

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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34 1. Introduction

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

50 Indirect interactions can be either density- or behaviorally-mediated. In density-mediated indirect
51 interactions the mediator species density changes. E.g., in apparent competition an increase in one
52 plant density increases herbivore density which, in turn, decreases density of the other plant species.
53 In behaviorally-mediated indirect interactions changes in one plant population density are transmitted
54 through changes in animal behavior when animal population density is fixed. In reality, both density-
55 and trait-mediated indirect interactions operate concurrently (Bolker et al., 2003; Křivan and Schmitz,
56 2004). Analysis of the apparent competition food web module with two plants and their common
57 consumers who undergo population dynamics and adaptively change their foraging preferences showed
58 that combination of density- and behaviorally-mediated interactions promotes plant coexistence that
59 would not be possible if consumer preferences were fixed (Křivan, 1997). Even when consumers were
60 kept at fixed densities but they adaptively changed their preferences for plants, plant coexistence was
61 still promoted by behaviorally-mediated interactions only (Křivan, 2003b). This suggests that in an-
62 tagonistic networks adaptive foraging promotes species coexistence by reducing apparent competition.
63 This was verified in more complex antagonistic di- and tri- trophic food web modules with many
64 species (Křivan, 2010). In simulated complex antagonistic food-webs adaptive prey switching also led
65 to increased species persistence (Kondoh, 2003; Berec et al., 2010).

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

84 In this article we analyze how behaviorally-mediated interactions transmitted by shared animals
85 influence plant competition. We demonstrate that foraging behavior of animal exploiters (e.g., her-
86 bivores) or mutualists (e.g., pollinators) can have important and predictable consequences for plant

87 competitive coexistence. By assuming that animal population densities are fixed, we eliminate density-
 88 mediated effects, e.g., apparent competition or apparent facilitation. In this way, we can focus entirely
 89 on indirect effects that are mediated only by changes in animal preferences (i.e., they are trait-mediated)
 90 for plants. We give conditions for plant coexistence at an equilibrium under exploitation or mutualism
 91 either when interaction strength is fixed, or when it is adaptive and maximizes animal fitness.

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

102 2. Model

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

$$\begin{aligned} \frac{dP_1}{dt} &= r_1 \left(1 - \frac{P_1 + c_2 P_2}{K_1} \right) P_1 + s u_1 P_1 A \\ \frac{dP_2}{dt} &= r_2 \left(1 - \frac{P_2 + c_1 P_1}{K_2} \right) P_2 + s u_2 P_2 A \end{aligned} \quad (1)$$

109 where $r_i > 0$ and $K_i > 0$ are plant intrinsic growth rates and environmental carrying capacities in
 110 absence of inter-specific interactions, and $c_i \geq 0$ is the competition coefficient that measures competitive
 111 effects of plant i on the other plant. The strength of plant–animal interactions depends on animal
 112 density (A) as well as on animal preferences u_1 and u_2 for plant 1 and 2, respectively ($u_i \geq 0$ for
 113 $i = 1, 2$ and $u_1 + u_2 = 1$). Preference for plant i can be interpreted as the proportion of time that an
 114 animal spends interacting with that plant, or, alternatively, as the fraction of the animal population
 115 ($u_i A$) interacting with that plant.

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

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

$$(\hat{P}_1, \hat{P}_2) = \left(\frac{K_1 r_2 (r_1 + s A u_1) - c_2 K_2 r_1 (r_2 + s A u_2)}{r_1 r_2 (1 - c_1 c_2)}, \frac{K_2 r_1 (r_2 + s A u_2) - c_1 K_1 r_2 (r_1 + s A u_1)}{r_1 r_2 (1 - c_1 c_2)} \right) \quad (2)$$

133 if and only if the ratio of carrying capacities satisfies¹

$$\frac{c_2(1 + s u_2 A / r_2)}{1 + s u_1 A / r_1} < \frac{K_1}{K_2} < \frac{1 + s u_2 A / r_2}{c_1(1 + s u_1 A / r_1)}. \quad (3)$$

134 Thus, stable plant coexistence requires that

$$c_1 c_2 < 1. \quad (4)$$

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

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

142 2.1. Adaptive animal preferences

143 Here we assume that animal preferences change in the direction that maximizes animal fitness. The
 144 payoff to an animal when feeding on plant $i (= 1, 2)$ is measured, e.g., as the amount of energy obtained
 145 per unit of time, i.e., $e_i P_i$ where e_i denotes the amount of energy obtained from a single plant per
 146 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
 147 $u_1 + u_2 = 1$ and $u_i \geq 0$. Under the ideal circumstances where individuals have a perfect knowledge
 148 about plant profitabilities and abundances, maximization of this fitness leads to the following optimal
 149 foraging strategy (Křivan, 2003b; Křivan and Vrkoč, 2007):

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

150 When plant densities are such that

$$e_1 P_1 = e_2 P_2, \quad (6)$$

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

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

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

¹When $A = 0$ 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.

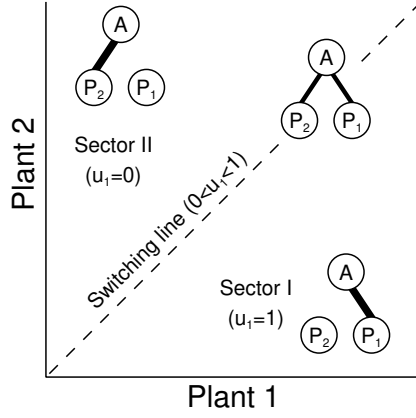


Figure 1. Interactions as a function of plant densities (axes) when animal preference changes according to the step-like rule (5). Below the switching line (6) animals specialize on plant 1, and above they specialize on plant 2. Generalism occurs along the switching line where animals display intermediate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

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

respectively. Here

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

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

$$\mathbf{E}_1 = (P_1^*, 0) = \left(K_1 \left(1 + \frac{sA}{r_1} \right), 0 \right) \quad (9)$$

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

$$\mathbf{E}_2 = (0, P_2^*) = \left(0, K_2 \left(1 + \frac{sA}{r_2} \right) \right) \quad (10)$$

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 $A < r_i$.

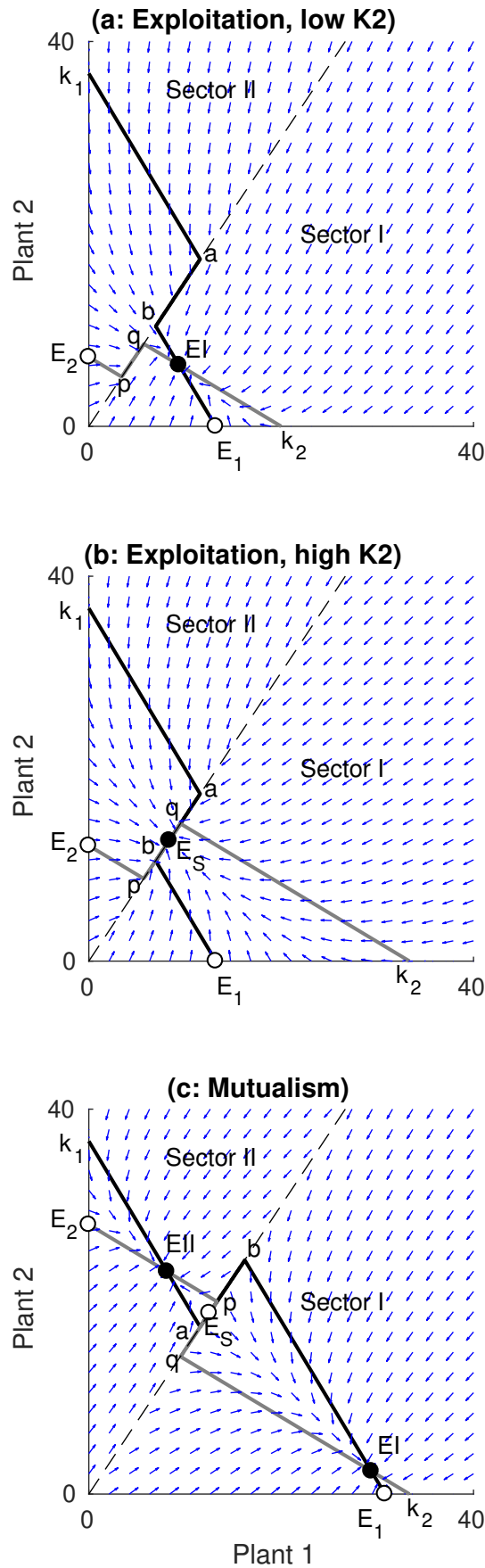


Figure 2. Generalized isoclines (plant 1: black, plant 2: gray) and plant dynamics under weak competition ($c_1 c_2 < 1$). The (dashed) switching line (6) splits the phase plane in sectors I and II. Stable equilibria are shown as dots, and unstable equilibria as circles. Panel a assumes low population 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 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 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.

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

193 We remark that under exploitation ($s = -1$) plant 1 (plant 2) generalized isocline consists of three
 194 segments if $r_1 > A$ ($r_2 > A$). Otherwise, the isocline has only two segments because \mathbf{E}_1 and \mathbf{b} (\mathbf{E}_2
 195 and \mathbf{p}) are not in the first quadrant. In case of mutualism ($s = 1$) generalized isoclines always consist
 196 of three segments because monocultures are viable since we assume that mutualism is facultative.

