

# Population dynamics of mutualism and intraspecific density dependence: how $\theta$ -logistic density dependence affects mutualistic positive feedback

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## Abstract

Mutualism describes the biological phenomenon where two or more species are reciprocally beneficial, regardless of their ecological intimacy or evolutionary history. Classic theory shows that mutualistic benefit must be relatively weak, or else it overpowers the stabilizing influence of intraspecific competition and leads to unrealistic, unbounded population growth. Interestingly, the conclusion that strong positive interactions lead to runaway population growth is strongly grounded in the behavior of a single model. This model—the Lotka-Volterra competition model with a sign change to generate mutualism rather than competition between species—assumes logistic growth of each species plus a linear interaction term to represent the mutualism. While it is commonly held that the linear interaction term is to blame for the model’s unrealistic behavior, we show here that a linear mutualism added to a  $\theta$ -logistic model of population growth can prevent unbounded growth. We find that when density dependence is decelerating, the benefit of mutualism at equilibrium is greater than when density dependence is accelerating. Although there is a greater benefit, however, decelerating density dependence tends to destabilize populations whereas accelerating density dependence is always stable. We interpret these findings tentatively, but with promise for the understanding of the population ecology of mutualism by generating several predictions relating growth rates of mutualist populations and the strength of mutualistic interaction.

*Keywords:* Mutualism, population dynamics, density dependence, Lotka-Volterra,  $\theta$ -logistic

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## 1. Introduction

Mutualistic interactions describe the ecology of two or more species that reciprocally increase each other’s fitness (Bronstein, 2015). These interactions are arguably the most common type of ecological interaction, and they have profoundly shaped biodiversity as we understand it. Examples include

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5 mutualisms between mycorrhizae and plants (van der Heijden et al., 2015), coral and zooxanthellae  
6 (Baker, 2003), plants and pollinators (Willmer, 2011), tending ants and aphids or Lepidoptera larvae  
7 (Rico-Gray and Oliveira, 2007; Stadler and Dixon, 2008), plants and seed-dispersing animals (Howe  
8 and Smallwood, 1982; Levey et al., 2002), lichens (fungi and algae) (Brodo et al., 2001), and plants  
9 and rhizobia (Sprent et al., 1987; Kiers et al., 2003). Despite mutualism’s obvious importance, it was  
10 not until the latter part of the 20<sup>th</sup> century that the natural history of mutualism underwent rigorous  
11 ecological study, the conceptual framework for mutualism was laid, and mutualism was no longer  
12 confounded with the concept of symbiosis. Thus, by the time mutualism was fully introduced to  
13 the larger ecological community, theoretical ecology had been developing in its absence for decades.  
14 This resulted in the paucity of theory for mutualisms still very much visible today.

15 Gause and Witt (1935) first used the Lotka-Volterra model of interspecific competition to inves-  
16 tigate the case of facultative “mutual aid” between two species by reversing the sign of the linear  
17 competition term from negative to positive. They noted that with enough “mutual aid” the zero-  
18 growth isoclines no longer cross to give a positive equilibrium point and species grow exponentially  
19 without bound—a biologically unrealistic scenario. More specifically, they found that if the product  
20 of the strength of mutualism between the two species is  $\geq$  the product of the strength of intraspecific  
21 competition for each species, then the positive feedback of mutualism would overpower the nega-  
22 tive feedback of intraspecific competition, resulting in unbounded growth. Following this pioneering  
23 study, no development of theory around mutualism would happen for over 30 years and ecologists  
24 were left lacking a basic theoretical explanation for what stabilizes mutualism in nature.

25 A key feature of the Lotka-Volterra model is its use of a linear functional response: the effect  
26 of a mutualist on its partner’s per capita growth rate is linearly proportional to the mutualist’s  
27 density. Early models of obligate mutualism also shared this feature. Albrecht et al. (1974), May  
28 (1976), Christiansen and Fenchel (1977), and Vandermeer and Boucher (1978) introduced the idea  
29 of modeling mutualism through the intrinsic growth rate, shifting it from positive, in the case  
30 of facultative mutualism, to negative for obligate mutualism. Using linear functional responses,  
31 they generally found that, first, two obligate mutualists cannot stably coexist and, second, stable  
32 coexistence is possible if one species is obligate and the other is not, depending on the strength of the  
33 mutualism. These papers and others (e.g. Wolin, 1985; DeAngelis et al., 1986) further postulated  
34 that mutualistic functional responses are nonlinear, and thus attributed the unrealistic behavior  
35 of the Lotka-Volterra and similar models to their use of a linear functional response. Nonlinear  
36 functional responses were later explicitly modeled (e.g., Wright, 1989; Holland et al., 2002; Holland  
37 and DeAngelis, 2010; Revilla, 2015), confirming that nonlinear functional responses can indeed

38 stabilize mutualistic populations.

