

Parameter Sensitivity of Transient Community Dynamics

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ABSTRACT: Transient dynamics have always intrigued ecologists, but current rapid environmental change (inducing transients even in previously undisturbed systems) has highlighted their importance more than ever. Here, I introduce a method for analyzing the sensitivity of transient ecological dynamics to parameter perturbations. The question the method answers is: how would the community dynamics have unfolded for some time horizon had the parameters been slightly different? I apply the method to three empirically parameterized models: competition between native forbs and exotic grasses in California, a host-parasitoid system, and an experimental chemostat predator-prey model. These applications showcase the ecological insights one can gain from models using transient sensitivity analysis. First, one can find parameters and their combinations whose perturbations disproportionately affect a system. Second, one can identify particular windows of time during which the predicted deviation from the unperturbed trajectories is especially large and utilize this information for management purposes. Third, there is an inverse relationship between transient and long-term sensitivities whenever the interacting populations are ecologically similar; paradoxically, the smaller the immediate response of the system, the more extreme its long-term response will be.

Keywords: community ecology, perturbations, sensitivity analysis, transient dynamics.

Introduction

The purpose of sensitivity analysis is to answer the question how a quantity of interest would change if some parameters were slightly perturbed. In population ecology, the most common form of sensitivity analysis looks at the response of the long-term population growth rate of a single species, calculated as the dominant eigenvalue λ of some population projection matrix, to changing one or more of the underlying life history parameters (Caswell 2001, chap. 9). Even though this type of sensitivity analysis ignores within-species density dependence as well as feedbacks between

different species, it has nevertheless led to important insights into the theory of senescence (Hamilton 1966; Gleeson 1984; Caswell 2011), life history trade-offs (Templeton 1980; Caswell 1982, 1984), classification of plant strategies (Silvertown et al. 1992; Franco and Silvertown 1996), and the assessment of extinction risk and suggestion of viable conservation measures (Crouse et al. 1987; Silvertown et al. 1993; Forsman et al. 1996; Noon and McKelvey 1996; Seamans et al. 1999; Fujiwara and Caswell 2001; Hunter et al. 2010).

The ecological relevance of sensitivity analysis can be greatly expanded by generalizing it to handle density dependence (Takada and Nakajima 1992, 1998; Grant and Benton 2000, 2003; Caswell et al. 2004; Caswell 2008) and communities of interacting populations (Levins 1974; Bender et al. 1984; Verdy and Caswell 2008). In these cases it makes less sense to look at the response of the long-term population growth rates, as that will simply be zero in the long run (but see Caswell et al. 2004). Instead, the quantity of interest is the eventual stationary population or community structure after perturbing environmental or life history parameters. Community-wide sensitivity analysis has been used for understanding the response of species-rich ecological networks, such as food webs, to press perturbations (Yodzis 1988, 2000; Dambacher et al. 2002; Novak et al. 2011; Aufderheide et al. 2013; Säterberg et al. 2013) and for grounding the concept of the ecological niche under simpler (Mészéna et al. 2006; Szilágyi and Mészéna 2009b) and more realistic (Szilágyi and Mészéna 2009a, 2010; Barabás et al. 2012; Barabás and Ostling 2013) assumptions. These advances have allowed for a wide range of ecological applications (Barabás et al. 2014).

The exclusive focus of these approaches on long-term stationary system behavior can be seen as a disadvantage. An equally important area of application is the analysis of transient dynamics (Hastings 2001, 2004). Transients have always been recognized as an important component of ecosystem dynamics, although theoreticians have had

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varied opinions on whether transients ought to be seen as a nuisance to be dealt with so one can better focus on more important questions or whether the study of transients possesses theoretical depth that is worthy of investigation in its own right. Recently, there has been a shift toward the latter attitude (Hastings et al. 2018; Tao et al. 2021), with a suite of techniques developed for dealing with transients (Morozov et al. 2016, 2020; Hastings et al. 2021). One likely impetus for this change has been the recently growing realization that long transients can superficially appear similar to stable dynamics, even though their correct identification as transients is critical for accurate forecasting and management (Abbott and Dakos 2021; Boettiger 2021; Francis et al. 2021).

While not entirely neglected, sensitivity methods for transient dynamics have been somewhat lagging behind. At the level of populations, it has long been recognized that the rate of approach to the stable stage distribution depends on the ratio of the second largest and largest eigenvalues (Tuljapurkar 1990). This ratio therefore provides a measure of how long the transient phase is expected to be; furthermore, its sensitivity can be easily calculated via standard eigenvalue perturbation theory (Caswell 2001, chap. 9). A more direct method to studying the sensitivity of population-level transients was introduced by Caswell (2007), who developed a formula for projecting the effects of a parameter perturbation forward in time without relying on the system being close to stationarity. At the community level, Neubert and Caswell (1997) introduced a way of characterizing the reactivity of ecological communities (maximum initial amplification rate of perturbations in systems that are stable yet initially may move away from the equilibrium point; Trefethen and Embree 2005). However, their approach considers dynamical perturbations of the population densities only, not those of the underlying model parameters. In the same spirit, Medeiros et al. (2023) have recently given a method for ranking species in communities on the basis of their sensitivities against perturbations of the population densities within a fixed window of time.

In accounting for parameter perturbations at the community level, important steps have been made by Gardner et al. (1981) and Richard et al. (2015). Their way of computing sensitivities reduces, in continuous time, an arbitrarily complicated system of ordinary differential equations to a set of strictly linear ones around some known solution. To obtain the perturbed transient behavior, one only needs to integrate the simpler linear system instead of the original equations. While their method is not tied to the analysis of ecological communities per se, it applies naturally in that context as well. More recently, Cenci and Saavedra (2019) have proposed using the trace of a community's Jacobian matrix for estimating whether a parameter perturbation

would have a large or small overall effect on its dynamical trajectory. Since the Jacobian takes on different values at different points in phase space, the same system may exhibit very different responses to parameter changes depending on the perturbation's timing. Even more recently, Ng et al. (2023) proposed a method for performing time-dependent sensitivity analysis based on optimal control theory.

Building on this body of work, here I introduce a technique for calculating community-level transient sensitivities in both discrete and continuous time. The continuous-time version is largely borrowed from Gardner et al. (1981) and Richard et al. (2015). Extending this to discrete time is a relatively straightforward exercise, although it has not been done before. The resulting method is applied to both empirically parameterized and theoretical models. The former include a model of competition in California grasslands between native forbs and exotic grasses, a host-parasitoid system, and an experimental chemostat predator-prey model. The applications demonstrate how the method can identify critical parameters (whose perturbations have a disproportionate effect on the system) as well as critical windows of time (defined as a time period during which the system is especially sensitive to perturbing some parameter). The theoretical models establish a connection between transient and long-term sensitivities when the dynamics start from near an equilibrium state: whenever interacting populations are ecologically similar, short-term and long-term sensitivities turn out to be inversely related. That is, a rapid short-term system response is accompanied by a tame long-term response, and vice versa. Along the way I also present some of the limitations of the approach. One such limitation is in the applicability of the framework to chaotic dynamical regimes, where successful prediction is possible only for short time horizons.

The Method of Community-Level Transient Sensitivity Analysis

Consider an ecological system with given dynamics, parameters, and initial conditions. Parameters are system characteristics that govern ecosystem dynamics but are in turn unaffected by it; they may include environmental factors like temperature, functional traits like bill depth in birds, or derived quantities (e.g., death rates) possibly containing the effects of both. We observe this system evolve for a given duration of time. The main question of transient sensitivity analysis is: how would the system's dynamics have unfolded for the same duration if one of the parameters had been slightly altered?

More concretely, sensitivity analysis starts out from a known solution to the ecological dynamics, generated by some original unperturbed parameter settings. Let this solution be $\mathbf{x}(t)$, representing the vector of state variables

(such as population densities) at time t . We then assume that some parameter ε is press perturbed (Bender et al. 1984) at the initial moment by a small amount $\Delta\varepsilon$, so that ε is replaced with $\varepsilon + \Delta\varepsilon$. The method approximates the perturbed solution $\mathbf{x}'(t)$ via a first-order Taylor expansion in $\Delta\varepsilon$:

$$\mathbf{x}'(t) \approx \mathbf{x}(t) + \boldsymbol{\sigma}(t)\Delta\varepsilon, \quad (1)$$

where $\boldsymbol{\sigma}(t)$ is the vector of sensitivities of each state variable at time t . The parameter ε is assumed to be time independent. If time-dependent external influences are important in a system—for instance, if temperature varies as $T(t) = a \cos(\omega t)$ with amplitude a and frequency ω —then ε could stand for either a or ω , instead of the time-varying function $T(t)$ itself. (For sensitivity methods that perturb entire functions at a time, see Cordoleani et al. 2011; Adamson and Morozov 2013; Aldebert et al. 2016.) The task of transient sensitivity analysis is to obtain $\boldsymbol{\sigma}(t)$ in equation (1). This section does this, first in discrete and then in continuous time.

