

1 ~~Essential resource provision can enhance persistence~~
2 Provision of essential resources as a persistence strategy in
3 **food webs**

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6 Pairwise interactions in food webs, including those between predator and prey are often
7 modulated by a third species. Such higher-order interactions are important structural
8 components of natural food webs that can increase the stability of communities against
9 perturbations and ensure continued ecosystem functioning. Particularly the flux of rare
10 organic and inorganic compounds that are essential to species in the community can
11 create higher-order interactions. Even though many such compounds exist, their effect
12 on structuring communities is little understood. In this study, I perform invasion analyses
13 on a general food web model that depicts apparent and exploitative competition. Intro-
14 ducing the provision of essential resources by a prey species to either its competitor or
15 its predator as a higher-order interaction, I find that this mechanism can ensure the focal
16 prey's persistence. Larger dietary essentiality, i.e. a stronger dependence of the predator
17 or the competitor on the essential resource can increase the invasion growth rate of the
18 focal prey to positive values, thus promoting its persistence when it would go extinct
19 for low essentiality. This research shows that essential resources and the higher-order
20 interactions created by them should be considered in community ecology.

21 Keywords: Higher-order interaction, Food webs, Food quality, Coexistence, Invasibility

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23 Introduction

24 Growth, reproduction and survival of organisms can be limited by organic and inorganic compounds,
25 which often are not present in the organism's diet in favourable concentrations or ratios. Particu-
26 larly consumers at the plant-herbivore interface are often affected by dietary mismatches (Elser et al.,
27 1996; Gaedke et al., 2002; Wacker and Martin-Creuzburg, 2012; Urabe et al., 2018). This motivated
28 considering besides food quantity also the quality of food when investigating performance measures of
29 aquatic consumers (~~Andersen et al., 2004; Anderson and Hessen, 2005; Wacker and Martin-Creuzburg, 2012; G~~
30 (Andersen et al., 2004; Anderson and Hessen, 2005; Wacker and Martin-Creuzburg, 2012; Guo et al., 2016; Sc
31 , terrestrial herbivores (Douglas, 2015; Eberl et al., 2020) and pollinators (Filipiak et al., 2017). ~~As~~
32 ~~dietary limitations induced by essential resources~~ The scarcity of resources that are essential for
33 growth and reproduction but cannot be easily acquired from the environment can constrain the flow
34 of matter and energy between trophic levels ~~they~~. Therefore, dietary limitations induced by essential
35 resources can have important effects on population and community dynamics (~~Muller et al., 2001; Gaedke et al.,~~
36 (Muller et al., 2001; Gaedke et al., 2002; Schade et al., 2003; Stiefs et al., 2010; Iwabuchi and Urabe, 2012; S
37 .

38 Dietary dependencies also regularly exist within the same trophic level, where uptake of essential
39 resources occurs from the environment, such as within the microbial loop when bacteria consume
40 dissolved organic carbon from phytoplankton exudates (Azam et al., 1983; Pomeroy et al., 2007)
41 or during the exchange of essential nutrients and metabolites between bacteria and microalgae
42 (~~Soria-Dengg et al., 2001; Croft et al., 2005; Kazamia et al., 2012; Suleiman et al., 2016; D'Souza et al., 2018~~
43 (Soria-Dengg et al., 2001; Croft et al., 2005; Kazamia et al., 2012; Suleiman et al., 2016; D'Souza et al., 2018
44 . Understanding the mechanisms and effects of such dependencies is crucial for ~~medical fields like~~
45 ~~human microbiome research (Herren, 2020) and antibiotic resistance research (Adamowicz et al., 2018)~~
46 ~~, but also for ecological research~~ biodiversity research given for example the importance of microalgae

47 such as diatoms for aquatic ecosystems and global carbon dynamics ([Croft et al., 2005](#); [Koedoo-](#)
48 [der et al., 2019](#)), but also for medical fields like human microbiome research ([Herren, 2020](#)) and
49 antibiotic resistance research ([Adamowicz et al., 2018](#)). Taken together, dietary mismatches and
50 dependencies of organisms from the same or different trophic levels are crucial determinants for the
51 structure of their communities.

52 Mechanistically, community structure is determined by direct interactions within pairs of species or
53 by indirect interactions across multiple species from the same or different trophic levels, e.g. through
54 trophic cascades or apparent competition. Additionally to direct and indirect interactions, higher-
55 order interactions, here defined as the density of a third species affecting the interaction of two other
56 species (sensu [Billick and Case, 1994](#)), were found to potentially structure communities. The effects
57 of higher-order interactions include stabilizing population dynamics ([Grilli et al., 2017](#)), increas-
58 ing robustness against perturbation (~~[Terry et al., 2019](#)~~) ([Terry et al., 2019](#); [Gibbs et al., 2023](#)), de-
59 termining fitness of competitors ([Mayfield and Stouffer, 2017](#)) and affecting biodiversity-ecosystem-
60 functioning relationships ([Miele et al., 2019](#)). Examples for higher-order interactions include trait-
61 mediated effects such as a predator affecting the foraging rate of its prey or the prey's predation
62 risk from other predators, and environment-mediated effects such as one species providing refuge to
63 another species ([Wootton, 2002](#); [Miele et al., 2019](#)).

64 In this paper, I will investigate another, so far unrecognized mechanism for creating higher-order
65 interactions that arises from the provisioning of essential resources. In the presence of dietary
66 mismatches one species, from here on referred to as the focal species, may provide resources that
67 are essential to other community members. Such interactions are possible both towards members
68 of the same trophic level, such as competitors, or towards members of different trophic levels,
69 e.g. shared predators that prey on multiple species. For example, a higher-order interaction within
70 the same trophic level is created when a competitor is co-limited by two resources but can only

71 obtain one of those two resources from its environment and relies on another prey (the focal prey)
72 to provide the other co-limiting resource. This provision may occur for example by leakage of
73 common goods (Gore et al., 2009) or carbon exudation in otherwise carbon-limited environments
74 (Bratbak and Thingstad, 1985; Raatz et al., 2018). A higher-order interaction between different
75 trophic levels can arise when a predator obtains energy from multiple prey species but only the
76 focal prey may provide additional, essential resources, e.g. vitamins or polyunsaturated fatty acids
77 (~~Wacker and Martin-Creuzburg, 2012; ?~~). (Wacker and Martin-Creuzburg, 2012). Excess essential
78 resources provided by the focal prey may then be used to efficiently convert other low-quality prey
79 into predator biomass (Raatz et al., 2017).

80 In these two cases the provision of essential resources by the focal prey creates a higher-order inter-
81 action that manifests as an interaction modification (sensu Terry et al., 2019) that regulates the flow
82 of matter to the competitor or predator compartment in these communities, respectively. Regulating
83 such fluxes has the potential to affect the biomass distribution in the community, ultimately deter-
84 mining the persistence of individual species. If such higher-order interactions increase the persistence
85 of the focal prey they pose as an example for a niche-improving form of niche construction and they
86 may thus even be adaptive (Kylafis and Loreau, 2008, 2011; Laland et al., 2016). Consequently, in
87 this paper, I will establish the provision of essential resources in a community as a mechanism driving
88 higher-order interactions that may increase the persistence of the focal prey species and prevent its
89 extinction either from predation or competition.

90 **Methods**

91 Investigating persistence of a focal species typically employs invasion analysis, which determines the
92 net growth rate of that species in the remaining resident community when it is rare (and assumed

93 to be invading) (MacArthur and Levins, 1967; Chesson, 1994; Ellner et al., 2019). If the focal
 94 prey provides the essential resources to some components of the community, being rare equates
 95 to switching off the higher-order interaction. Invasion analysis is therefore the perfect tool for
 96 determining the effect of essential resources both on the resident community and the persistence of
 97 the focal prey. Accordingly, I will investigate the invasion growth rate of the focal prey species X_1 in
 98 a community that contains an abiotic resource R , a competing species X_2 and a shared predator Y
 99 (Eqn. 1, Fig. 1), to incorporate essential resource provision in food webs. I assume a chemostat-type
 100 model in which the abiotic resource R is provided at a constant rate $R_0 \delta$ and all entities experience
 101 the same dilution, see Tab. 1 for parameter definitions and values. The two prey species X_1 and X_2
 102 take up the abiotic resource R at some rate $r u(R)$, where $u(R)$ defines the functional form of prey
 103 resource uptake. Both prey species are consumed by the predator following a functional response
 104 $f(X_1, X_2)$. I assume that the two prey species differ only in their attack probability (sensu Ehrlich
 105 and Gaedke, 2018) by a factor p and their maximum growth rate by a factor ϕ . For example, for
 106 $p < 1$ and $\phi < 1$ implements a growth-defense trade-off (Fig. 2b).

