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Ecological theory of mutualism: Robust patterns of stability and thresholds in two-species population models

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30 manuscript. F.S.V. and K.R.S.H. developed the conclusions and revised the manuscript.

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34 **Abstract**

35 Mutualisms are ubiquitous in nature, provide important ecosystem services, and involve
36 many species of interest for conservation. Theoretical progress on the population dynamics of
37 mutualistic interactions, however, comparatively lagged behind that of trophic and competitive
38 interactions, leading to the impression that ecologists still lack a generalized framework to
39 investigate the population dynamics of mutualisms. Yet, over the last 90 years, abundant
40 theoretical work has accumulated, ranging from abstract to detailed. Here, we review and
41 synthesize historical models of two-species mutualisms. We find that population dynamics of
42 mutualisms are qualitatively robust across derivations, including levels of detail, types of benefit,
43 and inspiring systems. Specifically, mutualisms tend to exhibit stable coexistence at high density
44 and destabilizing thresholds at low density. These dynamics emerge when benefits of mutualism
45 saturate, whether due to intrinsic or extrinsic density-dependence in intraspecific processes,
46 interspecific processes, or both. We distinguish between thresholds resulting from Allee effects,
47 low partner density, and high partner density, and their mathematical and conceptual causes. Our
48 synthesis suggests that there exists a robust population dynamic theory of mutualism that can
49 make general predictions.

50

51 **Introduction**

52 Mutualisms are ubiquitous in nature and serve indispensable roles in supporting biodiversity and
53 ecosystem function. Nearly all species on Earth participate in at least one of four main types of
54 mutualism: seed dispersal, pollination, protection, and resource exchange including with
55 symbionts (Janzen 1985, Bronstein 2015a, b). Moreover, up to $\sim 3/4$ of phosphorus and nitrogen
56 acquired by plants is provided by mycorrhizal fungi and nitrogen-fixing bacteria (van der
57 Heijden *et al.* 2008) and $\sim 1/3$ of crop production is dependent on animal pollination (Klein *et al.*

58 2007). The last 40 years has seen an important increase in studies on population ecology of
59 mutualism but with no (e.g., Gotelli 2008) to some representation in ecology textbooks (e.g., Kot
60 2001, Turchin 2003, Morin 2011, Vandermeer & Goldberg 2013, Mittlebach & McGill 2019)
61 and limited representation in recent syntheses of theoretical ecology (e.g., Hastings & Gross
62 2012; but see McCann & Gellner 2020 for a chapter on mutualistic networks by Bascompte &
63 Ferrara). This historical underrepresentation of mutualisms in general ecology texts has been
64 identified and explained by several authors (e.g., Boucher 1985, Bronstein 2015b, Raerinne
65 2020), part of which we briefly describe below. We submit that ecology will benefit from
66 integrating this coherent and robust body of theoretical work. Here, we contribute a first step
67 towards such integration by presenting the ecological theory of mutualism available to the
68 broader ecological community. Specifically, we review its historical literature and synthesize
69 generalities, both mathematical and conceptual, that can lay a foundation for a deeper
70 understanding and integration of mutualism in ecology.

71 Foundational theory in ecology was initially developed using Lotka-Volterra models. In
72 this framework, constant coefficients describe the positive or negative effects between two
73 interacting species as a linear function of the other species' density. The Lotka-Volterra model
74 for predation and competition predict stable cycles (oscillations, Lotka 1925, Volterra 1926) and
75 competitive exclusion (Volterra 1926, Gause 1934), respectively, which stimulated fruitful
76 empirical and theoretical work. Indeed, from the groundwork of Lotka-Volterra theory of
77 predation came more general consumer-resource theory, with useful and surprising results such
78 as the paradox of enrichment (Rosenzweig 1971) and a mathematical representation of seasonal
79 cycling in lake food webs (Boit *et al.* 2012).

80 In contrast, Lotka-Volterra models for mutualism have been a less useful simplification
81 than for predation and competition (Holland 2015). The original model (Gause & Witt 1935) and
82 other formulations in which species benefit as a linear function of each other's density (Addicott
83 1981) can predict unbounded population growth of both species. Additionally, the diversity of
84 mechanisms by which species may benefit each other and the non-reciprocity of many of them,
85 has cast suspicion on representing any "mutualistic" interaction as a simple exchange of positive
86 effects (Bronstein 2001a, b). Mutualisms are more likely to exhibit shifting net effects than other
87 interaction types (Chamberlain *et al.* 2014, Jones *et al.* 2015), with several exchanges dipping,
88 for example, into parasitism.

89 Despite all these interesting mechanisms and patterns ripe for study, mutualisms have
90 been subjected to less theoretical study than predation and competition. Many have speculated on
91 historical reasons (Boucher 1985, Bronstein 2015b, Raerinne 2020), but we highlight two here.
92 First, the terms used to identify interactions as “mutualism” have changed over time. Previous
93 theory treated mutualism as a subset of facilitation, in which one species alters the environment
94 to benefit a neighboring species (Callaway 2007), or symbiosis, in which species coexist in
95 “prolonged physical intimacy” (Bronstein 2015b), or used those terms interchangeably.
96 Additionally, the terms “mutualism,” “cooperation,” and “protocooperation” have been used
97 idiosyncratically for beneficial interactions within species as well as between them (Bronstein
98 2015b). Furthermore, some mutualisms are “indirect,” such that benefits to one partner can only
99 be realized in the presence of an external species or environmental condition (Holland &
100 DeAngelis 2010). In this review, we limit our scope to mutualism defined as reciprocally
101 beneficial interactions between two species (Bronstein 2015b). We largely focus on direct
102 mutualism or models that approximate the effects of indirect mutualism through two-species
103 models, though we touch on some other cases (e.g., Thompson *et al.* 2006).

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

114 As it stands now, mutualism has repeatedly been called a loose set of natural history
115 studies with little theory to unite or divide them (Addicott 1981, Bronstein 2015a). Despite an
116 increasing number of theoretical studies, an “ecological theory of mutualism” has not penetrated
117 the greater ecological community (Kot 2001, Turchin 2003, Gotelli 2008, Morin 2011,
118 Vandermeer & Goldberg 2013, Bronstein 2015a, Mittlebach & McGill 2019, Valdovinos 2019,
119 McCann & Gellner 2020). The studies that exist have suffered from a pattern of neglect and

150 indefinitely (*Saturating benefit models*). As costs of participating in mutualisms were
151 increasingly reported in empirical studies throughout the 1980s, theory sought to understand if
152 costs could account for limited net per-capita benefits more mechanistically, as well as the
153 conditions under which interactions could persist as mutualisms in light of context-dependency
154 of the net effects of the interaction (*Cost-benefit models and shifting net effects*). Most recently,
155 authors have sought to synthesize mutualism research into other bodies of interspecific
156 ecological understanding, including consumer-resource and ecological network theory
157 (*Consumer-resource approach to mutualism*).

158 Below, we provide an in-depth description of this theoretical development (summarized
159 in Table 1). We focus on the bulk of theory that conforms to the typical assumptions of
160 population dynamic approaches (Gotelli 2008). That is, we focus on models without immigration
161 or emigration (i.e., closed systems), without age, stage, or genetic structure, and under the
162 approximation that individuals encounter each other randomly with no spatial structure (mean
163 field assumption). These models have tended towards increasing analytical complexity as authors
164 included more ecological mechanisms and system-specific realism (Table 2), leveraging
165 numerical equation solvers. Accordingly, we use phase plane diagrams (Figs. 1-4) to visualize
166 the different qualitative dynamics of these models, as determined by species' curves of zero
167 growth ("nullclines") and fixed points ("equilibria") of the system (summarized in Table 3).

168 *Linear benefit models*

169 Gause and Witt (1935) proposed a model for "mutual aid" between a host and symbiont,
170 inspired by Konstitzin (1934; Wolin 1985). This model was a modification of the Lotka-Volterra
171 competition equations with positive (instead of negative) interaction coefficients (Eqn 1; see
172 Table 2 for numbered equations). Benefits increased linearly with increasing partner density,
173 while the strength of negative (intraspecific) density-dependence arising from processes external
174 to the mutualism also increased linearly with the density of the species receiving the benefit (i.e.,
175 the recipient species; Fig. 1). In this formulation, mutualism has two effects: it increases the low-
176 density growth rate of the recipient and the highest density at which the recipient can persist
177 (typically, the equilibrium density). The second effect has been called an increase in "carrying
178 capacity," but we reserve that term for density in the absence of the mutualistic partner. As
179 written, the model accommodates only what we now call "facultative" mutualists (Vandermeer
180 & Boucher 1978), those that can persist at positive density ("carrying capacity", K) in the

181 absence of their partner ($K > 0$). Gause and Witt also commented that increasing the strength of
182 mutualism (α_{ij} , Eqn 1) increases both species' equilibrium biomass until they pass to infinity, but
183 that infinite populations are obviously unreasonable and microcosm studies suggest that
184 interaction strength should decrease as species grow. These two studies (i.e., Konstitzin 1934,
185 Gause & Witt 1935) initiated theoretical research on what we now call mutualism around the
186 same time as theoretical research on predation and competition, but then paused for nearly 40
187 years.

188 Beginning in the 1970s, mutualism received attention as a destabilizing force in
189 ecological networks represented as random community matrices (May 1972, May 1973), with
190 the unbounded growth in the Lotka-Volterra models of mutualism being called a “silly solution”
191 (May 1976). Using Lotka-Volterra models, authors better characterized the conditions that lead
192 to unbounded growth found by Gause and Witt's original model of mutualism (Albrecht *et al.*
193 1974, Vandermeer & Boucher 1978, Goh 1979, Travis & Post 1979). Other forms of linear
194 benefits were investigated such as those that increase per-capita growth rate, equilibrium density,
195 or both (Fig. 1). Whittaker (1975) introduced a model in which mutualism increases the
196 equilibrium density of one partner and both the equilibrium density and per-capita growth rate of
197 the other partner. This model accommodates “obligate” mutualists like symbionts living on a
198 host that cannot persist in the absence of that host, that is, have zero carrying capacity ($K = 0$) in
199 the absence of their partners. The mutualistic symbiont-host interaction linearly increases the
200 carrying capacity for the symbiont (Eqn 2) while benefiting the host population by increasing its
201 low-density growth rate and its equilibrium density (Eqn 1). Later, Addicott (1981) introduced a
202 model in which mutualism only increases the per-capita growth rate (Eqn 4), inspired by the ant-
203 aphid mutualism described in Addicott (1979). Addicott emphasized that these different linear
204 benefit models could be used in a mix-and-match style to accommodate different types of
205 benefits exchanges.

