Trait–fitness relationships determine how trade-off shapes affect species coexistence

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Abstract. Trade-offs between functional traits are ubiquitous in nature and can promote species coexistence depending on their shape. Classic theory predicts that convex trade-offs facilitate coexistence of specialized species with extreme trait values (extreme species) while concave trade-offs promote species with intermediate trait values (intermediate species). We show here that this prediction becomes insufficient when the traits translate non-linearly into fitness which frequently occurs in nature, e.g., an increasing length of spines reduces grazing losses only up to a certain threshold resulting in a saturating or sigmoid trait-fitness function. We present a novel, general approach to evaluate the effect of different trade-off shapes on species coexistence. We compare the trade-off curve to the invasion boundary of an intermediate species invading the two extreme species. At this boundary, the invasion fitness is zero. Thus, it separates trait combinations where invasion is or is not possible. The invasion boundary is calculated based on measurable trait–fitness relationships. If at least one of these relationships is not linear, the invasion boundary becomes non-linear, implying that convex and concave trade-offs not necessarily lead to different coexistence patterns. Therefore, we suggest a new ecological classification of trade-offs into extreme-favoring and intermediate-favoring which differs from a purely mathematical description of their shape. We apply our approach to a well-established model of an empirical predator–prey system with competing prey types facing a trade-off between edibility and half-saturation constant for nutrient uptake. We show that the survival of the intermediate prey depends on the convexity of the trade-off. Overall, our approach provides a general tool to make a priori predictions on the outcome of competition among species facing a common trade-off in dependence of the shape of the trade-off and the shape of the trait–fitness relationships.

Key words: coexistence; competition; fitness; functional traits; invasion boundary; neutrality; predator–prey model; shape; trade-offs.

Introduction

Understanding the mechanisms of species coexistence still poses a major challenge in ecology. Trade-offs between different functional traits provide an essential basis for coexistence by allowing differentiation of ecological strategies through diverging trait values among coexisting species (Tilman 2000). Because species are unable to optimize the values of all their traits at the same time due to physiological, energetic, and genetic constraints, maximizing the value of one trait (e.g., defence against predation) generally implies costs regarding other traits (e.g., growth). Such trade-offs are common, occur for all types of species interactions, and may prevent the occurrence of a "superspecies" performing best under all conditions and outcompeting all others (Kneitel and Chase 2004).

The existence of a trade-off does not necessarily imply that different highly specialized species coexist. As first reported by Levins (1962, 1968), the species composition crucially depend on the shape of the trade-off between the traits. Assuming that fitness increases linearly with higher trait values, convex trade-offs imply that an intermediate value of one trait x comes with high fitness costs regarding the other trait y while the opposite holds for concave trade-offs (Fig. 1a). Accordingly, convex trade-offs which are mathematically defined by a positive second derivative ($\partial^2 y / \partial x^2$) were often called strong while concave trade-offs having a negative second derivative were named weak (Egas et al. 2004, Abrams 2006a, Rueffler et al. 2006). Previous theory commonly predicts that convex trade-offs select for extreme trait combinations (extreme species) while concave trade-offs promote species with intermediate trait values (intermediate species). This was shown for trade-offs of consumers using two different habitats/resources (Egas et al. 2004, Abrams 2006a), host trade-offs between growth rate and resistance against parasitism (Boots and Haraguchi 1999, Bowers and Hodgkinson 2001), trade-offs of pathogens transmitted to two different hosts (Gudelj et al. 2004), and prey trade-offs between reproduction/resource competition and vulnerability to predation
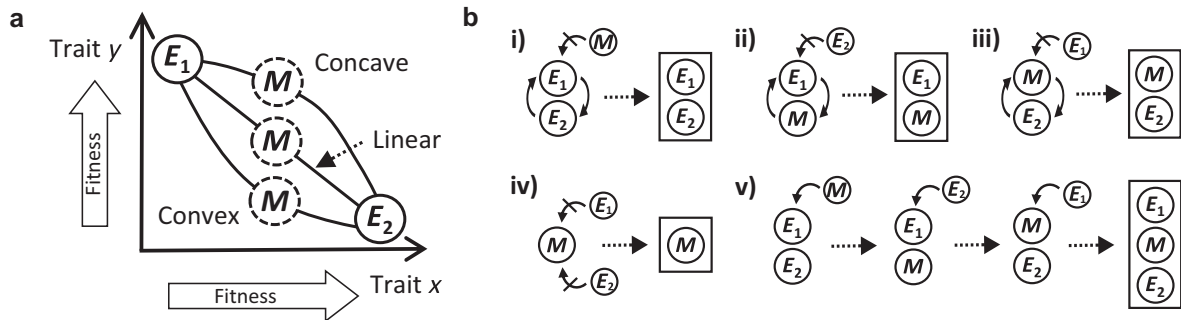
Fig. 1.   (a) Different shapes of a trade-off between trait x and trait y. The trait values of the extreme species E_1 and E_2 are fixed (solid circles) while the trait values of the intermediate species M (dashed circles) depend on the shape of the trade-off. (b) Coexistence analysis based on the invasion criterion. Assuming that the extreme species always coexist in the absence of M and no multi-stability occurs, five possible outcomes exist (i–v) which are illustrated behind the dashed arrows in the boxes. The necessary invasion tests are shown in front of the dashed arrows. Arrows indicate successful invasion paths while struck-through arrows represent impossible invasion paths. Two species coexist if they are mutuallly invasible and if they are non-invasible by the third species (i–iii). Only the intermediate species survives when both extreme species cannot invade it (iv). Coexistence of all three species occurs if each species can invade the others (v) (cf. general approach).

