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Competitive co-existence caused by adaptive predators

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ABSTRACT

Food web dynamics are usually studied using model systems in which food web features, such as distribution of interaction strength, are fixed. This neglects adaptive foraging behaviour, which makes interaction strength a function of consumer preferences. In an endeavour to understand the effects of adaptive foraging behaviour on food web persistence, I consider here a diamond-like food web consisting of resources, two consumer species and top predators. Using a simple Lotka-Volterra type food web dynamics, I compare stability of this model when top predators are inflexible with the case where they are adaptive foragers that maximize their fitness. I show that adaptive consumer switching by predators significantly enlarges the set of parameters for which the two consumer species co-exist in the food web. Moreover, adaptive consumer switching leads to the ideal free distribution of predators. The results suggest that predator species which behave in an adaptive way are more likely to be keystones than those species which are inflexible foragers.

Keywords: adaptive foraging, competition, food web, keystone predator, persistence, stability.

INTRODUCTION

Arising from the pioneering work of Gause (1934), the principle of competitive exclusion suggests that complete competitors cannot co-exist on a single resource. More generally, no stable equilibrium is possible if N species are limited by less than N factors (Levin, 1970). In accordance with this principle, simple models of competition that assume limitation by common resources (bottom-up control) do not predict species co-existence (Tilman, 1982). How, then, can competing species co-exist? It is the role of ecologists to search for other mechanisms that can explain long-term species survival. Paine (1966, 1969a,b, 1980) showed that removal of a starfish *Pisaster ochraceus* resulted in the competitive exclusion of most barnacle species on which the starfish normally feeds. Thus, co-existence of barnacle species was mediated by the presence of predators. Species like the starfish, whose impact on its community is disproportionally large relative to its abundance (Paine, 1992) or to its proportional biomass (Power *et al.*, 1996), are called keystone species. Identification of keystones in ecosystems is crucial in conservation ecology because their extinction is likely to affect several other species and can lead to a dramatic loss of biodiversity. A common

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mechanistic explanation for species co-existence in communities with keystone predators is that predation keeps the competitively dominant consumer species at low densities, which reduces interspecific competition and allows the competitors to survive indefinitely.

In this article, I consider a diamond-like food web that consists of three trophic levels: resources, two consumer species and top predators. The two consumer species compete directly for the shared resources, and indirectly (apparent competition; Holt, 1977, 1984; Holt *et al.*, 1994; Bonsall and Hassell, 1997; Abrams, 1998) through the shared predators. I ask: 'Under which circumstances can such a food web topology persist?' Following the extended principle of competitive exclusion (Levin, 1970), it is clear that the two consumers in a diamond-like food web cannot survive if the food web is controlled solely by resources or solely by predators. The reason is that there must be two limiting factors for consumer co-existence. For low predator densities, the food web is regulated by the lack of resources (bottom-up control), direct competition between consumers is strong and one of the two competing consumer species is outcompeted by exploitative competition. For high predator densities, the food web is regulated by predators (top-down control), apparent competition between consumers is strong and one of the two consumer species is again outcompeted. Naturally, the stronger competitor for exploitative competition can be the weaker competitor for apparent competition, and vice versa. Adding a constant number of predators to a purely exploitative system can lead to a switch in the surviving consumer species. Thus, consumers can co-exist only provided the food web is controlled both by predators and by resources (Levin, 1970). This requirement sets some constraints on system parameters that render the food web persistent (Leibold, 1996).

The above analysis assumes inflexible predators with fixed preferences for either consumer type. In this article, I focus on the case in which predators are flexible and they switch their diet adaptively (by which I mean that they maximize their fitness). I show that consumer switching enlarges the set of parameters for which the two competing species co-exist when compared with inflexible predators. I also show that adaptive switching leads to the ideal free distribution (IFD) of predators (Fretwell and Lucas, 1970) with respect to foraging on consumer 1 and consumer 2. The mechanisms that lead to species co-existence are similar to those for other models of population dynamics with adaptive predators (Gleeson and Wilson, 1986; Fryxell and Lundberg, 1993, 1994, 1997; Křivan, 1996, 1997, 1999, 2003; Hambäck, 1998; Genkai-Kato and Yamamura, 1999; Křivan and Sikder, 1999; van Baalen *et al.*, 2001; Křivan and Eisner, 2003; Křivan and Schmitz, 2003). Namely, adaptive consumer switching by predators relaxes the strength of both apparent and direct competition between consumer species, which allows for species co-existence. In fact, adaptive predators render the population equilibrium densities to the levels at which the food web is controlled both by top-down and bottom-up regulation, which is a necessary condition for species co-existence due to the extended exclusion principle (Levin, 1970). If I define keystone predators for the diamond-like food web as those species that allow for indefinite co-existence of the two competing consumer species, then the results of this study suggest that adaptive predators are more likely to be keystones than non-adaptive predators.

In this article, I consider two cases. The simpler case, with which I start, assumes that the density of the top predator is constant – that is, predators do not undergo population dynamics and they are treated as a component of the environment. This system allows for a straightforward analysis and for clear understanding of mechanisms that promote species co-existence. Then I consider the fully dynamical system, which is more difficult to analyse, but I show numerically that the conclusions derived from the simpler case still hold.

MODEL

I consider a diamond-like food web consisting of a common resource (R), two consumer populations (C_1 and C_2) and top predators (P). Population dynamics of the resource and consumer species are described by the following Lotka-Volterra model

$$
\begin{aligned}
\frac{\mathrm{d}R}{\mathrm{d}t} &= rR\left(1-\frac{R}{K}\right) - \lambda_1 C_1 R - \lambda_2 C_2 R \\
\frac{\mathrm{d}C_1}{\mathrm{d}t} &= C_1(e_1\lambda_1 R - m_1(P_1)) \\
\frac{\mathrm{d}C_2}{\mathrm{d}t} &= C_2(e_2\lambda_2 R - m_2(P_2))
\end{aligned}
\tag{1}
$$

where r is the resource per capita intrinsic growth rate, K is the resource environmental carrying capacity, λ_1 and λ_2 are consumer cropping rates of resources, e_1 and e_2 are efficiency rates with which resources are converted to new consumers, and m_1 and m_2 are consumer mortality rates. The model assumes tritrophic interactions between resources (R), two consumer species (C_1 and C_2) and predators (P). The predator population splits in two parts: those individuals that feed on consumer 1 (P_1) and those that feed on consumer 2 (P_2). The above model does not describe predator population dynamics explicitly. Instead, it assumes that predator dynamics are slow when compared with resource and consumer population dynamics and it treats the predator density as a constant. However, predators influence consumer mortality rates, which I indicate by writing $m_i(P_i)$. Thus, the above model treats resources and competitors dynamically, while predators are taken to be a component of the environment, which does not change in time, but predator preferences for either consumer 1 ($u_1 = P_1/P$) or consumer 2 ($u_2 = P_2/P$) can change. Thus, the distribution of interaction strength in the food web is not static, but it can vary as predator foraging preferences change in response to changes in consumer densities. In what follows, I consider two types of predator behaviours. First, I assume that predator preferences for consumers are fixed. This corresponds to a non-adaptive predator foraging behaviour. Second, I assume that predators are adaptive foragers that maximize their fitness, which corresponds to a more contemporary dynamic view of food webs, where not only interaction strength but also food web topologies are treated dynamically (Kondoh, 2003; Křivan and Schmitz, 2003). I compare both types of behaviours.

