# Plant coexistence mediated by adaptive foraging preferences of exploiters or mutualists

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Coexistence of plants depends on their competition for common resources and indirect interactions mediated by shared exploiters or mutualists. These interactions are driven either by changes in animal abundance (density-mediated interactions, e.g., apparent competition), or by changes in animal preferences for plants (behaviorally-mediated interactions). This article studies effects of behaviorally-mediated interactions on two plant population dynamics and animal preference dynamics when animal densities are fixed. Animals can be either adaptive exploiters or adaptive mutualists (e.g., herbivores or pollinators) that maximize their fitness. Analysis of the model shows that adaptive animal preferences for plants can lead to multiple outcomes of plant coexistence with different levels of specialization or generalism for the mediator animal species. In particular, exploiter generalism promotes plant coexistence even when inter-specific competition is too strong to make plant coexistence possible without exploiters, and mutualist specialization promotes plant coexistence at alternative stable states when plant inter-specific competition is weak. Introducing a new concept of generalized isoclines allows us to fully analyze the model with respect to the strength of competitive interactions between plants (weak or strong), and the type of interaction between plants and animals (exploitation or mutualism).

Keywords: *behaviorally-mediated interactions, competition for preference, differential inclusion, generalized isocline, switching, sliding and repelling regimes.*

Highlights:

- Adaptive exploiters make coexistence of two strongly competing plant species possible.
- Adaptive mutualists promote alternative plant coexistence states under weak competition.
- Adaptive mutualists always specialize on a single plant.
- The theory extends the isocline concept for ecological models with adaptive traits.

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# 1. Introduction

How do competing species coexist has been a puzzling question for ecologists. The competitive exclusion principle states that two species competing for the same resource cannot coexist at an equilibrium (Gause, 1934; Hardin, 1960). This view is supported by the Lotka–Volterra competition model which predicts that coexistence requires inter-specific competition to be weaker than intra-specific competition. The ecological interpretation is that niche overlap for competing species cannot be too large for species coexistence at an equilibrium (MacArthur and Levins, 1967). These early models of competition focused on two species competing either directly, or indirectly (i.e., interference vs. exploitative competition). Exploitative competition is an example of indirect interaction between two populations mediated by common resources (Grover, 1997). Another indirect interaction is apparent competition (Holt, 1977) that is mediated by shared consumers. In these competitive scenarios coexistence requires that species are limited by different factors. Thus, two exponentially growing plants will not coexist if they are limited by the same resource ("$R^*$" rule, Tilman 1982) or by the same single predator ("$P^*$" rule, Holt et al. 1994). Plant–animal mutualisms, on the other hand, can lead to apparent facilitation as in the case of pollination (Feinsinger, 1987; Ghazoul, 2006) where two plants flowering in different times can sustain large pollinator populations (Waser and Real, 1979).

Indirect interactions can be either density- or behaviorally-mediated. In density-mediated indirect interactions the mediator species density changes. E.g., in apparent competition an increase in one plant density increases herbivore density which, in turn, decreases density of the other plant species. In behaviorally-mediated indirect interactions changes in one plant population density are transmitted through changes in animal behavior when animal population density is fixed. In reality, both density- and trait-mediated indirect interactions operate concurrently (Bolker et al., 2003; Křivan and Schmitz, 2004). Analysis of the apparent competition food web module with two plants and their common consumers who undergo population dynamics and adaptively change their foraging preferences showed that combination of density- and behaviorally-mediated interactions promotes plant coexistence that would not be possible if consumer preferences were fixed (Křivan, 1997). Even when consumers were kept at fixed densities but they adaptively changed their preferences for plants, plant coexistence was still promoted by behaviorally-mediated interactions only (Křivan, 2003b). This suggests that in antagonistic networks adaptive foraging promotes species coexistence by reducing apparent competition. This was verified in more complex antagonistic di- and tri- trophic food web modules with many species (Křivan, 2010). In simulated complex antagonistic food-webs adaptive prey switching also led to increased species persistence (Kondoh, 2003; Berec et al., 2010).

Antagonistic interactions such as competition, predation and parasitism are cornerstones of the niche centric view of community structure (e.g., food webs, guilds), and theories of ecological dynamics and biodiversity (e.g., stability–complexity debate). Currently, there is a great interest about the role of mutualisms as factors shaping communities (Bastolla et al., 2009; Bronstein, 2015). As it turns out, many mutualisms are mediated by consumer–resource mechanisms, and several of them evolved from exploitative relationships such as parasitisms (Bronstein, 2015). Thus, we may be able to understand consequences of both mutualisms and antagonisms using common methodologies (Holland and DeAngelis, 2010). Several models considered apparent competition or apparent facilitation separately, and more recently, also together in the context of mixed mutualistic–antagonistic communities (Mougi and Kondoh, 2014; Sauve et al., 2016). A limited number of models consider density- and behaviorally-mediated effects transmitted by mutualisms. Some predict that adaptive mutualism promotes coexistence in the case of large communities (Valdovinos et al., 2013; Mougi and Kondoh, 2014), while others predict that adaptation constrain coexistence by favoring profitable partner species in detriment to rare ones (Revilla and Křivan, 2016). Thus, more research is required to evaluate the importance of adaptation and plasticity as drivers of population dynamics and community structure in interaction networks that combine both mutualistic and antagonistic interactions. And this motivates us to explore how adaptive behavior of exploiters or mutualists changes the outcomes of competition between the plants with which they interact.

In this article we analyze how behaviorally-mediated interactions transmitted by shared animals influence plant competition. We demonstrate that foraging behavior of animal exploiters (e.g., herbivores) or mutualists (e.g., pollinators) can have important and predictable consequences for plant competitive coexistence. By assuming that animal population densities are fixed, we eliminate density-mediated effects, e.g., apparent competition or apparent facilitation. In this way, we can focus entirely on indirect effects that are mediated only by changes in animal preferences (i.e., they are trait-mediated) for plants. We give conditions for plant coexistence at an equilibrium under exploitation or mutualism either when interaction strength is fixed, or when it is adaptive and maximizes animal fitness.

A plant competition model with adaptive preferences of one animal species for two plants is presented in Section 2. Because optimal animal strategy is not uniquely defined when both plants provide the same payoffs to animals, plant population dynamics are described by a differential inclusion (Aubin and Cellina, 1984; Colombo and Křivan, 1993). For such models we introduce generalized isoclines that allow us to fully analyze the model. Section 3 provides a complete classification of plant equilibria and corresponding animal preferences when animals are either exploiters or mutualists and when inter-specific plant competition is either weak or strong. We conclude that adaptive exploitation permits global stable coexistence when competition between plants is weak, and global or local stable coexistence when competition is strong. In the case of adaptive mutualism only weakly competing plants can coexist at a single equilibrium or at one of two alternative stable states.

## 2. Model

We consider an interaction module consisting of two competing plant species with population densities $P_1$ and $P_2$ and one animal species with population density $A$. The important feature of this interaction module is that plant–animal interactions can be either exploitative (e.g., folivory, granivory, modeled by parameter $s = -1$) or mutualistic (e.g., pollination, seed dispersal, $s = 1$). We assume that animal population density $A$ is fixed, and we are interested in plant population dynamics that are described by a Lotka–Volterra (LV) model

$$\begin{aligned}\frac{dP_1}{dt} &= r_1\left(1-\frac{P_1+c_2P_2}{K_1}\right)P_1 + su_1P_1A\\ \frac{dP_2}{dt} &= r_2\left(1-\frac{P_2+c_1P_1}{K_2}\right)P_2 + su_2P_2A\end{aligned} \tag{1}$$

where $r_i > 0$ and $K_i > 0$ are plant intrinsic growth rates and environmental carrying capacities in absence of inter-specific interactions, and $c_i \geq 0$ is the competition coefficient that measures competitive effects of plant $i$ on the other plant. The strength of plant–animal interactions depends on animal density ($A$) as well as on animal preferences $u_1$ and $u_2$ for plant 1 and 2, respectively ($u_i \geq 0$ for $i = 1, 2$ and $u_1 + u_2 = 1$). Preference for plant $i$ can be interpreted as the proportion of time that an animal spends interacting with that plant, or, alternatively, as the fraction of the animal population ($u_iA$) interacting with that plant.

When animals are mutualists ($s = 1$), model (1) assumes facultative mutualism for plants, i.e., plant populations can grow even without animals. This is a reasonable assumption because the great majority of plants do not rely on a single mutualist species. E.g., when the mutualist is a pollinator, plants can be pollinated by other means (e.g., by wind, or another pollinator species that is not being explicitly considered). Another feature of model (1) is that it assumes constant animal density. This can be a reasonable assumption if plant population dynamics are faster than animal population dynamics or model (1) describes plant dynamics in a small locality, saturated at level $A$ by a large regional population of highly mobile animals (Melián et al., 2009). In these scenarios effects of plants on animal population density (i.e., the numeric response) can be ignored. However, feedbacks between plant density and animal foraging behavior can remain important. Animal adaptation in response to changes in plant community composition affects animal fitness even when the numerical response is not considered. In turn, changes in animal preference influence population density of plants and alter plant community composition. The constant animal density assumption allows us to focus on behavior-mediated effects arising from adaptive animal preferences for plants.

For fixed animal preferences $u_i$ ($i = 1, 2$) model (1) is the classical Lotka–Volterra competitive system with well known dynamics (e.g., Case, 2000; Rohr et al., 2014). In particular, both plants coexist at a globally stable equilibrium

$$(\hat{P}_1, \hat{P}_2) = \left( \frac{K_1 r_2 (r_1 + sAu_1) - c_2 K_2 r_1 (r_2 + sAu_2)}{r_1 r_2 (1 - c_1 c_2)}, \frac{K_2 r_1 (r_2 + sAu_2) - c_1 K_1 r_2 (r_1 + sAu_1)}{r_1 r_2 (1 - c_1 c_2)} \right) \tag{2}$$

if and only if the ratio of carrying capacities satisfies[1]

$$\frac{c_2(1 + su_2 A/r_2)}{1 + su_1 A/r_1} < \frac{K_1}{K_2} < \frac{1 + su_2 A/r_2}{c_1(1 + su_1 A/r_1)}. \tag{3}$$

Thus, stable plant coexistence requires that

$$c_1 c_2 < 1. \tag{4}$$

When inequalities in (3) are reversed, equilibrium (2) is still feasible for intermediate $K_1/K_2$ ratios, but it is unstable, i.e., either plant 1 or 2 wins depending on initial conditions. This is the bistable outcome for the LV model when inter-specific competition is stronger relative to intra-specific competition ($c_1 c_2 > 1$). If under exploitation $u_i A > r_i$, plant $i$ is not viable and no interior equilibrium exists.

In the next sections we show that these predictions change when animals behave adaptively and they maximize their fitness.

## 2.1. Adaptive animal preferences

Here we assume that animal preferences change in the direction that maximizes animal fitness. The payoff to an animal when feeding on plant $i (= 1, 2)$ is measured, e.g., as the amount of energy obtained per unit of time, i.e., $e_i P_i$ where $e_i$ denotes the amount of energy obtained from a single plant per unit of time. Animal fitness is then defined as the average payoff, i.e., $W_A = e_1 u_1 P_1 + e_2 u_2 P_2$ where $u_1 + u_2 = 1$ and $u_i \geq 0$. Under the ideal circumstances where individuals have a perfect knowledge about plant profitabilities and abundances, maximization of this fitness leads to the following optimal foraging strategy (Křivan, 2003b; Křivan and Vrkoč, 2007):

$$u_1 \in U_1(P_1, P_2) = \begin{cases} \{0\} & \text{when} \quad e_1 P_1 < e_2 P_2 \\ [0, 1] & \text{when} \quad e_1 P_1 = e_2 P_2 \\ \{1\} & \text{when} \quad e_1 P_1 > e_2 P_2. \end{cases} \tag{5}$$

When plant densities are such that

$$e_1 P_1 = e_2 P_2, \tag{6}$$

animal preference for plant 1 ($u_1$) is not uniquely defined and can take any value between 0 and 1. This is because either of the two plants provides the same payoff for animals.

The switching line (6) splits the positive quadrant of plant density phase space in two sectors, as shown in Figure 1. In both of these sectors, animals behave as specialists. In sector I (sector II), which is below (above) the switching line, animals specialize on plant 1 (plant 2) only because this maximizes their fitness. For plant densities along the switching line, animals have intermediate preferences ($0 < u_1 < 1$), i.e., they are generalists that interact with both plants.

We observe that when $u_1$ is defined by (5), model (1) becomes a differential inclusion, or, equivalently, a Filippov (1988) regularization of a differential equation with a discontinuous right hand side (see Appendix A.1; Colombo and Křivan, 1993). To analyze such models we introduce in the next section generalized isoclines.

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[1] When $A = 0$ inequalities (3) reduce to $c_2 < \frac{K_1}{K_2} < \frac{1}{c_1}$ which are the classic conditions for stable coexistence in the Lotka–Volterra competition model.

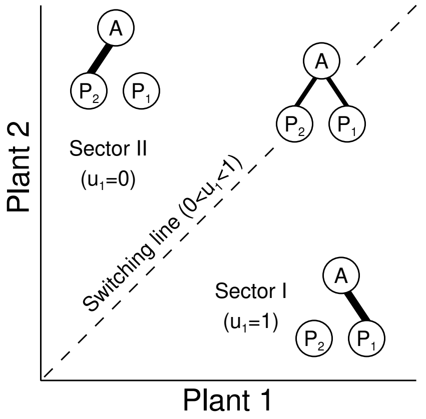

**Figure 1.** Interactions as a function of plant densities (axes) when animal preference changes according to the step-like rule (5). Below the switching line (6) animals specialize on plant 1, and above they specialize on plant 2. Generalism occurs along the switching line where animals display intermediate preferences for plants.

## 2.2. Interaction dynamics

### Generalized isoclines

The effect of adaptive animals on plant coexistence can be predicted by isocline analysis in the plant1–plant 2 phase plane. However, because population dynamics (1) together with animal preferences (5) are described by a differential inclusion, we need to define generalized plant isoclines for this model. Isoclines need to be defined in both sectors I and II, as well as in the switching line (6).

Within sectors I or II plant 1 and 2 isoclines are

$$\begin{aligned} P_1 + c_2 P_2 &= H_1 \\ P_2 + c_1 P_1 &= H_2, \end{aligned} \tag{7}$$

respectively. Here

$$(H_1\,,\,H_2) = \begin{cases} \left(K_1(1+\frac{sA}{r_1}),\,K_2\right) & \text{in sector I} \\ \left(K_1,\,K_2(1+\frac{sA}{r_2})\right) & \text{in sector II} \end{cases} \tag{8}$$

are sector-dependent adjusted carrying capacities that depend on exploitative ($s = -1$) or mutualistic animal effects ($s = 1$). For isoclines to exist in both sectors, $H_1$ and $H_2$ in (8) must be positive, i.e., $r_i + sA > 0$, $i = 1, 2$. Plant $i$ monoculture is viable under exploitation if $A < r_i$, i.e., plant $i$ has limited tolerance for exploitation. If $A > r_1$ ($A > r_2$), isocline for plant 1 (plant 2) does not exist in sector I (sector II) under exploitation. On the other hand, monocultures are always viable under facultative mutualism ($r_i + A > 0$).

