe differential responses to bottom-up and top-down forcing along alternative food chains (Stibor *et al.* 2004), but keeps ecosystem models much more tractable than complex, full-scale food web descriptions. While a number of food web modules with multiple food chains have been explored with dynamic models (Abrams 1993; Grover 1997; Hulot & Loreau 2006), a comprehensive theoretical treatment of the effects of bottom-up and top-down forcing on food webs with alternative energy pathways is lacking.

In this article we propose a general theoretical framework for such an analysis by reducing food web structure to two main energy pathways originating from distinct types of primary producers (e.g. edible vs. defended plants or plants in two different microhabitats). The primary producers are assumed to compete for limiting resources and to support separate food chains of varying length (up to the secondary carnivore level), which may or may not include a generalist top consumer reconnecting the chains. To explore the effects of bottom-up and top-down forcing on these food webs we analyse their equilibrium responses to changes in supply with a limiting plant resource and in mortality of a top consumer. We find that the response patterns depend on only two structural properties: the number of trophic levels in each food chain and the presence vs. absence of a generalist top consumer. Within our modelling framework, food web responses to bottom-up and top-down forcing can therefore be described by a surprisingly small set of rules. Many of the results extend to food webs where multiple pathways originate and reconnect elsewhere than at the producer and top consumer levels, and the model can be easily modified to describe food webs including a detritus-based pathway of energy flow.

MODEL STRUCTURE

We explored patterns of biomass and energy flow in model food webs consisting of two distinct chains that are linked at the bottom through a shared limiting nutrient. Webs where the two chains are additionally linked at the top through a shared (generalist) top consumer are referred to as 'looped' webs, webs lacking a shared top consumer are termed 'branched' webs (Fig. 1). Within each web, food chains are labelled chain 1 and chain 2 respectively. Each chain i can contain up to five trophic levels: the shared limiting nutrient (R), a primary producer (P_i), a herbivore (H_i), a primary carnivore (C_i) and a secondary carnivore (Fig. 1). The top consumer in a chain is labelled TC_i in branched webs and TC in looped webs, regardless of its trophic level.

Each food web is modelled with differential equations describing the rates of change in its constituent populations. The rate of change in the biomass density Y_i of each intermediate species (a species that is both a consumer and a prey/resource) in chain i is described by

$$\frac{dY_i}{dt} = Y_i(e_{X_i Y_i} A_{X_i Y_i} X_i - m_{Y_i} - A_{Y_i Z_i} Z_i) \quad (1a)$$

where X_i is the density of the prey/resource of species Y_i and Z_i is the density of the predator of Y_i . Depending on food web topology P_i , H_i and C_i take on the roles of prey (X_i), intermediate consumer (Y_i) or predator (Z_i) in different equations, whereas R and secondary carnivores only take on the roles of resource (X_i) and predator (Z_i) respectively. The term $e_{X_i Y_i} A_{X_i Y_i} X_i$ describes the specific growth rate of species Y_i and $A_{Y_i Z_i} Z_i$ its specific loss rate due to consumption by Z_i . The rate of change of a top consumer is described by

$$\frac{dTC_i}{dt} = TC_i(e_{X_i TC_i} A_{X_i TC_i} X_i - m_{TC_i}) \quad (1b)$$

in the case of a specialist top consumer feeding on a single prey/resource in chain i , and by

$$\frac{dTC}{dt} = TC(e_{X_1 TC} A_{X_1 TC} X_1 + e_{X_2 TC} A_{X_2 TC} X_2 - m_{TC}) \quad (1c)$$

in the case of a generalist predator feeding on prey/resources from both chains.

In all equations above, A_{JK} describes a type 2 functional response of consumer K feeding on prey/resource J . When consumer K feeds on a single prey/resource, A_{JK} takes the form

$$A_{JK} = \frac{a_{JK}}{1 + a_{JK} b_{JK} J} \quad (2a)$$

where J is the biomass density of the prey/resource. When consumer K is a generalist top consumer feeding on prey/resources from both chains, A_{JK} takes the form

$$A_{J,K} = \frac{a_{J,K}}{1 + a_{J_1,K} b_{J_1,K} J_1 + a_{J_2,K} b_{J_2,K} J_2}, \quad (2b)$$

where J_i stands for the prey/resource in chain i . Note that intermediate species take on the respective roles of consumer ($Y_i = K$) and prey ($Y_i = J_i$) in the left-most and right-most terms in the parenthesis of eqn 1a.

In eqns 1a–c, e_{JK} is the conversion efficiency of consumed prey/resources J into consumers K (biomass per biomass), and m is the density-independent specific mortality rate (per time). In eqns 2a and 2b, b_{JK} is handling time of consumer K for prey/resources J (time*consumer biomass/prey biomass), and a_{JK} is attack rate (area searched per biomass of consumer K per time). Note that functional responses are linear when handling times are zero.

The nutrient shared by the two chains in a web is assumed to limit primary production. For simplicity, the biomasses of all other food web components are expressed in units of the nutrient. We assume constant nutrient-to-carbon stoichiometries for all species. Consequently, nutrient and energy (= carbon) flows up a food chain are proportional. In the text we therefore describe the transfer of carbon and nutrients up a food chain in energetic terms rather than in terms of the nutrient currency used in the equations. For convenience we assume that the system is closed for nutrients. All results apply, however, equally to systems with chemostat-like

