Predator coexistence through emergent fitness equalization

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Abstract

The competitive exclusion principle is one of the oldest ideas in ecology, and states that without additional self-limitation two predators cannot coexist on a single prey. The search for mechanisms allowing coexistence despite this has identified niche differentiation between predators as crucial: without this, coexistence requires the predators to have exactly the same $R^*$ values, which is considered impossible. However, this reasoning misses a critical point: predators’ $R^*$ values are not static properties, but affected by defensive traits of their prey, which in turn can adapt in response to changes in predator densities. Here I show that this feedback between defense and predator dynamics enables stable predator coexistence without ecological niche differentiation. Instead, the mechanism driving coexistence is that prey adaptation causes defense to converge to the value where both predators have equal $R^*$ values (“fitness equalization”). This result is highly general, independent of specific model details, and applies to both rapid defense evolution and inducible defenses. It demonstrates the importance of considering long-standing ecological questions from an eco-evolutionary viewpoint, and showcases how the effects of adaptation can cascade through communities, driving diversity on higher trophic levels. These insights offer an important new perspective on coexistence theory.

Keywords: coexistence; competition; competitive exclusion; defense; emergent facilitation; predator-prey dynamics; eco-evolutionary feedbacks
Introduction

The competitive exclusion principle is one of the oldest ideas in community ecology, and states that two predators cannot coexist on a single prey (Gause 1934, Hardin 1960). Each predator suppresses prey density to the level where it is just barely able to persist (the $R^*$ principle, Tilman 1982), which prevents coexistence: whichever predator has the lower value for $R^*$ can suppress the prey to a density where its competitor can no longer persist, thereby driving it extinct. As a consequence, coexistence of two predators limited solely by the same prey would require them to have exactly the same $R^*$ value, which would require a coincidence of such magnitude that it is generally held to be impossible.

This mathematically rock-solid result stands in stark contrast with the rich diversity of many natural communities, and reconciling this contradiction has inspired a long search for mechanisms that may enable coexistence (Chesson 2000). This has uncovered a wide range of possibilities, falling into several broad categories. First, there are mechanisms directly causing a disadvantage to the more common competitor, such as self-limitation (Levin 1970) or frequency-dependent predation by a top predator (Huntly 1991). Second, there are mechanisms that operate by niche partitioning within a single prey species, so that a single prey essentially becomes multiple resources and can thus sustain multiple predators. For example, when the prey population consists of different prey phenotypes, and predators differ in which phenotypes they preferentially feed on, stable coexistence may be found (Schreiber et al. 2018). Similarly, predators feeding on different life stages of a stage-structured prey can coexist (De Roos et al. 2008) if at least one of the life stages is strongly resource-limited: its predator then causes competitive release that indirectly enables the competing predator to persist. Finally, a third class of mechanisms relies on temporal or spatial variation in prey density, which must be coupled with differences between the predators in how they cope with such variability (Armstrong and McGehee 1980, Chesson and Warner 1981, Chesson 1994).

One key feature connects all mechanisms outlined above: each predator species must suppress its own growth more than the growth of its competitor. This can be achieved by direct negative density-dependence, as would result from e.g. self-limitation (Levin 1970). However, most commonly it is the result of some form of ecological differentiation allowing the two predators to occupy at least partly separate niches, thereby reducing interspecific competition relative to intraspecific competition. This gives an advantage to any competitor falling to low
density, so that it will have a positive per capita growth rate and can recover (a “stabilizing mechanism”, Chesson 2000). Such ecological differences are held to be crucial for coexistence, which has led to the statement that the question of stable species coexistence is largely the question of the right sorts of ecological distinctions for the given circumstances (Chesson 2000).

However, there is an alternative explanation for coexistence which has not received nearly as much attention: predators could coexist, not because they are different, but because they are the same. In other words, two predators may coexist at a stable equilibrium because they do, in fact, have exactly equal $R^*$ values. The importance of mechanisms that reduce differences in $R^*$ values (“equalizing mechanisms”, Chesson 2000) is widely recognized, but equality of $R^*$ values is not accepted as a possible explanation for coexistence, for two important reasons. First, while e.g. adaptation of the competing predators can make their $R^*$ values more equal (Lankau 2011, Chen et al. 2018), it is highly unlikely that it will reduce the difference to exactly zero, which would be required for coexistence. Second, even if predator adaptation did cause exact equalization of the predators’ $R^*$ values, coexistence would still only be neutrally stable at best, and stochastic fluctuations will eventually drive one of the two competitors extinct. In short, equalizing mechanisms can only delay competitive exclusion, not prevent it (Chesson 2000).

