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Competition and Predation in Simple Food Webs: Intermediately Strong Trade-offs Maximize Coexistence

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Abstract

Competition and predation are fundamental interactions structuring food webs. However, rather than always following these neat theoretical categories, mixed interactions are ubiquitous in nature. Of particular importance are omnivorous species, such as intra-guild predators that can both compete with and predate on their prey. Here we examine trade-offs between competitive and predatory capacities by analysing the entire continuum of food web configurations existing between purely predator-prey and purely competitive interactions of two consumers subsisting on a single resource. Our results show that the range of conditions allowing for coexistence of the consumers is maximized at intermediately strong trade-offs. Even though coexistence under weak trade-offs and under very strong trade-offs is also possible, it occurs under much more restrictive conditions. We explain these findings by an intricate interplay between energy acquisition and interaction strength.

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Competition and Predation in Simple Food Webs: Intermediately Strong Trade-offs Miximize Coexistence

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1. Introduction

Competition and predation are interactions that have long been recognized as the key structural elements of ecological communities (e.g., Chase et al. 2002, and references therein). Much ecological theory has focused on how these basic interactions affect species coexistence in simple community modules, through population dynamics (Rosenzweig 1971; Armstrong & McGehee 1980; Oksanen et al. 1981; Tilman 1982; Diehl & Feissel 2000; Krivan 2000; Mylius et al. 2001). Competitive interactions in classical food webs have been linked to exclusion (Tilman 1982), while predation in the context of exploitative ecosystems has been linked to coexistence of predator and prey (Hairston et al. 1960; Oksanen et al. 1981). Exceptions from these simple trends have also been documented: see Rosenzweig (1971) for a case in which increasing productivity destabilizes a predator-prey interaction, and Armstrong & McGehee (1980) for conditions under which coexistence of competitors becomes possible through non-equilibrium population dynamics.

Studies linking competition and predation by investigating their joint impact on community structure have traditionally focused on the mediating effect of predation on competitive interactions (Fretwell & Lucas 1970; Lubchenko 1978; Chase et al. 2002, and references therein). We know that omnivory and intra-guild predation are ubiquitous in nature (Polis et al. 1989; Polis 1991; Polis & Strong 1996), yet only very few theoretical studies (Diehl & Feissel 2000; Krivan 2000; Mylius et al. 2001) have taken into account that a species may simultaneously compete with and predate on another species. These studies have shown that intra-guild predation can imply ecological bistability and lead to the exclusion of a prey by its intra-guild predator. In general, however, the effects of omnivory on coexistence and community structure are far from being well understood.

All organisms face certain constraints – whether physiological, morphological, energetic, or temporal – implying that increased allocation to one capacity must usually result in decreased allocation to another. The resulting trade-offs between life-history traits (Stearns 1992; Roff 1992) are central to the theory of species coexistence, both from a population dynamical and from an evolutionary perspective: a “Darwinian Demon” that is exempt from trade-offs (Law 1979) will always out-compete all other species by being, for example, in the case of intra-guild predation, both a better competitor and a better predator.

In this study we explore all possible food web configurations involving a resource and two consumer species (to which we shall refer as "antagonists") differentially investing, along a trade-off, in either resource feeding (competition) or antagonist feeding (predation). Systematically charting the community structures lying between the well-studied food web extremes – such as purely competitive and purely exploitative systems – allows us to determine which of these more general food webs are ecologically stable.

Even though the potential for coexistence, exclusion, and bistability to be affected by levels of investment into competition or predation has been documented in the literature (Oksanen et al. 1981; Tilman 1982; Diehl & Feissel 2000; Krivan 2000; Mylius et al. 2001), to our knowledge no study has yet investigated the continuum between purely competitive, omnivorous, and purely exploitative interactions, as analysed in this study. We find that only certain combinations of trade-offs and investment levels into competition or predation allow for the coexistence of all three involved species. In particular, we document the surprising result that the least restrictive conditions for coexistence arise for intermediately strong trade-offs. We discuss the relation between this result and earlier findings about weak to intermediately strong interactions between species promoting community persistence (May 1971; Gardner & Ashby 1970; McCann et al. 1998; McCann 2000).

2. Model Description

To explore the implications of differential investment into competition (for a basal resource) or predation (of an antagonistic consumer) for stable community structures, we consider the simple three-species food web illustrated in Figure 1. Capacities for competition and predation are linked through a trade-off, as shown in Figure 2.

(a) Antagonist dynamics

The population biomass, C and D, of the two antagonistic species vary according to

$$\frac{d}{dt}C = g_c(R,C,D)\;\; C \;, \tag{2.1}$$

$$\frac{d}{dt}D = g_d(R,C,D)\;\; D \;; \tag{2.2}$$

where $g_c(R,C,D)$ and $g_d(R,C,D)$ are the per capita growth rates of the two antagonists and depend on the biomass of all three species – R, C, and D – in the food web, with R denoting the basal resource biomass. These per capita growth rates are given by

$$g_c(R,C,D) = e_{cr}\alpha_{cr}R + e_{cd}\alpha_{cd}D - \alpha_{dc}D - \delta_c \;, \tag{2.3}$$

$$g_d(R,C,D) = e_{dr}\alpha_{dr}R + e_{dc}\alpha_{dc}C - \alpha_{cd}C - \delta_d \,. \tag{2.4}$$

