The effects of seasonality on competition for a limiting resource

Lluc Briganti Wiprachtiger[†]

Project Advisor: Lukas Eigentler[‡]

Abstract. Theoretical studies of PDE/ODE models describing ecosystem dynamics usually ignore seasonality in environmental conditions. In this paper I study a model of two generic consumer species that compete for a single limiting resource. I first consider constant resource input and then compare it to the case when resource input is dependent on time with a seasonal (periodic) pattern. The model with constant resource input is analysed analytically, by looking at the linear stability of every equilibrium. The model with seasonal resource input is analysed through numerical simulations. Results of the analysis show that seasonality has a significant effect on the outcome of the system, as when resource input is dependent on time, there could be stable coexistence, which is not possible under constant resource input. Moreover, metastable coexistence states exist for both resource input regimes if the average fitness difference between species is small. Finally, times until extinction become longer if resource input is not constant.

1. Introduction.

In a setting where two species compete for the same limiting resource, one of the species, even with the slightest advantage, will dominate over the other, and cause the extinction of its competitor. This is the competitive exclusion principle [9]. The species that dominates in this kind of system is determined by Tilman's R^* rule [16, 24], which states that the species that will outcompete the other will be the one that can survive with less amount of resource available.

A substantial amount of research using mathematical models has been done on coexistence under competition for one limiting resource. The term "limiting resource" refers to a resource that limits growth and therefore, if insufficient in quantity, can be the cause of one species dying out [6, 7, 16, 25]. According to the competitive exclusion principle, coexistence cannot occur in these circumstances [9, 17]. However, in nature coexistence is commonly observed. The competitive exclusion principle therefore suggests the presence of other coexistence-enabling mechanisms [16].

Even when no mechanism stabilising coexistence is present, species coexistence can occur through metastability [8]. A metastable state of an ecosystem in an inherently unstable state that nevertheless occurs as a long transient. In the context of competition dynamics, it can occur if two species have similar average fitness. In cases in which the competitive exclusion principle applies, the near balance between species causes the extinction process to take a long time. Therefore, coexistence can occur as a long transient in such cases. Mathematically, metastability is characterised by the small magnitude of one of the eigenvalues in the linear stability analysis of one (or more) of a model's equilibria [20]. This describes slow convergence or divergence to or from an equilibrium, meaning that coexistence may occur as a transient state in the system.

Another mechanism that enables coexistence in a system of competition for the same

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[†]Mathematics, School of Science and Engineering, University of Dundee, Dundee DD1 4HN, United Kingdom

[‡]Mathematics, School of Science and Engineering, University of Dundee, Dundee DD1 4HN, United Kingdom. Division of Molecular Microbiology, School of Life Sciences, University of Dundee, Dundee DD1 5EH, United Kingdom

limiting resource is seasonality in resource input over time [5, 14, 22]. Many ecosystems are fundamentally underpinned by seasonality, especially in temperate and continental climates [19].

Despite how common seasonal fluctuations are [26], resource input is considered to be constant in many ODE/PDE models describing resource-consumer interactions. Therefore, in this paper I will address the question of how seasonality affects metastable coexistence in resource limited ecosystems. In Section 2 I will introduce the model, then in Section 3 I will analyse the case with constant resource input, and finally in Section 4 I will compare it to the case with seasonal resource input.

2. Competition for nutrients model. In the standard Lotka-Volterra competition model, competition between species is modelled by combining all intra- and interspecific competitive mechanisms into single parameters, the competition coefficients. However, in many environments, species typically compete for limiting resources, which is not accounted for explicitly in the Lotka-Volterra model. The limiting nature of the resources requires explicit consideration of consumer-resource dynamics in mathematical models. The following model describes the interaction between two species competing for a single limiting resource:

(2.1)
$$
\begin{aligned}
\frac{dA_1}{dt} &= \frac{a_1 b_1 R A_1}{1 + a_1 h_1 R} - \mu_1 A_1, \\
\frac{dA_2}{dt} &= \frac{a_2 b_2 R A_2}{1 + a_2 h_2 R} - \mu_2 A_2, \\
\frac{dR}{dt} &= f(t) - jR - \frac{a_1 R A_1}{1 + a_1 h_1 R} - \frac{a_2 R A_2}{1 + a_2 h_2 R}.
\end{aligned}
$$

In this model, A_i represents population density of species, $i = 1, 2$, and R is resource density. a_i the rate at which species i reproduces, b_i the nutrient-to-biomass conversion coefficient (yield), h_i is the handling time, μ_i is the death rate, $f(t)$ is the nutrient input and j is the nutrient decay rate. The parameter $f = f(t)$ in this model will be considered as a constant at first, in which case it will represent a constant resource input over time. This is an approach commonly taken in many models describing consumer-resource interactions, despite being unable to account for temporal fluctuations in resource input in ecological systems. Therefore, I will also consider the case in which $f(t)$ is dependent on time in Section 4, meaning that the resource input will be affected by seasonality.

Parameter	Interpretation	Units
A_1	Population density of species 1	g
A_2	Population density of species 2	g
R	Resource density	g
t	Time	s
a_1	Rate at which species 1 reproduces	1/gs
a_2	Rate at which species 2 reproduces	1/gs
b_1	Nutrient to biomass conversion coefficient of species 1	dimensionless
b_2	Nutrient to biomass conversion coefficient of species 2	dimensionless
h_1	Handling time of species 1	s
h_2	Handling time of species 2	s
μ_1	Death rate of species 1	1/s
μ_2	Death rate of species 2	1/s
$f(t)$	Nutrient input	g/s
j	Nutrient decay rate	1/s

Table 1: Dimensional model parameters, interpretation and units.

