

Plant competition under simultaneous adaptation by herbivores and pollinators

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ABSTRACT

Two plants can influence one another indirectly by affecting population dynamics of shared exploiters and/or shared mutualists, giving rise to apparent competition or apparent mutualism, respectively. Indirect interactions between plants also occur when the preferences of exploiters and mutualists adapt to changes in relative plant densities. Here we study simultaneous effects of adaptive herbivore and pollinator preferences on the dynamics of two competing plant populations. As a result of feedbacks between plant dynamics and adaptive animal preferences, plants coexist at alternative stable states. This outcome is favored at low abundances of herbivores and pollinators when consumers tend to specialize on a single plant. As herbivore and pollinator abundances increase, generalism becomes more common. This promotes plant coexistence by balancing antagonistic and mutualistic effects between plants. Plant community dynamics become also more predictable due to reduction in the number of alternative stable states. This shows that the global decline in insect populations can lead to structural changes in plant communities that are difficult to predict.

1. Introduction

During the last three decades, populations of insects have decreased globally (Hallmann et al., 2017). This has important consequences, as insects play “a central role in a variety of processes, including pollination, herbivory and detritivory nutrient cycling and providing a food source for higher trophic levels such as birds, mammals and amphibians” (sic. Hallmann et al., 2017). This situation, associated with the expansion of monospecific crops (Holzschuh et al., 2011; Geslin et al., 2017), threatens the persistence and stability of natural communities. Both density and trait mediated effects of herbivores on plants and effects of pollinators on plants (see below) were analyzed theoretically using simple food web modules. In this article, our concern is to study how behavioral changes of both insect pollinators and herbivores impact coexistence of two plant populations.

Early models of “struggle for existence” focused on predator–prey interactions and consumer competition for resources (e.g., Volterra, 1926, 1928, 1938; Gause, 1934). These works that consider two interacting species were quickly extended to small food webs (also called community modules, Holt, 1997), consisting of three or four species. These early works considered fixed interaction strength between populations and led to an important general prediction that coexistence of several species is either difficult or impossible to achieve (e.g., the competitive exclusion principle, Gause, 1934; Hardin, 1960; Levin,

1970). Odum (1971) suggested that to explain a higher species richness more interactions (e.g., mutualism, commensalism, parasitism etc.) need to be considered. This view was challenged by May’s (1972) observation that for randomly assembled model interaction webs there is a sharp transition from stability to instability when complexity measured as the food-web connectance (i.e., the number of realized links in the food web divided by the number of all possible links) exceeds a critical threshold. Another research line focused on interaction strengths (e.g., Paine, 1980; McCann et al., 1998; Bascompte et al., 2005) that are assumed to be strong and fixed in these early models. E.g., in the predator–prey Lotka–Volterra model, the predator specializes on the particular prey that has no possibility to escape predation when even at low densities. Research on optimal foraging showed (Murdoch, 1969; Charnov, 1976; Stephens and Krebs, 1986) that animals often forage to maximize their food intake rate which is a proxy for their fitness. Other research also showed that prey try to avoid predators by using physical (Gause et al., 1936) or behavioral refuges either by reducing their activity, or changing their habitat (Sih, 1980, 1986; Lima and Dill, 1990; Peacor and Werner, 2001; Brown and Kotler, 2004). Such adaptive behaviors make interactions between consumers and their resources weaker and promote species persistence (e.g., Křivan, 1996, 1997; Fryxell and Lundberg, 1998; Huxel and McCann, 1998; van Baalen et al., 2001). These works mostly focus

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on food-web modules but similar predictions also carry-over to complex food-webs (e.g., Brose et al., 2003; Kondoh, 2006; Uchida and Drossel, 2007; Bercé et al., 2010; Křivan, 2014).

Early mathematical models of symbiosis and commensalism were studied by Kostitzin (1934) (for English translation see Scudo and Ziegler, 1978) and Gause and Witt (1935). These models have the form of the Lotka–Volterra type equations where originally negative interactions are replaced by positive interactions. Thus, presence of a symbiont increases the per capita population growth rate of the recipient species. The important aspect of these models is that they are phenomenological, i.e., they do not attempt to model causal mechanisms driving these positive interactions. They do allow researchers to model both facultative mutualism when a species can achieve a positive population growth without the mutualist, and obligate mutualism where positive population growth is possible only when a mutualist is present (e.g., Vandermeer and Boucher, 1978). A serious issue with Lotka–Volterra models is the prediction of limitless growth due to strong positive mutualistic feedbacks (the so called “orgy of mutual benefaction”, May, 1981). To prevent unbounded population growth modelers added negative feedbacks at high populations densities (Dean, 1983; Addicott and Freedman, 1984; Hernandez, 1998; Moore et al., 2017), or assumed saturating mutualistic feedbacks based on principles from consumer–resource theory, e.g., type II functional responses (Holland and DeAngelis, 2010; Revilla, 2015). Mathematical models of mutualism were also combined with models of competition, exploitation (e.g., predation, herbivory), commensalism, etc. (e.g., Ringel et al., 1996; Melián et al., 2009; Georgelin and Loeuille, 2014; Mougi and Kondoh, 2014; Sauve et al., 2014, 2015, 2016). These works showed that effects of mutualism on stability and species coexistence are diverse and complex due to combination of positive and negative feedbacks that can be either direct, but often are indirect and transmitted through a third species (Bolker et al., 2003). E.g., sharing a common pollinator leads to “apparent mutualism” between two plants where increase in population density of one species increases abundance of the pollinator, which, in turn, has a positive effect on the population of the other species (Feinsinger, 1987). When the two plants also share a common herbivore, there is yet another density mediated indirect interactions called “apparent competition” (Holt, 1977) where an increase in one plant increases the herbivore density which exerts negative effects on the other plant. Thus, in an interaction module with two plants sharing a mutualist and a herbivore, it is difficult to predict which of these indirect density mediated interactions will prevail. Models suggest that plant coexistence requires balances favoring indirect facilitation (apparent mutualism) over apparent competition (Sauve et al., 2015), and, in the case of large communities, a nested topology for mutualistic interactions (Bastolla et al., 2009; Thébault and Fontaine, 2010).

Many important mutualisms involve animals that pollinate flowers, disperse seeds, or defend plants, while obtaining plant food resources, e.g., nectar, pollen or fruits. Mutualistic consumers coexist with antagonistic consumers, e.g., folivores or granivores. Species coexistence in mutualistic–antagonistic systems was studied for small community modules (Georgelin and Loeuille, 2014; Sauve et al., 2015) and large interaction networks (Melián et al., 2009; Sauve et al., 2014, 2016). Some articles analyzed animal adaptation within these hybrid systems (Mougi and Kondoh, 2014; Georgelin and Loeuille, 2016).

In this article we study conditions for coexistence of two competing plants that interact both with herbivores and mutualists which are adaptive foragers. Adaptive foraging allows consumers to use the most profitable plants at a given time and place (Rosenzweig, 1981), i.e., those combining highest abundance and energetic reward. This has varied effects on the plant community. For example, adaptive herbivores that prefer abundant plants help rare plants indirectly, promoting plant diversity by weakening interaction strengths by excluding the rare plant from their diet. On the other hand, adaptive mutualists that prefer abundant plants create unfavorable conditions for rare plants that get less pollination, causing loss of plant diversity (Revilla and

Křivan, 2016, 2018). In our mutualistic–antagonistic model, direct interactions between plants, and plants and animals, combine with indirect interactions between plants that are mediated by changes in herbivores and mutualists preferences for plants. Due to the complexity of such interaction networks, we consider plant population dynamics at fixed herbivore and mutualist densities, i.e., herbivore and mutualist population dynamics are not modeled in this article. Instead, we manipulate animal densities, and we study their effects on the coexistence of the two plants. In particular, we are interested in effects when both pollinator and herbivore densities are decreasing, which reflects the current situation (Hallmann et al., 2017). In this setting the indirect interactions between plants are caused not by changes in animal population densities, but by changes in animal preferences for plants. This is an example of trait-mediated indirect interactions (TMII) where “indirect interaction between two [plant] species results from changes in traits [adaptive foraging behavior] of another species [herbivores and pollinators] in the community” (Bolker et al., 2003). As TMII can be as strong as or even stronger than density mediated interactions (Schmitz et al., 2004), we study combined density effects (i.e., direct competition between plants) and TMII effects caused by adaptive herbivore and mutualist foraging behavior on plant coexistence.

First, we study conditions for plant coexistence when animal preferences are fixed (i.e., animals have fixed preferences for plants, see Section 4.1). Second, we assume animals are adaptive foragers and we study how plant coexistence and interaction topology depend on population densities of herbivores and pollinators (Section 4.2). Finally, we study dependence of plant equilibria on population density of herbivores and mutualists (Sections 4.2.1 and 4.2.2) which allows us to predict possible scenarios of declining insect population numbers.

