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Reactivity and transient dynamics of discrete-time ecological systems

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On the occasion of the 62nd birthday of Jim Cushing

Most studies of ecological models focus exclusively on the asymptotic stability properties of equilibria. However, short-term transient effects can be important, and can in some cases dominate the dynamics seen in experimental or field studies. The reactivity of a stable equilibrium point measures the potential for short-term amplification of perturbations. The reactivity of a fixed point in a discrete-time system is given by the natural logarithm of the largest singular value of the Jacobian matrix of the linear approximation near the fixed point. If the reactivity is positive, the fixed point is said to be reactive. Here we examine the reactivity of discrete-time predator–prey models and density-dependent matrix population models. We find reactivity to be common (but not universal) and sometimes extremely high. Predator–prey or food web models that include a predator whose per-capita growth rate depends on the density of its prey, but not on its own density, are a special case. Any positive equilibrium of such a model must be reactive. Reactivity of discrete-time models depends on the timing of the census relative to the timing of reproduction. Perturbation analysis of singular values can be used to calculate the sensitivity and elasticity of reactivity to changes in model parameters. We conclude that transient amplification of perturbations should be a common ecological phenomenon. The interaction of these transient effects with the asymptotic nonlinear dynamics warrants further study.

Keywords: Reactivity; Resilience; Matrix population models; Predator-prey; Density-dependence; Food webs; Closure terms

1. Introduction

The typical analysis of a nonlinear ecological model begins with an enumeration of the model's equilibria and a characterization of their stability. For food-web and nutrient-cycle models [1], a next step often involves a calculation of the "resilience" of the stable equilibria. The resilience is the eventual rate of return to the equilibrium after a small perturbation [2]. Stability and resilience are important to ecologists because, the argument goes, more resilient systems are likely to be less variable and more persistent in the face of inevitable environmental perturbations.

Stability and resilience are both calculated from the dominant eigenvalue of the linearization of the model in the neighborhood of the equilibrium point in question. As such, both quantities characterize the asymptotic dynamics of small perturbations. Neither, however, provides any information about transient dynamics, and models with highly resilient equilibria can exhibit dramatic transient responses to perturbations [3]. For example,

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although perturbations to a stable equilibrium will eventually decay, they can grow rapidly at first, and the growth can continue for times on the order of the return time.

The question arises whether asymptotic behavior adequately characterizes system dynamics. In fact, real ecosystems typically do not complete their response to a perturbation before the next one occurs. Instead, they are buffeted by a more-or-less continual series of perturbations and the appearance of transient responses in our observations of nature may be the norm rather than the exception. For example, the elegant experimental and mathematical research of Cushing and colleagues on flour beetles of the genus *Tribolium* has shown that the interaction between perturbations and the stable manifolds of the system's invariant sets produce transient dynamics that are reflected in "distinctive temporal patterns in the data" [4].

As a practical matter, transient responses may be at least as important as asymptotic responses. Managers charged with ecosystem restoration, for example, are likely to be interested in both the short-term and long-term effects of their manipulations, particularly if the short-term effects can be large [5].

Empirical ecologists are only just beginning to shift their focus from asymptotic dynamics to transient dynamics. This is partly because they have not had a simple index for quantifying transient behavior. In an effort to focus more attention on transient dynamics, we recently introduced a set of such indices into the ecological literature [3].† Principal among these was "reactivity," the maximum instantaneous growth rate of a small perturbation. Positive reactivity has now been documented in a number of food web and ecosystem compartment models [3,12,13]. It has been shown to be a necessary condition for pattern formation via Turing instability in spatial ecological models [14], and has been shown to be a common property of the equilibria of continuous-time predator–prey models [15]. There are also methods for estimating reactivity from time series [16].

In our previous work, we defined reactivity only for systems of differential equations; it can also be defined for maps. Consider the linear system

$$\mathbf{x}(t+1) = \mathbf{B}\mathbf{x}(t) \tag{1}$$

(it might be the linearization of a nonlinear system in the neighborhood of an equilibrium point) with initial conditions $\mathbf{x}(0) = \mathbf{x}_0$. If $\hat{\mathbf{x}} = 0$ is an asymptotically stable equilibrium point of equation (1), then the maximum eigenvalue of $\mathbf{B}$ satisfies $|\lambda_1(\mathbf{B})| < 1$. The *resilience* of $\hat{\mathbf{x}}$, which is usually defined as the inverse of the asymptotic return time, can be measured by $-\log|\lambda_1|$.

We define reactivity ν as the maximum rate of departure from $\hat{\mathbf{x}}$ immediately following a perturbation; i.e.

$$\nu \equiv \log\left(\max_{\|\mathbf{x}_0\|\neq 0} \frac{\|\mathbf{x}(1)\|}{\|\mathbf{x}_0\|}\right) \tag{2a}$$

$$= \log\left(\max_{\|\mathbf{x}_0\|\neq 0} \frac{\|\mathbf{B}\mathbf{x}_0\|}{\|\mathbf{x}_0\|}\right) \tag{2b}$$

$$= \log |||\mathbf{B}||| \tag{2c}$$

$$= \log \sigma_1(\mathbf{B}), \tag{2d}$$

†These concepts and calculations will be familiar to many of the readers of this journal, as they arise in fluid dynamics [6,7] and in numerical analysis [8–11].

where $\|\cdot\|$ is the l_2 norm, $|||\cdot|||$ is the spectral norm and $\sigma_1(\mathbf{B})$ is the largest singular value of $\mathbf{B}$. If $\nu > 0$, the equilibrium point is said to be "reactive". The maximum rate of departure is realized for perturbations in the direction given by the right singular vector of $\mathbf{B}$ corresponding to σ_1.

Reactivity is just one feature of what we have termed the "amplification envelope,"

$$\rho(t) \equiv \max_{\mathbf{x}_0 \neq 0} \frac{\|\mathbf{x}(t)\|}{\|\mathbf{x}_0\|} = |||\mathbf{B}^t|||, \tag{3}$$

which gives the maximum possible amplification at time t of an initial perturbation. In particular, $\nu = \log \rho(1)$. Other features of possible interest are the maximum value of $\rho(t)$, the time at which the maximum is achieved, and the resilience of $\hat{\mathbf{x}}$, $\lim_{t\to\infty} (1/t) \log \rho(t)$.