A general S -species community model in discrete time can be written as

$$n_i(t+1) = n_i(t)R_i(n_1(t), \dots, n_S(t), \varepsilon, t), \quad (i = 1, \dots, S), \quad (2)$$

where $n_i(t)$ is species i 's population density at time t , R_i is its geometric rate of growth, and ε is some model parameter. It is often more convenient to work on the log scale: after introducing $x_i = \log(n_i)$ and $r_i = \log(R_i)$ (the per capita growth rate of species i), the model reads

$$x_i(t+1) = x_i(t) + r_i(x_1(t), \dots, x_S(t), \varepsilon, t). \quad (3)$$

To obtain the one-step sensitivity formula from time t to $t+1$, one can differentiate both sides by the parameter ε :

$$\frac{\partial x_i(t+1)}{\partial \varepsilon} = \frac{\partial x_i(t)}{\partial \varepsilon} + \frac{\partial r_i(t)}{\partial \varepsilon} + \sum_{j=1}^S \frac{\partial r_i(t)}{\partial x_j(t)} \frac{\partial x_j(t)}{\partial \varepsilon} \quad (4)$$

(the chain rule was used in the last term). This can also be interpreted as a recursion equation of its own, for the variable $\partial x_i(t)/\partial \varepsilon$. The meaning of this quantity is the local rate of change of the state variable i in response to a small change in the parameter ε . It is therefore precisely the sensitivity we are interested in. Using the notation of equation (1), one can write $\sigma_i(t) = \partial x_i(t)/\partial \varepsilon$ for the i th entry and $\boldsymbol{\sigma}(t)$ for the entire vector of sensitivities at time t .

When talking about transient sensitivities, we assume that the parameter ε is press perturbed at some given initial moment and then calculate the change this causes in the trajectory of the system. Choosing this initial moment as $t = 0$ without loss of generality, the initial conditions to the above recursion equation read $\partial x_i(0)/\partial \varepsilon = 0$ ($i = 1, \dots, S$), or $\boldsymbol{\sigma}(0) = 0$ for short.

In addition to $\boldsymbol{\sigma}(t)$, it is helpful to introduce the further simplifying notations $\mathbf{a}(t)$ and $\mathbf{z}(t)$, with entries

$$a_{ij}(t) = \frac{\partial r_i(t)}{\partial x_j(t)}, \quad (5a)$$

$$z_i(t) = \frac{\partial r_i(t)}{\partial \varepsilon}. \quad (5b)$$

Both are evaluated at the unperturbed solution $\mathbf{x}(t)$ at time t . Here, $\mathbf{a}(t)$ is an $S \times S$ matrix of derivatives of the growth rates with respect to the log densities, and $\mathbf{z}(t)$ is a vector of length $\mathbf{a}$ containing the growth rates' derivatives with respect to the parameter ε . With this notation, equation (4) is rewritten in the simple form $\boldsymbol{\sigma}(t+1) = \boldsymbol{\sigma}(t) + \mathbf{z}(t) + \mathbf{a}(t)\boldsymbol{\sigma}(t)$; or, after factoring out $\boldsymbol{\sigma}(t)$ from the right-hand side,

$$\boldsymbol{\sigma}(t+1) = \mathbf{z}(t) + [\mathbf{1} + \mathbf{a}(t)]\boldsymbol{\sigma}(t), \quad (6)$$

where $\mathbf{1}$ is the $S \times S$ identity matrix. The term $\mathbf{1} + \mathbf{a}(t)$ above is also the Jacobian matrix of equation (3).

By iterating this equation with the initial condition $\boldsymbol{\sigma}(0) = 0$, one can now obtain the transient sensitivities after any number of time steps. For example, $\boldsymbol{\sigma}(1)$ evaluates to $\mathbf{z}(0)$, $\boldsymbol{\sigma}(2)$ to $\mathbf{z}(1) + [\mathbf{1} + \mathbf{a}(1)]\mathbf{z}(0)$, and so on. More generally, equation (6) has an explicit analytical solution for arbitrary $t > 0$:

$$\boldsymbol{\sigma}(t) = \mathbf{z}(t-1) + \sum_{t'=0}^{t-2} \prod_{\tau=t'-1}^{t'+1} [\mathbf{1} + \mathbf{a}(\tau)]\mathbf{z}(t') \quad (7)$$

(supplement S1; supplements S1–S6 are available online), with the understanding that the summation evaluates to zero whenever its upper limit is negative.

Similar results attain in continuous time. A general continuous-time community model reads

$$\frac{dn_i(t)}{dt} = n_i(t)r_i(n_1(t), \dots, n_S(t), \varepsilon, t). \quad (8)$$

Introducing $x_i = \log(n_i)$, dividing both sides by $n_i(t)$, and using $dn_i(t)/(n_i(t)dt) = d\log(n_i)/dt = dx_i(t)/dt$, the model is transformed into the simpler

$$\frac{dx_i(t)}{dt} = r_i(x_1(t), \dots, x_S(t), \varepsilon, t). \quad (9)$$

Differentiating by ε , exchanging the order of differentiation with respect to ε and t on the left-hand side, and using the chain rule on the right yields the formula

$$\frac{d}{dt} \frac{\partial x_i(t)}{\partial \varepsilon} = \frac{\partial r_i(t)}{\partial \varepsilon} + \sum_{j=1}^S \frac{\partial r_i(t)}{\partial x_j(t)} \frac{\partial x_j(t)}{\partial \varepsilon}. \quad (10)$$

Keeping with the notations of equations (5) and $\sigma(t) = \partial x_i(t)/\partial e$, this can also be written as

$$\frac{d\sigma(t)}{dt} = z(t) + a(t)\sigma(t), \quad (11)$$

where t is now a continuous variable and $a(t)$ is the Jacobian of equation (9). The initial condition is once again $\sigma(0) = 0$, meaning that the perturbation has not yet had any effect at the moment it was turned on. Equation (11) was also derived by Gardner et al. (1981) and Richard et al. (2015), using a similar argument.

Just as in the discrete-time case, equation (11) also has an explicit, closed-form solution (see supplement S1 for the derivation):

$$\sigma(t) = \int_0^t T \text{Exp} \left(\int_{t'}^t a(\tau) d\tau \right) z(t') dt'. \quad (12)$$

Here, $\text{Exp}(\cdot)$ is the matrix exponential function (obtained by substituting the argument, which is a matrix, into the Taylor series of the exponential function), and T is a time-ordering operator that rearranges a product of matrices to decreasing order in time (e.g., Weinberg 1995, p. 143):

$$T a(t_1) a(t_2) = T a(t_2) a(t_1) = \begin{cases} a(t_1) a(t_2) & \text{if } t_2 \leq t_1, \\ a(t_2) a(t_1) & \text{if } t_2 > t_1. \end{cases} \quad (13)$$

Example Applications

In applying the sensitivity method, two approaches are possible. The first builds on the realization that equation (6) is a simpler equation than the original equation (3) (discrete time) and that equation (11) is simpler than equation (9) (continuous time), due to the latter systems being linear. One can therefore straightforwardly iterate (resp. integrate) them to estimate the perturbed dynamical trajectories. Second, the explicit solutions in equations (7) and (12) are useful for revealing the structure of the sensitivities and drawing general insights—however, they are impractical for numerical computations. Below I show applications using both approaches. I start with three specific model examples, using them to lay out how the analysis is done in practice. I then present a more general conclusion relying on the explicit analytical solutions, establishing a connection between long-term fixed point sensitivity analysis and transient sensitivities.

An Annual Plant Competition Model

The first example is a simple model of annual plant competition. It was originally proposed to describe a mechanism for the persistence of rare native forbs faced with

competition from exotic grasses on a California grassland (Levine and Rees 2004; Barabás et al. 2014). The model reads

$$n_i(t+1) = n_i(t) \left[(1 - g_i(t))(1 - d_i) + \frac{\lambda_i(t)g_i(t)}{1 + \alpha_i \mathcal{R}(t)} \right], \quad (14)$$

where i may be F (forb) or G (grass), $n_i(t)$ is the density of species i 's seeds in the seed bank at time t , d_i is their death rate, $\lambda_i(t)$ and $g_i(t)$ are the fecundity and germination rates of species i , α_i are competition coefficients with $\alpha_i = \alpha$ if $i = F$ and 1 if $i = G$, and

$$\mathcal{R}(t) = \frac{g_F(t)}{\alpha} n_F(t) + g_G(t) n_G(t) \quad (15)$$

summarizes the common factor jointly regulating the population growth of both forbs and grass.

In this model, environmental variability is required to generate coexistence via the storage effect (Chesson and Warner 1981; Chesson 1994; Barabás et al. 2018). That way, the otherwise rare forbs benefit from occasional good years while being buffered against bad years because of their superior seed banks (Levine and Rees 2004). For this reason, the environment fluctuates randomly between good and bad years. Each year is independently decided to be one or the other with 50% probability, and both the fraction of germinating seeds $g_i(t)$ and the annual fecundities $\lambda_i(t)$ take on different values depending on the type of year.