These issues, while absolutely valid, are not as insurmountable as they would appear. When searching for a mechanism that would operate through generating equality in the predators’ $R^*$ values, we only have to be careful that the mechanism we postulate for coexistence addresses them. The first requirement is therefore that such a mechanism must reduce the differences in $R^*$ values to zero: it must cause the system to converge towards the equal-$R^*$ state, and once achieved, the system must stay there. Any perturbation or displacement away from the equal-$R^*$ state must cause a feedback that drives it back. Second, such a mechanism must be stabilizing as well as equalizing: it must protect a predator falling to low density from extinction by changing the system in such a way that it becomes favored over its competitor. Ideally, we are searching for a mechanism in which these two properties are linked, so that achieving one will automatically also achieve the other.

I show here that prey adaptation can function as a mechanism fulfilling both criteria, and can enable stable coexistence of two predators. Defensive traits can adapt rapidly to changing predation pressure, either through rapid evolution (Yoshida et al. 2003, Frickel et al. 2017) or inducible defenses (Tollrian and Harvell 1999). As such traits affect how well predators can capture their prey, they affect the predators’ $R^*$ values; thus, defense adaptation changes the $R^*$
values. If it changes them in such a way that they become equal, this can enable coexistence of the predators by a mechanism I call “emergent fitness equalization”.

To demonstrate that this mechanism can work, I extend two one-prey two-predator models (the Lotka-Volterra and Rosenzweig-MacArthur models; Lotka 1925, Volterra 1928, Rosenzweig and MacArthur 1963) to include a continuous defensive trait in the prey. This trait either reduces predation by both predators, but is not equally effective against both of them (unidirectional defense; see Abrams 2000) or confers defense against one predator while increasing vulnerability to the second (bidirectional defense, Abrams 2000). Both defense scenarios enable the stable coexistence of the two predators for a broad parameter range. A necessary condition is that there must exist a level of defense where the predators have equal $R^*$ values, but this is not a sufficient condition: coexistence requires that defense converges exactly to this level where the $R^*$ values are equal. I demonstrate there is a critical role for the costs of defense relative to its benefits, which should not be too high (in both defense scenarios) or too low (only in the unidirectional scenario). These conditions can be mathematically proven and intuitively understood, and are highly general: they depend neither on the model investigated, nor on the specific functional forms by which the defensive trait affects the prey or the predators.

Thus, I show that at least one mechanism exists that enables coexistence through emergent fitness equalization. This novel result highlights the importance of the eco-evolutionary perspective on classic ecological questions such as competitive exclusion, which are too often still viewed from a purely ecological viewpoint.

Methods

A generic two-predator model is described by the following equations:

\[ \frac{dx}{dt} = (f - g_1 y_1 - g_2 y_2) x \]
\[ \frac{dy_i}{dt} = (e_i g_i x - d_i) y_i \]  

(1)

where $x$ is prey density and $y_1$ and $y_2$ are the densities of the two predators. $f$ and $g_i$ are general functions describing the prey growth rate and predators’ feeding rates, respectively; further, $e_i$ and $d_i$ refer to the predators’ conversion efficiencies and mortality rates. In this model, competitive exclusion occurs when the two predators have the same functional response, because
the coexistence equilibrium depends on the following condition being true (see Appendix S1: Section S1 for derivation):

\[ \frac{d_1}{e_1 g_1} = \frac{d_2}{e_2 g_2} \]  

(2)

The left-hand and right-hand terms are the $R^*$ values of predator 1 and predator 2, respectively. These must be exactly equal, otherwise the predator with the lower $R^*$ value will outcompete the other. A difference in $R^*$ values represents fitness differences (Chesson 2000); I will therefore refer to predators’ “fitness” throughout this manuscript, where higher fitness corresponds to a lower $R^*$ value, and “fitness equality” represents the two predators having equal $R^*$ values.

It should be noted here that, even if the condition in eq. (2) is met, coexistence is still only neutrally stable in the absence of a stabilizing mechanism. Defense adaptation in the prey (see below) will be the potential stabilizing mechanism in this study.

