

1 **Ecological theory of mutualism: Qualitative patterns in two-species population models**

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## Abstract

Mutualisms are ubiquitous in nature, provide important ecosystem services, and involve many species of interest for conservation. Theoretical progress on the population dynamics of mutualistic interactions, however, has comparatively lagged behind that of trophic and competitive interactions. Consequently, ecologists still lack a generalized framework to investigate the population dynamics of mutualisms. Here, we review historical models of two-species mutualisms from over the last 90 years. We find that population dynamics of mutualisms are qualitatively robust across derivations, including levels of detail, types of benefit, and inspiring systems. Specifically, mutualisms exhibit stable coexistence at high density and destabilizing thresholds at low density. We distinguish between thresholds resulting from Allee effects, low partner density, and high partner density, and their mathematical and conceptual causes. The dynamics of stable coexistence and thresholds in partner density emerge when benefits of mutualism saturate, whether due to intrinsic or extrinsic density dependence in intraspecific, interspecific, or both. These results suggest that there exists a robust population dynamic theory of mutualism that can make general predictions.

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## Introduction

Mutualisms are ubiquitous in nature and serve indispensable roles in supporting biodiversity and ecosystem function. Nearly all species on Earth participate in at least one of four main types of mutualism: seed dispersal, pollination, protection, and resource exchange including with symbionts (Janzen 1985, Bronstein 2015a,b). Moreover, up to  $\sim 3/4$  of phosphorus and nitrogen acquired by plants is provided by mycorrhizal fungi and nitrogen-fixing bacteria (van der Heijden *et al.* 2008) and  $\sim 1/3$  of crop production is dependent on animal pollination (Klein *et al.* 2007). The last 40 years has seen an important increase in studies on population ecology of mutualism but with little representation in textbooks (e.g., Kot 2001, Turchin 2003, Gotelli 2008, Morin 2011, Vandermeer & Goldberg 2013, Mittlebach & McGill 2019; but see McCann & Gellner 2020 for a chapter on mutualistic networks) and recent syntheses of theoretical ecology (e.g., Hastings & Gross 2019). This is, perhaps, due to disparate approaches and terminologies within this literature, on which we elaborate below. However, the qualitative predictions of this body of work are coherent and robust, and we submit that ecology will benefit from recognizing them as such. To make this ecological theory of mutualism available to the broader ecological community, we review the historical literature on the ecological theory of mutualism and synthesize generalities, both mathematical and conceptual, that can lay a foundation for deeper understanding of mutualism and, possibly, of community ecology as a whole.

Foundational theory in ecology was initially developed using Lotka-Volterra models. In this framework, constant coefficients describe the positive or negative effects between two interacting species as a linear function of the other species' density. The Lotka-Volterra model for predation and competition predict stable cycles (oscillations, Lotka 1925, Volterra 1926) and competitive exclusion (Volterra 1926, Gause 1934), respectively, which stimulated fruitful

66 empirical and theoretical work. Indeed, from the groundwork of Lotka-Volterra theory of  
67 predation came more general consumer-resource theory, with useful and surprising results such  
68 as the paradox of enrichment (Rosenzweig 1971) and a mathematical representation of seasonal  
69 cycling in lake food webs (Boit *et al.* 2012).

70 In contrast, Lotka-Volterra models for mutualism have been a less useful simplification  
71 than for predation and competition (Holland 2015). The original model (Gause & Witt 1935) and  
72 other formulations in which species benefit as a linear function of each other's density (Addicott  
73 1981) can predict unbounded population growth of both species (famously, "the orgy of mutual  
74 benefaction," May 1976). Additionally, the diversity of mechanisms by which species may  
75 benefit each other and the non-reciprocity of many of them, has cast suspicion on representing  
76 any "mutualistic" interaction as a simple exchange of positive effects (Bronstein 2001a,b).  
77 Mutualisms are more likely to exhibit shifting net effects than other interaction types  
78 (Chamberlain *et al.* 2014, Jones *et al.* 2015), with several exchanges dipping, for example, into  
79 parasitism.

80 Despite all these interesting mechanisms and patterns ripe for study, mutualisms have  
81 been subjected to less theoretical study than predation and competition. Many have speculated on  
82 historical reasons (Boucher 1985, Bronstein 2015b, Raerinne 2020), but we highlight two here.  
83 First, the terms used to identify interactions as "mutualism" have changed over time. Previous  
84 theory treated mutualism as a subset of facilitation, in which one species alters the environment  
85 to benefit a neighboring species (Callaway 2007), or symbiosis, in which species coexist in  
86 "prolonged physical intimacy" (Bronstein 2015b), or used those terms interchangeably.  
87 Additionally, the terms "mutualism," "cooperation," and "protocooperation" have been used  
88 idiosyncratically for beneficial interactions within species as well as between them (Bronstein

89 2015b). Furthermore, some mutualisms are “indirect,” such that benefits to one partner can only  
90 be realized in the presence of an external species or environmental condition (Holland &  
91 DeAngelis 2010). In this review, we limit our scope to mutualism defined as reciprocally  
92 beneficial interactions between two species without reference to the partners’ intimacy or  
93 environmental effects (Bronstein 2015b). We largely focus on direct mutualism or models that  
94 approximate the effects of indirect mutualism through two-species models, though we touch on  
95 some other cases (e.g., Thompson *et al.* 2006).

96         Second, the mechanisms by which species benefit each other in mutualisms are extremely  
97 diverse. These mechanisms include, but are not limited to, habitat provisioning, deterrence of  
98 predators or competitors, increased growth, faster maturation, facilitated reproduction, improved  
99 digestion, parasite grooming, and resource consumption. Conceptual frameworks have attempted  
100 to organize this rich diversity, for example, by the types of benefits exchanged (nutrition,  
101 protection, or transportation), the mechanisms of exchange, or the obligacy of each partner  
102 (reviewed in Bronstein 2015, Douglas 2015). This diversity of mechanisms makes the  
103 development of general but informative theory for mutualism more difficult than, for example,  
104 predator-prey theory, in which the interaction can be simply modeled as the consumption of  
105 individuals of one species by the individuals of the other species.

106         As it stands now, mutualism has repeatedly been called a loose set of natural history  
107 studies with little theory to unite or divide them (Addicott 1981, Bronstein 2015). Despite an  
108 increasing number of theoretical studies, an “ecological theory of mutualism” has not penetrated  
109 the greater ecological community (Bronstein 2015, Valdovinos 2019, recent textbooks). The  
110 studies that exist have suffered from a pattern of neglect and repeated rediscovery (Boucher  
111 1985, Morin 2011). Calls continue for simple but usable theory that synthesizes among



134 Gause and Witt (1935) proposed a model for mutual aid between a host and symbiont,  
135 inspired by Konstitzin (1934; Wolin 1985). This model was a modification of the Lotka-Volterra  
136 competition equations with positive (instead of negative) interaction coefficients (Eqn 1; see  
137 Table 2 for numbered equations). Benefits increased linearly with increasing partner density,  
138 while the strength of negative (intraspecific) density-dependence also increased linearly with the  
139 growth of the species receiving the benefit (i.e., the recipient species; Fig. 1B-F). In this  
140 formulation, mutualism has two effects: it increases the low-density growth rate of the recipient  
141 and the recipient's "equilibrium" density. The second effect means that mutualism increases the  
142 carrying capacity of the recipient species in the presence of its partner. However, hereafter, we  
143 reserve the term carrying capacity for density in the absence of the mutualistic partner. As  
144 written, the model accommodates only what we now call "facultative" mutualists (Vandermeer  
145 & Boucher 1978), those that can persist at positive density ("carrying capacity",  $K$ ) in the  
146 absence of their partner ( $K > 0$ ). Gause and Witt also commented that increasing the coefficients  
147 of mutual aid increases both species' equilibrium biomass until they pass to infinity, but that  
148 infinite populations are obviously unreasonable and microcosm studies suggest that the strength  
149 of mutual aid coefficients should decrease as species grow. These two studies (i.e., Konstitzin  
150 1934, Gause & Witt 1935) initiated theoretical research on what we now call mutualism around  
151 the same time as theoretical research on predation and competition, but then paused for nearly 40  
152 years (until 1970s).

153 Beginning in the 1970s, mutualism received attention as a destabilizing force in  
154 ecological networks represented as random community matrices (May 1972, May 1973), with  
155 the unbounded growth in the Lotka-Volterra models of mutualism being called a "silly solution"  
156 that leads to an "orgy of mutual benefaction" (May 1976). Using Lotka-Volterra models, authors

157 better characterized the conditions that lead to unbounded growth found by Gause and Witt's  
158 original model of mutualism (Albrecht *et al.* 1974, Vandermeer & Boucher 1978, Goh 1979,  
159 Travis & Post 1979). Other forms of linear benefits were investigated such as those that increase  
160 per-capita growth rate, equilibrium density, or both (Fig. 1). Whittaker (1975) introduced a  
161 model in which mutualism increases the equilibrium density of one partner and both the  
162 equilibrium density and per-capita growth rate of the other partner. This model accommodates  
163 "obligate" mutualists like symbionts living on a host that cannot persist in the absence of that  
164 host, that is, have zero carrying capacity ( $K = 0$ ) in the absence of their partners. The mutualistic  
165 symbiont-host interaction linearly increases the carrying capacity for the symbiont (Eqn 2) while  
166 benefiting the host population by increasing its low-density growth rate and its equilibrium  
167 density (Eqn 1). Later, Addicott (1981) introduced a model in which mutualism only increases  
168 the per-capita growth rate (Fig. 1A, Eqn 4), inspired by the ant-aphid mutualism described in  
169 Addicott (1979). Addicott emphasized that these different linear benefit models could be used in  
170 a mix-and-match style to accommodate different types of benefits exchanges.

171 Vandermeer and Boucher (1978) proposed the groundbreaking idea that mutualistic partners  
172 may exist along continuums of obligacy and interaction strength. The authors defined facultative  
173 mutualists as those with positive carrying capacity in absence of their partner. Obligate  
174 mutualists were defined more abstractly with zero or negative carrying capacity in absence of  
175 their partner ( $K \leq 0$ ), which represents the demographic drawdown that mutualism must exceed  
176 to allow persistence of the population. Negative carrying capacity arises mathematically when a  
177 population has a negative "intrinsic" growth rate, as is the case when its per-capita death rate  
178 exceeds its per-capita birth rate (Table 2). This choice is useful both mathematically and  
179 ecologically because it allows the strong demographic pulldown when death rates exceed birth

180 rates to be represented, without introducing numerical issues due to zero carrying capacity.  
181 Vandermeer and Boucher's analysis of Gause and Witt (1935)'s model found that obligate  
182 partnerships would either collapse to extinction when benefits are weak or exhibit a threshold  
183 population size under which they go extinct and above which they grow unboundedly when  
184 benefits are strong (Fig. 1E-F). They also found that facultative partners are likely to coexist  
185 stably when benefits are weak or exhibit unbounded growth when benefits are strong (Fig. 1C-D,  
186 also see Wolin 1985). Remarkably, Vandermeer and Boucher (1978; also see Christiansen &  
187 Fenchel 1977) anticipated the qualitative dynamics generated by extending these models to  
188 saturating benefit responses. However, the authors emphasized that unbounded growth was still  
189 an ecologically relevant result because it indicates persistence of the two-species mutualistic  
190 system. Indeed, they argue that persistence (whether species persist or go extinct) is a more  
191 biologically useful metric than neighborhood stability (whether the system returns to equilibrium  
192 after a small perturbation). Subsequent authors also emphasized other properties of stability of  
193 mutualism such as return time to equilibrium (Addicott 1981, Wolin 1985), species persistence  
194 (Valdovinos *et al.* 2013, 2016, 2018), or biomass variability (Hale *et al.* 2020).

