TRANSIENT SENSITIVITY ANALYSIS IN BIOLOGICAL AND ECOLOGICAL MODELS*

NATHANIAL BURCH†, LEVIS ENEYA , SEAN KRAMER , SAMANTHA TRACHT , AND OROU GAOUE

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Abstract. We investigate transient sensitivity analysis as an alternative to other sensitivity analyses that rely on long-term asymptotic dynamics. Since the transient dynamics often differ substantially from the long-term dynamics, such an analysis provides information about parameters and dynamics that are synergistic with short-term goals made by managers. We review the method for computing transient sensitivities for both discrete-time matrix models and systems of ordinary differential equations and then apply it in several examples with applications including disease modeling and populations.

Key words. transient dynamics, sensitivity analysis, conservation, management

Disclaimer. This is a working document and, at this stage, is very rough. Please read with a kind heart.

1. Introduction. Transient sensitivity analysis is well-understood to provide pertinent information that more traditional eigenvalue sensitivity does not provide, especially in a management setting, see, e.g., [3, 4, 14]. The so-called forward method, which computes derivatives of the *model output* with respect to a set of parameters, for performing transient sensitivity analyses of ecological models has been documented in [1], among other places.

Transient sensitivity analyses provide information over time-scales more applicable in management scenarios in contrast to the long time-scales associated with eigenvalue sensitivity analyses. This flexibility is ideal for adaptive management schemes and allows managers to balance short-term goals with long-term viability.

These approaches give managers the benefit of exploring sensitivity of population growth rate to demographic parameters over short management time-scales (e.g., annual adjusting of hunting and fishing regulations or land acquisition decisions for a species of concern) and thus better reflect the dynamic environmental conditions under which management strategies are implemented.

Other references we should look at: [2, 5, 6, 8, 9, 18].

Summary of the important messages:

- so-called equilibrium dynamics rely on the system to be in equilibrium, but the parameters and the model are not necessarily designed for this (often limited predictive power of the model)
- transient dynamics should not be ignored; in fact, the transient dynamics are often more relevant in many applications, e.g., short-term management plans
- equilibrium-type sensitivity analyses describe how parameters affect equilibrium behavior, but we are likely more interested in the behavior soon
- transient sensitivity analyses describe how parameters affect the transient dynamics and can thus be used in management scenarios

Outline of what we worked on over the last week:

- learned about transient sensitivity analysis (and how to compute it)
- coded (in MATLAB) examples of both linear and nonlinear matrix models and systems of ODEs
- we considered specific models:
  - Cannibalistic Flour Beetles (Tribolium) – from [1]
  - Fatal disease, Allee effect model – from Professor Yakubu [7]
  - Two-patch, fatal disease, Allee effect model – from Professor Yakubu [7]
  - Cholera – from Professor Lungu (need citation)
  - HIV and/or TB – from Professor Lungu [12] (is this the right source?)

2. A Motivating Example. Consider the discrete-time dynamical system (motivated from [1])

$$\mathbf{x}(t+1) = \begin{pmatrix} 0.32 & 0 & 8.43 \\ 0.17 & 0.51 & 0 \\ 0 & 0.11 & 0.42 \end{pmatrix} \mathbf{x}(t), \qquad \mathbf{x}(0) = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}.$$

The dominant eigenvalue is less than one, $\lambda \approx 0.96$, so that the population tends to extinction as $t \to \infty$, but the transient dynamics show population growth initially. In the situation that $\mathbf{x}(t)$ is a bacteria or an invasive species,

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†Please send correspondences to burchn@samsi.info

the transient growth of the population has an associated cost that we may wish to avoid. Moreover, parameter estimates and population dynamics are based on the current population so assuming the model is valid for long-time scales or significantly different population structures may be invalid.

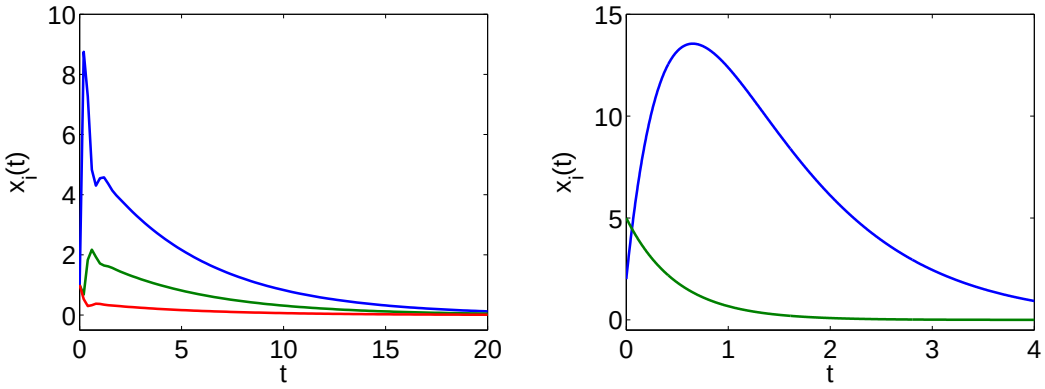
We similarly consider the case of a system of ordinary differential equations (motivated from [9])

$$\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \begin{pmatrix} -1 & 10 \\ 0 & -2 \end{pmatrix} \mathbf{x}(t), \qquad \mathbf{x}(0) = \begin{pmatrix} 2 \\ 5 \end{pmatrix}.$$

