

# The geometry of transient crashes and their dependence on demographic rates<sup>☆</sup>

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## Abstract

In theory and practice, many ecological communities possessing a stable coexistence steady state may, in actuality, be difficult to assemble species-by-species, due to temporarily low densities of one or more preexisting species after the introduction of a new community member. This article elucidates some of the conditions under which these transient near-extinctions are likely to occur. These conditions are given in terms of such geometric quantities as the position of the new coexistence state after an invasion, relative to the original coexistence state, and the severity of the post-invasion community's oscillations, as well as more directly biological quantities such as the demographic rates of the invader and the potential victim of a crash. Through graphical reasoning, numerical examples, and preliminary experimental results, the importance of these conditions is demonstrated.

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## 1. Introduction

Although for years the paradigm in mathematical ecology was to consider, chiefly if not exclusively, the existence and stability of fixed points of ecological models, much recent work has focused on the transient behavior of model communities (Hastings, 2004). Most of this research has focused on the existence of oscillatory or chaotic transients that act to postpone the inevitable extinction of some of the species in a system (McCann and Yodzis, 1994); often these transients can be of such a long duration, in ecological terms, that the theoretical steady state of the system is unimportant.

Some results have also highlighted the converse possibility – that transient dynamics approaching theoretical extinction can indicate the danger that a community with a stable coexistence steady state might undergo extinction in some of its component populations due to stochasticity or other factors not included in the model. Some simple models of shared predation, wherein one predator exploits two or more prey species, have been

seen to exhibit transient, and non-chaotic, crashing behavior after certain invasion events. In Holt and Hochberg (2001), this is seen upon introduction of the predator if one of the prey species has a significantly higher susceptibility to it than the other (denoted  $s_1$  or  $s_2$ ). Further raising the susceptibility of this species to the predator leads to stronger transient crashes in the corresponding prey, even if it does not affect the long-term coexistence densities. This result is taken much farther in Noonburg and Abrams (2005), where a keystone predator and its two prey species, along with an explicit resource, are modeled. It is found there that the possible parameter ranges allowing coexistence are significantly reduced if the requirements for coexistence are extended to include a feasible sequence of invasions leading to the final community, with no transient population densities beneath a specified threshold.

Another model of shared predation which exhibits transient crashes can be formed by the addition of a top-level exploiter to either of the multi-species competition models given in Huisman and Weissing (2001, 2002). It should be noted that in the latter, an example seven-consumer, three-resource system is given, assembled through a sequence of invasions; some of the invading species in that example undergo crashes after their introductions. The modified model I will use here to investigate

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transient dynamics is

$$\dot{P} = P \left( \sum_{i=1}^n e_i s_i N_i - m_P \right), \quad (1)$$

$$\dot{N}_i = N_i (\mu_i(R_1, \dots, R_k) - m_i - s_i P) \quad (2)$$

$$\dot{R}_j = D(S_j - R_j) - \sum_{i=1}^n c_{ji} \mu_i(R_1, \dots, R_k) N_i \quad (3)$$

where  $P$  is the exploiter,  $s_i$  are the susceptibilities of the prey species, and  $e_i$  are the corresponding conversion efficiencies. The growth rates of the prey species (i.e. the functions  $\mu_i$ ) and dynamics of the resources are as given in [Huisman and Weissing \(2002\)](#); however, the results I will present here are quite similar for growth rates as given in [Huisman and Weissing \(2001\)](#).

The dynamics of non-chaotic transient crashes so far have largely been explored through numerical analysis. Here I will use some simple geometric arguments and mathematical reasoning to describe general conditions leading to transient crashing after invasions in oscillatory models. I will first make a geometric analogy to an invasion event in an oscillatory system, which will allow a somewhat more exact understanding of the effects of various dynamical factors on crashing behavior. I will then show how and why the growth rates of the invader and the crashing species influence the transient danger to the latter. I will also briefly touch upon recent experimental work that may support the predictions discussed.

## 2. The geometry of transient crashes

### 2.1. Crashes and phase space

A transient crash occurs when one or more populations in a system momentarily approach extinction. It is often fruitful in mathematical modeling to consider the system's phase space. For ecological models, trajectories must remain in positive phase space – that is, their coordinates cannot be negative – because a negative population density has no physical meaning. So a crash occurs when a trajectory approaches the boundary between positive and negative phase spaces, where one or more of the coordinates is zero. We now investigate general dynamical causes which may lead to such a trajectory, by making a simplifying analogy to the possibly quite complicated shape of trajectories in phase space.

