# High food quality of prey lowers its risk of extinction

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The mineral and biochemical food quality of prey may limit predator production. This well-studied direct bottom-up effect is especially prominent for herbivore-plant interactions. Low-quality prey species, particularly when defended, are generally considered to be less prone to predator-driven extinction. Undefended high-quality prey species sustain high predator production thereby potentially increasing their own extinction risk. The food quality of primary producers is highly species-specific. In communities of competing prey species, predators thus may supplement their diets of low-quality prey with high-quality prey, leading to indirect horizontal interactions between prey species of different food quality. We explore how these predator-mediated indirect interactions affect species coexistence in a general predator-prey model that is parametrized for an experimental algae-rotifer system. To cover a broad range of three essential functional traits that shape many plant-herbivore interactions we consider differences in 1) the food quality of the prey species, 2) their competitive ability for nutrient uptake and 3) their defence against predation. As expected, low food quality of prey can, similarly to defence, provide protection against extinction by predation. Counterintuitively, our simulations demonstrate that being of high food quality also prevents extinction of that prey species and additionally promotes coexistence with a competing, low-quality prey. The persistence of the high-quality prey enables a high conversion efficiency and control of the low-quality prey by the predator and allows for re-allocation of nutrients to the high-quality competitor. Our results show that high food quality is not necessarily detrimental for a prey species but instead can protect against extinction and promote species richness and functional biodiversity.

Organisms can directly interact in numerous ways, such as predation, parasitism or allelopathy. Besides direct interactions, the importance of indirect interactions between organisms such as competition for shared resources (MacArthur 1970, Chesson 1990, Abrams 1998) or apparent competition are increasingly recognized. Organismal properties which shape species abundances and interactions are commonly referred to as functional traits. Food quality is an important trait of prey that is determined by the degree of biochemical and mineral mismatch between prey and predators and may directly limit predator production. Especially at the plant-herbivore interface, nutritional imbalances between the provision of minerals and biochemicals in the prey and the demands of the predators are a common phenomenon (Elser et al. 2000, Von Elert et al. 2003). The food quality of plants for herbivores is often evaluated by the plants' composition of minerals (phosphorus and nitrogen) (Elser et al. 2007, Sterner 2008) or biochemical compounds such as essential amino acids, vitamins, polyunsaturated fatty acids and sterols, which herbivores cannot synthesize on their own (Müller-Navarra 1995, Martin-Creuzburg et al. 2009, Sperfeld et al. 2012, Wacker and Martin-Creuzburg 2012). These biochemicals are not homogeneously distributed among prey species. In fact, the biochemical composition of primary producers is highly species-specific (Ahlgren et al. 1992, Volkman 2003, Piepho et al. 2012, Martin-Creuzburg and Merkel 2016). This creates an indirect horizontal interaction between the prey species as the overall food quality of the prey community is determined by the differences in food quality among different prey species. Low food quality of a prey species may function as a protection against predation as the predator is constrained by a deficiency in essential nutrients. A sufficiently high share of a second, high-quality prey in the diet releases the predator from food quality limitation as it provides biochemical nutrients to supplement the low-quality diet (Wacker and Martin-Creuzburg 2012). As the food is used with higher efficiency less nutrients are excreted and recycled.

Hence, this supplementation from a high quality to a low quality species increases predator production and decreases nutrient recycling. The balance between losses by predation and nutrient dependent growth determines the risk of a prey's extinction and therefore the prey community composition. Thus, we hypothesize that differences in food quality among prey species affect their coexistence. How exactly food quality affects coexistence (mediated by predation pressure and nutrient availability) is determined by the respective traits of the prey species. Consequently, we study the effect of food quality in the context of a variation in the prey's predation risk and competitiveness, which determine the prey's level of defence and its nutrient uptake ability at low nutrient concentrations, respectively. These two traits were shown to trade off against each other (Abrams and Matsuda 1997, Yoshida et al. 2004, Becks et al. 2012, Hiltunen et al. 2014), i.e. defence against predation may come at the cost of a lowered growth if resources are scarce.

Using numerical simulations, we evaluate how the indirect interactions between prey species of different food quality affect their coexistence and population dynamics at varying tradeoff strengths between defence and competitiveness. The biochemical food quality, determined by the mismatch between the biochemical composition of predator and prey, and the predation risk, determined e.g. by structural defences, are considered to be functionally independent. Both factors can individually affect the performance of the predator and thus the future grazing pressure by the prey species investing their energy and organic compounds into defence structures and easily accessible essential compounds. We cover a wide range of predator-prey systems by considering three different scenarios in which two prey species have different combinations of food quality and defence: 1) equal food quality scenario - both prey species are of high and identical food quality, thus eliminating the effects of food quality. This scenario was studied before (Abrams 1999, Jones and Ellner 2007) and serves as a reference. 2) undefended low quality scenario - the undefended prey species is of low food quality compared to the defended prey. This is a plausible scenario since low quality food is often easily accessible and available in large quantities, e.g. grass and leaves. 3) defended low quality scenario - the defended prey species is of low food quality compared to the undefended prey. This scenario is also ecologically reasonable as protective structures, such as thorns of terrestrial plants or thicker cell walls of algae mainly consist of carbon and thus decrease the food quality of the prey (Van Donk 1997).