(Day et al. 2002, Abrams 2003, Jones et al. 2009). In some of these studies, "convex" and "concave" were oppositely defined while we refer here to the mathematical definition mentioned before (see Fig. 1a).

Empiricists have made a strong effort to measure trade-off curves (Benkman 1993, Schluter 1995, O'Hara Hines et al. 2004, Jessup and Bohannan 2008) and recently tested Levins' theory with competition experiments (Maharjan et al. 2013, Meyer et al. 2015). However, the consequences of different trade-off curves for the outcome of competition may strongly depend on the considered traits trading off and how they relate to fitness (de Mazancourt and Dieckmann 2004, Rueffler et al. 2004, Bowers et al. 2005, White and Bowers 2005, Hoyle et al. 2008). For specific cases, the prediction may hold that convex trade-offs always favor extreme species while concave trade-offs promote intermediate species. In our paper, we abstract from specific cases and show that this distinction is insufficient when the traits translate non-linearly into fitness. To overcome this problem, we present a novel, general approach to evaluate consequences of different trade-off shapes for species coexistence based on measurable trait–fitness relationships. In order to do this, we calculate the invasion boundary of an intermediate species invading the two extreme species and compare the trade-off curve to it. This allows us to predict whether the extreme species will dominate for a given trade-off curve (invasion impossible) or whether an intermediate species will be part of the community (invasion possible). In addition, we evaluate when an intermediate species may stably coexist with one extreme species or both of them based on invasion criteria (Fig. 1b). Our approach is appropriate for systems without multi-stability implying that a species which is unable to invade can also not persist at high densities. Our results reveal that convex and concave trade-offs do often not imply different coexistence scenarios depending on the fitness functions. Therefore, we suggest a new classification of trade-offs into extreme-favoring (EF) and intermediate-favoring (MF) trade-offs which differs from a purely mathematical description of their shape. MF trade-offs allow for the invasion of an intermediate species into the extreme species while EF trade-offs do not.

Previous studies often examined trade-off shapes in an evolutionary context with adaptive dynamics where organisms could gradually adapt their trait values and reached maximal fitness due to selection (de Mazancourt and Dieckmann 2004, Rueffler et al. 2004, White and Bowers 2005). Here, we take an ecological perspective and analyse sorting of species (or genotypes) with fixed trait values facing an interspecific (or intraspecific) trade-off. Thus, in contrast to the previously mentioned studies, the considered community does not necessarily has to be evolutionary attainable via local mutations from a monomorphic population but can be assembled, e.g., by immigration. Typically, trade-offs are regarded to be species specific. However, interspecific trade-offs are also common in nature when organisms of different species share similar physiological constraints between functional traits (Tilman et al. 1982, Kneitel and Chase 2004), e.g., based on allometric relationships (Litchman et al. 2007). Mechanistically, there is no difference between competition of species facing an interspecific trade-off and sorting of genotypes of an asexually reproducing species with an intraspecific trade-off (assuming no horizontal gene transfer). In the following, we refer to species while the results are transferable to genotype sorting.

First, we introduce our general framework on how to calculate the shape of invasion boundaries based on given trait–fitness relationships and how to infer consequences of different trade-off shapes from that. We present illustrative cases where the invasion boundary is not linear but convex, concave, or a combination of both. In the second part, we apply the general approach to a well-established model of an empirical predator–prey system with competing prey types facing a trade-off

between edibility (probability of being attacked) and its half-saturation constant for nutrient uptake. We calculated the invasion boundary of an intermediate prey invading a defended extreme prey (low edibiblity) and a competitive extreme prey (low half-saturation constant) which was convex. Consequently, we found the same coexistence pattern for concave and slightly convex trade-offs lying above the invasion boundary. In addition to the analysis of stable coexistence, we considered the duration of co-occurrence in case of competitive exclusion which increased with trade-off curves getting closer to the invasion boundary as expected based on the theory on fitness equality (Hubbell 2001, He et al. 2012).

General Approach

Trait–fitness relationships and the invasion boundary

We consider a general system of three competing species that face an interspecific trade-off between two functional traits x and y: two species with extreme trait values (E_1, E_2) and one intermediate species (M). We assume niche differentiation of E_1 and E_2, i.e., their traits (x_1, y_1 and x_2, y_2) are fixed at the opposite extreme values of the trait range allowing them to stably coexist when M is absent. The aim of this approach is first to detect the invasion boundary of M invading a resident community of E_1 and E_2 (combinations of trait values x_M and y_M where the invasion fitness equals zero). The invasion boundary may be linear, convex, concave or a combination of convex and concave parts. This is described by the second derivative of one trait with respect to the other trait at the invasion boundary, i.e., $\partial y_M^2/\partial x_M^2$. In the following paragraphs, we achieve a general representation of this second derivative based on terms describing how x_M and y_M translate into fitness.

To achieve a criterion for the invasion success of M, we consider its per capita growth rate which is defined as its fitness. The fitness can be written as a function f of its traits x_M and y_M, its population density M and the population densities of the extreme species E_1 and E_2

$$\frac{1}{M}\frac{dM}{dt} = f(x_M, y_M, M, E_1, E_2). \quad (1)$$

For simplicity, we incorporate no further environmental variables, e.g., fluctuating abiotic factors, resource concentration, parasite or predator density, which can be added when considering a specific system. The fitness of M may also depend on the traits of E_1 and E_2. However, to simplify the notation, we drop them out of the function in Eq. 1 as they are fixed at constant values. Furthermore, we call the traits of M simply x and y from now on.