### 195 *Saturating benefit models*

196 The earliest models that incorporated saturating benefits within mutualism invoked  
197 unspecified (intraspecific) environmental constraints that limit population growth in the presence  
198 of a mutualist (Whittaker 1975, May 1976, Dean 1983, Wolin & Lawlor 1984). For example,  
199 Whittaker (1975) assumed extrinsic, intraspecific limiting factors to the benefits a host could  
200 receive from its symbiont (Eqn 3, Fig. 2A). This is the first of many models that exhibit  
201 thresholds (*sensu* Vandermeer & Boucher 1978), where the low density of one partner pushes the  
202 whole system to collapse. Some authors refer to these dynamics as "Allee thresholds" (e.g.,

203 Johnson & Amarasekare 2013), but these are not strictly Allee effects where populations decline  
204 due to their own low density.

205 This focus on extrinsic limits to benefit was epitomized by Wolin and Lawlor (1984). They  
206 derived models for five different ways in which mutualism could affect per-capita birth or death  
207 rates as functions of recipient density. For example, they compared models in which mutualism  
208 reduces intraspecific density-dependent limiting factors only in per-capita birth rates (Eqn 6, Fig.  
209 2C-D), only in per-capita birth rate but with saturating effects (Eqn 5, Fig. 2B), and both in birth  
210 and death rates with saturating effects (Eqn 2, Fig. 1B). These models were classified as  
211 describing mutualisms with effects primarily at high versus low self-density. Wolin and Lawlor  
212 concluded that low-density effects (i.e., primary effects on per-capita growth rate as opposed to  
213 equilibrium density) are stabilizing in terms of faster return times and the existence of a feasible,  
214 stable equilibrium. These models of “intraspecific density-dependence” (so called by later  
215 authors, Holland 2015) lacked biological mechanisms or reference to clear ecological examples,  
216 which perhaps pivoted the field away from this otherwise fruitful approach. In contrast, Soberón  
217 and Martinez del Rio (1981) proposed a detailed pollination model in which plant benefits are a  
218 function of pollinators’ visitation rate, modeled as a saturating Type II functional response. Thus,  
219 benefits to plants saturate as a function of their own density (intraspecific density-dependence),  
220 but due to factors intrinsic to the mutualism (that is, time constraints for pollinators handling  
221 flowers during foraging visits). Such an approach has seen a resurgence in recent literature (see  
222 *Consumer-resource models*, below) but was largely abandoned at the time.

223 Starting in the late 1980s, authors began to focus on “interspecific density-dependence,”  
224 which has been considered more consistent with other theories of interspecific interactions  
225 (Holland 2015). Wright (1989) proposed a model in which per-capita benefits saturate in terms

226 of partner density analogously to consumers foraging on resources due to limitations of  
227 consumer handling of resources or uptake rate (Fig. 2E-F). In the mutualistic case, benefits are  
228 assumed to saturate with increasing partner density, often as an additive, first order term to per-  
229 capita growth rate following a Holling Type II functional-response (Wright 1989, Bazykin *et al.*  
230 1997, Thompson *et al.* 2006, Holland & DeAngelis 2010, Wu *et al.* 2019, Hale *et al.* 2021). On  
231 the other hand, Thompson *et al.* (2006) proposed a theoretical framework that organized both  
232 terrestrial and aquatic mutualisms into those that affect birth rate, death rate, habitat acquisition  
233 or a combination of these benefits for each partner. Other authors have used different  
234 mathematical forms for analytical tractability (Pierce & Young 1986, García-Algarra *et al.*  
235 2014). Regardless, these assumptions result in both an increase in low-density growth rate and an  
236 increase in equilibrium density in the presence of mutualists.

237         These studies using the interspecific density-dependence approach included more  
238 ecological justification for mechanisms that limited benefit accrual. However, phenomenological  
239 accounts of environmental conditions limiting population growth were still present with most  
240 models via an undiscussed intraspecific limitation term (see discussion by Johnson &  
241 Amarasekare 2013). That is, authors assumed that at least one partner was limited by negative  
242 density-dependence to ensure curved nullclines and stable coexistence in the mutualism.  
243 Recently, Moore *et al.* (2018) introduced nonlinearities in intraspecific limitation while  
244 maintaining linear benefits. Mutualism is stable when density-dependence accelerates with  
245 increasing recipient density. Ecologically, this means that the growth rate of the population  
246 receiving the benefit decreases faster and faster at higher density, which has been observed  
247 empirically (Moore *et al.* 2018). This result highlights the importance of investigating the effect

248 of more realism in intraspecific limitation on the dynamics of mutualism, which has been largely  
249 under-explored.

250 Other authors derived models with benefits limited by both inter- and intraspecific  
251 density-dependence (May 1976, May 1978, Wells 1983, Fishman & Hadany 2010, Johnson &  
252 Amarasekare 2013). This added complexity was usually justified by system-specific  
253 considerations (e.g., May 1976, Wells 1983), but it also emerges from individual-level  
254 mechanisms in plant-pollinator systems (Fishman & Hadany 2010) or intraspecific competition  
255 for food or services (Johnson & Amarasekare 2013). In general, these limitations emerge when  
256 systems are limited both by availability of service providers (e.g., pollinators) and by the  
257 substrates that receive benefit (e.g., flowers to be pollinated, seeds to germinate, or individuals to  
258 protect from predators; Hale *et al.* 2021).

#### 259 *Cost-benefit models & shifting net effects*

260 A blooming of empirical work that started in the 1980s revealed that mutualisms are not  
261 only more (omni)present than previously expected but also context-dependent (Thompson 1988,  
262 Bronstein 1994, Herre *et al.* 1999, Chamberlain *et al.* 2014). That is, the effect of these  
263 interactions often shifts between mutualism and parasitism or competition due to the relative  
264 balance of costs and benefits of participating in the interaction. Moreover, costs and benefits  
265 themselves may be strongly varying across space, time, and other abiotic conditions. Early  
266 investigations of this topic used models that could accommodate different types of interactions  
267 through smooth transitions in parameter values (Whittaker 1975, Pierce & Young 1986). For  
268 example, Pierce and Young (1986) do not provide a specific mathematical form but use a  
269 geometric argument to investigate the dynamics of an ant-lycaenid butterfly interaction in which  
270 lycaenids may be mutualistic, commensalistic, or parasitic to tending ants.

271 Neuhauser and Fargione (2004) explored the mutualism-parasitism continuum using the  
272 classical predator-prey (or host-parasite) Lotka-Volterra model with the additional possibility of  
273 the parasite benefiting the host (Fig. 3A-B). The model includes both benefits and costs and it  
274 was applied to study plant-mycorrhizae interactions across gradients of soil fertility. The authors  
275 assumed that mycorrhizal fungi increase host-plant equilibrium density (benefits) but also  
276 linearly increase plant death rate due to exploitation (costs). This and other cost-benefit models  
277 can exhibit coexistence equilibria that are stable spirals, meaning that the populations densities  
278 will oscillate towards a fixed point (see *Patterns from Theory*). Zhang (2003) also modified a  
279 Lotka-Volterra model to accommodate mutualism but chose the competition instead of the  
280 predator-prey version of the model (Fig. 3C-E). The modified model assumed that the interaction  
281 between species was competitive at high density and mutualistic at low density, modeled  
282 phenomenologically as parabolic nullclines. This model can predict competitive exclusion,  
283 competitive coexistence where one partner dominates depending on initial density, thresholds in  
284 which low density of one partner drives the system to collapse, or “mutualism” according to the  
285 criterion that species coexistence stably at higher density than either could have achieved alone.  
286 Unfortunately, it is difficult to understand which of the diverse dynamics this model can exhibit  
287 are most ecologically relevant because interpretation is not provided for its parameters. A  
288 mechanistic derivation that achieves similar dynamics could be useful future work (but also see  
289 Gross 2008 for a similar approach on an explicit resource).

290 Other models also described different outcomes depending upon relative species' density  
291 (Hernandez 1998, Holland *et al.* 2002, Wang *et al.* 2019). In an important advance, Holland *et*  
292 *al.* (2002) proposed a suite of models in which different net effects result from the difference  
293 between increasing benefit functions and linear, saturating, or decreasing cost functions (see Fig.

294 1 of Holland *et al.* 2002). Their approach balances out different mechanisms that cause net  
295 effects of the interaction to shift as the relative densities of the populations change over time.

296 In seeking to represent the phenomena or mechanisms of shifting interaction outcomes,  
297 cost-benefit models revealed a much more complex set of potential dynamics for mutualism than  
298 had been previously reported. Saturating costs bends species' nullcline towards the partner's axis  
299 at high partner density, curving it back around towards the origin into a lobe shape (Fig. 3C-G).  
300 This is because high partner density exerts high saturating costs on the recipient due to resource  
301 consumption, which may exceed the benefits that can be acquired. Up to five non-trivial  
302 equilibria occur when coexistence is feasible. Moreover, separatrices running through saddle  
303 points define basins of attraction that lead to extinction or potential single-species persistence for  
304 facultative species. This ensures instability when one population is of substantially higher  
305 density than the other due to overexploitation of the rare partner (Fig. 4B). These dynamics  
306 contrast with the threshold effects (Fig. 4A) wherein the low-density partner benefits from  
307 mutualism but cannot provide sufficient reciprocal services. When the low-density partner  
308 becomes even rarer, it experiences an Allee effect, leading to its extinction (Fig. 4B). The high-  
309 density partner will also go extinct if it is obligate upon the low-density partner.

310 This much more complex set of potential dynamics that emerges from cost-benefit  
311 models exemplifies the criticism to mutualism theory as either too system-specific or too abstract  
312 to provide general insight into patterns and processes in mutualism (Bronstein 2001, Holland  
313 2015). Additionally, the field had not clearly connected the costs and benefits observed for  
314 individuals participating in a mutualism to potential population-level effects. The time was ripe  
315 for a conceptual synthesis.