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

200 Model equilibria

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

207 We start by analyzing position of isoclines in sectors I and II. Since isoclines are linear there they can
 208 intersect in either sector at most once. If they intersect, the corresponding equilibrium is locally stable²
 209 when $c_1c_2 < 1$ and unstable when $c_1c_2 > 1$. This follows from analysis of the classic LV competition
 210 model. We also observe that at these equilibria animals behave as specialists as they interact with a
 211 single plant only. To determine if isoclines intersect within a sector, we compare their intersections
 212 with the corresponding sector's axis and with the switching line (6). In sector I we compare position
 213 of equilibrium \mathbf{E}_1 with respect to point \mathbf{k}_2 on P_1 axis, and position of point \mathbf{b} with respect to point \mathbf{q}
 214 on the switching line. If \mathbf{E}_1 exists and

$$\mathbf{E}_1 < \mathbf{k}_2 \quad \text{and} \quad \mathbf{q} < \mathbf{b} \tag{11}$$

215 by which we mean that point \mathbf{E}_1 is to the left of point \mathbf{k}_2 on P_1 axes and point \mathbf{q} is to the left and
 216 down from point \mathbf{b} along the line $e_1P_1 = e_2P_2$, or

$$\mathbf{E}_1 > \mathbf{k}_2 \quad \text{and} \quad \mathbf{q} > \mathbf{b}, \tag{12}$$

217 Appendix A.1 shows that there is one coexistence equilibrium

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

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

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

221 If both inequalities in (14) are reversed, \mathbf{E}_I still exists because isoclines intersect in sector I but the
 222 equilibrium is unstable. If K_2/K_1 is larger or smaller than both γ_2 and τ_2 , there is no equilibrium in
 223 sector I because the two isoclines do not intersect there (e.g., Figure 2b where $\mathbf{E}_1 < \mathbf{k}_2$ but $\mathbf{b} < \mathbf{q}$).

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

224 Similarly, in sector II we compare position of \mathbf{k}_1 with respect to equilibrium \mathbf{E}_2 on the P_2 axis, and
 225 position of \mathbf{a} with respect to \mathbf{p} along the switching line. If equilibrium \mathbf{E}_2 exists and

$$\mathbf{E}_2 < \mathbf{k}_1 \quad \text{and} \quad \mathbf{a} < \mathbf{p} \quad (15)$$

226 OR

$$\mathbf{E}_2 > \mathbf{k}_1 \quad \text{and} \quad \mathbf{a} > \mathbf{p}, \quad (16)$$

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

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

228 This equilibrium is locally stable if and only if

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

229 As in sector I, instability of \mathbf{E}_{II} follows from inequality reversal in (18). When K_1/K_2 is larger or
 230 smaller than both γ_1 and τ_1 , no equilibrium exists in sector II.

231 We note that γ_1 and γ_2 are *invasion thresholds* that must be met by K_1/K_2 and K_2/K_1 , respectively,
 232 for plant 1 to invade at equilibrium \mathbf{E}_2 and for plant 2 to invade at equilibrium \mathbf{E}_1 , respectively.
 233 Invasion thresholds depend on resident plant parameters, plant–animal interaction type, and animal
 234 density. For example, γ_1 is directly proportional to the competitive effect of plant 2 on plant 1 (c_2)
 235 exactly as in standard LV models. This means that increasing inter-specific competition makes plant
 236 1 less likely to invade resident population consisting of plant 2 only. Under exploitation, increasing
 237 animal density decreases the threshold allowing plant 1 to invade, while increasing plant 2 intrinsic
 238 growth rate (r_2) makes this plant more difficult to invade. These predictions change under mutualism
 239 because the invasion threshold for plant 1 increases with increasing density of mutualists and decreases
 240 with plant 2 intrinsic growth rate.

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

$$\mathbf{E}_{\text{S}} = (\bar{P}_1, \bar{P}_2) = \left(\frac{e_2 K_1 K_2 (r_1 + r_2 + sA)}{K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)}, \frac{e_1 K_1 K_2 (r_1 + r_2 + sA)}{K_1 r_2 (e_1 + c_1 e_2) + K_2 r_1 (e_2 + c_2 e_1)} \right), \quad (19)$$

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

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

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

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

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

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

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

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

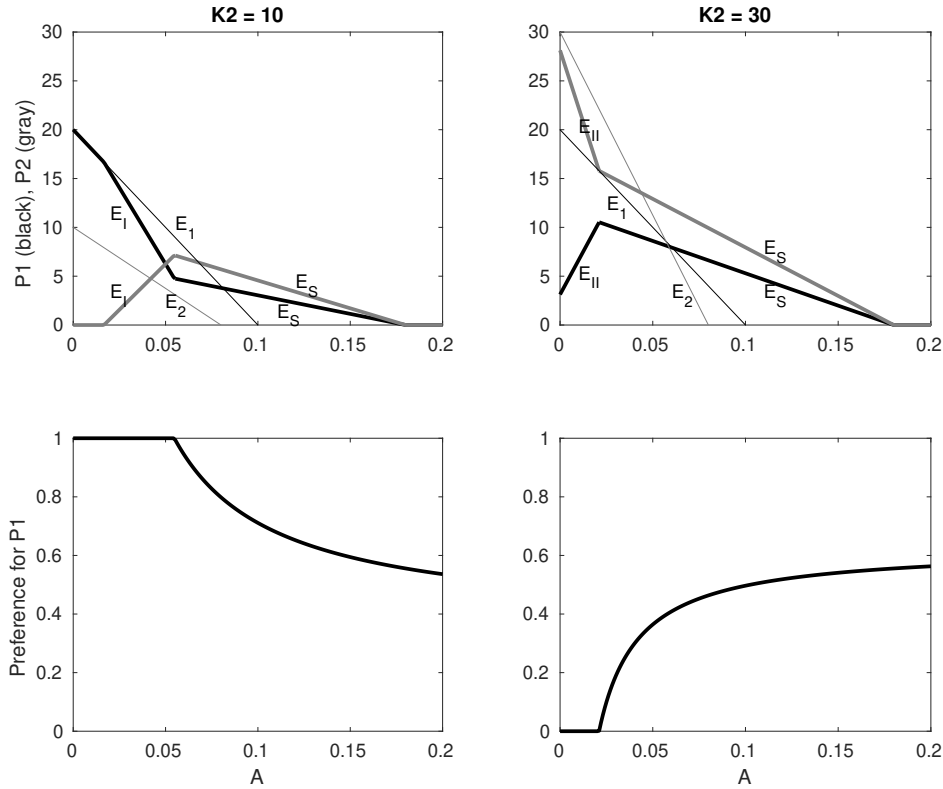


Figure 3. Plant coexistence under weak competition ($c_1c_2 < 1$) and adaptive exploitation ($s = -1$), for high (left column) or low (right column) K_1/K_2 ratios. Top panels show stable plant coexistence (thick lines) and monoculture (\mathbf{E}_1 and \mathbf{E}_2 , thin lines) equilibria as a function 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: $r_1 = 0.1, r_2 = 0.08, c_i = 0.6, e_1 = 1.5, e_2 = 1, K_1 = 20$.

255 holds and “ \mathbf{E}_S repels” trajectories away; see Appendix A.2). If only one attraction threshold is passed,
 256 equilibrium \mathbf{E}_S does not exist and there is no plant population equilibrium at which animals behave
 257 as generalists. Here the important observation is that existence and stability of equilibrium \mathbf{E}_S does
 258 not depend whether single plant monocultures are viable or not. In fact, even if neither of the two
 259 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).
 260 We show next how plant coexistence and animal preferences depend on animal abundance and model
 261 parameters.

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

$$\frac{K_1}{K_2} > \frac{e_2 + c_2e_1}{e_1 + c_1e_2} \quad (23)$$

264 (left column of Figure 3). Without exploiters ($A = 0$), plant 1 wins competition over plant 2. As
 265 the number of exploiters increases, exploiters are plant 1 specialists ($u_1 = 1$, bottom-left panel) and
 266 plant 1 equilibrium density decreases until $A \approx 0.017$. For higher exploiter density (approx. $0.017 <$
 267 $A < 0.055$) plant 2 invades plant 1 monoculture and both plants coexist at equilibrium \mathbf{E}_I given in
 268 (13). Plant 1 population density keeps decreasing with increasing A while plant 2 population density
 269 increases. Exploiters still behave as specialists on plant 1 till their population reaches another critical
 270 threshold $A \approx 0.055$. For yet higher exploiter density, animals behave as generalists feeding on both
 271 plants with decreasing preference for plant 1 given in (20) and plants coexist at equilibrium \mathbf{E}_S given
 272 in (19). Thus, both plant population densities now decrease with increasing animal abundance. The
 273 case where opposite inequality in (23) holds is shown in the right panels of Figure 3. In this case,
 274 exploiters start as plant 2 specialists ($u_1 = 0$, bottom-right panel) at plant equilibrium \mathbf{E}_{II} given in
 275 (17). Thus, plant 2 decreases monotonically while plant 1 increases for $0 \leq A < 0.021$. Once both
 276 plants are equally profitable for animals, animals become generalists and both plants start to decrease