### 2.2. An analogy

Consider the projection of phase space onto the plane that captures the dynamics of two interacting populations of interest. That is, instead of plotting the whole phase space, which could be quite difficult for three or more species, we trace a path representing only two populations – and therefore having only two coordinates – from the moment that an invasion takes place to the final state of the system. We will ignore the dynamics of the invader and treat the invasion itself as an instantaneous parameter change in the dynamics governing

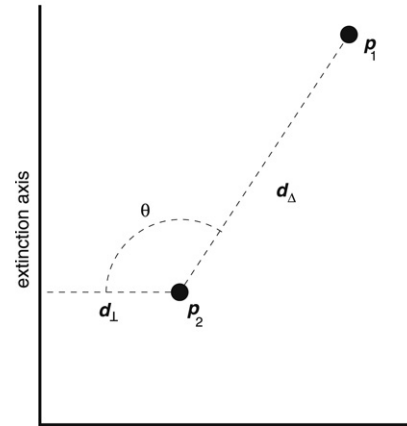


Fig. 1. Phase plane changes during an invasion.

behavior on the plane. Let  $p_1$  be the position of the system before invasion and  $p_2$  the asymptotically stable coexistence point after invasion. Let  $d_{\perp}$  be the distance from  $p_2$  to one of the two extinction axes. Let  $d_{\Delta}$  be the distance from  $p_1$  to  $p_2$ . For each eigenvalue  $\lambda_i$  of the post-invasion Jacobian  $\mathbf{J}(p_2)$ , let  $\varepsilon_i = -\text{Re } \lambda_i / |\text{Im } \lambda_i| > 0$ . Let  $\varepsilon$  be the smallest of these; that is,  $\varepsilon$  corresponds to the most imaginary eigenvalue, which means that it causes the most sustained oscillations. The linearization about the fixed point has a decay term of the form  $e^{(-\varepsilon x \pm i x)t} = e^{-\varepsilon x t} (\cos x t \pm i \sin x t)$  for some  $x$ . That is, trajectories in the phase plane should decay toward the fixed point like  $e^{-\varepsilon x t}$  and oscillate about it with period  $2\pi/x$ .

Let  $\theta$  be the angle from the line joining  $p_2$  to  $p_1$  to the line normal to the axis under consideration through the point  $p_2$ , where the angle is taken in the direction of the system dynamics. These quantities are shown in [Fig. 1](#) for counterclockwise oscillations. If oscillations roughly follow a logarithmic spiral, the linearization predicts that a trajectory starting at  $p_1$  will, after the invasion, traverse the angle  $\theta$  in time  $\theta/x$ . And since the trajectory begins at a distance  $d_{\Delta}$  from  $p_2$ , after  $\theta/x$  time it should be about  $e^{-\varepsilon x (\theta/x)} d_{\Delta} = e^{-\varepsilon \theta} d_{\Delta}$  from  $p_2$ . Therefore, in order for the trajectory not to intersect the extinction axis, we must have that  $d_{\perp} > e^{-\varepsilon \theta} d_{\Delta}$ .

This result is only analogous and approximate to the true situation under consideration. First of all, the invasion may not proceed like a simple parameter change, as it nearly does for the model of [Noonburg and Abrams \(2005\)](#) and the modified model (1)–(3) (see the first panels of [Figs. 4 and 5](#)). In [Holt and Hochberg \(2001\)](#), the invader undergoes lengthy oscillations after invasion. In general, oscillations occur in more than two dimensions, so even if they were to follow a perfect logarithmic spiral there, they would appear elliptic when projected onto two dimensions. Also, in continuous, deterministic ecological models, it is not possible for a trajectory starting in positive phase space to reach extinction in finite time. Trajectories that approach extinction are warped by nonlinear effects. Away from the coexistence fixed point, linearization fails.