Clearly, the eigenvalues of the matrix $\mathbf{A}$ are $\lambda_1 = -1$ and $\lambda_2 = -2$, with associated eigenvectors $\mathbf{v}_1 = \begin{pmatrix} 1 & 0 \end{pmatrix}^\top$ and $\mathbf{v}_2 = \begin{pmatrix} -10 & 1 \end{pmatrix}^\top$. Consequently,

$$\mathbf{x}(t) = 52 \exp(-t) \begin{pmatrix} 1 \\ 0 \end{pmatrix} + 5 \exp(-2t) \begin{pmatrix} -10 \\ 1 \end{pmatrix}$$

and the population tends to extinction as $t \to \infty$. However, the population exhibits growth in the transient time.



(a) population vs. time (b) population vs. time

FIG. 2.1. *Need to add a caption.*

3. Equilibrium Tools.

3.1. Dominant Eigenvalue and Stable Age Distribution. Consider the matrix population model

$$\begin{cases} \mathbf{x}(t+1) = \mathbf{A}\mathbf{x}(t), \\ \mathbf{x}(0) = \boldsymbol{\mu}. \end{cases}$$

The so-called eigenvalue sensitivity analysis focuses on the asymptotic population growth rate λ, the dominant eigenvalue of $\mathbf{A}$, once the population has reached a stable age distribution. Then, the sensitivity s_{ij} of λ with respect to an absolute change in the entry A_{ij} of of the matrix $\mathbf{A}$ is calculated by

$$s_{ij} = \frac{v_i w_j}{\mathbf{w}^\top \mathbf{v}},$$

where $\mathbf{w}$ and $\mathbf{v}$ are the right and left eigenvectors of $\mathbf{A}$ corresponding to the dominant eigenvalue λ. In equation (2), v and w represent the left and right eigenvectors, respectively, and is the inner product of two vectors.

3.2. The Effective Reproduction Number. The basic reproduction number, $\Re_0$, is the average number of secondary infections that occur when one infective is introduced into a completely susceptible population [10]. In an epidemic model the magnitude of the basic reproduction number determines whether or not a disease can invade a population. When $\Re_0 > 1$ the disease can invade and when $\Re_0 ¡ 1$ a disease is unlikely to invade a population. The basic reproduction number can be computed using the 'next-generation operator approach' [17]. This computation is done by linearizing the system of equations around the disease free equilibrium.

The effective reproduction number, $\Re_{eff}$, is the average number of secondary cases produced by a typical infective during the entire period of infectiousness once a disease has invaded [10]. Thus $\Re_0 > \Re_{eff}$. The effectiveness of intervention strategies is often measured by their ability to reduce the spread of disease in a given population. The effective reproduction number is one way in which to determine the effectiveness of a proposed intervention strategy in a disease model. Once an intervention strategy is introduced the goal is that the effective reproduction number will be reduced to less than one so that the disease will die out and the disease free equilibrium will be stable.

Epidemiological parameters are often hard to measure and there is uncertainty in their values. Thus it is important to determine how sensitive the model is to the parameter values. A small change in one parameter could lead to very different results, including the value of the basic and effective reproduction numbers.

4. Transient Sensitivity Analysis. We review the evolution equations for the sensitivities. The forthcoming analysis relies heavily on matrix calculus and we refer the reader to [1] for a nice review of matrix calculus.

4.1. Discrete-time Matrix Model. We first consider the discrete-time matrix model

$$\begin{cases} \mathbf{x}(t+1) = \mathbf{A}(\boldsymbol{\theta}, \mathbf{x}(t))\mathbf{x}(t), \\ \quad \mathbf{x}(0) = \boldsymbol{\mu}, \end{cases} \tag{4.1}$$

where $\mathbf{x}(t)$ is an $n \times 1$ state vector and $\mathbf{A}(\boldsymbol{\theta}, \mathbf{x}(t))$ is an $n \times n$ matrix that may depend on a vector of lower-level parameters $\boldsymbol{\theta}$ and the state vector $\mathbf{x}(t)$. Differentiating (4.1) with respect to the lower-level parameters gives