A meta-analysis showed that cyanobacteria are generally a bad food source for zooplankton (Wilson et al. 2006). The detrimental effects originated mostly from morphology or biochemical mismatches, whereas toxicity was less relevant. The above mentioned scenarios are therefore informative to the management of cyanobacterial blooms, depending on the level of defence and biochemical food quality of the cyanobacteria in focus relative to their competitors.

Although for better clarity we focus on the extreme cases where either one of the prey species is of very low quality, we present also intermediate cases to cover 1) the gradual transition between the scenarios and 2) a broader range of natural predator-prey systems.

It is often assumed that low quality itself already provides protection against predation, and thus also against predatormediated competition, as it prevents the predator to establish high grazing pressures (Moran and Hamilton 1980, Augner 1995). This reasoning suggests that high food quality is detrimental to a prey species as it increases predation pressure and may provide a niche for predator-mediated competitors. We show that high food quality of a prey species can instead increase its persistence and promote coexistence with low-quality prey. With this approach we study how tradeoffs between functional traits of species and their biochemical composition, two prominent features in ecology, in concert shape community composition and population dynamics.

## Model and methods

## Predator-prey model

We build on a predator-prey model that was first published by Fussmann et al. (2000) as an algae-rotifer chemostat model and its basic properties were discussed by Jones and Ellner (2004, 2007). The basic model assumptions are nitrogen limitation, nitrogen homoeostasis and asexual reproduction of all species. Therefore, all state variables are scaled to nitrogen by the organisms' respective nitrogen content. Nitrogen N is taken up by two algal prey species A and B which are consumed by one herbivore species Z, e.g. a rotifer.

$$\frac{dN}{dt} = \delta N_{\rm I} + R - \delta N - \frac{\beta N}{K_{\rm A} + N} A - \frac{\beta N}{K_{\rm B} + N} B \tag{1}$$

$$\frac{dA}{dt} = \frac{\beta N}{K_{\rm A} + N} A - f_{\rm A} Z - \delta A \tag{2}$$

$$\frac{dB}{dt} = \frac{\beta N}{K_{\rm B} + N} B - f_{\rm B} Z - \delta B \tag{3}$$

$$\frac{dZ}{dt} = \varepsilon_{\rm A} f_{\rm A} Z + \varepsilon_{\rm B} f_{\rm B} Z - \delta Z \tag{4}$$

$$f_{\rm A} = \frac{\rho \, p_{\rm A} \, A}{K_{\rm Z} + p_{\rm A} \, A + p_{\rm B} \, B} \tag{5}$$

$$f_{\rm B} = \frac{\rho \, p_{\rm B} \, B}{K_{\rm Z} + p_{\rm A} \, A + p_{\rm B} \, B} \tag{6}$$

$$R = (1 - \varepsilon_{\rm A}) f_{\rm A} Z + (1 - \varepsilon_{\rm B}) f_{\rm B} Z$$
<sup>(7)</sup>

While the model is parametrised for an algae-rotifer chemostat, the model structure is applicable for many predatorprey systems. The parameters can be found in Table 1. An inflow concentration N<sub>I</sub> constantly supplies nitrogen with a flow rate  $\delta$ . At the same flow rate all nitrogen is washed out of the chemostat volume, be it dissolved in the medium or bound within organisms. Natural mortality of organisms is considered to be small compared to grazing losses or wash-out and therefore omitted. The substrate uptake by the algae is modelled with Monod functions. The functional responses of the grazer on the algal species A and B,  $f_A$  and  $f_B$ , are assumed to follow a Holling type II and extended to multiple prey species (Holling 1959). Due to potential food quality differences between the algal species we assume different conversion efficiencies  $\varepsilon_A$  and  $\varepsilon_B$  for each prey. The derivation of these conversion efficiencies can be found in the supplementaries and we argue that they are prey-density dependent. An efficiency smaller than one implies that nitrogen is ingested by the herbivore but only partly converted into production. The remaining share is recycled via excretion and leads to the recycling rate R to ensure mass balance. As discussed by Jones and Ellner (2007), a tradeoff between defence and competitiveness of the prey is implemented for the two algal species A and B. The investment into a lowered predation risk p, e.g. by producing defensive structures, comes at the cost of an increased half-saturation constant Kand thus a lowered competitive ability at low nutrient con-

centrations (competitiveness)  $\frac{1}{K}$  (Yoshida et al. 2004). Algal

Table 1.	Parametrization o	f our model	for an a	lgae–rotifer	chemostat.	<sup>1</sup> see Tischner	and I	Lorenzen 1	1979,	<sup>2</sup> estimated f	or our	system	from
Fussmar	n et al. (2000) and	Becks et al.	(2010), 3	<sup>3</sup> estimated fi	om own me	asurements, "	<sup>4</sup> set ac	cording to	typica	al experimer	ital co	nditions,	<sup>5</sup> see
Gaedke	et al. 2002.							0	<i>.</i>				