206 Vandermeer and Boucher (1978) proposed the groundbreaking idea that mutualistic partners
207 may exist along continuums of obligacy and interaction strength. The authors defined facultative
208 mutualists as those with positive carrying capacity in absence of their partner. Obligate
209 mutualists were defined more abstractly with zero or negative carrying capacity in absence of
210 their partner ($K \leq 0$), which represents the demographic drawdown that mutualism must exceed
211 to allow persistence of the population. Negative carrying capacity arises mathematically when a

212 population has a negative “intrinsic” growth rate, as is the case when its per-capita death rate
213 exceeds its per-capita birth rate ($K_i = r_i/a_{ii} < 0$, where $a_{ii} > 0$ is a self-limitation coefficient,
214 Table 2). This choice is useful both mathematically and ecologically because it allows the strong
215 demographic pulldown when death rates exceed birth rates to be represented, without
216 introducing numerical issues due to zero carrying capacity. Vandermeer and Boucher’s analysis
217 of Gause and Witt (1935)’s model found that obligate-obligate partnerships would either collapse
218 to extinction when benefits are weak or exhibit a threshold population size under which they go
219 extinct and above which they grow unboundedly when benefits are strong (Fig. 1B, D). They
220 also found that facultative partners are likely to coexist stably when benefits are weak or exhibit
221 unbounded growth when benefits are strong (Fig. 1A, C, also see Wolin 1985). Remarkably,
222 Vandermeer and Boucher (1978; also see Christiansen & Fenchel 1977) anticipated the
223 qualitative dynamics generated by extending these models to saturating benefit responses.
224 However, the authors emphasized that unbounded growth was still an ecologically relevant result
225 because it indicates persistence of the two-species mutualistic system. Indeed, they argue that
226 persistence (whether species persist or go extinct) is a more biologically useful metric than
227 neighborhood stability (whether the system returns to equilibrium after a small perturbation).
228 Subsequent authors also emphasized other properties of stability of mutualism such as return
229 time to equilibrium (Addicott 1981, Wolin 1985), the domain of attraction to equilibrium
230 (Benadi *et al.* 2013a), species persistence (Valdovinos *et al.* 2013, 2016, 2018), maintenance of
231 diversity (Benadi *et al.* 2013b), and biomass variability (Hale *et al.* 2020).

232 *Saturating benefit models*

233 The earliest models that incorporated saturating benefits within mutualism invoked
234 unspecified (intraspecific) environmental constraints that limit population growth in the presence
235 of a mutualist (Whittaker 1975, May 1976, Dean 1983, Wolin & Lawlor 1984). For example,
236 Whittaker (1975) assumed extrinsic, intraspecific limiting factors to the benefits a host could
237 receive from its symbiont (Eqn 3, Fig. 2A). This is the first of many models that exhibit
238 thresholds (*sensu* Vandermeer & Boucher 1978), where the low density of one partner pushes the
239 whole system to collapse (sometimes called “Allee thresholds,” e.g., Johnson & Amarasekare
240 2013).

241 This focus on extrinsic limits to benefit was epitomized by Wolin and Lawlor (1984). They
242 derived models for five different ways in which mutualism could affect per-capita birth or death

243 rates as functions of recipient density. For example, they compared models in which mutualism
244 reduces intraspecific density-dependent limiting factors only in per-capita birth rates (Eqn 6, Fig.
245 2C-D), only in per-capita birth rate but with saturating effects (Eqn 5, Fig. 2E), and both in birth
246 and death rates with saturating effects (Eqn 2, Fig. 1A). These models were classified as
247 describing mutualisms with effects primarily at high versus low self-density. Wolin and Lawlor
248 concluded that low-density effects (i.e., primary effects on per-capita growth rate as opposed to
249 equilibrium density) are stabilizing in terms of faster return times and the existence of a feasible,
250 stable equilibrium. These models of “intraspecific density-dependence” (so called by later
251 authors, Holland 2015) lacked biological mechanisms or reference to clear ecological examples,
252 which perhaps pivoted the field away from this otherwise fruitful approach. In contrast, Soberón
253 and Martínez del Río (1981) proposed a detailed pollination model in which plant benefits are a
254 function of pollinators’ visitation rate, modeled as a saturating Type II functional response. Thus,
255 benefits to plants saturate as a function of their own density (intraspecific density-dependence),
256 but due to factors intrinsic to the mutualism (that is, time constraints for pollinators handling
257 flowers during foraging visits). Such an approach has seen a resurgence in recent literature (see
258 *Consumer-resource approach*, below) but was largely abandoned at the time.

259 Starting in the late 1980s, authors began to focus on “interspecific density-dependence,”
260 which has been considered more consistent with other theories of interspecific interactions
261 (Holland 2015). Wright (1989) proposed a model in which per-capita benefits saturate in terms
262 of partner density analogously to consumers foraging on resources due to limitations of
263 consumer handling of resources or uptake rate (Fig. 2E-F). In the mutualistic case, benefits are
264 assumed to saturate with increasing partner density, often as an additive, first order term to per-
265 capita growth rate following a Holling Type II functional-response (Wright 1989, Bazykin *et al.*
266 1997, Thompson *et al.* 2006, Holland & DeAngelis 2010, Wu *et al.* 2019, Hale *et al.* 2021). On
267 the other hand, Thompson *et al.* (2006) proposed a theoretical framework that organized both
268 terrestrial and aquatic mutualisms into those that affect birth rate, death rate, habitat acquisition
269 or a combination of these benefits for each partner. Other authors have used different
270 mathematical forms for analytical tractability (Pierce & Young 1986, García-Algarra *et al.*
271 2014). Regardless, these assumptions result in both an increase in low-density growth rate and an
272 increase in equilibrium density in the presence of mutualists.

304 Pierce & Young 1986). For example, Pierce and Young (1986) did not provide a specific
305 mathematical form but used a geometric argument to investigate the dynamics of an ant-lycaenid
306 butterfly interaction in which lycaenids may be mutualistic, commensalistic, or parasitic to
307 tending ants.

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

327 Other models also described different outcomes depending upon relative species' density
328 (Tonkyn 1986, Hernandez 1998, Holland *et al.* 2002, Wang 2019). In an important advance,
329 Holland *et al.* (2002) proposed a suite of models in which different net effects result from the
330 difference between increasing benefit functions and linear, saturating, or decreasing cost
331 functions (see Fig. 1 of Holland *et al.* 2002). Their approach balances out different mechanisms
332 that cause net effects of the interaction to shift as the relative densities of the populations change
333 over time.

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

348 This much more complex set of potential dynamics that emerges from cost-benefit
349 models exemplifies the criticism of mutualism theory as either too system-specific or too abstract
350 to provide general insight into patterns and processes in mutualism (Bronstein 2001a, Holland
351 2015). Additionally, the field had not clearly connected the costs and benefits observed for
352 individuals participating in a mutualism to potential population-level effects. The time was ripe
353 for a conceptual synthesis.

354 *Consumer-resource approach to mutualistic interactions*

355 In a landmark work, Holland and DeAngelis (2010) formalized a consumer-resource
356 approach to mutualism, providing a bridge between mutualism and the ecology of other
357 interspecific interactions. In their framework, mutualisms may be "unidirectional" or
358 "bidirectional" consumer-resource interactions, in which one or both partners benefit from
359 consuming costly resources provided by the other (Fig. 4B, Fig. 3E-F, respectively). Such
360 framework accommodated the shifting net effects of previous models (Holland & DeAngelis
361 2009, previous section), and formalized the concept of ecological costs and benefits as
362 modifications to demographic rates due to resource provisioning and nutrient or service
363 consumption. Notably, this framework allowed mutualisms to be modeled as a dynamic
364 continuum along a spectrum of other interspecific interactions, such as predator-prey and

365 competitive interactions (Holland & DeAngelis 2009, Holland 2015). This was possible by
366 clarifying the “currency” of the effects of mutualism as energy or biomass exchanges that
367 manifest in changes to per-capita growth rate (or its components: birth, death, immigration, etc.).
368 This framework stimulated recent development of theory for more specific systems (e.g., Kang *et*
369 *al.* 2011, Martignoni *et al.* 2020)

370 Holland and DeAngelis (2010) modeled specific study cases similarly to previous studies
371 (see *Saturating benefits*, above), but with costs defined separately from benefits via saturating
372 interspecific functions, accrued through provisioning resources. In contrast, service-provisioning
373 by consumers is assumed to incur only fixed costs that can be accounted for in parameter values,
374 like increased handling time when foraging for resources. The nonlinear costs cause lobe-shaped
375 nullclines allowing up to five coexistence equilibria. Like the earlier Zhang (2003) model, many
376 dynamics are possible including mutualistic stable coexistence and oscillations. However,
377 instead of the competitive exclusion and competitive coexistence outcomes of Zhang’s model,
378 “parasitism” by one partner is due to exploitation by a high-density partner that outweighs the
379 benefits it provides to the lower density partner. In most dynamics of the Holland and DeAngelis
380 model, parasitism collapses the system to extinction instead of allowing a stable but exploitative
381 interaction like in Zhang’s model.

382 Following Holland and DeAngelis’ publication, authors began to investigate accounting
383 for resource dynamics in consumer-resource mutualisms more mechanistically. Resource
384 dynamics were also considered in some earlier literature investigating mutualistic exchange of
385 resources and between guild-members sharing resources (bidirectional consumer-resource),
386 largely in the context of investigating coexistence mechanisms (e.g., Meyer 1975, McGill 2005,
387 Gross 2008). However, Benadi *et al.* (2012) and Valdovinos *et al.* (2013) proposed consumer-
388 resource models for pollination networks (unidirectional consumer-resource) in which
389 consumption was on nectar “rewards” rather than individuals of the resource populations directly
390 (but also see Scheuring 1992 for a similar stage-structured model). These models separated the
391 dynamics of the plants’ vegetative biomass from the dynamics of the plants’ floral rewards either
392 implicitly (Benadi *et al.* 2012, 2013a) or explicitly (Valdovinos *et al.* 2013). Explicitly
393 separating vegetative and rewards dynamics introduces complexity but allows (1) tracking of the
394 depletion of floral rewards by pollinator consumption, (2) evaluating exploitative competition
395 among pollinator species consuming the floral rewards provided by the same plant species, and

396 (3) incorporating the capability of pollinators to behaviorally increase their foraging effort on the
397 plant species in their diet with more floral rewards available (adaptive foraging). Though these
398 models were developed for plant-pollinator networks, their ideas paved the way for new
399 investigations of mutualism at the pairwise (Revilla 2015, Wang 2019, Hale *et al.* 2021) and
400 community (Benadi *et al.* 2013b, Valdovinos *et al.* 2016, Hale *et al.* 2020) scales. For example,
401 Revilla (2015) assumed rewards achieve steady state compared to changes in population density
402 and derived models in which the linear consumption rate on rewards mediates benefits to the
403 resource species. Hale *et al.* (2020) considered that pollinator visits can be approximated by
404 consumption of floral rewards, and assumed that benefit to both plant and pollinator species is
405 proportional to consumption rates on floral rewards. Hale *et al.* (2021) further specified whether
406 benefits should be proportional to per-capita consumption rate (as may be the case for animal-
407 dispersed plants) or to total consumption rate (as may be the case for animal-pollinated plants
408 which require obligate outcrossing). The latter leads to emergent Allee effects (Courchamp *et al.*
409 2018) for obligately animal-pollinated plants, explained by the plants' inability to attract
410 pollinators at low density.

411 **Patterns from Theory**

412 Historically, theory in mutualism has been focused on understanding how mutualisms can
413 stably persist. Here, we broaden our scope to ask, what dynamics does the theory predict
414 mutualisms will exhibit, and are they dependent upon ecological system or model formulation?
415 We found that predictions for the population dynamics of mutualisms are qualitatively robust
416 across the models reviewed, despite differences in level of detail, types of benefit, and inspiring
417 systems. We synthesize these general findings below.