$$\begin{cases} \dfrac{\mathrm{d}\mathbf{x}(t+1)}{\mathrm{d}\boldsymbol{\theta}^\top} = \left(\mathbf{A}(\boldsymbol{\theta}, \mathbf{x}(t)) + \left(\mathbf{x}(t)^\top \otimes \mathbf{I}_n\right) \dfrac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\mathbf{x}(t)^\top} \right) \dfrac{\mathrm{d}\mathbf{x}(t)}{\mathrm{d}\boldsymbol{\theta}^\top} + \left(\mathbf{x}(t)^\top \otimes \mathbf{I}_n\right) \dfrac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\boldsymbol{\theta}^\top}, \\ \dfrac{\mathrm{d}\mathbf{x}}{\mathrm{d}\boldsymbol{\theta}^\top}(0) = \dfrac{\mathrm{d}\boldsymbol{\mu}}{\mathrm{d}\boldsymbol{\theta}^\top}. \end{cases} \tag{4.2}$$

4.2. System of Ordinary Differential Equations Model. A similar approach is used for the case of a system of ordinary differential equations

$$\begin{cases} \dot{\mathbf{x}}(t) = \mathbf{A}(\boldsymbol{\theta}, \mathbf{x}(t))\mathbf{x}(t), \\ \mathbf{x}(0) = \boldsymbol{\mu}, \end{cases} \tag{4.3}$$

where $\mathbf{x}(t)$ is an $n \times 1$ state vector and $\mathbf{A}(\boldsymbol{\theta}, \mathbf{x}(t))$ is an $n \times n$ matrix that may depend on a vector of lower-level parameters $\boldsymbol{\theta}$ and the state vector $\mathbf{x}(t)$. The notation $\dot{\mathbf{x}}(t)$ denotes the temporal derivative of $\mathbf{x}(t)$. Differentiating (4.3) with respect to the lower-level parameters gives

$$\begin{cases} \dfrac{\mathrm{d}\dot{\mathbf{x}}(t)}{\mathrm{d}\boldsymbol{\theta}^\top} = \left(\mathbf{A}(\boldsymbol{\theta}, \mathbf{x}(t)) + \left(\mathbf{x}(t)^\top \otimes \mathbf{I}_n\right) \dfrac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\mathbf{x}(t)^\top} \right) \dfrac{\mathrm{d}\mathbf{x}(t)}{\mathrm{d}\boldsymbol{\theta}^\top} + \left(\mathbf{x}(t)^\top \otimes \mathbf{I}_n\right) \dfrac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\boldsymbol{\theta}^\top}, \\ \dfrac{\mathrm{d}\mathbf{x}_0}{\mathrm{d}\boldsymbol{\theta}^\top} = \dfrac{\mathrm{d}\boldsymbol{\mu}}{\mathrm{d}\boldsymbol{\theta}^\top}. \end{cases} \tag{4.4}$$

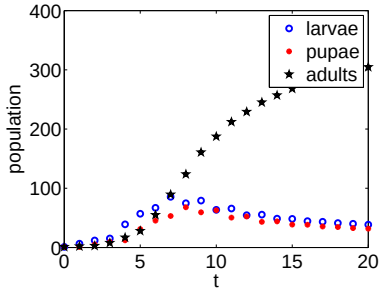
To solve (4.4), we choose Δt sufficiently small and use the forward Euler approximation (we also coded the improved Euler method)

$$\begin{cases} \dfrac{\mathrm{d}\mathbf{x}(t+\Delta t)}{\mathrm{d}\boldsymbol{\theta}^\top} = \dfrac{\mathrm{d}\mathbf{x}(t)}{\mathrm{d}\boldsymbol{\theta}^\top} + \Delta t \left\{ \left(\mathbf{A}(\boldsymbol{\theta}, \mathbf{x}(t)) + \left(\mathbf{x}(t)^\top \otimes \mathbf{I}_n\right) \dfrac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\mathbf{x}(t)^\top} \right) \dfrac{\mathrm{d}\mathbf{x}(t)}{\mathrm{d}\boldsymbol{\theta}^\top} + \left(\mathbf{x}(t)^\top \otimes \mathbf{I}_n\right) \dfrac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\boldsymbol{\theta}^\top} \right\}, \\ \quad \dfrac{\mathrm{d}\mathbf{x}(0)}{\mathrm{d}\boldsymbol{\theta}^\top} = \dfrac{\mathrm{d}\boldsymbol{\mu}}{\mathrm{d}\boldsymbol{\theta}^\top}. \end{cases} \tag{4.5}$$

5. Examples.

5.1. Flour Beetle (Tribolium). For now, we refer the reader to [1] for an introduction to the parameters.

$$\begin{cases} \mathbf{x}(t+1) = \begin{pmatrix} 0 & 0 & b\exp(-c_{e\ell}x_1(t) - c_{ea}x_3(t)) \\ 1-\mu_\ell & 0 & 0 \\ 0 & \exp(-c_{pa}x_3(t)) & 1-\mu_a \end{pmatrix} \mathbf{x}(t), \\ \quad \mathbf{x}(0) = \begin{pmatrix} 1 & 1 & 1 \end{pmatrix}^\top. \end{cases} \tag{5.1}$$



