COEXISTENCE OF COMPETING CONSUMERS ON A SINGLE RESOURCE IN A HYBRID MODEL

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Abstract. The question of whether and how two competing consumers can coexist on a single limiting resource has a long tradition in ecological theory. We build on a recent seasonal (hybrid) model for one consumer and one resource, and we extend it by introducing a second consumer. Consumers reproduce only once per year, the resource reproduces throughout the “summer” season. When we use linear consumer reproduction between years, we find explicit expressions for the trivial and semi-trivial equilibria, and we prove that there is no positive equilibrium generically. When we use non-linear consumer reproduction, we determine conditions for which both semi-trivial equilibria are unstable. We prove that a unique positive equilibrium exists in this case, and we find an explicit analytical expression for it. By linear analysis and numerical simulation, we find bifurcations from the stable equilibrium to population cycles that may appear through period-doubling or Hopf bifurcations. We interpret our results in terms of climate change that changes the length of the “summer” season.

1. Introduction. Many species live and interact in periodically varying environments with clearly distinct seasons of different environmental conditions. For example, many plants grow continually throughout the warmer summer season but remain dormant or are in decline during the colder winter season. Many mammals and birds reproduce only once per year, typically near the end of the winter season. Voles, hares and other rodents are intermediate in that they produce several generations within one summer season but none in the winter. The classical models for population dynamics are based on ordinary differential equations and are therefore unable to properly represent these life cycles [23]. Semi-discrete or hybrid models can include such seasonal details more accurately, see [4] for an early application of such models in population dynamics and [22] for a survey on the use of semi-discrete
modeling in population dynamics and ecology, plant pathology, epidemiology, and medicine. In this work, we derive and analyze a hybrid or semi-discrete model to investigate the population dynamic effects of such birth pulses.

Our particular focus is on competition dynamics. Competition between species is a fundamental building block of biological communities. The famous competitive exclusion principle states that at most one species can stably exist on a single limiting resource [30, 31]; see [21] for a history of the topic and an extension to several resources. However, it is known that two competing consumers can coexist along a periodic orbit generated by the consumer–resource interaction in a constant environment [12, 17, 18]. Seasonal reproduction is one of the most obvious causes of periodic temporal fluctuations in population dynamics. It seems therefore reasonable to expect that competition dynamics with seasonality in general and birth pulses in particular could allow for species coexistence.

A large body of literature has applied semi-discrete models to pulsed chemostat systems. Ebenhoh [5] first put forward an algae competition model where multiple species can coexist in the chemostat with pulsed nutrient input. Funasaki and Kot [7] followed the same modeling approach and studied a predator-prey-substrate model with periodic pulsing of the substrate. They showed that a holozoic protozoan can successfully invade (i.e. grow from low density) a chemostat containing substrate and bacteria. More recently, Smith and Wolkowicz [26] considered two-species competition on a single nonreproducing limiting nutrient in a self-cycling fermentation process. Competition between plasmid-bearing and plasmid-free organisms was studied in a chemostat with pulsed nutrient in [34, 35]. The authors of [32, 36] investigated competitive systems with a Beddington–DeAngelis functional response in a periodically pulsed chemostat. They derived criteria for the extinction or coexistence of competing species. More literature on pulsed chemostat dynamics exists but shall not be reviewed here.

Chemostats have very specific properties. The resource is abiotic (i.e., it does not reproduce) and an impulse typically consists of adding resource. Consumers are microbes and reproduce more or less continuously. In contrast, ecological dynamics typically focus on biotic resources, which reproduce continuously, and consumers often reproduce only once a year as described above. Semi-discrete models for ecological interactions have been used to derive mechanistic explanations of discrete-time population models [8, 6] and to study consumer–resource dynamics [23]. In these models, resource growth, consumption, and consumer mortality occur continuously throughout the summer season. During the winter, the species do not interact, and their populations independently decline at a constant rate [27]. Consumers store the energy gained from the resource until the end of the winter season, when the surviving consumers reproduce. Pachepsky et al. [23] showed that even with a linear functional response (describing the consumption of the resource) there can be complex dynamics, including stable equilibria, consumer–resource cycles, and overcompensation cycles. In contrast, consumer–resource models in continuous time only exhibit stable oscillations if the functional response is nonlinear, and do not exhibit overcompensation cycles at all [18]. We extend the model in [23] by introducing a second consumer, and we study whether and how the two competing consumers can coexist on a single biotic resource.

This paper is organized as follows. We first give a detailed model derivation in Section 2. Then we transform the semi-discrete model into a fully discrete model and analyze its steady states in Section 3. We find analytical expressions for steady
states with linear and nonlinear consumer reproduction terms. Generically, there is no positive equilibrium with linear consumer reproduction, but there is a unique positive equilibrium with non-linear reproduction. In Section 4, we study the stability of the steady states and visualize it numerically. We find Narmark–Sacker (Hopf) bifurcations and period-doubling bifurcations. Section 5 discusses possible extensions and future work.

2. Model formulation. We model the competition of two consumers for a single resource in a two-season environment. During the “summer” season, the resource grows logistically. Consumers reproduce only once per year, at the beginning of the summer season. They consume the resource throughout the summer season and store it as “energy” until reproduction. During the “winter” season, resource and consumers may die, so that only a fraction of them survive until the beginning of the following summer. The total stored energy also decreases as consumers die. The remaining energy is used after the winter for reproduction.

We denote by $T$ the length of the summer season and by $0 \leq \tau \leq T$ the time within a summer. The densities of the resource, two consumers and the total stored energy of consumers are denoted by $F(\tau), C_1(\tau), C_2(\tau), B_1(\tau), B_2(\tau)$. During the summer, these variables satisfy the differential equations:

$$
\frac{dF}{d\tau} = rF \left(1 - \frac{F}{K}\right) - a_1C_1F - a_2C_2F,
$$

$$
\frac{dC_1}{d\tau} = -m_1C_1,
$$

$$
\frac{dC_2}{d\tau} = -m_2C_2,
$$

$$
\frac{dB_1}{d\tau} = a_1C_1F - m_1B_1,
$$

$$
\frac{dB_2}{d\tau} = a_2C_2F - m_2B_2,
$$

where $r$ is the intrinsic resource growth rate, $K$ is the resource carrying capacity, $a_1$ and $a_2$ are the attack rates of consumers 1 and 2, and $m_1$ and $m_2$ are their death rates.