2.1. Nondimensionalisation. The model can be nondimensionalised by the following substitutions:

$$(2.2) \qquad B_i = \frac{A_i a_1}{\mu_1}, \qquad\qquad \widetilde{R} = \frac{R a_1 b_1}{\mu_1}, \qquad\qquad \widetilde{t} = \mu_1 t,$$

and by dropping the tildes for brevity, we get the nondimensional model

$$(2.3) \qquad \begin{aligned} \frac{dB_1}{dt} &= \frac{RB_1}{1 + K_1 R} - B_1, \\ \frac{dB_2}{dt} &= \frac{gcRB_2}{1 + K_2 R} - mB_2, \\ \frac{dR}{dt} &= r(t) - nR - \frac{RB_1}{1 + K_1 R} - \frac{gRB_2}{1 + K_2 R}, \end{aligned}$$

where

$$K_1 = \frac{h_1 \mu_1}{b_1}, \quad K_2 = \frac{a_2 h_2 \mu_1}{a_1 b_1}, \quad m = \frac{\mu_2}{\mu_1}, \quad r(t) = \frac{f(t)}{a_1 b_1}, \quad n = \frac{j}{\mu_1}, \quad g = \frac{a_2}{a_1}, \quad c = \frac{b_2}{b_1}.$$

The parameters K_1 and K_2 are are a combination of several constants of the original model, and they represent the handling time constant for species 1 and 2 respectively. The parameter $r(t)$ represents resource input, and n represents the decay rate of the resource. Finally, m represents the ratio of the death rates, g is the ratio of the reproduction rates and c is the ratio of the nutrient conversion coefficients.

3. Model analysis for constant resource input. In this section I will consider a constant resource input, i.e. $r(t) = r$.

3.1. Equilibria. I will start the investigation into possible coexistence mechanisms in the model by a calculation of the system's equilibria, determined by setting the right-hand sides of (2.3) equal to zero:

(3.1)
$$\frac{RB_1}{1 + K_1 R} - B_1 = 0,$$
$$\frac{gcRB_2}{1 + K_2 R} - mB = 0,$$
$$r - nR - \frac{RB_1}{1 + K_1 R} - \frac{gRB_2}{1 + K_2 R} = 0.$$

There are three possible steady states, which are the following:

$$S_1 = \left(\frac{K_1 r + n - r}{K_1 - 1}, 0, \frac{1}{1 - K_1} \right),$$
$$S_2 = \left(0, 0, \frac{r}{n} \right),$$
$$S_3 = \left(0, \frac{c(K_2 mr - cgr + mn)}{m(K_2 m - gc)}, \frac{m}{gc - K_2 m} \right).$$

Note that there is one extinction equilibrium (S_2) in which no species survives and two single-species equilibria (S_1 and S_3) in which one species competitively excludes the other, but no coexistence state. S_2 is always biologically relevant, i.e. it is always a positive real number. For S_1 to be biologically relevant, $K_1 < 1$ and $r > \frac{n}{1 - K_1}$ are required. For S_3 to be biologically relevant $K_2 < \frac{gc}{m}$ and $r > \frac{mn}{cg - K_2 m}$ are required.

3.2. Linear stability analysis. In this section I will look at the linear stability of the equilibria found in the previous section. To determine the stability of an equilibrium, it is necessary to first find the eigenvalues of the Jacobian matrix of the system, evaluated at the equilibrium. For model (2.3), the Jacobian is:

$$J = \begin{pmatrix} \dfrac{R}{K_1 R + 1} - 1 & 0 & \dfrac{B_1}{K_1 R + 1} - \dfrac{RB_1 K_1}{(K_1 R + 1)^2} \\[2ex] 0 & \dfrac{gcR}{K_2 R + 1} - m & \dfrac{gcB_2}{K_2 R + 1} - \dfrac{gcRB_2 K_2}{(K_2 R + 1)^2} \\[2ex] -\dfrac{R}{K_1 R + 1} & -\dfrac{gR}{K_2 R + 1} & -n - \dfrac{B_1}{K_1 R + 1} + \dfrac{RB_1 K_1}{(K_1 R + 1)^2} - \dfrac{gB_2}{K_2 R + 1} + \dfrac{gRB_2 K_2}{(K_2 R + 1)^2} \end{pmatrix}.$$

For an equilibrium to be stable, the real parts of all the eigenvalues of J need to be negative. Determination of stability conditions for the extinction steady state S_2 is straightforward through direct calculation of the Jacobian's eigenvalues, but for S_1 and S_3, I will take a different approach, as some of the eigenvalues are algebraically complex.

I will start by analysing S_2, for which the Jacobian is:

$$J_2 = \begin{pmatrix} \frac{-K_1-n+r}{K_1r+n} & 0 & 0 \\ 0 & \frac{-K_2mr+cgr-nm}{K_2r+n} & 0 \\ -\frac{r}{K_1r+n} & -\frac{gr}{K_2r+n} & -n \end{pmatrix}.$$

The eigenvalues of J_2 are:

$$\lambda_1^2 = -n, \qquad \lambda_2^2 = \frac{-K_2mr + cgr - nm}{K_2r + n}, \qquad \lambda_3^2 = \frac{-K_1r - n + r}{K_1r + n},$$

where the subscript is the index of the eigenvalue and the superscript is the index of the equilibrium. Note that $\lambda_1^2 < 0$ because $n > 0$, therefore the equilibrium is stable if and only if $\lambda_2^2 < 0$ and $\lambda_3^2 < 0$, which holds if $r < \min(\frac{mn}{cg-K_2m}, \frac{n}{1-K_1})$.

For S_1 and S_3, it is harder to analyse the eigenvalues this way. Substituting S_1, the Jacobian matrix J becomes:

$$J_1 = \begin{pmatrix} 0 & 0 & (K_1-1)((K_1-1)r+n) \\ 0 & \frac{(-K_1+K_2+1)m-gc}{-K_2+K_1-1} & 0 \\ -1 & \frac{g}{-K_2+K_1-1} & -K_1^2r+(-n+2r)K_1-r \end{pmatrix}.$$

To find the eigenvalues, the equation $|J_1 - \lambda I| = 0$ needs to be solved. The equation can be simplified to

$$\left(\frac{(-K_1+K_2+1)m-gc}{-K_2+K_1-1} - \lambda \right) \begin{vmatrix} -\lambda & (K_1-1)((K_1-1)r+n) \\ -1 & (-K_1^2r+(-n+2r)K_1-r) - \lambda \end{vmatrix} = 0.$$

Note that the eigenvalues of S_1 are found using the cofactor expansion. Therefore, S_1 is stable if and only if it is stable to the introduction a competitor species (determined by $\lambda_3^1 = \frac{(-K_1+K_2+1)m-gc}{-K_2+K_1-1}$) and stable in the sense of a single-species model (determined by the eigenvalues of $M_{22}(J_1)$, where $M_{22}(J_1)$ denotes the submatrix obtained from J_1 by deleting its second row and second column). $M_{22}(J_1)$ is the following matrix, and can be thought of the Jacobian matrix defining a single-species model:

$$M_{22}(J_1) = \begin{pmatrix} 0 & (K_1-1)((K_1-1)r+n) \\ -1 & -K_1^2r+(-n+2r)K_1-r \end{pmatrix}.$$

For $M_{22}(J_1)$, the trace is $\mathrm{tr}(M_{22}(J_1)) = -K_1^2r + 2K_1r - K_1n - r$, which for the first steady state, $\left(\frac{K_1r+n-r}{K_1-1}, \frac{1}{1-K_1} \right)$, to be stable, needs to be smaller than 0. Solving the inequality I get the condition that $r > \frac{K_1n}{2K_1-K_1^2-1}$. In this case $\det(M_{22}(J_1)) > 0$ for all parameter values, as $K_1 < 1$.

