

1       **Ecological theory of mutualism: Models generalizing across different mechanisms**

2                   Kayla R. S. Hale<sup>1\*</sup>, Daniel P. Maes<sup>1,2</sup>, & Fernanda S. Valdovinos<sup>1,3\*</sup>

3       <sup>1</sup> Department of Ecology and Evolutionary Biology, University of Michigan, Biological  
4       Sciences Building, 1105 North University Ave, Ann Arbor, MI 48109, USA.

5       <sup>2</sup> Department of Mathematics, University of Michigan, East Hall, 530 Church St, Ann  
6       Arbor, MI 48109, USA.

7       <sup>3</sup> Department of Environmental Science and Policy, University of California, Davis,  
8       Wickson Hall, One Shields Avenue, Davis, CA 95616.

9       The authors wish to be identified to the reviewers.

10      \*Corresponding authors; email: [kaylasal@umich.edu](mailto:kaylasal@umich.edu), [fvaldovinos@ucdavis.edu](mailto:fvaldovinos@ucdavis.edu)

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31 **Abstract**

32 Mutualisms are ubiquitous in nature, provide important ecosystem services, and  
33 involve many species of interest for conservation. Theoretical progress on the population  
34 dynamics of mutualistic interactions, however, has comparatively lagged behind that of  
35 trophic and competitive interactions. Consequently, ecologists still lack a generalized  
36 framework to investigate the population dynamics of mutualisms. Here, we propose  
37 extensible models for two-species mutualisms focusing on nutritional, protection, and  
38 transportation mechanisms and evaluate the population-level consequences of those  
39 mechanisms. We introduce a novel theoretical framework that highlights characteristic  
40 dynamics when the effects of mutualism are directly dependent or independent of recipient  
41 density and when they saturate due to inter- or intra-specific density-dependence. We end  
42 by integrating our work into the broader historical context of population-dynamic models of  
43 mutualism and conclude that a general ecological theory of mutualism exists.

44

## Introduction

45       Mutually beneficial interactions are ubiquitous in nature. Nearly all species on Earth  
46 participate in at least one of four main types of mutualism: seed dispersal, pollination,  
47 protection, and resource exchange including with symbionts (Janzen 1985, Bronstein  
48 2015a,b). These interactions also support an immense amount of ecosystem function. For  
49 example, up to  $\sim 3/4$  of phosphorus and nitrogen acquired by plants is provided by  
50 mycorrhizal fungi and nitrogen-fixing bacteria (van der Heijden *et al.* 2008) and  $\sim 1/3$  of  
51 crop production is dependent on animal pollination (Klein *et al.* 2007). Yet, the importance  
52 of mutualism for ecological communities has only recently been recognized (Bronstein  
53 2015b) and, accordingly, theory has lagged behind. Such theory is critical as anthropogenic  
54 perturbations like climate change, nutrient runoff, pesticide use, and invasive species  
55 increasingly threaten many mutualisms and the ecosystem services they provide  
56 (Stachowicz 2001, Tylianakis *et al.* 2008). Here, we develop simple but extensible theory  
57 (i.e., can be specified to particular systems or generalized to networks of species  
58 interactions) on the population dynamics of two-species mutualisms, which integrates  
59 mutualisms into the broader framework of community ecology.

60       Theoretical study of mutualism has lagged behind the other two “pillars” of  
61 community ecology: competition and predator-prey interactions (Callaway 2007). This has  
62 been attributed to many reasons, three of which we highlight here. First, the terms used to  
63 identify interactions as “mutualism” have changed over time. Previous theory treated  
64 mutualism as a subset of facilitation, in which one species alters the environment to benefit  
65 a neighboring species (Callaway 2007), or symbiosis, in which species coexist in

66 “prolonged physical intimacy” (Bronstein 2015b), or used those terms interchangeably. We  
67 limit our scope to mutualism defined as reciprocally beneficial interactions between species  
68 without reference to the partners’ intimacy or environmental effects, though our work could  
69 be adapted to these other cases (see, e.g., Thompson *et al.* 2006).

70 Second, incredible diversity among mutualisms led researchers to focus on natural  
71 history, resulting in a heterogeneous set of case studies with little to no theory to unify or  
72 partition them (Addicott 1981, Bronstein 2015b). Some conceptual frameworks have  
73 attempted to organize this rich diversity, for example, by the types of benefits exchanged,  
74 the mechanisms of exchange, or the obligacy of each partner (reviewed in Bronstein 2015b,  
75 Douglas 2015).

76 Third, the development of population dynamic models for mutualism was stifled by  
77 the belief that simple mathematical approaches make unrealistic predictions. Foundational  
78 theory in community ecology developed from Lotka-Volterra models, which use linear  
79 functional responses to describe the effect of the interaction on each species. The Lotka-  
80 Volterra model can predict stable cycles (oscillations) for predator-prey interactions (Lotka  
81 1925, Volterra 1926) or competitive exclusion for competition interactions (Volterra 1926,  
82 Gause 1934) – outcomes that stimulated fruitful empirical and theoretical work. In contrast,  
83 the Lotka-Volterra model for mutualistic interactions (Kostitzin 1934, Gause & Witt 1935)  
84 can predict unbounded population growth of both species (“the orgy of mutual  
85 benefaction,” May 1976). Theoretical work stagnated for nearly fifty years as authors  
86 attributed the supposed rarity of mutualism in natural ecosystems to the unstable nature of  
87 this outcome (e.g. Williamson 1972, May 1973, Goh 1979).

88 Population dynamic studies of mutualism began to reemerge in the 1980s, perhaps due  
89 to an increasing awareness of the prevalence and importance of mutualistic interactions  
90 (Boucher 1985, Bronstein 2015b). Authors showed that mutualism could be stabilized by  
91 incorporating negative density-dependence or mechanistic detail that explicitly limits  
92 benefit acquired from mutualism (see Table A1 of Appendix A). However, these models  
93 were criticized as either too case-specific to be useful or too abstract to be applicable  
94 (Bronstein 2015a). A handful of works have attempted to bridge this gap by organizing  
95 extant knowledge both conceptually and mathematically. For example, Addicott (1981)  
96 organized models by their effects on per-capita growth rate and/or equilibrium density for  
97 both participating species. Wolin and Lawlor (1984) categorized ways in which  
98 intraspecific density-dependence could limit benefits and stabilize mutualisms. Thompson  
99 *et al.* (2006) proposed a theoretical framework that organized mutualisms into those that  
100 affect birth rate, death rate, or habitat acquisition for each partner and predicted their  
101 ecological dynamics when immigration and emigration occur (i.e., in open systems). Most  
102 recently, Holland and DeAngelis (2010) categorized mutualisms as following  
103 “unidirectional” or “bidirectional” consumer-resource dynamics, in which one or both  
104 partners benefit from consuming costly resources provided by the other.

105 Despite these past advances, an “ecological theory of mutualism” has not penetrated  
106 into the greater ecological community (see recent textbooks, e.g., Gotelli 2008, Vandermeer  
107 & Goldberg 2013, Mittlebach & McGuill 2019). Calls continue for simple but usable  
108 theory that synthesizes among mutualisms to identify patterns in population dynamics and  
109 in the mechanisms that generate them (e.g. Addicott 1981, Callaway 2007, Bronstein

110 2015a). To that end, we develop theory in which the “benefits” of mutualism are an  
111 outcome of mechanisms that increase the per-capita growth rate of a population compared  
112 to that rate in the absence of its mutualistic partner. We derive models focusing on  
113 observable mechanisms so that each mathematical expression represents biological  
114 phenomena justified with empirical examples. Then, we synthesize a conceptual and  
115 mathematical framework that predicts population dynamics across mutualisms. Our work  
116 demonstrates that there is an ecological theory of mutualism that deserves attention from  
117 ecologists in general.

## 118 **Methods**

119 Growth rate of any population  $i$  can be described as the difference between the  
120 population’s reproduction and mortality rates, which are functions of the density-  
121 independent per-capita birth ( $b_i$ ) and death ( $d_i$ ) rates, as well as per-capita self-limitation  
122 and other density-dependent processes ( $s_i$ ). In the absence of mutualism, we represent  
123 changes in population density ( $N_i$ ) over time ( $t$ ) as:

$$124 \quad \frac{dN_i}{dt} = N_i[b_i(1 - s_i N_i) - d_i]. \quad \text{Eqn. 1}$$

125 Eqn. 1 is continuous, deterministic, and ignores migration, which accommodates species  
126 with overlapping generations and allows us to focus on how the balance of births and  
127 deaths in a population leads to different dynamics, unobscured by stochasticity and the  
128 dynamics of other patches.

129 Nearly all mutualisms consist of an exchange of nutrition, protection, or  
 130 transportation benefits. We derive and analyze models from Eqn. 1 for the most common  
 131 exchanges: nutrition-for-nutrition, nutrition-for-protection, and nutrition-for-transportation  
 132 (hereafter “nutrition,” “protection,” and “transport” mutualisms, respectively). Our  
 133 equations for each type of benefit can be mixed-and-matched for different systems, like the  
 134 protection-for-protection mutualism between clownfish and anemones (Table 1). Each of  
 135 our models accommodates populations of both “obligate” mutualists that cannot persist in  
 136 the absence of their partner and “facultative” mutualists that are self-sustaining. Table 2  
 137 summarizes our parameter definitions for all models.  
 138

Type of Mutualism	Examples Sp. 1 / Sp. 2	Dynamics of Sp. 1	Dynamics of Sp. 2
<i>Nutrition-for-Nutrition</i>	Plant / Microbe ( <i>mycorrhizae, rhizobia</i> )	Eqn. 2 w/ M-M	Eqn. 2 w/ M-M
<i>Nutrition-for-Protection</i>	Plant / Ant Animal ( <i>lycaenid caterpillars, scale insects, aphids</i> ) / Ant	Eqn. 3	Eqn. 2 w/ H-II
<i>Nutrition-for-Transportation</i>	Plant / Pollinator Plant / Seed Disperser ( <i>ants, frugivores</i> )	Eqn. 4 Eqn. 5	Eqn. 2 w/ H-II
<i>Protection-for-Protection</i>	Anemone / Clownfish	Eqn. 3	Eqn. 3

139 **Table 1. Population dynamic models for different types of mutualism.** Mutualisms are grouped by the  
 140 types of benefits exchanged (nutrition, protection, and transportation) between species (Sp. 1:  $N_1$ , Sp. 2:  $N_2$ ),  
 141 and their functional responses (M-M: Michaelis-Menten, H-II: Holling Type II). Additional models (with  
 142 qualitatively similar results) are presented in Appendices A, C.



143

### *Nutrition*

144 A unifying feature of many mutualisms is that they involve nutritional mechanisms,  
145 in which the benefit to one species is gained by consuming nutritional rewards from its  
146 partner (Thompson 1982, Janzen 1985, Table 1 of Holland & DeAngelis 2010). For  
147 example, pollinators forage on nectar from flowers and mycorrhizal fungi uptake carbon  
148 from root nodules. We modify Eqn. 1 so that when  $i$  consumes the rewards of  $j$  with rate  
149  $C_R(\mathbf{N}_j)$ , the per-capita growth rate of  $i$  increases proportionally:

$$150 \quad \frac{dN_i}{dt} = N_i [b_i(1 - s_i N_i) + c_{ij} C_R(\mathbf{N}_i, \mathbf{N}_j) - d_i] \quad \text{Eqn. 2}$$

151 where  $c_{ij}$  is the conversion efficiency of  $j$ 's rewards to new individuals of  $i$ . If  $i$  forages for  
152 the rewards, the per-capita consumption  $C_R(\mathbf{N}_i, \mathbf{N}_j) = \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j}$  follows a Holling Type II  
153 functional response with attack rate  $a_{ij}$  and handling time  $h_{ij}$ . If  $i$  uptakes the rewards  
154 directly (e.g., via diffusion), the per-capita consumption  $C_R(\mathbf{N}_i, \mathbf{N}_j) = \frac{v_i N_j}{k_{ij} + N_j}$  follows  
155 Michaelis-Menten kinetics with maximum uptake rate  $v_i$  and half-saturation constant  $k_{ij}$   
156 (i.e., the density of  $j$  at which half the maximum uptake rate is achieved). Both forms  
157 encode the reasonable assumption that  $i$ 's consumption rate on  $j$ 's rewards saturates with  
158 increasing density of  $j$ . Indeed, the expressions are identical when  $a_{ij} = v_i/k_{ij}$ ,  $h_{ij} =$   
159  $1/v_i$ . Species  $i$  is an obligate partner of  $j$  when  $r_i = b_i - d_i < 0$ ; otherwise ( $r_i \geq 0$ ),  $i$  is  
160 facultative.

161 Eqn. 2 is the most similar of our models to previous theory. It is an extension of the  
162 consumer equation of Rosenzweig and MacArthur's (1963) model when  $b_i > 0$ , and

163 identical to Wright’s (1989) model in which nutritional benefits saturate as a result of  
 164 constraints on handling time during foraging. It is also identical to Holland and DeAngelis’  
 165 (2010) equation for consumer mutualists that do not supply rewards (Table A1).  
 166

<b>Parameter</b>	<b>Interpretation</b> for recipient $i$ of benefit from resource or partner $j$	<b>Units</b>
$a_{ij}$	Per-resource attack rate	Resource <sup>-1</sup> Time <sup>-1</sup>
$b_i$	Per-capita birth rate or seed production	Time <sup>-1</sup>
$c_{ij}$	Conversion efficiency of resource to offspring	Unitless
$d_i$	Per-capita death rate	Time <sup>-1</sup>
$g_i$	Maximum fraction of seeds that recruit to maturity	Unitless
$h_{ij}$	Handling time on resource	Time
$k_{ij}$	Half-saturation density of resource	Resource
$s_i$	Per-birth, per-capita negative density-dependence due to, e.g. self-limitation during recruitment, Janzen-Connell effect	Density <sup>-2</sup>
$v_{ij}$	Maximum uptake rate of resource	Time <sup>-1</sup>
$y_{ij}$	Per-partner average seed set	Partner <sup>-1</sup>

167 **Table 2. Table of parameters.** All parameters in our models (Eqns. 1-5 and Appendices) are assumed to be  
 168 positive ( $> 0$ ). The unit “Density” refers to population  $i$ , while the units “Resource” and “Partner” (depending  
 169 on the system) refer to densities of population  $j$ . Subscripts *max*, *min*, and *diff* indicate the maximum,  
 170 minimum, and difference, respectively, in a parameter value due to mutualism.

171

## Protection

172

Protection mechanisms characterize a wide array of interactions in which the

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presence or behavior of a species protects another from natural enemies. The best-studied

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protection mutualisms are between ants and rewards-provisioning species like plants,

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lycaenid caterpillars, scale insects, and aphids (Ness *et al.* 2010). Ants harvest rewards like

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nectar, food bodies, and honeydew while cultivating and defending their resources through

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deterrence, attendance, and direct attack. Though these protection services have been

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observed to increase reproduction, the primary benefit to the resource species is a reduction

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in mortality due to, e.g., natural enemies including herbivores, predators, and parasitoids

180

(Ness *et al.* 2010, Trager *et al.* 2010). Therefore, we assume that benefits of protection

181

services ( $S$ ) are exclusively reductions in per-capita death rate. We model these reductions

182

as the difference between the maximum per-capita death rate of  $i$  inflicted by its natural

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enemies ( $d_{i_{max}}$ ) and the protection services provided by  $j$ ,  $d_{i_{diff}}S(\mathbf{N}_i, \mathbf{N}_j)$ , which

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incorporated in Eqn. 1 yields:

185

$$\frac{dN_i}{dt} = N_i \left[ b_i(1 - s_i N_i) - \left( d_{i_{max}} - d_{i_{diff}} S(\mathbf{N}_i, \mathbf{N}_j) \right) \right] \quad \text{Eqn. 3}$$

186

where  $d_{i_{diff}}$  is the maximum reduction in  $i$ 's death rate caused by  $j$ 's protection, with

187

minimum death rate  $d_{i_{min}} = d_{i_{max}} - d_{i_{diff}} \geq 0$ . Species  $i$  is obligate upon  $j$  when  $r_i =$

188

$b_i - d_i < 0$ ; otherwise  $i$  is facultative.

