

Adaptive foraging and flexible food web topology

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ABSTRACT

Ecological studies of direct and indirect interactions in food webs usually represent systems as unique configurations, such as keystone predation, exploitative competition, trophic cascades or intra-guild predation. Food web dynamics are then studied using model systems that are unique to the particular configuration. In an endeavour to develop a more unified theory of food web structure and function, we explore here model systems in which a consumer species forages adaptively on two resource species along a gradient of environmental productivity and predation mortality. We explore the nature of trophic interactions under three different assumptions about what constitutes a resource and the spatial distribution of resources. We first examine a consumer (herbivore) feeding on two resources (plants) that are distributed randomly in the environment. We extend this to the case in which each plant resource occurs in a discrete patch. Finally, we examine a variant of the patch selection case in which the consumer (an omnivore) feeds within and among two trophic levels. Our modelling shows that single systems of predators, adaptive herbivores and resources can display food chain and food web topologies under different levels of productivity and predator abundance. For example, adaptive omnivory causes the exploitative competition, linear food chain and multi-trophic level omnivory to be displayed by a single system. Thus, different food web topologies, normally thought to be unique configurations in nature, can be different manifestations of the same dynamical system. This suggests that tests for top-down or bottom-up control by manipulating predator abundance or nutrient supply to resources could be confounded by topological shifts in the system itself.

Keywords: adaptive foraging, food chain, food web, food web structure, omnivory, patch choice.

INTRODUCTION

Ecological studies of direct and indirect interactions in food webs typically represent systems in terms of simple but altogether unique configurations or topologies (e.g. Menge, 1995; Abrams *et al.*, 1996; McCann *et al.*, 1998). These topologies are then classified by the nature of the dominant ecological interaction – for example, keystone predation, exploitative competition, apparent competition, trophic cascade, intra-guild predation (Menge, 1995; Abrams *et al.*, 1996; McCann *et al.*, 1998). There is an advantage to using

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this kind of taxonomy when developing ecological theory. Models that characterize the essence of a dominant interaction using a conceptually simple species configuration can lead to powerful insights about the way direct and indirect effects may play themselves out over time. The downside to such an approach is that one is left with the impression that each topologically unique system is a fixed entity requiring a correspondingly unique model formalism to describe its dynamics. Such a perspective precludes any hope of developing a more unified theory of direct and indirect interactions in ecological systems.

We show here, using principles of adaptive foraging, that topologically different food web structures may in fact be different manifestations of the same dynamical system. Reaching this conclusion, however, requires a slight shift from the normal approach used to model dynamics of ecological food webs. Normally, a dynamical systems model is formalized to represent some specific configuration of interacting species. The dynamics of that system are then examined by altering factors intrinsic to the species populations themselves (e.g. parameters describing population growth rates and magnitudes of interaction strengths, or shapes of functional responses and the nature of density dependence). One then ascertains whether the qualitative structure of the system remains stable to quantitative changes in intrinsic factors.

Such an approach, however, overlooks a potentially rich range of qualitative outcomes that may arise when exploring the effects of changing extrinsic factors (e.g. changes in predator and resource abundance) on the structure of systems. Specifically, consumers are known to alter their resource choice in the face of changing resource and predator abundances, which has implications for community structure and dynamics. The interplay between diet choice and consumer–resource dynamics has been studied intensively under various assumptions on population dynamics and spatial distribution of resources (e.g. Tansky, 1978; Teramoto *et al.*, 1979; Gleeson and Wilson, 1986; Abrams, 1987, 1999; Abrams and Matsuda, 1993; Colombo and Křivan, 1993; Fryxell and Lundberg, 1993, 1994, 1997; Matsuda *et al.*, 1993; Křivan, 1996, 1997, 1998; Holt and Polis, 1997; McCann and Hastings, 1997; Boukal and Křivan, 1999; Genkai-Kato and Yamamura, 1999; Křivan and Sikder, 1999; Luttbeg and Schmitz, 2000; van Baalen *et al.*, 2001; Křivan and Eisner, 2003). We extend this line of research by considering how consumer adaptive foraging in response to such extrinsic factors can lead to topologically different states of a food web during the time evolution of the system's dynamics. This problem, although tightly related to previous studies, has not been, to our knowledge, addressed explicitly. Moreover, using a uniform modelling approach throughout this article allows us to compare effects of basic behavioural and population models on food web topologies. We show here that there may not be a single rigid topological structure that characterizes interactions among a given complement of species in a food web.

This has important implications for conclusions drawn from perturbation experiments that test for top-down or bottom-up control in food webs by manipulating predator abundance or nutrient supply to resources. The implicit assumption during the execution of these kinds of field experiments is that the feeding linkages among the species in the food web (food web topology) remains intact whenever nutrients or predators are manipulated. We show here that this assumption may not always hold. Thus, any conclusions that one draws about important drivers of trophic control in food webs (i.e. top-down *vs* bottom-up control in a system) may be confounded by shifting food web topology.

The core module in all of our modelling is a consumer–resource system in which a consumer species utilizes two resource species. We then explore the nature of trophic

interactions under three different assumptions about what constitutes a resource and the spatial distribution of resources. We first examine the case in which an adaptive consumer (herbivore) feeds on two resources (plants) that are distributed randomly in the environment. We then extend this to the case in which each resource occurs in a discrete patch and predators also display adaptive foraging behaviour. Finally, we examine a variant of the patch selection case in which the top predator (an adaptive omnivore) feeds within and among two trophic levels. We assume that the resource species have different nutritional value and that the adaptive consumer species is subject to mortality risk from a top predator species. We assume that consumers trade-off foraging against avoidance of predation mortality in ways that maximize per capita fitness, measured as net per capita reproduction. We characterize the link between resource distribution and consumption using the familiar prey and patch models of diet selection (Stephens and Krebs, 1986). Such models assume that consumers are completely omniscient.

RANDOM RESOURCE DISTRIBUTION

This scenario is based on the assumption that consumers are limited by search and handling time and encounter resources randomly, a case for which the classic prey model of adaptive foraging (Stephens and Krebs, 1986) is an appropriate descriptor of consumer–resource interactions. We explore how increasing consumer mortality caused by predation (i.e. the predation gradient) alters resource selection and hence food web topology as the consumer and resource species undergo dynamics.

We denote the primary resource as R_1 , the secondary resource as R_2 and consumers as C . In foraging jargon, resource 1 is the preferred resource and resource 2 is an alternative. Population dynamical consequences of the prey model have been studied in detail by, for example, Fryxell and Lundberg (1994, 1997), Křivan (1996), van Baalen *et al.* (2001) and Křivan and Eisner (2003). Here, we use an extension of the model of van Baalen *et al.* (2001), who assumed that the abundance of the alternative resource is relatively constant in the environment. This effectively means that uptake of the alternate resource by consumers is exactly compensated by resource production. This simplification is justified for many arthropod consumers because they can rely on alternative food such as pollen or nectar, the availability of which is unlikely to be influenced by the consumption (van Rijn and Sabelis, 1993; van Rijn and Tanigoshi, 1999). The presence of the alternative resource influences the consumer per capita growth rate, which, in turn, has consequences for the abundance and the dynamics of the primary resource population. The following model (without resource density dependence) was proposed by van Baalen *et al.* (2001):

$$\begin{aligned} \frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K} \right) - \frac{\lambda_1 R_1}{1 + h_1 \lambda_1 R_1 + u_2(R_1) h_2 \lambda_2 R_2} C \\ \frac{dC}{dt} &= C \left(\frac{e_1 \lambda_1 R_1 + e_2 u_2(R_1) \lambda_2 R_2}{1 + h_1 \lambda_1 R_1 + u_2(R_1) h_2 \lambda_2 R_2} - m \right) \end{aligned} \quad (1)$$

Here r_1 denotes resource 1 per capita growth rate, K is the resource 1 carrying capacity, e_i is the proportionality constant that describes the efficiency with which resources are converted to new consumers, h_i is the handling time an average consumer needs to process a unit of resource i , λ_i are the cropping rates of resource i by a searching consumer, and m is the consumer mortality rate which is dependent on predator (P) density ($m = m(P)$).

The above model assumes that the first resource is more profitable than the second resource ($e_1/h_1 > e_2/h_2$). Control parameter u_2 describes diet choice,

$$u_2(R_1) = \begin{cases} 0 & \text{if } R_1 > R_1^* \\ [0, 1] & \text{if } R_1 = R_1^* \\ 1 & \text{if } R_1 < R_1^* \end{cases}$$

where

$$R_1^* = \frac{e_2}{\lambda_1 (e_1 h_2 - e_2 h_1)} \quad (2)$$

These are well-known results of optimal diet selection theory, which extends to the case of diet selection for multiple resources (Werner and Hall, 1974; Charnov, 1976; Stephens and Krebs, 1986).

We now examine food web topology along the consumer mortality gradient. Depending on the consumer's diet choice, model (1) has two possible interior equilibria. Equilibrium E_2 corresponds to the case where consumers feed on the more profitable resource only, while equilibrium E_1 corresponds to the case of feeding on both resources (Fig. 1). Thus, equilibrium E_2 corresponds to a food chain topology, while E_1 corresponds to a food web with two resources. If the consumer cannot expect to produce sufficient numbers of offspring while feeding on resource 2 only to compensate for mortality, that is

$$m > e_2/h_2 \quad (3)$$

then both equilibria are in the region of the resource 1–consumer phase space where the food web topology is described as the linear chain (Fig. 1C and D). If the opposite inequality holds, then both equilibria are in the part of the phase space where food web topology is described as a food web (Fig. 1A and B). When resource limitation is strong (i.e. K is small), then the population dynamics are effectively stabilized at an equilibrium (Fig. 1A and C). In this case, we tend to see consumers specialize on the preferred resource when predation mortality (m) is high, so that inequality (3) holds. Accordingly, the food web topology will be a linear chain (Figs 1C and 2). The reason for this is that the profitability of the alternative resource is low relative to the magnitude of predation mortality, such that it is not worth eating the alternative resource. However, when predation mortality is reduced, we should see the topology switch from a linear chain to a food web with two resources (Figs 1A and 2).