316 *Consumer-resource approach to mutualistic interactions*

317           In a landmark work, Holland and DeAngelis (2010) formalized a consumer-resource  
318 approach to mutualism, providing a bridge between mutualism and the ecology of other  
319 interspecific interactions. In their framework, mutualisms may be “unidirectional” or  
320 “bidirectional” consumer-resource interactions, in which one or both partners benefit from  
321 consuming costly resources provided by the other (Fig. 4B, Fig. 3F-G, respectively). Such  
322 framework accommodated the shifting net effects of previous models (Holland & DeAngelis  
323 2009, previous section), and formalized the concept of ecological costs and benefits as  
324 modifications to demographic rates due to resource provisioning and nutrient or service  
325 consumption. Notably, this framework allowed mutualisms to be modeled as a dynamic  
326 continuum along a spectrum of other interspecific interactions, such as predator-prey and  
327 competitive interactions (Holland & DeAngelis 2009, Holland 2015). This was possible by  
328 clarifying the “currency” of the effects of mutualism as energy or biomass exchanges that  
329 manifest in changes to per-capita growth rate (or its components: birth, death, immigration, etc.).  
330 This framework stimulated recent development of theory for more specific systems (e.g., Kang *et*  
331 *al.* 2011, Martignoni *et al.* 2020)

332           Holland and DeAngelis (2010) modeled specific study cases similarly to previous studies  
333 (see *Saturating benefits* section), but with costs defined separately from benefits via saturating  
334 interspecific functions, accrued through provisioning resources. In contrast, service-provisioning  
335 by consumers is assumed to incur only fixed costs that can be accounted for in parameter values,  
336 like increased handling time when foraging for resources. The nonlinear costs cause lobe-shaped  
337 nullclines allowing up to five coexistence equilibria. Like the earlier Zhang (2003) model, many  
338 dynamics are possible including mutualistic stable coexistence and oscillations. However,  
339 instead of the competitive exclusion and competitive coexistence outcomes of Zhang’s model,

340 “parasitism” by one partner is due to exploitation by a high-density partner that outweighs the  
341 benefits it provides to the lower density partner. In most dynamics of the Holland and  
342 DeAngelis’ model, parasitism collapses the system to extinction instead of allowing a stable but  
343 exploitative interaction like in Zhang’s model.

344 Valdovinos *et al.* (2013) proposed a new type of consumer-resource model in which  
345 consumption is on “rewards” rather than individuals of the resource population directly (but also  
346 see Scheuring 1992 for a similar stage-structured model). Rewards are resources provided by one  
347 species to attract their mutualistic partners (Bronstein 2009). This model separates the dynamics  
348 of the plants’ vegetative biomass from the dynamics of the plants’ floral rewards. This key  
349 separation allows one to (1) track the depletion of floral rewards by pollinator consumption, (2)  
350 evaluate exploitative competition among pollinator species consuming the floral rewards  
351 provided by the same plant species, and (3) incorporate the capability of pollinators (adaptive  
352 foraging) to behaviorally increase their foraging effort on the plant species in their diet with  
353 more floral rewards available. Another advance of this model is incorporating the dilution of  
354 conspecific pollen carried by pollinators, which allows tracking competition among plant species  
355 for the quality of pollinator visits (see the next section). This model was developed for plant-  
356 pollinator networks, but its ideas paved the way for new investigations of mutualism at the  
357 pairwise (Revilla 2015, Wang 2019, Hale *et al.* 2021) and community (Valdovinos *et al.* 2016,  
358 Valdovinos & Marsland 2021, Hale *et al.* 2020) scales. For example, Revilla (2015) assumed  
359 rewards achieve steady state compared to changes in population density and derived models in  
360 which the linear consumption rate on rewards mediates benefits to the resource species. Hale *et*  
361 *al.* (2020) considered that pollinator visits can be approximated by consumption of floral  
362 rewards, and assumed that benefit to both plant and pollinator species is proportional to

363 consumption rates on floral rewards. Hale *et al.* (2021) further specified whether benefits should  
364 be proportional to per-capita consumption rate (as may be the case for animal-dispersed plants)  
365 or to total consumption rate (as may be the case for animal-pollinated plants which require  
366 obligate outcrossing). The latter leads to emergent Allee effects (Courchamp *et al.* 2018) for  
367 obligately animal-pollinated plants, explained by the plants' inability to attract pollinators at low  
368 density.

### 369 **Patterns from Theory**

370 We found that predictions for the population dynamics of mutualisms are qualitatively  
371 robust across the models reviewed, despite differences in level of detail, types of benefit, and  
372 inspiring systems. We synthesize these general findings below.

#### 373 *Mutualisms are stable with self-limitation and saturating benefits*

374 The stability of mutualistic interactions has generated controversy in the community  
375 ecology literature for decades (May 1972, May 1973, Bascompte *et al.* 2006, Holland &  
376 DeAngelis 2010, Allesina & Tang 2012, Johnson & Amarasekare 2013, Holland 2015,  
377 Valdovinos 2019, Hale *et al.* 2020). Topics of debate include definitions of stability (e.g., lack of  
378 positive feedbacks, robustness to perturbations), the scale at which they are assessed (e.g.,  
379 pairwise interactions, between guilds, within communities), and stabilizing mechanisms (e.g.,  
380 non-random interactions, environmental limits, consumer-resource dynamics).

381 Despite this debate, we found that theoretical investigation of pairwise mutualism has  
382 become conclusive: mutualisms are stable. Minimal realism in terms of limited benefits,  
383 accumulating costs, or accelerating intraspecific competition allow stable coexistence at high  
384 density according to the criteria of local stability analysis. That is, these systems will return to  
385 equilibrium after small perturbations to population densities. Under other definitions of stability,

386 such as persistence of populations or return time to equilibrium, mutualisms can be even more  
387 stable than predation and competition (Addicott 1981, Wolin & Lawlor 1984). Moreover, other  
388 mechanisms not reviewed here including spatial structure (Armstrong 1987, Amarasekare 2004,  
389 Mohammed *et al.* 2018), rewards or resource dynamics (Meyer *et al.* 1975, Scheuring 1992,  
390 Gross 2008, Revilla 2015, Cropp & Norbury 2019, Wang 2019), adaptive foraging (Valdovinos  
391 2013, 2016, 2018) and predators or competitors (Heithaus *et al.* 1980, Addicott & Freedman  
392 1984, Ringel *et al.* 1996, Mougi & Kondoh 2012, Hale *et al.* 2020) also stabilize mutualisms.

393         The pattern of stable coexistence of mutualists at high density is robust across  
394 mechanisms that limit benefit (Figs. 2-3). Both inter- and intraspecific density dependence lead  
395 to the same qualitative dynamics when they are present in at least one partner (also see  
396 *Thresholds*, below). One exception can occur when benefits accrue directly to a term that  
397 represents intraspecific density-dependence, which decreases per-capita growth rate at high  
398 density. If mutualism decreases this negative density-dependence to such an extent that it induces  
399 positive density-dependence at high partner density, the recipient population will begin accruing  
400 increasing benefit with its own increasing density (e.g., Eqns 5, 20). Then, the system can  
401 display unbounded growth (Fig. 2C-D) unless there are additional external limits to benefits  
402 accrued (Fig. 3K).

### 403         *Mutualisms exhibit thresholds when at least one partner is obligate*

404         Nearly all models that predict stable coexistence at high density also predict destabilizing  
405 thresholds at low density when one or more partners are obligate upon the mutualism (Fig. 2,  
406 Fig. 3A-B, H-K). Specifically, if either species dips below a critical threshold in population  
407 density, the obligate partner(s) will go extinct, even if initially at high density (Fig. 4A). This  
408 collapse occurs because, under the threshold, the low-density species cannot provide sufficient

409 benefits to its higher density partner. Threshold effects occur in systems with interaction  
410 strengths high enough to allow feasible coexistence, but with per-capita growth rates small  
411 enough (very negative for obligate partners, near-zero for facultative partners) that a partner can  
412 potentially achieve densities low enough for long enough that its obligate partner will go extinct.

413         Understanding threshold dynamics provides rich insight into interaction strength,  
414 obligacy, and positive feedbacks in mutualistic interaction. By definition, obligate mutualists  
415 have negative per-capita growth rate or carrying capacity in the absence of their partner. Thus,  
416 obligate mutualists can be only saved from population decline by benefits from mutualism that  
417 exceed their own negative intrinsic growth rate, that is, via strong mutualistic interactions. If  
418 both partners are initially at high enough density, obligate mutualists can achieve positive  
419 population growth, resulting in stable coexistence. However, if an obligate mutualist is at high  
420 density but its partner is at low density, the obligate mutualist will decline quickly due both to its  
421 negative intrinsic growth rate and due to strong intraspecific limitation at high density. The low-  
422 density partner may be growing due to mutualistic benefits, positive intrinsic growth, or release  
423 from intraspecific limitation. However, under the threshold, its population cannot recover fast  
424 enough to provide sufficient benefit to cancel out the negative intrinsic growth rate of the  
425 obligate partner and save it from decline. On the other hand, facultative partners can rely upon  
426 their own positive intrinsic growth rate to recover from low density, even after declines due to  
427 strong intraspecific competition or insufficient benefits provided by its partner. Thus, threshold  
428 effects do not occur in facultative partnerships.

429         These threshold dynamics emerge from the unique nature of mutualism and are  
430 potentially characteristic of this interaction. In predator-prey interactions, a low-density predator  
431 may benefit from a higher density prey population that is declining, but negative feedback in the

432 system also allows the crash of the predator population at high density and subsequent recovery  
433 of the prey population. In competition interactions, the higher density partner exerts stronger and  
434 stronger negative effects on the rare population, causing the rarer population to go extinct. In  
435 contrast, the positive feedback in the mutualistic system requires that both partners can provide  
436 sufficient benefits to the other to maintain the interaction. Notably, thresholds effects also occur  
437 in models that take very different approaches than those reviewed here. For example, Ingvarsson  
438 & Lundberg (1995) observed threshold effects dependent upon the ability for pollinators' ability  
439 to find flowers in a modified disease model for mutualism, while Wang (2019) showed that the  
440 thresholds observed in Revilla's (2015) model more precisely occur between pollinator and  
441 rewards density rather than pollinator and plant density directly. This further emphasizes the  
442 potential generality of thresholds in mutualisms.

#### 443 **Allee Effects**

444 Allee effects are another form of threshold but where the population declines below a  
445 threshold of its own density (instead of the partner's density). Here, we use "Allee effects" to  
446 refer specifically to strong, demographic Allee effects (Kramer *et al.* 2009) that emerge from the  
447 mutualism (i.e., are not hard coded into the population dynamics, Courchamp *et al.* 2018). Allee  
448 effects have been observed in food chains that include protection mutualism (Morales *et al.*  
449 2008) and in models of sequential colonization of patches by plants and mobile mutualists  
450 (Amarasekare 2004). As mentioned above, Hale *et al.* (2021) finds Allee effects in obligate  
451 plants when they become too rare to attract sufficient visitation from pollinators (Fig. 4C).  
452 Holland & DeAngelis (2010) find Allee effects in animal populations induced by  
453 overexploitation from another consumer mutualist.

454 *Strong interactions are needed for obligate mutualists to persist*

455 Research on mutualistic interactions has yet to firmly define interaction strength  
456 (Valdovinos 2019). In Lotka-Volterra models, interaction strength is simply defined by the  
457 benefit coefficient ( $\alpha_{ij}$  in Eqns 1, 2, 4). However, as authors have gained deeper mechanistic  
458 understanding of mutualism, it has become clear that interaction strength is a more complex  
459 topic related to the “effectiveness” of mutualistic partners (Vazquez *et al.* 2015, Schupp *et al.*  
460 2017). Schupp *et al.* defined the effectiveness of a population for providing mutualistic benefits  
461 to its partner as the product of the “quantity” and “quality” of benefits provided. The term  
462 “quality” accounts for the species-specific and interaction-specific traits, as well as the  
463 environmental context that determine how much benefit a partner can receive from a unit of  
464 benefit “quantity”. Examples of such benefit quality are the nutrition acquired from a foraging  
465 visit or the probability of a seed recruiting after being removed by a disperser.

