Hydra effects in discrete-time models of stable communities

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ABSTRACT

A species exhibits a hydra effect when, counter-intuitively, increased mortality of the species causes an increase in its abundance. Hydra effects have been studied in many continuous time (differential equation) multispecies models, but only rarely have hydra effects been observed in or studied with discrete time (difference equation) multispecies models. In addition most discrete time theory focuses on single-species models. Thus, it is unclear what unifying characteristics determine when hydra effects arise in discrete time models. Here, using discrete time multispecies models (where total abundance is the single variable describing each population), I show that a species exhibits a hydra effect in a stable system only when fixing that species' density at its equilibrium density destabilizes the system. This general characteristic is referred to as subsystem instability. I apply this result to two-species models and identify specific mechanisms that cause hydra effects in stable communities, e.g., in host–parasitoid models, host Allee effects and saturating parasitoid functional responses can cause parasitoid hydra effects. I discuss how the general characteristic can be used to identify mechanisms causing hydra effects in communities with three or more species. I also show that the condition for hydra effects at stable equilibria implies the system is reactive (i.e., density perturbations can grow before ultimately declining). This study extends previous work on conditions for hydra effects in single-species models by identifying necessary conditions for stable systems and sufficient conditions for cyclic systems. In total, these results show that hydra effects can arise in many more communities than previously appreciated and that hydra effects were present, but unrecognized, in previously studied discrete time models.

1. Introduction

Increased mortality of a species, e.g., due to culling, harvesting, or environment degradation, is expected to cause the abundance of that species to decline. However, in some cases increased mortality causes a species abundance to increase. This counter-intuitive response is known as a hydra effect (Abrams and Matsuda, 2005; Abrams, 2009). For example, in a study (Zipkin et al., 2008) on the invasive smallmouth bass *Micropterus dolomieu*, increased removal of the smallmouth bass resulted in an increase in its abundance; see Fig. 1 in Zipkin et al. (2008). Other empirical examples of hydra effects include blowflies (Nicholson, 1954, 1957), ciliates (Fryxell et al., 2005), and poeciliid fish (Schröder et al., 2009). Understanding when and how hydra effects arise in systems is important, because hydra effects can undermine species conservation or management strategies. For example, if the goal of the Zipkin et al. (2008) study had been to reduce the abundance of the invasive species, then counter-intuitively, increased removal would have had the opposite effect.

Hydra effects and the mechanisms that cause them have been studied using continuous time (ordinary differential equation) models and discrete time (difference equation) models, with Ricker (1954)

being the first to observe a hydra effect in a single-species discrete time model; see Abrams (2009) for a review. With continuous time models, hydra effects have been studied in a variety of two-, three- and four-species communities, including predator–prey systems with one or more species at each trophic level (Abrams, 2002; Abrams et al., 2003; Sieber and Hilker, 2012; Abrams and Cortez, 2015), predator–prey systems with size or stage structure (Abrams and Quince, 2005; de Roos et al., 2007; de Roos and Persson, 2013), 3-species food chain models (Sieber and Hilker, 2012), and versions of those systems that incorporate behavioral or evolutionary changes in foraging (Matsuda and Abrams, 2004; Abrams and Vos, 2003; Abrams and Matsuda, 2005; Abrams, 2012). Cortez and Abrams (2016) recently identified a general condition that defines when hydra effects can arise at stable equilibria of unstructured multispecies models. (Here, unstructured means that total abundance is the single variable describing each population.) That work identified conditions under which hydra effects can arise in the communities listed above in addition to communities with a single trophic level, e.g., three-species competition systems.

Hydra effects have been studied much less with discrete time community models. In particular, nearly all of the theoretical work has focused on single-species models with and without stage structure

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(Seno, 2008; Abrams, 2009; Liz and Pilarczyk, 2012; Liz and Ruiz-Herrera, 2012; Hilker and Liz, 2013). Only rarely have hydra effects been studied or identified in discrete time models with two or more species (Jonźen and Lundberg, 1999; Abrams, 2009; Guill et al., 2014). Because of the lack of examples and theory, it is unclear how often hydra effects arise in discrete time multispecies models. Moreover, it is unknown if there exists a unifying characteristic that determines when hydra effects arise in those models, or if that characteristic is related to mechanisms identified continuous time models.

Building on the work of Yodzis (1988) and Cortez and Abrams (2016) for continuous time models, this paper presents a general characteristic that determines when hydra effects arise in stable discrete time models with unstructured populations for any number of species. In particular, a species exhibits a hydra effect at a stable equilibrium of a discrete time model when fixing that species at its equilibrium density destabilizes the equilibrium; in this case, destabilization can result in large shifts in the community, including the possibility of extinction of one or more species. This result is surprising because the hydra-effect (HE) species is still present in the system and at the same density. However, what has changed is the ability of HE species to respond to changes in the densities of the other species. Thus, the dynamical feedback of the HE species is necessary for stable coexistence of all species. Following Cortez and Abrams (2016), the characteristic where destabilization occurs when the HE species is fixed at its equilibrium density is referred to as 'subsystem instability'.

In the following, I present a general discrete time n-species community model and derive the subsystem instability result. I then apply the result and identify when hydra effects arise in stable single-species models, cyclic single-species models, and stable two-species models. I also show that the presence of a hydra effect implies the system is reactive. I discuss how the subsystem instability result can be used to identify hydra effects in communities with more than two species and identify previous studies where hydra effects were present, but not recognized. This greatly increases the number of communities for which hydra effects occur when modeled using discrete time systems. I also discuss the relationship between the subsystem instability result for discrete time models in this study and the subsystem instability result for continuous time models in Cortez and Abrams (2016).