The invasion fitness of M is defined as its long-term mean per capita growth rate at very low densities ($M \approx 0$) in a resident system of E_1 and E_2, i.e.,

$$\left\langle \frac{1}{M}\frac{dM}{dt} \right\rangle = \langle f(x, y, 0, E_1, E_2) \rangle. \quad (2)$$

If the resident community is in a stable equilibrium, the angle brackets indicating the long-term mean can be omitted as the population densities are constant over time. In case of fluctuating densities, the mean is taken over one cycle. At the invasion boudary, $\langle f(x, y, 0, E_1, E_2) \rangle$ is equal to zero. In many cases, the traits affect different fitness components, e.g., growth based on resource consumption and loss due to predation. Therefore, we replace f by two additive functions f_x and f_y where each refers to one fitness component (for non-additive cases see Appendix S1)

$$\langle f_x(x, 0, E_1, E_2) \rangle + \langle f_y(y, 0, E_1, E_2) \rangle = 0 \quad (3)$$

Trade-offs imply that the value of one trait depends on the value of another trait. Thus, y can be expressed as a function of x and Eq. 3 can be rearranged to $\langle f_y(y(x), 0, E_1, E_2) \rangle = -\langle f_x(x, 0, E_1, E_2) \rangle$ while differentiating both sides of this equation with respect to x yields $\partial \langle f_y \rangle / \partial y \ \partial y/\partial x = -\partial \langle f_x \rangle/\partial x$ and thus

$$\frac{\partial y}{\partial x} = -\frac{\partial \langle f_x \rangle/\partial x}{\partial \langle f_y \rangle/\partial y}. \quad (4)$$

For simplicity, the arguments of f_x and f_y are not displayed any more. If $\partial y/\partial x$ is negative the invasion boundary has a negative slope and vice versa. The second derivative of y with respect to x describes the change of the slope of the invasion boundary along the gradient of x

$$\frac{\partial^2 y}{\partial x^2} = \frac{\frac{\partial \langle f_x \rangle}{\partial x}\frac{\partial^2 \langle f_y \rangle}{\partial y^2}\frac{\partial y}{\partial x} - \frac{\partial^2 \langle f_x \rangle}{\partial x^2}\frac{\partial \langle f_y \rangle}{\partial y}}{\left(\frac{\partial \langle f_y \rangle}{\partial y}\right)^2}. \quad (5)$$

The invasion boundary is concave if $\partial^2 y/\partial x^2$ is negative, convex for positive values, and linear when $\partial^2 y/\partial x^2 = 0$. Thus, Eq. 5 provides information about the shape of the invasion boundary. The individual terms of Eq. 5 or at least their signs are typically known or can be measured for specific systems: the signs of $\partial \langle f_x \rangle/\partial x$ and $\partial \langle f_y \rangle/\partial y$ describe whether an increasing trait value leads to a gain or a loss of fitness. The signs of $\partial^2 \langle f_x \rangle/\partial x^2$ and $\partial^2 \langle f_y \rangle/\partial y^2$ indicate whether this change in fitness accelerates or decelerates with increasing trait values.

Fig. 2 summarizes different cases of trait-invasion fitness relationships and the resulting directions and shapes of the invasion boundary based on Eqs. 4 and 5. Case 1 represents the standard case with positive, linear trait–fitness relationships resulting in a linear invasion boundary ($\partial^2 y/\partial x^2 = 0$) with a negative slope ($\partial y/\partial x < 0$). As shown in case 2, the slope can be positive when one of the traits affects the fitness negatively ($\partial \langle f_x \rangle/\partial x < 0$ or $\partial \langle f_y \rangle/\partial y < 0$), e.g., an increasing value of natural mortality reduces fitness.
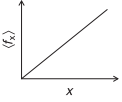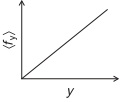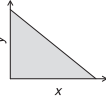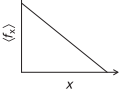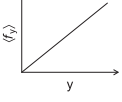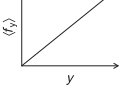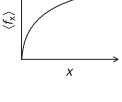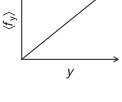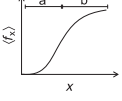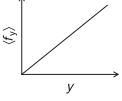
Case	$\langle f_x\rangle$	$\langle f_y\rangle$	$\dfrac{\partial\langle f_x\rangle}{\partial x}$	$\dfrac{\partial\langle f_y\rangle}{\partial y}$	$\dfrac{\partial y}{\partial x}$	$\dfrac{\partial^2\langle f_x\rangle}{\partial x^2}$	$\dfrac{\partial^2\langle f_y\rangle}{\partial y^2}$	$\dfrac{\partial^2 y}{\partial x^2}$	Invasion boundary
1			+	+	−	0	0	0	
2			−	+	+	0	0	0	
3			+	+	−	+	0	−	
4			+	+	−	−	0	+	
5			+	+	−	a) + b) −	0	a) − b) +	
6			−	−	−	0	+	+	

FIG. 2. Invasion boundaries of the intermediate species M resulting from different cases how its traits x and y translate into its additive invasion fitness components $\langle f_x\rangle$ and $\langle f_y\rangle$. The sign of $\partial y/\partial x$ determines the direction of the invasion boundary while its shape depends on the sign of $\partial^2 y/\partial x^2$. The black curve in the last column represents the invasion boundary and gray (white) areas refer to trait combinations where the invasion of M is impossible (possible).
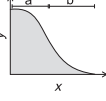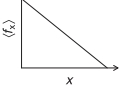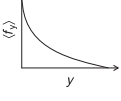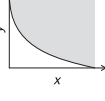
In cases 3–5, we focus on different shapes of the invasion boundary instead of different directions and consider only traits with a positive effect on the invasion fitness, i.e., the slope is always negative. The invasion boundary is concave when one trait has an increasingly higher effect on the invasion fitness with increasing trait values, i.e., $\partial^2\langle f_x\rangle/\partial x^2 > 0$ (case 3). As shown in case 4, it is convex when this effect is decreasingly higher ($\partial^2\langle f_x\rangle/\partial x^2 < 0$). Case 5 reveals that an invasion boundary can consist of convex and concave parts. Such special shapes occur when the range of trait values determines whether the effect of one trait on the invasion fitness is increasingly or decreasingly higher with increasing trait values. A typical example of such a trait is the neck length of giraffes feeding on tree leaves. Below a certain threshold, the leaves are out of reach. Above the threshold, a longer neck increases fitness as they have access to a larger number of leaves. However, once a giraffe's neck is sufficiently long so that most of the leaves are within reach, a further increase in neck length does not lead any more to a higher fitness. The often spheroid shape of tree crowns causes the sigmoid shape of the fitness function.