Enriching the system leads to resource 1–consumer low-amplitude fluctuations along a limit cycle due to the ‘paradox of enrichment’ (Fig. 1B and D; Rosenzweig, 1971). When the amplitude of the limit cycle is small (i.e. the resulting limit cycle does not reach the dashed vertical line in Fig. 1), the basic topologies associated with the different predation mortalities will be preserved (i.e. linear food chain under high mortality, food web topology under low mortality). For yet higher values of resource carrying capacity, the amplitude of the resulting limit cycle increases, but resource switching effectively sets the upper bound on the limit cycle amplitude by preventing it from crossing the switching line. Figure 1B and D show the limit cycle (dashed line cycle) for the resource–consumer model without switching and with switching (bold line cycle). It is clear that switching reduces fluctuations in population densities. When enrichment is strong enough so that the resulting limit

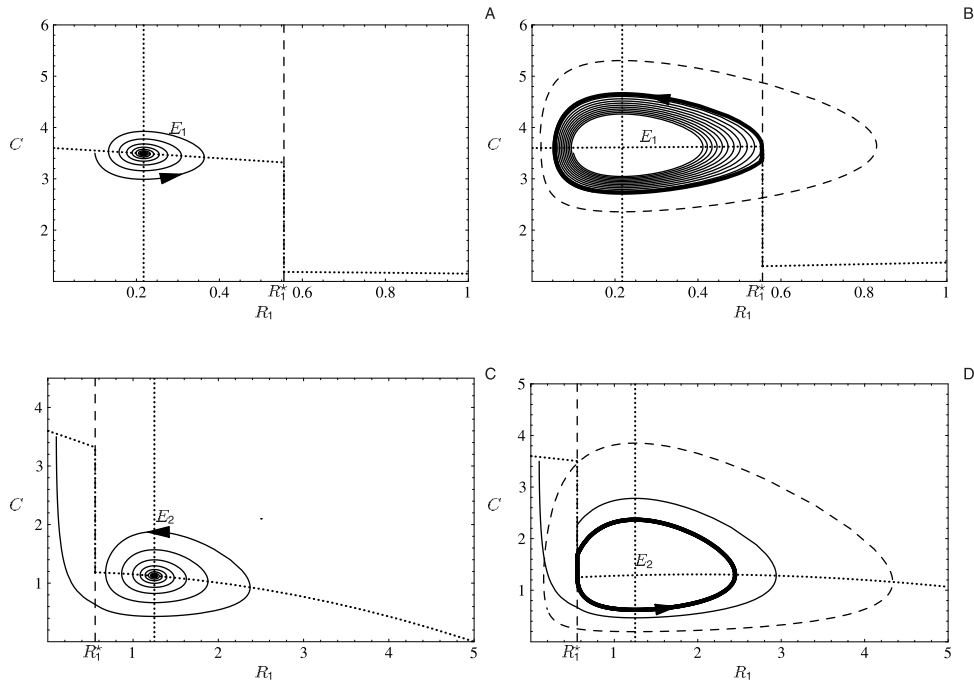


Fig. 1. Resource 1–consumer phase plane with resource and consumer isoclines (dotted lines) for optimal diet model. When the consumer mortality rate is low ($m = 0.4$), the resource 1 equilibrium density is lower than the switching density (A and B). In contrast, for higher resource mortality rates, the equilibril resource 1 density is above the switching density (C and D; $m = 1$). For low environmental productivities ($K = 5$ in A and C), population densities are stabilized at an equilibrium. Enriching the environment ($K = 20$ in B and $K = 9$ in D) leads to the emergence of a locally stable limit cycle (bold line) of smaller amplitude when compared with non-flexible consumers (dashed line cycle). Parameters: $R_2 = 10$, $r_1 = 1.2$, $e_1 = 1$, $e_2 = 0.1$, $h_1 = 0.2$, $h_2 = 0.2$, $\lambda_1 = 1$, $\lambda_2 = 1$.

cycle touches the switching line (as in Fig. 1B and D), then we should also see a periodic fluctuation from one food web topology to the other along the trajectory of the model system (1).

The topology fluctuates during the course of consumers and resources undergoing dynamics because, as resource abundance changes due to consumption, consumers must update their decision-making, which then feeds back on resource choice and ultimately on dynamics leading to new qualitative predictions about food web structure. This is an explicit consequence of blending two different organizational scales (i.e. behavioural vs population) in a single dynamical model.

The implication for field research is that manipulating mortality of consumers by predation (i.e. changing predator density) should not only cause a reduction in consumer density, but it should also alter food web topology to the extent that consumers may no longer eat all of the available resource types. Enriching the environment will also cause changes in food web topology, but in this case the strength of interactions among consumers and resources will also vary as population dynamics undergo periodic fluctuations. Thus, field experiments that are not sampled over the longer term may arrive at

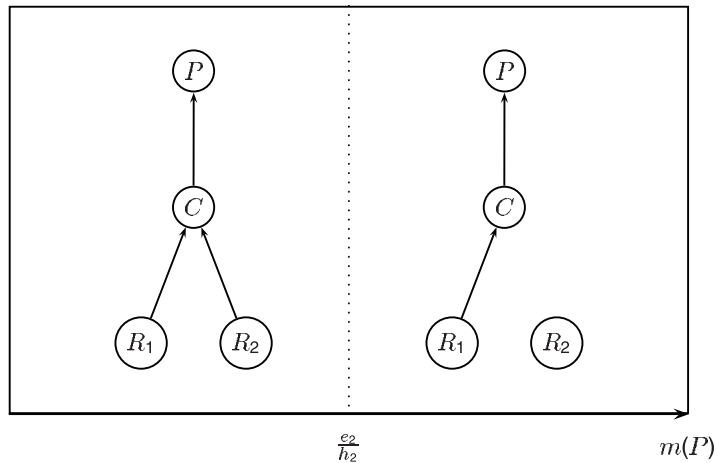


Fig. 2. Shift in the food web topology along the consumer mortality gradient for the optimal diet choice model with bottom-up regulation when the system is at the equilibrium. As consumer mortality increases due to increased predation, consumers switch (at $m = e_2/h_2$) from being generalist to more specialized feeding on the preferred food type.

a biased impression about the overall importance of cascading effects. Specifically, one may conclude that they either may be very important or extremely weak depending on the trajectory in abundance of species in each trophic level before the time of sampling. This analysis predicts that in environments with strong predation, consumers should be more specialized than in those where predation risk is low (Fig. 2). In essence, manipulating predation can cause the nature of the cascading effects in a single food web to be altered. Under certain levels of predation, we may see the system display a community cascade, *sensu* Polis (1999), in which the indirect effects of top predators are manifest widely among species of resources; under other levels of predation, we may see the same system switch to a species cascade, *sensu* Polis (1999), in which the indirect effects are manifest narrowly in a single resource species. This occurs despite the presence of other potential resources available in the system.

PATCHY RESOURCE DISTRIBUTION

We now turn to the case in which resources are distributed patchily in the environment. This case becomes a bit more complicated to model because it requires consideration of two types of predator hunting modes: sit-and-wait and actively hunting (Schmitz and Suttle, 2001).

In the case of the sit-and-wait predator, we will assume that consumers move from patch to patch to maximize their per capita fitness, but we also assume that top predators do not respond adaptively to changes in consumer use of patches. Predators merely cause a fixed level of mortality in one patch or another. To understand explicit linkages between model parameters and corresponding food web topologies, we assume instantaneous patch switching.

We then consider the case in which consumers select patches on the basis of resource quality and predation risk and predators actively hunt consumers as they move from one

patch to another. Thus, consumers and predators can be said to behave adaptively to each other's presence. Understanding interactions in this system requires taking a game-theoretic approach to identify the appropriate distribution of consumers between the two resource patches. This is because patch selection behaviour depends not only on resource abundance and predation mortality, but also on the density of conspecifics in a patch. This case can be examined by extending the ideal free distribution (IFD) concept originally defined for a single species (Fretwell and Lucas, 1970) to our two-species setting. This extension defines IFD for a predator-prey system as a Nash-Pareto (Křivan, 1997; Hofbauer and Sigmund, 1998) equilibrium of the corresponding game.

In any case of patch selection, consumers face a trade-off in that feeding on resources in one patch precludes them from physically being present in and feeding on resources in another patch. Thus, the most constraining factor on intake rate is the effort consumers expend feeding in a particular patch.

Predators do not actively hunt consumers

In the interest of keeping our models mathematically simple, we start our analyses under the assumption that resource handling times are zero. This allows us to consider population dynamics using an extension of the classical Lotka-Volterra consumer-resource model as a generic framework (Fryxell and Lundberg, 1994, 1997; Křivan, 1997):

$$\begin{aligned}\frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1}\right) - u_1 \lambda_1 R_1 C \\ \frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2}\right) - u_2 \lambda_2 R_2 C \\ \frac{dC}{dt} &= (e_1 \lambda_1 R_1 - m_1) u_1 C + (e_2 \lambda_2 R_2 - m_2) u_2 C\end{aligned}\tag{4}$$

In this model, the control u_i ($i = 1, 2$) specifies the proportion of an average consumer's lifetime that is spent feeding in patch i , thus $u_1 + u_2 = 1$. Following Křivan (1997), who analysed a similar system but without resource density dependence, we will assume that adaptive consumers maximize their net per capita reproduction rate ($dC/(Cdt)$), which leads to the following choice of controls. If $e_1 \lambda_1 R_1 - m_1 > e_2 \lambda_2 R_2 - m_2$, then patch 1 is more profitable ($u_1 = 1$); if the opposite inequality holds, then all consumers feed in patch 2 ($u_1 = 0$).

