Dynamics of pollination and seed dispersal mutualisms at low density

Kayla R. S. Hale[1*], Daniel P. Maes[1,2], & Fernanda S. Valdovinos[1,3*]

[1] Department of Ecology and Evolutionary Biology, University of Michigan, Biological Sciences Building, 1105 North University Ave, Ann Arbor, MI 48109, USA.

[2] Department of Mathematics, University of Michigan, East Hall, 530 Church St, Ann Arbor, MI 48109, USA.

[3] Department of Environmental Science and Policy, University of California, Davis, Wickson Hall, One Shields Avenue, Davis, CA 95616.

*Corresponding authors; email: kaylasal@umich.edu, fvaldovinos@ucdavis.edu

Manuscript elements: Figure 1, Figure 2, Figure 3, Table 1, Online Appendices A and B (including Table A1 and Figures A1-A3). Figures 1-3 are to print in color.

Keywords: transportation mutualism, reproductive services, population dynamics, thresholds, Allee effects, germination, negative density-dependence

Manuscript type: Major Article.

Running title: Dynamics of mutualisms at low density

Word count: 5545.

Acknowledgements: This research was supported by National Science Foundation Graduate Research Fellowship DGE-1143953 to K.R.S.H., National Science Foundation Graduate Research Fellowship DGE-1256260 to D.P.M., and National Science Foundation grant DEB-1834497 to F.S.V.

Competing interests: The authors declare no competing interests.

Statement of authorship: F.S.V. conceived the study; K.R.S.H. and D.P.M. analyzed the models; K.R.S.H. and F.S.V. developed the biological interpretation of the model results; K.R.S.H. wrote the manuscript with important contributions from F.S.V.; all authors developed the models.

Code availability: Mathematica notebooks used to analyze the models are available by request and will be available on GitHub upon acceptance.

Abstract

Pollination and seed dispersal mutualisms are critical for biodiversity and ecosystem services yet face mounting threats from anthropogenic perturbations that cause their populations to decline. Characterizing the dynamics of these mutualisms when populations are at low density is important to anticipate consequences of these perturbations. We developed simple population dynamic models detailed enough to distinguish different mechanisms by which plant populations benefit from animal pollination or seed dispersal. We modeled benefits as functions of foraging rate by animals on plant rewards and specified whether they affected plant seed set, germination, or negative density dependence during recruitment. We found that pollination and seed dispersal mutualisms are stable at high density but exhibit different dynamics at low density, depending on plant carrying capacity, animal foraging efficiency, and whether populations are obligate upon their partners for persistence. Under certain conditions, all mutualisms experience destabilizing thresholds in which one population declines because its partner is too rare. Plants additionally experience Allee effects when obligate upon pollinators. Finally, both pollination and seed dispersal mutualisms that reduce mortality during recruitment can exhibit bistable coexistence at low or high density. Insights from our models can inform conservation efforts, as mutualist populations continue to decline globally.

Introduction

Pollination and seed dispersal mutualisms support vast amounts of biodiversity and productivity in terrestrial ecosystems. Pollinators aid the reproduction of 78% and 94% of flowering plants in temperate and tropical regions, respectively (Ollerton *et al.* 2011), while seed dispersers aid the reproduction of 56% of plant species worldwide (Aslan *et al.* 2013). In addition, the production of 75% of the world's major crops partially or completely depend on pollinators (Klein *et al.* 2007). Unfortunately, these important mutualisms face threats globally. A recent meta-analysis of plant regeneration in forests (Neuschultz *et al.* 2016) found that pollination and seed dispersal are the processes most vulnerable to human disturbance including climate change, nutrient runoff, pesticide use, and invasive species (Stachowicz 2001, Traveset & Richardson 2006, Tylianakis *et al.* 2008, Zhou *et al.* 2013). In fact, there is clear evidence showing the abundance of pollinators and key seed disperser taxa such as frugivorous birds and mammals are declining globally (Potts *et al.* 2010, 2016, Wotton & Kelly 2011). Therefore, understanding the population dynamics of species involved in these mutualisms, especially at low abundances, can inform predictions of the consequences of those declines on the mutualisms, plant populations and crop production.

Historically, theoretical research (Gause & Witt 1935, Whittaker 1975, Vandermeer & Boucher 1978, Goh 1979, Addicott 1981, Wolin 1985, Bascompte *et al.* 2006, Okuyama & Holland 2008, Bastolla *et al.* 2009) mostly used Lotka-Volterra type models (*sensu* Valdovinos 2019) to investigate the dynamics of populations interacting mutualistically. This phenomenological representation of mutualistic interactions as net positive effects between interacting species provided insight for characterizing the effects of facultative,

obligate, linear, and saturating mutualisms on the long-term stability of mutualistic systems. However, representing mutualisms simply as positive effects between species overlooks important dynamics that emerge from the specific mechanisms by which species positively affect each other. More recent research advanced upon these phenomenological representations of mutualism by developing models that account for consumer-resource mechanisms (Wright 1989, Holland & DeAngelis 2010, Valdovinos *et al.* 2013, Revilla 2015). Accounting for consumer-resource mechanisms enabled the discovery of important dynamics, such Allee effects, alternative states, transitions between mutualism and parasitism, competition among species sharing mutualistic partners, and niche partitioning (May 1976, Soberón & Martinez del Rio 1981, Wells 1983, Wright 1989, Pierce & Young 1986, Holland & DeAngelis 2010, Valdovinos *et al.* 2013, 2016, Revilla 2015, Valdovinos & Marsland 2021) as well as the integration of these mutualisms into food web dynamics (Hale *et al.* 2020). This research, however, mostly focused on animal dynamics (i.e., the consumer) and the dynamics of plant resources available to the animals (but see Wells 1983). To investigate the consequences of pollinator and seed disperser declines on plant populations, more focus is needed on the mechanisms by which these animals affect plant reproduction (Beckman *et al.* 2020). Here, we improve mechanistic understanding of the ecological dynamics of these mutualisms by developing and analyzing consumer-resource models that also account for simple mechanisms of reproductive benefits to plants.

Pollination and seed dispersal mutualisms share similarities as “transportation mutualisms” (Bronstein 2015). In both cases, animals visit plants to feed upon rewards (such as nectar and fruit) and provide reproductive services (such as transport of pollen and

seeds) incidentally during foraging. However, these interactions differ in the mechanism of reproductive benefit to plants. Pollinators increase plant seed set by facilitating cross-fertilization, by moving pollen between conspecific plant individuals (Willmer 2011). Seed dispersers increase plant recruitment by lessening density-dependent seed(ling) mortality caused by predators, pathogens, and competitors (Wotton & Kelly 2011, Moore & Dittel 2020). Seed dispersal can also increase germination by improving seed condition during passage through dispersers' guts (Fricke *et al.* 2013). Here, we investigate the dynamical consequences of these various mechanisms of reproductive benefits to plants. We find distinct dynamical behaviors at low population densities, including thresholds, Allee effects, and bistable coexistence, depending on species obligacy (i.e., their ability to persist without their partner), plant carrying capacity, and animal foraging efficiency. We also show that pollination and seed dispersal mutualisms have similar dynamics and stability at high density but differ in the ecological conditions under which the populations are vulnerable to collapse.

Methods

We begin by deriving models for animal mutualists, which closely follow previous consumer-resource approaches (e.g., Wright 1989, Holland & DeAngelis 2010). Then, we derive novel models for plant mutualists, balancing simplicity with the necessary mechanistic detail to distinguish between the potential benefits of pollination versus seed dispersal interactions. We assume that the growth rate of animal and plant populations are functions of the density-independent per-capita birth (b_A, b_P) and death (b_A, b_P) rates in

absence of their mutualist, where subscripts A and P indicate animal and plant populations, respectively. These population growth rates are also function of per-capita self-limitation and other density-dependent processes (s_A, s_P), and the benefits provided by mutualists (see below). Our models are continuous, which accommodates species with overlapping generations. They are also deterministic and ignore migration, which allows us to focus on the dynamics that emerge from the mutualistic interactions, unobscured by stochasticity and the dynamics of other patches. Table 1 summarizes our parameter definitions for all models.

Population dynamics of animals

Pollinators and seed dispersers benefit from visiting plants by foraging for rewards that offer primarily nutritional benefit (Willmer 2011, Jordano 2014). We therefore model the change in animal population density ($\boldsymbol{A}$) over time t as

$$\frac{d\boldsymbol{A}}{dt} = b_A\boldsymbol{A} + \varepsilon C_R - s_A\boldsymbol{A} - d_A\boldsymbol{A} \qquad \text{Eqn. 1}$$

where the growth rate of the animal population increases proportionally to its consumption rate of plant rewards, C_R. Parameter ε is the efficiency of converting rewards to new animal individuals via birth and maturation. We choose total consumption rate $C_R = \frac{a\boldsymbol{AP}}{1+ah\boldsymbol{P}}$, following a Holling Type II functional response with attack rate a and handling time h. This encodes the reasonable assumption that animal consumption rate on plant rewards saturates with increasing density of the plant population. Reproduction fueled by resources other than plant rewards is included in b_A. We define an animal population ($\boldsymbol{A}$) as an "obligate" mutualist of the plant population ($\boldsymbol{P}$) when $r_A = b_A - d_A \leq 0$, that is, when $\boldsymbol{A}$

cannot persist in the absence of its mutualist plant. Otherwise ($r_A > 0$), $\boldsymbol{A}$ is "facultative" and its population is self-sustaining.

Population dynamics of plants

Plants receive reproductive services (S) from animals which increases the density of mature (reproductive) plant individuals. Reproductive services are functions of animal visitation to plants, which we assume to be well approximated by the foraging rate on rewards (C_R, Vázquez *et al*. 2005). Our pollination and seed-dispersal models both account for germination, g, and negative density-dependence, s_P, that limit the seeds that survive and mature to reproductive adults. This density-dependence represents, for example, natural enemies near a parent plant making the habitat inhospitable for the survival of seedlings (Janzen-Connell effect) or seeds competing during recruitment. Below, we derive separate models for pollination and seed dispersal based on the different mechanisms by which each affects the population dynamics of plants.

Pollination: Increase in seed set

We model animal-pollinated plant dynamics ($\boldsymbol{P}$) as:

$$\frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}[g(b_P + \beta S)(1 - s_P\boldsymbol{P}) - d_P] \qquad \text{Eqn. 2}$$

where β is the conversion efficiency of pollination services (S) to seed production. Pollination requires the transfer of pollen from one individual's flower to the stigma of a conspecific plant individual, which occurs when animals visit flowers to forage. We therefore assume $S = C_R$, where the contribution of the animal population to per-plant seed

set is the total foraging rate of animals on plant rewards (C_R). This expression accounts for the repeated interactions between plant and animal individuals required for conspecific pollen transfer (Vázquez *et al.* 2005, Schupp *et al.* 2017). Using the Holling Type II functional response for C_R from above yields our specific model for animal-pollination mutualisms:

$$\begin{cases} \frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[\left(b_P + \beta\frac{a\boldsymbol{AP}}{1+ah\boldsymbol{P}}\right)\, g(1 - s_P\boldsymbol{P}) - d_P\right] \\ \frac{d\boldsymbol{A}}{dt} = \boldsymbol{A}\left[b_A + \varepsilon\frac{a\boldsymbol{P}}{1+ah\boldsymbol{P}} - s_A\boldsymbol{A} - d_A\right] \end{cases} \qquad \text{Eqn. 3}$$

Following our previous definitions, plant population ($\boldsymbol{P}$) is an obligate mutualist of $\boldsymbol{A}$ when it cannot persist in its absence ($r_P = g_P b_P - d_P \leq 0$); otherwise, $\boldsymbol{P}$ is facultative ($r_P > 0$).