418 *Mutualisms are stable with intraspecific density-dependence and saturating* 419 *benefits*

420 The stability of mutualistic interactions has been discussed in the community ecology
421 literature for decades (May 1972, May 1973, Bascompte *et al.* 2006, Holland & DeAngelis 2010,
422 Allesina & Tang 2012, Johnson & Amarasekare 2013, Holland 2015, Valdovinos 2019, Hale *et*
423 *al.* 2020). Discussion has included definitions of stability (e.g., lack of positive feedbacks,
424 robustness to perturbations), the scale at which they are assessed (e.g., pairwise interactions,

425 between guilds, within communities), and stabilizing mechanisms (e.g., non-random interactions,
426 environmental limits, consumer-resource dynamics).

427 We found that theoretical investigation of pairwise mutualism has repeatedly and
428 robustly shown that mutualisms are stable. Minimal realism in terms of limited benefits,
429 accumulating costs, or accelerating intraspecific competition allow stable coexistence at high
430 density according to the criteria of local stability analysis. That is, these systems will return to
431 equilibrium after small perturbations to population densities. Under other definitions of stability,
432 such as persistence of populations or return time to equilibrium, mutualisms can be even more
433 stable than predation and competition (Addicott 1981, Wolin & Lawlor 1984). Moreover, other
434 mechanisms not reviewed here including spatial structure (Armstrong 1987, Amarasekare 2004,
435 Mohammed *et al.* 2018), rewards or resource dynamics (Meyer *et al.* 1975, Scheuring 1992,
436 Gross 2008, Revilla 2015, Cropp & Norbury 2019, Wang 2019), adaptive foraging (Valdovinos
437 2013, 2016, 2018) and predators or competitors (Heithaus *et al.* 1980, Rai *et al.* 1983, Addicott
438 & Freedman 1984, Tonkyn 1986, Ringel *et al.* 1996, Mougi & Kondoh 2012, Hale *et al.* 2020)
439 also stabilize mutualisms.

440 The pattern of stable coexistence of mutualists at high density is robust across
441 mechanisms that limit benefit (Figs. 2-3, Table 3). Both inter- and intraspecific density
442 dependence in saturating benefit functions lead to the same qualitative dynamics when they are
443 present in at least one partner (also see *Thresholds*, below). However, intraspecific density-
444 dependence and its effect on stability has been a source of confusion in the mutualism literature
445 for decades.

446 **Intraspecific density-dependence**

447 We found that authors described their models as exhibiting intraspecific density-
448 dependence in three (not necessarily distinct) cases. In the first case, authors are referring to the
449 negative density-dependence term in a simple population dynamic model (Case 1 of Table 3).
450 This term causes the decline in per-capita growth rate with increasing population density, and
451 historically was modeled through a carrying capacity function ($-N_i/K_i$ in Table 3). It is now
452 typically modeled through a “self-limitation” term ($-s_i N_i$ in Table 3), though it may represent
453 any form of negative density-dependence such as the Janzen-Connell effect, not just intraspecific
454 competition for limited resources. To display a nullcline in the relevant ecological quadrant, it is
455 necessary for mutualism models to include nonzero negative density-dependence unless they

456 include some other source of dependence on recipient density (e.g., s_i can be zero in Case 2 of
457 Table 3 because benefit saturates in terms of recipient density). Moore *et al.* (2018) found that
458 one species having an accelerating negative density-dependence term is also sufficient to allow
459 stable coexistence if per-capita benefits accrue linearly (Case 1.1.2). However, the form of
460 negative density-dependence (accelerating, decelerating, or constant) does not typically affect
461 nullcline geometry if per-capita benefits saturate (e.g., does not affect the qualitative dynamics of
462 Cases 1.2, 2.1, 2.2 of Table 3).

463 In the second case, authors refer to intraspecific density-dependence in their models when
464 benefits from mutualism increase per-capita growth rate directly (that is, affect density-
465 independent rates such as increased per-capita birth rate or decreased per-capita death rate), but
466 benefits saturate with increasing recipient density (Case 2 of Table 3). This emerges when
467 benefits are a function of the partner's visitation rate on the recipient or consumption rate on
468 rewards provided by the recipient or when the recipient has limited substrate with which to
469 convert interactions into benefits. This may generally be the case when mutualists provide
470 reproductive or protective services (e.g., Sóberon & Martinez del Rio 1981, Thompson *et al.*
471 2006, Johnson & Amarasekare 2013, Hale *et al.* 2021, but also see nutritional exchanges in
472 Parker 2001, Martignoni *et al.* 2020).

473 In the third case, authors refer to intraspecific density-dependence when benefits from
474 mutualism reduce negative density-dependence (Case 3 of Table 3), so that the effect of
475 mutualism is most prominent at high recipient density (Wolin & Lawlor 1984). Authors have
476 chosen this approach when mutualists provision habitat (e.g., Thompson *et al.* 2006), reduce
477 density-dependent mortality such as seed predation via the Janzen-Connell effect (e.g., Hale *et al.*
478 *et al.* 2021), or in the case of symbionts, which live within host populations (e.g., Whittaker 1975).
479 Here, benefits may be mediated through carrying capacity (Case 3.1) or through a self-limitation
480 term (Cases 3.2, 3.3), with different resulting nullecline geometries. Linear increases in carrying
481 capacity or decreases in self-limitation rate can yield unbounded population growth (Table 3).
482 More generally, even models with saturating benefits can exhibit unstable behavior when
483 benefits accrue directly to a term that represents intraspecific density-dependence, which
484 decreases per-capita growth rate at high density (not shown). If mutualism decreases negative
485 density-dependence to such an extent that it induces positive density-dependence at high partner
486 density, the recipient population will begin accruing increasing benefit with its own increasing

487 density (Case 3.2). Then, the system can display unbounded growth (Fig. 2C-D) unless benefits
488 are additionally limited by extrinsic or intrinsic factors such as the number of seeds that can
489 germinate after seed dispersal or the number of ovules that can be pollinated by pollinators (Case
490 3.3, Fig. 3H).

491 Though all three of the above cases have been called “intraspecific density-dependence”
492 in the mutualism literature, they refer to different ecological phenomena and have different
493 implications for the dynamics of mutualism. All models must include some form of per-capita
494 dependence on recipient density for feasible nullclines, but this may be manifest through a self-
495 limitation term or through per-capita benefit functions that decrease with increasing recipient
496 density. Models in which benefits reduce negative density-dependence in a recipient population
497 tend to allow unbounded population growth unless there are additional limits to benefits accrued.
498 In contrast, models in which per-capita benefits saturate with increasing recipient density are
499 stable, and exhibit the robust dynamics of high density stable coexistence and a low-density
500 threshold observed in models with benefits that saturate with increasing partner density (i.e.,
501 interspecific density-dependence).

502 *Mutualisms exhibit thresholds when at least one partner is obligate*

503 Nearly all models that predict stable coexistence at high density also predict destabilizing
504 thresholds at low density when one or more partners are obligate upon the mutualism (Fig. 2A-B,
505 E-F, Fig. 3A-B, G, H). Specifically, if either species dips below a critical threshold in population
506 density, the obligate partner(s) will go extinct, even if initially at high density (Fig. 4A). This
507 collapse occurs because, under the threshold, the low-density species cannot provide sufficient
508 benefits to its higher density partner. Threshold effects occur in systems with interaction
509 strengths high enough to allow feasible coexistence, but with per-capita growth rates small
510 enough (very negative for obligate partners, near-zero for facultative partners) that a partner can
511 potentially achieve densities low enough for long enough that its obligate partner will go extinct.

512 Understanding threshold dynamics provides rich insight into interaction strength,
513 obligacy, and positive feedbacks in mutualistic interaction. By definition, obligate mutualists
514 have negative per-capita growth rate in the absence of their partner. Thus, obligate mutualists can
515 be only saved from population decline by benefits from mutualism that exceed their own
516 negative intrinsic growth rate, that is, via strong mutualistic interactions. If both partners are
517 initially at high enough density, obligate mutualists can achieve positive population growth,

518 resulting in stable coexistence. However, if an obligate mutualist is at high density but its partner
519 is at low density, the obligate mutualist will decline quickly due both to its negative intrinsic
520 growth rate and due to strong intraspecific limitation at high density. The low-density partner
521 may be growing due to mutualistic benefits, positive intrinsic growth, or release from
522 intraspecific limitation. However, under the threshold, its population cannot recover fast enough
523 to provide sufficient benefit to cancel out the negative intrinsic growth rate of the obligate
524 partner and save it from decline. On the other hand, facultative partners can rely upon their own
525 positive intrinsic growth rate to recover from low density, even after declines due to strong
526 intraspecific competition or insufficient benefits provided by its partner. Thus, destabilizing
527 threshold effects do not occur when both partners are facultative. However, highly nonlinear
528 models can exhibit similar thresholds in facultative partnerships where coexistence occurs below
529 the threshold at low, rather than high densities (“bistable coexistence,” Parker 2001, Hale *et al.*
530 2021).

531 Threshold dynamics emerge from the unique nature of mutualism and are potentially
532 characteristic of this interaction. In predator-prey interactions, a low-density predator may
533 benefit from a higher density prey population that is declining, but negative feedback in the
534 system also limits the growth of the predator population at high density and subsequently allows
535 the recovery of the prey population from low density. In competition interactions, the higher
536 density partner exerts stronger and stronger negative effects on the rare population, causing the
537 rarer population to go extinct if interspecific competition exceeds intraspecific competition for at
538 least one of the competitors. In contrast, the positive feedback in the mutualistic system requires
539 that both partners can provide sufficient benefits to the other to maintain the interaction. Notably,
540 thresholds effects also occur in models that take very different approaches than those reviewed
541 here. For example, Ingvarsson & Lundberg (1995) observed threshold effects dependent upon
542 the ability for pollinators to find flowers in a modified disease model for mutualism, while Wang
543 (2019) showed that the thresholds observed in Revilla’s (2015) model more precisely occur
544 between pollinator and rewards density rather than pollinator and plant density directly. This
545 further emphasizes the potential generality of thresholds in mutualisms.

546 **Allee effects**

547 Allee effects are a form of threshold where the population exhibits negative per-capita
548 growth rate when rare. Here, we use “Allee effects” to refer specifically to strong, demographic

549 Allee effects (Kramer *et al.* 2009) that emerge from the mutualism (i.e., are not hard coded into
550 the population dynamics, Courchamp *et al.* 2018). Allee effects can emerge from many
551 mechanisms, but we distinguish between a few proximal causes that suggest differing
552 management recommendations for driving a collapsing system to high-density stable
553 coexistence. The most obvious case is also the least common form of threshold observed in
554 mutualism models: Allee effects driven by the inability of a population to support itself. This
555 type of Allee effect has also been observed in food chains that include protection mutualism
556 (Morales *et al.* 2008) and in models of sequential colonization of patches by plants and mobile
557 mutualists (Amarasekare 2004). As mentioned above, Hale *et al.* (2021) find Allee effects in
558 obligate plants when they become too rare to attract sufficient visitation from pollinators (Fig.
559 4C). From a management perspective, it would be necessary to supplement the population
560 experiencing the Allee effect (the declining, low-density partner) to prevent its extinction (Fig.
561 4C). The partner-induced threshold described above also leads to Allee effects, wherein species
562 decline when their partner is too low in density to support positive growth. In this case, it would
563 also be necessary to supplement the low-density species, though it may already appear to be
564 recovering due to positive population growth and high partner density. Indeed, from a
565 management perspective, this would achieve the counter-intuitive goal not of saving the low-
566 density population, but rather its high-density partner from extinction (Fig. 4A). Finally, Holland
567 & DeAngelis (2010) find Allee effects in animal populations induced by overexploitation from
568 another consumer mutualist. In this case, the management recommendation would be to equalize
569 partners' population densities to avoid overexploitation (Fig. 4B).