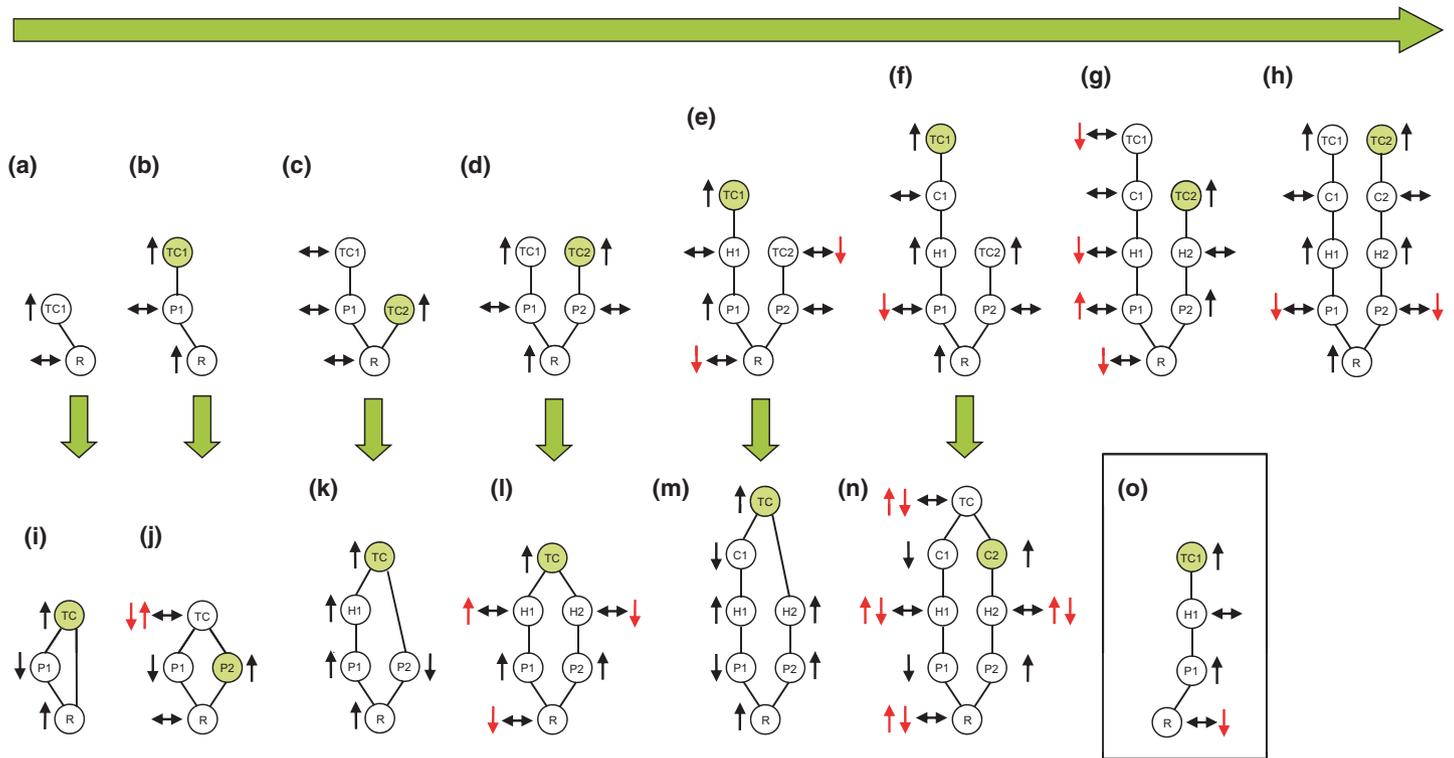


Figure 1 Equilibrium responses to nutrient enrichment. Webs are arranged in possible assembly sequences along enrichment gradients (green arrows), the last invader being highlighted in green. Circles represent resource (*R*), producers (*P*), herbivores (*H*) and carnivores (*C*) in chain *i* (*i* = 1, 2) and specialist (*TC*_{*i*}) or generalist top consumers (*TC*). Black arrows next to circles indicate the direction of change in equilibrium biomass of the compartment in response to enrichment, with horizontal arrows indicating no change. Where saturating functional responses produce qualitatively different outcomes than linear functional responses, the former are shown with red arrows. Pairs of opposed arrows indicate that compartments either increase or decrease, the equilibrium responses of *R*^{*}, *H*₁^{*} and *H*₂^{*} in panel n are being correlated. (a, b, o) 2-, 3-, 4-level food chains; (c–h) branched 3–2, 3–3, 4–3, 5–3, 5–4, 5–5 webs; (i–n) looped 3–2, 3–3, 4–3, 4–4, 5–4, 5–5 webs.

dynamics (results not shown), and likely for many other open systems provided that inputs and outputs have approached a long-term balance (i.e. $dR_{tot}/dt \rightarrow 0$; Grover 1997). The total amount of nutrients R_{tot} in the system remains constant over time and is a measure of nutrient enrichment. Nutrients not assimilated into living biomass are available for primary production (assuming instant recycling of excreted and dead biomass). The density of free mineral nutrients *R* can therefore be calculated from the mass balance eqns 3a (for branched webs) and 3b (for looped webs):

$$R = R_{tot} - \sum_i Y_i - \sum_i TC_i \tag{3a}$$

$$R = R_{tot} - \sum_i Y_i - TC. \tag{3b}$$

FOOD WEB ANALYSES

To investigate bottom-up and top-down influences we created branched and looped webs with up to five trophic levels and studied the signs of the equilibrium biomass changes of all web components in response to enrichment (increasing R_{tot}) and altered top consumer mortality (increasing m_{TC} or m_{TC_i}). For a given web topology, it is possible to gain analytical insights into the relationships among equilibrium biomasses of its components and their relationships to enrichment and top consumer mortality based on constraints to the

equilibrium solution (see Appendix S1 in Supporting Information). These constraints fully determine the responses of all components in a web when functional responses are linear (see Appendix S2), but usually not when functional responses are saturating. We therefore explored the responses of webs with type 2 functional responses numerically and checked the outcomes for consistency with analytical constraints (see Appendix S1, S3). When functional responses are linear it is also possible to solve for the equilibria and to calculate the derivatives of all equilibrium densities with respect to R_{tot} and m_{TC} or m_{TC_i} (see Appendix S2). These calculations were done in Matlab (Mathworks Inc., Natick, MA, USA). Numerical calculations assuming saturating functional responses were performed in Matcont 2.4 (Dhooge *et al.* 2003, as a package for Matlab).

When functional responses are saturating, equilibria are frequently unstable. It is well known that equilibrium and time-averaged population sizes may show opposite responses to enrichment when systems undergo sustained oscillations (Abrams & Roth 1994; Abrams & Fung 2010). Also, oscillating populations often go through long periods of very low population size with high risk of stochastic extinction. We therefore only present responses of stable equilibria. Moreover, the patterns obtained with saturating functional responses are very similar to, and more easily understood from, the patterns obtained with linear functional responses. We therefore present the patterns for linear functional responses first and subsequently highlight the similarities and differences arising from saturating functional responses.