Case 6 is further evaluated in the example below when we apply this approach to a predator–prey system with a trade-off between prey edibility and its half-saturation constant for nutrient uptake. Higher values of both traits have a negative effect on the invasion fitness which implies again

a negative slope of the invasion boundary but the assignment of areas in the trait space where invasion is possible or not is reversed as low values of both traits are beneficial. Moreover, the shape of the invasion boundary is convex and thus differs from the standard case because the trait y has a non-linear effect on fitness ($\partial^2\langle f_y\rangle/\partial y^2 > 0$).

So far, we have shown cases where only one trait translates non-linearly into fitness. In Appendix S1, we present the resulting invasion boundaries for cases where both traits affect the fitness non-linearly (Appendix S1: Fig. S1). Moreover, we show invasion boundaries for cases where the fitness components f_x and f_y are multiplicative rather than additive as assumed in Eq. 3. Remarkably, even for linear trait–fitness relationships the invasion boundary is non-linear when the fitness components are multiplicative (Appendix S1: Fig. S2). Applying our approach to a general resource competition model with a trade-off between specialization on two different resources (Appendix S2) reveals that the shape of the invasion boundary may depend on whether the residents cycle or are in steady-state which is line with previous results of Abrams (2006a).

Trade-off shapes, invasion boundaries, and coexistence

To assess the effect of different trade-off shapes on coexistence, we compare the trade-off curve to the

calculated invasion boundary. Both curves share the same terminal points, i.e., the trait combinations of the extreme species. Thus, a comparison of their shape allows direct conclusions on coexistence. We classify trade-offs as extreme-favoring (EF) when the invasion of an intermediate species is not possible leading to coexistence of only the extreme species and as intermediate-favoring (MF) if an intermediate species can invade the extreme species and becomes part of the community. We define a trade-off as neutral if it is identical to the invasion boundary. In Fig. 3, we show examples of different trade-off curves and the respective invasion boundary. In the standard case, the invasion boundary is linear, implying that convex trade-offs are EF while concave trade-offs are MF (Fig. 3a). For concave invasion boundaries, EF trade-offs can be convex, linear, and slightly concave while only strongly concave trade-offs are MF (Fig. 3b). The assignment of EF and MF trade-offs can be reversed depending on whether both traits translate positively into fitness (Fig. 3c) or negatively (Fig. 3d). If the trade-off curve or the invasion boundary is a combination of convex and concave parts, the trade-off may be MF and EF depending on the considered trait range (Fig. 3e, f). Thus, depending on the trait combination of the intermediate species, it will be part of the community or not.

Assuming that E_1 and E_2 stably coexist in the absence of M, EF trade-offs always lead to coexistence of the extreme species (Fig. 1b case i) while there are several possibilities of coexistence in case of MF trade-offs where M is part of the community. We use the invasion criterion (Chesson 2000) to test for the different coexistence scenarios. The invasion criterion states that two species stably coexist if each one is able to invade a system dominated by the other resident species (mutual invasibility). We extend this criterion to our three-species system. Assuming no multi-stability, four outcomes of coexistence are possible for MF trade-offs (Fig. 1b): (ii) Coexistence of E_1 and M when E_1+M are mutual invasible and not invasible by E_2, (iii) Coexistence of M and E_2 when $M+E_2$ are mutual invasible and not invasible by E_1, (iv) Survival of only M if M is not invasible by E_1 and E_2, (v) Coexistence of E_1, M and E_2 when E_1+E_2 is invasible by M, E_1+M by E_2 and $M+E_2$ by E_1. The three conditions for coexistence of all three species ensure that each species is able to increase after strong reduction in density. For example, if E_1 is reduced to very low densities, it can invade the remaining community whereby it is not important whether the invasion occurs directly into $M+E_2$ or whether there is a step in between, e.g., E_2 decreases also to very low densities followed by the invasion of E_1 into M and then the invasion of E_2 into E_1+M. The conditions of case v comprise all of these possible invasion paths.