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

571 Research on mutualistic interactions has yet to firmly define interaction strength
572 (Valdovinos 2019). In Lotka-Volterra models, interaction strength is simply defined by the
573 benefit coefficient (α_{ij} in Eqns 1, 2, 4). However, as authors have gained deeper mechanistic
574 understanding of mutualism, it has become clear that interaction strength is a more complex
575 topic related to the “effectiveness” of mutualistic partners (Vazquez *et al.* 2015, Schupp *et al.*
576 2017). Schupp *et al.* defined the effectiveness of a population for providing mutualistic benefits
577 to its partner as the product of the “quantity” and “quality” of benefits provided. The term
578 “quality” accounts for the species-specific and interaction-specific traits, as well as the
579 environmental context that determine how much benefit a partner can receive from a unit of

580 benefit “quantity”. Examples of such benefit quality are the nutrition acquired from a foraging
581 visit or the probability of a seed recruiting after being removed by a disperser.

582 The parameters that determine the quality of the mutualistic interaction are useful for
583 understanding the criteria for stable coexistence and thresholds. Weak interactions between
584 facultative partners in Lotka-Volterra models are considered stabilizing because they ensure
585 stable coexistence instead of permitting unbounded growth. Specifically, mutual benefits must be
586 weaker than species’ intraspecific limitation (Gause & Witt 1935, Travis & Post 1979).
587 However, stable coexistence always occurs between facultative mutualists in models with
588 saturating nullclines regardless of interaction strength. Conversely, in saturating systems with at
589 least one obligate partner, interactions must be sufficiently strong to overcome the negative
590 intrinsic growth rate of the obligate partner for coexistence to be feasible (Bazykin *et al.* 1997).
591 In this case, destabilizing threshold effects can occur not because of interaction strength, but due
592 to the low intrinsic growth rate of the partner. Overall, stronger interactions stabilize systems
593 with threshold effects by decreasing the threshold in population density that causes the system to
594 collapse, which allows positive growth from lower densities.

595 *Effects of mutualism varies between low and high population density*

596 Empirical work has shown that the effects of mutualism vary with both recipient (Wolin
597 & Lawlor 1984) and partner density (Holland 2015), and models show that this can lead to
598 different ecological dynamics. When benefits are strongest at low recipient density, we can
599 expect the robust dynamics of stable coexistence and threshold effects described previously (Fig.
600 2). When benefits are strongest at high recipient density, models predict unbounded growth
601 unless limited by other intrinsic or extrinsic factors (compare Fig. 2C-D to Fig. 3H). When
602 benefits are strongest at intermediate recipient density, we can expect saturating dynamics and
603 emergent Allee effects (Fig. 4B). On the other hand, if benefits are strongest at low partner
604 density and turn into net costs at high partner density, two outcomes are possible (Fig. 3, Fig.
605 4C): competitive or exploitative dynamics if the partner is at too high of an initial density, or
606 potential oscillations to stable coexistence if the partners are well-balanced.

607 Early syntheses reported that mutualism with the strongest effects at high recipient
608 density are less likely to be stable than those with the strongest effects at low recipient density
609 (Addicott 1981, Wolin 1985). At that time, authors represented high-density effects of mutualism
610 as direct modifications to species’ carrying capacity (Eqns 2, S9, S16; Wolin & Lawlor 1984).

611 Authors now represent the effects of mutualism exclusively through changes in demographic
612 rates (Holland 2015) unless explicitly representing habitat provisioning, e.g., corals or plants
613 with domatia and their animal partners (Thompson *et al.* 2006). Mutualism may still have the
614 strongest effects at high density (e.g., if benefits reduce negative density-dependence due to
615 intraspecific competition or the Janzen-Connell effect), but this would be represented by
616 modifying intraspecific limitation due to mutualism. Categorizing mutualisms by their relative
617 magnitude of costs and benefits at low versus high density of recipients versus partners is still a
618 profitable approach that could lead to a next-generation theoretical framework that organizes
619 mutualism by their population dynamics. Additionally, separating out the specific demographic
620 rates affected by mutualistic interactions (as in Thompson *et al.* 2006 and Hale *et al.* 2021) will
621 likely clarify the differences and similarities between mutualisms. Even if the population
622 dynamics of most models of mutualisms are qualitatively robust, the details of the low-density
623 dynamics and the criteria for collapse can provide insight for system-specific mechanisms and
624 patterns among them (Wu *et al.* 2019, Hale *et al.* 2021).

625 *Costs of mutualism can cause damped and undamped oscillations*

626 Models that incorporate costs to the mutualistic interaction can exhibit the same
627 qualitative dynamics described above. That is, they are stable when incorporating limiting factors
628 to benefits and self-limitation, exhibit thresholds when at least one partner is obligate, and need
629 strong interactions for obligate partners to persist. Additionally, these models can produce
630 oscillations. Linear costs can result in damped oscillations when the equilibrium is a stable spiral
631 (Fig. 3A-B, G; Neuhauser & Fargione 2004, Kang *et al.* 2011). Nonlinear costs can cause
632 undamped oscillations when the equilibrium is a stable center (Fig. 3F; Zhang 2003, Holland &
633 DeAngelis 2010).

634 Undamped oscillations occur when overexploitation by the consumer causes an Allee
635 effect in the resource, which does not necessarily lead to extinction (Fig. 3F). After depleting
636 their resource population, the consumer population also declines, eventually allowing the
637 resource to receive sufficient benefit compared to losses due to consumption. The system thus
638 recovers, and coexistence is maintained in this region via a limit cycle (i.e., oscillations) around a
639 stable center (left-most stable equilibrium, Fig. 3F). This outcome is not seen in simpler models
640 without cost terms, which predict stable coexistence at a non-oscillatory node (Fig. 2), or with
641 linear cost terms, which can predict damped-oscillations in a stable spiral (Fig. 3A-B, G).

642 Note that oscillation has been considered an important dynamic for mutualism models to
643 reiterate, as justified by observations that mutualist populations can vary in space and time
644 (Holland 2015). However, such variability need not necessarily be driven by the underlying
645 population dynamics. Far simpler models of mutualism can produce oscillations when
646 accounting for discrete time dynamics (e.g., Gilpin *et al.* 1982). Additionally, population
647 oscillations observed in nature may be caused by external factors, such as environmental
648 variation. This emphasizes that introducing explicit cost terms into mutualism should be
649 adequately justified at the population level. Regardless, the models in question suggest that
650 oscillations can be induced predictably, for example, by decreasing the density-dependent
651 mortality of an obligate symbiont (Neuhauser & Fargione 2004, e in Eqn. 9), which could
652 potentially be tested empirically by using different fungal strains in a plant-mycorrhizal system
653 (Martignoni *et al.* 2021).

654 Discussion

655 Theoretical study of mutualism has lagged behind the other two “pillars” of community
656 ecology: competition and predator-prey interactions (Callaway 2007, Holland 2015). Early
657 theory of mutualistic interactions was contemporaneous with early theory on predator-prey and
658 competition interactions. After a gap of nearly 40 years, the destabilizing influence of mutualistic
659 interactions in communities reignited theoretical attention. More recently, theory of mutualistic
660 networks has made faster progress than that of pairwise mutualisms (Bascompte *et al.* 2003,
661 2006, Holland *et al.* 2006, Okuyama & Holland 2008, Thébault & Fontaine 2010, Benadi *et al.*
662 2013b, Valdovinos *et al.* 2013, 2016, 2018, Valdovinos 2019, Hale *et al.* 2020), and has also
663 garnered more attention from broader community ecology (e.g., McCann & Gellner 2020).

664 Ecological theory of mutualism has been criticized as sparse, largely consisting of models
665 that are either too abstract to be useful or too case-specific to reveal general patterns (Bronstein
666 2015a). This is an accurate description of many of the models we reviewed, however,
667 remarkably, nearly all these models conformed to the same dynamics. We found that many
668 historical models make similar qualitative predictions despite their different derivations,
669 mechanisms, and inspiring systems. When feasible, coexistence is stable, and populations grow
670 with bound. Mutualisms with at least one obligate partner exhibit thresholds, under which the
671 low density of one partner destabilizes the system. If a species sustains nonlinear, population-

672 level costs from mutualism, it may be overexploited to extinction by its partner. These patterns
673 suggest that there exists a robust population dynamic theory of mutualism that can make general
674 predictions. With this groundwork of theory laid, authors can now focus on how relaxing the
675 assumptions of current models affects their predictions. For example, spatial and transmission
676 models reiterate the threshold predictions of models that conform to the mean-field assumption
677 (Ingvarsson & Lundberg 1995, Mohammed *et al.* 2018) as do models with explicit rewards
678 dynamics compared to those that approximate steady-state (Revilla 2015, Wang 2019).

679 *Avenues for future research*

680 Future work should also understand how predictions from pairwise models scale to the
681 network level. Threshold effects only occur when at least one partner is an obligate mutualist.
682 Most species have multiple potential partners and thus are not truly “obligate” in the sense that
683 only a specific pairwise interaction can allow positive population growth. Instead, most
684 mutualists are likely to be facultative, engaging in diffuse interactions with many potential
685 partners. However, it is likely that mortality exceeds reproduction in the absence of mutualistic
686 interactions for many species. In this sense, species may be obligate mutualists even though they
687 have multiple partners. Additionally, species are likely to have critical (cumulative) thresholds to
688 allow population growth. For example, Valdovinos and Marsland (2021) identify the quality of
689 visits needed from pollinators for plants to persist. Below such threshold, the plant species and
690 the animals depending on those plants go extinct. Understanding how destabilizing thresholds
691 may emerge or be ameliorated due to obligate mutualists in a network setting is an important
692 goal for future work. Moreover, emphasis on consumer-resource approaches with a common
693 “currency” of energy or biomass flows (Holland 2015) make mutualisms amenable to integration
694 into interspecific network models such as food webs (e.g., Hale *et al.* 2020). Such integration can
695 illuminate how context mediates interaction outcomes between potential mutualists, for example
696 by shifting interactions into overexploitation or competition regimes. Indeed, understanding the
697 structure and dynamics of these ‘multiplex’ ecological networks that include multiple types of
698 interactions has been identified as a primary goal in ecology (Kéfi *et al.* 2012).

699 Future work should interrogate the assumptions and predictions of these models with
700 empirical work. A main assumption is that mutualisms have population-level impacts. However,
701 most empirical studies quantify the benefits and costs of mutualisms at the individual level in
702 terms of fitness or even by using a single proxy for fitness (Bronstein 2001a, Ford *et al.* 2015).

703 Those effects do not necessarily imply population- and community-level impacts of mutualism
704 (Williamson 1972, Flatt & Weisser 2000, Palmer *et al.* 2010, Ford *et al.* 2015). Therefore,
705 empirical work is of foremost importance to evaluate whether mutualisms affect the population
706 dynamics of mutualistic partners. Among the predictions of these models (stable coexistence,
707 threshold effects, overexploitation), threshold effects have received the most attention (Latty &
708 Dakos 2019), but more empirical work is still needed. Wotton and Kelly (2011) and Kang *et al.*
709 (2011) observed threshold effects directly in frugivory systems and in ant-fungal gardens,
710 respectively, although the authors did not identify their results as such. Hale *et al.* (2021) showed
711 that threshold effects in obligate plants may be swamped out by Allee effects (e.g., Forsyth
712 2003), which suggests that targeted experiments to explore population trajectories should
713 consider the criteria for observing different dynamics (Fig. 4).

