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ORIGINAL RESEARCH

Not attackable or not crackable—How pre- and post-attack defenses with different competition costs affect prey coexistence and population dynamics

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Abstract

It is well-known that prey species often face trade-offs between defense against predation and competitiveness, enabling predator-mediated coexistence. However, we lack an understanding of how the large variety of different defense traits with different competition costs affects coexistence and population dynamics. Our study focusses on two general defense mechanisms, that is, pre-attack (e.g., camouflage) and post-attack defenses (e.g., weaponry) that act at different phases of the predator–prey interaction. We consider a food web model with one predator, two prey types and one resource. One prey type is undefended, while the other one is pre- or post-attack defended paying costs either by a higher half-saturation constant for resource uptake or a lower maximum growth rate. We show that post-attack defenses promote prey coexistence and stabilize the population dynamics more strongly than pre-attack defenses by interfering with the predator's functional response: Because the predator spends time handling “noncrackable” prey, the undefended prey is indirectly facilitated. A high half-saturation constant as defense costs promotes coexistence more and stabilizes the dynamics less than a low maximum growth rate. The former imposes high costs at low resource concentrations but allows for temporally high growth rates at predator-induced resource peaks preventing the extinction of the defended prey. We evaluate the effects of the different defense mechanisms and costs on coexistence under different enrichment levels in order to vary the importance of bottom-up and top-down control of the prey community.

KEYWORDS

coexistence, competition–defense trade-off, defense against predation, functional response, indirect facilitation, predator–prey cycles

1 | INTRODUCTION

Predation and competition for resources represent two major factors determining the survival of species at low and intermediate trophic levels (Sih, Crowley, McPeck, Petranka, & Strohmeier, 1985). Hence,

there is strong selection for increasing defense against predation and competitiveness. However, species optimizing one functional trait commonly have to pay costs regarding other traits due to physiological, energetic, and genetic constraints (Stearns, 1989). Trade-offs between defense and competitiveness have been frequently found

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in nature and may explain the high diversity of strategies along the gradient of being defended or highly competitive (Agrawal, 1998; Coley, Bryant, & Chapin, 1985; Hillebrand, Worm, & Lotze, 2000). Predation may enable coexistence of competing species facing a trade-off between defense and competitiveness. This mechanism is known as keystone predation (Leibold, 1996; Menge, Berlow, Blanchette, Navarrete, & Yamada, 1994; Paine, 1966) or analogously as killing the winner in a microbial context (Thingstad, 2000; Winter, Bouvier, Weinbauer, & Thingstad, 2010): A competitive superior species is suppressed by predation promoting the inferior but defended competitor which allows them to coexist. Several studies highlighted the importance of this predator-mediated coexistence in experimental and natural communities (e.g., Ciroso-Pérez, Carmona, Lapesa, & Serra, 2004; Fauth & Resetarits, 1991; McPeck, 1998).

Species evolved a variety of defense strategies to reduce their predation risk ranging from camouflage, apparent dead, mimicry, aposematism, warning calls, weaponry, chemical defense to escape behavior (Endler, 1991; Lima & Dill, 1990). These defense mechanisms interact in different ways with the predator. Some of them even hamper the predator, for example, chemical defenses, while others do not, for example, camouflage, which may have strong implications for the occurrence of predator-mediated coexistence. Furthermore, the type of defense costs regarding competitiveness (resource uptake affinity or growth rate) plays an important role for coexistence. Theory already showed that predator-mediated coexistence crucially depends on the environmental conditions (Chase et al., 2002), for example, the enrichment level (Genkai-Kato & Yamamura, 1999; Leibold, 1996; Proulx & Mazumder, 1998), the prey switching behavior of the predator (Abrams & Matsuda, 1993; Fryxell & Lundberg, 1994; Murdoch, 1969), the magnitude of the trade-off between defense and competitiveness (Abrams, 1999; Kasada, Yamamichi, & Yoshida, 2014; Tirok & Gaedke, 2010), and the difference in both the defense level and the competitiveness between the prey types (Becks, Ellner, Jones, & Hairston, 2010; Ehrlich, Becks, & Gaedke, 2017; Jones & Ellner, 2007). However, the role of different defense mechanisms and competition costs in prey communities remains unclear but holds promise to be decisive for their coexistence and the occurring population dynamics. Here, we want to evaluate explicitly the effects of different defense mechanisms and compare





the influence of different defense costs in terms of competitiveness on prey coexistence and population dynamics.

Following Bateman, Vos, and Anholt (2014), we distinguish between two general types of defense mechanisms: pre-attack and post-attack defenses that act at different phases of the predation sequence, that is, prey encounter, detection, attack, capture, manipulation, consumption, and digestion. A pre-attack defense implies that the predator does not attack the prey, for example, because it senses the defense, the prey is camouflaged or avoids habitats where predators occur. A post-attack defense means that the prey is attacked but survives, for example, due to weaponry, escape behavior or robustness. In contrast to pre-attack defenses, the predator invests time and energy to handle prey with a post-attack defense which reduces its potential to consume another undefended prey (see Table 1). Hence, a post-attack defended prey interferes with the functional response of the predator for edible prey which may result in a lower top-down control of the total prey community, while pre-attack defended prey does not. Thus, we expect different coexistence patterns and population dynamics in dependence of the defense mechanism.

We also distinguish between two general cost types of the defense in respect to resource competition: either having a reduced performance at low resource concentrations or growing slower independent of the resource concentrations. Referring to the Monod equation (Monod, 1950), this corresponds either to a higher half-saturation constant for resource uptake or a lower maximum growth rate. There is empirical evidence from phytoplankton and plant communities that both cost types are ecologically relevant (Agrawal, 1998; Lind et al., 2013; Meyer, Ellner, Hairston, Jones, & Yoshida, 2006; Yoshida, Hairston, & Ellner, 2004). However, a comparison of how both cost types affect the prey community is still missing.