We labelled each web with a two-number code (e.g. 4–3) for the lengths of its constituent food chains. Chain length was calculated as the number of nodes from the shared nutrient to the (shared or unshared) top consumer. We investigated plausible combinations of food chains of length 2 to 5 (Fig. 1) and distinguished three types of webs: (1) ‘odd–even webs’ consisting of one chain of odd and one of even length (3–2, 4–3, 5–4), (2) ‘even–even webs’ consisting of two even chains (4–4) and (iii) ‘odd–odd webs’ consisting of two odd chains (3–3, 5–3, 5–5). Feasibility of an equilibrium and responses to enrichment and top consumer mortality differ systematically between these three types of webs. To facilitate understanding of how trophic structure arises and how it affects dynamics we have arranged all webs in a possible sequence of community assembly along a gradient of nutrient enrichment, starting from a simple two-level food chain (Fig. 1). Some alternative assembly possibilities exist (e.g. web 1o instead of 1c may arise from 1b), but do not affect responses of a given web to enrichment.

We did not analyse webs with more than five nodes per chain, because it seems implausible that consumers linking the two chains would only occur at the top of such long food chains. We also did not analyse webs where the chains differ in length by more than two trophic levels (e.g. 5–2). For linear functional responses, the behaviour of any food web with either longer chains or greater differences in length between its two chains can, however, be easily inferred from the general rules derived below. When functional responses are saturating, the same is true for branched webs, whereas some looped webs show parameter dependent response patterns.

RESPONSES TO NUTRIENT ENRICHMENT: LINEAR FUNCTIONAL RESPONSES

The responses to nutrient enrichment in branched and looped food webs can be most easily understood if we first briefly review the well-known responses of single food chains. The top consumer in a model food chain is always strictly food limited and controls its prey/resource at a fixed equilibrium density where food consumption exactly meets the top consumer’s requirements to offset mortality. Consequently, the top consumer’s prey and all other populations at an odd distance below the top consumer remain at constant density, whereas the top consumer itself and all populations at an even distance from it increase with enrichment (Fig. 1a, b, o). With sufficient nutrient enrichment, the top consumer may reach an equilibrium density that permits the invasion of a higher level top consumer, adding one trophic level to the food chain and reversing the population responses to further enrichment (Oksanen *et al.* 1981). Alternatively, a second producer with a higher requirement for the basal nutrient may invade the resident food chain. The latter requires that enrichment has increased the nutrient to the density required by the invader, which is only possible if the resident food chain is of odd length (e.g. Fig. 1b to c).

Adding a generalist consumer to a two-level chain (Fig. 1i) or a second producer to a three-level chain (Fig. 1c) produces the simplest possible looped and branched webs respectively. Once there are two chains in a web, the response to nutrient enrichment depends on whether the web is branched or looped and on the type of web (i.e. odd–odd, odd–even or even–even).

Branched webs

Branched odd–even webs

In branched webs top consumers of both chains always control the populations at odd distance below themselves at constant biomass. For branched odd–even webs this implies that the shared nutrient is controlled by the top consumer of the even chain, whereas the producer in the odd chain is controlled by the top consumer of the odd chain. Because neither the nutrient nor the producer in the odd chain responds to enrichment, the odd chain as a whole cannot respond; in contrast, the chain of even length responds as it would in the absence of a second chain (Fig. 1c, e, g). In other words, in a branched odd–even web the even chain controls the odd chain. Consequently, biomass always increases with enrichment in the even chain but remains constant in the odd chain.

Branched even–even webs

Grover (1997) showed that a stable branched web of two even chains is not feasible. In the assembly scenario of Fig. 1 this would require a transition from an odd–even to an even–even web through invasion of a new top consumer into the odd chain. However, as the top species in the odd chain of an odd–even web stays constant with enrichment (Fig. 1c, e, g) its density cannot increase to the threshold required for invasion of a new top consumer preying on it, thus preventing the assembly of a branched even–even web. More generally, stable coexistence of two even chains depending on a single basal resource is impossible, because it requires that both food chains in isolation control the resource at the exact same equilibrium density R^* . Analogous to classical resource competition (where the species with the lower R^* excludes its competitor) two even chains with different R^* values cannot coexist, a phenomenon that Grover (1997) termed ‘cascade competition’.

Branched odd–odd webs

Invasion of the even chain in a branched odd–even web becomes possible once its top consumer has sufficiently increased after enrichment, giving rise to a branched odd–odd web (sequence Fig. 1c to d, e to f, g to h). The two odd chains in such a web respond to enrichment in the same way as they would in isolation (Fig. 1d, f, h).

Looped webs

We have just seen in branched webs that top-down control along one chain can suppress bottom-up responses along the other chain. Linking chains additionally through a generalist top consumer creates an opportunity for apparent competition, where bottom-up effects from one chain translate into top-down effects along the other chain. Looped webs therefore show more complex responses to enrichment than do branched webs.

Looped even–even webs

An even–even topology is possible when a food web is looped. In the assembly sequence looped even–even webs arise from branched odd–odd webs. Both top species in a branched odd–odd web increase with enrichment, eventually allowing a food limited generalist top consumer to invade (transition Fig. 1d to l). Once established, looped even–even webs respond to nutrient enrichment as would each of the constituent food chains in isolation (Fig. 1l).

Looped odd–odd webs

Because branched even–even webs are infeasible, looped odd–odd webs can only arise from branched odd–odd webs through invasion of a higher level consumer into one chain, which is immediately preyed upon by the resident top consumer of the other chain (Fig. 1b to j and f to n). In a looped odd–odd web the top consumer and all species at even distance below stay constant with enrichment, while species in odd distance from the top decrease along one chain and increase along the other (Fig. 1j, n). Total energy flow to the top remains thus constant with enrichment, while biomass accumulates in the chain with the lower transfer efficiency. The chain experiencing the biomass increase is always the one that was assembled last in the enrichment sequence (Fig. 1). With sufficient enrichment the decreasing prey of the top consumer will go extinct, the underlying mechanism being apparent competition. These patterns were first described for the simplest looped odd–odd web, the 3–3 web (Holt *et al.* 1994; Leibold 1996). Here, we have shown that the patterns apply to looped odd–odd webs in general.

Looped odd–even webs

Looped odd–even webs show the least intuitive responses to enrichment: all species in the even chain increase; in contrast, in the odd chain species at even distance from the top also increase but species at odd distance decrease (Fig. 1i, k, m). In Appendix S2 we derive this pattern analytically. It can also be intuitively understood by comparing branched and looped webs of identical chain lengths. Enrichment of a branched web always increases energy flow up the even chain which, in turn, controls the resource and the odd chain at a constant level (Fig. 1c, e, g). Now, if the even chain's top consumer is also the top consumer of the odd chain, increased energy flow up the even chain increases predation pressure down the odd chain, reducing the biomass of species in odd distance from the top along the odd chain (compare Fig. 1c vs. i, e vs. k and g vs. m by merging the top consumers of the branched chains into a single generalist top consumer). This will eventually lead to the extinction of the subterminal species in the odd chain, a theoretical result that is well established for the simplest looped odd–even web, an intra-guild predation web (Fig. 1i; Diehl & Feissel 2000).