39 Each of the aforementioned mutualism models, regardless of the functional response, assumes  
40 linear intraspecific density dependence; i.e., logistic within-species dynamics. However, nonlinear  
41 density dependence has been observed in controlled laboratory populations of organisms with simple  
42 life histories, such as *Daphnia* sp. and other Cladocera (Smith, 1963; Smith and Cooper, 1982) and  
43 *Drosophila* spp. (Ayala et al., 1973; Gilpin and Ayala, 1973; Pomerantz et al., 1980), and in long-term  
44 datasets on species with more complex life histories (Stubbs, 1977; Fowler, 1981; Sibly et al., 2005;  
45 Coulson et al., 2008). Models that relax the assumption of linear intraspecific density dependence  
46 have been proposed for single species (e.g., Richards, 1959; Schoener, 1973; Turchin, 2003; Sibly et al.,  
47 2005) and communities with two or more competitors (Ayala et al., 1973; Gilpin and Ayala, 1973;  
48 Schoener, 1976; Goh and Agnew, 1977; Gallagher et al., 1990), but never for mutualism (but see a  
49 generalized Verhulst-Lotka-Volterra model in Ribeiro et al. 2014 and a specific facultative-obligate  
50 model in Wang 2016). Given the prevalence of nonlinear intraspecific density dependence, and its  
51 known influence on dynamics in other ecological contexts, the dearth of mutualism models that  
52 assume anything besides logistic growth suggests that our understanding of mutualistic dynamics  
53 may be quite incomplete.

54 In sum, the Lotka-Volterra mutualism model makes two separate assumptions that are likely  
55 violated in many natural systems: a linear effect of mutualistic interactions, and linear intraspecific  
56 density dependence. The former is widely thought responsible for the Lotka-Volterra mutualism  
57 model's unrealistic behavior, but since the latter has never been investigated in the context of mu-  
58 tualisms, the relative importance of these two simplifying assumptions remains unclear. While we  
59 agree that many mutualistic interactions are likely nonlinear, the same could be said of competitive  
60 interactions, and yet Lotka-Volterra competition models endure. Is the need to eschew linear in-  
61 teraction rates truly fundamental for mutualisms? We approached this line of inquiry by returning  
62 to the original Lotka-Volterra mutualism model. To complement what is already known, we relax  
63 the assumption of linear intraspecific density dependence while leaving the assumption of a linear  
64 mutualistic functional response intact. We accomplish this by using the  $\theta$ -logistic equation, which  
65 can decelerate or accelerate as a function of intraspecific density. We found that any accelerating  
66 model was always stable, and that decelerating models were stable with weak mutualism. We there-  
67 fore conclude that relaxing *either* of the Lotka-Volterra model's major simplifying assumptions can  
68 prevent unrealistic model behavior. Given that nonlinear intraspecific density dependence appears  
69 to be widespread, nonlinearity in mutualistic interaction rates may be less important for stabilizing  
70 mutualisms than was previously believed.

71 **2. Methods**

72 The Lotka-Volterra mutualism model for population densities of two species,  $N_1$  and  $N_2$ , takes  
73 the form

$$\begin{aligned}
 \frac{1}{N_1} \frac{dN_1}{dt} &= f_1(N_1) + \beta_1 N_2 = r_1 - \alpha_1 N_1 + \beta_1 N_2 \\
 \frac{1}{N_2} \frac{dN_2}{dt} &= f_2(N_2) + \beta_2 N_1 = r_2 - \alpha_2 N_2 + \beta_2 N_1.
 \end{aligned}
 \tag{1}$$

76 That is, the per capita change in population  $i$ 's density is a function of intraspecific density,  $f_i(N_i)$ ,  
77 and a linear function of mutualist partner density,  $\beta_i N_j$ . It is further assumed that intraspecific  
78 density dependence,  $f_i(N_i)$ , is logistic. This means the per capita growth rate approaches  $r_i$  when  
79  $N_i$  approaches 0, and linearly decreases as intraspecific density increases, with slope  $-\alpha_i$ . Assuming  
80 positive parameter values, eq. (1) has the following behavior: each population grows when rare,  
81 each population has a stable positive abundance in the absence its mutualist partner, a feasible 2-  
82 species equilibrium exists if  $\beta_i \beta_j < \alpha_i \alpha_j$ , and unbounded exponential growth occurs if  $\beta_i \beta_j \geq \alpha_i \alpha_j$   
83 (Vandermeer and Boucher, 1978).