189

We assume that the protector population  $j$  benefits from foraging on rewards

190

provided by  $i$  and, therefore, model its dynamics with Eqn. 2 using the foraging functional

191 response (Table 1). If  $j$  reduces mortality via simple deterrence (“scaring off” natural  
192 enemies), we choose  $S(N_i, N_j) = \frac{N_j}{k_i + N_j}$  so that per-capita death rate declines proportional  
193 to  $j$ ’s perceived abundance around the recipient species, saturating when  $j$ ’s density is high.  
194 We consider other mechanisms of protection in Appendix C.

195 The nutrition (Eqn. 2) and protection (Eqn. 3) equations are identical when using  
196 the Michaelis-Menten functional response, with  $d_{i_{max}} = d_i, d_{i_{diff}} = c_{ij}v_i$ . Eqn. 3 is also  
197 similar to Thompson *et al.*’s (2006) model for protection mutualisms in open systems,  
198 when immigration and habitat provisioning are assumed to be negligible (Table A1).

### 199 *Transport*

200 Transportation mechanisms characterize the best studied mutualisms, perhaps due to  
201 the astonishing diversity by which immobile species attract more-mobile species to disperse  
202 their gametes. In the most common interactions (pollination and seed dispersal), animals  
203 visit plants to feed on rewards (including nectar and fruits), providing reproductive services  
204 (transport of pollen and seeds) incidentally during foraging. Except in special cases (e.g.,  
205 male bees visiting flowers to collect “perfume”), these rewards offer primarily nutritional  
206 benefit (Willmer 2011). Thus, we model the dynamics of transporter populations ( $j$ ) using  
207 Eqn. 2 with the foraging functional response (Table 1).

208 For plant populations ( $i$ ) that receive reproductive services ( $S$ ), we define  $b_i$  as per-  
209 capita seed set,  $g_i$  ( $> 0, \leq 1$ ) as the constant fraction of total seed set that germinates, and  
210  $s_i$  as negative density-dependence (e.g., Janzen-Connell effect, seed competition for  
211 recruitment). Plant  $i$  is obligate upon  $j$  when  $r_i = g_i b_i - d_i < 0$ ; otherwise  $i$  is facultative.

212 Reproductive services are functions of  $j$ 's visitation to  $i$  (see below) and increase the  
213 number of mature individuals in  $i$ . We derive separate models for pollination services  
214 (which increase seed set) and seed dispersal services (which decrease mortality during  
215 recruitment). We assume that foraging rate on rewards ( $C_R$ ) is a good proxy for visitation  
216 rate. Though some visits are unsuccessful due to depleted rewards or deception, we  
217 consider this mathematically similar to a predator unsuccessfully attacking a prey.

218 Modifying Eqn. 1 for pollination benefits yields:

$$219 \quad \frac{dN_i}{dt} = N_i [g_i(b_i + y_{ij}S(N_i, N_j))(1 - s_i N_i) - d_i] \quad \text{Eqn. 4}$$

220 where  $y_{ij}$  is the conversion efficiency of pollination services to seed production. Pollination  
221 requires the transfer of pollen from one individual's flower to the stigma of a conspecific  
222 plant individual, which occurs when animals visit flowers to forage. We therefore assume  
223  $S(N_i, N_j) = C_R(N_i, N_j) * N_i = \frac{a_{ji}N_j}{1+a_{ji}h_{ji}N_i} N_i$ , where the contribution of the animal  
224 population ( $j$ ) to per-capita seed set is proportional to  $j$ 's total foraging rate on  $i$ , calculated  
225 by multiplying  $j$ 's per-capita foraging rate on  $i$ 's rewards with plant density ( $N_i$ ). This  
226 expression accounts for the repeated interactions between plant and animal individuals  
227 required for conspecific pollen transfer (Vázquez *et al.* 2005).

228 In seed dispersal interactions, animals visit plants to forage on fruit or elaiosomes,  
229 later depositing the seed away from the parent plant. This process may increase germination  
230 rate by improving seed condition during passage through dispersers' guts, but more  
231 commonly increases recruitment by lessening density-dependent sources of mortality due to

232 predators and pathogens, which are most abundant near adult plants (Fricke *et al.* 2013).

233 We assume that negative density-dependence ( $s_{i_{max}}$ ) can be reduced to a minimum of

234  $s_{i_{min}} = s_{i_{max}} - s_{i_{diff}} \geq 0$  when dispersal services ( $S$ ) are maximally effective. Modifying

235 Eqn. 1 yields:

$$236 \quad \frac{dN_i}{dt} = N_i \left[ g_i b_i \left( 1 - \left( s_{i_{max}} - s_{i_{diff}} S(N_i, N_j) \right) N_i \right) - d_i \right] \quad \text{Eqn. 5}$$

237 We assume  $S(N_i, N_j) = C_R(N_i, N_j) = \frac{a_{ji}N_j}{1+a_{ji}h_{ji}N_i}$ , where the contribution of animals ( $j$ ) to

238 per-capita seed set is proportional to  $j$ 's per-capita (instead of total) foraging rate on  $i$ ,

239 because repeated interactions between plant and animal individuals are possible but not

240 required for effective seed dispersal (as opposed to the requirement for effective

241 pollination). To ensure that  $s_{i_{min}} = s_{i_{max}} - s_{i_{diff}} \geq 0$ , we choose parameter values that

242 fulfill  $s_{i_{max}} - \frac{s_{i_{diff}}}{h_{ji}} \geq 0$ .

243 Eqn. 5 differs from previous models mathematically, but is conceptually similar to

244 earlier theory that modeled mutualistic benefits as increasing carrying capacity (Whittaker

245 1975, Dean 1983, Wolin & Lawlor 1984, Neuhauser & Fargione 2004, Graves *et al.* 2006,

246 see Table A1), which is analogous to reducing the magnitude of negative density-

247 dependence. However, our pollination model (Eqn. 4) differs substantially from previous

248 work in the two-species population dynamic literature (Table A1). Its uniqueness is due to

249 the conceptually-important choice for negative density-dependence to limit (using a

250 multiplied term) the fraction of fertilized ovules that survive as seedlings to mature to

251 reproductive adults. If we instead assume that negative density-dependence limits overall

252 per-capita growth (using an additive term) as in previous works, our pollination and seed  
253 dispersal models would be mathematically identical.

### 254 *Rewards and Other Costs of Mutualism*

255 Species that receive services often offer nutritional “rewards” to attract their partner.  
256 These rewards are often partitioned from other components of the individual and have a  
257 unique chemical composition. Plants can produce nectar, a simple sugary solution, in  
258 flowers or nectaries separate from their vegetation, which is constructed from more  
259 complex carbohydrates and defensive compounds. Aphids and other hemipterans secrete  
260 honeydew that can be harvested separately from the rest of their body mass without killing  
261 individuals in the population. Nutritional mutualisms also follow this rewards paradigm  
262 with species provisioning a non-limiting resource in exchange for the acquisition of a  
263 limiting resource (Bronstein 2009).

264 Are rewards costly to offer? Evidence is sparse. Some rewards are waste products  
265 (Ness *et al.* 2010, e.g. honeydew is partially-digested phloem) that can even harm  
266 individuals if not removed (Gullan 1997), while other rewards are costly to individuals to  
267 construct (Brandenburg *et al.* 2012) or to have exploited (Yao & Akimoto 2001). However,  
268 these individual-level costs are likely to be buffered at the population level (see discussion  
269 in Appendix A). We therefore assume that costs associated with rewards do not  
270 substantially impact population density or, if they do, the impact could be represented as  
271 small changes to per-capita birth and death rates approximated as constant with respect to  
272 the producing species’ density. Other costs including increased handling time when  
273 foraging or increased exposure to parasites transported by visitors are also likely to be

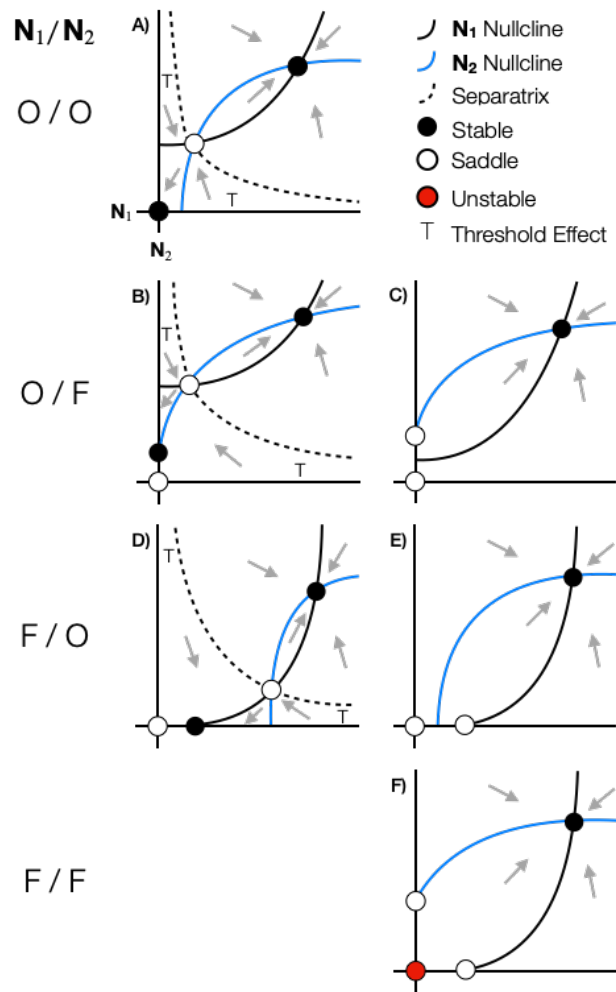
274 negligible or fixed at the population level (i.e., absorbed in parameter values, Holland &  
275 DeAngelis 2010). Therefore, we do not include explicit cost terms in our models.  
276 Nonetheless, individual-level costs that scale with rewards exploitation are often assumed  
277 to have population-level impacts (e.g. Aizen *et al.* 2014). To understand the impact of this  
278 assumption, we compare the dynamics of our simpler models to extended models with  
279 rewards exploitation (see Appendix C and discussion of overexploitation dynamics, below).

## 280 **Results**

281 We found that mutualisms have important similarities in their dynamics and  
282 stability. First, our models always predict stable coexistence when both species are  
283 facultative (Fig. 1F, 2F-G, 3F-G). Second, threshold or Allee effects may destabilize the  
284 system when at least one species is obligate and one or both partners are at low density  
285 (Figs. 1-3, left-column panels). Then, depending on initial conditions, both species go  
286 extinct or the facultative species persists at low density in the absence of its partner. Third,  
287 our models always display threshold effects when both partners are obligate which result in  
288 extinction at low densities (Fig. 1A, 2A, 3A).

289 Below we give a detailed description of the dynamic outcomes of each of our  
290 models, assuming coexistence is feasible. We organize our results by common and unique  
291 outcomes including Extinction, Single-Species Persistence, Coexistence, Threshold Effects,  
292 Allee Effects, and Bistability (see definitions below and Appendix B for mathematical  
293 details).





294

295 **Figure 1. Phase plane diagrams for nutritional and protection mutualisms.** Curves represent nullclines  
 296 along which population growth for each species is zero. Trivial nullclines (at  $N_1 = 0, N_2 = 0$ ) are omitted for  
 297 clarity. Rows illustrate all possible qualitative dynamics when coexistence is feasible for each combination of  
 298 obligate (O) and facultative (F) partners. The  $x$  and  $y$  axes are the densities of species 1 ( $N_1$ ) and 2 ( $N_2$ ),  
 299 respectively. Only the quadrant with positive abundances is shown. Arrows illustrate the direction of  
 300 population change in each region of the phase plane. Equilibria occur where the nullclines for  $N_1$  (black) and  
 301  $N_2$  (gray) intersect. Filled black equilibria are stable attractors, filled red equilibria are unstable repellers, and  
 302 hollow equilibria are half-stable saddle points. Here, saddle points induce *threshold effects* (T) in which one  
 303 population declines under a threshold of its partner's density (the separatrix, dashed line), leading to *single-*  
 304 *species persistence* of the facultative partner (B, D) or *extinction* when both partners are obligate (A). Above  
 305 the threshold (in A, B, D) or in systems without a threshold (C, E, F), the system always achieves *stable*  
 306 *coexistence*. In fact, stable coexistence is the only possible outcome when both partners are facultative (F) or  
 307 in some configurations of nullclines when one partner is facultative and the other obligate (C, D).

308

### *Nutrition and Protection*

309

Nutrition and protection mutualisms have the same mathematical form and identical

310

dynamical results despite their different derivations. We call  $N_1$  the plant (or attendee)

311

population and  $N_2$  the microbe (or protector) population for nutrition (or protection)

312

mutualisms (Table 1). Microbial and protector nullclines (gray curves, Fig. 1) are concave

313

down, increasing functions that saturate with respect to plant or attendee density. The plant

314

and attendee populations follow the same dynamics yielding symmetrical nullclines (black

315

curves, Fig. 1). Together, these result in the following outcomes:

316

1. **Extinction** (Fig. 1, all panels, circles at the origin). The extinction equilibrium is

317

attracting (a stable point) only when both partners are obligate (Fig. 1A). Otherwise,

318

one or both populations are repelled from extinction. The origin is a saddle point for

319

facultative-obligate pairs (Fig. 1B-E) or an unstable point when both partners are

320

facultative (Fig. 1F).

321

2. **Single-Species Persistence** (Fig. 1B-F, circles on axes). Facultative species can persist

322

at density  $r_i/b_i s_i$  in the absence of their partner. These single-species equilibria are

323

attracting when threshold effects are present (Fig. 1B, 1D). Otherwise (Fig. 1C, 1E, 1F),

324

they are saddle points and the system will tend towards stable coexistence.

325

3. **Stable Coexistence** (Fig. 1, all panels, off-axes black circles). The coexistence

326

equilibrium is a stable node (no oscillations) at higher density than either species could

327

achieve alone. Increased density past this equilibrium in either species causes its

328

population to decrease due to negative density-dependence. Therefore, the “orgy of

329

mutual benefaction” (May 1976) cannot occur.

330 4. **Threshold Effects** (Fig. 1, left-column panels, “T”). The nullclines intersect twice  
331 under some parameterizations when at least one species is an obligate partner. This  
332 yields a saddle point (Fig. 1A, 1B, 1D, off-axes unfilled circle) at densities intermediate  
333 to the stable coexistence and single-species persistence or extinction equilibria. The  
334 saddle determines a threshold (the “separatrix,” dashed line) below which obligate  
335 partners go extinct even if initially highly abundant (e.g., left “T” region in Fig. 1d).  
336 This means that one species is too low in density to provide sufficient benefits to its  
337 partner, causing the partner’s population to decline. The low-density species continues  
338 to benefit from mutualism but its increase in density cannot occur fast enough to save  
339 the system from extinction. Above the separatrix, one or both species are of high  
340 enough density that benefits from mutualism cause positive population growth in their  
341 partners and the system will achieve stable coexistence.