To model the dynamics from one year to the next, we denote by $t = 0, 1, 2, \ldots$ the year and by $U_t$, $V_t$, $W_t$ the densities of the resource, consumer 1 and consumer 2 at the beginning of the summer season. Then we write the initial conditions for (1) in year $t$:

$$
F(0) = U_t, \quad C_1(0) = V_t, \quad C_2(0) = W_t, \quad B_1(0) = 0, \quad B_2(0) = 0.
$$

Then the densities at the beginning of summer $t + 1$ can be obtained from the densities at the end of the preceding summer from the equations:

$$
U_{t+1} = \rho F(T^-),
$$

$$
V_{t+1} = \xi_1 C_1(T^-) + \theta_1 \xi_1 B_1(T^-),
$$

$$
W_{t+1} = \xi_2 C_2(T^-) + \theta_2 \xi_2 B_2(T^-),
$$

where $F(T^-), \quad C_1(T^-), \quad C_2(T^-), \quad B_1(T^-), \quad B_2(T^-)$ are the respective densities and stored energy at the end of summer $t$. Here, $0 < \rho, \xi_1, \xi_2 \leq 1$ are the survival probabilities of resource and two consumers, and $\theta_1, \theta_2$ are the reproduction rates of the two consumers. The expression in (3) assumes that the conversion efficiency
from stored energy to consumer density is linear. We also consider a nonlinear relationship below.

We non-dimensionalize the model to reduce the number of parameters and simplify the analysis, by taking

\[
 f = \frac{F}{K}, \quad s = \frac{\tau}{T}, \quad c_1 = a_1TC_1, \quad c_2 = a_2TC_2, \quad \mu_1 = m_1T, \quad \mu_2 = m_2T.
\]

\[
 b_1 = \frac{B_1}{K}, \quad b_2 = \frac{B_2}{K}, \quad u_t = \frac{U_t}{K}, \quad v_t = a_1TV_t, \quad w_t = a_2TW_t.
\]

Then the within-summer differential equations (1) become:

\[
 \frac{df}{ds} = \alpha f(1 - f) - c_1 f - c_2 f,
\]

\[
 \frac{dc_1}{ds} = -\mu_1 c_1,
\]

\[
 \frac{dc_2}{ds} = -\mu_2 c_2,
\]

\[
 \frac{db_1}{ds} = c_1 f - \mu_1 b_1,
\]

\[
 \frac{db_2}{ds} = c_2 f - \mu_2 b_2,
\]

with the initial conditions

\[
 f(0) = u_t, \quad c_1(0) = v_t, \quad c_2(0) = w_t, \quad b_1(0) = 0, \quad b_2(0) = 0,
\]

where \( \alpha = rT, \quad \mu_1 = m_1T, \quad \mu_2 = m_2T. \) The re-scaled difference equations between summers are

\[
 u_{t+1} = \rho f(T^-),
\]

\[
 v_{t+1} = \xi_1 c_1(T^-) + \eta_1 b_1(T^-),
\]

\[
 w_{t+1} = \xi_2 c_2(T^-) + \eta_2 b_2(T^-),
\]

where \( \eta_i = a_1\theta_1\xi_1 KT, \quad \eta_2 = a_2\theta_2\xi_2 KT. \)

The linear reproduction terms in (3) are realistic only with low stored energy. Even with these linear terms and a single consumer, the model can have complex dynamic behavior [23]. But the linear terms are not realistic with high stored energy, since consumers are limited by their capacity to produce offspring in the same period. Hence, we also explore the dynamics with the simplest nonlinear reproduction, namely the Beverton-Holt function [4]. This function is monotone increasing with decelerating rate. The updating equations from the end of one summer to the beginning of the next are then given by:

\[
 U_{t+1} = \rho F(T^-),
\]

\[
 V_{t+1} = \xi_1 c_1(T^-) + \frac{\theta_1\xi_1 B_1(T^-)}{1 + \delta_1\xi_1 B_1(T^-)},
\]

\[
 W_{t+1} = \xi_2 c_2(T^-) + \frac{\theta_2\xi_2 B_2(T^-)}{1 + \delta_2\xi_2 B_2(T^-)}.
\]

Here, \( \theta_i \) is the maximal reproduction rate and \( \delta_i \) denotes the strength of density dependence for consumer \( i. \) The factor of \( \xi_i \) appears since only surviving individuals
and the resource density at the end of the season as

$$f_{t+1} = \frac{\eta_2 b_2(1^-)}{1 + \varepsilon_2 b_2(1^-)},$$

where $\varepsilon_1 = K\delta_1 \xi_1$, $\varepsilon_2 = K\delta_2 \xi_2$. Parameters $\rho$, $\xi_1$, $\xi_2$, $\eta_1$, $\eta_2$ are the same as above. All the parameters of our model are positive.

3. Steady-state analysis. The hybrid dynamical systems (4), (6) and (4), (8) obviously have no steady states except for the trivial state where all populations are absent. Nontrivial steady states may arise for the period map and can then be studied by the standard theory of discrete dynamical systems. We convert the semi-discrete models (4), (6) and (4), (8) into a discrete map. In the case of a single consumer, this was previously done by [23, 33]. We generalize their approach to the case of two consumers. We solve the differential equations (4) to get expressions of $f$, $c_1$, $c_2$, $b_1$, $b_2$, and then substitute the respective values into difference equations (6) or (8) to obtain the discrete map. This allows us to study the existence and uniqueness of steady states through a discrete map.