APPLYING THE GENERAL APPROACH TO A PREDATOR–PREY SYSTEM

Model description

We applied the general framework to a model of an empirically well-studied chemostat system with the rotifer *Brachionus calyciflorus* as predator (*B*), different genotypes of the green algae *Chlamydomonas reinhardtii*
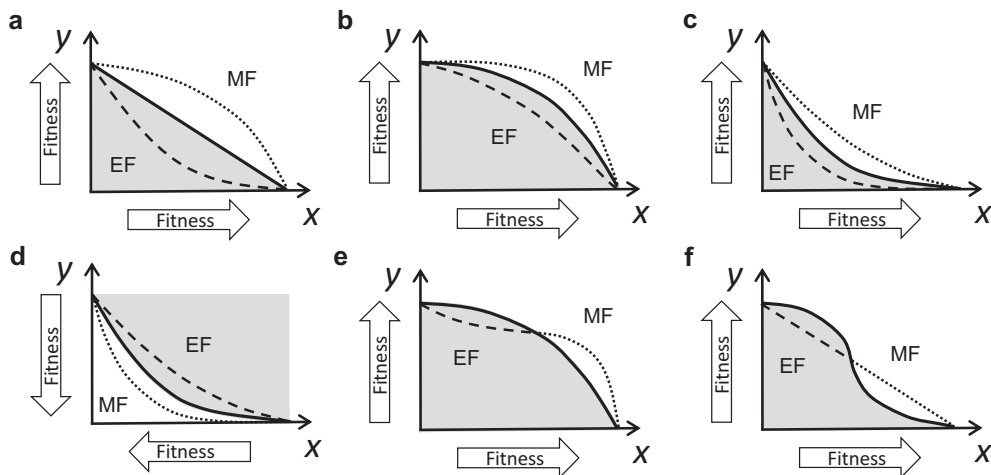
FIG. 3. Trade-offs are extreme-favoring (EF) or intermediate-favoring (MF) depending on their shape, the invasion boundary of the intermediate species M (solid line), and the direction of fitness increase (arrows). Dashed lines highlight examples of EF trade-offs while dotted lines indicate MF trade-offs. Trait combinations (x, y) of M where M cannot (can) invade the extreme species are marked with gray (white). (a) Standard case with a linear invasion boundary where convex trade-offs are EF while concave ones are MF. Non-linear invasion boundaries lead to deviations from the standard case. (b) For concave invasion boundaries, even slightly concave trade-offs are EF. (c) Convex invasion boundaries allow slightly convex trade-offs to be MF. (d) Inverse trait–fitness relationships reverse the assignment of EF and MF trade-offs. (e, f) More complex shapes of the trade-off or the invasion boundary allow for EF and MF parts within one trade-off curve.

as prey (E_1, M, and E_2) and a limiting nutrient (N) for the algae. The algal genotypes face a trade-off between edibility for the predator, i.e., probability of being attacked, and the half-saturation constant for the uptake of nutrients while we assume the other parameters to be identical (Becks et al. 2010, 2012). Some genotypes exhibit defence mechanisms (e.g., colony formation) which reduces their edibility but lowers also their affinity for nutrients (e.g., due to a lower diffusion velocity of nutrients through the matrix surrounding the colonies), i.e., increases their half-saturation constant (Becks et al. 2012, N. Woltermann and L. Becks, *unpublished data*). The trait values used in the model and stated below are based on Becks et al. (2010). The defended extreme prey E_1 has the lowest edibility ($p_1 = 0$) but the highest half-saturation constant ($K_1 = 8$ μmol N/L). The opposite holds for the competitive extreme prey E_2 ($p_2 = 1$, $K_2 = 2$ μmol N/L). We vary the trait values of the intermediate prey M between these extremes (p_M between 0 and 1, K_M between 2 and 8 μmol N/L).

The changes of the nutrient concentration and population densities over time are defined by the following differential equations

$$
\begin{aligned}
\frac{dN}{dt} &= \delta(N_I - N) - \frac{r}{\chi} \frac{NM}{K_M + N} - \frac{r}{\chi} \sum_{i=1}^{2} \frac{NE_i}{K_i + N} \\
\frac{dM}{dt} &= M\left[r \frac{N}{K_M + N} - \frac{gp_M B}{K_B + p_M M + \sum p_i E_i} - \delta \right] \\
\frac{dE_i}{dt} &= E_i\left[r \frac{N}{K_i + N} - \frac{gp_i B}{K_B + p_M M + \sum p_i E_i} - \delta \right] \\
\frac{dB}{dt} &= B\left[\chi_B \frac{g(p_M M + \sum p_i E_i)}{K_B + p_M M + \sum p_i E_i} - \delta \right]
\end{aligned}
\tag{6}
$$

with $i = 1, 2$. The chemostat system is characterized by a continuous inflow of medium with nutrients at the concentration N_I and outflow of medium with nutrients and organisms. The magnitude of the inflow and the outflow is described by the dilution rate δ. The consumption of nutrients by the prey and the consumption of prey by the predator are described by a classical Holling-type II functional response (Monod's Equation). For further details on the parameters and their values see Appendix S3: Table S1. In order to investigate the duration of co-occurrence and the population dynamics, we performed numerical integrations of this model with the lsoda solver of the deSolve package in R (Soetaert et al. 2010). In the simulations, we used the following initialization: $N = N_I$, $B = 1$ individual/mL and $E_1, M, E_2 = 10^5$ cells/mL. The simulations run for 200 d representing a relevant time scale for chemostat experiments. We determined the time until the first extinction event, i.e., the duration of co-occurrence, where the population density of one of the prey types falls below the extinction threshold (100 cells/mL), for each trait combination in a 1001×1001 grid covering the total trait space.

The invasion boundary of the intermediate prey

Here, we detect the shape of the invasion boundary of the intermediate prey M in a resident community of the defended extreme prey E_1 and the competitive extreme prey E_2. This specific system involves additionally nutrients N and the predator B. The invasion fitness of the intermediate prey ($M \approx 0$) equals

$$
\left\langle \frac{1}{M} \frac{dM}{dt} \right\rangle = r\left\langle \frac{N}{K_M + N} \right\rangle - p_M \left\langle \frac{gB}{K_B + \sum p_i E_i} \right\rangle - \delta .
\tag{7}
$$

Remarkably, the non-linear effect of p_M in the denominator of the functional response term cancels out in the invasion fitness due to $M = 0$ (compare Eqs. 6 and 7).