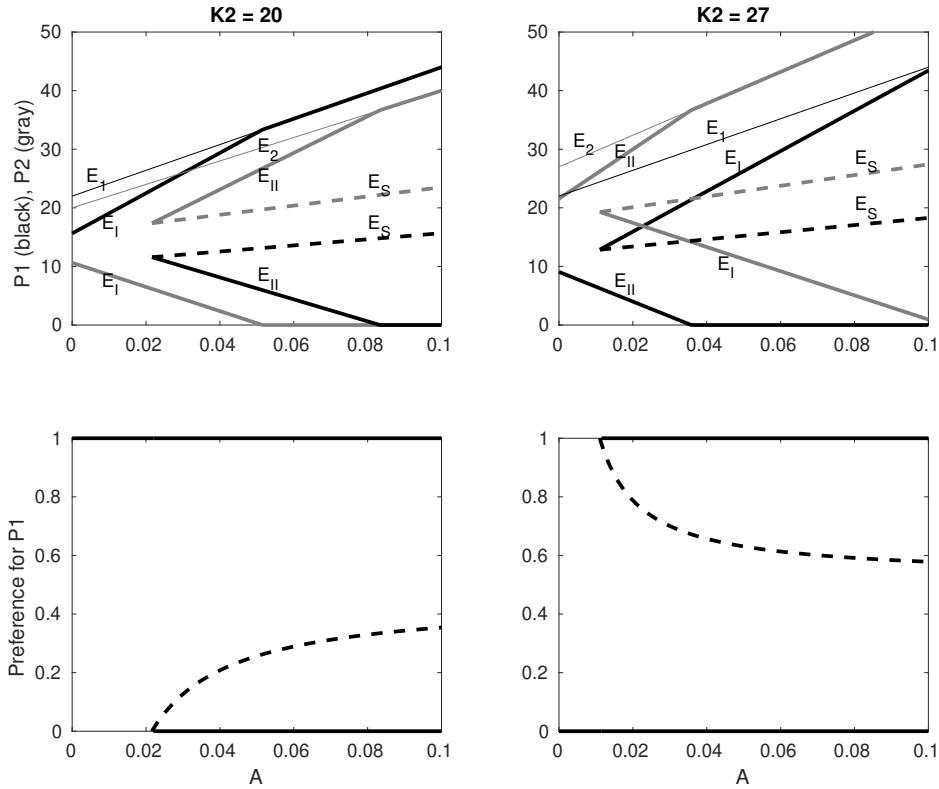


Figure 4. Plant coexistence under weak competition ($c_1 c_2 < 1$) and adaptive mutualism ($s = 1$), for high (left column) or low (right column) K_1/K_2 ratios. Top panels show stable coexistence (\mathbf{E}_I and \mathbf{E}_{II} , thick lines) and monoculture (\mathbf{E}_1 and \mathbf{E}_2 , thin lines) 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: $r_i = 0.1$, $c_i = 0.6$, $e_1 = 1.5$, $e_2 = 1$, $K_1 = 22$.

277 together as preference for plant 1 keeps increasing.

278 Figure 3 also shows that adaptive exploitation leads to indirect positive effects between plants. First,
 279 when animals are adaptive exploiters, plant equilibrium densities are positive for animal densities at
 280 which plant monocultures are not viable. E.g., plant 1 (plant 2) monoculture cannot exist for $A > 0.1$
 281 ($A > 0.08$) 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
 282 large exploiter densities viability of plant 1 relies on co-occurrence with plant 2 and vice-versa. Second,
 283 from (19) it follows that under generalism increasing K_1 or K_2 raises both plant equilibrium densities
 284 (cf. right vs. left top panels in Figure 3 for $A > 0.05$). This is unlike standard LV models where
 285 increasing K_2 causes increase of plant 2 equilibrium density and decrease of plant 1. The effect of
 286 other parameters on plant equilibria (\mathbf{E}_I , \mathbf{E}_{II} , \mathbf{E}_S) is given in Appendix B.

287 Effects of changes in parameters on plant equilibria in the case of mutualism are often in opposite
 288 directions as compared to exploiters (see Appendix B). Because we assume that mutualism is facultative,
 289 plant monocultures (\mathbf{E}_1 and \mathbf{E}_2) are always viable and they increase with A . Provided both
 290 plants coexist, plant 1 increases and plant 2 decreases with A at equilibrium \mathbf{E}_I , and the opposite
 291 happens at equilibrium \mathbf{E}_{II} . Equilibrium \mathbf{E}_S , if it exists, is always unstable. Figure 4 serves as a good
 292 illustration. The left column displays plant coexistence at equilibrium \mathbf{E}_I when $A < 0.022$ and animals
 293 specialize on plant 1 ($u_1 = 1$). For higher animal densities there are two stable equilibria \mathbf{E}_I and
 294 \mathbf{E}_{II} and unstable interior equilibrium \mathbf{E}_S at which animals are generalists. The right column shows
 295 situation where K_1/K_2 is lower and plants coexists at equilibrium \mathbf{E}_{II} when $A < 0.0115$ and animals
 296 specialize on plant 2. For higher animal densities there are two coexisting stable plant equilibria \mathbf{E}_I
 297 and \mathbf{E}_{II} and the unstable equilibrium \mathbf{E}_S .

298 3. Plant coexistence under exploitation or mutualism

299 By comparing K_1/K_2 with γ_1 and τ_1 thresholds in (18), and K_2/K_1 with γ_2 and τ_2 thresholds in
 300 (14), we provide a complete classification of model outcomes for all generic parameter combinations,
 301 see Appendix C. In the following sections we discuss all possible global dynamics when animals are
 302 exploiters or mutualists, and plant inter-specific competition is weak or strong. In the particular case
 303 of exploitation, we only display scenarios where $A < r_1$ and $A < r_2$, i.e., plant monocultures are viable
 304 and generalized isoclines display three segments. Scenarios where monocultures are not viable, i.e.,
 305 $A > r_i$, lead to similar global dynamics as long as $r_1 + r_2 > A$ (i.e., if $A > r_1 + r_2$ both plants go
 306 extinct like in Figure 3).

307 3.1. Exploitation ($s = -1$) and weak inter-specific plant competition ($c_1c_2 < 1$)

308 All qualitatively different patterns of isoclines intersections when inter-specific competition is weak and
 309 $A < r_i$ 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
 310 is always above its attraction threshold.³ This is why Figure 5a, b, d, e are blank, because there are
 311 no parameters that satisfy inequalities that define these four panels. With respect to plant equilibria,
 312 there are three mutually exclusive possible outcomes of plant competition.

313 First, the missing plant cannot invade the other plant monoculture equilibrium and plant coexistence
 314 is not possible. These are situations where generalized isoclines do not intersect nor overlap, and the
 315 dynamics globally converge toward the monoculture equilibrium of the plant that can invade (to \mathbf{E}_1
 316 in Figure 5c, and to \mathbf{E}_2 in panel g).

317 Second, both plants can invade one another and the generalized isoclines intersect in one of the two
 318 sectors. Thus, both plants coexist either at the globally stable equilibrium \mathbf{E}_I (panel f) at which ex-
 319 ploiteders specialize on plant 1, or globally stable equilibrium \mathbf{E}_{II} (panel h) at which exploiters specialize
 320 on plant 2.

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

324 3.2. Exploitation ($s = -1$) and strong inter-specific plant competition ($c_1c_2 > 1$)

325 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
 326 previous case of weak competition and there are 8 qualitative cases for isoclines intersections (Figure
 327 6).

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

333 If neither of the two invasion thresholds are met (Figure 6e), equilibrium \mathbf{E}_S is locally stable and
 334 depending on initial conditions there are three possible outcomes for plant population dynamics: (i)
 335 monoculture equilibrium \mathbf{E}_1 where exploiters specialize on plant 1 ($u_1 = 1$) and plant 2 is excluded,
 336 (ii) monoculture equilibrium \mathbf{E}_2 where exploiters specialize on plant 2 ($u_1 = 0$) and plant 1 is excluded,
 337 or (iii) plant coexistence equilibrium \mathbf{E}_S .

338 If only one plant invasion threshold is met, equilibrium \mathbf{E}_S stays locally stable and there is another
 339 monoculture equilibrium for the plant that meets its invasion threshold (i.e., \mathbf{E}_1 in panel f, or \mathbf{E}_2 in
 340 panel h).

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

³The 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.

