Oikos

Appendix oik-03863
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Appendix 1

Derivation of the conversion efficiency

Within the following we will present the derivation of the conversion efficiency for the food quality scenario where the defended prey B has low food quality (defended low quality scenario), see also Fig. A1. For the opposite case, the same arguments hold and only the prey species A and B need to be interchanged, as this derivation makes no assumptions on growth or defence of the respective prey species. Also, we assume the essential biochemical nutrients to be sterols, though the derivation equally holds for similar substances. For a compilation of symbols used in the following derivation we refer to Table A1.

The conversion efficiency determines how much nitrogen is invested into production at a certain time point if a certain amount of nitrogen is consumed. Predator production in our model is co-limited by the amount of sterols in the diet and the amount of biomass that is consumed. Since we assume homoeostasis in all organisms, we use nitrogen as a measurable surrogate for biomass. The amount of available prey nitrogen then shapes the functional response curve (Holling type II) which gives the amount of ingestion at a given point in time. Only part of the ingested nitrogen n^I is assimilated, the rest of the ingested nitrogen will be excreted. The amount of excretion is determined by the excretion constant e. At what efficiency the assimilated nitrogen can be transferred into new predator biomass depends on the amount of sterols σ^I that were ingested together with the nitrogen from each prey species, since new biomass can only be created at the sterol-to-nitrogen ratio S_Z of the predator. Here we assume that sterols are not excreted but completely assimilated as this should usually be the case. Also, neither nitrogen nor sterols are used up within respiration. The overall conversion efficiency ε measured in nitrogen (as a surrogate for biomass) will thus not only depend on excretion, but also on the available amount of sterols in the diet.

Our model assumes that the two prey species differ in their sterol content, whereas prey A contains more sterols per nitrogen than what would be needed to produce predator biomass and the other contains less. Therefore there will be surplus sterols left over from the high-quality prey A that can be used together with surplus nitrogen that was left over from the low-quality prey B. Altogether, this means that the lacking sterols in B reduce the conversion efficiency of Z from B, but can be complemented by sterols delivered by A.

We will now derive the conversion efficiency of Z from feeding on B by considering nitrogen and sterol balances for all processes described above. We will start with the sterol and nitrogen balances for independent reproduction on either of the two food sources. If an amount of nitrogen n_A^I is ingested by consuming prey species A, then $(1-e)\,n_A^I$ nitrogen is assimilated and therefore available for either reproduction (n_A^P) or to be left-over as surplus (n_A^S). The remaining nitrogen $e\,n_A^I$ will be recycled and added to the surrounding medium. The same should hold for sterols from A except they are not excreted and thus not recycled. Therefore we can formulate the basic mass balances for nitrogen and

sterols from the two prey species A and B.

$$n_A^I - n_A^{Recycling} = (1-e)\, n_A^I = n_A^P + n_A^S \tag{A1}$$
$$\sigma_A^I = \sigma_A^P + \sigma_A^S \tag{A2}$$

$$n_B^I - n_B^{Recycling} = (1-e)\, n_B^I = n_B^P + n_B^S \tag{A3}$$
$$\sigma_B^I = \sigma_B^P + \sigma_B^S \tag{A4}$$

With S, the amount of sterols per nitrogen unit in an organism, we can connect sterols and nitrogen used in reproduction ($\sigma_A^P = n_A^p S_A$, $\sigma_B^P = n_B^p S_B$). Thus, the sterol balances become

$$n_A^I\ S_A = n_A^P\ S_Z + \sigma_A^S \tag{A5}$$
$$n_B^I\ S_B = n_B^P\ S_Z + \sigma_B^S \tag{A6}$$

Now we can derive conditions for the sterol-to-nitrogen ratios of the three species so that there is no surplus nitrogen coming from A and no surplus sterols coming from B. What this means is that all nitrogen from A is used up with the sterols from A and all sterols from B are used up with the nitrogen from B. If we call for $n_A^S = 0$ we see in equation A5 that σ_A^S vanishes exactly at $S_A = (1-e)\ S_Z$. Therefore σ_A^S becomes larger than zero if $S_A > (1-e)\ S_Z$ resulting in surplus sterols which were not used in reproduction from A. Following the same rationale we see that for $(1-e)\ S_Z > S_B$ there will be no surplus sterols from B but left-over nitrogen that was not used up in reproduction from B. If we put these two conditions together we arrive at an expression for the sterol-to-nitrogen ratios of the three organisms that fulfils our requirements and allows for surplus nitrogen from B to be used with surplus sterols from A:

$$S_A > (1-e)\ S_Z > S_B \tag{A7}$$

which also represents our claim of one high-quality prey and one low-quality prey species. This ensures $n_A^S = 0$ and $\sigma_B^S = 0$ and turns equations A5 and A6 to

$$n_A^I\ S_A = (1-e)\, n_A^I\ S_Z + \sigma_A^S \tag{A8}$$
$$n_B^I\ S_B = n_B^P\ S_Z \tag{A9}$$

Now we can connect the surplus sterols σ_A^S from A with the surplus nitrogen n_B^S from B and define the amount of sterols (σ_A^{SP}) and nitrogen (n_B^{SP}) that will additionally lead to growth and reproduction due to supplementation. Since still not all sterols or nitrogen might be used up in reproduction, we will allow for nitrogen to be recycled and sterols to go to waste, as sterols are usually not recycled.