Previous studies on predator-mediated coexistence in diamond-shaped food web models often implicitly assumed pre-attack defenses (Abrams, 1999; Fryxell & Lundberg, 1994; Yamauchi & Yamamura, 2005) and considered either a higher half-saturation constant (Becks et al., 2010; Jones & Ellner, 2007; Yoshida, Jones, Ellner, Fussmann, & Hairston, 2003) or a lower maximum growth rate as costs (Abrams, 1999; Kasada et al., 2014; Yoshida et al.,

TABLE 1 Comparison of the predator's handling time spent per prey individual and the resulting energy gain of the predator for an undefended prey (a) and for prey types with three different defense mechanisms (b–d). T_a represents the time needed for attacking and capturing a prey individual and T_m is the manipulation and digestion time spent after capturing the prey

Defense mechanism		Handling time	Energy gain	Examples
a) Undefended ($p_2 = 1, q_2 = 1$)		$T_a + T_m$	Yes	–
b) Pre-attack defense ($p_1 = 0, q_1 = 1$)		0	No	Camouflage, mimicry, aposematism, apparent dead
c) Post-attack defense ($p_1 = 1, q_1 = 0$)		T_a	No	Weaponry, escape behavior, robustness, autotomy
d) Digestion resistance (see Appendix S1)		$T_a + T_m$	No	Algae with thickened cell walls or snails surviving gut passage in predators

2007). In this study, we explicitly model pre-attack and post-attack defenses and both cost types. The modeled diamond-shaped food web involves a basal resource, two competing prey types with a trade-off between defense and competitiveness, and one predator species. One prey type is undefended, while the other type is defended either by a reduced probability of being attacked or a lower probability of being consumed when attacked. We consider defense as a continuous trait with values ranging from completely defended to nearly undefended. The costs for defense are either a higher half-saturation constant or a lower maximum growth rate. By varying the values of both traits of the defended prey independently, we generate different magnitudes of the trade-off quantifying the costs of being more or less defended. For each trait combination, we test for coexistence and check whether the populations cycle or are in steady state. This enables us to evaluate how the different traits promote maintenance of prey diversity and stabilize the dynamics. We analyze these effects under different enrichment levels (different resource concentrations) in order to vary the relative importance of bottom-up and top-down control.

2 | METHODS

We consider a diamond-shaped food web model with one predator (P), two prey types (A_i), and one resource (N) limiting the growth of the prey. The two prey types face a trade-off: A_1 is defended but has costs in respect to resource competition while A_2 is undefended and highly competitive. The following model description is divided into four parts. At first, we present the different defense mechanisms of A_1 and derive the respective functional response of the predator. Second, we describe the different competition costs based on the resource-dependent growth function of the prey types. Third, we apply the model to a fully parametrized chemostat system, and finally, we explain how to analyze the effect of the different defense mechanisms and costs on prey coexistence and the population dynamics for the considered system.

2.1 | Defense mechanisms

The predator attacks the prey A_i with the probability p_i and then consumes the captured prey with the probability q_i . While A_2 is completely undefended ($p_2 = q_2 = 1$), A_1 is able to defend against predation at different phases of the predation sequence (Bateman et al., 2014). We distinguish between two general defense mechanisms: pre-attack defenses ($p_1 < 1$) and post-attack defenses ($q_1 < 1$). A third special defense mechanism where the prey is attacked and consumed ($p_1 = q_1 = 1$) but survives passing the digestive system of the predator is investigated in Appendix S1.

According to Brodie, Formanowicz, and Brodie (1991), we assume that the defended prey is specialized only on one defense mechanisms, that is, if $p_1 < 1$ then $q_1 = 1$ and vice versa, as investing in one strategy reduces the fitness advantage of the other. The main difference between the defense mechanisms lies in how they

affect the predator's functional response. We consider a Holling type II functional response of the predator implying that it spends a certain handling time for each attacked prey individual before it is able to attack the next prey item. Thus, the rate of consumption of the predator saturates with increasing prey density. The handling time comprises the time for attacking and capturing the prey (T_a), and, if the prey is consumed, the time for manipulating and digesting it (T_m). The two prey type version of the Holling disk equation is then given by

$$F_i = \frac{ap_i q_i A_i}{1 + ap_1(T_a + q_1 T_m)A_1 + ap_2(T_a + q_2 T_m)A_2} \quad (1)$$

where a represents the encounter rate (Bateman et al., 2014; Holling, 1959; Rueffler, Van Dooren, & Metz, 2006). It should be mentioned here that the attack probability p_i scales the encounter rate a in the presented version of the type II functional response (Equation 1). Therefore, the product of a and p_i can be interpreted as the effective attack rate on A_i .

The key to understand the effects of the different defense mechanisms on the functional response of predator is the handling time spent per prey individual. A completely undefended prey individual demands the full handling time of the predator attacking and manipulating it, that is, $T_a + T_m$ (Table 1a). A pre-attack defended prey individual with $p_1 = 0$ is not attacked and thus demands no handling time of the predator (Table 1b) allowing the predator to focus on the undefended prey. In contrast, for a post-attack defended prey individual with $q_1 = 0$, the predator invests the attack time T_a without making use out of it (Table 1c). The relative size of T_a compared to T_m determines how much the different prey types differ in their handling times. To approach this difference systematically, we replace T_a by $c_a T$ and T_m by $c_m T$ where T is the total handling time, c_a the fraction of T spent for attacking the prey, and c_m the fraction of T invested into manipulation which can be replaced by $c_m = 1 - c_a$. This leads us to

$$F_i = \frac{ap_i q_i A_i}{1 + ap_1(c_a T + q_1(1 - c_a)T)A_1 + ap_2(c_a T + q_2(1 - c_a)T)A_2} \quad (2)$$

If c_a has very low values, pre- and post-attack defenses do not differ substantially in their effect on the predator, while high values of c_a imply high differences in handling times needed for a pre- and post-attack defended prey (see Equation 2 and Table 1).

2.2 | Defense costs with respect to competitiveness

An empirically well-established resource-dependent growth model is the Monod equation with the parameters maximum per capita growth rate β_i and half-saturation constant K_i , that is, the resource concentration where the growth rate reaches half of the maximum (Monod, 1950). The Monod equation is equivalent to a Holling type II functional response but is not restricted to predator-prey

interactions and has been applied also to autotrophic organisms taking up nutrients (e.g., Becks et al., 2010; Raatz, Gaedke, & Wacker, 2017; Yoshida et al., 2003). The per capita growth rate of A_i in dependence of N is described by

$$G_i = \beta_i \frac{N}{K_i + N} \quad (3)$$

We distinguish here between two general types of defense costs of A_1 with respect to competitiveness: a reduced growth rate at low but not at high resource concentrations ($K_1 > K_2$) or a lower growth rate independent of the resource concentration ($\beta_1 < \beta_2$). Both cost traits (K_1 and β_1) are relevant in nature, and their implications can be understood based on two extreme cases. First, for very high resource concentrations ($N \gg K_1$), the per capita growth rate of A_1 reaches its maximum and is independent of the half-saturation constant ($G_1 = \beta_1$, see Equation 3). Second, for very low resource concentrations ($N \ll K_1$), the per capita growth rate of A_1 is given by $G_1 = (\beta_1/K_1)N$ (see Equation 3) and thus depends on both cost traits. According to that, β_1/K_1 can be interpreted as the slope of the growth function at very low N which is defined as the resource affinity. In the absence of mortality, the prey type with the higher resource affinity would be competitive superior (Button, 1978; Healey, 1980; Smith, Merico, Wirtz, & Pahlow, 2014). However, given a certain rate of natural mortality δ , the competitiveness depends on the