Inflexible predators

This case assumes that the proportions of predators feeding on consumer 1 (u_1) and on consumer 2 (u_2) do not change in time. Thus, predators are inflexible because they do not react to changing densities of consumers and the interaction strength in the food web does not change. The food web dynamics is controlled by a combination of predation and resource limitation, but these two factors are not independent for the two consumer species (e.g. both consumer species will decrease simultaneously if predator density increases). Due to the competitive exclusion principle, no stable species co-existence is possible (Levin, 1970). Moreover, the R^* rule implies that the consumer which suppresses resources to a lower equilibrial level will survive in the above model, while the other species will be outcompeted (Hsu, 1978; Waltman, 1983). Thus, if the second species is the weaker competitor, i.e.

$$\frac{m_1(P_1)}{e_1\lambda_1} < \frac{m_2(P_2)}{e_2\lambda_2} \tag{2}$$

then it will be eliminated from the food web and the resulting food web topology will be of the linear food chain (resource–consumer 1–predators; Fig. 1A). Similarly, if the opposite inequality holds, then consumer 1 will be eliminated from the food web. Figure 1A shows the switch in the food web topology along the consumer 1 mortality gradient (the unrealistic case where equality holds in (2) is not shown in Fig. 1A).

It is well known (Armstrong and McGehee, 1980; Hofbauer and Sigmund, 1984; Butler and Waltman, 1986; Hutson and Schmitt, 1992) that for species pesistence, it is necessary that at the equilibrium of a linear food chain where one consumer species is missing the

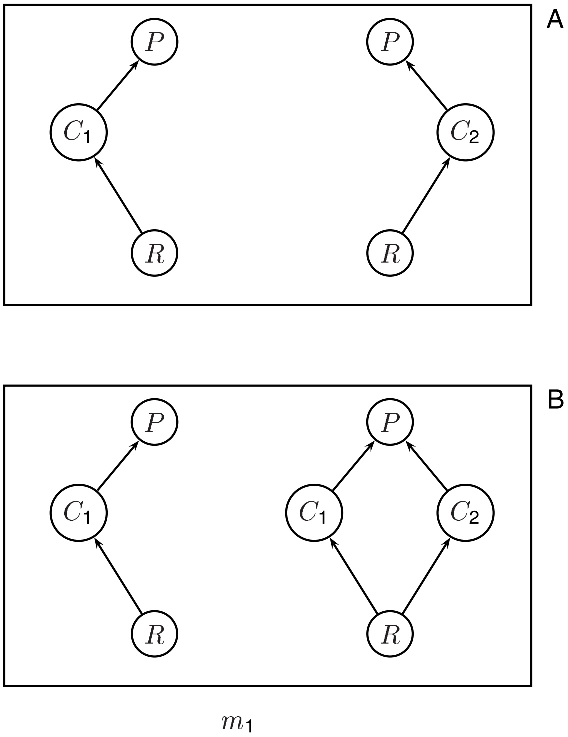

Fig. 1. The dependence of the food web topologies originating from the diamond-like food web topology along the consumer 1 mortality gradient. (A) assumes inflexible predators, while (B) assumes adaptive predators. In the case of inflexible predators, the food web topology is generically a linear food chain in which one consumer species is outcompeted. If predators are adaptive, then both consumer species can survive in the food web.

missing species can invade. This gives two necessary conditions for species permanence. While these conditions do not hold for inflexible predators (Appendix 1), I show in the next section that they can be satisfied if predators are adaptive foragers.

Adaptive predators

Now I assume that predators are adaptive foragers and that they choose their diet so that their per capita population growth rate is maximized. I assume that the per capita predator population growth rate is proportional to per capita food intake rate, i.e.

$$W = F_1 u_1 C_1 + F_2 u_2 C_2$$

where F_i denotes the instantaneous per capita population growth rate when feeding on consumer i ($i = 1, 2$). Thus, W is a surrogate for predator fitness. The optimal foraging strategy of predators is to feed on consumer 1 when $F_1C_1 > F_2C_2$ ($u_1 = 1$, $u_2 = 0$) and to feed on consumer 2 when the inequality is reversed ($u_1 = 0$, $u_2 = 1$). Here I assume that predators are omniscient and that they are perfect optimizers. This leads to dynamic changes in the food web topology as consumer densities change. When it is more profitable to feed on consumer 1, the food web topology is described by a linear food chain consisting of resources (R), consumer 1 (C_1) and predators (P). As the consumer not being preyed upon (consumer 2) grows, at a certain instant feeding on consumer 2 gives the same fitness as feeding on consumer 1. This can lead to the situation in which predators control densities of both consumer species at levels under which feeding on consumer 1 gives the same fitness as feeding on consumer 2. Such a distribution of predators was termed the ideal free distribution (IFD; Fretwell and Lucas, 1970) because predators are free to choose on which food resource to feed and they are assumed to be omniscient with respect to food abundance and quality. Although the original derivation of the IFD was a static concept, it was later extended to the case where predators and/or consumers undergo population dynamics (Lessells, 1995; Křivan, 1996, 2003). In what follows, I derive the ideal free distribution for predators and I study its consequences for the co-existence of the two consumer types. It is clear that if predators can regulate consumer populations so that the conditions for the IFD hold, then this should promote consumer co-existence because as one consumer population starts to decline, predators start to feed more on the other consumer population, which decreases predation strength on the first consumer population when compared with inflexible predators.

If predation on consumer 1 is more profitable than predation on consumer 2 ($F_1C_1 > F_2C_2$; the part of the consumer phase space below the dashed line in Fig. 2), the food web topology is that of the food chain with consumer 1 and the corresponding population dynamics are described by model (1) where I set $P_1 = P$ and $P_2 = 0$ as all predators feed on consumer 1.