For simplicity, the traits of the intermediate prey are represented by p and K from now on. The traits affect different components of the invasion fitness which are additive (see Eq. 7). Therefore, the invasion fitness can be represented by two additive functions each depending on one trait and the respective population densities

$$
\langle f_p(p, 0, E_1, E_2, B) \rangle = -p\left\langle \frac{gB}{K_B + \sum p_i E_i} \right\rangle - \delta
\tag{8}
$$

and

$$
\langle f_K(K, N) \rangle = r\left\langle \frac{N}{K + N} \right\rangle .
\tag{9}
$$

By deriving the fitness terms in Eqs. 8 and 9, we can infer how the traits of the intermediate prey translate into invasion fitness components which yields $\partial \langle f_p \rangle / \partial p < 0$, $\partial^2 \langle f_p \rangle / \partial p^2 = 0$, $\partial \langle f_K \rangle / \partial K < 0$ and $\partial^2 \langle f_K \rangle / \partial K^2 > 0$ (for details see Appendix S4). This implies that the invasion fitness decreases linearly with higher p. With higher values of K, it decreases whereby the slope of that decrease becomes less negative. These relationships determine the shape of the invasion boundary. By applying the procedure explained above (see Eqs. 3–5), we end up with the first and the second derivative of K with respect to p at the invasion boundary

$$
\frac{\partial K}{\partial p} = -\frac{\partial \langle f_p \rangle / \partial p}{\partial \langle f_K \rangle / \partial K} < 0
\tag{10}
$$

and

$$
\frac{\partial^2 K}{\partial p^2} = \frac{\frac{\partial \langle f_p \rangle}{\partial p} \frac{\partial^2 \langle f_K \rangle}{\partial K^2} \frac{\partial K}{\partial p} - \frac{\partial^2 \langle f_p \rangle}{\partial p^2} \frac{\partial \langle f_K \rangle}{\partial K}}{\left(\frac{\partial \langle f_K \rangle}{\partial K} \right)^2} > 0.
\tag{11}
$$

We can conclude that the slope of the invasion boundary for the traits p and K has a negative sign since the first derivative is negative (Eq. 10). Furthermore, the shape of the invasion boundary is convex, i.e., the

second derivative is larger than zero (Eq. 11). As higher values of both traits are unfavorable, a EF trade-off (invasion of M impossible) occurs for trait combinations above the invasion boundary. This corresponds to case 6 shown in Fig. 2 and Fig. 3d.

Coexistence and co-occurrence of different prey types

The coexistence analysis described here is based on the invasibility criterion (Fig. 1b) and demands the calculation of invasion fitness and invasion boundaries, which is documented in Appendix S5. EF trade-offs imply coexistence of the defended extreme prey E_1 and the competitive extreme prey E_2 as they cannot be invaded by the intermediate prey M (Fig. 1b case i, Fig. 4a, b). For MF trade-offs, M can invade and thus different outcomes are possible (Fig. 1b case ii–iv, Fig. 4a, c–e): At low p_M values, M coexists with E_2 (Fig. 4a, c) where M represents an additional defended prey type which outcompetes the defended extreme prey

E_1 by having the advantage of a lower half-saturation constant. In a narrow range of intermediate p_M values, neither E_1 nor E_2 can invade M since they are functionally not different enough from M. This leads to the survival of only M which is reasonably defended but can still sustain the predator and has a relatively low half-saturation constant (Fig. 4a, d). For high values of p_M, coexistence of E_1 and M occurs (Fig. 4a, e) where M outcompetes E_2 since it has also a relatively low half-saturation constant but a lower edibility compared to E_2.

Stable coexistence of three prey types demands that every prey type can invade the system of the two other prey types (Fig. 1b case v). This is precluded in our system due to the fact that the conditions for invasibility of $E_1 + E_2$ by M and of $E_1 + M$ by E_2 as well as $M + E_2$ by E_1 are mutually exclusive. Hence, the maximum number of stably coexisting prey types is two. However, all three prey types can co-occur for long periods (Fig. 4c). The duration of co-occurrence increases for trait combinations
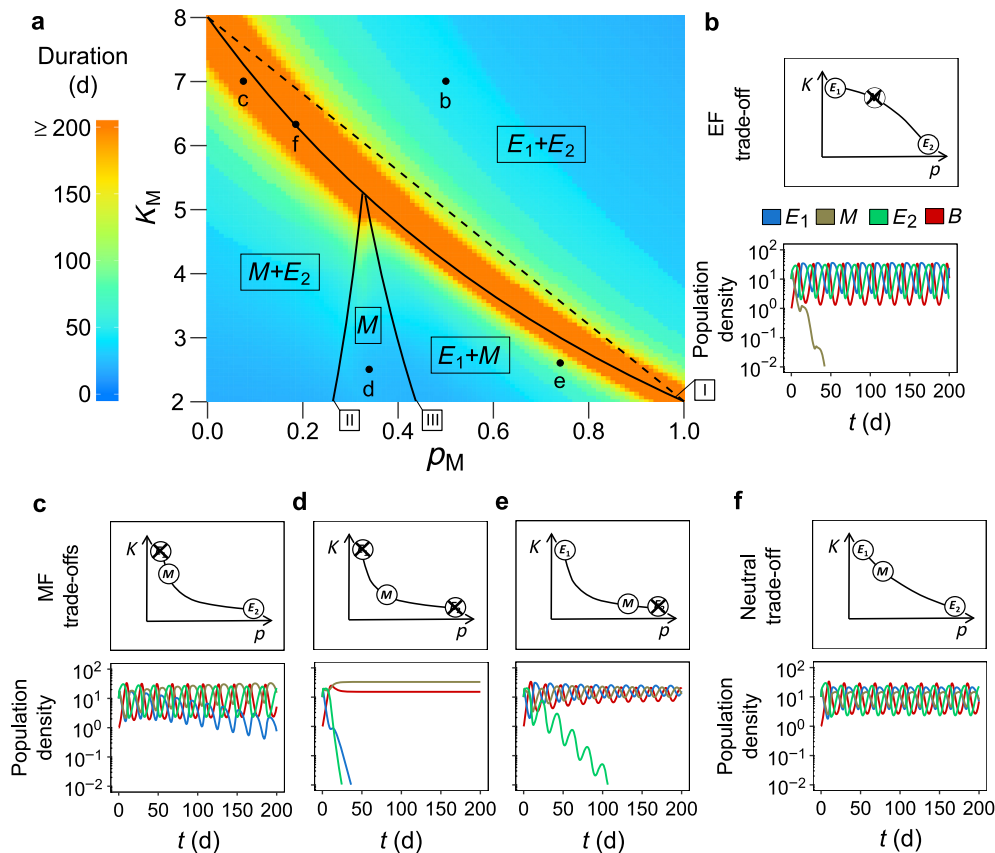