Parameter	Description	Value	Unit
δ	Chemostat dilution rate <sup>4</sup>	0.5	d-1
Nı	Chemostat inflow nitrogen concentration <sup>4</sup>	80	µmol N l−1
β	Maximum growth rate of algae	1	d <sup>-1</sup>
K <sub>A</sub>	Half-saturation constant of algal species $A^1$	4.3	µmol N I−1
K <sub>B</sub>	Half-saturation constant of algal species $B^4$	4.3-43	μmol N I-1
$p_{A}$	Predation risk of algal species $A$ (undefended) <sup>4</sup>	1	. 1
$p_{\rm B}$	Predation risk of algal species $B$ (defended) <sup>4</sup>	0-1	1
ρ	Maximum grazing rate of the predator <sup>2</sup>	1.76	d-1
, К <sub>7</sub>	Half-saturation constant of the predator <sup>2</sup>	28	µmol N I−1
ε	Conversion efficiency of $A$ into $Z$	0-0.66	. 1
ε <sub>R</sub>	Conversion efficiency of B into Z	0-0.66	1
S <sub>low</sub>	Sterol conc. of low-quality prey relative to that of $Z^3$	0	1
S <sub>Z</sub>			
$\underline{S_{\text{high}}}$	Sterol conc. of high-quality prey relative to that of $Z^3$	0.8	1
$S_{\rm Z}$			
е	Excretion factor <sup>5</sup>	0.33	1

species A is considered the undefended but better growing prey and B is defended against predation, but pays a cost for that defence, i.e.  $p_{\rm B} \le p_{\rm A}, \frac{1}{K_{\rm B}} \le \frac{1}{K_{\rm A}}$ . The position in trait-space of the defended prey will be varied to study the

effect of the strength of the tradeoff. Thus in our model we cover a broad range of defence, competitiveness and food quality; three key parameters that govern predator–prey systems in general and herbivore–plant interactions in particular.

#### Food quality of prey

The transfer of ingested prey biomass into predator biomass is governed by the predator's conversion efficiency. It can only be high if the demands for all essential biochemical nutrients (EBN) of the predator are met. Since the diet of a predator often consists of several prey species, with each of them having a different biochemical composition, its conversion efficiency depends on the community composition of the prey. A sufficiently high share of high-quality prey in the diet may provide the biochemical nutrients to also convert ingested low-quality prey into predator biomass. This links the conversion efficiency of the predator to population dynamics within the prey community and connects prey food quality with predator–prey interactions.

We vary the concentration of EBN among two prey species, resulting in either high or low food quality of a prey species. We assume that the EBN-to-nitrogen ratio of high quality food is well above the needs of the predator. Production from high quality food is therefore only nitrogen-limited. The EBN-to-nitrogen ratio of low-quality food is well below that of the predator. Thus, production from low-quality prey occurs with a low efficiency unless supplementary biochemical nutrients can be obtained from the ingestion of additional high-quality prey (see Fig. A1 in Supplementary material Appendix 1). The effect of these assumptions is captured by the conversion efficiencies  $\varepsilon_A$  and  $\varepsilon_B$ . Biochemical food quality thus affects only the numerical response of the predator but not its functional response. The conversion efficiency for the low-quality prey species  $\epsilon_{\rm low}$  is smaller than or equal to the conversion efficiency for the high-quality plant species  $\epsilon_{\rm high}$ . The following points thus hold for the conversion efficiency:

- If no high-quality prey is taken up, low-quality prey is consumed, but only leads to low production due to a limitation by EBN and ε<sub>low</sub> is minimal.
   If the predator ingests high-quality prey containing
- 2) If the predator ingests high-quality prey containing more EBN than it can use with the nitrogen from the high-quality prey, this surplus EBN enables further predator production from additionally consumed low-quality prey. The consumption of high-quality prey increases  $\epsilon_{low}$ .
- $\begin{array}{l} \epsilon_{low}. \\ 3) \ \ If \ a \ \ relatively \ large \ amount \ \ of \ high-quality \ prey \ is \ ingested, \ \epsilon_{low} \ becomes \ maximal \ (\epsilon_{low} = \epsilon_{high}) \ and \ predator \ production \ from \ low-quality \ prey \ is \ not \ limited \ by \ EBN, \ but \ entirely \ nitrogen-limited. \end{array}$

This reasoning results in a formulation of the conversion efficiency of the low-quality prey species  $\varepsilon_{low}$  which depends on the biomass ratio of high-quality prey to low-quality prey (Supplementary material Appendix 1 Fig. A2). For a formal derivation of Eq. 8 we refer to the supplementaries (Supplementary material Appendix 1).