2. Model and methods

We consider a community of two plants with population densities P_i ($i = 1, 2$), an antagonistic herbivore population with density H , and a mutualistic pollinator population with density M . Plants produce two types of resources. Foliar resources F_i , i.e., leaves, are consumed by herbivores, while pollination resources R_i , i.e., nectar or pollen, are consumed by mutualists. To model mutualism we assume that plant growth rates correlate with the consumption rate of R_i (Scheuring, 1992; Revilla, 2015). To model antagonism we assume that consumption of F_i increases plant mortality (Dobbertin and Brang, 2001). This assumption is valid for many terrestrial plants, where herbivores are folivores (e.g., lepidopterans), leaf cutters (e.g., ants), xylophages (e.g., beetles), or mucivores (e.g., aphids) that do not kill plants instantly (like predators do with prey), but the damage inflicted accelerates plant death by secondary causes, such as lower photosynthetic rates, nutrient loss, or infections (Kulman, 1971; Kosola et al., 2001; Cowie et al., 2016; Das et al., 2016). We then follow the mechanism described by Revilla (2015), where fast dynamics of resources (F_i and R_i), when compared with plant population dynamics, allow a steady-state equilibrium of resources at the current plant densities. In Appendix A we use these assumptions to derive differential equations for plant population dynamics

$$\frac{dP_1}{dt} = \left[\left(g_1 + \frac{r_1 v_1 M}{q_1 + v_1 M} \right) \left(1 - \frac{P_1 + c_2 P_2}{K_1} \right) - m_1 (p_1 + u_1 H) \right] P_1 \quad (1a)$$

$$\frac{dP_2}{dt} = \left[\left(g_2 + \frac{r_2 v_2 M}{q_2 + v_2 M} \right) \left(1 - \frac{P_2 + c_1 P_1}{K_2} \right) - m_2 (p_2 + u_2 H) \right] P_2, \quad (1b)$$

where g_i is the rate of vegetative growth in the absence of mutualism, r_i is the asymptotic growth rate due to pollination, and q_i is a half-saturation constant. Growth is regulated by competition with established plants, i.e., plant recruitment tends to zero as P_i approaches K_i , and c_j measures the competitive effect of plant j relative to the effect of plant i on itself. Herbivores raise intrinsic mortality rates according to parameter m_i . Non-herbivore mortality is accounted for by parameter p_i . The quantitative effect of herbivores on plants is

Table 1
Variables and parameters of Eqs. (1) and (2), and values used for numerical simulations.

Symbol	Description	Value
P_i	Plant i population density	variable
$u_i (v_i)$	Herbivore (mutualist) preference for plant i	variable
$W_H (W_M)$	Herbivore (mutualist) fitness	variable
H	Herbivore density	$0 \leq H \leq 2.5$
M	Mutualist density	$0 \leq M \leq 0.8$
g_i	Vegetative growth rate	0.005
K_i	Scale of plant's carrying capacity	$K_1 = 45, K_2 = 40$
c_i	Plant's inter-specific competition coefficient	0.3
r_i	Plant's growth rate due to mutualism	$r_1 = 0.022, r_2 = 0.02$
q_i	Half-saturation constant for mutualism	0.2
m_i	Plant's mortality rate due to herbivory	0.01
p_i	Non-herbivorous mortality scale	0.4
e_i	Herbivore's interaction payoffs	0.1
f_i	Mutualist's interaction payoffs	0.1

controlled by parameters $0 \leq u_i \leq 1$ ($u_1 + u_2 = 1$), i.e., the relative herbivore preference for plant i . Similarly, the effect of mutualists is controlled by relative mutualist preferences $0 \leq v_i \leq 1$ ($v_1 + v_2 = 1$) for plant i .

In this article we study effects of adaptive changes in animal preferences (u_i s and v_i s) on plants, and we define fitnesses in terms of animal payoffs. Fitnesses are given by (Appendix A)

$$W_H = \frac{e_1 u_1 P_1}{p_1 + u_1 H} + \frac{e_2 u_2 P_2}{p_2 + u_2 H} \tag{2a}$$

$$W_M = \frac{f_1 v_1 P_1}{q_1 + v_1 M} + \frac{f_2 v_2 P_2}{q_2 + v_2 M}, \tag{2b}$$

for herbivores and mutualists, respectively. Here e_i (f_i) are herbivore (mutualist) payoffs when feeding on plant i .

In order to obtain analytical results useful for this paper, we assume fixed herbivore and mutualist densities. This assumption requires that consumer dynamics are limited by factors different from plant resources, such as predators, availability of nesting sites, etc. This makes H and M critical parameters, i.e., independent variables that modify the feedbacks between plant dynamics and consumer preferences, which in turn determine plant coexistence and plant-animal interaction topologies.

Our results are presented in the following sections. Specifically, in Section 3 we employ methods from evolutionary game theory (Hofbauer and Sigmund, 1998) to derive the optimal foraging strategies for herbivores and mutualists according to fitnesses (2). In Section 4 we employ methods from the theory of dynamical systems (e.g., local stability & bifurcation analysis) to study the coexistence between plants 1 and 2. Table 1 lists our model variables, parameters, and numerical values used in simulations.

3. Herbivore and pollinator evolutionarily stable strategies at fixed plant population densities

When herbivores and pollinators are adaptive foragers, their preferences change in the direction that maximizes fitnesses given in (2). For given P_1, P_2, H and M , we want to find evolutionarily stable strategies (ESS) for herbivores and mutualists. In Appendix B we show that for the fitness function (2a) the herbivore ESS is given by

$$u_1^*(P_1, P_2, H) = \begin{cases} 1 & \text{if } P_2 < \frac{e_1 p_2 P_1}{e_2(p_1 + H)} \\ \frac{e_1 P_1}{e_1 P_1 + e_2 P_2} + \frac{e_1 p_2 P_1 - e_2 p_1 P_2}{H(e_1 P_1 + e_2 P_2)} & \text{if } \frac{e_1 p_2 P_1}{e_2(p_1 + H)} < P_2 < \frac{e_1(p_2 + H)P_1}{e_2 p_1} \\ 0 & \text{if } P_2 > \frac{e_1(p_2 + H)P_1}{e_2 p_1}, \end{cases} \tag{3}$$

and the mutualist ESS is given by

$$v_1^*(P_1, P_2, M) = \begin{cases} 1 & \text{if } P_2 < \frac{f_1 q_2 P_1}{f_2(q_1 + M)} \\ \frac{f_1 P_1}{f_1 P_1 + f_2 P_2} + \frac{f_1 q_2 P_1 - f_2 q_1 P_2}{M(f_1 P_1 + f_2 P_2)} & \text{if } \frac{f_1 q_2 P_1}{f_2(q_1 + M)} < P_2 < \frac{f_1(q_2 + M)P_1}{f_2 q_1} \\ 0 & \text{if } P_2 > \frac{f_1(q_2 + M)P_1}{f_2 q_1}. \end{cases} \tag{4}$$

These optimal preferences show that the more abundant a plant is, the more it attracts both herbivores and mutualists, i.e., preferences are *frequency-dependent*. However there are minimum thresholds that must be met for a plant to attract animals at all. These expressions also show that as herbivore (mutualist) population density increases, u_1^* (v_1^*) converges to $\frac{e_1 P_1}{e_1 P_1 + e_2 P_2}$ ($\frac{f_1 P_1}{f_1 P_1 + f_2 P_2}$) which corresponds to the proportional product of quality and quantity of resource 1 for herbivores (mutualists).

Table 2 lists all possible qualitatively different ESSs given by (3) and (4). For given herbivore H and pollinator M abundances, the positive part of the plant abundance plane can be divided into five sectors that specify qualitatively different foraging preferences of herbivores (H) and mutualists (M). The sector boundaries for herbivores

$$I_H^0 : P_2 = \left(\frac{e_1(p_2 + H)}{e_2 p_1} \right) P_1 \tag{5a}$$

$$I_H^1 : P_2 = \left(\frac{e_1 p_2}{e_2(p_1 + H)} \right) P_1, \tag{5b}$$

and pollinators

$$I_M^0 : P_2 = \left(\frac{f_1(q_2 + M)}{f_2 q_1} \right) P_1 \tag{5c}$$

$$I_M^1 : P_2 = \left(\frac{f_1 q_2}{f_2(q_1 + M)} \right) P_1, \tag{5d}$$

are straight lines radiating from the origin as shown in Fig. 1. These lines are called “isolegs” in the optimal foraging literature (e.g., Rosenzweig, 1986; Rosenzweig and Abramsky, 1986; Revilla and Křivan, 2018). In the sector between I_H^0 and I_H^1 isolegs, herbivores are generalists (i.e., $0 < u_1 < 1$), and optimal herbivore preferences given in (3) change continuously with P_1 and P_2 . We call this sector the “cone of herbivore generalism” from here onward. In the region above the cone of generalism (above I_H^0 isoleg in Fig. 1) herbivores specialize exclusively on plant 2 (i.e., $u_1 = 0$), and in the region below the cone (i.e., below I_H^1 isoleg in Fig. 1) they specialize on plant 1 (i.e., $u_1 = 1$). For mutualists, isolegs I_M^0 and I_M^1 define the corresponding “cone of mutualist generalism”. Fig. 1 shows that there are four qualitative arrangements for herbivore and mutualist cones of generalism: the cones do not overlap (Fig. 1a), they overlap partially (Fig. 1b), the herbivore's cone lies within the mutualist's cone (Fig. 1c), or the mutualist's cone lies within the herbivore's cone (Fig. 1d). As foragers densities increase, their cones of generalism get wider, and overlaps of the two cones become more likely. Different arrangements of cones give rise to different combinations of herbivore and mutualist preferences that modify plant population dynamics, which in turn, modify herbivore and mutualist preference, as we will see in the next sections.

4. Plant population dynamics

In this section we study plant population dynamics. First, we assume that herbivore and pollinator preferences for plants are fixed, i.e., animals are inflexible consumers. This leads to the classic Lotka–Volterra plant population dynamics. Second, we consider the case where animals are adaptive foragers that change their preferences so as to maximize their fitness. We assume that these adaptations are very fast when compared to population dynamics so that animal preferences track instantaneously plant population densities.

Table 2

Combined herbivore and mutualist ESSs. The first (second) symbol on a label indicates if herbivores (mutualists) are 1: plant 1 specialists, 2: plant 2 specialists, G: generalists. The occurrence of all except 21 on the plant density plane $P_1 P_2$ is sketched by Fig. 1.