equilibrium resource concentration N_i^* at which the gross growth rate equals the mortality, that is, $G_i = \delta$ (Tilman, 1982). Following Equation 3, the equilibrium resource concentration of a prey type A_i in monoculture is given by

$$N_i^* = \frac{K_i}{\frac{\beta_i}{\delta} - 1} \quad (4)$$

The undefended prey A_2 has a lower equilibrium resource concentration than the defended prey A_1 ($N_2^* < N_1^*$) and thus outcompetes A_1 in the absence of predation. We use the ratio N_2^*/N_1^* as a measure of relative competitiveness of A_1 which allows us to compare the effects of the different defense costs (higher K_1 or lower β_1) on competition. For costs arising from $K_1 > K_2$ ($\beta_1 = \beta_2$), N_2^*/N_1^* equals K_2/K_1 . For costs originating from $\beta_1 < \beta_2$ ($K_1 = K_2$), it is given by $(\beta_1 - \delta)/(\beta_2 - \delta)$ (see Equation 4).

2.3 | Chemostat model

Here, we put the diamond-shaped food web model with the previously derived functional responses and growth functions into an ecologically relevant context. We consider a chemostat system which is characterized by a continuous inflow of medium with resources and outflow of medium with resources and organisms (Smith

Parameter/Variable	Value	Unit	References
N	–	$\mu\text{mol N/L}$	–
A_i	–	ind./mL	–
P	–	ind./mL	–
N_i	80, 160 or 240	$\mu\text{mol N/L}$	TVC
δ	0.8	per day	TVC
χ	2.7×10^6	ind./ $\mu\text{mol N}$	Lutz Becks, unpublished data
χ_P	170×10^{-6}	–	Becks et al. (2010)
a	0.073	mL/day	Calculated from Becks et al. (2010)
T	9.091×10^{-5}	day	Calculated from Becks et al. (2010)
c_a	0.5	–	NM
p_i	p_1 varied, $p_2 = 1.0$	–	Lutz Becks, unpublished data
q_i	q_1 varied, $q_2 = 1.0$	–	Lutz Becks, unpublished data
K_i	K_1 varied, $K_2 = 2.2$	$\mu\text{mol N/L}$	Lutz Becks, unpublished data
β_i	β_1 varied, $\beta_2 = 1.6$	per day	Noemi Woltermann, unpublished data

TABLE 2 Values and units of state variables and parameters used in the predator-prey chemostat model parametrized for a rotifer-algae system (Becks et al., 2010, 2012)

TVC, Typical values used in chemostat experiments with rotifers and algae as they enable sufficient rotifer densities but avoid light limitation (e.g., Becks et al., 2010; Yoshida et al., 2003); NM, No measurements available. For simplicity, we assume that the fraction of T spent for attacking and manipulating the prey is equal, that is, $c_a = 0.5$ (sensitivity analysis in Appendix S3).

& Waltman, 1995). The magnitude of the in- and outflow is described by the dilution rate δ which represents the mortality rate of the prey and the predator. The resource concentration in the supplied medium N_i determines the quantity of inflowing resources. An increase in N_i implies an enrichment of the system. The changes of the resource concentration and population densities over time are defined by the following differential equations

$$\begin{aligned} \frac{dN}{dt} &= \delta(N_i - N) - \frac{1}{\chi}G_1A_1 - \frac{1}{\chi}G_2A_2 \\ \frac{dA_i}{dt} &= G_iA_i - F_iP - \delta A_i \\ \frac{dP}{dt} &= \chi_p F_1P + \chi_p F_2P - \delta P \end{aligned} \tag{5}$$

with $i = 1, 2$. The parameter χ describes the prey's conversion efficiency of resources into prey individuals. The parameter χ_p describes the efficiency with which consumed prey individuals are converted into predator individuals. To reach a suitable parametrization, we refer our model to an empirically well-studied rotifer-algae system with *Brachionus calyciflorus* as a predator and different genotypes of *Chlamydomonas reinhardtii* as prey (Becks, Ellner, Jones, & Hairston, 2012; Becks et al., 2010). For details on the values and units of the parameters and the state variables, see Table 2. For the given system, A_1 and A_2 represent different genotypes of the same algal species. However, mechanistically, there is no difference between analyzing coexistence of different species or genotypes of an asexually reproducing species without horizontal gene transfer.

2.4 | Analysis of coexistence and population dynamics

The traits of the undefended prey A_2 are fixed. By varying the defense level and the defense costs of A_1 independently, we generate different slopes of the trade-offs. In order to understand the individual effects of the different traits, we vary only the value of one defense trait and one cost trait at a time. The other trait values are

equal to those of A_2 . This results in four different types of trade-offs (TO) which we consider: p-K-TO, q-K-TO, p- β -TO, and q- β -TO. First, we analyze how the different defense mechanisms ($p_1 < p_2$ or $q_1 < q_2$) affect prey coexistence and the population dynamics, that is, whether cycles or steady state occur. Secondly, we compare the effect of different costs of defense ($K_1 > K_2$ or $\beta_1 < \beta_2$) on these properties.

In order to find the coexistence regions in the trait space, we applied an analytical approach of Jones and Ellner (2007) which calculates the condition for a coexistence equilibrium where all net growth rates equal zero. A following linear stability analysis of these equilibria informs about the population dynamics. A steady-state occurs in case of a stable equilibrium. For an unstable equilibrium, coexistence with cycling population densities is possible. To check the basin of attraction of the respective attractor, that is, the range of possible initial conditions leading to it, we perform an invasion analysis. We check whether A_1 can invade a resident community with N, A_2 and P which reveals whether coexistence is also reached with very low population densities of A_1 . For further details on the analysis, see Appendix S2 in Supporting information. To investigate details of the population dynamics, we did numerical integrations for selected parameter combinations with the odeint solver of the SciPy package in Python (Jones, Oliphant, & Peterson, 2001). For all simulations shown in the main text, we use the same setting of initial population densities ($N = N_i, A_1 = A_2 = 10^5$ ind./mL, $P = 1$ ind./mL) and a simulation time of 60 days.