Specific models

I investigate two predator-prey models that are specific versions of the model in eq. (1). The Lotka-Volterra model is the simplest representation of predator-prey dynamics, where prey grow exponentially and both predators have a linear functional response:

\[ \frac{dx}{dt} = (r - a_1 y_1 - a_2 y_2) x \]

\[ \frac{dy_i}{dt} = (e_i a_i x - d_i) y_i \]  

(3)

where $r$ is the prey intrinsic growth rate and $a_i$ are the predators’ attack rates. I investigate this model as it is simple enough to be analytically tractable even after defense dynamics are added (see below), and mathematical proof for the existence and stability of the coexistence equilibrium can be derived (Appendix S1: Sections S2 and S3). However, as its simplicity renders it biologically unrealistic, I also investigate the commonly used Rosenzweig-MacArthur model:

\[ \frac{dx}{dt} = \left( r \left(1 - \frac{x}{K}\right) - \frac{a_1 y_1}{1 + a_1 h x} - \frac{a_2 y_2}{1 + a_2 h x} \right) x \]

\[ \frac{dy_i}{dt} = \left( \frac{e_i a_i x}{1 + a_i h x} - d_i \right) y_i \]  

(4)
Exponential growth in the prey is replaced with logistic growth, with $K$ being the carrying capacity; and the predators have a Holling type II functional response, with $h_i$ representing the handling times of the predators.

**Defense**

I extend the models in (3) and (4) by assuming the prey has a certain level of defense, $u$, which affects the predators’ attack rates but comes at the cost of a lower growth rate (Herms and Mattson 1992, Loose and Dawidowicz 1994, Kraaijeveld and Godfray 1997). This defense trait is assumed to be a quantitative, continuous trait, which can adapt (through evolution or phenotypic plasticity) to optimally balance the conflicting needs of growth and defense. Following the framework of adaptive dynamics (Abrams 2001), the direction and speed of trait changes are determined by the fitness gradient:

$$
\frac{du}{dt} = G \frac{\partial w_x}{\partial u}
$$

where $w_x$ represents the prey per capita net growth rate and $G$ determines the speed of trait changes relative to ecological dynamics. Even under contemporary (“rapid”) evolution, trait changes are still generally slower than population dynamics (DeLong et al. 2016); however, the adaptive dynamics approach also represents trait changes driven by phenotypic plasticity (Yamamichi et al. 2019), which are generally expected to be faster than evolutionary changes. $G = 0.02$ was chosen as the standard value (see Table 1 for all parameters and values used), but I confirm that changing the speed of adaptation does not affect the equilibrium location or stability (Appendix S1: Sections S2 and S3), although it of course affects how rapidly the equilibrium is reached.

The location and stability of the equilibrium can be mathematically derived without specifying the functions for $r$, $a_1$ and $a_2$ (see Appendix S1: Sections S2.2 and S3.2), confirming that the results I obtain here do not depend on the specific forms chosen. However, for the main results I use the following functions:

$$
\begin{align*}
    r &= r_0 \left(1 - c \cdot u^2\right) \\
    a_i &= a_0 \left(1 - \theta_i (u - v)\right)
\end{align*}
$$

where $r_0$ is the maximum prey growth rate (achieved when $u = 0$), and $c$ is the costliness of defense; the quadratic function generates accelerating costs for increasing defense, which causes
the defense trait to be under stabilizing selection. This is an important requirement for coexistence (see Appendix S1: Section S3.2).

The attack rates $a_i$ are characterized by the three parameters $a_0$, $\theta_i$, and $v$ (Fig. 1). Here $\theta_i$ denotes the effectiveness of defense against each predator (i.e. the slope of the lines in Fig. 1); $v$ denotes the value of $u$ where the lines for $a_1$ and $a_2$ cross; and $a_0$ is the attack rate at this crossing point. The existence of such a crossing point is a strict requirement for coexistence driven by the mechanism I investigate here, as otherwise one predator would always achieve higher fitness than the other. However, it is not an unrealistic assumption, and can easily be accommodated by both unidirectional and bidirectional defense traits (Fig. 1) (Abrams 2000).