714 One difficulty of empirical applications is that an out-of-the-box consumer-resource
715 approach following Holland and DeAngelis' (2010) framework can be logistically
716 overwhelming. Nonlinear cost and benefit functions generate so many dynamics that they are
717 nearly intractable analytically (but see numerical toolkit by Wu *et al.* 2019). Moreover, with up
718 to four separate functional responses to parameterize, this framework requires an extremely high
719 number of parameters to estimate empirically. This level of detail may be necessary to describe
720 some two-species mutualism but is likely not general. Simplifications like approximating costs
721 and benefits as proportional to consumers' foraging rate (Soberón & Martinez 1981, Revilla
722 2015, Hale *et al.* 2021) can facilitate integration between theoretical and empirical approaches.
723 Additionally, costs that scale with rewards construction can be approximated as fixed reductions
724 to benefit, and thus accounted for in the measured parameters (Revilla 2015, Hale *et al.* 2021,
725 Fig. 3H). Systems with these complementary saturating benefits and fixed costs are likely to
726 display much more limited dynamics than those shown in Fig. 3C-F. For example, Kang *et al.*
727 (2011) and Martignoni *et al.* (2020, 2021) adapted Holland and DeAngelis' approach to specific
728 empirical systems, leading to models which predict the threshold and stable coexistence
729 dynamics of simpler saturating benefit models (Fig. 3G).

730 Reviewers for an earlier version of this manuscript commented that our results cement
731 the idea that pairwise models of mutualism have been "pushed...as far as they will go," that "this
732 literature has limited usefulness for motivating the theory of the future," and that it may be "the
733 nature of mutualism" that its dynamics are "not very interesting...for a broad audience in

734 ecology and evolution.” Though we cannot speak to whether mutualism is of interest to specific
735 individuals, we do believe that this attitude may have contributed to the long-term stagnation and
736 repeated loss and rediscovery of theory in mutualism. A clear summary of the population
737 dynamics of pairwise mutualisms (as we presented here) is an important groundwork for
738 directing research into modules and networks including mutualistic interactions, the evolutionary
739 origins of mutualism, and, pressingly, directing conservation efforts across systems (Fig. 4).
740 Both within the discipline and more broadly, there is an impression that theory is lacking. But it
741 is simply not the case that ecological theory of mutualism is incoherent or under-developed: we
742 find here that it is remarkably self-consistent despite the diversity of inspiring systems and
743 modeling frameworks. It is not a mystery how pairwise mutualisms can persist stably, at least
744 theoretically. Mutualisms are highly stable at high density, and the network setting may diffuse
745 the risk of low density-thresholds leading to population collapse. A similar set of empirical
746 literature to support or dispute the models’ results has yet to accumulate, but we hope that by
747 clearly outlining dynamical expectations of mutualistic theory, such work will be more
748 accessible to empiricists.

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1001

1002

Legends

1003 **Fig. 1. Characteristic dynamics for linear benefit models.** In early models of mutualism,
1004 benefits were represented by a constant coefficient (interactions strength) multiplying a linear

1005 function of partner density. Benefits were modeled as affecting per-capita growth rate (low-
1006 density effect, Eqn 4), equilibrium density (high-density effect, Eqn 2), or both (Eqn 1, see Table
1007 2). When benefits have exclusively low-density effects, nullclines (curves of zero growth), are
1008 simply vertical (N_1) and horizontal (N_2) lines, always resulting in stable coexistence
1009 (qualitatively similar dynamics to those in **A**). Otherwise, the nullclines are linear, increasing
1010 curves, with different potential dynamics (**A-D**). When both partners are facultative mutualists (
1011 $N_i = K_i > 0$ when $N_j = 0$), they display stable coexistence when benefits are weak (**A**) or grow
1012 without bound (unstable coexistence) when benefits are strong (**C**). When both mutualists are
1013 obligate upon their partner ($N_i = K_i \leq 0$ when $N_j = 0$) and benefits are weak, the system exhibits
1014 a threshold in density above which species exhibit unbounded growth and below which
1015 extinctions occur (**B**), whereas if benefits are strong, only extinctions occur (**D**). When mutualists
1016 are a facultative-obligate pair, any of the previous results can occur depending on relative
1017 interaction strength and obligacy. Benefit strength (weak or strong) is relative to intraspecific
1018 limitation. Arrows are vectors showing the ‘flow’ of the system: arrow angle shows the direction
1019 of changes in density of N_1 (x-direction) and N_2 (y-direction) and arrow color shows the
1020 magnitudes of change in that direction (lighter colors are stronger changes). Nullclines are curves
1021 of zero change of density for one partner. Equilibria (colored or hollow dots) occur when both
1022 partners have zero change in density. Equilibria are locally stable (black dots) or unstable (red
1023 dots) if the system is attracted or repelled, respectively, the equilibrium after a small
1024 perturbation. Equilibria are half-stable “saddles” (hollow dots) if the system is attracted in some
1025 dimensions by repelled in others. Panels were generated using the model in Case 1.1.1 of Table
1026 3.

1027
1028 **Fig. 2. Characteristic dynamics for saturating benefit models.** Density-dependent benefit
1029 functions stabilize linear benefit models (Fig. 1). Benefits may saturate (decrease in strength)
1030 with increasing recipient density (“intraspecific density-dependence,” Case 2.1), increasing
1031 partner density (“interspecific density-dependence,” Case 1.2), or both (Case 2.2), resulting in
1032 stable coexistence (see Table 3). Specifically, when paired with a partner with linear (**A-B**) or
1033 saturating (**E-F**) benefits, feasible systems exhibit the same qualitative dynamics: stable
1034 coexistence at densities higher than either partner could achieve alone (off-axes black point), and
1035 potential or guaranteed threshold effects when one or both partners are obligate mutualists.

1036 Under a certain threshold (red dashed line), one population is at too low density to support its
1037 partner, collapsing the system (**B, F**). This threshold causes extinction of obligate partners, even
1038 if initially highly abundant (e.g., follow lighter colored trajectories in panel **F**). These dynamics
1039 of coexistence and threshold effects are robust across models of mutualism with saturating
1040 benefits, regardless of the mechanism by which benefit saturates (Cases 1.2, 2.1, 2.2). Benefits
1041 may also increase in strength with increasing recipient density (also called “intraspecific density-
1042 dependence,” Case 3.2), causing unbounded growth in the absence of other limitations.
1043 Specifically, feasible systems between two facultative partners of this form exhibit unstable
1044 coexistence (**C-D**) and a potential threshold under which the system exhibits stable coexistence
1045 at low density or explodes with unbounded population growth at high density (**D**). Panels were
1046 generated using models in Case 1.1.1 (N_1 only, **A-B**), Case 1.2 for (N_2 only **A-B**, both **E-F**), or
1047 Case 3.2 (**C-D**) of Table 3.

1048 **Fig. 3. Characteristic dynamics for shifting net-effects and consumer-resource models.**

1049 Models that investigated shifts in net effects as a balance of costs and benefits (“context-
1050 dependency”) led to a synthesis of mutualism into a consumer-resource framework. Models with
1051 saturating benefit functions and linear costs (**A-B**) tend to display stable coexistence (**A**) and
1052 threshold effects (**B**) like earlier models (Fig. 2). Stable coexistence is “mutualistic” if the
1053 nullclines intersect such that both species achieve higher density than they would alone, or if
1054 increasing the density of one species from equilibrium permit growth of its partner. Otherwise,
1055 the interaction is “parasitic.” Linear costs can make the coexistence equilibrium a stable spiral,
1056 with damped oscillations towards equilibrium (**B, D, F, G**). Models with unimodal benefit
1057 response that allow negative effects (net costs) at high density (**C-D**) or that include both
1058 separately saturating costs and benefits (**E-F**) display more complex dynamics. Depending on its
1059 parameterization, the mutualism-competition model by Zhang (2003) displays mutualistic stable
1060 coexistence (not shown), competitive exclusion (**C**), or competitive dominance (**D**), with
1061 dominant species dependent on initial densities (i.e., system initialized to the left or right of the
1062 separatrix). The consumer-resource model by Holland & DeAngelis (2010) also displays a range
1063 of dynamics depending on parameterization (**E-F**), including multiple stable coexistence
1064 equilibria (**F**). Mutualistic coexistence occurs when the ratio of consumers to their resources is
1065 not above a certain threshold (i.e., to the left of the left separatrix, or below the bottom
1066 separatrix). Otherwise, consumers overexploit their resources (causing more costs than provided

1067 benefits), leading to system collapse. Recent works use a consumer-resource approach with
1068 system-specific mechanisms (**G**, **H**), but often exhibit the simpler qualitative dynamics of
1069 saturating benefit models (Fig. 2) with the potential for oscillations (**G**). Panels show the
1070 following models: (**A-B**) Neuhauser & Fargione 2004, plant-mycorrhizae; (**C-D**) Zhang 2003,
1071 competitor-mutualists; (**E-F**) Holland & DeAngelis 2010, bidirectional consumer-resource
1072 mutualism (e.g., corals); (**G**) Kang *et al.* 2011, ant-fungal garden; (**H**) Hale *et al.* 2021, plant-
1073 seed disperser.

1074

1075 **Fig. 4. Distinguishing characteristic dynamics.** N_1 (x-axis) is obligate mutualist and N_2 (y-
1076 axis) is facultative in all panels. (**A**) Threshold effects: N_1 goes extinct when the density of N_2 is
1077 below a threshold (separatrix). The system achieves stable coexistence when N_2 is above the
1078 threshold, and both species achieve higher densities than either would attain alone. (**B**)
1079 Overexploitation dynamics: the system collapses above a threshold in the ratio of consumer (N_2)
1080 to resource (N_1) species density. At low density, both partners will grow due to benefits from
1081 mutualism until they reach stable coexistence at higher density than either species could achieve
1082 alone. Above a threshold of N_2 density (separatrix), both populations will grow but N_2 will
1083 increase to such an extent that it exerts more costs than benefits it provides (exploitation). N_1
1084 will begin to decline at low density while N_2 continues to grow, eventually leading to both going
1085 extinct. At even higher initial densities of N_2 , N_2 will immediately overexploit N_1 and both
1086 species will go extinct, without even acquiring enough benefits to allow its own population to
1087 grow. (**C**) Allee effects: N_1 will go extinct if its density is under a threshold of its own density
1088 (left side of N_1 non-trivial nullcline) because it becomes too rare to receive benefits from the
1089 mutualistic interaction. The system tends towards stable coexistence at higher density than either
1090 partner could achieve alone when N_1 is above such threshold of its own density. Note that
1091 threshold effects induced by partner decline (**A**) cause Allee effects in both species because at
1092 low density they cannot support a sufficient partner population density to allow their own
1093 population growth. Overexploitation (**B**) by the high-density consumer (N_2) also induces an
1094 Allee effect in the resource species (N_1) where lower resource density causes lower benefits
1095 from the interaction. Example systems: (**A**) Graves *et al.* 2006, lichens; (**B**) Holland &

1096 DeAngelis 2010, unidirectional consumer resource mutualism (e.g., seed dispersal); (C) Hale *et*
1097 *al.* 2021, pollination.