$$\varepsilon_{\text{low}} = \min\left(1 - e, \frac{S_{\text{low}}}{S_Z} + \frac{f_{\text{high}}}{f_{\text{low}}} \left(\frac{S_{\text{high}}}{S_Z} - (1 - e)\right)\right)$$
(8)

The conversion efficiency of the high-quality prey species is constant and given by

$$\varepsilon_{\rm high} = 1 - e \tag{9}$$

Here, *e* is the excretion factor of the predator,  $S_{\text{low}}$ ,  $S_{\text{high}}$  and  $S_Z$  are the EBN-to-nitrogen ratios of low-quality prey, high-quality prey and predator, respectively, and  $f_{\text{high}}$  and  $f_{\text{low}}$  are the functional responses of the predator on highand low-quality prey, respectively. Since the biochemical nutrients are labile substances we assume that they are not recycled. The respective food quality scenario determines which prey species obtains which conversion efficiency:

 $\begin{array}{ll} \mbox{Equal food quality scenario} & \epsilon_{\rm A} = \epsilon_{\rm high} & \epsilon_{\rm B} = \epsilon_{\rm high} \\ \mbox{Undefended low quality scenario} & \epsilon_{\rm A} = \epsilon_{\rm low} & \epsilon_{\rm B} = \epsilon_{\rm high} \\ \mbox{Defended low quality scenario} & \epsilon_{\rm A} = \epsilon_{\rm high} & \epsilon_{\rm B} = \epsilon_{\rm low} \\ \end{array}$ 

Our formulation of  $\epsilon_B$  results in a partial co-limitation of predator growth by the quantity of available food,

 $\frac{p_{\rm A}{\rm A}+p_{\rm B}{\rm B}}{N_{\rm I}}$  , and its overall food quality, i.e. the relative

portion of high-quality food among the available food. Fig. 1 shows the per capita growth rate of the predator for both quality and quantity of available food. If less than 80% of the available food are represented by the high-quality prey species, predator growth is co-limited by EBN and the quantity of available food. Above 80% of high-quality prey, food quality is not limiting and only food quantity determines predator growth via its functional response.

#### Simulations and determination of dynamics

By combining vectorization and parallel computing the system of ordinary differential equations (Eq. 1–4) was integrated over a wide range of the trait space of the defended prey species *B* with the *ode23* algorithm in MatLab (The MathWorks). The simulations were run for 400 000 time units (days) to overcome any transients. The simulations were initialized at  $N(0) = \frac{1}{8}N_{\rm I}$ ,  $A(0) = \frac{3}{8}N_{\rm I}$ ,  $B(0) = \frac{3}{8}N_{\rm I}$  and  $Z(0) = \frac{1}{8}N_{\rm I}$ , except when we studied the dependence on initial conditions where different starting points were chosen. To distinguish between cycling and steady state dynamics, local peaks in herbivore density and the period length of cycles were determined using the 'findpeaks' algorithm from the time-series toolbox in MatLab. Only the last 10 000 days were considered in this analysis and the period



Figure 1. Co-limitation of predator growth by the quantity of available food,  $\frac{p_A A + p_B B}{N_I}$ , and its overall quality  $\frac{p_A A}{p_A A + p_B B}$ , assuming that A is the high-quality and B the low-quality prey. Parameters are  $\frac{S_B}{S_Z} = 0$ ,  $\frac{S_A}{S_Z} = 0.8$  and e = 0.33.

lengths were averaged. For peaks to be recognized, their relative size (prominence) had to exceed the simulation accuracy of 10<sup>-6</sup>. The bifurcation between different dynamic states of the system were studied using the continuation and bifurcation software MatCont (Dhooge et al. 2003).

## Results

Our simulations reveal how food quality influences species coexistence and population dynamics in a general predator-prey model. This holds in particular for the plantherbivore interface as primary producers often differ in their biochemical composition from their consumers. We use an algae-rotifer system to examine three different combinations of prey food quality and defence: 1) equal food quality scenario, 2) undefended low quality scenario and 3) defended low quality scenario. Predator production is not limited by biochemical nutrients in the first scenario but potentially in the two others (Fig. 1). First, we evaluate species coexistence along the defence-competitiveness tradeoff for the three different food quality scenarios (Fig. 2). Within each scenario, we vary the predation risk and the competitive ability at low nutrient concentrations of the defended prey species, relative to the undefended. Subsequently, the general types of species composition and population dynamics are discussed. Finally, we conclude by describing two ecologically relevant bistabilities between the system's long-term states. The results for the food quality scenarios are presented in detail for the extreme cases of prey food quality, as here the qualitative differences are clearest, but we present also the transition between these scenarios along a gradient of declining food quality.