The biomass of C grows according to the encounter and sequestration of R and D (with attack coefficients α_{cr} and α_{cd}) and the corresponding conversion into C-biomass

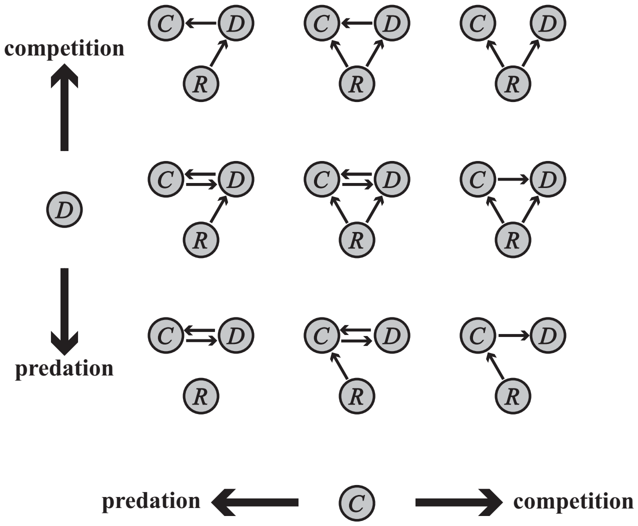

Figure 1. Elementary food webs based on competition-predation trade-offs in two antagonistic consumers (*C* and *D*) feeding on a basal resource (*R*). Arrows indicate the direction of energy flows between organisms. The horizontal (vertical) axis shows the relative investment into competition and predation for species *C* (*D*). (Note that "competition" and "predation" in these axis labels refer to the investment of a species into competitive or predatory abilities, and not to the resulting food web configurations.)

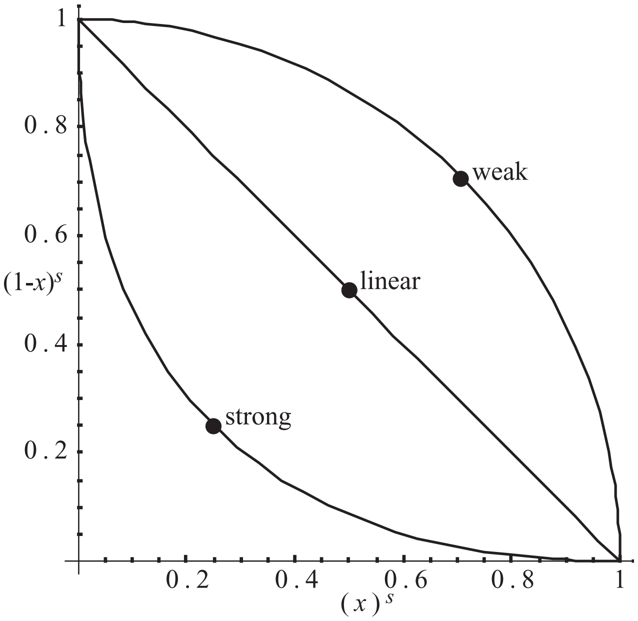

Figure 2. Illustration of strong, weak, and linear trade-offs between predation capacity x^s and competition capacity $(1 - x)^s$, where x is the investment into the former. Circles indicate where the two capacities are equal. For strong trade-offs ($s > 1$), total capacity is minimized at the circle. For weak trade-offs ($s < 1$), total capacity is maximized at the circle. For linear trade-offs ($s = 1$), total capacity is constant.

(with efficiencies e_{cr} and e_{cd}). The population biomass of *C* is reduced through predation by *D* (with attack coefficient α_{dc}) and a species-specific, density independent background mortality (at rate δ_c). Per capita rates for *D* are analogous. Table 1 provides a summary of, variables, parameters, and default parameter values.

We have assumed a linear dependence of attack rates on resource or antagonist biomass. However, our results do not qualitatively change if we allow for attack rates to saturate with increasing resource or antagonist levels.

(b) Resource dynamics

Resources in isolation grow according to semi-chemostat dynamics, with semi-chemostatic carrying capacity *K* and inflow rate ρ. In the absence of species *C* and *D*, resource biomass thus equilibrates at *K*. Species *C* and *D* impose additional mortality on the resource through consumption,

$$\frac{d}{dt}R = \rho(K-R) - R(\alpha_{cr}C + \alpha_{dr}D) \ . \tag{2.5}$$

Conclusions presented in this study remain qualitatively unchanged when assuming logistic instead of semi-chemostatic growth.

(c) Trade-offs

We model the trade-offs between resource consumption and prey consumption describing the attack coefficients as follows,

$$\alpha_{cr} = a_{\max} x_c^{s_c} \ , \tag{2.6}$$

$$\alpha_{cd} = a_{\max}(1-x_c)^{s_c} \ , \tag{2.7}$$

$$\alpha_{dr} = a_{\max} x_d^{s_d} \ , \tag{2.8}$$

$$\alpha_{dc} = a_{\max}(1-x_d)^{s_d} \ , \tag{2.9}$$

where $a_{\max}$ determines the maximal attack coefficient. The two adaptive traits x_c and x_d (x in the generic case) range from 0 to 1 and determine to which extent *C* and *D* invest into predation. For example, when $x_c = 1$, *C* consumes only resources: the attack coefficient α_{cr} equals $a_{\max}$, while α_{cd} is zero. By contrast, when $x_c = 0$, *C* focuses entirely on prey consumption at a rate $\alpha_{cd} = a_{\max}$, while $\alpha_{cr} = 0$.