Seed dispersal: Reduction in negative density-dependence or increase in germination

Seed dispersers visit plants to forage on fruit, elaiosomes, or even seeds directly, later depositing the seed away from the parent plant. This process increases recruitment by reducing density-dependent mortality caused by predators or pathogens, which are most abundant near adult plants (Wotton & Kelly 2011, Fricke *et al.* 2013, Moore & Dittel 2020). Seed dispersal may also increase germination by improving seed condition during passage through dispersers' guts, which removes pathogens or provides "chemical camouflage" from natural enemies (Fricke *et al.* 2013). We consider both cases below.

First, animals rescue seeds from predators, pathogens, and intraspecific competition by transporting them away from parent plants. This can increase successful recruitment:

$$\frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}[b_P g(1 - (s_P - \sigma S)\boldsymbol{P}) - d_P] \qquad \text{Eqn. 4}$$

where σ converts dispersal services into reductions in negative density-dependence (s_P). Eqn. 4 implies that plants must be potentially persistent (have positive demographic rates, $r_P = b_P g - d_P > 0$) to benefit from reductions to negative density-dependence. Therefore, we only consider facultative plants ($r_P > 0$) for this case.

Second, animals may increase seed condition by masticating or digesting fruits. This can improve germinability or germination rate:

$$\frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}[b_P(g + \gamma S)(1 - s_P\boldsymbol{P}) - d_P]. \qquad \text{Eqn. 5}$$

where γ converts dispersal services into increased germination g. Plants may be obligate ($r_P \leq 0$) or facultative ($r_P > 0$) upon their animal partner for population persistence.

In both seed dispersal cases, services are directly related to consumption rate of animals on plant rewards. We use $S = C_R/\boldsymbol{P}$, where the per-plant benefit of seed dispersal is proportional to the per-capita (i.e., per-plant) visitation rate of animals on plants. This is because repeated interactions between plant and animal individuals are possible but not required for effective seed dispersal, as it is for effective pollination (Schupp *et al.* 2017). Using the Holling Type II functional response from above yields our specific models for animal seed-dispersal mutualisms in which plants benefit via escape from negative density-dependence:

$$\begin{cases} \frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[b_P g\left(1 - \left(s_P - \sigma\frac{a\boldsymbol{A}}{1+ah\boldsymbol{P}}\right)\boldsymbol{P}\right) - d_P\right] \\ \frac{d\boldsymbol{A}}{dt} = \boldsymbol{A}\left[b_A + \varepsilon\frac{a\boldsymbol{P}}{1+ah\boldsymbol{P}} - s_A\boldsymbol{A} - d_A\right] \end{cases} \qquad \text{Eqn. 6}$$

or increased germination:

192 $$\begin{cases} \frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[b_P\left(g + \gamma\frac{a\boldsymbol{A}}{1+ah\boldsymbol{P}}\right)(1 - s_P\boldsymbol{P}) - d_P\right] \\ \frac{d\boldsymbol{A}}{dt} = \boldsymbol{A}\left[b_A + \varepsilon\frac{a\boldsymbol{P}}{1+ah\boldsymbol{P}} - s_A\boldsymbol{A} - d_A\right] \end{cases} \quad \text{Eqn. 7}$$

193 Notice that Eqn. 7 is only biologically reasonable when $s_P - \sigma S \geq 0$, which is not
194 guaranteed when the ratio of animal to plant density is high. We restrict our analysis to the
195 space in which this condition holds, though our results are qualitatively the same outside of
196 this regime as well.

197 **Costs of mutualism**

198 The potential costs of pollination and seed dispersal mutualisms on plant
199 populations are less clear than their benefits. Plants tend to provide nutritional rewards such
200 as nectar or fruits to attract their animal transporters of pollen or seeds. The available
201 evidence suggests that the costs of providing these rewards tend to suppress seed set or
202 other aspects of an individual plant's reproduction (Edwards *et al.* 2006, Willmer 2011).
203 However, these individual-level costs are likely to be buffered at the population level for
204 several reasons. First, costs associated with rewards can simply act to reduce benefit
205 provided by mutualism (e.g., reduced seed set due to nectar production, Brandenburg *et al.*
206 2012; seed predation by scatterhoarders, Gómez *et al.* 2019). Second, rewards and the
207 organs that produce them are typically ephemeral in comparison to individuals in the
208 population. These organs can be damaged or decay, but these costs are unlikely to
209 instantaneously result in death or damage to individuals (Revilla 2015). More generally,
210 costs associated with rewards may be "fixed" in that they are independent of partner density
211 (e.g., sunk costs of molecular machinery used to produce rewards, Holland *et al.* 2002).

Finally, changes in metrics of individual fitness like fecundity do not necessarily manifest in changes in the per-capita growth rate of the population (Ford *et al.* 2015). In summary, rewards costs, even if highly impactful to individuals or a certain vital rate, may not have a measurable impact on population growth. Therefore, we assume that costs associated with rewards do not substantially impact population density or, if they do, the impact could be represented as small, fixed changes to plants' per-capita birth and death rates approximated as constant with respect to the producing species' density.

Analysis

We performed phase plane analyses on our pollination (Eqn. 3) and seed dispersal models (Eqns. 5, 6) using Wolfram Mathematica 11. Mathematical analysis and simulation code are presented in Appendix A and online, respectively. In the main text, we only present results for the ecologically relevant cases where populations have positive densities and can potentially coexist (i.e., are feasible). We investigated the behavior of populations at low density, assessing our models for conditions under which Allee effects, thresholds, and other alternative stable states occur. We use the term "Allee effects" for strong, demographic Allee effects, in which a population declines under a certain threshold of its own density (Kramer *et al.* 2009). We define "threshold effects" as population declines caused by the decline of its partner's density under a certain threshold (Vandermeer & Boucher 1978, Revilla 2015). Alternative stable states, such as single-species persistence or bistability, occur when a system can settle stably into more than one equilibrium depending only upon initial conditions ("historical accidents," May 1977).

Results

We found that pollination and seed dispersal mutualisms have similar dynamics and stability at high density but differ in the ecological conditions under which the populations are vulnerable to collapse. Different parameter regimes, in combination with whether each partner is obligate or facultative, lead to different dynamics at low population densities. Below, we describe these different dynamics for each of our models, assuming that coexistence is feasible (but see Appendix A for results on feasibility). Then, we describe some ecological scenarios under which each outcome is likely to occur. We provide these scenarios rather than providing formal mathematical conditions, because the latter are complex and difficult to interpret due to the nonlinearities in our models.

Pollination

The shape and intersections of the plant and animal "nullclines" (curves of zero change in population density) determine the dynamics of the system. The animal nullclines (black curves) are concave down, increasing functions that saturate with respect to plant density (Figs. 1-3). The animal-pollinated plant nullclines (green curves) differ according to whether the plant is obligate or facultative (Fig. 1). When obligate (Fig. 1A-B), the plant nullcline is U-shaped bounded between vertical asymptotes at zero and at $1/s_P$. When facultative (Fig. 1C-G), the plant nullcline is increasing and concave up at high densities. Depending on the parameter regime, the plant nullcline may exhibit an inflection point at low densities in which it transitions from concave down to up (e.g., Fig. 1D). When facultative, animals or plants may persist in the absence of their partners at density $K_A =$

254 r_A/s_A or $K_P = r_P/b_P g s_P$, respectively. These densities are "carrying capacities" in the
255 original sense of single-species equilibrium densities (Vandermeer & Boucher 1978).

256 When plants are obligate (Fig. 1A-B), the system exhibits two equilibria: (1) A
257 stable coexistence equilibrium (off-axes filled circle). Density past this equilibrium in either
258 species causes its population to decrease due to negative density-dependence. Therefore,
259 unbounded population growth cannot occur. (2) A half-stable saddle point that attracts in
260 one dimension but repels in the other (off-axes hollow circle), bisecting the plane into two
261 portions, as marked by the "separatrix" (dashed line). This separatrix marks out a threshold
262 under which obligate partners go extinct even if initially highly abundant ("threshold
263 effects," regions shaded light red). For example, following a trajectory from the lower-right
264 region in Fig. 1B, initially highly abundant obligate plants go extinct while initially rare
265 pollinators persist at K_A. These threshold effects occur because one species is too low in
266 density to provide sufficient benefits to its partner, causing the partner's population to
267 decline. The low-density species continues to benefit from mutualism but its increase in
268 density cannot occur fast enough to save the system from extinction. Above the separatrix,
269 one or both species are of high enough density that benefits from mutualism cause positive
270 population growth in their partners and the system will achieve stable coexistence.

271 Obligate animal-pollinated plants are additionally susceptible to Allee effects
272 (regions shaded dark red), where their population declines under a threshold of their own
273 density regardless of the density of their partner (Fig. 1A-B). This occurs because benefit is
274 proportional to the total consumption rate by animals, i.e., plants require obligate

outcrossing for successful pollination behavior. At very low plant density, even highly abundant pollinators are limited by the time required to harvest and (incidentally) transfer pollen between two plant individuals, and thus cannot provide pollination services at a rate sufficient to allow plant population growth. Unsurprisingly, animals cannot acquire enough food and decline either to extinction (Fig. 1A) or to K_A once plants are fully extirpated (Fig. 1B).

When animal-pollinated plants are facultative (Fig. 1C-G), more diverse dynamics are possible, depending on the relative growth rates and efficiency of plants and animals as mutualists. High-density stable coexistence always occurs if partners are originally at high enough density. At lower density, threshold effects can also occur when animals are obligate mutualists (Fig.1 C) or even population growth from low densities (Fig. 1D-G) with the potential for bistable coexistence (Fig. 1D, 1F).

When both partners exhibit population growth from low densities (Fig. 1D-G), stable coexistence at higher densities than either species could achieve alone will always occur. However, in a relatively small parameter range, the system exhibits three equilibria: low-density stable, half-stable saddle, and high-density stable (Fig. 1D, 1F). Thus, there are two possible points of stable coexistence – one at lower density and one at higher – to which the system will be attracted, based upon initial conditions ("bistable coexistence"). A separatrix (dashed line) running through the saddle point (hollow circle) marks out a threshold under which the system will persist at the lower-density coexistence equilibrium.

Growth from low density (Fig. 1D-G) can occur when $-\frac{r_A}{a(\varepsilon+hr_A)} < K_P$. That is, when the intercept of the animal nullcline in the x-axis (representing plant density) is higher than the intercept of the plant nullcline. In this case, bistable coexistence (Fig. 1D, 1F) is most likely when plants have low carrying capacity, K_P. That is, when the environment is hostile to plants due to, for example, high density-dependence (s_P) or density-independent mortality (d_P). In addition, bistable coexistence is most likely when pollinators are inefficient at accessing nutrients from rewards when foraging upon plants (low a, low ε, high h) and have near-zero population growth rate (r_A) in the absence of plants, regardless of whether they are obligate or facultative. The single stable coexistence equilibrium at high density is most likely under the opposite conditions (Fig. 1E, 1G). That is, when plants have high carrying capacities and pollinators are efficient foragers. Finally, threshold effects can occur instead (Fig. 1C) when $-\frac{r_A}{a(\varepsilon+hr_A)} > K_P$, that is, when the intercept of the animal nullcline is lower than the intercept of the plant nullcline in the x-axis. This happens when pollinators are highly obligate upon plants ($r_A \ll 0$). Threshold effects are also more likely when pollinators are efficient foragers (high a, high ε, low h) but the environment is hostile to plants (low K_P).

Seed Dispersal

Our seed dispersal model with benefit to plants as reduced negative density-dependence displays a range of low-density outcomes (Fig. 2) like those described for pollination mutualisms. Seed dispersers follow the same dynamics as pollinators. Plants are always facultative (see Methods) and can persist in the absence of animal mutualists at

density K_P. The plant nullcline is a concave down, increasing function with linear slope of $\frac{hs_P}{\sigma} \geq h$ at high densities. Therefore, based on the plant nullcline alone, benefits to plants would increase indefinitely with increasing animal density. However, animal visitation rate saturates due to satiation (encoded in the Holling type II functional response) and this animal saturation bounds the benefits to plants by intersecting the plant nullcline at high densities. At low densities, the plant nullcline can exhibit an inflection point in which it transitions from concave down to linear growth. The same qualitative conditions hold as described for the pollination model as to whether the system exhibits bistable coexistence (Fig. 2B, 2D), a single high-density stable coexistence equilibrium (Fig. 2C, 2E), or threshold effects when animals are obligate mutualists (Fig. 2A). Note that as negative density dependence increases due to the Janzen-Connell effect or intraspecific competition (high s_P), plant carrying capacity shifts to lower density, making the cases in which threshold effects or bistable coexistence can occur more likely. Conversely, increasing the effectiveness of escape from negative density-dependence due to seed dispersal (high σ) makes the single high-density coexistence case more likely.