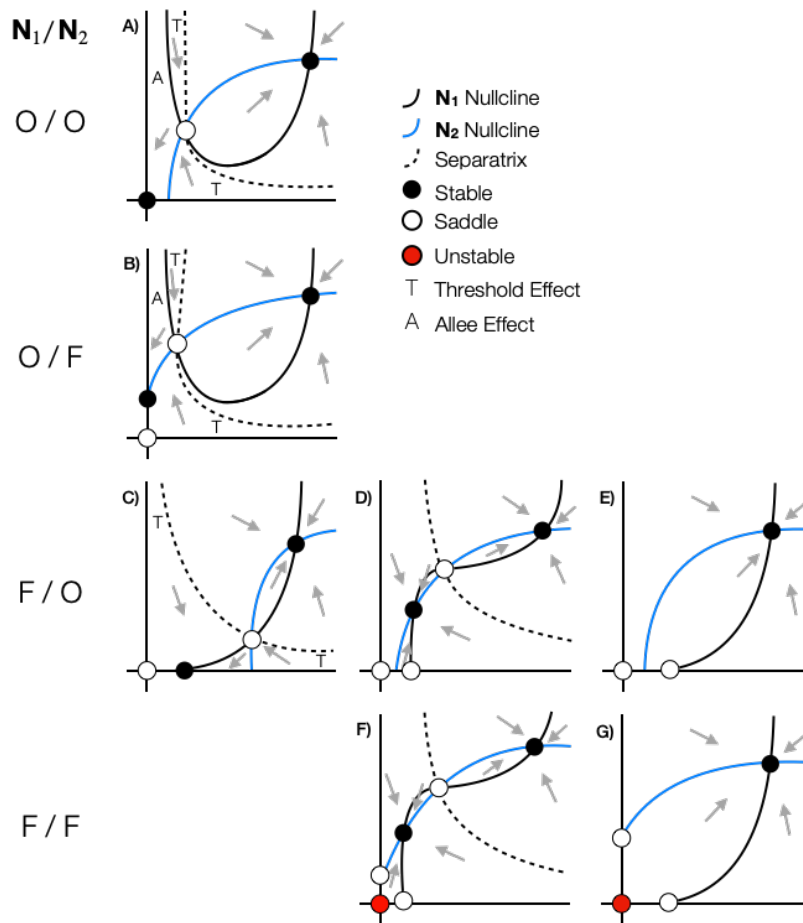
342 Alternative protection mechanisms of different mathematical forms yield qualitatively  
343 similar results (Appendix C).

#### 344 *Transport*

345 We call  $N_1$  the plant population and  $N_2$  the animal population (Table 1). The  
346 animal nullclines (gray curves) are identical to the microbe/protector nullclines in Fig. 1.  
347 The plant nullclines in the pollination and seed dispersal models are both top-open humps  
348 bounded on the left side by a vertical asymptote at zero (Figs. 2A-B, 3A-B) despite  
349 different derivations. These nullclines differ in their high-density behaviors, where the  
350 pollination nullcline is concave up and saturates to  $1/s_1$  (Fig. 2), while the seed-dispersal

351 nullcline is concave down when facultative (Fig. 3C-G) and continues to increase with a

352 linear slope  $\frac{h_{21}s_{1max}}{s_{1diff}} \geq 1$ .



353

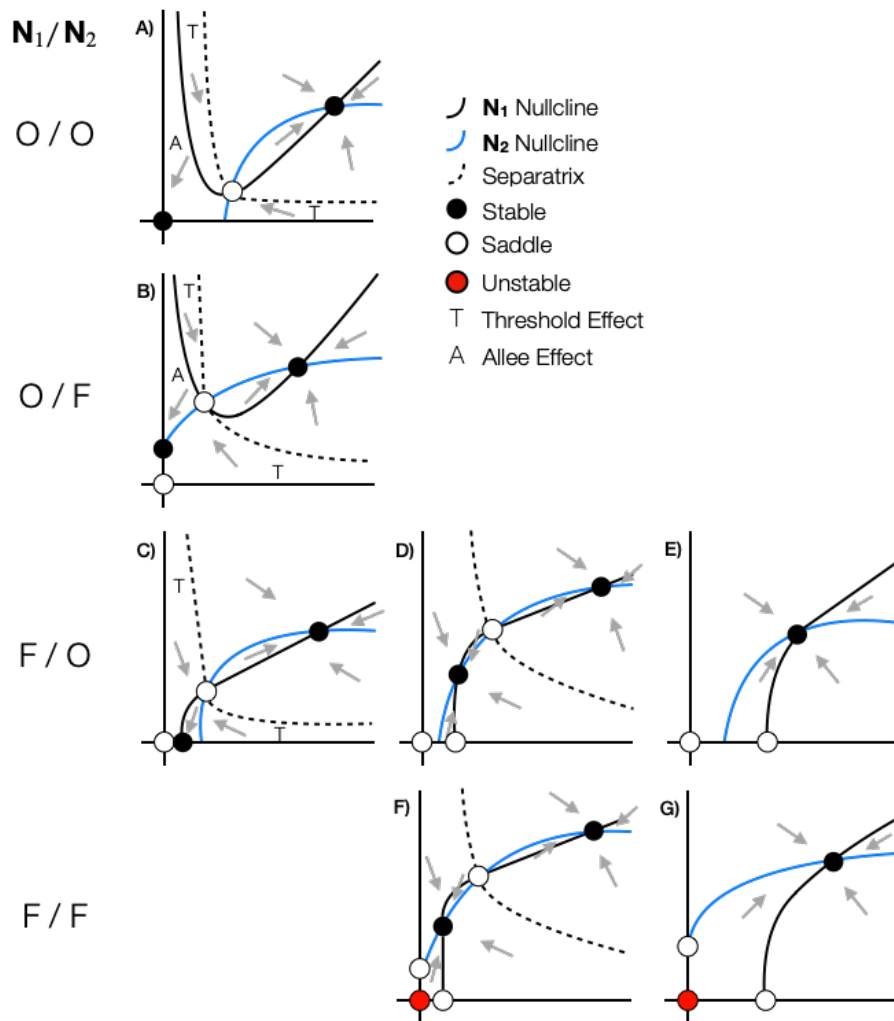
354 **Figure 2. Phase plane diagrams for pollination mutualisms.** All formatting and terminology follows Fig. 1.

355 Here, saddle points can induce threshold effects (T) when at least one species is obligate (A, B, C). When  
 356 species' densities are above the threshold, they achieve stable coexistence; below the threshold, the system  
 357 collapses to extinction (A) or single-species persistence (B, C) of the facultative partner. When the plant  
 358 partner ( $N_1$ , black) is obligate (A, B), threshold effects additionally lead to strong, demographic Allee effects  
 359 (A, Kramer et al. 2009) in which the plant population declines under a threshold of its own density. Saddle  
 360 points can also induce bistability (i.e., two stable coexistence equilibria, D, F), where species stably coexist at  
 361 the low-density equilibrium if their density were initially below the separatrix (dashed line) or at the high-  
 362 density equilibrium otherwise. Finally, when plants are facultative, stable coexistence is the only possible  
 363 outcome for some nullclines configurations (E, G).

364 Differences in the plant nullclines between seed dispersal and pollination  
365 interactions manifest in different nullcline geometries but similar dynamical outcomes.  
366 Many of the outcomes are similar to those described for nutrition and protection  
367 mutualisms, which we do not restate. We describe only dynamics unique to the transport  
368 models:

- 369 1. **Extinction** (Figs. 2-3, all panels, circles at the origin).
- 370 2. **Single-Species Persistence** (Figs. 2B-G, 3B-G, circles on axes). Facultative plants can  
371 persist at density  $r_1/g_1b_1s_1$  in the absence of their partner.
- 372 3. **Stable Coexistence** (Figs. 2-3, all panels, off-axes black circles). One stable  
373 coexistence equilibrium is present when plants are obligate mutualists (Fig. 2A-B, Fig.  
374 3A-B). Two stable coexistence equilibria (bistability) are possible when plants are  
375 facultative (Fig. 2D, 2F, 3D, 3F).
- 376 4. **Bistability** (Figs. 2-3, middle-column panels). When plants are facultative, the plant  
377 and animal nullclines intersect three times under some parameterizations. This yields a  
378 saddle point (off-axes unfilled circle) bisected by a separatrix (dashed line) that divides  
379 the plane into two basins of attraction corresponding to a lower- and higher-density  
380 stable coexistence, both at higher density than either species could achieve alone. The  
381 system will tend to either coexistence equilibrium depending on initial conditions.
- 382 5. **Threshold Effects** (Figs. 2-3, left-column panels, “T”).
- 383 6. **Allee Effects** (Figs. 2A-B, 3A-B, “A”). When plants are obligate, their population  
384 declines under a threshold of their own density regardless of the density of their partner.  
385 This results from the asymptotic behavior of the plant nullcline at  $N_1 = 0$ , which occurs

386 by different mechanisms depending on the transport model. In the pollination model, it  
 387 occurs because benefit is proportional to the total consumption rate by animals, whereas  
 388 in the seed-dispersal model it occurs because benefit affects the density-dependent term.  
 389



390

391 **Figure 3. Phase plane diagrams for seed dispersal mutualisms.** All formatting and terminology follows  
 392 Figs. 1-2. All dynamics described in Fig. 1 also apply here. Pollination and seed dispersal mutualisms differ  
 393 only the geometry of the plant nullcline ( $N_1$ , black), but not in their dynamical outcomes.

394

## Discussion

395           Previous models have been criticized as too case-specific or too phenomenological  
396 to further empirical and theoretical understanding of generalities in the ecologies of diverse  
397 mutualisms (Bronstein 2015a). To address this, we derived models that balance mechanistic  
398 detail with the potential for mechanisms to have population-level effects. We found that  
399 predictions for the population dynamics of mutualisms are qualitatively robust across  
400 derivations, including level of detail, types of benefit, and inspiring systems. We now  
401 organize these predictions in a (novel) theoretical framework that synthesizes our  
402 conceptual and mathematical results (Table 3, Fig. 4). We then highlight the assumptions  
403 that restrict the applicability of our work and identify how these assumptions can be  
404 relaxed. We conclude that a coherent and well-developed ecological theory of mutualism  
405 exists.

406

### *Synthesizing Mechanisms in a Mathematical Framework*

407           We followed previous conceptual work to develop models for species benefiting  
408 from nutritional, protection, and transportation mechanisms, as these putatively mapped  
409 onto the processes of consumption, mortality, and reproduction (Table 3). Our  
410 mathematical results revealed that nutritional and protection mechanisms are similar to  
411 each other because they modify density-independent rates (per-capita birth, death, or both)  
412 by saturating processes directly dependent on partner density or per-capita behavior rates  
413 (i.e., partner or recipient consumption, deterrence, attendance; see Appendices A, C).  
414 Similarly, transportation mechanisms are similar to each other because they both directly  
415 depend on and saturate in terms of recipient density, either because they are proportional to

CONCEPTUAL					MATHEMATICAL						
Type of Benefit	Process	Mechanism	Means of Effect	Effect	Nullcline Geometry			Dynamical Outcomes			
					Obligacy (recipient)	Low Density	High Density	Low Density		High Density	
								O <sup>P</sup>	F <sup>P</sup>	O <sup>P</sup>	F <sup>P</sup>
<i>Nutrition</i>	Consumption	Consumption	<b>Per-capita consumption on partner</b>	Density-independent (↑ $b_i$ , ↓ $d_i$ or both)	O	–	Saturating, concave up	T	T	Stable coexistence	
					F	–		T	–		
<i>Protection</i>	Mortality	↓ Mortality	<b>Per-capita deterrence/attendance by partner</b>	Density-independent (↓ $d_i$ )	O	–	Saturating, concave up	T	T	Stable coexistence	
					F	–		T	–		
<i>Transportation: Pollination</i>	Reproduction	↑ Seed production	<b>Total consumption by partner</b>	Density-dependent (↑ $b_i$ )	O	Asymptote at 0	Saturating, concave up	T, A	T, A	Stable coexistence	
					F	Changing concavity		T, A	B		
Seed dispersal	Reproduction	↓ Density-dependent mortality during recruitment	<b>Per-capita consumption by partner</b>	Density-dependent (↓ $s_i$ )	O	Asymptote at 0	Linear growth	T, A	T, A	Stable coexistence	
					F	Concave down		T, A	B;		

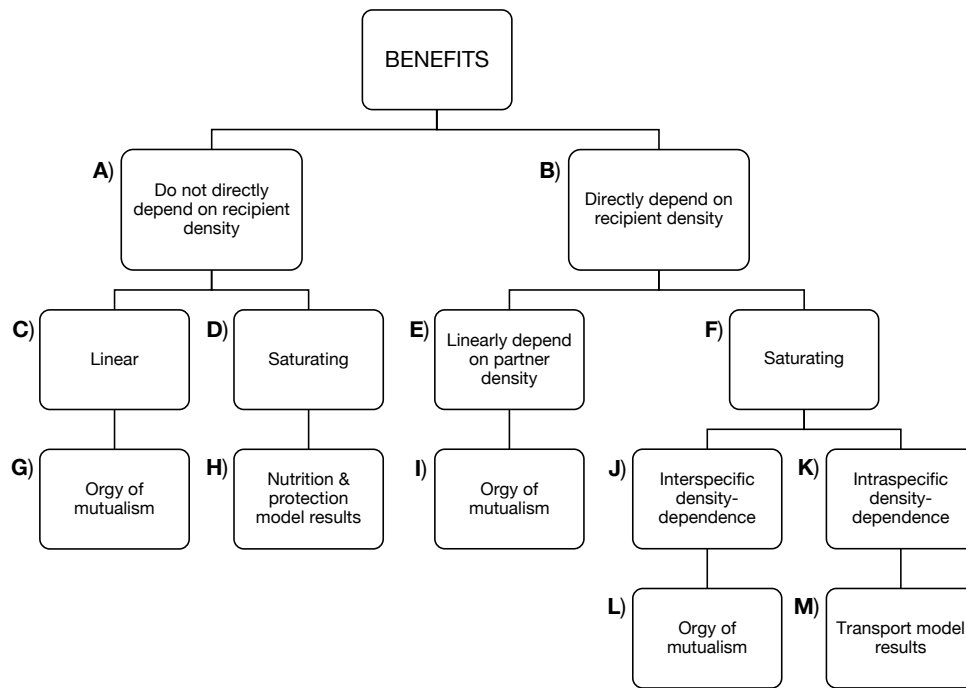


417 **Table 3. Theoretical framework.** Synthesis of Conceptual and Mathematical results for each type of mutualism. All  
418 entries are with respect to the recipient of mutualistic benefits (Eqns. 2-5) and assume that the partner is a nutritional  
419 mutualist as in our Figs. 1-3. Dashes (–) indicate no notable behavior in that region. The mapping of different “Types  
420 of Benefits” to “Processes” and “Mechanisms” is a conceptual simplification that represents general patterns among  
421 mutualisms. Mechanisms can result from different behaviors of partners and recipients; we specify one characteristic  
422 behavior for each of our models (“Means of Effect”). In all cases, per-capita benefits are a function of partner  
423 density. Additionally, the “Effects” of mutualism are either directly dependent or independent of recipient density.  
424 All effects are saturating, either due to interspecific density-dependence (nutrition, protection) or intraspecific  
425 density-dependence (transport, alternate protection models [Appendix C]). These distinctions, in addition to whether  
426 the recipient species is obligate (O) or facultative (F), determine different “Nullcline Geometries” and “Dynamical  
427 Outcomes”. For example, both models with “density-dependent” effects have nullclines with a vertical asymptote at  
428 zero when obligate, and can change concavity between low and high density when facultative. Different dynamical  
429 outcomes are dependent on parameterization of the model, the type of partner species, and whether the partner is  
430 obligate or facultative. Outcomes are separated into columns (headed O/F) when dependent on partner obligacy  
431 (highlighted with a superscripted *P*) and are separated by line-breaks when dependent on parameterization. In all our  
432 models, stable coexistence can always occur at higher density than either species could achieve alone. Our models  
433 are thus distinguished by their low density-behavior: “T” and “A” refer to threshold and Allee effects,  
434 respectively. “B” refers to stable coexistence at low density, which gives two stable coexistence equilibria  
435 (bistability). When facultative, species can also potentially persist at a low-density, single-species equilibrium (not  
436 included in the table).

437

438 the partner’s total behavior rates (pollination) or because the partner’s per-capita behavior  
439 modifies a density-dependent rate (seed dispersal).