466 The parameters that determine the quality of the mutualistic interaction are useful for  
467 understanding the criteria for stable coexistence and thresholds. Weak interactions between  
468 facultative partners in Lotka-Volterra models are considered stabilizing because they ensure  
469 stable coexistence instead of permitting unbounded growth. Specifically, mutual benefits must be  
470 weaker than species’ intraspecific limitation (Gause & Witt 1935, Travis & Post 1979).  
471 However, stable coexistence always occurs between facultative mutualists in models with  
472 saturating nullclines regardless of interaction strength. Conversely, in systems with at least one  
473 obligate partner, interactions must be sufficiently strong to overcome the negative intrinsic  
474 growth rate of the obligate partner for coexistence to be feasible (Bazykin *et al.* 1997). In this  
475 case, threshold effects can occur, not because of interaction strength but due to the low intrinsic  
476 growth rate of the partner. Overall, stronger interactions stabilize systems with threshold effects

477 by decreasing the threshold in population density that causes the system to collapse, which  
478 allows positive growth from lower densities.

479 In a network setting, weak, diffuse mutualistic interactions are considered stabilizing  
480 because their positive feedbacks are limited, and thus less likely to push the system away from  
481 equilibrium after a small perturbation (Bascompte *et al.* 2006, Allesina & Tang 2012). However,  
482 these studies have relied upon Lotka-Volterra-style models to represent mutualism. Theory that  
483 models mutualism with saturating benefits show that strong mutualistic interactions are  
484 stabilizing as expected from pairwise models (Holland *et al.* 2006, Okuyama & Holland 2008).

#### 485 *Effects of mutualism varies between low and high population density*

486 Empirical work has shown that the effects of mutualism vary with both recipient (Wolin  
487 & Lawlor 1984) and partner density (Holland 2015), and models show that this can lead to  
488 different ecological dynamics. When benefits are strongest at low recipient density, we can  
489 expect the robust dynamics of stable coexistence and threshold effects described previously (Fig.  
490 2). When benefits are strongest at high recipient density, models predict unbounded growth  
491 unless limited by other intrinsic or extrinsic factors (compare Fig. 2C-D to Fig. 3I-K). When  
492 benefits are strongest at intermediate recipient density, we can expect saturating dynamics and  
493 emergent Allee effects (Fig. 4B). On the other hand, if benefits are strongest at low partner  
494 density and turn into net costs at high partner density, two outcomes are possible (Fig. 3, Fig.  
495 4C): competitive or exploitative dynamics if the partner is at too high of an initial density, or  
496 potential oscillations to stable coexistence if the partners are well-balanced.

497 Early syntheses reported that mutualism with the strongest effects at high recipient  
498 density are less likely to be stable than those with the strongest effects at low recipient density  
499 (Addicott 1981, Wolin 1985). At that time, authors represented high-density effects of mutualism

500 as direct modifications to species' carrying capacity (Eqns 2, S9, S16; Wolin & Lawlor 1984).  
501 Authors now represent the effects of mutualism exclusively through changes in demographic  
502 rates (Holland 2015) unless explicitly representing habitat provisioning, e.g., corals or plants  
503 with domatia and their animal partners (Thompson *et al.* 2006). Mutualism may still have the  
504 strongest effects at high density (e.g., if benefits reduce negative density-dependence due to  
505 intraspecific competition or the Janzen-Connell effect), but this would be represented by  
506 modifying intraspecific limitation due to mutualism. Categorizing mutualisms by their relative  
507 magnitude of costs and benefits at low versus high density of recipients versus partners is still a  
508 profitable approach that could lead to a next-generation theoretical framework that organizes  
509 mutualism by their population dynamics. Additionally, separating out the specific demographic  
510 rates affected by mutualistic interactions (as in Thompson *et al.* 2006 and Hale *et al.* 2021) will  
511 likely clarify the differences and similarities between mutualisms. Even if the population  
512 dynamics of most models of mutualisms are qualitatively robust, the details of the low-density  
513 dynamics and the criteria for collapse can provide insight for system-specific mechanisms and  
514 patterns among them (Wu *et al.* 2019, Hale *et al.* 2021).

### 515 *Costs of mutualism can cause damped and undamped oscillations*

516 Models that incorporate costs to the mutualistic interaction can exhibit the same  
517 qualitative dynamics described above. That is, they are stable when incorporating limiting factors  
518 to benefits and self-limitation, exhibit thresholds when at least one partner is obligate, and need  
519 strong interactions for obligate partners to persist. Additionally, these models can produce  
520 oscillations. Linear costs can result in damped oscillations when the equilibrium is a stable spiral  
521 (Fig. 3A-B; Neuhauser & Fargione 2004, Kang *et al.* 2011). Nonlinear costs can cause



545 2006, Holland *et al.* 2006, Okuyama & Holland 2008, Thébault & Fontaine 2010, Valdovinos *et*  
546 *al.* 2013, 2016, 2018, Valdovinos 2019, Hale *et al.* 2020), and has also garnered more attention  
547 from broader community ecology (e.g., McCann & Gellner 2020).

548         We found that many historical models make similar qualitative predictions despite their  
549 different derivations, mechanisms, and inspiring systems. When feasible, coexistence is stable,  
550 and populations grow with bound. Mutualisms with at least one obligate partner exhibit  
551 thresholds, under which the low density of one partner destabilizes the system. If a species  
552 sustains nonlinear, population-level costs from mutualism, it may be overexploited to extinction  
553 by its partner. These patterns suggest that there exists a robust population dynamic theory of  
554 mutualism that can make general predictions. With this groundwork of theory laid, authors can  
555 now focus on how relaxing the assumptions of current models affects their predictions. For  
556 example, spatial and transmission models reiterate the threshold predictions of models that  
557 conform to the mean-field assumption (Ingvarsson & Lundberg 1995, Mohammed *et al.* 2018) as  
558 do models with explicit rewards dynamics compared to those that approximate steady-state  
559 (Revilla 2015, Wang 2019).

560         Future work should also understand how predictions from pairwise models scale to the  
561 network level. Threshold effects only occur when at least one partner is an obligate mutualist.  
562 Most species have multiple potential partners and thus are not truly “obligate” in the sense that  
563 only a specific pairwise interaction can allow positive population growth. Instead, most  
564 mutualists are likely to be facultative, engaging in diffuse interactions with many potential  
565 partners. However, it is likely that mortality exceeds reproduction in the absence of mutualistic  
566 interactions for many species. In this sense, species may be obligate mutualists even though they  
567 have multiple partners. Additionally, species are likely to have critical (cumulative) thresholds to

568 allow population growth. For example, Valdovinos and Marsland (2021) identify the quality of  
569 visits needed from pollinators for plants to persist. Below such threshold, the plant species and  
570 the animals depending on those plants go extinct. Understanding how destabilizing thresholds  
571 may emerge or be ameliorated due to obligate mutualists in a network setting is an important  
572 goal for future work. Moreover, emphasis on consumer-resource approaches with a common  
573 “currency” of energy or biomass flows (Holland 2015) make mutualisms amenable to integration  
574 into interspecific network models such as food webs (e.g., Hale *et al.* 2020). Such integration can  
575 illuminate how context mediates interaction outcomes between potential mutualists, for example  
576 by shifting interactions into overexploitation or competition regimes. Indeed, understanding the  
577 structure and dynamics of these ‘multiplex’ ecological networks that include multiple types of  
578 interactions has been identified as a primary goal in ecology (Kéfi *et al.* 2012).

579         Future work should interrogate the assumptions and predictions of these models with  
580 empirical work. A main assumption is that mutualisms have population-level impacts. However,  
581 most empirical studies quantify the benefits and costs of mutualisms at the individual level in  
582 terms of fitness or even by using a single proxy for fitness (Bronstein 2001a, Ford *et al.* 2015).  
583 Those effects do not necessarily imply population- and community-level impacts of mutualism  
584 (Williamson 1972, Flatt & Weisser 2000, Palmer *et al.* 2010, Ford *et al.* 2015). Therefore,  
585 empirical work is of foremost importance to evaluate whether mutualisms affect the population  
586 dynamics of mutualistic partners. Among the predictions of these models (stable coexistence,  
587 threshold effects, overexploitation), threshold effects have received the most attention (Latty &  
588 Dakos 2019), but more empirical work is still needed. Wotton and Kelly (2011) and Kang *et al.*  
589 (2011) observed threshold effects directly in frugivory systems and in ant-fungal gardens,  
590 respectively, although the authors did not identify their results as such. Hale *et al.* (2021) showed

591 that threshold effects in obligate plants may be swamped out by Allee effects, which suggests  
592 that targeted experiments to explore population trajectories should consider the criteria for  
593 observing different dynamics (Fig. 4).

594 One difficulty of empirical applications is that an out-of-the-box consumer-resource  
595 approach following Holland and DeAngelis' (2010) framework can be logistically  
596 overwhelming. Nonlinear cost and benefit functions generate so many dynamics that they are  
597 nearly intractable analytically (but see numerical toolkit by Wu *et al.* 2019). Moreover, with up  
598 to four separate functional responses to parameterize, this framework requires an extremely high  
599 number of parameters to estimate empirically. This level of detail may be necessary to describe  
600 some two-species mutualism but is likely not general. Simplifications like approximating costs  
601 and benefits as proportional to consumers' foraging rate (Soberón & Martinez 1981, Revilla  
602 2015, Hale *et al.* 2021) can facilitate integration between theoretical and empirical approaches.  
603 Additionally, costs that scale with rewards construction can be approximated as fixed reductions  
604 to benefit, and thus accounted for in the measured parameters (Revilla 2015, Hale *et al.* 2021).  
605 Systems with these complementary saturating benefits and fixed costs are likely to display much  
606 more limited dynamics than those shown in Fig. 3C-G. For example, Kang *et al.* (2011) and  
607 Martignoni *et al.* (2020) adapted Holland and DeAngelis' approach to specific empirical  
608 systems, leading to models which predict the threshold and stable coexistence dynamics of  
609 simpler saturating benefit models (Fig. 3H-J).

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824

825

## Legends

826 **Fig. 1. Characteristic dynamics for linear benefit models.** In early models of mutualism,  
827 benefits were represented by a constant coefficient (interactions strength) multiplying a linear  
828 function of partner density. Benefits affected per-capita growth rate (low-density effect, **A**),  
829 equilibrium density (high-density effect, **B**), or both (**C-F**). High- and both low- and high-density  
830 effects (**B-F**) yield the same nullclines (curves of the zero growth), but species achieve  
831 equilibrium density faster when mutualism affects both their equilibrium density and their per-  
832 capita growth rate. When mutualists are facultative partners ( $N_i = K_i > 0$  when  $N_j = 0$ ), they can  
833 display unbounded growth or stable coexistence depending on whether benefits were strong (**C**)  
834 or weak (**D**). When mutualists are obligate partners ( $N_i = K_i \leq 0$  when  $N_j = 0$ ), they observed  
835 stable coexistence or extinctions when mutualists were strong (**E**) or weak (**F**). When mutualists  
836 are a facultative-obligate pair, they display any of the previous four results depending on relative  
837 interaction strength and obligacy (e.g., **B**, see Vandermeer & Boucher for full results). Panels  
838 show: (**A**) Addicott 1981, (**B**) Whittaker 1978, (**C-F**) Gause & Witt 1935, Vandermeer &  
839 Boucher 1978. Benefit strength (weak or strong) is relative to intraspecific limitation. Arrows are  
840 vectors showing the ‘flow’ of the system: arrow angle shows the direction of changes in density  
841 of  $N_1$  (x-direction) and  $N_2$  (y-direction) and arrow color shows the magnitudes of change in that  
842 direction (lighter colors are stronger changes). Nullclines are curves of zero change of density for  
843 one partner. Equilibria (colored or hollow dots) occur when both partners have zero change in  
844 density. Equilibria are locally stable (black dots) or unstable (red dots) if the system is attracted  
845 or repelled, respectively, the equilibrium after a small perturbation. Equilibria are half-stable  
846 “saddles” (hollow dots) if the system is attracted in some dimensions by repelled in others.