Despite the analogy's shortcomings, it suggests that the severity of transient crashes after an invasion should be related

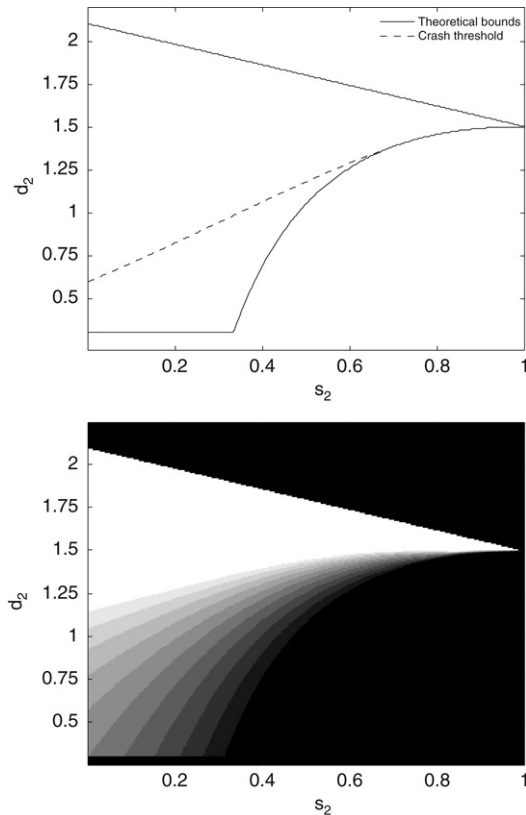


Fig. 2. Crashing as a function of  $s_2$  and  $d_2$ : crash boundaries (top) and  $\kappa$  (bottom). Fixed parameters are  $r = K = c_1 = c_2 = b_1 = s_1 = 1$ ,  $b_2 = 3$ ,  $d_1 = e_1 = e_2 = 0.1$ , and  $D = 0.03$ .

to the relative magnitudes of  $d_\perp$  and  $e^{-\varepsilon\theta} d_\Delta$ . Specifically, as

$$\kappa = \frac{d_\perp e^{\varepsilon\theta}}{d_\Delta} \quad (4)$$

decreases, population crashes should become more severe.

### 2.3. The predictive quality of $\kappa$

To test the extent to which crashing depends on the quantities named above in the relationship deduced above, let us compare crashing behavior to the value of  $\kappa$  for some of the models previously mentioned.

A parameter slice for the keystone predation model

$$\dot{R} = rR(1 - R/K) - c_1 N_1 R - c_2 N_2 R \quad (5)$$

$$\dot{N}_1 = N_1(b_1 c_1 R - d_1 - s_1 P) \quad (6)$$

$$\dot{N}_2 = N_2(b_2 c_2 R - d_2 - s_2 P) \quad (7)$$

$$\dot{P} = P(e_1 s_1 N_1 + e_2 s_2 N_2 - D) \quad (8)$$

was examined by Noonburg and Abrams. On that slice,  $s_2$  and  $d_2$  vary; it is shown in Noonburg and Abrams (2005) that the region exhibiting simple long-term coexistence is significantly larger than the region for which no drastic crashes occur after invasion by the second prey. Fig. 2 shows the  $s_2$ – $d_2$  parameter slice and the corresponding values of  $\kappa$ . In the first plot, the boundary of parameter values with a long-term outcome of coexistence is marked, along with the boundary found when

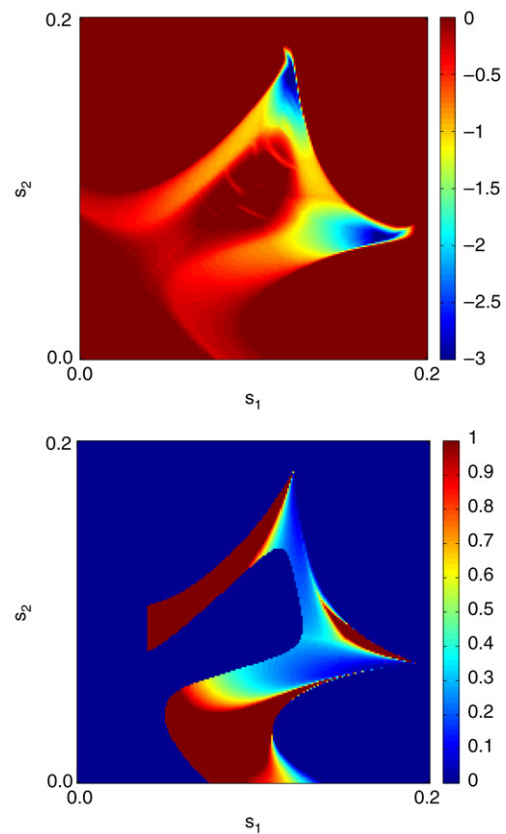


Fig. 3. Crashing as a function of  $s_1$  and  $s_2$ : crash magnitude (top) and  $\kappa$  (bottom). Fixed parameters are given in the text.

