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Population dynamics of mutualism and intraspecific density dependence: how θ-logistic-like 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 many other models of population growth will not lead to unbounded growth. We find that when density dependence is decelerative, the effect of mutualism is greater than when density dependence is accelerative. Although there is a greater benefit at equilibrium of a mutualist partner, decelerative density dependence tends to destabilize populations whereas accelerative density dependence is always stable. Incidentally, even when we model density dependence in birth and death rates separately, as long as one of the rates shows accelerative density dependence, populations will always be 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 · θ-logistic

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 mutualisms between mycorrhizae and plants (van der Heijden et al, 2015), coral and zooxanthellae (Baker, 2003), plants and pollinators (Willmer, 2011), tending ants and aphids or Lepidoptera larvae (Rico-Gray and Oliveira, 2007; Stadler and Dixon, 2008), plants and seed-dispersing animals (Howe and Smallwood, 1982; Levey et al, 2002), lichens (fungi and algae) (Brodo et al, 2001), and plants and rhizobia (Sprent et al, 1987; Kiers et al, 2003). Despite mutualism's obvious importance, it was not until the latter part of the 20th century that the natural history of mutualism underwent rigorous ecological study, the conceptual framework for mutualism was laid, and mutualism was no longer confounded with the concept of symbiosis. Thus, by the time mutualism was fully introduced to the

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larger ecological community, theoretical ecology had been developing in its absence for decades. This resulted in the paucity of theory for mutualisms still very much visible today.

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

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

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

In sum, the Lotka-Volterra mutualism model makes two separate assumptions that are likely violated in many natural systems: a linear effect of mutualistic interactions, and linear intraspecific density dependence. The former is widely thought responsible for the Lotka-Volterra mutualism model's unrealistic behavior, but since the latter has never been investigated in the context of mutualisms, the relative importance of these two simplifying assumptions remains unclear. While we agree that many mutualistic interactions are likely nonlinear, the same could be said of competitive interactions, and yet Lotka-Volterra competition models endure. Is the need to eschew linear interaction rates truly fundamental for mutualisms? We approached this line of inquiry by returning to the original Lotka-Volterra mutualism model. To complement what is already known, we relax the assumption of linear intraspecific density dependence while leaving the assumption of a linear mutualistic functional response intact. We accomplish this by replacing the logistic term in the Lotka-Volterra mutualism model with a pair of θ-logistic terms that represent density dependent birth and death rates that can each accelerate or decelerate nonlinearly with intraspecific density. We found that most models with nonlinear intraspecific density dependence lead to stable coexistence, irrespective of the strength of mutualism. We therefore conclude that relaxing *either* of the Lotka-Volterra model's major simplifying assumptions is sufficient to prevent unrealistic model behavior. Given that nonlinear intraspecific density dependence

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appears widespread, nonlinearity in mutualistic interaction rates may be less important for stabilizing mutualisms than was previously believed.

2 Methods

The Lotka-Volterra mutualism model for populations of two species, N_1 and N_2, takes the form

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

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

We chose to use the Verhulst logistic equation (r-α) over the Pearl-Reed logistic equation (K) because it is a simpler model with more clearly interpretable parameters (see Mallet (2012) for a detailed comparison). Primarily relevant to us is that the Verhulst logistic formulation has parameters that can be independently measured and independently statistically estimated. Also, it allows us to avoid the terminological baggage of 'carrying capacity' (see Sayre (2008) for a historical review, and references in Mallet (2012) for paradoxes and more modern disagreements), whose exact meaning is ambiguous when the 'maximum population density' is uncreased by mutualism.

Unfortunately, there are pitifully few empirical studies on functional responses in mutualistic systems, especially given the breadth of functional and taxonomic diversity of types of mutualistic interactions; e.g., facultative and obligate; transient and permanent; species-specific and diffuse; symbiotic and free-living; bi-product, invested, and purloined; direct and indirect; transportation, protection, and nutritional; and bi- and unidirectional mutualisms. The few studies that have directly or indirectly focused on the functional responses of a population to its mutualist partner's population have found evidence for different functional forms, including linear (e.g., Fonseca, 1999; Morales, 2011), saturating (e.g., Holland et al, 2002), and hyperbolic (e.g., Gange and Ayres, 1999; Vannette and Hunter, 2011), albeit with some statistical limitations (e.g., Morales, 2011; Vannette and Hunter, 2011). Nevertheless, linear responses can provide realistic descriptions in some settings. For example, Fonseca (1999) found that population growth of Amazonian ants is limited by the number of plant-producing domatia, and as the density of domatia increased, ant colonies proportionally increased. As a second example, Morales (2011) found that the emigration of predators from treehopper aggregations increased linearly with the density of the ants that defend the treehoppers. As a third example, in by-product mutualisms (see Connor, 1995), where there is no cost or a fixed cost to engage in a mutualism, the conferment of benefits are likely linear. Ultimately, if linear responses can provide realistic descriptions in some settings, they will usually be preferable because they are more easily tractable and have a straightforward biological interpretation, with β_i as an interaction coefficient. As explained in the Introduction, we do not yet know whether the linear functional response uniquely explains the Lotka-Volterra model's unrealistic description of mutualisms, nor when its use can be justified on the grounds of tractability. This is one thing we seek to discover with this study, and so we retain the Lotka-Volterra's linear functional response in our initial model before subsequently replacing it with a nonlinear response.

The first terms in eq. (1) have not received the same scrutiny as the last terms. We suspect this has more to do with the ubiquity of the logistic model than any careful evaluation of its application here. To explore this, we relax the assumption of logistic growth—the assumption that the difference between per capita births and deaths linearly decreases as density increases. We relax this assumption by modeling per capita births and deaths as separate, nonlinear functions, using the θ-logistic model for each. This causes the per capita birth (or death) rate to be a decelerating function of density if the exponent is < 1 and an accelerating function if the exponent is > 1 (Fig. 1). An exponent of 0 yields a

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density independent model and an exponent of 1 recovers the logistic model. We write each birth and death function as a density independent term, b_i or d_i with a density dependent term, $\mu_i N_i^{\eta_i}$ or $\nu_i N_i^{\theta_i}$.