(a) population vs. time

FIG. 5.1. *Add caption.*

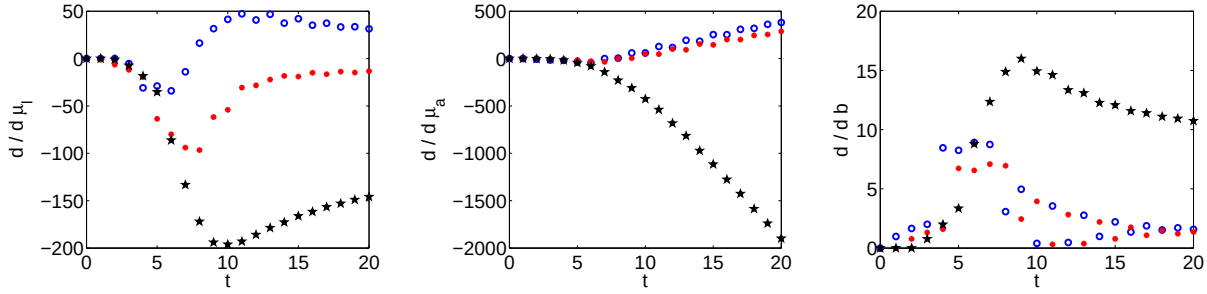
The parameters were selected to be

$$\begin{pmatrix} b & \mu_\ell & \mu_a & c_{ea} & c_{e\ell} & c_{pa} \end{pmatrix} = \begin{pmatrix} 6.598 & 0.2055 & 0.007629 & 0.001155 & 0.01209 & 0.0047 \end{pmatrix}$$

Suppose we have three pesticides,

- one that effectively increases μ_ℓ
- one that effectively increases μ_a
- and one that decreases b.

Which pesticide would be most effective at reducing the total population of the Flour Beetles?



(a) sensitivity wrt μ_ℓ (b) sensitivity wrt μ_a (c) sensitivity wrt b

FIG. 5.2. *Add a caption.*

5.2. Fatal Disease Model with the Allee Effect. We let $\mathbf{x}(t) = \begin{pmatrix} p(t) \\ i(t) \end{pmatrix}$ and consider the model for a fatal disease with an Allee effect found in [7],

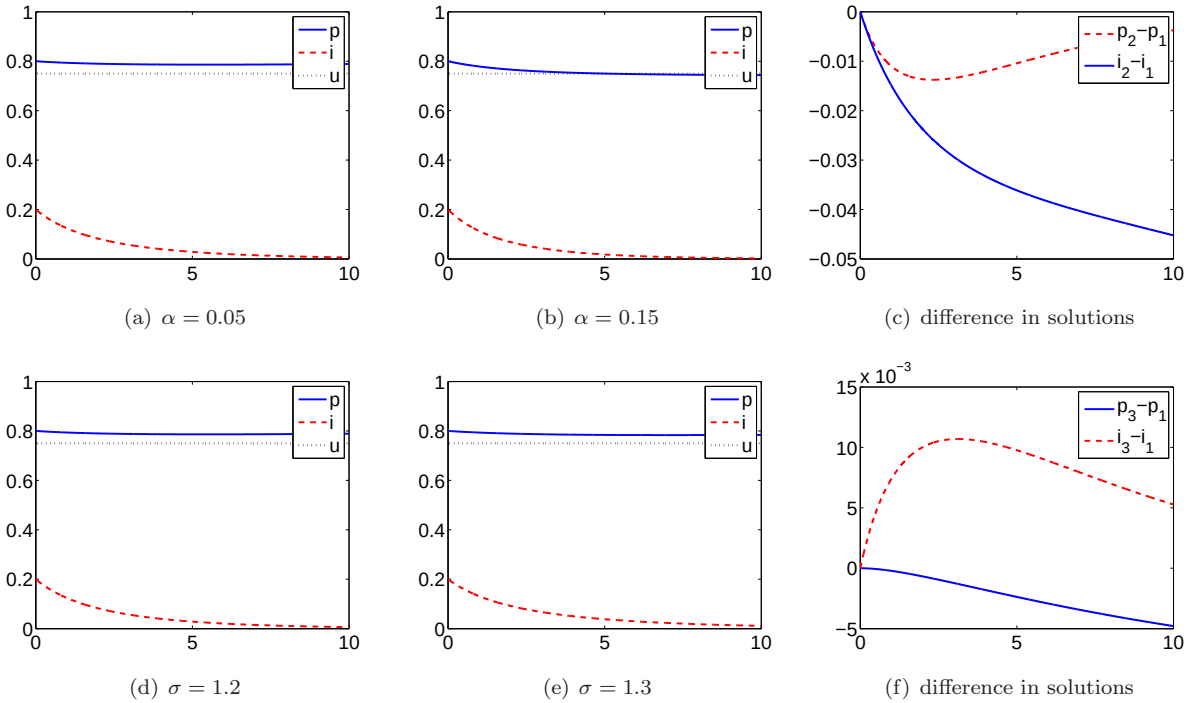
$$\begin{cases} \dot{\mathbf{x}}(t) = \begin{pmatrix} r(1-x_1(t))(x_1(t)-u) & -\alpha \\ (\sigma-1)x_2(t) & -(\alpha+d+ru)-\sigma x_2(t) \end{pmatrix} \mathbf{x}(t), \\ \mathbf{x}(0) = \begin{pmatrix} p_0 & i_0 \end{pmatrix}^\top. \end{cases} \tag{5.2}$$