Omnivorous strategies are described by values of x between 0 and 1. The realized attack coefficient at these intermediate strategies is a function of the maximum attack coefficient, and the strength of the trade-off s_c or s_d (s in the generic case). The case $s = 1$ describes a simple linear trade-off (Figure 2). Here the relationship between the trait variable and the attack coefficients are such that a change in one attack coefficient implies an equal, but opposite change in the other attack coefficient. This means that the sum of the attack coefficients always equals $a_{\max}$. For $s < 1$ (weak trade-off) attack coefficients at all intermediate values of x sum to values greater than $a_{\max}$. At $s = 0$ the sum of attack coefficients is 2 $a_{\max}$ for all values of x except 0 or 1. For $s > 1$ (strong trade-off) intermediate values of x lead to a total attack coefficient that is

Table 1. Variables, parameters and default parameter values used in the model.

Symbol	Description	Default value
	Variables	
t	Time	-
C	Biomass of antagonist *C*	-
D	Biomass of antagonist *D*	-
R	Biomass of basal resource *R*	-
	Parameters	
ρ	Semi-chemostatic inflow rate of resource	0.2
K	Semi-chemostatic carrying capacity of resource	100
α_{cr}	Attack coefficient of *C* on *R*	$a_{\max}\left(x_c\right)^{s_c}$
α_{dr}	Attack coefficient of *D* on *R*	$a_{\max}\left(x_d\right)^{s_d}$
α_{cd}	Attack coefficient of *C* on *D*	$a_{\max}\left(1-x_c\right)^{s_c}$
α_{dc}	Attack coefficient of *D* on *C*	$a_{\max}\left(1-x_d\right)^{s_d}$
e_{cr}	Conversion efficiency of *R* to *C*	0.1
e_{dr}	Conversion efficiency of *R* to *D*	0.1
e_{cd}	Conversion efficiency of *D* to *C*	0.01
e_{dc}	Conversion efficiency of *C* to *D*	0.01
δ_c	Intrinsic death rate of *C*	0.05
δ_d	Intrinsic death rate of *D*	0.05
	Trade-off parameters	
s_c	Trade-off strength for *C*	-
s_d	Trade-off strength for *D*	-
x_c	Trait value of *C*	-
x_d	Trait value of *D*	-
$a_{\max}$	Maximal attack coefficient	0.4

always less than $a_{\max}$. At $s=\infty$ any intermediate trait value results in a total attack coefficient of 0.

Attack coefficients determine the energy antagonists can take in, as well as the strength of their interaction. For weak trade-offs, attack coefficients at intermediate trait values give rise to high total attack coefficients. Here a consumer experiences both a high potential energy intake and high interaction strength. For strong trade-offs, intermediate-values of x result in low attack coefficients, low interaction strength, and thus also in a low energy intake.

Such weak or strong trade-offs can arise through physiological, morphological, behavioural, or temporal constraints. Consider, for instance, a behavioural constraint: if searching for food strongly depends on search images, synergistic effects at intermediate strategies could lead to situations in which searching for one type of food increases the chances to find another type, resulting in a weak trade-off. By contrast, in a “jack of all trades, but master of none” scenario, an intermediate search image might lead to total attack coefficients that fall below those of specialists.

(d) Coexistence

In the absence of *C* or *D, R* equilibrates at $\bar{R}=K$. From this starting point, we consider the potential for invasion of either antagonist. If such invasion is possible, then a stable

$\overline{C}\overline{R}$- or $\overline{D}\overline{R}$-equilibrium exists. We use the subsequent ability (or disability) of *C* or *D* to invade, respectively, a $\overline{D}\overline{R}$- or $\overline{C}\overline{R}$-equilibrium to determine whether coexistence is possible. Community states for which a three-species equilibrium is possible but not attainable through invasion are not considered here, since such polymorphisms are not protected against accidental extinctions and thus unlikely to persist in nature (Prout 1968).

The invasion fitness (Metz *et al.* 1992) of *C* in a population comprising solely of *R* is given by *C*'s per capita growth rate evaluated at $\overline{R}$,

$$Inv(C \to R) = e_{cr}\alpha_{cr}K - \delta_c \ . \tag{2.10}$$

Similarly, one obtains the rate of invasion for an antagonist into an environment composed of the other antagonist monopolizing a resource,

$$Inv(C \to DR) = e_{cr}\alpha_{cr}\overline{R} + \overline{D}(e_{cd}\alpha_{cd} - \alpha_{dc}) - \delta_c \ , \tag{2.11}$$

where $\overline{R}$ and $\overline{D}$ denote the biomasses of *R* and *D* at their joint equilibrium. Calculation of $Inv(D \to R)$ and $Inv(D \to CR)$ is analogous,

$$Inv(D \to R) = e_{dr}\alpha_{dr}K - \delta_d \ , \tag{2.12}$$

$$Inv(D \to CR) = e_{dr}\alpha_{dr}\overline{R} + \overline{C}(e_{dc}\alpha_{dc} - \alpha_{cd}) - \delta_d \ . \tag{2.13}$$

Invasion of *C* into $\overline{R}$, of *C* into $\overline{D}\overline{R}$, of *D* into $\overline{R}$, or of *D* into $\overline{C}\overline{R}$ is possible when, respectively, $Inv(C \to R) > 0$, $Inv(C \to DR) > 0$, $Inv(D \to R) > 0$, or $Inv(D \to CR) > 0$.