As a result, isoclines in sectors I and II are piece-wise linear as illustrated in Figure 2. Plant 1 isocline in sector I is the line segment connecting points $\mathbf{b}$ and $\mathbf{E_1}$, and in sector II is the line segment connecting points $\mathbf{k_1}$ and $\mathbf{a}$. Point

$$\mathbf{E_1} = (P_1^*, 0) = \left(K_1\left(1 + \frac{sA}{r_1}\right)\,,\,0\right) \tag{9}$$

is plant 1 monoculture equilibrium of model (1), and formulas for intersection points $\mathbf{a}$, $\mathbf{b}$ (with switching line) and $\mathbf{k_1}$ (with $P_2$ axis) are given in Appendix A.1. Similarly, plant 2 isocline consists of line segments connecting points $\mathbf{E_2}$ and $\mathbf{p}$ in sector II, and $\mathbf{q}$ and $\mathbf{k_2}$ in sector I. Point

$$\mathbf{E_2} = (0, P_2^*) = \left(0\,,\,K_2\left(1 + \frac{sA}{r_2}\right)\right) \tag{10}$$

is plant 2 monoculture equilibrium of model (1), and intersection points $\mathbf{p}$, $\mathbf{q}$ (with switching line) and $\mathbf{k_2}$ (with $P_1$ axis) are given in Appendix A.1. We remark that both monoculture equilibria exist for mutualists while for exploiters, plant $i$ monoculture equilibrium exists if $A < r_i$.

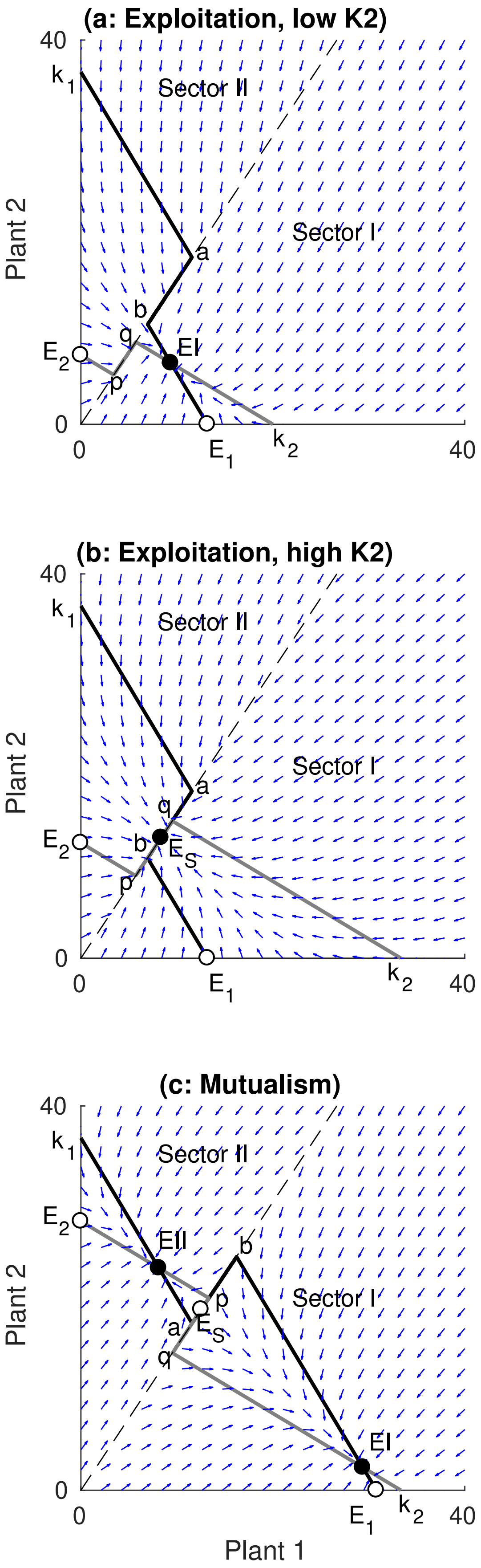

**Figure 2.** Generalized isoclines (plant 1: black, plant 2: gray) and plant dynamics under weak competition ($c_1 c_2 < 1$). The (dashed) switching line (6) splits the phase plane in sectors I and II. Stable equilibria are shown as dots, and unstable equilibria as circles. Panel a assumes low population of exploiters and isoclines intersect at a stable equilibrium in sector I. As the number of exploiters increases (panel b), plants coexist at stable equilibrium $\mathbf{E_S}$ at the switching line where animals are generalists. In panel c animals are mutualists and isoclines intersect at two stable equilibria, one in each sector. Equilibrium $\mathbf{E_S}$ is unstable. Parameter values: $r_i = 0.1, c_i = 0.6, e_1 = 1.5, e_2 = 1, A = 0.04, K_1 = 22$; $K_2 = 12$ in (a) and $K_2 = 20$ in (b,c); $s = -1$ in panels a,b, and $s = 1$ in panel c.

We define *generalized isoclines* by adding the segment **a**—**b** to plant 1 isocline, and segment **p**—**q** to plant 2 isocline. Thus, both plant isoclines are continuous, piece-wise linear curves in plant phase space. Plant 1 (plant 2) isocline is shown as the black (gray) line in Figure 2. We stress here, that along their central segments (**a**—**b** for plant 1 isocline, and **p**—**q** for plant 2 isocline) the usual definition of isoclines as points of zero growth for particular plant species does not hold for generalized isoclines. In particular, we show in the next section that when the two segments partially overlap along the switching line as in Figure 2b, c, the overlap segment (**b**—**q** in panel b and **a**—**p** in panel c) does not consist of equilibria only, as we explain in the next section.

We remark that under exploitation ($s = -1$) plant 1 (plant 2) generalized isocline consists of three segments if $r_1 > A$ ($r_2 > A$). Otherwise, the isocline has only two segments because $\mathbf{E_1}$ and **b** ($\mathbf{E_2}$ and **p**) are not in the first quadrant. In case of mutualism ($s = 1$) generalized isoclines always consist of three segments because monocultures are viable since we assume that mutualism is facultative.

Appendix D shows that generalized isoclines obtained for step-like preferences given in (5) are well approximated by smooth (usual) isoclines when preferences are more gradual. However, the generalized isoclines allow us to fully analyze the model.

## Model equilibria

In the classic Lotka–Volterra (LV) model (1) stable plant coexistence requires that the missing species can invade when the other plant is at its population equilibrium. This is a consequence of linear isoclines that generically intersect at most once. The case where animals behave adaptively is more complex, because generalized isoclines are piece-wise linear and there can be interior equilibria in both sectors (e.g., Figure 2c). In addition, we show in this section that there is one equilibrium at the segment of the switching line where the two isoclines coincide (e.g., Figure 2b, c).

We start by analyzing position of isoclines in sectors I and II. Since isoclines are linear there they can intersect in either sector at most once. If they intersect, the corresponding equilibrium is locally stable[2] when $c_1c_2 < 1$ and unstable when $c_1c_2 > 1$. This follows from analysis of the classic LV competition model. We also observe that at these equilibria animals behave as specialists as they interact with a single plant only. To determine if isoclines intersect within a sector, we compare their intersections with the corresponding sector's axis and with the switching line (6). In sector I we compare position of equilibrium $\mathbf{E_1}$ with respect to point $\mathbf{k_2}$ on $P_1$ axis, and position of point **b** with respect to point **q** on the switching line. If $\mathbf{E_1}$ exists and

$$\mathbf{E_1} < \mathbf{k_2} \quad \text{and} \quad \mathbf{q} < \mathbf{b} \tag{11}$$

by which we mean that point $\mathbf{E_1}$ is to the left of point $\mathbf{k_2}$ on $P_1$ axes and point **q** is to the left and down from point **b** along the line $e_1P_1 = e_2P_2$, or

$$\mathbf{E_1} > \mathbf{k_2} \quad \text{and} \quad \mathbf{q} > \mathbf{b}, \tag{12}$$

Appendix A.1 shows that there is one coexistence equilibrium

$$\mathbf{E_I} = \left(\hat{P}_1, \hat{P}_2\right) = \left(\frac{K_1r_2(r_1 + sA) - c_2K_2r_1r_2}{r_1r_2(1 - c_1c_2)}, \frac{K_2r_1r_2 - c_1K_1r_2(r_1 + sA)}{r_1r_2(1 - c_1c_2)}\right) \tag{13}$$

in sector I and this equilibrium is locally stable when (11) holds because in this case $c_1c_2 < 1$ (Figure 2a, c). If conditions in (12) hold, the equilibrium is unstable. Appendix A.1 shows that (11) is equivalent with

$$\gamma_2 \equiv c_1\left(1 + \frac{sA}{r_1}\right) < \frac{K_2}{K_1} < \left(\frac{e_1 + c_1e_2}{e_2 + c_2e_1}\right)\left(1 + \frac{sA}{r_1}\right) \equiv \tau_2. \tag{14}$$

If both inequalities in (14) are reversed, $\mathbf{E_I}$ still exists because isoclines intersect in sector I but the equilibrium is unstable. If $K_2/K_1$ is larger or smaller than both $\gamma_2$ and $\tau_2$, there is no equilibrium in sector I because the two isoclines do not intersect there (e.g., Figure 2b where $\mathbf{E_1} < \mathbf{k_2}$ but $\mathbf{b} < \mathbf{q}$).

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[2] By local stability we mean local asymptotic stability throughout this article.

Similarly, in sector II we compare position of $\mathbf{k_1}$ with respect to equilibrium $\mathbf{E_2}$ on the $P_2$ axis, and position of $\mathbf{a}$ with respect to $\mathbf{p}$ along the switching line. If equilibrium $\mathbf{E_2}$ exists and

$$\mathbf{E_2} < \mathbf{k_1} \quad \text{and} \quad \mathbf{a} < \mathbf{p} \tag{15}$$

or

$$\mathbf{E_2} > \mathbf{k_1} \quad \text{and} \quad \mathbf{a} > \mathbf{p}, \tag{16}$$

Appendix A.1 shows that there is one equilibrium in sector II

$$\mathbf{E_{II}} = \left(\hat{P}_1, \hat{P}_2\right) = \left(\frac{K_1 r_1 r_2 - c_2 K_2 r_1 (r_2 + sA)}{r_1 r_2 (1 - c_1 c_2)}, \frac{K_2 r_1 (r_2 + sA) - c_1 K_1 r_1 r_2}{r_1 r_2 (1 - c_1 c_2)}\right). \tag{17}$$

This equilibrium is locally stable if and only if

$$\gamma_1 \equiv c_2 \left(1 + \frac{sA}{r_2}\right) < \frac{K_1}{K_2} < \left(\frac{e_2 + c_2 e_1}{e_1 + c_1 e_2}\right)\left(1 + \frac{sA}{r_2}\right) \equiv \tau_1. \tag{18}$$

As in sector I, instability of $\mathbf{E_{II}}$ follows from inequality reversal in (18). When $K_1/K_2$ is larger or smaller than both $\gamma_1$ and $\tau_1$, no equilibrium exists in sector II.

We note that $\gamma_1$ and $\gamma_2$ are *invasion thresholds* that must be met by $K_1/K_2$ and $K_2/K_1$, respectively, for plant 1 to invade at equilibrium $\mathbf{E_2}$ and for plant 2 to invade at equilibrium $\mathbf{E_1}$, respectively. Invasion thresholds depend on resident plant parameters, plant–animal interaction type, and animal density. For example, $\gamma_1$ is directly proportional to the competitive effect of plant 2 on plant 1 ($c_2$) exactly as in standard LV models. This means that increasing inter-specific competition makes plant 1 less likely to invade resident population consisting of plant 2 only. Under exploitation, increasing animal density decreases the threshold allowing plant 1 to invade, while increasing plant 2 intrinsic growth rate ($r_2$) makes this plant more difficult to invade. These predictions change under mutualism because the invasion threshold for plant 1 increases with increasing density of mutualists and decreases with plant 2 intrinsic growth rate.

Now we look for plant equilibria in the segment of the switching line where the two generalized isoclines overlap. To answer this question we have to analyze plant dynamics (1) with optimal animal behavior (5) on the switching line where animal preference for either plant is not uniquely defined. Analysis in Appendix A.2 shows that when the two generalized isoclines partially overlap along the switching line, there exists a single equilibrium in the overlap segment

$$\mathbf{E_S} = (\bar{P}_1, \bar{P}_2) = \left(\frac{e_2 K_1 K_2 (r_1 + r_2 + sA)}{K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)}, \frac{e_1 K_1 K_2 (r_1 + r_2 + sA)}{K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)}\right), \tag{19}$$

see Figure 2b, c. This equilibrium is locally stable under exploitation (Figure 2b) and unstable under mutualism (Figure 2c). Appendix A.2 also shows that animal preference for plant 1 at this equilibrium is

$$\bar{u}_1 = \frac{K_2 r_1 (r_2 + sA)(e_2 + c_2 e_1) - K_1 r_1 r_2 (e_1 + c_1 e_2)}{sA\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]}, \tag{20}$$

i.e., animals behave as generalists at this equilibrium.