transient crashes are considered as limitations on possible coexistence. In the second plot, the twelve shades represent  $\kappa \leq 0$ ,  $0 < \kappa \leq 0.1$ ,  $0.1 < \kappa \leq 0.2$ , ..., and  $\kappa \geq 1.0$ . Judging visually, Noonburg and Abrams' crash cutoff seems to correspond to a value of  $\kappa$  around 0.6. Calculation of  $\kappa$  is a simple matter for this model, since the coexistence steady states can be found by solving a  $4 \times 4$  linear system, and the Jacobian and its eigenvalues are easily computed. Parameters for which a coexistence density is negative or the coexistence fixed point is unstable are assigned  $\kappa = 0$ .

Fig. 3 shows an  $s_1$ – $s_2$  parameter slice for the modified model (1)–(3), comparing crash magnitude after a predator invasion to  $\kappa$  on the slice. Regions where crashing occurs are highly correlated with low  $\kappa$ . In the first plot, crash magnitude is defined as the minimum of the densities of the prey species shortly after invasion divided by the minimum of the long-term densities of the prey species, and then minimized over a small set of distinct invasion times (the same set is used for each parameter combination), since before invasion the system is on a limit cycle. This returns a value greater than 1 for non-crashing parameters (including asymptotic extinction outcomes), and roughly gives a worst-case scenario for each parameter combination, although generally crashing behavior in this model does not greatly depend on the moment at which invasion occurs. Crash magnitude is plotted on a log scale, from  $10^{-3}$  and below to 1 and above. In the second plot, calculation of  $\kappa$  was accomplished by a combination of Runge–Kutta

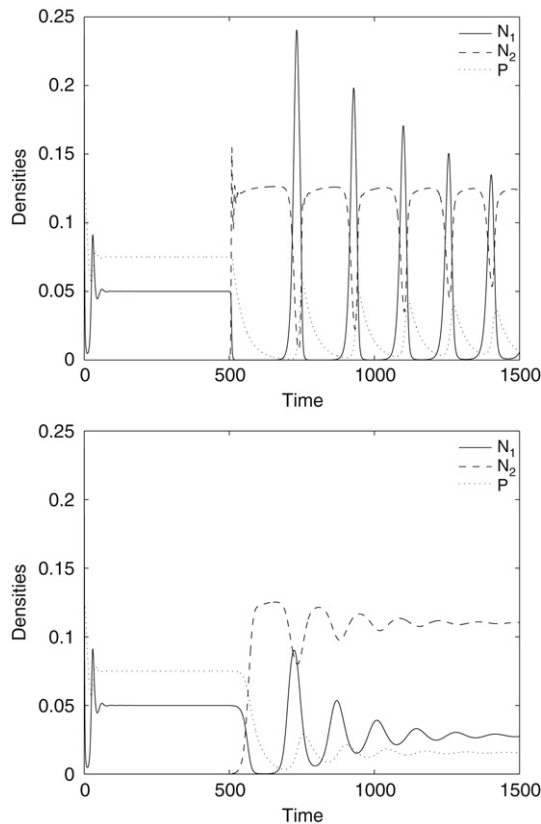


Fig. 4. Invasion by  $N_2$  at  $t = 500$  with fast (top) and slow (bottom) dynamics. Parameters are  $r = K = 1$ ,  $c_1 = 3$ ,  $c_2 = 6$ ,  $b_1 = b_2 = 1/3$ ,  $d_1 = e_1 = e_2 = 0.1$ ,  $d_2 = 0.48$ ,  $s_1 = 10$ ,  $s_2 = 2$ , and  $D = 0.05$ .

iteration and nonlinear solution via the BFGS method. Again, untenable coexistence points are assigned  $\kappa = 0$ .

Fixed parameters for Fig. 3 are  $r_1 = r_2 = r_3 = 1$ ,  $m_1 = m_2 = m_3 = D = 0.25$ ,  $\mathbf{K} = \begin{pmatrix} 1 & 0.9 & 0.25 \\ 0.25 & 1 & 0.9 \\ 0.9 & 0.25 & 1 \end{pmatrix}$ ,  $\mathbf{c} = \begin{pmatrix} 0.1 & 0.2 & 0.15 \\ 0.15 & 0.1 & 0.2 \\ 0.2 & 0.15 & 0.1 \end{pmatrix}$ ,  $S_1 = S_2 = S_3 = 10$ ,  $s_3 = 0.1$ ,  $e_1 = e_2 = e_3 = 0.1$ , and  $m_P = 0.3$ . The above values for  $\mathbf{K}$  and  $\mathbf{c}$  are shown in Huisman and Weissing (2002) to produce limit cycles in the system without a predator. For further discussion of the meaning and effects of these parameters, see Huisman and Weissing (2001, 2002).