Considering (4) and (5), we obtain the solution of the consumer equations as

$$c_1(s) = v_1 e^{-\mu_1 s}, \quad c_2(s) = w_1 e^{-\mu_2 s},$$

and their densities at the end of the season as

$$c_1(1^-) = v_1 e^{-\mu_1}, \quad c_2(1^-) = w_1 e^{-\mu_2}.$$  

The equation for $f(s)$ can be rewritten as the Riccati equation

$$\frac{df}{ds} = \alpha f - \alpha f^2 - v_1 e^{-\mu_1 s} f - w_1 e^{-\mu_2 s} f.$$ 

To solve the equation, we set $y = \frac{1}{f}$. Then

$$\frac{dy}{ds} = \alpha - \left(\alpha - v_1 e^{-\mu_1 s} - w_1 e^{-\mu_2 s}\right) y,$$

which has the solution

$$y(s) = e^{-\alpha s-v_1 e^{-\mu_1 s}/\mu_1-w_1 e^{-\mu_2 s}/\mu_2} \left(\alpha \int_0^se^{\alpha \tau+v_1 e^{-\mu_1 \tau}/\mu_1+w_1 e^{-\mu_2 \tau}/\mu_2 d\tau + \frac{e^{\mu_1}+w_1}{u_1}\right).$$

Hence, we find the solution for $f$ in equation (4) as

$$f(s) = \frac{u_1 e^{\alpha s+v_1 e^{-\mu_1 s}/\mu_1+w_1 e^{-\mu_2 s}/\mu_2}}{1 + \alpha u_1 \int_0^se^{\alpha \tau+v_1 e^{-\mu_1 \tau}/\mu_1+w_1 e^{-\mu_2 \tau}/\mu_2 d\tau + \frac{e^{\mu_1}+w_1}{u_1}},$$

and the resource density at the end of the season as

$$f(1^-) = \frac{u_1 e^{\alpha s-v_1 e^{-\mu_1 s}/\mu_1-w_1 e^{-\mu_2 s}/\mu_2}}{1 + \alpha u_1 \int_0^se^{\alpha \tau-v_1 e^{-\mu_1 \tau}/\mu_1-w_1 e^{-\mu_2 \tau}/\mu_2 d\tau}.$$
Substituting (9) and (11) into (4), we rewrite the equation for $b_1(s)$,

$$\frac{db_1}{ds} = \frac{u_t v_t e^{\mu s - \mu s - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2}}{1 + \alpha u_t \int_0^s e^{\alpha \tau - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2} d\tau} - \mu_1 b_1.$$  

The solution of this equation is given by

$$b_1(s) = u_t v_t e^{-\mu_1 s} \int_0^s \frac{e^{\alpha \tau - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2}}{1 + \alpha u_t \int_0^\tau e^{\alpha \tau - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2} d\tau} d\tau.$$  

Therefore, at the end of the summer season, we have

$$b_1(1^-) = \frac{v_t}{e^{\mu_1 \alpha}} \ln \left(1 + \alpha u_t \int_0^1 e^{\alpha \tau - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2} d\tau \right).$$  

Similarly, for $b_2$ we find

$$b_2(1^-) = \frac{w_t}{e^{\mu_2 \alpha}} \ln \left(1 + \alpha u_t \int_0^1 e^{\alpha \tau - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2} d\tau \right).$$  

We use these explicit expressions to study the dynamics between years as discrete systems. We treat the cases of linear and nonlinear reproduction separately.

### 3.1. Linear consumer reproduction

First, we analyze the case where consumers reproduce linearly. Our main result is that the two consumers cannot coexist at a steady state in general. We substitute (10), (12), (13) and (14) into the linear difference equations (6). Thus, the discrete map from the beginning of summer $t$ to summer $t + 1$ is

$$u_{t+1} = \frac{\rho e^{\alpha s - \bar{v}_t(1-e^{-\mu})/\mu_1 - v_1(1-e^{-\mu})/\mu_2}}{1 + \alpha \bar{u} \int_0^1 e^{\alpha \tau - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2} d\tau},$$  

$$v_{t+1} = \frac{\eta_1 u_t}{e^{\mu_1 \alpha}} \ln \left(1 + \alpha u_t \int_0^1 e^{\alpha \tau - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2} d\tau \right),$$  

$$w_{t+1} = \frac{\eta_2 w_t}{e^{\mu_2 \alpha}} \ln \left(1 + \alpha u_t \int_0^1 e^{\alpha \tau - v_1(1-e^{-\mu})/\mu_1 - w_1(1-e^{-\mu})/\mu_2} d\tau \right).$$  

The model has several possible equilibria. At the trivial equilibrium $(0, 0, 0)$, all species are absent. When $\rho e^{\alpha} > 1$, we have the resource-only equilibrium $(\rho e^{\alpha - 1}, 0, 0)$. If there is an equilibrium $(\bar{u}, \bar{v}, 0)$ with $\bar{u} > 0, \bar{v} > 0$, that equilibrium point satisfies the following equations:

$$\frac{\rho e^{\alpha s - \bar{v}_t(1-e^{-\mu})/\mu_1}}{1 + \alpha \bar{u} \int_0^1 e^{\alpha \tau - \bar{v}_t(1-e^{-\mu})/\mu_1} d\tau} = 1,$$  

$$\frac{\eta_1 u_t}{e^{\mu_1 \alpha}} \ln \left(1 + \alpha \bar{u} \int_0^1 e^{\alpha \tau - \bar{v}_t(1-e^{-\mu})/\mu_1} d\tau \right) = 1.$$  

Combining (18) with (19), we solve (similar to [23, 33])

$$\bar{v} = \frac{u_t (\alpha + \ln \rho + \alpha(\xi_1 - e^{\mu_1})/\eta_1)}{1 - e^{-\mu_1}}.$$  

which is positive if the condition \( \eta_1 (\ln \rho + \alpha) > (e^{\mu_2} - \xi_1) \alpha \) holds. We also get

\[
\bar{u} = \frac{e^{\alpha (e^{\mu_1} - \xi_1)/\mu_1} - 1}{\alpha \int_0^1 e^{g_1(s)} ds},
\]

where \( g_1(s) = \alpha s - \frac{(\alpha + \ln \rho + \alpha (\xi_1 - e^{\mu_1})/\eta_1)(1 - e^{-\mu_1 s})}{1 - e^{-\mu_1}} \).