847

848 **Fig. 2. Characteristic dynamics for saturating benefit models.** Density-dependent benefit  
849 functions stabilize linear benefit models (Fig. 1). Benefits may saturate (decrease in strength)  
850 with increasing recipient density (“intraspecific density-dependence,” **A-B**), increasing partner  
851 density (“interspecific density-dependence,” **E-J**), or both (**K**), resulting in stable coexistence.  
852 Benefits may also increase in strength with increasing recipient density (another form of  
853 intraspecific density-dependence), causing unbounded growth in the absence of other limitations  
854 (**C-D**). Models where at least one partner exhibits saturating benefits and intraspecific limitation  
855 exhibit the same qualitative dynamics (**A-B, E-K**): feasible systems display stable coexistence at  
856 densities higher than either partner could achieve alone (off-axes black point), and potential or  
857 guaranteed threshold effects when one or both partners are obligate mutualists. Under a certain  
858 threshold (red dashed line), one population is at too low density to support its partner, collapsing  
859 the system (**F, H, J, K**). This threshold causes extinction of obligate partners, even if initially  
860 highly abundant (e.g., follow lighter colored trajectories in panel **F**). These dynamics of  
861 coexistence and threshold effects are robust across models of mutualism with saturating benefits,  
862 regardless of the mechanism by which benefit saturates. Panels show models ordered  
863 chronologically: (**A**) Whittaker 1975, (**B-D**) Wolin & Lawlor 1985, (**E-F**) Wright 1989, (**G-H**)  
864 Graves *et al.* 2006, (**I-J**) Thompson *et al.* 2006, (**K**) Fishman & Hadany 2010. Models are also  
865 ordered by increasing mechanistic detail, from arbitrary limiting factors applied to Lotka-  
866 Volterra models (**A**) to a population-level approximation of benefit functions from an individual-  
867 based model (**K**). These models represent diverse inspiring systems, including host-symbiont  
868 (**A**), pollination (**E-F, K**), lichens (**G-H**), and protection mutualism (**I-J**).  
869

870 **Fig. 3. Characteristic dynamics for shifting net-effects and consumer-resource models.**

871 Models that investigated shifts in net effects as a balance of costs and benefits led to a synthesis  
872 of mutualism into a consumer-resource framework. Models with saturating benefit functions and  
873 linear costs (**A-B**) tend to display stable coexistence (**A**) and threshold effects (**B**) like earlier  
874 models (Fig. 2). Stable coexistence is “mutualistic” if the nullclines intersect such that both  
875 species achieve higher density than they would alone, or if increasing the density of one species  
876 from equilibrium permit growth of its partner. Otherwise, the interaction is “parasitic” (in this  
877 case, if the linear nullcline intersected above the vertex of the curved nullcline). Linear costs can  
878 make the coexistence equilibrium a stable spiral, with damped oscillations towards equilibrium  
879 (**B, D, E, G, H**). Models with unimodal benefit response that allow negative effects (net costs) at  
880 high density (**C-E**) or that include both separately saturating costs and benefits (**F-G**) display  
881 more complex dynamics. Depending on its parameterization, the mutualism-competition model  
882 by Zhang (2003) displays competitive exclusion (**C**), mutualistic stable coexistence (**D**), or  
883 competitive dominance (**E**), with dominant species dependent on initial densities (i.e., system  
884 initialized to the left or right of the separatrix). The consumer-resource model by Holland &  
885 DeAngelis (2010) also displays a range of dynamics depending on parameterization (**E-F**),  
886 including multiple stable coexistence equilibria (**F**). Mutualistic coexistence occurs when the  
887 ratio of consumers to their resources is not above a certain threshold (i.e., to the left of the left  
888 separatrix, or below the bottom separatrix). Otherwise, consumers overexploit their resources  
889 (causing more costs than provided benefits), leading to system collapse. Panels show the  
890 following models: (**A-B**) Neuhauser & Fargione 2004 (plant-mycorrhizae), (**C-E**) Zhang 2003  
891 (competitor-mutualists), (**F-G**) Holland & DeAngelis 2010 (bidirectional consumer-resource

892 mutualism, e.g., corals), **(H)** Kang *et al.* 2011 (ant-fungal garden), **(I-J)** Martignoni *et al.* 2020  
893 (plant-mycorrhizae), **(K)** Hale *et al.* 2021 (plant-seed disperser).

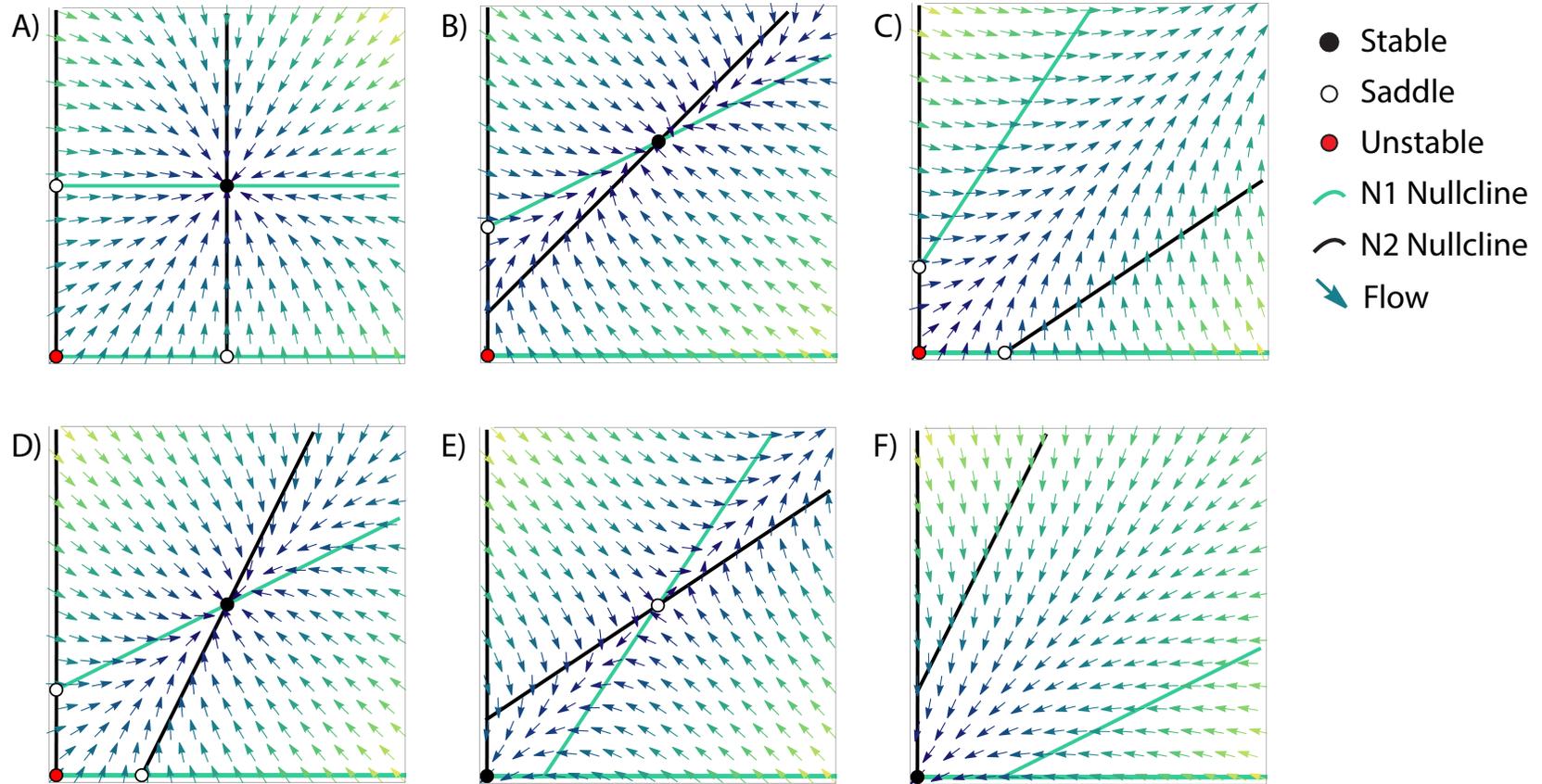
894

895 **Fig. 4. Distinguishing characteristic dynamics.** N1 (x-axis) is obligate mutualist and N2 (y-  
896 axis) is facultative in all panels. **(A)** Threshold effects: N1 goes extinct when the density of N2 is  
897 below certain threshold (separatrix), or the system achieves stable coexistence when N2 is above  
898 such threshold, where both species achieve higher densities than each would attain alone. **(B)**  
899 Overexploitation dynamics: the system collapses above a threshold in the ratio of consumer (N2)  
900 to resource (N1) species density. At low density, both partners will grow due to benefits from  
901 mutualism until they reach stable coexistence at higher density than either species could achieve  
902 alone. Above a threshold of N2 density (separatrix), both populations will grow but N2 will  
903 increase to such an extent that it exerts more costs than benefits it provides (exploitation). N1  
904 will begin to decline at low density while N2 continues to grow, eventually leading to both going  
905 extinct. At even higher initial densities of N2, N2 will immediately overexploit N1 and both  
906 species will go extinct, without even acquiring enough benefits to allow its own population to  
907 grow. **(C)** Allee effects: N1 will go extinct if its density is under certain threshold (separatrix)  
908 because it becomes too rare to receive benefits from the mutualistic interaction. The system tends  
909 towards stable coexistence at higher density than either partner could achieve alone when N1 is  
910 above such threshold of its own density. Note that overexploitation **(B)** by the high-density  
911 consumer (N2) induces an Allee effect in the resource species (N1) where lower resource density  
912 causes lower benefits from the interaction. Example systems: **(A)** Graves *et al.* 2006, lichens; **(B)**  
913 Holland & DeAngelis 2010, unidirectional consumer resource mutualism (e.g., seed dispersal);  
914 **(C)** Hale *et al.* 2021, pollination.