The quantity  $\kappa$  is a good predictor of transient crashing behavior for these two models. This indicates that crash intensity depends upon fixed point movement and oscillatory behavior in the way I have outlined, at least in these cases.

#### 2.4. Implications

A naive geometric argument suggests that highly oscillatory – though ultimately stable – dynamics and a particular condition on the movement of a system's fixed point during an invasion may be sufficient to cause transient crashes in population densities en route to the system's final state. It has been argued that oscillations in certain broad classes of biological systems should be common (Gilpin, 1975; Turchin, 2001) and often arise from indirect interactions, as for example

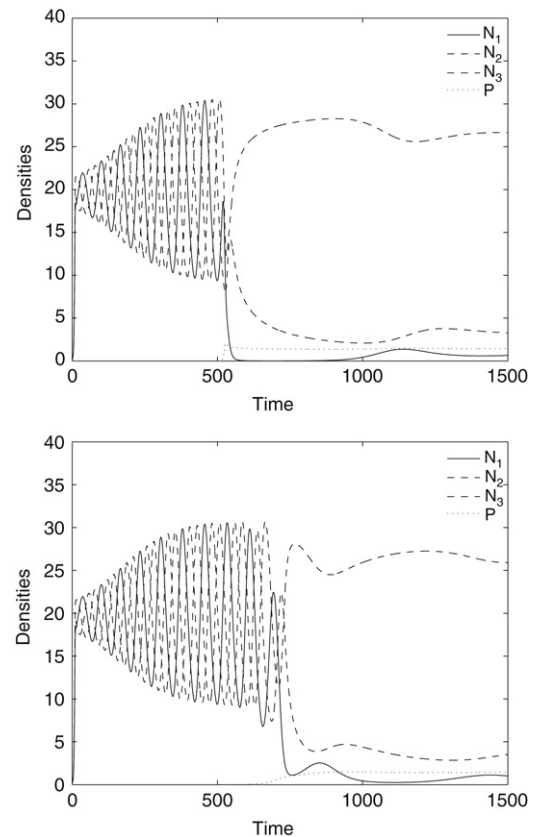


Fig. 5. Invasion by  $P$  at  $t = 500$  with fast (top) and slow (bottom) dynamics. Parameters are the same as in Fig. 3, with  $s_1 = 0.165$  and  $s_2 = 0.07$ .

apparent competition. It is already well recognized that these oscillations can have drastic effects on the ability of populations to coexist (Abrams, 1999; Bonsall and Hassell, 1998).

The specific form of the dependence of  $\kappa$  on fixed point movement has interesting consequences. An invasion event may cause a transient crash in a population whose long-term density is unaffected – or, conceivably, even increased – by the invasion. For example, in the model (5)–(8), if the invading prey is invulnerable to the predator ( $s_2 = 0$ ), we are guaranteed that the equilibrium value of the other prey is the same before and after invasion. If we were to plot that prey on the horizontal axis and the predator on the vertical in Fig. 1, during invasion the fixed point would move vertically down toward predator extinction. But as intuition from that figure might suggest, and as reported in Noonburg and Abrams (2005), the transient crash in the prey can be even more severe with that parameter choice than with positive invader susceptibility.

### 3. Dependence on demographic rates

#### 3.1. The outcome of slowed invasions

It was assumed in the analogy above that the invasion acts like an instantaneous parameter change. The dynamics of the invader must be relatively fast in order to cause a severe crash. For slow invader dynamics, the rest of the system is entrained by the invader (Ludwig et al., 1978; Rinaldi and Scheffer, 2000); instead of an immediate jump from one fixed point



to another as if a parameter were instantaneously altered, the system moves more smoothly toward its new state. This is shown in Fig. 4 for the models (5)–(8) and Fig. 5 for the models (1)–(3). In each case crashes are shown in the first plot with the original model, and in the second with invader dynamics slowed by an order of magnitude. In these the crashing behavior is much less severe than with the original invader dynamics. This result also holds for the model from Holt and Hochberg (2001).