Our first model pairs the θ-logistic birth and death functions with a linear functional response, to arrive at

$$\begin{aligned} \frac{1}{N_1}\frac{dN_1}{dt} &= \left(b_1 - \mu_1 N_1^{\eta_1}\right) - \left(d_1 + \nu_1 N_1^{\theta_1}\right) + \beta_1 N_2 \\ \frac{1}{N_2}\frac{dN_2}{dt} &= \left(b_2 - \mu_2 N_2^{\eta_2}\right) - \left(d_2 + \nu_2 N_2^{\theta_2}\right) + \beta_2 N_1. \end{aligned} \tag{2}$$

Rearranged to group the density independent, density dependent, and mutualism terms, our model with a linear functional response is,

$$\begin{aligned} \frac{1}{N_1}\frac{dN_1}{dt} &= (b_1 - d_1) - \left(\mu_1 N_1^{\eta_1} + \nu_1 N_1^{\theta_1}\right) + \beta_1 N_2 \\ \frac{1}{N_2}\frac{dN_2}{dt} &= (b_2 - d_2) - \left(\mu_2 N_2^{\eta_2} + \nu_2 N_2^{\theta_2}\right) + \beta_2 N_1. \end{aligned} \tag{3}$$

In these eqs., $b_i - d_i$ is equal to r_i in eq. (1). Similarly, when $\eta_i = \theta_i = 1$ in eq. (3), $-(\mu_i + \nu_i)$ is equal to $-\alpha_i$ in eq. (1).

Finally, to more fully understand the effect of relaxing the assumption of linear intraspecific density dependence, we extend our approach to include a saturating functional response. Specifically, we replace the $\beta_i N_j$ in eq. (3) with a saturating function (following Wright, 1989; Holland et al, 2002; Holland and DeAngelis, 2010, and others), to create equations:

$$\begin{aligned} \frac{1}{N_1}\frac{dN_1}{dt} &= (b_1 - d_1) - \left(\mu_1 N_1^{\eta_1} + \nu_1 N_1^{\theta_1}\right) + \frac{\gamma_1 N_2}{\delta_1 + N_2} \\ \frac{1}{N_2}\frac{dN_2}{dt} &= (b_2 - d_2) - \left(\mu_2 N_2^{\eta_2} + \nu_2 N_2^{\theta_2}\right) + \frac{\gamma_2 N_1}{\delta_2 + N_1}, \end{aligned} \tag{4}$$

with γ_i being the maximum benefit species j can confer to species i and δ_i as the half-saturation constant, which controls how quickly the saturation of benefits occurs. For a more mechanistic, consumer-resource-based interpretation of the parameters in the saturating functional response for mutualisms, see Revilla (2015).

2.1 Analyses

Our main experiment involved assessing stability of eq. (3) by modifying the four types of intraspecific density dependence (density independent, decelerating, linear, accelerating) for births and deaths in a model of mutualism with a linear functional response. Fig. 2 graphically depicts the 16 qualitatively different combinations of types of birth and death rates. We refer to cases where $\eta_i = \theta_i$, along the diagonal of Fig. 2, as "symmetrical"; in these cases, the intraspecific part of our model is the familiar θ-logistic equation. In our analysis, we consider the symmetrical cases first, before considering non-symmetrical examples in which $\eta_i \neq \theta_i$. In all analyses we assumed the same parameters between species i and species j. Lastly, we compared our results to those obtained from model (4).

We analyzed eqs. (3) and (4) using a combination of analytical, numerical, and graphical techniques to assess model behavior. Specifically, we (i) found equilibria and (ii) determined the behavior around each equilibrium using local stability analysis. When analytical solutions were not possible (η_i or $\theta_i \neq 0$ or 1), we solved for stable equilibria numerically using the Livermore Solver for Ordinary Differential Equations, Automatic (LSODA) (Hindmarsh, 1983; Petzold, 1983) and solved for unstable equilibria using Newton's method. LSODA is an integrator that was used because of its generality and ability to automatically handle stiff and non-stiff initial value problems, which were properties of our models. Newton's method is an iterative root-finding algorithm we used to find unstable equilibria to a precision of 10^{-15}, across state-space, from $N_i = 0$–10^{100} by orders of 10. Analyses were conducted in the R language and environment (R Core Team, 2016), with LSODA implemented in the deSolve package (Soetaert et al, 2010; Soetaert, 2010) and Newton's method in the rootSolve package (Soetaert and Herman, 2009; Soetaert, 2009). Code to run numerical analysis can be found at `https://github.com/dispersing/Mutualism-NonlinearDensityDependence`.

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Parameter values for numerical analyses focused on the type of nonlinear per capita intraspecific density dependence (i.e., η_i and θ_i) and the strength of mutualism (i.e., β_i, but also the maximum saturation in eq. (4), γ_i). For both of these types of parameters, we considered values ranging from 10^{-2}–10^{2}. The other parameter values—b_i, d_i, μ_i, and ν_i—did not qualitatively affect the model behavior in terms of number or stability of equilibria (C. Moore, unpublished results), so we do not discuss their effects in detail.

Graphical analyses were conducted using a modified version of the R package phaseR (Grayling, 2014a,b). Specifically, phase plots were created, using direction fields and zero-growth isoclines (i.e., nullclines) to corroborate and visualize our numerical findings.

3 Results

3.1 General results

For all analyses with linear functional responses we found between 3 and 5 non-negative equilibrium population sizes (Fig. 3). Analytically, we found that (0,0) was always an equilibrium and always unstable. Further, there were always two boundary equilibria ($N_1 > 0, 0$) and ($0, N_2 > 0$), both of which were saddle nodes. The instability of the trivial and boundary equilibria means that populations always grow when rare, as expected. Numerically, we found that in cases where interior equilibria were present ($N_1^* > 0, N_2^* > 0$), there were either one or two points. In cases where there was only one equilibrium point, it was always stable; in cases where there were two equilibrium points, the point proximal to the origin (0,0) was always stable and the point distal to the origin was a saddle node. Fig. 4 shows the six qualitatively different types of phase planes found in this study: (i) a trivial density independent case $\eta_i = \theta_i = 0$; (ii & iii) unstable and stable configurations when intraspecific density dependence was decelerating, $0 < \eta_i = \theta_i < 1$; (iv & v) unstable and stable configurations when intraspecific density dependence was linear, $\eta_i = \theta_i = 1$; and (vi) a stable configuration when intraspecific density dependence was accelerating, $\eta_i = \theta_i > 1$.