Our seed dispersal model with benefit to plants as increased seed germination displays simpler dynamics than the other two models. The plant nullcline for both obligate and facultative plants is a concave up, increasing function, bounded by a vertical asymptote at $1/s_P$. Animal-seed dispersers follow the same dynamics as animal-pollinators, described above. Like the pollination model, stable coexistence at higher densities than either can achieve alone is always possible (Fig. 3A-F). When at least one partner is an obligate

337 mutualist, threshold effects can always occur, leading to extinction if at least one partner is
338 at low enough density (Fig. 3A, B, D). These effects are most likely when one partner is
339 highly obligate ($r_i \ll 0$) and when plants are difficult to find on the landscape (search time
340 $(1/a) \to \infty$). Specifically, they can occur in feasible systems when $K_A < -\frac{r_P}{b_P \gamma a}$ or
341 $-\frac{r_A}{a(\varepsilon + h r_A)} > K_P$. Alternatively, growth from low density and ultimate stable coexistence is
342 the only outcome when both partners are facultative (Fig. 3F).

343 **Discussion**

344 Pollination and seed dispersal mutualisms support the reproduction of a vast number
345 of plant species globally, including crops (Klein *et al.* 2007, Aslan *et al.* 2013, Garibaldi *et*
346 *al.* 2013, Neuschultz *et al.* 2016). Anthropogenic stressors threaten these mutualisms by
347 causing population declines that can disrupt the benefits provided by the mutualists
348 (Tylianakis *et al.* 2008, Traveset & Richardson 2006, 2014, Potts *et al.* 2010, 2016,
349 Beckman *et al.* 2020). These potential disruptions increase the need to study the dynamics
350 of mutualisms when the interacting populations exhibit low density. Historically, however,
351 theoretical studies have focused on the dynamics of mutualisms at high density. Authors
352 grappled with the unbounded growth predicted by the simplest models of mutualism
353 (Robert May's (1976) "orgy of mutual benefaction") and searched for mechanisms that
354 would lead to stable coexistence (Wolin & Lawlor 1984). This research found that the
355 saturation of mutualistic benefit stabilizes the population dynamics of mutualistic
356 interactions at high density (Holland *et al.* 2006, Okuyama & Holland 2008). Theoretical

research should now focus on the dynamics of mutualisms at low density, especially given the global population declines of pollinators and seed dispersers.

We investigated the dynamics, especially at low density, of novel consumer-resource models that incorporate the mechanisms by which pollinators and seed-dispersers benefit plant populations. We found thresholds, Allee effects, and bistable coexistence, and characterized when each of those dynamics occur. Thresholds occur when mutualists are obligate because low-density populations cannot provide enough benefit to rescue their higher density partner (Figs. 1A-C, 2A, 3A-B, D). Allee effects occur in obligate animal-pollinated plants because the plants can become too low in density to attract sufficient pollinator visits to save their own population (Figs. 1A-B). Bistable coexistence occurs in pollination (Figs. 1D, F) and seed dispersal mutualisms when plants benefit through a reduction in negative density-dependence during recruitment (Figs. 2B, D). In both mutualisms, bistable coexistence occurs when plants are facultative but have low carrying capacity while animals are inefficient foragers with near-zero per-capita growth rate. Conversely, when facultative plants have high carrying capacity and animals are efficient foragers, plant and animal populations grow from low density with subsequent stable coexistence at a single, high-density equilibrium (Figs. 1E, 1G, 2C, 2E, 3C, 3E). This high-density equilibrium is guaranteed for facultative seed dispersal mutualisms when animals benefit plants via increased seed germination (Fig. 3F).

Threshold effects in mutualisms were first described in the late 1970s, specifically in cases of obligate mutualists that strongly benefit each other (May 1976, Vandermeer and Boucher 1978). The strong mutualistic interaction allowed the species to persist at high

379 densities, but was not sufficient for coexistence at densities below the threshold. The
380 authors also found that obligate mutualists interacting weakly always go extinct, that is,
381 thresholds effects do not occur in those mutualisms. This research used the Lotka-Volterra
382 model for mutualism with positive interacting coefficients and linear functional responses,
383 but the same qualitative results at low density are found when saturation is added to the
384 functional responses (Vandermeer & Goldberg 2013). Indeed, models incorporating
385 consumer-resource mechanisms also find these thresholds (May 1976, Soberón & Martinez
386 del Rio 1981, Wells 1983, Wright 1989, Fishman & Hadany 2010). Most recently, Revilla
387 (2015) predicts threshold effects in obligate plants, in which plants at low density cannot
388 recover fast enough to save their animal partners from decline, even if the animal
389 population was originally at very high density. Finally, Valdovinos and Marsland (2021)
390 identify the quality of visits needed from pollinators for plants to persist. Below such
391 threshold, the plant species and the animals depending on those plants go extinct. Here, we
392 also find that threshold effects occur when at least one mutualist is obligate and when the
393 benefits among species (in terms of efficient foraging) are strong enough to sustain
394 populations at high densities.

395 Allee effects may also cause irrecoverable declines in populations at low density.
396 We find Allee effects in plant populations that are obligate mutualists of pollinators, due to,
397 e.g., high self-incompatibility. This result is consistent with pollination ecology because
398 pollinators' benefits to plants tend to decrease at low plant density due to increased search
399 time, leading to a decrease in visitation rate and pollen limitation (Forsyth 2003). Low plant
400 density may also decrease visitation rate due to insufficient floral displays or reduce visit

401 quality due to pollen dilution (Forsyth 2003). Indeed, pollinator-mediated Allee effects
402 have been observed empirically in highly self-incompatible plant species (Kramer *et al.*
403 2009). We show that reductions in visit quantity alone are sufficient to induce an Allee
404 effect, whereas natural populations likely experience both a decrease in visit quality and
405 quantity at low plant density. In contrast, we did not find Allee effects in our seed dispersal
406 models. This is consistent with the mechanisms by which seed dispersers benefit plants.
407 Seed dispersers benefit plants by increasing the seed germination or their survival to
408 adulthood through refuge from intraspecific competition and natural enemies (seed
409 predators, herbivores) that are attracted to regions of high food densities (i.e., the Janzen-
410 Connell effect, Janzen 1970, Connell 1971, Wotton & Kelly 2011, Fricke *et al.* 2013,
411 Moore & Dittel 2020). These plants are thus less likely to experience Allee effects, because
412 at low density the primary threats are similarly reduced. However, plants that are obligate
413 upon animal dispersers for germination can experience Allee effects in our models when
414 animals follow a Type III functional response (Appendix A); this is because plants become
415 too rare to attract animals that are less active at low food density (also see Courchamp *et al.*
416 2018). Finally, Holland and DeAngelis (2010) predict an Allee effect in "unidirectional"
417 consumer-resource mutualisms, which include both animal-pollination and seed dispersal
418 interactions. However, their Allee effect occurs due to animal overexploitation of plant
419 rewards, which induces more costs to plants from supplying rewards than benefits, though
420 they comment that this is unlikely to lead to the extinction of seed dispersal systems.
421 Bistable coexistence, where partners coexist stably either at low or high density,
422 depending upon if at least one population dips below a certain threshold of density, is, to

our knowledge, a novel result. Ecologically, bistable coexistence results from the dependence on plant density caused by the required transfer of pollen between conspecific plants in pollination or refuge from threats at high conspecific density in seed dispersal mutualism. Mathematically, it results from the change in concavity in the plant nullclines of both models. As a result, bistable coexistence can also occur in our germination model when seed dispersers follow a Holling Type III functional response. In such case, the animal nullcline inflects because animals consume faster at medium, compared to low or high, plant densities (Appendix A). Bistable coexistence occurs when plants have low carrying capacity (K_P) and animals have near-zero growth rate and low foraging efficiency, particularly due to low "attack rate" (a) on plants' rewards. High search times for plants ($1/a$) can cause low attack rate, potentially because the plant is not very visible to the pollinator on the landscape, or because pollinators have low preference for that plants' rewards (Valdovinos *et al.* 2013, 2016). Bistable coexistence is probably less likely to occur in natural systems than our stable coexistence or threshold effects scenarios, in which pollinators have higher a and plants have high or low K_P, respectively. However, anthropogenic perturbations leading to population decline, as well as spatial and temporal mismatches between compatible partners, may increase the occurrence of bistable coexistence.

Overall, we find that obligate mutualisms are most at risk for experiencing destabilizing thresholds, which may have cascading effects on the rest of the ecological community (Latty & Dakos 2019). The existence of thresholds suggests that environmental change could shift a pollination system from above a separatrix to below it. This will lead

445 to collapse of the system under certain conditions, but in very special cases, the system may
446 instead shift to a lower stable coexistence equilibrium, and still exhibit positive growth at
447 low density. Though this is a preferable outcome to deterministic extinction, these
448 dynamics still allow the system to reach very low population densities, and thus to be more
449 vulnerable to environmental or demographic stochasticity. However, the highly stable
450 outcomes for facultative mutualists, and particularly for facultative plants with high
451 carrying capacity, suggest that these species may buffer communities from perturbations to
452 low density in a network setting (also see van der Heide *et al.* 2020). This is because
453 mutualistic networks are typically highly nested, which means that generalist species tend
454 to interact with both generalist and specialist species but specialist species with only
455 generalists (Bascompte *et al.* 2003). Then, a nested network with generalist plants (by
456 definition facultative to each of their animal mutualists), that also have sufficiently high
457 carrying capacity, may not suffer threshold effects caused by rare, obligate animal
458 populations. In other words, those generalist plants with high carrying capacity may make
459 the network robust to potential threshold effects.

460 A unique aspect of our modelling approach is that we specify whether plants benefit
461 according to animal total or per-capita visitation rate. Our choice for pollination benefits to
462 plants to scale with animal total visitation rate accounts for outcrossing (Vázquez *et al.*
463 2005). This, to the best of our knowledge, makes our pollination model unique in the
464 literature of two-species models (but see Valdovinos *et al.* 2013, 2016, Hale *et al*. 2020 for
465 network models). In addition, visitation in our models differs from previous work (e.g.,
466 Revilla 2015) because we use nonlinear (specifically, Holling Type II) saturating functional

467 responses for consumption rate. This allows both plants and animals to experience intra-
468 specific competition for benefits, set by the maximum time animals can spend foraging on
469 rewards. We could follow previous work (Revilla 2015) and impose a direct limitation to
470 plant benefits, so that they saturate due to limited ovules or seeds (Appendix B). This does
471 not qualitatively change our results, except for the negative density-dependence seed
472 dispersal model, which displays the simpler results of our germination model (i.e., no
473 bistable coexistence).