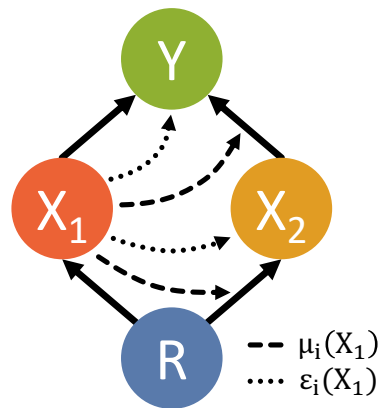


Figure 1 Food web structure. The model equations (Eq. 1) describe a diamond-shaped food web module. Solid arrows depict flows of matter due to resource or prey uptake. Dashed arrows show the interaction modification $\mu_i(X_1)$ of the uptake rates that are caused by the provision of essential resources by the focal prey. The other potential higher-order interaction from essential resource provision $\varepsilon_i(X_1)$ affects the conversion efficiency of the competitor or the predator and is depicted by dotted arrows. Only one of these higher-order interaction is investigated at a time in the following.

$$\begin{aligned}
\frac{dR}{dt} &= (R_0 - R) \delta - r u(R) X_1 - \mu_X(X_1) \phi r u(R) X_2 \\
\frac{dX_1}{dt} &= r u(R) X_1 - f(X_1, X_2) X_1 Y - \delta X_1 \\
\frac{dX_2}{dt} &= \varepsilon_X(X_1) \mu_X(X_1) \phi r u(R) X_2 - \mu_Y(X_1) p f(X_1, X_2) X_2 Y - \delta X_2 \\
\frac{dY}{dt} &= f(X_1, X_2) X_1 Y + \varepsilon_Y(X_1) \mu_Y(X_1) p f(X_1, X_2) X_2 Y - \delta Y
\end{aligned} \tag{1}$$

107 Throughout this paper, I use a Monod-type term to indicate resource limitation of the prey

$$u(R) = \frac{R}{K + R} \tag{2}$$

108 and a Holling Type-2 functional response for multiple prey species to describe the predation rate by
109 an individual predator:

$$f(X_1, X_2) = g \frac{1}{H + X_1 + p X_2} \tag{3}$$

110 I introduce the higher-order interactions due to essential resource provision as interaction modifica-
111 tions $\mu_i(X_1)$ and $\varepsilon_i(X_1)$ driven by the density of the focal prey species (Arditi et al., 2005). For
112 generality, I include all possible options where these modifications affect the uptake rates of abiotic
113 resources or prey, or the efficiency at which new biomass is produced, respectively. Accordingly,
114 $\mu_X(X_1)$ defines how an increasing density of the focal prey increases the resource uptake rate of
115 the competing prey and $\varepsilon_X(X_1)$ gives the conversion efficiency of those resources into new competi-
116 tor biomass depending on the density of the focal prey. The same logic translates to $\mu_Y(X_1)$ and
117 $\varepsilon_Y(X_1)$ for the predator. ~~I assume that these modification functions~~ Note that in this model, I am
118 investigating only the provision of essential resources, thus assuming that the focal prey itself always
119 contains the essential resources. Predator consumption and conversion of focal prey biomass is thus
120 kept constant. I assume that the modification functions $\mu_i(X_1)$ and $\varepsilon_i(X_1)$ monotonically increase
121 with focal prey density, eventually approaching unity for large focal prey densities, as here their effect

122 should vanish, as the essential resource should be abundantly present and thus non-limiting.

$$\lim_{X_1 \rightarrow \infty} \mu_i(X_1) = 1$$

$$\lim_{X_1 \rightarrow \infty} \varepsilon_i(X_1) = 1$$

123 The interaction modifications pose an implicit way of representing the temporal dynamics of produc-
124 tion, distribution, stability, uptake and usage of the essential resource molecules and thus avoid the
125 difficulties involved in modelling these processes explicitly, but explicit approaches also exist (Sun
126 et al., 2019; Hammarlund et al., 2019).

127 I define essentiality e as the relative reduction of uptake rates or conversion efficiencies in the absence
128 of the focal prey compared to when it's abundantly present and neither the uptake rates nor the
129 conversion efficiencies are reduced. For the uptake rate modifications $\mu_i(X_1)$ this results in

$$\begin{aligned} e &= \frac{\lim_{X_1 \rightarrow \infty} \mu_i(X_1) - \mu_i(0)}{\lim_{X_1 \rightarrow \infty} \mu_i(X_1)} \\ &= 1 - \mu_i(0) \end{aligned} \quad (4)$$

130 A high essentiality thus implies a strong reduction in the uptake rates when the focal prey is absent.

131 Similarly, if the higher-order interaction is incorporated into the conversion efficiencies ~~we~~ I define

$$e = 1 - \varepsilon_i(0) \quad (5)$$

132 Note that for the sake of simplicity I investigate only the effect of one higher-order interaction at a
133 time, i.e. only one interaction modification will be dependent on the focal prey density, keeping the
134 other three constant at unity.

135 To determine the effect of essential resource provision on persistence of the focal prey I employ
136 invasion analysis and study whether the focal prey can re-invade the resident community once it
137 ~~should go~~ has gone extinct. This is ensured by a positive invasion growth rate which is defined as
138 the average per-capita growth rate when rare (Ellner et al., 2019). Specifically, the invasion growth

Table 1 Reference parameter set. Resource concentrations and organism abundances or densities are assumed to be normalized appropriately such that their units become unity. Deviations from the reference parameter values are reported where applicable. For an illustration of the different food web scenarios see Fig. 2.

Parameter	Biological meaning	Value			
R_0	Input concentration of abiotic resource	1			
δ	Chemostat dilution rate	1 time unit ⁻¹			
r	Prey's uptake rate	2 time unit ⁻¹			
K	Prey's half-saturation constant	0.1			
g	Predator's consumption rate	1.5 time unit ⁻¹			
H	Predator's half-saturation constant	0.1			
		Food web scenarios			
		I	II	III	IV
ϕ	Relative competitiveness of the competitor	1.05	0.95	0.95	1.05
p	Relative vulnerability of the competitor to predation	0.8	0.8	1.2	1.2

139 rate of the focal prey in [our my](#) model is

$$\left\langle \frac{1}{X_1} \frac{dX_1}{dt} \Big|_{X_1=0} \right\rangle = \langle r u(R) - f(0, X_2) Y - \delta \rangle \quad (6)$$

140 where the angle brackets denote the temporal average. If the resident community's attractor is
141 a limit cycle, the temporal average can be obtained numerically from one period of such cycles
142 ([Ehrlich et al., 2017](#)). As at least some of the parameter combinations investigated in this paper
143 result in limit cycles I used this numerical approach throughout and confirmed the results with the
144 analytically computable solutions for those cases where the resident community was in a steady
145 state. For numerically determining the invasion growth rate of the focal prey, the resident com-
146 munity dynamics were numerically integrated for 2000 time units until they reached their attractor.
147 [Convergence was determined visually](#). The period length was determined as in [Raatz et al. \(2019\)](#)
148 by determining the average time spans between predator maxima during the last 200 time units us-
149 ing the FindMaximum algorithm in Mathematica. The average of the invasion growth rates for
150 each time step during one period was computed. All computations were performed in Mathematica
151 ([Wolfram Research, Inc., 2019](#)) and can be re-run using the provided Mathematica notebooks (DOI
152 [10.5281/zenodo.7575589.8093740](https://doi.org/10.5281/zenodo.7575589.8093740)). The analytical solutions are lengthy and can also be found in

153 the notebook [and the corresponding pdf exports](#).

154 For evaluating the state of the resident community as well as the invasion growth rate of the focal
155 prey, the interaction modifications $\mu_i(X_1)$ and $\varepsilon_i(X_1)$ reduce to $\mu_i(0) = \mu_i^0$ and $\varepsilon_i(0) = \varepsilon_i^0$, which I
156 can relate to the essentiality e via Eqs. 4 and 5. Therefore, we obtain direct relationships between
157 the essentiality of the resource that is provided by the focal prey and its invasion growth rate.
158 Notably, the invasion analysis does not require a specific choice of the [functional form of the](#) interac-
159 tion modifications. Only those numerical integrations where the focal prey is not set to zero require
160 a particular definition. In those cases I use the following functions that monotonically increase and
161 saturate at unity for large X_1 .

$$\begin{aligned}\mu_i(X_1) &= \mu_i^0 + (1 - \mu_i^0) \frac{X_1}{0.5 R_0 + X_1} \\ \varepsilon_i(X_1) &= \varepsilon_i^0 + (1 - \varepsilon_i^0) \frac{X_1}{0.5 R_0 + X_1}\end{aligned}\tag{7}$$

162 To investigate under which conditions the provision of essential resources can ensure persistence
163 I will focus on four food web scenarios that account for the non-trivial coexistence outcomes in
164 the diamond-shaped food web module. In the first food web scenario the focal prey is the inferior
165 competitor for resource R and is more vulnerable to predation than its competitor, which would imply
166 extinction of the focal prey without essentiality (Fig. 2a [2a, see black arrows](#)). In the second food
167 web scenario the focal prey is again more vulnerable to predation but now the superior competitor
168 for resource R , which allows for predator-mediated coexistence for a subset of the parameter space,
169 but focal prey extinction otherwise (Abrams, 1999; Jones and Ellner, 2007) (Fig. 2b). The third
170 and fourth food web scenarios are the mirror images of scenarios one and two (Fig. 2c and d).
171 Complementing these scenarios, I will scan the parameter space of vulnerability to predation p and
172 resource competitiveness ϕ of the competitor relative to the focal prey.