## Equally high food quality

The equal food quality scenario (Fig. 2, top) was studied before (Abrams 1999, Jones and Ellner 2007) and serves as a reference that excludes differences in food quality of prey. It exhibits three different final species compositions (Fig. 2). For high competitiveness and a moderately lowered predation risk of the defended prey species, the undefended prey is outcompeted (blue region, Fig. 2). This corresponds to low costs for relatively high gains in defence. The defence therefore pays off. If the competitiveness is too low, the defended prey species goes extinct as irrespective of the gain in defence the costs of maintaining the defensive strategy are too high (yellow region, Fig. 2). For very low predation risks both prey species coexist over a large range of the competitiveness of the defended prey (green region, Fig. 2). Here, the defended cannot sustain the predator alone as its defence is too high. Only if some undefended prey remains the predator is kept from extinction, which in turn ensures that the costs for defence pay off and the defended prey species persists.

#### Undefended prey is of low food quality

The outcome of prey competition changes drastically if the undefended prey is of low food quality (Fig. 2, left scenario).



Figure 2. Competition outcome between the undefended prey A and the defended prey B growing on nitrogen N under predation by the predator Z for the three different food quality scenarios (above – equal food quality, far left – undefended low quality, far right – defended low quality) and the transitions. The trait differences between defended and undefended prey are varied by varying predation risk

 $p_{\rm B} \le p_{\rm A}$  and competitiveness  $\frac{1}{K_{\rm B}} \le \frac{1}{K_{\rm A}}, \left[ \left( \mu \text{molNI}^{-1} \right)^{-1} \right]$  of the defended prey. The colors depict the ratio between undefended and

defended prey averaged over the last 10 000 days. Dotted and crossed regions show quarter phase lag and antiphase cycling dynamics, respectively. Regions without markers are in steady state. The boundaries of the different regions in the equal food quality scenario are shown in grey also in the other scenarios. Exemplary dynamics for parameter combinations I–VI are shown in Fig. 3. The predator goes extinct only in the yellow, unmarked region. Similar behaviour was found at a lower dilution rate of  $\delta = 0.2$  (Supplementary material Appendix Fig. A5).

Only if the defended prey has a slightly lowered predation risk and a slightly lowered competitiveness compared to the undefended prey the competition outcome remains unchanged. Here, the defended prey is still able to dominate over the undefended prey as its defence pays off and costs are not too high (blue region, Fig. 2). Since the defended prey is of high food quality, it is able to sustain the predator. If the competitiveness of the defended prey is too low, the costs for defence become too high and the defended prey is outcompeted, as it was the case for equally high food quality in this region. However, now the undefended prey is of low food quality and cannot sustain the predator. Thus the predator goes extinct and only the undefended, low-quality prey remains (yellow region, Fig. 2). The same reasoning explains the outcome for a very low predation risk of the defended prey. In the equal food quality scenario, coexistence in this region was mediated by the predator, which was sustained only by the undefended prey as the defended prey was too defended. Since now the undefended prey is of low food quality, it does not sustain the predator which then cannot mediate coexistence. The resulting dominance of the undefended prey explains the spread of the yellow region over the steady state coexistence region and part of the region where the defended prey dominated in the equal food quality scenario. The extent of this overlap depends on the initial conditions and will be discussed later.

#### Defended prey is of low food quality

If the defended prey is of low food quality (Fig. 2, right scenario), we again see strong changes in the competition outcome compared to the other scenarios. The region in trait space where the defended prey outcompeted the undefended prey completely vanishes. In the equally high quality scenario the defence of the defended prey paid off while the defended prey was still able to sustain the predator on its own. Since it is now of poor nutritional value to the predator, it cannot sustain the predator which now depends on the high food quality of the undefended prey. If the undefended prey is grazed down to low biomasses the predator also decreases, thereby weakening the advantage of the defended over the undefended prey. This allows the undefended prey to withstand both competition with the defended prey as well as grazing from the predator. Consequently, the coexistence region which was only found for strong defences (low predation risk) in the equal food quality scenario now spreads across the entire range of predation risks (green region). If the costs of defence are too high for the defended prey, the undefended prey can persist with the predator due to its high food quality (yellow region). The upper boundary of this region, which defines at which competitiveness the defence pays off, is slightly shifted upwards. This implies that the defended prey needs an even higher competitiveness for its defence to pay off and to coexist with the undefended prey if it is of low food quality. Due to the increased coexistence of high and low-quality prey the effect of nutrient recycling is potentially large in this scenario. To study this effect we compared the prey competition outcome with (Fig. 2, right scenario) and without recycling (Supplementary material Appendix 1 Fig. A3). We observed no qualitative changes in the coexistence pattern or the distribution of biomass (Supplementary material Appendix 1

Fig. A4), but found less parameter combinations of cycling coexistence.

The outcome of prey competition is substantiated by the average biomasses of each species during the last 10 000 days of each simulation (Supplementary material Appendix 1 Fig. A4). Within the coexistence region of the equal food quality scenario the defended prey on average reaches higher biomasses than the undefended prey. The predator attains high average biomasses for more parameter combinations in this scenario than in the other ones as it is never limited by food quality. The undefended prey has extremely high average biomasses in the undefended low quality scenario as it outcompetes its competitor and does not sustain the predator. Within the defended low quality scenario, the average biomasses are more evenly distributed across the parameter space compared to the other scenarios. Removing nutrient recycling reduces the average biomasses for most parameter combinations.