3 | RESULTS

3.1 | General patterns of prey coexistence and population dynamics

To explain the patterns of coexistence and population dynamics in general, we focus initially on the trade-off (TO) between attack probability p , that is, pre-attack defense, and half-saturation

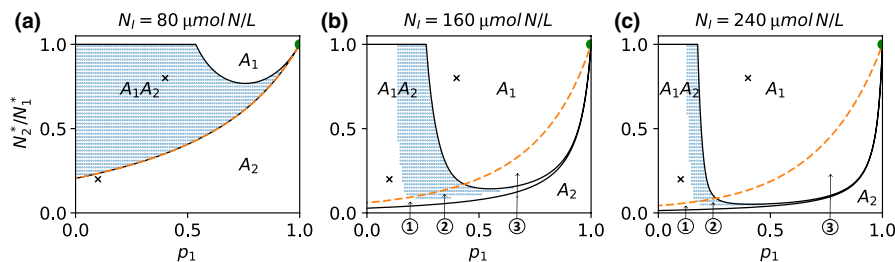


FIGURE 1 Prey coexistence and population dynamics for a trade-off (TO) between pre-attack defense, p , and half-saturation constant K (p-K-TO) under three levels of resource supply, that is, $N_i = 80, 160, 240 \mu\text{mol N/L}$ (a–c). The traits of the undefended prey A_2 are kept constant (green dot). The attack probability p_1 and the half-saturation constant K_1 of the defended prey A_1 which determines its relative competitiveness N_2^*/N_1^* (cf. Methods, Equation 4) are varied within the shown trait space. The capital letters display which prey types survive in the different parts of the trait space. The black lines enclose the part of the trait space where a coexistence equilibrium exists while blue dots mark where it is locally stable (steady state). The dashed orange line represents the invasion boundary above which A_1 can invade a resident community with A_2 . The numbers indicate special cases which occur at intermediate and high enrichment levels (b, c): ① Only A_2 survives as the coexistence equilibrium is unstable and A_1 cannot invade, ② multistability between coexistence and survival of only A_2 , ③ multistability between survival of A_1 and survival of A_2 . The crosses mark trait combinations used in Figure 5

constant K (p-K-TO). We consider three different enrichment levels, that is, $N_I = 80, 160,$ and $240 \mu\text{mol N/L}$, to reveal the sensitivity of these patterns to the productivity of the system (Figure 1a–c).

For a low resource supply ($N_I = 80 \mu\text{mol N/L}$), the defended prey A_1 dies out and only the undefended prey A_2 survives if the relative competitiveness N_2^*/N_1^* (cf. Methods, Equation 4) of A_1 is very low, that is, A_1 has a high half-saturation constant K_1 (Figure 1a). For higher values of N_2^*/N_1^* , A_1 and A_2 may coexist. The range of possible N_2^*/N_1^* values enabling coexistence increases with a decreasing attack probability p_1 (Figure 1a). At low values of p_1 , both prey types coexist for relatively low N_2^*/N_1^* values and even for high N_2^*/N_1^* values close to 1 (very low defense costs). The latter case implies a very high fitness of A_1 as it has favorable values for both traits. However, such a highly defended A_1 cannot outcompete A_2 as long as its competitiveness is lower than that of A_2 ($N_2^*/N_1^* < 1$) because A_1 needs A_2 to maintain the predator P and thus its advantage of being defended. In the absence of P , A_1 would be inferior compared to A_2 as long as its competitiveness is slightly lower than that of A_2 . At high values of p_1 , A_1 can maintain P by itself for N_2^*/N_1^* close to 1 and thus outcompetes A_2 (Figure 1a).

For low levels of resource supply ($N_I = 80 \mu\text{mol N/L}$), both prey types coexist in a steady state; that is, the coexistence equilibrium is always stable (Figure 1a). Furthermore, the outcome of coexistence is independent of the initial conditions as the invasion boundary of A_1 is identical to the boundary of the region where coexistence equilibria exist, indicating that they are globally stable. This pattern changes if we enrich the system, that is, increase N_I to 160 or 240 $\mu\text{mol N/L}$. A higher resource supply enhances the occurrence of coexistence in cycles, that is, unstable coexistence equilibria (Figure 1b,c). The higher concentration of resources reduces the bottom-up control which promotes the fitness of A_1 as its disadvantage regarding competition for resources gets less important. Therefore, the part of the trait space where A_1 goes extinct decreases while the part where A_1 outcompetes A_2 strongly increases which alters also the trait space of coexistence (Figure 1b,c). Moreover, the invasion boundary of A_1 is not identical to the boundary of coexistence equilibria any more, implying that even if a coexistence equilibrium exists, the two prey types may not coexist. In parts of the trait space below the invasion boundary of A_1 where the coexistence equilibrium is unstable, there is no attractor enabling coexistence and only A_2 survives (① in Figure 1b,c). In the region where a locally stable coexistence equilibrium exists but A_1 cannot invade (② in Figure 1b,c), either both prey types coexist or A_1 goes extinct depending on the initial conditions. Multistability occurs also at trait ranges above the region of coexistence equilibria where A_1 cannot invade A_2 (③ in Figure 1b,c). Here, priority effects matter: either A_1 outcompetes A_2 when present at initially high densities or goes extinct when A_2 is initially dominant (for details on multistability see Appendix S4).

The predator P survives in all trait areas stated above for all enrichment levels. It would only die out when a highly defended A_1 has a higher competitiveness than A_2 ($N_2^*/N_1^* > 1$) leading to the extinction of A_2 , the only suitable food source of P in this case.

3.2 | Comparison of different defense mechanisms

To demonstrate the effects of the different defense mechanisms on coexistence and population dynamics, we chose an intermediate resource supply ($N_I = 160 \mu\text{mol N/L}$) where coexistence with population cycles occurs and the defended prey A_1 is able to outcompete the undefended prey A_2 for a significant part of the trait space (Figure 1b). The results for $N_I = 80$ and $240 \mu\text{mol N/L}$ are given in Appendix S3 (Figures C1 and C2).

Comparing the different types of defense–competition trade-offs, we find qualitatively the same regions of coexistence in the trait space but with greatly differing importance (Figure 2a–d). A post-attack defense ($p_1 = 1, q_1 < 1$) promotes coexistence more strongly than a pre-attack defense ($p_1 < 1, q_1 = 1$) and stabilizes the dynamics. This observation is independent of the type of costs for the defense (Figure 2a–d). We elucidate the effects of the different defense mechanisms based on the comparison of the attack probability–half-saturation constant trade-off (p-K-TO, Figure 2a) and the consumption probability–half-saturation constant trade-off (q-K-TO, Figure 2c). The part of the trait space where the defended prey A_1 outcompetes the undefended prey A_2 is smaller for the q-K-TO while the coexistence region increases (Figure 2a,c). The region where A_1 goes extinct remains constant. The changes in the coexistence patterns can be explained with the different growth functions of the predator P resulting from the different defense mechanisms. We consider two comparable levels of the different defenses ($p_1 = 0.45$ or $q_1 = 0.45$) having the same costs ($N_2^*/N_1^* = 0.5$). The population dynamics clearly reveal that the growth rate of P is higher for the p-K-TO compared to the q-K-TO although the amount of total available prey ($\Sigma p_i q_i A_i$) is slightly lower during the predator growing phase (Figure 3a,b). The resulting higher biomass of P , that is, the higher top-down control, in case of the p-K-TO drives the undefended prey A_2 to extinction (Figure 3a).