RESPONSES TO NUTRIENT ENRICHMENT: TYPE 2 FUNCTIONAL RESPONSES

Again, we first consider single food chains. Food chains up to length three respond identically to enrichment whether functional responses are linear or saturating (Fig. 1a, b). Responses differ, however, for longer chains. Per capita mortality of a prey decreases with its own density when the functional response of its predator is saturating. This happens with enrichment to the third species from the top. In chains of length four or more, the third species from the top can therefore only be in equilibrium if the density of its food decreases with enrichment (Fig. 1o). While this has consequences for webs with longer chains, most enrichment responses of webs observed in the linear case are either conserved or accentuated when functional responses are saturating.

Branched webs

Branched even–even webs remain impossible with saturating functional responses because of 'cascade competition' between the two food chains (Grover 1997).

Branched odd–even webs

As in the linear case, enrichment increases biomass in the even chain but not in the odd chain, because the even chain controls the resource. In a 3–2 web, enrichment responses are identical to the linear case (Fig. 1c, see Appendix S4). When the even chain is of length four, however, the resource decreases with enrichment. Consequently, the odd chain suffers from 'de-richment' and responds accordingly; i.e. the top consumer of the odd chain and all species at even distance from it decrease (Fig. 1e, g). In odd–even webs with one chain of length four, dominance of the even over the odd chain is therefore more pronounced than in the linear case; i.e. increased energy flow up the even chain is accompanied by decreased energy flow up the odd chain (Fig. 1e, g).

Branched odd–odd webs

As in the linear case, both chains respond to enrichment as would the corresponding food chains in isolation (Fig. 1d, f, h). If one chain is of length five its producer decreases with enrichment; all other populations respond to enrichment as in the linear case (Fig. 1f, h).

Looped webs

Results for looped webs with saturating functional responses are based on numerical exploration backed up by analytical results (see Appendix S1, S3, S5, S6). Most response patterns from the linear case are conserved, but deviations occur in most compartments that remain constant in the linear case. For odd–even webs, we only found examples where the response patterns of the linear system are fully conserved (Fig. 1i, k, m). Biomass constancy, observed for several members of linear webs, is, however, not a robust feature (Fig. 1j, l, n). With saturating functional responses we found constancy of a food web member only in the 3–3 web, where the basal resource remains constant (Fig. 1j, see Appendix S5). Generally, in odd–odd webs the top consumer may increase or decrease depending on parameter values, and so may all web members at even distance from the top in the looped 5–5 web (Fig. 1j, n). In the latter web the responses of the resource and the two herbivores are correlated (this follows from eqs. A1–3, A1–4 and A1–6, Appendix S1) and were also correlated with the top consumer in all our numerical runs with stable equilibria (Fig. 1 n).

RESPONSES TO TOP CONSUMER MORTALITY: LINEAR FUNCTIONAL RESPONSES

In any food chain with linear functional responses the top consumer always decreases with increasing own mortality (Fig. 2a, b, s). At equilibrium, this increase in the top consumer's mortality must be balanced by an increase in the density of its prey, the effects of which cascade to the nutrient level. The nutrient therefore decreases with increasing top consumer mortality in an odd food chain (Fig. 2b), but increases in an even food chain (Fig. 2a, s). In webs consisting of two food chains, effects of increasing top consumer mortality then propagate through both chains, the exact responses depending on the type of web (branched or looped; odd–odd, odd–even, or even–even). In the case of branched odd–even webs we must also distinguish between cases where the top consumer of either the odd or the even chain experiences increased mortality. To more easily describe these