In the next sections, we analyze several examples of discrete-time predator–prey models and nonlinear matrix population models. We then consider the perturbation analysis of reactivity, and end with a discussion of the ecological implications.

2. Discrete predator–prey models

There is a large literature on discrete-time models for predator–prey or host-parasitoid interactions, dating back to the Nicholson–Bailey model [17] (see [18] for a review). These models can be written

$$n_1(t+1) = f(n_1(t), n_2(t)) \tag{4}$$

$$n_2(t+1) = g(n_1(t), n_2(t)) \tag{5}$$

where n_1 and n_2 denote prey and predators, respectively. Choices of the functions $f(\cdot)$ and $g(\cdot)$ reflect hypotheses about the growth of the prey, the rate of consumption of prey by predators, and the mortality rate of the predators. Many of these models have similar stability and bifurcation patterns [19,20]. The following example is typical.

Example 1 *The Hadeler–Gerstman model.* Hadeler and Gerstman [21] studied a discrete version of the Rosenzweig–MacArthur predator–prey model. In the absence of predation, prey grow logistically. The predators exhibit a saturating Type II functional response. In non-dimensional form,

$$n_1(t+1) = (r+1)n_1(t) - r\,n_1^2(t) - \frac{cn_1(t)n_2(t)}{n_1(t)+\gamma} \tag{6}$$

$$n_2(t+1) = \frac{cn_1(t)n_2(t)}{n_1(t)+\gamma} \tag{7}$$

where n_1 and n_2 are prey and predators, r is the prey growth rate, c is the maximum predation rate and γ is the half-saturation constant. The model has an equilibrium at

$$\hat{n}_1 = \frac{\gamma}{c-1} \tag{8}$$

$$\hat{n}_2 = r\hat{n}_1(1-\hat{n}_1). \tag{9}$$

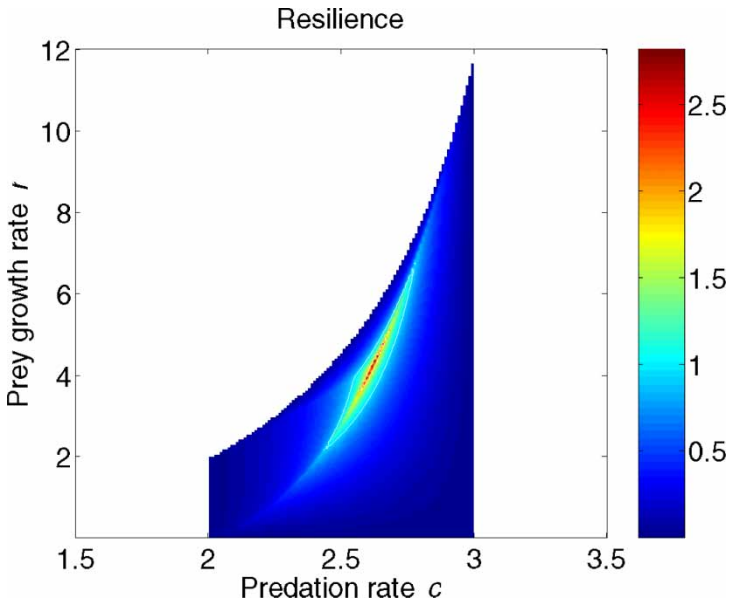

Figure 1. The resilience of the coexistence equilibrium for the Hadeler–Gerstman predator–prey model as a function of the predation rate c and the prey growth rate r. Resilience is plotted only within the stability region.

The Jacobian at the equilibrium is

$$\mathbf{B} = \begin{pmatrix} r + 1 - 2r\hat{n}_1 - \dfrac{c\hat{n}_2\gamma}{(\hat{n}_1+\gamma)^2} & -\frac{c\hat{n}_1}{\hat{n}_1+\gamma} \\ \frac{c\hat{n}_2\gamma}{(\hat{n}_1+\gamma)^2} & \frac{c\hat{n}_1}{\hat{n}_1+\gamma} \end{pmatrix}. \tag{10}$$

The stability properties of this model were analyzed by Neubert and Kot [20]. For the case where $\gamma = 1$ (other values are similar), there is a roughly trapezoidal stability region in the $r - c$ parameter space (figure 1). Crossing the left-hand boundary of this region produces a transcritical bifurcation, crossing the right-hand boundary produces a Hopf bifurcation, and crossing the upper boundary produces a subcritical flip bifurcation. Within the stability region, resilience is maximized near the center (where $|\lambda|$ is at a minimum), and decreases dramatically towards the stability boundaries (figure 1).

The coexistence equilibrium of this model is always reactive (figure 2). That is, there is always at least one perturbation of $\hat{\mathbf{n}}$ that results in transient amplification of the distance from $\hat{\mathbf{n}}$. Reactivity is nearly independent of the predation rate c, but increases dramatically with the prey growth rate r, to values on the order of $\nu \approx 1.6$. If $\mathbf{x}(t) = \mathbf{n}(t) - \hat{\mathbf{n}}$, then a reactivity of $\nu \approx 1.6$ implies $\|\mathbf{x}(1)\|/\|\mathbf{x}(0)\| \approx 5$. Figure 3 shows the result of a perturbation in the direction of maximum amplification ($r = 9$, $c = 2.9$).