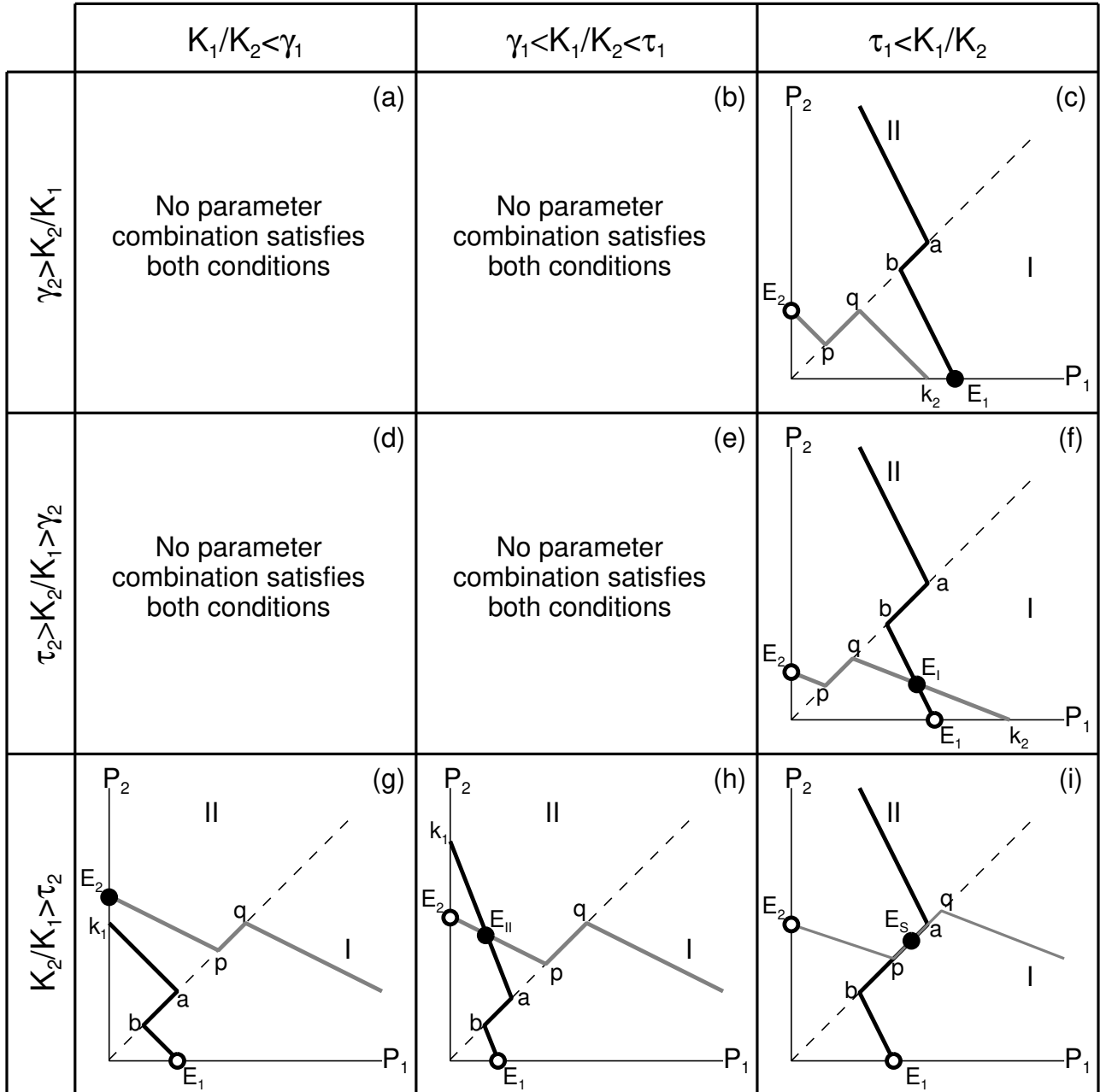


Figure 5. Plant generalized isoclines (plant 1: black, plant 2: gray) under exploitation ($s = -1$) and weak competition ($c_1 c_2 < 1$). Isoclines intersect the dashed switching line (6) at four points **a**, **b**, **p**, **q**. Animals specialize on plant 1 (2) in sector I (II) that is below (above) the switching line in the $P_1 P_2$ 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 (γ_1, γ_2) and attraction (τ_1, τ_2) thresholds.

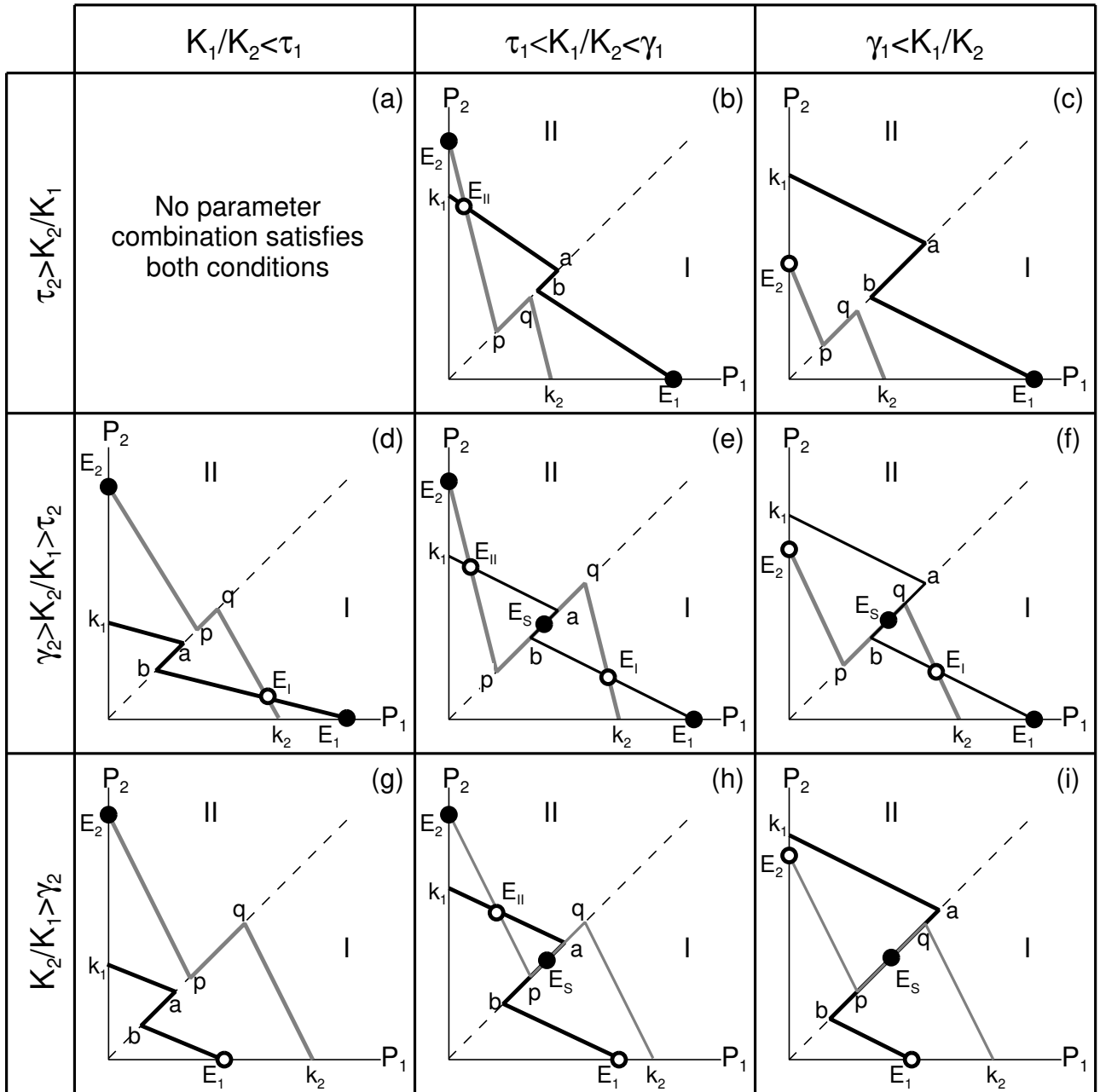


Figure 6. Plant generalized isoclines under exploitation ($s = -1$) and strong competition ($c_1 c_2 > 1$). Notation like in Figure 5.

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

347 3.3. Mutualism ($s = 1$) and weak inter-specific plant competition ($c_1 c_2 < 1$)

348 All possible qualitative intersections of isoclines under mutualism and weak inter-specific plant compe-
 349 tition are shown in Figure 7. As inter-specific competition is weak ($c_1 c_2 < 1$), plant invasion thresholds
 350 are smaller than attraction thresholds ($\gamma_1 < \tau_1$ and $\gamma_2 < \tau_2$) and there are no parameter values such
 351 that $K_1/K_2 > \tau_1$ and $K_2/K_1 > \tau_2$, i.e., panel i in Figure 7 is empty.⁴

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

361 First, if neither plant invasion threshold is met (Figure 7a) initial conditions lead towards mono-
 362 culture equilibrium \mathbf{E}_1 or \mathbf{E}_2 , where mutualists specialize on plant 1 or plant 2 respectively. This
 363 outcome is analogous to the bi-stable case of the standard LV competition model when competition
 364 is strong ($c_1 c_2 > 1$) and the interior equilibrium is a saddle point. But here, instead, competition is
 365 weak ($c_1 c_2 < 1$), and bi-stability arises because equilibrium \mathbf{E}_S on the switching line behaves like a
 366 saddle point. We described similar outcomes of mutual exclusion in previous obligatory mutualism
 367 models (Revilla and Křivan, 2016), where plants competed exclusively for pollinator preferences (i.e.,
 368 $c_1 = c_2 = 0$).

369 Second, when plant 1 (2) meets its invasion threshold and the other plant 2 (1) does not, initial
 370 conditions lead either to a monoculture of plant 1 (2) or to stable coexistence of both plants with
 371 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).

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

375 3.4. Mutualism ($s = 1$) and strong inter-specific plant competition ($c_1 c_2 > 1$)

376 When animals are mutualists ($s = 1$) and inter-specific plant competition is strong ($c_1 c_2 > 1$) attraction
 377 thresholds are smaller than invasion thresholds ($\gamma_i > \tau_i, i = 1, 2$) and there are no parameters satisfying
 378 $K_2/K_1 > \gamma_2$ and $K_1/K_2 > \gamma_1$ (i.e., panels e, f, h and i in Figure 8 are empty). Moreover, plant
 379 coexistence is impossible (Figure 8) which is in a sharp contrast with the case of exploiters (Figure 6)
 380 where plant coexistence is possible depending on initial conditions.