Herbivore ESS	Mutualist ESS	Description	Label
$u_1^* = 1$	$v_1^* = 1$	Herbivores and mutualists specialize on P1	11
$u_1^* = 0$	$v_1^* = 0$	Herbivores and mutualists specialize on P2	22
$u_1^* = 1$	$v_1^* = 0$	Herbivores specialize on P1, mutualists specialize on P2	12
$u_1^* = 0$	$v_1^* = 1$	Herbivores specialize on P2, mutualists specialize on P1	21
$0 < u_1^* < 1$	$v_1^* = 1$	Herbivores are generalists, mutualists specialize on P1	G1
$0 < u_1^* < 1$	$v_1^* = 0$	Herbivores are generalists, mutualists specialize on P2	G2
$u_1^* = 1$	$0 < v_1^* < 1$	Herbivores specialize on P1, mutualists are generalists	1G
$u_1^* = 0$	$0 < v_1^* < 1$	Herbivores specialize on P2, mutualists are generalists	2G
$0 < u_1^* < 1$	$0 < v_1^* < 1$	Herbivores and mutualists are generalists	GG

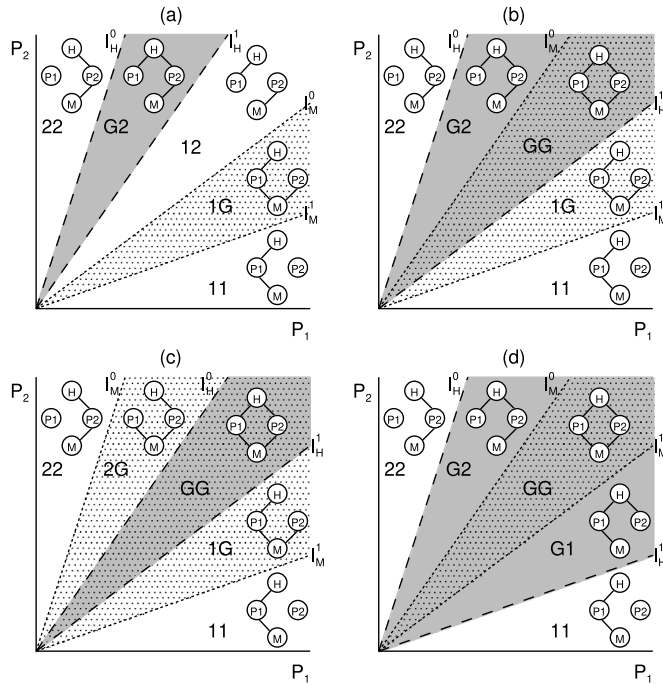


Fig. 1. Plant-animal interactions patterns on $P_1 P_2$ plant plane. Graphs are labeled according to Table 2. Herbivores are generalist within the gray cone formed by isocles I_H^0 and I_H^1 (dash lines, Eqs. (5a), (5b)), and mutualist are generalist within the dotted cone formed by I_M^0 and I_M^1 (dot lines, Eqs. (5c), (5d)). Consumers specialize on plant 1 (plant 2) in sectors below (above) their respective cones of generalism. Cones may not overlap (a), overlap partially (b), the herbivore's cone lies within the mutualist's cone (c), or the mutualist's cone lies within the herbivore's cone (d).

4.1. Plant dynamics with fixed animal preferences

When herbivore and pollinator preferences are fixed, system (1) becomes the Lotka-Volterra (LV) competition model that has a trivial equilibrium (0,0) and two single plant (i.e., monoculture) equilibria $(P_1, 0) = (Q_1, 0)$ and $(0, P_2) = (0, Q_2)$ where plants reach their environmental carrying capacities

$$Q_i = K_i \left(1 - \frac{m_i(p_i + u_i H)}{g_i + \frac{r_i v_i M}{q_i + v_i M}} \right). \tag{6}$$

A plant's carrying capacity increases with mutualist preference and density ($v_i M$) and decreases with herbivore preference and density ($u_i H$). A plant is *viable*, at given herbivore and mutualist densities, if Q_i is positive, i.e., when

$$g_i + \frac{r_i v_i M}{q_i + v_i M} > m_i(p_i + u_i H), \tag{7}$$

and *not viable* otherwise. We observe that plant viability requires that the plant growth rate, which is the sum of the plant vegetative growth rate and the growth rate due to pollination, must be larger than plant mortality caused by herbivory. In particular, a necessary condition for plant i viability (obtained for $v_i M$ tending to infinity in (7)) is

$$g_i + r_i > m_i(p_i + u_i H).$$

Furthermore, mutualism is *facultative* if $g_i > m_i p_i$, i.e., when in absence of herbivory ($u_i H = 0$) a plant overcomes mortality solely by vegetative growth. On the contrary if $m_i p_i > g_i$, mutualism is obligate for the plant, i.e., vegetative growth alone is not enough to compensate mortality, even without herbivory ($u_i H = 0$).

Provided (7) holds for $i = 1, 2$, a plant community equilibrium is at the intersection of the plant isoclines¹

$$P_1 + c_2 P_2 = Q_1 \tag{8a}$$

$$P_2 + c_1 P_1 = Q_2, \tag{8b}$$

and such coexistence is globally stable if each plant can invade the other's monoculture, i.e., when both monoculture plant equilibria $(0, Q_2)$ and $(Q_1, 0)$ are unstable. The invasion conditions for plant 1 and 2 are, respectively,

$$Q_1 > c_2 Q_2 \tag{9a}$$

$$Q_2 > c_1 Q_1. \tag{9b}$$

From these conditions

$$c_1 c_2 < 1, \tag{10}$$

that is interpreted as “intra-specific competition is stronger than inter-specific”. If invasibility conditions in (9) hold, the stable plant coexistence equilibrium is

$$(\hat{P}_1, \hat{P}_2) = \left(\frac{Q_1 - c_2 Q_2}{1 - c_1 c_2}, \frac{Q_2 - c_1 Q_1}{1 - c_1 c_2} \right). \tag{11}$$

If opposite inequalities in (9) hold, $c_1 c_2 > 1$, the equilibrium is unstable, and plant population dynamics are bi-stable. Depending on the initial conditions plant 1 or plant 2 wins the competition, reaches its carrying capacity and the other plant goes extinct. If (9a) holds but (9b) does not, plant 1 excludes plant 2. Vice-versa, if (9b) holds but (9a) does not, plant 2 excludes plant 1. The last two cases show that (10) is necessary but not sufficient for stable coexistence.

In the next section we consider adaptive herbivores and mutualists that maximize their fitnesses.

4.2. Plant population dynamics with adaptive animal preferences

For the rest of this article we assume that herbivores preferences u_i given in (3) and mutualists preferences v_i given in (4) track current

¹ By isoclines we mean non-trivial ones. Trivial isoclines $P_1 = 0$ and $P_2 = 0$ are considered only implicitly.

plant population densities instantaneously, and we substitute these formulas in plant population dynamics (1). The resulting model is highly non-linear, and analytical formulas for equilibria and stability are very complex expressions. Thus, we study the dynamics of the interaction network using numerical methods.

Fig. 2 shows the dependence of the interaction network topology on herbivore and mutualist densities. This figure assumes that inter-specific competition between plants is weaker than intra-specific competition (i.e., the inequality in (10) holds) and both plants coexist at a single stable state in absence of herbivores and pollinators ($H = M = 0$). In the dark shaded region of the plot both plant monocultures are viable, because parameters are such that inequality in (7) holds for both plants. Plant 1 monoculture (which has a slightly higher $r_1 = 0.022$ when compared to plant 2 $r_2 = 0.02$) is also viable in the light-shaded region where plant 2 monoculture goes extinct. In the white region the negative effect of herbivory overweighs the positive effect of mutualism and neither plant monoculture survives. However, as we see, this does not mean that the two plants cannot coexist when they are together (e.g., see the upper right white region GG where both plans coexist).

Stable plant coexistence is possible in 15 (out of total 17) regions shown in Fig. 2 at one, two or three alternative stable states that are labeled according to interaction patterns listed in Table 2. These labels indicate preference of herbivores (the symbol at the first position) and mutualists (the symbol at the second position) for plants at the corresponding stable plant equilibrium. Animal generalism is indicated by G, following the convention introduced in Table 2. For example, G1 means that herbivores are generalists and mutualists specialize on plant 1 at the corresponding plant equilibrium. These labels also indicate the interaction topology (see Fig. 1).

There are two regions where plant coexistence is not possible. In region “E” the negative effect of herbivory on plants is too strong when compared to the positive effect of mutualism and plants go globally extinct. This is because the density of herbivores when compared to density of mutualists is too high. In the region denoted by “B” in Fig. 2, either plant 1 or plant 2 is excluded depending on initial conditions, and herbivores and mutualists specialize on the surviving monoculture.

We observe that most regions allow plant coexistence at several alternative stable states. E.g., in the region denoted by “G1, G2, GG”, plants coexistence is possible at three different stable states. Here G1 means that at the plant equilibrium, herbivores are generalists feeding on both plants while pollinators specialize on plant 1, at equilibrium G2 herbivores are generalists while mutualists specialize on plant 2, and at equilibrium GG both herbivores and mutualists are generalists. At which of these alternative equilibria plants settle depends on initial conditions (see the next section). Fig. 2 suggests that the number of states at which plants can coexist is highest and equal to three at intermediate densities of herbivores and mutualists. When herbivore and mutualist densities are very low the number of stable states tends to be one or two, with at least one specialist consumer (e.g., regions “22”, “11, 22”, “11, G2”, or “G1, G2”). When herbivore and mutualist densities are large enough, plants coexist at a single stable state where both consumers are generalist (“GG” region) and where neither of the two plants can survive at positive densities without the other plant being present.

Since model (1) is two-dimensional, we can use phase plane analysis to gain insights about plant community dynamics when herbivores and mutualists preferences for plants quickly adapt to changes in plant densities. For this purpose we graph the plant isoclines (8) with u_i and v_i given in (3) and (4), respectively, in formulas (6). In the following paragraph we describe the general features of the isoclines and we illustrate plant population dynamics at herbivores and mutualists densities marked with “x” in Fig. 2.