440 This suggests a more informative way to group mutualisms: by whether their effects are  
441 directly dependent on recipient populations (Fig. 4). This scheme predicts that some interactions  
442 will be dynamically similar despite differing in their types of benefit. For example, protection  
443 services in some systems may reduce density-dependent sources of mortality such as disease  
444 (e.g., cleaning by ants reduces aphid mortality, Nielsen *et al.* 2010, Durak *et al.* 2016). Modeling  
445 this similarly to seed dispersal, where benefits are directly dependent on recipient density,



446

447 **Figure 4. An ecological theory of mutualism.** By synthesizing the results of our models with historical models  
 448 derived with varying levels of mechanism for diverse motivating systems (Appendix A), we demonstrate that  
 449 ecological models of mutualism have predictable dynamical outcomes. This synthesis assumes that benefits of  
 450 mutualisms strictly increase per-capita growth rate of the recipient population, affect only a single ecological  
 451 process, and depend on partner density. Benefits may furthermore (B) directly depend or (A) not directly depend on  
 452 recipient density. (C) If benefits simply accumulate linearly as function of partner density (i.e., do not directly  
 453 depend on recipient density), models predict (G) unstable coexistence – the “orgy of mutual[ism].” (D) If benefits  
 454 instead saturate (either due to interspecific density-dependence, intraspecific density-dependence, or both),  
 455 mutualisms exhibit (H) the same dynamical outcomes as our nutrition and protection models. That is, stable  
 456 coexistence and threshold effects when one partner is obligate. Many historical models fall into this category and  
 457 predict identical outcomes. (B) When benefits directly depend on recipient density, they may additionally (E)  
 458 accumulate linearly as a function of partner density, leading to (I) the orgy of mutualism, or (F) saturate. (J) If  
 459 benefits saturate with respect to partner density, models predict (L) the orgy of mutualism. (K) If benefits instead  
 460 saturate with respect to recipient density, as in our pollination and seed dispersal models, mutualisms exhibit (M)  
 461 stable coexistence, threshold effects when one partner is obligate, Allee effects when plants are obligate, and  
 462 potential bistability when plants are facultative. The combination of both direct dependence and saturation in terms  
 463 of recipient density in our transport models appears to be unique among historical models. See Appendix A for  
 464 historical models and descriptions of their dynamical outcomes.

465 predicts an Allee effect at low density in obligate partners (Appendix C). Alternatively,  
466 when its effects are not directly dependent on recipient density, mutualism will have  
467 indistinguishable impacts on population dynamics, whether resulting from nutritional, protection,  
468 or transportation mechanisms (of the same functional form). For example, seed dispersal services  
469 (per-capita visitation) may increase (density-independent) germination rate ( $g_i$ ) in some systems  
470 (e.g., Fricke *et al.* 2013). Modeling this yields qualitatively identical results to our nutrition and  
471 protection models (Appendix C).

### 472 *Synthesizing Population Dynamic Behavior*

473 All four mutualism models studied here exhibit similar dynamical outcomes (Table 3),  
474 which were also predicted by several historical models (Appendix A). Specifically, when  
475 feasible, coexistence is stable, non-oscillatory, and populations grow with bound. All obligate-  
476 obligate mutualisms and certain interactions between obligate and facultative mutualists exhibit  
477 thresholds, under which the low density of one partner destabilizes the system.

478 Mutualisms are commonly modeled as having effects independent of recipient density  
479 (Appendix A). We modeled the benefits provided by pollination and seed dispersal as both  
480 directly dependent on and saturating in terms of recipient (plant) density, yielding the additional  
481 dynamical outcomes of Allee effects or bistability when plants are obligate or facultative,  
482 respectively. Other mutualisms may exhibit these outcomes if they: i) modify a density-  
483 dependent process, ii) affect a total rate (e.g., visitation) on the recipient population, or iii)  
484 include a facultative partner that follows a Type III functional response (Appendix C).  
485 Understanding how frequently the effects of mutualisms are directly dependent or independent of

486 recipient density is an important avenue for future work. For example, empirical work could  
487 distinguish between these effects by testing for a dynamical transition from threshold to Allee  
488 effects in obligate plants when their pollinators are at very high density (compare Fig. 1A-B to  
489 Fig. 2A-B).

490 Our nutrition and protection models are identical to those proposed by Holland and  
491 DeAngelis (2010) when excluding their cost terms for supplying resources (like rewards). The  
492 cost terms in their models lead to lobe-shaped nullclines and substantially different dynamical  
493 outcomes. Specifically, our models (no cost terms) predict a threshold effect where the high-  
494 density partner decreases and the low-density partner increases, while their models (with cost  
495 terms) predict overexploitation where the high-density partner increases and the low-density  
496 partner decreases (shifting the interaction from mutualism to parasitism), eventually causing an  
497 Allee effect and extinction of one or both partners. Empirical studies could test these alternative  
498 predictions by tracking population sizes over time when one partner is at low density.  
499 Interestingly, overexploitation in their models occurs due to the increased costs to the exploited  
500 partner of supplying resources. Extensions to our models with exploitation (as opposed to  
501 rewards production) costs can also predict overexploitation dynamics with fewer parameters  
502 (Appendices C).

### 503 *Population-Level Impacts of Benefits and Costs Occurring at the Individual Level*

504 Population dynamic models of mutualistic interactions, including ours, assume that  
505 mutualisms have population-level impacts. However, most empirical studies quantify the benefits  
506 and costs of mutualisms at the individual level in terms of fitness or even by using a single proxy

507 for fitness (Bronstein 2001, Ford *et al.* 2015). Those effects do not necessarily imply population-  
508 and community-level impacts of mutualism (Williamson 1972, Flatt & Weisser 2000, Ford *et al.*  
509 2015, Fredrickson 2015). Therefore, empirical work on population dynamics of mutualisms is of  
510 foremost importance to evaluate historical and current ecological theory on mutualisms.

511 To derive our models, we synthesized available knowledge across mutualisms on  
512 population-level costs of offering rewards (Appendix A). Using this synthesis, we assumed that  
513 costs associated with rewards did not have population-level effects or that they were of low or  
514 “fixed” cost which could be accounted for in demographic parameters. In contrast, high  
515 magnitude or “variable” costs that are a function of partner density should be accounted for  
516 explicitly (Holland *et al.* 2002, Morris *et al.* 2010). More generally, we expect that “construction”  
517 costs (attracting partners, rewards production) are more likely to be negligible than “exploitation”  
518 costs (rewards consumption, interference, destruction, mortality; Holland *et al.* 2002) which scale  
519 with a partner’s visitation rate, and thus are more likely to have impacts on the recipient  
520 population (see extensions, Appendix C). Similar conceptual and empirical syntheses among  
521 mutualisms are needed to provide insight into how mechanisms that affect fitness also impact  
522 population dynamics.

### 523 *Applying Our Models*

524 Our simple models can be applied to a variety of mutualisms. This final subsection  
525 discusses our most important assumptions in order to clarify the conditions under which our  
526 models apply. See Gotelli (2008) for a review of basic assumptions of population dynamic  
527 models and their consequences.

528 **Benefit via a single mechanism.** The predictions of our models apply when there is one primary  
529 mechanism of mutualistic benefit to each partner. For example, we assume that a nutritional  
530 mutualist benefits exclusively from consuming its partner's rewards – not other components of  
531 the partner's biomass and not from other aspects of the interaction that affect different vital rates.  
532 An interesting extension of our work would be to synthesize population dynamic behavior for  
533 “double mutualisms,” in which there are two mechanisms of mutualistic benefit to a partner  
534 (Fuster *et al.* 2019). Double mutualisms may play important ecological roles in ecosystems with  
535 limited resources, such as islands.

536 **Negative density-dependence.** We made the broad assumption that resources for reproduction  
537 and growth are limited, so vital rates are dependent on population size (Gotelli 2008). We  
538 included a negative density-dependence term in each of our population dynamic equations to  
539 represent, e.g., self-limitation due to competition or the Janzen-Connell effect (a common  
540 assumption, Table A1). The combination of negative density-dependence and saturating  
541 functional responses in our models curves the nullclines so that they intersect and result in stable  
542 coexistence.

543 **Functional forms.** Density-dependent functional responses limit positive feedbacks that cause  
544 unbounded population growth (the “orgy of mutual[ism]”) observed, e.g., in Lotka-Volterra  
545 models with density-independent (linear) functional responses. Historically, authors focused on  
546 intraspecific density dependence, where per-capita benefits decrease and saturate with increasing  
547 recipient density (but see Appendix A). Recent work advocates for interspecific density  
548 dependence, where per-capita benefits saturate with increasing *partner* density, to integrate

549 mutualism into broader consumer-resource theory (Wright 1989, Holland & DeAngelis 2010,  
550 Holland 2015). Our work primarily studied saturating (Holling Type II and Michaelis-Menten)  
551 functional responses with either inter- or intraspecific density-dependence (also see Appendix C).  
552 We used interspecific density-dependence for nutritional and protection mutualists, where  
553 recipients benefit from consuming their partners' rewards or from deterrence of enemies by their  
554 partners, respectively. We used intraspecific density-dependence for transportation mutualists,  
555 where recipients benefit from their partners' consumption of their own rewards. However, the  
556 distinction between intra- and inter-specific density dependence is not predictive of different  
557 population dynamics when the effects of mutualism do not directly depend on recipient density  
558 (Fig. 4). For example, protection services could instead be modeled with intraspecific density  
559 dependence if benefits are proportional to protectors' recruitment on recipients (e.g., Morales  
560 2000). This does not modify the qualitative dynamics of our protection model (Appendix C).

561 In summary, we proposed a theoretical framework that ties mechanisms to predicted  
562 population dynamics (Table 3, Fig. 4). The predictions of this framework apply when population-  
563 level benefits accumulate via a single mechanism and when population-level costs are negligible,  
564 are fixed effects, or simply diminish population-level benefits. Additionally, functional forms  
565 should be chosen according to the system. Then, effects of mutualism could potentially be  
566 identified experimentally by testing where per-capita benefits increase proportionally to or are  
567 independent of recipient density, respectively. Finally, our models could be falsified by assessing  
568 transient population dynamics for threshold effects, Allee effects, or overexploitation when one  
569 species is at low density.

570

## Conclusion

571 A critical part of elevating mutualism to the “third pillar of ecology” is developing theory  
572 that underpins fitness, population dynamics, and community dynamics of mutualistic interactions  
573 – but work on population dynamics is notably underrepresented. Here, we united conceptual  
574 mathematical approaches to identify patterns in the processes that generate mutualisms and the  
575 population dynamics that result. Despite different derivations, mechanisms, and inspiring  
576 systems, our models and many historical models make similar qualitative predictions when  
577 grouped by whether the effects of mutualism are directly dependent or independent of recipient  
578 density. This suggests that there exists a robust population dynamic theory of mutualism that can  
579 make general predictions. These predictions (including stable coexistence, threshold effects,  
580 Allee effects, and overexploitation) can be tested by combining empirical and theoretical  
581 approaches (e.g. Breton & Addicott 1992, Morales 2000, Palmer *et al.* 2010, Kang *et al.* 2011,  
582 Ford *et al.* 2015, also see Holland 2015). Such work will contribute to our understanding of  
583 general patterns and processes within and among mutualisms, and inform efforts to preserve  
584 mutualistic systems (Bronstein 2001, Callaway 2007, Bronstein 2015a,b).

585

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## 704 **Appendix A: Additional Discussion**

### 705 *Costs of Rewards at the Population Level*

706 Offering rewards to mutualistic partners can incur costs to individuals (Bronstein 2001).  
707 To our knowledge, however, there are not empirical studies that have measured how these costs  
708 result in changes to population growth. Given this lack of empirical information, we chose to  
709 assume that costs associated with rewards are negligible at the population level (or can otherwise  
710 be accounted for in parameter values). This is justified for at least four reasons: First, costs  
711 associated with rewards can simply act to reduce benefit provided by mutualism (e.g., reduced  
712 seed set due to nectar production, Brandenburg *et al.* 2012). Second, rewards and the organs that  
713 produce them are typically ephemeral in comparison to individuals in the population. They can be  
714 damaged or decay, but, instantaneously, these costs are unlikely to result in death or damage to  
715 individuals (Revilla 2015). Third, many costs associated with rewards are “fixed” in that they are  
716 independent of partner density (e.g., sunk costs of molecular machinery used to produce rewards,  
717 Holland *et al.* 2002) or are otherwise compensated for within individuals (e.g., carbon costs of  
718 supporting microbial mutualists stimulate compensatory photosynthesis, Kaschuk *et al.* 2010).  
719 Fourth, changes in metrics of individual fitness like fecundity do not necessarily manifest in  
720 changes in the per-capita growth rate of the population (Ford *et al.* 2015; e.g., soil rhizobia  
721 populations often stay constant despite the >100,000-fold increase in descendants released into  
722 soil produced by a plant-associated rhizobium, Denison & Kiers 2011).



723 *Patterns in Historical Models*

724 A surprising result of our work is that many of our model predictions are robust across  
725 types of mutualism and their mechanistic derivations – even among historical models (Table A1).  
726 Despite diverse approaches, many historical models predict stable coexistence and threshold  
727 effects when at least one species is obligate (May 1978, Soberón & Martínez Del Rio 1981,  
728 Wells 1983, Wolin & Lawlor 1984: Eqn. A8, Pierce & Young 1986, Wright 1989, Graves *et al.*  
729 2006, Thompson *et al.* 2006: Eqns. A12-A13, Kang *et al.* 2011, Revilla 2015), suggesting that  
730 these outcomes could be general among mutualisms. Some historical models are even  
731 mathematically identical, despite derivations ranging from phenomenological to extremely  
732 detailed (e.g., Soberón & Martínez del Rio 1981: Eqn. A6, Wright 1989, Bazykin 1998, our Eqns.  
733 2-3).

734 A theme among these historical models is that the benefits of mutualism (Fig. 4A) do not  
735 directly depend on recipient density and (Fig. 4D) are saturating, either due to interspecific  
736 density-dependence (Soberón & Martínez del Rio 1981: Eqn. A6, Dean 1983, Wright 1989,  
737 Graves *et al.* 2006, Thompson *et al.* 2006: Eqn. A12-A13, Holland & DeAngelis 2010, Kang *et*  
738 *al.* 2011), intraspecific density-dependence (Soberón & Martínez del Rio 1981: Eqn. A5, Wolin  
739 & Lawlor 1984: Eqn. A8, Revilla 2015: Eqn. A17), or both (May 1978, Wells 1983). Our  
740 nutrition and protection models are also in this tradition: benefits do not directly depend on  
741 recipient density and saturate due to interspecific (main text models, Eqns. 2-3) or intraspecific  
742 (alternative protection models, Appendix C) density-dependence, with qualitatively identical  
743 results (Fig. 4H).

744 Historical models in which mutualistic benefits directly depend on recipient density (Fig.  
745 4B) typically describe an increase in carrying capacity due to mutualism (Whittaker 1975, Wolin  
746 & Lawlor 1984: Eqns. A6, A7, Pierce & Young 1986: Eqn. A10, Neuhauser & Fargione 2004,  
747 Thompson *et al.* 2006: Eqn. A14). Interestingly, both models with saturating benefits (Wolin &  
748 Lawlor 1984: Eqns. A6-A7) saturate without inflection (no changes in concavity) due to  
749 interspecific density-dependence (Fig. 4J). Note though that these models have been referred to  
750 as examples of *intra*-specific density dependence (e.g. Holland 2015), presumably because  
751 saturating benefits reduce negative density-dependence in the recipient population. The models  
752 predict stable coexistence (Eqns. A6-A7) or unstable coexistence (Eqn. A7, Fig. 4L), but not  
753 bistability, and can be applied to facultative mutualists only. This is in contrast to our transport  
754 models (Eqns. 4-5), which are both directly dependent on recipient density and saturate due to  
755 intraspecific density-dependence because benefits are proportional to a partner's per-capita  
756 visitation or consumption rate on the recipient population (Fig. 4K, 4M). Additionally, high  
757 degree terms ( $N_i^2, N_i N_j$ ) in their nullclines allow inflection points that can lead to bistability.