Unidirectional defense means that both predators suffer negative effects from increased defense. Here a crossing point exists when defense is more effective against one of the predators (Fig. 1a). For example, as many predators are gape-limited, a larger prey body size is a strong defensive trait against small predators, but is less effective against larger ones (Scharf et al. 2000). Similarly, faster running or swimming speed is effective for escaping predators hunting by active pursuit, but does little against ambush predators that aim to strike before their prey has a chance to run (Kiørboe et al. 2009, Bro-Jørgensen 2013); accordingly, prey evolve greater running speeds when they are more at risk from pursuit predators (Bro-Jørgensen 2013).

Bidirectional defense means that the predators respond to an increase in defense in opposite directions: while the attack rate of one predator declines, the other increases (Fig. 1b). For example, copepod migration to deeper waters allows them to escape fish predation, but makes them vulnerable to predation by Chaoboros larvae (Neill 1990); biofilm-forming bacteria can attach to surfaces to avoid suspension-feeding protozoans, but then become available to surface-grazers like amoebae (Seiler et al. 2017). A morphological example is shell morphology in snails: elongated (but weaker) snail shells protect against predators that attack through shell entry, but increase vulnerability to predators that crush shells (DeWitt et al. 2000, Bourdeau 2009).

In the analysis here I will assume that defense is always most effective against predator 1 (i.e. $\theta_1 > \theta_2$); in the unidirectional case both $\theta_1$ and $\theta_2$ have positive values (Fig. 1a), while in the bidirectional case, $\theta_2$ is negative (Fig. 1b).

Simulations

Numerical analyses were performed using Wolfram Mathematica 10.0. For the bifurcation plots (Fig. 2), simulations were run for 50,000 time steps, after which a time series was generated.
of the last 2,000 time steps with a temporal resolution of 0.01. The maxima and minima of these
time series were recorded. For the defense equilibria (Fig. 3, Fig. S6 in Appendix S1) and the
contour plots (Fig. 4, Figs. S4 and S5 in Appendix S1), analytical expressions of the equilibrium
densities $y_1^*$ and $y_2^*$ were derived, which were then evaluated numerically over the parameter
ranges chosen.

**Results**

To investigate coexistence I start with a mathematical analysis of the Lotka-Volterra
model. For mathematical convenience, I assume that the predators have equal conversion
efficiencies and mortality rates ($e_1 = e_2 = e$ and $d_1 = d_2 = d$), but the results by no means depend on
this assumption (a full analysis of the general case can be found in Appendix S1: Section S2). This
assumption means that the coexistence condition in eq. (2) simplifies to $a_1 = a_2$, which means that
to enable coexistence, the equilibrium value of defense must be $u^* = v$ (Fig. 1; see eq. (6)). It can
be mathematically shown (Appendix S1: Section S2) that the existence of a crossing point is by
itself not sufficient for coexistence. The costliness of defense $c$ plays a vital role. Coexistence is
only possible when

$$
\frac{\theta_2}{v(2 + \theta_2 v)} < c < \frac{\theta_1}{v(2 + \theta_1 v)}
$$

That is, the costliness of defense must not be too high or too low; and the upper and lower
boundaries are determined by the predators’ susceptibilities to defense. The more dissimilar the
values for $\theta_1$ and $\theta_2$ are, the broader the range under which the predators can coexist. For the
standard parameter values (see Table 1), these coexistence boundaries are $0.8 < c < 2.22$ for the
unidirectional scenario, and $c < 2.22$ for the bidirectional scenario. Within these boundaries, both
predators have positive equilibrium densities, and the coexistence equilibrium can be proven to be
stable (Appendix S1: Sections S2 and S3).

The results of this mathematical analysis are confirmed by numerical simulations of the
Lotka-Volterra model (Fig. 2a-b). If $c$ is within the coexistence boundaries, the equilibrium value
for defense is at $u^* = v = 0.5$ (Fig. 2a-b, light blue points). The equilibrium prey density $x^*$ (dark
blue points) also remains constant over this range ($x^* = d/ea_0 = 0.2$; eq. (2)). Finally, and most
importantly, both predators have positive density (Fig. 2a-b, red and orange points) and coexist at
a stable equilibrium, where oscillations are quickly dampened to a stationary state (Appendix S1: Fig. S2).