Similarly, if predation on consumer 2 is more profitable than predation on consumer 1 ($F_1C_1 < F_2C_2$; the part of the consumer phase space above the dashed line in Fig. 2), the corresponding food web topology is that of the food chain with consumer 2 and the corresponding population dynamics are given by model (1) where I set $P_1 = 0$ and $P_2 = P$ as all predators feed on consumer 2. I assume that consumer mortality rates $m_1(P)$ and $m_2(P)$ increase with increasing predator densities and that without predators the second consumer is the weaker competitor [$m_1(0)/(e_1\lambda_1) < m_2(0)/(e_2\lambda_2)$]. Invasibility analysis shows (Appendix 2) that for low predator densities that satisfy inequality

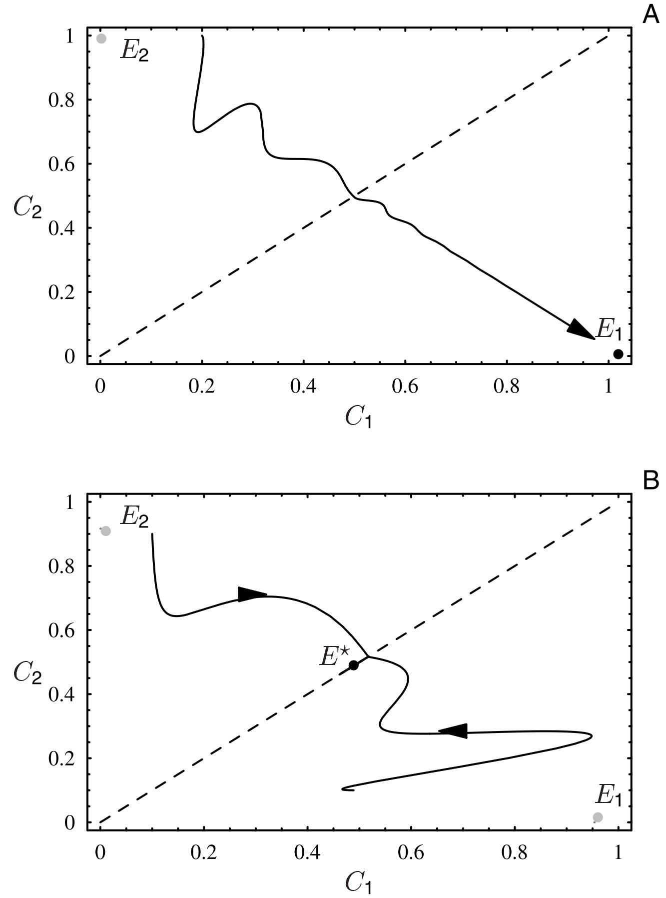

Fig. 2. Population dynamics for adaptive predators in consumer phase space. (A) assumes low predator densities ($P = 0.01$) and the competitively weaker consumer 2 is outcompeted by the dominant consumer 1 as in the case of inflexible predators. (B) assumes higher predator densities ($P = 0.1$), in which case predators reach ideal free distribution because they suppress consumer densities to the level at which predator fitness is the same regardless of whether they feed on consumer 1 or consumer 2 (shown as the dashed line). Population dynamics converge to an interior equilibrium. Parameters: $r = 1.1$, $e_1 = 0.1$, $e_2 = 0.08$, $\lambda_1 = \lambda_2 = 1$, $\mu_1 = \mu_2 = 0.1$, $\Lambda_1 = \Lambda_2 = 1$, $F_1 = F_2 = 1$, $K = 15$.

$$\frac{m_1(P)}{e_1\lambda_1} < \frac{m_2(0)}{e_2\lambda_2} \tag{3}$$

the second consumer remains the weaker competitor and it cannot invade the linear food chain with consumer 1, exactly as in the case of inflexible predators (Fig. 2A). The corresponding food web topology is the food chain with consumer 1 present (Fig. 1B, low consumer 1 mortality rates).

The situation changes when predator density is high enough in the sense that the opposite to inequality (3) holds. Then, both equilibria can be invaded by the missing species and the diamond-like food web topology can persist (Appendix 2; Fig. 1B, high consumer 1 mortality rates). In this case, predator density is high enough to control consumer densities at the level where feeding on consumer 1 provides the same fitness as feeding on consumer 2. Figure 2 shows adaptive population dynamics in the case where consumer mortality rates are linear functions of predator densities:

$$m_i(P_i) = \mu_i + \Lambda_i P_i \qquad i = 1, 2 \tag{4}$$

Here μ_i denotes the background consumer mortality rate in the absence of predators ($m_i(0) = \mu_i$) and Λ_i is the cropping rate of predators when feeding on consumer type i. Trajectories of model (1) with adaptive predators are pushed from both sides to the switching plane $F_1C_1 = F_2C_2$ (shown as the dashed line in Fig. 2). Population dynamics in the switching plane are described by the following model (Appendix 3):

$$\begin{aligned}
\frac{\mathrm{d}R}{\mathrm{d}t} &= rR\left(1 - \frac{R}{K}\right) - \frac{\lambda_1 F_2 \Lambda_2 - \lambda_2 F_1 \Lambda_1}{F_2 \Lambda_2} RC_1 \\
\frac{\mathrm{d}C_1}{\mathrm{d}t} &= C_1\left(\frac{e_2\Lambda_1\lambda_2 + e_1\lambda_1\Lambda_2}{\Lambda_1 + \Lambda_2} R - \frac{\mu_1\,\Lambda_2 + \mu_2\Lambda_1 + P\Lambda_1\Lambda_2}{\Lambda_1 + \Lambda_2}\right) \\
\frac{\mathrm{d}C_2}{\mathrm{d}t} &= C_2\left(\frac{e_2\Lambda_1\lambda_2 + e_1\lambda_1\Lambda_2}{\Lambda_1 + \Lambda_2} R - \frac{\mu_1\Lambda_2 + \mu_2\Lambda_1 + P\Lambda_1\Lambda_2}{\Lambda_1 + \Lambda_2}\right)
\end{aligned} \tag{5}$$

with an interior equilibrium E^* (Fig. 2B) in the IFD plane:

$$\begin{aligned}
R^* &= \frac{\mu_1\Lambda_2 + \mu_2\Lambda_1 + \Lambda_1\Lambda_2 P}{e_1\lambda_1\Lambda_2 + e_2\lambda_2\Lambda_1} \\
C_1^* &= \frac{F_2 r(e_2 K\Lambda_1\lambda_2 + e_1 K\lambda_1\Lambda_2 - P\Lambda_1\Lambda_2 - \Lambda_2\mu_1 - \Lambda_1\mu_2)}{K\,(F_2\lambda_1 + F_1\lambda_2)\,(e_2\Lambda_1\lambda_2 + e_1\lambda_1\Lambda_2)} \\
C_2^* &= \frac{F_1}{F_2} C_1^*
\end{aligned}$$

At this equilibrium, predators will feed on both species and the ideal free distribution of predators is (Appendix 3):

$$\frac{u_1}{u_2} = \frac{e_2\mu_1\lambda_2 - e_1\lambda_1\,(\mu_2 + P\Lambda_2)}{e_1\mu_2\lambda_1 - e_2\lambda_2\,(\mu_1 + P\Lambda_1)}$$

(Fig. 3). As the overall predator density increases, predator preferences for consumer 1 decrease at the population equilibrium. Co-existence of the two consumer species at the switching plane is possible because the coefficients in model (5) for the two consumer species are the same. Thus, the co-existence in the switching plane does not contradict the exclusion principle (Levin, 1970). Figure 4A shows the range of parameters in the P–K parameter space for which the diamond-like food web is persistent. The minimal predator density for persistence

$$P > \frac{e_1\lambda_1\mu_2 - e_2\lambda_2\mu_1}{e_2\lambda_2\Lambda_1}$$

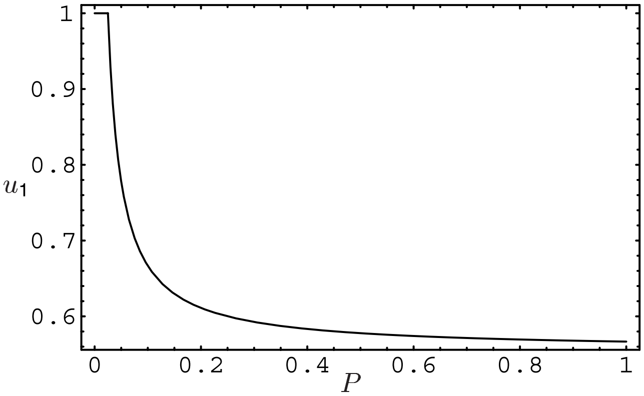

Fig. 3. The ideal free distribution of predators at the population equilibrium as a function of the overall predator density. Parameters are the same as those in Fig. 2.