FIG. 4.   (a) Coexistence and duration of co-occurrence of the three prey types depending on the edibility p_M and the half-saturation constant K_M (μmol N/L) of the intermediate prey type M. The capital letters E_1, E_2, and M indicate which prey types coexist in the different regions framed by the solid lines representing the invasion boundaries (line I: M into E_1+E_2; line II: E_2 into M; line III: E_1 into M). The invasion boundary of M (line I) is convex and differs distinctly from the often assumed linear case (dashed line). The color grid indicates the duration of co-occurrence (i.e., time until first extinction) which increases when getting closer to the invasion boundary of M. The dots labeled with lowercase letters mark trait combinations for which potential shapes of the trade-off and the population dynamics of the prey types (10^4 cells/mL) and the predator B (individuals/mL) are shown in panels b–f. The lower limit of the population density axis equals the extinction threshold of the prey types, 100 cells/mL. Trade-off curves are defined as extreme-favoring (EF), intermediate-favoring (MF) or neutral depending on whether they are above, below or identical to the invasion boundary of M. [Color figure can be viewed at wileyonlinelibrary.com]

closer to the invasion boundary (Fig. 4a–e). Exactly on the invasion boundary, i.e., for neutral trade-offs, none of the prey types is outcompeted due to fitness equality (Fig. 4a, f). This is called unstable coexistence as none of the prey types can invade the others because the invasion fitness equals zero. They only coexist if they are present at sufficiently high initial densities.

Discussion

We developed a novel and general approach to analyse the consequences of different trade-off curves for coexistence based on measurable trait–fitness relationships. We revealed limitations of the common prediction that convex trade-offs favor species with extreme trait values while concave trade-offs enable survival of intermediate species. These limitations arise from the implicit assumption of linear trait–fitness relationships implying that the invasion boundary of an intermediate species invading the extreme species is linear. Here, we infer the shape of the invasion boundary directly from the trait–fitness relationships and show that it is often non-linear. This holds when the relationship between at least one trait and the fitness is non-linear (Fig. 2, Fig. 4) or when the fitness components are non-additive (Appendix S1). We show how information on the shape of the invasion boundary can be used to infer consequences of different trade-off curves for coexistence. Depending on the relative position of the trade-off curve to the invasion boundary, we classify trade-offs as extreme-favoring (EF, invasion of intermediate species not possible) or intermediate-favoring (MF, invasion possible; Fig. 3). We apply our approach to an illustrative example of a predator–prey system with a trade-off between prey edibility and half-saturation constant for nutrients where the invasion boundary of an intermediate prey is convex.

The impacts of non-linear invasion boundaries on evolution were already highlighted by Rueffler et al. (2004) and de Mazancourt and Dieckmann (2004) who extended Levins' approach by allowing for density- and frequency-dependent fitness. They compared trade-off curves and invasion boundaries of mutant strategies in a monomorphic resident population to assess the direction of selection with gradual evolution. Rueffler et al. (2004) discussed under which conditions the invasion boundaries are non-linear but they did not specify their shape. For instance, non-linear invasion boundaries occur in stage-structured models when the traits are characteristic for different stages (Ebenman et al. 1996, Hoyle et al. 2008) and different resource competition models depending on the state of the resident community (Abrams 2006b, Abrams and Rueffler 2009). Further studies underline the importance of assessing the curvature of invasion boundaries for predicting evolutionary outcomes (Bowers et al. 2005, White and Bowers 2005). However, our study is the first which explicitly addresses the question of when the invasion boundary becomes convex, concave or has a more complex shape depending on the trait–fitness relationships (Fig. 2). Moreover, our approach is released from the

limitation that coexistence has to be evolutionary attainable via local mutations. We consider coexistence within an existing pool of species with fixed trait values.

Our approach is based on the assumption that two extreme species facing a two-dimensional trade-off stably coexist in the absence of an intermediate species independent of the shape of the trade-off, i.e., they are mutual invasible. However, depending on the magnitude of the trade-off and the environment, only one extreme species may survive. For example, a defended prey cannot coexist with a fast-growing prey if the defence costs in terms of growth are very high (Abrams 1999, Kasada et al. 2014). Moreover, if the physiologically feasible trait range is very narrow, the extreme types may be too similar for stable coexistence. In such cases, we can adapt our approach and consider a resident community of only one extreme species to check for the invasion of an intermediate species. In the previously described case with two coexisting resident extreme species, the trade-off curve and the invasion boundary shared the same terminal points (see Fig. 3). This needs not to be the case when only one resident extreme species is present. The trade-off curve and the invasion boundary still converge at the trait combination of the resident species which is neutrally invasible while at the other end of the trait range they may diverge. Nevertheless, it is possible to distinguish between EF and MF trade-offs just by detecting whether the trade-off curve lies below or above the invasion boundary of the intermediate species invading the one resident species.