If we now assume that consumers move from a patch of one resource type to a patch of another resource type in such a way that consumer fitness is maximized, we arrive at two 'pure' strategies (i.e. stay in patch 1 only or stay in patch 2 only) with the corresponding equilibria

$$\begin{aligned}R_1 &= \frac{m_1}{e_1 \lambda_1} \\ R_2 &= K_2 \\ C &= \frac{r_1 (e_1 \lambda_1 K_1 - m_1)}{e_1 K_1 \lambda_1^2}\end{aligned}$$

and

$$R_1 = K_1$$

$$R_2 = \frac{m_2}{e_2 \lambda_2}$$

$$C = \frac{r_2(e_2 K_2 \lambda_2 - m_2)}{e_2 K_2 \lambda_2^2}$$

If both equilibria are positive – that is, resource productivities are high enough ($K_i > m_i/(e_i \lambda_i)$) – then it turns out that neither of these equilibria is feasible. This is because the first equilibrium (computed under the assumption that consumers stay in patch 1) lies in the upper triangular part of the resource 1–resource 2 phase space (this equilibrium is denoted as E_1 in Fig. 3B and C) where all animals should occupy patch 2 only. Similarly, the second equilibrium (computed under the assumption that consumers stay in patch 2) lies in the part of the resource 1–resource 2 phase space where all consumers should occupy patch 1 only (equilibrium E_2 in the lower triangular part of the phase space in Fig. 3B).

The population trajectories of model (4) tend to converge on the first equilibrium (denoted as E_1 in Fig. 3) whenever resource densities are such that the consumer fitness in patch 1 is higher than that in patch 2 (i.e. when resource densities are in the lower right triangle of the resource 1–resource 2 phase space, $e_1 \lambda_1 R_1 - m_1 > e_2 \lambda_2 R_2 - m_2$); otherwise, densities converge to the second equilibrium (denoted as E_2 in Fig. 3). Thus, trajectories are pushed from both sides to the IFD plane – the location in the phase space where fitness in both patch types equalizes

$$e_1 \lambda_1 R_1 - m_1 = e_2 \lambda_2 R_2 - m_2$$

which is presented graphically in Fig. 3A as a shaded plane and in Fig. 3B and C as a dashed line. Numerical analyses of population dynamics of this system indicate that the trajectories will converge to a new equilibrium point on the IFD plane (denoted as E_{IFD} in Fig. 3B). This equilibrium point lies at the intersection of the IFD line (dashed line in Fig. 3) with a curve that is obtained by varying consumer patch preference u_1 from zero to one (see dotted line in Fig. 3B and C). This implies that the IFD distribution of consumers at this equilibrium is

$$\frac{u_1^*}{u_2^*} = \frac{r_1 e_2 \lambda_2^2 K_2 (e_1 \lambda_1 K_1 - m_1)}{r_2 e_1 \lambda_1^2 K_1 (e_2 \lambda_2 K_2 - m_2)}$$

Because the consumer IFD at the population equilibrium is a linearly decreasing function of consumer mortality rate in patches containing more profitable resource 1 (m_1 ; Fig. 4A), adaptive consumers will spend progressively more time in patches containing resource 2 as mortality rate when feeding on resource 1 increases. That is, we tend to see the emergence of a linear food chain configuration. Computing explicitly the interior equilibrium of model (4) and substituting the IFD for the controls u_i , we can solve explicitly for the equilibrium solution:

$$R_1^{\text{IFD}} = \frac{m_1}{e_1 \lambda_1}$$

$$R_2^{\text{IFD}} = \frac{m_2}{e_2 \lambda_2}$$

$$C^{\text{IFD}} = \frac{r_1(e_1\lambda_1K_1 - m_1)}{e_1K_1\lambda_1^2} + \frac{r_2(e_2K_2\lambda_2 - m_2)}{e_2K_2\lambda_2^2}$$

Note that without density dependence, the population dynamics will converge to the IFD plane but the equilibrium in this plane will not be asymptotically stable (Křivan, 1997).

So far we have assumed that the environmental carrying capacities in both patches are high enough to support viable populations in the patches. We now consider the case in which the productivity in one patch (say patch 1) is not sufficient to support consumers at positive densities ($K_1 < m_1/(e_1\lambda_1)$). This condition can arise if resource productivity itself is low or if predation risk is high relative to resource productivity, such that consumer mortality from either food shortage or predation exceeds consumer reproduction – in essence, the patch is a population sink. In this case, equilibrium E_2 belongs to the upper triangular part of the phase space where all consumers are in patch 2. Thus, E_2 is feasible and population dynamics settle at this equilibrium (Fig. 3C).

In this case, consumer–resource abundance at equilibrium can be qualitatively different depending on the consumer mortality rate in patch 1 (Fig. 4B). Thus, as predation mortality in patch 1 increases and remains unchanged in patch 2, we expect resource abundance in patch 1 to increase (solid line in Fig. 4B) – that is, a positive indirect effect of predators on resource 1 and little or no change in resource 2 (dashed line in Fig. 4B). Thus, we will see cascading effects along one feeding chain in the food web, which would appear as a species cascade if we were to sample resources in a field experiment, despite the fact that consumers utilize both resources.

The above analysis shows that manipulating resource carrying capacities and/or predation mortality on consumers will cause changes in food web topology (Fig. 5). If the predation mortality is high relative to resource carrying capacity in both patches (i.e. K_i/m_i low), then the system will not persist (Fig. 5). Alternatively, if both values are high, consumers will use both resource patches (i.e. the IFD food web). In the other cases, only the patch with the higher K_i/m_i will be used, and the food web topology becomes a linear food chain. The point is that bottom-up or top-down manipulations can lead to three different topological manifestations of the food web.

Predators actively hunt consumers and behave adaptively

Up until now we have considered interactions between consumers and their resources independently of predators. However, if consumers behave adaptively, their predators should also respond to changes in consumer behaviour (Lima, 2002). Changes in consumer behaviour will necessarily influence the per capita consumer mortality rate as well as predator-caused mortality risk in both patches. As a consequence, predators must respond to the changes in consumer dynamics caused by their presence in a community. This effectively results in a game between consumers and predators: consumers try to avoid predators by choosing a patch with low predation risk, while predators try to maximize their resource consumption by choosing the patch with highest consumer density. Computing an IFD in this case becomes more complicated because, as we explained above, the maximization of consumer fitness depends on the behaviour of predators and vice versa.

To gain some sense of the interplay that arises among predators, consumers and resources, we begin our analysis without considering population dynamics – that is, the

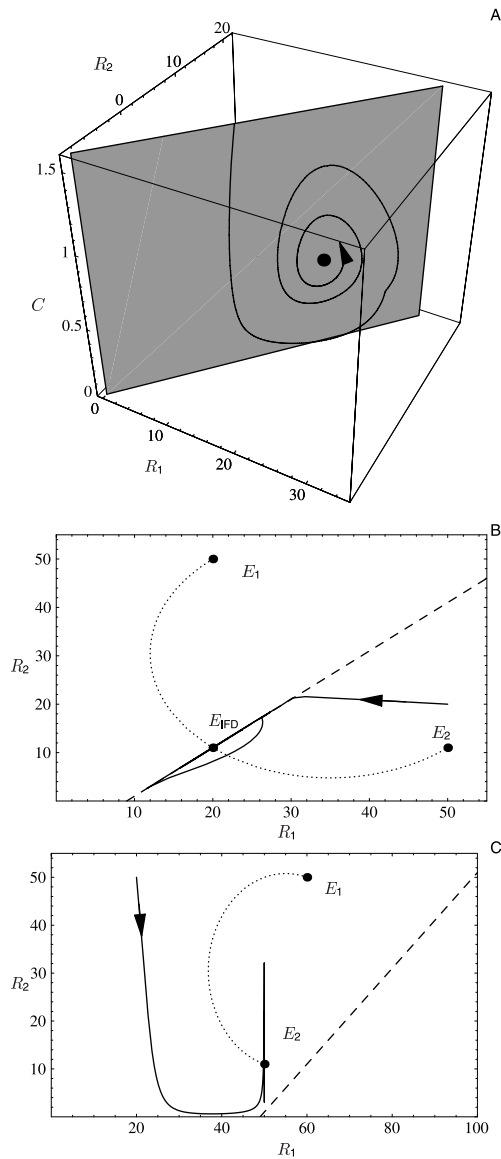


Fig. 3. Trajectories of patch model (4) which are driven by the optimal patch choice. For low consumer mortality rates in patch 1 ($m_1 < e_1 \lambda_1 K_1$, $m_1 = 2$), the trajectory converges to an equilibrium E_{IFD} at which the consumer population splits across both patches: (A) shows a trajectory in the three-dimensional phase space, while (B) shows the projection of the same trajectory to the resource 1–resource 2 phase space. When consumer mortality rate is high enough so that patch 1 cannot support consumers at positive levels ($m_1 > e_1 \lambda_1 K_1$, $m_1 = 6$), all consumers will be in patch 2 (C). The dashed line is the projection of the IFD plane to the resource 1–resource 2 density phase space. E_1 is the equilibrium of the linear food chain consisting of resource 1, consumers and predators. As consumers include resource 2 in their diet, the equilibrium moves along the dotted curve towards E_2 , which corresponds to a complete diet shift of consumers to resource 2. Parameters: $r_1 = 0.5$, $r_2 = 0.4$, $\lambda_1 = 1$, $\lambda_2 = 1$, $K_1 = 50$, $K_2 = 50$, $e_1 = 0.1$, $e_2 = 0.1$, $m_2 = 1.1$.