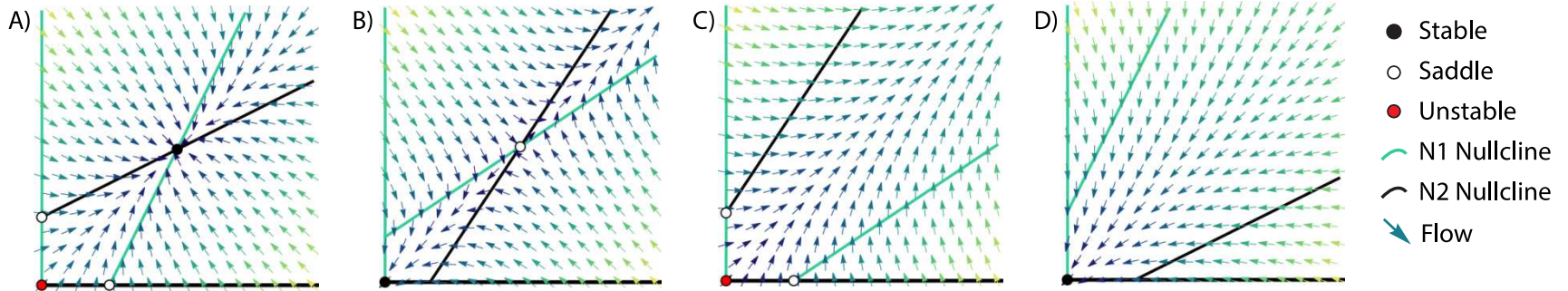
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Figures

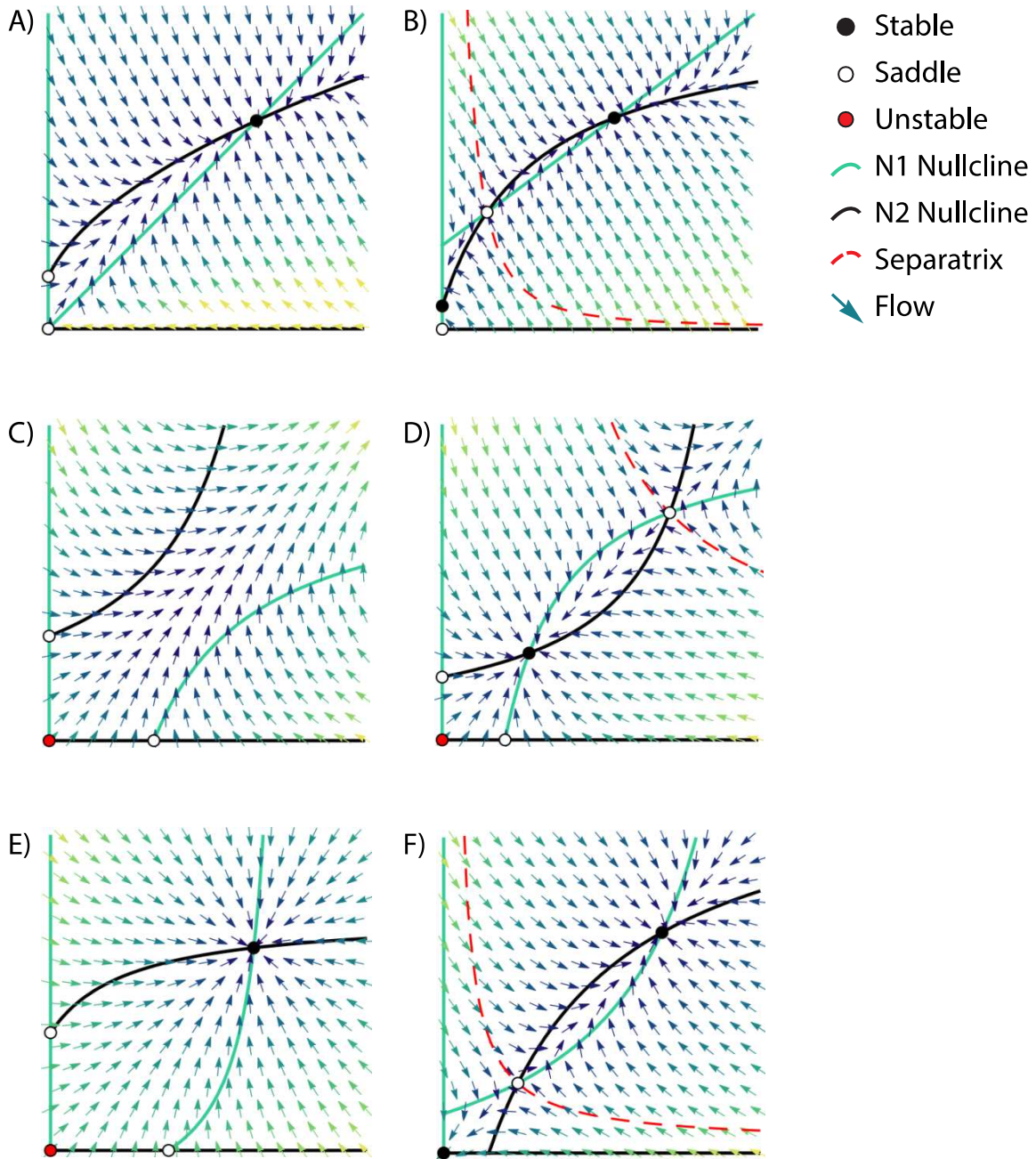
1099 **Fig. 1. Characteristic dynamics for linear benefit models.**

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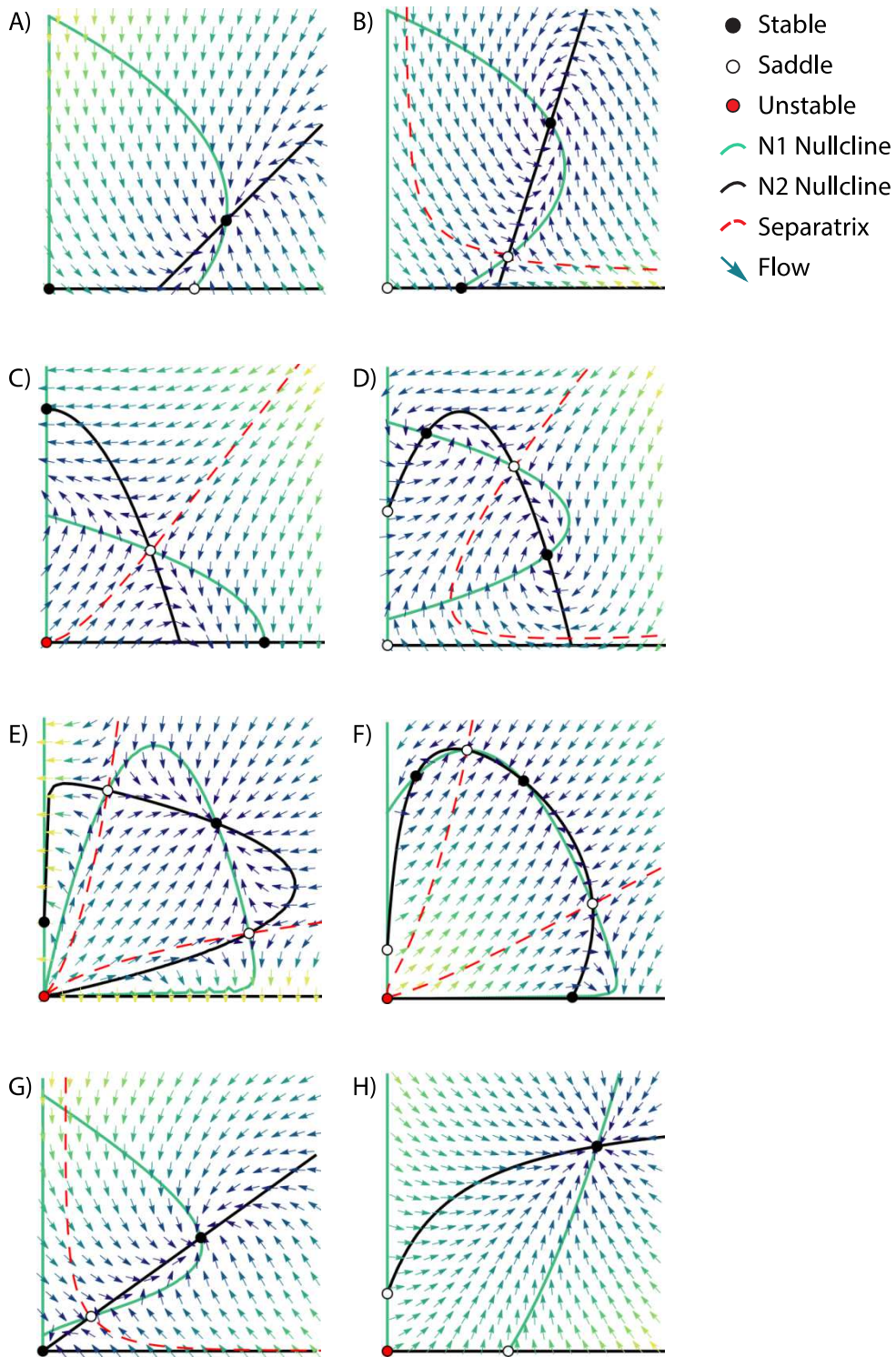
1102 **Fig. 2. Characteristic dynamics for saturating benefit models.**



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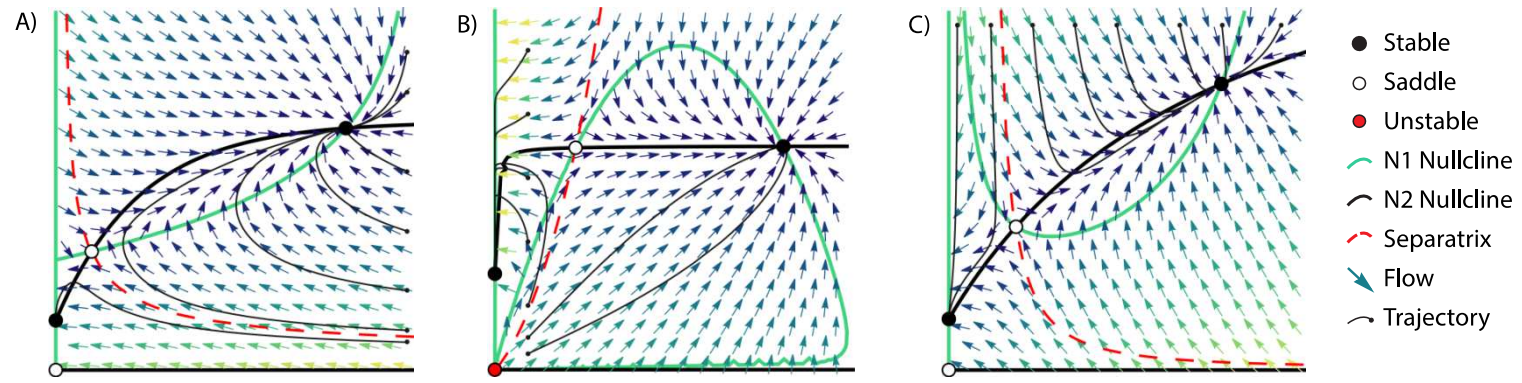
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1105 **Fig. 3. Characteristic dynamics for shifting net-effects and consumer-resource models.**



1107 **Fig. 4. Distinguishing characteristic dynamics.**

1108



1110 **Table 1. The historical development of theory of mutualism.**

	Linear benefits	Saturating benefits <i>(intraspecific)</i>	Saturating benefits <i>(interspecific)</i>	Cost-benefit models & shifting net effects	Consumer-resource approach
Representative work	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.
Mechanisms included	Benefit increases per-capita growth rate (low-density effect), equilibrium density (high-density effect), or both.	Per-capita benefit accrual decreases 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 recipient or partner densities and negative effects (net costs) at high densities. Benefits accrue due to 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.