The eigenvalue determining stability to the introduction of a competitor is:

$$\lambda_3^1 = \frac{(-K_1 + K_2 + 1)m - gc}{-K_2 + K_1 - 1}.$$

For the steady state $\left(\frac{K_1 r + n - r}{K_1 - 1}, 0, \frac{1}{1 - K_1}\right)$ to be stable, $\lambda_3^1 < 0$ is needed, and $m > \frac{cg}{K_2 - K_1 + 1}$ is required for stability.

Combined, for S_1 to be stable, the following conditions must hold:

$$(3.2) \qquad r > \frac{K_1 n}{2K_1 - K_1^2 - 1}, \qquad\qquad m > \frac{cg}{K_2 - K_1 + 1}.$$

Similarly, for S_3, the Jacobian matrix becomes:

$$J_3 = \begin{pmatrix} \frac{(-K_1 + K_2 + 1)m - gc}{(K_1 - K_2)m + gc} & 0 & 0 \\ 0 & 0 & \frac{(-K_2 m + gc)((-K_2 r - n)m + cgr)}{gm} \\ -\frac{m}{(K_1 - K_2)m + gc} & -\frac{m}{c} & \frac{-K_2^2 m^2 r + 2K_2 cgmr - c^2 g^2 r - K_2 m^2 n}{gcm} \end{pmatrix}.$$

To find the eigenvalues, the equation $|J_3 - \lambda I| = 0$ needs to be solved. The equation can be simplified to:

$$\left(\frac{(-K_1 + K_2 + 1)m - gc}{(K_1 - K_2)m + gc} - \lambda\right) \begin{vmatrix} -\lambda & \frac{(-K_2 m + gc)((-K_2 r - n)m + cgr)}{gm} \\ -\frac{m}{c} & \left(\frac{-K_2^2 m^2 r + 2K_2 cgmr - c^2 g^2 r - K_2 m^2 n}{gcm}\right) - \lambda \end{vmatrix} = 0.$$

Again, the eigenvalues of S_3 are found using the cofactor expansion. Two of the eigenvalues are found from the reduced matrix and the remaining eigenvalue $\lambda_3^3 = \frac{(-K_1 + K_2 + 1)m - gc}{(K_1 - K_2)m + gc}$ determines the stability of the steady state to the introduction of a competitor species. $M_{11}(J_3)$ is defined in a similar manner as $M_{22}(J_1)$.

For $M_{11}(J_3)$, where $M_{11}(J_3)$ denotes the submatrix obtained from J_3 by deleting its first row and first column, determining the stability in the sense of the single-species model, the trace is

$$\text{tr}(M_{11}(J_3)) = \frac{K_2^2 m^2 r + 2K_2 cgmr - c^2 g^2 r - K_2 m^2 n}{cgm},$$

which for the third steady state, $\left(\frac{c(K_2 mr - cgr + mn)}{m(K_2 m - gc)}, \frac{m}{gc - K_2 m}\right)$, to be stable, $\text{tr}(M_{11}(J_3)) < 0$ is needed. Solving the inequality, we get the condition $r > \frac{K_2 m^2 n}{2K_2 cgm - K_2^2 m^2 - c^2 g^2}$. In this case $\det(M_{11}(J_3)) > 0$ for all parameter values.

The remaining eigenvalue determining stability to the introduction of a competitor is:

$$\lambda_3^3 = \frac{(-K_1 + K_2 + 1)m - gc}{(K_1 - K_2)m + gc},$$

which needs to be smaller than 0 for the third steady state, $\left(0, \frac{c(K_2mr - cgr + mn)}{m(K_2m - gc)}, \frac{m}{gc - K_2m}\right)$, to be stable. Thus, $m < \frac{cg}{K_1 - K_2 - 1}$ is required for stability.

Therefore for the steady state S_3 to be stable the following conditions must hold:

$$(3.3) \qquad r > \frac{K_2 m^2 n}{2K_2 cgm - K_2^2 m^2 - c^2 g^2}, \qquad\qquad m < \frac{cg}{K_1 - K_2 - 1}.$$

For any given parameter set, only one competitor species can survive (Table 2), as S_1 and S_3 have opposite stability conditions on m. Therefore these two equilibria cannot be stable at the same time.

Equilibrium	Conditions for stability
$S_1 = \left(\frac{K_1 r + n - r}{K_1 - 1}, 0, \frac{1}{1 - K_1}\right)$	$r > \frac{K_1 n}{2K_1 - K_1^2 - 1}$ and $m > \frac{cg}{K_2 - K_1 + 1}$
$S_2 = \left(0, 0, \frac{r}{n}\right)$	$r < \frac{mn}{cg - K_2 m}$ and $r < \frac{n}{1 - K_1}$
$S_3 = \left(0, \frac{c(K_2 mr - cgr + mn)}{m(K_2 m - cg)}, \frac{m}{cg - K_2 m}\right)$	$r > \frac{K_2 m^2 n}{2K_2 cgm - K_2^2 m^2 - c^2 g^2}$ and $m < \frac{cg}{K_2 - K_1 + 1}$

Table 2: Conditions for stability for each of the equilibria

3.3. The special case when $m = \frac{cg}{K_2 - K_1 + 1}$**.** It was shown in the linear stability analysis above that the steady states S_1 and S_3 cannot be stable at the same time. But, what happens if $m = \frac{cg}{K_2 - K_1 + 1}$?