A central parameter in all chemostat studies is the dilution rate as it determines residence times of organisms and nutrients, and the relative importance of fresh nutrient supply versus recycling. Reducing the dilution rate from  $0.5 \, d^{-1}$  to  $0.2 \, d^{-1}$  enlarges the parameter space where defence pays off in the equal food quality scenario. Also the region in the defended low quality scenario where we predict coexistence mediated by the high quality of the undefended prey increases strongly (Supplementary material Appendix 1 Fig. A5).

#### **Population dynamics**

Our system exhibits six different types of population dynamics for different parameter combinations of competitiveness and predation risk of the defended prey (Fig. 3). If both prey species coexist with the predator, the sum of the prey



Figure 3. Population dynamics for the parameter combinations marked in Fig. 2. Populations are scaled to the inflow concentration of the chemostat and transients of 399 900 days have been omitted. Combinations I and IV show coexistence of predator and both prey in antiphase cycling and steady state, respectively. In combinations II and III only one prey cycles with an approximately quarter phase lag with the predator. Combination V shows the steady state of the defended prey and the predator and in combination VI only the undefended prey, which is of low food quality in this case, remains in the system.

biomasses cycles antiphase with the predator biomass for lower predation risks (Fig. 2, crossed green region; Fig. 3, combination I). Within this antiphase cycling we observe temporal niching. If the predator biomass is high, the undefended prey is grazed down which releases the defended prey from nutrient competition. The predator declines as now the defended prey dominates the prey biomass. This releases the undefended prey from predation pressure and it outcompetes the defended prey. Therefore the temporal niche for the defended prey precedes the temporal niche of the undefended prey.

Prey coexistence in a steady state is attained for higher predation risks of the defended prey (Fig. 2, non-crossed green region; Fig. 3, combination IV). If one prey goes extinct and the remaining prey can sustain the predator population, prey and predator either cycle in a classic quarterperiod phase lag (Fig. 2, dotted blue and dotted yellow region; Fig. 3, combinations II and III) or attain a steady state (Fig. 2, unmarked blue region; Fig. 3, combination V). If the predator is not sustained, the remaining prey grows to its steady-state capacity (Fig. 2, yellow unmarked region; Fig. 3, combination VI).

#### **Bifurcations and bistability**

We investigated the dependence of the dynamics on initial conditions and found a bistability in the undefended low quality scenario between dominance of the low-quality, undefended prey on the one hand and the species composition pattern found for equal food quality on the other hand (Supplementary material Appendix 1 Fig. A6). Initially very low biomasses of the undefended, low-quality prey result in a smaller dominance region. If it has high initial biomasses, it dominates from the beginning and suppresses the establishment of either prey coexistence or the predator being sustained by the defended, high-quality prey, respectively.

We found a second bistability at the transition from cycling to steady state coexistence in the defended low quality scenario (Fig. 2, right scenario). In the reference model with equal biochemical food quality, coexistence in antiphase cycles and coexistence in steady state are connected by a supercritical Hopf-bifurcation (Fussmann et al. 2000, Jones and Ellner 2007). Within the defended low quality scenario, we find that the antiphase cycling at low predation risks of the defended prey and steady state prey coexistence are also connected by a supercritical Hopf-bifurcation. Interestingly, at intermediate predation risks, when decreasing the competitiveness of the defended prey, the transition from steady-state to antiphase cycling is instead mediated by a subcritical Hopf-bifurcation in combination with a cyclic-fold bifurcation (Supplementary material Appendix 1 Fig. A7, A8). This bifurcation pattern creates a bistability between steady state and antiphase cycling at the intersecting parameter region. This bistability becomes even more pronounced at lower dilution rates (Supplementary material Appendix 1 Fig. A9).

## Discussion

#### Food quality affects species coexistence

Under most natural conditions predators rely on a diverse community of prey species differing in their biochemical food quality. We show that these differences determine both prey species' coexistence and population dynamics. Our study reveals that within a diverse prey community, higher food quality does not necessarily imply a higher vulnerability to predation and extinction, but may favour survival under competition with a second defended prey species of lower food quality (Fig. 2, defended low quality scenario). In contrast, for a single prey species, low food quality is expected to serve as protection against extinction by predation (Moran and Hamilton 1980) as the predator cannot acquire enough



Figure 4. Predator production and nutrient recycling depend on both the ingested individual's food quality and the food quality of the whole prey community, i.e. the food quality conditions. (A) – under high-quality conditions the predator can grow equally well on highand low-quality prey due to supplementation. Under low-quality conditions, i.e. the predator is generally quality-limited, a high-quality prey individual can be converted efficiently into predator biomass. Also, it contributes surplus essential biochemical nutrients (EBN) that allow for additional predator production from low-quality prey. Under the same conditions an ingested low-quality prey individual is not supplemented and predator production is low. (B) – under high-quality conditions nutrient recycling is proportional to the excretion factor *e*. Under low-quality conditions surplus EBN from an ingested high-quality prey individual reduce the net recycled nutrients below normal excretion as nitrogen from additional ingestion can also be converted, while most of the nutrients from a low-quality prey are recycled.

biomass to graze down the prey population. Our results indicate that this protection is reduced as soon as there is a second, high-quality prey that can sustain a predator population (Fig. 2, undefended low quality scenario) and may thus be less relevant in nature.