2.1 Closure terms and reactivity

Many discrete-time predator–prey models (including the model in Example 1), can be written in the special form

$$n_1(t+1) = f_1(n_1(t), n_2(t)) \tag{11a}$$

$$n_2(t+1) = n_2(t) f_2(n_1(t)), \tag{11b}$$

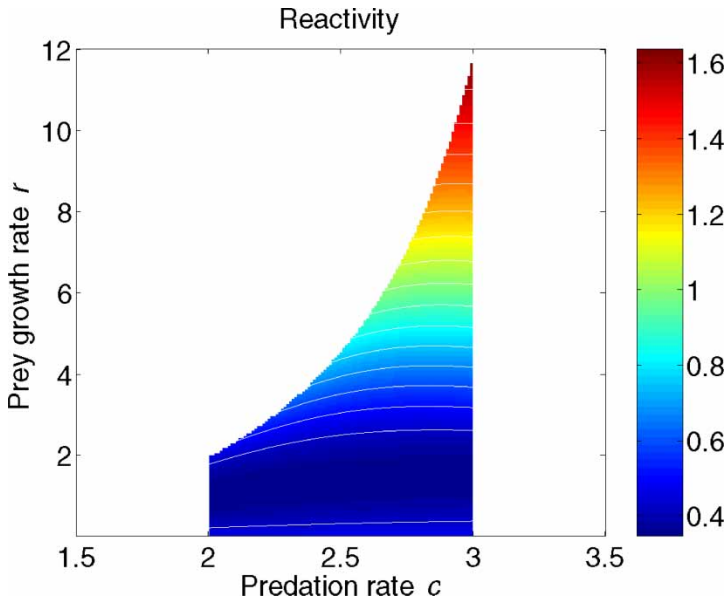

Figure 2. Reactivity of the coexistence equilibrium for the Hadeler–Gerstman predator–prey model as a function of the predation rate c and the prey growth rate r. Reactivity is plotted only within the stability region.

where n_1 and n_2 are the population density of the prey and predator, respectively. The function $f_2(\cdot)$ is the per-capita growth rate of the predator. As written in equation (11b), it depends on the prey density but is independent of the predator density. This function can be interpreted in terms of two ecological processes. One is competition among the predators, caused by reduction in the availability of their prey. The second is predator mortality due to their consumption by higher trophic levels not explicitly included in the model. When used in this way to truncate a food chain, the per-capita predator growth rate is sometimes called

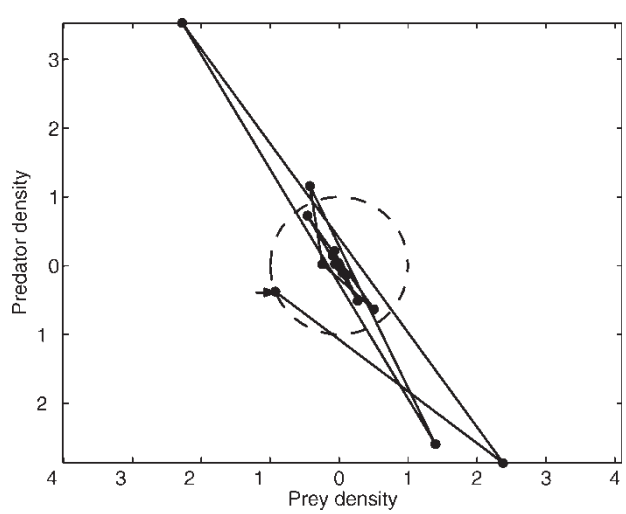

Figure 3. A trajectory calculated from the linear approximation to the Hadeler–Gerstman predator–prey model (7) for $c = 2.9$, $r = 9$. The equilibrium is at the center of the circle; the initial perturbation (indicated by the arrow) was in the direction of maximum amplification.

a "closure term". It has been suggested that the effects of higher trophic levels might be better captured by a nonlinear closure term that depends on n_2 [22], but most predator–prey models have linear closure terms.

Linear closure terms have important implications for transient dynamics. If model (11a,b) has a linearly stable equilibrium point with $\hat{n}_2 > 0$, then $f_2(\hat{n}_1) = 1$. As a consequence, the Jacobian matrix has the form

$$\mathbf{B} = \left.\begin{pmatrix} \frac{\partial f_1}{\partial n_1} & \frac{\partial f_1}{\partial n_2} \\ n_2 \frac{\partial f_2}{\partial n_1} & f_2(n_1) \end{pmatrix}\right|_{\mathbf{n}=\hat{\mathbf{n}}} = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & 1 \end{pmatrix}, \tag{12}$$

with $b_{12} \neq 0$. It is then easy to show that $\sigma_1(\mathbf{B}) > 1$ and the equilibrium $\hat{\mathbf{n}}$ must be reactive. The matrix $\mathbf{C} = \mathbf{B}^{\mathsf{T}}\mathbf{B}$ has the form

$$\mathbf{C} = \begin{pmatrix} b_{11}^2 + b_{21}^2 & b_{11}b_{12} + b_{21} \\ b_{11}b_{12} + b_{21} & 1 + b_{12}^2 \end{pmatrix}. \tag{13}$$

A corollary of the inclusion principle (see [23], Theorem 4.3.15) tells us that the largest eigenvalue of $\mathbf{C}$ is not smaller than any of the diagonal entries of $\mathbf{C}$. Thus

$$\sigma_1(\mathbf{B}) = \sqrt{\lambda_1(\mathbf{C})} \geq \sqrt{1 + b_{12}^2} > 1. \tag{14}$$

The same argument can be applied to *any* m-species food-web model in which at least one species, typically a top predator, has a per capita growth rate independent of its own density. Without loss of generality, one can label this species n_m. The Jacobian matrix will then necessarily have $b_{mm} = 1$, and as a result, the equilibrium must be reactive. If, on the other hand, the web contains no species whose per capita growth rate is independent of its own density, the above arguments do not apply. This situation often arises when the closure terms are density-dependent. Neubert *et al.* [15] showed that biologically reasonable density-dependent closure terms typically reduce the reactivity of continuous-time predator–prey models. We conjecture that this is also the case for discrete models.

Example 2 *The Beddington-Free-Lawton model.* Beddington *et al.* [19] created a host-parisitoid model by adding prey density-dependence to the (always unstable) Nicholson–Bailey model (see p. 190 of [24] for a derivation). Neubert and Kot [20] showed that it can be reduced to the non-dimensional form

$$n_1(t+1) = n_1(t)\exp(r[1 - n_1(t)] - n_2(t)) \tag{15}$$

$$n_2(t+1) = cn_1(t)[1 - \exp(-n_2(t))] \tag{16}$$

where n_1 and n_2 are the host and the parasitoid, r is the intrinsic host growth rate and c is the maximum parasitoid attack rate. This model has a nonlinear closure term. The stability region in the $r - c$ plane for the unique positive equilibrium point is similar in shape to that of the Hadeler–Gerstman model, and figure 4 shows the reactivity within the stability region. Even though the closure term is nonlinear, the coexistence equilibrium is always reactive, although over much of the parameter region it is only slightly so.