is given by the invasibility condition (Appendix 2) and the lower boundary on the resource carrying capacity is given by

$$K = \frac{P\Lambda_1\Lambda_2 + \Lambda_1\mu_2 + \Lambda_2\mu_1}{e_1\lambda_1\Lambda_2 + e_2\lambda_2\Lambda_1}$$

For lower resource carrying capacities, the interior equilibrium E^* is not positive because consumers die out due to strong predation mortality.

PREDATORS UNDERGO POPULATION DYNAMICS

So far, I have assumed that the predator density is fixed. Now I want to extend previous results to the full dynamical setting where predators are treated dynamically. I consider the following model describing the four-species population dynamics:

$$\begin{aligned}
\frac{\mathrm{d}R}{\mathrm{d}t} &= rR\left(1 - \frac{R}{K}\right) - \lambda_1 C_1 R - \lambda_2 C_2 R \\
\frac{\mathrm{d}C_1}{\mathrm{d}t} &= C_1(e_1\lambda_1 R - \Lambda_1 u_1 P - \mu_1) \\
\frac{\mathrm{d}C_2}{\mathrm{d}t} &= C_2(e_2\lambda_2 R - \Lambda_2 u_2 P - \mu_2) \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= P(F_1 u_1 C_1 + F_2 u_2 C_2 - m)
\end{aligned} \tag{6}$$

where μ_i and m are the backround consumer and predator mortality rates, respectively. Leibold (1996) analysed model (6) assuming that predator preferences for either consumer (u_i) are fixed and he showed that model (6) can have a locally stable interior equilibrium at which all species can co-exist indefinitely. Thus, when predators are treated dynamically, they can promote co-existence of the two consumer species. However, the co-existence can be limited to a narow range of parameters. Here I study the range of parameters for which the diamond-like food web is persistent and I ask whether adaptive predator behaviour enhances species co-existence as my previous analysis for fixed predator densities suggests.

The two necessary conditions for consumer invasibility are given in Appendix 4. Figure 4B shows graphically the range in predator mortality rate (m) and the resource carrying capacity (K) parameter space for which the two invasibility conditions hold and all species co-exist. The range is either quite narrow (such as in Fig. 4B) or void because the two invasibility conditions may not be satisfied. A similar analysis for adaptive predators shows (Appendix 4; Fig. 4C) that adaptive consumer switching strongly enlarges the range of parameters for which the diamond-like food web is persistent. The reason for this increase in the range of parameters is the same as that I have already discussed for the model with fixed predator density. Adaptive predator behaviour relaxes apparent competition between the two consumer species, which allows both consumers to survive in the food web. This is numerically documented in Fig. 5, where dependence of the stable equilibrium on the resource carrying capacity is shown. The left-hand panels show a simulation for inflexible predators, while the right-hand panels show simulations for adaptive predators. In the left-hand panels, consumer 1 is outcompeted from the food web at high resource carrying capacities. In contrast, when predators are adaptive, the two consumers co-exist even at high resource carrying capacities (right-hand panels), which makes the diamond food web permanent. This is because at high enrichment levels, adaptive predation relaxes apparent competition between the two consumer species.

The mechanism that leads to consumer co-existence in the food web with adpative predators is similar to that we have already observed for model (1). In the lower triangular region of the consumer phase space (Fig. 6, bottom panels) where predators feed on consumer 1 only ($u_1 = 1$, $u_2 = 0$), the corresponding food web has the following interior equilibrium:

$$E_a = \left\{ \frac{\mu_2}{e_2\lambda_2},\ \frac{m}{F_1},\ \frac{e_2K(F_1r - m\lambda_1)\lambda_2 - F_1r\mu_2}{e_2F_1K\lambda_2^2},\ \frac{e_1\lambda_1\mu_2 - e_2\lambda_2\mu_1}{e_2\Lambda_1\lambda_2} \right\}$$

Similarly, in the upper triangular region of the consumer phase space where predators feed on consumer 2 ($u_1 = 0$, $u_2 = 1$), the corresponding food web has the following interior equilibrium:

$$E_b = \left\{ \frac{\mu_1}{e_1\lambda_1},\ \frac{e_1K\lambda_1(F_2r - m\lambda_2) - F_2r\mu_1}{e_1F_2K\lambda_1^2},\ \frac{m}{F_2},\ \frac{e_2\lambda_2\mu_1 - e_1\lambda_1\mu_2}{e_1\Lambda_2\lambda_1} \right\}$$

Thus, only one of these two equilibria can be positive. Following our assumption (2), I assume that

$$\frac{\mu_1}{e_1\lambda_1} < \frac{\mu_2}{e_2\lambda_2}$$

This means that equilibrium E_b is never positive, because the predator density at this equilibrium is always negative. There are two possibilities. Either equilibrium E_a belongs to the lower triangular region of the consumer phase space, in which case the predators will feed on consumer 1 only at this equilibrium (Fig. 6, left). Or, the equilibrium is in the upper triangular region of the phase space, which occurs if