We define the vector of parameters $\boldsymbol{\theta} = \begin{pmatrix} r & \alpha & u & d & \sigma & p(0) & i(0) \end{pmatrix}^\top$. Then, tedious calculations yield

$$\frac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\boldsymbol{\theta}^\top} = \begin{pmatrix} (1-p)(p-u) & 0 & -r(1-p) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & i & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 & 0 \\ -u & -1 & -r & -1 & -i & 0 & 0 \end{pmatrix} \tag{5.3}$$

and

$$\frac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\mathbf{x}(t)^\top} = \begin{pmatrix} r(-2x_1(t)+1+u) & 0 \\ 0 & \sigma-1 \\ 0 & 0 \\ 0 & -\sigma \end{pmatrix} \tag{5.4}$$



(a) $\alpha = 0.05$ (b) $\alpha = 0.15$ (c) difference in solutions

(d) $\sigma = 1.2$ (e) $\sigma = 1.3$ (f) difference in solutions

FIG. 5.3. *Need to add a caption.*

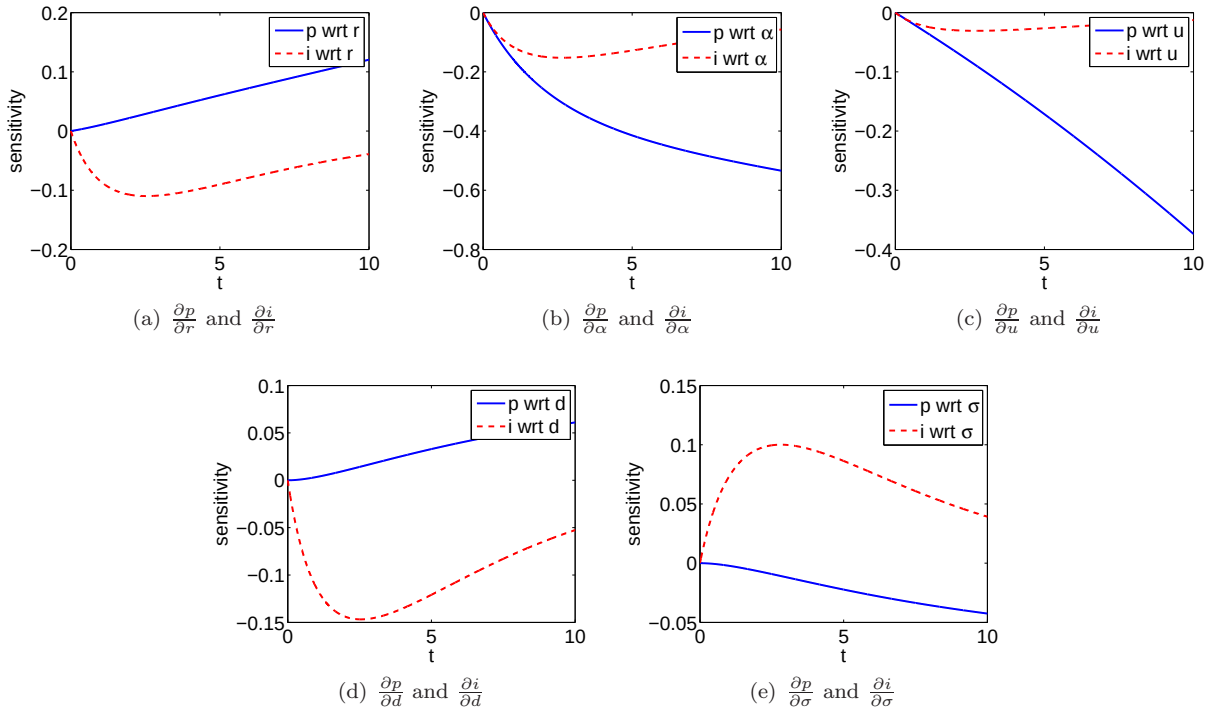
5.3. Two-Patch Disease Model. We now extend Aziz's model with the Allee affect to a two-patch model where species migrate between patches. A small disease is introduced into the population and transient sensitivities are analyzed with respect to migration rates. The two-patch model is given as