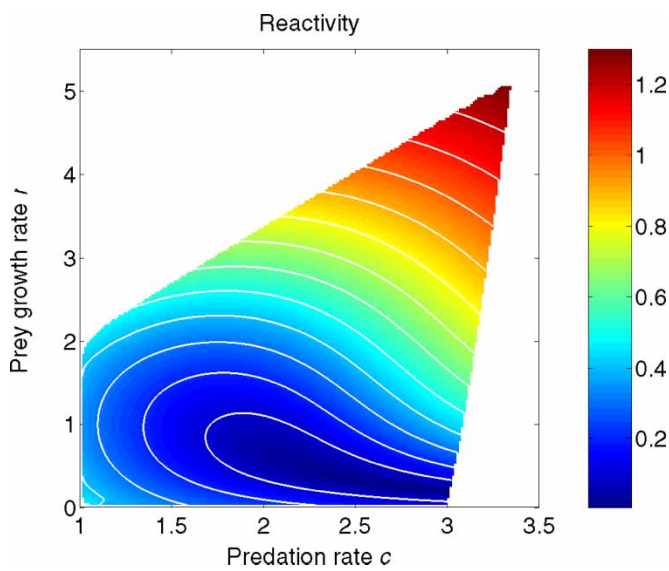

Figure 4. Reactivity for the Beddington-Free-Lawton model as a function of the predation rate c and the prey growth rate r. Reactivity is plotted only within the stability region.

3. Nonlinear matrix population models

Nonlinear matrix population models are a useful way to describe density-dependent dynamics of an age- or stage-structured population [25,26]. A nonlinear matrix population model can be written

$$\mathbf{n}(t+1) = \mathbf{A}_{\mathbf{n}(t)}\,\mathbf{n}(t) \tag{17}$$

where $\mathbf{n}$ is an s-vector whose entries give the abundance of each of s stages in the life cycle and $\mathbf{A}_{\mathbf{n}}$ is an $s \times s$ non-negative matrix some or all of whose entries are functions of $\mathbf{n}$. If $\hat{\mathbf{n}}$ is an equilibrium of equation (17), then the dynamics of small perturbations $\mathbf{x}$ from $\hat{\mathbf{n}}$ are given by

$$\mathbf{x}(t+1) = \mathbf{B}\mathbf{x}(t) \tag{18}$$

where the Jacobian matrix $\mathbf{B}$ can be computed as

$$\mathbf{B} = \mathbf{A}_{\hat{\mathbf{n}}} + \left(\frac{\partial \mathbf{A}}{\partial n_1}\hat{\mathbf{n}} \;\; \frac{\partial \mathbf{A}}{\partial n_2}\hat{\mathbf{n}} \;\; \cdots \;\; \frac{\partial \mathbf{A}}{\partial n_s}\hat{\mathbf{n}} \right) \tag{19}$$

where all partial derivatives are evaluated at $\hat{\mathbf{n}}$ [26,27]. The stability of $\hat{\mathbf{n}}$ is determined by the largest eigenvalue of $\mathbf{B}$; its reactivity is determined by the largest singular value of $\mathbf{B}$.

In this section, we will examine the reactivity of several nonlinear matrix population models.

Example 3 Tribolium *population dynamics.* The most thoroughly analyzed nonlinear matrix population model, both mathematically and experimentally, is the model for flour beetles of the genus *Tribolium*, developed by Cushing and his collaborators ([4] and references therein). These beetles are small insects living in flour and stored grain products. Their life cycle includes egg, larva, pupa and adult stages. Adults and larvae cannibalize eggs, and adults also cannibalize larvae. This cannibalistic interaction provides the nonlinearity that regulates

the populations and determines a rich array of bifurcations, attractors and both asymptotic and transient dynamics. The model studied by Cushing and his colleagues is obtained by letting n_1, n_2 and n_3 be the numbers of larvae, pupae and adults, respectively. The population projection matrix is

$$\mathbf{A_n} = \begin{pmatrix} 0 & 0 & b\exp(-c_{\mathrm{el}}n_1 - c_{\mathrm{ea}}n_3) \\ 1-\mu_l & 0 & 0 \\ 0 & \exp(-c_{\mathrm{pa}}n_3) & 1-\mu_{\mathrm{a}} \end{pmatrix} \tag{20}$$

where b is the fecundity, c_{ea}, c_{el} and c_{pa} are coefficients describing cannibalism, and μ_{l} and μ_{a} are larval and adult mortality rates (see [4] for a detailed description of the model and its underlying biology).

The parameters of the model depend on the environment in which the beetles are living. One experiment (Table 2.1 of [4]) led to parameter estimates of $c_{\mathrm{ea}} = 1.097 \times 10^{-2}$, $c_{\mathrm{el}} = 9.264 \times 10^{-3}$, $c_{\mathrm{pa}} = 1.779 \times 10^{-2}$, $\mu_{\mathrm{a}} = 0.1108$ and $\mu_{\mathrm{l}} = 0.5129$. The model has a stable positive equilibrium for fecundities from $b = 0.23$ to $b \approx 8.74$. Figure 5 shows the resilience and the reactivity of this equilibrium. The reactivity is positive for low and for high values of b, and negative for intermediate values. Over this range of parameter values, the reactivity is never very large ($\nu = 0.1$ implies $\|\mathbf{x}(1)\|/\|\mathbf{x}(0)\| = 1.105$).

Example 4 *Dungeness crab populations: effects of census timing.* The Dungeness crab (*Cancer magister*) is distributed along the west coast of North America, and is the subject of an important commercial harvest. Female crabs lay millions of eggs at one time and the resulting larvae spend some months in the plankton. Adult crabs may live for as long as 10 years.

Higgins *et al.* [28] presented a nonlinear discrete-time model for Dungeness crab, keyed to the point in the year (December) when a pulse of eggs is produced. According to their model, density-dependence operates in egg production, survival of eggs to their first birthday, and survival of adults from age 1 to 2.