474 Our qualitative results (Figs. 1-3) are generally robust to varying functional forms
475 from Type I (linear) to Type III (Appendix A). The exceptions are our negative density-
476 dependence seed dispersal model, in which unbounded population growth can occur when
477 dispersers follow a linear functional response, and our germination seed dispersal model
478 which has similar dynamics to our pollination model when dispersers follow a Type III
479 functional response. Our models can also accommodate functional responses interpreted as
480 "net benefit" curves (e.g., Holland *et al.* 2002, Morris *et al.* 2010) if costs and benefits
481 affect the same vital rate. That is, if "costs" simply reduce the benefits that accrue to a
482 given vital rate (e.g., Brandenburg *et al.* 2012). Under this interpretation, unimodal
483 functional forms may arise (e.g., Morris *et al.* 2010) which could lead to substantially
484 different dynamical predictions than those presented here. Another of our unique
485 assumptions is that negative density-dependence specifically reduces the potential plant
486 "births" that mature to reproductive adults. Our models exhibit qualitatively similar
487 dynamics if we instead assume that negative density-dependence limits overall per-capita
488 growth (using an additive term) as in previous works (e.g., Holland & DeAngelis 2010,

Revilla 2015). Finally, our models, as well as previous ones, assume that mutualisms have population-level impacts. Most empirical studies, however, quantify the benefits and costs of mutualisms at the individual level in terms of fitness or even by using a single proxy for fitness (Bronstein 2001, Ford *et al.* 2015). Those effects do not necessarily imply population- or community-level impacts of mutualism (Flatt & Weisser 2000, Ford *et al.* 2015). Therefore, empirical work on population dynamics of mutualisms is of foremost importance to evaluate historical and current ecological theory on mutualisms.

Conclusion

This research increased mechanistic understanding of the dynamics of plant-animal mutualisms by analyzing consumer-resource models that incorporate simple mechanisms of reproductive benefits to plants. We found that these mutualisms may be vulnerable to declines at low density due to Allee and threshold effects and identified bistable coexistence in some cases. We also characterized the ecological scenarios under which those dynamical behaviors are most likely to occur, which has been recognized a conservation priority (Latty & Dakos 2019). Future work should continue to investigate how different mechanisms of mutualism manifest in different population dynamics at low density, both to advance ecological understanding and to aid in conservation objectives.

References

Addicott, J. F. 1981. Stability properties of 2-species models of mutualism: Simulation studies. Oecologia 49:42–49.

Aslan, C. E., E. S. Zavaleta, B. Tershy, and D. Croll. 2013. Mutualism disruption Threatens global plant biodiversity: A Systematic Review. PloS ONE 8.

Bascompte, J., Jordano, P., Melian, C.J. and Olesen, J.M. 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences USA 100:9383–9387.

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 1:3-5.

Bastolla, U., M. A. Fortuna, A. Pascual-García, A. Ferrera, B. Luque, and J. Bascompte. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018-1020.

Beckman, N. G., C. E. Aslan, H. S. Rogers, O. Kogan, J. L. Bronstein, J. M. Bullock, F. Hartig, et al. 2020. Advancing an interdisciplinary framework to study seed dispersal ecology. AoB PLANTS 12:1–18.

Bronstein, J. L. 2001. The costs of mutualism. American Zoologist 41:825–839.

Bronstein, J. L. 2015. The study of mutualism. Pages 3-19 *in* J. L. Bronstein, ed. Mutualism. Oxford University Press, Oxford.

Courchamp, F., L. Berec, and J. Gascoigne 2008. Population dynamics: modelling demographic Allee effects. *In* Allee Effects in Ecology and Conservation, Oxford University Press, Oxford.

Edwards, W., M. Dunlop, and L. Rodgerson. 2006. The evolution of rewards: Seed dispersal, seed size and elaiosome size. Journal of Ecology 94:687–694.

Fishman, M. A., and L. Hadany. 2010. Plant-pollinator population dynamics. Theoretical Population Biology 78:270–277.

Flatt, T., and W. W. Weisser. 2000. The effects of mutualistic ants on aphid life. Ecology 81:3522–3529.

Ford, K. R., J. H. Ness, J. L. Bronstein, and W. F. Morris. 2015. The demographic consequences of mutualism: ants increase host-plant fruit production but not population growth. Oecologia 179:435–446.

Forsyth, S. A. 2003. Density-dependent seed set in the Haleakala silversword: Evidence for an Allee effect. Oecologia 136:551–557.

Fricke, E. C., M. J. Simon, K. M. Reagan, D. J. Levey, J. A. Riffell, T. A. Carlo, and J. J. Tewksbury. 2013. When condition trumps location: Seed consumption by fruit-eating birds removes pathogens and predator attractants. Ecology Letters 16:1031–1036.

Gause, G. F., and A. A. Witt. 1935. Behavior of mixed populations and the problem of natural selection. American Naturalist 69:596–609.

Goh, B. S. 1979. Stability in models of mutualism. American Naturalist 113:261–275.

Gómez, J. M., E. W. Schupp, and P. Jordano. 2019. Synzoochory: the ecological and evolutionary relevance of a dual interaction. Biological Reviews 94:874–902.

Hale, K. R. S., F. S. Valdovinos, and N. D. Martinez. 2020. Mutualism increases diversity, stability, and function of multiplex networks that integrate pollinators into food webs. Nature Communications 11.

Holland, J. N., and D. L. DeAngelis. 2010. A consumer-resource approach to the density-dependent population dynamics of mutualism. Ecology 91:1286–1295.

Holland, J. N., D. L. DeAngelis, and J. L. Bronstein. 2002. Population dynamics and mutualism: Functional responses of benefits and costs. American Naturalist 159:231–244.

Holland, J. N., Okuyama, T., & DeAngelis, D. L. 2006. Comment on "Asymmetric coevolutionary networks facilitate biodiversity maintenance." Science, 313:1887–1887.

Janzen, D. H. 1970. Herbivores and number of tree species in tropical forests. American Naturalist 104:501–508.

Jordano P. 2014. Fruits and frugivory. Pages 125–166 *in* R. S. Gallagher, ed. Seeds: The ecology of regeneration in plant communities. CABI, Boston.

Klein, A. M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences 274:303–313.

Kramer, A. M., B. Dennis, A. M. Liebhold, and J. M. Drake. 2009. The evidence for Allee effects. Population Ecology 51:341–354.

Latty, T., and V. Dakos. 2019. The risk of threshold responses, tipping points, and cascading failures in pollination systems. Biodiversity and Conservation 28:3389–3406.

May, R. M. 1976. Theoretical Ecology, Principles and Applications. Blackwell Scientific, Oxford.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–477.

Moore, C. M., and J. W. Dittel. 2020. On mutualism, models, and masting: The effects of seed-dispersing animals on the plants they disperse. Journal of Ecology 108:1775–1783.

Morris, W. F., D. P. Vázquez, and N. P. Chacoff. 2010. Benefit and cost curves for typical pollination mutualisms. Ecology 91:1276–1285.

Neuschulz, E. L., T. Mueller, M. Schleuning, and K. Böhning-Gaese. 2016. Pollination and seed dispersal are the most threatened processes of plant regeneration. Scientific Reports 6:6–11.

Okuyama, T., and J. N. Holland. 2008. Network structural properties mediate the stability of mutualistic communities. Ecology Letters 11:208–216.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos 120:321–326.

Pierce, N. E., and W. R. Young. 1986. Lycaenid butterflies and ants: Two-species stable equilibria in mutualistic, commensal, and parasitic Interactions. American Naturalist 128:216–227.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: Trends, impacts and drivers. Trends in Ecology and Evolution 25:345–353.

Potts, S. G., V. Imperatriz-Fonseca, H. T. Ngo, M. A. Aizen, J. C. Biesmeijer, T. D. Breeze, L. v. Dicks, et al. 2016. Safeguarding pollinators and their values to human well-being. Nature 540:220–229.

Revilla, T. A. 2015. Numerical responses in resource-based mutualisms: A time scale approach. Journal of Theoretical Biology 378:39–46.

Schupp, E. W., P. Jordano, and J. M. Gómez. 2017. A general framework for effectiveness concepts in mutualisms. Ecology Letters 20:577–590.

Soberón, J. M., and C. Martinez del Rio. 1981. The dynamics of a plant-pollinator interaction. Journal of Theoretical Biology 91:363–378.

Stachowicz, J. J. 2001. The structure of ecological communities. BioScience 51:235–246.

Traveset, A. and Richardson, D. M. 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology and Evolution 21:208–216.

Traveset, A. and Richardson, D. M. 2014. Mutualistic interactions and biological invasions. Annual Review of Ecology, Evolution, and Systematics 45:89–113.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Valdovinos, F. S. 2019. Mutualistic networks: moving closer to a predictive theory. Ecology Letters 22:1517–1534.

Valdovinos, F.S., Moisset de Espanes, P., Flores, J.D. & Ramos-Jiliberto, R. 2013. Adaptive foraging allows the maintenance of biodiversity of pollination networks. Oikos 122:907–917.

Valdovinos, F. S., B. J. Brosi, H. M. Briggs, P. Moisset de Espanés, R. Ramos-Jiliberto, and N. D. Martinez. 2016. Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. Ecology Letters 19:1277–1286.

Valdovinos, F.S., and Marsland, R. 2021. Niche theory for mutualism: A graphical approach to plant-pollinator network dynamics. American Naturalist 197:393–404.

Van der Heide, T., C. Angelini, J. de Fouw, and J. S. Eklöf. 2021. Facultative mutualisms: A double-edged sword for foundation species in the face of anthropogenic global change. Ecology and Evolution 11:29–44.

Vandermeer, J. H., and D. H. Boucher. 1978. Varieties of mutualistic interaction in population models. Journal of Theoretical Biology 74:549–558.

620 Vandermeer, J. H., and Goldberg, D. E. 2013. Pages 225-238 *in* Population ecology: First
621 principles. Princeton University Press, Princeton.

622 Vázquez, D. P., W. F. Morris, and P. Jordano. 2005. Interaction frequency as a surrogate
623 for the total effect of animal mutualists on plants. Ecology Letters 8:1088-1094.

624 Wells, H. 1983. Population equilibria and stability in plant-animal pollination systems.
625 Journal of Theoretical Biology 100:685–699.

626 Whittaker, R. H. 1975. Communities and Ecosystems. 2d ed. Macmillan, New York.

627 Willmer, P. 2011. Pollination and Floral Ecology. Princeton University Press, Princeton.

628 Wolin, C. L., and L. R. Lawlor. 1984. Models of facultative mutualism: Density effects.
629 American Naturalist 124:843–862.

630 Wolin, C.L. 1985. The population dynamics of mutualistic systems. Pages *in* 248–269. D.
631 H. Boucher, ed. The Biology of Mutualism. Oxford University Press, Oxford.

632 Wotton, D. M., and D. Kelly. 2011. Frugivore loss limits recruitment of large-seeded trees.
633 Proceedings of the Royal Society B: Biological Sciences 278:3345–3354.

634 Wright, D. H. 1989. A simple, stable model of mutualism incorporating handling time.
635 American Naturalist 134:664–667.

636 Zhou, Y., C. Newman, J. Chen, Z. Xie, and D. W. Macdonald. 2013. Anomalous, extreme
637 weather disrupts obligate seed dispersal mutualism: Snow in a subtropical forest ecosystem.
638 Global Change Biology 19:2867–2877.

639

Legends

Figure 1.