By symmetry, we also have an equilibrium \( (\bar{u}, 0, \bar{w}) \) with \( \bar{u}, \bar{w} > 0 \), where

\[
\bar{w} = \frac{\mu_2 (\alpha + \ln \rho + \alpha (\xi_2 - e^{\mu_2})/\eta_2)}{1 - e^{-\mu_2}} - 1,
\]

\[
\bar{u} = \frac{e^{\alpha (e^{\mu_2} - \xi_2)/\eta_2} - 1}{\alpha \int_0^1 e^{g_2(s)} ds},
\]

with \( g_2(s) = \alpha s - \frac{(\alpha + \ln \rho + \alpha (\xi_2 - e^{\mu_2})/\eta_2)(1 - e^{-\mu_2 s})}{1 - e^{-\mu_2}} \), provided \( \eta_2 (\ln \rho + \alpha) > (e^{\mu_2} - \xi_2) \alpha \).

The plane \( v = 0 \) (or \( w = 0 \)) is invariant for the system. Only one consumer exists. This subsystem is similar to the one studied by Pachepsky et al [23]. Its dynamics range from stable nonzero equilibrium, period-doubling bifurcation to 2-cycles and Hopf bifurcation to oscillations.

Whether or not a species can persist in a given system can often be studied by what is called invasion analysis, i.e., by asking whether the species can grow when rare. Mathematically, this is done by linearizing at the state where the species is absent and asking whether this state is linearly stable (i.e., no invasion) or unstable (i.e., invasion is possible).

Turelli [29] conjectures that mutual invasibility is a sufficient condition for coexistence. If either of the two consumer species is able to grow when the other consumer is at equilibrium with the resource, then they are able to coexist. This criterion of mutual invasibility is widely used to simplify theoretical investigations of coexistence [9, 24, 28]. Hence, we study the stability of the equilibria \( (\bar{u}, \bar{v}, 0) \) and \( (\bar{u}, 0, \bar{w}) \) to evaluate the possibility of mutual invasion.

**Proposition 1.** Assume that \( (\bar{u}, \bar{v}, 0) \) is stable in the \( u-v \) plane, and \( (\bar{u}, 0, \bar{w}) \) is stable in the \( u-w \) plane. Then there is no mutual invasion.

**Proof.** We linearize equations (15), (16), (17) at \( (\bar{u}, \bar{v}, 0) \) to obtain the eigenvalues of the Jacobian matrix. The equations decouple. Two eigenvalues are inside the unit circle since we assumed that the point is stable within the \( u-v \) plane. The equation for \( w \) determines the remaining eigenvalue as

\[
\lambda = \xi_2 e^{-\mu_2} + \frac{\eta_2}{\mu_2} \ln \left( \frac{1 + \alpha \bar{u}}{1 + \alpha \bar{w}} \right) \int_0^1 e^{\alpha \tau - \bar{v} (1 - e^{-\mu_1 \tau})} d\tau
\]

\[
= \xi_2 e^{-\mu_2} + \frac{\eta_2 (\mu_1 - \xi_1)}{\eta_1 e^{\mu_1}} > 0.
\]

The equilibrium \( (\bar{u}, \bar{v}, 0) \) is unstable and consumer 2 can invade if and only if the positive eigenvalue \( \lambda \) is greater than one. And \( \lambda > 1 \) is equivalent to \( \frac{e^{\mu_1} - \xi_1}{\eta_1} > \frac{e^{\mu_2} - \xi_2}{\eta_2} \). By symmetry, consumer 1 can invade the \( (\bar{u}, 0, \bar{w}) \) steady state if the reverse inequality \( \frac{e^{\mu_1} - \xi_1}{\eta_1} < \frac{e^{\mu_2} - \xi_2}{\eta_2} \) holds. Hence, the equilibrium \( (\bar{u}, \bar{v}, 0) \) is unstable when the equilibrium \( (\bar{u}, 0, \bar{w}) \) is locally stable, and vice versa. Therefore, in the linear consumer reproduction model, mutual invasion cannot occur.

We conjecture that there is no steady state where all species coexist. In fact, we can prove the following.
Proposition 2. If \((e^{\mu_1} - \xi_1)/\eta_1 = (e^{\mu_2} - \xi_2)/\eta_2\), there is a continuum of steady states. If not, there is no positive equilibrium.

Proof. If there is a positive equilibrium \((\bar{u}, \bar{v}, \bar{w})\), it is required to satisfy the following equations

\[
\frac{\rho e^{\alpha - \varepsilon(1-e^{-\mu_1})}/\mu_1 - \bar{w}(1-e^{-\mu_2})/\mu_2}{1 + \alpha \bar{u} \int_0^1 e^{\alpha \tau - \varepsilon(1-e^{-\mu_1})}/\mu_1 - \bar{w}(1-e^{-\mu_2})/\mu_2 d\tau} = 1,
\]

\[
\xi_1 e^{-\mu_1} + \frac{\eta_1}{e^{\mu_1} \alpha} \ln \left(1 + \alpha \bar{u} \int_0^1 e^{\alpha \tau - \varepsilon(1-e^{-\mu_1})}/\mu_1 - \bar{w}(1-e^{-\mu_2})/\mu_2 d\tau\right) = 1, \quad (24)
\]

\[
\xi_2 e^{-\mu_2} + \frac{\eta_2}{e^{\mu_2} \alpha} \ln \left(1 + \alpha \bar{u} \int_0^1 e^{\alpha \tau - \varepsilon(1-e^{-\mu_1})}/\mu_1 - \bar{w}(1-e^{-\mu_2})/\mu_2 d\tau\right) = 1. \quad (25)
\]

We combine (24) with (25) to derive

\[
\frac{e^{\mu_1} - \xi_1}{\eta_1} = \frac{e^{\mu_2} - \xi_2}{\eta_2} = \frac{\ln \rho + \alpha - \bar{v}(1-e^{-\mu_1})/\mu_1 - \bar{w}(1-e^{-\mu_2})/\mu_2}{\alpha}. \quad (26)
\]

In the special case where \((e^{\mu_1} - \xi_1)/\eta_1 = (e^{\mu_2} - \xi_2)/\eta_2\), there is a continuum of equilibria and the three species coexist. Generically, if \((e^{\mu_1} - \xi_1)/\eta_1 \neq (e^{\mu_2} - \xi_2)/\eta_2\), there is no positive equilibrium where all species coexist. \(\square\)

Remark 1. When \((e^{\mu_1} - \xi_1)/\eta_1 = (e^{\mu_2} - \xi_2)/\eta_2\), one eigenvalue of the Jacobian matrix at \((\bar{u}, \bar{v}, 0)\) and \((\bar{u}, 0, \bar{w})\) is \(\lambda = 1\).