We can thus look at the conditions for community assembly as a function of $Inv(C \to R)$, $Inv(C \to DR)$, $Inv(D \to R)$, and $Inv(D \to CR)$. On this basis, we can discern five qualitatively different types of possible community (Table 2):

- *R alone* (R): Neither *C* nor *D* is able to persist on the resource alone.
- *C and R* (C): *C* is able to persist on the resource alone, while *D* is not able to invade.
- *D and R* (D): *D* is able to persist on the resource alone, while *C* is not able to invade.
- *Bistability between C and D* (C/D): Both *C* and *D* are able to persist on the resource alone, but are not able to invade each other's equilibria.
- *Three-species coexistence* (CD): At least one antagonist is able to persist on the resource alone, while the other is able to invade the ensuing two-species equilibrium.

All equilibria mentioned below were checked with CONTENT (Kuzsnetsov *et al.* 1996), a software package for numerical bifurcation analysis.

3. Results

We graphically present our results by detailing community states as a function of the trait values x_c and x_d, referring to this two-dimensional space as the system's trait space. To facilitate understanding, we first consider symmetric cases, characterized by the following constraints: $s_c = s_d = s$, $e_{cd} = e_{dc} = e_p$, $e_{dr} = e_{cr} = e_r$, and $\delta_c = \delta_d = \delta$. In such symmetric cases, the two antagonists differ only in their trait values x_c and x_d, and thus in their attack coefficients. We first obtain the resulting patterns of community states for the symmetric case and then show the robustness of these patterns to asymmetry.

Table 2. Invasion conditions and resulting community structure. CD refers to a three-species equilibrium. C to a *C*-only equilibrium, D to a *D*-only equilibrium, C/D to bistability between *C* and *D*, and R to a *R*-only equilibrium. An asterisk indicates that conditions for invasion can either be >0 or <0.

Invasion fitness	**Community structure**						
	CD			**C**	**D**	**C/D**	**R**
$Inv(C \rightarrow R)$	$*$		>0	>0	$*$	>0	<0
$Inv(D \rightarrow R)$	>0	or	$*$	$*$	>0	>0	<0
$Inv(C \rightarrow DR)$	>0		>0	$*$	<0	<0	$*$
$Inv(D \rightarrow CR)$	>0		>0	<0	$*$	<0	$*$

Figure 3 illustrates the construction of community states from the zero-isoclines of invasion fitness at default parameter values (Table 1) and $s = 5$ (a strong trade–off). Invasion zero-isoclines (depicted as transitions from black to white in Figures 3a to 3d) allow detailing community states in trait space (Figure 3e) following the relations in Table 2. Areas marked R, C, or D denote regions where, respectively, R, CR, or DR equilibria are feasible and stable. The region marked C/D corresponds to bistability between CR and DR equilibria. In these regions, priority effects determine the ultimate establishment of *C*, respectively *D*, as both antagonists can build up high enough population levels on the resource alone so as to prevent invasion of the other.

At $(x_c, x_d) = (0,1)$, *D* purely consumes the resource, while *C* purely consumes *D*. This point in trait space thus lets *C* and *D* assume the roles of predator and prey, respectively. Trait values near this upper left corner therefore describe interactions that are mostly of predator-prey type; the same applies, by symmetry, to the neighbourhood of the lower right corner. At $(x_c, x_d) = (1,1)$, both species consume only the resource. The upper right corner thus harbours communities in which competitive interactions prevail. In accordance with Tilman's (1982) *R** theory of competition, the antagonist with the highest attack coefficient on the resource, and thus the one that can reduce the resource to its lowest level, then wins. At $(x_c, x_d) = (0,0)$ both antagonists consume only each other. Near this lower left corner both species specialize to such an extent on predation that there is not enough energy influx from the resource to support them, resulting in the extinction of both antagonists.

Figures 4a and 5a illustrate three trends that result from increasing trade-off strength:

- With increasing strength of the trade-off, conditions for coexistence first relax, peaking at intermediately strong trade offs, and then tighten again.
- Bistability dominates for weak trade offs, while it dwindles and then disappears for stronger trade-offs.
- The stronger the trade-off, the larger the regions in trait space that allow only for the existence of the resource.

What happens to these findings when primary productivity is two times as high than (*K*=200)? This is shown in Figures 4b and 5b. We observe larger regions of coexistence