758 A more recent pattern in population dynamic models of mutualism investigates the  
759 stability of interactions that can shift from mutualism to parasitism, either as controlled by an  
760 interaction coefficient that increases or depresses, respectively, equilibrium density in the  
761 presence of the partner (Pierce & Young 1986, Neuhauser & Fargione 2004), or as a balance  
762 between costs and benefits that depend dynamically on partner density (Holland & DeAngelis  
763 2010, Kang *et al.* 2011). Pierce and Young's (1986) and Neuhauser and Fargione's (2004)  
764 models reproduce the qualitative results of our nutrition and protection models when the

765 interactions are mutualistic. Kang *et al.*'s (2011) model for leaf-cutter ants and their fungal  
766 gardens includes a linear cost term of fungal biomass consumption, but still reproduces the  
767 qualitative results of our nutrition and protection models between partners with Type I and Type  
768 III functional responses. Holland and DeAngelis' (2010) models also reproduce our qualitative  
769 results when costs, which they specify are saturating costs of supplying resources to consumers,  
770 are set to zero ( $q_i = 0$  in Eqn. A15). However, their full models (when  $q_i > 0$ ) are unique  
771 because nonzero costs may exceed benefits instantaneously ("parasitism") due to the unique  
772 dynamical outcome of overexploitation even if in the long run benefits are greater ("mutualism").  
773 Testing for overexploitation dynamics may illuminate the prevalence of nonlinear population-  
774 level costs among mutualisms. Also see our proposed models with cost terms and comparison to  
775 Holland and DeAngelis' work in Appendix C.

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822 Naturalist 134:664–667.

Reference	Model	Unique Eqn. Number	Motivating System	Notes
Gause & Witt 1935	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i + \alpha_{ij} N_j - N_i}{K_i} \right)$	A1	n/a	Facultative only
Whittaker 1975	$\left\{ \begin{array}{l} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 + \alpha_{12} N_2 - N_1}{K_1 + \alpha_{12} N_2} \right) \\ N_2 \text{ follows Eqn. A1} \end{array} \right.$	A2 A1	Symbiont ( $N_1$ )- Host ( $N_2$ ) mutualism	$N_1$ is obligate when $K_1 = 0$
May 1978	$\left\{ \begin{array}{l} \frac{dN_1}{dt} = N_1 \left( \frac{I_{12} N_2}{CD + CN_1 + N_1 N_2} - d_1 \right) \\ N_2 \text{ follows Eqn. A2} \end{array} \right.$	A3 A2	Plant ( $N_1$ )- Pollinator ( $N_2$ ) and others	$N_2$ is obligate as defined by Whittaker 1975
Vandermeer & Boucher 1978	$\frac{dN_i}{dt} = N_i (r_i + \alpha_{ij} N_j - \alpha_{ii} N_i),$	A1	Legume ( $N_1$ )- Rhizobium ( $N_2$ ) and others	Obligate when $K_i =$ $r_i / \alpha_{ii} \leq 0$
Addicott 1981	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i - N_i}{K_i} \right) \left( 1 + \frac{\alpha_{ij} N_j}{K_i} \right)$	A4	Aphid ( $N_1$ )-Ant ( $N_2$ )	Facultative only
Soberón & Martinez del Rio 1981	$\left\{ \begin{array}{l} \frac{dN_1}{dt} = N_1 \left( \frac{k_1 \sigma \mu N_2}{1 + \sigma \phi \mu^2 N_1} - \gamma \right) \\ \frac{dN_2}{dt} = N_2 \left( \epsilon (K_2 - N_2) + \frac{k_2 \sigma \mu^2 N_1}{1 + \sigma \phi \mu^2 N_1} \right) \end{array} \right.$	A5 A6	Plant ( $N_1$ )- Pollinator ( $N_2$ )	$N_1$ is always obligate; $N_2$ is obligate when $K_2 =$ 0

Dean 1983	$\frac{dN_i}{dt} = r_i N_i \left( \frac{k_i - N_i}{k_i} \right)$ <p>where <math>k_i = K_{i_{max}} \left( 1 - e^{-((a_i N_j + c_i)/K_{i_{max}})} \right)</math></p>	A7	n/a	Unintended behaviors; replaced by Graves <i>et al.</i> 2006
Wells 1983	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{b_{12} N_2}{a_1 N_1 + N_2 + h_{12}} - d_1 f_1 N_1 - d_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( \frac{b_{21} N_1}{a_2 N_2 + N_1 + h_{21}} - d_2 \right) \end{cases}$	A8 A9	Plant ( $N_1$ )- Pollinator ( $N_2$ )	Obligate only
Wolin & Lawlor 1984	$\frac{dN_i}{dt} = N_i \left( r_i - \frac{bN_i}{1 + mN_j} - dN_i \right)$ $\frac{dN_i}{dt} = N_i (r_i - (b - mN_j + d)N_i)$ $\frac{dN_i}{dt} = N_i \left( r_i \left( 1 - \frac{N_i}{K} \right) + mN_j e^{-\alpha N_i} \right)$	A6 A7 A8	n/a	Multiple models presented with proposed similar derivations for mutualisms that reduce mortality. Facultative only
Pierce & Young 1986	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1(N_2) - \frac{N_1}{K_1} \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( 1 - \frac{N_2}{K_2(N_1)} \right) \end{cases}$	A9 A10	Lycaenid ( $N_1$ )- Ant ( $N_2$ )	$r_1(N_2)$ is 1's growth rate as a fn. of $N_2$ ; $K_2(N_1)$ is 2's equilibrium density of 2 as a fn. of $N_1$
Wright 1989	$\frac{dN_i}{dt} = N_i \left( r_i (1 - c_i N_i) + b_{ij} \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j} \right)$	A6	Pollinators and other mutualists that behave as foragers	Obligate when $r_i < 0$



Neuhauser & Fargione 2004	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1 + \gamma_{12} N_2}\right) - a N_1 N_2 \\ N_2 \text{ follows Eqn. A1} \end{cases}$	A11 A1	Plant ( $N_1$ )- Mycorrhizae ( $N_2$ )	Facultative only
Graves <i>et al.</i> 2006	$\frac{dN_i}{dt} = N_i (r_{i0} + (r_{i1} - r_{i0})(1 - e^{-k_{ij} N_j}) - s_i N_i)$	A7	Lichens and other nutritional mutualisms	Replaces Dean's 1983 model. Obligate when $r_{i0} < 0, r_{i1} + r_{i0} > 0$
Thompson <i>et al.</i> 2006	$\frac{dN_i}{dt} = \left( \rho_i \left( b_i N_i + \frac{\alpha_i N_j}{\beta_i + N_j} N_i \right) + I_i \right) \left( 1 - \frac{N_i}{S_i} \right) - d_{i_{max}} N_i$	A12	Many; systems where mutualism: Increases birth	Multiple models are presented with different combinations of benefit. Alosed system when $I_i = 0$ . Obligate when $\rho_i b_i < d_{i_{max}}$
	$\frac{dN_i}{dt} = (\rho_i b_i N_i + I_i) \left( 1 - \frac{N_i}{S_i} \right) - \left( d_{i_{min}} + \frac{d_{i_{diff}}}{1 + c_i N_j} \right) N_i$	A13	Decreases death	
	$\frac{dN_i}{dt} = (\rho_i b_i N_i + I_i) \left( 1 - \frac{N_i}{S_i + N_j} \right) - d_{i_{max}} N_i$	A14	Increases carrying capacity	
Holland & DeAngelis 2010	$\frac{dN_i}{dt} = N_i \left( r_i + c_i \left( \frac{a_{ij} N_j}{h_j + N_j} \right) - q_i \left( \frac{\beta_{ij} N_j}{e_i + N_i} \right) - s_i N_i \right), i \in 1, 2$	A15	Bidirectional, e.g. Plant ( $N_1$ )- Mycorrhizae ( $N_2$ )	Aconsumer-resource models of mutualism
	$\begin{cases} N_1 \text{ follows Eqn. A15} \\ N_2 \text{ follows Eqn. A6} \end{cases}$		Unidirectional, e.g. Plant ( $N_1$ )- Pollinator ( $N_2$ )	Obligate when $r_i = 0$
Kang <i>et al.</i> 2011	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1 \left( \frac{a_{12} N_2^2}{b_{12} + a_{12} N_2^2} \right) - c_{12} N_2 - d_1 N_1 \right) \\ N_2 \text{ follows Eqn. C1} \end{cases}$	A16	Fungus ( $N_1$ )- Leaf-cutter Ant ( $N_2$ )	$N_2$ is obligate with $r_2 = 0$

Revilla 2015

$$\frac{dN_i}{dt} = N_i \left( r_i - c_i N_i + \frac{\sigma_i \beta_i \alpha_j N_j}{\omega_j + \beta_i N_i} \right), i \in 1,2$$

A17

Exchanges of  
resources for  
resources, e.g.  
LichensAssuming the  
timescale of  
rewards  
replenishment is  
much faster than  
population change

$$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1 - c_1 N_1 + \frac{\sigma_0 \beta_0 \alpha_0 N_0 + \sigma_1 \beta \alpha N_2}{\omega + \beta_0 N_0 + \beta N_2} \right) \\ \frac{dN_2}{dt} = N_2 \left( r_2 - c_2 N_2 + \frac{\sigma_2 \beta \alpha N_1}{\omega + \beta_0 N_0 + \beta N_2} \right) \end{cases}$$

A6

Exchanges of  
resources for  
services, e.g. e.g.  
Plant ( $N_1$ )-  
Disperser ( $N_2$ )

A17

823 **Table A1. Historic population dynamic models of mutualism.** This list is not comprehensive. In general, we  
824 included only a sampling of deterministic, continuous-time population dynamic models of two equations for two  
825 species that were intended by the authors to generalize across mutualistic systems. However, we also included a few  
826 specific models (e.g. Soberón & Martinez del Rio 1981, Pierce & Young 1986, Kang *et al.* 2011) if we considered  
827 their approach notable or reference their work in the text. Equations with the same numbering are not significantly  
828 different mathematically. Additionally, many models, despite different mathematical features, predict similar  
829 qualitative dynamics in the ecologically-relevant region (Appendix A). Equations largely follow the notation from  
830 the original citations. Only unique models from each citation were included. We encourage the readers to refer to the  
831 citations for the model derivations and interpretation of parameters.

## 832 **Appendix B: Mathematical Details**

### 833 *Analysis*

834 We first analyze Eqn. 1 to serve as a reference for the effects of mutualism. In the  
835 absence of a potential partner ( $N_j$ ), the nullclines for Eqn. 1 are also equilibria. There are  
836 two: one “trivial” ( $\bar{N}_i = 0$ , “extinction”) and one nontrivial:

$$837 \quad \bar{N}_i = \frac{r_i}{b_i s_i}. \quad \text{Eqn. B1}$$

838 The nontrivial equilibrium is feasible (exists) when  $r_i = b_i - d_i \geq 0$ . Because we are  
839 concerned only with dynamics when both species have non-negative density, in this work  
840 we call equilibria “stable” or “unstable” when they are attracting or repelling, respectively,  
841 in this ecological region (when  $N_i \geq 0$ ). When  $r_i > 0$ , the trivial equilibrium is always  
842 unstable, allowing positive population growth when  $N_i$  is at low density, and the nontrivial  
843 equilibrium is stable allowing population persistence at constant density. Specifically, when  
844  $N_i < r_i/b_i s_i$  population density increases due to positive intrinsic growth whereas when  
845  $N_i > r_i/b_i s_i$ , population density decreases due to negative density-dependence.

846 In all of our models (Table 1), both species have “trivial” nullclines:  $\bar{N}_1 = 0$ , a  
847 vertical line along the y-axis, and  $\bar{N}_2 = 0$ , a horizontal line along the x-axis. The  
848 intersection of both species’ trivial nullclines gives a trivial extinction equilibrium ( $\bar{N}_1 = 0$ ,  
849  $\bar{N}_2 = 0$ ) in every model. Additionally, one species  $N_2$  follows the same dynamic equation  
850 (Eqn. 2) and thus has the same nontrivial nullclines (hereafter, simply “nullclines”). We use  
851 the Holling Type II notation in the following analysis but it is easy to substitute parameters

852 for Michaelis-Menten kinetics. The nullcline (Figs. 1-3, gray) is a concave down,  
853 increasing function that saturates with respect to its partner's abundance:

$$854 \quad \overline{N}_2 = \frac{r_2}{b_2 s_2} + \frac{c_2}{b_2 s_2} \frac{a_{21} N_1}{(1 + a_{21} h_{21} N_1)}. \quad \text{Eqn. B2}$$

855 Eqn. B2 is the curve showing the balance between negative density-dependence (exerted by  
856 the  $(1 - s_i N_i)$  term in Eqn. 2), benefit from mutualism, and positive intrinsic growth (when  
857  $N_2$  is facultative). When  $N_2 > \overline{N}_2$ , negative density-dependence is stronger than benefit  
858 from mutualism and/or intrinsic growth causing  $N_2$  to decrease. When  $N_2 < \overline{N}_2$ , negative  
859 density-dependence is weaker and  $N_2$  increases.

860 Comparing Eqns. B1 and B2, we can isolate the benefits of mutualism to  $N_2$  as  
861  $\frac{c_{21}}{b_2 s_2} \frac{a_{21} N_1}{(1 + a_{21} h_{21} N_1)}$ . Importantly, benefits saturate with respect to partner density. In particular,  
862 as plant density becomes extremely high,  $N_2$  saturates to a higher value than it could  
863 achieve in the absence of its partner:

$$864 \quad \lim_{N_1 \rightarrow \infty} \overline{N}_2 = \frac{r_2}{b_2 s_2} + \frac{c_{21}}{b_2 h_{21} s_2}. \quad \text{Eqn. B3}$$

865 This horizontal asymptote is an upper bound on the density of  $N_2$ . When  $N_2$  is facultative  
866 ( $r_2 > 0$ ), its nullcline intersects the y-axis in the ecological region (when  $N_i \geq 0$ ) at

$$867 \quad \overline{N}_{2,0,y} = \frac{r_2}{b_2 s_2}. \quad \text{Eqn. B4}$$

868 All else being equal, decreasing  $r_2$  pushes the visible part of  $N_2$ 's nullcline down so that  
869 when  $N_2$  is obligate ( $r_2 \leq 0$ ), it intersects the at y-axis at zero or negative values (not  
870 shown). Then, in the ecological region, the nullcline instead intersects the x-axis at

$$871 \quad \overline{N}_{2,x,0} = \frac{-r_2}{a_{21}(c_{21}+h_{21}r_2)}. \quad \text{Eqn. B5}$$

872 Below, we calculate the nontrivial nullclines for  $N_1$  (Figs. 1-3, black) and similarly analyze  
873 their dynamics in the ecological region of the plane. See Methods and Tables 1-2 for  
874 terminology.

## 875 **Nutrition**

876 Plants ( $N_1$ ) follow the same dynamics as microbes ( $N_2$ ), so their nullcline is  
877 symmetrical to Eqn. B2:

$$878 \quad \overline{N}_1 = \frac{r_1}{b_1s_1} + \frac{c_{12}}{b_1s_1} \frac{a_{12}N_2}{(1+a_{12}h_{12}N_2)}. \quad \text{Eqn. B6}$$

879 Clearly, Eqn. B6 is an increasing function that saturates with respect to microbe density. It  
880 can be rearranged to be a function of  $N_1$ :

$$881 \quad N_2 = \frac{r_1 - b_1s_1\overline{N}_1}{a_{12}(b_1h_{12}s_1\overline{N}_1 - h_{12}r_1 - c_{12})}. \quad \text{Eqn. B7}$$

882 Then, plant density increases to the left of its nullcline (Fig. 1, black) due to mutualism and  
883 decreases to the right of it due to strong negative density-dependence. All other properties  
884 are likewise symmetrical (i.e. Eqns. B3-B5 apply with the  $x$  and  $y$  axes switched and  
885 indices 1 and 2 swapped).