$$\begin{aligned} \frac{\mathrm{d}p_j}{\mathrm{d}t} &= r_j(1-p_j)(p_j-u_j)p_j - \alpha_j i_j + \delta \sum_{k=1,2}(L_{kj}p_k - L_{kj}p_j), \\ \frac{\mathrm{d}i_j}{\mathrm{d}t} &= [-A_j + (\sigma_j - 1)p_j - \sigma_j i_j]i_j + \delta \sum_{k=1,2}(L_{kj}i_k - L_{kj}i_j), \end{aligned} \tag{5.5}$$

where $A_j = \alpha_j + d_j + r_j u_j$ on each patch $k \in \{1,2\}$ and δ is the non-negative diffusion coefficient for the population. Furthermore, the Allee threshold is given by $u_j \in (0,1)$ and the rate of movement from patch k to j is L_{kj}.

For computing the sensitivities, we let $\mathbf{x}(t) = \begin{pmatrix} p1(t) \\ p2(t) \\ i1(t) \\ i2(t) \end{pmatrix}$ and write the two-patch model as

$$\begin{cases} \dot{\mathbf{x}}(t) = \begin{pmatrix} r_1(1-x_1(t))(x_1(t)-u) - L_{12} & \delta L_{21} & -\alpha_1 & 0 \\ \delta L_{12} & r_2(1-x_2(t))(x_2(t)-u) - \delta L_{21} & 0 & -\alpha_2 \\ (\sigma-1)x_3(t) & 0 & -(\alpha_1+d_1+r_1u) - \sigma x_3(t) - \delta L_{12} & \delta L_{21} \\ 0 & (\sigma-1)x_4(t) & \delta L_{12} & -(\alpha_2+d_2+r_2u) - \sigma x_4(t) - \delta L_{21} \end{pmatrix} \mathbf{x}(t), \\ \mathbf{x}(0) = (p_{1_0} \quad p_{2_0} \quad i_{1_0} \quad i_{2_0})^\top, \end{cases} \tag{5.6}$$



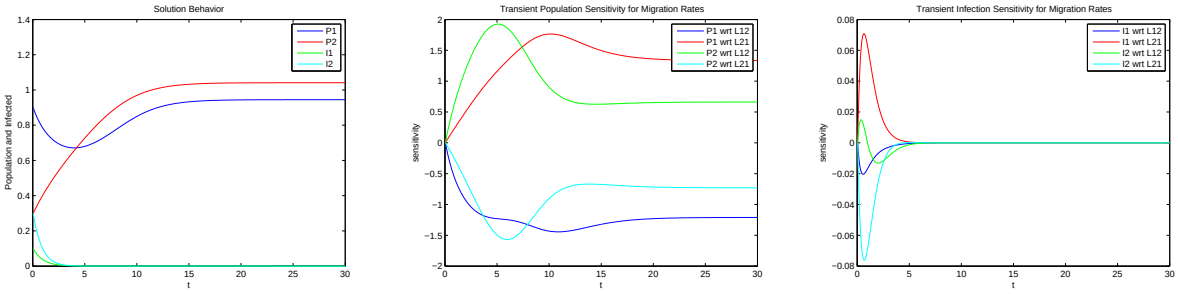
(a) $\frac{\partial p}{\partial r}$ and $\frac{\partial i}{\partial r}$ (b) $\frac{\partial p}{\partial \alpha}$ and $\frac{\partial i}{\partial \alpha}$ (c) $\frac{\partial p}{\partial u}$ and $\frac{\partial i}{\partial u}$

(d) $\frac{\partial p}{\partial d}$ and $\frac{\partial i}{\partial d}$ (e) $\frac{\partial p}{\partial \sigma}$ and $\frac{\partial i}{\partial \sigma}$

FIG. 5.4. *Need to add a caption.*

Here, we are mostly interested in the sensitivities of transient solution behavior with respect to perturbations in migration rates so we define the vector of parameters as $\boldsymbol{\theta} = \begin{pmatrix} L_{12} & L_{21} \end{pmatrix}^\top$. In this case, a very tedious calculation yields a sparse matrix for $\frac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\mathbf{x}(t)^\top}$ and $\frac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\theta(t)^\top}$.

Below are the computed sensitivities for the disease model along with solution behavior for given parameters.



(a) $\alpha = 0.05$ (b) $\alpha = 0.05$ (c) $\alpha = 0.05$

FIG. 5.5. *The quantities* $M_\Omega^{\Gamma_i}$ *for* $t \in [0, 0.25]$ *and two different values of* ε.