This analysis allows us to give meaning to *attraction thresholds* $\tau_i$ defined in (14) and (18). For equilibrium $\mathbf{E_S}$ to exist, $\bar{u}_1$ must be between 0 and 1. Under exploitation ($s = -1$) this happens when

$$\frac{K_1}{K_2} > \tau_1 \quad \text{and} \quad \frac{K_2}{K_1} > \tau_2 \tag{21}$$

while under mutualism ($s = 1$) the conditions are

$$\frac{K_1}{K_2} < \tau_1 \quad \text{and} \quad \frac{K_2}{K_1} < \tau_2. \tag{22}$$

Equilibrium $\mathbf{E_S}$ exists when $r_1 + r_2 + sA > 0$ and it is always locally stable for exploitation (i.e., (21) holds and "$\mathbf{E_S}$ attracts" locally trajectories from both sectors) and unstable for mutualism (i.e., (22)

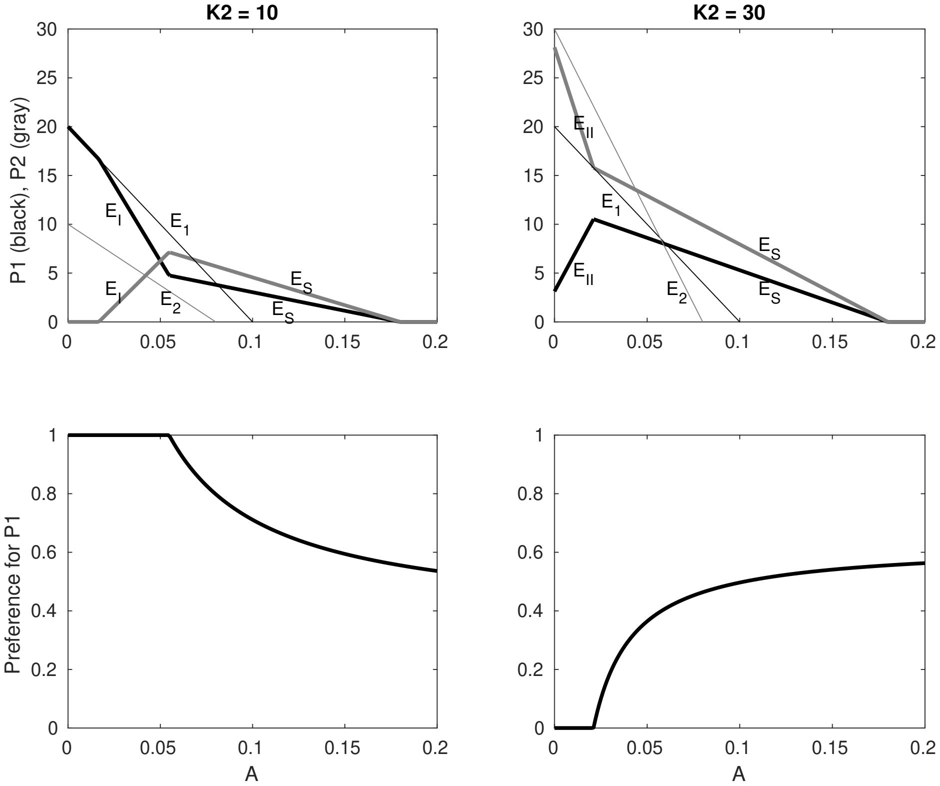

**Figure 3.** Plant coexistence under weak competition ($c_1c_2 < 1$) and adaptive exploitation ($s = -1$), for high (left column) or low (right column) $K_1/K_2$ ratios. Top panels show stable plant coexistence (thick lines) and monoculture ($\mathbf{E_1}$ and $\mathbf{E_2}$, thin lines) equilibria as a function of exploiter density. Bottom panels show corresponding exploiter preference for plant 1 ($u_1$). It is interesting to observe that plant $i(= 1, 2)$ monoculture is viable only when $A \leq r_i$ while when together, both plants form viable community for higher animal densities satisfying $A \leq r_1 + r_2$. Parameter values: $r_1 = 0.1, r_2 = 0.08, c_i = 0.6, e_1 = 1.5, e_2 = 1, K_1 = 20$.

holds and "$\mathbf{E_S}$ repels" trajectories away; see Appendix A.2). If only one attraction threshold is passed, equilibrium $\mathbf{E_S}$ does not exist and there is no plant population equilibrium at which animals behave as generalists. Here the important observation is that existence and stability of equilibrium $\mathbf{E_S}$ does not depend whether single plant monocultures are viable or not. In fact, even if neither of the two plants is viable (i.e., $A > r_i$, $i = 1, 2$), equilibrium $\mathbf{E_S}$ still exists provided $A < r_1 + r_2$ (Figure 3). We show next how plant coexistence and animal preferences depend on animal abundance and model parameters.

Figure 3 illustrates the effects of adaptive exploiters on plant equilibria and exploiter preferences for plants. Let us consider the situation where

$$\frac{K_1}{K_2} > \frac{e_2 + c_2e_1}{e_1 + c_1e_2} \tag{23}$$

(left column of Figure 3). Without exploiters ($A = 0$), plant 1 wins competition over plant 2. As the number of exploiters increases, exploiters are plant 1 specialists ($u_1 = 1$, bottom-left panel) and plant 1 equilibrium density decreases until $A \approx 0.017$. For higher exploiter density (approx. $0.017 < A < 0.055$) plant 2 invades plant 1 monoculture and both plants coexist at equilibrium $\mathbf{E_I}$ given in (13). Plant 1 population density keeps decreasing with increasing $A$ while plant 2 population density increases. Exploiters still behave as specialists on plant 1 till their population reaches another critical threshold $A \approx 0.055$. For yet higher exploiter density, animals behave as generalists feeding on both plants with decreasing preference for plant 1 given in (20) and plants coexist at equilibrium $\mathbf{E_S}$ given in (19). Thus, both plant population densities now decrease with increasing animal abundance. The case where opposite inequality in (23) holds is shown in the right panels of Figure 3. In this case, exploiters start as plant 2 specialists ($u_1 = 0$, bottom-right panel) at plant equilibrium $\mathbf{E_{II}}$ given in (17). Thus, plant 2 decreases monotonically while plant 1 increases for $0 \leq A < 0.021$. Once both plants are equally profitable for animals, animals become generalists and both plants start to decrease

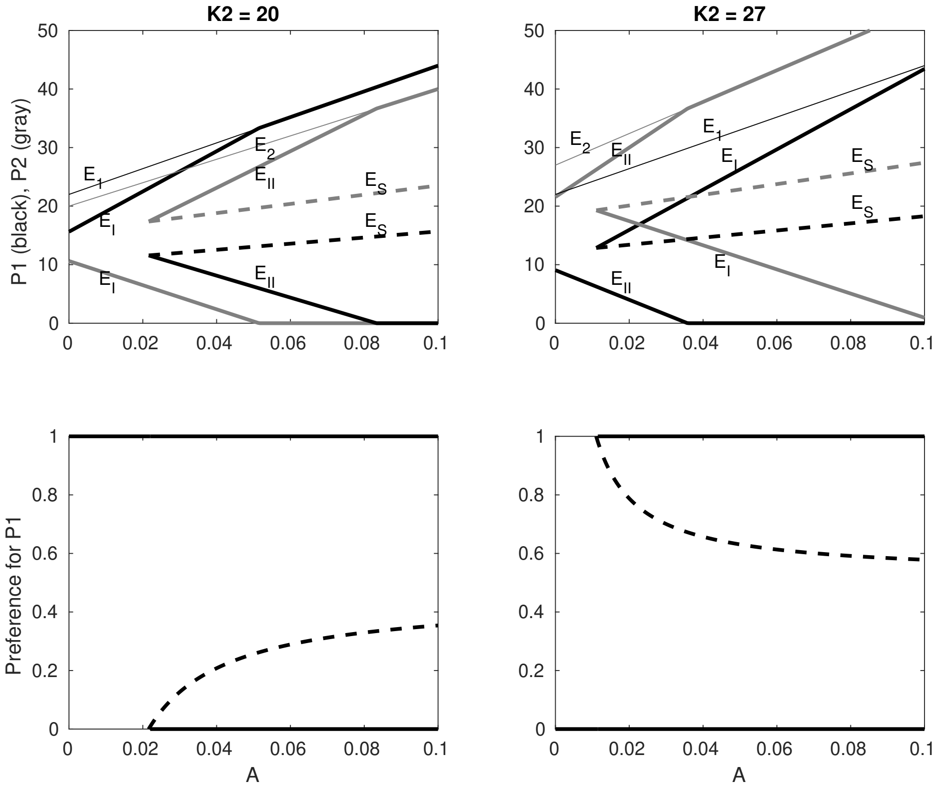

**Figure 4.** Plant coexistence under weak competition ($c_1 c_2 < 1$) and adaptive mutualism ($s = 1$), for high (left column) or low (right column) $K_1/K_2$ ratios. Top panels show stable coexistence ($\mathbf{E_I}$ and $\mathbf{E_{II}}$, thick lines) and monoculture ($\mathbf{E_1}$ and $\mathbf{E_2}$, thin lines) equilibria as a function of exploiter density. Bottom panels show corresponding mutualist preference for plant 1 ($u_1$). An alternative stable state (thick gray lines) emerges when $u_1$ changes from 1 or 0 into $0 < u_1 < 1$. Parameter values: $r_i = 0.1, c_i = 0.6, e_1 = 1.5, e_2 = 1, K_1 = 22$.

together as preference for plant 1 keeps increasing.

Figure 3 also shows that adaptive exploitation leads to indirect positive effects between plants. First, when animals are adaptive exploiters, plant equilibrium densities are positive for animal densities at which plant monocultures are not viable. E.g., plant 1 (plant 2) monoculture cannot exist for $A > 0.1$ ($A > 0.08$) in Figure 3 but both plants do coexist at $\mathbf{E_S}$ as long as $A \leq r_1 + r_2 = 0.18$. Thus, for large exploiter densities viability of plant 1 relies on co-occurrence with plant 2 and vice-versa. Second, from (19) it follows that under generalism increasing $K_1$ or $K_2$ raises both plant equilibrium densities (cf. right vs. left top panels in Figure 3 for $A > 0.05$). This is unlike standard LV models where increasing $K_2$ causes increase of plant 2 equilibrium density and decrease of plant 1. The effect of other parameters on plant equilibria ($\mathbf{E_I}, \mathbf{E_{II}}, \mathbf{E_S}$) is given in Appendix B.

Effects of changes in parameters on plant equilibria in the case of mutualism are often in opposite directions as compared to exploiters (see Appendix B). Because we assume that mutualism is facultative, plant monocultures ($\mathbf{E_1}$ and $\mathbf{E_2}$) are always viable and they increase with $A$. Provided both plants coexist, plant 1 increases and plant 2 decreases with $A$ at equilibrium $\mathbf{E_I}$, and the opposite happens at equilibrium $\mathbf{E_{II}}$. Equilibrium $\mathbf{E_S}$, if it exists, is always unstable. Figure 4 serves as a good illustration. The left column displays plant coexistence at equilibrium $\mathbf{E_I}$ when $A < 0.022$ and animals specialize on plant 1 ($u_1 = 1$). For higher animal densities there are two stable equilibria $\mathbf{E_I}$ and $\mathbf{E_{II}}$ and unstable interior equilibrium $\mathbf{E_S}$ at which animals are generalists. The right column shows situation where $K_1/K_2$ is lower and plants coexists at equilibrium $\mathbf{E_{II}}$ when $A < 0.0115$ and animals specialize on plant 2. For higher animal densities there are two coexisting stable plant equilibria $\mathbf{E_I}$ and $\mathbf{E_{II}}$ and the unstable equilibrium $\mathbf{E_S}$.

# 3. Plant coexistence under exploitation or mutualism

By comparing $K_1/K_2$ with $\gamma_1$ and $\tau_1$ thresholds in (18), and $K_2/K_1$ with $\gamma_2$ and $\tau_2$ thresholds in (14), we provide a complete classification of model outcomes for all generic parameter combinations, see Appendix C. In the following sections we discuss all possible global dynamics when animals are exploiters or mutualists, and plant inter-specific competition is weak or strong. In the particular case of exploitation, we only display scenarios where $A < r_1$ and $A < r_2$, i.e., plant monocultures are viable and generalized isoclines display three segments. Scenarios where monocultures are not viable, i.e., $A > r_i$, lead to similar global dynamics as long as $r_1 + r_2 > A$ (i.e., if $A > r_1 + r_2$ both plants go extinct like in Figure 3).

## 3.1. Exploitation ($s = -1$) and weak inter-specific plant competition ($c_1c_2 < 1$)

All qualitatively different patterns of isoclines intersections when inter-specific competition is weak and $A < r_i$ are shown in Figure 5. Since $s = -1$, either $K_1/K_2 > \tau_1$ or $K_2/K_1 > \tau_2$, i.e., at least one plant is always above its attraction threshold.[3] This is why Figure 5a, b, d, e are blank, because there are no parameters that satisfy inequalities that define these four panels. With respect to plant equilibria, there are three mutually exclusive possible outcomes of plant competition.

First, the missing plant cannot invade the other plant monoculture equilibrium and plant coexistence is not possible. These are situations where generalized isoclines do not intersect nor overlap, and the dynamics globally converge toward the monoculture equilibrium of the plant that can invade (to $\mathbf{E_1}$ in Figure 5c, and to $\mathbf{E_2}$ in panel g).

Second, both plants can invade one another and the generalized isoclines intersect in one of the two sectors. Thus, both plants coexist either at the globally stable equilibrium $\mathbf{E_I}$ (panel f) at which exploiters specialize on plant 1, or globally stable equilibrium $\mathbf{E_{II}}$ (panel h) at which exploiters specialize on plant 2.

Third, generalized isoclines partially overlap along the switching line (Figure 5i), so that there is globally stable equilibrium $\mathbf{E_S}$ at which animals behave as generalists with intermediate preferences for plant 1 given by $\bar{u}_1$ in (20).

## 3.2. Exploitation ($s = -1$) and strong inter-specific plant competition ($c_1c_2 > 1$)

Since $s = -1$, there are no parameters satisfying $K_2/K_1 < \tau_2$ and $K_1/K_2 < \tau_1$ exactly as in the previous case of weak competition and there are 8 qualitative cases for isoclines intersections (Figure 6).

Due to strong competition, stable plant coexistence is impossible in sector I or sector II, but when both attraction thresholds are met (i.e., $K_1/K_2 > \tau_1$ and $K_2/K_1 > \tau_2$), the isoclines partially overlap along the switching line and plants can coexist at equilibrium $\mathbf{E_S}$ where exploiters behave as adaptive generalists with intermediate preference $\bar{u}_1$ for plant 1. This state of coexistence can be locally or globally stable, depending on whether invasion thresholds are met, as we will see next.

If neither of the two invasion thresholds are met (Figure 6e), equilibrium $\mathbf{E_S}$ is locally stable and depending on initial conditions there are three possible outcomes for plant population dynamics: (i) monoculture equilibrium $\mathbf{E_1}$ where exploiters specialize on plant 1 ($u_1 = 1$) and plant 2 is excluded, (ii) monoculture equilibrium $\mathbf{E_2}$ where exploiters specialize on plant 2 ($u_1 = 0$) and plant 1 is excluded, or (iii) plant coexistence equilibrium $\mathbf{E_S}$.

If only one plant invasion threshold is met, equilibrium $\mathbf{E_S}$ stays locally stable and there is another monoculture equilibrium for the plant that meets its invasion threshold (i.e., $\mathbf{E_1}$ in panel f, or $\mathbf{E_2}$ in panel h).

If both plants are above their invasion thresholds, $\mathbf{E_S}$ is globally stable (Figure 6i), despite of intra-specific competition being stronger than inter-specific ($c_1c_2 > 1$) that would not permit stable coexistence in the standard LV competition model.

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[3] The case where both $K_1/K_2 < \tau_1$ and $K_2/K_1 < \tau_2$ is not possible because then $1 < \tau_1\tau_2 = (1 - \frac{A}{r_1})(1 - \frac{A}{r_2}) < 1$, a contradiction.