Fig. 3 displays global dynamics at 9 points marked by “x” in Fig. 2. The nonlinear dependence of herbivore (3) and mutualist (4) preferences on plant densities leads to nonlinear isoclines that are

defined separately at each sector. In marginal sectors that are adjacent to the axes (i.e., below isocles I_H^1 and I_M^1 , or above isocles I_H^0 and I_M^0) corresponding isocline segments are linear and given by the Lotka–Volterra model because animal preferences are either 1 or 0 there (i.e., $u_1 = v_1 = 1$ or $u_1 = v_1 = 0$). Plant i ($i = 1, 2$) isocline meets the P_i axis at $P_i = Q_i$ (denoted by diamond symbols in Fig. 3), given by Eq. (6). Between isocles, i.e., within the cones of generalism, one or both of animal preferences for plants (u_1 and v_1 given in (3)) are nonlinear functions of plant densities, and the corresponding isocline segments are polynomial curves of degree 2 or 3. Like with the LV model, plant P_i has positive net growth ($dP_i/dt > 0$) in the positive part of the $P_1 P_2$ plane bounded by its isocline and P_i axes, and negative net growth ($dP_i/dt < 0$) outside. Stable (unstable) plant equilibria are denoted by dots (circles).

First, we observe that unlike the LV competition model with fixed animal preferences where plants can only coexist at a single equilibrium for our choice of parameters, nonlinear isoclines allow multiple plant equilibria (see panels (a)–(g) in Fig. 3). Coexistence of multiple stable states implies that the fate of the system depends on initial conditions and not knowing this information, it cannot be predicted where the system will converge to. In particular, the priority effect (Young et al., 2001) will have a strong effect on the community composition. The priority effect is due to adaptive mutualism, which causes strong competition for pollination services that favors resident or abundant plants (e.g., agricultural crops, see Holzschuh et al., 2011) in detriment to rarer plants (e.g., invaders). We also observe that besides multiple stable states where both plant species coexist, there are stable equilibria with one plant only (panels (d) and (g) in Fig. 3).

Second, we observe the effect of herbivores and mutualists on plant monoculture equilibrium densities (denoted by the diamond symbol on the axes in Fig. 3). It is obvious that the negative effect of herbivores on plant monocultures is much stronger than is the positive effect of mutualists. This already follows from formula (6) which shows that plant population densities linearly decrease as herbivore density increases, while the positive effect of mutualists on plant densities is saturating. Thus, when mutualists are abundant, an increase in their density will have a negligible effect on plant density (e.g., cf. Fig. 3d vs. Fig. 3g).

Third, we observe facilitation effects of one plant on the other at the stable coexistence equilibrium (e.g., Figs. 3f, h). Indeed, in these panels the plant densities at the GG equilibrium are higher when compared with their monoculture densities. Such facilitation effect requires herbivore generalism, so that both plants share the costs of herbivory, and also mutualist generalism, so that neither plant is the sole winner of mutualist benefits. Thus, facilitation happens at plant equilibria that are in the overlap of herbivore and mutualist cones of generalism (i.e., a “GG” equilibrium point). When extreme levels of herbivory turn monocultures nonviable (i.e., (7) does not hold), the facilitation effect is the only mean by which plants can persist at all (e.g., panel (i)).

Fig. 3 also shows how plant population dynamics determines plant–animal interaction topologies (i.e., consumer preferences). For example, Figs. 3e, f display qualitatively similar plant dynamics with three coexistence equilibria. However, at the two equilibria that are dominated by one of the two plants, interaction dynamics differ between the two panels. While in panel (e) herbivores specialize on the more abundant plant at these two equilibria, they generalize in panel (f). This is because herbivore density is higher in panel (f) and generalism of herbivores prevents one plant to be excluded which, in turn, increases herbivore fitness.

In the next section we examine the dependence of stable plant equilibria on herbivore and mutualist densities.

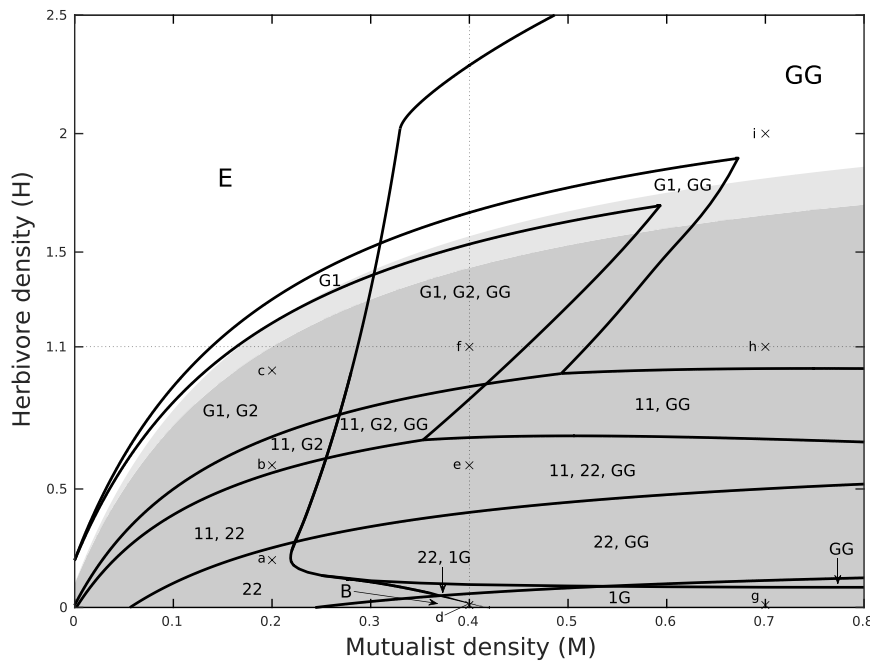


Fig. 2. Dependence of interaction topology at stable equilibria on herbivore and mutualist densities. Labels correspond to animal preferences (Table 2) at corresponding plant equilibria. Region B corresponds to plant mutual exclusion (i.e. bi-stability) and region E corresponds to global plant extinction. Plant monocultures are viable in shaded regions (P1: light & dark, P2: dark). Fig. 3 shows dynamics for herbivore and mutualist densities corresponding to points a, b, ..., i marked with “x”. Fig. 4 shows density profiles along the vertical dotted line at fixed mutualist density $M = 0.4$ and Fig. 5 along the horizontal dotted line at fixed herbivore density $H = 1.1$. Other parameters used in simulations: $g_i = 0.005$, $r_1 = 0.022$, $r_2 = 0.02$, $K_1 = 45$, $K_2 = 40$, $m_i = 0.01$, $c_i = 0.3$, $p_i = 0.4$, $q_i = 0.2$, $e_i = f_i = 0.1$.

4.2.1. Effect of adaptive herbivory on plant densities

Fig. 4 shows dependence of plant 1 (top panel) and plant 2 (bottom panel) equilibrium densities along the herbivore gradient when mutualist density is fixed at $M = 0.4$. This corresponds to moving along the vertical dotted line in Fig. 2. Solid (dotted) lines denote stable (unstable) equilibria.

In general, plant densities decrease with increasing herbivore density, which is expected from the antagonistic relationship between plants and herbivores. For example, monocultures decrease linearly with H according to Eq. (6). Exceptions happen when herbivores or mutualists specialize on a single plant, as we describe next.

At very low herbivore density, both monocultures are stable against invasion and the system is bi-stable. This is evident from Fig. 4 that shows stable monoculture equilibria (solid) Q_1 and Q_2 respectively, and one line of unstable equilibria starting at $H = 0$ (dotted line), which corresponds to the unstable equilibrium in Fig. 3d. Plant 1 (plant 2) monoculture becomes invasible (i.e., unstable, indicated by dashes) at the branching point bp_1 (bp_2) in Fig. 4, where an interior stable plant equilibrium at which both animals specialize on plant 1 (on plant 2) branches from Q_1 (Q_2). These branches are straight lines given by (6) with $u_1 = v_1 = 1$ (“11” line) or $u_1 = v_1 = 0$ (“22” line) and they correspond to LV equilibria on marginal sectors adjacent to the axes (e.g., Fig. 3e). The branching point bp_1 ($H \approx 0.4$) lies on the boundary between regions “22,GG” and “11,22,1G” in Fig. 2, whereas bp_2 ($H \approx 0.058$) lies on the boundary between “1G” and “22,1G”. As H increases further, plant 1 experiences more herbivory but plant 2 none, so that the equilibrium density of plant 1 decreases while that of plant 2 increases. At $H \approx 0.932$ this equilibrium reaches I_H^1 isoleg (5b) where herbivores become generalists, i.e., interaction topology changes to “G1”. From this point on, both plants are affected by herbivory and both equilibria densities decrease until they disappear at $H \approx 1.667$ (denoted as ep_1 in Fig. 4). The circle in Fig. 4 denotes the point at which herbivores switch from plant 1 specialization to generalism. This point corresponds to herbivore density on the boundary between regions “11,G2,GG” and “G1,G2,GG” in Fig. 2.

In the case of branch line “22” that describes the interior plant equilibria where both animals specialize on plant 2, equilibrium density of plant 2 decreases while density of plant 1 increases with H . But unlike the switch in interaction topology from “11” to “G1” described before, we observe a gap between lines denoted by “22” and “G2”. At limit point lp_1 where $H \approx 0.717$, the “22” equilibrium hits the I_M^0 isoleg (5b) and this equilibrium vanishes. Then at limit point lp_2 where $H \approx 0.879$, the isoclines intersect again within the herbivore’s cone of generalism, and the equilibrium “G2” appears until the joint extinction of plants due to herbivory at $H \approx 1.533$ (denoted as ep_2). Limit point lp_1 lies on the boundary between regions “11,22,GG” and “11,GG” in Fig. 2, whereas lp_2 lies on the boundary between “11,GG” and “11,G2,GG”.