In this case, calculation of the Jacobian's eigenvalues for both S_1 and S_3 yield a zero eigenvalue. Therefore, linear stability analysis is unable to provide information on the equilibria's stability. Tools from non-linear analysis could be used to acquire more information on the equilibria's stability in this special case [12], but this is not attempted here. Instead, I use numerical simulations to investigate the system's dynamics for $m = \frac{cg}{K_2 - K_1 + 1}$. The system can be solved numerically using Matlab's ODE solver ode15s. Visualisations of the model solution show that in this case, there is stable coexistence (Figure 1).
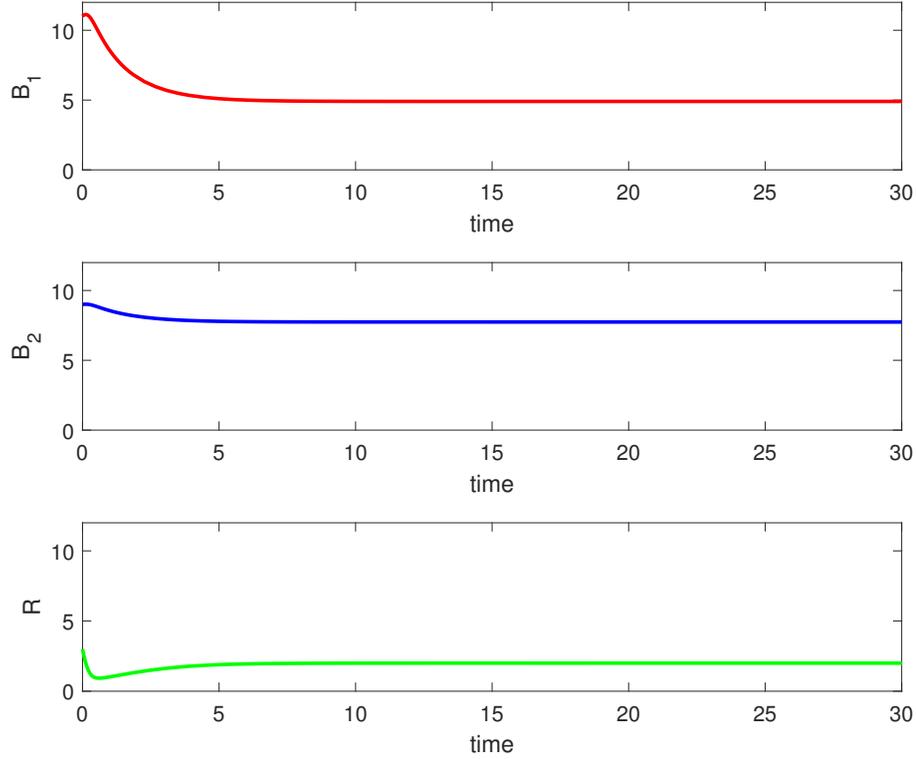
Figure 1: Numerical simulation for the threshold case $m = \frac{cg}{K_2 - K_1 + 1}$, with values $K_1 = \frac{1}{2}$, $K_2 = 2$, $g = 1$, $c = 1$, $m = \frac{2}{5}$, $r = 10$ and $n = 1$.

3.4. Biological interpretation. The previous section revealed the behaviour of the model for the cases $m < \frac{cg}{K_2 - K_1 + 1}$, $m = \frac{cg}{K_2 - K_1 + 1}$ and $m > \frac{cg}{K_2 - K_1 + 1}$ from a mathematical point of view. In this section I will interpret these model dynamics from a biological viewpoint.

I will start comparing the resource components of the first and third equilibria, which I will call R_1^* and R_3^*, respectively. Recall that they are given by

$$R_1^* = \frac{1}{1 - K_1},$$
$$R_3^* = \frac{m}{cg - K_2 m}.$$

Solving the equation $R_1 = R_3$, the resources are equal if and only if $m = \frac{cg}{K_2 - K_1 + 1}$. Thus, $R_1 < R_3$, then $m > \frac{cg}{K_2 - K_1 + 1}$, and if $R_1 > R_3$, then $m < \frac{cg}{K_2 - K_1 + 1}$.

The threshold on m is the same as one of the conditions for stability for the first and third equilibria (S_1 and S_3). Therefore, provided that resource input r is sufficiently large, S_3 is

stable if and only if $R_1 > R_3$ and S_1 is stable if and only if $R_1 < R_3$. Thus, it can be concluded that the species that survives is the one that can reduce the resource the most. This is known as Tilman's R^* rule [16]. Hence, a species' ability to reduce the limiting resource can also be associated with its average fitness. Moreover,

$$(3.4) \qquad \underbrace{m}_{\text{mortality}} - \underbrace{\overbrace{cg}^{\text{growth rate}}}_{\substack{K_2 - K_1 + 1 \\ \text{handling time}}}$$

can be regarded as the average fitness difference between both species, meaning the ability to survive depends on a species' mortality rate, growth rate and handling time relative to its competitor. That is, if the average fitness difference is negative, then S_3 is stable and B_2 competitively excludes B_1, and vice versa if the average fitness difference is positive, then S_1 is stable and B_1 competitively excludes B_2. Furthermore, if $m = \frac{cg}{K_2 - K_1 + 1}$, then $R_1 = R_3$. This means that both species have the same capacity to reduce the resource and identical average fitness, and there is coexistence. All of this is shown in Figure 2.

3.5. Metastability. The analysis above highlights that stable coexistence is only possible if the two species have exactly the same average fitness (i.e. $m = \frac{cg}{K_2 - K_1 + 1}$) and any slight variation from this would lead to the extinction of one of the species. Extinction in this paper is defined as the time t_{ext}, such that $\min(B_1(t), B_2(t)) < 1$ for all $t \geq t_{ext}$. However, in biological systems it is highly unrealistic for two species to have exactly the same average fitness. Nevertheless, if m is close to the critical value, numerical simulations reveal that it takes a long time for one of the species to go extinct (a long time being of an order of 10^4). This means that the two species will be able to coexist for a long period of time before one of them vanishes. This phenomenon is called metastability and it occurs if the species' average fitness is similar. The sign of $m - \frac{cg}{K_2 - K_1 + 1}$ determines to which equilibrium the system converges eventually and its magnitude determines whether metastability occurs or not. Metastability occurs if the largest absolute value of the eigenvalue of the stable single-species equilibrium is small. Thus, for initial conditions where the species coexist, the system transits to the stable equilibrium very slowly, making the system spend a long time in a transient coexistence state. This phenomenon is called metastability, because solutions observed in a short time interval appear to be stable despite their inherent instability. Figure 3 shows an example in which metastability occurs:

Furthermore, the time it takes until one of the species goes extinct can be predicted with excellent accuracy using the eigenvalues from the linear stability analysis, considering a species extinct when the density is less than 1 for all $t > t_{ext}$. This can be demonstrated by plotting the time until extinction against $\frac{1}{\lambda_{max}}$, where λ_{max} is the biggest eigenvalue of the unstable single-species steady state (Figure 4).