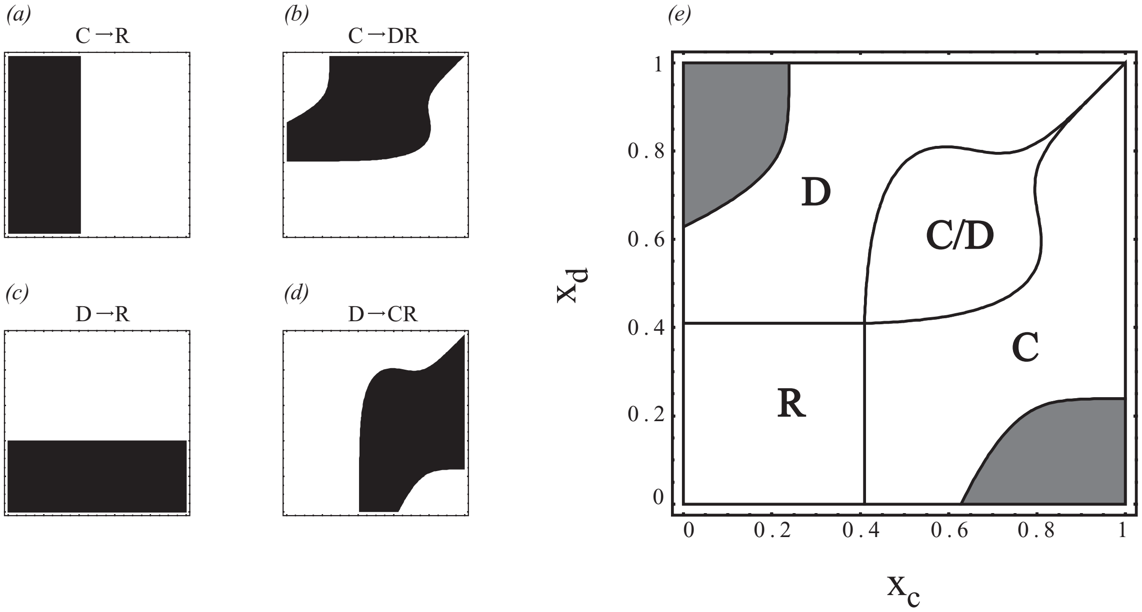

Figure 3. Partitioning of trait space at default parameter values and s = 5. (a-d) Panels marked C→R, D→R, C→DR, and D→CR show, respectively, regions where C can invade an R equilibrium (white region in a), D can invade an R equilibrium (white region in b), C can invade a DR equilibrium (white regions in c), and where D can invade a CR equilibrium (white regions in d). (e) Resulting partitioning of trait space according to community states. Shaded regions indicate areas where all three species can coexist. In regions marked C (D), only C (D) is viable on the resource. The region marked C/D involve bistability between C and D: here either a CR equilibrium or a DR equilibrium is attained. The region marked R indicate that neither C nor D are viable on the resource R.

before, especially for stronger trade-offs (i.e., for $s = 5$, $s = 10$, and $s = 20$), while the facilitating effect is less pronounced for weaker trade-offs. At $s = 2$ and $s = 5$, regions of bistability are enlarged, whereas regions in which just the resource can persist have shrunk. All these effects are strengthened when the resource's carrying capacity is further enhanced (results not shown).

Figures 4c-f and 5c-f explore the robustness of the observed trends to asymmetric parameter settings. These cases therefore refer to antagonists that differ in more than their trait values and attack coefficients. It is hence remarkable that for all these cases the three patterns highlighted above robustly prevail. Some slight differences between the cases are briefly described in the next four paragraphs.

In Figures 4c and 5c, *C* is superior to *D* in terms of its conversion efficiency of the resources ($e_{cr} = 0.5$). As a result, we observe, especially at $s = 2$ and $s = 5$, markedly enlarged regions over which *C* can persist (these can be partitioned in regions of coexistence, CD; regions of bistability, C/D; and regions in which C exists alone with the resource, C). Also the region of viable predator-prey systems in the lower right corner has become much larger, where *D* benefits from the higher biomass that *C* can sustain. Other effects include shifting of the left boundary of the R region towards lower levels of x_c, shifting of the C region outwards towards areas where normally there would be C/D bistability, and shifting of the C/D bistability regions to where *D* always ousts *C* at $s = 5$ in Figure 4a. At $s = 10$ and $s = 20$, differences are less marked, except for larger regions of coexistence in the lower right corner. At $s = 1$ and below,