The condition \((e^{\mu_1} - \xi_1)/\eta_1 = (e^{\mu_2} - \xi_2)/\eta_2\) is too strict to be satisfied in real biological systems. Generically, the resource and two consumers cannot coexist at a steady state.

3.2. Non-linear consumer reproduction. We now turn to the model with non-linear consumer reproduction. We can extend the analysis from the linear case to the non-linear case, but the calculations are more cumbersome. It will turn out that under certain conditions, there is a positive equilibrium, and it is unique. We can give a complete analytical expression for it. Substituting (10), (12), (13) and (14) into the difference equations (8), the discrete map is given by

\[
u_{t+1} = \frac{\rho u_t e^{\alpha - v_t(1-e^{-\mu_1})}/\mu_1 - w_t(1-e^{-\mu_2})/\mu_2}{1 + \alpha u_t \int_0^1 e^{\alpha \tau - v_t(1-e^{-\mu_1})}/\mu_1 - w_t(1-e^{-\mu_2})/\mu_2 d\tau},
\]

\[
u_{t+1} = \xi_1 v_t e^{-\mu_1} + \frac{\eta_1 v_t e^{-\mu_1} \ln \left(1 + \alpha u_t \int_0^1 e^{\alpha \tau - v_t(1-e^{-\mu_1})}/\mu_1 - w_t(1-e^{-\mu_2})/\mu_2 d\tau\right)}{\alpha + \varepsilon_1 v_t e^{-\mu_1}}, \quad (28)
\]

\[
u_{t+1} = \xi_2 w_t e^{-\mu_2} + \frac{\eta_2 w_t e^{-\mu_2} \ln \left(1 + \alpha u_t \int_0^1 e^{\alpha \tau - v_t(1-e^{-\mu_1})}/\mu_1 - w_t(1-e^{-\mu_2})/\mu_2 d\tau\right)}{\alpha + \varepsilon_2 w_t e^{-\mu_2}}. \quad (29)
\]

As before, there exists the trivial equilibrium \((0, 0, 0)\) and, if \(\rho e^\alpha > 1\), the resource-only equilibrium \((e^{\alpha-1}, 0, 0)\). We can calculate the semi-trivial equilibrium points as follows.
Proposition 3. If \( \eta_1(\ln \rho + \alpha) > (e^{\mu_1} - \xi_1)\alpha \), there is a semi-trivial equilibrium \((\bar{u}, \bar{v}, 0)\), where

\[
\bar{v} = \left(\frac{(e^{\mu_1} - \xi_1)\varepsilon_1\mu_1(\ln \rho + \alpha) + \eta_1(e^{\mu_1} - 1)}{2(e^{\mu_1} - \xi_1)\varepsilon_1(1 - e^{-\mu_1})} \right) \sqrt{\left(\frac{(e^{\mu_1} - \xi_1)\varepsilon_1\mu_1(\ln \rho + \alpha) - \eta_1(e^{\mu_1} - 1)^2 + 4(e^{\mu_1} - \xi_1)^2\alpha\varepsilon_1\mu_1(e^{\mu_1} - 1)}{2(e^{\mu_1} - \xi_1)\varepsilon_1(1 - e^{-\mu_1})}\right)^2}.
\]

and

\[
\bar{u} = \frac{\rho e^{\alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1} - 1}{\alpha \int_0^1 e^{\alpha\bar{v}(1 - e^{-\mu_1})/\mu_1} d\tau}.
\]

Proof. The semi-trivial equilibrium \((\bar{u}, \bar{v}, 0)\) satisfies the following equations:

\[
\xi_1 e^{-\mu_1} + \frac{\eta_1 e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1)}{\alpha + \varepsilon_1 \bar{v} e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1)} = 1.
\]

From the first of these, we can get expression (31) for \(\bar{v}\) in terms of \(\bar{v}\) and rewrite (32) as

\[
\xi_1 e^{-\mu_1} + \frac{\eta_1 e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1)}{\alpha + \varepsilon_1 \bar{v} e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1)} = 1,
\]

which is equivalent to the quadratic equation

\[
(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (1 - e^{-\mu_1})/\mu_1 \bar{v}^2 + \eta_1(\ln \rho + \alpha) - (e^{\mu_1} - \xi_1)\alpha
\]

\[
- [(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) + \eta_1(1 - e^{-\mu_1})/\mu_1] \bar{v} = 0.
\]

The discriminant of (33) is

\[
\Delta_1 = [(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) + \eta_1(1 - e^{-\mu_1})/\mu_1]^2 - 4(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (1 - e^{-\mu_1})/\mu_1 \eta_1(\ln \rho + \alpha) - (e^{\mu_1} - \xi_1)\alpha
\]

\[
= [(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha)]^2 - 2(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) \eta_1(1 - e^{-\mu_1})/\mu_1
\]

\[
+ \eta_1(1 - e^{-\mu_1})/\mu_1]^2 + 4(e^{\mu_1} - \xi_1)^2\alpha\varepsilon_1 e^{-\mu_1} (1 - e^{-\mu_1})/\mu_1
\]

\[
= [(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) - \eta_1(1 - e^{-\mu_1})/\mu_1]^2
\]

\[
+ 4(e^{\mu_1} - \xi_1)^2\alpha\varepsilon_1 e^{-\mu_1} (1 - e^{-\mu_1})/\mu_1,
\]

which is positive. Hence, we obtain two solutions for the quadratic equation as

\[
\bar{v} = \frac{(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) + \eta_1(1 - e^{-\mu_1})/\mu_1 \pm \sqrt{\Delta_1}}{2(e^{\mu_1} - \xi_1)\varepsilon_1 e^{-\mu_1} (1 - e^{-\mu_1})/\mu_1}.
\]

We show that only one solution may satisfy \(\bar{u} > 0\) and \(\bar{v} > 0\).