4. Time-dependent fluctuations in resource input. In a real life setting, the resource input is never constant, due to it being dependent on weather and many other factors. While resource input is typically underpinned by stochastic mechanisms, seasonal trends play a role
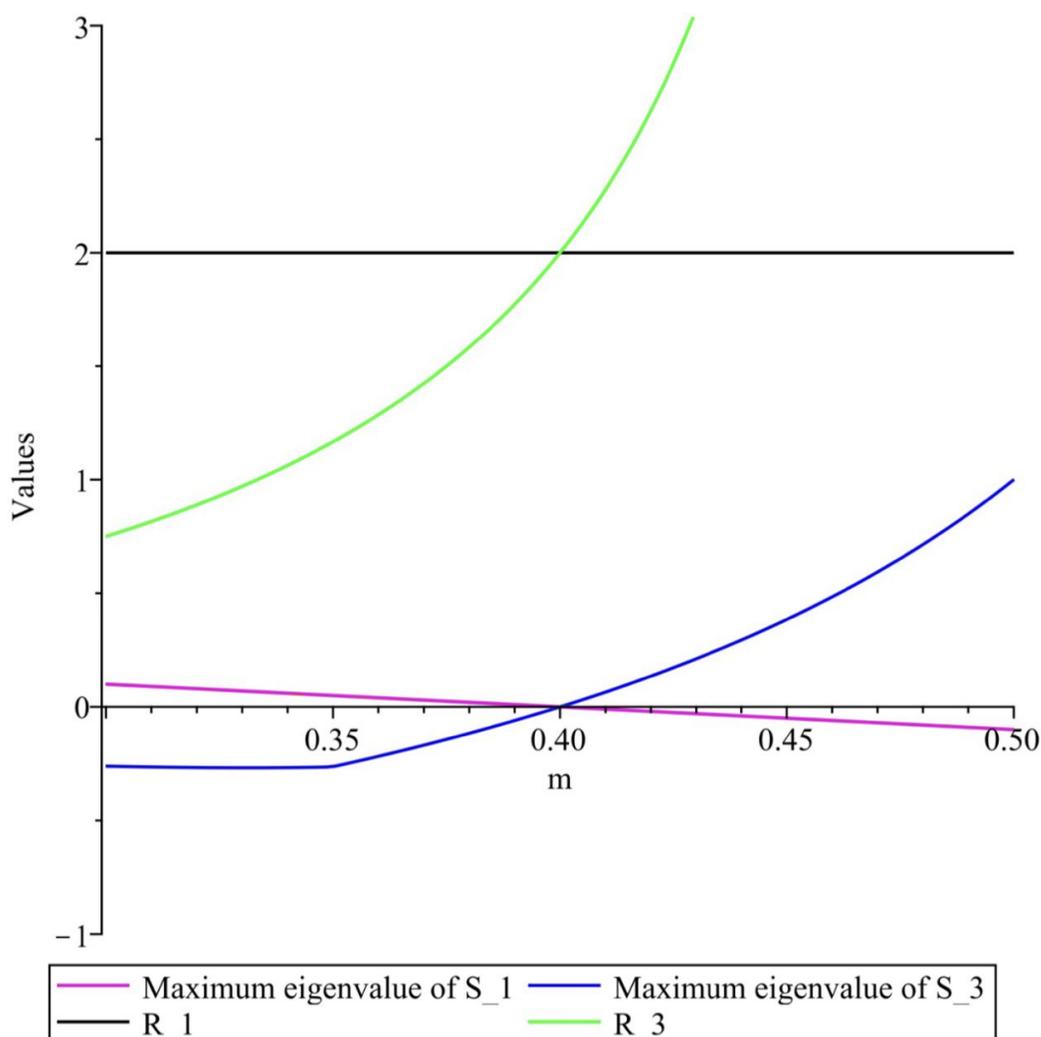
Figure 2: This figure shows the maximum eigenvalues (blue and red) and resource densities (black and green) of S_1 and S_3. Note that at the point where both species have the same average fitness both species have the same ability to reduce the resource.

in temperate and continental climates [21]. This can be represented in the model by making $r(t)$, the nutrient input, dependent on time.

There are many potential ways to impose time dependence on $r(t)$. Here I compare two choices to the case where r is constant. One is having the value for r change every 50 time units in a periodic fashion with period $T = 100$:

$$r_1(t) = \begin{cases} a, & 100n \leq t < 100n + 50 \\ b, & 100n + 50 \leq t < 100(n + 1) \end{cases},$$
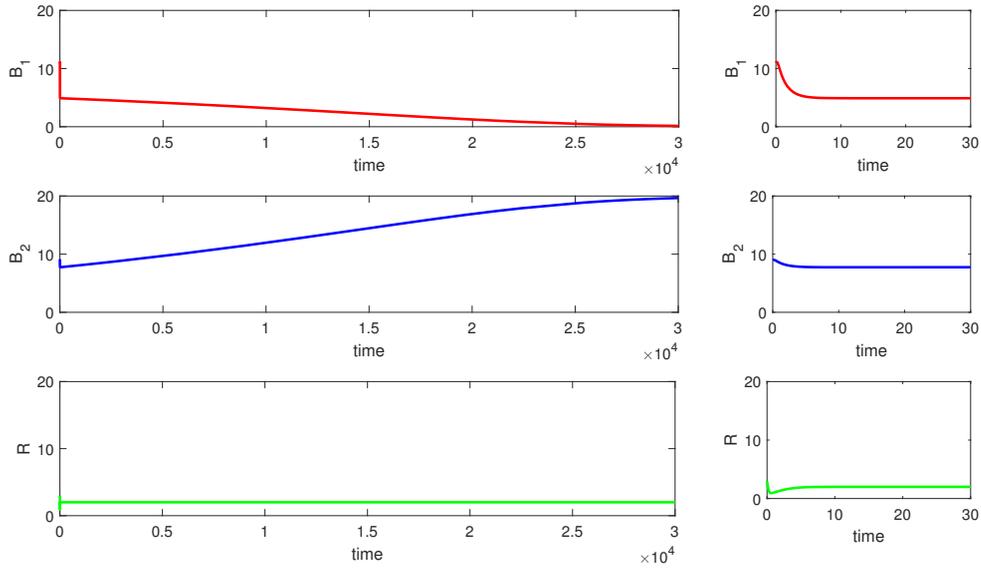
Figure 3: Numerical simulation with $m = 0.39995$, $K_1 = \frac{1}{2}$, $K_2 = 2$, $g = 1$, $c = 1$, $r = 10$ and $n = 1$. The left column shows the behaviour of the system after a long time, while the right column is zoomed in on the first 30 time points.

where $a,b \in \mathbb{R}$ and $n \in [0, \infty)$. In the numerical simulations I use $a = 5$ and $b = 15$, which means that the average resource input is 10, the same as in the numerical simulations with constant resource input.