We applied our general approach to an empirically well understood predator–prey chemostat system with a trade-off between prey edibility (probability of being attacked) and its half-saturation constant for nutrient uptake. We found that the invasion boundary of an intermediate prey invading the two extreme prey types was convex and had a negative slope. A subsequent invasion analysis (Fig. 1b) could explain the coexistence of different prey types (Fig. 4). Remarkably, for MF trade-offs, the intermediate prey outcompeted both extreme prey types or stably coexisted with one of them depending on its trait values while stable coexistence of all three prey types is impossible in this system even under cycling population densities. This follows the general theorem stating that at most n species can coexist on n regulating variables (Meszéna et al. 2006), i.e., two different prey types can coexist based on one resource and one predator. However, previous theory revealed that fluctuating population densities may allow for a higher number of coexisting species. For example, Abrams (2006b) showed that two specialist and one generalist consumer can stably coexist on two resources for slightly convex trade-offs when the resources cycle asynchronously. This was possible due to the relative non-linearity arising from the different saturating functional responses of the consumers to the resources which promoted the fitness of the generalist. In models on interactions of prey species sharing one resource and a common predator, non-linear functional responses also promote cycles and allow for coexistence

of two different prey strategies (Abrams and Matsuda 1997, Abrams et al. 1998, Abrams 1999, Yoshida et al. 2007). However, relative non-linearities enabling stable coexistence of three prey strategies under fluctuating densities have not been found in these predator–prey systems, as shown in our study.

The three prey types cannot stably coexist but they may co-occur on long, ecologically relevant time scales when fitness differences are small, i.e., the trade-off is nearly neutral. Studies on the role of neutrality and nearly neutral trade-offs for maintaining functional diversity in natural communities have a long tradition in ecology (e.g., Hubbell 2001, 2005, Adler et al. 2007). High fitness equality extends the duration of co-occurrence and may increase the possibility of coexistence even if only weak stabilizing mechanisms are present (Chesson 2000, He et al. 2012, Pedruski et al. 2015). We argue here that nearly neutral trade-offs and the resulting low differences in fitness may help to explain the partly observed high functional diversity in simple, short-term experimental systems like the predator–prey system considered in our study. Chemostat experiments mostly cover up to 100 generations (Becks et al. 2010, Hiltunen et al. 2014). Within this time scale, all prey types maintain empirically detectable population densities for nearly neutral trade-offs even if one prey type would die out in the long term (Fig. 4c). It should be mentioned here that the duration of co-occurrence depends not only on the degree of fitness equality but also on the extinction threshold and the initial population densities, e.g., low initial densities of an inferior competitor decrease the duration of co-occurrence.

So far, we focused on two-dimensional trade-offs. However, multiple traits may trade off in nature (e.g., Edwards et al. 2011) and our approach can be extended to multi-dimensional trade-offs. For example, a trade-off among three traits can be represented by a plane in a three-dimensional trait space. We can calculate the invasion boundary of an intermediate species invading the three possible extreme strategies. By comparing the planes of the trade-off and the invasion boundary, we can conclude whether the trade-off is EF or MF. Furthermore, there is the possibility that a trait affects more than one fitness component, e.g., the size of phytoplankton cells determines their growth, nutrient uptake, sedimentation and grazing losses (Litchman and Klausmeier 2008, Finkel et al. 2010). Accordingly, such traits were often called "master traits." Dividing a "master trait" into the associated functional parameters like maximum growth rate, nutrient affinity, sedimentation velocity, and vulnerability to predation leads us to individual fitness functions that can be handled with our approach.

Previous research has documented that trade-offs often tend to be EF and found specialization of strategies indicating high costs of intermediate strategies (Benkman 1993, Schluter 1995, O'Hara Hines et al. 2004, Mealor and Boots 2006). However, evidently, MF trade-offs are also relevant, e.g., for trade-offs between stress tolerance and resource-dependent growth in different *Escherichia*

coli strains (Maharjan et al. 2013). Empirical evidence for trade-offs consisting of EF and MF parts is currently lacking but development of theory on trade-off curves combining concave and convex parts, which have the potential to be EF and MF, has been intensified (Zu et al. 2011, Zu and Takeuchi 2012). Our approach contributes to this theoretical work and allows to assess consequences of more complex trade-off shapes. Furthermore, previous research showed that the shape of trade-offs may depend on the environment (Jessup and Bohannan 2008), which would allow for a continuous switching between EF and MF under fluctuating conditions. This also implies that neutral trade-offs may be of low relevance in natural systems because a trade-off curve identical to the invasion boundary is unlikely to prevail for extended periods of time. Nevertheless, nearly neutral trade-offs may be relevant. For instance, trait measurements on the edibility and maximum growth rate of different phytoplankton species indicate a nearly linear trade-off (Wirtz and Eckhardt 1996). According to our study, the invasion boundary for these traits is linear as well (Fig. 2, case 2) suggesting that these phytoplankton species co-occur due to low fitness differences instead of strong niche differentiation.

Conclusion

We conclude that the common prediction that convex trade-offs promote species with extreme trait values while concave trade-offs favor species with intermediate trait values fails in case of non-linear trait–fitness relationships, which frequently occur in nature. Our approach stating how the shape of a trade-off affects coexistence in dependence of the fitness functions overcomes this limitation and can be readily used in practice: establishing the trait–fitness relationships enables to calculate the invasion boundary of an intermediate species invading a community of species with extreme trait values. A comparison of this boundary with the shape of the trade-off allows to predict coexistence. This leads us to a new classification of trade-offs into extreme-favoring and intermediate-favoring which is more specific in terms of the ecological consequences than a purely mathematical description of their curvature, i.e., convex or concave.

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