From (31), we find that \(\bar{u} > 0\) if and only if \(\rho e^{\alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1} - 1 > 0\), which is equivalent to

\[
\bar{v}(1 - e^{-\mu_1})/\mu_1 < \alpha + \ln \rho.
\]
On the other hand, from

\[ \bar{v} = \left( e^{\mu_1} - \xi_1 \right) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) + \eta_1 (1 - e^{-\mu_1}) / \mu_1 + \sqrt{\Delta}, \]

we calculate

\[ \bar{v}(1 - e^{-\mu_1}) / \mu_1 \]

\[ = \left( e^{\mu_1} - \xi_1 \right) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) + \eta_1 (1 - e^{-\mu_1}) / \mu_1 + \]

\[ \sqrt{\left[ (e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) - \eta_1 (1 - e^{-\mu_1}) / \mu_1 \right]^2 + 4 \left( e^{\mu_1} - \xi_1 \right)^2 \alpha \varepsilon_1 e^{-\mu_1} (1 - e^{-\mu_1}) / \mu_1} \]

Then

\[ > \left( e^{\mu_1} - \xi_1 \right) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) + \eta_1 (1 - e^{-\mu_1}) / \mu_1 \]

\[ + \sqrt{\left[ (e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) - \eta_1 (1 - e^{-\mu_1}) / \mu_1 \right]^2} \]

There are two cases: if

\[ (e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) \geq \eta_1 (1 - e^{-\mu_1}) / \mu_1, \]

then

\[ \bar{v}(1 - e^{-\mu_1}) / \mu_1 > \frac{2 \left( e^{\mu_1} - \xi_1 \right) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha)}{2 \left( e^{\mu_1} - \xi_1 \right) \varepsilon_1 e^{-\mu_1}} \]

\[ \quad = \ln \rho + \alpha. \]

If, on the other hand,

\[ (e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) < \eta_1 (1 - e^{-\mu_1}) / \mu_1, \]

then

\[ \bar{v}(1 - e^{-\mu_1}) / \mu_1 > \frac{\eta_1 (1 - e^{-\mu_1}) / \mu_1}{(e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1}} \]

\[ > \frac{(e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha)}{(e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1}} \]

\[ = \ln \rho + \alpha. \]

By this calculation, we always have \( \bar{v}(1 - e^{-\mu_1}) / \mu_1 > \ln \rho + \alpha \), which contradicts (36). Hence, we cannot choose the ‘+’ sign in (35). Instead, using the ‘-’ sign in (35), we check:

\[ \bar{v}(1 - e^{-\mu_1}) / \mu_1 \]

\[ = \left( e^{\mu_1} - \xi_1 \right) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) + \eta_1 (1 - e^{-\mu_1}) / \mu_1 - \]

\[ \sqrt{\left[ (e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) - \eta_1 (1 - e^{-\mu_1}) / \mu_1 \right]^2 + 4 \left( e^{\mu_1} - \xi_1 \right)^2 \alpha \varepsilon_1 e^{-\mu_1} (1 - e^{-\mu_1}) / \mu_1} \]

\[ < \left( e^{\mu_1} - \xi_1 \right) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) + \eta_1 (1 - e^{-\mu_1}) / \mu_1 - \]

\[ \sqrt{\left[ (e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) - \eta_1 (1 - e^{-\mu_1}) / \mu_1 \right]^2} \]

There are also two cases: if

\[ (e^{\mu_1} - \xi_1) \varepsilon_1 e^{-\mu_1} (\ln \rho + \alpha) < \eta_1 (1 - e^{-\mu_1}) / \mu_1, \]
Assume that the Proposition 4. semi-trivial state. Here, we formulate the conditions for invasion of one consumer into the values. Instead, we will evaluate the stability conditions numerically in the next linearization, we cannot obtain simple analytical explicit expressions for the eigenvalues. Therefore, if the condition (37) is met, we can obtain \( \bar{w} \) from (31).

By symmetry, there is another semi-trivial equilibrium.

**Corollary 1.** If \( \eta_2(\ln \rho + \alpha) > (e^{\mu_2} - \xi_2)\alpha \), there is a semi-trivial equilibrium \((\bar{u}, 0, \bar{w})\), where

\[
\bar{w} = \frac{(e^{\mu_2} - \xi_2)\varepsilon_2\mu_2(\ln \rho + \alpha) + \eta_2(e^{\mu_2} - 1)}{2(e^{\mu_2} - \xi_2)\varepsilon_2(1 - e^{-\mu_2})} - \sqrt{\left[(e^{\mu_2} - \xi_2)\varepsilon_2\mu_2(\ln \rho + \alpha) - \eta_2(e^{\mu_2} - 1)^2 + 4(e^{\mu_2} - \xi_2)^2\varepsilon_2\mu_2(e^{\mu_2} - 1)\right]} - \frac{2(e^{\mu_2} - \xi_2)\varepsilon_2(1 - e^{-\mu_2})}{2(e^{\mu_2} - \xi_2)\varepsilon_2(1 - e^{-\mu_2})},
\]

and

\[
\bar{u} = \frac{\rho e^{\alpha \bar{w}(1 - e^{-\mu_2})/\mu_2} - 1}{\alpha \int_0^1 e^{\alpha \tau - \bar{w}(1 - e^{-\mu_2})/\mu_2}d\tau}.
\]

As before, we expect that all three species can coexist if each semi-trivial equilibrium can be invaded by the absent consumer. Although we can calculate the linearization, we cannot obtain simple analytical explicit expressions for the eigenvalues. Instead, we will evaluate the stability conditions numerically in the next section. Here, we formulate the conditions for invasion of one consumer into the semi-trivial state.