The other approach is to impose a sinusoidal oscillation on the resource input by setting:

$$r_2(t) = \bar{r} + C \sin\left(\frac{2\pi}{T}t\right),$$

where $\bar{r} \in \mathbb{R}$, C is a constant between 0 and $\bar{r}$, to ensure that resource input is never smaller than 0, which would not be biologically relevant. In this case I also set $T = 100$ and $\bar{r} = 10$. Note that $\bar{r}$ is set to the constant value of r used in the analysis in Section 3.

Because $r(t)$ is dependent on time, in these cases the linear stability analysis is considerably more challenging. Therefore I will restrict the analysis to numerical simulations.

Model simulations (Figure 5) suggest that equilibria are, just like the fluctuations in resource input, time-periodic. They also show that stable coexistence is possible even if $m \neq \frac{cg}{K_2 - K_1 + 1}$, and furthermore, the time spent in transient state increases with increase of the amplitude C of the fluctuations around $\bar{r}$.
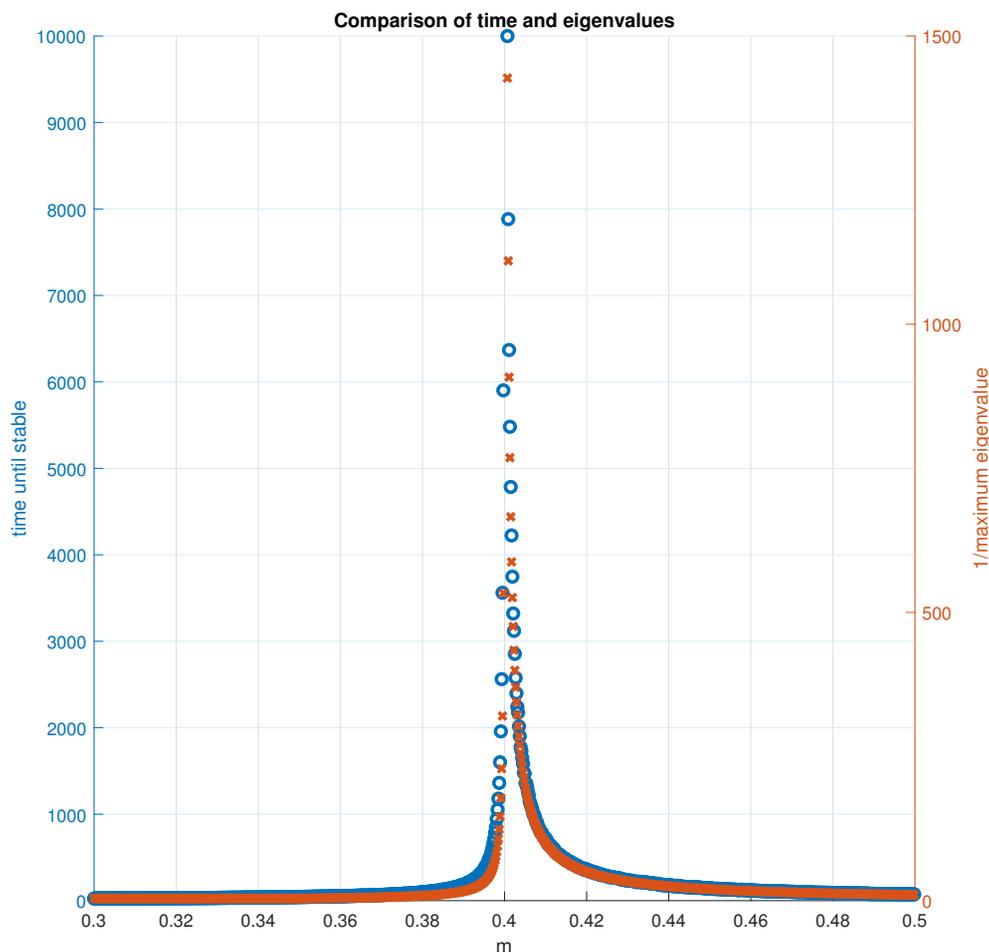
Figure 4: The time for one species to go extinct in numerical simulations is compared with $1/\lambda_{\max}$, where $\lambda_{\max}$ denotes the maximum eigenvalue of the unstable steady state. Other parameter values are $K_1 = \frac{1}{2}$, $K_2 = 2$, $g = 1$, $c = 1$, $r = 10$, $n = 1$, the same as Figures 2, 3