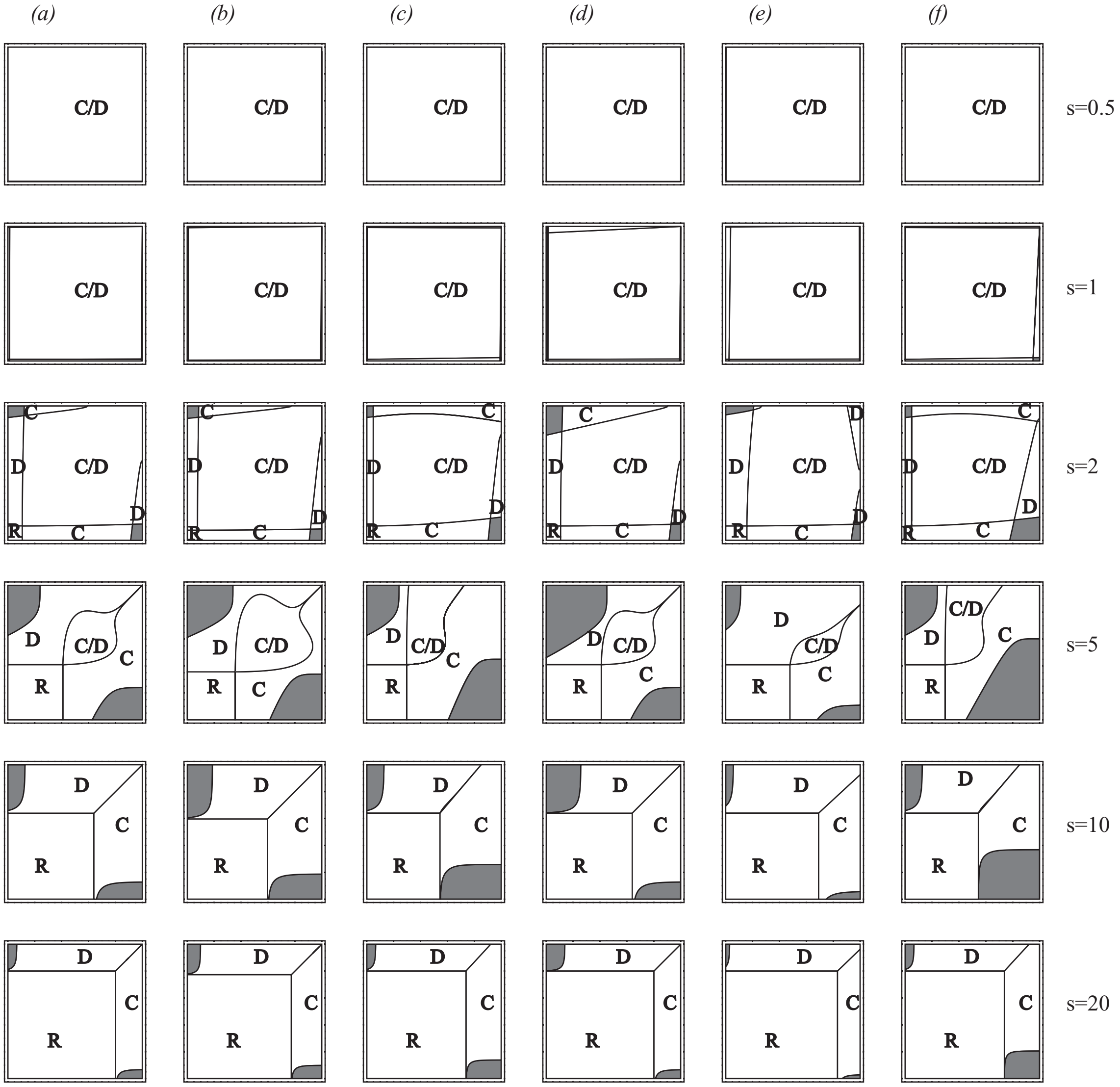

Figure 4. Partitioning of trait space for varying trade-off strengths. (a) Symmetric case at default parameter values. (b) Symmetric case with *K*=200. (c) Asymmetric case where *C* feeds on the resource five times as efficiently as *D*, $e_{cr} = 0.5$. (d) Asymmetric case where *C* is five times as efficient on *D*, as *D* is on *C*, $e_{cd} = 0.05$. (e) Asymmetric case where *C* has a higher death rate than *D*, $\delta_c = 0.1$. (f) Asymmetric case where *C* is five times as efficient on the resource and *D* is five times as efficient on *C*, $e_{cr} = 0.5$ and $e_{dc} = 0.05$. In each column, the trade-off strength *s* varies from weak (*s* = 0.5) through linear (*s* = 1) through moderately strong (*s* = 2 and *s* = 5) to very strong (*s* = 10 and *s* = 20). Shading and labels as in Figure 3.

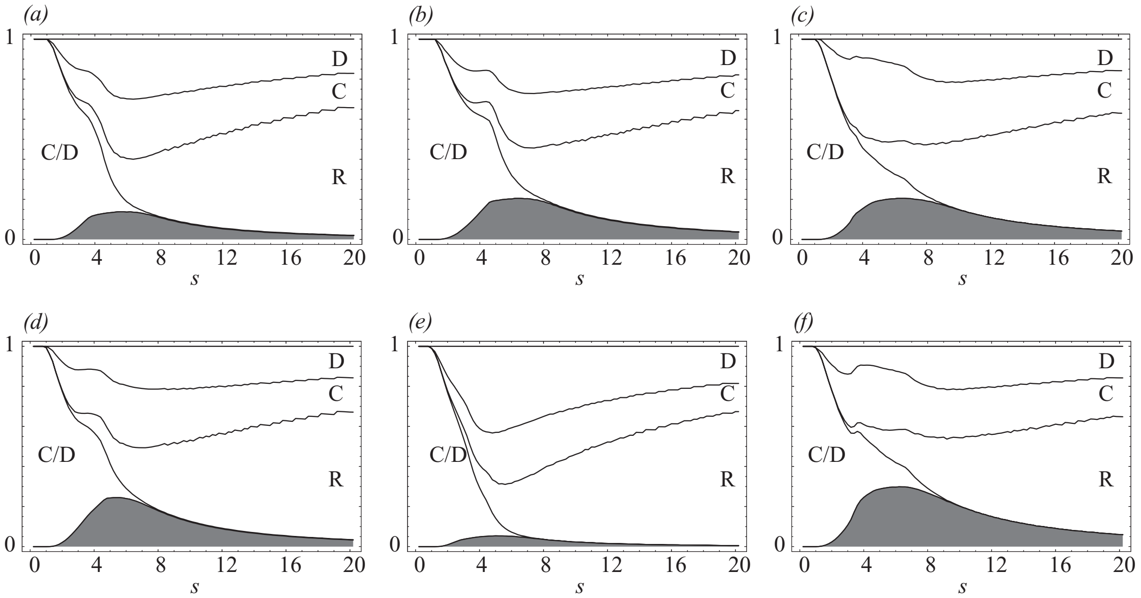

Figure 5. Proportion of trait space occupied by different community states as a function of trade-off strength *s*. Panels (a) to (f) correspond to Figures 4a to 4f. Labels as in Figure 3.