$$\sigma_A^S = \sigma_A^{SP} + \sigma_A^{Waste} \tag{A10}$$
$$n_B^S = n_B^{SP} + n_B^{S,\ Recycling} \tag{A11}$$

The conversion efficiency now can be defined as the ratio of nitrogen from B used for reproduction and the amount of ingested nitrogen from B:

$$\varepsilon_B = \frac{n_B^P + n_B^{SP}}{n_B^I} \tag{A12}$$

From here on there are two possible outcomes, either there are too many sterols left over which cannot be used up with the surplus nitrogen, or there is too much nitrogen left over which cannot be used up

with the surplus sterols. Which option is chosen depends on whether the ratio of surplus sterols over surplus nitrogen is larger or smaller than the body content ratio of sterols to nitrogen in the predator S_Z.
In option one no nitrogen is recycled and some sterols will go to waste. In the second case no sterols will go to waste but some nitrogen is recycled. Since we are computing the conversion efficiency in nitrogen units the first scenario with zero recycling leads to maximum efficiency, whereas the latter will result in a reduced conversion efficiency in nitrogen units as sterols are lacking.

Case I - $\sigma_A^S / n_B^S > S_Z$

In this case, there are enough sterols available and no additional nitrogen has to be recycled, which means $\sigma_A^{Waste} > 0$ and $n_B^{S,\,Recycling} = 0$ in equations A10 and A11. Therefore $n_B^S = n_B^{SP}$ and equation A3 becomes

$$(1-e)\, n_B^I - n_B^P = n_B^{SP}$$

and we arrive at a conversion efficiency of

$$\begin{aligned} \varepsilon_{B1} &= \frac{n_B^P + (1-e)\, n_B^I - n_B^P}{n_B^I} \\ &= 1 - e \end{aligned} \tag{A13}$$

which is exactly the maximum possible efficiency if only excretion reduces the amount of nitrogen used for reproduction.

Case II - $\sigma_A^S / n_B^S < S_Z$

In the second scenario, sterols are limiting the amount of nitrogen to be used for reproduction, which translates to $\sigma_A^{Waste} = 0$ and $n_B^{S,\,Recycling} > 0$ in equations A10 and A11. Thus we have $\sigma_A^S = \sigma_A^{SP}$ which we can rewrite with equation A8 to

$$\begin{aligned} \sigma_A^S &= n_B^{SP}\, S_Z \\ &= n_A^I (S_A - (1-e)\, S_Z) \end{aligned}$$

With equation A9 the conversion efficiency for the case of limiting sterols becomes

$$\begin{aligned} \varepsilon_{B2} &= \frac{n_B^P + n_B^{SP}}{n_B^I} \\ &= \frac{S_B}{S_Z} + \frac{n_A^I}{n_B^I} \left(\frac{S_A - (1-e)\, S_Z}{S_Z} \right) \end{aligned} \tag{A14}$$

Connecting the two cases

The condition for the second case can be rewritten to obtain an upper limit of the conversion efficiency that equals the conversion efficiency of the first case.

$$\begin{aligned} \sigma_A^S &< n_B^S\, S_Z \\ n_A^I (S_A - (1-e)\, S_Z) &< S_Z \left((1-e)\, n_B^I - n_B^P \right) \\ n_A^I (S_A - (1-e)\, S_Z) &< S_Z ((1-e)\, n_B^I - n_B^I \frac{S_B}{S_Z}) \\ n_A^I (S_A - (1-e)\, S_Z) &< n_B^I ((1-e)\, S_Z - S_B) \end{aligned}$$

$$\frac{n_A^I}{n_B^I} < \frac{(1-e)\, S_Z - S_B}{S_A - (1-e)\, S_Z} \tag{A15}$$

Equation A15 can now be inserted into equation A14 to obtain the upper limit of ε_{B2} since the term within the brackets is always positive after condition A7.

$$\varepsilon_{B2} < \frac{S_B}{S_Z} + \frac{(1-e)\,S_Z - S_B}{S_A - (1-e)\,S_Z}\left(\frac{S_A - (1-e)\,S_Z}{S_Z}\right) = 1 - e$$

Therefore whenever the condition of the second case holds, the conversion efficiency will stay below that of the first case and we can use the minimum function to bring the two formulations of the conversion efficiency together.

$$\begin{aligned}\varepsilon_B &= \min(\varepsilon_{B1}, \varepsilon_{B2}) \\ &= \min\left(1 - e\ ,\ \frac{S_B}{S_Z} + \frac{n_A^I}{n_B^I}\left(\frac{S_A - (1-e)\,S_Z}{S_Z}\right)\right)\end{aligned} \tag{A16}$$

to obtain an expression of the conversion efficiency in units of nitrogen which holds for all n_A^I and n_B^I if the species' sterol to nitrogen ratios fulfil condition A7.
As we have seen, the conversion efficiency from feeding on A under condition A7 is

$$\varepsilon_A = 1 - e \tag{A17}$$

and the amount of recycled nitrogen from A and B becomes

$$n_A^{Recycling} = (1 - \varepsilon_A)\, n_A^I \tag{A18}$$

$$n_B^{Recycling} = (1 - \varepsilon_B)\, n_B^I \tag{A19}$$

where $n_A^{Recycling}$ is only determined by excretion but $n_B^{Recycling}$ is given by excretion together with unused nitrogen due to sterol limitation.
If we now define a certain time unit τ over which a nitrogen amount of n^I was consumed by one predator unit Z we can relate the ingested nitrogen to the functional responses f which gives the rate of nitrogen ingestion at a given time point by writing

$$f = \frac{n^I}{\tau}$$

and the conversion efficiency can be expressed in terms of the functional responses f_A and f_B given in the ordinary differential equations 2-4 (Fig. A2).