84 The first terms in eq. (1) have not received the same scrutiny as the last terms. We suspect this  
85 has more to do with the ubiquity of the logistic model than careful evaluation of its application here.  
86 To explore this, we relax the assumption of logistic growth—the assumption that the difference be-  
87 tween per capita births and deaths linearly decreases as density increases. We relax this assumption  
88 by modeling per capita growth rates using the  $\theta$ -logistic model. This causes the per capita growth  
89 rate to be a decelerating function of density if the exponent ( $\theta$ ) is  $< 1$  and an accelerating function  
90 if it is  $> 1$  (Fig. 1). An exponent of 0 yields a density independent model and an exponent of 1  
91 recovers the logistic model. We write each density dependent term,  $f_i(N_i)$ , as  $-\alpha_i N^{\theta_i}$ :

$$\begin{aligned}
 \frac{1}{N_1} \frac{dN_1}{dt} &= r_1 - \alpha_1 N_1^{\theta_1} + \beta_1 N_2 \\
 \frac{1}{N_2} \frac{dN_2}{dt} &= r_2 - \alpha_2 N_2^{\theta_2} + \beta_2 N_1.
 \end{aligned}
 \tag{2}$$

94 Our main experiment involved assessing stability of eq. (2) by modifying the four types of in-  
95 traspecific density dependence (density independent, decelerating, linear, accelerating) in a model  
96 of mutualism with a linear functional response. Additionally, in the Supplementary Material, we  
97 (1) modeled per capita birth and death rates as separate nonlinear functions, each with their own  
98 exponent, (2) considered when exponents are different between the two populations, and (3) used  
99 a saturating functional response instead of a linear one using the procedures described in the re-

100 mainder of this section. A combination of analytical, numerical, and graphical techniques were  
101 used to assess the behavior of eq. (2). Specifically, we (i) found equilibria and (ii) determined the  
102 behavior around each equilibrium using local stability analysis. When analytical solutions were not  
103 possible (i.e.,  $\theta_i \neq 0$  or 1), we solved for stable equilibria numerically using the Livermore Solver  
104 for Ordinary Differential Equations, Automatic (LSODA) (Hindmarsh, 1983; Petzold, 1983) and  
105 solved for unstable equilibria using Newton’s method. LSODA is an integrator that was used be-  
106 cause of its generality and ability to automatically handle stiff and non-stiff initial value problems,  
107 which were properties of our models. Newton’s method is an iterative root-finding algorithm we  
108 used to find unstable equilibria to a precision of  $10^{-15}$ , across state-space, from  $N_i = 0-10^{100}$  by  
109 orders of 10. Analyses were conducted in the R language and environment (R Core Team, 2016),  
110 with LSODA implemented in the deSolve package (Soetaert et al., 2010; Soetaert, 2010) and New-  
111 ton’s method in the rootSolve package (Soetaert and Herman, 2009; Soetaert, 2009). Graphical  
112 analyses were conducted using a modified version of the R package phaseR (Grayling, 2014). Specif-  
113 ically, phase plots were created, using direction fields and zero-growth isoclines (i.e., nullclines)  
114 to corroborate and visualize our numerical findings. Code to run our analyses can be found at  
115 <https://github.com/dispersing/Mutualism-NonlinearDensityDependence>.

116 Parameter values for numerical analyses focused on the type of nonlinear per capita intraspecific  
117 density dependence (i.e.,  $\theta_i$ ) and the strength of mutualism (i.e.,  $\beta_i$ ). For both of these types of  
118 parameters, we considered values ranging from  $10^{-2}$ – $10^2$ . The other parameter values ( $r_i$  and  $\alpha_i$ ) did  
119 not qualitatively affect the model behavior in terms of number or stability of equilibria (C. Moore,  
120 unpublished results), so we do not discuss their effects in detail.

### 121 3. Results

122 *General results.* For all analyses with linear functional responses we found between 3 and 5 non-  
123 negative equilibrium population sizes (Fig. 2). Analytically, we found that (0,0) was always an  
124 equilibrium and always unstable. Further, there were always two boundary equilibria ( $N_1 > 0, 0$ )  
125 and ( $0, N_2 > 0$ ), both of which were saddle nodes. The instability of the trivial and boundary  
126 equilibria means that populations always grow when rare, as expected. Numerically, we found that  
127 in cases where interior equilibria were present ( $N_1^* > 0, N_2^* > 0$ ), there were either one or two points.  
128 In cases where there was only one equilibrium point, it was always stable; in cases where there were  
129 two equilibrium points, the point proximal to the origin (0,0) was always stable and the point distal  
130 to the origin was a saddle node. Fig. 3 shows the six qualitatively different types of phase planes

131 found in this study: (i) a trivial density independent case  $\theta_i = 0$ ; (ii & iii) unstable and stable  
 132 configurations when intraspecific density dependence was decelerating,  $0 < \theta_i < 1$ ; (iv & v) unstable  
 133 and stable configurations when intraspecific density dependence was linear,  $\theta_i = 1$ ; and (vi) a stable  
 134 configuration when intraspecific density dependence was accelerating,  $\theta_i > 1$ .