In general, in the absence of mutualism, decelerating intraspecific density dependence increased both species' densities at equilibrium ($\beta_i = 0$ plane in Fig. 5, left panel). Oppositely, accelerating intraspecific density dependence decreased the equilibrium densities. Strong mutualism (high β_i) destabilized populations with decelerating intraspecific density dependence, but populations with accelerating intraspecific density dependence were always stable (Fig. 5, center panel; note that only stable equilibria are shown, so missing portions of the surface (at high β_i and low η_i and θ_i) denote loss of stability). Further, when a stable interior equilibrium was present, adding mutualism to populations with decelerating intraspecific density dependence generated a larger benefit of mutualism than with accelerating intraspecific density dependence (Fig. 5, right panel). Adding mutualism to populations when birth and death rates were subject to independent intraspecific density dependence (i.e., non-symmetrical, $\eta_i \neq \theta_i$) was always stable if either η_i or θ_i was accelerating (> 1), and destabilized populations if $\eta_i \neq \theta_i$ were both decelerating (< 1) if the mutualistic effect was sufficiently large (Fig. 6). Below we describe results based on symmetrical cases when $\eta_i = \theta_i$ and non-symmetrical cases when $\eta_i \neq \theta_i$, in greater depth.

3.2 Symmetrical density dependence, $\eta_i = \theta_i$

3.2.1 Decelerating density dependence, $0 < \eta_i = \theta_i < 1$

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

$$\left(\left(\frac{b_1 - d_1}{\mu_1 + \nu_1} \right)^{\eta_1^{-1}}, \left(\frac{b_2 - d_2}{\mu_2 + \nu_2} \right)^{\eta_2^{-1}} \right). \tag{5}$$

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

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Adding mutualism to populations with decelerating density dependence changed the dynamics in either of two ways: (i) it destabilized the populations resulting in unbounded population growth (Fig. 4, top-center panel) or (ii) it created both a stable and saddle node (Fig. 4, top-right panel). For very small values of $\eta_i = \theta_i$, populations were always unstable with mutualism added (i.e., $\beta_i > 0$). As decelerating density dependence became more linear (i.e., as $\eta_i = \theta_i \to 1$), however, weak mutualism (small values of β_i) resulted in an alternative configuration in which zero-growth isoclines crossed twice. Of these two equilibria, the stable equilibrium point was always larger than in the absence of mutualism ($\beta_i = 0$) and the saddle node was always larger than the stable point. For the same values of $\eta_i = \theta_i$ with stable and saddle nodes, increasing β_i increased the stable point and decreased the saddle point. Continuing to increase β_i ultimately resulted in a saddle-node bifurcation, beyond which all configurations were unstable, illustrated as the light-dark gray boundary in Fig. 3.

3.2.2 Linear density dependence, $\eta_i = \theta_i = 1$

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

$$\left(\frac{b_1 - d_1}{\mu_1 + \nu_1}, \frac{b_2 - d_2}{\mu_2 + \nu_2}\right).$$

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

$$\left(\frac{b_1 - d_1}{\mu_1 + \nu_1} + \frac{\beta_1(b_1 - d_1)(\beta_1 + \mu_1 + \nu_1)}{(\mu_1 + \nu_1)^2((\mu_1 + \nu_1) - \beta_1^2)}, \frac{b_2 - d_2}{\mu_2 + \nu_2} + \frac{\beta_2(b_2 - d_2)(\beta_2 + \mu_2 + \nu_2)}{(\mu_2 + \nu_2)^2((\mu_2 + \nu_2) - \beta_2^2)}\right).$$

3.2.3 Accelerating density dependence, $1 < \eta_i = \theta_i$

When $1 < \eta_i = \theta_i$, there was always one interior equilibrium (4 total equilibria), irrespective of the strength of mutualism (Figs. 3, 5). In the absence of mutualism, the interior equilibrium is again given by (5). Again, note the η_i^{-1} in the exponent. In these cases of accelerating density dependence, as $\eta_i = \theta_i$ increase from 1, the greatest change in growth rate occurs at higher densities (Fig. 1). Furthermore, the equilibrium point in the absence of mutualism decreases as $\eta_i = \theta_i$ increased (Fig. 5, left panel). With mutualism ($\beta_i > 0$), in addition to always being stable, the benefit decreased as $\eta_i = \theta_i$ increased.

3.3 Non-symmetrical density dependence, $\eta_i \neq \theta_i$

When $\eta_i \neq \theta_i$, we found no dynamics qualitatively different from what we found in the symmetrical cases. When either of the birth or death functions were density independent ($\eta_i = 0$ or $\theta_i = 0$), the population growth rates and model dynamics behaved according to the function without the non-zero exponent. Further, when either of the birth of death functions responded linearly density, or both of the birth and death functions responded at a decelerating rate, the population growth rates and model dynamics were behaved similarly to cases with decelerating density dependence (Fig. 6, $\eta_i \leq 1$ and $\theta_i \leq 1$).

There was one important difference in non-symmetrical cases. Specifically, if either of the birth and death functions were accelerating, then there was always one interior stable equilibrium (Fig. 6, $\eta_i > 1$ and $\theta_i > 1$). This finding is irrespective of the strength of mutualism.

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3.4 Comparison of nonlinear density dependence with a saturating functional response

We investigated relaxing the assumption of linear intraspecific density dependence and have thus far focused on a linear functional response between mutualist partners (eq. (3)). We further compared this model with a different functional response, a nonlinear saturating function (eq. (4)) (Fig. 7). In general, our findings with respect to the benefit of mutualism were the same: as intraspecific density dependence shifted from decelerating to accelerating, for a given strength of mutualism (γ_i is roughly analogous to β_i in the linear functional response), the benefit of mutualism decreased (Fig. 7, right panel). Also, increasing the strength of mutualism (γ_i) always increased the benefit of mutualism for any type of density dependence. There were three major differences between the linear and saturating models. First, in the saturating model, there were no unstable configurations (Fig. 5, center panel, compared with Fig. 7, center panel). Second, again in the saturating model, across all values of strength of mutualism and density dependence there were always four equilibria, with a single, stable interior equilibrium. Third, weak accelerating density dependence with a linear functional response produced a disproportionally large spike in benefit from mutualism (Fig. 5, right panel, compared with Fig. 7, right panel).