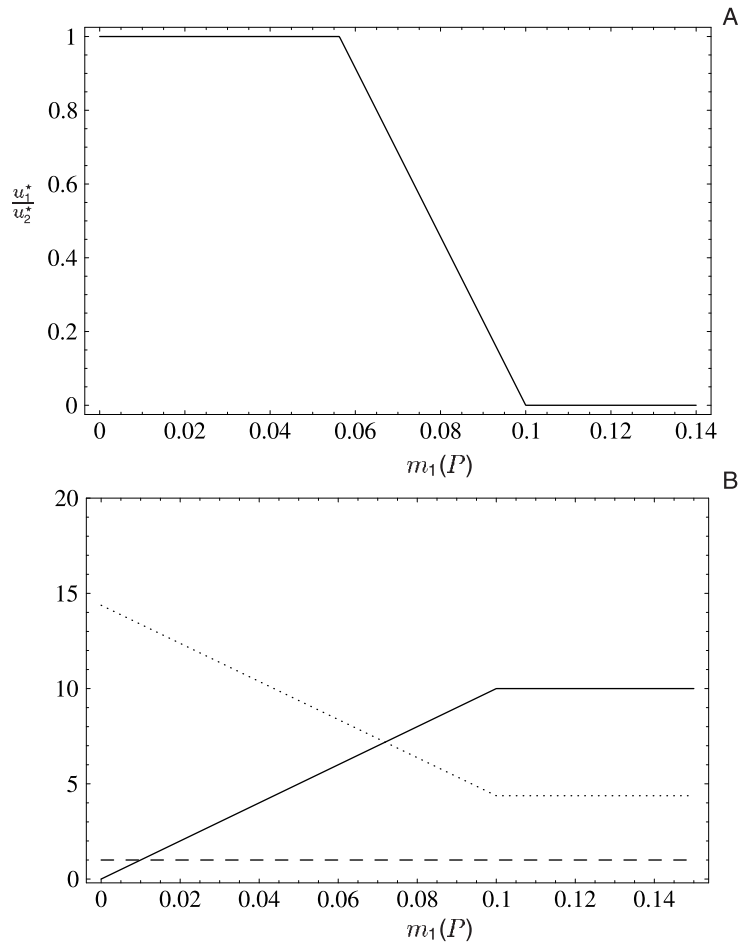


Fig. 4. Ideal free distribution of consumer population at the equilibrium as a function of consumer mortality rate in patch 1 (A). (B) shows dependence of the equilibril resource density in patch 1 (solid line) and in patch 2 (dashed line) and consumer density (dotted line) on mortality rate in patch 1 when consumers adaptively respond to predation risk. Consumer mortality in patch 2 (refuge) is fixed ($m_2 = 0.01$). Other parameters are: $r_1 = 1$, $r_2 = 0.5$, $\lambda_1 = 0.1$, $\lambda_2 = 0.1$, $K_1 = 10$, $K_2 = 8$, $m_2 = 0.01$, $e_1 = 0.1$, $e_2 = 0.1$.

behavioural ecology of the game. Once the static behaviour of the system is understood, we explore further how the interactions play themselves out when consumers and resources are allowed to undergo dynamics.

To model the interplay between consumers and their predators, we express explicitly the consumer per capita mortality rate as a function of the predator’s patch choice strategy. We assume that v_i specifies the proportion of an average predator’s lifetime that is spent in patch i ($i = 1, 2$). If P is the overall predator density and Λ_i is the predator cropping rate in patch i , then the mean per capita consumer mortality rate in patch i can be described as

$$m_i = \Lambda_i v_i P$$

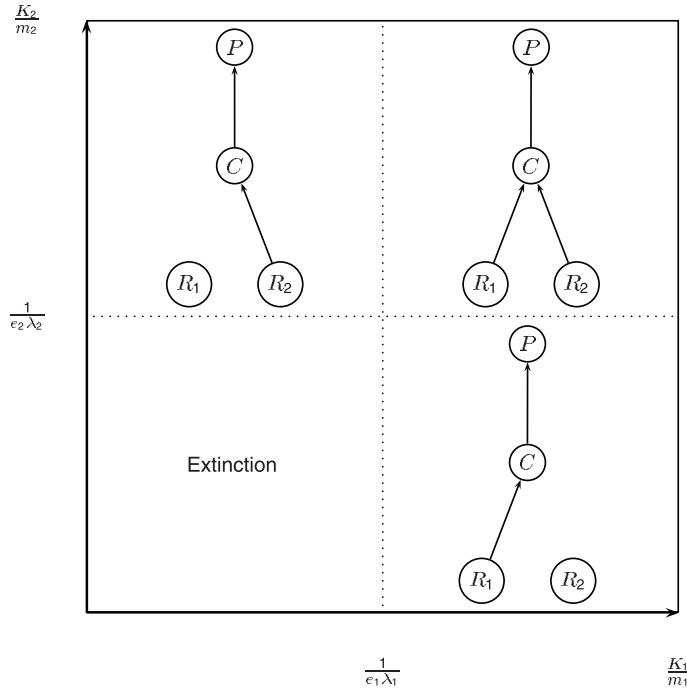


Fig. 5. Shift in the food web topology along the patch resource carrying capacity/predation mortality gradients for the optimal patch choice model with bottom-up regulation. When these ratios are low in both patches, the consumers cannot survive in either patch. When both ratios are high, consumers distribute at the equilibrium over both patches. In the other two cases, consumers feed only in the patch with the higher carrying capacity/mortality ratio and the corresponding food web topology is of the linear food chain.

To estimate fitness, we embed these functions in a model of population dynamics by substituting the above mortality rates to model (4). That is:

$$\begin{aligned} \frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1}\right) - u_1 \lambda_1 R_1 C \\ \frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2}\right) - u_2 \lambda_2 R_2 C \\ \frac{dC}{dt} &= (e_1 \lambda_1 R_1 - \Lambda_1 v_1 P) u_1 C + (e_2 \lambda_2 R_2 - \Lambda_2 v_2 P) u_2 C \end{aligned} \tag{5}$$

The fitness of an average consumer, expressed in terms of the per capita consumer population growth rate, is given by

$$(e_1 \lambda_1 R_1 - \Lambda_1 v_1 P) u_1 + (e_2 \lambda_2 R_2 - \Lambda_2 v_2 P) u_2 \tag{6}$$

and fitness of an average predator (measured again by the instantaneous per capita predator population growth $dP/(Pdt)$) is proportional to the predators' intake rate

$$\Lambda_1 u_1 v_1 + \Lambda_2 u_2 v_2 \tag{7}$$

The joint IFD for consumers and predators is computed in Appendix 1. It follows from this computation that provided predator density is at a level such that $e_1 R_1 \lambda_1 - P \Lambda_1 < e_2 \lambda_2 R_2 < e_1 R_1 \lambda_1 + P \Lambda_2$, the IFD for both consumer and predator is to occupy both patches and the corresponding food web topology includes both resources (see the middle region in Fig. 6). Appendix 1 shows that the corresponding IFD is given by

$$u_1^* = \frac{\Lambda_2}{\Lambda_1 + \Lambda_2}$$

and

$$v_1^* = \frac{e_1 \lambda_1 R_1 - e_2 \lambda_2 R_2 + \Lambda_2 P}{(\Lambda_1 + \Lambda_2) P}$$

If predator density is low (i.e. either $P \Lambda_1 < e_1 R_1 \lambda_1 - e_2 \lambda_2 R_2$ or $P \Lambda_2 < e_2 \lambda_2 R_2 - e_1 R_1 \lambda_1$, see lower and upper triangular region in Fig. 6), meaning that consumer mortality rates in both patches are low, then consumers and predators will occupy only the patch which provides consumers with higher per capita intake rate measured by the product $e_i \lambda_i R_i$. The corresponding food web topology is described by a linear food chain where consumers specialize on the more abundant resource. Thus, if enrichment experiments differentially alter the abundance of resource patches (e.g. increasing the abundance of resource 1 much more than resource 2), those experiments may also alter the topology of the system from a food web to a linear food chain. The implication for field research is that experimental tests of bottom-up control may again be confounded by the alteration of feeding linkages in the food web as a consequence of consumer and predator adaptive foraging.

We now relax the assumption that resource and consumer densities are held constant and consider the implication of the dynamic patch choice game between consumers and predators on population dynamics and on food web structure. We assume, without loss of generality, that the following inequality holds:

$$\frac{r_1 \Lambda_1}{\lambda_1} > \frac{r_2 \Lambda_2}{\lambda_2} \quad (8)$$

For example, if the respective cropping rates for consumers and for predators are identical in each patch (i.e. $\lambda_1 = \lambda_2$ and $\Lambda_1 = \Lambda_2$), then the above condition holds if the resource growth rate in patch 1 is higher than that in patch 2. Or, if patch 2 is a refuge for consumers, by which we mean that the predator cropping rate (Λ_2) there is either zero or negligible, then the above inequality again holds. Population dynamics in the upper triangular part of the state space where resource 2 is more abundant than resource 1 (Fig. 6) is described by a linear food chain ($u_1 = v_1 = 0$ in model (5)) where consumers specialize on resource 2. The corresponding equilibrium of this food chain is, however, not located in the upper triangular part of the resource 1–resource 2 phase space and it is not, therefore, feasible (see Appendix 1). Also, patch 1 is consumer-free in this case, so resource 1 grows logistically, and trajectories will enter the middle region of the phase space where it becomes more profitable to use both resources. That is:

$$e_1 \lambda_1 R_1 - P \Lambda_1 < e_2 \lambda_2 R_2 < e_1 \lambda_1 R_1 + P \Lambda_2$$

