Appendix B. – Stability analysis of the OBE model

In this appendix, we provide details of the stability analysis of the dimensionless OBE model Eq. (2),

$$\frac{d\hat{I}_j}{d\hat{t}} = \left(1 + \hat{b}^\theta\right)\frac{\hat{H}^\theta_{j,\hat{t}-\hat{\tau}}}{\hat{b}^\theta + \hat{H}^\theta_{j,\hat{t}-\hat{\tau}}} - \hat{I}_j$$

$$\frac{d\hat{H}_j}{d\hat{t}} = \hat{m}\left(1 - \hat{H}_j\right) - \left(\hat{d} + \hat{\chi}\hat{I}_j\right)\hat{H}_j + \frac{1}{2}\left(\hat{d} + \hat{\chi}\hat{I}_{j-1}\right)\hat{H}_{j-1} + \frac{1}{2}\left(\hat{d} + \hat{\chi}\hat{I}_{j+1}\right)\hat{H}_{j+1}$$

, (B.1)

which is a delay-differential equation. The model in Eq. (B.1) is not analytically tractable because of non-linearities. In order to examine the propensity of Eq. (B.1) to exhibit persistent variability in induction levels and herbivore densities, we turn to linear stability analysis. The basic technique is to approximate a non-linear system with a linear one near enough to equilibrium that influences of non-linearities are very small. The benefit of making such an approximation is that linear systems are analytically tractable, and can effectively describe the stability properties of equilibria of non-linear models under most conditions (Murray 2003). Analyses based on linear approximation were confirmed with numerical simulations of non-linear models (not shown).

Defining the perturbations as $I_j = \bar{I}^* + i_j$ and $H_j = \bar{H}^* + h_j$, substituting these into Eq. (B.1) and ignoring small non-linear terms yields a linear equation with the general form

$$\frac{di_j}{dt} = a_{11}i_j + a_{12}h_{t-\tau,j}$$

$$\frac{dh_j}{dt} = a_{21}i_{j-1} + a_{22}i_j + a_{23}i_{j+1} + a_{24}h_{j-1} + a_{25}h_j + a_{26}h_{j+1}$$

(B.2)

where $a_{11} = -1, a_{12} = \frac{b^\theta \theta}{1+b^\theta}, a_{21} = \frac{\chi}{2}\bar{H}^*, a_{22} = -\chi\bar{H}^*, a_{23} = \frac{\chi}{2}\bar{H}^*, a_{24} = \frac{d + \chi\bar{I}^*}{2}$,

$a_{25} = -m - \left(d + \chi \overline{I}^* \right)$, and $a_{26} = \dfrac{d + \chi \overline{I}^*}{2}$. Note that, because of our choices of base units during

dimensional analysis, $\overline{I}^* = \overline{H}^* = 1$. Perturbations i and h that grow indicate instability and the

presence of persistent spatial variation in both induction and herbivore densities.

Given that we are looking at the stability of perturbations with a spatial signal, further

progress is facilitated with the use of Fourier transforms. The Fourier transform characterizes any

signal as the sum of sinusoids with—in our case—different spatial frequencies k and spatial

wavelengths $2\pi/k$. The Fourier transforms of i and h are defined as $\tilde{i}(k) = \sum_{j=1}^{n} i_j e^{-Ijk}$ and

$\tilde{h}(k) = \sum_{j=1}^{n} h_j e^{-Ijk}$ where $I = \sqrt{-1}$. Applying these to Eq. (B.2)—noting that the Fourier

transform of a discrete lagged function is $\tilde{n}_{j-1} = \tilde{n}_j e^{-Ik}$ (Nisbet and Gurney 2003)—gives

$$
\begin{aligned}
\frac{d\tilde{i}}{dt} &= -\tilde{i} + \frac{b^\theta \theta}{1 + b^\theta} \tilde{h}_{t-\tau} \\
\frac{d\tilde{h}}{dt} &= \chi \overline{H}^* \left(\frac{1}{2} e^{-Ik} - 1 + \frac{1}{2} e^{Ik} \right) \tilde{i} + \left(d + \chi \overline{I}^* \right) \left(\frac{1}{2} e^{-Ik} - 1 + \frac{1}{2} e^{Ik} \right) \tilde{h} - m\tilde{h}
\end{aligned}
\tag{B.3}
$$

Note how the equations now describe the dynamics of a spatial distribution with frequency k

rather than resistance levels and herbivore densities in a given patch j.

To simplify further analyses, it is desirable to replace the complex exponentials above

with more tractable quantities. For ease of presentation, we opt to replace these terms with

approximations obtained using second-order Taylor series expansions around $k = 0$, where

$e^{-Ik} \approx 1 - Ik - \dfrac{k^2}{2} + O[k]^3$. From this approximation, we can make the substitution

$\left(\dfrac{1}{2} e^{-Ik} - 1 + \dfrac{1}{2} e^{Ik} \right) \approx -\dfrac{k^2}{2}$. An exact (real) substitution can be made for the complex exponentials

in the bracketed expression using Euler's formula; however, the Taylor approximation is easier to interpret by avoiding trigonomic functions and is extremely accurate up to at least $k = \pi$. After some simplification,

$$\frac{d\tilde{i}}{dt} = -\tilde{i} + \frac{b^{\theta}\theta}{1+b^{\theta}}\tilde{h}_{t-\tau}$$
$$\frac{d\tilde{h}}{dt} = -\chi\bar{H}^{*}\frac{k^2}{2}\tilde{i} - \left(m + \left(d + \chi\bar{I}^{*}\right)\frac{k^2}{2}\right)\tilde{h}$$
\hfill (B.4)