More generally, the growth rates of P are equal for the p-K-TO and the q-K-TO in the absence of A_1 , but they diverge for the different types of defenses with an increasing density of the defended prey A_1 (Figure 3c). With higher shares of A_1 , the predator is increasingly handling “noncrackable” prey for the q-K-TO which dampens its growth in comparison with the p-K-TO. At high densities of A_2 , an increasing density of A_1 leads even to a reduction of growth in case of the q-K-TO, while there is a slight increase in growth for the p-K-TO (Figure 3c). When A_2 is absent, P dies out in case of the q-K-TO because the gross growth rate of P based on a post-attack defended A_1 lies below the mortality rate even for high densities of A_1 resulting in a negative net growth of P (Figure 3c). Therefore, A_1 cannot outcompete A_2 as it needs A_2 to maintain the predator and thus its advantage in respect to defense. In addition, A_1 indirectly facilitates A_2 as it reduces the grazing loss of A_2 by keeping the predator handling “noncrackable” food items (Figure 3c). The described effects of the post-attack defense on predator growth result in the coexistence of both prey types for an extended trait space. These effects are absent in case of the pre-attack defense leading to the extinction of A_2 . The lower growth rates of P in case of the q-K-TO explain also the more

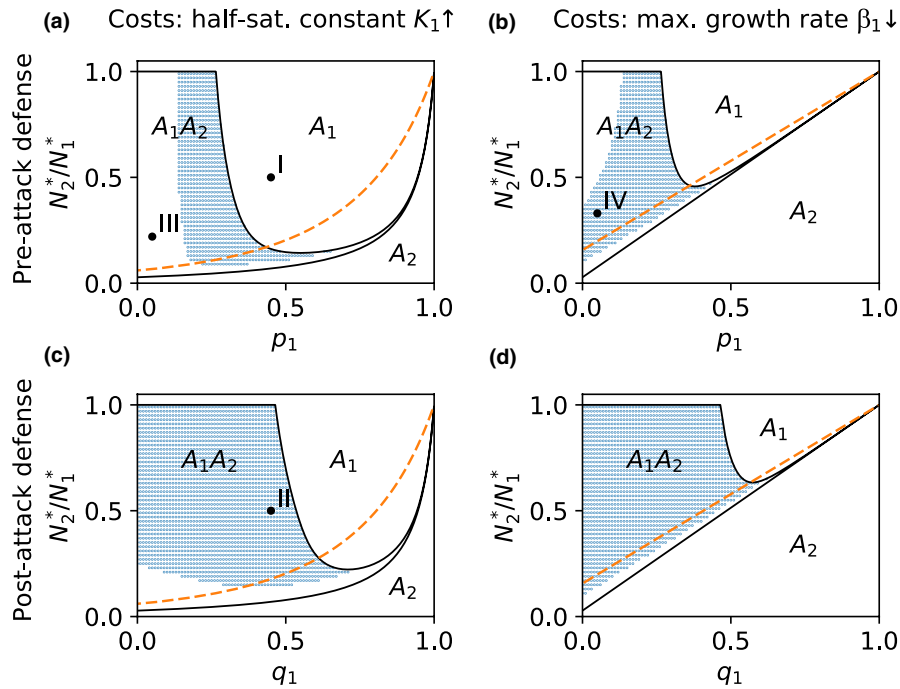


FIGURE 2 Comparison of different types of trade-offs between defense and resource competition regarding their effect on coexistence and population dynamics of a defended prey A_1 and an undefended prey A_2 at an intermediate resource supply ($N_I = 160 \mu\text{mol N/L}$). The trait values of A_1 are varied within the shown trait space. The defense occurs either prior to an attack by a predator via a lower attack probability p_1 (a, b) or after being attacked by a lower consumption probability q_1 (c, d). The costs of the defense are either a higher half-saturation constant K_1 (a, c) or a reduced maximum growth rate β_1 (b, d). Both cost traits affect the relative competitiveness N_2^*/N_1^* of A_1 compared to A_2 (cf. Methods, Equation 4). The capital letters display main regions in the trait space with different competition outcomes: Only the undefended prey survives (A_2), only the defended prey survives (A_1), or both prey types coexist (A_1A_2). Coexistence equilibria exist within the region surrounded by black lines, while blue dots indicate where they are locally stable. The dashed orange line marks the invasion boundary of A_1 . For further details on other regions with multistability, see Figure 1. The black dots with Roman numerals mark trait combinations for which population dynamics and growth functions are shown in Figure 3 (I, II) and Figure 4 (III, IV)

frequent occurrence of steady states (Figure 2c). Cycles require sufficient deflections of population densities, that is, high minima of prey densities, which are prevented due to the lower growth rates of P .

3.3 | Comparison of different defense costs

We now compare the effects of different cost types based on the trade-off between attack probability and half-saturation constant (p-K-TO) or maximum growth rate (p- β -TO). A higher half-saturation constant K_1 rather than a lower maximum growth rate β_1 as defense costs allows the defended prey A_1 to survive even at lower values of relative competitiveness N_2^*/N_1^* and promotes cycles more strongly at high and intermediate defense levels, that is, low and intermediate p_1 (Figure 2a,b). The advantage of A_1 facing a p-K-TO and the altered stability of coexistence equilibria can be explained based on the population dynamics and growth functions of the prey types shown in Figure 4 for the trait combinations (III, IV) marked in Figure 2a,b.