Finally, we have the third line of stable plant coexistence where mutualists are generalist. This line starts at the limit point $H \approx 0.022$ (denoted as lp_3) where the dynamic turns from bi-stable (i.e., region B in Fig. 2, e.g., Fig. 3d) to locally stable coexistence with herbivores specializing on plant 1, i.e., line “1G”. Like in the case of equilibrium line “11”, plant 1 decreases with H while plant 2 increases, until this equilibrium crosses the I_H^1 isoleg at $H \approx 0.097$ and herbivores become generalist, i.e., the “GG” line starts (indicated with the open circle). From this point on both plants decrease with H until joint extinction at $H \approx 2.288$ (denoted as ep_3).

4.2.2. Effect of adaptive mutualism on plant densities

Fig. 5 shows dependence of plant 1 (top panel) and plant 2 (bottom panel) equilibrium densities along the mutualist gradient when herbivore density is fixed at $H = 1.1$ which corresponds to moving along the horizontal dotted line in Fig. 2. Solid (dotted) lines denote stable (unstable) equilibria.

Monocultures are viable for $M > 0.167$ in the case of plant 1 (Q_1 line), and for $M > 0.2$ in the case of plant 2 (Q_2 line), when condition (7) holds. They are unstable against invasion by the missing plant, and increase with diminishing returns as M increases to infinity, according to (6).

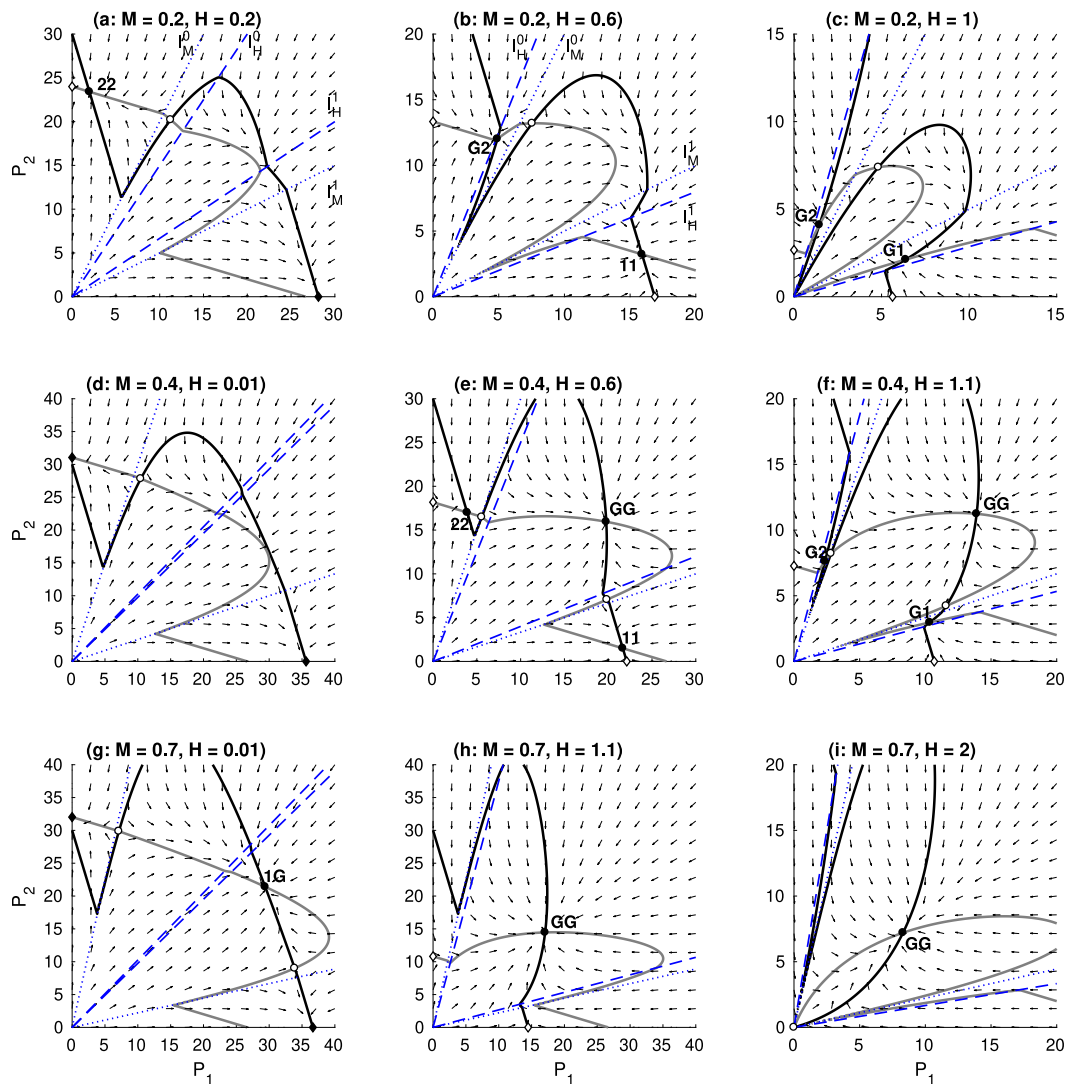


Fig. 3. Plant population dynamics (vector fields). Panels correspond to points “a” to “i” marked by “x” in Fig. 2. The P_1P_2 plane is divided by herbivore and mutualist isocles (dash or dot lines, respectively, like in Fig. 1). Isoclines of plant 1 (black) and 2 (gray) intersect at stable (dots) and unstable (circles) states. Stable states are labeled according to animal preferences (Table 2). Monocultures can be stable (black diamonds) or unstable/invadable (white diamonds).

We observe three lines of stable coexistence, “G1”, “G2” and “GG”. The “G1” line starts at the extinction point $M \approx 0.139$ (denoted as ep_1) where mutualist density is insufficient to compensate for herbivory. For similar reasons, line “G2” starts at $M \approx 0.167$ (denoted as ep_2). These equilibria branches terminate at limit point $M \approx 0.519$ (lp_1 for “G1”) or $M \approx 0.457$ (lp_2 for “G2”). Since then on plant coexistence is possible along the “GG” branch where both animals are generalists, which starts at the limit point lp_3 where $M \approx 0.287$ (which is connected to branch “G1” by an unstable branch, i.e., dots connecting lp_3 to lp_1 in Fig. 5). Thus, at the current herbivore density ($H = 1.1$), mutualists turn generalist when their densities are large enough, or specialists (on plant 1 or 2) when their densities are low enough.

Fig. 5 also shows that plants can attain larger densities when together compared with their monocultures. This happens for both plants along the whole “GG” branch, only for plant 1 along a part of the “G1” branch where $M < 0.333$, or only for plant 2 along the whole “G2” branch. This is due to the indirect facilitation when herbivores are generalists.

Both plant densities increase along branch “GG” since both benefit from increased level of mutualism. However, both plants also increase along branches “G1” and “G2”, despite mutualist specialization. In

“G1”, as mutualists specialize on plant 1, plant 1 density increases with M because plant 1 gets more pollination, but also more herbivory as herbivores preference for plant 1 increases. This decreases herbivory on plant 2, which can also increase with M . This mechanism operates along the G2 branch too, *mutatis mutandis*. The plant monopolizing mutualists increases faster with M , i.e., $\frac{dP_1}{dM} > \frac{dP_2}{dM}$ along “G1” and $\frac{dP_2}{dM} > \frac{dP_1}{dM}$ along “G2”.

We observe that as mutualist density increases, the number of alternative stable coexistence states increases from 0 (for $M < 0.139$), to 1 (for $0.139 < M < 0.167$), to 2 (for $0.167 < M < 0.287$), to 3 (for $0.287 < M < 0.457$). For yet higher mutualist densities the number of coexistence stable states decreases to a single one for $M > 0.519$.

5. Discussion

In this article we study direct and indirect interactions between two competing plants that are mediated by shared herbivores and pollinators (both called consumers here). We consider plant population dynamics under the assumption that consumer density is fixed, but preferences for plants are adaptive and maximize consumer fitness. While without consumers plants can coexist at most at a single equilibrium

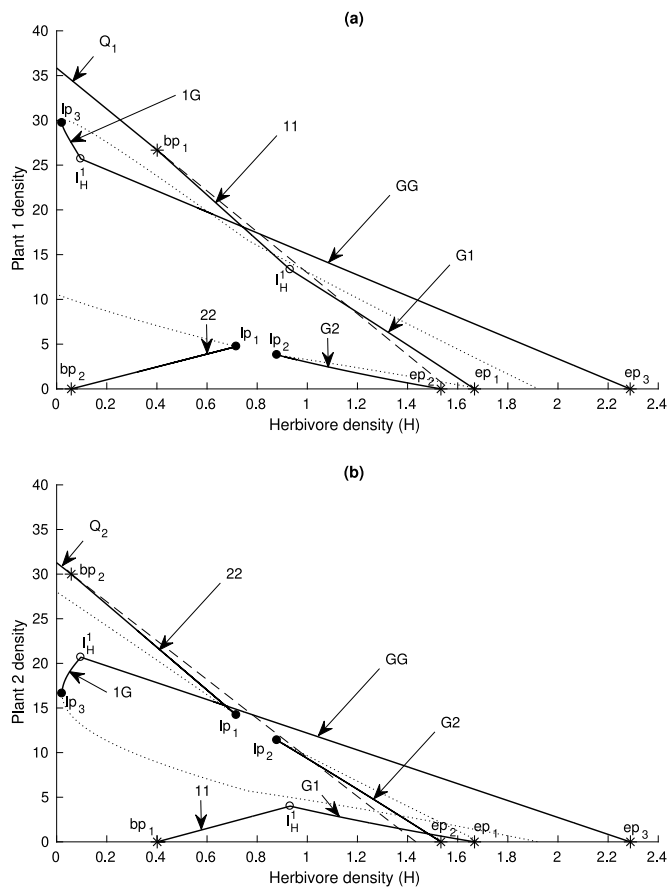


Fig. 4. Plant equilibria as function of herbivore density at fixed mutualist density $M = 0.4$, and parameters from Fig. 2. Solid lines represent stable equilibria, dotted lines are unstable states, and dashed lines are for invasible (unstable) monocultures. Plant 1 and 2 monocultures are labeled Q_1 and Q_2 respectively, and the other stable states according to Table 2 and Eq. (5). Asterisks mark branching (bp) of communities from monocultures, or extinction (ep) of communities due to herbivory. Black dots are limit points (lp) where coexistence starts without invasion or ends without extinction. An open circle indicates a stable state lying on an isocline.

we show that adaptive consumer behavior promotes plant coexistence at alternative stable states through apparent plant facilitation which increases plant densities above those that each plant can achieve when alone. We also show that decrease in insect (i.e., consumer) population densities can lead to unpredictable patterns of plant extinction.