We now look for solutions to Eq. (B.4) of the form $e^{\lambda t}$. Substituting the ansatz $\tilde{i} = \Psi e^{\lambda t}$ and $\tilde{h} = \Phi e^{\lambda t}$ and re-arranging yields the corresponding characteristic equation for the system,

$$0 = \lambda^2 + B_1\lambda + B_2 + B_3 e^{-\lambda\tau}$$
\hfill (B.5)

where $B_1 = 1 + m + \frac{k^2}{2}\left(d + \chi\bar{I}^{*}\right)$, $B_2 = m + \left(d + \chi\bar{I}^{*}\right)\frac{k^2}{2}$, and $B_3 = \frac{\chi\bar{H}^{*}k^2 b^{\theta}\theta}{2\left(1+b^{\theta}\right)}$. A perturbation to

induction levels or herbivore densities with spatial frequency k will increase to form persistent aggregations if the real part of λ, $\mathrm{Re}(\lambda)$, is greater than zero; we refer to this quantity in the text as the perturbation growth rate ξ. Equation (B.5) is a transcendental equation, meaning that we cannot algebraically find closed form representations for λ. However, systems with characteristic equations in the form of Eq. (B.5), especially conditions on their stability, have been well studied (Kuang 1993). Transitions to instability happen through a Hopf bifurcation such that we have solutions to Eq. (B.5) in the form of $\lambda = I\omega$ at a some critical time delay τ_C. This implies (see (Kuang 1993 for details),

$$\omega_{\pm} = \sqrt{\frac{2B_2 - B_3^2 \pm \sqrt{\left(2B_2 - B_3^2\right)^2 - 4\left(B_2^2 - B_3^2\right)}}{2}}$$
\hfill (B.6)

There are two cases we need to consider to determine whether there exists a solution

$\lambda = I\omega$ to Eq. (B.5). First, when $B_3^2 - B_2^2 \geq 0$, there exists one solution $\lambda = I\omega_+$. When the time delay exceeds the critical time delay τ_C, the system loses stability through this root and does not regain it for any $\tau > \tau_C$. When $B_3^2 - B_2^2 < 0$, there can be two solutions, $\lambda_\pm = I\omega_\pm$, given other conditions hold true. A necessary (but not sufficient) condition is $2B_2 - B_1^2 > 0$. For the OBE model, $2B_2 - B_1^2 = -1 - \left(m + (d + \chi \overline{I}^*) \dfrac{k^2}{2} \right)^2$. Thus, stability can only be lost when

$$\Lambda = B_3^2 - B_2^2 \geq 0 \tag{B.7}$$

where

$$\lambda = I\omega_+, \quad \omega_+ = \sqrt{\dfrac{2B_2 - B_3^2 + \sqrt{\left(2B_2 - B_3^2\right)^2 - 4\left(B_2^2 - B_3^2\right)}}{2}} . \tag{B.8}$$

We refer to Λ as the "instability metric" in the text. The critical time delay τ_C that makes Eq. (B.8) is true is derived in (Kuang 1993) as

$$\tau_C = \dfrac{\cos^{-1}\left(\dfrac{\omega^2 - B_2}{B_3}\right)}{\omega} . \tag{B.9}$$

Stability analyses of the OBME and LBME are accomplished in the same manner as outlined for the OBE model above.

For Eq. (B.4), $B_3^2 - B_2^2 \geq 0$ is

$$\dfrac{\theta b^\theta}{1 + b^\theta} - \dfrac{2m}{\chi k^2} - \dfrac{d}{\chi} - 1 \geq 0 \tag{B.10}$$

In the best case for stability, where m and d approach zero, we see that instability requires

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$$\frac{\theta b^{\theta}}{1+b^{\theta}} > 1.$$

The importance of the induction time delay can be demonstrated by examining the case where the time delay is absent, as the model is always stable in this instance. Setting $\tau = 0$ sets the exponential term $e^{-\lambda\tau}$ in Eq. (B.5) to one, transforming the characteristic equation into a simple quadratic equation commonly encountered in two-species consumer-resource models (Murdoch et al. 2003). Routh-Hurwitz stability conditions for such a two state variable system guarantee stability when

$$B_1 > 0 \quad \text{and} \quad B_2 + B_3 > 0. \tag{B.11}$$

For the OBE equation with no time delay, $B_1 = 1 + m + \frac{k^2}{2}(d + \chi)$ and

$B_2 + B_3 = m + \frac{b^{\theta}k^2\theta\chi}{2(1+b^{\theta})} + \frac{k^2}{2}(d + \chi)$, both satisfying the inequalities in Eq. (B.11).

The OBE model is always stable in the face of global perturbations. Such global perturbations have a frequency $k = 0$, meaning an essentially infinite spatial wavelength (i.e., the wave becomes flat). Setting $k = 0$ in Eq. (B.5) causes it to simplify in such a way that $\lambda = \text{Max}\{-m, -1\}$. Thus, the system is always stable in the face of global perturbations and, because λ is always a real number in this case, does not even show transient oscillations.

Some level of herbivore movement sensitivity χ is required for spatial patterns to develop. When $\chi = 0$, $B_3^2 - B_2^2 = -\frac{1}{4}(dk^2 + 2m)^2$ and the stability criterion Eq. (B.7) can never be satisfied.

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