135 In general, in the absence of mutualism, decelerating intraspecific density dependence increased  
 136 both species' densities at equilibrium ( $\beta_i = 0$  plane in Fig. 4, left panel). Oppositely, accelerating  
 137 intraspecific density dependence decreased the equilibrium densities. Strong mutualism (high  $\beta_i$ )  
 138 destabilized populations with decelerating intraspecific density dependence, but populations with  
 139 accelerating intraspecific density dependence were always stable (Fig. 4, center panel; note that only  
 140 stable equilibria are shown, so missing portions of the surface at high  $\beta_i$  and low  $\theta_i$  denote loss of  
 141 stability; see also Supplemental Material, section 2). Further, when a stable interior equilibrium  
 142 was present, adding mutualism to populations with decelerating intraspecific density dependence  
 143 generated a larger benefit of mutualism than with accelerating intraspecific density dependence  
 144 (Fig. 4, right panel).

145 *Decelerating density dependence,  $0 < \theta_i < 1$ .* When  $0 < \theta_i < 1$ , we found that there were 1–2  
 146 interior equilibria (3–5 total equilibria), depending on the strength of mutualism. In the absence  
 147 of mutualism, the interior equilibrium (and consequently the boundary equilibria by setting either  
 148 coordinate to 0) is at

$$\left( \left( \frac{r_1}{\alpha_1} \right)^{\theta_1^{-1}}, \left( \frac{r_2}{\alpha_2} \right)^{\theta_2^{-1}} \right). \quad (3)$$

149 Notice the  $\theta_i^{-1}$  exponent. In these cases of decelerating density dependence, as  $\theta_i$  decreases from 1,  
 150 the greatest change in growth rate occurs at lower densities (Fig. 1). Furthermore, the equilibrium  
 151 density in the absence of mutualism grows larger as  $\theta_i$  decreases.

152 Adding mutualism to populations with decelerating density dependence changed the dynamics  
 153 in either of two ways: (i) it destabilized the populations resulting in unbounded population growth  
 154 (Fig. 3, top-center panel) or (ii) it created both a stable and saddle node (Fig. 3, top-right panel).  
 155 For very small values of  $\theta_i$ , populations were always unstable with mutualism added (i.e.,  $\beta_i > 0$ ).  
 156 As decelerating density dependence became more linear (i.e., as  $\theta_i \rightarrow 1$ ), however, weak mutualism  
 157 (small values of  $\beta_i$ ) resulted in an alternative configuration in which zero-growth isoclines crossed  
 158 twice. Of these two equilibria, the stable equilibrium point was always larger than in the absence  
 159 of mutualism ( $\beta_i = 0$ ) and the saddle node was always larger than the stable point. For the same  
 160 values of  $\theta_i$  with stable and saddle nodes, increasing  $\beta_i$  increased the stable point and decreased

161 the saddle point. Continuing to increase  $\beta_i$  ultimately resulted in a saddle-node bifurcation, beyond  
 162 which all configurations were unstable, illustrated as the light-dark gray boundary in Fig. 2.

163 *Linear density dependence*,  $\theta_i = 1$ . When  $\theta_i = 1$ , there were either 0 or 1 interior equilibrium  
 164 configurations (3 or 4 total equilibria) that respectively corresponded to the absence of presence of  
 165 an interior stable point. Linear density dependence is equivalent to the most traditional formulation  
 166 of mutualism, the Lotka-Volterra competition model with the sign reversed of the effect of another  
 167 population. Although the behavior of this model is well-known, we summarize its properties briefly  
 168 here for ease of comparison. In the absence of mutualism, the interior equilibrium (and consequently  
 169 the boundary equilibria by setting either value to 0) is at

$$\left( \frac{r_1}{\alpha_1}, \frac{r_2}{\alpha_2} \right). \quad (4)$$

170 The slope of the zero-growth isocline as it increases from the boundary equilibrium is  $\frac{\beta_i N_j}{\alpha_i}$ ,  
 171 and zero-growth isoclines form a stable interior equilibrium point anytime  $\beta_i \beta_j < \alpha_i \alpha_j$ . This is  
 172 equivalent to the more traditional notation,  $\alpha_{ij} \alpha_{ji} < \alpha_{ii} \alpha_{jj}$  found in ecology texts (e.g., May, 1981;  
 173 DeAngelis et al., 1986; Kot, 2001). The location of the stable interior equilibrium point is

$$\left( \frac{r_1}{\alpha_1} + \frac{\beta_1 r_1 (\beta_1 + \alpha_1)}{\alpha_1^2 (\alpha_1 - \beta_1^2)}, \frac{r_2}{\alpha_2} + \frac{\beta_2 r_2 (\beta_2 + \alpha_2)}{\alpha_2^2 (\alpha_2 - \beta_2^2)} \right) \quad (5)$$