**Proposition 4.** Assume that the \((\bar{u}, \bar{v}, 0)\) equilibrium is stable in the \(u-v\) plane. If

\[
\frac{e^{\mu_1} - 1}{\mu_1}((e^{\mu_1} - \xi_1)\eta_2 - (e^{\mu_2} - \xi_2)\eta_2) + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_1(\ln \rho + \alpha - \frac{(e^{\mu_2} - \xi_2)\alpha}{\eta_2}) > 0,
\]

then the \((\bar{u}, \bar{v}, 0)\) equilibrium is unstable and invaded by \(w\).
Proof. We linearize equations (27), (28), (29) at \((\bar{u}, \bar{v}, 0)\) to obtain the eigenvalues of the Jacobian matrix. Two eigenvalues are inside the unit circle since we assumed that the point is stable within the \(u-v\) plane. The equation for \(w\) determines the remaining eigenvalue as

\[
\lambda = \xi_2 e^{-\mu_2} + \frac{\eta_2[(e^{\mu_1} - \xi_1)(\ln\rho + \alpha)\varepsilon_1 - \eta_1(e^{\mu_1} - 1)/\mu_1]}{2\alpha e^{\mu_2}(e^{\mu_1} - \xi_1)\varepsilon_1} + \frac{\eta_2\sqrt{[(e^{\mu_1} - \xi_1)\varepsilon_1(\ln\rho + \alpha) - \eta_1(e^{\mu_1} - 1)/\mu_1]^2 + 4(e^{\mu_1} - \xi_1)^2\alpha\varepsilon_1(e^{\mu_1} - 1)/\mu_1}}{2\alpha e^{\mu_2}(e^{\mu_1} - \xi_1)\varepsilon_1}.
\]

Consumer 2 can invade the \((\bar{u}, \bar{v}, 0)\) equilibrium if this eigenvalue is greater than one. \(\lambda > 1\) is equivalent to

\[
\sqrt{[(e^{\mu_1} - \xi_1)\varepsilon_1(\ln\rho + \alpha) - \eta_1(e^{\mu_1} - 1)/\mu_1]^2 + 4(e^{\mu_1} - \xi_1)^2\alpha\varepsilon_1(e^{\mu_1} - 1)/\mu_1} > 2(e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_1\alpha/\eta_2 + \eta_1(e^{\mu_1} - 1)/\mu_1 - (e^{\mu_1} - \xi_1)(\ln\rho + \alpha)\varepsilon_1.
\] (40)

If

\[
2(e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_1\alpha/\eta_2 + \eta_1(e^{\mu_1} - 1)/\mu_1 - (e^{\mu_1} - \xi_1)(\ln\rho + \alpha)\varepsilon_1 \leq 0,
\] (41)

inequality (40) is always true. If, on the other hand,

\[
2(e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_1\alpha/\eta_2 + \eta_1(e^{\mu_1} - 1)/\mu_1 - (e^{\mu_1} - \xi_1)(\ln\rho + \alpha)\varepsilon_1 > 0,
\] (42)

then we square both sides of (40) and rearrange terms to obtain (39) as

\[
e^{\mu_1} - 1 \mu_1 (e^{\mu_1} - \xi_1)\eta_2 - (e^{\mu_2} - \xi_2)\eta_1 + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_1(\ln\rho + \alpha - \frac{(e^{\mu_2} - \xi_2)\alpha}{\eta_2}) > 0.
\]

Because (42) is equivalent to

\[
e^{\mu_1} - 1 \mu_1 (e^{\mu_1} - \xi_1)\eta_2 - (e^{\mu_2} - \xi_2)\eta_1 + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_1(\ln\rho + \alpha - \frac{(e^{\mu_2} - \xi_2)\alpha}{\eta_2}) < (e^{\mu_1} - 1)(e^{\mu_1} - \xi_1)\eta_2/\mu_1 + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_1\alpha/\eta_2,
\] (43)

(41) becomes

\[
e^{\mu_1} - 1 \mu_1 (e^{\mu_1} - \xi_1)\eta_2 - (e^{\mu_2} - \xi_2)\eta_1 + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_1(\ln\rho + \alpha - \frac{(e^{\mu_2} - \xi_2)\alpha}{\eta_2}) \geq (e^{\mu_1} - 1)(e^{\mu_1} - \xi_1)\eta_2/\mu_1 + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)^2\varepsilon_1\alpha/\eta_2.
\] (44)

Combining two cases (44), (43) and (39), we draw the conclusion that if (39) is satisfied, then the eigenvalue \(\lambda > 1\) and the \((\bar{u}, \bar{v}, 0)\) equilibrium can be invaded by \(w\).

Corollary 2. Assume that \((\bar{u}, 0, \bar{w})\) is stable in the \(u-w\) plane. If

\[
e^{\mu_2} - 1 \mu_2 (e^{\mu_2} - \xi_2)\eta_1 - (e^{\mu_1} - \xi_1)\eta_2 + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_2(\ln\rho + \alpha - \frac{(e^{\mu_1} - \xi_1)\alpha}{\eta_1}) > 0,
\] (45)

then \((\bar{u}, 0, \bar{w})\) equilibrium is unstable and \(v\) can invade.
According to invasibility criterion, we expect stable coexistence [19] if the conditions of proposition 4 and corollary 2 are satisfied. It turns out that we can derive an explicit analytical expression of the positive equilibrium. We find that (39) and (45) are necessary and sufficient conditions for the positive equilibrium to exist. Since we have an explicit expression, we also find that the positive equilibrium is unique.

**Proposition 5.** A positive equilibrium exists if and only if (39) and (45) are satisfied. This equilibrium $\bar{v}$, $\bar{\tilde{v}}$, $\bar{u}$ is unique and is given by:

$$\bar{v} = \frac{2\varepsilon_1 e^{-\mu_1} (e^{\mu_2} - 1) \eta_1 + \varepsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \varepsilon_1 \varepsilon_2 \mu_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha)}{2(\varepsilon_1 e^{-\mu_1} (e^{\mu_2} - 1) + \varepsilon_2 \mu_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1) - \varepsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2) - \sqrt{\Delta}}$$

$$\bar{\tilde{v}} = \frac{\varepsilon_1 \varepsilon_2 \mu_2 e^{-\mu_1} (e^{\mu_2} - 1) (\ln \rho + \alpha) + \varepsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \varepsilon_1 \varepsilon_2 \mu_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1}{2e^{\mu_2} (\varepsilon_1 e^{\mu_2} (e^{\mu_2} - 1) + \varepsilon_2 (1 - e^{\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1)} - \frac{\varepsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \varepsilon_1 \varepsilon_2 \mu_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1 - \sqrt{\Delta}}{2e^{\mu_2} (\varepsilon_1 e^{\mu_2} (e^{\mu_2} - 1) + \varepsilon_2 (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1)},$$

where

$$\Delta = (\varepsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_2} - 1) (\ln \rho + \alpha) + \varepsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1)^2 + 4\varepsilon_1 \varepsilon_2 \alpha e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1)^2 \mu_2 / \mu_1 + 4\varepsilon_1 \varepsilon_2 \alpha e^{-\mu_1} (e^{\mu_1} - \xi_1)^2 (e^{\mu_2} - 1),$$

and

$$\bar{u} = \frac{\rho e^{-\gamma(1 - e^{-\mu_1}) / \mu_1 - \bar{u}(1 - e^{-\mu_2}) / \mu_2}}{\alpha + \bar{u} \int_0^\tau e^{\gamma(1 - e^{-\mu_1}) / \mu_1 - \bar{u}(1 - e^{-\mu_2}) / \mu_2} d\tau} = 1.$$  