173 A priori one would expect that essentiality that limits the growth and competitiveness of the com-
174 petitor should favour the persistence of the focal prey. Further, I hypothesize that within predator-

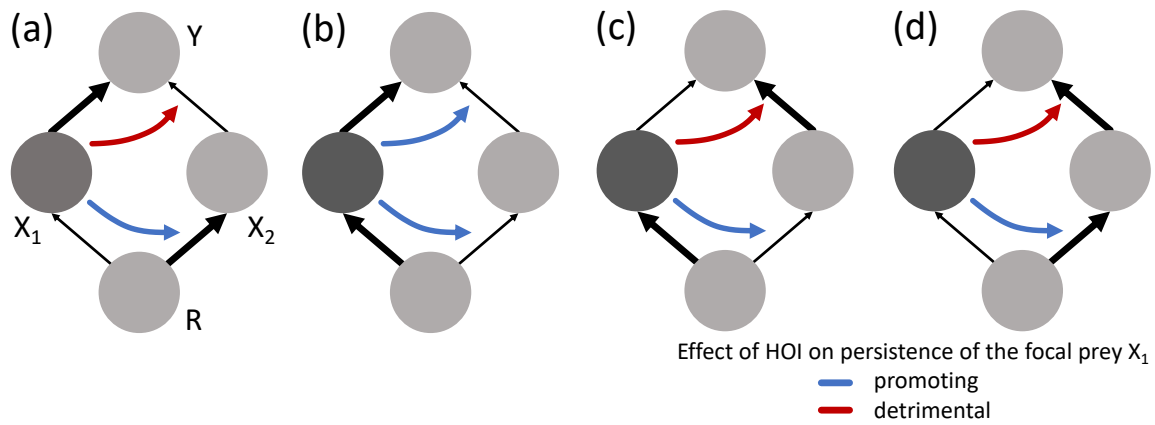


Figure 2 The effect of higher-order interactions depends on the food web scenario. In the first food web scenario (a), the focal prey X_1 is more vulnerable to predation and less competitive than its competitor X_2 , whereas it is more vulnerable to predation but also more competitive in the second food web scenario (b). The third (c) and fourth (d) food web scenarios are mirror images of the first and second food web scenario. Essentiality-mediated higher-order interactions that limit the growth of the competitor should favour persistence of the focal prey X_1 (blue curved arrows). Essentiality should promote persistence of the focal prey in food webs that permit predator-mediated coexistence (blue curved arrow in (b)), but likely is detrimental otherwise (red curved arrows) as it can render the competitor effectively less vulnerable to predation than the focal prey.

175 mediated coexistence an increasing essentiality should make the focal prey more indispensable to
 176 the community and therefore increase its invasion growth rate, possibly even eventually fulfilling the
 177 invasion criterion

$$\left\langle \frac{1}{X_1} \frac{dX_1}{dt} \Big|_{X_1=0} \right\rangle > 0$$

178 that would prove an ensured persistence of the focal prey.

179 Results

180 Scanning the parameter space of vulnerability to predation p and resource competitiveness ϕ of
 181 the competitor relative to the focal prey provides an overview of the effects of essentiality on the
 182 persistence of the focal prey (Fig. 3). Comparing the invasion growth rates at vanishing and complete
 183 essentiality, I find that depending on these parameters, and thus the respective food web scenario,
 184 essentiality-mediated higher-order interactions can promote but also counter-act the persistence of

185 the focal prey, or have no effect as the focal prey persists or goes extinct ~~independent~~ irrespective of
 186 its essentiality. Analysing the four food web scenarios in more detail provides a detailed understanding
 of the mechanisms behind these patterns.

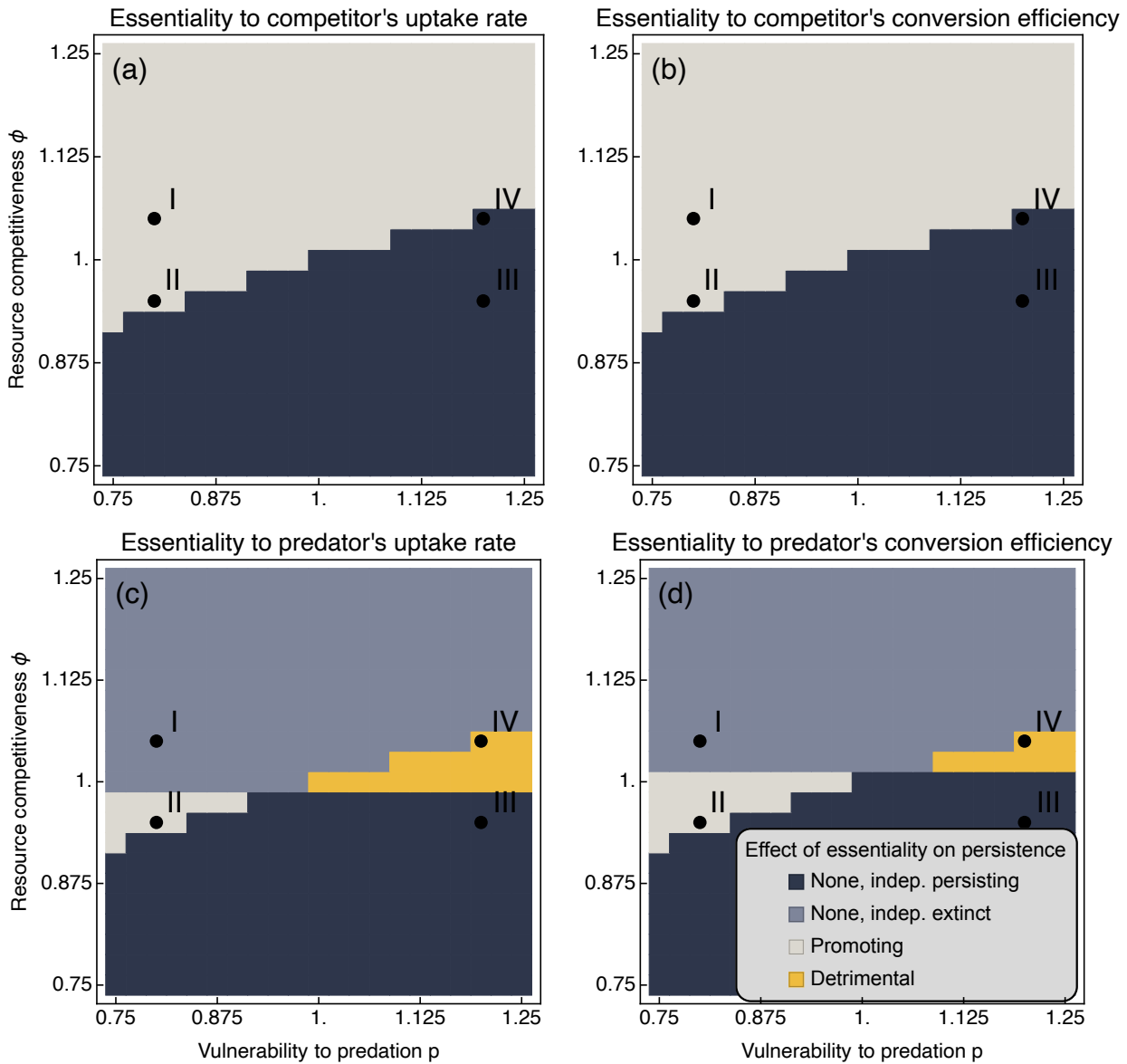


Figure 3 Effect of essentiality on the persistence of the focal prey Comparing the invasion growth rates of the focal prey for essentialities of $e = 0$ and $e = 1$ allows to classify the effects of essentiality on persistence for the four higher-order interactions indicated in Fig. 1. If the invasion growth rate for vanishing and complete essentiality are both positive then the focal prey persists independent of its essentiality (dark blue region). Vice versa, if both invasion growth rates are negative the focal prey goes extinct independent of its essentiality (light blue region). Sign changes from negative to positive for increasing essentiality indicate a persistence-promoting effect of essentiality (light-grey region), whereas sign changes from positive to negative depict a detrimental effect of essentiality on persistence of the focal prey (yellow region). The parameters of the four food web scenarios of Fig. 2 are indicated by Roman numerals.