For the p-K-TO, the system cycles (Figure 4a) while damped oscillation occur at the shown p- β -TO (Figure 4b). The trait combinations III, IV are chosen as they lead to a similar level of resource concentrations and predator densities in the first growing phase of A_1 (marked phase in Figure 4a,b). Despite the similar environmental conditions in this phase, A_1 reaches a much higher growth rate

for the p-K-TO than for the p- β -TO (Figure 4a-c). In general, under (at least transient) cyclic conditions, A_1 increases in density when the predator strongly consumes A_2 leading to an increased resource availability (Figure 4a,b). Accordingly, A_1 grows at a resource peak. At high resource concentrations, the growth function of A_1 is getting close to that of A_2 for the p-K-TO as they have the same maximum growth rate, but it remains consistently lower in case of the p- β -TO (Figure 4c). The higher growth rate of A_1 in case of the p-K-TO leads to more unstable equilibria and increases the occurrence of cycles compared to the p- β -TO. This explains also why A_1 survives also for a lower competitiveness N_2^*/N_1^* over a large range of p_1 values in case of the p-K-TO. Costs regarding K_1 can be seen as a more temporal disadvantage which only becomes relevant during pronounced resource depletion, that is, bottom-up control. During top-down control (high predator densities), this disadvantage is less important as the resource conditions are good. The lower competitiveness of A_1 under resource depletion is counteracted by the relatively high growth rate at resource peaks enabling it to survive.

We find basically the same effects of the different cost types when considering the other defense mechanism with the reduced consumption probability (q-K-TO and q- β -TO). However, the reduced occurrence of cycles in case of the β -costs is less evident as the post-attack defense mechanism is already stabilizing (Figure 2c,d).

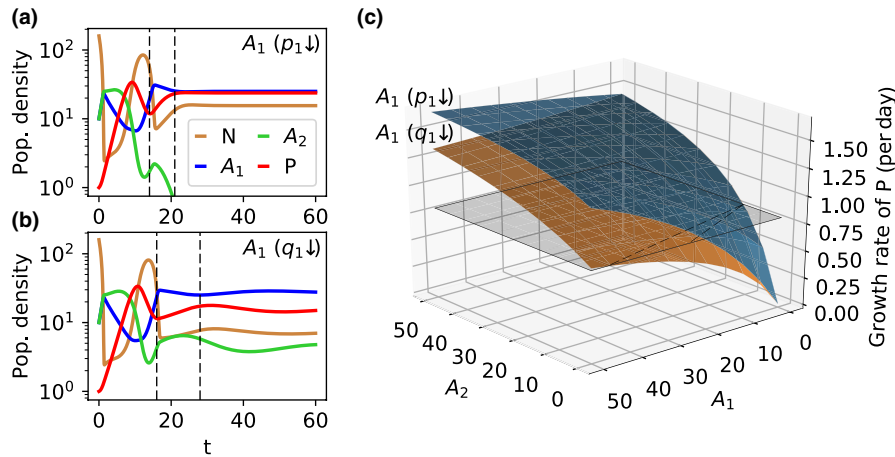


FIGURE 3 (a) Population dynamics for a pre-attack defense–half-saturation constant trade-off (trait combination I in Figure 2a, $p_1 = 0.45$ and $K_1 = 4.4 \mu\text{mol N/L}$) and (b) a post-attack defense–half-saturation constant trade-off (trait combination II in Figure 2c, $q_1 = 0.45$ and $K_1 = 4.4 \mu\text{mol N/L}$). The population densities of the resource N ($\mu\text{mol N/L}$), the two prey types A_i (10^4 ind./mL), and the predator P (ind./mL) are plotted over time t (day). The vertical dashed lines enclose one growing phase of P . (c) Per capita growth rate of P without mortality in dependence of the densities of the defended prey A_1 and the undefended prey A_2 . The blue surface shows the growth function when A_1 is pre-attack defended (like in a), while the orange surface represents the growth function in case of a post-attack defended A_1 (like in b). The post-attack defense reduces the growth rate of P by keeping it unprofitably handling with defended prey individuals while there is no handling of pre-attack defended prey. The gray surface shows the dilution rate which represents the mortality of the predator. The black dashed lines illustrate where the growth rate of P equals its mortality, that is, where its net growth rate is zero

3.4 | The effect of the enrichment level

So far, we analyzed how the different defense mechanisms and costs affect the proportion of the trait space leading to coexistence at a certain resource supply (Figure 2). Now, we fix the trait values of both prey types but vary the enrichment level (N_i) to evaluate the maintenance of coexistence under altered environmental conditions. Pre-attack and post-attack defenses differ in their implications for coexistence within a broad range of intermediate defense levels (Figure 2). The type of costs is most relevant at high cost levels and intermediate to high defense levels (Figure 2). Accordingly, we chose such trait combinations of the defended prey, that is, an intermediate defense level with low costs and a high defense level with high costs (marked in Figure 1), to examine how the differences in coexistence patterns depend on the enrichment level (Figure 5a,b).

At an intermediate level of defense with low costs, coexistence is promoted by the post-attack defense in comparison with the pre-attack defense, independent of the type of costs (Figure 5a). The post-attack defense allows the prey types to stably coexist over a wide range of enrichment levels from low to very high resource supplies while in case of the pre-attack defense coexistence is only possible for a low resource supply (Figure 5a). Contrastingly, at a high level of defense and costs, the coexistence patterns diverge between the different cost types but are rather independent from the defense mechanism. Costs with respect to the half-saturation constant enable coexistence for lower and especially higher enrichment levels compared to costs regarding the maximum growth rate (Figure 5b).

3.5 | Sensitivity analysis

In Appendix S3, we show how the coexistence and population dynamics of the prey types depend on the amount of the attack time relative to the manipulation time which is defined by c_a (fraction of total handling time spent for attacking). With higher values of c_a , the post-attack defense increasingly promotes coexistence and stabilizes the dynamics, while the results for the pre-attack defense are independent of c_a (Appendix S3: Figures C3 and C4). Furthermore, we check the sensitivity of our results with respect to the encounter rate a , the total handling time T , the conversion efficiency of the predator χ_{p_i} , the conversion efficiency of the prey χ , the resource concentration in the supplied medium N_i , the dilution rate δ , the maximum growth rate of the undefended prey β_2 , and its half-saturation constant K_2 . The general pattern that post-attack defenses promote coexistence and stabilize the dynamics compared to pre-attack defenses is independent of these parameter values. The same holds for the observed pattern that costs regarding the half-saturation constant promote coexistence and the occurrence of cycles more strongly than costs with respect to the maximum growth rate (Appendix S3: Figures C5–C7). Obviously, the exact trait values for the occurrence of coexistence equilibria and their local stability depend on the values of all parameters.