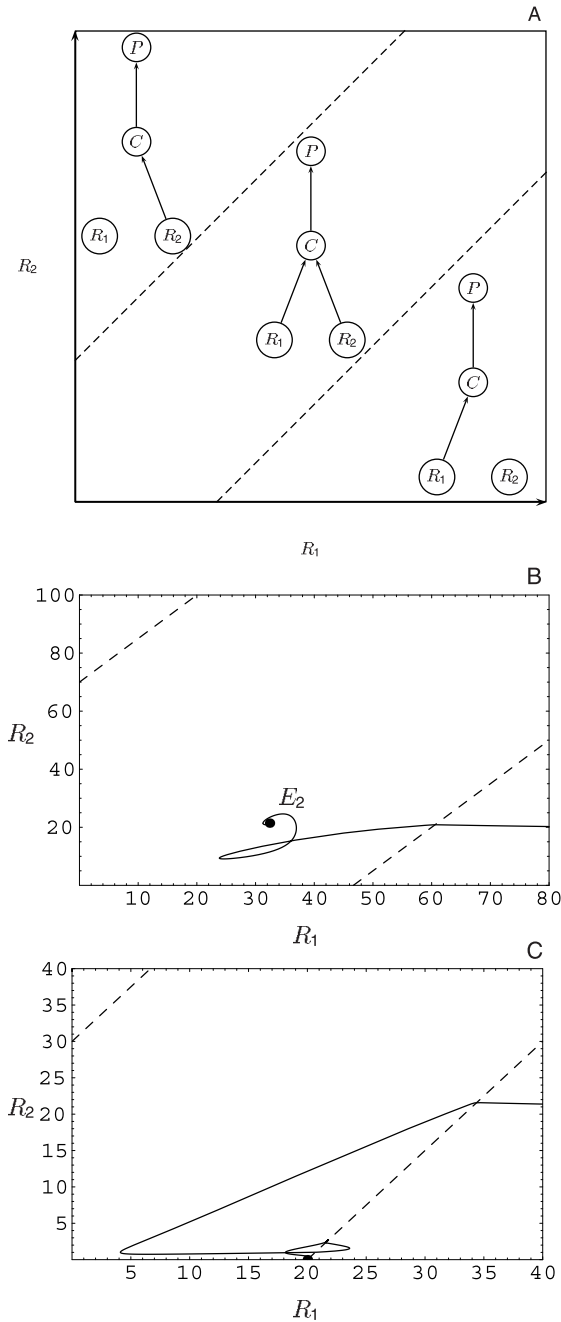


Fig. 6. Food web topologies and population dynamics for the patch model in which both consumers and predators behave adaptively. (A) shows the food web topologies along the resource gradients. (B) and (C) show corresponding population dynamics. (B) assumes that the equilibrium E_2 is in the middle region ($P = 7$) of the phase space, while (C) assumes that this equilibrium is not positive ($P = 3$). Parameters: $r_1 = 1.5$, $r_2 = 0.5$, $\lambda_1 = \lambda_2 = 1$, $e_2 = 0.1$, $e_1 = 0.15$, $\Lambda_1 = \Lambda_2 = 1$, $K_1 = 40$, $K_2 = 50$.

In this middle region of the phase space, both predator and consumer populations co-exist in both patch types in accordance with the above derived IFD. The corresponding food web topology includes both resources and the population dynamics are described by substituting the IFD (see Appendix 1) in model (4), which implies:

$$\begin{aligned}\frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1}\right) - \frac{\lambda_1 \Lambda_2}{\Lambda_1 + \Lambda_2} R_1 C \\ \frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2}\right) - \frac{\lambda_2 \Lambda_1}{\Lambda_1 + \Lambda_2} R_2 C \\ \frac{dC}{dt} &= C \left(\frac{e_1 \lambda_1 \Lambda_2 R_1 + e_2 \lambda_2 \Lambda_1 R_2}{\Lambda_1 + \Lambda_2} - \frac{\Lambda_1 \Lambda_2}{\Lambda_1 + \Lambda_2} P \right)\end{aligned}$$

Appendix 1 shows that provided

$$\frac{e_1 K_1 \lambda_1 \Lambda_2 + e_2 K_2 \Lambda_1 \lambda_2}{\Lambda_1 \Lambda_2} > P > \frac{K_1 e_1 \lambda_1 (r_1 \lambda_2 \Lambda_1 - r_2 \lambda_1 \Lambda_2)}{r_1 \lambda_2 \Lambda_1^2} \quad (9)$$

then there exists an interior equilibrium of the above model which is denoted as E_2 in Appendix 1 and in Fig. 6B. As predator density decreases, the equilibrium level of resource 2 decreases due to increasing apparent competition between resources [because of our assumption (8), which implies that at low predator densities consumer 2 is outcompeted from the system; see formula (A2) in Appendix 1]. At the moment when condition (9) ceases to hold, the resource 2 equilibrium level is zero and for yet lower predator densities the corresponding population equilibrium is as shown in Fig. 6C.

In the lower triangular region of the resource 1–resource 2 phase space, the population dynamics are described by a linear food chain with resource 2 and, because the corresponding equilibrium does not belong to this region of the phase space (Appendix 1), trajectories that start at this lower region will necessarily enter the middle region where they converge to equilibrium E_2 .

Unlike the case for sit-and-wait predators in which we see the predominance of a linear food chain topology, actively hunting (adaptive) predators cause consumers to utilize both patches and we see the predominance of a food web topology with two resources. The point is that predator hunting mode can have an important bearing on the nature of the food web topology and thus top-down and bottom-up effects.

FOOD CHAINS WITH ADAPTIVE OMNIVORY

The concept that natural systems can be arrayed into a chain, in which species at a higher level consume species at adjacent, lower levels only, has been a powerful way to organize thinking about the structure of food webs and the direct and indirect interactions that occur therein. In such a conception, we assume that the trophic status of species is narrowly fixed. So, predators will only interact directly with consumers; consumers will only interact directly with resources. This ignores important dimensions of complexity that we see in real-world systems. One source of complexity in particular is that many species engage in consumer–resource interactions with species at more than one trophic level, known in the broad sense as omnivory (Polis, 1991; Diehl, 1992, 1993, 1995; Dawah *et al.*, 1995;

Morin and Lawler, 1996; Winemiller, 1996; Fagan, 1997; McCann and Hastings, 1997; Holyoak and Sachdev, 1998; Diehl and Feissel, 2000, 2001).

Omnivory can take on many forms. One form that immediately comes to mind is the classic case in which a top predator preys on both consumers (herbivores) and resources (plants). Other examples include predator species that share consumer prey and also feed on each other, called intra-guild predation (Polis *et al.*, 1989; Polis and Holt, 1992; Holt and Polis, 1997; Rosenheim, 1998), and predator species that feed on individuals of their own species in addition to feeding on consumers, called cannibalism (Wise, 1993; Claessen *et al.*, 2000). The omnivory link in a food web adds complexity because, in addition to direct predator–consumer or consumer–resource interactions and indirect predator–resource interactions (cascading effects), we now have another direct predator–resource interaction and indirect interaction (exploitative competition) between an omnivorous predator and its consumer prey.

Omnivory presents challenges to consumers. Not only must they avoid being captured by their omnivorous predators, but they must also compete with them for resources. Classical ecological theory (Pimm and Lawton, 1977, 1978; Pimm, 1991) indicates that, for this reason, the likelihood of having an equilibrium in which all species stably co-exist becomes extremely rare. As a consequence of this theory, and apparently confirming empirical observations based on data with low taxonomic resolution (i.e. many different species aggregated into a trophic category), ecologists have long operated under the belief that omnivory is not an important food web interaction because it should be rare, or non-existent, under natural conditions. Recent efforts have revisited this issue by refining the taxonomic resolution of food web data and precisely quantifying food web linkages. This research has revealed that, contrary to past beliefs, omnivory is fairly widespread in food webs (Polis, 1991; Diehl, 1993; Dawah *et al.*, 1995; Winemiller, 1996; Fagan, 1997; Holyoak and Sachdev, 1998, and references therein). This revelation naturally led to a re-examination of theory on the role of omnivory in food webs. Specifically, theorists began trying to identify the kinds of mechanisms that might explain why food webs with omnivorous links tend to exhibit a high degree of permanence (Law and Blackford, 1992; Polis and Holt, 1992; Holt and Polis, 1997; McCann and Hastings, 1997; Sterner *et al.*, 1997). These analyses generally show that consumers will persist in food webs at equilibrium only if the omnivorous predators are inferior to the consumers at exploiting the shared resource. If predators are superior competitors for the shared resource, then even without predation the consumers will be excluded from the system via competitive exclusion. These analyses have largely assumed that the strength of omnivory remains fixed. Křivan (2000) showed that when the strength of omnivory varies adaptively in a system in which there is a trade-off between predation and competition, then behaviour may increase the range of conditions in which species may persist in a food web.

To examine the effect of adaptive foraging on the topology of food webs with omnivory, we use a generalization of the linear food chain by adding to it an omnivorous link (see middle food web in Fig. 7A). We again assume that predator density is relatively constant in time, and thus represents a component of the environment of the consumer–resource interaction.