4 Discussion

4.1 Main findings

Lotka-Volterra models of mutualism assume that intraspecific density linearly decreases per capita growth rates. Other population models of mutualism have inherited this assumption and have generally concluded that 2-species models of mutualism are inherently unstable. In real populations, however, not only do nonlinear per capita growth rates exist, but they seem to be the rule rather than the exception (Stubbs, 1977; Fowler, 1981; Sibly et al, 2005). In this study, we examined how relaxing the assumption of linearly dependent per capita birth and death rates affects the stability and mutualistic benefit in these models. We found that when per capita growth rates decrease most strongly at low densities and are decelerating, mutualism usually destabilizes the model. In contrast, when growth rates decrease most strongly at high densities and are accelerating, models are always stable with mutualism. Despite the tendency for mutualism to destabilize the 2-species equilibrium with decelerating density dependence, the benefit was greater compared to stabilizing, accelerating density dependence. We additionally found that if either the birth or death functions exhibited accelerating density dependence, the models always had a single, stable interior equilibrium irrespective of the strength of mutualism.

4.2 Forms of intraspecific density dependence

Our paper presents an alternative way that classic Lotka-Volterra mutualism models can be modified to stabilize mutualism. Simply put, we added a layer of biological realism (nonlinear intraspecific density dependence) to the Lotka-Volterra mutualism model and we found informative ways that within-species properties could stabilize mutualism, even with a linear functional response modeling the interaction between species. Support for decelerating and accelerating density dependence has largely been based on large datasets from observational studies (e.g., 1750 species of mammals, birds, fish, and insects in Sibly et al, 2005). Most of the data suggest that decelerating density dependence is the most common form (Sibly et al, 2005). In our models, decelerating density dependence was largely unstable with mutualism added. The reason that our decelerating models were unstable was that for strong deceleration (i.e., η_i and $\theta_i \to 0$), after the initial steep decline in birth or death rates, the population growth rate continues to decrease, but at decreasing rate. For biologically-realistic densities, after the initial steep decline in birth or death rates, the population growth rate is asymptotic and therefore does not meaningfully decrease with increasing density, allowing the benefit of mutualism to overpower and destabilize the system.

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

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

From an evolutionary perspective, a long-standing theory about why we see nonlinear density dependence comes from evolutionary theories of life-history strategies; i.e., r- and K-selected populations (Gilpin and Ayala, 1973; Stubbs, 1977; Fowler, 1981), but also θ-selection (Gilpin et al, 1976). Setting aside historical controversies, this body of theory has generated very useful quantities like the specific growth rate of a population. The most general prediction made is that populations with a high specific growth rate (commonly referred to as r-selected) should exhibit decelerating density dependence since their survival probability drops off precipitously at relatively low densities. On the other hand, populations with a low specific growth rate (commonly referred to as K-selected) should exhibit accelerating density dependence since their survival probabilities drop off at relatively high densities (see Figs. 1, 2 in Fowler, 1981). Another illuminating example of how traits associated with life-history strategies may be driving nonlinear density dependence was in a study of bird populations (Sæther and Engen, 2002). Sæther and Engen (2002) found that intrinsic growth rate, r, was correlated with the type of nonlinear density dependence exhibited by the population, as well as metrics like clutch size and adult survival rates. Interestingly, they also found a correlation between environmental stochasticity and intrinsic growth rate, suggesting that intrinsic growth rate may be a confounding factor if studies try to find a relationship between environmental stochasticity and the shape of a population's density dependence (Sæther and Engen, 2002).

4.3 Comparison with a saturating mutualism

We compared both linear and saturating functional responses because the latter response is now widely used as an alternative that prevents unrealistic outcomes of the Lotka-Volterra mutualism model (e.g., Holland et al, 2002, 2006; Okuyama and Holland, 2008; Holland and DeAngelis, 2010; Bastolla et al, 2009; Rohr et al, 2014). The effects of nonlinear per capita intraspecific density dependence was largely the same for both models, with the mutualistic benefit being greatest with decelerating density dependence. We postulate that this is a general phenomenon that we expect to see with other types of mutualistic functional responses. As an example, in a hypothetical seed-caching seed-dispersal mutualism, we can expect that the per capita effect of the seed-caching animals on the nut-producing plants will be constant; i.e., seed-caching animals disperse all nuts, regardless of the density of seed-caching animals. In this case, we may model the functional response as a constant function $g_i(N_j) = \epsilon_i$, with ϵ_i being the constant per capita benefit of having any amount of seed-caching animals present. Coincidentally, this example is actually a special case of to the saturating functional response, as the upper limit of the saturating function as $N_j \to \infty$ or $\delta_i \to 0$ is a constant (γ_i in eq. (4)).

The two major differences between the dynamics of our models with linear and saturating functional responses were (i) the saturating functional response model always had a stable interior equilibrium and (ii) there was a strong peak in the population densities with weak accelerating density dependence with a linear functional response that was not present with a saturating functional response (Fig. 5, center and right panels). Unlike the linear functional response, the model with a saturating functional response withstood destabilization with linear and decelerative density dependence when relatively strong mutualism was added. Indeed, persistent stabilization is one of the most attractive features of the saturating functional response. Although it remained stable with stronger deceleration, we found that the mutualistic benefit continued to increase, which does not seem to be a realistic feature of our models. The peak in the mutualistic benefit in the model with a linear functional response was the other difference compared with the saturating functional response model, which also does not seem to be a realistic feature. This peak arose from parameter space where accelerating density dependence was weak and the strength of the linear functional response was strong (for $1 < \eta_i$ or $\theta_i < 2$). We

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did not observe a similar peak in the models with a saturating functional response because at higher densities the benefit of the mutualism is diminished.