4 | DISCUSSION

We compared the effects of pre-attack and post-attack defenses with different costs in respect to resource competition on

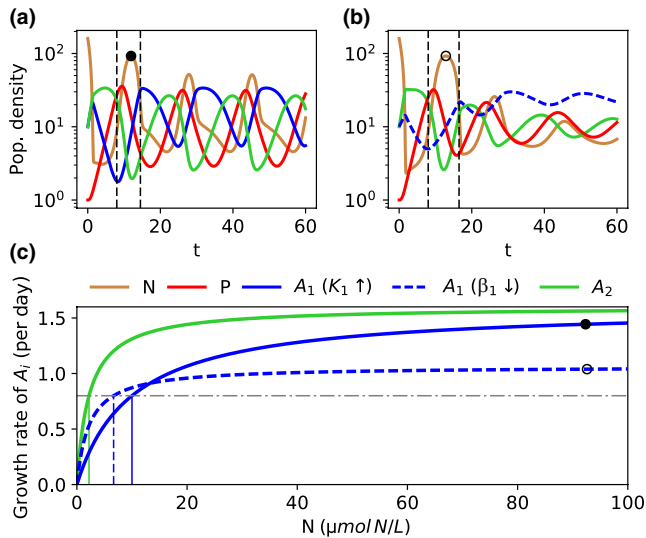


FIGURE 4 (a) Population dynamics for a trade-off between pre-attack defense and half-saturation constant (trait combination III in Figure 2a) or (b) maximum growth rate (trait combination IV in Figure 2b). The population densities of the resource N ($\mu\text{mol N/L}$), both prey types A_i (10^4 ind./mL) and the predator P (ind./mL) are plotted over time t (d). The pre-attack defended prey A_1 ($p_1 = 0.05$) has either a higher half-saturation constant ($K_1 = 10 \mu\text{mol N/L}$) (a) or a reduced maximum growth rate ($\beta_1 = 1.064$ per day) (b) compared to the undefended prey A_2 . The black dashed lines enclose one growing phase of A_1 at high resource concentrations (peak marked with dot) after strong grazing of A_2 by P . (c) Per capita growth rates of the prey types without mortality in dependence of the resource concentration are represented by the thick lines. The thin vertical green and blue lines show the resource concentration at equilibrium in monoculture N_i^* of each prey type where lower values of N_i^* imply higher competitiveness. The horizontal black dashed-dotted line represents the dilution rate, that is, the mortality of the prey without the predator. The dots illustrate the realized growth rate of the respective defended prey at the resource peaks shown in (a, b)

coexistence and population dynamics in a diamond-shaped food web. The post-attack defense promoted coexistence and stabilized the dynamics more than a pre-attack defense. Post-attack defended individuals damped the growth of the predator by keeping it handling them which indirectly facilitates the undefended prey. This

mechanism enabled coexistence at trait combinations where the defended prey would outcompete the undefended one in case of a pre-attack defense. Costs regarding resource competition were either a higher half-saturation constant or a lower maximum growth rate. The former cost type promoted coexistence and cycling population densities more than a lower maximum growth rate by allowing the defended prey to realize high growth rates at temporally high resource concentrations which prevents its extinction even if it has a very low competitiveness.

The main difference between both defense mechanisms is that a post-attack defended prey affects the functional response of the predator consuming an undefended prey while a pre-attack defended prey does not. In a previous study of Grover (1995), inedible plants were generally described as interfering when they negatively affect the growth of the herbivore consuming an edible plant. This interference weakens the interaction between the predator and its prey. In food web theory, weak interactions are known to stabilize the population dynamics (McCann, 2011; McCann, Hastings, & Huxel, 1998). In fact, several authors (Grover, 1995; Kretzschmar, Nisbet, & Mccauley, 1993; Vos, Berrocal, Karamaouna, Hemerik, & Vet, 2001) showed that interfering inedible species stabilized dynamics in comparison with noninterfering inedible ones which resembles the effect observed in our study, while they did not reveal the potential of interfering defended prey to enhance coexistence. This was not possible in their systems because the defended prey was completely inedible. Thus, it could not maintain the predator by itself and always had to coexist with the undefended prey. Contrastingly, we considered defense as a continuous trait. At low and intermediate defense levels, the defended prey is able to outcompete the undefended prey. The trait range where this competitive exclusion of the undefended prey occurred was strongly reduced by the post-attack defense, while the trait range allowing coexistence increased in comparison with a noninterfering pre-attack defense due to indirect facilitation. The relevance of our results is supported by empirical studies revealing that low to intermediate defense levels frequently occur in nature (White, Kaul, Knoll, Wilson, & Sarnelle, 2011) and that defended prey types may outcompete undefended prey types even if they have costs for their defense (Kasada et al., 2014). The

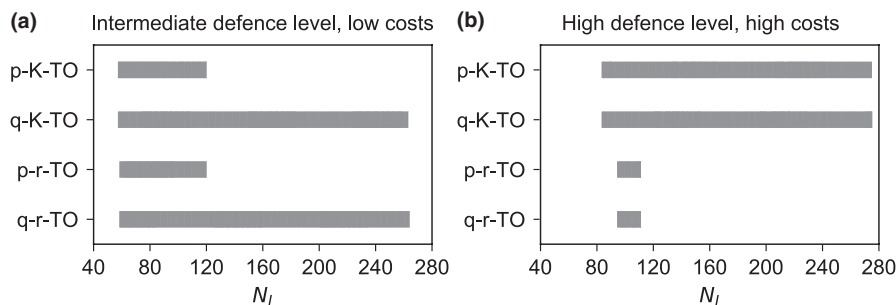


FIGURE 5 Coexistence of two prey types depending on the level of resource supply N_i (in $\mu\text{mol N/L}$), that is, the enrichment level, for different trade-offs (TO) between pre-attack (p) or post-attack defense (q) and the half-saturation constant (K) or maximum growth rate (β). The bars indicate the range where both prey types stably coexist, implying that a coexistence equilibrium exists and the defended prey can invade the undefended prey. The defended prey has either (a) an intermediate defense level and low costs (p_1 or $q_1 = 0.4$, $N_2^*/N_1^* = 0.8$) or (b) a high defense level and high costs (p_1 or $q_1 = 0.1$, $N_2^*/N_1^* = 0.2$). These trait combinations are indicated in Figure 1

presented mechanism of indirect facilitation among prey species may provide an explanation why apparent competition, that is, an increasing density of one prey species indirectly reduces the density of the other prey species via the predator (Holt, 1977), is not always observed in nature (Chaneton & Bonsall, 2000).