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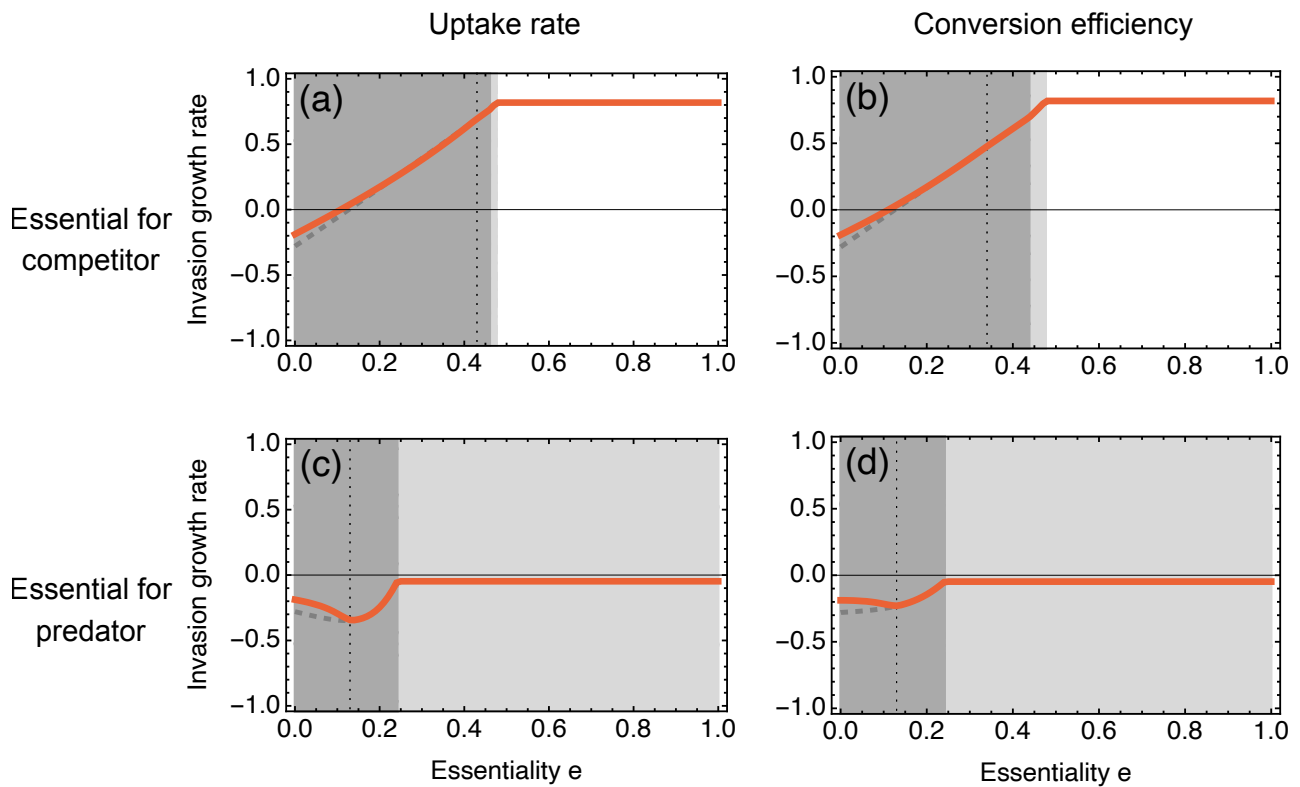


Figure 4 Invasion growth rate of the focal prey for the first food web scenario (Fig. 2a). Here, the focal prey is more vulnerable to predation and competitively inferior to the competitor. Essential resource provisioning affects (a) the uptake rate or (b) the conversion efficiency of the competitor, or (c) the uptake rate or (d) the conversion efficiency of the shared predator. The grey shading indicates the states of the resident community (Fig. A1). For dark shading both predator and competitor coexist, for light-grey shading only the competitor persists and for no shading only the resource remains. The analytically computed invasion growth rate (dashed line) deviates from the numerical observation (full line) once the dynamics become cyclic. The vertical dotted line marks the bifurcation point.

188 In the first food web scenario (Fig. 2a) the focal prey does not persist for vanishing essentiality,
 189 as indicated by a negative invasion growth rate. However, increasing essentiality when the higher-
 190 order interaction affects the resource uptake rate or conversion efficiency of the competitor turns the
 191 invasion growth rate positive (Fig. 4a,b) and thus ensures the persistence of the focal prey (Fig. 5).
 192 This includes a drastic shift in the resident community shortly beyond $e = 0.4$ where first the predator
 193 and then the prey go extinct (Fig. A1a,b). An essentiality of $e = 0.4$ implies that the resource uptake
 194 rate or the conversion efficiency of the competitor are reduced to 60% in the absence of the focal
 195 prey. In our my model formulation this implies that the competitor cannot sustain the predator

196 further which, in the absence of the focal prey, therefore goes extinct. A slight additional reduction
 197 hinders the competitor from outgrowing dilution and thus drives it to extinction as well. In this food
 198 web scenario, higher-order interactions that target the uptake rate or the conversion efficiency of
 199 the predator do not benefit the persistence of the focal prey (Fig. 4c,d) due to unfavourable trait
 200 combinations. As the focal prey is the inferior competitor for the resource R and also more vulnerable
 201 to predation it can persist neither in the absence nor in the presence of the predator. Supporting the
 202 predator by providing essential resources harms the focal prey more than the competitor. For the
 203 predator, a larger dependence on the focal prey is also disadvantageous as this decreases its uptake
 204 rate and conversion efficiency, and results in extinction at approximately $e = 0.25$ (Fig. A1c,d).

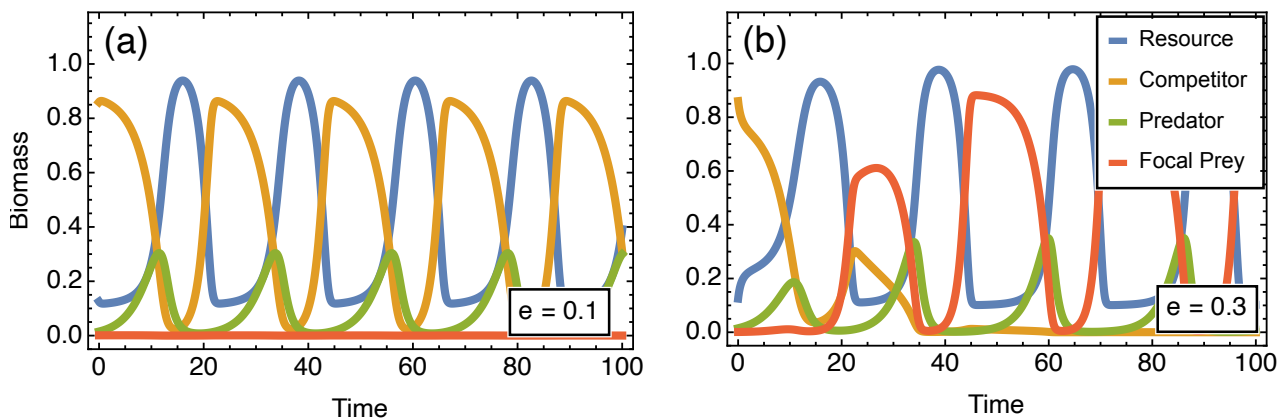


Figure 5 Population dynamics for the first food web scenario when the higher-order interaction targets the resource uptake rate of the competitor (Fig. 4a). (a) For small essentialities the invasion rate of the focal prey is negative and it thus cannot invade. (b) A larger essentiality ensures the persistence of the focal prey. To obtain these dynamics, I chose the interaction modification according to Eq. 7, integrated the resident community to its stable state and then introduced the focal prey at an initial biomass of $X_{1,0} = 10^{-3}$.

205 In the second food web scenario, the focal prey is still more vulnerable to predation than its competitor
 206 but now it is also the superior competitor for the resource R (Fig. 3). While the invasion
 207 analysis outcomes are similar to the first food web scenario for higher-order interactions targeting
 208 the competitor's uptake rate or conversion efficiency (Fig. 6a,b), the trait combinations now allow
 209 for positive invasion growth rates also when the higher-order interaction targets the predator's up-

210 take rate or conversion efficiency (Fig. 6c,d). Therefore, increasing essentiality can promote the
211 persistence of the focal prey for intermediate to large essentiality in this food web scenario. This
212 persistence-promoting effect of essentiality appears in a parameter range of predator-mediated coex-
213 istence of prey (Fig. 7). Here, the predator goes extinct in the resident community as the competing
214 prey alone does not sustain the predator given the reduction in uptake rate or conversion efficiency
215 for large essentiality of the focal prey (Fig. A2). In the absence of the predator the focal prey ben-
216 efits from its higher competitiveness for the resource R and thus persists. Once it invades it may
217 additionally sustain the predator (Fig. 7b). Conditional on the presence or absence of the predator
218 when the focal prey invades two community states are therefore possible. Without the predator the
219 focal prey out-competes the competitor which thus goes extinct (Fig. 7b, solid lines). If the predator
220 is present or is re-introduced it however mediates coexistence of the focal prey and the competitor
221 (Fig. 7b, dashed lines). This shows that providing essential resources can affect not only the focal
222 prey itself, but also the whole community structure.