Interaction webs are driven by direct (e.g., direct feeding of predators on their prey) and indirect interactions (e.g., trophic cascades Hairston et al., 1960, apparent competition Holt, 1977). All these interactions are caused by changes in population densities. It has been argued (Schmitz et al., 2004) that interactions caused by changes in animal behavior even when population densities stay constant (i.e., trait mediated interactions) can cause effects of similar or even larger magnitude. Such effects can be either direct (i.e., direct trait mediated interactions), or indirect (for a review see Bolker et al., 2003). In this article we study two indirect trait mediated interactions between two competing plant populations mediated by changes in foraging preferences of shared pollinators and herbivores. Understanding effects of trait mediated interactions in model systems is important, because in reality it is often impossible to separate trait and density mediated interactions. E.g., in plant communities sharing a common herbivore both trait and density mediated interactions will occur. While density mediated apparent competition between plants is detrimental to plant

coexistence, because an increase in one plant density increases population density of the herbivore which, in turn, exerts a negative effect on the other plant, the trait mediated indirect interactions caused by changes in herbivore preference for the more abundant plant promotes plant coexistence and we call this trait mediated facilitation. It was shown that such apparent facilitation can be stronger than apparent competition and lead to plant coexistence in two-resource–single consumer system (Křivan, 1997). The other trait mediated interaction in our interaction network is mediated by adaptive pollinator preferences for plants. As one plant density increases, pollinator preference for this plant increases which is detrimental for the other plant that receives less pollination. We call this trait mediated apparent competition.

In this article we developed a new plant–herbivore–pollinator model where the plants supply one resource for pollinators (e.g., pollen, or nectar) and a different resource for herbivores (e.g., leaves). This extends the mechanism used in previous papers to model “resource-for-services” mutualisms (Revilla, 2015; Revilla and Křivan, 2016, 2018) to the realm of exploitative interactions, e.g., “resource-for-antagonism”. This causes resource competition (Schoener, 1978) within the herbivore and within the pollinator populations, which are the driving forces behind adaptation towards specialization or generalism in foraging preferences.

When pollinator and herbivore densities are fixed as well as their preferences for either plant, plant dynamics are described by the classic Lotka–Volterra competition model where either both plants coexist, only one plant survives, or the model is bi-stable in that the fate of the system depends on the history. The situation dramatically changes when both herbivore and pollinator foraging preferences for plants are adaptive so that consumers maximize their fitnesses at current plant population densities. As mentioned before, trait mediated interactions via herbivore adaptation tends to equalize plant densities and promotes plant coexistence. On the other hand, mutualist adaptation works in the opposite direction, i.e., positive feedbacks between preferences and population densities increase competitive asymmetries between plants (Mougi and Kondoh, 2014; Revilla and Křivan, 2016) and promote exclusion of one plant by the other. When these two mechanisms are considered together, it is difficult to predict which mechanism (i.e., trait mediated facilitation or competition) will drive the system.

With two animal consumers, the preferences of one of them can drive plant population dynamics in directions that affect the preference of the other consumer and vice-versa. We show that the chain of indirect feedbacks between plants and animals creates a rich set of population dynamics where plants can attain coexistence at up to three alternative stable states (Fig. 3). Adaptive mutualism tends to increase differences in plant abundances by specialization on the more common plant, which leads to alternative stable states. This was also observed in interaction modules with two plants and mutualists (Revilla and Křivan, 2016, 2018; Křivan and Revilla, 2019). On the other hand, adaptive herbivory tends to prevent competitive exclusion by steering preferences towards common plants and away from rare which are at risk of extinction.

By fixing animal densities, we remove indirect density-mediated effects such as apparent competition (Holt, 1977) and facilitation (Feinsinger, 1987), but frequency-dependent effects mediated by animal preferences remain and can be analyzed. The joint effects of density- and trait-mediated interactions are more difficult to study because the number of variables involved increases (i.e., 4 species densities). We know that for two prey and one predator adaptive foraging counteracts apparent competition (e.g., Křivan, 1996, 1997). And for two plants and one pollinator, competition for plant resources promotes pollinator generalism which allows plant–plant facilitation (Revilla and Křivan, 2016). In both situations, antagonistic or mutualistic, the growth of consumer populations promotes their generalism, which in turn promotes the stability of plant communities for the reasons discussed in previous paragraphs.

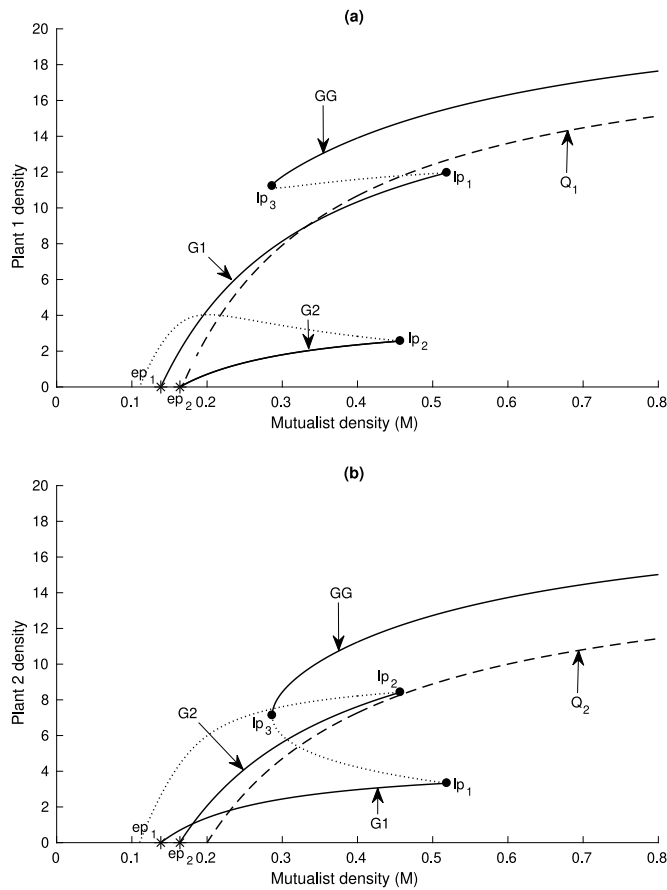


Fig. 5. Plant equilibria as function of mutualist density at fixed herbivore density $H = 1.1$, and parameters from Fig. 2. Solid lines represent stable equilibria, dotted lines unstable states, and dashed lines are for invisable (unstable) monocultures. Plant 1 and 2 monocultures are labeled Q_1 and Q_2 respectively, and the other stable states according to Table 2 and Eq. (5). Asterisks mark extinction points (ep) for two-plant communities due to low mutualism. Black dots are limit points (lp) where coexistence starts without invasion or ends without extinction.

Our results highlight the importance that trait-mediated interactions can have for plant coexistence. This has important implications in current times of insect declines (Hallmann et al., 2017), and large scale perturbations of pollination services (Holzschuh et al., 2011; Geslin et al., 2017) caused by human activities. We can hypothesize that the decrease of insect populations leads to regimes of alternative states, caused by adaptive specialization. As a result, predictability of plant–insect dynamics becomes difficult. Some alternative states can be very unbalanced in plant abundances (e.g., coexistence states denoted by “11” and “22” in Fig. 3e), making species loss easier as a result of small perturbations. On the other hand, management policies that sustain reasonably large and diverse insect populations would promote their generalism. In such conditions, the provision of mutualistic services is favorable for a large number of plant species, and potential pests can be kept in check by the dynamic control by herbivores.

CRediT authorship contribution statement

Tomás A. Revilla: Conceived the study, Model analysis, Manuscript writing. **Thomas Marcou:** Model analysis, Manuscript revision. **Vlastimil Křivan:** Model analysis, Manuscript writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Model derivation

Herbivore F_i (leaves) and mutualist R_i (nectar or pollen) resources of plant $i = 1, 2$ follow supply–consumption dynamics

$$\begin{aligned} \frac{dF_i}{dt} &= \pi_i P_i - \omega_i F_i - u_i \alpha_i F_i H \\ \frac{dR_i}{dt} &= \sigma_i P_i - \lambda_i R_i - v_i \beta_i R_i M, \end{aligned} \quad (\text{A.1})$$

where P_i is plant population density, π_i and σ_i represent production/supply (e.g., leafing, nectar secretion) rates per plant, and λ_i and ω_i are non-consumptive decay rates (e.g., falling, withering, re-absorption). Herbivores (mutualists) with population density $H(M)$ consume resources with specific rates $\alpha_i(\beta_i)$ and relative preference $0 \leq u_i \leq 1$ ($u_1 + u_2 = 1$) for plant i .

We consider plant P_i population dynamics

$$\frac{dP_i}{dt} = (g_i P_i + \rho_i v_i \beta_i R_i M) \left(1 - \frac{P_i + c_j P_j}{K_i} \right) - \frac{\mu_i}{(F_i/P_i)} P_i, \quad i = 1, 2, \quad (\text{A.2})$$

where the growth rate $g_i P_i + \rho_i v_i \beta_i R_i M$ consists of two terms. The first term corresponds to growth without mutualism with vegetative rate g_i . The second term links plant growth to consumption of mutualistic resources R_i in (A.1) by means of the constant ρ_i that translates pollination to seed numbers. Plant i experiences intra-specific competition and inter-specific competition from plant j according to the competition coefficient c_j . K_i is the density of plant P_i at which competition results in zero recruitment of new plants. In order to relate plant mortality with consumption of herbivore resources F_i in (A.1), we assume that mortality increases with the intensity of defoliation caused by the herbivores. A simple and convenient way to state this dependency is by making intrinsic mortality inversely proportional to foliar biomass per plant F_i/P_i with a proportionality constant μ_i , under the assumption that foliage is evenly distributed among individual plants.