It is mentioned in Noonburg and Abrams (2005) that for some models, a predator with slower dynamics leads to crashing, while the opposite holds in other models. It turns out that the former models are those in which the predator is not the invader, while models like that in Holt and Hochberg (2001), in which the predator invades, comprise the latter. The key to severe crashes is that invaders have demographic rates at least comparable to those of the other species.

Note that it is during the invasion itself, while the system corrects toward a new long-term state, that the speed of the invader's dynamics is most important. Since Allee effects reduce the initial growth rates of invaders (Stephens and Sutherland, 1999), this makes the question of whether an invader exhibits an Allee effect of even greater interest than it has been. Many authors have considered the ramifications of an Allee effect in an invading species (Courchamp et al., 1999; Drake, 2004). These works have largely focused on the reduced probability of successful establishment from low numbers. However, here I have also shown how the slowing of an invading population's growth can severely mitigate the transient effects of an invasion, whether that invasion turns out to be successful or not.

### 3.2. The crashing population

Certain useful mathematical simplifications apply to systems of ordinary differential equations such as some of those employed here, if one of the populations under consideration has high demographic rates. For example, in Noonburg and Abrams (2005), the prey population that crashes after the introduction of a second prey generally has very high susceptibility to the keystone predator, and it is found that greatly increasing this vulnerable prey's other parameters leads to even more severe crashing after invasion by the other prey.

A system of this kind, in which a population has potentially high rates of change, can be analyzed using a singular perturbation approach, as explained in fairly ecological terms in Ludwig et al. (1978). Approximate analysis is possible under the assumption that populations with fast dynamics, such as the more susceptible prey in the model (5)–(8), change instantaneously relative to slower populations, the densities of which can be taken as constant parameters during that fast change. Upon invasion by a second prey, the resource density begins to decrease and the predator density, in most cases, begins to increase. Since, prior to invasion, the first prey's dynamics were at equilibrium, these changes lead to a negative trend in its density. Once away from equilibrium, that prey has rapid dynamics relative to the resource and predator, so we

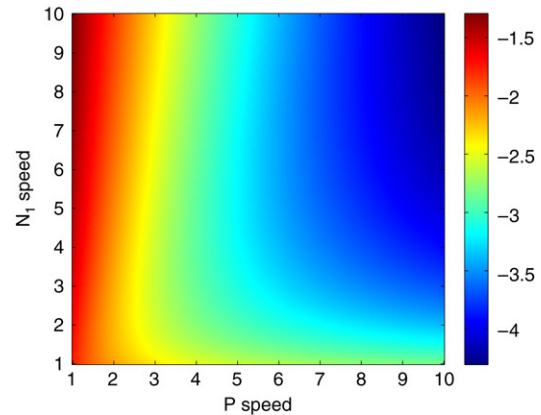


Fig. 6. Dependence of crashing behavior on speed of invader and victim. Parameters are  $r_1 = 1$ ,  $r_2 = 1/4$ ,  $K_1 = K_2 = 1$ ,  $s_1 = 1$ ,  $s_2 = 1/4$ ,  $e_1 = e_2 = 1$ ,  $r_P = 7/4$ , and  $D = 1/4$ .

hold these as constants and see that the prey should crash to low densities, where it remains until the predator and resource slowly return to more favorable levels in its absence. This argument can be made more formal using classical results such as that presented in Tikhonov (1952).

A system in which a prey is highly susceptible to a predator, or generally has high demographic rates – regardless of whether long-term coexistence is in danger – is prone to transient crashing during invasions, if the invader's presence has an immediate negative effect on the susceptible prey. This can be seen in all of the models mentioned here. The basic form of most ecological models, in which the growth of a given organism is proportional to its density – i.e.  $\dot{N} = Nf(N, \dots)$  for some function  $f$  – lends itself to the existence, in the language of singular perturbation theory, of slow manifolds along phase axes – i.e. along  $N = 0$ . To put simply, after invasion by a competitor or predator, a population with high demographic rates is likely to be pulled for a time toward zero population density, near which stochasticity or an otherwise unimportant Allee effect may cause extinction. Such attraction toward extinction on an extended interval would look like permanent, asymptotic extinction on the time scales of many empirical studies.