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

386 Bi-stability can also be caused by instability of equilibrium \mathbf{E}_S when the two plant isoclines partially
 387 overlap (Figure 8a), similarly to the case where competition is weak as discussed in the previous Section
 388 3.3.

⁴Indeed 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 $s = 1$.

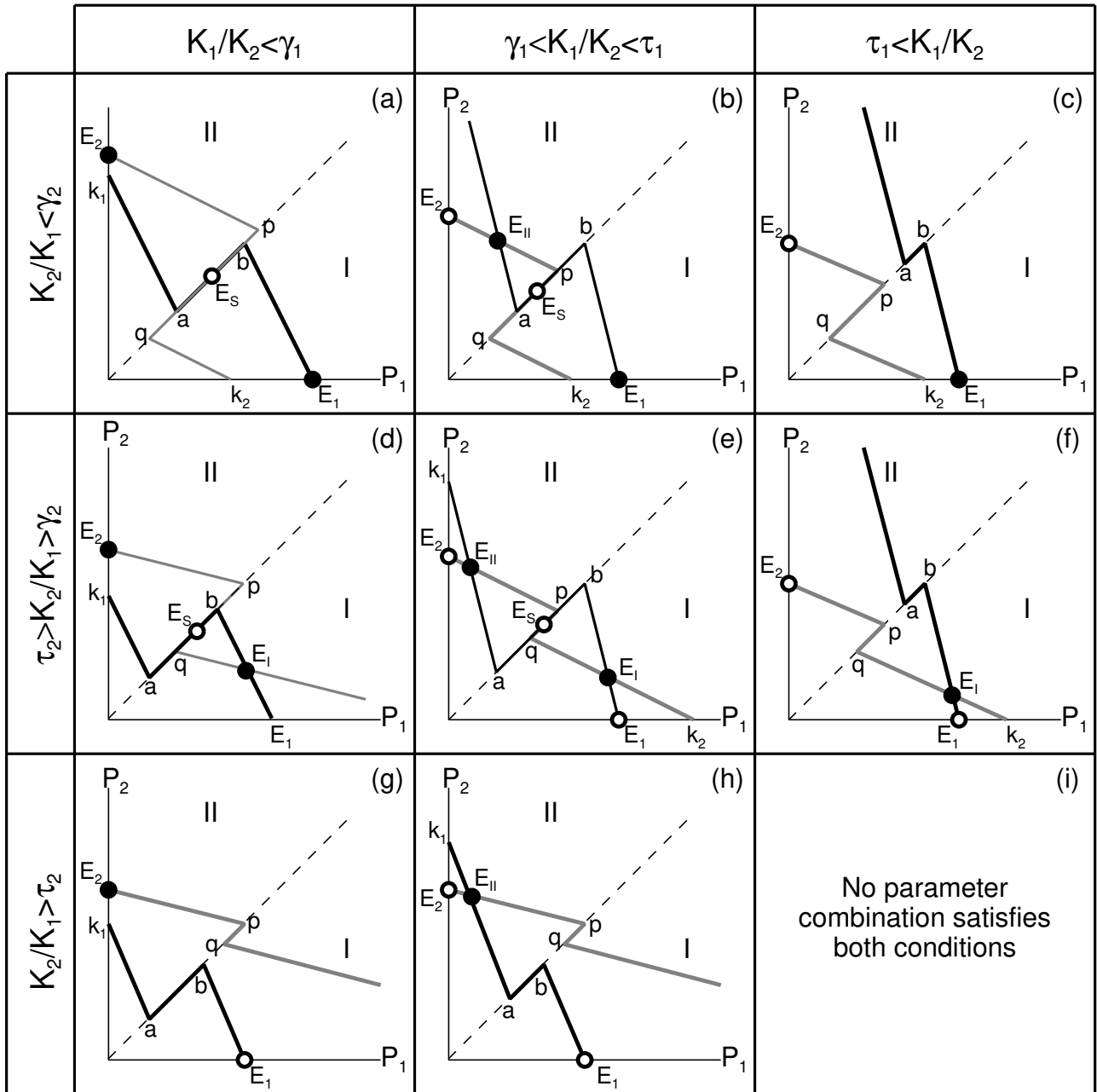


Figure 7. Plant generalized isoclines under mutualism ($s = 1$) and weak competition ($c_1 c_2 < 1$). Notation like in Figure 5.

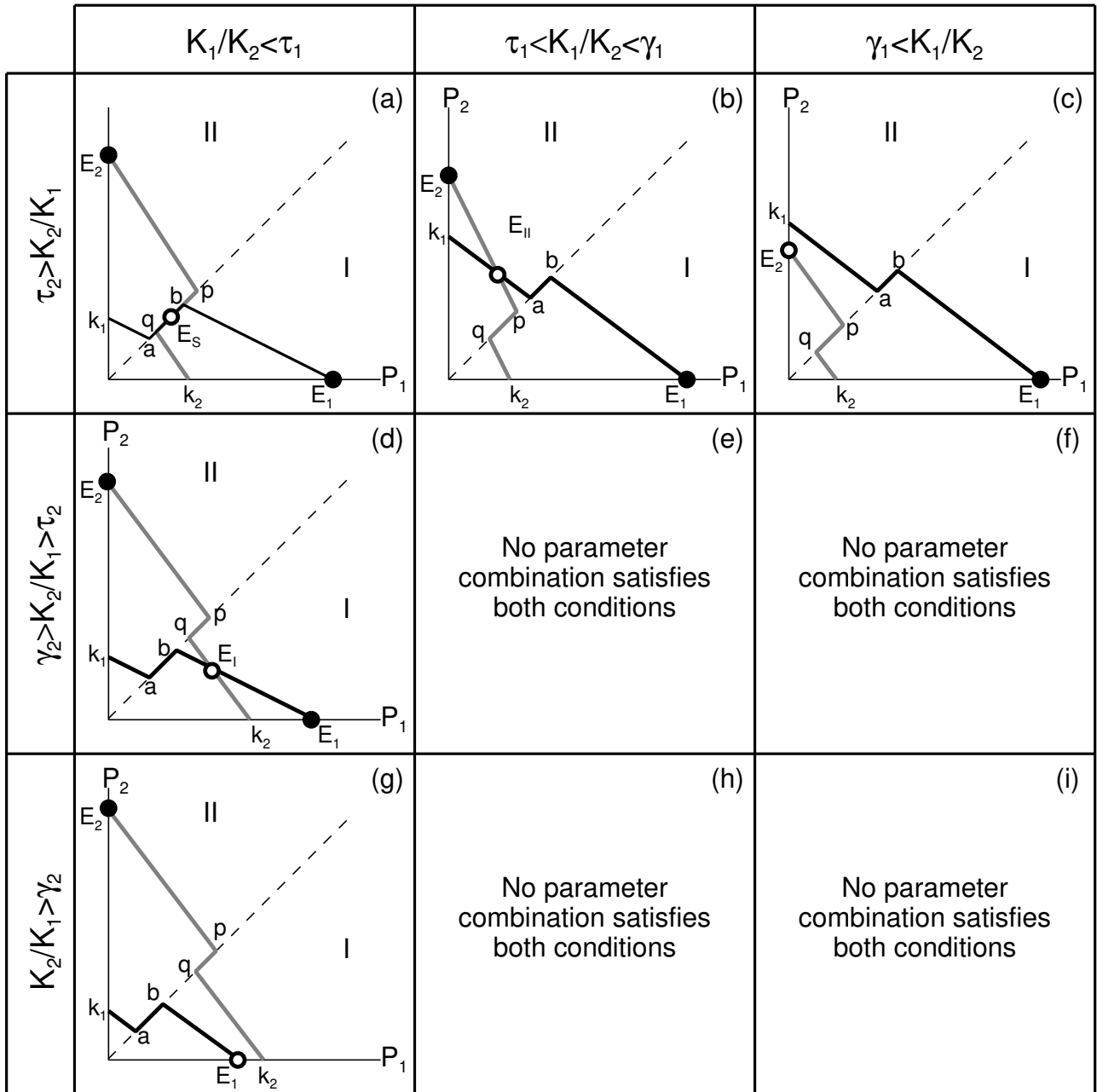


Figure 8. Plant generalized isoclines under mutualism ($s = 1$) and strong competition ($c_1 c_2 > 1$). Notation like in Figure 5.

389 4. Discussion

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

398 Model analysis leads to the following general predictions:

- 399 1. Under exploitation and weak competition a globally stable plant coexistence equilibrium exists
 400 when carrying capacities are not very unbalanced. At plant coexistence equilibrium exploiters
 401 are specialist when at low densities while at high densities they are generalists. Plant coexistence
 402 is possible even if neither of the two plants is viable as a monoculture.
- 403 2. Plant coexistence under exploitation and strong competition is possible but conditional, i.e., de-
 404 pends on initial conditions. Up to three plant equilibria can co-exist. Plant coexistence is possible
 405 only due to adaptive behavior of exploiters when exploiters behave as adaptive generalists.
- 406 3. Plant coexistence under mutualism and weak competition can be global or conditional on initial
 407 plant population densities. Under mutualism animals always specialize on the more profitable
 408 plant only.
- 409 4. Plant coexistence under mutualism and strong competition is impossible.