4.4 Future directions

Mutualism is incredibly important in virtually every ecosystem, yet we are missing fundamental theoretical and empirical information like the role of intraspecific density dependence in mediating its effect. Very few empirical studies on the population ecology of mutualism exist, and we hope that this will be remedied. This is especially true because ecologists are extending population models into larger, more complex community models where functional forms can have important consequences (see the exchange, for example: Bascompte et al, 2006a; Holland et al, 2006; Bascompte et al, 2006b). Most importantly, we need studies examining both the relationship between intraspecific density and population growth rate and the functional and numerical responses of mutualist pairs for the multifarious forms of mutualisms (e.g., interspecific-resource defense, tropic-resource, spatial-resource mutualisms). As argued in the methods, there is no *a priori* reason to reject a linear functional response for all mutualisms based on the few empirical studies of mutualism population dynamics that exist. Identifying more examples of linear functional responses could help reveal what other processes stabilize the interaction, and whether nonlinear intraspecific density dependence can be a stabilizing process as suggested by our study.

There were many empirical predictions and questions that arose from relaxing linear per capita intraspecific density dependence in this study. Foremost, we predict that in species with accelerating intraspecific density dependence, the benefit of engaging in mutualism is less than in species with decelerating intraspecific density dependence. Does this mean that we expect fewer species with accelerating intraspecific density dependence to engage in mutualistic interactions than those with decelerating intraspecific density dependence? Or do we expect more species with accelerating intraspecific density dependence to engage in mutualistic interactions than those with decelerating intraspecific density dependence because the interaction is inherently more stable? Contrasting the trade-off between the benefit of mutualism and, at least in the models with a linear functional response, stability may reveal which species with different life histories are involved with mutualisms while others are not. We found this tradeoff with both the linear and saturating functional responses.

4.5 Conclusion

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

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

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

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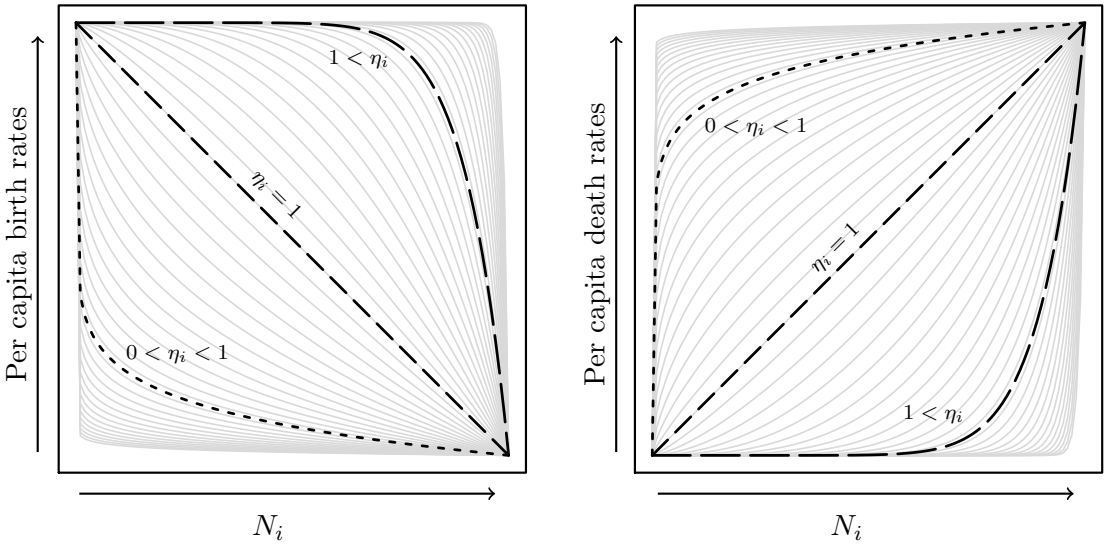

Fig. 1 Values of η_i and θ_i used in eqs. (3) and (4) to represent nonlinear per capita birth and death rates before accounting for the effects of mutualism. Panels show how the per capita birth (left) and death (right) rates change as functions of intraspecific density, N_i. The actual values used for numerical analyses are presented in light gray, with highlighted examples of decelerating intraspecific density dependence (η_i or $\theta_i = 1/10$; short dashes, ▪▪▪▪▪), linear intraspecific density dependence (η_i or $\theta_i = 1$; medium dashes, ▬ ▬ ▬), and accelerating intraspecific density dependence (η_i or $\theta_i = 10$; long dashes, ▬ ▬).