little effect is observed. Other effects include shifting of the left boundary of the R region towards lower levels of x_c, shifting of the C region outwards towards areas where normally there would be C/D bistability, and shifting of the C/D bistability regions to where *D* always ousts *C* at $s = 5$ in Figure 4a. At $s = 10$ and $s = 20$,differences are less marked, except for larger regions of coexistence in the lower right corner. At $s = 1$ and below, little effect is observed.

In Figures 4d and 5d, *C* is superior to *D* in terms of prey conversion efficiency ($e_{cd} = 0.05$). Marked effects on coexistence are seen in regions where *C* is predator and *D* is prey. C regions expand noticeably at $s = 2$, where there is some encroachment on C/D regions (in the upper left corner). D regions do not noticeably shrink except for stronger trade-offs, whereas at $s = 2$ and above coexistence regions have grown at the expense of D regions.

Figures 4e and 5e examine the consequences of a higher death rate for *C* ($\delta_c = 0.1$). In this case, regions of coexistence are shrunk for all trade-off strengths s and in both predator-prey corners. C regions are also reduced and encroached upon by C/D regions at $s = 5$. Regions of C/D bistability are decreased for all trade-off strengths, while R regions are increased. D regions expand most noticeably at $s = 2$ and $s = 5$, while at $s = 10$ this effect is less pronounced.

Figures 4f and 5f examine the robustness of results to making species *C* five times as efficient in resource consumption, and *D* five times as efficient in preying upon *C*. ($e_{cr} = 0.5$ and $e_{dc} = 0.05$). The region of coexistence around the lower right (predator-prey) corner is greatly enlarged for all trade-off strengths. In regions where *C* is more of a competitor, C regions encroach on regions of bistability (particularly clear at $s = 5$), as well as on R regions.

Figures 5a-f gives an overview of the areas of trait space occupied by different community states for the cases shown in Figures 4a-f, with the trade-off strength s varying continuously from 0 to 20. Figure 5 clearly demonstrates how robustly in all

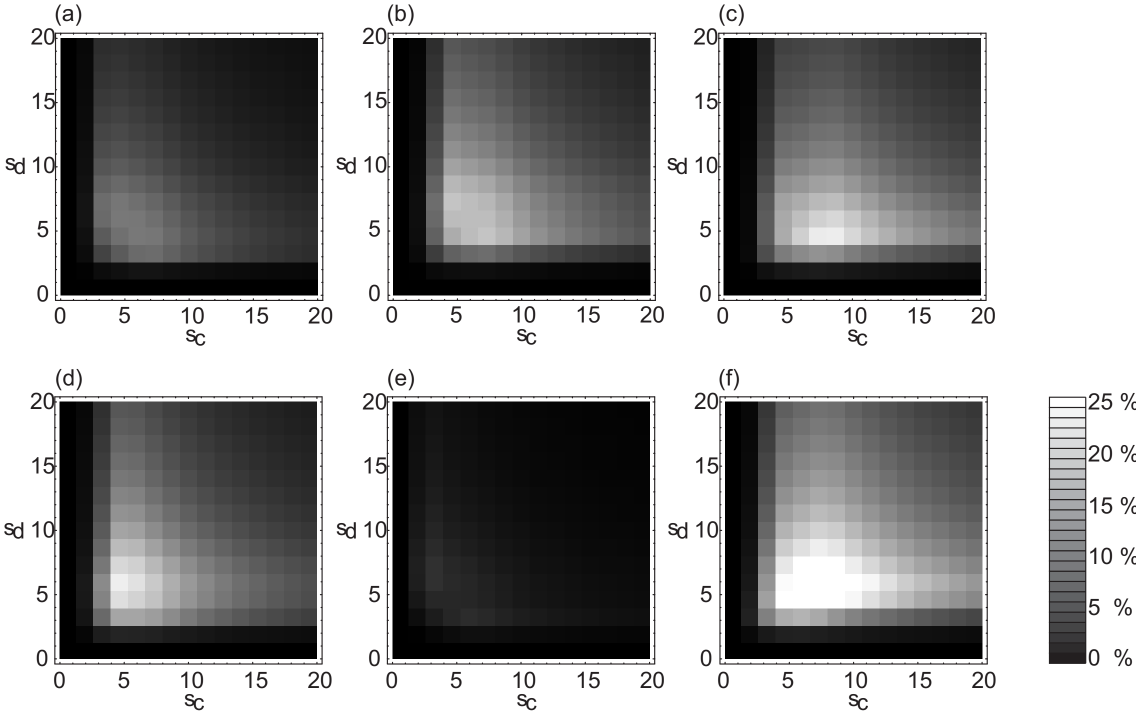

Figure 6. Percentage of trait space for which coexistence is possible as a function of asymmetric trade-off strengths s_c and s_d. Lighter shading indicates a greater potential for coexistence. Parameters for panels (a) to (f) are as in Figures 4a to 4f.

these cases regions of coexistence first grow with increasing s, then peak at intermediately high trade-offs, and finally dwindle again.