915

## Figures

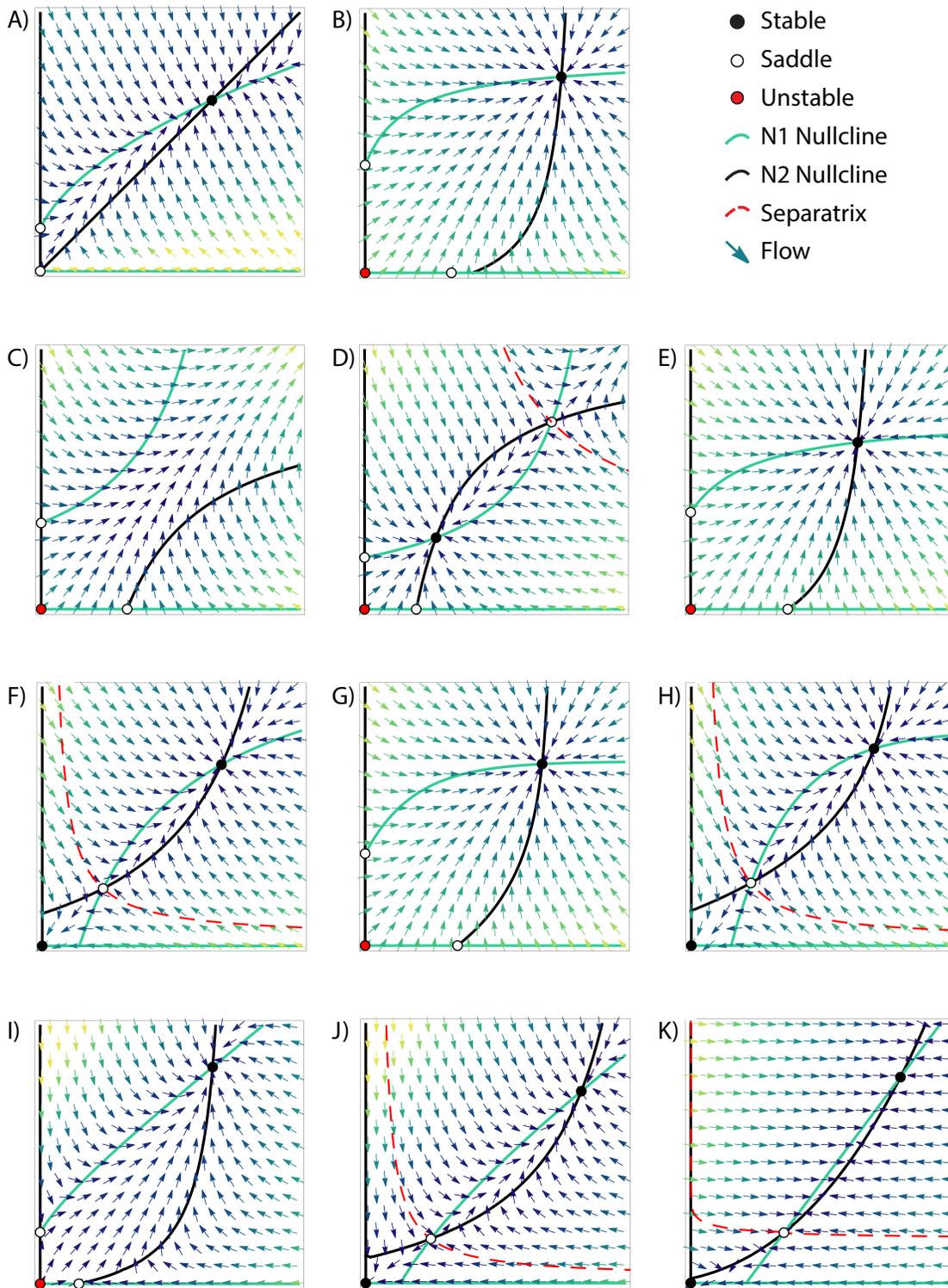
916 **Fig. 1. Characteristic dynamics for linear benefit models.**



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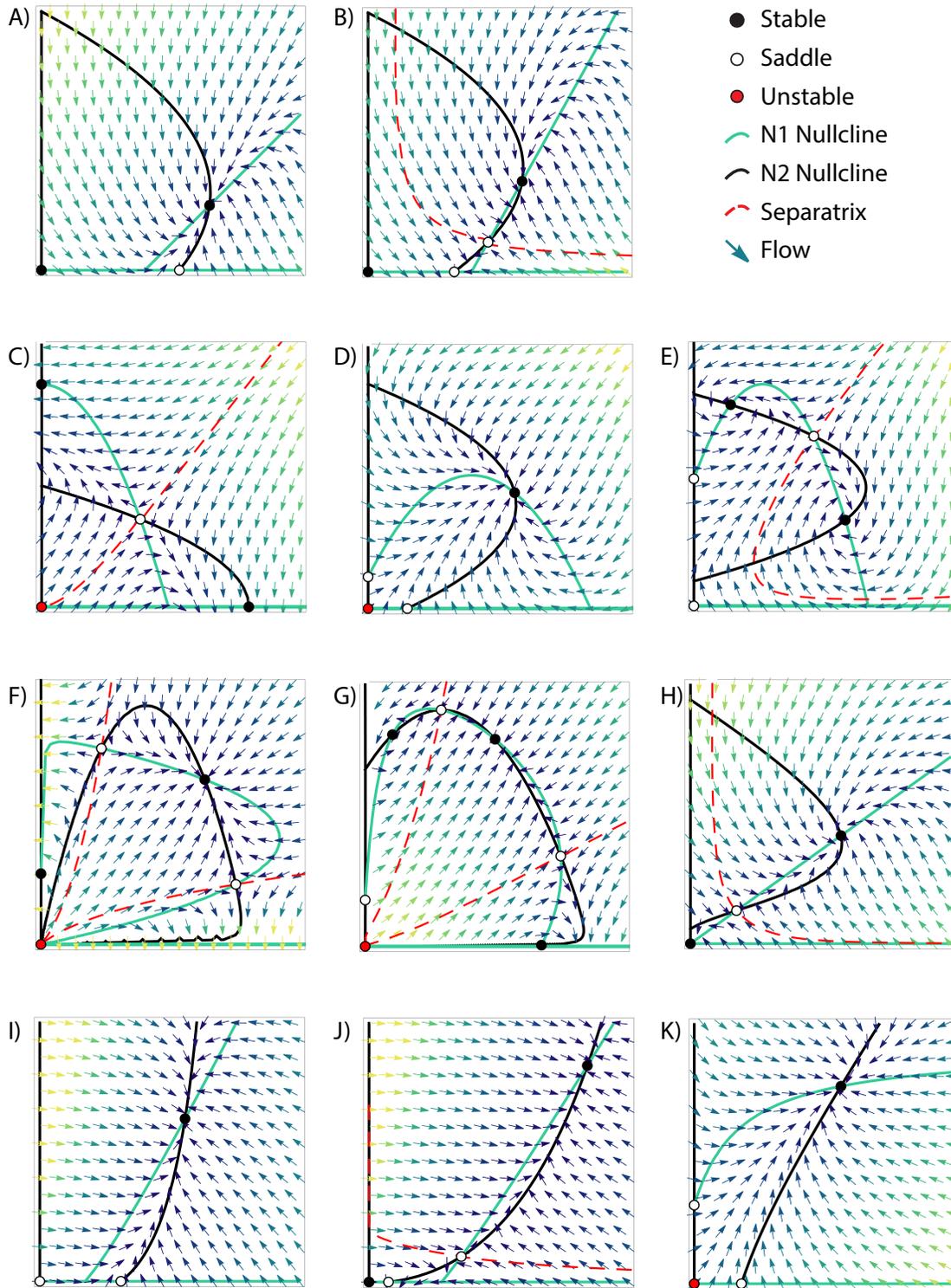
919 **Fig. 2. Characteristic dynamics for saturating benefit models.**



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921

922 **Fig. 3. Characteristic dynamics for shifting net-effects and consumer-resource models.**

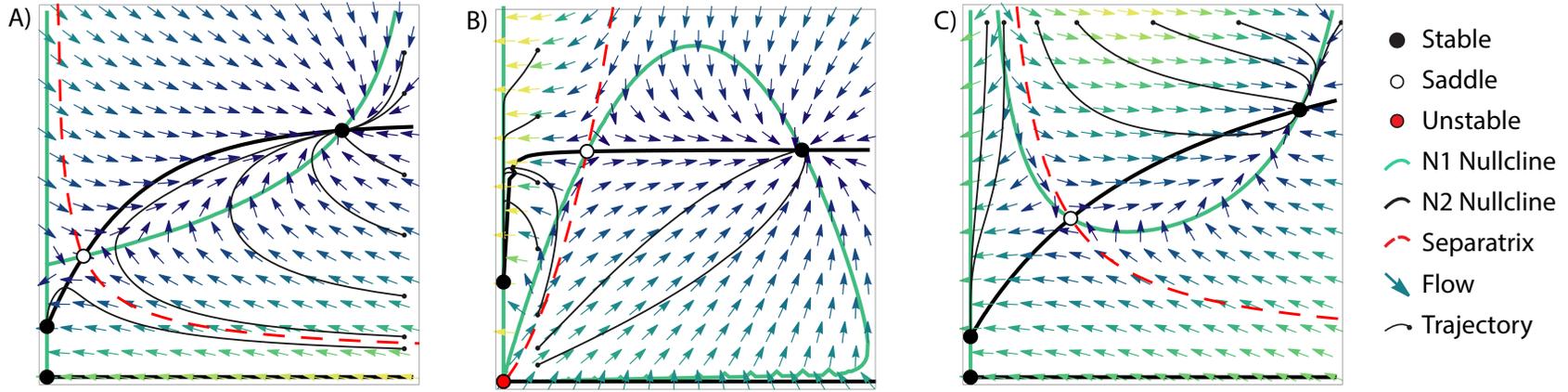


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924

925 **Fig. 4. Distinguishing characteristic dynamics.**

926



928 **Table 1. The historical development of theory of mutualism.**

	<b>Linear benefits</b>	<b>Saturating benefits</b> ( <i>intraspecific</i> )	<b>Saturating benefits</b> ( <i>interspecific</i> )	<b>Cost-benefit models &amp; shifting net effects</b>	<b>Consumer-resource approach</b>
<b>Beginning</b>	Gause & Witt (1935) proposed the first mutualism model as a modification of the Lotka-Volterra equations.	Whittaker (1975) proposed that benefits to a host population from a symbiont should saturate per host individual due to extrinsic factors.	Wright (1989) proposed that benefits should saturate with interspecific density, due to constraints on handling time.	Hernandez (1998) proposed that benefits increase at low partner density, but interaction becomes negative at high partner density.	Holland & DeAngelis (2010) proposed that resource supply and consumption processes directly affect per-capita growth rate.
<b>Mechanisms included</b>	Benefit increases per-capita growth rate (low-density effect), equilibrium density (high-density effect), or both.	Benefits decrease as: Resources or space become limiting*, Substrates to receive or attract benefits become limiting, Competition for benefits increases. * “extrinsic” factors; all other listed limitations are “intrinsic” to the mutualism	Rate of benefit accrual decreases as (effective) partner density becomes limiting, or due to satiation, search time, or handling time. Benefits may also be subject to intraspecific limitations.	Partners have nonlinear effects, with positive effects (net benefits) at low partner density and negative effects (net costs) at high partner density. Benefits accrue due to exploitation/facilitation at low density. Costs accrue due to exploitation or competition at high density.	Benefits accrue due to consumption of resources (or services) supplied by a partner. Costs accrue by supplying resources to a partner or having resources consumed.
<b>Characteristic assumptions</b>	Benefit is a linear function of partner density.	Benefit increases per-capita growth rate and equilibrium density, but saturates with increasing recipient density. At least one partner experiences additional self-limitation.	Benefit increases per-capita growth rate and equilibrium density, but saturates with increasing partner density. At least one partner experiences additional self-limitation	Net effects are represented directly as a non-monotonic interspecific function or emerge from the balance between interspecific benefit and cost functions	Consumption is an interspecific process. Services are approximated as function of partner density or consumption rate. Costs accrue in demographic or foraging parameters (“fixed costs”), or are functions