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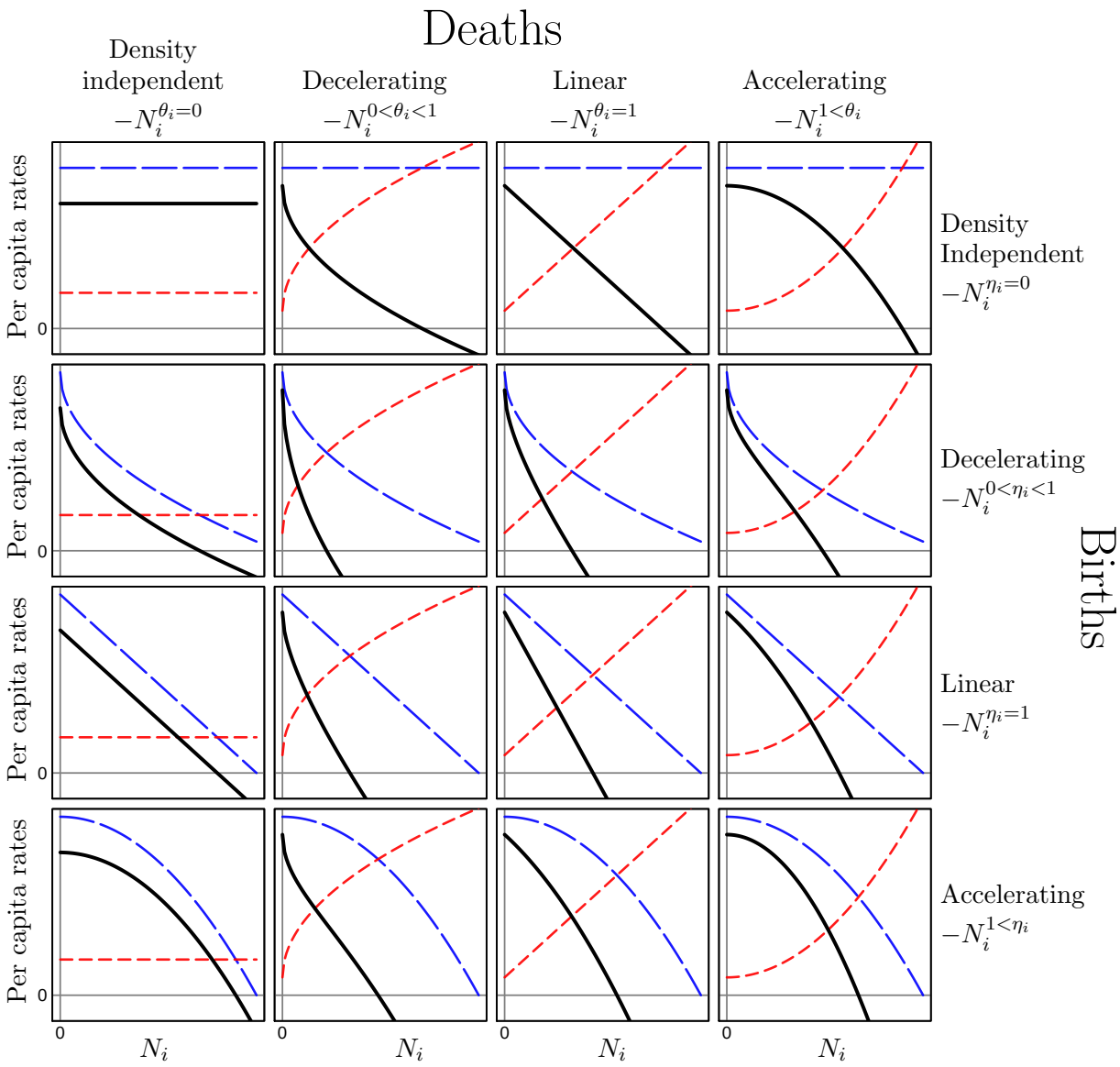

Fig. 2 The qualitative range of per capita birth and death functions used in this study to examine how relaxing the assumption of linear per capita intraspecific density dependence could affect the population dynamics of mutualism. Each panel's x-axis is population density, N_i, and the y-axis is the per capita birth, death, or growth rate. Per capita birth (— — —) and death (- - - -) rates respectively increase or decrease as a function of density. Across rows of panels the shape of density dependent births changes as η_i increases and across columns of panels the shape of density-dependent deaths changes as θ_i increases. The difference between the birth and death rates, the per capita population growth rate (———), is superimposed to show that similar overall population growth functions can arise from different birth and death processes.

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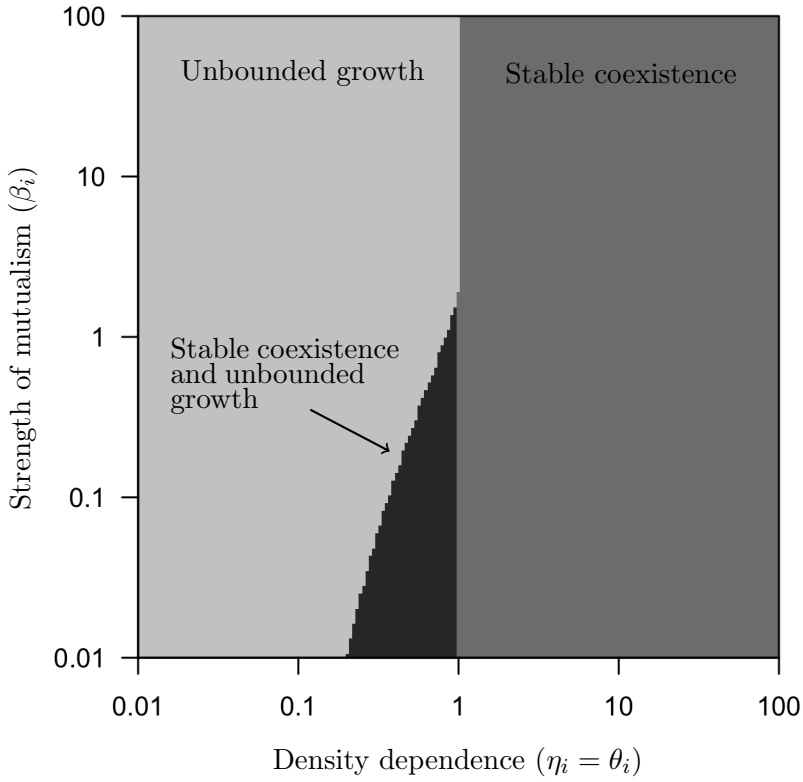

Fig. 3 Number of equilibrium points (shades of gray) across all values of intraspecific density dependence ($\eta_i = \theta_i$) and strength of mutualism (β_i), while holding the remaining parameters constant at $b_i = 5$, $d_i = 1$, $\mu_i = 1$, and $\nu_i = 1$. Across all analyses, there were always 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.