174 *Accelerating density dependence*,  $\theta_i > 1$ . When  $\theta_i > 1$ , there was always one interior equilibrium (4  
 175 total equilibria), irrespective of the strength of mutualism (Figs. 2, 4). In the absence of mutualism,  
 176 the interior equilibrium is again given by (3). Again, note the  $\theta_i^{-1}$  in the exponent. In these cases of  
 177 accelerating density dependence, as  $\theta_i$  increase from 1, the greatest change in growth rate occurs at  
 178 higher densities (Fig. 1). Furthermore, the equilibrium point in the absence of mutualism decreases  
 179 as  $\theta_i$  increased (Fig. 4, left panel). With mutualism ( $\beta_i > 0$ ), in addition to always being stable, the  
 180 benefit decreased as  $\theta_i$  increased.

181 *Supplementary Material: Births and deaths as separate processes, interspecific differences in in-*  
 182 *traspecific density dependence, and saturating functional response.* Assuming per capita birth and  
 183 death rates were independent processes, we modeled them as separate nonlinear functions. Our  
 184 main finding was that as long as one of the exponents was accelerating, the interior equilibrium  
 185 point would always be stable. We found no qualitatively new model behaviors when we allowed the  
 186 two species to have differently shaped intraspecific density dependent functions. Notably, the pres-

187 ence of a single, stable interior equilibrium point is possible as long as *either* species has accelerating  
188 density dependence. We also replaced the linear functional response in eq. (2) with a saturating  
189 functional response, finding that the saturating function would always stabilize the interior equilib-  
190 rium point, but with less mutualistic benefit (the difference in density in the absence and presence  
191 of a mutualist partner).

#### 192 4. Discussion

193 Lotka-Volterra models of mutualism assume that intraspecific density linearly decreases per  
194 capita growth rates. Other population models of mutualism have inherited this assumption and  
195 have generally concluded that 2-species models of mutualism are inherently unstable. In real popu-  
196 lations, however, not only do nonlinear per capita growth rates exist, but they seem to be the rule  
197 rather than the exception (Stubbs, 1977; Fowler, 1981; Sibly et al., 2005). In this study, we exam-  
198 ined how relaxing the assumption of linearly dependent per capita growth rates affected stability  
199 and mutualistic benefit in these models. We found that when per capita growth rates decrease most  
200 strongly at low densities and are decelerating, mutualism usually destabilizes the model. In contrast,  
201 when growth rates decrease most strongly at high densities and are accelerating, models are always  
202 stable with mutualism. Despite the tendency for mutualism to destabilize the 2-species equilibrium  
203 with decelerating density dependence, the benefit was greater compared to stabilizing, accelerating  
204 density dependence.

205 Our paper presents an alternative way that the classic Lotka-Volterra mutualism model can be  
206 modified to stabilize mutualism. Simply put, we added a layer of biological realism (nonlinear in-  
207 traspecific density dependence) to the Lotka-Volterra mutualism model and we found informative  
208 ways that within-species properties could stabilize mutualism, even with a linear functional response  
209 modeling the interaction between species. Support for decelerating and accelerating density depen-  
210 dence has largely been based on large datasets from observational studies (e.g., 1750 species of  
211 mammals, birds, fish, and insects in Sibly et al., 2005). Further work to determine whether species  
212 that engage in mutualism are more likely to have accelerating intraspecific density dependence,  
213 which we found to be stabilizing, would be useful.

214 From an ecological perspective, species' nonlinear responses to intraspecific density arise from  
215 differences in ecological habits or population structure. Sedentary organisms, like many plants for  
216 example, exhibit a more-or-less-constant death rate at low-to-intermediate population densities,  
217 and then at higher densities death rates tend to rapidly increase (as in scramble competition or



218 self-thinning, Yoda et al., 1963) or increase linearly (as in contest competition, Crawley and Ross,  
219 1990), resulting in accelerating density dependence. Subsets of populations, such as age or stage,  
220 can experience different vital rates and generate nonlinear density dependence for populations as a  
221 whole. In African ungulates, for example, increases in density led to increases in adult mortality,  
222 while juvenile mortality remained relatively constant at all population densities (Owen-Smith, 2006).  
223 In fact, many mutualisms occur between species with structured populations, so our study may lend  
224 insights into these interactions. As examples, many plant-mycorrhizal associations are mutualistic  
225 in the seedling stage (Grime et al., 1987; Jones and Smith, 2004; van der Heijden and Horton, 2009)  
226 and adult plants engage in mutualistic interactions with pollinators when they reach a reproductive  
227 stage.