886 **Protection**

887 Species that benefit from protection mutualisms ( $N_1$ ) follow the same dynamics as  
 888 nutritional mutualists. In the protection notation, their nontrivial nullcline (Fig. 1, black) is:

889 
$$\overline{N}_1 = \frac{r_1}{b_1 s_1} + \frac{d_{1diff}}{b_1 s_1} \frac{N_2}{(k_{12} + N_2)}. \quad \text{Eqn. B8}$$

890  $\overline{N}_1$  approaches a vertical asymptote at

891 
$$\lim_{N_2 \rightarrow \infty} \overline{N}_1 = \frac{r_1}{b_1 s_1} + \frac{d_{1diff}}{b_1 s_1}. \quad \text{Eqn. B9}$$

892 When obligate ( $r_1 < 0$ ),  $\overline{N}_1$  intersects the y-axis in at

893 
$$\overline{N}_{20,y} = -\frac{r_1 k_{12}}{b_1 - d_{1min}}. \quad \text{Eqn. B10}$$

894 When facultative ( $r_1 > 0$ ),  $\overline{N}_1$  intersects the x-axis at

895 
$$\overline{N}_{2x,0} = \frac{r_1}{b_1 s_1}. \quad \text{Eqn. B11}$$

896 **Transport**

897 The equation for the nullcline of animal-pollinated plants (Fig. 2, black) is:

898 
$$N_2 = \frac{(b_1 g_1 s_1 \overline{N}_1 - r_1)(1 + a_{21} h_{21} \overline{N}_1)}{y_{12} a_{21} g_1 (1 - s_1 \overline{N}_1) \overline{N}_1}. \quad \text{Eqn. B12}$$

899 When plants are obligate ( $r_1 = g_1 b_1 - d_1 \leq 0$ , Fig. 2a-b), the nullcline is a top-open hump

900 bounded by vertical asymptotes at  $N_1 = 0$  and  $N_1 = 1/s_1$ . When plants are facultative

901 ( $r_1 > 0$ , Fig. 2c-g), at high density the nullcline is increasing, concave up, and saturates at

902  $1/s_1$ . At low density, the nullcline is concave down, though this may not be visible in the  
903 ecological region of the plane. Regardless, it has x-intercept

904 
$$\overline{N}_{10,y} = \frac{r_1}{g_1 b_1 s_1}. \quad \text{Eqn. B13}$$

905 The equation for the nullcline of animal-dispersed plants (Fig. 3, black) is:

906 
$$N_2 = \frac{(b_1 g_1 s_{1max} \overline{N}_1 - r_1)(1 + a_{21} h_{21} \overline{N}_1)}{s_{1diff} a_{21} \overline{N}_1}. \quad \text{Eqn. B14}$$

907 At high plant density, the nullcline has a linear slope of  $h_{21} s_{1max} / s_{1diff}$ , which is  $\geq 1$  due  
908 to our condition that negative density-dependence can be reduced at most to zero (see  
909 Methods). When plants are obligate ( $r_1 = g_1 b_1 - d_1 \leq 0$ , Fig. 3a-b), the nullcline is a top-  
910 open hump bounded on the left side by a vertical asymptote at  $N_1 = 0$ . When plants are  
911 facultative ( $r_1 > 0$ , Fig. 3c-g), the nullcline is concave down at low density, with x-  
912 intercept

913 
$$\overline{N}_{10,y} = \frac{r_1}{g_1 b_1 s_{1max}}. \quad \text{Eqn. B15}$$

914 For both Eqns. B12 and B14, inside the hump or to the left of the curve plant density  
915 increases; to the right, plant density decreases due to strong negative density-dependence.

### 916 *Feasibility*

917 All of our models are structurally unstable (Rohr et al. 2014), such that smooth  
918 transitions in parameter values shift the nontrivial nullclines (hereafter, “nullclines”) so that  
919 they may intersect in various ways or even fail to intersect, with different dynamical

920 outcomes for each case (Fig. B1). In the main text, we focused on “feasible” systems, that  
921 is, where coexistence of the partners with non-negative density (i.e. in the ecological  
922 region) was possible. There are many parameterizations that lead to feasibility, but it is not  
923 easy to provide an ecological interpretation for the conditions to achieve them. Below we  
924 enumerate the geometric conditions that lead to feasibility by describing the required  
925 positioning of the nullclines.

## 926 **Nutrition and Protection**

927 There are three cases for how the nullclines of  $N_1$  and  $N_2$  intersect:

928 (1) The nullclines never intersect (Fig. B1a). Coexistence is not possible. Depending on the  
929 initial conditions, both species may be extinct or a facultative species may persist at  $N_i =$   
930  $\frac{r_i}{b_i s_i}$  with  $N_j = 0$ .

931 (2) The nullclines intersect exactly once (Fig. B1b). This case is extremely sensitive to the  
932 vital rates like birth and death rates of both species; it is highly unlikely in nature these  
933 rates would be maintained at such precise values, especially in the presence of stochasticity.  
934 We neglect this case.

935 (3) The nullclines intersect twice (Fig. B1c-d), yielding exactly one saddle point at low  
936 density and one stable equilibrium at high density. Coexistence is feasible when at least one  
937 of the intersections is in the ecological region (Fig. B1c, d: two, one intersection(s) in the  
938 ecological region, respectively). When only one intersection occurs in the ecological  
939 region, it is the stable coexistence equilibrium.



940 **Transport**

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

942 (1) If the nullclines never intersect (Fig. B1e), then coexistence is not possible.

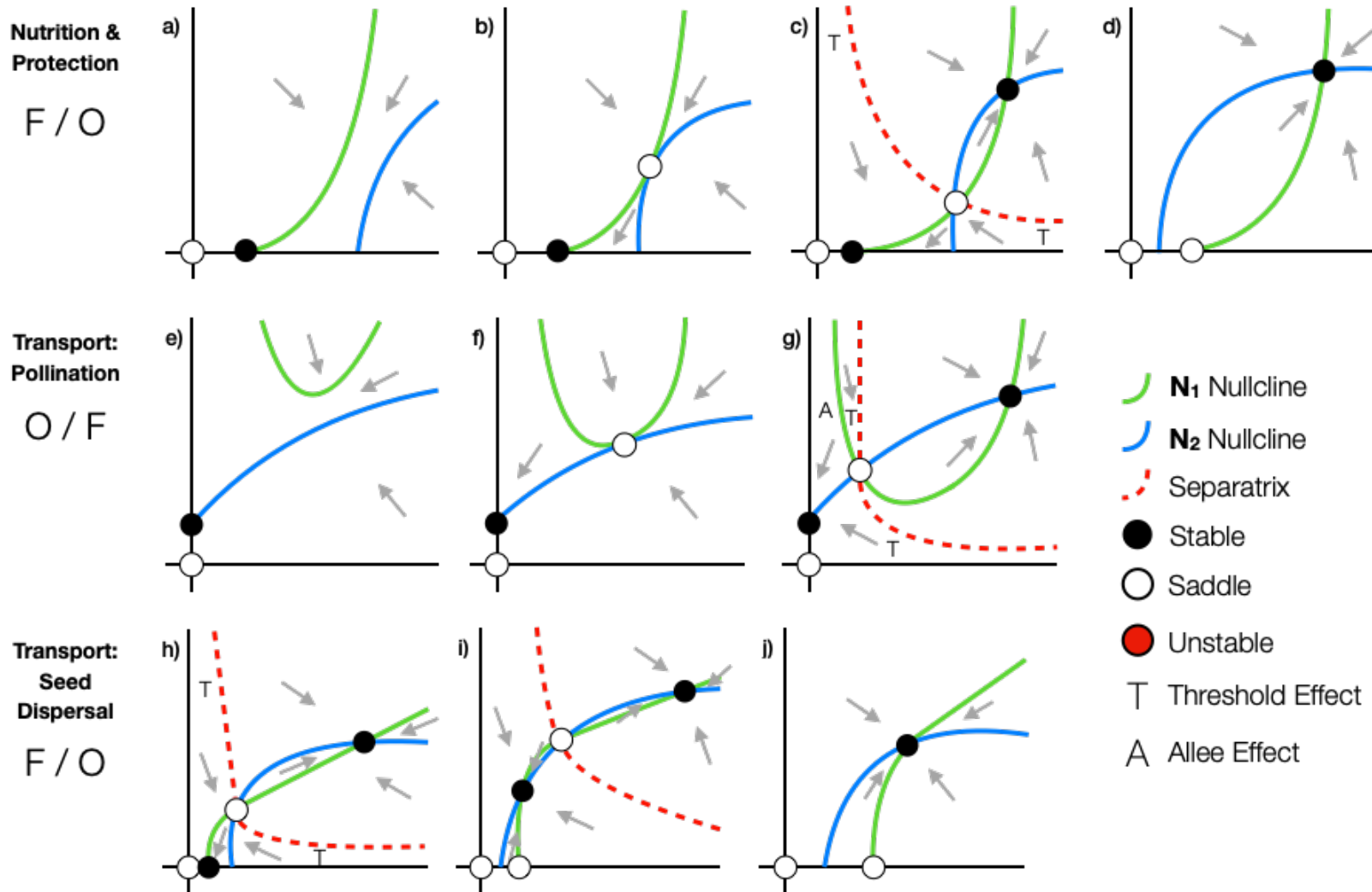
943 (2) If the nullclines intersect exactly once when plants are obligate (Fig. B1f), this is an  
944 ecologically unlikely case that we neglect.

945 (3) If the nullclines intersect twice with at least one intersection in the ecological region  
946 (e.g. Fig. B1g, B1h), then coexistence is feasible. The low-density equilibrium is a saddle  
947 point while the high-density equilibrium is stable. When only one intersection occurs in the  
948 ecological region, it is the stable coexistence equilibrium.

949 (4) If the nullclines intersect three times in the ecological region (e.g. Fig. B1i), then  
950 coexistence is feasible. The low and high density equilibria are stable (“bistability”) and the  
951 intermediate equilibrium is a saddle point. Bistability appears to only occur when at least  
952 one nullcline changes concavity in the ecological region. Our transport models display  
953 bistability because their nullclines change from concave up to concave down (pollination,  
954 Figs. 2d, 2f) or from concave down to linear growth (seed dispersal, Figs. 3d, 3f). However,  
955 bistability can more generally result from Type III functional responses in facultative  
956 mutualists (see Appendix C).

957 *References*

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



960

961 **Figure B1. Examples of structural instability.** Phase plane diagrams illustrating smooth transitions from infeasible to feasible coexistence (from left to right  
 962 panels within a row). Formatting follows Figs. 1-3. Labels for each row identify the models being illustrated (Table 1) and species 1 / species 2 as obligate (O) or

963 facultative (F). **(a-d)** The  $N_2$  nullcline shifts smoothly to the left, due to, for example, increasing conversion efficiency ( $c_{21}$ ). This moves the system from **(a)**  
964 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  
965 densities fall below a threshold, to **(d)** guaranteed stable coexistence. This type of structural instability occurs in both our nutrition and protection models (shown)  
966 and in our pollination model when plants are facultative (not shown). **(e-g)** the vertex of the  $N_1$  nullcline shifts smoothly down, due to, for example, increasing  
967 partner quality ( $y_{12}$ ). This moves the system from **(e)** infeasible, to **(f)** ecologically unlikely, through a blue sky bifurcation in which **(g)** coexistence is feasible  
968 and stable but threshold and Allee effects are present. **(h-j)** The  $N_1$  nullcline shifts smoothly to the right, due to, for example, decreasing maximum negative  
969 density-dependence ( $s_{1max}$ ), i.e. negative density-dependence in the absence of the partner. This moves the system from infeasible (not shown), to ecologically  
970 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  
971 stable coexistence is guaranteed but occurs either at a low- or high-density equilibrium, to **(j)** guaranteed stable coexistence. This type of structural instability  
972 occurs in both our seed dispersal model (shown) and in our pollination model when plants are facultative (not shown).

973

## Appendix C

974

### *Functional Forms*

975       To understand the robustness of our results, we analyzed our models (Table 1) using other  
976 functional forms in addition to the saturating forms presented in the main text. Specifically, we  
977 report all possible dynamical outcomes for every combination of obligate and facultative partners  
978 with Holling Type I, II, and III functional responses. Table C1 specifies the mathematical  
979 expressions used for each model. Notice that in the transport models, reproductive services ( $S$ ) to  
980 population  $i$  are a function of partner  $j$ 's consumption or visitation rate ( $C_R$ ) on  $i$ , so only the  
981 functional form for  $j$  needs to be specified.

982       Our results are generally robust to variation in functional form (Figs. C1-C3). We  
983 highlight the exceptions to that pattern here. In our nutrition and protection models (Fig. C1),  
984 coexistence is infeasible or leads to the orgy of mutualism (that is, unstable coexistence) when  
985 both partners have Type I functional responses. Additionally, bistability becomes a possible  
986 dynamical outcome when a facultative partner has a Type III functional response. In our  
987 pollination model (Fig. C2), all dynamical outcomes are as reported in the main text, even when  
988 pollinators follow a Type I functional response. In our seed dispersal model (Fig. C3), the orgy of  
989 mutualism always occurs when dispersers follow a Type I functional response.

990       Though we do not analyze them here, other functional forms including the Beddington-  
991 DeAngelis formula, ratio-dependent forms, and unimodal forms should be used in our models  
992 according to the specific system (reviewed by Holland 2015). Note that for nutrition and transport  
993 mutualisms, we derived models in which the functional responses (or more precisely, numerical

994 responses, Revilla 2015) are direct functions of recipient or partner consumption rate. However,  
995 our models can also accommodate functional responses interpreted as “net benefit” curves (e.g.,  
996 Holland *et al.* 2002, Morris *et al.* 2010) if costs and benefits affect the same vital rate (i.e., if  
997 “costs” simply reduce the benefits that accrue to a given vital rate). Under this interpretation,  
998 unimodal functional forms may arise (e.g. Morris *et al.* 2010) which could lead to substantially  
999 different dynamical predictions than those presented here.

### 1000 *Alternative Models*

1001 In the main text, we presented a protection model for species  $i$  in which the partner  
1002 population ( $N_j$ ) reduces mortality ( $d$ ) by deterring natural enemies (Eqn. 3). If  $j$  instead reduces  
1003 mortality via attendance on the recipient population (e.g. Morales 2000), we choose  $S(N_i, N_j) =$   
1004  $\frac{N_j}{k+N_i}$  or  $S(N_i, N_j) = C_R(N_i, N_j) = \frac{a_{ij}N_j}{1+a_{ij}h_{ij}N_i}$  so that per-capita death rate declines proportional to  
1005  $j$ 's recruitment rate or consumption rate on  $i$ 's rewards, respectively. Then, benefit saturates  
1006 when  $i$ 's density is high. Here, we analyze the specific model:

$$1007 \quad \frac{dN_1}{dt} = N_1 \left[ b_1(1 - s_1N_1) - \left( d_{1_{max}} - d_{1_{diff}} \frac{a_{12}N_2}{1+a_{12}h_{12}N_1} \right) \right] \quad \text{Eqn. C1}$$

1008 where attendees ( $N_1$ ) are obligate on protectors ( $N_2$ ) when  $r_1 = b_1 - d_{1_{max}} < 0$  and facultative  
1009 otherwise. We additionally require  $d_{1_{diff}} = d_{1_{max}} - d_{1_{min}} \leq d_{1_{max}}h_{ij}$ , so that net mortality is  
1010 always non-negative.