223 In the third food web scenario, the focal prey persists independent of essentiality as indicated by a
224 positive invasion growth rate for all possible types of essentiality-mediated higher order interactions
225 (Fig. 3 and Fig. A3). If essentiality affects the competitor the focal prey's invasion growth rate
226 increases further. If, however, essentiality causes limitations for the predator the invasion growth
227 rate tends to decrease for larger essentiality (albeit not turning negative) as this effectively reduces
228 the energy flow from the competitor to the predator and thus eventually renders the competitor less
229 vulnerable to predation than the focal prey.

230 Similarly, higher-order interactions affecting the competitor increase the invasion growth rate of the
231 focal prey with higher essentiality in the fourth food web scenario. ~~For not too high~~ If the resource
232 competitiveness of the competitor the is only slightly exceeding the resource competitiveness of the
233 focal prey the invasion growth rate of the focal prey is positive even for zero essentiality and only

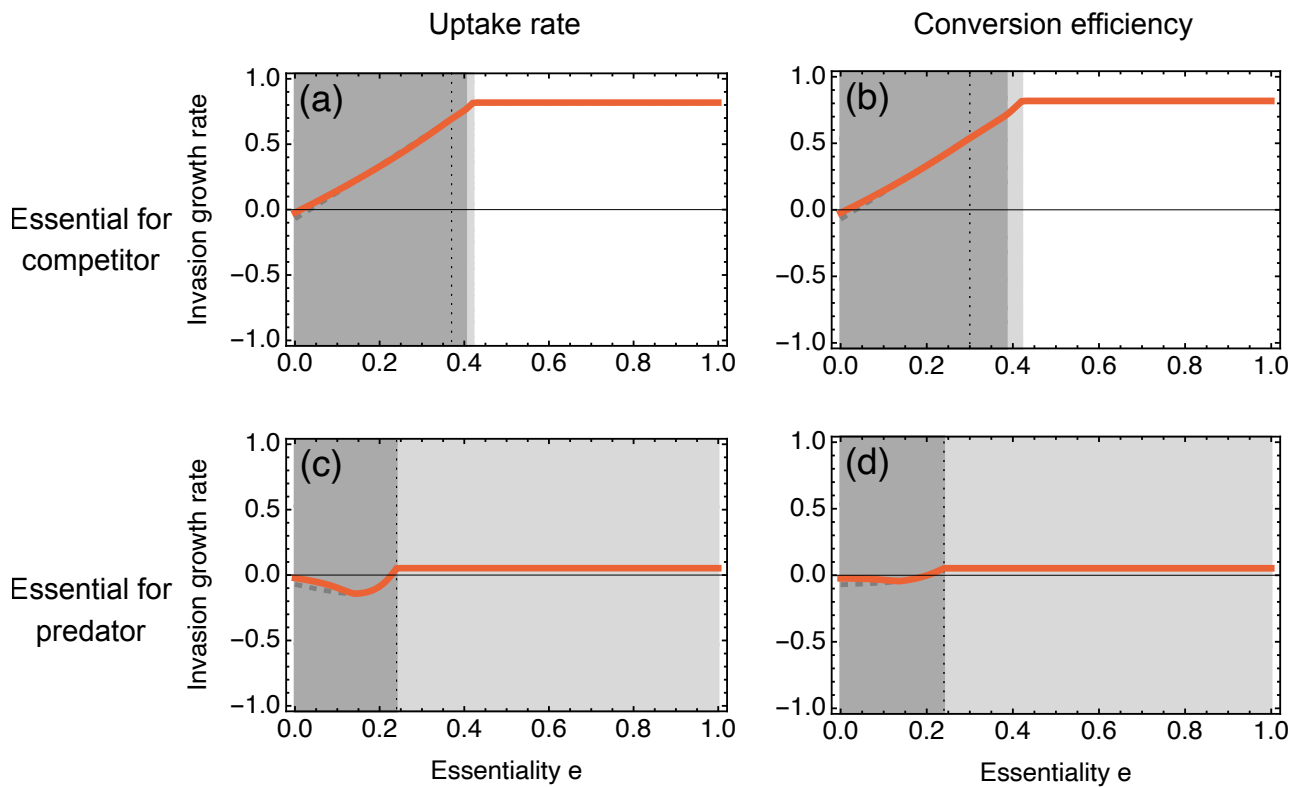


Figure 6 Invasion growth rate for the second food web scenario. Here, the focal prey is more vulnerable to predation but also competitively superior to the competitor. In the absence of the focal prey its essentiality determines the reduction in (a) the uptake rate or (b) the conversion efficiency of the competitor, or (c) the uptake rate or (d) the conversion efficiency of the shared predator. The plot specifics are identical to Fig. 4.

234 increases further for higher essentiality (Fig. A4). For higher competitiveness of the competitor
 235 the invasion growth rate at zero essentiality is negative and turns positive for higher essentiality,
 236 again resulting in promoted persistence already (Fig. 3a,b). In this scenario, however, higher-order
 237 interactions affecting the predator can result in a negative invasion growth rate, which can become
 238 even smaller if the essentiality becomes larger. Here again, an increasing essentiality counteracts
 239 the larger vulnerability of the competitor to predation, and allows the competitor to outcompete the
 240 focal prey given its higher resource competitiveness.

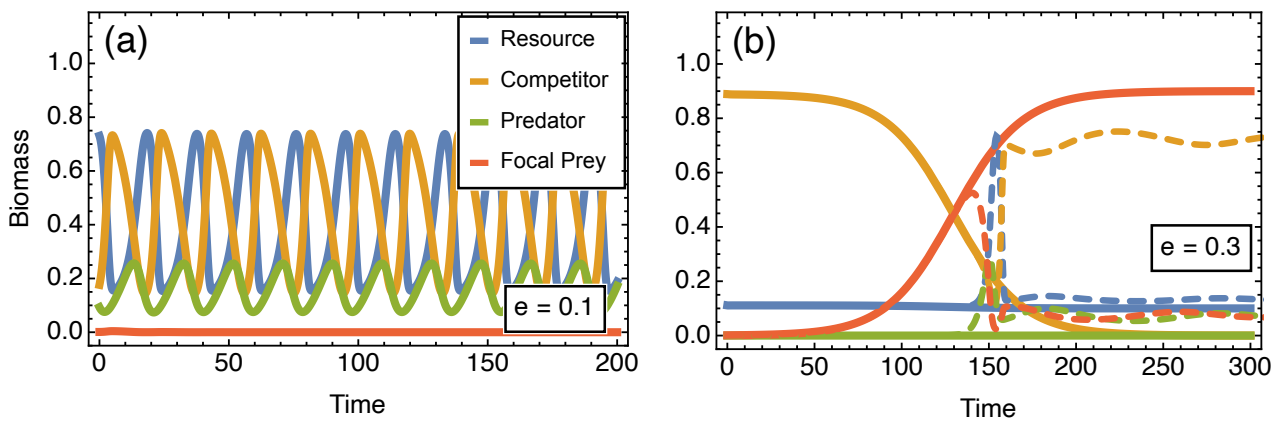


Figure 7 Population dynamics for the second food web scenario when the higher-order interaction targets the resource uptake rate of the shared predator (Fig. 6c). (a) For small essentialities the invasion rate of the focal prey is negative and it thus cannot invade. (b) A larger essentiality ensures the persistence of the focal prey. To obtain these dynamics, I chose the interaction modification according to Eq. 7, integrated the resident community to its stable state and then introduced the focal prey at an initial biomass of $X_{1,0} = 10^{-3}$. In panel (b) the predator goes extinct in the residence community, thus I assumed $Y_0 = 0$ (thick lines). If, however, the predator is reintroduced together with the focal prey ($Y_0 = 10^{-3}$, thin dashed lines), it is supported by the focal prey, re-establishes and mediates the coexistence of both prey types.

241 Discussion

242 Higher-order interactions have the potential to shape community structure and dynamics (Grilli et al.,
 243 2017; Mayfield and Stouffer, 2017; Terry et al., 2019). In this paper, I showed how the provision
 244 of essential resources creates a higher-order interaction that decisively ~~affect~~ affects the persistence
 245 of the focal prey and the resulting community structure. I investigated both the case of essential
 246 resource provision to community members from the same trophic level as well as from a higher
 247 trophic level. Whether these higher-order interactions in the end ensure persistence depends both
 248 on their strength as well as on the food web scenario (see Fig. 2 for a summary of the results).