With increasing costliness of defense, the relative densities of the two predators shift: predator 1 increases, while predator 2 declines (Fig. 2a-b). Consequently, if defense is too costly, predator 2 goes extinct; defense then converges to a different equilibrium value $u_1^*$, its optimal strategy when facing only predator 1 (see Appendix S1: Section S5). Conversely, predator 1 goes extinct if the costliness is too low, but only in the unidirectional scenario (Fig. 2a), and defense converges to its optimal strategy $u_2^*$ when defending only against predator 2. This optimal value increases rapidly as the costliness declines further, until it reaches the point where the attack rate of predator 2 becomes zero (Appendix S1: Section S5). At this point both predators go extinct, and the prey, now facing no mortality at all, grows exponentially to infinite abundance; there is no longer an equilibrium (Fig. 2a, $c < 0.44$).

Due to this lack of prey self-limitation, the Lotka-Volterra model is generally considered highly unrealistic. However, the same results were found for the Rosenzweig-MacArthur model (Fig. 2c-f), which does account for self-limitation as well as handling limitation in the predators. When the predators’ handling times are short, the equilibria are stable (Fig. 2c-d); with longer handling times, sustained predator-prey cycles can occur for part of the range (Fig. 2e-f), as is typical for this model. However, the presence of cycles has no impact on coexistence: the predators can coexist on a limit cycle, rather than a stable equilibrium, as long as the costliness remains within the coexistence boundaries (Fig. 2f).

The locations of the coexistence boundaries can be understood by how the prey would defend against each of the two predators in isolation. In a one-predator context, the equilibrium level of defense ($u_1^*, u_2^*$) optimally balances the costs and benefits to the prey. Thus, $u_1^* > u_2^*$, as defense is more beneficial against predator 1; and both $u_1^*$ and $u_2^*$ decrease as the costliness increases (Fig. 3a; derivation in Appendix S1: Section S5). The coexistence boundaries are located where $u_1^*$ and $u_2^*$ cross the line where $u^* = v$ (Fig. 3). In the bidirectional scenario this means that the lower boundary is absent: increased defense makes the prey more vulnerable to predator 2, so the equilibrium defense against predator 2 is always $u_2^* = 0$ (Fig. 3b).

Between the coexistence boundaries, $u_1^* > v$ and $u_2^* < v$, which drives the feedback between defense and predator densities that enables coexistence. If predator 2 is low, the prey is effectively only facing predator 1, and its defense will increase towards $u_1^*$; this gives the advantage to predator 2 ($a_2 > a_1$, see Fig. 1) and allows it to increase. The reverse happens if
predator 1 is at low density. Thus, neither predator can maintain the competitive edge for long; in the long run, defense will converge to the level where the attack rates are equal.

Thus, the range for coexistence is determined by how far apart the crossing points of the single-species curves ($u_1^*$ and $u_2^*$) with $u^* = v$ are (Fig. 3). The more dissimilar the impact of defense on the two predators (i.e. the more dissimilar $\theta_1$ and $\theta_2$ are), the broader the range of coexistence; it is broadest in the bidirectional case, when $\theta_2 \leq 0$ (Fig. 4a). The boundaries can be shifted to the left or the right by changes in other parameters, but the general pattern always holds. For example, increasing the predators’ handling times shifts the coexistence boundaries to lower values of $c$ (Fig. 4b): the predation rates are lower with longer handling times, so the benefit of defense is smaller and the single-species curves in Fig. 3 shift to the left. Such shifts are also found when the predators’ mortality rates or conversion efficiencies are varied, whereas changing the prey maximum growth rate, the carrying capacity, or the equilibrium attack rate does not affect the coexistence boundaries (Appendix S1: Figs. S4 and S5).

Interestingly, for a large part of the coexistence range there is not only coexistence, but emergent facilitation in both defense scenarios: if $c \leq 2.04$, predator 1 is unable to survive by itself, as the prey would increase its defense high enough to drive predator 1 extinct (Fig. 3; Appendix S1: Section S5). However, the presence of predator 2 enables it to persist: lower defense becomes the better strategy when predator 1 falls to low density, allowing it to recover and persist over a much broader parameter range.