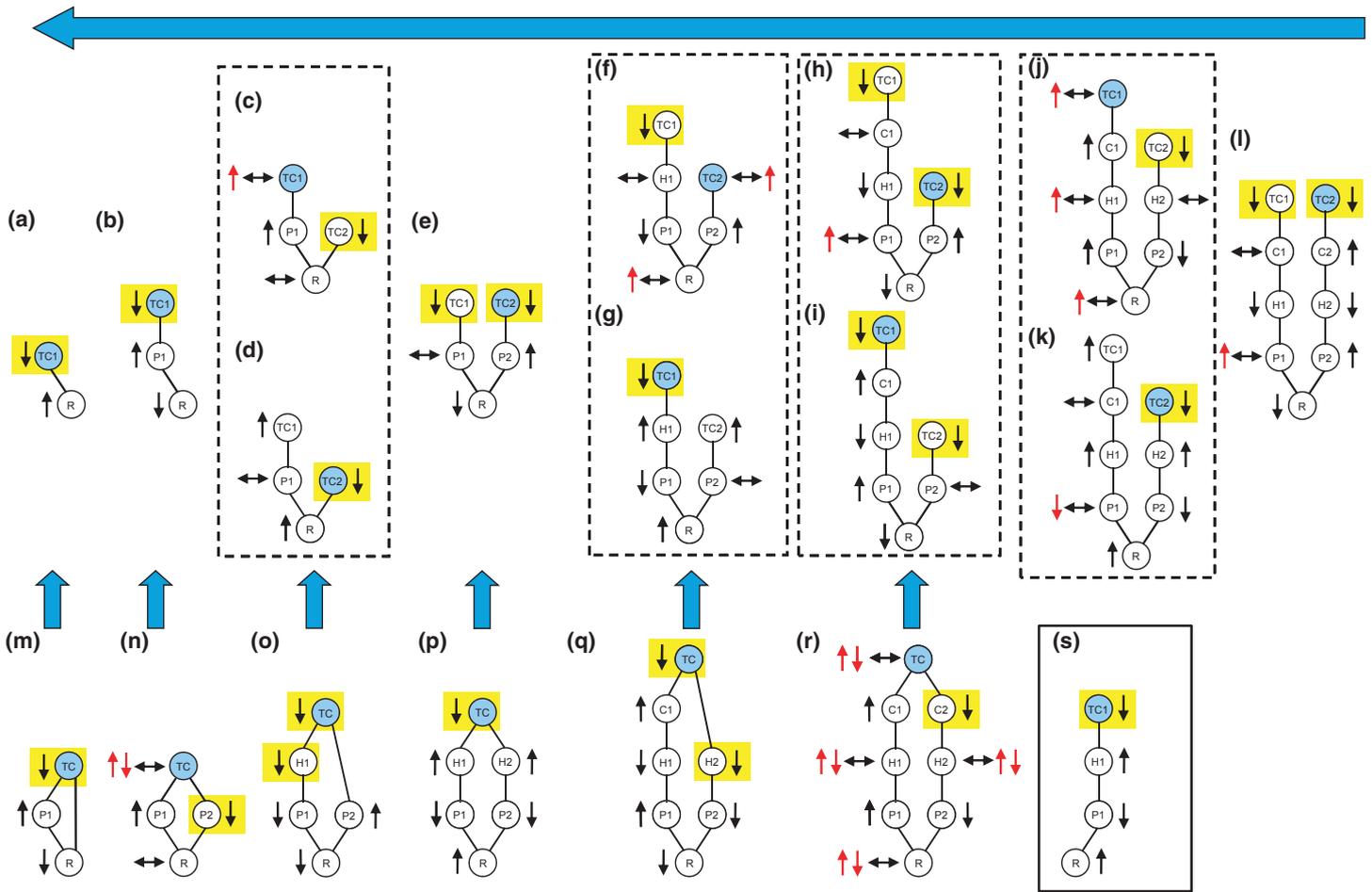


Figure 2 Equilibrium responses to increased mortality of the top consumer highlighted in blue shading. Symbols and black and red arrows are defined as in Fig. 1. The responses of R^* , H_1^* and H_2^* indicated by red arrows in panel r are correlated. Yellow background shading indicates species that may go extinct with sufficiently high top consumer mortality. Thick blue arrows point at webs resulting from such extinctions. When there are two possibilities for which species goes extinct, the outcome is shown that results in a reversal of the enrichment sequence of Fig. 1. This illustrates that, for a given community with fixed parameters, increasing its top consumer's mortality will reverse the enrichment assembly.

responses we call a change in top consumer mortality a ‘manipulation’.

Common to all webs is that increasing top consumer mortality will eventually cause an extinction. Interestingly, however, it is not always the manipulated top consumer that dies out. Instead, the species going extinct is always the one that invaded last along the enrichment sequence (Fig. 2), owing to its more precarious energetic balance. This implies that the top consumer of an odd chain cannot go extinct in response to increasing own mortality, if the remaining community would form an ‘impossible’ branched even–even web. In such cases extinction always hits either the top consumer of the even chain (branched odd–even webs, Fig. 2c, f, j), or a subterminal consumer (looped odd–odd webs, Fig. 2n, r).

Branched webs

In a branched web, the (top-down) effects of top consumer mortality in one chain propagate via the shared nutrient up the other chain, with often counter-intuitive consequences. When the manipulated chain is even, increasing top consumer mortality translates into increased nutrient density and, thus, enriches the other chain. Total

biomass therefore decreases in the manipulated chain and increases in the other chain, where the non-manipulated top consumer and every other population increases (Fig. 2d, g, k). In contrast, when the manipulated chain is odd, increasing its top consumer's mortality translates into increased plant biomass in the manipulated chain. Plants in the manipulated odd chain then consume a larger fraction of the nutrient, thus ‘de-riching’ the other chain. Total biomass therefore decreases in the non-manipulated chain and increases in the manipulated chain (Fig. 2c, e, f, h, j, l). The manipulated top consumer of the odd chain itself decreases if both chains are of odd length. Seemingly paradoxically, however, the manipulated top consumer of the odd chain does not respond to its own mortality if the non-manipulated chain is even. In the latter case the non-manipulated even chain controls the nutrient – and all populations at even distance from the nutrient (including the manipulated top consumer) – at a constant level (Fig. 2c, f, j).

Looped webs

In looped webs all populations that increase with enrichment, decrease with increasing top consumer mortality and vice versa

(Fig. 2m–r). In looped odd–even webs, the response pattern to increased top consumer mortality is therefore exactly opposite to the enrichment pattern (Fig. 2m, o, q). Populations that stay constant with enrichment remain, however, either constant (in looped odd–odd-webs, Fig. 2n, r) or increase (in looped even–even webs, Fig. 2p) with increasing top consumer mortality. These results were derived analytically (see Appendix S2), but can, for most food webs, be understood from three conditions: (1) with increasing top consumer mortality, at least one of its prey must increase to maintain top consumer mortality in balance with growth; (2) at least one other population must decrease to maintain mass balance; and (3) populations at even distance from each other within a food chain must change in the same direction (otherwise the population between them is not in equilibrium).

RESPONSES TO TOP CONSUMER MORTALITY: TYPE 2 FUNCTIONAL RESPONSES

Again, most responses of webs observed in the linear case are preserved when functional responses are saturating. Deviations from the linear case occur largely in the same webs and links as the deviations in enrichment patterns and exclusively concern compartments that remain constant in the linear case (Fig. 2).

Branched webs

Identical to the linear case, increasing top consumer mortality in an even chain always enriches (increases nutrient flow into) the non-manipulated chain and hence decreases flow up the manipulated chain (Fig. 2d, g, k). Conversely, increasing top consumer mortality in an odd chain always ‘de-riches’ (decreases nutrient flow into) the non-manipulated chain and increases flow up the manipulated chain (Fig. 2c, e, f, h, j, l). Deviating from the linear case, in odd–even webs this increased flow causes an increase in all members of the manipulated odd chain including the nutrient and the top consumer; seemingly paradoxically, the top consumer of the odd chain thus increases in response to increased own mortality (Fig. 2c, f, j). While this increase with own mortality cannot go on indefinitely, in all numerical analyses the top consumer of the non-manipulated even chain went extinct before this threshold mortality was reached, reversing the enrichment assembly sequence and avoiding ‘impossible’ even–even webs (Fig. 2c, f, j). Also, with saturating functional responses, the fourth highest level in a non-manipulated chain responds non-intuitively to effects propagating from the other chain; i.e. it decreases with enrichment (Fig. 2k) and increases with ‘de-richment’ (Fig. 2f, h, l).

Looped webs

Again, results for looped webs are based on numerical investigations backed up by analytical results. The response patterns of looped odd–even and looped even–even webs were always preserved under the assumption of saturating functional responses (Fig. 2m, o–q). Odd–odd webs deviate in that compartments that stay constant in the linear case may either increase or decrease with top consumer mortality, when functional responses are saturating (Fig. 2n, r). As with enrichment, constancy only holds for the resource in looped 3–3 webs, whereas in looped 5–5 webs all compartments at even distance to the top were positively correlated to the mortality

response of the top consumer. The responses of these compartments to increased mortality need, however, not always be reversed to their enrichment responses (see Appendix S5).