2. n-Species community model

Let $x_{i,t}$ denote the density (or abundance) of species i at time point t. The general n-species discrete-time community model describes the changes in each species density over time,

$$x_{i,t+1} = x_{i,t} f_i(x_{1,t}, \ldots, x_{n,t}, \delta_i), \quad 1 \le i \le n \tag{1}$$

where f_i accounts for the per capita production in the density of species i due to all ecological processes. Throughout this study, the parameter δ_i will be related to the mortality of the species i. Thus, with the exception of some results pertaining to single-species communities ($n=1$), throughout I assume that increases in the mortality of species i reduce its per capita growth rate, i.e., $\partial f_i/\partial \delta_i < 0$. Let $\vec{x}^* = (x_1^*, \ldots, x_n^*)$ be a stable coexistence equilibrium of model (1). Throughout we use f_i^* to denote when a function is evaluated at the equilibrium point. Species i exhibits a hydra effect at an equilibrium point if $\partial x_i^*/\partial \delta_i > 0$, i.e., if an increase in the mortality of species i causes the equilibrium density of that species to increase.

Note that while this study focuses on increases in mortality, my results also apply to counterintuitive responses to changes in other parameters, provided that the parameter does not directly affect the per capita fitnesses of the other species in the system (f_j does not depend on δ_i for $i \ne j$). This means that the conditions under which hydra effects arise in stable systems due to increased mortality are the same as the conditions under which changes in other parameters have effects of opposite sign on a species' population-level response and its per

capita fitness. For example, hydra effects in response to increased mortality occur under the same conditions that increased emigration (which decreases per capita fitness) increases population size, or increased reproduction rates (which increase per capita fitness) decrease population size.

The Jacobian of model (1) determines whether small perturbations to the equilibrium densities will grow (implying equilibrium instability) or decrease (implying equilibrium stability). When evaluated at the coexistence equilibrium, the Jacobian has the form $\mathbf{J} = \overline{\mathbf{J}} + \mathbf{I}_{n \times n}$, where $\mathbf{I}_{n \times n}$ is the $n \times n$ identity matrix and

$$\overline{\mathbf{J}} = \begin{pmatrix} x_1^* \frac{\partial f_1^*}{\partial x_1} & \cdots & x_1^* \frac{\partial f_1^*}{\partial x_n} \\ \vdots & \ddots & \vdots \\ x_n^* \frac{\partial f_n^*}{\partial x_1} & \cdots & x_n^* \frac{\partial f_n^*}{\partial x_n} \end{pmatrix}. \tag{2}$$

Note that the coexistence equilibrium point $\vec{x}^*$ is stable when all eigenvalues of the Jacobian have modulus less than one. Equilibrium stability also implies that all eigenvalues of $\overline{\mathbf{J}}$ lie within the unit circle centered at $-1 + 0i$.

3. Results

In the following sections, I derive a formula for how the equilibrium density of a species responds to increased mortality (i.e., a formula for $\partial x_i^*/\partial \delta_i$) and give a biological interpretation for that formula. I then apply that formula to stable one-species communities, cyclic one-species communities, and stable two-species communities.

The following conditions for hydra effects depend on whether species have positive or negative self-effects at equilibrium and, for single-species communities, if the density dependence of the species is overcompensatory. Positive self-effects means that the per capita fitness of the species increases with increases in its density, i.e., $\partial f_i/\partial x_i > 0$. Positive self-effects can arise through intraspecific interactions, e.g., Allee effects, or through interspecific interactions, e.g. saturating predator functional responses. Negative self-effects are decreases in per capita fitness with increased density, i.e., $\partial f_i/\partial x_i < 0$. A common cause for negative self-effects is intraspecific competition. The density dependence of a species is overcompensatory if the fitness of the species, $x_i f_i(N_i)$, decreases with increased density, i.e., $(\partial/\partial x_i)(x_i f_i) = f_i + x_i(\partial f_i/\partial x_i) < 0$. Note that overcompensation requires negative self-effects.

3.1. Hydra effects imply subsystem instability

To derive a formula for $\partial x_i^*/\partial \delta_i$, I implicitly differentiate model (1) evaluated at $\vec{x}^*$ with respect to δ_i and solve for the partial derivative. This approach is the same as that used in Yodzis (1988) and Cortez and Abrams (2016) to study responses to mortality perturbations and hydra effects in continuous time models. This approach has also been used previously to study stable discrete time models (e.g., Seno, 2008) and it has been extended to models exhibiting cyclic dynamics (Liz and Ruiz-Herrera, 2012; Sieber and Hilker, 2012). As shown in the appendix, the response of the equilibrium density of species i to an increase in its mortality is

$$\frac{\partial x_i^*}{\partial \delta_i} = \left(-\frac{\partial f_i^*}{\partial \delta_i} \right) \frac{x_i^* \overline{\mathbf{M}}_{ii}}{|\overline{\mathbf{J}}|} \tag{3}$$

where $|\overline{\mathbf{J}}|$ is the determinant of $\overline{\mathbf{J}}$ and $\overline{\mathbf{M}}_{ii}$ is the i, i minor of $\overline{\mathbf{J}}$, i.e., the determinant of the matrix where the ith row and column of $\overline{\mathbf{J}}$ are removed. Under the assumption that increased mortality reduces a species per capita growth rate, the term in parentheses is positive. Thus, hydra effects only arise when $\overline{\mathbf{M}}_{ii}$ and $|\overline{\mathbf{J}}|$ have the same sign.

The signs of $\overline{\mathbf{M}}_{ii}$ and $|\overline{\mathbf{J}}|$ can be interpreted in terms of system stability. For a system with an even number of species (n even), $|\overline{\mathbf{J}}|$ is positive at a stable equilibrium. For an odd number of species (n odd),