5.4. Cholera Model with no Recruitment.

$$\begin{aligned}
\frac{dS}{dt} &= -\frac{\beta SB}{N} + bV - \theta S - \mu S + \alpha I \\
\frac{dV}{dt} &= \theta S + -bV - \mu V \\
\frac{dI}{dt} &= \frac{\beta SB}{N} - (d + \alpha + \mu) \\
\frac{dB}{dt} &= \gamma B + \eta I
\end{aligned}$$

$$N = S + V + I$$

Parameter	Description
β	Transmission Rate
μ	Natural Death Rate
d	Death due to Disease
σ	Vaccination Rate
b	Loss of Immunity from Vaccination
γ	Bacteria Growth
η	Infectious Individual's Contribution to Bacteria Growth
α	Recovery Rate

TABLE 5.1
Parameters

$$\frac{d}{dt}\begin{bmatrix} S \\ V \\ I \\ B \end{bmatrix} = \begin{bmatrix} -(\sigma+\mu) & b & \alpha & -\frac{\beta S}{N} \\ \sigma & -(b+\mu) & 0 & 0 \\ 0 & 0 & -(d+\alpha+\mu) & \frac{\beta S}{N} \\ 0 & 0 & \eta & \gamma \end{bmatrix} \begin{bmatrix} S \\ V \\ I \\ B \end{bmatrix}$$

$$\boldsymbol{\theta} = \begin{bmatrix} \beta & d & \sigma & b & \gamma & \eta & \alpha \end{bmatrix}^\top$$

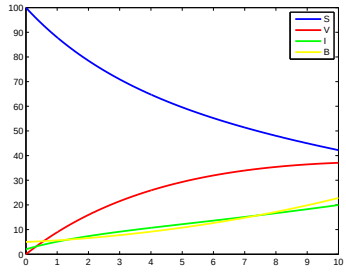


FIG. 5.6. *Cholera model with no recruitment in matrix form.*

(refer to Fig. 5.7 The transient sensitivity of susceptible, vaccinated, infected, and bacteria classes to the transmission rate, β. As the transmission rate, β, increases the susceptible population (blue line) and vaccinated population (red line) decrease while the infectious population (green line) and the bacteria population (yellow line) increase, which is the expected behavior.

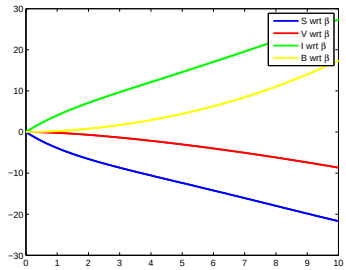


FIG. 5.7. *Need to add a caption.*

(refer Fig. 5.8) to The transient sensitivity of susceptible, vaccinated, infected, and bacteria classes to the loss of immunity from vaccination, b. This graph shows the effect on S, V, I, and B of increasing the parameter b, the loss of immunity from vaccination. The susceptible population (blue line) increases due to people leaving the vaccination class and returning to the susceptible class and the vaccinated class (red line) decreases. The infected class (green line) increases, this makes sense because as b increases there are fewer people with immunity. The bacteria (yellow line) also increases since there are more people who are infectious.

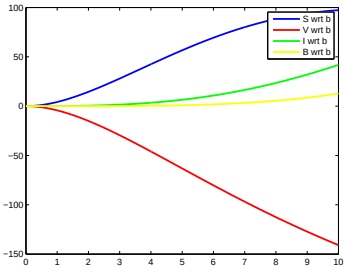


FIG. 5.8. *Need to add a caption*

5.5. Lungu's HIV Model. As yet another example, we consider the HIV epidemic model which has attracted a lot of interest from researchers in the field of diseases modeling; see for example [11, 12, 13, 15, 16]. We refer the reader to the above sources for details of infectious diseases modeling. For now, it suffices to point out that when a susceptible individual is infected with HIV, s/he goes through a latent period, or incubation period, before becoming infectious. For this reason, in addition to the susceptible (S), infected (I) and removed (R) classes, it is reasonable to introduce an exposed class (E) to obtain the model

$$\begin{aligned} \frac{dS}{dt} &= bN - dS - \lambda IS/N \\ \frac{dE}{dt} &= IS/N - (\epsilon + d)E \\ \frac{dI}{dt} &= \epsilon E - (\gamma + \alpha d)I \\ \frac{dR}{dt} &= \gamma I - dR \end{aligned} \tag{5.7}$$

where b is the recruitment rate, d is the mortality rate, λ, the infection rate, α, ..., ϵ, ..., and γ, ...

With the substitutions $s = S/N$, $e = E/N$, $i = I/N$, and $r = R/N$, and some rigorous algebraic manipulations, the model in (5.7) reduces to one with state variables that add to unity (i.e., $s + e + i + r = 1$) :

$$\begin{aligned} \frac{ds}{dt} &= b - bs - \lambda is + \alpha is \\ \frac{de}{dt} &= \lambda is - (\epsilon + b)e + \alpha ie \\ \frac{di}{dt} &= \epsilon e - (\gamma + \alpha + b)i + \alpha i^2 \end{aligned} \tag{5.8}$$

where the equation involving r has been omitted since the first three equations do not involve r, a parameter that can after all be obtained from the relation $s + e + i + r = 1$.