GENERALISATION TO EXTENDED FOOD WEB TOPOLOGIES

While our analysis has so far focussed on parallel energy pathways originating at the primary producer level, our results generalize to food webs where the branching occurs at higher trophic levels. We illustrate this with the looped 4–3 web (Fig. 3a–d), but the results apply to any branched or looped web with a single branching. When one or more linearly linked compartments are present below a branching node, enrichment at the base of this lower, linear structure will always propagate up to the branching node. Thus, the upper part of the web responds to enrichment at the base exactly as it would if the branching node was directly enriched (compare Figs 3a–b with 1k). Similarly, links below a branching node do not influence how top-down effects propagate through the branched or looped upper parts of a web. Consequently, responses of that upper part of the web to top consumer mortality are also not altered (compare Figs 3c–d with 2o).

It is also straightforward to see how our results extend to looped webs where the chains reconnect below the apex predator level. The response of the looped module to enrichment and top consumer mortality then depends on whether the chain beginning at (and including) the reconnecting node is of length two or three. We have only explored this for linear functional responses and illustrate the results again with the looped 4–3 module (Fig. 3e–h). Generally, a subterminal population is always held constant by a specialist top consumer in an enrichment situation, but must increase in response to increased top consumer mortality. For the reconnecting node this implies constant (Fig. 3f) vs. increasing (Fig. 3h) per capita mortality, respectively, when the top chain has length three. The responses of a looped module to enrichment and top consumer mortality are then the same as for the looped module in isolation (Figs 3f vs. 1k; Figs 3h vs. 2o). In contrast, when the subterminal population is the reconnecting node (top chain has length two), responses of the looped module to top consumer mortality are opposite to the responses of a looped web in isolation (Figs 3g vs. 2o). Moreover, apparent competition between the two food chains cannot occur. Their members therefore respond to enrichment as would a branched web lacking the reconnecting species altogether (compare Figs 3e with 1c).

DISCUSSION

We have theoretically explored bottom-up and top-down control in food webs with two alternative energy pathways. We propose that this relatively simple structure can serve as a useful, general abstraction of many real food webs, being representative of at least three common scenarios: (1) communities in which competing primary producers can be broadly lumped into edible and less edible categories which support different suites of herbivores (Armstrong 1994; Olff *et al.* 2009); (2) communities in which different types of primary producers occur in different (micro-)habitats that are sufficiently close in space for resource competition to occur among producers, e.g. benthic vs. pelagic lake habitats (Vadeboncoeur *et al.* 2005) or terrestrial canopy vs. understory habitats (Pringle & Fox-Dobbs 2008); and (3) communities in which energy flow is dominated by a few species in alternative food chains, e.g. the

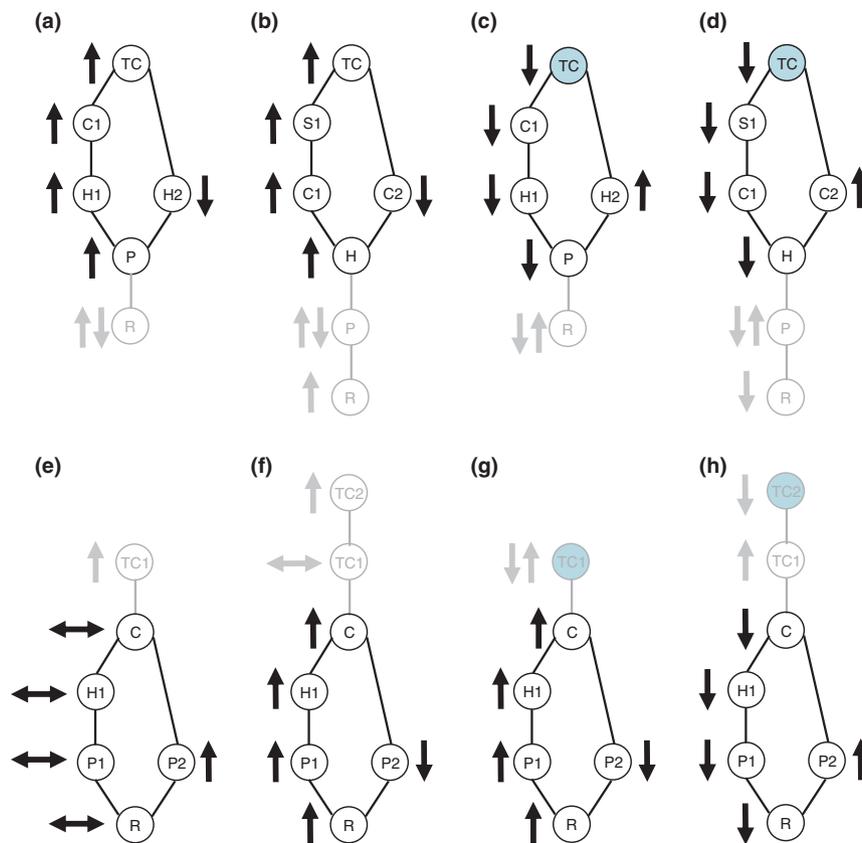


Figure 3 Equilibrium responses to enrichment (a, b, e, f) and to increased top consumer mortality (c, d, g, h; top consumer highlighted in blue) of a looped 4–3 web module with one or two additional trophic levels below (a–d) or above (e–h). S_1 = secondary carnivore in chain 1; TC_1 = consumer one trophic level above the 4–3 module; TC_2 = consumer two trophic levels above the 4–3 module. Other symbols and arrows as in Fig. 1. Response patterns were derived analytically assuming linear functional responses. To focus on the looped 4–3 module other compartments are outlined in grey. Responses of some compartments outside the looped module are parameter dependent.

‘sardine’ vs. ‘anchovy’ pathways in coastal upwelling systems (Cury *et al.* 2008). Our analyses can be easily extended to food webs where energy pathways branch at higher trophic levels or reconnect below the apex predator level. The modelling framework is therefore applicable to other food web topologies, including webs where parallel energy channels are based on living plants and on plant detritus respectively (see below).