### 3.3. Numerical example

I will now demonstrate the importance of demographic rates to transient crashing behavior for the model from Holt and Hochberg (2001),

$$\dot{N}_1 = r_1 N_1 (1 - N_1/K_1) - s_1 N_1 P \quad (9)$$

$$\dot{N}_2 = r_2 N_2 (1 - N_2/K_2) - s_2 N_2 P \quad (10)$$

$$\dot{P} = r_P P (e_1 s_1 N_1 + e_2 s_2 N_2 - D). \quad (11)$$

I will adjust the dynamics of prey 1 and the invading predator by multiplying the right-hand side of their respective equations by constants, which I will refer to as their speeds. Note that this adjustment does not affect the long-term state of the system. I choose parameters such that the two prey species have the same density at the stable coexistence point. Fig. 6 shows how

the severity of crashes depends on the demographic rates of the invading predator and prey 1. The minimum density of that prey is plotted on a log scale.

If either species has speed 1, increasing the speed of the other species has fairly little effect on crashing behavior. In fact, even for larger predator speeds, increasing the speed of prey 1 can reduce transient crashing. This is due to the entrainment effect spoken of earlier. Severe crashes require the speeds of both species to be large.

#### 4. Discussion

The estimate of the dependence of transient crash intensity on factors such as the movement of a system's fixed point and the value of the most oscillatory post-invasion eigenvalue proved fairly accurate for two of the models considered here. In addition to research on ecological introductions, the study of catastrophic regime shifts (see for example Scheffer and Carpenter (2003)) and other consequences of multiple steady states might be well served by considering the possibility of transient crashing behavior, especially since a catastrophic shift between states in an oscillatory system would likely meet the conditions for transient crashes given here.

The fact that an ecological invader's Allee effect should dramatically reduce the severity of initial crashes draws attention to a general problem with using simple models to explore post-invasion transient behavior. Typically, these models are best suited to the study of asymptotic coexistence dynamics. They do not take into account the true behavior of very small populations. Though a basic model may be very accurate for reasonably-sized populations, it may break down for the small numbers involved in an invasion event. For an example of this possibly drastic difference in accuracy between densities of reasonable magnitude and negligible densities, see the boundary layer model of Hastings et al. (1981).

As stated in Noonburg and Abrams (2005), there is little empirical evidence to date for transient (and non-chaotic) crashing behavior in natural systems. This may be partially due to its not being sought after. There are reasons for such evidence to be overlooked; for example, as noted before, the time scales of many studies are such that their apparent end result is actual extinction. Also, the very reason that theoretically transient extinctions are important – that stochasticity and other factors can cause them to be permanent in a natural system – leads to an inherent difficulty in their experimental detection.

There are some scant data with which to compare our the predictions presented here. In Warren et al. (2003), a systematic program of experiments is described in which stable communities are invaded and the results recorded. Of particular interest are initial communities containing *Paramecium caudatum*, *Colpidium striatum*, and *Tetrahymena pyriformis* (all of which share a common bacterial resource), and invaded by predators *Blepharisma japonicum* and *Euplotes patella*. The results of that work demonstrate that a single kind of invasion event can have differing outcomes. This strongly suggests that, when an extinction takes place in one case but not another, transient crashing is occurring. The

highly stochastic nature of extinction during a crash would account for the variability between experimental replicates. As noted in Warren et al. (2003), the lengths of *Paramecium*, *Colpidium*, and *Tetrahymena* are about 150, 70, and 35 microns, respectively. The generation time of *P. caudatum* is given in Fok and Allen (1979) as 20–26 hours. That of *C. striatum* is about 5 hours in Holyoak and Lawler (1996). That of *T. pyriformis* is about 4 hours in Meyer et al. (1972). In Warren et al. (2003), the consumers with faster dynamics and smaller size are prone to extinction during invasions, either by a predator or by *Paramecium*, though *Paramecium* itself is never driven to extinction by similar invasions. Also, *Blepharisma* exhibits the ability to drive prey to extinction during invasion, and at the same time it shows a tendency to become extinct during prey invasions. While these are not direct evidences for our arguments here, they are consistent under those arguments.

The arguments and examples presented here contribute to the ongoing study of the importance of short- to medium-term model dynamics to actual ecological phenomena (Hastings, 2004). The transient behavior of a community after a new invasion may be of vital importance to the long-term composition of that community. As such, it is hoped that the insights given here will aid in the search for rules of community assembly (Drake, 1990), the knowledge of which will improve the understanding of how communities may be formed by chance or human design.

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