249 Confirming the expectations, I find in all food web scenarios that a larger essentiality for the com-
 250 petitor ~~increases~~ can increase the invasion growth rate of the focal prey. In the first and second
 251 food web scenario where the invasion growth rate is negative for zero essentiality this leads to a
 252 sign-change in the invasion growth rate and thus a promoting effect of essentiality on persistence. In

253 the third and fourth food web scenarios the invasion growth rate of the focal prey is already positive
254 for zero essentiality and only increases further for larger essentiality. Essentiality for the predator can
255 indeed favour the persistence of the focal prey in food web scenarios that permit predator-mediated
256 coexistence of the prey species (second food web scenario), but can also be detrimental for persis-
257 tence if it renders the competitor effectively less vulnerable to predation (fourth food web scenario).
258 Further, I find that essentiality determines the resident community structure, with larger essentiality
259 driving extinct first the predator and then, depending on the higher-order interaction, potentially also
260 the competitor. As seen in the second food web scenario this allows for multiple possible community
261 states, depending on whether the coexistence-mediating predator is re-introduced together with the
262 focal prey. Further, no qualitative differences between higher-order interactions affecting the uptake
263 rate or the conversion efficiency were observed.

264 Experimental support exists for both higher-order interactions that affect the uptake rate or the
265 conversion efficiency. Essential resources affecting the uptake rate could result from adaptive foraging
266 behaviour, as predicted by nutritional geometry ([Raubenheimer and Simpson, 1993](#); [Simpson et al.,](#)
267 [2004](#)), selective feeding ([Buskey, 1997](#); [Elser et al., 2016](#); [Meunier et al., 2016](#); [Eberl et al., 2020](#)),
268 or changed behaviour due to the provision of essential micronutrients, as recently reported for a
269 nematode feeding on larvae of other nematodes ([Akduman et al., 2020](#)). Here, the attack rate of
270 the predatory nematode increased when reared on vitamin B₁₂ producing bacteria compared to B₁₂
271 deficient controls. However, feeding rate was not increased in this study, so only the prey's loss
272 term would be affected by this higher-order interaction when transferring these results to ~~our~~ [my](#)
273 model. Another possibility would be generally better physiological conditions that increase fitness,
274 as reported for *Daphnia magna* and vitamin B₁₂ ([Kusari et al., 2017](#)), which could also translate to
275 generally increased activity.

276 The most direct and intuitive mechanism for a higher-order interaction that affects the conversion ef-

277 ficiency of a consumer via essential resource provision is that those lacking essential nutrients that are
278 halting biomass production are directly provided. This is the case in the above example with *Daphnia*
279 *magna* and vitamin B₁₂ (Keating, 1985), other nutrients like phosphorous (Urabe et al., 2018) or
280 biochemicals (~~(Martin-Creuzburg et al., 2009; ?)~~(Martin-Creuzburg et al., 2009; Raatz et al., 2017)
281 . Similarly, supplementing herbivory with fungivory was found to significantly speed up growth in
282 moth larvae (Eberl et al., 2020). Microbial cross-feeding likely represents the case of higher-order
283 interactions affecting the conversion efficiency of organisms on the same trophic level (D'Souza et al.,
284 2018). In the absence of another carbon source bacteria depend on algal carbon fixation and exuda-
285 tion (Bratbak and Thingstad, 1985; Raatz et al., 2018), which was proposed as the mutualistic trade
286 in return for bacterial vitamin B₁₂ provision (Croft et al., 2005) during this type of cross-feeding
287 between different kingdoms.

288 ~~I worked out that essentiality, defined as the reduction of uptake rates or conversion efficiencies when~~
289 ~~the focal prey is absent, is an appropriate measure to determine the effect of the~~ There has been
290 a long history of investigating the effect of higher-order ~~interaction on the persistence of the focal~~
291 ~~prey, particularly when using invasion analysis. One of the benefits from this definitions is that the~~
292 ~~density-dependent functional form of the~~ interactions in small ecological interaction networks, such as
293 trait-mediated indirect interactions (?Werner and Peacor, 2003) or non-trophic interactions (?), e.g.
294 facilitation (Gross, 2008). The effect of higher-order interactions ~~does not need to be specified, which~~
295 ~~largely facilitates experimental approaches of measuring the presence and effect of the~~ on community
296 stability is investigated also in larger networks, both empirical (González González et al., 2021) and
297 theoretical, randomly sampled ones (e.g. Arditi et al., 2005; Grilli et al., 2017; Gibbs et al., 2023),
298 and innovative approaches of analyzing their effects have been proposed (Golubski et al., 2016). The
299 effect of trait-mediated indirect interactions and higher-order interactions in general have been shown
300 to depend on many specifics, such as network structure and interaction strengths. In my **analysis**

301 ~~I focussed on the persistence of the focal prey. It should be noted that determining coexistence~~
302 ~~of species, and not only persistence of a focal species, can be complicated by the existence of~~
303 ~~multiple stable states (e.g. Yamamichi et al., 2014; ?) which constrain the interpretation of invasion~~
304 ~~growth rates (Grainger et al., 2019) model, a higher essentiality corresponds to a higher strength of~~
305 ~~the higher-order interaction. I found that depending on the food web scenario, food-quality-provision-mediated~~
306 ~~higher-order interactions can be both promoting but also detrimental to persistence and thus community~~
307 ~~stability, a finding that resonates with this overall complexity. Exploring the effect of multiple,~~
308 ~~simultaneously occurring higher-order interactions presents an interesting avenue for future research.~~

309 The provision of essential resources changes the abiotic environment of the competitors or predators
310 via changing the pool of available essential resources. It can be seen as a form of niche construction
311 that is implicitly included via an interaction modification between two biotic food web components
312 ~~(similar to Kylafis and Loreau, 2011)~~ (similar to Kylafis and Loreau, 2011; Oña et al., 2021). Obvi-
313 ously, the niches of predator and competitor are impacted directly by the presence of the focal
314 prey. Interestingly, however, this niche construction operates also indirectly in the second food web
315 scenario, as the niche of the focal prey is extended through a feedback loop via predator-mediated
316 coexistence of competitor and focal prey.

317 ~~Bridging theory and experiments on higher-order-interactions is challenging (Levine et al., 2017).~~
318 ~~I worked out that essentiality, defined as the reduction of uptake rates or conversion efficiencies~~
319 ~~when the focal prey is absent, is an appropriate measure to determine the effect of the higher-order~~
320 ~~interaction on the persistence of the focal prey, particularly when using invasion analysis. One of~~
321 ~~the benefits from this definition is that the density-dependent functional form of the higher-order~~
322 ~~interactions does not need to be specified, which largely facilitates experimental approaches of~~
323 ~~measuring the presence and effect of the higher-order interactions. In my analysis I focussed on~~
324 ~~the persistence of the focal prey. It should be noted that determining coexistence of species, and~~

325 not only persistence of a focal species, can be complicated by the existence of multiple stable
326 states (e.g. Yamamichi et al., 2014) which constrains the interpretation of invasion growth rates
327 (Grainger et al., 2019).

328 Measuring higher-order interactions experimentally is difficult, however, some advances have been
329 reported that employ different strategies. A first line of research infers the higher-order interactions
330 statistically from community dynamics data (e.g. Kéfi et al., 2015; Mayfield and Stouffer, 2017).
331 A second, more mechanistic approach aims to disable hypothesized higher-order interactions and
332 compare the outcomes with the non-manipulated scenario. One prominent example is the study by
333 Wootton (1993) where the disguising effect of barnacles for limpets was discovered by removing
334 barnacles partially or completely. Removing the species that initiates the higher-order interaction to
335 quantify the effect of the higher-order interaction however is complicated by other direct and indirect
336 effects that are then also removed, which would lead to false evaluations of the effect size of the
337 higher-order interaction. The essential resource context provides a different way of determining the
338 effect size of higher-order interactions. Experimentally providing the essential resource in excess by
339 supplementation removes its potential to cause higher-order interactions and decreases its essentiality.
340 This approach has been used in investigations of microbial cross-feeding, such as in Kazamia et al.
341 (2012) and Hammarlund et al. (2019) where supplementation with the essential resource alleviated
342 the dependence on the interaction partner, shifting the coexistence pattern towards the beneficiary
343 of the supplementation. In the context of herbivore limitation by biochemicals, supplementation was
344 used to show the mechanistic basis for the higher-order interaction (Wacker and Martin-Creuzburg,
345 2012). In a predator-prey context ~~it is also possible to~~ Bayesian inference from population size time
346 series can be used to obtain uptake rates and conversion efficiencies independently (?). Applying the
347 inference for different supplementation levels should allow to disentangle whether the essential re-
348 source affects the uptake rate or the conversion efficiency of the predator ~~by obtaining and comparing~~

349 ~~short population size time series of both predator and prey~~. This may be less feasible for a prey
350 consuming abiotic resources, but even here methods such as isotopic labelling could be used to track
351 uptake and conversion separately. The community-structuring effect of essential resource provision
352 remains to be tested, which requires tracking the population feedback mechanisms over larger time
353 scales of many prey generations, but chemostat or mesocosm experiments will be useful here. The
354 central focus of this article on persistence of the focal prey, however, facilitates experimental valida-
355 tion. As argued before, only the invasion growth rate of the focal prey would have to be obtained for
356 different levels of supplementation with potentially different resident communities. This reduces the
357 time that experimental cultures would have to be operated and avoids experimental difficulties often
358 entailed by long-term observations, ultimately illuminating the potential effect of essential resource
359 provision on prey persistence.