Our analysis suggests that the presence of two alternative energy pathways affects food web responses to bottom-up and top-down forcing in easily predictable ways. Surprisingly few and simple rules govern the equilibrium responses of the investigated food webs, and only two pieces of information are needed to understand most of these responses: (1) Is the food web branched or looped? and (2) Are the component food chains (counted from the branching node) of odd or of even length? These two pieces of information fully determine the responses of all food web members when functional responses are linear, which is an appropriate approximation when small changes in equilibrium densities are investigated. When functional responses are saturating and equilibria are stable, the response patterns are very similar, with only a few deviations occurring in some populations that remain constant in the linear case (Figs 1 and 2). Note, however, that, when functional responses are far from saturation, predicted deviations from constancy would be weak and therefore difficult to distinguish from true constancy in

empirical data. In summary, our analyses suggest that the equilibrium behaviour of food webs with two alternative energy pathways can be closely predicted from easily measured descriptors of food web topology.

Energy flow along odd vs. even chains

A pervasive pattern emerging from our analysis is that energy flow along even chains has precedence over energy flow along odd chains. In branched odd–even webs top consumers of the odd chain remain constant or decrease with enrichment, while top consumers of the even chain always increase. This pattern is even more pronounced in looped odd–even webs, where all members of the even chain increase with enrichment, whereas at least one member of the odd chain decreases and eventually may go extinct. With respect to the simplest looped odd–even web, the intraguild predation web (Fig. 1i), a corollary of this finding is that the frequently predicted extinction of the intraguild prey with enrichment (Diehl & Feissel 2000; Mylius *et al.* 2001) is not the consequence of a direct, energetic shortcut to the top consumer (bypassing the longer 3-level chain). On the contrary, if the even chain in a looped odd–even web is longer than the odd chain (Fig. 1k), it is nevertheless a member of the (shorter) odd chain that may go extinct, highlighting the precedence of energy flow along even chains.

The primacy of energy flow along even chains appears to extend to food webs where energy pathways branch at higher trophic levels and/or reconnect below the apex predator level, as illustrated in Fig. 3. Importantly, odd vs. even chain length is defined starting from (and including) the branching node. This makes intuitive sense, because it is the branching node that transmits top-down effects between chains. Starting from the branching node, enrichment thus increases energy flow along pathways of length 4 (Fig. 3a, b, e) and 6 (Fig. 3f), respectively, whereas energy flow is constant (Fig. 3e) or decreases (Fig. 3a, b, f) along pathways of length 3 and 5.

Comparisons with food chain theory

The responses of food webs with alternative energy pathways to nutrient enrichment and top consumer mortality often deviate from predictions of classical food chain theory. The latter is particularly evident in looped odd–even webs, in which all trophic levels in the even chain increase with enrichment and decrease with increasing top consumer mortality. This is a remarkable phenomenon in models with purely prey-dependent functional responses. It suggests that, if dominant alternative pathways of energy flow in real food webs are frequently of odd vs. even length, one would not expect to observe community-wide trophic cascades (*sensu* Polis *et al.* 2000). More generally, it seems to be a rule that summed trophic level responses of food webs with one or more loops do not respond to enrichment in the way predicted for simple food chains (Fig. 1i–n; see also Abrams 1993; Hulot & Loreau 2006).

The propagation of effects through looped web structures may be relevant to a remarkable phenomenon described from many coastal upwelling areas, the regime shift between anchovy and sardine dominated food webs (Alheit & Niquen 2004; Barange *et al.* 2009). Available data suggest that the involved components can be described as a looped 5–5 web linking nutrients and top predators via a flagellate–small zooplankton–sardine chain and a diatom–large zooplankton–anchovy chain (Lingen *et al.* 2006). Scattered evidence indicates that periods of intensified upwelling (= nutrient enrichment) are accompanied by increased abundances of all members of the nutrient–diatom–large zooplankton–anchovy–top predator chain and by alternating changes along the other chain (flagellates decrease, small zooplankton increases, sardines decrease) (Verheye 2000; Taylor *et al.* 2008; Montecino & Lange 2009). While such an enrichment response is clearly compatible with a looped 5–5 web (Fig. 1n) other explanations have been proposed, including one involving mutual intraguild predation between anchovies and sardines (Irigoien & Roos 2011). Importantly, both hypotheses assume a looped topology of competing food chains reconnected by consumers.

Also in branched webs, deviations from food chain theory are commonplace. For example, the top consumer controlling the response of a branched web to enrichment need not be the top consumer of the longest food chain. If the odd chain in a branched odd–even web is longer than the even chain, the summed trophic level responses to enrichment will differ markedly from the predictions of food chain theory; i.e. the highest trophic level (and every second level below) will remain constant or even decrease rather than increase, and the second highest trophic level (and every second level below) will increase rather than remain constant (Fig. 1c, g). These observations may lend rigour to the discussion of when a

top trophic level should be considered ‘functional’ in the sense of exerting a regulating influence on a food web (Power 1992).

Indirect antagonisms and mutualisms

Vandermeer (1980) conjectured that herbivores in different food chains should be indirect mutualists and carnivores indirect antagonists, the interactions being mediated by resource competition between the respective food chains’ primary producers. While apparent competition between chains precludes such regularities in looped webs, our study supports the conjecture for herbivores in branched webs, both of which usually respond to enrichment or top consumer mortality in the same direction (indicating mutualism). In contrast, however, carnivores in different chains of branched webs often respond in opposite or orthogonal directions, indicating antagonism or independence (Figs 1d–h and 2e–l). A much clearer pattern in branched webs is instead that, independent of trophic level, top consumers of odd chains are indirect mutualists, and top consumers of even chains are indirect antagonists, of the other chain’s top consumer. This frequently leads to counter-intuitive consequences of harvesting. For example, in branched webs, harvested top consumers may increase while non-harvested top consumers in the other chain decrease, which cautions against harvesting as a straightforward management tool. In line with this Yodzis (1998) concluded from an analysis of the Benguela food web that harvesting of fish eating marine mammals may frequently reduce fisheries returns.

Empirical evidence of cascading effects, including counter-intuitive ones, from apex predators into other food chains is indeed accumulating (Kerfoot 1987; Ellis *et al.* 2011; Estes *et al.* 2011). For example, Anthony *et al.* (2008) reported that a sea otter decline on Aleutian islands was, unexpectedly, accompanied by increased bald eagle production. Sea otter declines are known to cascade to the dominant primary producers, kelp, via release of herbivorous sea urchins (Estes & Palmisan 1974). Anthony *et al.* therefore expected bald eagles to suffer from the sea otter decline, mediated through a decline in kelp forest habitat and associated prey fish production. However, the authors also observed a diet shift in bald eagles from fish to sea birds, suggesting an alternative scenario compatible with the response of a branched 3–2 web to increasing top consumer mortality in the even chain (Fig. 2d). Sea urchins are a food of several sea birds (Estes *et al.* 2009; Bustnes *et al.* 2010). Thus, the increase in sea urchins following the otter decline may have increased energy flow up the 3-linked urchin–sea bird–bald eagle chain.