In particular, Levine and Rees (2004) gave an empirically motivated parameterization of this model, with $\alpha = 2$, $d_F = 0.1$, $d_G = 0.7$, $\lambda_i = 30$ in good and 5 in bad years for both species, $g_F = 0.7$ in good and 0.1 in bad years, and $g_G = 0.9$ regardless of year quality.

The discrete-time geometric growth rates are given by the bracketed term in equation (14). To write the model in the form of equation (3), we take its logarithm to obtain the per capita rates $R_i(t)$:

$$r_i(t) = \log \left[(1 - g_i(t))(1 - d_i) + \frac{\lambda_i(t)g_i(t)}{1 + \alpha_i \mathcal{R}(t)} \right], \quad (16)$$

with the understanding that $\mathcal{R}(t)$ is expressed via the log densities $x_i(t) = \log(n_i(t))$ as

$$\mathcal{R}(t) = \frac{g_F(t)}{\alpha} e^{x_F(t)} + g_G(t) e^{x_G(t)}. \quad (17)$$

With the parameter values above and for a given sequence of good/bad years, the model can be iterated to obtain the log population densities in each year. Since a time horizon of about 100 years is needed for the dynamics to converge on a stationary attractor (supplement S2), I ran the model for 100 years to focus on the transient phase (fig. 1, top row).

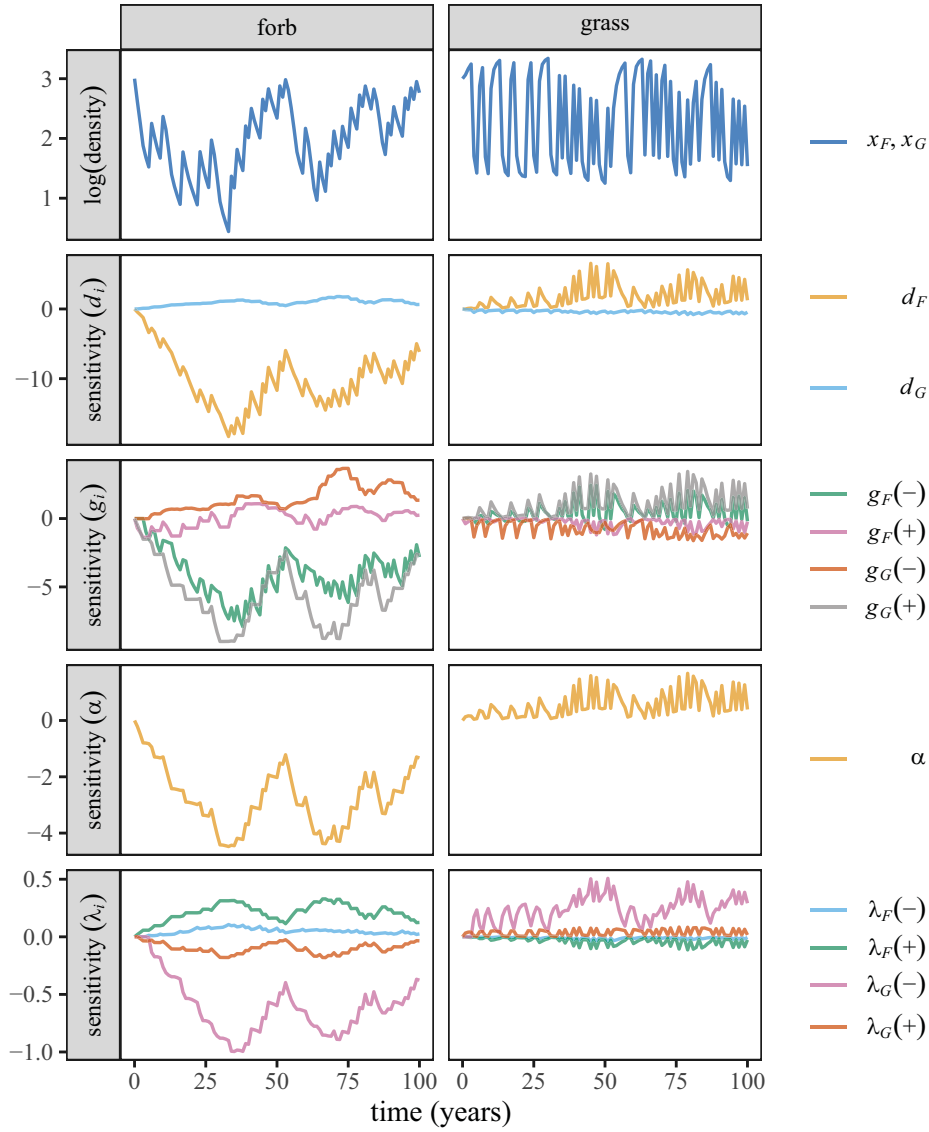


Figure 1: Baseline solution of the annual plant model from initial log densities $x_F(0) = x_G(0) = 3$ for 100 years (*top row*) and the corresponding sensitivities of the forb and grass log densities to perturbing the model parameters (*bottom four rows*). Columns show results for the forb (*left*) and grass (*right*). The (+) and (−) next to the parameters refer to their values in good and bad years, respectively.

To begin the sensitivity analysis, we first calculate $\mathbf{a}(t)$. From its definition in equation (5a) and the expression for $r_i(t)$ in equation (16),

$$a_{ij}(t) = \frac{\partial r_i(t)}{\partial x_j(t)} = \frac{\partial r_i(t)}{\partial \mathcal{R}(t)} \frac{\partial \mathcal{R}(t)}{\partial x_j(t)}$$

$$= - \frac{\lambda_i(t) g_i(t) \alpha_i}{(1-d_i)(1-g_i(t))(1+\alpha_i \mathcal{R}(t))^2 + \lambda_i(t) g_i(t)(1+\alpha_i \mathcal{R}(t))}$$

$$\times \frac{g_j(t) \exp(x_j(t))}{\alpha_j}.$$
(18)

Calculating $\mathbf{z}(t)$ from equation (5b) proceeds by first designating a focal parameter with respect to which the sensitivities are evaluated. For example, let that parameter be $\varepsilon = d_F$. Then,

$$z_i(t) = \frac{\partial r_i(t)}{\partial \varepsilon} = \frac{\partial r_i(t)}{\partial d_F}$$

$$= \frac{g_i(t) - 1}{(1-d_i)(1-g_i(t)) + g_i(t)\lambda_i(t)/(1+\alpha \mathcal{R}(t))} \delta_{iF}$$
(19)

(δ_{if} is 1 for $i = F$ and 0 for $i = G$). The sensitivities $\sigma(t)$ to perturbing the parameter d_F are obtained by first evaluating $\mathbf{a}(t)$ and $\mathbf{z}(t)$ at every moment of time (using the unperturbed $x_i(t)$ for the log densities) and then iterating equation (6).

The derivative $\mathbf{z}(t)$ can be calculated analogously for any other parameter. However, there is no need to do this by hand, as the procedure can be automated. I am providing a Mathematica package¹ (Wolfram Research 2019) as a supplement to this work, which takes an arbitrary model as its input, calculates $\mathbf{a}(t)$ and $\mathbf{z}(t)$ analytically for all model parameters, and automatically performs sensitivity analysis. Using this package, I have calculated the sensitivities to perturbations in all 11 model parameters of the annual plant model (fig. 1).

With these sensitivities in hand, one can apply equation (1) to estimate what trajectories the model would take if the parameters were slightly different. Figure 2 illustrates this, for perturbing the forb death rate $d_F = 0.1$ by $\pm 10\%$, $\pm 50\%$, and $\pm 100\%$. In each case, both the prediction of the sensitivity formula and the exact solution are shown (the exact solution is obtained by reiterating the dynamics from scratch, with the modified parameter values). As expected, the results from the sensitivity formula match the true solution very closely for parameter perturbations that are not too large. Even for substantial changes, however, the qualitative trends are accurately captured—although since the ordinates in figure 2 are on the log scale, the quantitative differences do become large eventually. Given that the method is based on a linear approximation in the perturbed parameters (eq. [1]), this is already more than one could in general aspire for.

When interpreting the raw sensitivities in figure 1, one must take the differing scales of the parameters' perturbations into account. The impact of a parameter perturbation on the dynamical trajectory can be large for two reasons: either because the sensitivities $\sigma(t)$ are large or because the parameter perturbation $\Delta\epsilon$ is large (eq. [1]). The sensitivity of forb density to its death rate in the seed bank d_F hovers around -10 , whereas the sensitivity of forb density to the fecundities λ_i hardly ever reaches 1 in absolute value. However, since d_F is a number between 0 and 1 whereas the λ_i may take on any nonnegative value, the range of perturbations in the latter may in principle be much larger than for d_F . Whether that is in fact the case is a question to be decided on a case-by-case basis, with the aid of empirical information if necessary. (One way of resolving the problem of differing scales is to use elasticities instead of sensitivities—these, however, have their own limitations; see “Discussion.”)