Phase plane diagrams for plant-pollinator mutualisms. Nullclines are curves of zero growth for plant (green) or animal pollinator (black) populations. Equilibria (dots) occur at the intersection of plant and animal nullclines. Filled black equilibria are stable attractors, filled red equilibria are unstable repellers, and hollow equilibria are half-stable saddle points. Arrows show the directions of population change for plants (x-axis) and animals (y-axis), with lighter colors indicating a faster rate of change. Dynamics depend upon the parameterization of the model and whether plants and animals are obligate (O) or facultative (F) mutualists (rows). When plants are obligate (**A, B**), they experience Allee effects at low density (dark red shaded region). Plants cannot attract sufficient pollinator visitation to support their own population growth, leading to collapse. When either plants or animals are obligate, both partners experience threshold effects (light red shaded region). Below the threshold marked by the separatrix (dashed line), one population's density is too low to support its partner's growth, resulting in system collapse to extinction (**A**), animal-only persistence at $K_A = (b_A - d_A)/s_A$ (**B**), or plant-only persistence at $K_P = (b_P g - d_P)/b_P g s_P$ (**D**). Thus, depending upon the initial densities of both partners, the mutualism may persist stably or collapse. When one partner is facultative, stable coexistence may be the only outcome (**C, E, G**). However, in a small parameter space, bistable coexistence may occur (**D, F**). Here, the separatrix divides the region in which the system will be attracted to the low- or high-density stable coexistence equilibrium, depending upon whether initial densities are below or above the separatrix, respectively. Parameter values are fixed to the

following: $a = 0.6, h = 0.75$; plants: $\beta = 2, g = 0.8, s_P = 0.15$; obligate: $b_P = 0.3, d_P = 2.2$; facultative: $b_P = 2, d_P = 1$; animals: $\varepsilon = 1, d_A = 1.5$; obligate: $b_A = 1.2, s_A = 0.11$; facultative animals: $b_A = 2, s_A = 0.2$; except for: (**B**) $a = 0.4$, (**C**) $h = 0.5, \beta = 1, d_P = 1.4, b_A = 0.7, s_A = 0.07$, (**D**) $a = 0.05, b_P = 0.1, d_P = 0.05, g = 0.55, \beta = 0.55, s_P = 0.25, b_A = 0.19, d_A = 0.2, s_A = 0.05$, (**F**) $a = 0.014, b_P = 0.19, d_P = 0.11, g = 0.6, \beta = 0.55, s_P = 0.1, b_A = 0.18, \varepsilon = 2.5, d_A = 0.15, s_A = 0.04$, (**G**) $a = 0.4$.

Figure 2.

Phase plane diagrams for plant seed-disperser mutualisms, where animals reduce negative density-dependence in plants. Nullclines are curves of zero growth for plant (green) and animal seed-disperser (black) populations. Here, plants must be able to persist at low density ($K_P = (b_P g - d_P)/b_P g s_P > 0$) to benefit from reductions in negative density-dependence; therefore, we consider only facultative plant populations. All other formatting and terminology follow Fig. 1. When animals are obligate mutualists (**A**), both partners may experience threshold effects. Otherwise, both partners experience growth from low density (**B, C, D, E**), resulting in either a single (**C, E**) or two (bi)stable (**B, D**) coexistence equilibria. Parameter values are fixed to the following: $a = 1, h = 0.5$; plants: $b_P = 1, g = 1, s_P = 0.2, \sigma = 0.15, d_P = 0.4$; animals: $\varepsilon = 1$; obligate: $b_A = 1, d_A = 2, s_A = 0.15$; facultative: $b_A = 2$; except for: (**A**) $g = 0.6, \sigma = 0.2$, (**B**) $g = 0.5, a = 0.36, b_A = 1.75, s_A = 0.12$; (**D**) $g = 0.45, \sigma = 0.175, s_A = 0.12, d_A = 1.75$; (**E**) $\varepsilon = 0.5$, $s_A = 0.2$, $d_A = 1.5$.

Figure 3.

Phase plane diagrams for plant seed-disperser mutualisms, where animals increase seed germination in plants. Nullclines are curves of zero growth for plant (green) and animal seed-disperser (black) populations. Dynamics depend upon the parameterization of the model and whether plants and animals are obligate (O) or facultative (F) mutualists (rows). When either partner is an obligate mutualist, both partners may experience threshold effects (**A, B, D**). When either partner is a facultative mutualist, the system may instead exhibit a single coexistence equilibrium with growth from low density for both partners (**C, E, F**). Parameter values are fixed to the following: $a = 1, h = 0.5$; plants: $b_P = 1, g = 0.5, \gamma = 0.5, s_P = 0.1$; obligate: $d_P = 1$; animals: $b_A = 1, \varepsilon = 1$; obligate: $s_A = 0.1, d_A = 1.4$; facultative: $s_A = 0.2, d_A = 0.2$; except for: (**A**) $s_A = 0.15$; (**B**) $s_P = 0.2, d_P = 1.6$, $d_A = 0.9$; (**C**) $a = 0.5$, $g = 1$; (**D**) $a = 0.5$, $s_P = 0.17, d_P = 0.4$; (**E**) $h = 1, d_P = 0.2$; (**F**) $h = 1, d_P = 0.3, \varepsilon = 0.8$.

Figures and Tables

Figure 1.

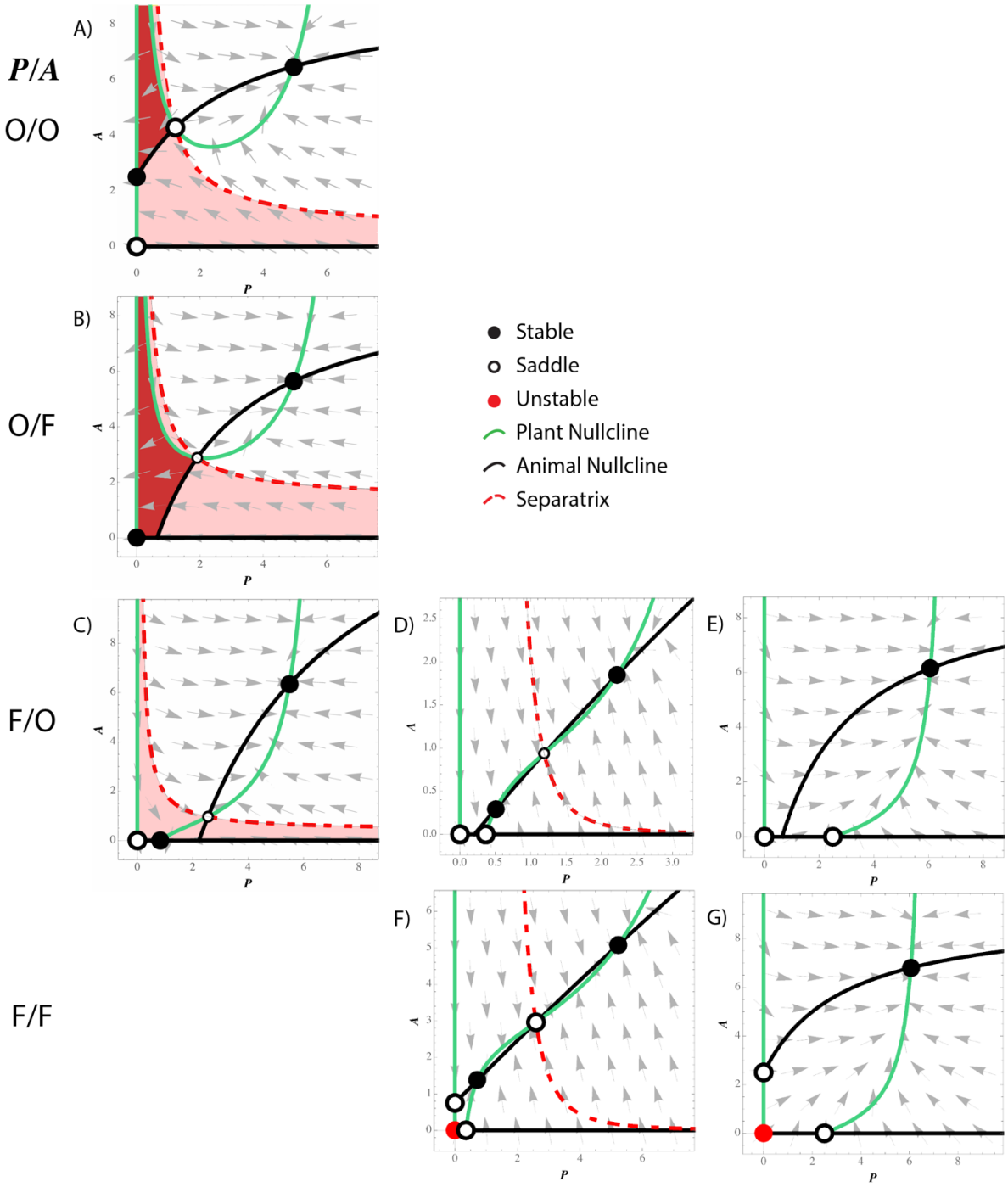


Figure 2.

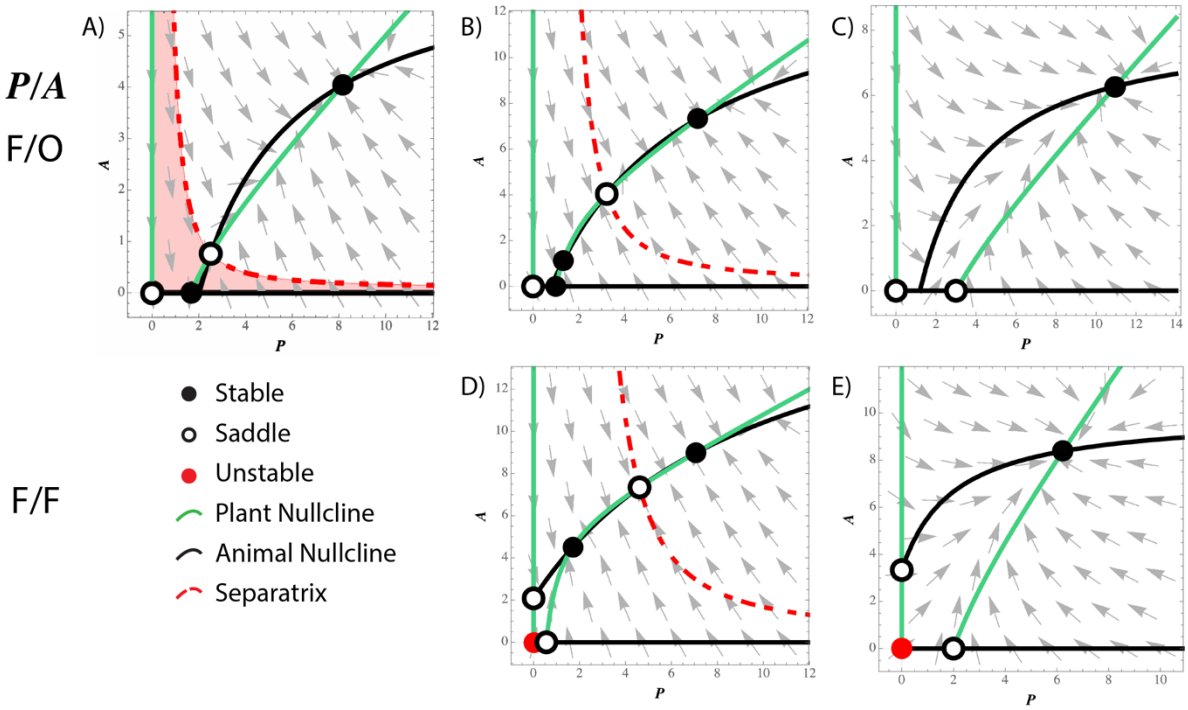

A)
B)
C)
D)
E)
P/A
F/O
F/F
Stable
Saddle
Unstable
Plant Nullcline
Animal Nullcline
Separatrix
P
A

Figure 3.