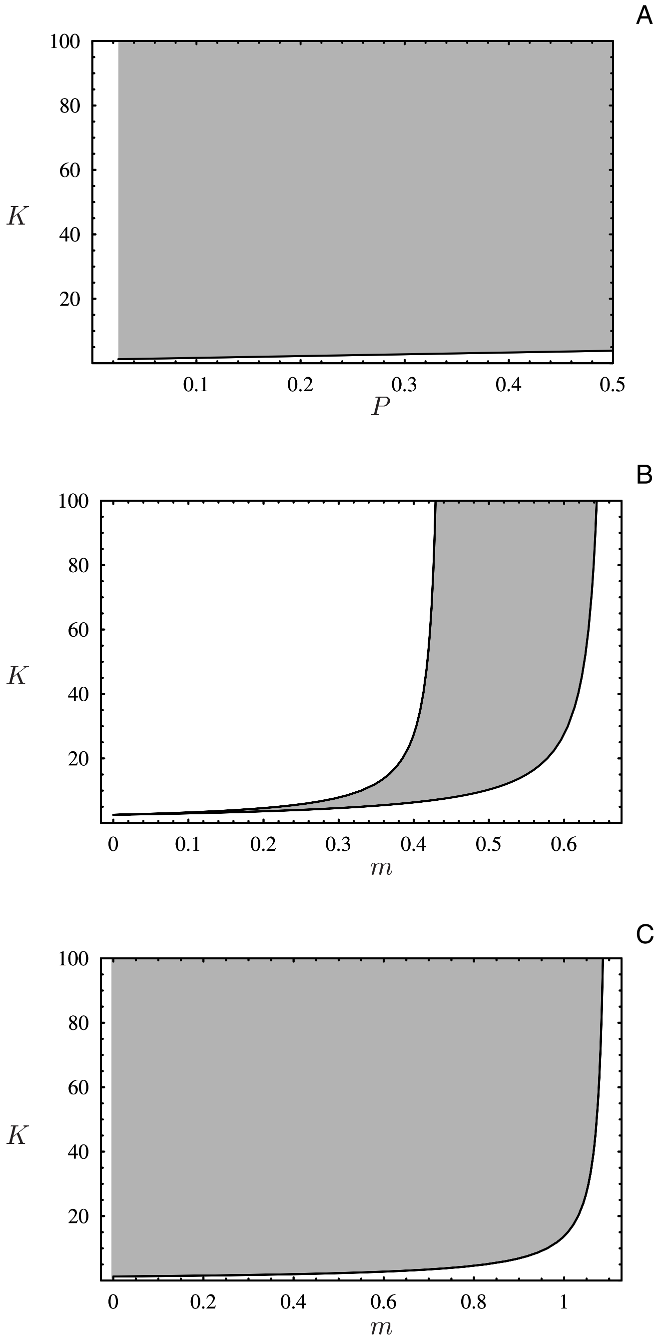

Fig. 4. (A) The range of parameters in (P, K) parameter space for which the diamond-like food web is persistent when predators do not undergo population dynamics. (B) and (C) The range of parameters in (m, K) parameter space for which the diamond-like food web is persistent when predators undergo population dynamics. (B) assumes inflexible predators ($u_1 = 0.6$, $u_2 = 0.4$), while (C) assumes adaptive predators. The parameters are the same as those in Fig. 2.

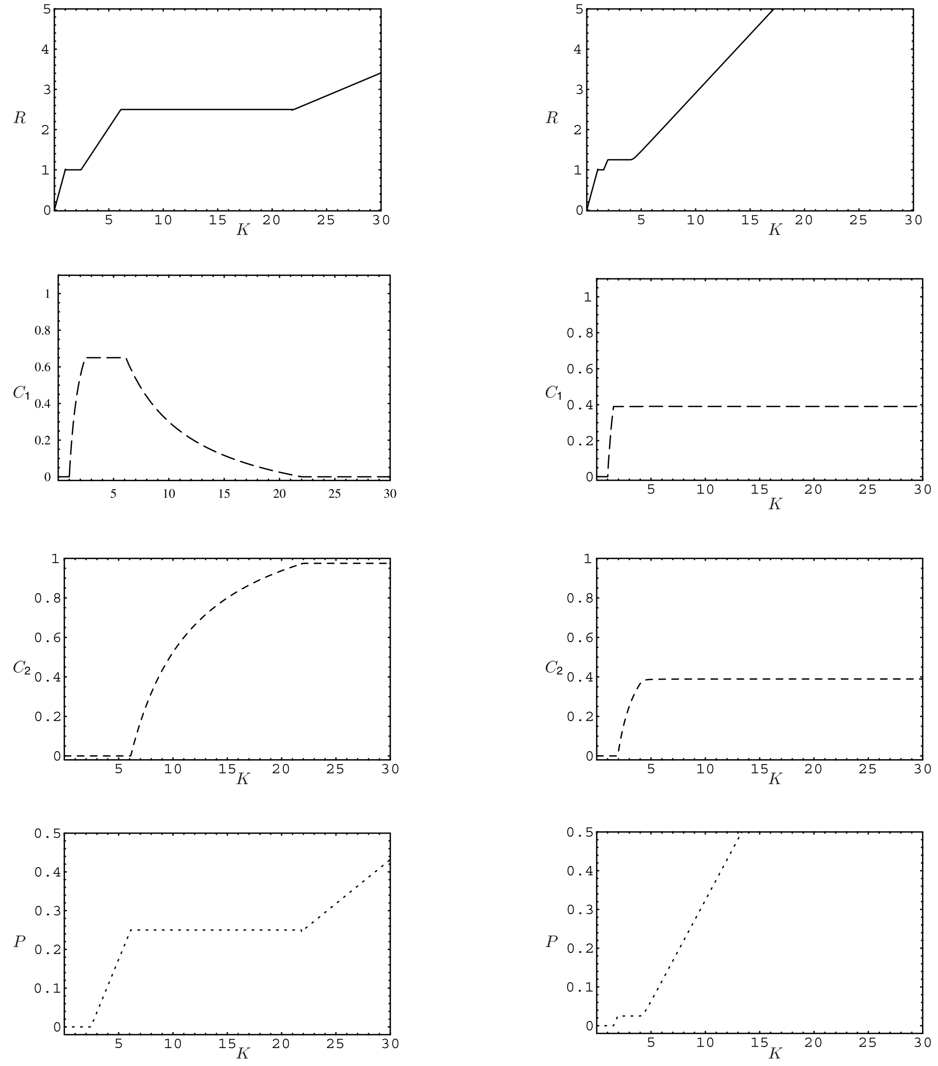

Fig. 5. Dependence of species equilibrium on resource carrying capacity K for a model with inflexible predators (left-hand panels, $u_1 = 0.6$, $u_2 = 0.4$) and adaptive predators (right-hand panels). Parameters: $m = 0.39$; other parameters are the same as those in Fig. 2.

$$K[F_1F_2e_2r\lambda_2 - e_2\lambda_2m(\lambda_1F_2 + \lambda_2F_1)] > F_1r\mu_2 \tag{7}$$

Then, the trajectories of model (6) that start in the lower triangular part of the consumer phase space tend to equilibrium E_a and the trajectories that start in the upper triangular part of the consumer phase space tend to the lower triangular region because the competitively weaker consumer 2 tends to be outcompeted by consumer 1. Once again, this leads to conflict along the switching plane (dashed line in Fig. 6) and to the emergence of a new equilibrium at the switching plane (Fig. 6, right; Appendix 5). For inequality (7) to hold, predator mortality rates cannot be too high, and the resource carrying capacity