Now we assume that the turnover of plant resources is fast and they instantaneously track plant population densities, i.e., $dF_i/dt = 0$ and $dR_i/dt = 0$ in (A.1) which yields

$$\begin{aligned} F_i &= \frac{\pi_i P_i}{\omega_i + u_i \alpha_i H} \\ R_i &= \frac{\sigma_i P_i}{\lambda_i + v_i \beta_i M}. \end{aligned} \quad (\text{A.3})$$

Substituting these expressions in (A.2) leads to the system of two differential equations (1) studied in the main text, where we group $r_i = \rho_i \sigma_i$, $m_i = \mu_i \alpha_i / \pi_i$, $p_i = \omega_i / \alpha_i$, $q_i = \lambda_i / \beta_i$.

Next, animal payoffs when feeding on plant i are measured by the instantaneous plant consumption rate multiplied by conversion factors ϵ_i (ϕ_i) for herbivores (pollinators). For example, herbivore payoff when feeding on plant 1 only is $\epsilon_1 \alpha_1 F_1$. Animal fitnesses are then defined as mean animal payoffs

$$\begin{aligned} W_H &= \epsilon_1 u_1 \alpha_1 F_1 + \epsilon_2 u_2 \alpha_2 F_2 \\ W_M &= \phi_1 v_1 \beta_1 R_1 + \phi_2 v_2 \beta_2 R_2, \end{aligned} \quad (\text{A.4})$$

for herbivores and pollinators, respectively. Substituting expressions (A.3) into (A.4) leads to herbivore and mutualists fitnesses (2) in the main text, grouping $e_i = \epsilon_i \pi_i$, $f_i = \phi_i \sigma_i$.

Appendix B. Evolutionarily stable strategy

Let us consider herbivores and their fitness function (2a). In a population where $u_1 H$ herbivores forage on plant 1 and $u_2 H = (1-u_1)H$ on plant 2, the payoffs that a herbivore gets from interaction with plant 1 or plant 2 are

$$U_1(u_1) = \frac{e_1 P_1}{p_1 + u_1 H}, U_2(u_1) = \frac{e_2 P_2}{p_2 + (1-u_1)H}. \quad (\text{A.5})$$

These payoffs depend on plant densities, herbivore densities and herbivore preferences. The herbivore with preference \tilde{u}_1 for plant 1 in a resident population with preference u_1 obtains fitness given by the average payoff

$$W_H(\tilde{u}_1, u_1) = \tilde{u}_1 U_1(u_1) + (1-\tilde{u}_1)U_2(u_1). \quad (\text{A.6})$$

The optimal preference u_1^* is calculated as the Nash equilibrium (NE) for the fitness function (A.6). At an interior (i.e., generalist) NE the two payoffs (A.5) must be the same, i.e., $U_1 = U_2$, which yields

$$u_1^* = \frac{e_1 P_1}{e_1 P_1 + e_2 P_2} + \frac{e_1 p_2 P_1 - e_2 p_1 P_2}{H(e_1 P_1 + e_2 P_2)},$$

provided $0 < u_1^* < 1$. If $U_1(u_1) > U_2(u_1)$ ($U_1(u_1) < U_2(u_1)$) for all $0 \leq u_1 \leq 1$, the NE and the only evolutionary outcome is $u_1^* = 1$ ($u_1^* = 0$).

Because for $u_1 \neq u_1^*$

$$W_H(u_1^*, u_1) - W_H(u_1, u_1) = \frac{(e_1 P_1 (p_2 + (1-u_1)H) - e_2 P_2 (p_1 + u_1 H))^2}{H(e_1 P_1 + e_2 P_2)(p_2 + (1-u_1)H)(p_1 + u_1 H)} > 0,$$

the interior Nash equilibrium u_1^* is also resistant to mutant invasions, i.e., $W_H(u_1^*, u_1) > W_H(u_1, u_1)$ for all strategies $u_1 \neq u_1^*$, and it is an Evolutionarily stable strategy (Hofbauer and Sigmund, 1998). Thus,

$$u_1^*(P_1, P_2, H) = \begin{cases} 1 & \text{if } P_2 < \frac{e_1 p_2 P_1}{e_2 (p_1 + H)} \\ \frac{e_1 P_1}{e_1 P_1 + e_2 P_2} + \frac{e_1 p_2 P_1 - e_2 p_1 P_2}{H(e_1 P_1 + e_2 P_2)} & \text{if } \frac{e_1 p_2 P_1}{e_2 (p_1 + H)} < P_2 < \frac{e_1 (p_2 + H) P_1}{e_2 p_1} \\ 0 & \text{if } P_2 > \frac{e_1 (p_2 + H) P_1}{e_2 p_1}, \end{cases}$$

which is function (3) in the main text. Making appropriate changes of symbols and using fitness function (2b) instead, we can derive function (4) for the mutualists in the main text.

References

Addicott, J.F., Freedman, H.I., 1984. On the structure and stability of mutualistic systems: analysis of predator-prey and competition models as modified by the action of a slow-growing mutualist. *Theor. Popul. Biol.* 26 (3), 320–339. [http://dx.doi.org/10.1016/0040-5809\(84\)90037-6](http://dx.doi.org/10.1016/0040-5809(84)90037-6).

van Baalen, M., Křivan, V., van Rijn, P.C.J., Sabelis, M.W., 2001. Alternative food, switching predators, and the persistence of predator-prey systems. *Am. Nat.* 157 (5), 1–16. <http://dx.doi.org/10.1086/319933>.

Bascompte, J., Melián, C.J., Sala, E., 2005. Interaction strength combinations and the overfishing of a marine food web. *Proc. Natl. Acad. Sci. USA* 102 (15), 5443–5447.

Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458, 1018–1020. <http://dx.doi.org/10.1038/nature07950>.

Berec, L., Eisner, J., Křivan, V., 2010. Adaptive foraging does not always lead to more complex food webs. *J. Theor. Biol.* 266, 211–218. <http://dx.doi.org/10.1016/j.jtbi.2010.06.034>.

Bolker, B., Holyoak, M., Křivan, V., Rowe, L., Schmitz, O., 2003. Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* 84 (5), 1101–1114. [http://dx.doi.org/10.1890/0012-9658\(2003\)084\[1101:CTAESO\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2003)084[1101:CTAESO]2.0.CO;2).

Brose, U., Williams, R.J., Martinez, N.D., 2003. Comment on “foraging adaptation and the relationship between food-web complexity and stability”. *Science* 301, 918. <http://dx.doi.org/10.1126/science.1085902>.

Brown, J.S., Kotler, B.P., 2004. Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* 7 (10), 999–1014. <http://dx.doi.org/10.1111/j.1461-0248.2004.00661.x>.

Charnov, E.L., 1976. Optimal foraging: attack strategy of a mantid. *Am. Nat.* 110, 141–151.

Cowie, B.W., Byrne, M.J., Witkowski, E.T., Venter, N., 2016. Exacerbation of photosynthetic damage through increased heat–light stress resulting from gargaphia decoris sap-feeding. *Biol. Control* 94, 82–89. <http://dx.doi.org/10.1016/j.biocontrol.2015.12.008>.

Das, A.J., Stephenson, N.L., Davis, K.P., 2016. Why do trees die? Characterizing the drivers of background tree mortality. *Ecology* 97 (10), 2616–2627. <http://dx.doi.org/10.1002/ecy.1497>.

Dean, A.M., 1983. A simple model of mutualism. *Am. Nat.* 121 (3), 409–417.

Dobbertin, M., Brang, P., 2001. Crown defoliation improves tree mortality models. *Forest Ecol. Manag.* 141 (3), 271–284. [http://dx.doi.org/10.1016/S0378-1127\(00\)00335-2](http://dx.doi.org/10.1016/S0378-1127(00)00335-2).

Feinsinger, P., 1987. Effects of plant species on each other's pollination: is community structure influenced? *Trends Ecol. Evol.* 2 (5), 123–126. [http://dx.doi.org/10.1016/0169-5347\(87\)90052-8](http://dx.doi.org/10.1016/0169-5347(87)90052-8).

Fryxell, J.M., Lundberg, P., 1998. Individual Behavior and Community Dynamics. In: Population and Community Biology Series, (20), Chapman & Hall, New York, p. 211.

Gause, G.F., 1934. *The Struggle for Existence*. Williams & Wilkins, Baltimore, MD.

Gause, G.F., Smaragdova, N.P., Witt, A.A., 1936. Further studies of interaction between predators and prey. *J. Anim. Ecol.* 5 (1), 1–18. <http://dx.doi.org/10.2307/1087>.

Gause, G.F., Witt, A.A., 1935. Behavior of mixed populations and the problem of natural selection. *Am. Nat.* 69 (725), 596–609.

Georgelin, E., Loeuille, N., 2014. Dynamics of coupled mutualistic and antagonistic interactions, and their implications for ecosystem management. *J. Theor. Biol.* 346 (7), 67–74. <http://dx.doi.org/10.1016/j.jtbi.2013.12.012>.

Georgelin, E., Loeuille, N., 2016. Evolutionary response of plant interaction traits to nutrient enrichment modifies the assembly and structure of antagonistic-mutualistic communities. *J. Ecol.* 104 (1), 193–205. <http://dx.doi.org/10.1111/1365-2745.12485>.

Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébaud, E., Vereecken, N., 2017. Massively introduced managed species and their consequences for plant–pollinator interactions. *Adv. Ecol. Res.* 57, 147–199. <http://dx.doi.org/10.1016/bs.aecr.2016.10.007>.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. *Am. Nat.* 94, 421–425.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörrn, T., nad Hans de Kroon, D.G., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* 12 (10), e0185809. <http://dx.doi.org/10.1371/journal.pone.0185809>.