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363 **Competing Interests**

364 The author states no competing financial interests.

365 **Data ~~archiving statement~~, script and code availability**

366 The Mathematica scripts used for the calculations and for creating the figures have been de-
367 posited [both as Mathematica notebooks and also as pdf exports](#) in a zenodo repository with DOI

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602 **Appendix**

603 **Supporting figures**

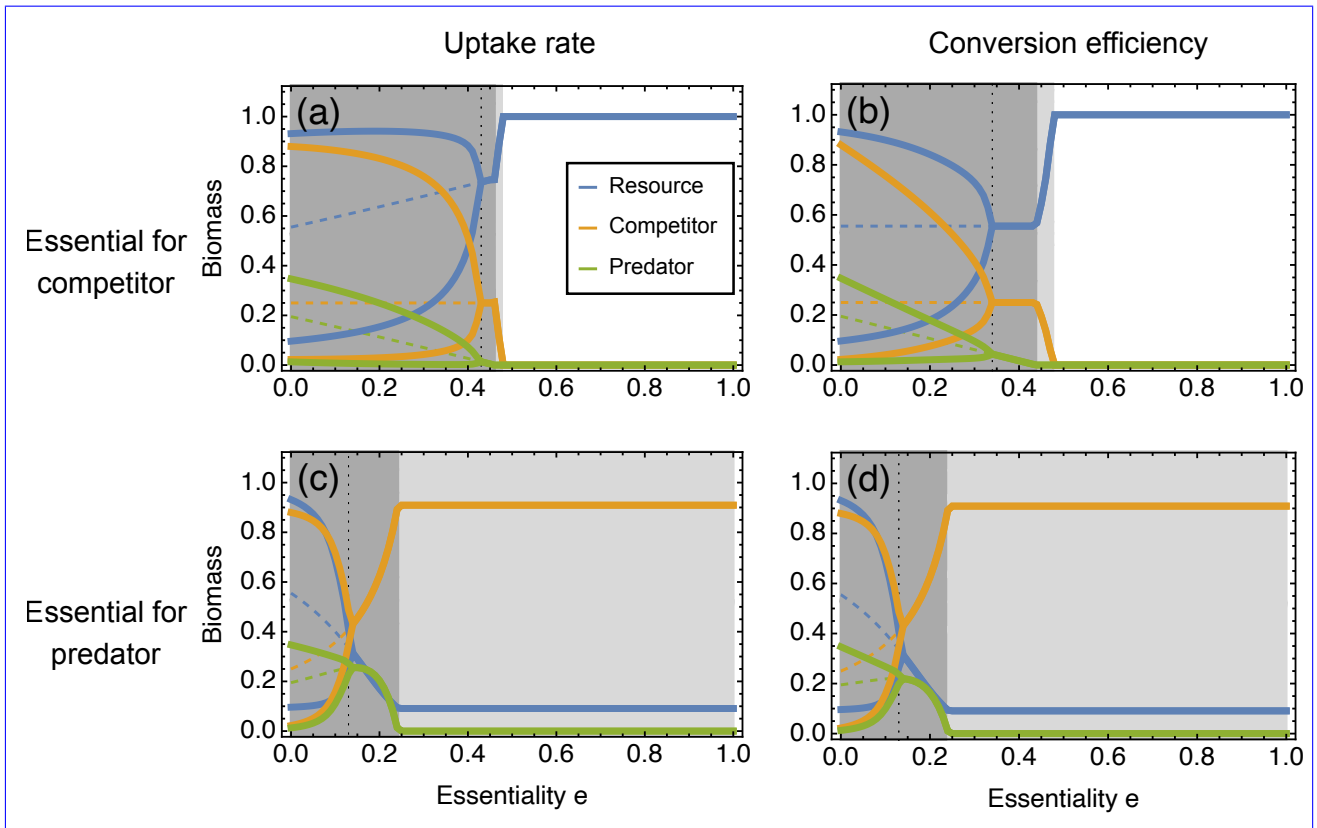


Figure A1 Resident community states for the first food web scenario. In the absence of the focal prey its essentiality determines the reduction in (a) the uptake rate or (b) the conversion efficiency of the competitor, or (c) the uptake rate or (d) the conversion efficiency of the shared predator, which affects their community dynamics. Full lines represent the minima and maxima of one population cycle, if the population is cycling, or otherwise the steady state biomass. The vertical dotted line indicates the bifurcation point. Population dynamics were defined as cyclic if the difference between predator extrema exceeded 10^{-5} . During cycles, the unstable fixed point is indicated by the dashed line. As in Fig. 4, the grey shading indicates the states of the resident community. For dark shading both predator and competitor coexist, for light-grey shading only the competitor persists and for no shading only the resource remains.

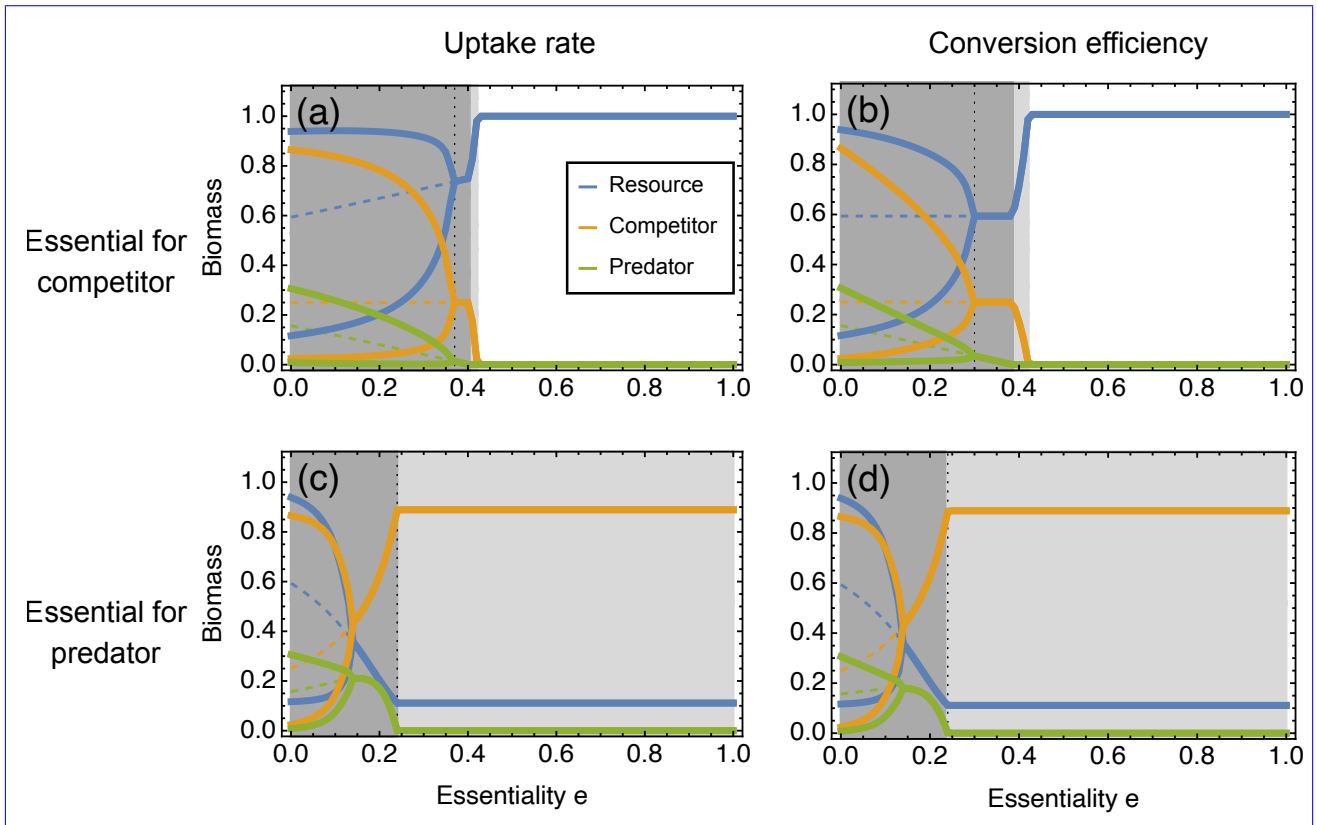


Figure A2 Resident community states for the second food web scenario. Here, the focal prey is more vulnerable to predation but also the superior competitor for the abiotic resource. In the absence of the focal prey its essentiality determines the reduction in (a) the uptake rate or (b) the conversion efficiency of the competitor, or (c) the uptake rate or (d) the conversion efficiency of the shared predator. The plot specifics are identical to Fig. A1.