Based on figure 1, it is fair to say that the death rate d_F of the forb in the seed bank, grass fecundity $\lambda_G(-)$ in bad

years, and the competition coefficient α have a disproportionately large effect on forb densities. This is especially true during the critical window of time between years 30 and 39 when forb sensitivities with respect to these three parameters are near their highest, because this also coincides with times of low forb population densities. When managing this system, these three parameters are therefore particularly important to monitor and favorably manipulate if possible: by keeping each of them at reduced values from the outset at $t = 0$, they will lend a disproportionate boost to the forb densities down the road. (Their values should be reduced because the forb sensitivities with respect to these parameters are negative; see fig. 1). The same might be true for the germination rates $g_F(-)$ and $g_G(+)$, although since their sensitivity values are about half of d_F 's while still being bounded between 0 and 1, there is no reason to think they will be as important as d_F without further supporting evidence. By contrast, the analysis reveals that forb sensitivity to changing some other parameters—for example, d_G , $g_F(+)$, and $g_G(-)$ —is low and more or less unrelated to forb densities. Consequently, they are much less important to keep track of.

Some of the sensitivity profiles in figure 1 appear to be strongly correlated. For example, the competition coefficient α and the germination rate $g_G(+)$ of grass in good years follow a very similar pattern. While there is no obvious biological connection between them, it is possible to show mathematically why the correlation exists (supplement S2). Second, the sensitivity profiles of the good-year fecundities $\lambda_F(+)$ and $\lambda_G(+)$ appear mirror symmetric. A closer look reveals that this is mostly an illusion—for example, the largest value of the sensitivity with respect to $\lambda_F(+)$ is 0.33, and the corresponding value for $\lambda_G(+)$ is 0.18. That said, there is a biological connection between the two: since the unperturbed values of $\lambda_i(t)$ are symmetric across the two species (30 in good years and 5 in bad years for both forb and grass), it stands to reason that the forb will be helped at least approximately as much by an increase in its own good-year fecundity as it will be hindered by an increase in its competitor's. Third, not only are the sensitivity curves occasionally correlated with one another, they correlate with the log density profile of the forb as well (e.g., the sensitivity with respect to d_F follows a similar pattern to $x_F(t)$ in fig. 1). As discussed in supplement S2, while higher initial forb densities do increase the propensity for a positive correlation, this is by no means given, and different sequences of good/bad years may or may not lead to similar patterns.

Finally, one potential complicating factor is when two or more parameters jointly depend on some unmodeled environmental factor—a hidden underlying parameter. For example, $\lambda_F(+)$ and $\lambda_G(+)$ might both depend on soil pH, in which case a change in pH will affect both. This may

1. Available at <https://zenodo.org/record/8379960>.

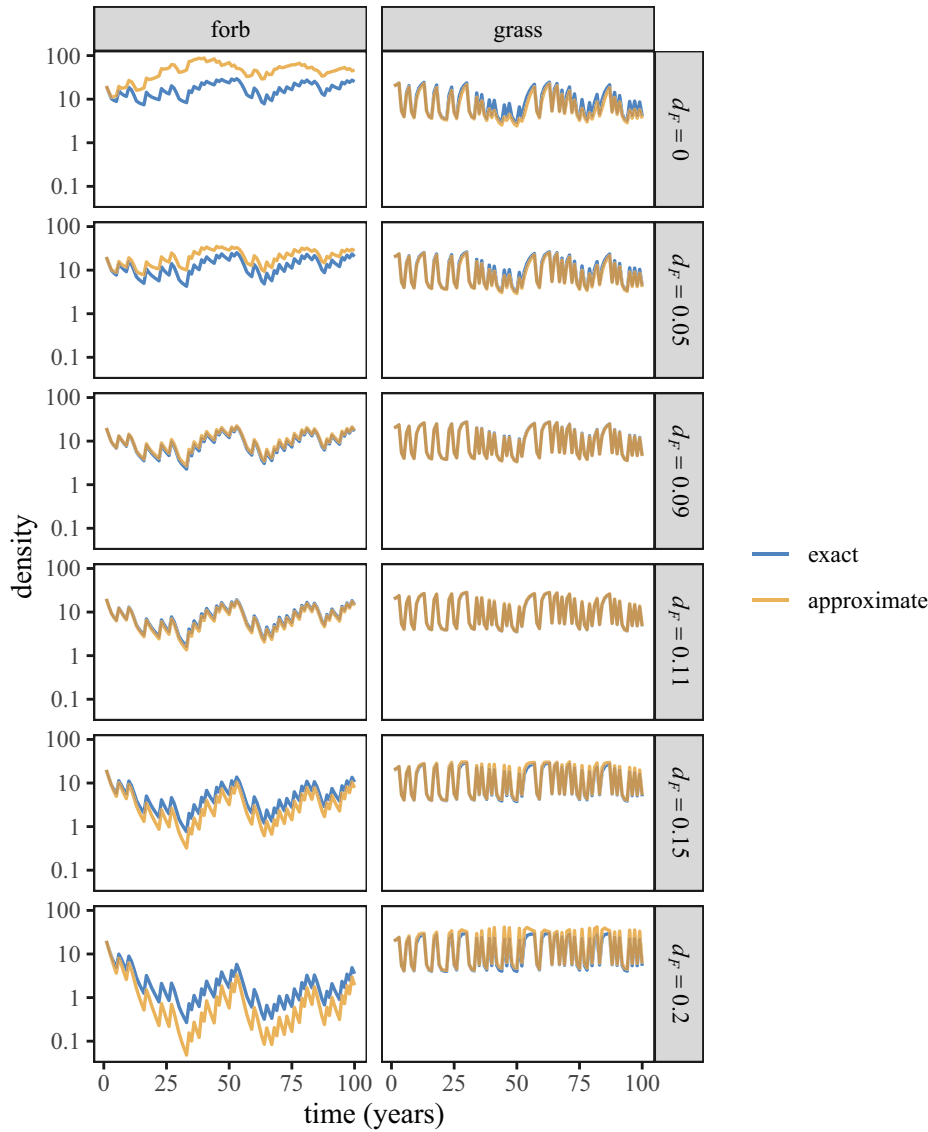


Figure 2: Exact and approximated solutions (colors) of the annual plant model, for both the forb and grass (columns), for various values of the forb death rate d_F (rows). The unperturbed value of the parameter is $d_F = 0.1$; the solution thus generated is seen in the top row of figure 1. The exact curves (blue) are obtained by reiterating the model with the modified parameter, and the approximations (yellow) are from equation (1). In applying this equation, $\Delta\varepsilon$ is equal to the displayed parameter value minus the original $d_F = 0.1$, and the $\sigma(t)$ are those calculated and displayed in figure 1 for d_F . For small perturbations, the approximation matches the exact solution very well. For larger ones, it gradually becomes less accurate, even though it still predicts the correct trends.

get worrisome if soil pH has opposing effects on these fecundities, so an increase in $\lambda_G(+)$ is always accompanied by a decrease in $\lambda_F(+)$. This would cause the two otherwise moderately sized and opposite-signed effects to add up to a single substantial negative effect on the forb. Mathematically it is easy to handle such indirect dependencies: if $\varepsilon(\eta)$ is the dependence of the parameter ε on some other factor η , such as pH, then $\sigma_i(t)$ is simply $(\partial x_i(t)/\partial \varepsilon) \times (\partial \varepsilon/\partial \eta)$ by the chain rule. But their biological ramifications

could be anything but trivial: they can mitigate otherwise serious-looking sensitivities or else exacerbate effects that otherwise would have appeared minor.

A Host-Parasitoid Model

The transient sensitivities calculated in the annual plant model were able to predict the future expected behavior of the system for a long stretch of time. This is due to the

fact that while the environment is erratically fluctuating, the dynamics of the system are otherwise simple. Such long-term predictive power should not be expected if, for example, the dynamics are chaotic. To demonstrate this limitation, I use a model of host-parasitoid interactions that again has been parameterized using field data and has a chaotic attractor (Turchin et al. 2003; Dwyer et al. 2004). Given the host population densities $n_H(t)$ and those of the parasitoid $n_P(t)$, the model reads

$$n_H(t+1) = \lambda n_H(t) \left(1 - \frac{2abn_H(t)}{b^2 + n_H^2(t)} \right) (1 - I), \quad (20)$$

$$n_P(t+1) = \omega n_H(t) I, \quad (21)$$

where λ is the host fecundity, ω is the survival rate of the parasitoid, the bracketed term is the fraction of hosts that did not succumb to predation (by a generalist predator whose density does not respond to that of the host but that nevertheless exerts chronic predation with a type III numerical response), and

$$I = 1 - \exp\left(-\frac{sn_P(t)}{1 + scn_H(t) + sd n_P(t)}\right) \quad (22)$$

is the fraction of hosts attacked by the parasitoid between two adjacent time steps (time is measured in units of host generations). With the parameters $\lambda = 30$, $\omega = 10$, $c = 0.01$, $d = 0.2$, $a = 0.961$, $b = 0.14$, and $s = 0.7$ (Dwyer et al. 2004), the dynamics converge on a chaotic attractor (fig. 3).