Incorporation of detrital pathways

In many ecosystems a major fraction of primary production enters the food web as detritus rather than as living producer biomass (Hairston & Hairston 1993; Wetzel 1995; Cebrian 1999). A ‘green world’ view of trophic dynamics has therefore been criticised and it has been argued that prediction of bottom-up and top-down effects in real ecosystems requires consideration of detrital pathways (Polis & Strong 1996; Moore *et al.* 2004). We have deliberately studied a model of pure grazing chains, which makes the most general assumptions about interactions. Specifically, all interactions are reciprocal, i.e. energy flow between two compartments depends on the densities of both the resource and the consumer, whereas the link

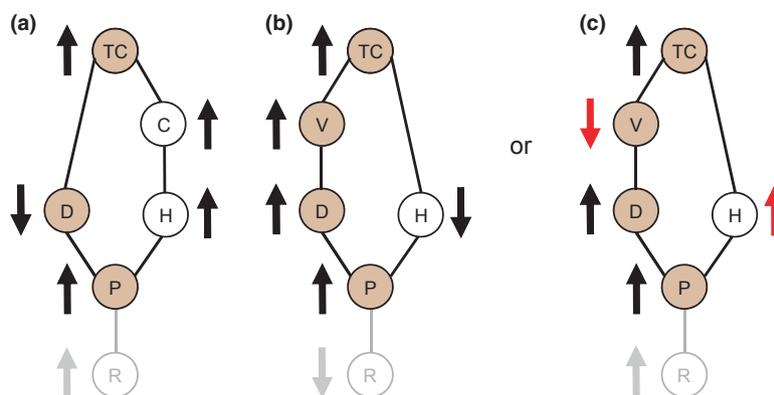


Figure 4 Equilibrium responses to enrichment of 4–3 webs with one detritus-based pathway. *D* = detritus; *V* = detritivore. Other symbols and arrows as in Fig. 1. To focus on the 4–3 module the nutrient is outlined in grey. The detritus chain is highlighted in brown. Response patterns were derived analytically assuming linear functional responses and donor-controlled input of dead plant material $m_p P$ to the detritus compartment. (a) Detritus in 3-link chain: 4–3 module responds like a 4–3 web with two grazing chains (Figs 1k and 3a). (b, c) Detritus in 4-link chain: responses of V^* and H^* depend on the top consumer's attack rates on detritivores (a_{VTC}) and herbivores (a_{HTC}) relative to the detritivores' and herbivores' mortality rates (m_V and m_H). (b) When $\frac{a_{VTC}}{m_V} < \frac{a_{HTC}}{m_H}$, the 4–3 module responds like a 4–3 web with two grazing chains. (c) When $\frac{a_{VTC}}{m_V} > \frac{a_{HTC}}{m_H}$ the response deviates as indicated by red arrows.

from plants to plant detritus is donor controlled. Topology, however, need not differ between grazing and detritus chains, and any food web including a grazing and a detritus chain (e.g. Fig. 4) has a 'topological twin' consisting of two grazing chains that branch off at the plant level (e.g. Fig. 3a). An obvious question is then whether the topological rules derived in this article extend to food webs including a detrital pathway.

While a thorough exploration of this issue is beyond the scope of this article, preliminary analyses suggest that responses of detrital food webs are also governed by simple, topological rules. For example, webs with a detritus pathway respond similarly to enrichment as do pure grazing webs when the plant-detritus link is in an odd chain (unpublished results, Fig. 4a), but can respond differently (though in predictable ways) when the plant-detritus link is in an even chain (Fig. 4b, c; chain length is counted from and includes the branching node in all cases). The important message is that conversion of a single link to donor control is all that is needed to apply our model to ecosystems with a detritus pathway, and that equilibrium responses of detritus webs are, again, related to topology. For the particular topology in Fig. 4b/c, numerical analyses of a more sophisticated model (including top predator switching and saturating functional responses) corroborate the existence of the depicted two alternative response patterns to nutrient enrichment (Attayde & Ripa 2008).

Outlook

A challenge in the application of our approach to real ecosystems is the identification of major interaction pathways and their simplification to tractable branched or looped webs. This will require decisions on how to aggregate species into functional groups and which feeding links to neglect. From a conceptual perspective, it seems most meaningful to distinguish between 'fast' and 'slow' energy channels (consisting of strong vs. weak interactions respectively). Coupling to slow channels buffers oscillatory tendencies in fast channels, and has been proposed to be the most critical, stabilising structural component of real food webs (Rip *et al.* 2010; Rooney & McCann 2012). From an empirical perspective, quanti-

tative approaches such as multivariate autoregressive models (Ives *et al.* 2003; Hampton *et al.* 2006) and structural equation modelling (Wootton 1994; Gotelli & Ellison 2006) applied to observational and experimental data can guide food web simplification. Ideally, tests of model predictions will involve carefully designed new experiments, but existing ones could be re-analysed based on a functional grouping into dominant interaction pathways. We caution, however, that many manipulative experiments with natural communities typically capture transients rather than the equilibrium states addressed by theory (Englund & Moen 2003). Long-term observational data of systems undergoing environmental changes may therefore be an important testing ground for our approach.

We conclude that the recently advocated reduction of food webs to major pathways of energy flow (Fulton 2010; Shin *et al.* 2010) holds promise. While there remain both practical and conceptual challenges when applying this approach to real food webs, we believe that our study assembles and organises important theoretical insights into how topology affects food web dynamics, something food web theory has long been striving for. Given the productive impact of 'simple' food chain theory on ecology in the past, we propose that models with alternative energy pathways will serve both ecosystem and community ecologists as a useful conceptual framework for the future.

ACKNOWLEDGEMENTS

The research has been supported by the German Science Foundation (DFG grant no. DI745/7–1). We thank Stephano Allesina for comments on the manuscripts and intense discussions, as well as two anonymous referees for helpful comments on the manuscript.

AUTHOR CONTRIBUTIONS

All authors contributed to the conceptual ideas and the design of the modelling work. SW performed all numerical analyses and pro-

vided most of the analytical results. SD and AdR suggested additional analyses and checked analytical results. SW wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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Editor, Andrew Beckerman

Manuscript received 12 March 2012

First decision made 12 April 2012

Manuscript accepted 28 May 2012