The basic resource–consumer linear food chain model can be extended to include omnivory by adding a term that accounts for resource mortality due to consumption by predators. This leads to the following model of food web dynamics:

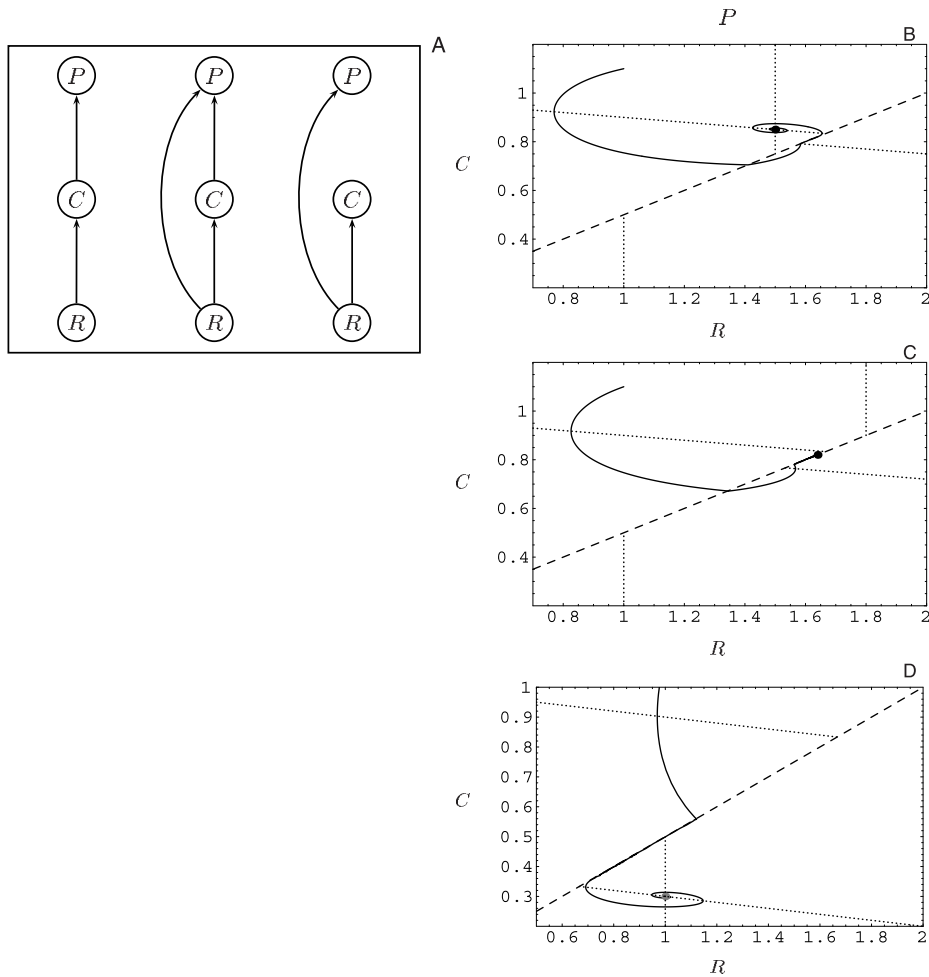


Fig. 7. Food web topologies and population dynamics of a food chain with adaptive omnivory. (A) The food web topologies along the predator gradients. (B–D) The corresponding population dynamics. When predator density is low (B: $P = 0.05$), trajectories converge to the equilibrium (denoted by the solid dot), which corresponds to a linear food chain topology without omnivory. At intermediate predator densities (C: $P = 0.8$), a new locally stable equilibrium point (solid dot) emerges. At the equilibrium, omnivory strength is strictly between zero and one (see formula (13)) and the food web topology is one of a linear food web with omnivory. For yet higher predator densities, trajectories converge to the equilibrium, which corresponds to a purely competitive system (D: $P = 0.6$). Resource and consumer isoclines are shown as dotted lines. Parameter values are: $K = 10$, $r = 1$, $\lambda = 1$, $e = 0.1$, $e_R = 0.5$, $e_C = 1$, $\lambda_R = 1$, $\lambda_C = 1$, $m = 0.1$.

$$\frac{dR}{dt} = R \left(r \left(1 - \frac{R}{K} \right) - \lambda C - M(u, P) \right)$$

$$\frac{dC}{dt} = C (e\lambda R - m(u, P))$$
(10)

where R denotes the resource population density, C denotes the consumer population density and M denotes the additional mortality imposed on resources by the omnivorous link. The control parameter u ($0 \leq u \leq 1$) defines the strength of omnivory qualitatively as the proportion of the resource in the diet of an average omnivorous predator (see also McCann and Hastings, 1997; Křivan, 2000). This is effectively like a patch choice model in which resource species are discrete entities and predators choose among one or the other or both resources. Thus an omnivorous strength equal to zero means that there is no omnivory, effectively making the food web a linear chain. At the other extreme, an omnivory strength equal to 1 implies pure exploitative competition between the omnivorous predators (technically, they no longer are predators in this case because they do not feed on consumers) and consumers for the shared resources. Thus strength values greater than 0 and less than 1 indicate varying degrees of omnivory in this system.

We consider the case in which the strength of omnivory (u) changes adaptively with resource and consumer densities. This issue is especially relevant if omnivorous predators trade-off foraging on resources with foraging on consumers. We assume that consumer and resource mortality rates caused by omnivorous predators in model (10) are related linearly to predator density (P). That is, the consumer mortality rate becomes

$$m(u, P) = m + (1 - u)\lambda_C P$$

and the resource mortality rate becomes

$$M(u, P) = u\lambda_R P$$

where λ_R is the maximum cropping rate of resources by predators whenever they feed exclusively on resources and λ_C is the maximum cropping rate of consumers by predators. As we assume that there is a linear trade-off between feeding on resources versus feeding on consumers, then, for a given omnivory strength u , fitness of an average predator is described as in the case of the patch model of optimal foraging by

$$e_C(1 - u)\lambda_C C + e_R u\lambda_R R$$

where e_C and e_R are constants that convert units of consumer or resource items into predator fitness. Here $e_C\lambda_C C$ is the fitness of predators that feed exclusively on resources and $e_R\lambda_R R$ is the fitness of predators that specialize on consumers, respectively. The above fitness is then the average of these two pure strategies. The optimal strategy of the omnivorous predators is to feed exclusively on consumers whenever consumer density is high – that is, whenever $e_C\lambda_C C > e_R\lambda_R R$. In consumer–resource phase space, this strategy corresponds to population densities that fall within the upper-left triangular region of the phase space in Fig. 7B–D. The strength of omnivory u is then equal to zero, which effectively reduces the topology of the system from a food web with omnivory to a linear food chain. If the opposite inequality holds – that is, if resources are abundant relative to consumer densities (when population densities fall within the lower-right triangular region of the phase space in Fig. 7B–D) – then the predator optimal foraging strategy is to feed exclusively on the resource. In this case, the strength of omnivory equals 1 and, as explained above, we obtain a topology in which the omnivorous predator no longer feeds on the consumer and, instead, becomes an exploitative competitor of the consumer for the resource. There is also a boundary between these two regions (dashed line in Fig. 7B–D) that has an important bearing on dynamics. Along this boundary line, the extent of omnivory is not determined

uniquely by fitness maximization as it is in the triangular regions. Rather, it depends on the population dynamics of consumers and resources, as we show below.

We now examine the effects of manipulating predator density on population dynamics and on the food web topology. We show that the dynamics of the system do not merely involve changes in consumer and resource densities over time. Rather, adaptive omnivory also causes the topology of the system to switch to different states – that is, exploitative competition versus linear food web with or without omnivory – as the abundances of consumers and resources fluctuate. To this end, we examine the system in phase space by plotting the consumer–resource isoclines and population trajectories. The adaptive behaviour of predators leads to discontinuities in isoclines (dotted lines in Fig. 7). The isoclines are discontinuous along the switching line (dashed line in Fig. 7). Let us consider the case where the food web topology is of the linear food chain – that is, no omnivory occurs ($u = 0$). The corresponding equilibrium

$$R_{\text{eq}} = \frac{m + \lambda_c P}{\lambda_e}$$

and

$$C_{\text{eq}} = \frac{r(e\lambda K - m - \lambda_c P)}{e\lambda^2 K}$$

can be either in the upper triangular region or in the lower triangular region. Let us assume that it is in the upper triangular region (Fig. 7B), which happens when predator density is not too high and parameters of the model are such that the following inequality holds:

$$P < \frac{e_c \lambda_c r (eK\lambda - m) - e_R \lambda_R m K \lambda}{\lambda_c (e_R \lambda_R \lambda K + \lambda_c e_c r)} \quad (11)$$

Under this inequality, there is one equilibrium which lies in the upper-left triangle of the phase space where food web topology is described by the food chain. All trajectories are driven to this equilibrium (Fig. 7B).

As predator densities increase, the consumer equilibrium decreases, too, and when

$$\frac{e_c \lambda_c r (eK\lambda - m) - e_R \lambda_R m K \lambda}{\lambda_c (e_R \lambda_R \lambda K + \lambda_c e_c r)} < P < \frac{e_c \lambda_c r (eK\lambda - m) - e_R \lambda_R m K \lambda}{\lambda_c \lambda_R \lambda K e_c} \quad (12)$$

the two isoclines do not intersect in the upper or lower triangular regions (Fig. 7C). Despite this we find that a new, locally stable equilibrium appears on the boundary between the two triangular regions (Fig. 7C). This equilibrium is given by (see Appendix 2)

$$R_{\text{eq}} = \frac{e_c K ((m + P \lambda_c) \lambda_R - r \lambda_c)}{(e e_c - e_R) K \lambda \lambda_R - e_c r \lambda_c}$$

and

$$C_{\text{eq}} = \frac{e_R \lambda_R}{e_c \lambda_c} R_{\text{eq}}$$

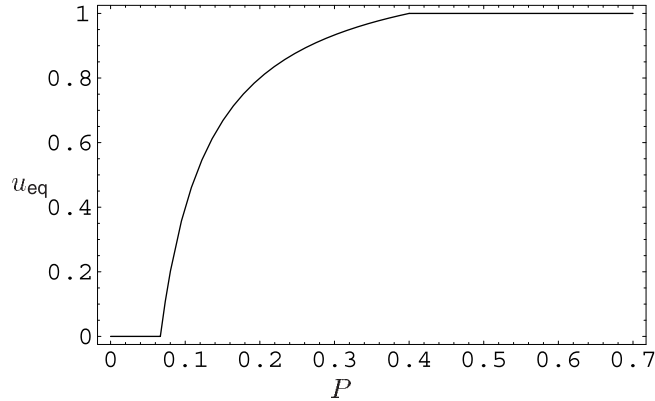


Fig. 8. Strength of omnivory u_{eq} at the equilibrium as a function of predator density. Parameters are the same as those in Fig. 7.

At this equilibrium, the strength of omnivory is given by the formula

$$u_{eq} = \frac{e_R K(m + P)\lambda + e_C \mathcal{I}(m + P - eK\lambda)}{P(e_C \mathcal{I} + (e_R - ee_C)K\lambda)} \tag{13}$$

(Appendix 2). Figure 8 illustrates that the strength of omnivory at the equilibrium increases at a decreasing rate with increasing predator density. Thus, for intermediate predator densities, the food web topology will be described by a linear food chain with omnivory.