Introducing $x_H(t) = \log(n_H(t))$ and $x_P(t) = \log(n_P(t))$, the model can be rewritten by taking logarithms in equations (20) and (21):

$$x_H(t+1) = x_H(t) + \log\left[\lambda \left(1 - \frac{2abe^{x_H(t)}}{b^2 + e^{2x_H(t)}} \right) (1 - I)\right], \quad (23)$$

$$x_P(t+1) = x_P(t) + \log[\omega e^{x_H(t) - x_P(t)} I], \quad (24)$$

where the per capita growth rates are given by the log terms on the right-hand sides. These growth rates can then be used to perform the sensitivity analysis (supplement S3).

Let us focus on the parameter s and its perturbations. Comparing the predictions of the sensitivities with the true solutions (generated by iterating the model from scratch with the perturbed parameter values), one can assess the quality of the approximation (fig. 4). Notably, unlike in the case of the annual plant model, the approximated solution only works for a short time span, quickly breaking

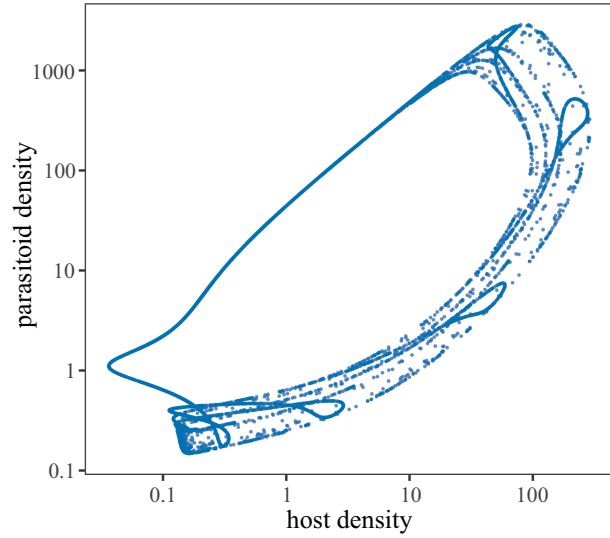


Figure 3: Chaotic attractor of the host-parasitoid system, obtained by iterating the model for $t = 10,000$ time steps and discarding the first 200 to eliminate transients.

down for longer time stretches. This is not surprising because perturbative series do not converge under chaotic dynamics, regardless of how small the parameter perturbation may otherwise be (the same is true for small changes in initial conditions). In a system with a positive largest Lyapunov exponent L , predictability is generally confined to a time duration on the scale of $1/L$ (Bezruchko and Smirnov 2010). The implication is that the method's projections will be acceptable only for short time horizons (in this example, about 30 generations), beyond which any accuracy is quickly lost.

A Chemostat Predator-Prey Model

This model, used here for illustrating the use of the continuous-time framework, has been developed to study population cycles induced by combined eco-evolutionary processes (Fussmann et al. 2000; Yoshida et al. 2003). The equations model the dynamics of the available limiting nutrient nitrogen (n_N), the green alga *Chlorella vulgaris* utilizing the nitrogen (n_c), and the rotifer consumers of the algae, *Brachionus calyciflorus* (n_b). At any point in time, only a fraction of these rotifers can reproduce, so n_r denotes the fertile part of the *Brachionus* population. To simplify the original model formulation, I express each of the n_i (where i is N , c , b , or r) relative to the volume $V = 0.33$ L of the chemostat they are placed in; so n_i here translates to n_i/V in Yoshida et al. (2003). With this convention, the model equations read

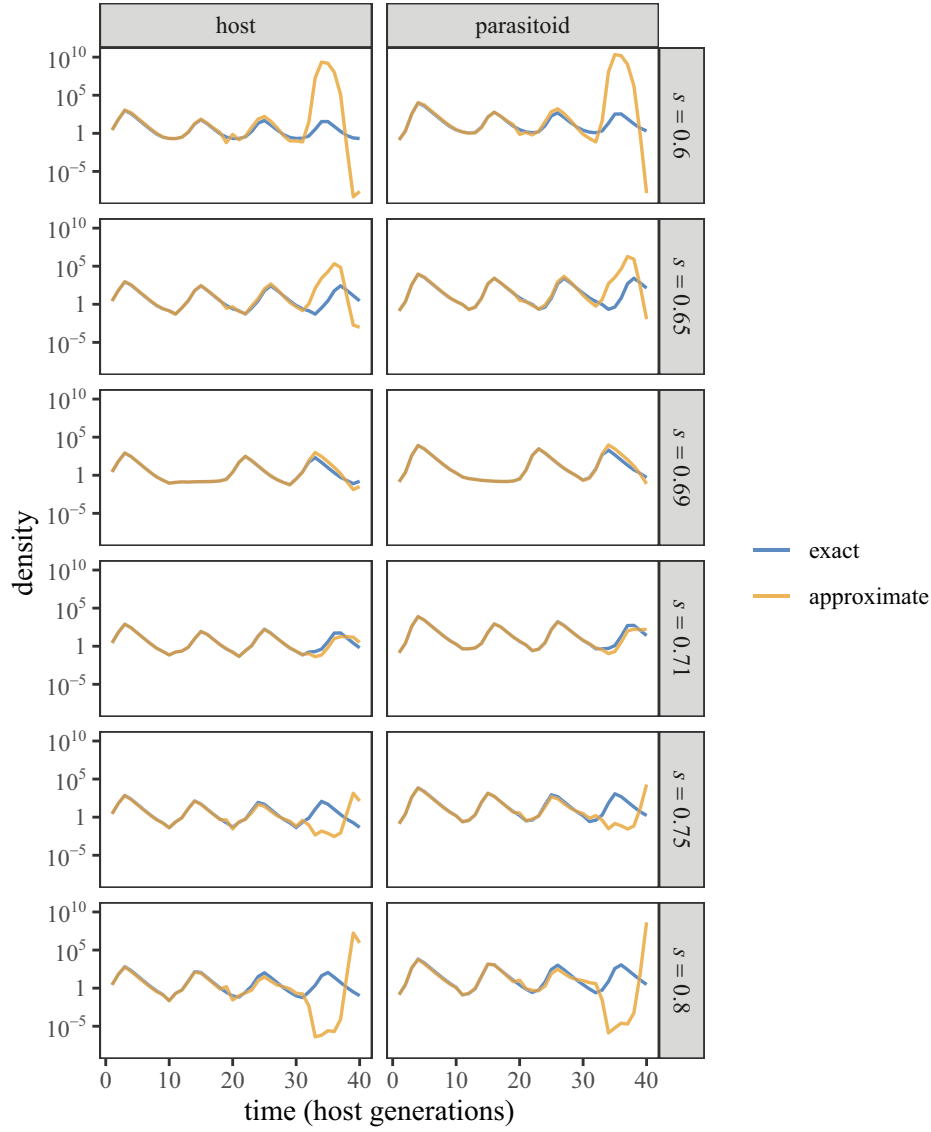


Figure 4: As figure 2, but for the host-parasitoid model and the parameter s (rows), whose unperturbed value is $s = 0.7$. The approximation is good only for much shorter time horizons than in figure 2: with the exception of very small perturbations, it already starts breaking down around $t = 30$ (note the extreme scale of the ordinate).

$$\frac{dn_N(t)}{dt} = \delta(N_i - n_N(t)) - f_c(n_N(t))n_N(t)n_c(t), \quad (25)$$

$$\begin{aligned} \frac{dn_c(t)}{dt} &= \chi_c f_c(n_N(t))n_N(t)n_c(t) \\ &\quad - f_b(n_c(t))n_c(t)n_b(t) - \delta n_c(t), \end{aligned} \quad (26)$$

$$\frac{dn_b(t)}{dt} = \chi_b f_b(n_c(t))n_c(t)n_r(t) - (\delta + m)n_b(t), \quad (27)$$

$$\frac{dn_r(t)}{dt} = \chi_b f_b(n_c(t))n_c(t)n_r(t) - (\delta + m + \lambda)n_r(t), \quad (28)$$

where $\delta = 0.69 \text{ day}^{-1}$ is the chemostat's dilution rate, $N_i = 80 \text{ mol/L}$ is the inflow concentration of nitrogen, $\chi_c = 0.05$ and $\chi_b = 5,400$ are unitless algal and rotifer conversion coefficients, $\lambda = 0.4 \text{ day}^{-1}$ is the rotifer senescence rate, and $m = 0.055 \text{ day}^{-1}$ is the rotifer mortality rate (Yoshida et al. 2003). The two functions

$$f_c(n_N) = \frac{\omega_c \beta_c / \kappa_c}{K_c + n_N(t)} \quad (29)$$

and

$$f_b(n_c) = \frac{G}{K_b + \max(n_c(t), n_c^*)} \quad (30)$$

are the algal and rotifer functional responses, normalized by the densities of their respective resources (the nitrogen $n_N(t)$ in the case of the algae and the algae $n_c(t)$ in the case of the rotifers). Here, $\kappa_c = 1$ is the algal assimilation efficiency, $\omega_c = 20$ mol is the nitrogen content in 10^9 *Chlorella* cells, $\beta_c = 3.3 \text{ day}^{-1}$ is the maximum *Chlorella* recruitment rate, $K_c = 4.3 \text{ mol/L}$ and $K_b = 0.292 \text{ per } 10^9 \text{ } Chlorella \text{ cells}$ are half-saturation constants for the *Chlorella* and *Brachionus* functional responses, $G = 3.3 \times 10^{-4} \text{ day}^{-1}$ is the maximum *Brachionus* clearance rate, and $n_c^* = 0.437 \text{ L per } 10^9 \text{ cells}$ is the critical *Chlorella* concentration above which the linear trend in the functional response switches to a saturating curve.