410 An important special case when plants do not compete directly ($c_1 = c_2 = 0$), e.g., when plants grow in
 411 separate pots, or plants are separated by a fence or a road (Geslin et al., 2017), was analyzed in Křivan
 412 (2003b) for exploiters. In this case plant 1 (plant 2) isocline is vertical (horizontal) in sectors I and
 413 II, invasion thresholds are zero so that they play no role at all, and attraction thresholds simplify to
 414 $\tau_1 = \frac{e_2}{e_1} \left(1 + \frac{sA}{r_2}\right)$ 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
 415 is either global extinction (when exploiter density is too high) or global coexistence where animals can
 416 be specialists (when exploiter density is low) or generalists (when exploiter density is intermediate).
 417 In the case of mutualism ($s = 1$) possible outcomes always predict coexistence, including alternative
 418 stable states, as shown in Figure 7e, f, h.

419 We stress here that our predictions concern a small community, and it would be incorrect to ex-
 420 trapolate them to larger plant–animal interaction networks without proper consideration of model (1)
 421 limitations and assumptions (see section Model assumption below). For example, our model predicts
 422 that both plants can coexist with generalist exploiters but not with generalists mutualists, while there
 423 is empirical evidence that insect pollinators are more generalist than insect herbivores (Fontaine et al.,
 424 2009). Disagreement arises, e.g., because our Lotka–Volterra model does not consider competition for
 425 plants among the animals that are kept at fixed density. When mutualism is modeled under explicit
 426 consumer–resource dynamics where animal population densities change (Valdovinos et al., 2013; Revilla
 427 and Křivan, 2016), resource depletion (e.g., nectar consumption) can promote mutualist generalism,
 428 countering the tendency towards exclusive specialization on the most profitable plant.

429 Another counter-intuitive prediction is that exploitation coupled with flexible foraging enables indi-
 430 rect facilitation between plants. Once again, this is due to fixed animal population densities, because
 431 increase in one plant population density does not lead to increase in exploiter population density, a
 432 necessary condition for apparent competition (Holt, 1977) to occur. Similarly, switching can reduce or
 433 even eliminate apparent competition when there is interference between consumers (Abrams, 1995).
 434 Thus by coexisting, plants share exploitation costs, which leads to facilitation (i.e., higher equilibrium
 435 densities). Such indirect positive effect can be extreme, i.e., plants that cannot tolerate exploita-
 436 tion alone can survive when sharing exploitative stress with another plant (e.g., Figure 3). Similarly,
 437 adaptive mutualism makes plant coexistence more difficult, because it makes plant competition even

438 stronger (Figure 4). Once again, this is because we assume a fixed mutualist density while the con-
439 ventional view of indirect facilitation between plants mediated by shared mutualists assumes that that
440 mutualism raises shared pollinator densities (Waser and Real, 1979). In this respect, experiments
441 show that competition between plants for pollinator preferences can overcome such facilitation effects
442 (Ghazoul, 2006).

443 Population dynamics and adaptive animal preferences

444 To model effects of adaptive animal preferences on population dynamics of two competing plant species,
445 we combine the Lotka–Volterra competitive model with a behavioral model that describes changes
446 in animal preferences for plants. This is a common scenario in plant communities interacting with
447 guilds of herbivores, parasites, pollinators or seed dispersers (Melián et al., 2009; Sauve et al., 2016;
448 Bronstein, 2015). We assume that animal preferences for plants track instantaneously current plant
449 population densities which, in turn, influence plant population dynamics. To model this feedback,
450 we assume that animal preferences maximize animal fitness at current plant population densities. As
451 optimal animal preferences when both plants are equally profitable are not uniquely given, the resulting
452 plant population dynamics are described by a Lotka–Volterra differential inclusion (e.g., Colombo and
453 Křivan, 1993; Křivan, 1996, 1997, 2007; Křivan et al., 2008). We analyze this model by generalizing
454 the concept of isoclines which allows us to provide a complete classification of all plant equilibria. To
455 this end, we split the plant phase space into two sectors (Figures 2a, c, e and 5–8). The boundary that
456 separates these sectors is called the switching line because animals switch their preferences for plants
457 when plant population numbers cross this line. Along the switching line animal fitness is independent
458 from animal preferences because payoffs from both plants are the same. Inside the sectors, animals
459 specialize on one plant only⁵. Thus, plant isoclines inside each sector coincide with the classical
460 isoclines for the Lotka–Volterra competition model. In this article we define generalized plant isoclines
461 that are formed by sector-wise pieces of isoclines that are connected with segments of the switching line
462 (Figures 5–8). Thus, globally, generalized plant isoclines are piece-wise linear, which leads to multiple
463 isocline intersections and multiple steady states. In particular, the segments of the two plant isoclines
464 that are subsets of the switching line can partially overlap (Figure 5i; Figure 6e, f, h, i; Figure 7a,
465 b, d, e; Figure 8a). If so, we show that plant population dynamics have a unique equilibrium in this
466 overlapping segment (e.g., Figure 2b, c). This equilibrium is either locally stable when animals are
467 exploiters or unstable when animals are mutualists. There are important differences between plant
468 equilibria in the switching line and those that are inside sectors because animals are specialists inside
469 sectors, but they are generalists at the equilibrium that is in the switching line.

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

⁵Similar concepts, called isodars and isolegs, are used in the habitat selection theory (Pimm and Rosenzweig, 1981; Rosenzweig, 1981; Křivan and Siroť, 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.

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

488 **Model assumptions**

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

502 Another important assumption is that animal adaptation is much faster than plant population
503 dynamics. This requires that changes of foraging behavior occur within individual lifetimes, e.g.,
504 highly mobile consumers dispersing between plant species, like in the ideal free distribution (Křivan,
505 2003b). The assumption of fast adaptation can be relaxed by modeling preference dynamics explicitly
506 using, e.g., replicator equation (Kondoh, 2003). In Revilla and Křivan (2016) we showed that qualitative
507 predictions related to mutualist generalism vs. specialism are preserved even when adaptation runs on a
508 similar time scale as population dynamics. However, when adaptation was much slower than population
509 dynamics, predictions frequently diverged due to extreme dependence on animal initial preferences. For
510 example, if animals initially strongly prefer one plant over the other despite the fact that such behavior
511 is not optimal, the initially preferred plant can die out before animal preferences could change. In
512 addition, when adaptation occurs over multiple generations, specialization or generalism also depends
513 on the evolution of fitness related traits such as conversion efficiencies (e_i), which scale interactions
514 with payoffs. Parameters like these depend on complex morphological and physiological constraints,
515 and they generally relate to one another via non-linear trade-offs (Egas et al., 2004). Accounting for
516 long term change of these parameters requires different approaches (e.g., adaptive dynamics, Kisdi
517 2002; Egas et al. 2004; Rueffler et al. 2006).

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

524 **Conditional coexistence and alternative plant stable states**

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

533 Conditional coexistence and coexistence at alternative stable states are common predictions of mod-
534 els that combine positive and negative density-dependent interactions (e.g., Hernandez, 1998; Holland
535 and DeAngelis, 2010; Revilla and Encinas-Viso, 2015). In the present model, however, plants always

536 interact negatively due to inter-specific competition, and additional positive or negative effects arise
537 due to adaptive preference of common exploiters or mutualists. Since animal densities are fixed, these
538 indirect effects are behavior-mediated, but triggered by changes in plant densities. It is very important
539 to remark that such abundance–preference feedbacks between trophic levels leads to very different
540 predictions when compared to abundance–abundance feedbacks between trophic levels. In this latter
541 case where animals respond numerically to plant densities, exploitation leads to *apparent competition*
542 (Holt, 1977) and mutualism to *apparent mutualism* (or apparent facilitation) between plants, which
543 respectively opposes and favors coexistence (Sauve et al., 2016). When animal preferences respond
544 to plant densities, exploitation leads to a *competitive release* that promotes stable plant coexistence
545 (Křivan, 1997, 2003a) while mutualism leads to *competition for mutualists preferences* between plants
546 that destabilizes plant coexistence and leads to plant exclusion (Revilla and Křivan, 2018).

547 In this article we showed that conditional plant coexistence is expected in scenarios where generalist
548 exploiters regulate strongly competing plants (i.e., $c_1c_2 > 1$, Figure 6e, f, h, i). On the other hand,
549 outcomes like coexistence at alternative stable states are expected between weakly competing plants
550 (i.e., $c_1c_2 < 1$) that are regulated by specialized mutualists. How relevant these predictions are in
551 the real world depends on how widespread are situations where intra-specific competition is stronger
552 than inter-specific, and vice-versa. On the one hand, meta-analyses suggest that intra- and inter-
553 specific effects are too similar to be discerned (Gurevitch et al., 1992), or that intra-specific effects are
554 actually much stronger than inter-specific (i.e., $c_1c_2 \leq 1$; Adler et al., 2018). However, recent pair-wise
555 competition experiments (Sheppard, 2019) suggest that inter-specific competition can be strong (i.e.,
556 $c_1c_2 > 1$). Such uncertainty is rooted in the fact that these surveys assume models like (1) that treat
557 competition phenomenologically, and there can be multiple underlying factors that can lead to strong
558 net competition. For example, competition can be strengthened by allelopathy (Inderjit and Del Moral,
559 1997), which is decidedly stronger against non-specifics compared to con-specifics.