228 From an evolutionary perspective, a long-standing theory about why we see nonlinear density  
229 dependence comes from evolutionary theories of life-history strategies; i.e.,  $r$ - and  $K$ -selected species  
230 (Gilpin and Ayala, 1973; Stubbs, 1977; Fowler, 1981), including  $\theta$ -selection (Gilpin et al., 1976).  
231 Setting aside historical controversies, this body of theory has generated very useful quantities like  
232 the specific growth rate of a population. The most general prediction made is that populations with  
233 a high specific growth rate (commonly referred to as  $r$ -selected) should exhibit decelerating density  
234 dependence since their survival probability drops off precipitously at relatively low densities. On the  
235 other hand, populations with a low specific growth rate (commonly referred to as  $K$ -selected) should  
236 exhibit accelerating density dependence since their survival probabilities drop off at relatively high  
237 densities (see Figs. 1, 2 in Fowler, 1981). Based on our study we suspect that different life-history  
238 strategies may both be a result of and a causative factor in the evolution of mutualistic interactions,  
239 and further work should examine how engaging in a mutualistic interaction should change the shape  
240 of density dependence and how changing density dependence affects a species ability to engage in a  
241 mutualistic interaction.

242 In conclusion, the linear functional response has historically been the scapegoat for theoretical  
243 studies of the population dynamics of mutualism. For example, the eminent Lord Robert May (1976)  
244 writes:

245 *... the simple, quadratically nonlinear, Lotka-Volterra models ... are inadequate for even*  
246 *a first discussion of mutualism, as they tend to lead to silly solutions in which both*  
247 *populations undergo unbounded exponential growth, in an orgy of mutual benefaction.*  
248 *Minimally realistic models for two mutualists must allow for saturation in the magnitude*  
249 *of at least one of the reciprocal benefits.*

250 In this paper, we build on May's idea of modifying the Lotka-Volterra mutualism model; not through  
251 the saturation of benefits, but through intraspecific density dependence. We found that biologically-  
252 realistic nonlinear density dependence significantly changes the dynamics of the original Lotka-  
253 Volterra mutualism model, where we found that accelerating density dependence always stabilized  
254 our models but with weaker mutualistic benefit relative to decelerating density dependence. We hope  
255 that this study will further stimulate ecologists to consider all simplifying of assumptions of even the  
256 most basic models and also to investigate more deeply into the relationships between intraspecific  
257 density, interspecific density, and population growth to gain a better grasp on mutualistic population  
258 dynamics.

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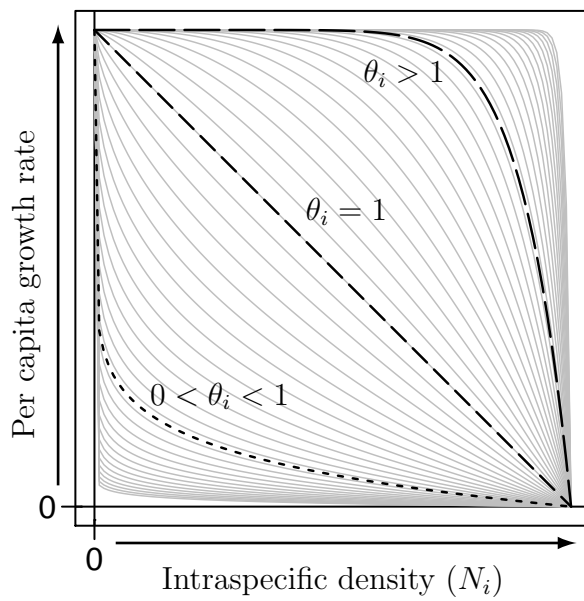


Figure 1: Values of  $\theta_i$  used in eq. (2) to represent nonlinear per capita growth rates before accounting for the effects of mutualism. The figure shows how the per capita growth rates change as a function of intraspecific density,  $N_i$ . The actual values used for numerical analyses are presented in light gray, with highlighted examples of decelerating intraspecific density dependence ( $\theta_i = 1/10$ ; short dashes,  $\cdots$ ), linear intraspecific density dependence ( $\theta_i = 1$ ; medium dashes,  $- - -$ ), and accelerating intraspecific density dependence ( $\theta_i = 10$ ; long dashes,  $- - -$ ).