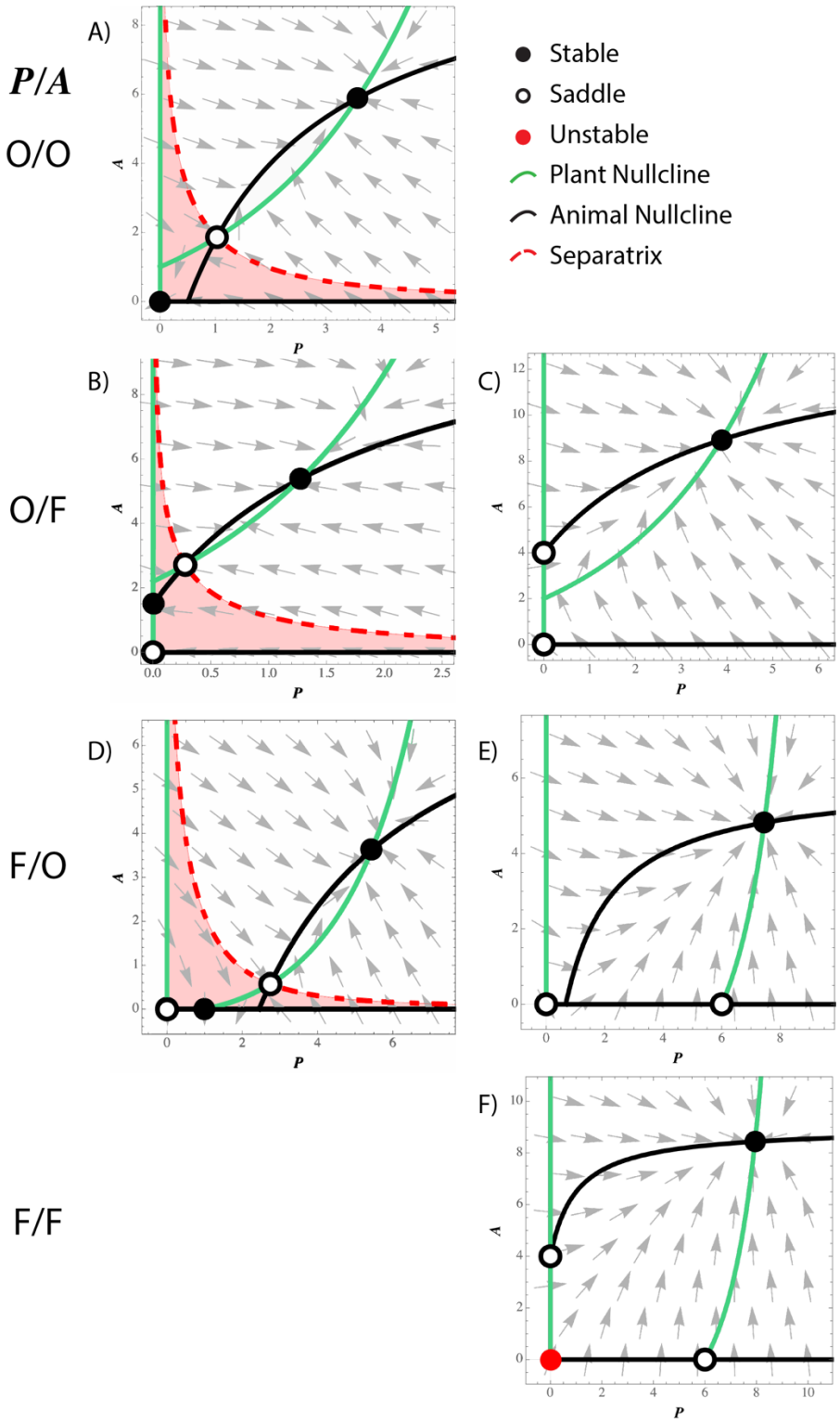

P/A
O/O
O/F
F/O
F/F
A)
B)
C)
D)
E)
F)
Stable
Saddle
Unstable
Plant Nullcline
Animal Nullcline
Separatrix
P
A

Table 1. Table of parameters.

Parameter	**Interpretation**	**Units**
a	Per-plant attack rate on rewards	$[P^{-1}\ t^{-1}]$
b_i	Per-capita birth or seed production rate	$[t^{-1}]$
β	Per-animal seed set	$[A^{-1}]$
d_i	Per-capita death rate	$[t^{-1}]$
ε	Efficiency of converting food rewards to animal offspring	*Unitless*
g	Per-plant seed germination	*Unitless*
γ	Seed germination per animal visitation rate	$[A^{-1}\ P\ t]$
h	Handling time on rewards	$[t]$
s_i	Negative density-dependence due to, e.g., intraspecific competition, Janzen-Connell effect	s_P: $[P^{-1}]$ or s_A: $[A^{-1}\ t^{-1}]$
σ	Reduced negative density-dependence per animal visitation rate	$[A^{-1}\ t]$

All parameters are assumed to be positive (> 0). The units A, P, and t refer to animal density, plant density, and time, respectively. Subscript i is used to specify the parameter for the plant (P) or animal (A) population. We use Greek letters (β, ε, γ, σ) to indicate conversion coefficients for benefits due to mutualism, while Roman letters (a, b, d, g, h, s) indicate plant and animal demographic and feeding parameters.

Appendix A: Mathematical Analysis

In all three of our models (Eqns. 3, 6, 7), plant and animal populations have "trivial" nullclines: $\overline{\boldsymbol{P}} = 0$, a vertical line along the y-axis, and $\overline{\boldsymbol{A}} = 0$, a horizontal line along the x-axis. The intersection of both species' trivial nullclines gives a trivial extinction equilibrium ($\overline{\boldsymbol{P}} = 0,\ \overline{\boldsymbol{A}} = 0$) in every model. The animal population, $\boldsymbol{A}$, follows the same dynamic equation (Eqn. 1) in all of our models and thus has the same nontrivial nullclines (hereafter, simply "nullclines").

The animal nullcline (Figs. 1-3, black) is a concave down, increasing function that saturates with respect to its partner's abundance:

$$\overline{\boldsymbol{A}} = \frac{r_A}{s_A} + \frac{\varepsilon}{s_A}\frac{a\boldsymbol{P}}{(1+ah\boldsymbol{P})}. \qquad \text{Eqn. A1}$$

Eqn. A1 describes the balance between negative density-dependence, benefit from mutualism, and intrinsic growth or decay for facultative or obligate animal populations, respectively. When $\boldsymbol{A} > \overline{\boldsymbol{A}}$, negative density-dependence is stronger than benefit from mutualism and/or intrinsic growth, causing $\boldsymbol{A}$ to decrease. When $\boldsymbol{A} < \overline{\boldsymbol{A}}$, negative density-dependence is weaker and $\boldsymbol{A}$ increases.

The benefit of mutualism to $\boldsymbol{A}$ is $\frac{\varepsilon}{s_A}\frac{a\boldsymbol{P}}{(1+ah\boldsymbol{P})}$, which saturates with respect to plant density. As plant density becomes extremely high, $\boldsymbol{A}$ saturates to a higher value than it could achieve in the absence of its partner:

$$\lim_{P\to\infty} \bar{A} = \frac{r_A}{s_A} + \frac{\varepsilon}{s_A h}. \qquad \text{Eqn. A2}$$

This horizontal asymptote is an upper bound on the density of $\boldsymbol{A}$. When $\boldsymbol{A}$ is facultative ($r_A > 0$), its nullcline intersects the y-axis in the ecological region (positive quadrant) at

$$\overline{\boldsymbol{A}}_{0,y} = \frac{r_A}{s_A} = K_A. \qquad \text{Eqn. A3}$$

This is animal density in the absence of plants; we call it the carrying capacity (K_A). All else being equal, decreasing r_A pushes the visible part of the animal nullcline down so that when the animal population is obligate ($r_A \leq 0$), its nullcline intersects the y-axis at zero or negative values (not shown). The animal nullcline intersects the x-axis in the positive quadrant at

$$\overline{\boldsymbol{A}}_{x,0} = \frac{-r_A}{a(\varepsilon + hr_A)}. \qquad \text{Eqn. A4}$$

When the animal population is obligate, this intersection occurs in the positive quadrant, whereas when the animal population is facultative, the intersection occurs at negative values of the plant population.

The equation for the nullcline of animal-pollinated plants (Fig. 1, green) is:

$$\boldsymbol{A} = \frac{(b_P g s_P \overline{\boldsymbol{P}} - r_P)(1 + ah\overline{\boldsymbol{P}})}{\beta a g (1 - s_P \overline{\boldsymbol{P}})\overline{\boldsymbol{P}}}. \qquad \text{Eqn. A5}$$

When plants are obligate ($r_P = b_P g - d_P \leq 0$, Fig. 1a-b), the nullcline is a U-shape bounded by vertical asymptotes at $\boldsymbol{P} = 0$ and $\boldsymbol{P} = 1/s_P$. Note that the asymptote $\boldsymbol{P} = 1/s_P$ represents the plant's maximum population density. When plants are facultative ($r_P > 0$, Fig. 1c-g), the nullcline is concave up at high density and keeps increasing asymptotically towards its maximum, $\boldsymbol{P} = 1/s_P$. At low density, the nullcline is concave down, though

this may not be visible in the ecological region of the plane (positive quadrant). Its x-intercept is

$$\overline{\boldsymbol{P}}_{x,0} = \frac{r_P}{b_P g s_P} = K_P > 0. \qquad \text{Eqn. A6}$$

This is plant density in the absence of animals; we call it the carrying capacity (K_P). Inside the U or to the left of the nullcline, plant density increases; to the right or under, plant density decreases due to strong negative density-dependence.

The equation for the nullcline of animal-dispersed plants that benefit through reduced negative density-dependence (Fig. 2, green) is:

$$\boldsymbol{A} = \frac{(b_P g s_P \overline{\boldsymbol{P}} - r_P)(1 + a h \overline{\boldsymbol{P}})}{b_P g \sigma a \overline{\boldsymbol{P}}}. \qquad \text{Eqn. A7}$$

At high plant density, the nullcline has a linear slope of $\frac{h s_P}{\sigma} \geq h$. At low plant density, the nullcline is concave down, bounded on the left side by a vertical asymptote at $\boldsymbol{P} = 0$. Because we consider only facultative plants for this mutualism ($r_P > 0$), the nullcline always has an x-intercept visible in the ecological region at

$$\overline{P}_{x,0} = \frac{r_P}{b_P g s_P} = K_P > 0. \qquad \text{Eqn. A8}$$

The equation for the nullcline of animal-dispersed plants that benefit through germination (Fig. 3, green) is:

$$\boldsymbol{A} = \frac{(b_P g s_P \overline{\boldsymbol{P}} - r_P)(1 + a h \overline{\boldsymbol{P}})}{b_P \gamma a (1 - s_P \overline{\boldsymbol{P}})}. \qquad \text{Eqn. A9}$$

In the ecological region, the nullcline is an increasing, concave up curve. At high plant density, the nullcline has a vertical asymptote at $\boldsymbol{P} = 1/s_P$, the maximum plant density in the presence of animal mutualists. At low plant density, the nullcline is concave down, bounded on the left side by a vertical asymptote at $\boldsymbol{P} = 0$. The nullcline intersects the x-axis at

$$\overline{\boldsymbol{P}}_{x,0} = \frac{r_P}{b_P g s_P} = K_P \qquad \text{Eqn. A10}$$

which is visible in the ecological region when plants are facultative ($r_P > 0$). It intersects the y-axis at

$$\overline{\boldsymbol{P}}_{0,y} = \frac{-r_P}{b_P \gamma a} \qquad \text{Eqn. A11}$$

which is visible in the ecological region when plants are obligate ($r_P \leq 0$).

Feasibility

All our models are structurally unstable (Rohr *et al*. 2014), such that smooth transitions in parameter values shift the nontrivial nullclines (hereafter, "nullclines") so that they may intersect in various ways or even fail to intersect, with different dynamical outcomes for each case (Fig. A1). In the main text, we focused on "feasible" systems, that is, where coexistence of the partners with non-negative density (i.e. in the ecological region) was possible. There are many parameterizations that lead to feasibility, but it is not easy to provide an ecological interpretation for the conditions to achieve them. Here, we enumerate the geometric conditions that lead to feasibility by describing the required positioning of the nullclines.

There are four cases for how the plant and animal nullclines intersect:

(1) If the nullclines never intersect (e.g., Fig. A1A, A1E), then coexistence is not possible.

(2) If the nullclines intersect exactly once (e.g., Fig. A1B, A1F), this is an ecologically unlikely case that we neglect.

(3) If the nullclines intersect twice with at least one intersection in the ecological region (e.g., Fig. A1C-D, A1G-J), then coexistence is feasible. The low-density equilibrium is a saddle point while the high-density equilibrium is stable (e.g., Fig. A1C, A1G, A1H). When only one intersection occurs in the ecological region, it is the stable coexistence equilibrium (e.g., Fig. A1D, A1J).