Such a model can be written in two ways: as a pre-breeding or post-breeding birth pulse model [26, Section 2.4]. The choice affects the nature of the individuals in each age class and

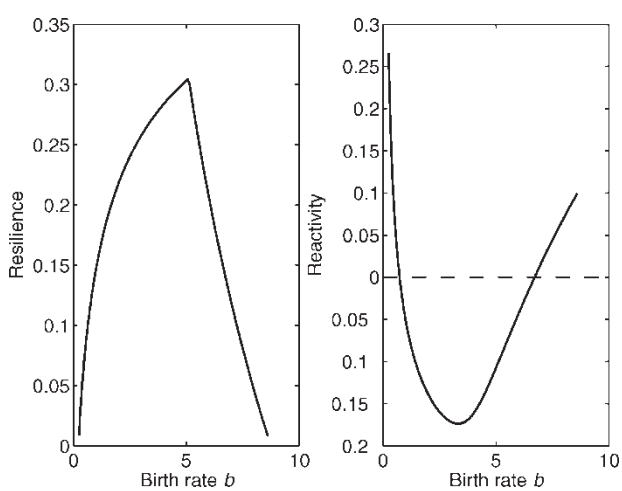

Figure 5. The resilience and reactivity of the non-trivial equilibrium of the *Tribolium* model, as a function of the fecundity parameter b. The equilibrium becomes unstable via a flip bifurcation at $b \approx 8.74$.

in which transitions the density-dependent effects occur. Consider a species that reproduces at one fixed point in the year. A pre-breeding census model, projects the population from just before one birth pulse to just before the next. In such a model, individuals in each age class are, when censused, just about to celebrate their birthday and move to the next age class. A post-breeding census model projects the population from just after one birth pulse to just after the next. Individuals in each age class, when censused, have just celebrated their birthday and moved into the age class. The first age class consists of newly-laid eggs.

Because of the high fecundity of the Dungeness crab, the number of eggs in the post-breeding census model is enormous, but the numbers of individuals of ages $1, 2, \ldots$ is the same in the two models. However, individuals appear in different age classes. The 1-year old individuals that appear in the first age class in the pre-breeding model appear in the second age class in the post-breeding model.

Using the equations from Higgins *et al.* [28], the projection matrix for the pre-breeding model is:

$$\mathbf{A}_{\text{pre}} = \left(\begin{array}{cccc|cccc} 0 & 0 & f_3(\mathbf{n}) & f_4(\mathbf{n}) & 0 & 0 & 0 & 0 \\ p_1(\mathbf{n}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{\text{a}} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{\text{a}} & 0 & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & f_3(\mathbf{n}) & f_4(\mathbf{n}) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & q_1(\mathbf{n}) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{\text{a}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_a & s_h(1-h) \end{array}\right) \tag{21}$$

where the first four components of $\mathbf{n}$ are females of age-classes $1, \ldots, 4$ and the last four components are the corresponding male age classes. Here, s_{l} is larval survival, s_{a} is adult survival, s_{h} is survival of the harvested stage, c, c_0 and c_1 are competition coefficients, and the density-dependent vital rates are

$$f_3(\mathbf{n}) = f_4(\mathbf{n}) = 0.5bs_{\text{l}}\sqrt{s_{\text{a}}}\exp\left(-c(n_3+n_4) - c_0\sqrt{s_{\text{a}}}n_1\right) \tag{22}$$

$$p_1(\mathbf{n}) = s_{\text{a}}\exp\left(-c_1 n_2\right) \tag{23}$$

$$q_1(\mathbf{n}) = s_{\text{a}}\exp\left(-c_1 n_6\right) \tag{24}$$

The matrix for the post-breeding model is

$$\mathbf{A}_{\text{pre}} = \left(\begin{array}{c|ccc|cccc} 0 & 0 & f_3(\mathbf{n}) & f_4(\mathbf{n}) & 0 & 0 & 0 & 0 \\ \hline p_1(\mathbf{n}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & p_2(\mathbf{n}) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{\text{a}} & 0 & 0 & 0 & 0 & 0 \\ \hline q_1(\mathbf{n}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & q_2(\mathbf{n}) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{\text{a}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_{\text{a}} & s_h(1-h) \end{array}\right) \tag{25}$$

where the first component of $\mathbf{n}$ is eggs, the next three components are females and the last four components are males. The density-dependent functions for fertility and survival are

$$f_3(\mathbf{n}) = f_4(\mathbf{n}) = bs_{\mathrm{a}} \exp\left(-cs_{\mathrm{a}}(n_3 + n_4)\right) \tag{26}$$

$$p_1(\mathbf{n}) = 0.5s_{\mathrm{l}}\sqrt{s_{\mathrm{a}}} \exp\left(-c_0\sqrt{s_{\mathrm{a}}}n_2\right) \tag{27}$$

$$p_2(\mathbf{n}) = s_{\mathrm{a}} \exp\left(-c_1 n_3\right) \tag{28}$$

$$q_1(\mathbf{n}) = 0.5s_{\mathrm{l}}\sqrt{s_{\mathrm{a}}} \exp\left(-c_0\sqrt{s_{\mathrm{a}}}n_5\right) \tag{29}$$

$$q_2(\mathbf{n}) = s_{\mathrm{a}} \exp\left(-c_1 n_6\right) \tag{30}$$

Except for the presence of eggs in the post-breeding model and their absence in the pre-breeding model, the equilibria of these two formulations are identical, as are the eigenvalues of their Jacobian matrices. The reactivities of the post-breeding model, however, are much larger than those of the pre-breeding model (Table 1). The initial amplification of a perturbation ($\|\mathbf{x}(1)\|/\|\mathbf{x}(0)\|$) differs by a factor of about 10^5 between the two models. The reactivities of the post-breeding model are the largest we have ever encountered. This example emphasizes a point not often appreciated: while the asymptotic properties of an equilibrium may be independent of the choice of a point in the annual breeding cycle at which a census is carried out, the transient dynamics are not.