As a further test of robustness, Figure 6 shows the area occupied by regions of coexistence as a function of the (now asymmetric) trade-off strengths s_c and s_d. Obviously, for very asymmetric trade-offs ($s_c \gg s_d$ or $s_d \gg s_c$) the antagonist with the weaker trade-off captures most of trait space, since it possesses both higher predatory and competitive capacity at intermediate trait values. Remarkably, however, throughout all six cases considered here, maximal opportunities for coexistence are again to be found at intermediate values of s_c and s_d.

4. Discussion

We have analysed a three-species community model consisting of two antagonists on a dynamic resource. The antagonists can invest in competitive or predatory interactions along a trade-off. When analysing the potential for coexistence in dependence on the relative investment into competition vs. predation our results show a remarkably robust pattern of intermediately strong trade-offs maximizing coexistence. We now explain how this result can be understood by considering the balance between energy intake and interaction strength: in particular coexistence is maximized when attack coefficients are strong enough to guarantee viability through energy inflow, but still weak enough to allow the existence of an antagonist.

Energy intake and population dynamic interactions are key determinants of community structure, as can be seen from Figure 3: When antagonists feed mostly on each other and not on the resource (lower left corner) energy intake is too low for antagonist populations to subsist. When species concentrate primarily on resource consumption (upper right corner) energy intake ensures antagonist viability when monopolizing the resource. However, here an increased strength of population dynamic interactions makes competitive exclusion more likely (Tilman 1982).

Trade-off strengths determine the magnitude of both energy intake and population dynamic interactions at all but the extreme traits. Under strong trade-offs, realized attack coefficients across trait space are low, and thus both potential energy intake and interaction strength are low. Weak trade-offs, by contrast, ensure that realized attack coefficients, and thus potential energy intake and interaction strength, are both high. While a species' existence becomes more feasible with increased energy inflow, coexistence becomes increasingly difficult with stronger interaction strengths. Maximum coexistence is realized where trade-off strength is such that attack coefficients are low enough to allow for coexistence, but still high enough for energy inflow to allow existence. This can be seen in Figures 4 and 5: with stronger trade-offs regions increase where species are energetically limited, and thus only resources can exist. With weakening trade-offs, bistable regions increase, reflecting areas where energetic inflow is sufficient for existence, but interaction strengths are such that coexistence is impossible.

Additional support for our explanations above comes from our test of increasing primary productivity (Figures 4b and 5b). Here resource-only regions decrease and bistable regions increase across all trade-off strengths. Coexistence increases at higher trade-off strengths, not lower ones. At stronger trade-offs, species are primarily energy-limited and thus benefit from the increase in productivity as shown by both the increase in regions of coexistence and the decrease in resource-only regions. At lower trade-offs, energy is not a limiting factor and coexistence is instead limited by the magnitude of interaction strengths. An increase in carrying capacity only serves to increase bistable regions, where priority effects determine community composition. In these regions, energy levels are high enough for existence, but population dynamics are such that coexistence is not possible.

Trade-offs in our study determine both energy intake and interaction strengths. The debate about the expected relation between interaction strength and community structure has been varied and long (May 1971, McCann 2000, and references therein); however, consensus nowadays seems to be that weak to intermediately strong interactions between species offer the greatest scope for community persistence (e.g., McCann 2000; Neutel et al 2002). Our study concurs with this. Notice, however, that these other findings address the absolute strength of interactions, and not, as in our case, the relative partitioning of such strength between targets at different trophic levels. Our results focus on trade-off strengths; with interaction strengths coming into play only indirectly.

Wrapping up, we highlight two limitations of our results. First, most real organisms, obviously, do not live in simple three-species food webs. For example, if one or both of the two antagonists considered here can also forage on an external food source, the potential for coexistence might change. If this (these) other food source(s) are *weakly* coupled to the dynamics of the focal species, they can be approximated by a small constant inflow term in the growth functions. This would lower both death rates for one or both antagonists, thus making room for extra coexistence. Figures 4e and 5e showed that the maximization of coexistence under intermediately strong trade-offs robustly persists, even under varying mortality rates. However, if the coupling of one of our antagonists with an external food source were *strong*, analysis of an expanded model, involving four or more equations instead of three, would become necessary. We predict that potential for coexistence would be increased but note that this case is beyond the scope of this paper.

Second, food webs set the stage for the adaptation of their component species – either on short, population dynamical time scales due to plastic responses and optimal foraging, or on longer, evolutionary time scales due to natural selection. Like in many classic studies (Armstrong & McGehee 1980; Oksanen *et al.* 1981; Tilman 1982), as well as in newer investigations (Huisman & Weissing 1999; Diehl & Feissel 2000; Mylius *et al.* 2001), we have not attempted to study these additional, yet important, questions in the present paper, which has concentrated on charting the potential for ecological coexistence. While we have shown here that intermediately strong trade-offs promote ecological coexistence, questions about how this result fares when also considering behavioural or evolutionary adaptations point the way towards further fruitful research on this topic.

Keeping these caveats in mind, the results presented here lead us to conclude that the potential for coexistence is maximized whenever species are moderately impeded from simultaneously being good at too many things.

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