(4) If the nullclines intersect three times in the ecological region (e.g., Fig. B1I), then coexistence is feasible. The low- and high-density equilibria are stable ("bistable coexistence") and the intermediate equilibrium is a saddle point. Bistable coexistence appears to only occur when at least one nullcline changes concavity in the ecological region. Our main-text models display bistable coexistence because their nullclines change from concave up to concave down (pollination, Figs. 1D, 1F) or from concave down to linear growth (seed dispersal, Figs. 2B, 2D). However, bistability can more generally result from Type III functional responses in facultative mutualists.

Functional Forms

To understand the robustness of our results, we analyzed our models using Holling Type I and III functional forms in addition to the saturating Holling Type II forms presented in the main text (Table B1, Figs. B1-B3).

References

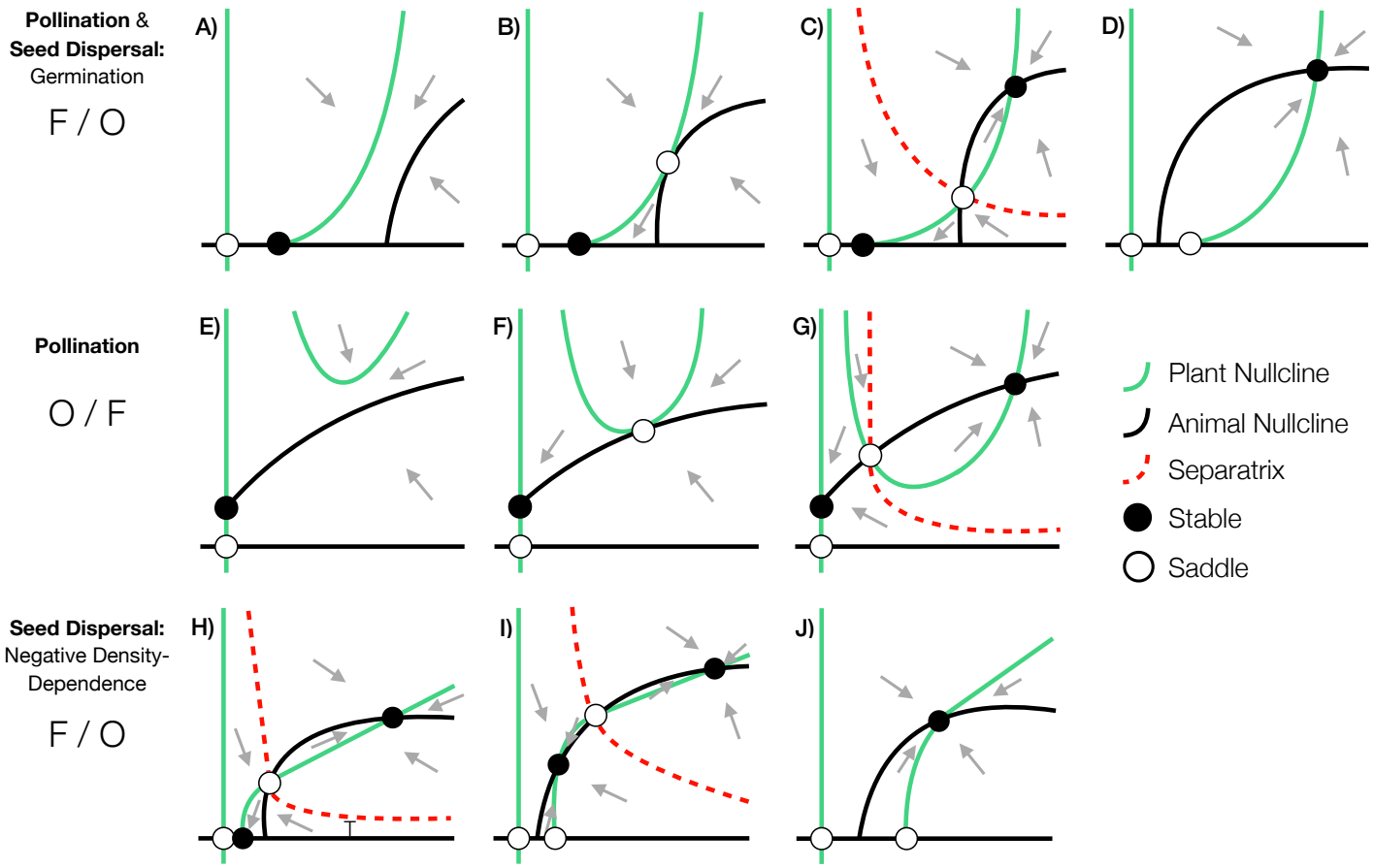
Rohr, R. P., S. Saavedra, and J. Bascompte. 2014. On the structural stability of mutualistic systems. Science 345(6195):1–9.

Table A1. Functional forms

Reproductive Services	**Type I**	**Type II**	**Type III**
Pollination $S = C_R$	$\boldsymbol{AP}$	$\frac{a\boldsymbol{AP}}{1 + ah\boldsymbol{P}}$	$\frac{a\boldsymbol{AP}^2}{1 + ah\boldsymbol{P}^2}$
Seed Dispersal $S = C_R/\boldsymbol{P}$	$\boldsymbol{A}$	$\frac{a\boldsymbol{A}}{1 + ah\boldsymbol{P}}$	$\frac{a\boldsymbol{AP}}{1 + ah\boldsymbol{P}^2}$

Expressions for Holling Type I-III functional forms used to model reproductive services (S) and consumption rate (C_R) in our pollination (Eqns. 1 & 2) and seed dispersal models: reduced negative density-dependence (Eqns. 1 & 4), increased germination (Eqns. 1 & 5). Because reproductive services (S) provided animals are a function of their consumption rate on plant rewards (C_R), only one functional form needs to be specified. Pollination services are assumed to be equal to total consumption rate, while seed dispersal services (both germination and negative density-dependence) are assumed to be equal to per-capita consumption rate.

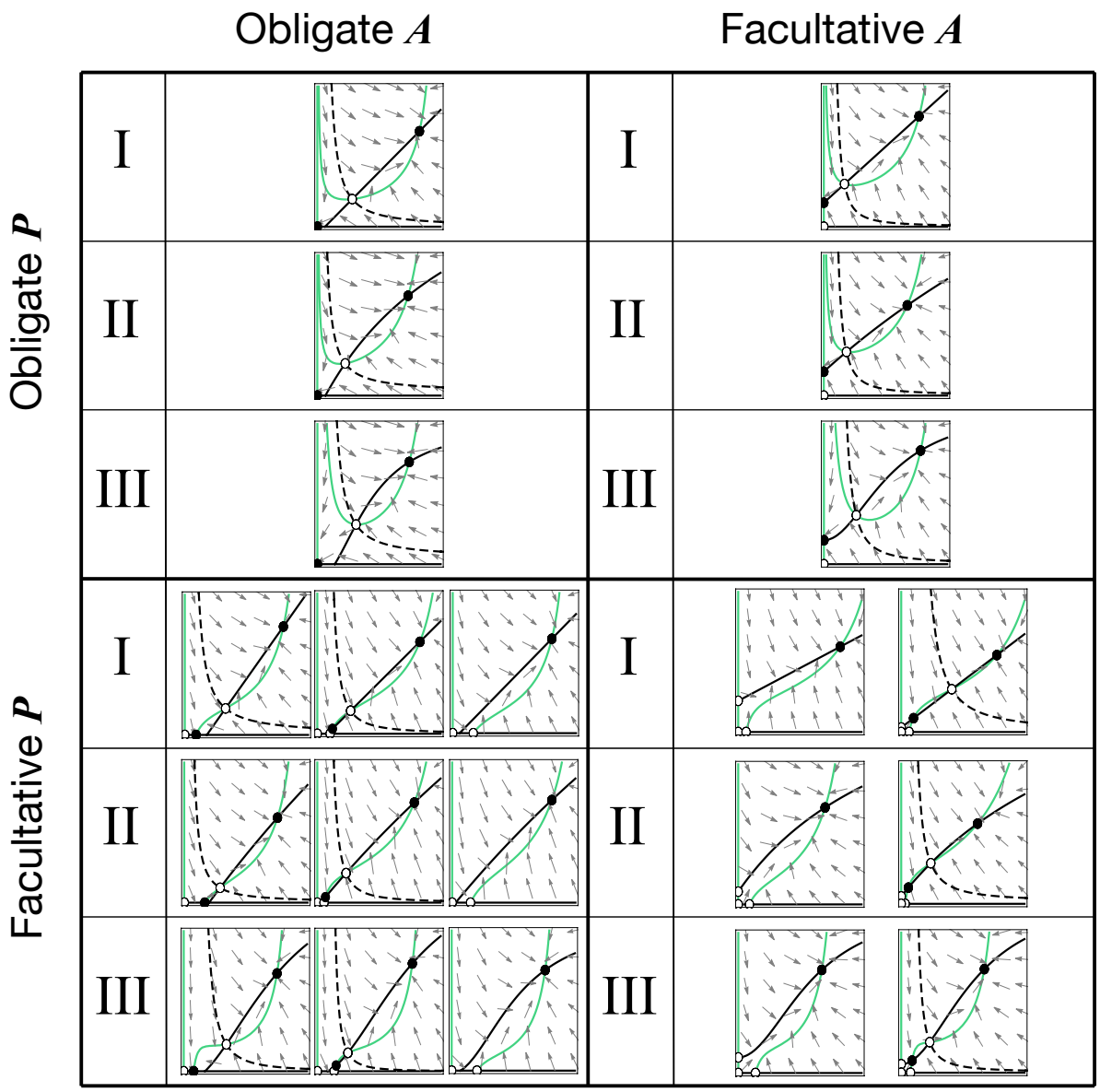
Figure A1.



Examples of structural instability. Phase plane diagrams illustrating smooth transitions from infeasible to feasible coexistence (from left to right panels within a row). Labels for each row identify the relevant models and Plants / Animals as obligate (O) or facultative (F). (**A-D**) The ***A*** nullcline shifts smoothly to the left, due to, for example, increasing conversion efficiency (ε). This moves the system