$$\varepsilon_B = \min\left(1 - e\ ,\ \frac{S_B}{S_Z} + \frac{f_A}{f_B}\left(\frac{S_A - (1-e)\,S_Z}{S_Z}\right)\right) \tag{A20}$$

and the total recycling term R becomes the sum already given in equation 7.

$$R = (1 - \varepsilon_A)\, f_A\, Z + (1 - \varepsilon_B)\, f_B\, Z$$

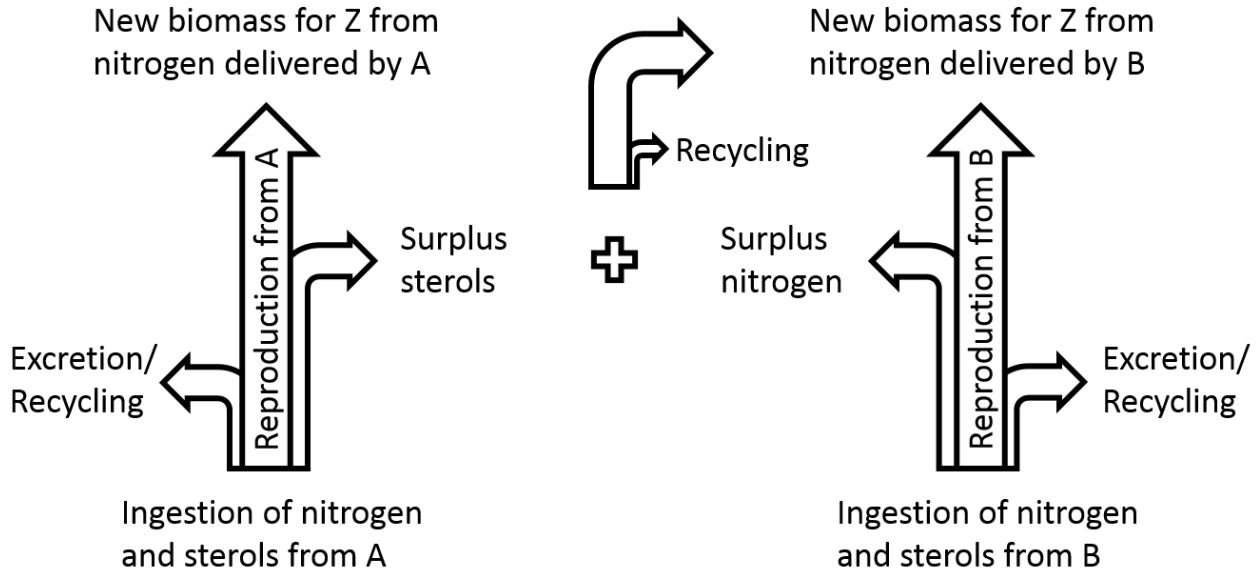


Figure A1 Illustration of the flow of mass from the producers A and B to the consumer Z and the concept of surplus nitrogen and surplus EBN (here sterols) to increase the nitrogen flow from B to Z. The ratio of A to B determines the relative amounts of surpluses. How those are processed determines the conversion efficiency of feeding on B. Here, it is assumed that the defended prey B has low food quality (defended low quality scenario). For the opposite case A and B can be interchanged deliberately within this derivation.

Table A1 List of symbols used for the derivation of the conversion efficiency.

Parameter	Description	Unit
ε_A	conversion efficiency of Z on A with respect to N	1
ε_B	conversion efficiency of Z on B with respect to N	1
f_A	Functional response of Z on A	µmol N/s
f_B	Functional response of Z on B	µmol N/s
S_A	Sterol to N ratio of prey A	nmol Sterol/µmol N
S_B	Sterol to N ratio of prey B	nmol Sterol/µmol N
S_Z	Sterol to N ratio of predator Z	nmol Sterol/µmol N
e	Excretion factor	1
τ	Arbitrary time relating functional responses to consumed N	day
n_A^I	Ingested amount of N from A at a given time per unit predator	µmol N
$n_A^{Recycling}$	Ingested N from A not assimilated but immediately recycled	µmol N
n_A^P	N from A directly used up for reproduction with sterols from A	µmol N
n_A^S	Surplus N from A not used up for reproduction with sterols from A	µmol N
σ_A^I	Ingested amount of sterols from A at a given time per unit predator	nmol Sterols
σ_A^P	Sterols from A that are directly used up for reproduction with N from A	nmol Sterols
σ_A^S	Surplus sterols from A not used up for reproduction with N from A	nmol Sterols
n_B^I	Ingested amount of N from B at a given time per unit predator	µmol N
$n_B^{Recycling}$	Ingested N from B that is not assimilated but immediately recycled	µmol N
n_B^P	N from B that is directly used up for reproduction with sterols from B	µmol N
n_B^S	Surplus N from B not used up for reproduction with sterols from B	µmol N
σ_B^I	Ingested amount of sterols from B at a given time per unit predator	nmol Sterols
σ_B^P	Sterols from B directly used up for reproduction with N from B	nmol Sterols
σ_B^S	Surplus sterols from B not used up for reproduction with N from B	nmol Sterols
σ_A^{SP}	Surplus sterols from A enabling reproduction with surplus N from B	nmol Sterols
n_B^{SP}	Surplus N from B enabling reproduction with surplus sterols from A	µmol N
σ_A^{Waste}	Surplus sterols from A for which no surplus N from B is left	nmol Sterols
$n_B^{S,Recycling}$	Surplus N from B for which no surplus sterols from A are left	µmol N