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

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687 **A. Plant population dynamics**

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

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

689 and

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

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

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

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

$$\begin{aligned}\frac{dP_1}{dt} &= \left(r_1 \left(1 - \frac{P_1 + c_2 P_2}{K_1} \right) \right) P_1 \\ \frac{dP_2}{dt} &= \left(r_2 \left(1 - \frac{P_2 + c_1 P_1}{K_2} \right) + sA \right) P_2.\end{aligned}\tag{A.2}$$

693 Along the switching line $e_1 P_1 = e_2 P_2$ animal strategy is not uniquely defined and population dy-
694 namics satisfy

$$\begin{aligned}\frac{dP_1}{dt} &= r_1 \left(1 - \frac{P_1 + c_2 P_2}{K_1} \right) P_1 + s u_1 P_1 A \\ \frac{dP_2}{dt} &= r_2 \left(1 - \frac{P_2 + c_1 P_1}{K_2} \right) P_2 + s u_2 P_2 A \\ (u_1, u_2) &\in \{(v_1, v_2) \mid v_1 + v_2 = 1, v_1 \geq 0, v_2 \geq 0\}.\end{aligned}\tag{A.3}$$

695 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

$$P_1 + c_2 P_2 = K_1 \left(1 + \frac{sA}{r_1} \right)\tag{A.4}$$

$$P_1 + c_2 P_2 = K_1,\tag{A.5}$$

696 respectively. We observe that plant 1 isocline exists in sector I iff $r_1 + sA > 0$. For mutualists ($s = 1$)
697 this is always the case, but for exploiters this holds only if $A < r_1$ which we assume now. The segment
698 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]
699 and switching line (6) at

$$\mathbf{b} = \left(\frac{e_2 K_1 (r_1 + sA)}{r_1 (e_2 + c_2 e_1)}, \frac{e_1 K_1 (r_1 + sA)}{r_1 (e_2 + c_2 e_1)} \right),\tag{A.6}$$

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

$$\mathbf{k}_1 = \left(0, \frac{K_1}{c_2} \right)\tag{A.7}$$

$$\mathbf{a} = \left(\frac{e_2 K_1}{e_2 + c_2 e_1}, \frac{e_1 K_1}{e_2 + c_2 e_1} \right),\tag{A.8}$$

700 respectively.

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

$$P_2 + c_1 P_1 = K_2\tag{A.9}$$

and in sector II

$$P_2 + c_1 P_1 = K_2 \left(1 + \frac{sA}{r_2} \right),\tag{A.10}$$

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

$$\mathbf{k}_2 = \left(\frac{K_2}{c_1}, 0 \right)\tag{A.11}$$

$$\mathbf{q} = \left(\frac{e_2 K_2}{e_1 + c_1 e_2}, \frac{e_1 K_2}{e_1 + c_1 e_2} \right),\tag{A.12}$$

701 respectively. Isocline (A.10) intersects the P_2 axis at \mathbf{E}_2 [given by (10) in the main text] and the
 702 switching line at

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

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

$$\mathbf{k}_2 > \mathbf{E}_1 \iff \frac{K_2}{K_1} > c_1 \left(1 + \frac{sA}{r_1} \right) \equiv \gamma_2 \quad (\text{A.14})$$

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

703 If both conditions above are true, plant 2 isocline is above plant 1 isocline in sector I and there is no
 704 interior equilibrium in this sector (e.g., Figure 2c, sector I). If both conditions are false, then plant 1
 705 isocline is above plant 2 isocline in sector I (Figure 5c, sector I). If (A.14) is true and (A.15) false,
 706 isoclines intersect at point \mathbf{E}_I [given by (13) in the main text], and because plant 1 isocline is steeper
 707 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
 708 and (A.15) true, isoclines intersect again but because plant 2 isocline is steeper than plant 1 isocline
 709 ($\frac{1}{c_2} < c_1$), \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

$$\mathbf{k}_1 > \mathbf{E}_2 \iff \frac{K_1}{K_2} > c_2 \left(1 + \frac{sA}{r_2} \right) \equiv \gamma_1 \quad (\text{A.16})$$

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

710 If both conditions above are true (e.g., Figure 2a,c) or both are false (e.g., Figure 5g), there is no
 711 interior equilibrium in sector II because the two plant isoclines do not intersect there. If (A.16) is true
 712 and (A.17) false, isoclines intersect at the point \mathbf{E}_{II} [given by (17) in the main text], and because plant
 713 1 isocline is steeper than plant 2 isocline ($\frac{1}{c_2} > c_1$) the equilibrium is stable (e.g., Figure 2e, sector II).
 714 And if (A.16) is false and (A.17) true, isoclines intersect and because plant 2 isocline is steeper than
 715 plant 1 isocline ($\frac{1}{c_2} < c_1$), \mathbf{E}_{II} is unstable (e.g., Figure 6b, sector II).

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

717 Here we are interested in plant population dynamics at the switching line. Let $\mathbf{n} = (e_1, -e_2)$ be a
 718 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)
 719 and (A.2) by \mathbf{f}^I and \mathbf{f}^{II} , respectively. The dynamics close to the switching line depend on the following
 720 scalar products

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

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

- 722 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
 723 I to sector II.
- 724 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
 725 II to sector I.
- 726 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
 727 for some positive time on the switching line. This is called the sliding regime.

	Cases	$\langle \mathbf{n}, \mathbf{f}^I \rangle$	$\langle \mathbf{n}, \mathbf{f}^{II} \rangle$	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.

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

731 We observe that

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

732 Thus, when $s = 1$, $\langle \mathbf{n}, \mathbf{f}^{II} \rangle > 0$ implies $\langle \mathbf{n}, \mathbf{f}^I \rangle > 0$ which excludes the sliding regime. Similarly, when
733 $s = -1$, $\langle \mathbf{n}, \mathbf{f}^{II} \rangle < 0$ implies $\langle \mathbf{n}, \mathbf{f}^I \rangle < 0$ which excludes the repelling regime.

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

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

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

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

743

744 A.2.1. Equilibrium \mathbf{E}_S

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

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

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

749 0 and 1. This happens iff either (21) or (22) holds. Using (A.6) and (A.12), plant 1 population
 750 equilibrium given in (19) can be written as a convex combination of points b_1 and q_1

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

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

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

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

753 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
 754 where the plant generalized isoclines overlap. Now we study stability of \mathbf{E}_S .

755 First we consider the exploitation case where $s = -1$. Table A.1 shows that at points where the
 756 generalized isoclines overlap, trajectories are driven toward the switching line from both sectors. In
 757 this case trajectories cannot cross the switching line inside the isoclines overlap segment. Thus, once
 758 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
 759 that when the trajectory moves along the overlap segment, preferences for plants (u_1, u_2) must satisfy
 760 $e_1 P_1'(t) = e_2 P_2'(t)$, i.e.,

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

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

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

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

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

765 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
 766 stable, because trajectories close to this equilibrium are attracted from both sector I and II toward the
 767 switching line (Table A.1) and they converge along the switching line to the equilibrium.

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

772 B. Effect of parameters on equilibria

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

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

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

$$\begin{aligned} \frac{\partial \hat{P}_1}{\partial r_1} &= \frac{-s K_1 A}{r_1^2 (1 - c_1 c_2)}, & \frac{\partial \hat{P}_2}{\partial r_1} &= \frac{s c_1 K_1 A}{r_1^2 (1 - c_1 c_2)}, & \frac{\partial \hat{P}_1}{\partial A} &= \frac{s K_1}{r_1 (1 - c_1 c_2)}, & \frac{\partial \hat{P}_2}{\partial A} &= \frac{-s K_1 c_1}{r_1 (1 - c_1 c_2)}, \\ \frac{\partial \hat{P}_1}{\partial K_1} &= \frac{1}{1 - c_1 c_2} \left(1 + \frac{sA}{r_1} \right), & \frac{\partial \hat{P}_2}{\partial K_1} &= \frac{-c_1}{1 - c_1 c_2} \left(1 + \frac{sA}{r_1} \right), & \frac{\partial \hat{P}_1}{\partial K_2} &= \frac{-c_2}{1 - c_1 c_2}, & \frac{\partial \hat{P}_2}{\partial K_2} &= \frac{1}{1 - c_1 c_2}, \\ \frac{\partial \hat{P}_1}{\partial c_1} &= \frac{c_2 \hat{P}_1}{1 - c_1 c_2}, & \frac{\partial \hat{P}_2}{\partial c_1} &= \frac{-\hat{P}_1}{1 - c_1 c_2}, & \frac{\partial \hat{P}_1}{\partial c_2} &= \frac{-\hat{P}_2}{1 - c_1 c_2}, & \frac{\partial \hat{P}_2}{\partial c_2} &= \frac{c_1 \hat{P}_2}{1 - c_1 c_2}. \end{aligned}$$

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

776 At equilibrium \mathbf{E}_S (19) plant densities take the form

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

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

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

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

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

777 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.

778 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

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

779 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
 780 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

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

781 where the quantities between curly braces are positive (because feasibility of \mathbf{E}_S requires $r_1 + r_2 + sA >$
 782 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

783 ($s = 1$), $\frac{\partial \bar{u}_1}{\partial K_1} < 0$ 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
 784 as follows

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

785 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
 786 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
 787 compared with the corresponding derivatives with respect r_1, K_1, c_1, e_1 above.