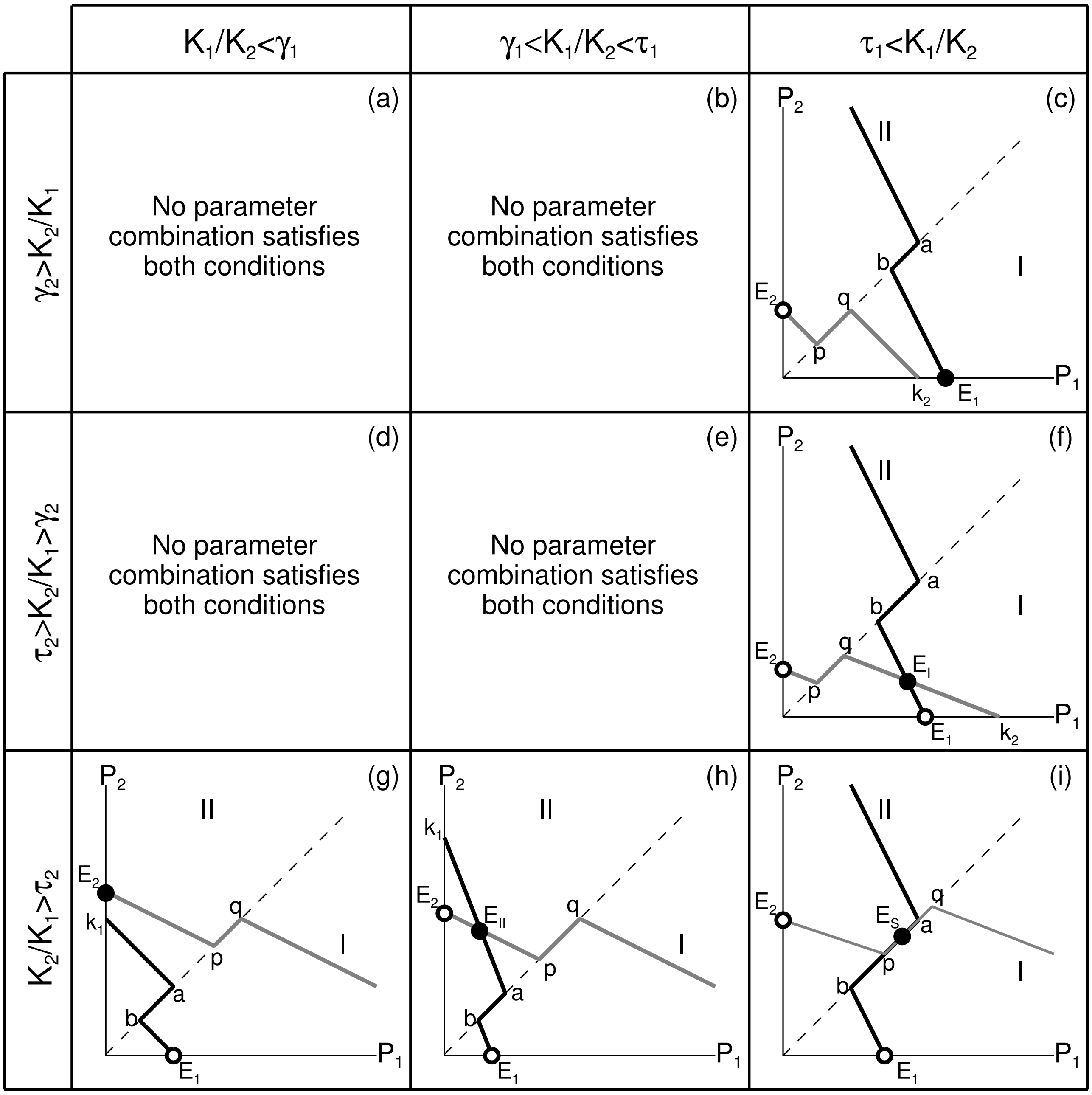

**Figure 5.** Plant generalized isoclines (plant 1: black, plant 2: gray) under exploitation ($s = -1$) and weak competition ($c_1c_2 < 1$). Isoclines intersect the dashed switching line (6) at four points **a**, **b**, **p**, **q**. Animals specialize on plant 1 (2) in sector I (II) that is below (above) the switching line in the $P_1P_2$ plane. Dots and circles denote stable and unstable equilibria (9,10,13,17,19), respectively. Representative configurations are sketched according to carrying capacity ratios in relation to invasion ($\gamma_1$, $\gamma_2$) and attraction ($\tau_1$, $\tau_2$) thresholds.

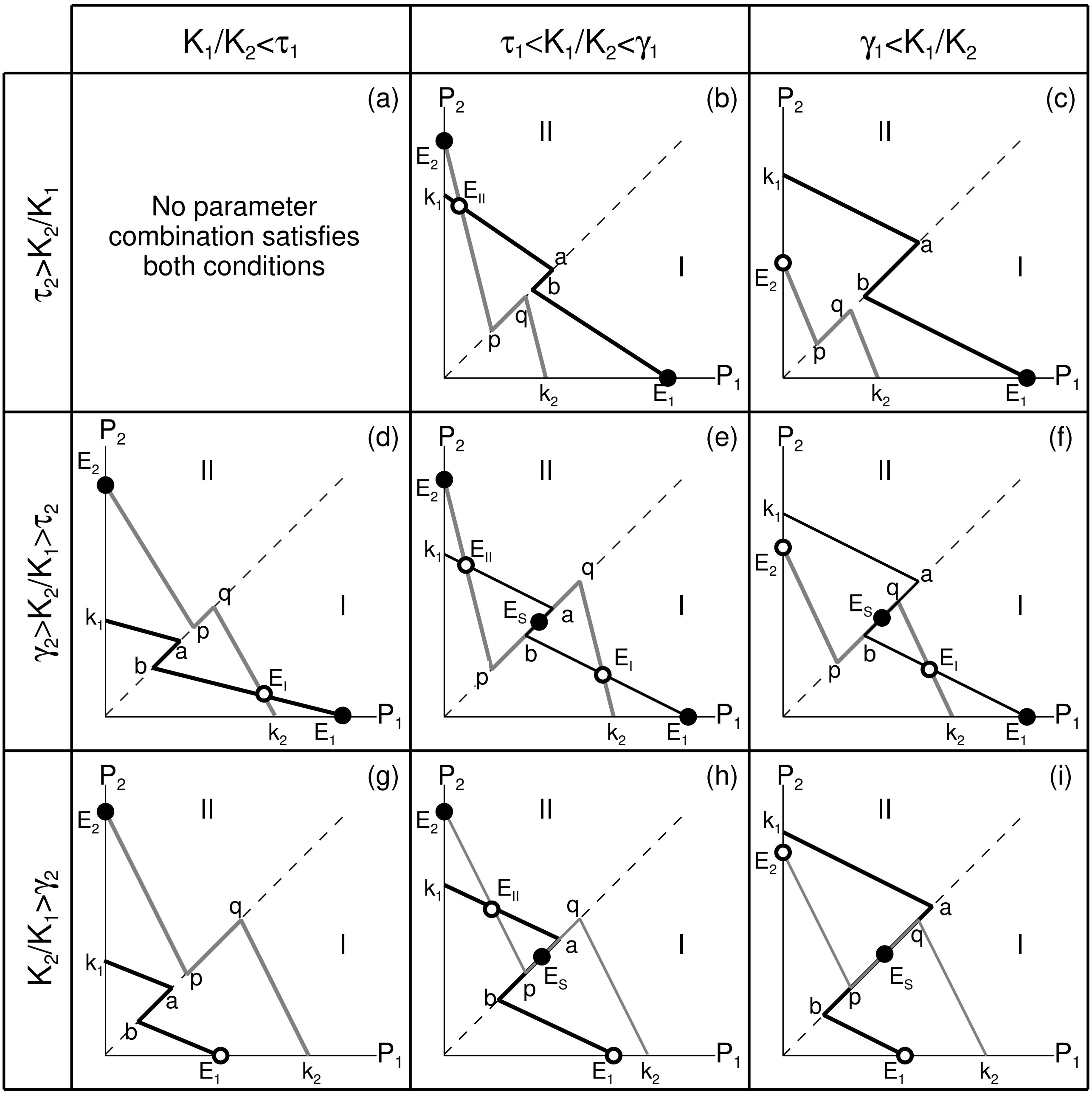

**Figure 6.** Plant generalized isoclines under exploitation ($s = -1$) and strong competition ($c_1c_2 > 1$). Notation like in Figure 5.

Like in standard LV models with strong competition, there are parameter values for which generalized isoclines intersect in a single unstable equilibrium, leading to the well known bi-stable outcome where plant 1 or plant 2 wins depending on initial conditions (Figure 6b,d).

## 3.3. Mutualism ($s = 1$) and weak inter-specific plant competition ($c_1c_2 < 1$)

All possible qualitative intersections of isoclines under mutualism and weak inter-specific plant competition are shown in Figure 7. As inter-specific competition is weak ($c_1c_2 < 1$), plant invasion thresholds are smaller than attraction thresholds ($\gamma_1 < \tau_1$ and $\gamma_2 < \tau_2$) and there are no parameter values such that $K_1/K_2 > \tau_1$ and $K_2/K_1 > \tau_2$, i.e., panel i in Figure 7 is empty.[4]

There are important differences in plant competition dynamics under mutualism when compared to the exploitative case (cf. Figure 7 vs. Figure 5). The main difference is that the interior equilibrium $\mathbf{E_S}$, when it exists, is unstable for mutualism (Figure 7a, b, d, e). As this is the only plant coexistence equilibrium at which animals behave as generalists, this predicts that mutualists will always behave as specialists when plants are at a locally stable equilibrium, whether both plants coexist (Figure 7b, d, e, f, h) or not (Figure 7a, c, g). The other important difference between mutualists vs. exploiters is that mutualism leads to alternative locally stable plant equilibria (Figure 7a, b, d, e). Where the plant dynamics converge depends on initial plant population densities, and there are three general cases that we describe next.

First, if neither plant invasion threshold is met (Figure 7a) initial conditions lead towards monoculture equilibrium $\mathbf{E_1}$ or $\mathbf{E_2}$, where mutualists specialize on plant 1 or plant 2 respectively. This outcome is analogous to the bi-stable case of the standard LV competition model when competition is strong ($c_1c_2 > 1$) and the interior equilibrium is a saddle point. But here, instead, competition is weak ($c_1c_2 < 1$), and bi-stability arises because equilibrium $\mathbf{E_S}$ on the switching line behaves like a saddle point. We described similar outcomes of mutual exclusion in previous obligatory mutualism models (Revilla and Křivan, 2016), where plants competed exclusively for pollinator preferences (i.e., $c_1 = c_2 = 0$).

Second, when plant 1 (2) meets its invasion threshold and the other plant 2 (1) does not, initial conditions lead either to a monoculture of plant 1 (2) or to stable coexistence of both plants with mutualists specializing on plant 2 (1) (e.g., $\mathbf{E_1}$ or $\mathbf{E_{II}}$ in Figure 7b; $\mathbf{E_2}$ or $\mathbf{E_I}$ in panel d).

Third, when both plants are above their invasion thresholds there are locally stable equilibria in both sectors, and initial conditions determine whether coexistence takes place at equilibrium $\mathbf{E_I}$ where mutualists specialize on plant 1, or at $\mathbf{E_{II}}$ where they specialize on plant 2 (Figure 7e).

## 3.4. Mutualism ($s = 1$) and strong inter-specific plant competition ($c_1c_2 > 1$)

When animals are mutualists ($s = 1$) and inter-specific plant competition is strong ($c_1c_2 > 1$) attraction thresholds are smaller than invasion thresholds ($\gamma_i > \tau_i$, $i = 1, 2$) and there are no parameters satisfying $K_2/K_1 > \gamma_2$ and $K_1/K_2 > \gamma_1$ (i.e., panels e, f, h and i in Figure 8 are empty). Moreover, plant coexistence is impossible (Figure 8) which is in a sharp contrast with the case of exploiters (Figure 6) where plant coexistence is possible depending on initial conditions.

When isoclines intersect in sector I or II, and do not overlap along the switching line, one plant competitively excludes the other plant, and plant population dynamics are bi-stable (Figure 8b, d). These bi-stable scenarios can be attributed entirely to strong inter-specific competition, like in standard LV competition models. But again, as in the case of exploitation with strong competition, bi-stability leads to mutualists specializing either on plant 1, or on plant 2.

Bi-stability can also be caused by instability of equilibrium $\mathbf{E_S}$ when the two plant isoclines partially overlap (Figure 8a), similarly to the case where competition is weak as discussed in the previous Section 3.3.

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[4] Indeed inequalities $K_1/K_2 > \tau_1$ and $K_2/K_1 > \tau_2$ imply that $\tau_1\tau_2 = (1 + \frac{sA}{r_1})(1 + \frac{sA}{r_2}) < 1$ which is false under mutualism when $s = 1$ .

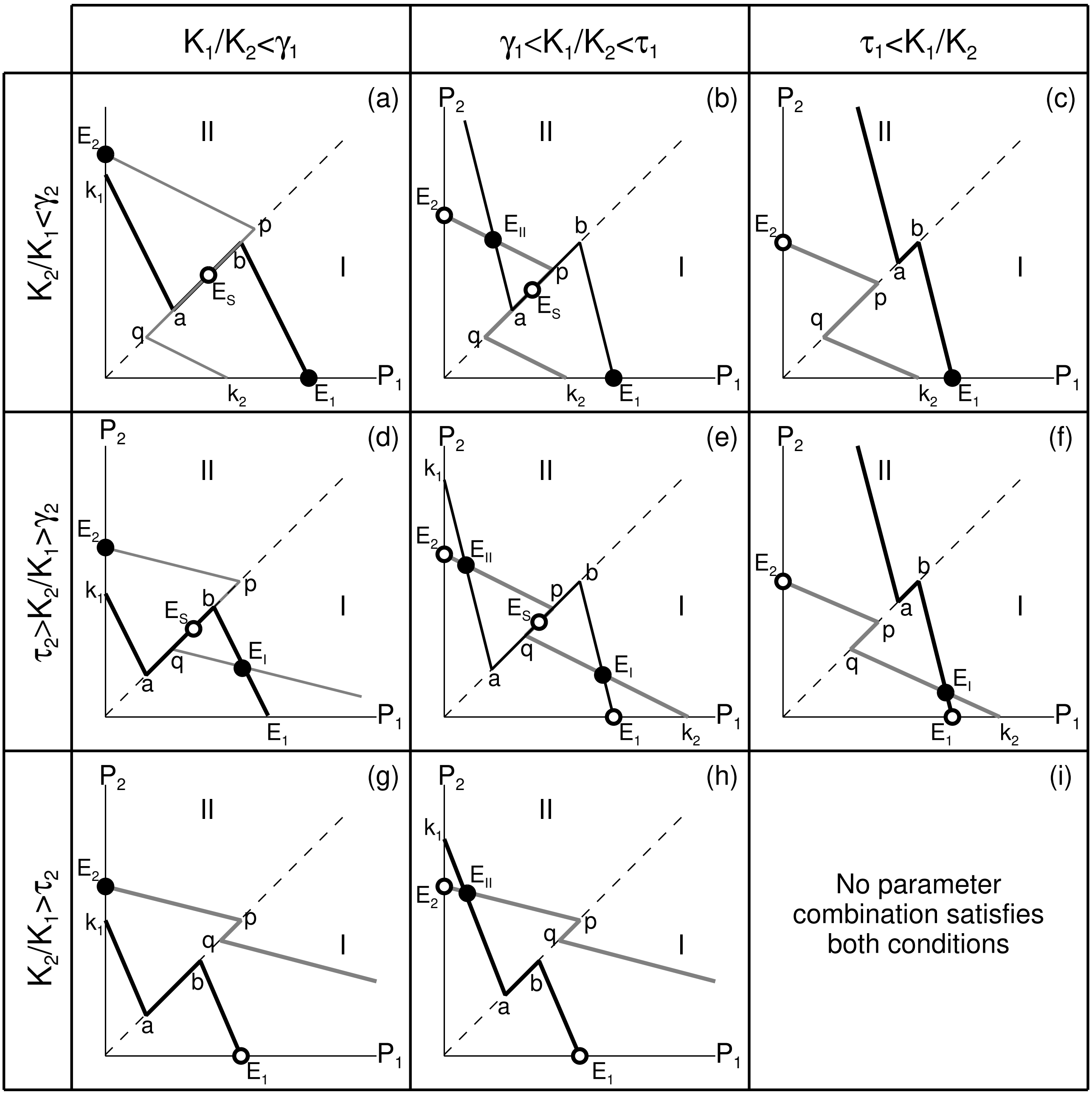

**Figure 7.** Plant generalized isoclines under mutualism ($s = 1$) and weak competition ($c_1c_2 < 1$). Notation like in Figure 5.