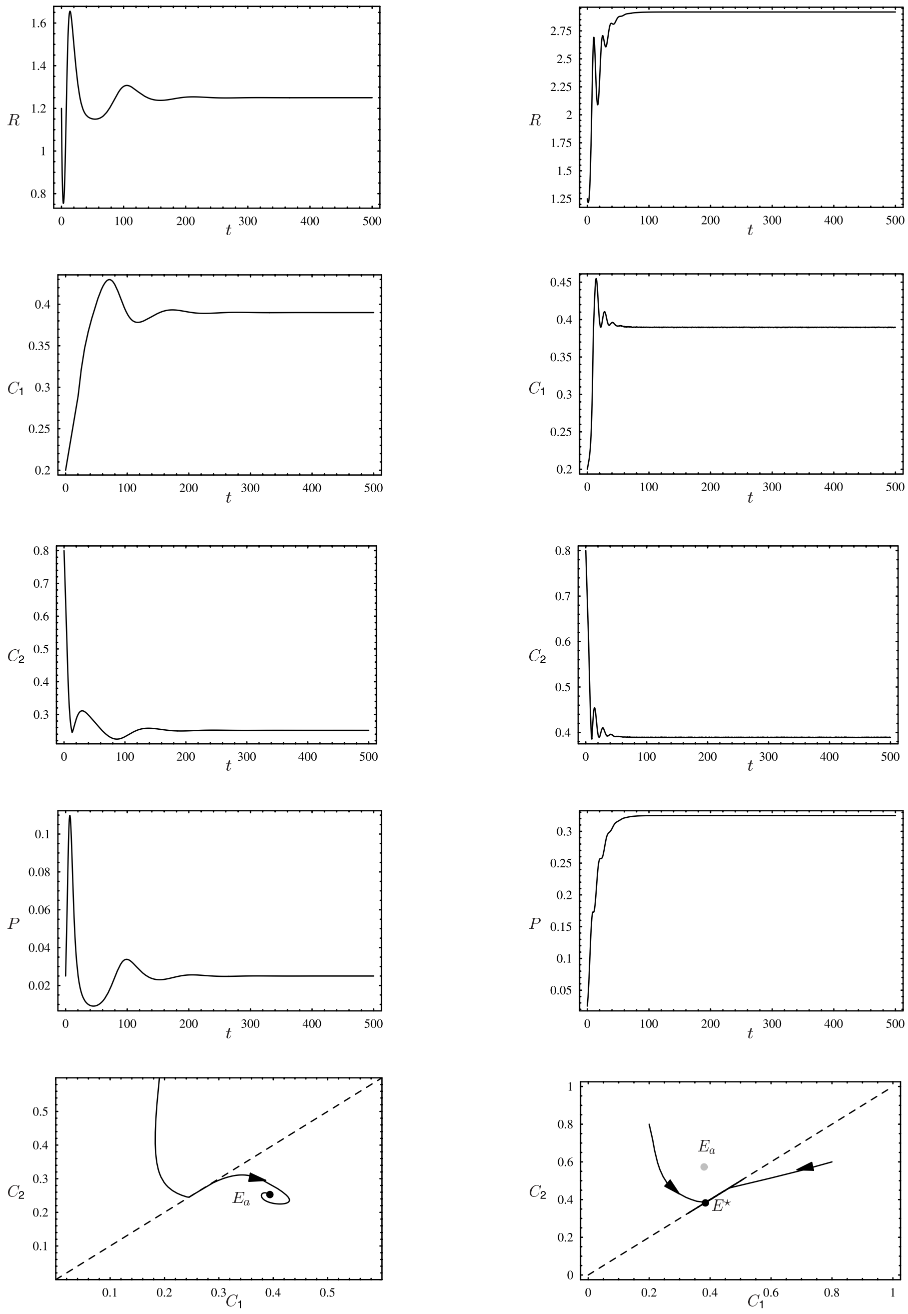

Fig. 6. Population dynamics when predators are adaptive foragers. The left-hand panels assume a low resource carrying capacity ($K = 3$) so that inequality (7) does not hold. Trajectories converge to the equilibrium at which predators feed on consumer 1 only. The right-hand panels show the case where the resource carrying capacity is high ($K = 10$) so that inequality (7) holds. In this case, a new equilibrium (E^*, Appendix 5) appears in the IFD plane (shown as the dashed line). Parameters are the same as are those in Fig. 5.

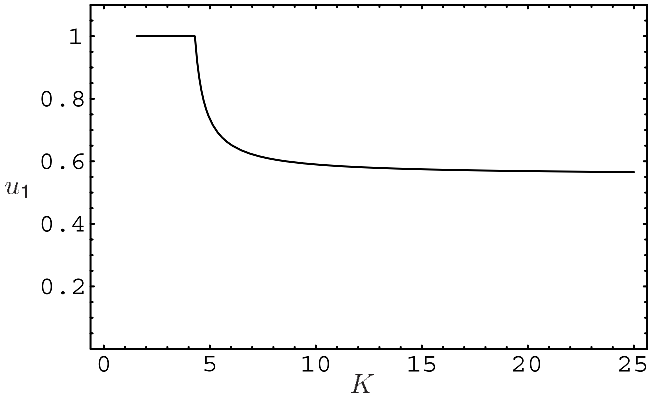

Fig. 7. The proportion of the equilibrium predator population feeding on consumer 1 as a function of the resource carrying capacity. Parameters are the same as those in Fig. 6.

cannot be too low. Figure 7 shows the proportion of the equilibrium predator population feeding on consumer 1 as a function of the resource carrying capacity. For low resource carrying capacities for which inequality (7) holds, both consumers co-exist in the food web and predators feed on consumer 1 only. For higher resource carrying capacities for which inequality (7) does not hold, predators feed on both consumers and the corresponding food web topology is diamond-like.

DISCUSSION

Ecological theory suggests, based on the principle of competitive exclusion (Gause, 1934; Levin, 1970), that competition is a strong driving force in food webs, which sets an upper limit on the number of co-existing species. Although this principle is one of the cornerstones of contemporary ecology, it is based on the assumption that food webs are static in the sense that their basic features (e.g. interaction strength, food web topology) do not change in time. Such an assumption does not reflect consumers' adaptive behavioural or evolutionary switches in food choice that lead to dynamic changes in interaction strength (Kondoh, 2003) and food web topologies (Křivan and Schmitz, 2003). Many studies have shown clearly that adaptive behaviours promote species co-existence when compared with inflexible animals (see review in Bolker *et al.*, 2003). In this article, I have considered a diamond-like food web consisting of common resources, two consumer species and top predators. I have compared two types of top predators: inflexible predators with fixed preferences for either consumer type, and flexible predators that adaptively change their feeding preferences with changing consumer densities. According to the competitive exclusion principle (Levin, 1970), the two consumer species in the diamond-like food web can co-exist if each is limited by an independent combination of predation and resource limitation. In this article, I ask two questions: (1) what is the range of parameters for which the two consumer species do co-exist and (2) does adaptive feeding by top predators enlarge this parameter range – that is, does it make co-existence more likely? I have considered two cases with increasing complexity. The first case assumed that predator density is fixed – that is, predators were treated as a component of the environment. Then I studied the full dynamical case where predators also undergo population dynamics. In a diamond-like food web, consumers compete twice. First, they compete for common resources; second, they compete indirectly through the shared predators. This latter type of indirect competition has been termed 'apparent competition' (Holt, 1977, 1984; Holt *et al.*, 1994; Bonsall and Hassell, 1997; Abrams, 1998). For the case in which inflexible predators do not undergo population dynamics, apparent competition can reverse the outcome of consumer direct competition for resources, but it cannot (with the exception of the unrealistic case in which the density of predators is such that both consumers are equally strong competitors) lead to the indefinite co-existence of both consumer species. This is because of the trade-off between direct exploitative competition and apparent competition. For low predator densities, the food web is controlled by the lack of resources and one competitor is outcompeted due to exploitative competition. As predator densities increase, the food web is controlled by predation (top-down control) and apparent competition leads to extinction of one competitor. This result is consistent with the extended competition exclusion principle (Levin, 1970), because the two factors (resources and predation) that limit the two consumer species are not independent. Second, I considered flexible (constant density) predators that adjust their food preferences to consumer densities. Thus, if consumer 1 density is low, it pays predators to feed on consumer 2 only and vice versa. It is clear that this mechanism reduces apparent competition between the two consumer types when one consumer density is low because predators do not prey on this consumer. Using invasibility analysis, I showed that for adaptive predators the diamond-like food web topology can persist provided the predator density is high enough to regulate consumer densities at levels for which predator fitness is the same regardless on which consumer species predators feed. The corresponding predator distribution is then the ideal free distribution, because by changing its feeding strategy a mutant predator cannot increase its fitness. I studied population dynamics under the assumption that the consumer mortality rate is a linear function of predator densities. In this case, population densities tend to an interior equilibrium at which predator distribution corresponds to the IFD – that is, at the equilibrium, predators feed on both consumer species. Moreover, consumer population dynamics that correspond to the predator IFD are identical, which makes consumer co-existence at the equilibrium possible (see consumer dynamics described by model (5)). If keystone predators are those that make survival of both consumer species possible, then my analysis suggests that for a tritrophic diamond-like food web described by a Lotka-Volterra model with a fixed predator density, a necessary condition for predators to act as the keystone species is that they are adaptive foragers. Otherwise, they cannot increase diversity of the system by allowing indefinite co-existence of the two consumer species.