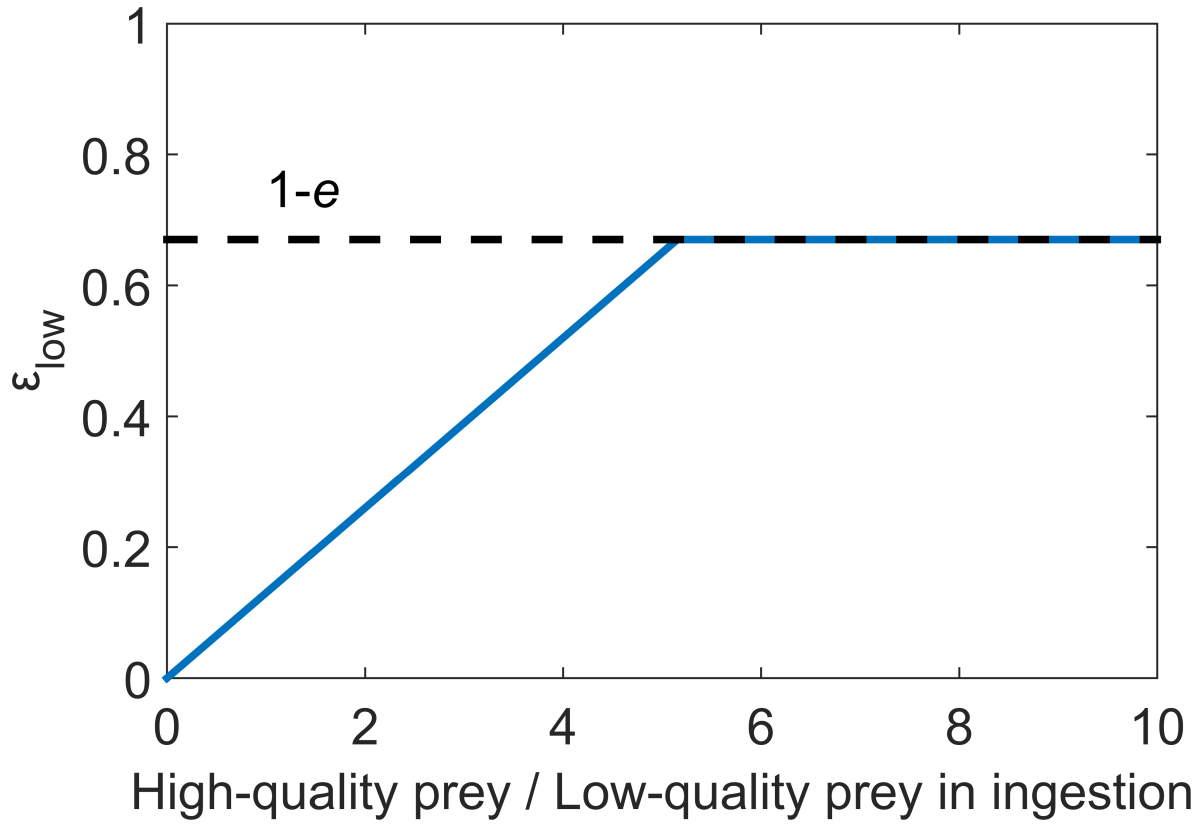


Figure A2 The conversion efficiency of the predator for the low-quality prey depends on the functional responses for low-quality and high-quality prey as given in equation A20. Parameters that determine the shape of the conversion efficiency are chosen as $\frac{S_{\text{low}}}{S_Z} = 0$, $\frac{S_{\text{high}}}{S_Z} = 0.8$ and $e = 0.33$.