1011 Alternatively, we could choose the simplest function so that mortality is reduced  
1012 monotonically with saturation when partner density is high, as proposed by Thompson *et al.*  
1013 (2006). In this case, we modify Eqn. 3 to give the specific model:

1014 
$$\frac{dN_1}{dt} = N_1 \left[ b_1(1 - s_1 N_1) - \left( d_{1_{min}} + d_{1_{diff}} \frac{1}{k + N_2} \right) \right] \quad \text{Eqn. C2}$$

1015 where, again, attendees ( $N_1$ ) are obligate on protectors ( $N_2$ ) when  $r_1 = b_1 - d_{1_{max}} < 0$  and  
1016 facultative otherwise.

1017 Another alternative is to assume that protection services increase attendees' maturation  
1018 rate ( $b$ ) as in the case where ants ( $N_2$ ) guard the pupae of lycaenid butterflies ( $N_1$ , Travassos &  
1019 Pierce 2000). Then, we modify Eqn. 3 to give the specific model:

1020 
$$\frac{dN_1}{dt} = N_1 \left[ \left( b_{1_{min}} + b_{1_{diff}} S(N_1, N_2) \right) (1 - s_1 N_1) - d_1 \right] \quad \text{Eqn. C3}$$

1021 where we choose  $S(N_1, N_2) = \frac{N_2}{k + N_1}$  to represent ant recruitment rate. Lycaenids are obligate on  
1022 ants when  $r_1 = b_{1_{min}} - d_1 < 0$  and facultative otherwise.

1023 Finally, we could assume that tending by protectors decrease attendees' mortality due to  
1024 density-dependent processes ( $s$ ), which may act over the course of attendees' lives. For example,  
1025 ants reduce aphid mortality through cleaning and quarantining practices that (presumably)  
1026 prevent the spread of fungal infections (Nielsen *et al.* 2010, Durak *et al.* 2016). Then, we modify  
1027 Eqn. 3 to give the specific model:

1028 
$$\frac{dN_1}{dt} = N_1 \left[ b_1 - d_1 - \left( s_{1_{max}} - s_{1_{diff}} S(N_1, N_2) \right) N_1 \right] \quad \text{Eqn. C4}$$

1029 where we again choose  $S(N_1, N_2) = \frac{N_2}{k + N_1}$  to represent ant recruitment rate. Aphids ( $N_1$ ) are  
1030 obligate on ants ( $N_2$ ) when  $r_1 = b_1 - d_1 < 0$  and facultative otherwise.

1031 We can also consider an alternative model for seed dispersal. In the main text, we  
1032 presented a model (Eqn. 5) wherein plants benefit from seed dispersal by escaping density-  
1033 dependent sources of mortality during maturation ( $s$ ). Some plants ( $N_1$ ) instead benefit  
1034 exclusively via an increase in seed survival/germination rate ( $g$ ) because gut passage through  
1035 avian or mammal dispersers ( $N_2$ ) removes pathogens from seeds and provides chemical  
1036 camouflage from seed predators (Fricke *et al.* 2013). In this case, we modify Eqn. 5 to give the  
1037 specific model:

1038 
$$\frac{dN_1}{dt} = N_1 \left[ b_1 \left( g_{1_{min}} + g_{1_{diff}} S(N_1, N_2) \right) (1 - s_1 N_1) - d_1 \right] \quad \text{Eqn. C5}$$

1039 where plants are obligate on dispersers when  $r_1 = b_1 g_{1_{min}} - d_1 < 0$  and facultative otherwise.

1040 We choose  $S(N_1, N_2) = C_R(N_1, N_2) = \frac{a_{12} N_2}{1 + a_{12} h_{12} N_1}$  to represent the consumption rate of fruit by

1041 dispersers. Since we originally defined  $g$  as the fraction of seeds that germinate, we additionally

1042 require  $g_{1_{diff}} = g_{1_{max}} - g_{1_{min}} \leq (1 - g_{1_{min}}) h_{12}$ , so that net germination fraction is always

1043 between 0 and 1.

1044 Protection models C1-C3 have similar qualitatively nullcline geometries as our main text  
1045 protection model (Fig. C4a-d). Though the nullcline for model C1 does not saturate (Fig. C4b), it  
1046 will yield the same dynamical outcomes as our main text model (Fig. 2) when paired with a  
1047 partner such as a nutritional mutualist with a concave down saturating or linear nullcline. Models  
1048 C2-C3 have exactly the same qualitative nullcline geometries as our main text model, despite  
1049 mutualism potentially affecting different vital rates in these models (Fig. C4c-d). In all cases  
1050 (Eqns. C1-C3), as in our main text model (Eqn. 3), the effect of mutualism is independent of  
1051 recipient density.

1052 In contrast, protection model C4 has qualitatively identical nullcline geometry to our main  
1053 text seed dispersal model (Fig. C4e), because in both cases the effect of mutualism is dependent  
1054 on and saturating in terms of recipient density. In model C4, protection services affect a density-  
1055 dependent process (modifying  $s$ ) and benefit is proportional to attendance or recruitment rate by  
1056 protectors on the recipient species (saturates via intraspecific density-dependence).

1057 Finally, seed dispersal model C5 has qualitatively similar nullcline geometry to our main  
1058 text nutrition and protection models (and to protection models C1-C3), because the benefits of  
1059 seed dispersal (increased germination) are not directly dependent on recipient density.

### 1060 *Extensions*

1061 The extensions proposed here are not mutually exclusive and can be applied to any of our  
1062 main text models. First, we consider an extension that accounts for the costs of rewards  
1063 exploitation, including the special case in which depletion of rewards due to exploitation induces  
1064 variable and potentially high costs of rewards production. Exploitation costs are those incurred  
1065 while a partner is acquiring rewards, such as damage to flowers by pollinators during foraging for  
1066 nectar and pollen. Such costs accumulate proportionally to the exploiter's visitation or rewards  
1067 consumption rate, which can affect individual fitness and demographic rates, and is often  
1068 assumed to affect population growth rate as well (e.g. Aizen *et al.* 2014). Interestingly, rewards  
1069 production costs can also accumulate proportionally to rewards consumption rate. For example,  
1070 when tended by ants, some aphid species enrich their honeydew with synthesized sugars, which  
1071 decreases their fecundity and body size, presumably due to carbohydrate depletion (Yao *et al.*  
1072 2000, Yao & Akimoto 2001). Though honeydew enrichment is a construction cost (rewards



1073 production), it can be modeled as proportional to rewards consumption (exploitation) because  
1074 ants' consumption behavior induces the metabolic costs of enriching depleted honeydew.

1075 For easy comparison to previous works that include costs (e.g. Holland & DeAngelis  
1076 2010, Table A1), we modify our nutritional model with Michaelis-Menten functional responses  
1077 to include rewards exploitation costs as follows:

$$1078 \quad \frac{dN_i}{dt} = N_i \left[ b_i (1 - s_i N_i) + c_i C_R(N_j, N_i) - q_i C_R(N_i, N_j) - d_i \right] \quad \text{Eqn. C6}$$

1079 where costs to population  $i$  are related to the benefits to population  $j$  because they occur via the  
1080 same mechanism:  $j$ 's exploitation of  $i$ 's rewards. Mathematically, this is a special case of  
1081 Holland and DeAngelis' (2010) model (specifically, our model has four fewer parameters), which  
1082 assumed independently parameterized functional responses for benefits and costs. The coefficient  
1083  $q_i$  controls the effect of rewards exploitation on population density. If rewards exploitation has  
1084 minimal population-level effects,  $0 \leq q_i \ll 1$ . Assuming both species incur exploitation costs  
1085 yields the specific model:

$$1086 \quad \begin{cases} \frac{dN_1}{dt} = N_1 \left[ b_1 (1 - s_1 N_1) + c_1 \frac{v_1 N_2}{k_1 + N_2} - q_1 \frac{v_2 N_2}{k_2 + N_1} - d_1 \right] \\ \frac{dN_2}{dt} = N_2 \left[ b_2 (1 - s_2 N_2) + c_2 \frac{v_2 N_1}{k_2 + N_1} - q_2 \frac{v_1 N_1}{k_1 + N_2} - d_2 \right] \end{cases} \quad \text{Eqn. C7}$$

1087 Our simple nutrition model (Eqn. 2) yields an increasing, concave down nullcline that  
1088 saturates with respect to the partner's density. Including an explicit term for saturating costs of  
1089 rewards consumption (Eqn. C7) bends species' nullcline towards the partner's axis at high  
1090 partner density, eventually curving it back around towards the origin into a lobe shape (Fig. C5a).  
1091 This is because high partner density exerts high saturating costs on the recipient due to rewards

1092 consumption, which may exceed the benefits that can be acquired. When coexistence is feasible,  
1093 up to three non-trivial equilibria occur: a stable node flanked by two saddle points. Stable  
1094 coexistence can occur at higher densities than either species could achieve alone. However,  
1095 separatrices running through the saddle points define basins of attraction that lead to extinction  
1096 or, if at least one species is facultative, single-species persistence. This ensures instability when  
1097 one population is of substantially higher density than the other due to overexploitation of the rare  
1098 partner (regions labeled “E,” Fig. C5a). This is contrast to threshold effects defined in the main  
1099 text wherein the low-density partner benefits from mutualism but cannot provide sufficient  
1100 reciprocal services. When the low-density partner becomes even rarer, it experiences an Allee  
1101 effect, leading to its extinction (“A,” Fig. C35a). The high-density partner will also go extinct if it  
1102 is obligate upon the low-density partner. See Holland and DeAngelis (2010) for a complete  
1103 analysis and Cropp and Norbury (2018) for a summary of the model’s behavior.

1104         Second, we consider an extension that accounts for dynamics of consumption of  
1105 individuals in a partner population. For example, butterflies and moths often act as herbivores as  
1106 larvae (damaging or killing plant vegetation,  $V$ ) and as pollinators (consuming nectar rewards,  $R$ )  
1107 when mature. Similarly, protector ants sometimes consume individuals of their attendee  
1108 population (aphids, lycaenids, plants, etc.) in addition to the provided rewards (honeydew, nectar,  
1109 etc.). This ‘vegetative’ consumption ( $C_V(\mathbf{N}_i)$ ) directly reduces the attendees’ density:

1110                     
$$\frac{dN_i}{dt} = N_i \left[ b_i(1 - s_i N_i) - C_V(N_i, N_j) - \left( d_{i_{max}} - d_{i_{diff}} S(N_j) \right) \right] \quad \text{Eqn. C8}$$

1111 and increases the protectors’ density:

1112 
$$\frac{dN_i}{dt} = N_i [b_i(1 - s_i N_i) + C_R(N_j, N_i) + C_V(N_j, N_i) - d_i] \quad \text{Eqn. C9}$$

1113 Specifically, we assume that rewards density is proportional to the attendees' density  
 1114 ( $N_1$ ), and that ants ( $N_2$ ) forage according to a Holling Type II functional response on both  
 1115 rewards and  $N_1$  (attendee individuals) but with different attack rates ( $a_{2R}, a_{2V}$ ) and handling  
 1116 times ( $h_{2R}, h_{2V}$ ):

1117 
$$\begin{cases} \frac{dN_1}{dt} = N_1 \left[ b_1(1 - s_1 N_1) - \frac{a_{2V} N_2}{1 + a_{2V} h_{2V} N_1} - \left( d_{1max} - d_{1diff} \frac{N_2}{k_1 + N_2} \right) \right] \\ \frac{dN_2}{dt} = N_2 \left[ b_2(1 - s_2 N_2) + c_{2R} \frac{a_{2R} N_1}{1 + a_{2R} h_{2R} N_1} + c_{2V} \frac{a_{2V} N_1}{1 + a_{2V} h_{2V} N_1} - d_2 \right] \end{cases} \quad \text{Eqn. C10}$$

1118 Then, attendees exhibit dynamics of an identical mathematical form to nutritional mutualists with  
 1119 rewards exploitation costs (Eqn. C6 with  $q = 1$  indicating consumption of individuals in the  
 1120 population). Protectors that access both rewards and individuals from their partner population  
 1121 exhibit qualitatively similar dynamics to protectors that consume only rewards (Eqn. 2): the  
 1122 nullclines are concave down, increasing curves that saturate with respect to attendee density.  
 1123 However, accessing an additional resource allows the protector population to saturate to a higher  
 1124 density (of  $\bar{N}_2 = \frac{r_2}{b_2 s_2} + \frac{c_V}{b_2 h_V} + \frac{c_R}{b_2 h_R}$ ) than could be supported by rewards alone.

1125 In our extended model (Eqn. C10), protector and attendee nullclines may intersect once or  
 1126 twice with similar dynamical outcomes as in our simple model (Fig. 1). When the nullclines  
 1127 intersect exactly twice, the lower-density equilibrium is a saddle point that induces a separatrix,  
 1128 under which overexploitation of attendees by protectors destabilizes the system by inducing an  
 1129 Allee effect in the attendee population that causes extinction of facultative partners. Our simpler

1130 model also exhibits destabilization that can result in extinction, but due to threshold effects  
1131 instead of overexploitation (Fig. 1A, B, D).

1132 Our extended model also allows for the protector and attendee to intersect three times,  
1133 leading to unique dynamical outcomes (Fig. C5b). Here, a separatrix divides the phase plane into  
1134 two regions. On the right side, a basin of attraction allows stable coexistence to be maintained at  
1135 a single high-density node (non-oscillatory coexistence). On the left side, overexploitation (“E,”  
1136 Fig. C5b) by the protector population causes an Allee effect (“A”) in the attendee population,  
1137 which does not necessarily lead to extinction. After depleting their resource population, the  
1138 protector population also declines, eventually allowing the attendee population to receive  
1139 sufficient benefit via protection compared to losses due to consumption. The system thus  
1140 recovers and coexistence is maintained in this region via a limit cycle (i.e. oscillations) around a  
1141 stable center, an outcome not seen in our simpler models.