Then I extended these results to the case where predators are treated dynamically. Such a model was studied in detail by Leibold (1996), who showed that parameters exist for which the model (with inflexible predators) possesses a locally stable interior equilibrium. However, the necessary conditions for co-existence of the two consumer species are rather stringent as Fig. 4B shows. In fact, for some other parameters, the two consumer species may not co-exist at all. Again, adaptive feeding behaviour of predators enlarges substantially the range of parameters for which the necessary condition for consumer co-existence holds (Fig. 4C). The mechanism that allows for consumer co-existence is the same as that in the case of fixed predator density. Namely, adaptive predation reduces the apparent competition between consumer species and drives the interior equilibrium to the IFD plane where profitability of both consumer species for predators is the same.

Species whose impact on their community is large are called keystone species (Paine, 1992; Power *et al.*, 1996). The identification of keystones in ecosystems is crucial in conservation ecology because extinction of keystones can cause a dramatic loss of biodiversity. Because experimental identification of keystone species through extensive pairwise species manipulations is either difficult or impossible, Power *et al.* (1996) suggested identification of traits that characterize keystone species in natural communities. For several traits, preferential feeding on dominant prey species seems to be naturally associated with keystone predation (Menge *et al.*, 1994; Power *et al.*, 1996). However, in a survey of well-studied marine and freshwater communities (Menge *et al.*, 1994), preferential predation on dominant prey species appeared both in systems with and without keystones. My analysis suggests that it is adaptive feeding that distinguishes between keystones and other predators because adaptive predators can more effectively regulate the food web than inflexible predators.

My results show, once again, that adaptive food choice is a key factor for species co-existence. Similar conclusions can be drawn from other population dynamical models that incorporate optimal foraging behaviour (e.g. Gleeson and Wilson, 1986; Fryxell and Lundberg, 1993, 1994, 1997; Křivan, 1996, 1997, 1999, 2003; Hambäck, 1998; Genkai-Kato and Yamamura, 1999; Křivan and Sikder, 1999; van Baalen *et al.*, 2001; Křivan and Eisner, 2003; Křivan and Schmitz, 2003). These studies suggest that adaptive foraging promotes species co-existence without necessarily stabilizing population densities at an equilibrium. This is because adaptive foraging changes interaction strength in food webs, which relaxes the competition (either apparent or exploitative) between species. Although most of these studies considered simple community modules consisting of three or four species, a recent study by Kondoh (2003) shows that similar mechanisms promote species persistence in complex food webs.

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APPENDIX 1: INVASIBILITY CONDITIONS WHEN PREDATORS ARE INFLEXIBLE FORAGERS

Model (1) has no interior equilibrium. It has, however, two equilibria with one consumer species missing. These are:

$$E_1 = \left(\frac{m_1(P_1)}{e_1\lambda_1}, \frac{r(e_1\lambda_1 K - m_1(P_1))}{e_1\lambda_1^2 K}, 0 \right)$$

and

$$E_2 = \left(\frac{m_2(P_2)}{e_2\lambda_2}, 0, \frac{r(e_2\lambda_2 K - m_2(P_2))}{e_2\lambda_2^2 K} \right)$$

Note that conditions

$$K > \frac{m_1(P_1)}{e_1\lambda_1} \quad \text{and} \quad K > \frac{m_2(P_2)}{e_2\lambda_2} \tag{A1}$$

are necessary for consumer co-existence. Indeed, if one of these inequalities does not hold, then the corresponding consumer species cannot survive in the food web because its per capita population growth rate will be negative.

Consumer 1 can invade the equilibrium E_1 of the linear food chain if $\mathrm{d}C_1/(C_1\mathrm{d}t)$ evaluated at the equilibrium is positive. This condition gives

$$\left. \frac{1}{C_1}\frac{\mathrm{d}C_1}{\mathrm{d}t} \right|_{E_1} = e_2\lambda_2 m_1(P_1) - e_1\lambda_1 m_2(P_2) > 0$$

Similarly, consumer 2 can invade the equilibrium E_2 of the linear food chain if $\mathrm{d}C_2/(C_2\mathrm{d}t)$ evaluated at the equilibrium is positive. This condition gives

$$\left. \frac{1}{C_2}\frac{\mathrm{d}C_2}{\mathrm{d}t} \right|_{E_2} = e_1\lambda_1 m_2(P_2) - e_2\lambda_2 m_1(P_1) > 0$$

The two conditions for permanence of the diamond-like food web cannot hold simultaneously and the system is impermanent.

APPENDIX 2: INVASIBILITY CONDITIONS WHEN PREDATORS ARE ADAPTIVE FORAGERS

Consumer 2 can invade the equilibrium E_1 (provided this equilibrium is positive) if $\mathrm{d}C_2/(C_2\mathrm{d}t)$ evaluated at the equilibrium is positive. As predators do not feed on consumer 2 at this equilibrium, this condition gives

$$\left.\frac{1}{C_2}\frac{\mathrm{d}C_2}{\mathrm{d}t}\right|_{E_1} = e_2\lambda_2 m_1(P) - e_1\lambda_1 m_2(0) > 0$$

Thus, consumer 2 can invade provided

$$m_1(P) > \frac{e_1\lambda_1 m_2\,(0)}{e_2\lambda_2}$$

Similarly, consumer 1 can invade the equilibrium E_2 of the linear food chain if $\mathrm{d}C_1/(C_1\mathrm{d}t)$ evaluated at the equilibrium is positive. As predators do not feed on consumer 1 at this equilibrium, this condition gives

$$\left.\frac{1}{C_1}\frac{\mathrm{d}C_1}{\mathrm{d}t}\right|_{E_2} = e_1\lambda_1 m_2(P) - e_2\lambda_2 m_1(0) > 0$$