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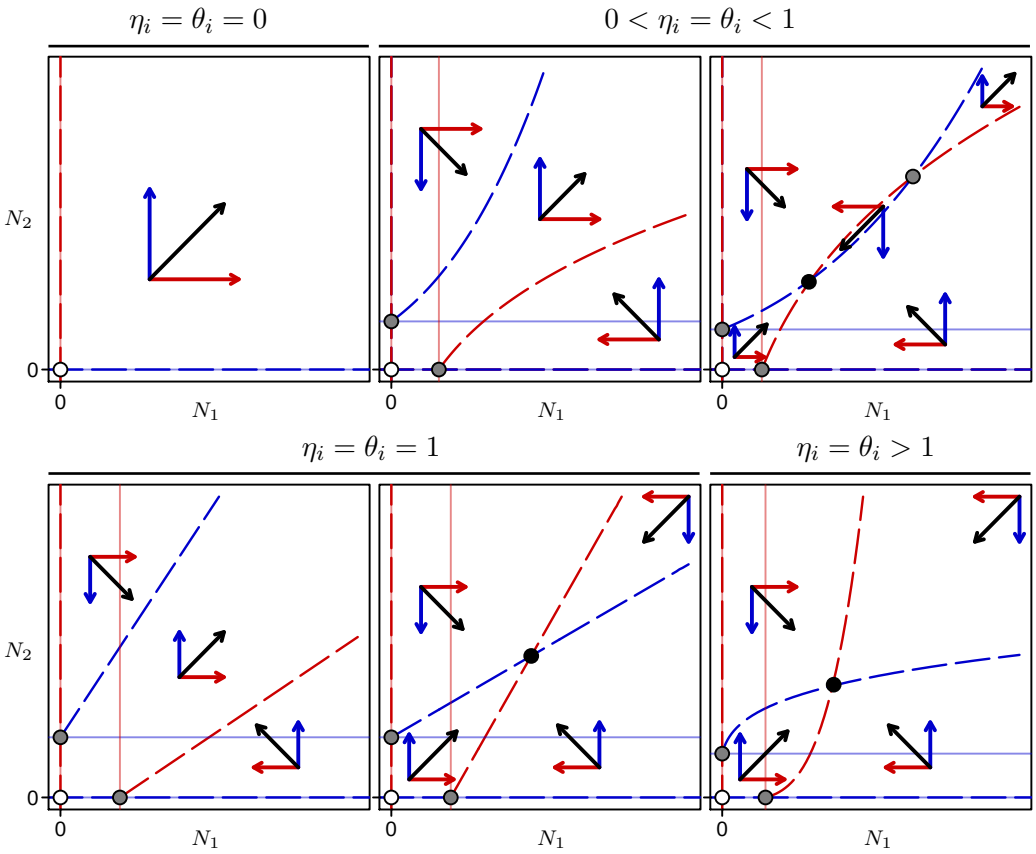

Fig. 4 Phase planes representing the qualitative dynamics of 2-species mutualistic interactions for different models of per capita intraspecific density dependence. Each panel shows the densities of N_1 and N_2 on the x- and y-axes. Within each panel, zero-growth isoclines (nullclines) are shown for 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 ($\beta_i > 0$) in dashed, red or blue (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. Point within panels represent unstable (white), stable (black), or saddle nodes (gray). The trivial intraspecific density independent result ($\eta_i = \theta_i = 0$) is shown in the *top left* panel, the two results of decelerating intraspecific density dependence ($0 < \eta_i = \theta_i < 1$) are shown in the *second and third columns of the top row*, linear intraspecific density dependence ($\eta_i = \theta_i = 1$) is shown in the *first and second columns of the bottom row*, and accelerating intraspecific density dependence ($\eta_i = \theta_i > 1$) is shown in the *bottom right panel*.

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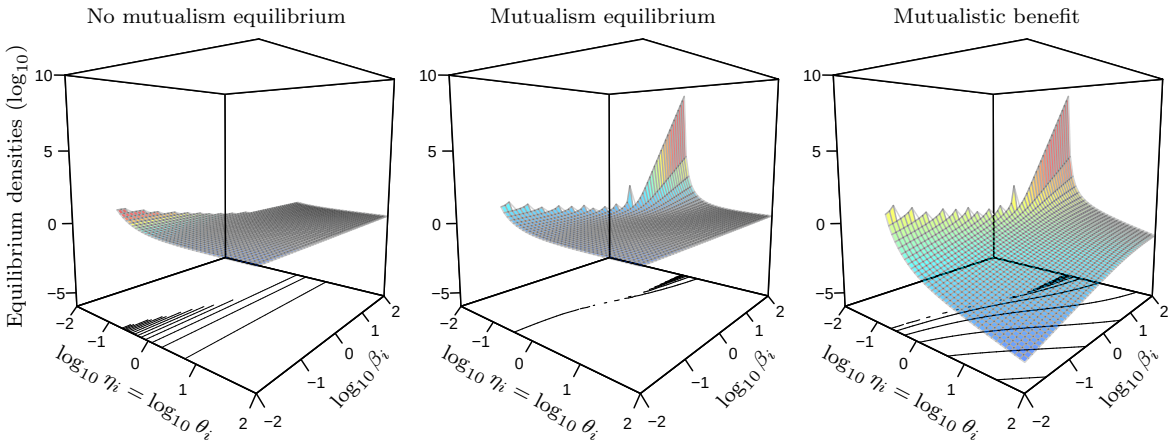

Fig. 5 For model (3), nonlinear per capita birth and death rates with a linear functional response of mutualism, the location of the interior equilibrium in the absence of mutualism ($\beta_i = 0$, left), stable interior equilibrium with mutualism (center), and the benefit of mutualism as the difference between the two (right). The locations of equilibria were identified as the Euclidian distance from the origin, $\sqrt{(N_i^*)^2 + (N_j^*)^2}$, for identical parameters for each species: $b_i = 5$, $d_i = 1$, $\mu_i = 1$, and $\nu_i = 1$. Each panel shows the aforementioned response on the vertical axis, the type of intraspecific density dependence ($\eta_i = \theta_i$ from 10^{-2}–10^2) on the left horizontal axis, and the strength of mutualism (β_i from 10^{-2}–10^2) on the right horizontal axis. Further, 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. In the left panel, we extend the result at $\beta_i = 0$ across the right horizontal axis to aid comparison with the center panel. 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 there were stable interior equilibria across all values of η_i and θ_i, but we removed the same part of the surface to aid comparison across panels. Because there is no mutualism in the left panel, if we showed the entire surface is would be the same as Fig. 7, left panel.