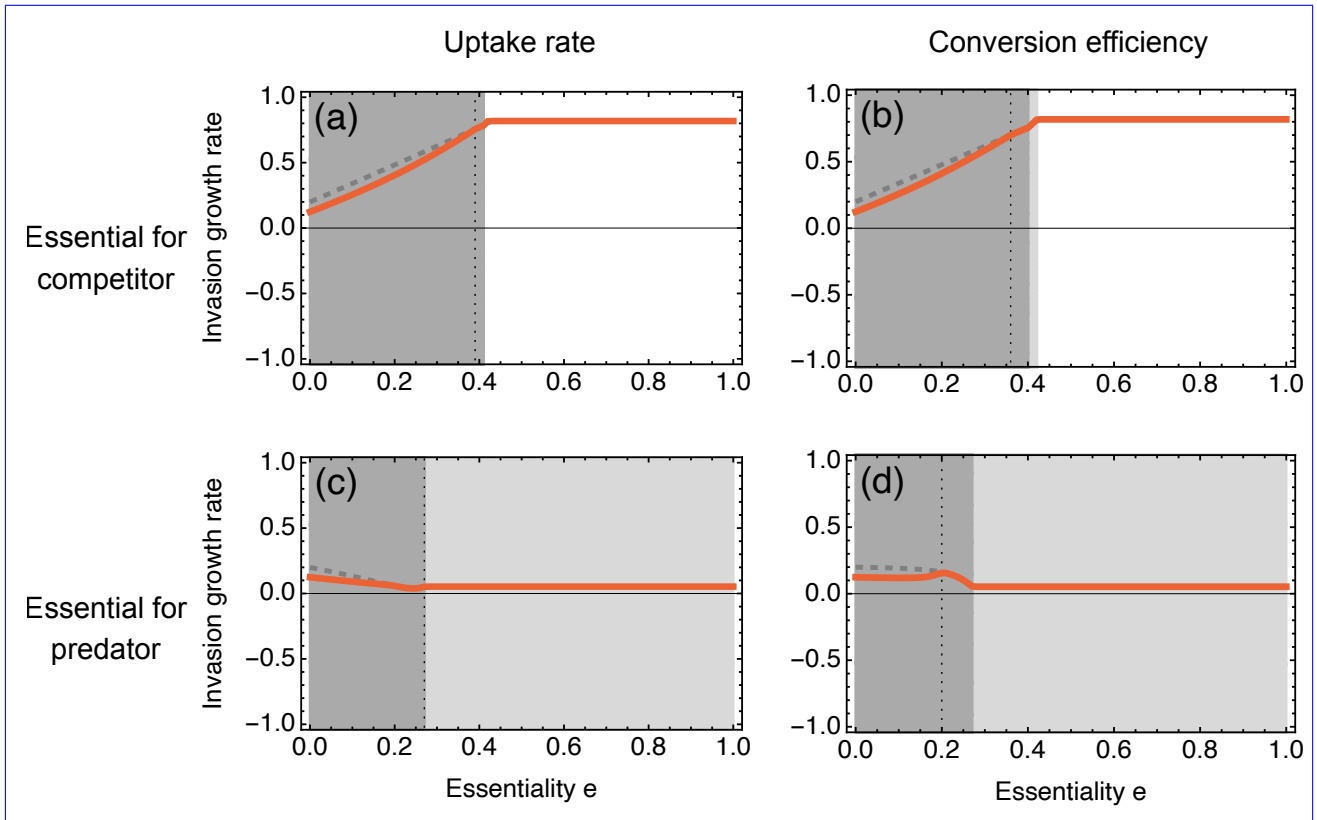


Figure A3 Invasion growth rate of the focal prey for the third food web scenario (Fig. 2c). Here, the focal prey is less vulnerable to predation and more competitive for the resource than the competitor. Essential resource provisioning affects (a) the uptake rate or (b) the conversion efficiency of the competitor, or (c) the uptake rate or (d) the conversion efficiency of the shared predator. Further plot specifics are identical to Figs. 4 and 6.

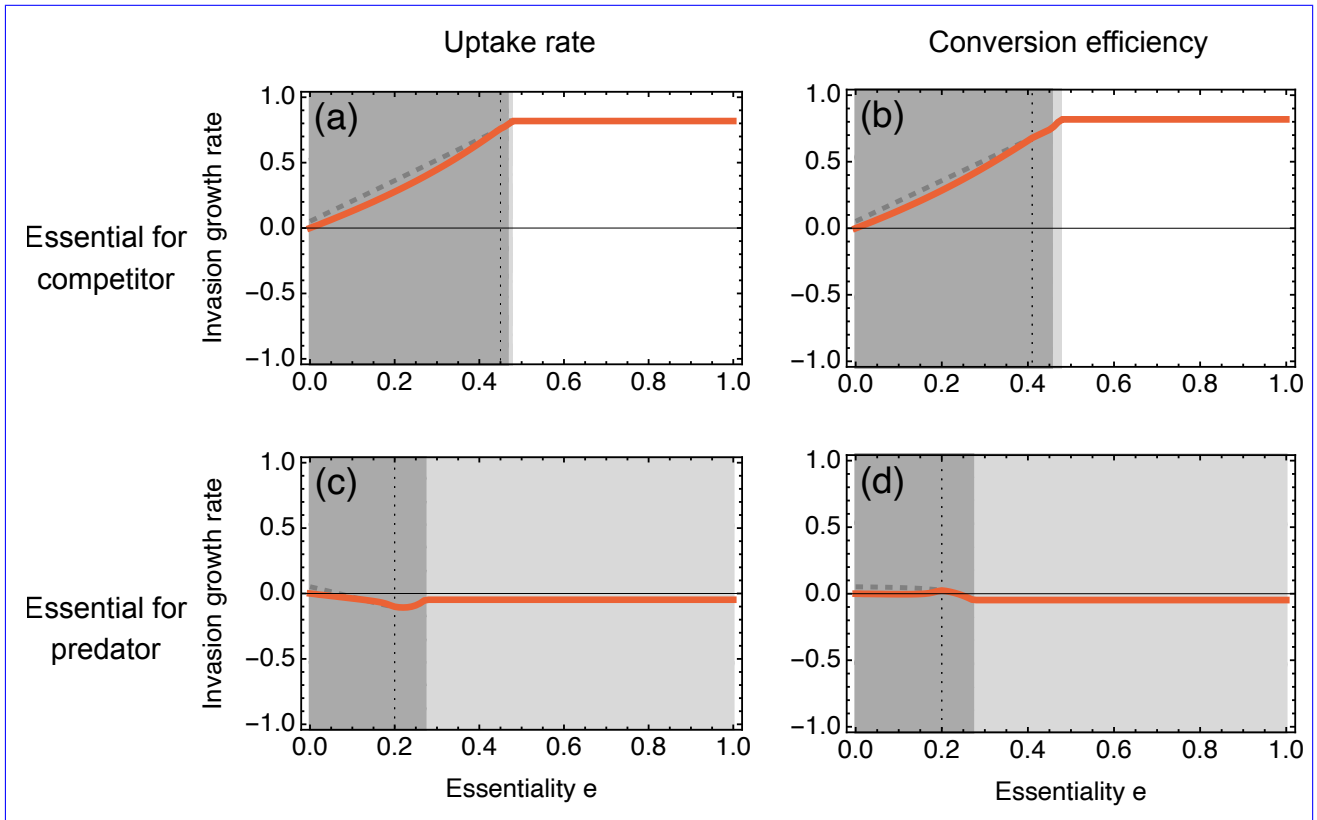


Figure A4 Invasion growth rate of the focal prey for the fourth food web scenario (Fig. 2d). Here, the focal prey is less vulnerable to predation and less competitive for the resource than the competitor. Essential resource provisioning affects (a) the uptake rate or (b) the conversion efficiency of the competitor, or (c) the uptake rate or (d) the conversion efficiency of the shared predator. Further plot specifics are identical to Figs. 4 and 6.