Thus, consumer 1 can invade provided

$$m_2(P) > \frac{e_2\lambda_2 m_1(0)}{e_1\lambda_1}$$

In contrast to the inflexible predators, the two invasibility conditions can be satisfied when predators are flexible. For example, if predation mortality rates are linear functions of predator density (4) and the second consumer is the weaker competitor, then the two invasibility conditions hold if

$$P > \frac{e_1\lambda_1\mu_2 - e_2\lambda_2\mu_1}{e_2\lambda_2\Lambda_1}$$

APPENDIX 3: POPULATION DYNAMICS UNDER IFD

If the system moves in the IFD plane given by $F_1C_1 = F_2C_2$, then trajectories of (1) satisfy:

$$F_1\frac{\mathrm{d}C_1(t)}{\mathrm{d}t} = F_2\frac{\mathrm{d}C_2(t)}{\mathrm{d}t}$$

(Colombo and Křivan, 1993; Křivan, 1997; van Baalen *et al.*, 2001). Thus, along the IFD plane we have:

$$F_1C_1(t)(e_1\lambda_1R(t) - \mu_1 - \Lambda_1P_1) = F_2C_2(t)(e_2\lambda_2R(t) - \mu_2 - \Lambda_2P_2)$$

As $P_1 + P_2 = P$, we get:

$$P_1 = \frac{e_1\lambda_1(P\Lambda_2 + \mu_2) - e_2\lambda_2\mu_1}{e_2\lambda_2\Lambda_1 + e_1\lambda_1\Lambda_2}$$

and

$$P_2 = \frac{e_2\lambda_2(P\Lambda_1 + \mu_1) - e_1\lambda_1\mu_2}{e_2\lambda_2\Lambda_1 + e_1\lambda_1\Lambda_2}$$

Substituting these values in model (1), we obtain model (5).

APPENDIX 4: PREDATORS UNDERGO POPULATION DYNAMICS

Model (6) has two equilibria where one of the two consumer species is missing:

$$E_1 = \left(K\left(1 - \frac{m\lambda_1}{F_1ru_1}\right), \frac{m}{F_1u_1},\ 0,\ \frac{e_1K\lambda_1(F_1ru_1 - m\lambda_1) - F_1ru_1\mu_1}{F_1ru_1^2\Lambda_1}\right)$$
$$E_2 = \left(K\left(1 - \frac{m\lambda_2}{F_2ru_2}\right),\ 0, \frac{m}{F_2u_2},\ \frac{e_2K\lambda_2(F_2ru_2 - m\lambda_2) - F_2ru_2\mu_2}{F_2ru_2^2\Lambda_2}\right)$$

Consumer 1 can invade the equilibrium E_2 (provided it is positive) if $\mathrm{d}C_1/(C_1\mathrm{d}t)$ evaluated at the equilibrium is positive. This condition gives

$$\frac{1}{C_1}\frac{\mathrm{d}C_1}{\mathrm{d}t}\bigg|_{E_2} = \frac{K(F_2ru_2 - m\lambda_2)(e_1u_2\lambda_1\Lambda_2 - e_2u_1\lambda_2\Lambda_1) + F_2ru_2(-u_2\Lambda_2\mu_1 + u_1\Lambda_1\mu_2)}{F_2ru_2^2\Lambda_2} > 0$$

Similarly, consumer 2 can invade the equilibrium E_1 (provided it is positive) if $\mathrm{d}C_2/(C_2\mathrm{d}t)$ evaluated at the equilibrium is positive. This condition gives

$$\frac{1}{C_2}\frac{\mathrm{d}C_2}{\mathrm{d}t}\bigg|_{E_1} = \frac{K(F_1ru_1 - m\lambda_1)(e_2u_1\lambda_2\Lambda_1 - e_1u_2\lambda_1\Lambda_2) + F_1ru_1(u_2\Lambda_2\mu_1 - u_1\Lambda_1\mu_2)}{F_1ru_1^2\Lambda_1} > 0$$

In contrast to the case where predators do not undergo population dynamics, the two conditions for permanence of the diamond-like food web can hold simultaneously provided $F_1ru_1 - m\lambda_1 \neq F_2ru_2 - m\lambda_2$. However, the two conditions strongly restrict the set of possible parameters for which model (6) can be permanent (Fig. 4B).

Now I consider the case where predators are adaptive foragers. First, I consider equilibrium E_2 where I set $u_2 = 1$. Consumer 1 can invade this equilibrium (provided it is positive) if

$$\frac{1}{C_1}\frac{\mathrm{d}C_1}{\mathrm{d}t}\bigg|_{E_2} = \frac{K(F_2r - m\lambda_2)e_1\lambda_1 - F_2r\mu_1}{F_2r} > 0$$

Second, I consider equilibrium E_1 where I set $u_1 = 1$. Consumer 2 can invade this equilibrium (provided it is positive) if

$$\frac{1}{C_2}\frac{\mathrm{d}C_2}{\mathrm{d}t}\bigg|_{E_1} = \frac{K(F_1r - m\lambda_1)e_2\lambda_2) - F_1r\mu_2}{F_1r} > 0$$

These two conditions are then necessary for species co-existence when predators are optimal foragers (Fig. 4C).

APPENDIX 5: POPULATION DYNAMICS UNDER IFD

If condition (7) holds, then trajectories of model (6) that start in the lower triangular region of the consumer phase space tend to equilibrium E_a, which lies in the upper triangular region of the same phase space. In contrast, trajectories that start in the upper triangular region of the consumer phase space tend to the IFD plane because I assume that consumer 2 is competitively weaker than consumer 1. This causes a tension along the IFD plane and leads to the emergence of a new equilibrium in the IFD plane. Because this equilibrium lies in the IFD plane

$$F_1 C_1 = F_2 C_2$$

this (together with $u_1 + u_2 = 1$) gives the formulae for species equilibrium densities and the interaction strength at the equilibrium:

$$R^* = K\left(1 - \frac{m\lambda_1}{F_1 r} - \frac{m\lambda_2}{F_2 r}\right)$$

$$C_1^* = \frac{m}{F_1}$$

$$C_2^* = \frac{F_2 m}{F_1}$$

$$P^* = \frac{K(F_1F_2r - m(F_2\lambda_1 + F_1\lambda_2))(e_2\Lambda_1\lambda_2 + e_1\lambda_1\Lambda_2)}{F_1F_2r\Lambda_1\Lambda_2} - \frac{\Lambda_2\mu_1 + \Lambda_1\mu_2}{\Lambda_1\Lambda_2}$$

$$u_1^* = \frac{\Lambda_2(e_1K\lambda_1(F_2m\lambda_1 + F_1m\lambda_2 - F_1F_2r) + F_1F_2r\mu_1)}{K(F_2m\lambda_1 + F_1m\lambda_2 - F_1F_2r)(e_1\lambda_1\Lambda_2 + e_2\lambda_2\Lambda_1) + F_1F_2r(\Lambda_2\mu_1 + \Lambda_1\mu_2)}$$