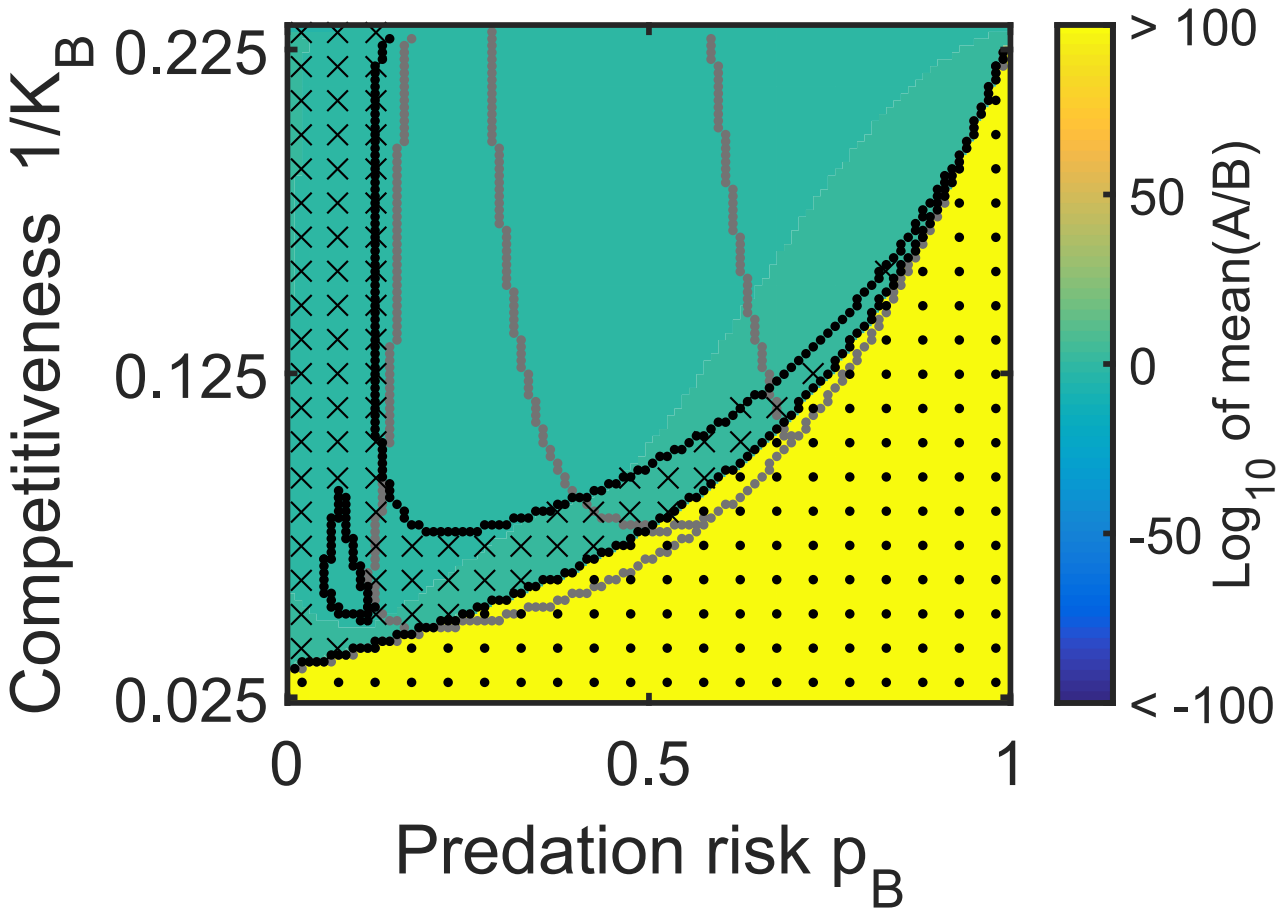
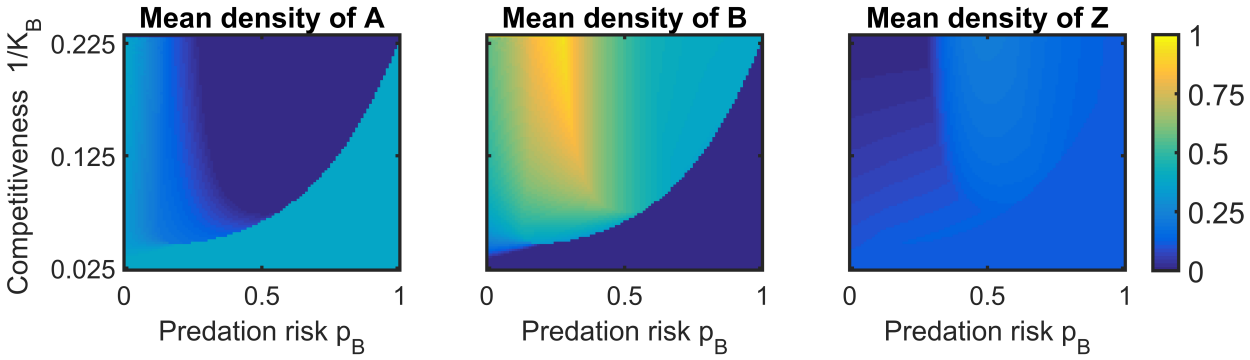
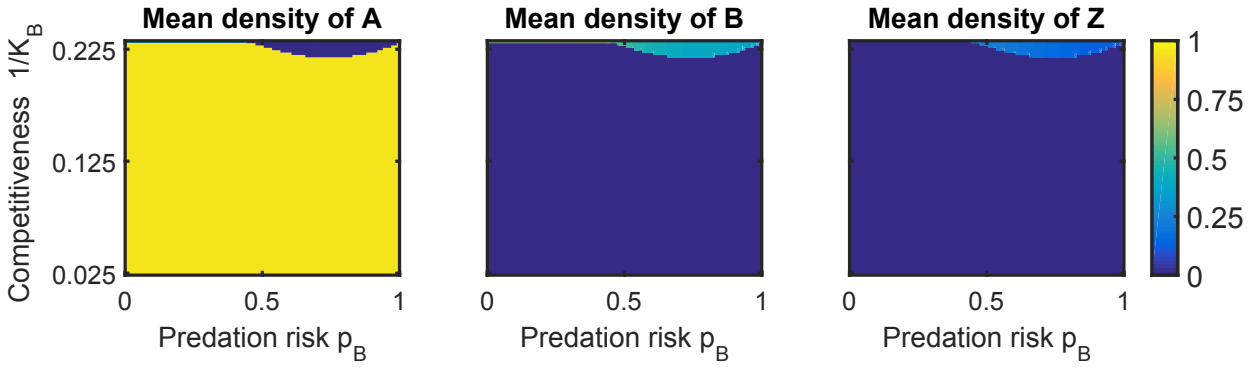


Figure A3 Coexistence without recycling at high food quality of undefended prey. Plot specifics are the same as in Fig. 2.