Hardin, G., 1960. The competitive exclusion principle. *Science* 131, 1292–1297. <http://dx.doi.org/10.1126/science.131.3409.1292>.

Hernandez, M.J., 1998. Dynamics of transitions between population interactions: a nonlinear interaction α -function defined. *Proc. R. Soc. B* 265, 1433–1440. <http://dx.doi.org/10.1098/rspb.1998.0454>.

Hofbauer, J., Sigmund, K., 1998. *Evolutionary Games and Population Dynamics*. Cambridge University Press, p. 351.

Holland, J.N., DeAngelis, D.L., 2010. A consumer-resource approach to the density-dependent population dynamics of mutualism. *Ecology* 91, 1286–1295. <http://dx.doi.org/10.1890/09-1163.1>.

Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.* 12, 197–229. [http://dx.doi.org/10.1016/0040-5809\(77\)90042-9](http://dx.doi.org/10.1016/0040-5809(77)90042-9).

Holt, R.D., 1997. Community modules. In: Gange, A.C., Brown, V.K. (Eds.), *Multi-trophic Interactions in Terrestrial Ecosystems*. Blackwell Science, pp. 333–349, 36th Symposium of the British Ecological Society.

Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc. R. Soc. B* 278 (1723), 3444–3451. <http://dx.doi.org/10.1098/rspb.2011.0268>.

Huxel, G.R., McCann, K.S., 1998. Food web stability: the influence of trophic flows across habitats. *Am. Nat.* 152 (3), 460–469. <http://dx.doi.org/10.1086/286182>.

Kondoh, M., 2006. Does foraging adaptation create the positive complexity? stability relationship in realistic food-web structure? *J. Theor. Biol.* 238, 646–651. <http://dx.doi.org/10.1016/j.jtbi.2005.06.028>.

Kosola, K.R., Dickmann, D.I., Paul, E.A., Parry, D., 2001. Repeated insect defoliation effects on growth, nitrogen acquisition, carbohydrates, and root demography of poplars. *Oecologia* 129 (1), 65–74. <http://dx.doi.org/10.1007/s004420100694>.

Kostitzin, V., 1934. *Symbiose, Parasitisme Et Évolution, ActualitéS Scientifiques Et Culturelles Et Industrielles*. Hermann, Paris.

Kulman, H., 1971. Effects of insect defoliation on growth and mortality of trees. *Ann. Rev. Entomol.* 16 (1), 289–324. <http://dx.doi.org/10.1146/annurev.en.16.010171.001445>.

Křivan, V., 1996. Optimal foraging and predator prey dynamics. *Theor. Popul. Biol.* 49, 265–290. <http://dx.doi.org/10.1006/tpbi.1996.0014>.

Křivan, V., 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. *Am. Nat.* 149 (1), 164–178. <http://dx.doi.org/10.1086/285984>.

Křivan, V., 2014. Competition in di- and tri-trophic food web modules. *J. Theor. Biol.* 343, 127–137. <http://dx.doi.org/10.1016/j.jtbi.2013.11.020>.

- Křivan, V., Revilla, T.A., 2019. Plant coexistence mediated by adaptive foraging preferences of exploiters or mutualists. *J. Theor. Biol.* 480, 112–128. <http://dx.doi.org/10.1016/j.jtbi.2019.08.003>.
- Levin, S.A., 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat.* 104, 413–423. <http://dx.doi.org/10.1086/282676>.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68 (4), 619–640. <http://dx.doi.org/10.1139/z90-092>.
- May, R.M., 1972. Will a large complex system be stable? *Nature* 238 (5364), 413. <http://dx.doi.org/10.1038/238413a0>.
- May, R.M., 1981. *Theoretical Ecology: Principles and Applications*, second ed. Blackwell.
- McCann, K.S., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. *Nature* 395, 794–798. <http://dx.doi.org/10.1038/27427>.
- Melián, C.J., Bascompte, J., Jordano, P., Křivan, V., 2009. Diversity in a complex ecological network with two interaction types. *Oikos* 118 (1), 122–130. <http://dx.doi.org/10.1111/j.1600-0706.2008.16751.x>.
- Moore, C.M., Catella, S.A., Abbott, K.C., 2017. Population dynamics of mutualism and intraspecific density dependence: How θ -logistic density dependence affects mutualistic positive feedback. *Ecol. Model.* 368, 191–197. <http://dx.doi.org/10.1016/j.ecolmodel.2017.11.016>.
- Mougi, A., Kondoh, M., 2014. Adaptation in a hybrid world with multiple interaction types: a new mechanism for species coexistence. *Ecol. Res.* 29 (2), 113–119. <http://dx.doi.org/10.1007/s11284-013-1111-4>.
- Murdoch, W.W., 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39 (4), 335–354.
- Odum, E.P., 1971. *Fundamentals of Ecology*. Saunders.
- Paine, R.T., 1980. Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49 (3), 667–685.
- Peacor, S.D., Werner, E.E., 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl. Acad. Sci. USA* 98 (7), 3904–3908. <http://dx.doi.org/10.1073/pnas.071061998>.
- Revilla, T.A., 2015. Numerical responses in resource-based mutualisms: a time scale approach. *J. Theor. Biol.* 387, 39–46. <http://dx.doi.org/10.1016/j.jtbi.2015.04.012>.
- Revilla, T.A., Křivan, V., 2016. Pollinator foraging adaptation and the coexistence of competing plants. *PLoS One* 11 (8), e0160076. <http://dx.doi.org/10.1371/journal.pone.0160076>.
- Revilla, T.A., Křivan, V., 2018. Competition, trait-mediated facilitation, and the structure of plant-pollinator communities. *J. Theor. Biol.* 440, 42–57. <http://dx.doi.org/10.1016/j.jtbi.2017.12.019>.
- Ringel, M.S., Hu, H.H., Anderson, G., 1996. The stability and persistence of mutualisms embedded in community interactions. *Theor. Popul. Biol.* 50 (3), 281–297. <http://dx.doi.org/10.1006/tpbi.1996.0032>.
- Rosenzweig, M.L., 1981. A theory of habitat selection. *Ecology* 62 (2), 327–335. <http://dx.doi.org/10.2307/1936707>.
- Rosenzweig, M.L., 1986. Hummingbird isolegs in an experimental system. *Behav. Ecol. Sociobiol.* 19 (5), 313–322. <http://dx.doi.org/10.1007/BF00295704>.
- Rosenzweig, M.L., Abramsky, Z., 1986. Centrifugal community organization. *Oikos* 46 (3), 339–348. <http://dx.doi.org/10.2307/3565832>.
- Sauve, A., Fontaine, C., Thébault, E., 2014. Structure–stability relationships in networks combining mutualistic and antagonistic interactions. *Oikos* 123 (3), 378–384. <http://dx.doi.org/10.1111/j.1600-0706.2013.00743.x>.
- Sauve, A.M.C., Fontaine, C., Thébault, E., 2015. Stability of a diamond-shaped module with multiple interaction types. *Theor. Ecol.* 9 (1), 27–37. <http://dx.doi.org/10.1007/s12080-015-0260-1>.
- Sauve, A.M.C., Thébault, E., Poccock, M.J.O., Fontaine, C., 2016. How plants connect pollination and herbivory networks and their contribution to community stability. *Ecology* 97 (4), 908–917. <http://dx.doi.org/10.1890/15-0132.1>.
- Scheuring, I., 1992. “The orgy of mutualism” as an artefact: a stage structured model of plant-pollinator and seed-dispersal systems. *Abstracta Bot.* 16 (1), 65–70.
- Schmitz, O.J., Křivan, V., Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* 7 (2), 153–163. <http://dx.doi.org/10.1111/j.1461-0248.2003.00560.x>.
- Schoener, T.W., 1978. Effects of density-restricted food encounter on some single-level competition models. *Theor. Popul. Biol.* 13 (3), 365–381. [http://dx.doi.org/10.1016/0040-5809\(78\)90052-7](http://dx.doi.org/10.1016/0040-5809(78)90052-7).
- Scudo, F.M., Ziegler, J.R., 1978. In: Levin, S.A. (Ed.), *The Golden Age of Theoretical Ecology, 1923–1940: A Collection of Works By V. Volterra, VA Kostitzin, AJ Lotka, and an Kolmogoroff*. In: *Lecture Notes in Biomathematics*, (22), Springer, p. 490.
- Sih, A., 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210 (4473), 1041–1043.
- Sih, A., 1986. Antipredator responses and the perception of danger by mosquito larvae. *Ecology* 67 (2), 434–441.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press.
- Thébault, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329 (5993), 853–856. <http://dx.doi.org/10.1126/science.1188321>.
- Uchida, S., Drossel, B., 2007. Relation between complexity and stability in food webs with adaptive behavior. *J. Theor. Biol.* 247 (4), 713–722.
- Vandermeer, J., Boucher, D.H., 1978. Varieties of mutualistic interaction in population models. *J. Theor. Biol.* 74, 549–558. [http://dx.doi.org/10.1016/0022-5193\(78\)90241-2](http://dx.doi.org/10.1016/0022-5193(78)90241-2).
- Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. *Nature* 118 (2972), 558–560. <http://dx.doi.org/10.1038/118558a0>.
- Volterra, V., 1928. Variations and fluctuations of the number of individuals in animal species living together. *J. Conseil* 3 (1), 3–51. <http://dx.doi.org/10.1093/icesjms/3.1.3>.
- Volterra, V., 1938. Population growth, equilibria, and extinction under specified breeding conditions: a development and extension of the theory of the logistic curve. *Hum. Biol.* 10 (1), 1–11.
- Young, T.P., Chase, J.M., Huddleston, R.T., 2001. Community succession and assembly comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecol. Restor.* 19 (1), 5–18.