Discussion

In the absence of self-limitation (Levin 1970) or some form of niche partitioning (Chesson 2000), two competing predators can only coexist on a single prey if their $R^*$ values are exactly equal (Tilman 1982). Ever since the first formulation of the competitive exclusion principle (Hardin 1960) this scenario has been considered self-evidently impossible for any natural system. While it is certainly true that two predators will not coincidentally have exactly equal $R^*$ values, it is critical to recognize that the $R^*$ values are far from random. Defensive traits are vital for survival and are often under strong selective pressure, and can thus change rapidly via evolution or phenotypic plasticity when predation pressure changes (e.g. Tollrian and Harvell 1999, Yoshida et al. 2003, Frickel et al. 2017). Here I show that prey adaptation can enable predator coexistence by causing emergence of fitness equality between the predators.
A strict condition for this result is that the defense trait is not equally effective against both predators, so that the two predators exert opposing selective pressures. In nature prey generally face multiple predators with different sizes, morphologies or hunting styles; traits that defend against one predator are often less effective against others (unidirectional traits) or even counterproductive (bidirectional traits) (Scharf et al. 2000, Sih et al. 1998, Turner et al. 2000, Relyea 2003). That different predators can push a defense trait in opposite directions is obvious in the case of bidirectional traits, where defending against one predator directly means becoming more vulnerable to the other. However, the same holds for unidirectional traits, which defend against both predators but typically come at a metabolic or resource allocation cost (Herms and Mattson 1992, Loose and Dawidowicz 1994, Kraaijeveld and Godfray 1997): defense should be lower when it offers less benefit (Bro-Jørgensen 2013, Hettyey et al. 2011). Thus, for both unidirectional and bidirectional traits, the presence of two different predators can result in an eco-evolutionary feedback (Fussmann et al. 2007): the composition of the predator guild, i.e. which predators are present and in what numbers, determines whether the overall selective pressure pushes for higher or lower defense; in turn, the current level of defense determines which of the predators has the advantage. This feedback loop is critical for stabilizing coexistence, as this is what causes defense adaptation to act as both an equalizing and a stabilizing mechanism (Chesson 2000). Whenever a predator falls to low density, the prey adapts to disfavor its competitor, thereby preventing extinction. Eventually, when the defense trait is under stabilizing selection, it will converge to the level where the predators have equal fitness, thereby enabling coexistence.

This mechanism is highly general, independent of details such as the predators’ functional responses, the exact way that defense affects the predators, or whether defense traits are unidirectional or bidirectional. It is also independent of whether adaptation occurs through evolution or phenotypic plasticity, as they can both be described by the adaptive dynamics approach used here (Abrams 2001, Yamamichi et al. 2019). The generality of the mechanism makes it widely applicable to coexistence of predators, herbivores, parasites, and any other consumer-resource system with adapting prey.

For a substantial part of the parameter range, I found that coexistence was enabled via emergent facilitation, similar to a previous study on predators feeding on different life stages of their prey (De Roos et al. 2008). When the cost of defense is too low, the predator that is more affected by defense cannot persist by itself. Its persistence is enabled by the presence of a second predator, which prevents the prey’s defense becoming too strong. Such indirect predator effects
have been shown experimentally in inducible defenses, where the vulnerability to one predator can be increased by the presence of a second one (Sih et al. 1998, Soluk 1993, Hoverman and Relyea 2007). However, whether this could enable the persistence of a predator that might go extinct by itself has not been studied.

While the speed of adaptation does not affect the location or stability of the coexistence equilibrium, faster adaptation will likely promote coexistence by shortening transient periods in which one of the predators is at a clear disadvantage. Evolution and phenotypic plasticity may thus not be entirely interchangeable: inducible defenses can respond rapidly to changing predation pressure, often within the same generation (Tollrian and Harvell 1999), whereas a trait change through rapid evolution by necessity requires multiple generations of selection. Thus, inducible defenses will probably be most effective at enabling coexistence. When the prey adapts through evolution, coexistence will depend critically on whether the prey can evolve rapidly enough. Since this is a form of evolutionary rescue, if indirectly (Yamamichi and Miner 2015), the same conditions should apply: coexistence is favored by high initial standing genetic variation (corresponding to fast evolution), small initial fitness differences, and high initial population size of the endangered predator (Bell 2017).