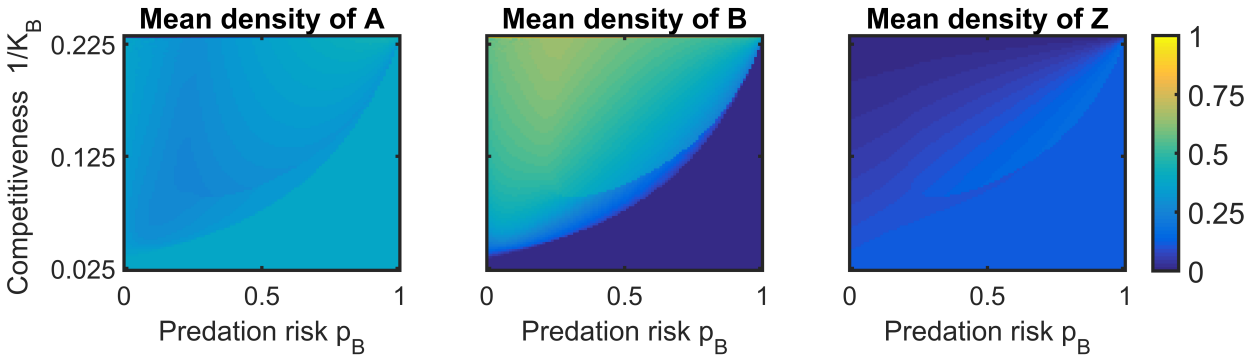
(a) Equal food quality scenario



(b) Undefended low quality scenario



(c) Defended low quality scenario



(d) Defended low quality scenario with recycling term R set to zero

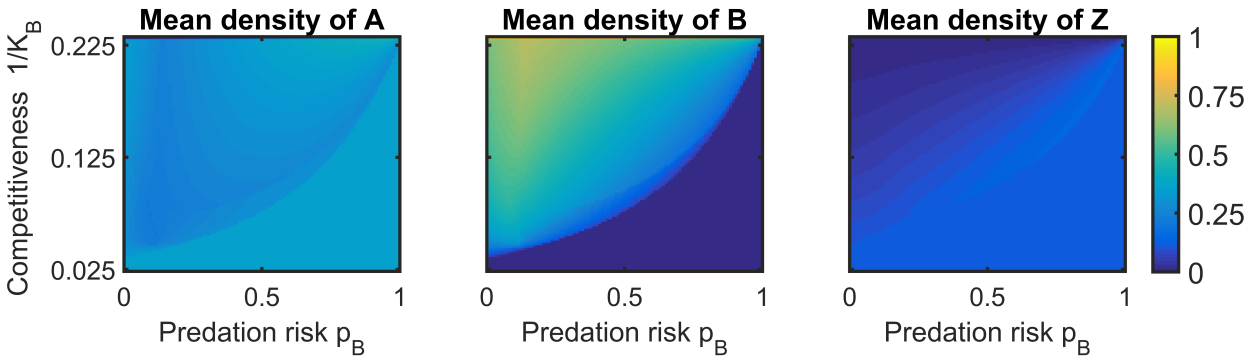
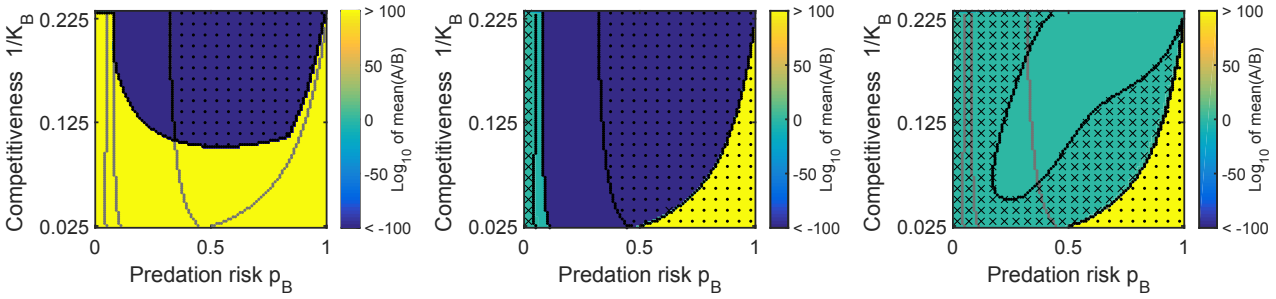
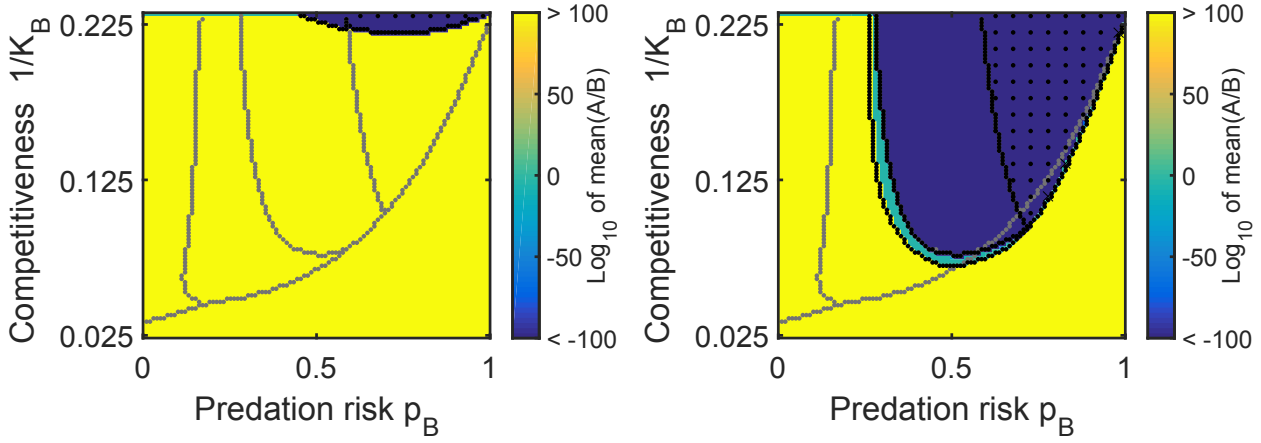