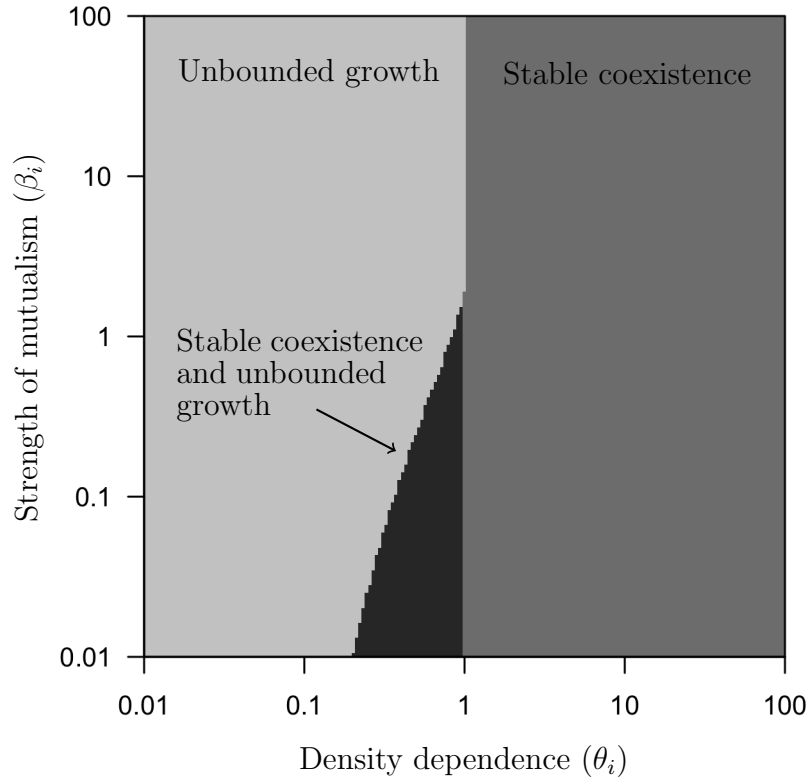


Figure 2: Number of equilibrium points (shades of gray) across all values of intraspecific density dependence ( $\theta_i$ ) and strength of mutualism ( $\beta_i$ ), while holding the remaining parameters constant at  $r_i = 4$ ,  $\alpha_i = 2$ . Across all analyses, there were always between 1 and 2 interior equilibria (3 and 5 total equilibria, including the trivial and boundary equilibria). The light-gray regions corresponds to unstable configurations where no interior equilibrium existed, the medium-gray regions correspond to stable configurations where one stable interior equilibrium existed, and the dark-gray regions correspond to areas with two interior equilibria, one stable at low densities and one saddle at high densities.