Characteristic assumptions	Benefit is a linear function of partner density.	Benefit increases per-capita growth rate and equilibrium density, but saturates with increasing recipient density.	Benefit increases per-capita growth rate and equilibrium density, but saturates with increasing partner density. Recipient 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”)
Characteristic predictions	Unbounded growth between facultative partners with strong interactions. Stable coexistence between facultative partners with weak interactions. Extinction of obligate partners below a certain density threshold or unbounded growth above such threshold with	Stable coexistence in feasible interactions, regardless of interaction strength or obligacy. Threshold between extinction of obligate partners and stable coexistence when at least one partner is obligate. Coexistence is non-oscillatory (stable node).	Same predictions as in intraspecific saturating models.	Diverse dynamics, depending on the model and its parameterization: Predictions of saturating models, but coexistence may be oscillatory (stable spiral). Mutualistic coexistence, competitive coexistence, or competitive exclusion. Mutualistic coexistence, parasitic coexistence, or extinctions.	Fixed costs: same predictions as in saturating models. Variable, linear costs: same predictions as saturating models, but coexistence may be oscillatory. Variable, nonlinear costs: mutualistic coexistence or overexploitation by consumers leading to collapse; coexistence may

	strong interactions. Extinction of obligate partners with weak interactions.				be oscillatory.
Citations	Gause & Witt 1935, Whittaker 1974, Vandermeer & Boucher 1978, Goh 1979, Addicott 1981, Gilpin 1982.	Whittaker 1975, May 1976, Soberón & Martínez del Rio 1981, Dean 1983, Wolin & Lawlor 1984, Parker 2001.	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.	Tonkyn 1986, 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.

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1113 **Table 2. Selected models of pairwise mutualism.**

1114 A full list of models cited in the main text is included in the supplementary information (Table
 1115 S1). Equations largely follow the notation from the original citations. All parameters are positive
 1116 (> 0) unless otherwise specified. Models with unique mathematical forms are given unique
 1117 equation numbers. We encourage the readers to refer to the original references for the model
 1118 derivations and interpretation of parameters. Notes include inspiring system and obligacy, if
 1119 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	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 + \alpha_{12} N_2 - N_1}{K_1 + \alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 + \alpha_{21} N_1 - N_2}{K_2} \right) \end{cases}$	Symbiont (N_1)-Host (N_2)
	1		Obligate N_1 when $K_1 = 0$ Parasitism when $\alpha_{21} < 0$
	2	$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left(\frac{\alpha_{12} N_2 - N_1}{\alpha_{12} N_2} \right) \\ \frac{dN_2}{dt} = \frac{r_2 N_2}{K_2} \left(K_2 + \frac{a D N_1}{D + N_2} - N_2 \right) \end{cases}$	Symbiont (N_1)-Host (N_2)
	3		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	$\frac{dN_i}{dt} = N_i(r_i - (b - mN_j + d)N_i)$	Reduces b without limit
Wright 1989	7	$\frac{dN_i}{dt} = N_i\left(r_i - c_iN_i + b_{ij}\frac{a_{ij}N_j}{1 + a_{ij}h_{ij}N_j}\right)$	Pollinators & other forager mutualists See Table S1
Zhang 2003	8	$\frac{dN_i}{dt} = R_iN_i(c_i - N_i - a_i(N_j - b_i)^2)$	Interactions between species at the same trophic level $-\infty < b_i < \infty$
Neuhauser & Fargione 2004	9 1	$\begin{cases} \frac{dN_1}{dt} = r_1N_1\left(\frac{K_1 + \gamma_{12}N_2 - N_1}{K_1 + \gamma_{12}N_2} - aN_2\right) \\ \frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 + \alpha_{21}N_1 - N_2}{K_2}\right) \end{cases}$	Plant (N_1)-Mycorrhizae (N_2) Facultative only
Graves <i>et al.</i> 2006	10	$\frac{dN_i}{dt} = N_i(r_{i0} + (r_{i1} - r_{i0})(1 - e^{-k_iN_j}) - a_iN_i)$	Lichens Obligate when $r_{i0} < 0$, $r_{i1} + r_{i0} > 0$ See Table S1
Thompson <i>et al.</i> 2006	11 12	$\begin{cases} \frac{dN_1}{dt} = (\rho_1b_1N_1 + I_1)\left(1 - \frac{N_1}{S_1}\right) - \left(d_{1min} + \frac{d_{1max} - d_{1min}}{1 + c_1N_2}\right)N_1 \\ \frac{dN_2}{dt} = (\rho_2b_2N_2 + I_2)\left(1 - \frac{N_2}{S_2 + N_1}\right) - \left(d_{2min} + \frac{d_{2max} - d_{2min}}{1 + c_2N_1}\right)N_2 \end{cases}$	Hermit crabs (N_1)- Anemones (N_2) Closed system when I_i $= 0$, $\rho_i = 1$ Obligate when $\rho_i b_i < d_{i,max}$ See Table S1
Holland & DeAngelis 2010	13	$\frac{dN_i}{dt} = N_i\left(r_i + c_i\left(\frac{a_{ij}N_j}{h_j + N_j}\right) - q_i\left(\frac{\beta_{ij}N_j}{e_i + N_i}\right) - s_iN_i\right)$	Bidirectional Consumer-Resource e.g., Plant (N_1)- Mycorrhizae (N_2) Obligate when $r_i = 0$
	13 7	$\begin{cases} \frac{dN_1}{dt} = N_1\left(r_1 + c_1\left(\frac{a_{12}N_2}{h_2 + N_2}\right) - q_1\left(\frac{\beta_{12}N_2}{e_1 + N_1}\right) - s_1N_1\right) \\ \frac{dN_2}{dt} = N_2\left(r_2 + c_2\left(\frac{a_{21}N_1}{h_1 + N_1}\right) - s_2N_2\right) \end{cases}$	Unidirectional e.g., Plant (N_1)- Pollinator (N_2)

Fishman & Hadany 2010	14	$\begin{cases} \frac{dN_1}{dt} = N_1 \left(\frac{\eta\alpha N_2}{1 + \alpha N_1 + \alpha\beta N_2} - b - cN_1 \right) \\ \frac{dN_2}{dt} = N_2 \left(\frac{\mu\alpha N_1}{1 + \alpha N_1 + \alpha\beta N_2} - d \right) \end{cases}$	Plant (N_1)-Pollinator (N_2)
	15		Obligate only
Kang <i>et al.</i> 2011	16	$\begin{cases} \frac{dN_1}{dt} = N_1 \left(r_f \left(\frac{aN_2^2}{b + aN_2^2} \right) - r_c N_2 - d_1 N_1 \right) \\ \frac{dN_2}{dt} = N_2 (r_a N_1 - d_2 N_2) \end{cases}$	Fungal garden (N_1)- Leaf cutter ant (N_2)
	1		Obligate only
Martignoni <i>et al.</i> 2020	17	$\begin{cases} \frac{dN_1}{dt} = N_1 \left(r_p + \frac{q_{hp}\alpha N_2}{d + N_1} - q_{cp}\beta N_2 - \mu_p N_1 \right) \\ \frac{dN_2}{dt} = N_2 \left(q_{cm}\beta N_1 - \frac{q_{hm}\alpha N_1}{d + N_1} - \mu_m N_2 \right) \end{cases}$	Plant (N_1)-Mycorrhizae (N_2)
	18		Obligate N_2
Hale <i>et al.</i> 2021	19	$\begin{cases} \frac{dP}{dt} = P \left[b_p \left(f + \varphi \frac{aAP}{1 + ahP + aAP} \right) g - s_p P - d_p \right] \\ \frac{dA}{dt} = A \left[b_A + \varepsilon \frac{aP}{1 + ahP} - s_A A - d_A \right] \end{cases}$	Plant (N_1)-Pollinator (N_2)
	7		Obligate N_1 when $b_1 f g - d_1 \leq 0$; obligate N_2 when $b_2 - d_2 \leq 0$
	20	$\begin{cases} \frac{dP}{dt} = P \left[b_p f g - \left(s_p - \sigma \frac{aA}{1 + ahP + aA} \right) P - d_p \right] \\ \frac{dA}{dt} = A \left[b_A + \varepsilon \frac{aP}{1 + ahP} - s_A A - d_A \right] \end{cases}$	Plant (N_1)-Seed Disperser (N_2)
	7		Facultative N_1 only Obligate N_2 when $b_2 - d_2 \leq 0$

1121 **Table 3. Generic models of mutualism.**

1122 Description of nullcline geometry, qualitative dynamics, and empirical assumptions under which seven generic models of mutualism
 1123 may arise. In all models, benefits of mutualism are a function of partner density (N_j). All models also include a form of intraspecific
 1124 density-dependence, that is per-capita growth rate is dependent upon recipient density (N_i). To better interpret the historical literature,
 1125 we categorize models into three cases of intraspecific density-dependence (see text). Only Case 2 yields feasible dynamics in the
 1126 absence of self-limitation (i.e., when $s_i = 0$). Intrinsic (per-capita) growth rate determines obligacy in all models ($r_i \leq 0$: i is obligate
 1127 upon j , $r_i > 0$: i is facultative), with one exception. Case 3.1 uses the (deprecated) historical convention in which carrying capacity
 1128 directly determines obligacy ($K_i = 0$: i is obligate upon j , $K_i > 0$: i is facultative). All other parameters are assumed to be positive.
 1129 Nullcline geometry is restricted to the ecologically relevant region ($N_1 \geq 0, N_2 \geq 0$). Only feasible dynamics are listed: “SC” is stable
 1130 coexistence, “UC” is unstable coexistence,” “UC/E threshold” is a threshold dividing the plane into unstable coexistence at higher
 1131 density or extinction at lower density, “HD” is high density, etc. Alternative qualitative dynamics (listed on separate lines) are possible
 1132 based on parameterization of the models.