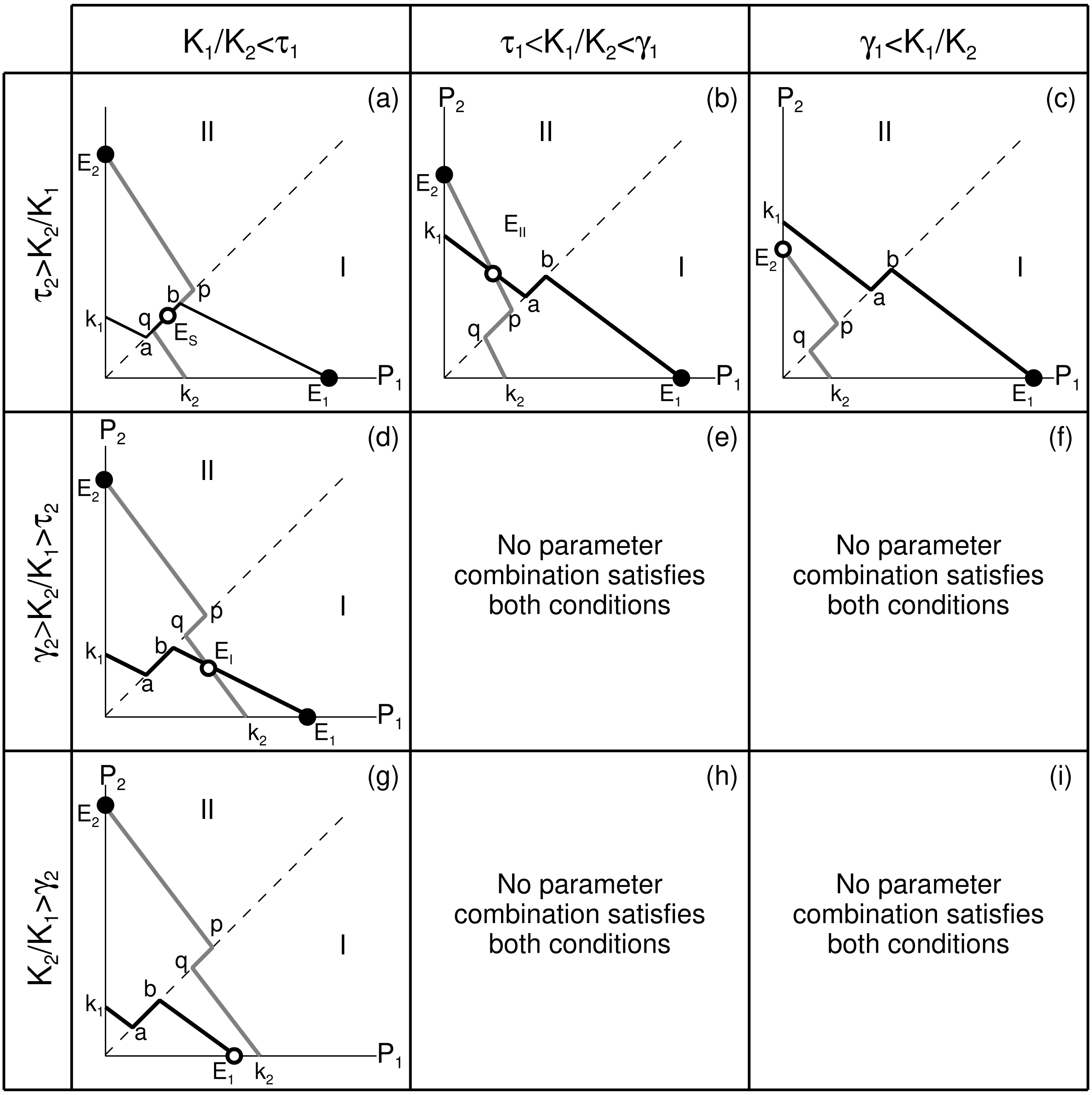

**Figure 8.** Plant generalized isoclines under mutualism ($s = 1$) and strong competition ($c_1 c_2 > 1$). Notation like in Figure 5.

# 4. Discussion

In this article we study effects of adaptive exploiters or mutualists on two competing plant population dynamics, and on animal preference for plants. For plant population dynamics described by the Lotka–Volterra competition model we provide a complete classification (Figures 5–8, Appendix C) of coexistence states when plants interact either with adaptive exploiters or mutualists that have fixed population densities. This classification is based on comparing plant *invasion* ($\gamma_i$ given in (14)) and *attraction* ($\tau_i$ given in (18)) thresholds. These critical numbers capture the combined influences of (i) plant–animal interaction type (exploitation vs. mutualism), (ii) inter-specific plant competition (weak vs. strong), and (iii) indirect effects between plants mediated by changes in animal preferences.

Model analysis leads to the following general predictions:

1. Under exploitation and weak competition a globally stable plant coexistence equilibrium exists when carrying capacities are not very unbalanced. At plant coexistence equilibrium exploiters are specialist when at low densities while at high densities they are generalists. Plant coexistence is possible even if neither of the two plants is viable as a monoculture.

2. Plant coexistence under exploitation and strong competition is possible but conditional, i.e., depends on initial conditions. Up to three plant equilibria can co-exist. Plant coexistence is possible only due to adaptive behavior of exploiters when exploiters behave as adaptive generalists.

3. Plant coexistence under mutualism and weak competition can be global or conditional on initial plant population densities. Under mutualism animals always specialize on the more profitable plant only.

4. Plant coexistence under mutualism and strong competition is impossible.

An important special case when plants do not compete directly ($c_1 = c_2 = 0$), e.g., when plants grow in separate pots, or plants are separated by a fence or a road (Geslin et al., 2017), was analyzed in Křivan (2003b) for exploiters. In this case plant 1 (plant 2) isocline is vertical (horizontal) in sectors I and II, invasion thresholds are zero so that they play no role at all, and attraction thresholds simplify to $\tau_1 = \frac{e_2}{e_1}\left(1 + \frac{sA}{r_2}\right)$ and $\tau_2 = \frac{e_1}{e_2}\left(1 + \frac{sA}{r_1}\right)$. In the case of exploitation ($s = -1$) the only possible outcome is either global extinction (when exploiter density is too high) or global coexistence where animals can be specialists (when exploiter density is low) or generalists (when exploiter density is intermediate). In the case of mutualism ($s = 1$) possible outcomes always predict coexistence, including alternative stable states, as shown in Figure 7e, f, h.

We stress here that our predictions concern a small community, and it would be incorrect to extrapolate them to larger plant–animal interaction networks without proper consideration of model (1) limitations and assumptions (see section Model assumption below). For example, our model predicts that both plants can coexist with generalist exploiters but not with generalists mutualists, while there is empirical evidence that insect pollinators are more generalist than insect herbivores (Fontaine et al., 2009). Disagreement arises, e.g., because our Lotka–Volterra model does not consider competition for plants among the animals that are kept at fixed density. When mutualism is modeled under explicit consumer–resource dynamics where animal population densities change (Valdovinos et al., 2013; Revilla and Křivan, 2016), resource depletion (e.g., nectar consumption) can promote mutualist generalism, countering the tendency towards exclusive specialization on the most profitable plant.

Another counter-intuitive prediction is that exploitation coupled with flexible foraging enables indirect facilitation between plants. Once again, this is due to fixed animal population densities, because increase in one plant population density does not lead to increase in exploiter population density, a necessary condition for apparent competition (Holt, 1977) to occur. Similarly, switching can reduce or even eliminate apparent competition when there is interference between consumers (Abrams, 1995). Thus by coexisting, plants share exploitation costs, which leads to facilitation (i.e., higher equilibrium densities). Such indirect positive effect can be extreme, i.e., plants that cannot tolerate exploitation alone can survive when sharing exploitative stress with another plant (e.g., Figure 3). Similarly, adaptive mutualism makes plant coexistence more difficult, because it makes plant competition even stronger (Figure 4). Once again, this is because we assume a fixed mutualist density while the conventional view of indirect facilitation between plants mediated by shared mutualists assumes that that mutualism raises shared pollinator densities (Waser and Real, 1979). In this respect, experiments show that competition between plants for pollinator preferences can overcome such facilitation effects (Ghazoul, 2006).

## Population dynamics and adaptive animal preferences

To model effects of adaptive animal preferences on population dynamics of two competing plant species, we combine the Lotka–Volterra competitive model with a behavioral model that describes changes in animal preferences for plants. This is a common scenario in plant communities interacting with guilds of herbivores, parasites, pollinators or seed dispersers (Melián et al., 2009; Sauve et al., 2016; Bronstein, 2015). We assume that animal preferences for plants track instantaneously current plant population densities which, in turn, influence plant population dynamics. To model this feedback, we assume that animal preferences maximize animal fitness at current plant population densities. As optimal animal preferences when both plants are equally profitable are not uniquely given, the resulting plant population dynamics are described by a Lotka–Volterra differential inclusion (e.g., Colombo and Křivan, 1993; Křivan, 1996, 1997, 2007; Křivan et al., 2008). We analyze this model by generalizing the concept of isoclines which allows us to provide a complete classification of all plant equilibria. To this end, we split the plant phase space into two sectors (Figures 2a, c, e and 5–8). The boundary that separates these sectors is called the switching line because animals switch their preferences for plants when plant population numbers cross this line. Along the switching line animal fitness is independent from animal preferences because payoffs from both plants are the same. Inside the sectors, animals specialize on one plant only[5]. Thus, plant isoclines inside each sector coincide with the classical isoclines for the Lotka–Volterra competition model. In this article we define generalized plant isoclines that are formed by sector-wise pieces of isoclines that are connected with segments of the switching line (Figures 5–8). Thus, globally, generalized plant isoclines are piece-wise linear, which leads to multiple isocline intersections and multiple steady states. In particular, the segments of the two plant isoclines that are subsets of the switching line can partially overlap (Figure 5i; Figure 6e, f, h, i; Figure 7a, b, d, e; Figure 8a). If so, we show that plant population dynamics have a unique equilibrium in this overlapping segment (e.g., Figure 2b, c). This equilibrium is either locally stable when animals are exploiters or unstable when animals are mutualists. There are important differences between plant equilibria in the switching line and those that are inside sectors because animals are specialists inside sectors, but they are generalists at the equilibrium that is in the switching line.

The configuration of generalized isoclines depends on plant *invasion thresholds* (14) and *attraction thresholds* (18). Invasion thresholds $\gamma_i$ determine whether the missing plant species can invade the other plant monoculture at the equilibrium. For the standard Lotka–Volterra competition model with fixed animal preferences, coexistence as well as global dynamics can be predicted entirely in terms of invasion thresholds. However, when interactions between plants and animals are adaptive, we have to consider animal preferences which leads to non-linear generalized isoclines, and the concept of attraction thresholds. Attraction threshold $\tau_i$ determines whether the plant coexistence equilibrium at the switching line, where animals behave as plant generalists, locally attracts or repels orbits. This is analogous to the invasion threshold which determines whether the boundary equilibria attract or repel orbits. Attraction thresholds depend on animal density, inter-specific competition, and on payoffs ($e_i$) animals obtain from plants. These payoffs define animal fitness which is a function of plant densities. Despite the fact that we assume fixed animal densities, animal preferences (i.e., animal behavioral traits) change with changes in plant numbers. In other words, we observe indirect interactions between plants mediated by changes in animal preferences (i.e., trait-mediated indirect interactions between plants sensu Bolker et al., 2003). Thus, attraction thresholds capture the combined effects of inter-specific plant competition and behaviorally-mediated indirect effects, and their positions relative to

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[5] Similar concepts, called isodars and isolegs, are used in the habitat selection theory (Pimm and Rosenzweig, 1981; Rosenzweig, 1981; Křivan and Sirot, 2002; Morris, 2003; Křivan and Vrkoč, 2007) where distribution of a single population is studied as a function of the number of individuals of that population. In this article distribution of animals depends not only on animal population density, but also on plant densities.

invasion thresholds determine global interaction dynamics as summarized at the start of the discussion section.

## Model assumptions

The plant–animal model assumes constant animal density. This allows us to focus on behavior-mediated indirect interactions between plants not affected by simultaneous density-mediated interactions caused by changes in animal density (i.e., apparent competition and facilitation). This is reasonable assumption if animal populations are regulated mainly by external factors not explicitly considered. A good example is the case of common bees with large managed populations (Geslin et al., 2017), spilling over natural communities. Constant animal density is also enforced in short term experiments that study the effect of foraging behavior on plant success (Fontaine et al., 2005). Another plausible scenario is that the animal population dynamics is very slow when compared with plants due to differences in generation time (e.g., ungulate recruitment being slower than grass regrowth). An important prediction of the model is that exploitation favors animal generalism, while mutualism favors specialization. When animal population dynamics are considered, animal benefits must decrease due to intra-specific competition for plant resources, favoring generalism over specialization, even under mutualism (Revilla and Křivan, 2016).

Another important assumption is that animal adaptation is much faster than plant population dynamics. This requires that changes of foraging behavior occur within individual lifetimes, e.g., highly mobile consumers dispersing between plant species, like in the ideal free distribution (Křivan, 2003b). The assumption of fast adaptation can be relaxed by modeling preference dynamics explicitly using, e.g., replicator equation (Kondoh, 2003). In Revilla and Křivan (2016) we showed that qualitative predictions related to mutualist generalism vs. specialism are preserved even when adaptation runs on a similar time scale as population dynamics. However, when adaptation was much slower than population dynamics, predictions frequently diverged due to extreme dependence on animal initial preferences. For example, if animals initially strongly prefer one plant over the other despite the fact that such behavior is not optimal, the initially preferred plant can die out before animal preferences could change. In addition, when adaptation occurs over multiple generations, specialization or generalism also depends on the evolution of fitness related traits such as conversion efficiencies ($e_i$), which scale interactions with payoffs. Parameters like these depend on complex morphological and physiological constraints, and they generally relate to one another via non-linear trade-offs (Egas et al., 2004). Accounting for long term change of these parameters requires different approaches (e.g., adaptive dynamics, Kisdi 2002; Egas et al. 2004; Rueffler et al. 2006).

Finally, we only consider facultative mutualism because many plants have multiple pollinators or seed dispersers (Melián et al., 2009). Obligate mutualism can be modeled with Lotka–Volterra equations (Vandermeer and Boucher, 1978), but adaptive preference rules out coexistence trivially because mutualists interact with the more profitable plant only and the less profitable plant will die. Obligate mutualisms are better studied using mechanistic models (Revilla and Křivan, 2016, 2018), that predict coexistence depending on initial conditions because of mutualistic Allee effects (Bronstein, 2015).