As stated above, stabilizing selection on the defense trait is a requirement for emergent fitness equalization; thus, the growth-defense trade-off must favor intermediate trait values over the extremes. This can be the result of diminishing benefits or increasing costs. Although both are easy to imagine (e.g. increased running or swimming speed will become increasingly costly as higher speeds increase drag), very little is known on the shape of the growth-defense trade-off in empirical systems. However, one line of investigation from which the prevalence of stabilizing selection can be inferred is the expression of inducible defenses under gradients of predation risk. A defense trait under disruptive selection should show a step-function response: individuals should either express no defense, or high defense, with nothing in between. A trait under stabilizing selection, on the other hand, should show a graded response where individuals’ expression of defense is fine-tuned to the current cost/benefit balance. Numerous studies have shown such a graded response to increasing predation risk (e.g. Loose and Dawidowicz 1994, Wiackowski and Staronska 1999, Relyea 2004, Schoeppner and Relyea 2008, Hettyey et al. 2011), suggesting that stabilizing selection is a reasonable assumption for many defense traits.

While both rapid evolution and phenotypic plasticity have been recognized as mechanisms promoting competitive coexistence, studies on this topic have focused almost entirely on
adaptation of the competing species themselves (Lankau 2011, Turcotte and Levine 2016). While this can reduce fitness differences and thereby slow down competitive exclusion, it cannot prevent exclusion in the long run (Chen et al. 2018). In contrast, the role of adaptation on a different trophic level – the competitors’ prey or predators – has not received the attention it deserves. This absence is striking, since the impact of prey adaptation on predator-prey dynamics (Yoshida et al. 2003, Becks et al. 2012) and even community structure and ecosystem functioning (Post et al. 2008, Palkovacs et al. 2009) is well-known in the field of eco-evolutionary dynamics. That such community effects can extend to promoting predator coexistence was recently demonstrated in an experimental predator-prey system, where algal prey were faced with viruses and rotifer predators (Frickel et al. 2017). While initially the virus rapidly reduced the algae to very low densities, resulting in the extinction of the rotifers, the two enemies coexisted after the algae evolved defense against the virus. Although the prediction of fitness equalization remains to be explicitly tested experimentally, this study provides a critical confirmation of the idea that rapid prey adaptation can drive coexistence of multiple predators.

Even though the role of prey adaptation in enabling predator coexistence has been underappreciated, the concept itself is not entirely new. Bengfort et al. (2017) showed coexistence of two predators on a single prey evolving along a bidirectional trait axis, but did not unravel the underlying mechanism as coexistence was not the focus of that study. Schreiber et al. (2018) did explicitly study the potential for prey evolution to enable predator coexistence, but under a very different scenario: evolution was modelled as a change in the frequencies of discrete phenotypes, where each phenotype was defended against one predator but vulnerable to the other. That predator coexistence is possible in such a scenario is not entirely surprising, as the prey species is divided into multiple resources, which can then support multiple predators via classic niche partitioning (Chesson 2000). The mechanism I propose here is fundamentally different from that of Schreiber et al. (2018), and I derive an entirely new set of conditions for coexistence. There are critical roles for the costs of defense, and for the dissimilarity in how the two predators are affected by defense. Investigations into eco-evolutionary dynamics have recently started moving beyond simple predator-prey pairs to the dynamics of prey faced with multiple enemies (Friman and Buckling 2014, Frickel et al. 2017). Such systems have already provided important first results (Frickel et al. 2017) and form an ideal opportunity for further experimental testing of predictions on when coexistence through emergent fitness equalization should be found.
Outlook: future directions

The processes governing species diversity across trophic levels are not well understood, but it is commonly argued that diversity begets diversity (Janz et al. 2006): an increasing number of prey species results in an increasing number of ways to exploit them, leading to increased potential for predator diversity. While this argument has only been made for prey species diversity, diversity in prey traits – particularly those traits governing how vulnerable they are to various predators – should be equally important. In this study I modelled prey adaptation with a single defensive trait, but prey may possess many traits that affect their predation risk. Several studies on induced defenses indeed showed a combination of morphological and behavioral traits working in concert (Relyea 2003, Van Buskirk 2001), and this is likely representative for most prey. Increasing the diversity of defensive traits in a single prey may promote predator diversity, analogous to increased species diversity, by generating a higher number of feedbacks between defensive traits and predator densities. What role this type of intra-specific trait diversity might play in maintaining predator diversity is an open question for future theoretical and experimental investigation.