Introducing $x_i(t) = \log(n_i(t))$ with i being N , c , b , or r , one can rewrite the equations in the form of equation (9) and then perform the sensitivity calculations (supplement S4). The dynamics reach a stable limit cycle after about 18 time units (days). Focusing on the transient period $t \leq 18$, figure 5 shows transient sensitivities for four of the model parameters. The top row shows the log densities $x_i(t)$ of the unperturbed solution: the *Brachionus* population first undergoes exponential growth while *Chlorella* and nitrogen stay more or less constant, after which the depletion of *Chlorella* puts a stop to the growth of the rotifer predators. Regardless of which parameter is perturbed, the $\sigma(t)$ (bottom four rows) reveal a sensitive phase of the dynamics right around $t \approx 15$, where the exponential *Brachionus* growth halts. Before then, nitrogen levels respond only to changes in χ_c , and *Chlorella* densities to both N_i and χ_c . The magnitudes of *Brachionus* sensitivities increase more or less linearly in all cases except for the threshold algal concentration n_c^* . In fact, consistent with equation (30), n_c^* plays no role at all as long as the *Chlorella* population exceeds this threshold and only starts being important after $n_c(t) = \exp(x_c(t))$ drops below this point.

The sensitivity profiles of *Chlorella* to perturbing N_i and χ_c are similar in shape. Just as in the case of the annual plant model and its parameters with similarly shaped sensitivity curves, one can ask which of these parameters is more important for influencing *Chlorella* dynamics. If one naively assumes that an x percent change (assuming x is small) is equally plausible in the original $N_i = 80 \text{ mol/L}$ and $\chi_c = 0.05$, then one can use equation (1) to reason that the expected effect on *Chlorella* densities is the sensitivity times the value of the perturbed parameter times x . Looking at figure 5, the maximum sensitivity of *Chlorella* around day 15 is -0.02 to perturbing N_i and -20 to perturbing χ_c . So an $x = 10\%$ parameter change will generate perturbations of $10\% \times 80 \times (-0.02) = -0.16$ for N_i and $10\% \times 0.05 \times (-20) = -0.1$ for χ_c . While this might suggest that N_i is 1.6 times as important as χ_c , there is no good reason to expect perturbations of x percent to be equally plausible in N_i and χ_c . In fact, since the conversion

coefficient χ_c emerges by averaging over a very large number of individuals, it is unlikely to be manipulable. By contrast, the nitrogen inflow concentration N_i can vary broadly under natural conditions. This means that, ceteris paribus, N_i will be much more important for influencing *Chlorella* dynamics than χ_c simply by virtue of the latter not being able to vary much in the first place.

The Connection between Transient and Long-Term Sensitivities

Fixed point sensitivity analysis (Levins 1974; Bender et al. 1984; Yodzis 1988; Dambacher et al. 2002; Mesz  na et al. 2006; Novak et al. 2011; Aufderheide et al. 2013; S  terberg et al. 2013) asks: given an equilibrium point in phase space, how does its position shift in response to a parameter perturbation? Transient sensitivity analysis asks: for given initial conditions and time horizon, how does the trajectory of the system shift in response to changing a parameter at $t = 0$? These are two distinct questions. Nevertheless, there is one point of connection between them: when the initial conditions themselves are at a stable equilibrium point. Without any parameter perturbations, this means that the system remains where it is: $\mathbf{x}(t) = \mathbf{x}(0)$ for all times. As the dynamical trajectory is constant, $\mathbf{a}(t)$ and $\mathbf{z}(t)$ are always evaluated at the same point in phase space and are also constant. Let us denote their values at the fixed point by $\hat{\mathbf{a}}$ and $\hat{\mathbf{z}}$, respectively, and use them to calculate the transient sensitivity of such a system. This section focuses on discrete-time dynamics, but the same results obtain in continuous time as well (supplement S5).

Starting from the general solution of equation (7) in discrete time and using $\mathbf{a}(t) = \hat{\mathbf{a}}$, $\mathbf{z}(t) = \hat{\mathbf{z}}$,

$$\sigma(t) = \hat{\mathbf{z}} + \left(\sum_{t'=0}^{t-2} \prod_{\tau=t'-1}^{t+1} (1 + \hat{\mathbf{a}}) \right) \hat{\mathbf{z}} \quad (31)$$

for arbitrary $t > 0$. As time goes on, the perturbed system will eventually reach its new, slightly shifted equilibrium and settle there. Since the original equilibrium is stable by assumption, the perturbed equilibrium is also stable (a hyperbolic equilibrium point cannot change stability from an infinitesimal perturbation). One can follow the sensitivities in this limit by letting t go to infinity. Denoting $\sigma(t \rightarrow \infty)$ by $\hat{\sigma}$, we obtain, from equation (31),

$$\hat{\sigma} = \hat{\mathbf{z}} + \lim_{t \rightarrow \infty} \left(\sum_{t'=0}^{t-2} \prod_{\tau=t'-1}^{t+1} (1 + \hat{\mathbf{a}}) \right) \hat{\mathbf{z}}. \quad (32)$$

A short calculation (supplement S5) shows that as long as the fixed point is assumed stable, this expression reduces to

$$\hat{\sigma} = -\hat{\mathbf{a}}^{-1} \hat{\mathbf{z}}, \quad (33)$$

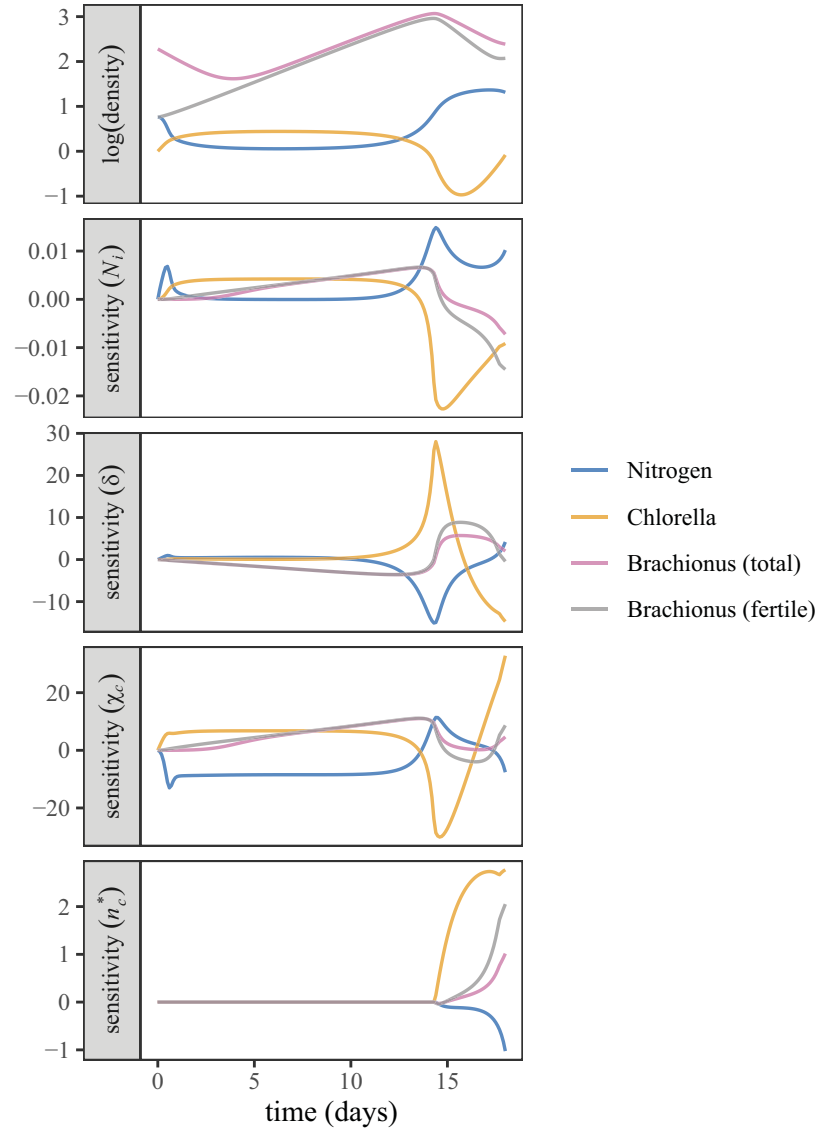


Figure 5: Solution of the *Chlorella-Brachionus* consumer-resource system, for the transient state before it reaches a stable limit cycle (*top panel*). The initial conditions are $x_N(0) = \log(10)$ for nitrogen, $x_c(0) = \log(1)$ for *Chlorella*, and $x_b(0) = \log(1,000)$ for total and $x_f(0) = \log(10)$ for fertile *Brachionus*. Subsequent panels show the transient sensitivities around this solution, for four different model parameters: the nitrogen inflow N_i , the chemostat dilution rate δ , the algal conversion efficiency of nitrogen χ_c , and the threshold *Chlorella* concentration n_c^* .

where $\hat{\mathbf{a}}^{-1}$ is the inverse of the matrix $\hat{\mathbf{a}}$. This is precisely the formula for the sensitivity of a fixed point, in both discrete and continuous time (Levins 1974; Bender et al. 1984; Yodzis 1988; Dambacher et al. 2002; Meszéna et al. 2006; Novak et al. 2011; Aufderheide et al. 2013; Säterberg et al. 2013; Barabás et al. 2014). It therefore can and usually is obtained directly, by setting $\sigma(t) = \hat{\sigma}$ to be at equilibrium and solving for $\hat{\sigma}$ in the dynamical equations (in our case, eq. [6] or eq. [11]). Approaching the same problem from the viewpoint of transients in the long-term limit therefore recovers this known formula.