The preceding examples make it clear that the equilibria of density-dependent stage-structured models are often reactive. Each of these cases, though, refers to a specific species and life cycle. In the next example, we turn to a simple model in which we can explore the effect of life history type and the type of density-dependence.

Example 5 *A simple density-dependent life cycle.* Plant and animal life histories exhibit enormous diversity. Some species live for hours, some for centuries. Some lavish parental care on a single offspring; others abandon millions of larvae to take their chances on life in the plankton. Here, we examine a model [29] that includes only the most basic life cycle division: that between reproducing adults and non-reproducing juveniles. The demography is parameterized by the survival of juveniles and adults (s_1 and s_2), the maturation or growth rate of juveniles (γ), and the fertility of adults (ϕ). Each of these parameters may depend on population density. The resulting density-dependent projection matrix (assuming a pre-breeding model) is

$$\mathbf{A_n} = \begin{pmatrix} s_1(1-\gamma) & \phi \\ s_1\gamma & s_2 \end{pmatrix}. \tag{31}$$

TABLE 1. The reactivity and resilience for the pre-breeding and post-breeding census models of the Dungeness crab, based on parameter values for eight locations in California [28].

Pre-breeding		*Post-breeding*	
Reactivity ν	*Resilience*	*Reactivity* ν	*Resilience*
−0.0479	1.9443	6.4172	1.9443
−0.2230	0.7407	10.6438	0.7407
0.0221	0.4004	12.5088	0.4004
0.7851	0.1857	13.7936	0.1857
0.1487	0.7944	10.5765	0.7944
0.4332	0.2595	13.7847	0.2595
0.3631	0.0526	12.8085	0.0526
0.1868	0.4354	12.1708	0.4354

Neubert and Caswell [29] applied this model to four important classes of idealized life histories, depending on reproductive strategy and developmental rate. Reproduction may be semelparous (reproducing only once) or iteroparous (reproducing repeatedly). Semelparity is obtained as $s_2 \to 0$, iteroparity when $s_2 > 0$. Development may be precocious (rapid development to maturity) or delayed. Precocious development is obtained as $\gamma \to 1$, delayed development when $\gamma < 1$. The combination of these two dichotomies gives four classes of life histories: precocious semelparity (e.g. many annual plants and insects), precocious iteroparity (e.g. small mammals and birds), delayed semelparity (e.g. periodical cicadas) and delayed iteroparity (e.g. humans, whales and other large mammals).

Because the matrix (31) contains four parameters, there are four possible locations for the operation of density-dependence within the life cycle. Here we examine three of these: density-dependent reproduction ($\phi \to \phi e^{-bN}$), density-dependent growth ($\gamma \to \gamma e^{-bN}$), and density-dependent juvenile survival ($s_1 \to s_1 e^{-bN}$), where $N = n_1 + n_2$. We eliminate the parameter b by implicitly scaling $\mathbf{n}$ relative to the strength of density-dependence. Neubert and Caswell [29] obtained the equilibria and linear approximations and categorized the bifurcation patterns for each of the models. Here, we examine the reactivity of each of the 12 models (four life history types and three modes of density-dependence).

The stability regions in $s_1 - \phi$ space for the non-trivial equilibrium $\hat{\mathbf{n}}$ are shown in figure 6. At the bottom boundary of each region, $\hat{\mathbf{n}}$ collides with 0 and exchanges stability in a transcritical bifurcation. At the upper boundary, $\hat{\mathbf{n}}$ loses stability via a bifurcation that is characteristic of each type of density-dependence (a flip bifurcation for density-dependent reproduction, a Hopf bifurcation for density-dependent growth or juvenile survival).

Within the stability region, reactivity is common. When reproductive output is density-dependent, equilibria are reactive in 50% or more of the parameter space, and are most reactive when s_1 and ϕ are both low (the left-hand tip of the stability region). In contrast, in the density-dependent growth and density-dependent juvenile survival models, the equilibrium is almost always reactive, sometimes extremely so ($\nu \approx 15$, implying that initial perturbations may be magnified by as much as 3×10^6 times). Reactivity is nearly independent of juvenile survival, but increases strongly with reproductive output.

4. Perturbation analysis

To explore how reactivity responds to changes in parameters, we want to calculate $\mathrm{d}\nu/\mathrm{d}\theta$, where θ is a specified parameter in the model. To do so we use the notation for matrix calculus of [30]. If $\mathbf{y}(\theta)$ is an $s \times 1$ vector-valued function of a scalar argument θ, then $\partial \mathbf{y}/\partial \theta$ is the $s \times 1$ vector whose ith entry is $\partial y_i/\partial \theta$. If $\mathbf{f}(\mathbf{x})$ is an $s \times 1$ vector-valued function of the $r \times 1$ vector $\mathbf{x}$, then $\partial \mathbf{f}/\partial \mathbf{x}$ is the $s \times r$ matrix whose (i,j) entry is $\partial f_i/\partial x_j$. Derivatives of matrix-valued functions and derivatives with respect to matrix-valued arguments are calculated by applying these rules to the vec of the matrices, where $\mathrm{vec}(\mathbf{X})$ stacks the columns of $\mathbf{X}$ one above the other, with the second beneath the first, and so on.

We consider a discrete-time model of the form

$$\mathbf{x}(t+1) = \mathbf{f}(\mathbf{x}(t), \theta). \tag{32}$$

The Jacobian matrix at the equilibrium $\hat{\mathbf{x}}$ is

$$\mathbf{B}(\hat{\mathbf{x}}, \theta) = \left.\frac{\partial \mathbf{f}(\mathbf{x}, \theta)}{\partial \mathbf{x}}\right|_{\hat{\mathbf{x}}}. \tag{33}$$