Increasing the number of eco-evolutionary feedbacks can also be achieved through accounting for predator-prey coevolution, rather than prey evolution alone; but the effects of this are more difficult to predict. Predator adaptation may act as an equalizing mechanism, thereby promoting coexistence (Lankau 2011); or it may counteract the effects of prey adaptation and hinder coexistence. A modelling study using a multi-prey multi-predator framework (Klauschies et al. 2016) found “supersaturated” predator coexistence: a single rapidly-evolving prey supported two predators with very distinct offense strategies. At the very least, this indicates that coexistence is not impossible under predator-prey coevolution; moreover, prey evolution may have been the critical part of this scenario. But to what extent these results can be generalized is not clear at this point.

Finally, fitness equality has always been disregarded as a possible explanation for competitive coexistence, but I demonstrate here that this dismissal is undeserved: the simple, omnipresent mechanism of prey defense adaptation can cause such equality to emerge. It is possible, perhaps even likely, that more mechanisms for emergent fitness equalization exist, but the dismissal of this scenario has left this avenue entirely unexplored. Ecologists have long
focused on mechanisms allowing consumers to be different enough for coexistence (Chesson 2000); it is time to start looking for mechanisms allowing them to be the same.

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### Tables

**Table 1. Model parameters and standard values used in numerical simulations**

| Parameter | Description                                                                 | Standard value         |
|-----------|-----------------------------------------------------------------------------|------------------------|
| $r_0$     | Maximum prey growth rate                                                     | 0.5                    |
| $e_1, e_2$| Predator-prey conversion efficiencies                                        | 0.5                    |
| $d_1, d_2$| Predator mortality rates                                                     | 0.1                    |
| $\nu$     | Level of defense where predators have equal attack rates                     | 0.5                    |
| $\alpha_0$| Attack rate at $u = \nu$                                                     | 1.0                    |
| $\theta_1$| Sensitivity of predator 1 to defense                                         | 5.0                    |
| $\theta_2$| Sensitivity of predator 2 to defense                                         | 1.0 (unidirectional)   |
|           |                                                                             | -1.0 (bidirectional)   |
| $c$       | Costliness of defense                                                        | varied                 |
| $K$       | Prey carrying capacity                                                       | 1.0                    |
| $h_1, h_2$| Handling time                                                               | 0.1, 1.0               |
Figure captions

Figure 1. Schematic representation of how the attack rates depend on defense $u$. (a) The attack rates $a_1$ and $a_2$ both decline with an increase in defense (unidirectional scenario), with $a_1$ declining more rapidly; (b) $a_1$ declines with an increase in defense, but $a_2$ increases (bidirectional scenario). In both defense scenarios, the attack rates are equal when $u = v$. See Methods (“Defense”) and eq. (6) for details on the meaning of the parameters.

Figure 2. Bifurcation plots of the Lotka-Volterra model (a-b) and the Rosenzweig-MacArthur model (c-f). Points represent the maxima and minima of the prey, predator and defense dynamics in the last 5000 steps of the simulated timeseries (see Methods); vertical dashed lines indicate the coexistence boundaries (see eq. (7)). In (c) and (d), $h_1 = h_2 = 0.1$; in (e) and (f), $h_1 = h_2 = 1$. See Table 1 for other parameter values.

Figure 3. Equilibrium levels of defense in the single-predator and two-predator scenarios. Red line: equilibrium defense $u_1^*$ in the absence of predator 2; orange line: equilibrium defense $u_2^*$ in the absence of predator 1 (see Appendix S1: Section S5 for derivation of $u_1^*$ and $u_2^*$). Note that the line for $u_1^*$ starts at $c = 2.04$; predator 1 goes extinct when $c \leq 2.04$ in the single-predator scenario (see Appendix S1: Section S5). Light blue line: $u^* = v = 0.5$, the defense value enabling coexistence. Solid lines indicate the equilibrium level of defense found in the simulations (cf. Fig. 2a-b, light blue points). Dashed vertical lines indicate the coexistence boundaries (cf. the boundaries in Fig. 2a-b and eq. (7)).

Figure 4. Coexistence regions in the Rosenzweig-MacArthur model. Coexistence is found in the colored regions; colors indicate the contribution of predator 1 to the total predator density at equilibrium, $y_1^*/(y_1^* + y_2^*)$ (see scale on the right). In the black regions, one of the two predators goes extinct. In (a), $h_1 = h_2 = 1$; in (b), $\theta_2 = 1$ (unidirectional defense). For all other parameter values, see Table 1.
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