Figure A4 Biomasses of the undefended prey A (left), the defended prey B (middle) and the predator Z (right) relative to the inflow concentration, averaged over the last 10 000 days of the simulations.



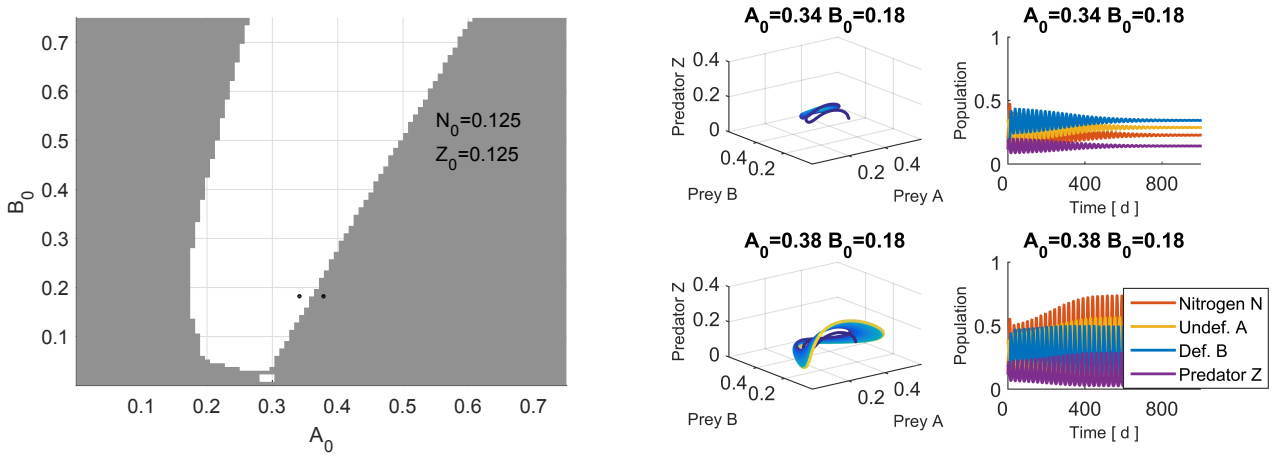
(a) Undefended low quality (b) Equal food quality (c) Defended low quality

Figure A5 Competition outcome at lower dilution rate $\delta = 0.2$ d^{-1}. Plot specifics are the same as in Fig. 2. A dilution rate of $\delta = 0.3$ d^{-1} produces intermediate results compared to Fig. 2.



(a) $A_0 = 3/8 N_I$ (b) $A_0 = 1/80 N_I$

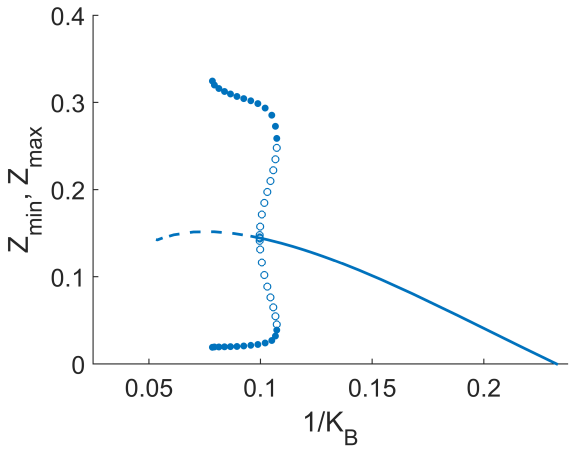
Figure A6 Bistability in the system where the undefended prey A has the low food quality, shown by using different initial conditions for the undefended prey A and the same plot as in Fig. 2.