If attacking defended prey types hampers predator's growth, the question arises whether the predator adapts and entirely disregards the defended prey implying that post-attack defenses become pre-attack defenses. Pre-attack defenses are also favorable from the point of view of the defended prey which is then able to better out-compete a competing undefended prey. Accordingly, predator and defended prey may evolve toward avoiding interactions with each other which would mean that being not attacked is the prevailing defense strategy. This reasoning is supported by the observation that many defended prey species show warning signals to deter the predator from attacking them (Blount et al., 2012; Stevens & Ruxton, 2012) and that predators often show behavioral changes to avoid defended prey species (White et al., 2011; Xu, Nielsen, & Kiørboe, 2018). However, not attacking defended prey species implies a higher grazing pressure on undefended prey species which may reduce their population densities leading to the dominance of defended prey species. The resulting lack in food may cause predator attacks on the defended prey (Barnett, Bateson, & Rowe, 2007; Fryxell & Lundberg, 1994). However, if the defense of the prey is very effective, such prey switching behavior of the predator is unlikely. Several studies highlighted the importance of the interplay between the predator's diet choice and the level of defense for prey coexistence and population dynamics (Abrams & Matsuda, 1993; Fryxell & Lundberg, 1994; Yamauchi & Yamamura, 2005). Another argument for the occurrence of post-attack defenses in nature is the inability of predators to discriminate between undefended and defended prey. This may hold especially for predators with nonselective feeding strategies, like, for example, filter feeding *Daphnia* sp. consuming filamentous algae (Peter & Lampert, 1989). Furthermore, it strongly depends on the costs of the prey which defense mechanisms evolve (Bateman et al., 2014). Post-attack defenses may evolve if pre-attack defenses are very costly, for example, if avoiding habitats with predators substantially lowers the possibility of resource acquisition (Verdolin, 2006).

The used categorization into pre- and post-attack defenses is based on mechanistic considerations regarding their effect on the invested handling time of the predator. Even if these categories are relevant for a broad range of defense mechanisms, they may not apply to every specific defense strategy. For example, several algal species are digestion-resistant; that is, they are attacked and ingested by the zooplankton but survive the gut passage (Demott & McKinney, 2015; Meyer et al., 2006; Porter, 1973). The same holds also for some species of aquatic snails eaten by mallards (van Leeuwen, van der Velde, van Lith, & Klaassen, 2012; Wada, Kawakami, & Chiba, 2012). Such digestion resistance may promote coexistence and stabilize the dynamics even more than post-attack defended prey (see Appendix S1). Furthermore, toxicity of a prey may differ in the consequences on prey coexistence from the defense mechanisms considered here,

especially when it interferes not only with the predator but also with the competitor (Hiltunen, Barreiro, & Hairston, 2012). However, for a large variety of defense strategies, for example, aposematism, weaponry or mimicry, the used classification regarding the phase at which the defense interrupts the predation sequence is adequate. We distinguished between early (pre-attack) and late (post-attack) defenses (Bateman et al., 2014). Of course, in nature there are gradients between pre- and post-attack defenses, that is, the handling of the predator aborts at different points in time which can be mimicked by varying the parameter c_a (see Appendix S3). In the presented model, c_a was defined as the fraction of handling time invested in attacking prey. However, in a more general sense, c_a can be interpreted as the timing of a defended prey to abort the predation sequence relative to the total handling time, that is, a large c_a corresponds to a late defense and vice versa. Therefore, the given equation of the predator's functional response for two prey types (Equation 2) can be applied to multiple defense mechanisms acting at different phases of the predation sequence.

Hammill, Kratina, Vos, Petchey, and Anholt (2015) provided first empirical evidence that inedible prey species promote persistence of edible ones based on an experiment with a flatworm feeding on ciliates. However, despite the wide-spread occurrence of post-attack defenses, we found no study specifically analyzing their effect on coexistence and comparing it to pre-attack defenses. Thus, our research may serve as a starting point for future empirical studies on the maintenance of functional diversity within prey communities due to indirect facilitation of undefended prey species by post-attack defended prey species.

Quantifying defense costs is often difficult as it requires knowledge about the functional property of the prey which is influenced by an altered allocation of resources to implement the defense. Furthermore, the costs may be system specific and may vary depending on the environment (Siemens, Garner, Mitchell-Olds, & Callaway, 2002; Strauss, Rudgers, Lau, & Irwin, 2002); for example, they may occur only when a competitor is present (van Velzen & Etienne, 2015). We focussed on two major cost traits of defended prey types which describe their resource-dependent growth kinetics: a higher half-saturation constant which implies a reduced competitiveness at low resource concentration, and a lower maximum growth rate which reduces growth independent of the resource concentrations. Studies on plankton organisms revealed that trade-offs between maximum growth rates and defenses frequently occur (Agrawal, 1998; Meyer et al., 2006) but half-saturation constant-defense trade-offs were found as well (Becks et al., 2010; Yoshida et al., 2004). Furthermore, there is indication from phytoplankton organisms that the maximum growth rate and the half-saturation constant are often positively correlated (Edwards, Klausmeier, & Litchman, 2013; Litchman, Edwards, & Klausmeier, 2015). Thus, Aksnes and Egge (1991) and Smith et al. (2014) suggested an alternative mechanistic formulation of nutrient-uptake kinetics for phytoplankton organisms which accounted implicitly for this correlation. They used the affinity, that is, the slope of the uptake function at resource concentrations close to zero, instead

of the half-saturation constant as a parameter describing the performance at low resource concentrations. However, the outcome would be similar: a lower affinity rather than a lower maximum growth rate as defense costs promotes coexistence and destabilizes the dynamics because it allows for temporally high growth rates of the defended prey at resource peaks.

In the context of plant communities, there is an ongoing debate on the costs of defenses against herbivory. Several studies indicated that there is often no interspecific trade-off between defense and competitiveness as a higher resource supply adversely affected defended plants (Lind et al., 2013; Viola et al., 2010). In fact, Lind et al. (2013) demonstrated that defended plants are commonly the better competitor when resources are depleted but perform less well at high resource concentrations. Such multidimensional trade-offs may be included in future studies considering specific prey communities and their cost type/s of defense.

The coexistence of defended and undefended prey types critically depends on the relative importance of bottom-up and top-down control, that is, the enrichment level of the system (Bohannan & Lenski, 2000; Leibold, 1996; Proulx & Mazumder, 1998). Higher enrichment levels promote the defended prey as its disadvantage regarding resource competition gets less important relative to its advantage of being defended against predation. Thus, our insights on how the competitive exclusion of an undefended prey by an intermediately defended prey is prevented in case of post-attack defense may prevail more in systems with an intermediate or high resource supply (Figure 5a). A high system productivity reduces also the potential extinction risk of the defended prey if the defense costs arise from a high half-saturation costs where resource peaks permit temporally high growth rates of the defended prey (Figure 5b). Hence, we conclude that the current trend of anthropogenic eutrophication of ecosystems enhances the necessity to discriminate between different defense mechanisms and their associated costs.

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CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTION

EE had the principal idea; EE and UG designed the study; EE did the mathematical and numerical analyses and wrote the manuscript on which UG commented.

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