## Conditional coexistence and alternative plant stable states

The interplay between plant competition and animal adaptation gives rise to complex plant population–animal preference dynamics. As plant isoclines are non-linear (e.g., Figure 7) multiple equilibria can co-exist. This has important implications for the diversity of communities under perturbations (Yan and Zhang, 2014; Zhang et al., 2015). On the one hand, perturbations in plant abundances can lead to loss of coexistence under exploitation and strong competition, i.e. coexistence conditioned by initial conditions (e.g., Figure 6e, f, h). On the other hand, they can trigger transitions between alternative stable states of coexistence when mutualism and weak inter-plant competition combine (e.g., Figure 7e).

Conditional coexistence and coexistence at alternative stable states are common predictions of models that combine positive and negative density-dependent interactions (e.g., Hernandez, 1998; Holland and DeAngelis, 2010; Revilla and Encinas-Viso, 2015). In the present model, however, plants always interact negatively due to inter-specific competition, and additional positive or negative effects arise due to adaptive preference of common exploiters or mutualists. Since animal densities are fixed, these indirect effects are behavior-mediated, but triggered by changes in plant densities. It is very important to remark that such abundance–preference feedbacks between trophic levels leads to very different predictions when compared to abundance–abundance feedbacks between trophic levels. In this latter case where animals respond numerically to plant densities, exploitation leads to *apparent competition* (Holt, 1977) and mutualism to *apparent mutualism* (or apparent facilitation) between plants, which respectively opposes and favors coexistence (Sauve et al., 2016). When animal preferences respond to plant densities, exploitation leads to a *competitive release* that promotes stable plant coexistence (Křivan, 1997, 2003a) while mutualism leads to *competition for mutualists preferences* between plants that destabilizes plant coexistence and leads to plant exclusion (Revilla and Křivan, 2018).

In this article we showed that conditional plant coexistence is expected in scenarios where generalist exploiters regulate strongly competing plants (i.e., $c_1c_2 > 1$, Figure 6e, f, h, i). On the other hand, outcomes like coexistence at alternative stable states are expected between weakly competing plants (i.e., $c_1c_2 < 1$) that are regulated by specialized mutualists. How relevant these predictions are in the real world depends on how widespread are situations where intra-specific competition is stronger than inter-specific, and vice-versa. On the one hand, meta-analyses suggest that intra- and inter-specific effects are too similar to be discerned (Gurevitch et al., 1992), or that intra-specific effects are actually much stronger than inter-specific (i.e., $c_1c_2 \leq 1$; Adler et al., 2018). However, recent pair-wise competition experiments (Sheppard, 2019) suggest that inter-specific competition can be strong (i.e., $c_1c_2 > 1$). Such uncertainty is rooted in the fact that these surveys assume models like (1) that treat competition phenomenologically, and there can be multiple underlying factors that can lead to strong net competition. For example, competition can be strengthened by allelopathy (Inderjit and Del Moral, 1997), which is decidedly stronger against non-specifics compared to con-specifics.

It will be interesting to explore to what extent our conclusions can be extrapolated to larger communities, consisting of several animal and plant species. For such diverse scenarios coexistence must result from intricate balances between multiple positive and negative effects (Melián et al., 2009; Georgelin and Loeuille, 2014; Mougi and Kondoh, 2014; Revilla and Křivan, 2016), where density- and behaviorally-mediated effects mix up. The analytical study of combined exploitative and mutualist effects is more difficult. For an illustration, let us consider a second exploiter or mutualist. This modification of model (1) will result in two switching lines (one for each animal species), three sectors and piece-wise continuous generalized isoclines that will consist of five segments. Mathematical analysis given in this article can be extended to describe this case as well, but as the number of species increases, complete mathematical classification will be intractable due to combinatorial complexity of possible outcomes. In these cases simulation approaches can be useful for studying the likelihood of multiple equilibria, as a function of competition intensity and the proportion of exploitative vs. mutualistic interactions (e.g., Melián et al. 2009).

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# A. Plant population dynamics

The switching line $e_1P_1 = e_2P_2$ of the animal splits the positive quadrant into

$$\text{sector I} = \{(P_1, P_2) \mid e_1P_1 > e_2P_2, P_1 \geq 0, P_2 \geq 0\}$$

and

$$\text{sector II} = \{(P_1, P_2) \mid e_1P_1 < e_2P_2, P_1 \geq 0, P_2 \geq 0\}.$$

In sector I animals interact with plant 1 only and plant population dynamics [system (1) in the main text] are

$$\begin{aligned}\frac{dP_1}{dt} &= \left(r_1\left(1 - \frac{P_1 + c_2P_2}{K_1}\right) + sA\right)P_1 \\ \frac{dP_2}{dt} &= \left(r_2\left(1 - \frac{P_2 + c_1P_1}{K_2}\right)\right)P_2,\end{aligned} \tag{A.1}$$

whereas in sector II animals interact with plant 2 only and population dynamics are

$$\begin{aligned}\frac{dP_1}{dt} &= \left(r_1\left(1-\frac{P_1+c_2P_2}{K_1}\right)\right)P_1\\ \frac{dP_2}{dt} &= \left(r_2\left(1-\frac{P_2+c_1P_1}{K_2}\right)+sA\right)P_2.\end{aligned}\tag{A.2}$$

Along the switching line $e_1P_1 = e_2P_2$ animal strategy is not uniquely defined and population dynamics satisfy

$$\begin{aligned}\frac{dP_1}{dt} =& r_1\left(1-\frac{P_1+c_2P_2}{K_1}\right)P_1 + su_1P_1A\\ \frac{dP_2}{dt} =& r_2\left(1-\frac{P_2+c_1P_1}{K_2}\right)P_2 + su_2P_2A\\ (u_1,u_2) \in& \{(v_1,v_2) \mid v_1+v_2=1, v_1\geq 0, v_2\geq 0\}.\end{aligned}\tag{A.3}$$

## A.1. Plant dynamics in sectors I and II

From (A.1) and (A.2), the isoclines of plant 1 in sectors I and II are

$$P_1 + c_2P_2 = K_1\left(1+\frac{sA}{r_1}\right)\tag{A.4}$$

$$P_1 + c_2P_2 = K_1,\tag{A.5}$$

respectively. We observe that plant 1 isocline exists in sector I iff $r_1 + sA > 0$. For mutualists ($s = 1$) this is always the case, but for exploiters this holds only if $A < r_1$ which we assume now. The segment of plant 1 isocline in sector I given in (A.4) intersects the $P_1$ axis at $\mathbf{E_1}$ [given by (9) in the main text] and switching line (6) at

$$\mathbf{b} = \left(\frac{e_2K_1(r_1+sA)}{r_1(e_2+c_2e_1)}, \frac{e_1K_1(r_1+sA)}{r_1(e_2+c_2e_1)}\right),\tag{A.6}$$

and the segment of plant 1 isocline in sector II given in (A.5) intersects the $P_2$ axis and the switching line at points

$$\mathbf{k_1} = \left(0, \frac{K_1}{c_2}\right)\tag{A.7}$$

$$\mathbf{a} = \left(\frac{e_2K_1}{e_2+c_2e_1}, \frac{e_1K_1}{e_2+c_2e_1}\right),\tag{A.8}$$

respectively.

Similarly from (A.1) and (A.2), plant 2 isocline in sector I is

$$P_2 + c_1P_1 = K_2\tag{A.9}$$

and in sector II

$$P_2 + c_1P_1 = K_2\left(1+\frac{sA}{r_2}\right),\tag{A.10}$$

respectively. Once again, plant 2 isocline exists in sector II iff $r_2 + sA > 0$. Isocline (A.9) intersects the $P_1$ axis and the switching line at points

$$\mathbf{k_2} = \left(\frac{K_2}{c_1}, 0\right)\tag{A.11}$$

$$\mathbf{q} = \left(\frac{e_2K_2}{e_1+c_1e_2}, \frac{e_1K_2}{e_1+c_1e_2}\right),\tag{A.12}$$

respectively. Isocline (A.10) intersects the $P_2$ axis at $\mathbf{E_2}$ [given by (10) in the main text] and the switching line at

$$\mathbf{p} = \left( \frac{e_2 K_2 (r_2 + sA)}{r_2(e_1 + c_1 e_2)}, \frac{e_1 K_2 (r_2 + sA)}{r_2(e_1 + c_1 e_2)} \right). \tag{A.13}$$

Isoclines position in sector I is determined by position of $\mathbf{k_2}$ with respect to $\mathbf{E_1}$ on the $P_1$ axis, and position of $\mathbf{b}$ with respect to $\mathbf{q}$ along the switching line. The following statements apply in this sector

$$\mathbf{k_2} > \mathbf{E_1} \Longleftrightarrow \frac{K_2}{K_1} > c_1 \left(1 + \frac{sA}{r_1}\right) \equiv \gamma_2 \tag{A.14}$$

$$\mathbf{q} > \mathbf{b} \Longleftrightarrow \frac{K_2}{K_1} > \left(\frac{e_1 + c_1 e_2}{e_2 + c_2 e_1}\right) \left(1 + \frac{sA}{r_1}\right) \equiv \tau_2. \tag{A.15}$$

If both conditions above are true, plant 2 isocline is above plant 1 isocline in sector I and there is no interior equilibrium in this sector (e.g., Figure 2c, sector I). If both conditions are false, then plant 1 isocline is above plant 2 isocline in sector I (Figure 5c, sector I). If (A.14) is true and (A.15) false, isoclines intersect at point $\mathbf{E_I}$ [given by (13) in the main text], and because plant 1 isocline is steeper than plant 2 isocline ($\frac{1}{c_2} > c_1$) this equilibrium is stable (e.g., Figure 5f, sector I). If (A.14) is false and (A.15) true, isoclines intersect again but because plant 2 isocline is steeper than plant 1 isocline ($\frac{1}{c_2} < c_1$), $\mathbf{E_I}$ is unstable (e.g., Figure 6d, sector I).

For sector II we compare $\mathbf{k_1}$ with $\mathbf{E_2}$ on the $P_2$ axis, and $\mathbf{a}$ with $\mathbf{p}$ along the switching line. We obtain

$$\mathbf{k_1} > \mathbf{E_2} \Longleftrightarrow \frac{K_1}{K_2} > c_2 \left(1 + \frac{sA}{r_2}\right) \equiv \gamma_1 \tag{A.16}$$

$$\mathbf{a} > \mathbf{p} \Longleftrightarrow \frac{K_1}{K_2} > \left(\frac{e_2 + c_2 e_1}{e_1 + c_1 e_2}\right) \left(1 + \frac{sA}{r_2}\right) \equiv \tau_1. \tag{A.17}$$

If both conditions above are true (e.g., Figure 2a,c) or both are false (e.g., Figure 5g), there is no interior equilibrium in sector II because the two plant isoclines do not intersect there. If (A.16) is true and (A.17) false, isoclines intersect at the point $\mathbf{E_{II}}$ [given by (17) in the main text], and because plant 1 isocline is steeper than plant 2 isocline ($\frac{1}{c_2} > c_1$) the equilibrium is stable (e.g., Figure 2e, sector II). And if (A.16) is false and (A.17) true, isoclines intersect and because plant 2 isocline is steeper than plant 1 isocline ($\frac{1}{c_2} < c_1$), $\mathbf{E_{II}}$ is unstable (e.g., Figure 6b, sector II).

## A.2. Plant population dynamics along the switching line

Here we are interested in plant population dynamics at the switching line. Let $\mathbf{n} = (e_1, -e_2)$ be a perpendicular vector to the switching line $e_1 P_1 = e_2 P_2$ and let us denote the right hand sides of (A.1) and (A.2) by $\mathbf{f^I}$ and $\mathbf{f^{II}}$, respectively. The dynamics close to the switching line depend on the following scalar products

$$\begin{aligned} \langle \mathbf{n}, \mathbf{f^I} \rangle &= e_1 P_1 \left\{ (r_1 + sA) - r_2 + P_1 \frac{K_1 r_2 (e_1 + c_1 e_2) - K_2 r_1 (e_2 + c_2 e_1)}{e_2 K_1 K_2} \right\} \\ \langle \mathbf{n}, \mathbf{f^{II}} \rangle &= e_1 P_1 \left\{ r_1 - (r_2 + sA) + P_1 \frac{K_1 r_2 (e_1 + c_1 e_2) - K_2 r_1 (e_2 + c_2 e_1)}{e_2 K_1 K_2} \right\}. \end{aligned} \tag{A.18}$$

There are four possibilities (Filippov, 1988; Colombo and Křivan, 1993):

1. If $\langle \mathbf{n}, \mathbf{f^I} \rangle < 0$ and $\langle \mathbf{n}, \mathbf{f^{II}} \rangle < 0$ trajectories are crossing the switching line in direction from sector I to sector II.

2. If $\langle \mathbf{n}, \mathbf{f^I} \rangle > 0$ and $\langle \mathbf{n}, \mathbf{f^{II}} \rangle > 0$ trajectories are crossing the switching line in direction from sector II to sector I.

3. If $\langle \mathbf{n}, \mathbf{f^I} \rangle < 0$ and $\langle \mathbf{n}, \mathbf{f^{II}} \rangle > 0$ trajectories do not cross the switching line and they have to stay for some positive time on the switching line. This is called the sliding regime.

| | Cases | $\langle \mathbf{n}, \mathbf{f}^{\mathbf{I}} \rangle$ | $\langle \mathbf{n}, \mathbf{f}^{\mathbf{II}} \rangle$ | overlap segment | $\mathbf{E_S}$ | dynamics at the overlap segment |
|---|---|---|---|---|---|---|
| $s = -1$ | $p_1 < b_1 < a_1 < q_1$ | <0 | >0 | **ba** | Yes | sliding regime |
| | $b_1 < p_1 < q_1 < a_1$ | <0 | >0 | **pq** | Yes | sliding regime |
| | $p_1 < b_1 < q_1 < a_1$ | <0 | >0 | **bq** | Yes | sliding regime |
| | $b_1 < p_1 < a_1 < q_1$ | <0 | >0 | **pa** | Yes | sliding regime |
| | $p_1 < q_1 < b_1 < a_1$ | >0 | >0 | no overlap | No | crossing from sector II to I |
| | $b_1 < a_1 < p_1 < q_1$ | <0 | <0 | no overlap | No | crossing from sector I to II |
| $s = 1$ | $q_1 < a_1 < b_1 < p_1$ | >0 | <0 | **ab** | Yes | repelling regime |
| | $a_1 < q_1 < p_1 < b_1$ | >0 | <0 | **qp** | Yes | repelling regime |
| | $q_1 < a_1 < p_1 < b_1$ | >0 | <0 | **ap** | Yes | repelling regime |
| | $a_1 < q_1 < b_1 < p_1$ | >0 | <0 | **qb** | Yes | repelling regime |
| | $q_1 < p_1 < a_1 < b_1$ | >0 | >0 | no overlap | No | crossing from sector II to I |
| | $a_1 < b_1 < q_1 < p_1$ | <0 | <0 | no overlap | No | crossing from sector I to II |

**Table A.1.** List of all possible overlaps of generalized isoclines along the switching line.

4. If $\langle \mathbf{n}, \mathbf{f}^{\mathbf{I}} \rangle > 0$ and $\langle \mathbf{n}, \mathbf{f}^{\mathbf{II}} \rangle < 0$ trajectories that start at such points are not uniquely defined. They can move along the switching line for some time and then leave the line either to sector I or to sector II. This is called the repelling regime.