788 C. Classification of equilibria

789 Table A.2 summarizes our previous analyzes given in Appendices A.1 and A.2, and lists all feasible
 790 (i.e., non-negative) stable equilibria for system (1) under exploitation ($s = -1$) or mutualism ($s = 1$),
 791 and weak ($c_1 c_2 < 1$) or strong ($c_1 c_2 > 1$) competition. Empty (\emptyset) cells indicate that no parameter
 792 combination satisfies row or column conditions. Cells with only one equilibrium indicate that this
 793 equilibrium is globally stable. Cells with multiple equilibria indicate that these equilibria are locally
 794 stable. There are 56 non-empty cells in Table A.2, each of them corresponding to a unique isocline
 795 configuration. The configurations shown in Figures 5–8 are indicated by figure number and panel. Out
 796 of these 56 configurations, there are 11 possible combinations (i.e., $\mathbf{E}_1, \mathbf{E}_2, \mathbf{E}_I, \mathbf{E}_{II}, \mathbf{E}_S, \{\mathbf{E}_I, \mathbf{E}_{II}\},$
 797 $\{\mathbf{E}_S, \mathbf{E}_1\}, \{\mathbf{E}_S, \mathbf{E}_2\}, \{\mathbf{E}_1, \mathbf{E}_{II}\}, \{\mathbf{E}_2, \mathbf{E}_I\}, \{\mathbf{E}_S, \mathbf{E}_1, \mathbf{E}_2\}$) with respect to stable equilibria.

798 Equilibria $\mathbf{E}_1, \mathbf{E}_2$ given in (9), (10) are boundary (i.e., monoculture) equilibria for plant 1 and 2,
 799 respectively; $\mathbf{E}_I, \mathbf{E}_{II}, \mathbf{E}_S$ given in (13), (17), and (19) are interior equilibria in sector I (where $u_1 = 1$),
 800 sector II (where $u_1 = 0$), and the switching line (where $u_1 = \bar{u}_1$ is given by (20)), respectively. Cases
 801 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
 802 \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.
 803 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
 804 remark that for exploitation when $A > r_1$ ($A > r_2$), point \mathbf{b} (\mathbf{p}) is in the third quadrant and boundary
 805 equilibrium \mathbf{E}_1 (\mathbf{E}_2) is not feasible. Table A.2 considers all generic cases excluding those cases where
 806 one or more inequalities between points and parameters are replaced by equalities.

807

808 D. Gradual change in preference

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

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

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

818 We observe (cf. Figure A.1 here vs. Figure 2 in the main text) that for sufficiently large values of the
 819 Hill exponent the dynamics of model (1) in the main text with step-like preferences are well approx-
 820 imated by plant population dynamics where animal preferences for plants are gradual and described
 821 by (A.21). In Figure A.1 that matches Figure 2 of the main text we show a cone of intermediate plant
 822 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			
		$k_1 > E_2, k_2 > E_1$	$k_1 > E_2, k_2 < E_1$	$k_1 < E_2, k_2 > E_1$	$k_1 < E_2, k_2 < E_1$
$c_1 c_2 < 1$	$p < q < b < a$	E_I (Fig. 5f)	E_I (Fig. 5c)	\emptyset	\emptyset
	$b < a < p < q$	E_{II} (Fig. 5h)	\emptyset	E_2 (Fig. 5g)	\emptyset
$s = -1$	$p < b < a < q$	E_S	\emptyset	\emptyset	\emptyset
	$b < p < q < a$	E_S	\emptyset	\emptyset	\emptyset
$c_1 c_2 > 1$	$p < b < q < a$	E_S	\emptyset	\emptyset	\emptyset
	$b < p < a < q$	E_S (Fig. 5i)	\emptyset	\emptyset	\emptyset
$c_1 c_2 < 1$	$p < q < b < a$	\emptyset	E_I (Fig. 6c)	\emptyset	$\{E_1, E_2\}$ (Fig. 6b)
	$b < a < p < q$	\emptyset	\emptyset	E_2 (Fig. 6g)	$\{E_1, E_2\}$ (Fig. 6d)
$s = 1$	$p < b < a < q$	E_S	$\{E_S, E_1\}$ (Fig. 6f)	$\{E_S, E_2\}$	$\{E_S, E_1, E_2\}$ (Fig. 6e)
	$b < p < q < a$	E_S (Fig. 6i)	$\{E_S, E_1\}$	$\{E_S, E_2\}$	$\{E_S, E_1, E_2\}$
$c_1 c_2 < 1$	$p < b < q < a$	E_S	$\{E_S, E_1\}$	$\{E_S, E_2\}$ (Fig. 6h)	$\{E_S, E_1, E_2\}$
	$b < p < a < q$	E_S	$\{E_S, E_1\}$	\emptyset	\emptyset
$c_1 c_2 > 1$	$q < p < a < b$	E_I (Fig. 7f)	E_I (Fig. 7c)	E_2 (Fig. 7g)	$\{E_1, E_2\}$ (Fig. 7a)
	$a < b < q < p$	E_{II} (Fig. 7h)	\emptyset	$\{E_1, E_2\}$	$\{E_1, E_2\}$
$s = 1$	$q < a < b < p$	$\{E_I, E_{II}\}$	$\{E_{II}, E_1\}$	$\{E_1, E_2\}$	$\{E_1, E_2\}$
	$a < q < p < b$	$\{E_I, E_{II}\}$ (Fig. 7e)	$\{E_{II}, E_1\}$	$\{E_1, E_2\}$	$\{E_1, E_2\}$
$c_1 c_2 < 1$	$q < a < p < b$	$\{E_I, E_{II}\}$	$\{E_I, E_1\}$ (Fig. 7b)	$\{E_1, E_2\}$	$\{E_1, E_2\}$
	$a < q < b < p$	$\{E_I, E_{II}\}$	$\{E_{II}, E_1\}$	$\{E_1, E_2\}$ (Fig. 7d)	$\{E_1, E_2\}$
$c_1 c_2 > 1$	$q < p < a < b$	\emptyset	E_I (Fig. 8c)	\emptyset	$\{E_1, E_2\}$ (Fig. 8b)
	$a < b < q < p$	\emptyset	\emptyset	E_2 (Fig. 8g)	$\{E_1, E_2\}$ (Fig. 8d)
$s = 1$	$q < a < b < p$	\emptyset	\emptyset	\emptyset	$\{E_1, E_2\}$
	$a < q < p < b$	\emptyset	\emptyset	\emptyset	$\{E_1, E_2\}$
$c_1 c_2 < 1$	$q < a < p < b$	\emptyset	\emptyset	\emptyset	$\{E_1, E_2\}$
	$a < q < b < p$	\emptyset	\emptyset	\emptyset	$\{E_1, E_2\}$

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

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

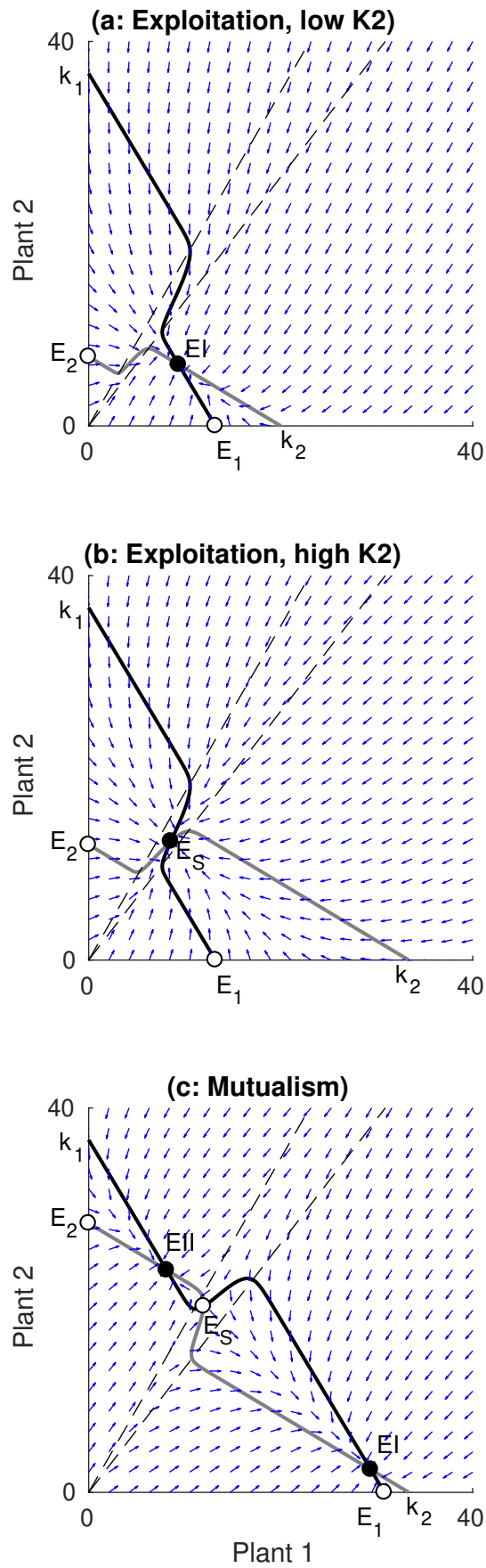


Figure A.1. Plant isoclines (plant 1: black, plant 2: gray) and population dynamics under weak competition ($c_1 c_2 < 1$) and preferences given by the Hill function with $z = 20$ (dashed lines correspond to contour lines for which $u_1 = 0.05$ and $u_1 = 0.95$). Panels and parameters correspond to those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