Now letting $\dot{\mathbf{x}} = (ds/dt,\ de/dt,\ di/dt)^\top$, the system of differential equations in (5.8) can be written in the matrix form

$$\dot{\mathbf{x}} = \mathbf{A}\mathbf{x} + \mathbf{b} \tag{5.9}$$

where

$$\mathbf{A} = \begin{pmatrix} -(b + \lambda i - \alpha i) & 0 & 0 \\ \lambda i & -(\epsilon + b - \alpha i) & 0 \\ 0 & \epsilon & -(\gamma + \alpha + b - \alpha i) \end{pmatrix}; \quad \mathbf{x} = \begin{pmatrix} s \\ e \\ i \end{pmatrix}; \quad \mathbf{b} = \begin{pmatrix} b \\ 0 \\ 0 \end{pmatrix}$$

Now, in a similar vein as in Example 5.2, we set the parameter vector $\boldsymbol{\theta} = (b, \lambda, \alpha, \epsilon, \gamma)$, and obtain

$$\frac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\boldsymbol{\theta}^\top} = \begin{pmatrix} -1 & -i & i & 0 & 0 \\ 0 & i & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ -1 & 0 & i & -1 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ -1 & 0 & i-1 & 0 & -1 \end{pmatrix}; \qquad \frac{\mathrm{d}(\mathbf{b})}{\mathrm{d}\boldsymbol{\theta}^\top} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

and

$$\frac{\mathrm{dvec}(\mathbf{A})}{\mathrm{d}\mathbf{x}^\top} = \begin{pmatrix} 0 & 0 & \alpha - \lambda \\ 0 & 0 & \lambda \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \alpha \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \alpha \end{pmatrix}$$

These matrix derivatives are then used to find the approximate solution of (4.4) as outlined in (4.5).

6. Future Directions. WE NEED A NICE SUMMARY AND FUTURE DIRECTIONS

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7. Appendix 1: Matlab Code for Example 5.2.

```
function f = Amat(t,y)

global r u alpha d sigma C;

C = alpha+d+r*u;
f = [ r*(1-y(1))*(y(1)-u) -alpha ; (sigma-1)*y(2) (-C-sigma*y(2)) ];
```

```
function f = DVEC1(t,y)

global r u alpha d sigma C;

f = [(1-y(1))*(y(1)-u) 0 -r*(1-y(1)) 0 0 0 0 ; 0 0 0 0 y(2) 0 0 ;  0 -1 0 0 0 0 0 ; -u -1 -r -1 ...
    -y(2) 0 0];
```

```
function f = DVEC2(t,y)

global r u alpha d sigma C;

f = [r*(-2*y(1)+1+u) 0 ; 0 sigma-1 ;  0 0 ; 0 -sigma];
```

```
global r u alpha d sigma C;

r = 0.2; alpha = 0.05; u = 0.75; d = 0.25; sigma = 1.2;

x0 = [ 0.8 ; 0.2 ];

t = linspace(0,10,10000);
delta_t = t(2)-t(1);

x = zeros(size(x0,1),size(t,2));
x(:,1) = x0;

for k = 2:size(x,2)
    temp = x(:,k-1) + delta_t*Amat(t(k-1),x(:,k-1))*x(:,k-1);
    x(:,k) = x(:,k-1) + delta_t/2*(Amat(t(k-1),x(:,k-1))*x(:,k-1)+Amat(t(k),temp)*temp);
end

x_sens = zeros(14,size(t,2));
x_sens([11,14],1) = [1 ; 1];
temp1 = zeros(2,7);
temp1(:,6:7) = eye(2);
% the sensitivity vector is
% theta = [ 'r' ; 'alpha' ; 'u' ; 'd' ; 'sigma' ; 'p(0)' ; 'i(0)' ];
for k = 2:size(x,2)
    temp2 = temp1 + delta_t*(Amat(t(k-1),x(:,k-1))*temp1 + ...
        kron((x(:,k-1))',eye(2))*DVEC1(t(k-1),x(:,k-1)) + ...
        kron((x(:,k-1))',eye(2))*DVEC2(t(k-1),x(:,k-1))*temp1);
    temp3 = temp1 + delta_t/2*(Amat(t(k-1),x(:,k-1))*temp1 + ...
        kron((x(:,k-1))',eye(2))*DVEC1(t(k-1),x(:,k-1)) + ...
        kron((x(:,k-1))',eye(2))*DVEC2(t(k-1),x(:,k-1))*temp1  +  Amat(t(k),x(:,k))*temp2 + ...
        kron((x(:,k))',eye(2))*DVEC1(t(k),x(:,k)) + kron((x(:,k))',eye(2))*DVEC2(t(k),x(:,k))*temp2);
    x_sens(:,k) = temp3(:);
    temp1 = temp3;
end
```