We observe that

$$\langle \mathbf{n}, \mathbf{f}^{\mathbf{I}} \rangle = \langle \mathbf{n}, \mathbf{f}^{\mathbf{II}} \rangle + 2se_1P_1A.$$

Thus, when $s = 1$, $\langle \mathbf{n}, \mathbf{f}^{\mathbf{II}} \rangle > 0$ implies $\langle \mathbf{n}, \mathbf{f}^{\mathbf{I}} \rangle > 0$ which excludes the sliding regime. Similarly, when $s = -1$, $\langle \mathbf{n}, \mathbf{f}^{\mathbf{II}} \rangle < 0$ implies $\langle \mathbf{n}, \mathbf{f}^{\mathbf{I}} \rangle < 0$ which excludes the repelling regime.

To analyze all possible situations under which sliding or repelling regime occurs, using (A.6), (A.8), (A.12), and (A.13) we rewrite (A.18) as

$$\begin{aligned} \langle \mathbf{n}, \mathbf{f}^{\mathbf{I}} \rangle &= \frac{e_1P_1\left\{K_1r_2(e_1+c_1e_2)\left[P_1-q_1\right]-K_2r_1(e_2+c_2e_1)\left[P_1-b_1\right]\right\}}{e_2K_1K_2} \\ \langle \mathbf{n}, \mathbf{f}^{\mathbf{II}} \rangle &= \frac{e_1P_1\left\{K_1r_2(e_1+c_1e_2)\left[P_1-p_1\right]-K_2r_1(e_2+c_2e_1)\left[P_1-a_1\right]\right\}}{e_2K_1K_2}. \end{aligned} \tag{A.19}$$

For exploiters ($s = -1$) $\mathbf{b} < \mathbf{a}$ and $\mathbf{p} < \mathbf{q}$ so that there are four possibilities for isoclines overlap at the switching line. All these possibilities together with the overlap segment of the two generalized isoclines are listed in Table A.1. Moreover, scalar products given in (A.19) show that in the overlap segment plant dynamics are in the sliding regime.

Similarly, for mutualists ($s = 1$) $\mathbf{b} > \mathbf{a}$ and $\mathbf{p} > \mathbf{q}$ and again there are four possibilities where the two isoclines overlap at the switching line (Table A.1). However, in this case, the overlap segment repels trajectories.

### A.2.1. Equilibrium $\mathbf{E_S}$

Now we look for equilibria of model (1) and (5) in the switching line. Every non-trivial equilibrium there must satisfy

$$\begin{aligned} e_1P_1 =& e_2P_2 \\ 0 =& r_1\left(1-\frac{P_1+c_2P_2}{K_1}\right)P_1 + su_1P_1A \\ 0 =& r_2\left(1-\frac{P_2+c_1P_1}{K_2}\right)P_2 + s(1-u_1)P_2A. \end{aligned}$$

These equations have a single non-trivial solution that gives equilibrium $\mathbf{E_S}$ given in (19) and the corresponding preference for plant 1, $\bar{u}_1$, given in (20). For $\mathbf{E_S}$ to be feasible, $\bar{u}_1$ must be between

0 and 1. This happens iff either (21) or (22) holds. Using (A.6) and (A.12), plant 1 population equilibrium given in (19) can be written as a convex combination of points $b_1$ and $q_1$

$$\bar{P}_1 = \left[\frac{K_2 r_1(e_2 + c_2 e_1)}{K_1 r_2(e_1 + c_1 e_2) + K_2 r_1(e_2 + c_2 e_1)}\right] b_1 + \left[\frac{K_1 r_2(e_1 + c_1 e_2)}{K_1 r_2(e_1 + c_1 e_2) + K_2 r_1(e_2 + c_2 e_1)}\right] q_1,$$

which shows that $b_1 < \bar{P}_1 < q_1$.

Similarly, using (A.8) and (A.13), plant 1 population equilibrium becomes

$$\bar{P}_1 = \left[\frac{K_2 r_1(e_2 + c_2 e_1)}{K_1 r_2(e_1 + c_1 e_2) + K_2 r_1(e_2 + c_2 e_1)}\right] a_1 + \left[\frac{K_1 r_2(e_1 + c_1 e_2)}{K_1 r_2(e_1 + c_1 e_2) + K_2 r_1(e_2 + c_2 e_1)}\right] p_1$$

which shows that $p_1 < \bar{P}_1 < a_1$. It follows from Table A.1 that equilibrium $\mathbf{E_S}$ is in the sliding regime where the plant generalized isoclines overlap. Now we study stability of $\mathbf{E_S}$.

First we consider the exploitation case where $s = -1$. Table A.1 shows that at points where the generalized isoclines overlap, trajectories are driven toward the switching line from both sectors. In this case trajectories cannot cross the switching line inside the isoclines overlap segment. Thus, once a trajectory reaches the overlap segment, it must move along it, i.e., $e_1 P_1(t) = e_2 P_2(t)$. This means that when the trajectory moves along the overlap segment, preferences for plants $(u_1, u_2)$ must satisfy $e_1 P_1'(t) = e_2 P_2'(t)$, i.e.,

$$e_1\left[r_1\left(1 - \frac{P_1 + c_2 P_2}{K_1}\right) + s u_1 A\right] = e_2\left[r_2\left(1 - \frac{P_2 + c_1 P_1}{K_2} + s(1 - u_1)A\right)\right],$$

where we used the fact that $e_1 P_1(t) = e_2 P_2(t)$. The corresponding preference for plant plant 1 along the trajectory is

$$u_1 = \frac{e_2 K_2(sAe_1K_1 + c_2 e_1 P_1 r_1 + e_2 r_1(P_1 - K_1)) - e_1 K_1 r_2(c_1 e_2 P_1 + e_1 P_1 - e_2 K_2)}{sAe_2 K_1 K_2(e_1 + e_2)}.$$

With this preference for plant 1, plant population dynamics in the sliding regime are described by the logistic equation

$$\frac{dP_1}{dt} = \frac{e_1(r_1 + r_2 + sA)}{e_1 + e_2}\left[1 - \left(\frac{K_1 r_2(e_1 + c_1 e_2) + K_2 r_1(e_2 + c_2 e_1)}{e_2 K_1 K_2(r_1 + r_2 + sA)}\right) P_1\right] P_1, \qquad \text{(A.20)}$$

with equilibrium $\bar{P}_1$ corresponding to $\mathbf{E_S} = (\bar{P}_1, e_1/e_2 \bar{P}_1)$. This shows that equilibrium $\mathbf{E_S}$ is locally stable, because trajectories close to this equilibrium are attracted from both sector I and II toward the switching line (Table A.1) and they converge along the switching line to the equilibrium.

Second, we consider stability of $\mathbf{E_S}$ for mutualisms when $s = 1$. Table A.1 shows that the overlap segment of the two isoclines repels nearby trajectories, equilibrium $\mathbf{E_S}$ is unstable. Moreover, trajectories that start at the overlap of the two plant generalized isoclines are not uniquely defined, because they can leave this segment of the switching line either to sector I, or to sector II.

# B. Effect of parameters on equilibria

Using (7) and (8) for sector I, equilibrium densities at $\mathbf{E_I}$ (13) take the form

$$\hat{P}_1 = \frac{H_1 - c_2 K_2}{1 - c_1 c_2},\ \hat{P}_2 = \frac{K_2 - c_1 H_1}{1 - c_1 c_2},$$

where $H_1 = K_1\left(1 + \frac{sA}{r_1}\right)$. Thus, $\partial\hat{P}_i/\partial r_2, \partial\hat{P}_i/\partial e_1, \partial\hat{P}_i/\partial e_2\ (i = 1, 2)$ are all zero, and

$$\frac{\partial\hat{P}_1}{\partial r_1} = \frac{-sK_1 A}{r_1^2(1 - c_1 c_2)}, \quad \frac{\partial\hat{P}_2}{\partial r_1} = \frac{sc_1 K_1 A}{r_1^2(1 - c_1 c_2)}, \quad \frac{\partial\hat{P}_1}{\partial A} = \frac{sK_1}{r_1(1 - c_1 c_2)}, \quad \frac{\partial\hat{P}_2}{\partial A} = \frac{-sK_1 c_1}{r_1(1 - c_1 c_2)},$$

$$\frac{\partial\hat{P}_1}{\partial K_1} = \frac{1}{1 - c_1 c_2}\left(1 + \frac{sA}{r_1}\right), \quad \frac{\partial\hat{P}_2}{\partial K_1} = \frac{-c_1}{1 - c_1 c_2}\left(1 + \frac{sA}{r_1}\right), \quad \frac{\partial\hat{P}_1}{\partial K_2} = \frac{-c_2}{1 - c_1 c_2}, \quad \frac{\partial\hat{P}_2}{\partial K_2} = \frac{1}{1 - c_1 c_2},$$

$$\frac{\partial\hat{P}_1}{\partial c_1} = \frac{c_2\hat{P}_1}{1 - c_1 c_2}, \quad \frac{\partial\hat{P}_2}{\partial c_1} = \frac{-\hat{P}_1}{1 - c_1 c_2}, \quad \frac{\partial\hat{P}_1}{\partial c_2} = \frac{-\hat{P}_2}{1 - c_1 c_2}, \quad \frac{\partial\hat{P}_2}{\partial c_2} = \frac{c_1\hat{P}_2}{1 - c_1 c_2}.$$

We remark that because $r_1 + sA > 0$ is required for $\mathbf{E_I}$ to be feasible, the sign of $\frac{\partial \hat{P}_1}{\partial K_1}$ and $\frac{\partial \hat{P}_2}{\partial K_1}$ is independent of $1 + \frac{sA}{r_1}$. Parameter effects on $\mathbf{E_{II}}$ are obtained analogously.

At equilibrium $\mathbf{E_S}$ (19) plant densities take the form

$$\bar{P}_1 = e_2 G\,,\ \bar{P}_2 = e_1 G,$$

where $G = \dfrac{K_1 K_2 (r_1 + r_2 + sA)}{K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)}$. This quantity varies with parameters as

$$\begin{aligned}
\frac{\partial G}{\partial r_1} &= \left(\frac{K_1}{K_2} - \tau_1\right)\left\{\frac{r_2(e_1 + c_1 e_2) K_1 K_2^2}{\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]^2}\right\} \\
\frac{\partial G}{\partial K_1} &= \left\{\frac{r_1 (r_1 + r_2 + sA)(e_2 + c_2 e_1) K_2^2}{\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]^2}\right\} \\
\frac{\partial G}{\partial c_1} &= -\left\{\frac{e_2 r_2 (r_1 + r_2 + sA) K_1^2 K_2}{\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]^2}\right\} \\
\frac{\partial G}{\partial A} &= s\left\{\frac{K_1 K_2}{K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)}\right\} \\
\frac{\partial G}{\partial e_1} &= -\left\{\frac{K_1 K_2 (r_1 + r_2 + sA)(K_1 r_2 + K_2 r_1 c_2)}{\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]^2}\right\},
\end{aligned}$$

where the quantities between curly braces are positive (because feasibility of $\mathbf{E_S}$ requires $r_1 + r_2 + sA > 0$). Thus $\frac{\partial G}{\partial K_1} > 0$, $\frac{\partial G}{\partial c_1} < 0$, and $\frac{\partial G}{\partial e_1} < 0$. Moreover, $\frac{\partial G}{\partial A} < 0$ under exploitation ($s = -1$) and $\frac{\partial G}{\partial A} > 0$ under mutualism ($s = 1$). Under exploitation $\frac{\partial G}{\partial r_1} > 0$ because $\mathbf{E_S}$ is feasible iff both plants are *above* their attraction thresholds (i.e., $K_1/K_2 > \tau_1$ and $K_2/K_1 > \tau_2$). Conversely, $\frac{\partial G}{\partial r_1} < 0$ under mutualism. Since $\bar{P}_i = e_j G$ where $i, j = 1, 2$ but $i \neq j$, we can conclude

$$\frac{\partial \bar{P}_i}{\partial K_1} > 0, \qquad \frac{\partial \bar{P}_i}{\partial c_1} < 0, \qquad \frac{\partial \bar{P}_i}{\partial r_1}\begin{cases} > 0 & \text{exploitation} \\ < 0 & \text{mutualism,}\end{cases} \qquad \frac{\partial \bar{P}_i}{\partial A}\begin{cases} < 0 & \text{exploitation} \\ > 0 & \text{mutualism,}\end{cases},$$

i.e., both plant densities change in the same direction (i.e., $\partial \bar{P}_1 / \partial \bar{P}_2 > 0$) when $r_1, K_1, c_1, A$ change. Now when $e_1$ varies we have $\frac{\partial \bar{P}_1}{\partial e_1} = e_2 \frac{\partial G}{\partial e_1} < 0$, but

$$\frac{\partial \bar{P}_2}{\partial e_1} = G + e_1 \frac{\partial G}{\partial r_1} = \frac{e_2 K_1 K_2 (K_2 r_1 + c_1 K_1 r_2)(r_1 + r_2 + sA)}{\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]^2}$$

which is positive. *Mutatis mutandis* $\frac{\partial \bar{P}_1}{\partial e_2} > 0$ and $\frac{\partial \bar{P}_2}{\partial e_2} < 0$. Thus, when $e_1$ or $e_2$ change, plant densities change in opposite directions (i.e., $\partial \bar{P}_1 / \partial \bar{P}_2 < 0$).