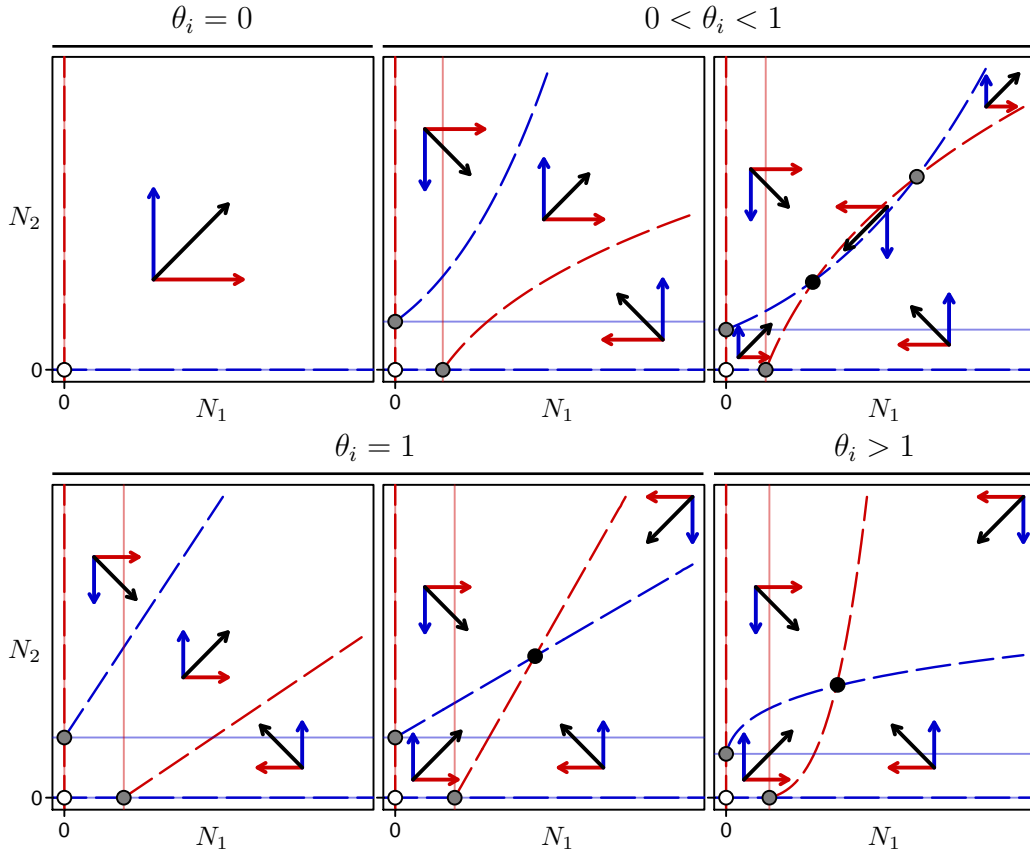


Figure 3: Phase planes representing the qualitative dynamics of 2-species mutualistic interactions for different models of per capita intraspecific density dependence. Each panel shows the densities of  $N_1$  and  $N_2$  on the  $x$ - and  $y$ -axes. Within each panel, zero-growth isoclines (nullclines) are shown for  $N_1$  (red) and  $N_2$  (blue): (i) when there is no mutualism ( $\beta_i = 0$ ) as solid, light lines (— or —) and (ii) when mutualism is present ( $\beta_i > 0$ ) as dashed lines (--- or ---). Arrows within panels show the qualitative direction vectors for  $N_1$  (red),  $N_2$  (blue), and together (black) for all changes in direction for each phase plane. Points within panels represent unstable (white), stable (black), or saddle nodes (gray). The trivial intraspecific density independent result ( $\theta_i = 0$ ) is shown in the *top-left* panel, the two results of decelerating intraspecific density dependence ( $0 < \theta_i < 1$ ) are shown in the *top-center* and *-right* panels, linear intraspecific density dependence ( $\theta_i = 1$ ) is shown in the *bottom-left* and *-center* panels, and accelerating intraspecific density dependence ( $\theta_i > 1$ ) is shown in the *bottom-right* panel.

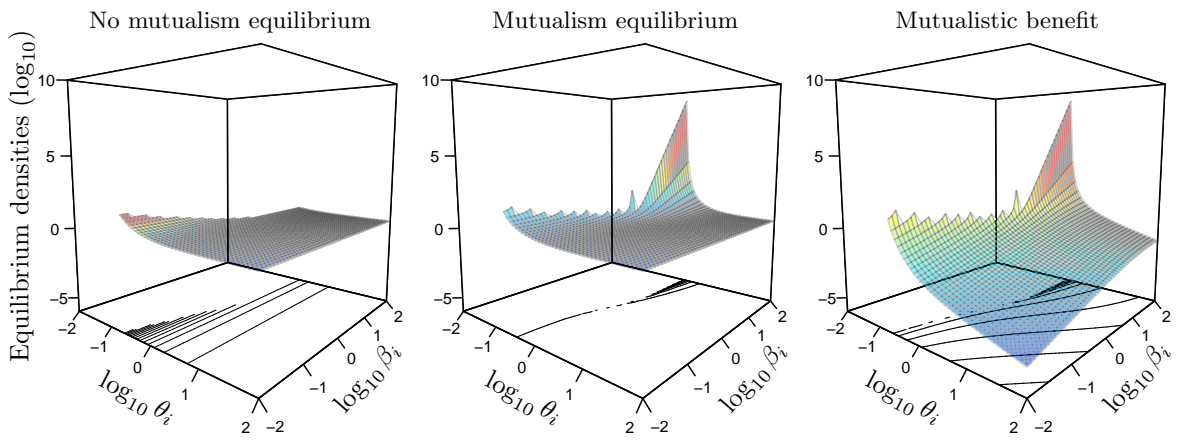


Figure 4: For model (2), nonlinear per capita growth rates with a linear functional response of mutualism, the location of the interior equilibrium in the absence of mutualism ( $\beta_i = 0$ , left), stable interior equilibrium with mutualism (center), and the benefit of mutualism as the difference between the two (right). The locations of equilibria were identified as the Euclidean distance from the origin,  $\sqrt{(N_i^*)^2 + (N_j^*)^2}$ , for identical parameters for each species:  $r_i = 4$ ,  $\alpha_i = 2$ . Each panel shows the aforementioned response on the vertical axis, the type of intraspecific density dependence ( $\theta_i$  from  $10^{-2}$ – $10^2$ ) on the left horizontal axis, and the strength of mutualism ( $\beta_i$  from  $10^{-2}$ – $10^2$ ) on the right horizontal axis. Additionally, each panel shows the relative values of each surface (colors), the absolute values of each surface (same axes across panels), and contour lines at the base of each plot show changes in the surface. Further, in areas where there is no surface, there was no stable interior equilibrium when  $\beta_i \neq 0$  (center). In the left panel without mutualism, there were stable interior equilibria across all values of  $\theta_i$ , but we removed the same part of the surface to aid comparison across panels.

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