					of partner consumption rate (“variable costs”)
<b>Predictions</b>	<p>Unbounded growth between facultative partners with strong interactions.</p> <p>Stable coexistence between facultative partners with weak interactions.</p> <p>Extinction of obligate partners below a certain density threshold or unbounded growth above such threshold with strong interactions.</p> <p>Extinction of obligate partners with weak interactions.</p>	<p>Stable coexistence in feasible interactions, regardless of interaction strength or obligacy.</p> <p>Threshold between extinction of obligate partners and stable coexistence when at least one partner is obligate.</p> <p>Coexistence is non-oscillatory (stable node).</p>	Same predictions as in intraspecific saturating models.	<p>Diverse dynamics, depending on the model and its parameterization:</p> <p>Predictions of saturating models, but coexistence may be oscillatory (stable spiral)</p> <p>Mutualistic coexistence, competitive coexistence, or competitive exclusion</p> <p>Mutualistic coexistence, parasitic coexistence, or extinctions.</p>	<p>Fixed costs: same predictions as in saturating models.</p> <p>Variable, linear costs: same predictions as saturating models, but coexistence may be oscillatory.</p> <p>Variable, nonlinear costs: mutualistic coexistence or overexploitation by consumers leading to collapse; coexistence may be oscillatory.</p>
<b>Citations</b>	Gause & Witt 1935, Whittaker 1974, Vandermeer & Boucher 1978, Goh 1979, Addicott 1981.	Whittaker 1975, May 1976, Soberón & Martínez del Rio 1981, Dean 1983, Wolin & Lawlor 1984.	Wells 1983, Pierce & Young 1986, Wright 1989, Graves <i>et al.</i> 2006, Thompson <i>et al.</i> 2006, Fishman & Hadany 2010, Johnson & Amarasekare 2013, García-Algarra <i>et al.</i> 2014.	Hernandez 1998, Holland <i>et al.</i> 2002, Neuhauser & Fargione 2004, Wu <i>et al.</i> 2019.	Holland & DeAngelis 2010, Kang <i>et al.</i> 2011, Revilla 2015, Martignoni <i>et al.</i> 2020, Hale <i>et al.</i> 2021.

929

930

931 **Table 2. Selected models of pairwise mutualism.** A full list of models cited in the main text is  
932 included in the supplementary information (Table S1). Equations largely follow the notation  
933 from the original citations. All parameters are positive ( $> 0$ ) unless otherwise specified. Models  
934 with unique mathematical forms are given unique equation numbers. We encourage the readers  
935 to refer to the original references for the model derivations and interpretation of parameters.  
936 Notes include inspiring system and obligacy, if specified by authors.

Reference	Eqn	Models for Pairwise Mutualism ( $i = 1, 2$ )	Notes
Gause & Witt 1935	1	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i + \alpha_{ij} N_j - N_i}{K_i} \right)$	Facultative only
Whittaker 1975	2 1	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 + \alpha_{12} N_2 - N_1}{K_1 + \alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 + \alpha_{21} N_1 - N_2}{K_2} \right) \end{cases}$	Symbiont ( $N_1$ )-Host ( $N_2$ ) Obligate $N_1$ when $K_1 = 0$ Parasitism when $\alpha_{21} < 0$
	2 3	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{\alpha_{12} N_2 - N_1}{\alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = \frac{r_2 N_2}{K_2} \left( K_2 + \frac{a D N_1}{D + N_2} - N_2 \right) \end{cases}$	Symbiont ( $N_1$ )-Host ( $N_2$ ) Obligate $N_1$
Vandermeer & Boucher 1978	1	$\frac{dN_i}{dt} = N_i (r_i + \alpha_{ij} N_j - \alpha_{ii} N_i)$	Legume ( $N_1$ )- <i>Rhizobium</i> ( $N_2$ ) Obligate when $K_i = r_i / \alpha_{ii} \leq 0$
Addicott 1981	4	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i - N_i}{K_i} \right) \left( 1 + \frac{\alpha_{ij} N_j}{K_i} \right)$	Aphid ( $N_1$ )-Ant ( $N_2$ ) Facultative only See Table S1
Wolin & Lawlor 1984	5	$\frac{dN_i}{dt} = N_i \left( r_i - \frac{b N_i}{1 + m N_j} - d N_i \right)$	Facultative only Reduces intra-specific limitation in birth ( $b$ ) to at most 0 See Table S1
	6	$\frac{dN_i}{dt} = N_i (r_i - (b - m N_j + d) N_i)$	Reduces $b$ without limit
Wright 1989	7	$\frac{dN_i}{dt} = N_i \left( r_i - c_i N_i + b_{ij} \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j} \right)$	Pollinators & other forager mutualists See Table S1
Zhang 2003	8	$\frac{dN_i}{dt} = R_i N_i (c_i - N_i - a_i (N_j - b_i)^2)$	Interactions between species at the same trophic level $-\infty < b_i < \infty$

Neuhauser & Fargione 2004	9 1	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 + \gamma_{12} N_2 - N_1}{K_1 + \gamma_{12} N_2} - a N_2 \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 + \alpha_{21} N_1 - N_2}{K_2} \right) \end{cases}$	Plant ( $N_1$ )-Mycorrhizae ( $N_2$ ) Facultative only
Graves <i>et al.</i> 2006	10	$\frac{dN_i}{dt} = N_i (r_{i0} + (r_{i1} - r_{i0})(1 - e^{-k_i N_j}) - a_i N_i)$	Lichens Obligate when $r_{i0} < 0, r_{i1} + r_{i0} > 0$ See Table S1
Thompson <i>et al.</i> 2006	11 12	$\begin{cases} \frac{dN_1}{dt} = (\rho_1 b_1 N_1 + I_1) \left( 1 - \frac{N_1}{S_1} \right) - \left( d_{1min} + \frac{d_{1max} - d_{1min}}{1 + c_1 N_2} \right) N_1 \\ \frac{dN_2}{dt} = (\rho_2 b_2 N_2 + I_2) \left( 1 - \frac{N_2}{S_2 + N_1} \right) - \left( d_{2min} + \frac{d_{2max} - d_{2min}}{1 + c_2 N_1} \right) N_2 \end{cases}$	Hermit crabs ( $N_1$ )-Anemones ( $N_2$ ) Closed system when $I_i = 0, \rho_i = 1$ Obligate when $\rho_i b_i < d_{imax}$ See Table S1
Holland & DeAngelis 2010	13	$\frac{dN_i}{dt} = N_i \left( r_i + c_i \left( \frac{a_{ij} N_j}{h_j + N_j} \right) - q_i \left( \frac{\beta_{ij} N_j}{e_i + N_i} \right) - s_i N_i \right)$	Bidirectional Consumer-Resource e.g., Plant ( $N_1$ )-Mycorrhizae ( $N_2$ ) Obligate when $r_i = 0$
	13 7	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1 + c_1 \left( \frac{a_{12} N_2}{h_2 + N_2} \right) - q_1 \left( \frac{\beta_{12} N_2}{e_1 + N_1} \right) - s_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( r_2 + c_2 \left( \frac{a_{21} N_1}{h_1 + N_1} \right) - s_2 N_2 \right) \end{cases}$	Unidirectional e.g., Plant ( $N_1$ )-Pollinator ( $N_2$ )
Fishman & Hadany 2010	14 15	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{\eta \alpha N_2}{1 + \alpha N_1 + \alpha \beta N_2} - b - c N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( \frac{\mu \alpha N_1}{1 + \alpha N_1 + \alpha \beta N_2} - d \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate only
Kang <i>et al.</i> 2011	16 1	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_f \left( \frac{a N_2^2}{b + a N_2^2} \right) - r_c N_2 - d_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 (r_a N_1 - d_2 N_2) \end{cases}$	Fungal garden ( $N_1$ )-Leaf cutter ant ( $N_2$ ) Obligate only
Martignoni <i>et al.</i> 2020	17 18	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_p + \frac{q_{hp} \alpha N_2}{d + N_1} - q_{cp} \beta N_2 - \mu_p N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( q_{cm} \beta N_1 - \frac{q_{hm} \alpha N_1}{d + N_1} - \mu_m N_2 \right) \end{cases}$	Plant ( $N_1$ )-Mycorrhizae ( $N_2$ ) Obligate $N_2$
Hale <i>et al.</i> 2021	19 7	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \left( b_1 + \beta \frac{a N_2 N_1}{1 + ah N_1} \right) g (1 - s_1 N_1) - d_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( b_2 + \varepsilon \frac{a N_1}{1 + ah N_1} - s_2 N_2 - d_2 \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate $N_1$ when $b_1 g - d_1 \leq 0$ ; obligate $N_2$ when $b_2 - d_2 \leq 0$
	20 7	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( b_1 g \left( 1 - \left( s_1 - \sigma \frac{a N_2}{1 + ah N_1} \right) N_1 \right) - d_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( b_2 + \varepsilon \frac{a N_1}{1 + ah N_1} - s_2 N_2 - d_2 \right) \end{cases}$	Facultative $N_1$ only

Supplementary Information

938 **Table S1. Models of pairwise mutualism.** Equations largely follow the notation from the  
 939 original citations. All parameters are positive ( $> 0$ ) unless otherwise specified. Models with  
 940 unique mathematical forms are given unique equation numbers, starting chronologically  
 941 (compared to the selected models from main text). We encourage the readers to refer to the  
 942 original references for the model derivations and interpretation of parameters. Notes include  
 943 inspiring system and obligacy, if specified by authors.

Reference	Eq n	Models for Pairwise Mutualism ( $i = 1, 2$ )	Notes (inspiring system, obligacy, etc.)
Gause & Witt 1935	S1	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i + \alpha_{ij} N_j - N_i}{K_i} \right)$	Facultative only
Whittaker 1975	S2	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 + \alpha_{12} N_2 - N_1}{K_1 + \alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 + \alpha_{21} N_1 - N_2}{K_2} \right) \end{cases}$	Symbiont ( $N_1$ )-Host ( $N_2$ ) Obligate $N_1$ when $K_1 = 0$ Parasitism when $\alpha_{21} < 0$
	S1		
	S2	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( \frac{\alpha_{12} N_2 - N_1}{\alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = \frac{r_2 N_2}{K_2} \left( K_2 + \frac{a d N_1}{D + N_2} - N_2 \right) \end{cases}$	Obligate Symbiont ( $N_1$ )-Host ( $N_2$ ) Arbitrary external factors limit benefit to $N_2$
	S3		
May 1976	S4	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{I N_2}{C D + C N_1 + N_1 N_2} - d_1 \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{\alpha_{21} N_1 - N_2}{\alpha_{21} N_1} \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) and others
	S2		
Vandermeer & Boucher 1978	S1	$\frac{dN_i}{dt} = N_i (r_i + \alpha_{ij} N_j - \alpha_{ii} N_i)$	Legume ( $N_1$ )- <i>Rhizobium</i> ( $N_2$ ) Obligate when $K_i = r_i / \alpha_{ii} \leq 0$
Addicott 1981	S5	$\frac{dN_i}{dt} = r_i \left( \frac{K_i - N_i}{K_i} \right) \left( 1 + \frac{\alpha_{ij} N_j}{K_i} \right)$	Aphid ( $N_1$ )-Ant ( $N_2$ ) Facultative only
	S6	$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i - N_i}{K_i} \right) \left( 1 + \frac{\alpha_{ij} N_j}{K_i} \right)$	*Reference reports Eqn. 5. Figures suggest Eqn. 6 & subsequent authors use Eqn. 6
Soberón & Martinez del Rio 1981	S7	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{k_1 \sigma \mu N_2}{1 + \sigma \phi \mu^2 N_1} - \gamma \right) \\ \frac{dN_2}{dt} = N_2 \left( \epsilon (K_2 - N_2) + \frac{k_2 \sigma \mu^2 N_1}{1 + \sigma \phi \mu^2 N_1} \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate $N_1$ ; obligate $N_2$ when $K_2 = 0$
	S8		
Dean 1983	S9	$\frac{dN_i}{dt} = r_i N_i \left( \frac{k_i - N_i}{k_i} \right)$ $k_i = K_{i,max} (1 - e^{-(\alpha_i N_j + c_i) / K_{i,max}})$	Unintended behaviors; updated by Graves <i>et al.</i> 2006
Wells 1983	S10	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{b N_2}{a N_1 + N_2 + c} - d f N_1 - d \right) \\ \frac{dN_2}{dt} = N_2 \left( \frac{m N_1}{r N_2 + N_1 + h} - g \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate only
	S11		
Wolin & Lawlor 1984	S12	$\frac{dN_i}{dt} = N_i \left( r_i - \frac{b N_i}{1 + m N_j} - d N_i \right)$	Multiple models (including S2, S6) where benefits are a fn. of intra-specific limitation in birth ( $b$ ) & death ( $d$ ) processes Facultative only Reduces $b$ to at most 0