First, I investigate how systematically changing m affects e xtinction t imes (Figure 6). Figure 6 compares extinction times at different v alues o f m f or t he t hree c ases o f resource input that have been introduced. It can be seen that if the resource input is dependent on time, extinction times are much larger. For the cases when $r(t)$ is dependent on time, there are some plateaus at 10000. These plateaus indicate those parameter values for which coexistence is stable and the simulation is terminated after 10000 time units as no extinction is detected.
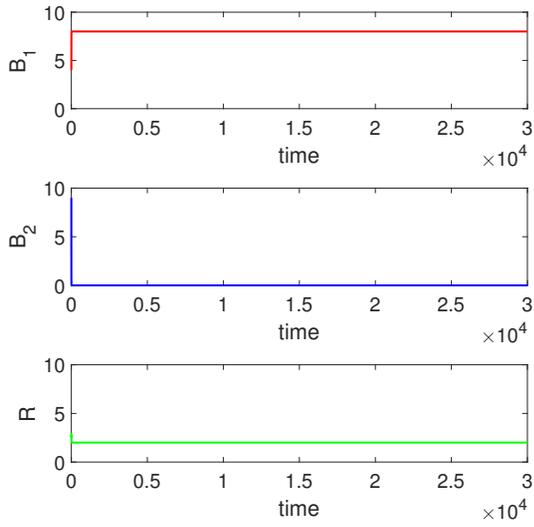
(a) constant $r = 10$, $m = 1$
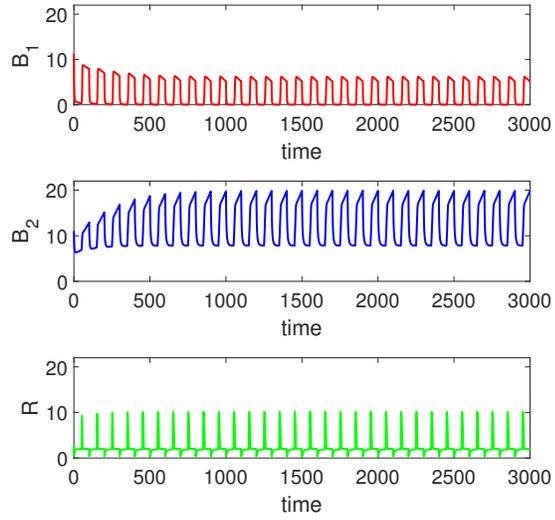
(b) $r = r_1(t)$ is a piecewise constant with a 100 unit period, $m = 0.395$
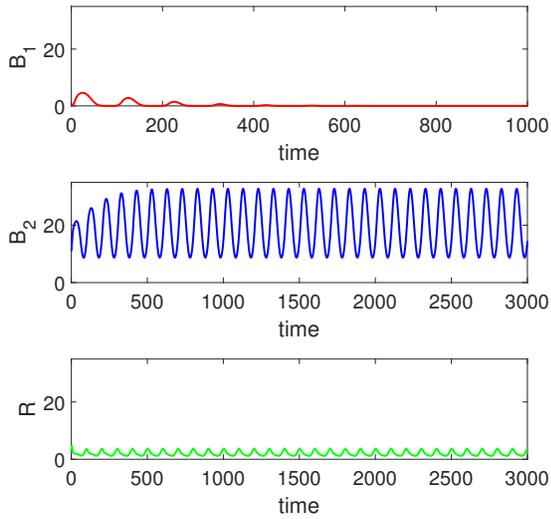
(c) $r = r_2(t)$ is sinusoidal with $C = 5$, $m = 0.395$ and $\bar{r} = 10$
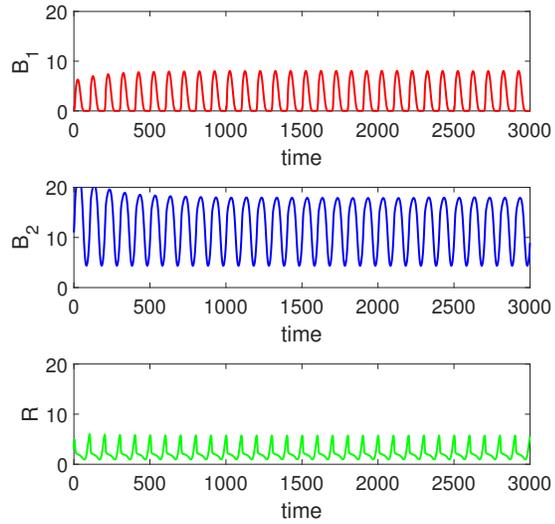
(d) $r = r_2(t)$ is sinusoidal with $C = 7$, $m = 0.395$ and $\bar{r} = 10$

Figure 5: Numerical simulations with constant and periodic resource availability. Other parameter values are $K_1 = \frac{1}{2}$, $K_2 = 2$, $g = 1$, $n = 1$, $a = 5$ and $b = 15$.
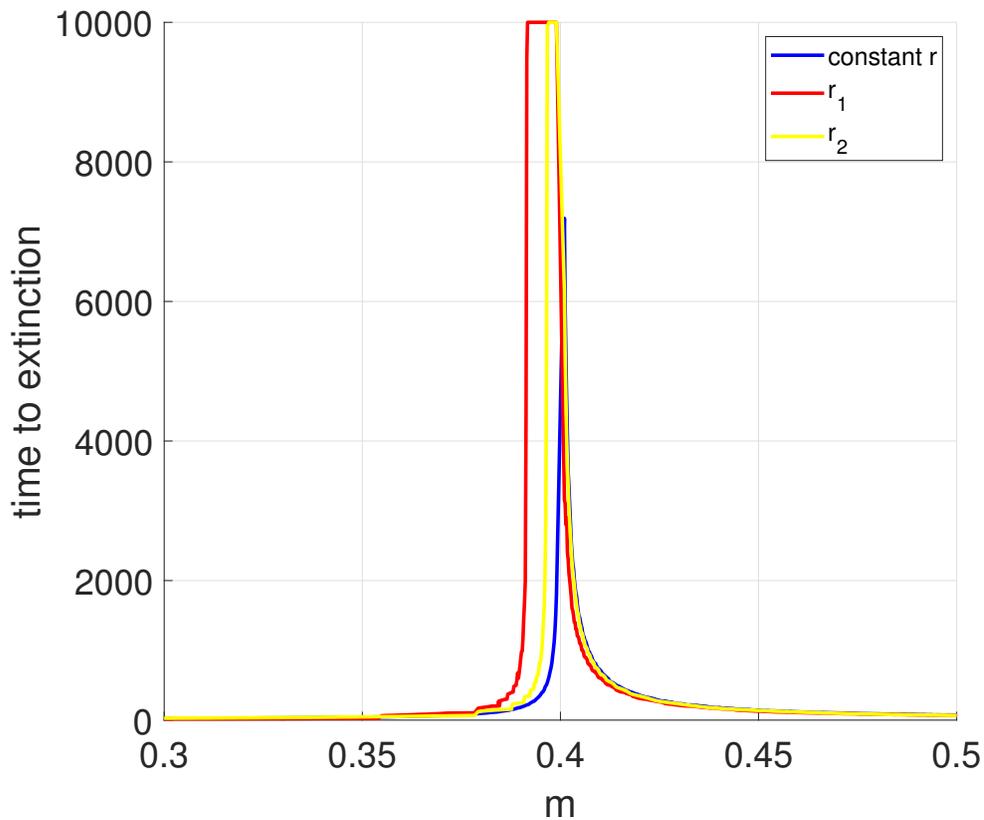
Figure 6: The time until species extinction occurs in numerical simulations of (2.3) is compared across the different resource input functions. Plateaus at t = 10000 signify stable coexistence. Other parameter values are $K_1 = \frac{1}{2}$, $K_2 = 2$, $g = 1$, $c = 1$, $n = 1$, $\bar{r} = 10$, $a = 5$, $b = 15$, $T = 100$, $C = 5$.