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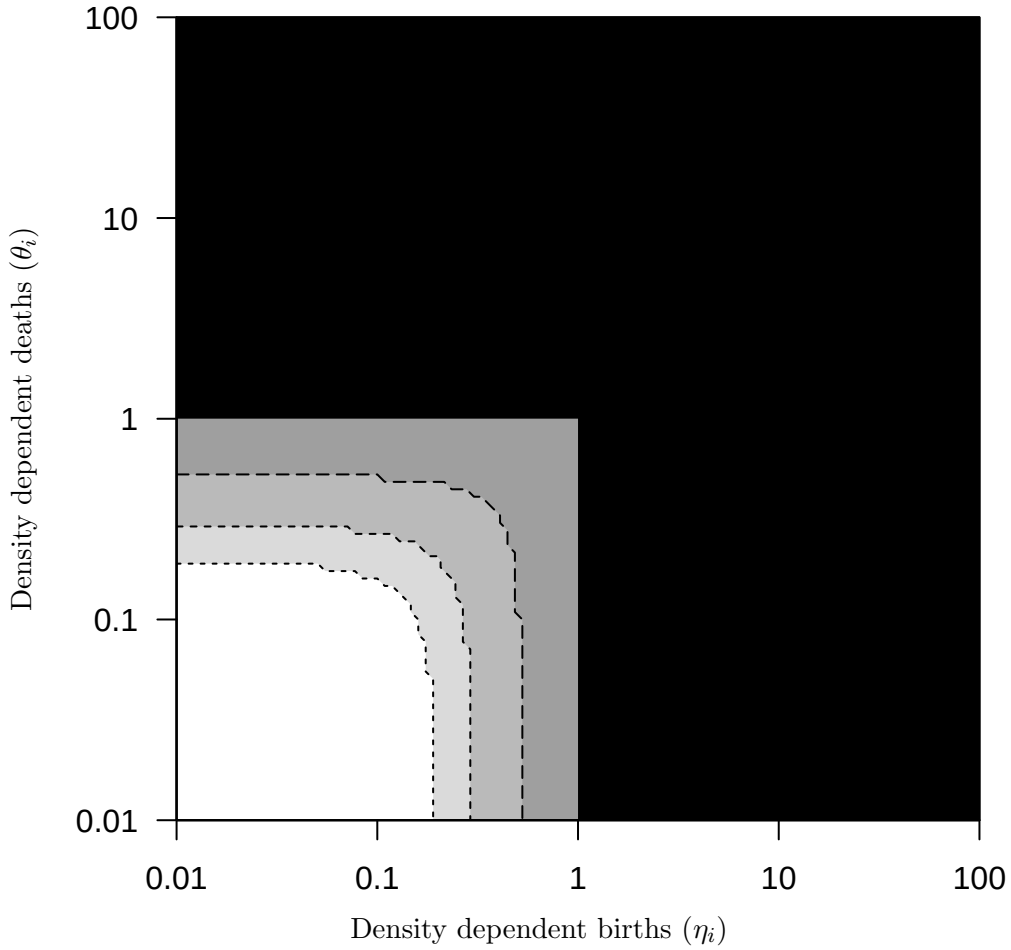

Fig. 6 Number of equilibrium points given non-symmetrical intraspecific density dependent birth (η_i; x-axis) and death (θ_i; y-axis) functions, for different strengths of a linear mutualism functional response (β_i; grayscale). If either birth (η_i) or death (θ_i) functions were accelerating (> 1), then there was always one interior equilibrium and it was stable (black), irrespective of the strength of mutualism (β_i). We only show parameter space up to 10^2, but a stable interior equilibrium was present for any value greater than 1. If both birth and death functions were decelerating (< 1), then the strength of mutualism determined if there was no interior equilibrium or two interior equilibria. Contours lines delineate the no-interior- (white) and two-interior-equilibrium (gray) boundaries for several strengths of mutualism (10^{-1} (▬ ▬, darkest gray), 10^{-2} (▬ ▬, medium gray), and 10^{-3} (▪ ▪, lightest gray)).

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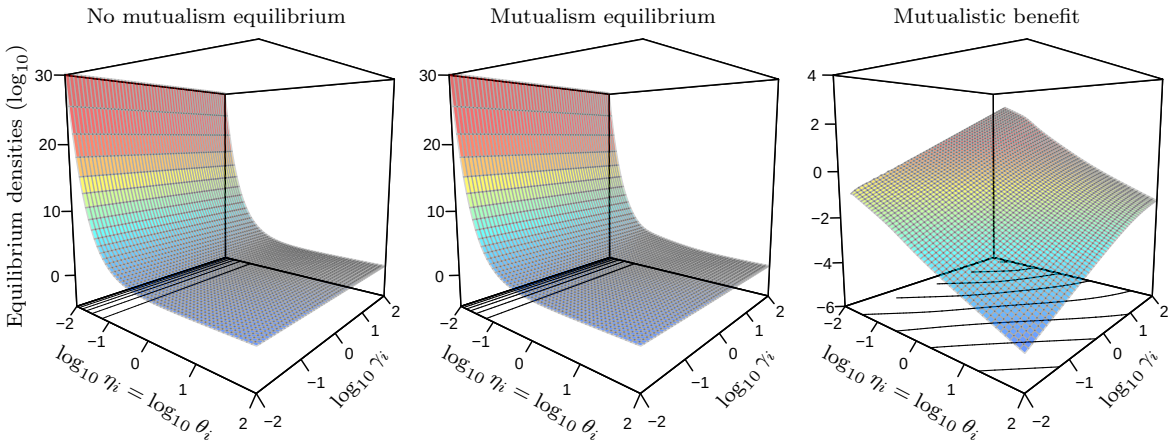

Fig. 7 For model (4), nonlinear per capita birth and death rates with a saturating functional response of mutualism, the location of the interior equilibrium in the absence of mutualism (left), stable interior equilibrium with mutualism (center), and the benefit of mutualism, as the difference between the two (right). The locations of equilibria were identified as the Euclidian distance from the origin, $\sqrt{(N_i^*)^2 + (N_j^*)^2}$, for identical parameters for each species: $b_i = 5$, $d_i = 1$, $\mu_i = 1$, and $\nu_i = 1$. Each panel shows the aforementioned response on the vertical axis, the type of intraspecific density dependence ($\eta_i = \theta_i$ from 10^{-2}–10^{2}) on the left horizontal axis, and the strength of mutualism (γ_i from 10^{-2}–10^{2}) on the right horizontal axis. Further, 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.

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