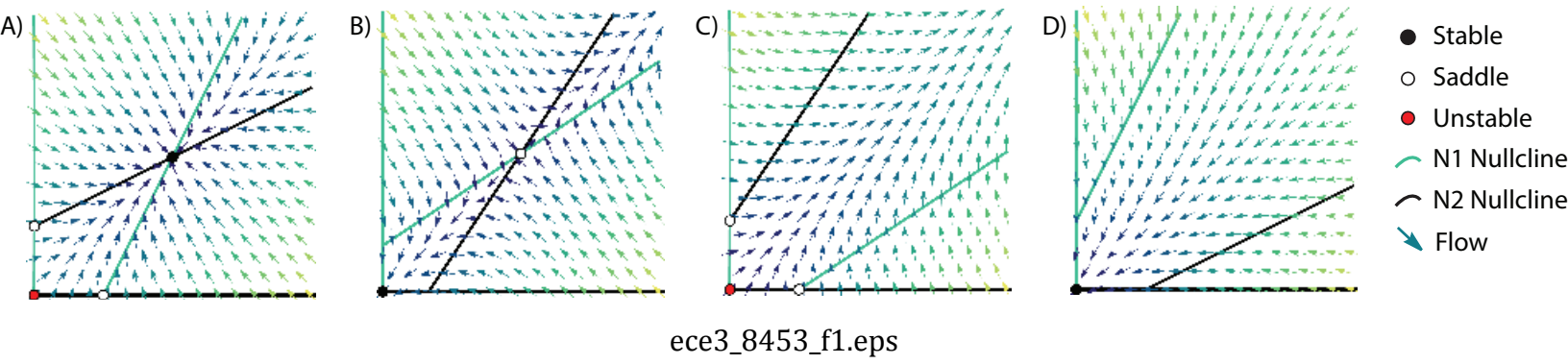
1133

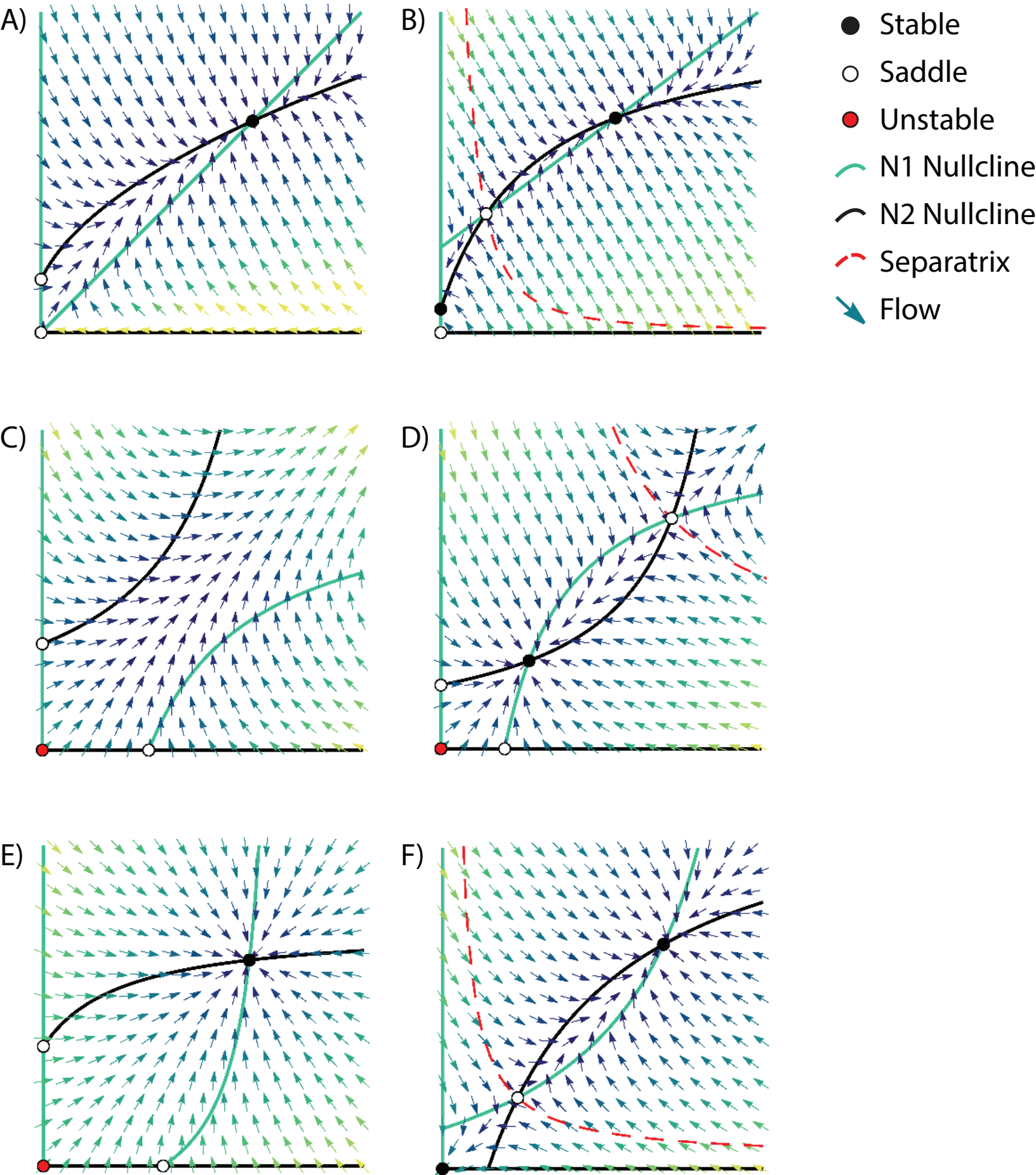
		Qualitative dynamics with N_2			
	Change in population density of N_i with benefits from N_j	N_1 Nullcline geometry	Stability with Case 1.1.1 (linear)	Stability with Case 1.2 (increasing, concave down)	Empirical justification (Table S1 reference)
Case 1: Intraspecific density-dependence in population dynamics only: self-limitation or negative density-dependence terms					
Benefits accrue directly to per-capita growth rate...					
1.1.1	...as a linear function of partner density $\frac{dN_i}{dt} = N_i(r_i + \beta_{ij}N_j - s_iN_i^{\theta_i})$	$\theta_1 = 1$: Increasing, linear	SC (Fig. 1A) UC (Fig. 1C) UC/E threshold (Fig. 1B)	SC (Fig. 2A) HD SC & SC/E threshold (Fig. 2B)	S1: Early ant colonies consume fungus, self-limit due to larval care, etc. (Kang <i>et al.</i> 2011)

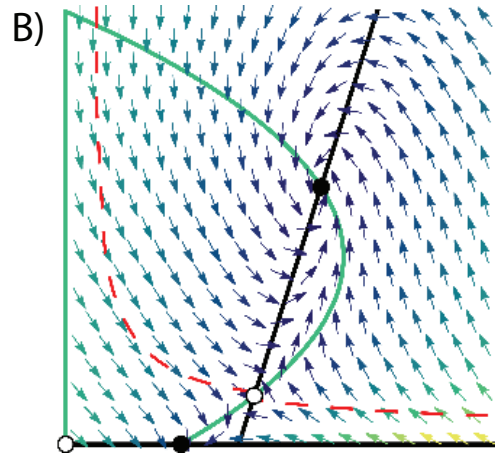
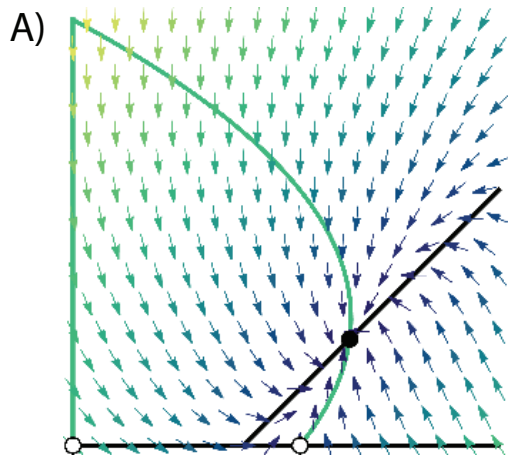
1.1.2		$0 < \theta_1 < 1$, $r_1 > 0$: Increasing concave down	UC UC/E threshold HD UC & SC/E threshold	SC UC UC/E threshold HD UC & SC/E threshold	S35: Decelerating negative density-dependence; “r-selected” organisms (Moore <i>et al.</i> 2018)
1.1.3		$\theta_1 > 1$, $r_1 > 0$: Increasing, concave up	SC HD SC & SC/E threshold	SC (Fig. 2E) HD SC & SC/E threshold (Fig. 2F)	S35: Accelerating negative density-dependence; “K-selected,” sedentary, & stage-structured organisms, e.g., flowering plants (Moore <i>et al.</i> 2018)
1.2	...as a function that saturates with increasing partner density $\frac{dN_i}{dt} = N_i \left(r_i + \beta_{ij} \frac{N_j}{h_{ij} + N_j} - s_i N_i \right)$	Increasing, concave up	SC HD SC & SC/E threshold	SC (Fig. 2E) HD SC & SC/E threshold (Fig. 2F)	Servicers such as pollinators forage... S8: limited by handling time (Type II, Soberón & Martínez del Rio 1981, Wright 1989, Holland & DeAngelis 2010, Hale <i>et al.</i> 2021) S34: limited by rewards availability (Type I, on saturating plant rewards (Revilla 2015) S27: Mortality declines due to protection or deterrence by partners (Thompson <i>et al.</i> 2006)
Case 2: Intraspecific density-dependence in mutualism only: benefits saturate with increasing recipient density					
	Benefits accrue directly to per-capita growth rate...				

2.1with increasing recipient density $\frac{dN_i}{dt} = N_i \left(r_i + \beta_{ij} \frac{N_j}{h_{ij} + N_i} - s_i N_i \right)$	Increasing, concave up	SC HD SC & SC/E threshold	SC (Fig. 2E) HD SC & SC/E threshold (Fig. 2F)	Plant reproduction is a function of pollinator visitation... S7: Type II, on plants (Soberón & Martínez del Río 1981) S33: Type I, on saturating plant rewards (Revilla 2015) Also see S3
2.2with increasing recipient & partner density $\frac{dN_i}{dt} = N_i \left(r_i + \beta_{ij} \frac{N_j}{h_{ij} + N_i + N_j} - s_i N_i \right)$	Increasing, concave up	SC HD SC & SC/E threshold	SC (Fig. 2E) HD SC & SC/E threshold (Fig. 2F)	S10: Plant reproduction is a function of pollinator visitation (Type II), limited by ovule availability (Wells 1983) S11: Pollinators forage on plants (Type II), limited by search time (Wells 1983) Also see S4, S31
Case 3: Benefits of mutualism reduce intraspecific density-dependence in population dynamics					
	Benefits reduce negative density-dependence...				
3.1	...via increasing carrying capacity as a linear function of partner density $\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i + N_j} \right)$	Increasing, linear	SC (Fig. 1A) UC (Fig. 1C) UC/E threshold (Fig. 1B)	SC (Fig. 2A) HD SC & SC/E threshold (Fig. 2B)	S2: Hosts for symbionts (Whittaker 1975, May 1976) S28: Partners supply substrate or habitat, e.g., domatia for aphids (Thompson <i>et al.</i> 2006) Also see S12
	...via decreasing self-limitation				

3.2as a linear function of partner density $\frac{dN_i}{dt} = N_i(r_i - (s_i - \beta_{ij}N_j)N_i)$	Increasing, concave down	UC HD UC & UC/SC threshold	UC HD UC & UC/SC threshold	S13: Benefits accrue primarily at high recipient density (Wolin & Lawlor 1984)
3.3as a function that saturates with increasing recipient & partner density $\frac{dN_i}{dt} = N_i\left(r_i - \left(s_i - \beta_{ij}\frac{N_j}{h_{ij} + N_i + N_j}\right)N_i\right)$	Decreasing, concave up to linear	SC HD SC & SC/E threshold	SC (Fig. 3H) HD SC & SC/E threshold (Fig. 3H)	S40: Disperser visitation (Type II) reduces seed mortality from the Janzen-Connell effect (Hale <i>et al.</i> 2021)







- Stable
- Saddle
- Unstable
- N1 Nullcline
- N2 Nullcline
- - - Separatrix
- ↘ Flow