From the model simulations (Figure 5), it can also be seen that changing C in the sinusoidal regime also affects coexistence. As C becomes larger (Figure 7), the extinction time increases and at some point, if C is sufficiently large, stable coexistence is possible (indicated by an extinction time of 10000).
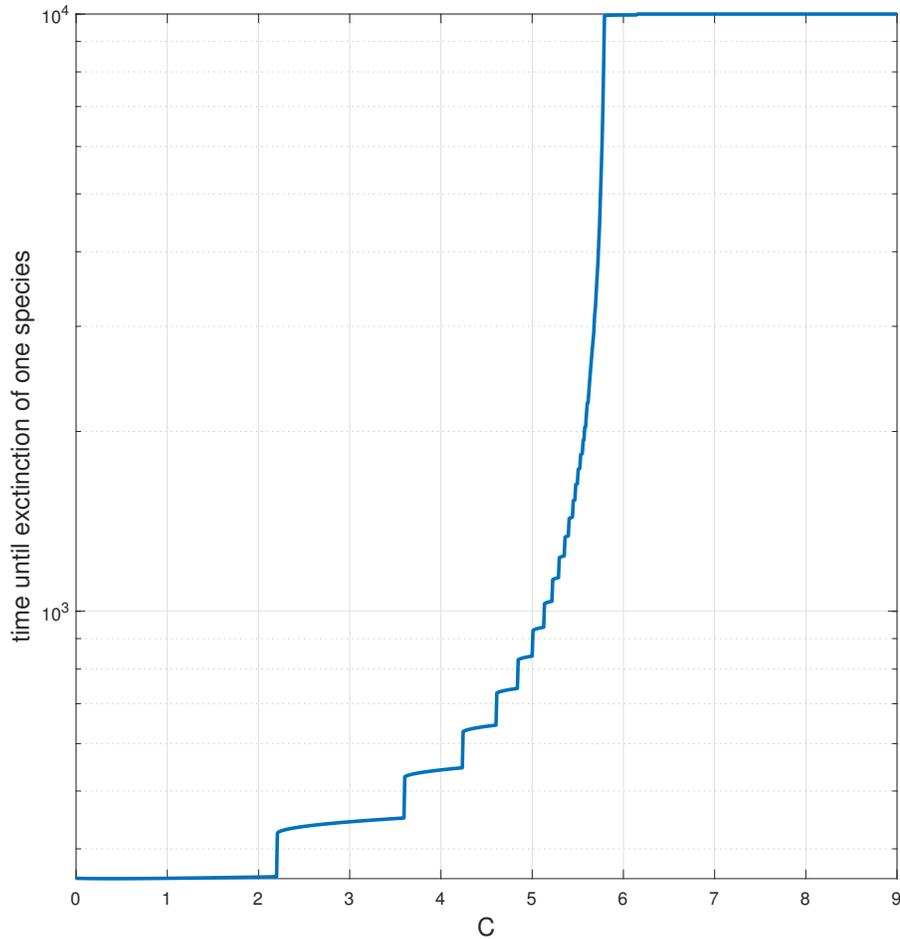
Figure 7: Effect of changing the amplitude C on time to extinction. The time until species extinction occurs in numerical simulations of (2.3) with resource input fluctuating in a sinusoidal manner are compared by changing C. Other parameter values are $K_1 = \frac{1}{2}$, $K_2 = 2$, $g = 1$, $c = 1$, $n = 1$, $m = 0.395$, $\bar{r} = 10$.

5. Discussion. Seasonality and other temporal variability in environmental conditions are often ignored in theoretical studies of consumer-resource dynamics utilising PDE/ODE models. This paper highlights the impact of seasonal fluctuations in resource input on the coexistence of two species competing for the same resource. My analysis shows that seasonal resource input promotes coexistence of species if they have similar average fitness (defined by Eq (3.4)) by stabilising coexistence and prolonging the duration of the occurrence of meta-stable coexistence states.

If resource input is constant, stable coexistence is not possible and that is why metastability takes an important role. The competitive exclusion principle [9] applies, but if both species have similar (but not identical) average fitness, the time to extinction is large. Therefore, coexistence can be observed for a significant duration, despite its inherent instability. This is of potential significance for ecological field studies. If extinction of a "weaker" species requires a long time, short durations of field studies may falsely identify metastable coexistence states as stable. The time to extinction becomes even larger under fluctuating resource input, making both species able to coexist in a transient state for longer. This enhances the importance of metastable states in seasonal climates. Mathematically, metastability is characterised by the small magnitude of an eigenvalue describing the linear growth rate of a perturbation to an equilibrium. I have indeed shown that there is a strong correlation between eigenvalue magnitude and transient times in the system. Therefore, eigenvalues are very useful to predict the time required for one species to competitively exclude the other.

The importance of metastable states in mathematical models models of ecological systems has been discussed previously (restricted to constant resource input) [8, 10]. However, the concept of metastability has also been reported from other types of mathematical models, such as the Cahn Hilliard equation [1, 2], microwave heating models [11], chemotactic models [18, 20], Burgers' equation [3] and models of the Lotus effect [15].

On the other hand, in the case when resource input fluctuates, stable coexistence is also possible if the species have similar average fitness. This has been studied before and it has been discovered that coexistence is possible due to a "gleaner-opportunist trade-off" [4, 14]. It has been revealed that seasonal variations in resource input can stabilise coexistence if one species thrives in a lower resource input, due to lower minimum resource requirement (the "gleaner"), and if the other species is superior for higher resource input, due to a high ratio of maximum growth rate and death rate (the "opportunist"). In my results it can also be appreciated that there is a shift to the right for the m in regards to time to extinction; this is really interesting, however I have not been able to determine the cause of this shift.

In this paper the model with non-constant resource input was only analysed by conducting numerical simulations. However, analytical results could be achieved in the future by analysing the linear stability of the equilibria through a calculation of Floquet multipliers [13, 23]. This would allow me to analyse the case with seasonal rainfall more analytically and in a more formal way, which would result in a better comparison with the linear stability analysis I have done for the constant resource input case.

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