When predator density is increased so that

$$P > \frac{e_C \lambda_C \mathcal{I}(eK\lambda - m) - e_R \lambda_R m K \lambda}{\lambda_C \lambda_R \lambda K e e_C}$$

the isoclines intersect in the lower-right triangular part of the phase space where food web topology is of the purely competitive system. Trajectories converge to this equilibrium (Fig. 7D).

These analyses show that changes in omnivorous predator density can lead to different food web topologies (Fig. 7A). Again, food webs that we would normally characterize as having distinct kinds of indirect effects (e.g. exploitative competition, trophic cascade, food chain omnivory: Menge, 1995; Abrams *et al.*, 1996) can be treated as different manifestations of the same dynamical system.

DISCUSSION

A central goal in community ecology is to derive a conceptualization of food web structure and function that both faithfully characterizes the trophic linkages among species in a system, and predicts contingency in the nature and strength of species effects (Polis and Strong, 1996). Most current analyses approach this issue by characterizing different systems by the nature of the dominant interaction driving dynamics – for example, keystone predation, exploitative competition, apparent competition, trophic cascade, intra-guild predation (Menge, 1995; Abrams *et al.*, 1996; McCann *et al.*, 1998). Accordingly, theory is developed around each type of food web configuration, giving the indication that food web

ecology requires myriad models of interactions to characterize the rich diversity found in the real world.

We instead argue here that considerable contingency in food web structure and interactions can be understood using single-model frameworks that include adaptive foraging behaviour of intermediate and top consumers. We focused our analysis on a conceptualization of a consumer–resource system in which a consumer species utilizes two resource species. We explored how the nature of trophic interactions varied under three different assumptions about what constitutes a resource and the spatial distribution of resources. We examined the case in which a consumer (herbivore) feeds on two resources (plants) that are distributed randomly in the environment. We then extended this to the case in which each plant resource occurs in a discrete patch. Finally, we examined a variant of the patch selection case in which the consumer (an omnivore) feeds within and among two trophic levels.

When resources are randomly distributed, we found that adaptive foraging by consumers along a productivity and predation mortality gradient can vary between a food chain and a food web with two resources. When resource productivity is low, then resource–consumer population dynamics settle to an equilibrium. Under high levels of predation mortality, consumers tend to feed on the more profitable resource only, which results in the linear food chain (Fig. 1C). At low consumer mortality rates, consumers will be less selective and they will feed on both resources (Fig. 1A). The equilibrium becomes destabilized by enrichment, in which case the population dynamics will periodically fluctuate around their equilibrium. There are two emergent outcomes of this periodicity. When fluctuations are small, food web topology will exhibit the same pattern as in the case of stable equilibrium. For higher enrichments, the limit cycle will result in periodic resource switching by the consumer and, correspondingly, the food web topology will periodically change as resources and consumer densities fluctuate. For high consumer mortality rates, the food web topology will periodically switch from the food chain to food web with two resources (Fig. 1D), while for low consumer mortality rates, the food web dynamics will be that of the food web with two resources along the whole cycle (Fig. 1B). This implies that enrichment experiments can both enhance the abundance of different species in trophic levels as well as alter the nature of the trophic interactions. In essence, we may see both species cascades and trophic cascades arise in a single system depending on the level of productivity.

When resources are distributed in discrete patches, we see an even richer range of food web topology depending again on the level of productivity and on the nature of the top predator hunting mode. Top predators that display sit-and-wait behaviour associated with a given resource patch cause consumers to settle in the patch which provides them with the highest per capita population growth rate – that is, the one that best balances the trade-off between predation mortality and nutrient intake. We showed that depending on the ratio of the resource productivity (resource carrying capacity)/consumer mortality rate in each patch, there are three possible topologies: two of the food chain, either with resource 1 or resource 2 as the sole resource, and one of the food web with two resources (Fig. 5). When these ratios are low in both patches, consumers cannot survive in either of them and we get extinction. If these ratios are high enough in both patches, then the equilibrium corresponds to the ideal free distribution of consumers among the two patches – that is, both patches are occupied and we get a food web with two resources. In the other two possible cases, consumers can survive in one patch only and we get a linear food chain. When top predators are actively hunting adaptive foragers – that is, predators that track changes in consumer

density in a patch in ways that maximize their own fitness – we get a game between consumers and predators. We showed that adaptive predator movement between patches causes consumers to distribute themselves over both patches, thus leading to a food web topology rather than to a linear chain topology.

Finally, adaptive omnivory leads to an even richer range of possible topologies for a given set of species. Again, depending on resource productivity and predator density, we may see the emergence of exploitative resource competition between an omnivorous predator and its consumer prey, a food chain in which the ‘omnivorous’ predator feeds on the consumer and the consumer feeds on the resource, or a bona fide omnivorous chain in which the predator feeds on both the consumer and the resource and competes exploitatively with the consumer for the resource. Given the newly discovered ubiquity of omnivory in natural systems (Polis, 1991; Diehl, 1993; Winemiller, 1996; Fagan, 1997; Diehl and Feissel, 2000, 2001), it may prove worthwhile to explore further how food web topology changes when resource, consumer and especially omnivorous predator abundance is systematically changed in experiments. Adaptive omnivorous behaviour may be one conceptualization that offers the broadest possibility of unifying thinking about the nature of different community structures (topologies) in nature.

So far, we have considered only direct predation on consumers. However, recent empirical studies of food web interactions (Messina, 1981; Power *et al.*, 1985; Turner and Mittelbach, 1990; Huang and Sih, 1991; Diehl and Eklöv, 1995; McIntosh and Townsend, 1996; Beckerman *et al.*, 1997; Turner, 1997; Peckarsky and McIntosh, 1998; Schmitz, 1998, 2000; Gastreich, 1999) have shown that predators also cause changes in consumer behaviour such as lower foraging activity or habitat shift to seek refuge from predation. This effect of predators on consumers is known as a trait effect. Our models allow us to study, at least partially, implications of such trait effects on food web topology in the same way as we did for direct predation. We do this by assuming that the presence of top predators decreases the activity of consumers, which we model as a decrease in cropping rates. We can then isolate the effects of risk from those of direct predation. For example, in the case of the random resource distribution model (1), we keep consumer mortality rate m constant and decrease the cropping rates. We observe that introducing increasing predation risk leads to an increase in the critical switching density for resource 1 (see formula 2) because the cropping rate λ_1 decreases. At the same time, equilibrium density of resource 1 compensates by increasing, with the net result that the relative position of the resource 1 equilibrium with respect to the switching line remains unchanged with the introduction of predation risk (see inequality (3), which does not depend on the cropping rates). Thus, we conclude that predation risk alone does not cause any qualitative changes in food web topology when consumers search for resources randomly. For the patchy resource distribution model, Fig. 5 shows that decreasing the consumer cropping rates increases the two thresholds below which extinction occurs. Thus, allowing only risk effects can cause a switch in topology from a food web with two resources to either a food web with one resource only (consumers become specialists on one resource) or a collapse of the food web structure. We never see the converse, where predation risk results in specialist consumers becoming more generalized in the face of predation risk (i.e. we never see a switch from food chain topology to food web topology). Similarly, consumers in the omnivorous predator–consumer–resource chain can respond behaviourally to the risk of predation. These situations often arise when the consumer and omnivorous predator are intra-guild prey and predator (Sih *et al.*, 1998). In such cases, there may be less impact of the predator and consumer

species on resources because of risk-reducing effects (Sih *et al.*, 1998). Risk reduction arises because the predator and consumer species engage in 'lateral' intra-guild interactions that reduce the strength of the downward effect on the resources in the food web. These intra-guild effects can arise because the predator reduces the numerical abundance of the consumer or the consumer avoids the risk of being consumed by seeking refuge in other habitats. The net effects of risk-avoidance behaviour by the consumer can be as strong or stronger than the net effects of the numerical change in consumer abundance (Peacor and Werner, 2001). Predictions about the net effects of risk reduction hinges entirely on the relative importance of behavioural versus density effects. This is one important area that needs much more experimental analysis before we can obtain the empirical insight required to allow generalizations (Sih *et al.*, 1998).

Our predictions are only qualitative in the sense that they show general trends, not the exact strength of trophic interactions. Nevertheless, our modelling has some important implications for perturbations experiments that test for top-down or bottom-up control by manipulating predator abundance or nutrient supply to resources. Namely, the experimental results and interpretation of the primacy for top-down versus bottom-up effects may be confounded by topological changes. Thus, empirical research needs to appreciate that food web linkages (interaction strengths) and topology may not remain static when adaptive consumers switch their resource choice in response to changes in extrinsic environmental factors such as nutrient addition or top predator manipulation.

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APPENDIX 1: ANALYSIS OF THE PATCH MODEL IN WHICH BOTH CONSUMERS AND PREDATORS BEHAVE ADAPTIVELY

The IFD strategy u_1 of consumers for every fixed distribution v_1 of predators is

$$u_1(v_1) = \begin{cases} 1 & \text{if } e_1\lambda_1R_1 - \Lambda_1v_1P > e_2\lambda_2R_2 - \Lambda_2v_2P \\ [0, 1] & \text{if } e_1\lambda_1R_1 - \Lambda_1v_1P = e_2\lambda_2R_2 - \Lambda_2v_2P \\ 0 & \text{if } e_1\lambda_1R_1 - \Lambda_1v_1P < e_2\lambda_2R_2 - \Lambda_2v_2P \end{cases}$$

Similarly, for a fixed strategy u_1 of consumers, the IFD strategy v_1 of predators satisfies

$$v_1(u_1) = \begin{cases} 1 & \text{if } \Lambda_1u_1 > \Lambda_2u_2 \\ [0, 1] & \text{if } \Lambda_1u_1 = \Lambda_2u_2 \\ 0 & \text{if } \Lambda_1u_1 < \Lambda_2u_2 \end{cases}$$

The points where the graphs of $u_1(v_1)$ and $v_1(u_1)$ intersect define the Nash-Pareto equilibrium (Hofbauer and Sigmund, 1998) of the game between consumers and predators. At the Nash-Pareto equilibrium, it is impossible for both consumers and predators to simultaneously deviate from the equilibrium: fitness of at least one of them would decrease. In this sense, the Nash-Pareto equilibrium defines the ideal free distribution of consumers and predators.