The food quality of one prey species can modulate the growth of and predation on competing prey species and the resulting effect of food quality depends on differences and trade-offs between functional traits of the prey community. Consumption of a single individual directly decreases that species' density, but also impacts the whole prey community by two processes that directly depend on prey food quality: 1) additional predator production that increases the predation pressure on the whole prey community (numerical response) and 2) nutrient recycling that makes nutrients from a consumed prey available to the whole prey community. These community effects of predation depend on both, the food quality of the consumed individual and the food quality composition of the whole prey community and are therefore highly context-dependent (Fig. 4).

Under high-quality conditions, i.e. in an environment dominated by high-quality prey, the predator production per consumed low-quality prey individual equals that of a high-quality prey since additionally consumed high-quality prey supplements the low-quality prey. Under low-quality conditions, however, an ingested individual of low-quality prey cannot be supplemented, leading to a low predator production. Under the same conditions an ingested high-quality prey allows for predator production from its own biomass and also delivers a surplus of biochemical nutrients that may be used to supplement additional predator production from low-quality prey.

Recycling behaves oppositely: under high-quality conditions only few of the nutrients bound within a consumed prey are recycled, irrespective of its own quality. The same holds for a high-quality prey that is consumed under low-quality conditions, while all of the nutrients from a low-quality prey are routed to the medium as there is no supplementation by high-quality prey (Fig. 4).

Whether and how the prey species are impacted by these indirect effects depends on their functional traits. The probability for a prey individual to be consumed and how it is affected by an increase in predation pressure are determined by its defence. Whether an increase of nutrient recycling matters depends on the competitiveness of the prey. Thus food quality gives rise to indirect species interactions between prey that shape the different competition outcomes within the trait space of the defended prey (Fig. 2).

Figure 4 implies that only strong competitors for nutrients can counteract predation with low food quality as most of their nutrients are recycled upon consumption and can only be regained if the low-quality prey is competitively superior. Therefore, under low-quality conditions, implying high recycling, low food quality is rather detrimental for a defended prey. Consumption of a low-quality prey individual does not increase the predation pressure on the prey community. This prevents a competitive advantage for the defended prey. Instead, most of the nutrients from the ingested low-quality prey are recycled and made accessible to competitors, allowing for growth of an undefended prey species that is a better competitor for nutrients. If this species is of high food quality it increases the predator production by dietary supplementation of the low-quality species. Eventually, the supplementation limits its further net growth since now the defence of the defended prey pays off. Thus, the combination of limitation of predator production and recycling shifts biomass from the low-quality to the highquality prey and promotes the persistence of the undefended high-quality prey species.

We assumed a rather high dilution rate typical for experimental systems studying predator-prey relationships (Fussmann et al. 2000). However, lower dilution rates in fact increase the significance of our results (Supplementary material Appendix 1 Fig. A5). At low dilution prey growth is more bottom-up limited which makes being defended even more valuable as it protects already established biomasses. This allows the defended prey to outcompete the undefended prey already at lower competitiveness in the equal food quality scenario. As a consequence, also the coexistence region is enlarged which is mediated by quality limitation of the predator in the defended low quality scenario (Supplementary material Appendix 1 Fig. A5). Additionally, lower dilution increases the importance of recycled nutrients relative to fresh supply (Vadstein et al. 2012). This impedes the competitive ability of a low-quality species of which a higher portion is recycled by grazing (Fig. 4) and these recycled nutrients remain longer available to competitors due to the lower dilution rate.

## Food quality affects population dynamics

Populations tend to switch from steady state to predatorprey cycles if the energy flux to the predators increases and food chains become more top-heavy (Abrams 1999, Rip and McCann 2011) and we observed corresponding patterns in our simulations. These switches are of ecological importance as within the cycles, populations may reach very small numbers making them vulnerable to stochastic extinctions (Rosenzweig 1971). Depending on the strength of the defence-competitiveness tradeoff we found two types of population dynamics that enable both prey species to coexist with the predator (Fig. 3). Within the antiphase cycles of total prey and predator biomass, the niches that both prey occupy are temporally separated as the prey competes for a single nutrient (Gilpin 1975, Armstrong and McGehee 1980). At high competitiveness and high predation risk of the defended prey (weak tradeoff) both prey species become more similar. This tends to increase the competition of the prey species as their temporal niches overlap to a larger extent. Therefore, prey growth becomes more bottomup limited and its density dependence increases, which promotes steady-state dynamics. Similarly, competition between the two prey species increases without recycling. The amount of substrate in the system is reduced as a nitrogen export is created which becomes high at high grazing and low prey food quality. Thus, without recycling, we find cycling coexistence only for half as many parameter combinations (Supplementary material Appendix 1 Fig. A3). At the transition from steady state of defended prey and predator to quarter phase lag cycling an increasing predation risk of the defended prey results in a higher prey availability for the predator and higher predator production, promoting predator-prey cycles.