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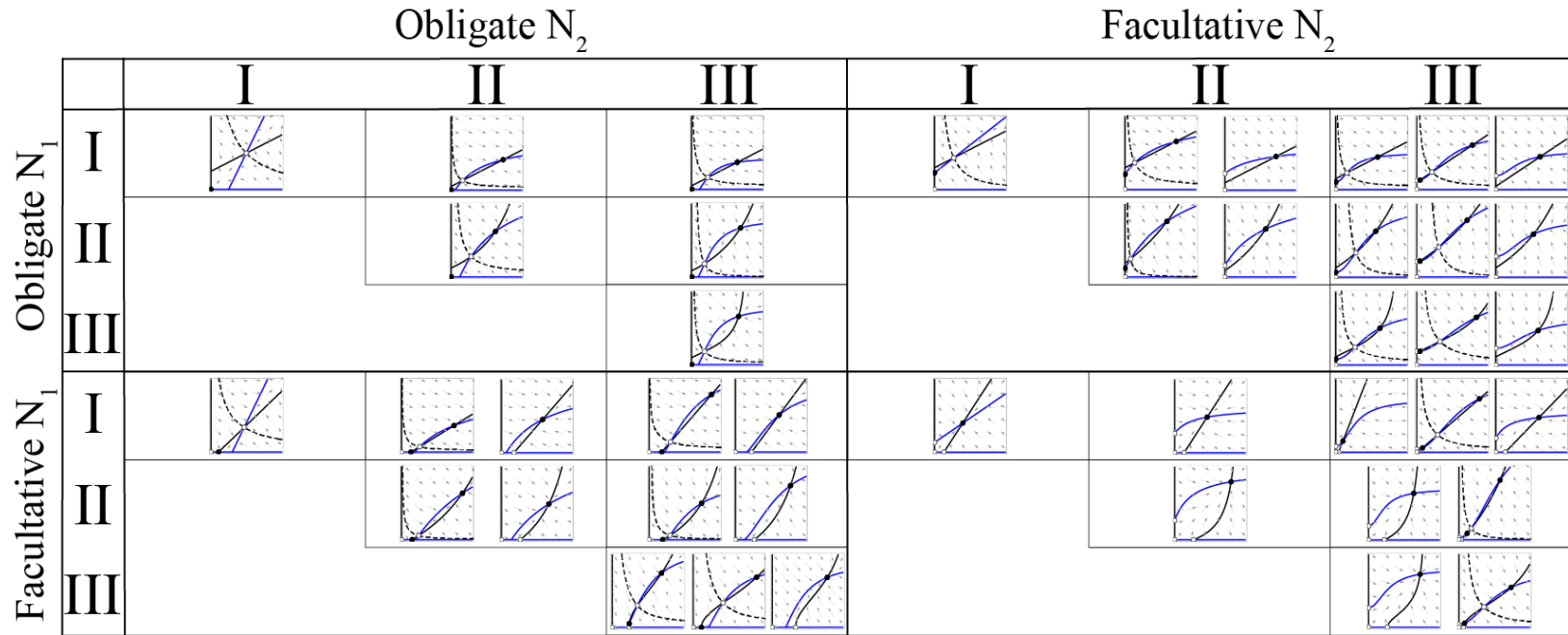
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1170

Type of Benefit	Type I	Type II	Type III
Nutrition $C_R(N_j)$	$a_{ij}N_j$	$\frac{a_{ij}N_j}{1 + a_{ij}h_{ij}N_j}$	$\frac{a_{ij}N_j^2}{1 + a_{ij}h_{ij}N_j^2}$
Protection $S(N_j)$	$N_j$	$\frac{N_j}{k_{ij} + N_j}$	$\frac{N_j^2}{k_{ij} + N_j^2}$
Transportation: Pollination $S(N_i, N_j) = C_R(N_i, N_j) * N_i$	$N_j N_i$	$\frac{a_{ji}N_j N_i}{1 + a_{ji}h_{ji}N_i}$	$\frac{a_{ji}N_j N_i^2}{1 + a_{ji}h_{ji}N_i^2}$
Seed Dispersal $S(N_i, N_j) = C_R(N_i, N_j)$	$N_j$	$\frac{a_{ji}N_j}{1 + a_{ji}h_{ji}N_i}$	$\frac{a_{ji}N_j N_i}{1 + a_{ji}h_{ji}N_i^2}$

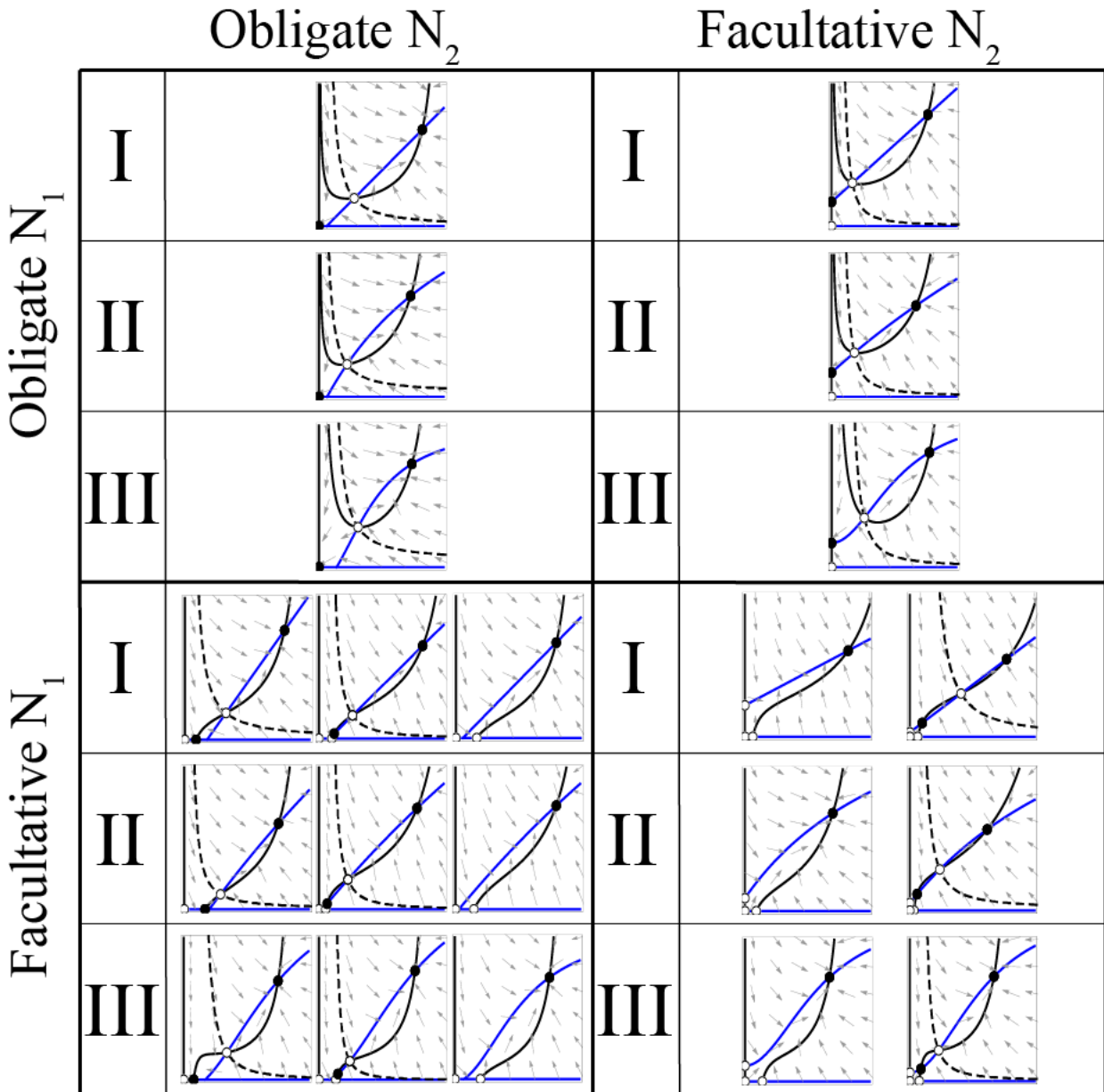
1171 **Table C1. Functional forms.** Functional forms used to assess robustness of results for each model. Functional forms describe the consumption rate on a  
1172 partner's rewards ( $C_R$ ) or the accrual of services provided by a partner ( $S$ ), which, in the transportation models, are a function of the partner's consumption  
1173 rate. Indices  $i$  and  $j$  refer to the recipient and partner population, respectively. For the nutrition model, we use the Holling notation for convenience.



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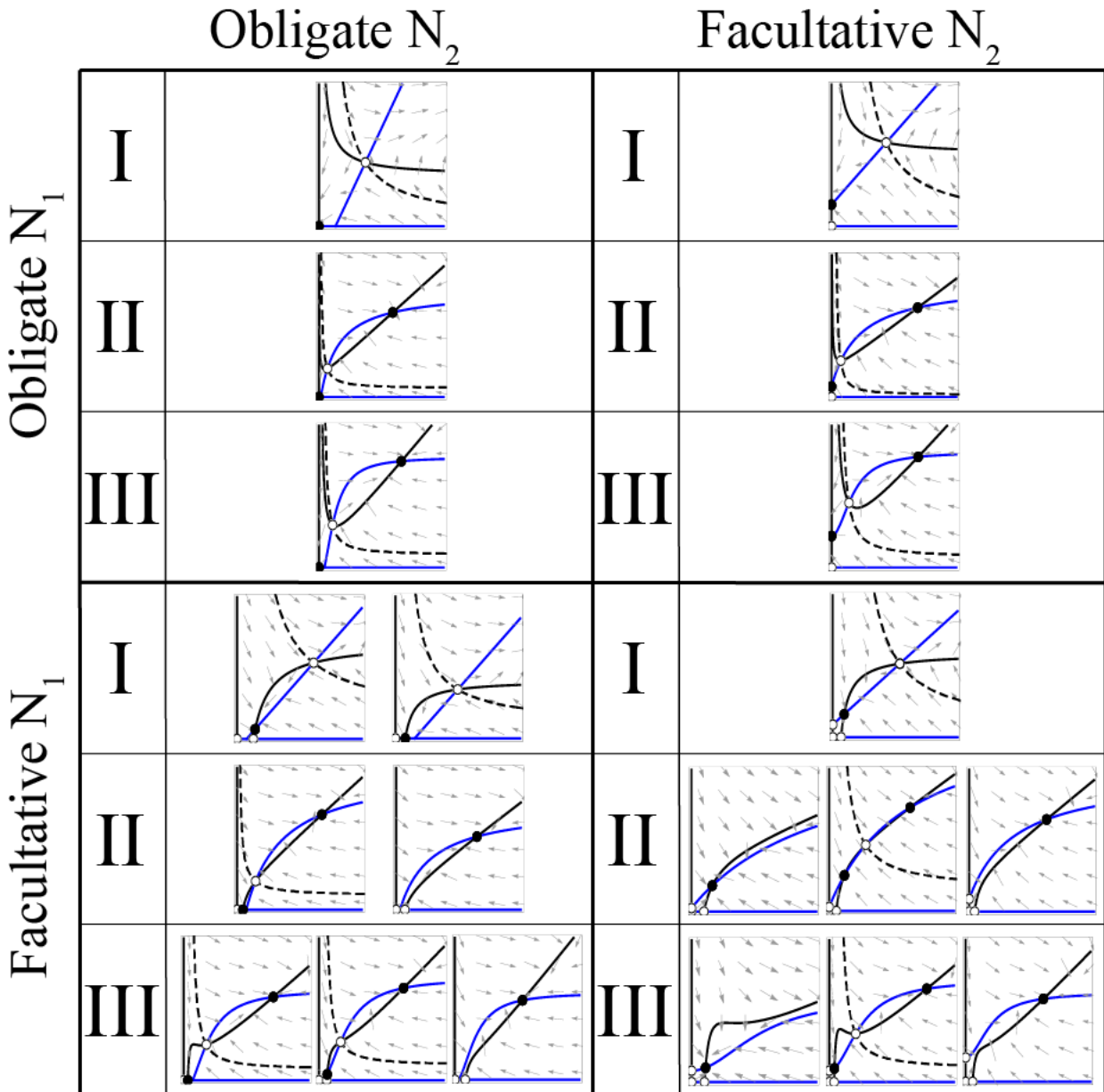
1175 **Figure C1. Effect of functional form on nutrition and protection mutualisms.** Panels show phase plane diagrams with unique dynamical outcomes  
 1176 when each partner population ( $N_1$ , black;  $N_2$ , blue) is an obligate or facultative mutualist following a Holling Type I, II, or III functional response (Table  
 1177 C1). Equilibria are stable (filled, black) or unstable or saddle points (hollow). Saddle points are bisected by a separatrix (dashed black line) that divides the  
 1178 plane into two regions.





1179

1180 **Figure C2. Effect of functional form on pollination mutualisms.** Formatting follows Figure C1. Plants ( $N_1$ )  
 1181 accumulate benefit proportionally to the functional form of animal pollinators ( $N_2$ ).

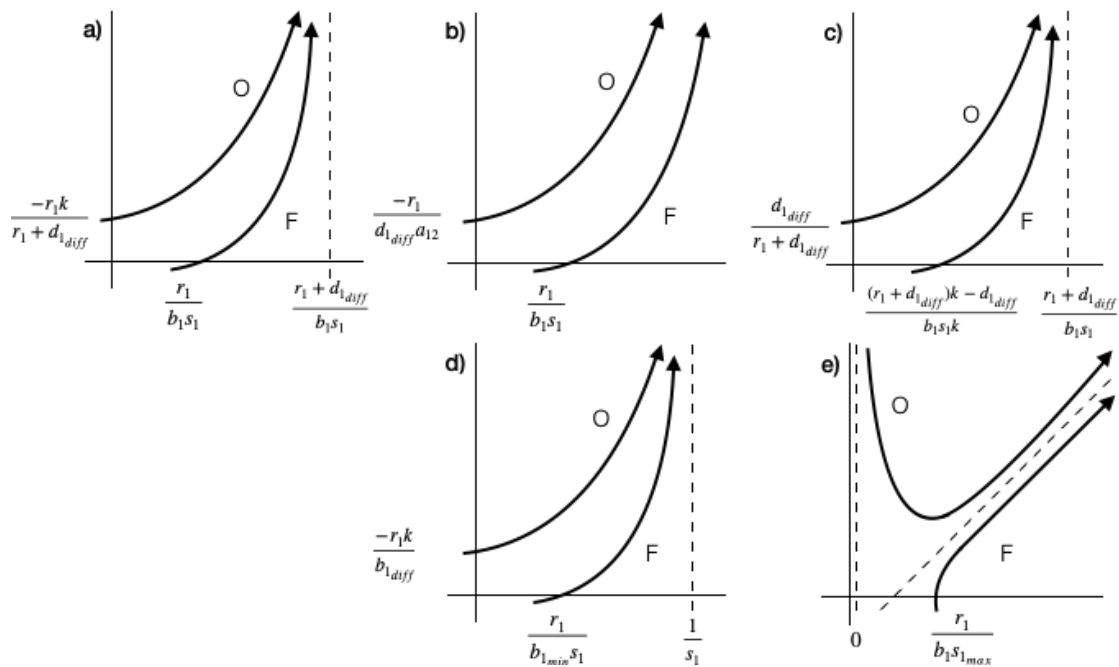


1182

1183 **Figure C3. Effect of functional form on seed dispersal mutualisms.** Formatting follows Figure

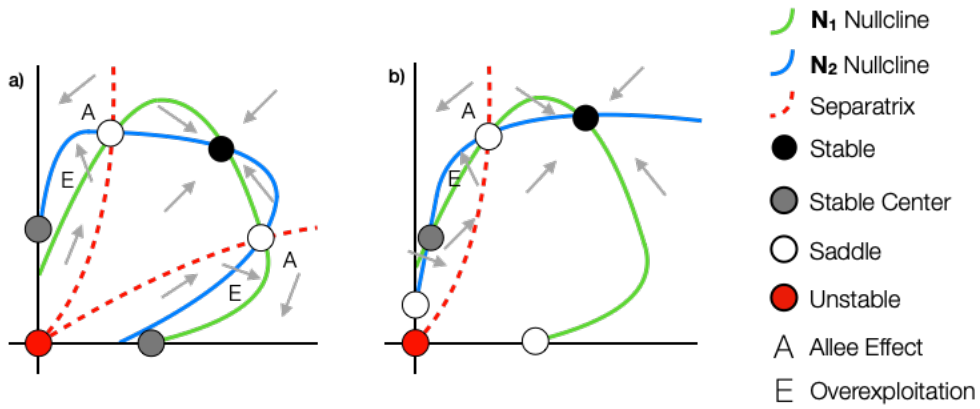
1184 C1. Plants ( $N_1$ ) accumulate benefit proportionally to the functional form of animal pollinators

1185 ( $N_2$ ).



1186

1187 **Figure C4. Nullcline geometry of alternative protection models.** Only geometries when coexistence is feasible are  
 1188 shown. Nullclines (black lines) intersect the x-axis when recipients of protection services are facultative (F)  
 1189 mutualists or the y-axis when they are obligate (O). Asymptotes are shown with dashed lines. (a) Main text model  
 1190 (Eqn. 3). (b) Model C1. (c) Model C2. (d) Model C3. (e) Model C4. (b-d) Benefits are not directly dependent on  
 1191 recipient density, but saturate due to (c) inter- or (b, d) intraspecific density-dependence. (d) Benefits are  
 1192 additionally limited by negative density-dependence. (e) Benefits are directly dependent on recipient density and  
 1193 saturate due to intraspecific density-dependence.



1194

1195 **Figure C5. Phase plane diagrams for our extensions.** Only a sampling of cases is shown for comparison to our  
1196 main text models (Figs. 1-3) and Holland and DeAngelis' (2010) models including cost terms (Table A1). **(a)** Model  
1197 C7. **(b)** Model C10.