There is one important difference between the equilibrium and transient results, though. In the context of fixed point sensitivity analysis, equation (33) applies to both stable and unstable equilibria. Whereas in deriving the equation from transient analysis, stability has to be assumed. This discrepancy stems from a difference in the original questions asked by the two sensitivity approaches. The question “how does the position of the fixed point change in phase space after a parameter perturbation?” can be answered regardless of the fixed point’s stability. But when one asks about the future of dynamical trajectories, those

will be repelled by the unstable equilibrium point and thus diverge: the limit in equation (32) will no longer exist. It is therefore natural that transient sensitivity analysis establishes equation (33) only when the fixed point is stable.

Finally, it is interesting to compare the behavior of short- and long-term transient sensitivities for the above scenario. Applying equation (31) for $t = 1$ and $t = 2$, one gets $\sigma(1) = \hat{z}$ and $\sigma(2) = \hat{z} + (\mathbf{1} + \hat{\mathbf{a}})\hat{z}$, the latter being proportional to $\hat{\mathbf{a}}\hat{z}$. This, in a way, is the opposite of the long-term sensitivity $\hat{\sigma}$ in equation (33), which is proportional to $\hat{\mathbf{a}}^{-1}\hat{z}$. The difference can be biologically meaningful. For example, two species that are almost identical will have a matrix $\hat{\mathbf{a}}$ with nearly equal rows and columns because they respond to any change in the biotic environment almost identically. This near equality of rows and columns makes the matrix ill-conditioned, however. The entries of the inverse matrix will then be very large. By equation (33), this causes the long-term sensitivities to also be large: even a small parameter perturbation will cause a large shift in where the dynamics will eventually wind up. Such large shifts always run the risk of moving outside the feasibility domain (Rohr et al. 2014; Saavedra et al. 2017; Song et al. 2018, 2021), leading to the extinction of at least one of the species (Meszéna et al. 2006; Barabás et al. 2014). However, even if a small parameter change does result in coexistence turning to exclusion in the long run, the exclusion process itself will be slow, precisely because the species are similar and therefore respond to any change in conditions in near-identical ways (Deng et al. 2022). That is, the relative densities of the two species do not change much during any one single time step, even though the overall change is drastic in the long run. Supplement S6 illustrates this point through a simple example.

Another way of making sense of this result is to relate it to the process of natural selection. Variants of the same species will almost always be ecologically similar, and they will have a hard time coexisting because of the very small feasibility domain stemming precisely from this similarity. This, of course, is the engine behind adaptive evolution: once a slightly better-adapted mutant reaches an appreciable population size, it is practically guaranteed to go to fixation and exclude the other mutants. On the other hand, similar variants will respond similarly to any environment, which limits the selective advantage of the more fit variant to a relatively narrow range. Since the time to exclusion scales with the inverse of this selective advantage (Gillespie 2004; Mallet 2012), reaching the long-term steady state of exclusion will be a relatively slow process.

Discussion

Ecology is a subject where counterfactual statements (what would have been the outcome if something had been dif-

ferent) are perhaps more important than in other fields of science, where data are more readily available and experiments are easier and quicker to perform. Sensitivity analysis offers one way of arriving at such counterfactuals, by extrapolating the effects of perturbations to the system. This work described a method, in both discrete and continuous time, that can be used to estimate the sensitivity of transient behavior to altering model parameters. The continuous-time formalism has been derived before by Gardner et al. (1981) and Richard et al. (2015), although without the general solution of equation (12). Caswell (2007) developed a discrete-time approach, without equation (7), for just a single age- or stage-structured population. After extending the discrete-time method to communities of unstructured species, the sensitivity technique was applied to three empirically parameterized ecological models, as well as theoretical scenarios, to showcase its use as well as some of its limitations. The requisite sensitivity computations can be automated: the supplied scripts can perform both the analytical and the numerical calculations on any specified model.

The applications illustrated how one can use transient sensitivities to identify critical parameters whose perturbations have disproportionate effects on a system's dynamics. Equally important, one can pinpoint particular windows of time when sensitivities are highest. This is in contrast with the more traditional sensitivity analysis of long-term stationary behavior, where it is only possible to talk of the sensitivity of the stationary state to parameter perturbations. In the case of transients, the effects of perturbations are themselves dependent on time (figs. 1, 5). If transient sensitivity analysis is used in service of conservation efforts, then one can map out the times at which an initial parameter change will make its effects most strongly felt. This is less relevant if periods of high sensitivity are accompanied by large population densities (as was the case with *Brachionus* in the chemostat predator-prey model). But it becomes especially important when high sensitivities coincide with low densities of the target population. In that case, one can use the foresight gained via the use of sensitivity analysis to identify parameters whose press perturbations will, down the road, cause the greatest benefit to species in a vulnerable state.

The annual plant model of competing native forbs and exotic grasses provided one such example. Here, the sensitivity of the forb to seed mortality, to the competition coefficient, and to its competitor's fecundity in poor years was extreme whenever forb densities were very low. Population collapse during this window of time could therefore be prevented by implementing and maintaining improved values of these parameters from the beginning. Of course, whether effective management is possible depends on a number of other factors, such as whether the parameters

are independent (see the earlier discussion of the annual plant model), how uncertain the original parameter values are in the first place, to what extent one can manipulate parameters, and whether doing so is feasible given the monetary and resource constraints of the conservation project. These and other points are outlined in a practical flowchart in figure 6.

Any kind of sensitivity analysis, including the present one, plays a supporting role in achieving the ultimate goal of understanding the dynamics of ecological communities. Real ecosystems are fraught with uncertainty: knowledge of population densities, parameter values, and even the model chosen to describe them is incomplete. Sensitivity

analysis helps in dealing with one particular type of uncertainty, the one in the model parameters. This already assumes having a parameterized model at hand and is therefore different from methods that can in principle be used without assuming a predetermined model structure (Sugihara et al. 2012; Cenci and Saavedra 2019). By exploring how parameter perturbations influence model outcomes, sensitivity calculations offer a way of getting a grip on parameter uncertainty—provided that the proposed mathematical model of the community is sufficiently accurate in the first place. Incorporating the effects of uncertainty in population densities into this framework involves computing the derivatives with respect to the initial conditions