Here we give a complete classification of IFD as a function of parameters. The interior intersection point of the two graphs is denoted by (u_1^*, v_1^*) , where

$$u_1^* = \frac{\Lambda_2}{\Lambda_1 + \Lambda_2}$$

and

$$v_1^* = \frac{e_1\lambda_1 R_1 - e_2\lambda_2 R_2 + \Lambda_2 P}{(\Lambda_1 + \Lambda_2) P}$$

Qualitatively, the following possibilities exist (Křivan, 1997; Boukal and Křivan, 1999):

(a) If $(e_1 R_1 \lambda_1 - P \Lambda_1) / (e_2 \lambda_2) < R_2 < (e_1 R_1 \lambda_1 + P \Lambda_2) / (e_2 \lambda_2)$, then the IFD is (u_1^*, v_1^*) ; for the position of $u_1(v_1)$ and $v_1(u_1)$, see Fig. 9A. The corresponding population dynamics are described by the model:

$$\begin{aligned} \frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1} \right) - \frac{\lambda_1 \Lambda_2}{\Lambda_1 + \Lambda_2} R_1 C \\ \frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2} \right) - \frac{\lambda_2 \Lambda_1}{\Lambda_1 + \Lambda_2} R_2 C \\ \frac{dC}{dt} &= \frac{C}{\Lambda_1 + \Lambda_2} (e_1 \lambda_1 \Lambda_2 R_1 + e_2 \lambda_2 \Lambda_1 R_2 - \Lambda_1 \Lambda_2 P) \end{aligned} \tag{A1}$$

Interior equilibrium E_2 is

$$\begin{aligned} R_1 &= \frac{K_1(r_2\lambda_1\Lambda_2P\Lambda_1\Lambda_2 + e_2K_2\Lambda_1\lambda_2(r_1\Lambda_1\lambda_2 - r_2\lambda_1\Lambda_2))}{e_2K_2r_1\Lambda_1^2\lambda_2^2 + e_1K_1r_2\lambda_1^2\Lambda_2^2} \\ R_2 &= \frac{K_2(r_1\Lambda_1\lambda_2P\Lambda_1\Lambda_2 - e_1K_1\lambda_1\Lambda_2(r_1\Lambda_1\lambda_2 - r_2\lambda_1\Lambda_2))}{e_2K_2r_1\Lambda_1^2\lambda_2^2 + e_1K_1r_2\lambda_1^2\Lambda_2^2} \\ C &= \frac{r_1r_2(\Lambda_1 + \Lambda_2)(e_2K_2\Lambda_1\lambda_2 + e_1K_1\lambda_1\Lambda_2 - P\Lambda_1\Lambda_2)}{e_2K_2r_1\Lambda_1^2\lambda_2^2 + e_1K_1r_2\lambda_1^2\Lambda_2^2} \end{aligned}$$

Due to our assumption (8), resource 1 at this equilibrium is always at a positive level, while the positivity of resource 2 requires that

$$\frac{K_1}{P} < \frac{r_1\lambda_2\Lambda_1^2}{e_1\lambda_1(r_1\lambda_2\Lambda_1 - r_2\lambda_1\Lambda_2)} \tag{A2}$$

This condition also ensures that the equilibrium belongs to the part of the species density phase space where population dynamics are described by model (A2). Consumers exist at the equilibrium at positive levels provided

$$P < \frac{e_1K_1\lambda_1\Lambda_2 + e_2K_2\Lambda_1\lambda_2}{\Lambda_1\Lambda_2}$$

(b) If $R_2 < (e_1 R_1 \lambda_1 - P\Lambda_1)/(e_2 \lambda_2)$, then the IFD is $(1, 1)$; for the position of $u_1(v_1)$ and $v_1(u_1)$, see Fig. 9B. The corresponding population dynamics are described by the model:

$$\begin{aligned}\frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1}\right) - R_1 C \lambda_1 \\ \frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2}\right) \\ \frac{dC}{dt} &= C(e_1 R_1 \lambda_1 - P\Lambda_1)\end{aligned}\tag{A3}$$

with interior equilibrium

$$E_1 = \left(\frac{P\Lambda_1}{e_1 \lambda_1}, K_2, \frac{r_1(e_1 K_1 \lambda_1 - P\Lambda_1)}{e_1 K_1 \lambda_1^2} \right)$$

This equilibrium never belongs to the lower triangular region of the phase space where the population dynamics are described by model (A3). Therefore, it is not feasible because population densities cannot settle at this equilibrium.

(c) If $R_2 > (e_1 R_1 \lambda_1 + P\Lambda_2)/(e_2 \lambda_2)$, then the IFD is $(0, 0)$; for the position of $u_1(v_1)$ and $v_1(u_1)$, see Fig. 9C. The corresponding population dynamics are described by the model:

$$\begin{aligned}\frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1}\right) \\ \frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2}\right) - R_2 C \lambda_2 \\ \frac{dC}{dt} &= C(e_2 R_2 \lambda_2 - P\Lambda_2)\end{aligned}\tag{A4}$$

with interior equilibrium

$$E_3 = \left(K_1, \frac{P\Lambda_2}{e_2 \lambda_2}, \frac{r_2(e_2 K_2 \lambda_2 - P\Lambda_2)}{e_2 K_2 \lambda_2^2} \right)$$

This equilibrium never belongs to the upper triangular region of the phase space where the dynamics are described by model (A4). Once again, the equilibrium is not feasible and population densities cannot settle at this equilibrium.

(d) If $R_2 = (e_1 R_1 \lambda_1 - P\Lambda_1)/(e_2 \lambda_2)$, then the IFD is not uniquely defined because $v_1 = 1$ and u_1 is anywhere between u_1^* and 1.

(e) If $R_2 = (e_1 R_1 \lambda_1 + P\Lambda_2)/(e_2 \lambda_2)$, then the IFD is not uniquely defined because $v_1 = 0$ and u_1 is anywhere between 0 and u_1^* .

Now we study the population dynamics driven by the adaptive strategies. There are two possibilities. Either condition (A2) holds and equilibrium E_2 is positive, in which case it is the only equilibrium

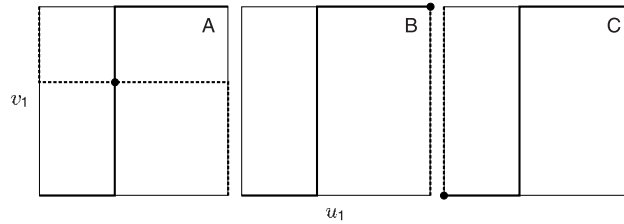


Fig. 9. Three possible generic IFDs for the model in which both consumers and predators behave adaptively. The figure shows $u_1(v_1)$ (dotted line) and $v_1(u_1)$ (solid line); for details, see Appendix 1.

for population dynamics. If condition (A2) does not hold, then equilibrium E_2 is not positive and equilibrium E_1 belongs either to the upper triangular part of the phase space or to the middle region of the phase space and E_3 belongs to the lower triangular part of the phase space. As numerical simulations show, this leads to extinction of one resource.

APPENDIX 2: POPULATION DYNAMICS OF SYSTEM WITH ADAPTIVE OMNIVOROUS PREDATORS

Here we compute the equilibrium that lies at the switching line where the food web topologies change. When trajectories are pushed from both sides towards the switching line (which happens when inequality (12) holds), once a trajectory reaches the switching line it cannot leave it. We can derive explicitly equations describing population dynamics along the switching line. As $e_c \lambda_c C = e_R \lambda_R R$ along the switching line, trajectories must satisfy there the following differential equation:

$$e_c \lambda_c \frac{dC}{dt} = e_R \lambda_R \frac{dR}{dt}$$

Substituting to this equation expressions for derivatives of population densities from model (10) and functional dependence of mortality rates on the strength of omnivory, we can compute explicitly the strength of omnivory:

$$u = \frac{e_c \lambda_c (-rR + K(m + r - e_R \lambda + P \lambda_c)) - e_R K R \lambda \lambda_R}{e_c K P \lambda_c (\lambda_c + \lambda_R)}$$

Substituting this control back to model (10) we get a description of the population dynamics along the switching line:

$$\frac{dR}{dt} = \frac{e_R R \lambda_R (e_R K R \lambda \lambda_R^2 + e_c \lambda_c (-rR \lambda_c + K(r - C \lambda) \lambda_c - K(m + C \lambda - e_R \lambda + P \lambda_c) \lambda_R))}{e_c K \lambda_c (\lambda_c + \lambda_R)}$$

$$\frac{dC}{dt} = \frac{C \lambda_c (e_c r (K - R) \lambda_c - K(e_R R \lambda + e_c (m - e_R \lambda + P \lambda_c)) \lambda_R)}{K(\lambda_c + \lambda_R)}$$

The above system has one non-zero equilibrium:

$$R_{eq} = \frac{e_c K (-r \lambda_c + (m + P \lambda_c) \lambda_R)}{-e_c r \lambda_c + (e_c - e_R) K \lambda \lambda_R}$$

and

$$C_{\text{eq}} = \frac{e_R \lambda_R}{e_C \lambda_C} R_{\text{eq}}$$

which is shown in Fig. 7C as a dot on the switching line. The strength of omnivory evaluated at the equilibrium is given by formula (13).