Finally the derivatives of generalist preference $\bar{u}_1$ (20) at $\mathbf{E_S}$ are

$$\begin{aligned}
\frac{\partial \bar{u}_1}{\partial r_1} &= \left\{\frac{r_2 (e_2 + c_2 e_1) K_1\, \bar{u}_1}{r_1 \left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]}\right\} \\
\frac{\partial \bar{u}_1}{\partial K_1} &= -s\left\{\frac{r_1 r_2 K_2 (e_1 + c_1 e_2)(e_2 + c_2 e_1)(r_1 + r_2 + sA)}{A\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]^2}\right\} \\
\frac{\partial \bar{u}_1}{\partial c_1} &= -s\left\{\frac{r_1 r_2 e_2 K_1 K_2 (e_2 + c_2 e_1)(r_1 + r_2 + sA)}{A\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]^2}\right\} \\
\frac{\partial \bar{u}_1}{\partial e_1} &= s(c_1 c_2 - 1)\left\{\frac{e_2 r_1 r_2 K_1 K_2 (r_1 + r_2 + sA)}{A\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]^2}\right\} \\
\frac{\partial \bar{u}_1}{\partial A} &= s\left(\frac{K_1}{K_2} - \frac{e_2 + c_2 e_1}{e_1 + c_1 e_2}\right)\left\{\frac{r_1 r_2 K_2 (e_1 + c_1 e_2)}{A^2\left[K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)\right]}\right\},
\end{aligned}$$

where the quantities between curly braces are positive (because feasibility of $\mathbf{E_S}$ requires $r_1 + r_2 + sA > 0$). Thus $\frac{\partial \bar{u}_1}{\partial r_1} > 0$ trivially. Under exploitation ($s = -1$), $\frac{\partial \bar{u}_1}{\partial K_1} > 0$, and $\frac{\partial \bar{u}_1}{\partial c_1} > 0$. And under mutualism

$(s = 1)$, $\frac{\partial \bar{u}_1}{\partial K_1} < 0$ and $\frac{\partial \bar{u}_1}{\partial c_1} < 0$. The sign of $\frac{\partial \bar{u}_1}{\partial e_1}$ depends on interaction type and strength of competition as follows

$$\frac{\partial \bar{u}_1}{\partial e_1} \begin{cases} > 0 & \text{for exploitation } \& \ c_1 c_2 < 1 \\ < 0 & \text{for exploitation } \& \ c_1 c_2 > 1 \\ < 0 & \text{for mutualism } \& \ c_1 c_2 < 1 \\ > 0 & \text{for mutualism } \& \ c_1 c_2 > 1 \end{cases}$$

and the sign of $\partial \bar{u}_1 / \partial A$ depends on interaction type and the sign of the $\frac{K_1}{K_2} - \frac{e_2 + c_2 e_1}{e_1 + c_1 e_2}$. Since $u_1$ and $u_2$ vary in opposite directions, the derivatives of $\bar{u}_1$ with respect to $r_2, K_2, c_2, e_2$ are of opposite signs compared with the corresponding derivatives with respect $r_1, K_1, c_1, e_1$ above.

# C. Classification of equilibria

Table A.2 summarizes our previous analyzes given in Appendices A.1 and A.2, and lists all feasible (i.e., non-negative) stable equilibria for system (1) under exploitation $(s = -1)$ or mutualism $(s = 1)$, and weak $(c_1 c_2 < 1)$ or strong $(c_1 c_2 > 1)$ competition. Empty $(\emptyset)$ cells indicate that no parameter combination satisfies row or column conditions. Cells with only one equilibrium indicate that this equilibrium is globally stable. Cells with multiple equilibria indicate that these equilibria are locally stable. There are 56 non-empty cells in Table A.2, each of them corresponding to a unique isocline configuration. The configurations shown in Figures 5–8 are indicated by figure number and panel. Out of these 56 configurations, there are 11 possible combinations (i.e., $\mathbf{E_1}$, $\mathbf{E_2}$, $\mathbf{E_I}$, $\mathbf{E_{II}}$, $\mathbf{E_S}$, $\{\mathbf{E_I}, \mathbf{E_{II}}\}$, $\{\mathbf{E_S}, \mathbf{E_1}\}$, $\{\mathbf{E_S}, \mathbf{E_2}\}$, $\{\mathbf{E_1}, \mathbf{E_{II}}\}$, $\{\mathbf{E_2}, \mathbf{E_I}\}$, $\{\mathbf{E_S}, \mathbf{E_1}, \mathbf{E_2}\}$) with respect to stable equilibria.

Equilibria $\mathbf{E_1}, \mathbf{E_2}$ given in (9), (10) are boundary (i.e., monoculture) equilibria for plant 1 and 2, respectively; $\mathbf{E_I}, \mathbf{E_{II}}, \mathbf{E_S}$ given in (13), (17), and (19) are interior equilibria in sector I (where $u_1 = 1$), sector II (where $u_1 = 0$), and the switching line (where $u_1 = \bar{u}_1$ is given by (20)), respectively. Cases are classified with respect to position of $\mathbf{k_1}$ given in (A.7) and $\mathbf{E_1}$ on $P_1$ axes, $\mathbf{k_2}$ given in (A.11) and $\mathbf{E_2}$ on $P_2$ axes, and points $\mathbf{a}$, $\mathbf{b}$, $\mathbf{p}$, $\mathbf{q}$ given in (A.8), (A.6), (A.13), (A.12) along the switching line. For mutualisms $(s = 1)$, $\mathbf{q} < \mathbf{p}$ and $\mathbf{a} < \mathbf{b}$ while for exploitation $(s = -1)$, $\mathbf{p} < \mathbf{q}$ and $\mathbf{b} < \mathbf{a}$. We remark that for exploitation when $A > r_1$ $(A > r_2)$, point $\mathbf{b}$ $(\mathbf{p})$ is in the third quadrant and boundary equilibrium $\mathbf{E_1}$ $(\mathbf{E_2})$ is not feasible. Table A.2 considers all generic cases excluding those cases where one or more inequalities between points and parameters are replaced by equalities.

# D. Gradual change in preference

Preference modeled by equation (5) in the main text assumes ideal animals that are omniscient and perfect optimizers that switch instantaneously on the plant that is more profitable. Now let us consider a more realistic animal that adjusts its plant preferences more gradually with changes in plant densities. This can be modeled by the Hill function

$$u_1(P_1, P_2) = \frac{(e_1 P_1)^z}{(e_1 P_1)^z + (e_2 P_2)^z} \tag{A.21}$$

where the exponent $z > 0$ controls the steepness of preference transitions. As $z$ converges to infinity, graphs of the Hill functions converge to the graph of the step-like preference (5) in the main text. When we substitute this gradual switching function in the Lotka–Volterra equations (1) of the main text, piece-wise isoclines change into smooth curves. As the steepness exponent $z$ increases and switching becomes more step-like, these isoclines converge to generalized isoclines from the main text.

We observe (cf. Figure A.1 here vs. Figure 2 in the main text) that for sufficiently large values of the Hill exponent the dynamics of model (1) in the main text with step-like preferences are well approximated by plant population dynamics where animal preferences for plants are gradual and described by (A.21). In Figure A.1 that matches Figure 2 of the main text we show a cone of intermediate plant 1 preferences (area between 5% and 95% preference contour lines). Increasing the Hill exponent $(z)$

| Interacting conditions | | Position of isoclines intersections along the switching line | Position of isoclines intersections along $P_1$ and $P_2$ axes | | | |
|---|---|---|---|---|---|---|
| | | | $\mathbf{k_1 > E_2, k_2 > E_1}$ | $\mathbf{k_1 > E_2, k_2 < E_1}$ | $\mathbf{k_1 < E_2, k_2 > E_1}$ | $\mathbf{k_1 < E_2, k_2 < E_1}$ |
| $s = -1$ | $c_1c_2 < 1$ | $\mathbf{p < q < b < a}$ | $\mathbf{E_I}$(Fig. 5f) | $\mathbf{E_1}$(Fig. 5c) | $\emptyset$ | $\emptyset$ |
| | | $\mathbf{b < a < p < q}$ | $\mathbf{E_{II}}$(Fig. 5h) | $\emptyset$ | $\mathbf{E_2}$(Fig. 5g) | $\emptyset$ |
| | | $\mathbf{p < b < a < q}$ | $\mathbf{E_S}$ | $\emptyset$ | $\emptyset$ | $\emptyset$ |
| | | $\mathbf{b < p < q < a}$ | $\mathbf{E_S}$ | $\emptyset$ | $\emptyset$ | $\emptyset$ |
| | | $\mathbf{p < b < q < a}$ | $\mathbf{E_S}$ | $\emptyset$ | $\emptyset$ | $\emptyset$ |
| | | $\mathbf{b < p < a < q}$ | $\mathbf{E_S}$(Fig. 5i) | $\emptyset$ | $\emptyset$ | $\emptyset$ |
| | $c_1c_2 > 1$ | $\mathbf{p < q < b < a}$ | $\emptyset$ | $\mathbf{E_1}$(Fig. 6c) | $\emptyset$ | $\{\mathbf{E_1, E_2}\}$(Fig. 6b) |
| | | $\mathbf{b < a < p < q}$ | $\emptyset$ | $\emptyset$ | $\mathbf{E_2}$(Fig. 6g) | $\{\mathbf{E_1, E_2}\}$(Fig. 6d) |
| | | $\mathbf{p < b < a < q}$ | $\mathbf{E_S}$ | $\{\mathbf{E_S, E_1}\}$(Fig. 6f) | $\{\mathbf{E_S, E_2}\}$ | $\{\mathbf{E_S, E_1, E_2}\}$(Fig. 6e) |
| | | $\mathbf{b < p < q < a}$ | $\mathbf{E_S}$ (Fig. 6i) | $\{\mathbf{E_S, E_1}\}$ | $\{\mathbf{E_S, E_2}\}$ | $\{\mathbf{E_S, E_1, E_2}\}$ |
| | | $\mathbf{p < b < q < a}$ | $\mathbf{E_S}$ | $\{\mathbf{E_S, E_1}\}$ | $\{\mathbf{E_S, E_2}\}$ | $\{\mathbf{E_S, E_1, E_2}\}$ |
| | | $\mathbf{b < p < a < q}$ | $\mathbf{E_S}$ | $\{\mathbf{E_S, E_1}\}$ | $\{\mathbf{E_S, E_2}\}$(Fig. 6h) | $\{\mathbf{E_S, E_1, E_2}\}$ |
| $s = 1$ | $c_1c_2 < 1$ | $\mathbf{q < p < a < b}$ | $\mathbf{E_I}$(Fig. 7f) | $\mathbf{E_1}$(Fig. 7c) | $\emptyset$ | $\emptyset$ |
| | | $\mathbf{a < b < q < p}$ | $\mathbf{E_{II}}$(Fig. 7h) | $\emptyset$ | $\mathbf{E_2}$(Fig. 7g) | $\emptyset$ |
| | | $\mathbf{q < a < b < p}$ | $\{\mathbf{E_I, E_{II}}\}$ | $\{\mathbf{E_{II}, E_1}\}$ | $\{\mathbf{E_I, E_2}\}$ | $\{\mathbf{E_1, E_2}\}$(Fig. 7a) |
| | | $\mathbf{a < q < p < b}$ | $\{\mathbf{E_I, E_{II}}\}$(Fig. 7e) | $\{\mathbf{E_{II}, E_1}\}$ | $\{\mathbf{E_I, E_2}\}$ | $\{\mathbf{E_1, E_2}\}$ |
| | | $\mathbf{q < a < p < b}$ | $\{\mathbf{E_I, E_{II}}\}$ | $\{\mathbf{E_{II}, E_1}\}$(Fig. 7b) | $\{\mathbf{E_I, E_2}\}$ | $\{\mathbf{E_1, E_2}\}$ |
| | | $\mathbf{a < q < b < p}$ | $\{\mathbf{E_I, E_{II}}\}$ | $\{\mathbf{E_{II}, E_1}\}$ | $\{\mathbf{E_I, E_2}\}$(Fig. 7d) | $\{\mathbf{E_1, E_2}\}$ |
| | $c_1c_2 > 1$ | $\mathbf{q < p < a < b}$ | $\emptyset$ | $\mathbf{E_1}$(Fig. 8c) | $\emptyset$ | $\{\mathbf{E_1, E_2}\}$(Fig. 8b) |
| | | $\mathbf{a < b < q < p}$ | $\emptyset$ | $\emptyset$ | $\mathbf{E_2}$(Fig. 8g) | $\{\mathbf{E_1, E_2}\}$(Fig. 8d) |
| | | $\mathbf{q < a < b < p}$ | $\emptyset$ | $\emptyset$ | $\emptyset$ | $\{\mathbf{E_1, E_2}\}$ |
| | | $\mathbf{a < q < p < b}$ | $\emptyset$ | $\emptyset$ | $\emptyset$ | $\{\mathbf{E_1, E_2}\}$ |
| | | $\mathbf{q < a < p < b}$ | $\emptyset$ | $\emptyset$ | $\emptyset$ | $\{\mathbf{E_1, E_2}\}$ |
| | | $\mathbf{a < q < b < p}$ | $\emptyset$ | $\emptyset$ | $\emptyset$ | $\{\mathbf{E_1, E_2}\}$ (Fig. 8a) |

**Table A.2.** Classification of all possible stable equilibria of model (1) with adaptive animal behavior for all generic parameter cases.

towards infinity collapses the cone into the switching line (equation (6) in the main text) and in panel b the intersection of isoclines converges to $\mathbf{E_S}$ given in equation (19) in the main text. Isoclines in the cone converge to the segments of generalized isoclines that are in the switching line.

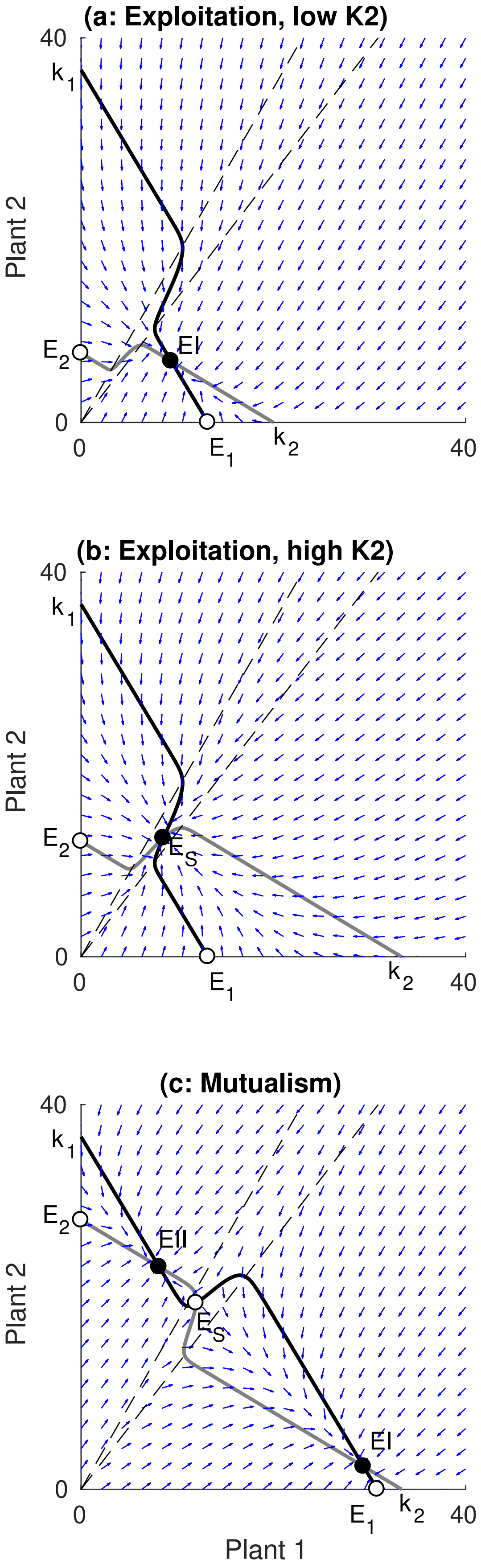

**Figure A.1.** Plant isoclines (plant 1: black, plant 2: gray) and population dynamics under weak competition ($c_1 c_2 < 1$) and preferences given by the Hill function with $z = 20$ (dashed lines correspond to contour lines for which $u_1 = 0.05$ and $u_1 = 0.95$). Panels and parameters correspond to those of Figure 2 in the main text.