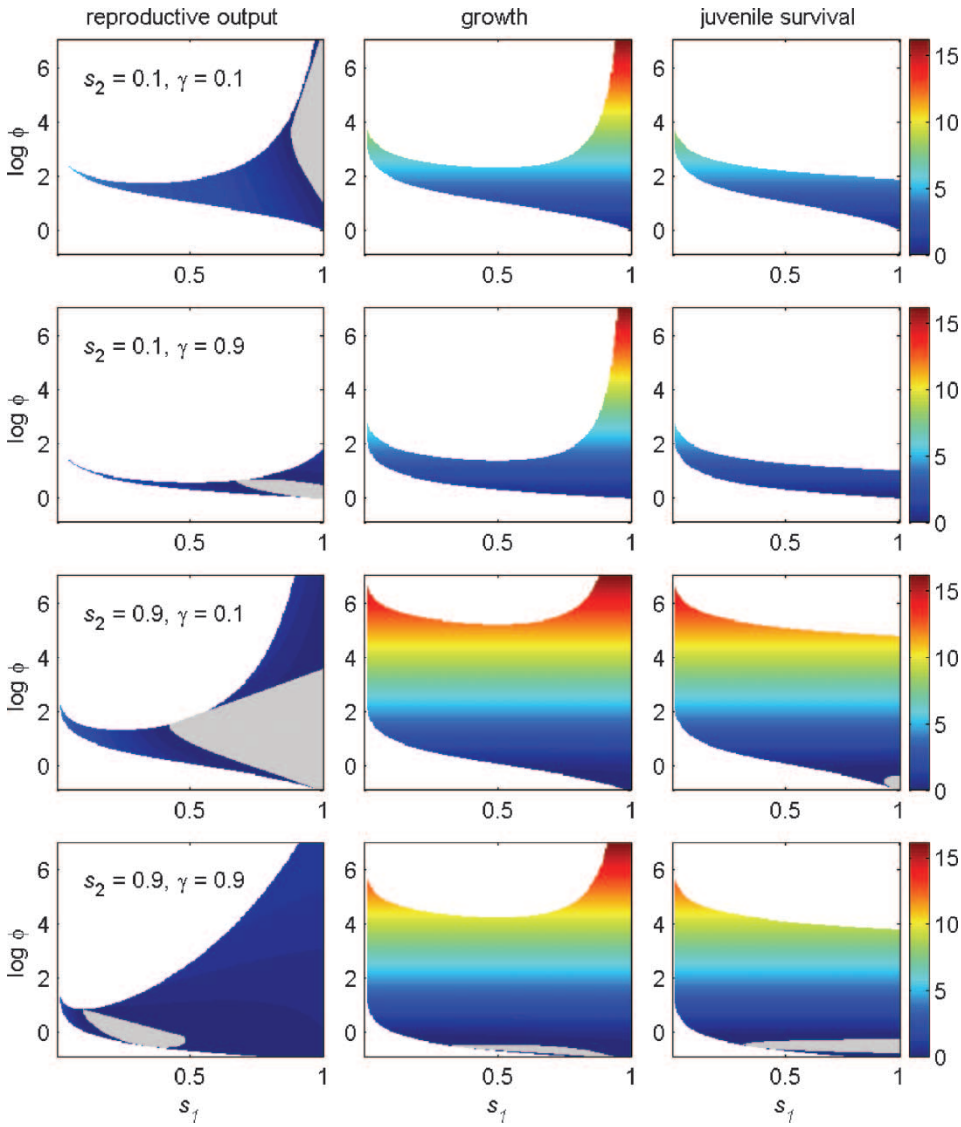

Figure 6. Reactivity for the two-stage density-dependent matrix population model, within the stability region, as a function of juvenile survival s_1 and the $\log_{10}$ of adult fecundity ϕ. Grey areas are stable but not reactive. Results are shown for three types of density-dependence (density-dependent fertility, density-dependent growth and density-dependent juvenile survival) and four life histories. The life histories are defined by adult survival s_2 and juvenile growth rate γ: delayed semelparity ($\gamma = 0.1$, $s_2 = 0.1$), precocious semelparity ($\gamma = 0.9$, $s_2 = 0.9$), delayed iteroparity ($\gamma = 0.1$, $s_2 = 0.9$), and precocious iteroparity ($\gamma = 0.9$, $s_2 = 0.9$).

The reactivity $\nu = \log \sigma(\mathbf{B})$, where σ is the largest singular value. The sensitivity of σ to changes in the elements of $\mathbf{B}$ is

$$\frac{\partial \sigma}{\partial b_{ij}} = u_i v_j, \tag{34}$$

where $\mathbf{u}$ and $\mathbf{v}$ are the left and right singular vectors of $\mathbf{B}$ corresponding to σ [31].

TABLE 2. The sensitivity of ν and the elasticity of σ to changes in each of the parameters in the *Tribolium* model of Example 3.

Parameter	*Sensitivity*	*Elasticity*
b	0.0505	0.5903
c_{ea}	−37.5876	−0.4123
c_{el}	43.9692	0.4073
c_{pa}	0.2814	0.0050
μ_{a}	0.0279	0.0031
μ_{l}	−0.4168	−0.2138

We consider a parameter θ that affects the elements of $\mathbf{B}$ both directly and also through changes in $\hat{\mathbf{x}}$. We write

$$\frac{\mathrm{d}\nu}{\mathrm{d}\theta} = \frac{1}{\sigma}\frac{\mathrm{d}\sigma}{\mathrm{d}\theta} \tag{35}$$

$$= \frac{1}{\sigma}\frac{\mathrm{d}\sigma}{\mathrm{d}\mathbf{B}}\frac{\mathrm{d}\mathbf{B}}{\mathrm{d}\theta} \tag{36}$$

$$= \frac{1}{\sigma}\frac{\mathrm{d}\sigma}{\mathrm{d}\mathbf{B}}\left(\frac{\partial\mathbf{B}}{\partial\theta} + \frac{\partial\mathbf{B}}{\partial\hat{\mathbf{x}}}\frac{\partial\hat{\mathbf{x}}}{\partial\theta}\right). \tag{37}$$

Note that the rules for matrix differentiation guarantee conformability of these matrices. The sensitivity of $\hat{\mathbf{x}}$ is given by implicit differentiation as

$$\frac{\partial\hat{\mathbf{x}}}{\partial\theta} = (\mathbf{I} - \mathbf{B})^{-1}\frac{\partial\mathbf{f}}{\partial\theta}, \tag{38}$$

where $\mathbf{I} - \mathbf{B}$ is nonsingular if the spectral radius of $\mathbf{B}$ is strictly less than 1. Thus, finally,

$$\frac{\mathrm{d}\nu}{\mathrm{d}\theta} = \frac{1}{\sigma}\frac{\mathrm{d}\sigma}{\mathrm{d}\mathbf{B}}\left(\frac{\partial\mathbf{B}}{\partial\theta} + \frac{\partial\mathbf{B}}{\partial\mathbf{x}}(\mathbf{I} - \mathbf{B})^{-1}\frac{\partial\mathbf{f}}{\partial\theta}\right). \tag{39}$$

Example 6 *Sensitivity analysis of the* Tribolium *model.* The *Tribolium* model (20) contains six parameters. Its reactivity depends on the value of the fecundity b (figure 5). Arbitrarily choosing $b = 8$ gives a reactivity of $\nu = 0.07$. Applying equation (39) gives the sensitivity results shown in Table 2 and figure 7.