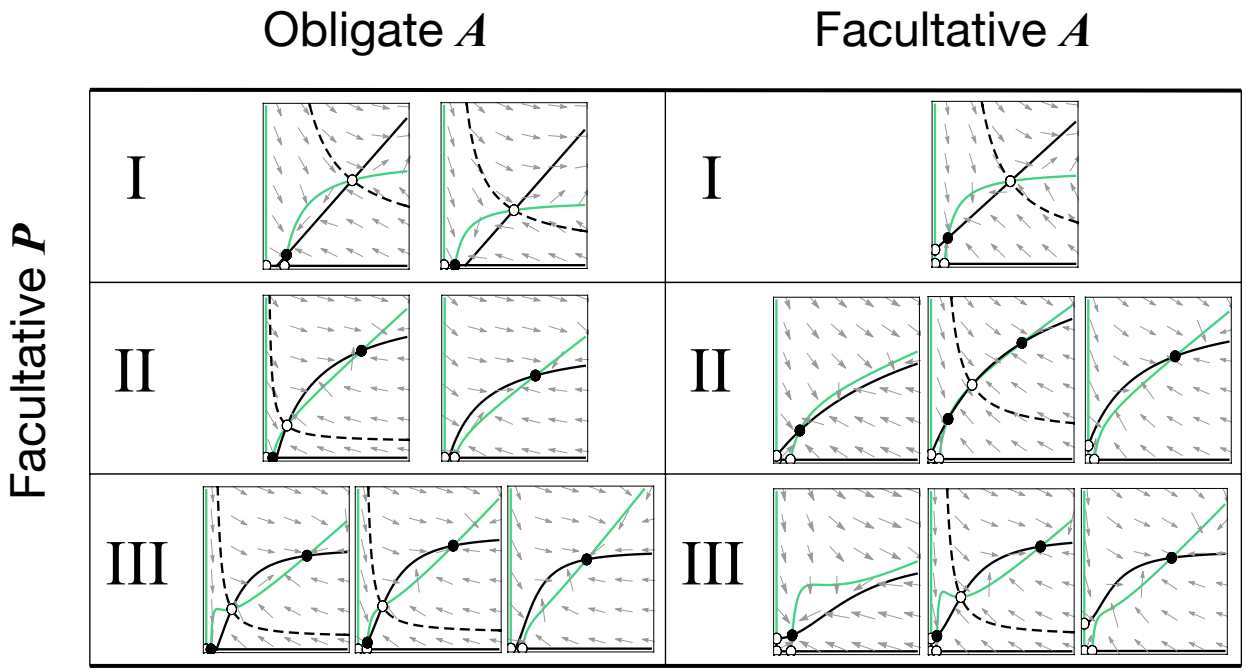
from (**A**) infeasible, to (**B**) ecologically unlikely, through a "blue sky" bifurcation in which (**C**) coexistence is feasible and stable but will not occur if species' initial densities fall below a threshold, to (**D**) guaranteed stable coexistence. This type of structural instability occurs in both our pollination model when plants are facultative and in our seed dispersal: germination benefits model. (**E-G**) The vertex of the ***P*** nullcline shifts smoothly down, due to, for example, increasing partner quality (β). This moves the system from (**E**) infeasible, to (**F**) ecologically unlikely, through a blue-sky bifurcation in which (**G**) coexistence is feasible and stable but threshold and Allee effects are present. (**H-J**) The ***P*** nullcline shifts smoothly to the right, due to, for example, decreasing negative density-dependence (s_P). This moves the system from infeasible (not shown), to ecologically unlikely (not shown), through a blue-sky bifurcation in which (**H**) coexistence is feasible and stable but threshold effects are present, to (**I**) bistability in which stable coexistence is guaranteed but occurs either at a low- or high-density equilibrium, to (**J**) guaranteed stable coexistence. This type of structural instability occurs in both our seed dispersal model (shown) and in our pollination model when plants are facultative (not shown).

Figure A2.



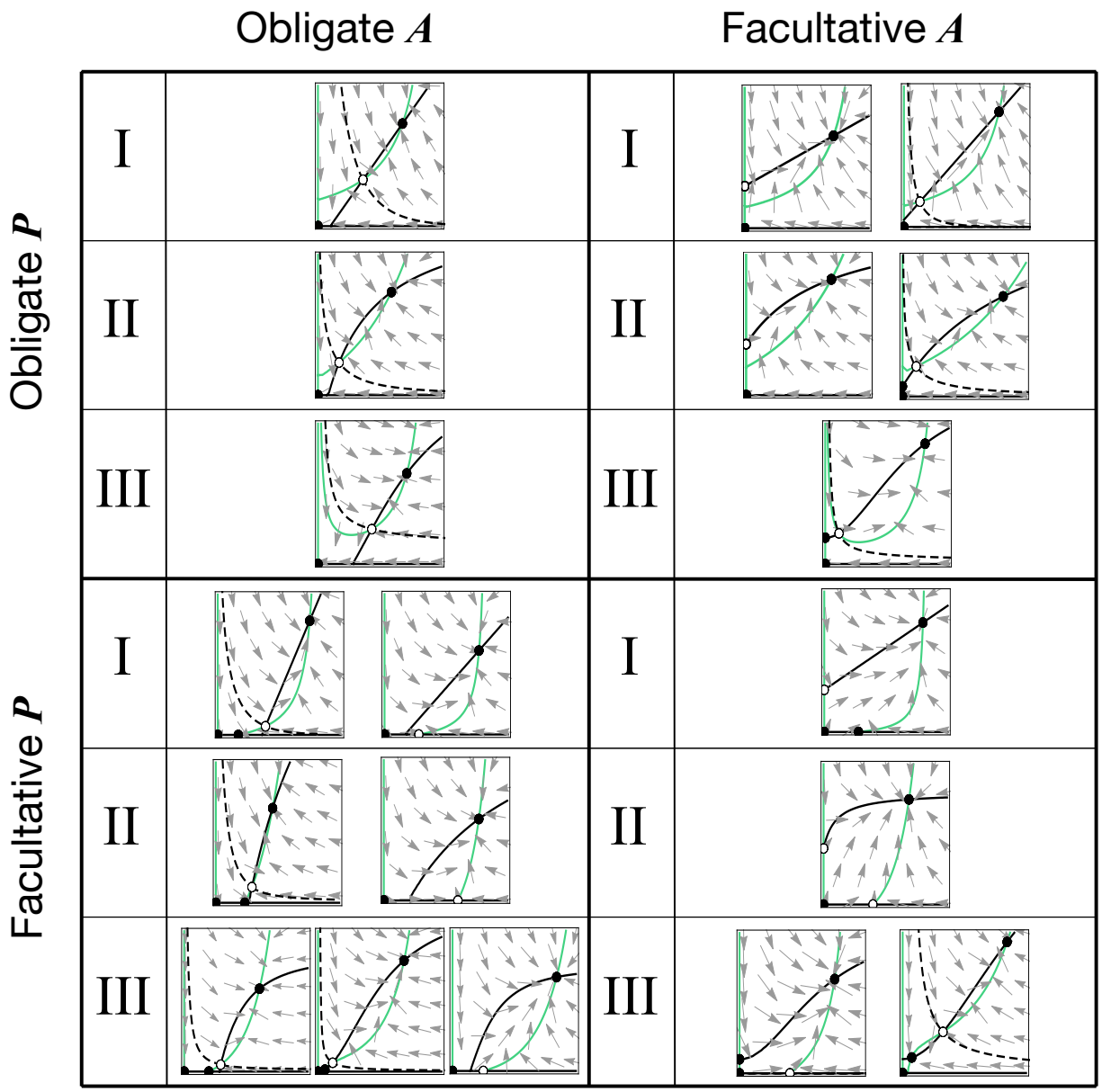
Effect of functional form on pollination mutualisms. Panels show phase plane diagrams with unique dynamical outcomes when each partner population (***P***, green; ***A***, black) is an obligate or facultative mutualist following a Holling Type I, II, or III functional response (Table A1). Equilibria are stable (filled, black) or unstable or saddle points (hollow). Saddle points are bisected by a separatrix (dashed black line) that divides the plane into two regions.

Figure A3.



Effect of functional form on seed dispersal mutualisms that reduce negative density-dependence in plants. Formatting follows figure A2.

Figure A3.



Effect of functional form on seed dispersal mutualisms that increase germination in plants. Formatting follows figure A2.

Appendix B: Saturating Services

In our main text, benefits to plants saturate indirectly, due to the limited time available for animals to forage upon rewards. In natural systems, benefits also saturate directly in terms of the number of flowers available to be fertilized, seeds available to germinate, etc. We can ensure this by writing benefit as a saturating function of reproductive services $S/(1+S)$. However, simpler models are desirable both for analytical tractability and because they can perform sufficiently or even better than more complicated models when confronted with messy or ecologically constrained data reflective of natural systems (Novak & Stouffer 2020). Indeed, our pollination and germination models retain identical qualitative dynamics when modeling plant benefit with saturating services, though our negative density-dependence model exhibits simpler dynamics that are qualitatively like the germination model. For this reason, we presented the simpler models in the main text, but we derive the more detailed models below. The more detailed approach allows more specific parameter defintions that may be easier to measure empirically.

For plant populations ($\boldsymbol{P}$), we define b_P as per-capita seed set, d_P as the per-capita death rate, and s_P as negative density-dependence in the absence of mutualism. We assume that negative density-dependence limits the seeds that survive and mature to reproductive adults, due to, e.g., the Janzen-Connell effect and seed competition for recruitment. Additionally, we assume that plant reproduction is limited by the fraction of flowers that can be fertilized through wind pollination or selfing ($0 \leq f \leq 1$) and the fraction of seeds that can germinate ($0 \leq g \leq 1$) even when subjected to low negative density-dependence. Reproductive services (S) from animals increase the density of mature (reproductive) plant individuals by pollinating flowers (φ),

improving germinability (γ), or providing refuge from seed predation and other sources of density-dependent mortality during recruitment (σ).

When animals pollinate flowers by transferring pollen between them (reproductive services, S), the fraction of flowers that are pollinated (f) can increase in the presence of animals to a maximum of $f + \varphi \leq 1$. We can then model animal-pollinated plant population dynamics ($\boldsymbol{P}$) as

$$\frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[b_P(f + \varphi\frac{S}{1+S})g(1 - s_P\boldsymbol{P}) - d_P\right] \qquad \text{Eqn. B1}$$

where benefit from pollination services (S) saturates as the fraction of flowers that are pollinated approaches its maximum. As in the main text, we assume $S = C_R$, total foraging rate of animals on plant rewards. Using a Holling Type II functional response for C_R and simplifying the algebra yields:

$$\begin{cases} \frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[b_P(f + \varphi\frac{a\boldsymbol{AP}}{1+ah\boldsymbol{P}+a\boldsymbol{AP}})g(1 - s_P\boldsymbol{P}) - d_P\right] \\ \frac{d\boldsymbol{A}}{dt} = \boldsymbol{A}\left[b_A + \varepsilon\frac{a\boldsymbol{P}}{1+ah\boldsymbol{P}} - s_A\boldsymbol{A} - d_A\right] \end{cases} \qquad \text{Eqn. B2}$$

In this specific form of the model, plant benefits are limited both by the fraction of flowers available to pollinate (φ) and by pollinators' handling time on flowers (h).

Similarly, when animals rescue seeds from predators, pathogens, and intraspecific competition by transporting them away from parent trees dispersal services, negative density-dependence (s) can be reduced to a minimum of $s - \sigma \geq 0$ in the presence of animals. Modeling this yields:

$$\frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[b_P f g\left(1 - \left(s - \sigma\frac{S}{1+S}\right)\boldsymbol{P}\right) - d_P\right] \qquad \text{Eqn. B3}$$

When animals increase germinability of seeds by masticating and/or digesting fruits (reproductive services, S), the fraction of seeds that germinate (g) can increase in the presence of animals to a maximum of $g + \gamma \leq 1$. Modeling this yields:

$$\frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[b_P f(g + \gamma \frac{S}{1+S})(1 - s_P \boldsymbol{P}) - d_P\right] \qquad \text{Eqn. B4}$$

As in the main text, we assume $S = C_R/\boldsymbol{P}$, per-plant foraging rate of animals on plant rewards, for both seed dispersal models. Using a Holling Type II functional response for C_R and simplifying the algebra yields our specific model for escape from negative density-dependence in animal seed-dispersal mutualisms:

$$\begin{cases} \frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[b_P f g\left(1 - \left(s_P - \sigma \frac{a\boldsymbol{A}}{1+ah\boldsymbol{P}+a\boldsymbol{A}}\right)\boldsymbol{P}\right) - d_P\right] \\ \frac{d\boldsymbol{A}}{dt} = \boldsymbol{A}\left[b_A + \varepsilon \frac{a\boldsymbol{P}}{1+ah\boldsymbol{P}} - s_A \boldsymbol{A} - d_A\right] \end{cases} \qquad \text{Eqn. B5}$$

and for increased germinability in animal seed-dispersal mutualisms:

$$\begin{cases} \frac{d\boldsymbol{P}}{dt} = \boldsymbol{P}\left[b_P f(g + \gamma \frac{a\boldsymbol{A}}{1+ah\boldsymbol{P}+a\boldsymbol{A}})(1 - s_P \boldsymbol{P}) - d_P\right] \\ \frac{d\boldsymbol{A}}{dt} = \boldsymbol{A}\left[b_A + \varepsilon \frac{a\boldsymbol{P}}{1+ah\boldsymbol{P}} - s_A \boldsymbol{A} - d_A\right] \end{cases} \qquad \text{Eqn. B6}$$

In these specific forms, plant benefits are limited both by the fraction of seeds available to germinate (γ) or the negative density-dependent effects to reduce (σ) and by dispersers' handling time on rewards (h).