	S13	$\frac{dN_i}{dt} = N_i(r_i - (b - mN_j + d)N_i)$	Reduces $b$ without limit
	S14	$\frac{dN_i}{dt} = N_i \left( r_i \left( 1 - \frac{N_i}{K} \right) + mN_j e^{-\alpha N_i} \right)$	Benefits decrease exponentially
Pierce & Young 1986	S15 S16	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1(N_2) - \frac{N_1}{K_1} \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( 1 - \frac{N_2}{K_2(N_1)} \right) \end{cases}$	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 $N_1$ . Parasitism when $K_2(N_1)$ is decreasing
Wright 1989	S17	$\frac{dN_i}{dt} = N_i \left( r_i(1 - c_i N_i) + b_{ij} \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j} \right)$	Pollinators & other forager mutualists
	S8	$\frac{dN_i}{dt} = N_i \left( r_i - c_i N_i + b_{ij} \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j} \right)$	*Reference reports Eqn 17. Figures suggest Eqn 8 & subsequent authors use Eqn 8 Obligate when $r_i < 0$
Hernandez 1998	S18	$\frac{dN_i}{dt} = r_i N_i \left( 1 - \frac{N_i}{K_i} + \left( \frac{b_i N_j - c_i N_j^2}{1 + d_i N_j^2} \right) \frac{N_j}{K_i} \right)$	Facultative Parasitism at high $N_j$
	S19	$\frac{dN_i}{dt} = r_i N_i \left( -1 + \left( \frac{b_i N_j - c_i N_j^2}{1 + d_i N_j^2} \right) \frac{N_j}{K_i} \right)$	Obligate Parasitism at high $N_j$
Holland <i>et al.</i> 2002	S20 S21	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( (1-a)\alpha F \left( 1 - e^{\left( \frac{-\gamma_1 N_2}{FN_1} \right)} \right) \left( e^{\left( \frac{-\gamma_2 N_2}{FN_1} \right)} \right) - d_1 - gN_1 \right) \\ \frac{dN_2}{dt} = (1-a)\alpha F \left( 1 - e^{\left( \frac{-\gamma_1 N_2}{FN_1} \right)} \right) \left( e^{\left( \frac{-\gamma_2 N_2}{FN_1} \right)} \right) - d_2 N_2 \end{cases}$	Obligate Senita Cactus ( $N_1$ ) – Moth ( $N_2$ ) Detailed application of more general theory
Zhang 2003	S22	$\frac{dN_i}{dt} = R_i N_i (c_i - N_i - a_i(N_j - b_i)^2)$	Interactions between species at the same trophic level Competition at high $N_j$ $\infty < b_i < \infty$
Neuhauser & Fargione 2004	S23 S1	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left( 1 - \frac{N_1}{K_1 + \gamma_{12} N_2} - aN_2 \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 + \alpha_{21} N_1 - N_2}{K_2} \right) \end{cases}$	Plant ( $N_1$ )-Mycorrhizae ( $N_2$ ) Facultative only
Graves <i>et al.</i> 2006	S9	$\frac{dN_i}{dt} = N_i(r_{i0} + (r_{i1} - r_{i0})(1 - e^{-k_i N_j}) - a_i N_i)$	Lichens and other N-fixing symbioses Updates Dean's (1983) model so that mutualism affects per-capita growth rate instead of equilb. density directly. Obligate when $r_{i0} < 0, r_{i1} + r_{i0} > 0$
Thompson <i>et al.</i> 2006	S24	$\frac{dN_i}{dt} = \left( \rho_i \left( b_i N_i + \frac{\alpha_i N_j}{\beta_i + N_j} N_i \right) + I_i \right) \left( 1 - \frac{N_i}{S_i} \right) - d_{i_{max}} N_i$	Set of models with different combinations of benefit. Closed system when $I_i = 0, \rho_i = 1$ . Obligate when $\rho_i b_i < d_{i_{max}}$ Benefit: increases birth
	S25	$\frac{dN_i}{dt} = (\rho_i b_i N_i + I_i) \left( 1 - \frac{N_i}{S_i} \right) - \left( d_{i_{min}} + \frac{d_{i_{diff}}}{1 + c_i N_j} \right) N_i$	Decreases death
	S26	$\frac{dN_i}{dt} = (\rho_i b_i N_i + I_i) \left( 1 - \frac{N_i}{S_i + N_j} \right) - d_{i_{max}} N_i$	Increases carrying capacity

Holland & DeAngelis 2010	S27	$\frac{dN_i}{dt} = N_i \left( r_i + c_i \left( \frac{a_{ij}N_j}{h_j + N_j} \right) - q_i \left( \frac{\beta_{ij}N_j}{e_i + N_i} \right) - s_i N_i \right)$	Bidirectional Consumer - Resource e.g., Plant ( $N_1$ )-Mycorrhizae ( $N_2$ )
	S27 S8	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1 + c_1 \left( \frac{a_{12}N_2}{h_2 + N_2} \right) - q_1 \left( \frac{\beta_{12}N_2}{e_1 + N_1} \right) - s_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( r_2 + c_2 \left( \frac{a_{21}N_1}{h_1 + N_1} \right) - s_2 N_2 \right) \end{cases}$	Unidirectional e.g., Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate when $r_i = 0$
Fishman & Hadany 2010	S10 S11	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( \frac{\eta\alpha N_2}{1 + \alpha N_1 + \alpha\beta N_2} - b - cN_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( \frac{\mu\alpha N_1}{1 + \alpha N_1 + \alpha\beta N_2} - d \right) \end{cases}$	Plant ( $N_1$ )-Pollinator ( $N_2$ ) Obligate only Approx. from individual-based model
Kang <i>et al.</i> 2011	S28 S1	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_f \left( \frac{aN_2^2}{b + aN_2^2} \right) - r_c N_2 - d_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 (r_a N_1 - d_2 N_2) \end{cases}$	Fungal garden ( $N_1$ )-Leaf cutter ant ( $N_2$ ) Obligate only
Johnson & Amarasekare 2013	S29	$\frac{dN_i}{dt} = N_i \left( r_i + \frac{m_{ij}N_j}{1 + m_{ij}\tau_i N_j + \alpha_i N_i^2} \right)$	Obligate when $r_i < 0$
García-Algarra <i>et al.</i> 2014	S30	$\frac{dN_i}{dt} = N_i (r_i + b_{ij}N_j - (\alpha_i + c_i b_{ij}N_j)N_i)$	Obligate when $r_i \leq 0$
Revilla 2015	S31	$\frac{dN_i}{dt} = N_i \left( r_i + \frac{\sigma_i \beta_i \alpha_j N_j}{\omega_j + \beta_i N_i} - c_i N_i \right)$	Assuming steady-state reward dynamics Exchanges of resources for resources, e.g., Lichens Obligate when $r_i \leq 0$
	S32 S31	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_1 + \frac{\sigma_0 \beta_0 \alpha_0 N_0 + \sigma_1 \beta \alpha N_2}{\omega + \beta_0 N_0 + \beta N_2} - c_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( r_2 + \frac{\sigma_2 \beta \alpha N_1}{\omega + \beta_0 N_0 + \beta N_2} - c_2 N_2 \right) \end{cases}$	Exchanges of resources for services, e.g., Plant ( $N_1$ )-Disperser ( $N_2$ ) Obligate when $r_i \leq 0$
Moore <i>et al.</i> 2018	S34	$\frac{dN_i}{dt} = N_i (r_i + \beta_j N_j - \alpha_i N_i^{\theta_i})$	Accelerating intraspecific density-dependence when $\theta_i > 1$ ; Eqn 1 when $\theta_i = 1$ Facultative only ( $r_i > 0$ )
Cropp & Norbury 2019	S33	$\frac{dN_i}{dt} = N_i \left( r_i \left( \frac{N_j}{\varepsilon_j + N_j} \right) R + a_{ij}N_j - a_{ii}N_i \right)$ where $R = 1 - N_1 - N_2$	Autotrophs ( $N_1$ )-( $N_2$ ) Conservation of mass limits a shared resource $R$ “Obligation” ( $\varepsilon_j > 0$ ) is a separate process from costs & benefits
Wu <i>et al.</i> 2019		Analyzed conditions for system collapse in 81 models of mutualism representing different combinations of saturating benefits due to interspecific density-dependence; zero, linear, or saturating costs due to interspecific density-dependence; and effects of external stress.	
Martignoni <i>et al.</i> 2020	S35 S36	$\begin{cases} \frac{dN_1}{dt} = N_1 \left( r_p + \frac{q_{hp}\alpha N_2}{d + N_1} - q_{cp}\beta N_2 - \mu_p N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left( q_{cm}\beta N_1 - \frac{q_{hm}\alpha N_1}{d + N_1} - \mu_m N_2 \right) \end{cases}$	Plant ( $N_1$ )-Mycorrhizae ( $N_2$ )

Hale <i>et al.</i> 2021	S8	$\frac{dN_2}{dt} = N_2 \left( b_2 + \varepsilon \frac{aN_1}{1 + ahN_1} - s_2N_2 - d_2 \right)$	Set of models for Plants ( $N_1$ , below)- Animal Transporters ( $N_2$ ) Obligate when $b_2 - d_2 \leq 0$
	S37	$\frac{dN_1}{dt} = N_1 \left( \left( b_1 + \beta \frac{aN_2N_1}{1 + ahN_1} \right) g(1 - s_1N_1) - d_1 \right)$	Pollinators increase seed set Obligate when $b_1g - d_1 \leq 0$
	S38	$\frac{dN_1}{dt} = N_1 \left( b_1g \left( 1 - \left( s_1 - \sigma \frac{aN_2}{1 + ahN_1} \right) N_1 \right) - d_1 \right)$	Dispersers reduce negative density-dependence Facultative only
	S39	$\frac{dN_1}{dt} = N_1 \left( b_1 \left( g + \gamma \frac{aN_2}{1 + ahN_1} \right) (1 - s_1N_1) - d_1 \right)$	Dispersers increase germination Obligate when $b_1g - d_1 \leq 0$