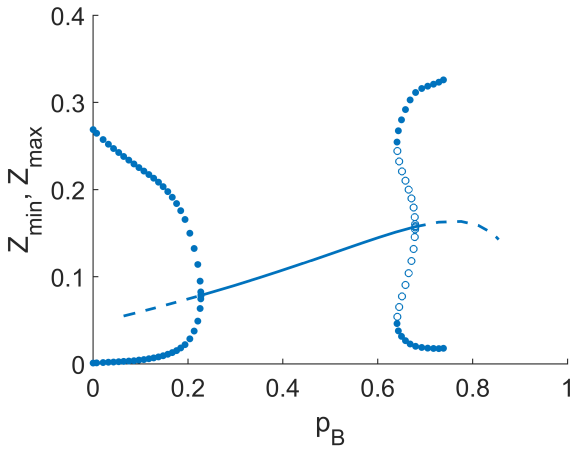
(a) Bistability check

(b) Population dynamics at the bistability boundary

Figure A7 Bistability in the dynamics of the system with an undefended high-quality prey was found by varying the initial conditions for a given parameter set. Densities are given relative to inflow concentration N_{I}. (a) Bistability at $1/K_B = 0.1042(\mu\mathrm{mol\ N/l})^{-1}$ and $p_{\mathrm{B}} = 0.5$. In the grey regions the population is cycling, the white region depicts steady state. (b) Visualization of the two basins of attraction and the corresponding population dynamics at the boundary between steady state dynamics and cycling. The colouring in the phase-space plots moves from blue to yellow in time. Mean biomasses differ between both states, e.g. $\overline{Z_{ss}} = 0.14\,N_{\mathrm{I}} > \overline{Z_{cycl}} = 0.11\,N_{\mathrm{I}}$.

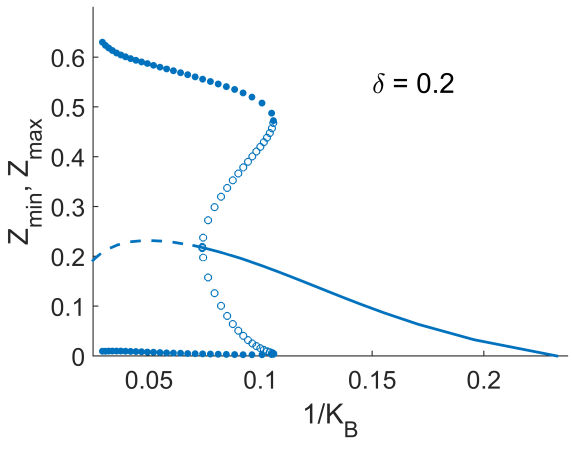


(a) Fixed predation risk $p_\mathrm{B} = 0.5$, variation along the competitiveness $1/K_B$

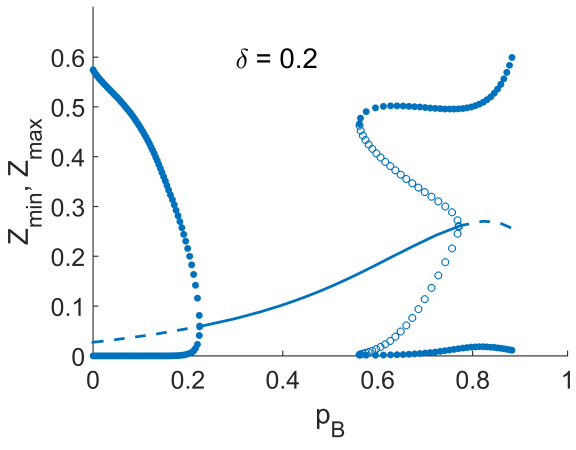


(b) Fixed competitiveness $1/K_B = 0.125\,(\mu\mathrm{mol\ N/l})^{-1}$, variation along the predation risk p_B

Figure A8 Bifurcation plots of the transitions between steady state coexistence and cycling coexistence with an undefended high-quality prey along (a) the competitiveness $1/K_B$ and (b) the predation risk p_B. (a) Above $1/K_B = 0.1\,(\mu\mathrm{mol\ N/l})^{-}1$ the steady state is stable. Between $1/K_B = 0.1\,(\mu\mathrm{mol\ N/l})^{-}1$ and $1/K_B = 0.11\,(\mu\mathrm{mol\ N/l})^{-1}$ both steady state and large amplitude antiphase limit cycle are stable. They are separated by an unstable limit cycle, which emerges from the steady state in a subcritical Hopf-bifurcation and falls onto the stable limit cycle in a cyclic-fold bifurcation. Below $1/K_B = 0.1\,(\mu\mathrm{mol\ N/l})^{-1}$ the steady state is unstable and below $1/K_B = 0.075\,(\mu\mathrm{mol\ N/l})^{-1}$ reaches the region where B goes extinct and the coexistence attractor therefore becomes unstable. (b) Below $p_B = 0.22$ only the antiphase cycling is stable, above the steady state becomes stable in a supercritical Hopf bifurcation. Between $p_B = 0.62$ and $p_B = 0.68$ both steady state and large amplitude antiphase limit cycle are stable. They are separated by an unstable limit cycle emerging from the steady state in a subcritical Hopf-bifurcation and falling onto the stable limit cycle in a cyclic-fold bifurcation. Above $p_B = 0.75$ the steady state reaches the region where B goes extinct and the coexistence attractor therefore becomes unstable.



(a) Fixed predation risk $p_\mathrm{B} = 0.5$, variation along the competitiveness $1/K_B$



(b) Fixed competitiveness $1/K_B = 0.125\,(\mu\mathrm{mol\ N/l})^{-1}$, variation along the predation risk p_B

Figure A9 Plot specifics as in Fig. A8, but at a dilution rate of $\delta = 0.2\ \mathrm{d}^{-1}$.