## Food quality may cause a bistability

In our system, the coexistence in antiphase cycles and the coexistence in steady-state is partly bistable giving rise to two possible long-term dynamics for the same species. This bistability is ecologically important for two reasons: 1) the mean biomasses of the species differ between the two states (Supplementary material Appendix 1 Fig. A7). This affects system properties such as the mean food quality of the prey trophic level, but also the biomass of the predator is different. This can for example determine the system's invasibility for a top-predator or potential ecosystem services, e.g. production of essential biochemicals. 2) Due to the non-linear dependence of grazing on prey biomass mean clearance rates differ between a cycling system and a system at steady state, even if the mean biomasses were equal (Jensen's inequality). This again can cause different energy fluxes between trophic levels for the same species or impact possible top-predators that may average over fluctuating biomasses due to their larger body size. Which of these states is attained depends on the initial conditions. Switching between the two attractors by directed perturbations can occur, e.g. by loss of a certain amount of the high-quality prey. Knowledge of such bistabilities in natural systems is important as it impacts their long-term predictability and may explain regime shifts (Andersen et al. 2009).

### **Biological relevance of our results**

Intuitively, one expects low food quality of prey to be an indirect protection against predation as it prevents the predator to thrive and we can confirm this hypothesis for the undefended low quality scenario for a substantial parameter range. Counterintuitively, we also found that combining low food quality with a defence against predation can be unfavourable for that species. In this case, low food quality promotes coexistence with a second species that is especially vulnerable to predation as it is both undefended and of high food quality. This unexpected result is ecologically relevant as the underlying scenario is supported by experimental findings. Defensive physiological structures, such as thicker cell walls (Van Donk 1997, Hamm et al. 2003) or spines and thorns (Milewski et al. 1991, Tollrian and Harvell 1999) are mainly made of carbon (e.g. cellulose) and therefore, by increasing the carbon-to-nutrient ratio, decrease the food quality of the defended prey. The defended low quality scenario that comprises the coexistence promoting effect of food quality thus may regularly occur in natural systems.

While in general our approach makes no assumptions of a distinct ecosystem, an intriguing and economically relevant example where our model may be informative are cyanobacterial blooms. Firstly, reports of the low biochemical quality of cyanobacteria for grazers accumulate (Martin-Creuzburg et al. 2009, Wacker and Martin-Creuzburg 2012). Secondly, the morphology of cyanobacteria is diverse ranging from single-celled forms over colonies to filamentous species and largely affects zooplankton performance analogous to the predation risk we defined (Wilson et al. 2006). Thus, both the undefended low quality scenario and the defended low quality scenario are realistic situations for pelagic ecosystems as predation risk and food quality are always measured relative to the respective competitors of the cyanobacteria. The undefended low quality scenario (Fig. 2, left side) is representative for cyanobacterial blooms when no better competitor for nutrients is present, and grazers and competitors go extinct. The defended low quality scenario (Fig. 2, right side) holds for defended cyanobacteria (e.g. by colonyforming or mat-building) which are worse competitors for nutrients than other high-quality algal species due to their defence (e.g. by limited diffusion through the clumps). For this situation, our study predicts that the complete take-over of the cyanobacteria is prevented by the high quality of the competitor which fits with observations (Nixdorf and Hoeg 1993).

The nutritional imbalance at the plant-herbivore interface is a general feature in nature (Elser et al. 2000). Thus, food quality plays an important role across scales and ecosystems and supplementary feeding might be a prominent strategy of many herbivores. Our work shows that food quality can determine species coexistence and population dynamics and that a prey species can shape the predation on the whole prey community. Together with other species' traits and tradeoffs among these traits, low food quality can reduce predation pressure while high food quality can promote predator-mediated coexistence of prey. Nature comprises more than direct species interactions and food quality should be considered an important factor that mediates indirect interactions and shapes functional biodiversity.

*Acknowledgements* – We thank Apostolos-Manuel Koussoroplis, Elias Ehrlich, Dominik Martin-Creuzburg and Teppo Hiltunen for helpful discussions and insightful comments on the manuscript. *Funding* – This work was funded by DFG (WA 2445/8-1, WA 2445/11-1, GA 401/26-1) as part of the Priority Programme 1704 (DynaTrait).

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Supplementary material (available online as Appendix oik-03863 at <www.oikosjournal.org/appendix/oik-03863>). Appendix 1.

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