Reactivity is most sensitive to changes in the rate of cannibalism of eggs, but cannibalism of eggs by adults and cannibalism of eggs by larvae have opposite effects on ν. All the other sensitivities are much smaller in magnitude.

The parameters of the *Tribolium* model range over several orders of magnitude (Example 3). In such cases, it may be useful to evaluate the effect of a proportional change in the parameter; this is calculated as the elasticity of σ to the parameter:

$$\frac{\theta}{\sigma}\frac{\partial\sigma}{\partial\theta}. \tag{40}$$

The elasticities are shown in figure 7. A proportional increase in the fecundity b has a large positive effect on reactivity, the proportional responses to c_{ea} and c_{el} are similar to those shown in the sensitivity results, and increases in μ_{l} reduce reactivity.

To us, none of these effects is intuitive, but their interpretation will be easier when more examples are available.

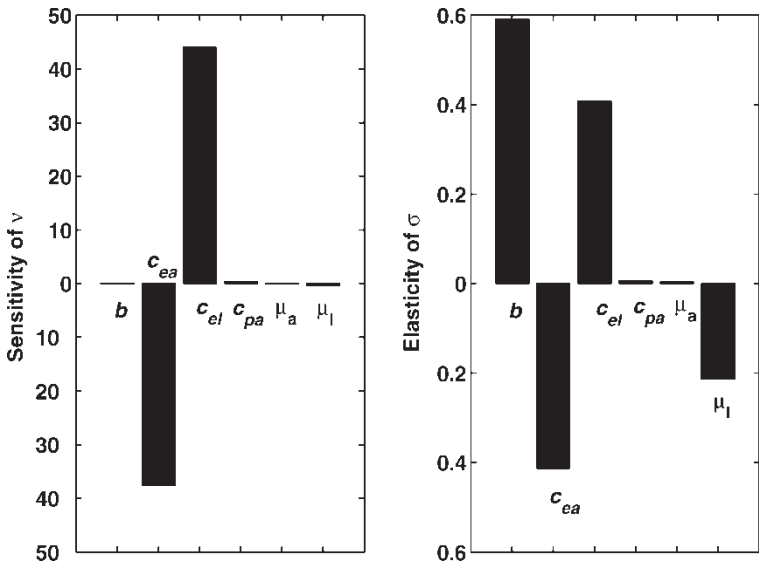

Figure 7. The sensitivity of reactivity ν, and the elasticity of the largest singular value σ, to changes in each of the parameters of the *Tribolium* model.

5. Discussion

1. Reactivity is a common property of discrete-time ecological systems. Thus, it should come as no surprise if stable ecological systems exhibit transient amplification of perturbations.
2. However, reactivity is not universal. This implies that transient amplification is a truly interesting property of a nonlinear model, along with the nature of its invariant sets (equilibria, cycles, invariant loops, strange attractors) and its bifurcation structure. Perturbation analysis shows that reactivity responds to parameter changes in ways that are not (yet, at least) intuitively obvious.
3. As in continuous-time models [3], reactivity is related to the normality of **B**. The largest singular value of a normal matrix is equal to the magnitude of its largest eigenvalue. If $\hat{\mathbf{x}}$ is stable, then the spectral radius of **B** is less than 1, so if **B** is normal, the equilibrium cannot be both stable and reactive.
4. In predator–prey and food-web models, the presence of a predator with a linear closure term (i.e. with a per-capita growth rate independent of its own density) is sufficient to guarantee reactivity. Linear closure terms are common in ecological models; this may or may not imply that they are common in ecological systems.
5. Many ecologists, including the authors of this paper, must struggle to avoid assuming that reactivity increases dramatically as an equilibrium becomes unstable. That is, that there should be a consistent negative relation between reactivity and resilience. But this is not always so. Although reactivity and resilience do behave this way as a function of the birth rate in the *Tribolium* model of Example 3 (figure 5), in both predator–prey models and the two-stage density-dependent matrix model, changes in reactivity near the boundaries of stability regions depend on which parameter is varied, and do not mirror the changes in resilience (cf. figures 1 and 2).

6. The case of the Dungeness crab (Example 4) shows that reactivity can change dramatically in response to a change in model formulation that leaves the equilibrium and stability properties of the model unchanged. It will be important to learn how to interpret transient results in the context of the model formulation that produces them (and the corresponding assumptions about how and when the system is observed).
7. Reactivity is only one piece of the puzzle of transient dynamics. Cushing *et al.* [4] have emphasized the importance of the diverse array of invariant sets—both stable and unstable—that may inhabit the state space of a nonlinear system. Trajectories resulting from perturbations of attracting sets may be strongly influenced by unstable sets in their vicinity. As Cushing *et al.* [4, p. 25] state:

"Thus, in time series data under the influence of nonlinear dynamics and stochasticity, one should expect to see a complicated dance of attractors, transients and unstable entities. It is more fruitful, in attempting to explain patterns observed in data, to study the relative influences of these various components, rather than try to explain the data in terms of a specific type of deterministic attractor."

It seems possible that the transient amplification of perturbations, which carry trajectories temporarily away from equilibria, may increase the chance of passing close enough to an unstable set for its influence to be apparent in the resulting dynamics. At least, such connections warrant further research.

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