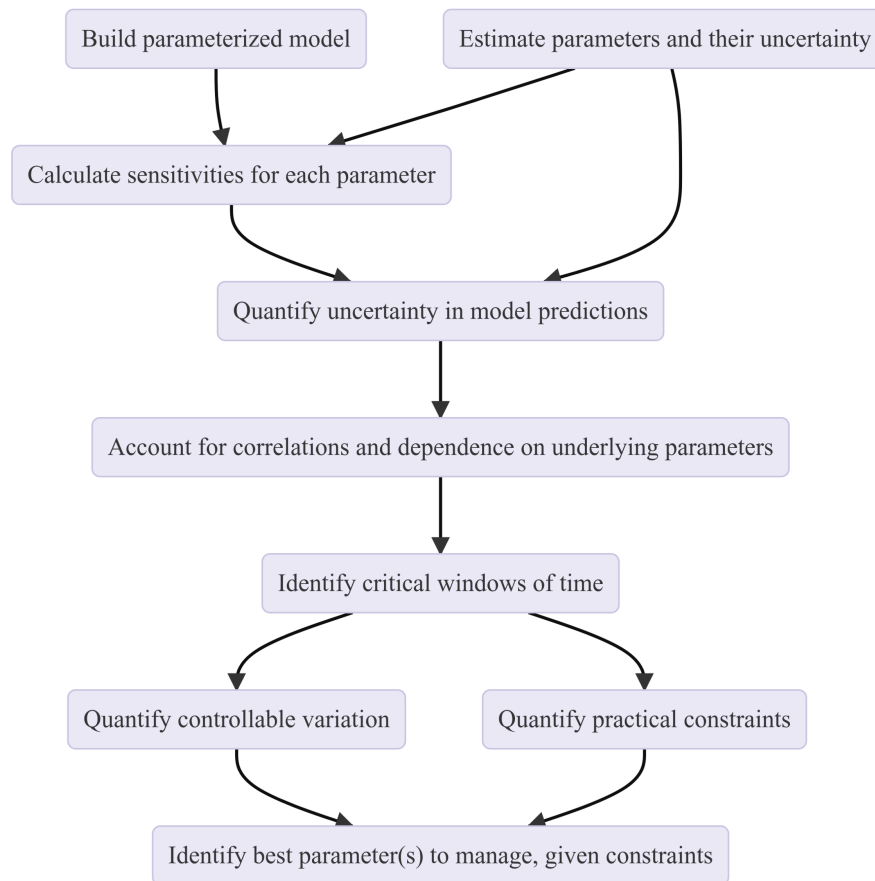


Figure 6: Schematic outline of how transient sensitivity analysis can aid management decisions. After creating a parameterized model, the time-dependent sensitivities are calculated. Uncertainty in parameter values can then be translated to uncertainty in dynamical trajectories using equation (1). To correctly assess the effects of parameter changes, any correlation between them and/or joint dependence on underlying parameters should be taken into account (e.g., if both seed death rates and germination rates strongly depend on soil pH, then they cannot be changed independently). It can additionally be useful to identify windows of time during which sensitivities are high, especially if these times coincide with low populations of a target species. Parameters to manipulate might be selected on the basis of their effects during these critical windows rather than their overall effect. (If changing parameter 1 yields the greatest overall increase in abundance but at the cost of likely extinction at an earlier time whereas changing parameter 2 gives more modest overall increases while practically eliminating any chance of extinction, then there are good reasons to favor parameter 2 over parameter 1.) The next step is to quantify the extent to which the parameters can be manipulated given biological, physical, and resource constraints. Finally, one can then rank parameters on the basis of how much of an improvement they would yield to the dynamics, given these constraints and equation (1).

$x_i(0)$ and using an analogous formula to equations (6) and (11). But there is no way of getting around the need for a parameterized model to apply the method. For a recent technique that attempts to circumvent the need for an explicit model specification, see Cenci and Saavedra (2019). For a very interesting and flexible new approach that does rely on a parameterized model but also utilizes optimal control theory to aid transient sensitivity calculations, see Ng et al. (2023).

Sensitivity analysis, which is based on a first-order Taylor expansion assuming small parameter perturbations, has the disadvantage of being an approximate method. Its predictions are in principle perfect only when the magnitude of the parameter perturbation $\Delta\epsilon$ approaches zero, and they generally lose accuracy as the perturbation size increases. This drawback originates from the fact that most quantities in ecology whose sensitivity we are interested in depend nonlinearly on the parameters we change. This is true even in the context of the linear population growth model of age- or stage-structured populations (Caswell 2001). In these models, the long-term growth rate is the dominant eigenvalue of the population projection matrix, and since eigenvalues are polynomial (i.e., nonlinear) functions of the matrix entries, one cannot in general hope to gain a full understanding of their parameter dependence. On the bright side, flattening out problems into (locally) linear ones means that the sensitivity technique can be applied to many seemingly very different use cases. While the formulas are more involved, one can obtain general sensitivity expressions for density-dependent population models (Takada and Nakajima 1992, 1998; Grant and Benton 2000, 2003; Caswell et al. 2004; Caswell 2008). Similarly, it is possible to extend the calculations to communities of interacting species (Levins 1974; Bender et al. 1984; Meszéna et al. 2006; Verdy and Caswell 2008; Barabás et al. 2014). And as discussed here and elsewhere (Caswell 2007; Richard et al. 2015; Medeiros et al. 2023; Ng et al. 2023), sensitivity analysis can be applied to transient dynamics as well.

That said, there are many cases where local sensitivity methods are insufficient because the goal is to get a broad overview of the dynamical possibilities of a system instead of extrapolating its behavior to trajectories that fall near some known solution. Fortunately, there are tools available for that kind of model exploration as well. These include nullcline and bifurcation analysis, which aid in delineating parameter domains with given dynamical regimes. Such techniques can become unfeasible for species-rich systems, in which case one can still rely on global sensitivity methods to map out a model's behavior over the entire parameter space (Sheikholeslami et al. 2019). One common strategy for conducting such global analyses is to perform the sampling of parameter space in two steps. The first is a

crude exploratory step, which is sufficient to classify the parameters (or other inputs, such as initial conditions; Medeiros et al. 2023) as noninfluential or as possibly highly sensitive (Becker et al. 2018). Then in the second step, only the potentially sensitive inputs are investigated, in greater detail. Such methods might be the only viable way of analyzing sensitivities under chaotic dynamics. As we have seen when discussing the host-parasitoid model, local sensitivity methods based on analytical Taylor expansions are accurate only for a handful of time steps at most. Global sensitivity methods could, at the very least, answer questions about the sensitivity of the long-term average behavior of a chaotic system: by foregoing the details of dynamical trajectories, one could map out, for example, the approximate center and basin of attraction of chaotic attractors and their parameter dependence.

Sensitivities measure a system's response to additive perturbations. This can potentially confound the effects of parameters that operate on very different scales, because the same additive perturbation of 0.5 (say) means very different things for a probability parameter ranging from 0 to 1 and for fecundities on the order of thousands. One common way of trying to resolve this issue is by changing from additive perturbations to proportional ones via elasticities (Caswell et al. 1984). Instead of asking what happens after a small additive change to the parameter, one asks what happens when the parameter is changed by 1% or some other small percentage. Elasticities are computed by taking the derivative of the log response with respect to the log of the parameter. Since the $x(t)$ are already the logarithms of the population densities, the elasticities of the densities $n(t)$ are obtained as $\partial x(t)/\partial \log(\epsilon) = \epsilon(\partial x(t)/\partial \epsilon) = \epsilon \sigma(t)$. One should be aware, though, that elasticities do not solve every problem. First, thanks to the logarithm, they can be used only for parameters that are strictly positive. Second, resolving one issue of scale introduces another: imposing a change by a fixed percentage means that instead of comparing parameters on different scales, we are now comparing perturbations that are on different scales (Caswell 2001, chap. 9). And third, the main interpretational advantage of elasticities in standard eigenvalue perturbation theory is that they sum to 1, but this does not hold for $\epsilon \sigma(t)$.² Despite these problems, elasticities may of course still be used and be useful.

Finally, the sensitivity methods developed and discussed here rely on scalar parameters and their perturbations. This means that if the dynamics depend on some function (say, a type II functional response in a predator-prey

2. Elasticities summing to 1 are contingent on $x(t)$ being a homogeneous function of ϵ (Mesterton-Gibbons 1993). In the case of eigenvalues λ of a matrix A , homogeneity holds by the definition $Ax = \lambda x$, implying $A^k x = \lambda^k x$ for any integer k . There is no reason for the same to be true here.

model), the perturbation cannot affect the function in arbitrary ways. Instead, only the parameters used to describe the function's shape will change—such as the maximum attack rate and the handling time in this example. This restricts the types of changes one can apply to the function, and the resulting lack of flexibility can demonstrably create overly optimistic sensitivity predictions (Aldebert et al. 2016). Fortunately, methods for gauging the sensitivity of a model to all possible perturbations of a given size to the function exist (Cordoleani et al. 2011; Adamson and Morozov 2013). Incorporating this methodology in other sensitivity calculations, such as the transient sensitivities here, would be desirable. In principle, this could be achieved by replacing the partial derivatives with respect to ε in equations (4) and (10) by functional derivatives with respect to entire functions. Whether it is possible to go beyond merely defining such sensitivities and make the procedure practical for real-world calculations remains to be seen.

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Data and Code Availability

Code for automating transient sensitivity analysis, along with example applications, are archived on Zenodo (<https://doi.org/10.5281/zenodo.8379960>).

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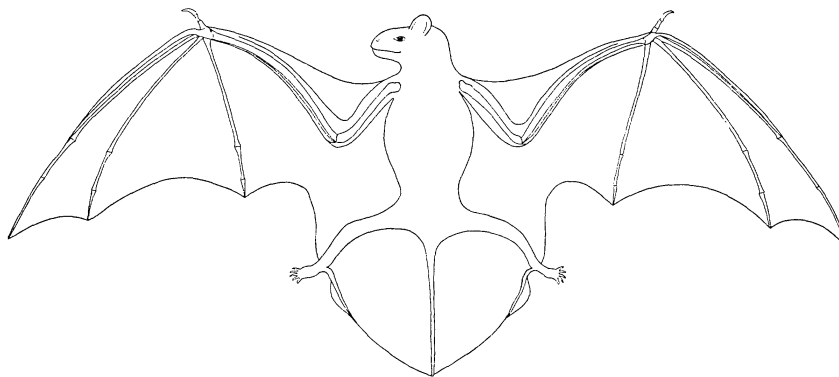
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“In the bats one sees the culmination of volant adaptation on the part of the Mammalia and the entire order has reached a state of perfection excelled only by the birds and pterodactyls.” From “Volant Adaptation in Vertebrates” by Richard S. Lull (*The American Naturalist*, 1906, 40:537–566).