**Proof.** If there is a positive equilibrium $(\bar{u}, \bar{v}, \bar{\tilde{v}})$, it must satisfy

$$\frac{\rho e^{-\gamma(1 - e^{-\mu_1}) / \mu_1 - \bar{u}(1 - e^{-\mu_2}) / \mu_2}}{1 + \alpha \bar{u} \int_0^\tau e^{\gamma(1 - e^{-\mu_1}) / \mu_1 - \bar{u}(1 - e^{-\mu_2}) / \mu_2} d\tau} = 1,$$

$$\xi_1 e^{-\mu_1} + \frac{\eta_1 e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2)}{\alpha + \varepsilon_1 \bar{v} e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2) \int_0^\tau e^{\gamma(1 - e^{-\mu_1}) / \mu_1 - \bar{u}(1 - e^{-\mu_2}) / \mu_2} d\tau} = 1,$$

$$\xi_2 e^{-\mu_2} + \frac{\eta_2 e^{-\mu_2} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2)}{\alpha + \varepsilon_2 \bar{w} e^{-\mu_2} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2) \int_0^\tau e^{\gamma(1 - e^{-\mu_1}) / \mu_1 - \bar{u}(1 - e^{-\mu_2}) / \mu_2} d\tau} = 1.$$  

From (50), we obtain the expression (49) for $\bar{u}$ in terms of $\bar{v}$ and $\bar{\tilde{v}}$. Using (49), we can rewrite (51) and (52) as

$$\xi_1 e^{-\mu_1} + \frac{\eta_1 e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2)}{\alpha + \varepsilon_1 \bar{v} e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2) \int_0^\tau e^{\gamma(1 - e^{-\mu_1}) / \mu_1 - \bar{u}(1 - e^{-\mu_2}) / \mu_2} d\tau} = 1,$$

$$\xi_2 e^{-\mu_2} + \frac{\eta_2 e^{-\mu_2} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2)}{\alpha + \varepsilon_2 \bar{w} e^{-\mu_2} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2) \int_0^\tau e^{\gamma(1 - e^{-\mu_1}) / \mu_1 - \bar{u}(1 - e^{-\mu_2}) / \mu_2} d\tau} = 1.$$
After rearranging, we get
\[
\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1 - \bar{v}(1 - e^{-\mu_2})/\mu_2 = \frac{(\epsilon_{\mu_1} - \xi_1)\alpha}{\eta_1 - \epsilon_1 \bar{v} e^{-\mu_1}(e^{\mu_1} - \xi_1)} - \frac{(\epsilon_{\mu_2} - \xi_2)\alpha}{\eta_2 - \epsilon_2 \bar{v} e^{-\mu_2}(e^{\mu_2} - \xi_2)},
\]
and derive
\[
\bar{v} = \frac{\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1 - \bar{v}(1 - e^{-\mu_2})/\mu_2}{1 - e^{-\mu_2}} = \frac{\eta_2 e^{\mu_2}}{\epsilon_2 (e^{\mu_2} - \xi_2)} - \frac{\eta_1 e^{\mu_2}}{\epsilon_2 (e^{\mu_2} - \xi_1)} + \frac{\epsilon_1 e^{\mu_2}}{\epsilon_2 e^{\mu_2} \bar{v}},
\]
(53)
Hence, \( \bar{v} \) satisfies the quadratic equation
\[
A_2 \bar{v}^2 - A_1 \bar{v} + A_0 = 0,
\]
(54)
where
\[
A_2 = \epsilon_1^2 e^{-2\mu_1} (e^{\mu_1} - \xi_1)(e^{\mu_2} - 1) + \epsilon_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1,
\]
\[
A_1 = 2 \epsilon_1 e^{-\mu_1} (e^{\mu_2} - 1) \eta_1 + \epsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \epsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha) - \epsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2),
\]
\[
A_0 = \epsilon_2 \mu_2 \eta_1 (\ln \rho + \alpha) + \left( \frac{\eta_1}{e^{\mu_1} - \xi_1} - \frac{\eta_2}{e^{\mu_2} - \xi_2} \right) \eta_1 (e^{\mu_2} - 1) - (e^{\mu_1} - \xi_1) \alpha e^{\mu_2}.
\]
The discriminant of (54) is
\[
\Delta = (2 \epsilon_1 e^{-\mu_1} (e^{\mu_2} - 1) \eta_1 + \epsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \epsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha) - \epsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2))^2 - 4 (\epsilon_1^2 e^{-2\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \epsilon_1 \eta_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1) (\ln \rho + \alpha) + (\eta_1 / (e^{\mu_1} - \xi_1) - \eta_2 / (e^{\mu_2} - \xi_2)) \eta_1 (e^{\mu_2} - 1) - (e^{\mu_1} - \xi_1) \alpha e^{\mu_2})
\]
\[
\times \left( \frac{\epsilon_2^2 e^{-2\mu_1} (e^{\mu_1} - \xi_1)(e^{\mu_2} - 1) + \epsilon_2 e^{-\mu_1} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1}{e^{\mu_1} - \xi_1} \right) + 2 \epsilon_1 \epsilon_2 \eta_1 \eta_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_2} - 1) \left( e^{\mu_2} - 1 \right) \left( e^{\mu_2} - \xi_2 \right)
\]
\[
- 2 \epsilon_1^2 \epsilon_2 \eta_2 e^{-2\mu_1} (e^{\mu_2} - 1) (\ln \rho + \alpha) (e^{\mu_1} - \xi_1)^2 / (e^{\mu_2} - \xi_2) + 4 \epsilon_1^2 \epsilon_2 \eta_2 e^{-2\mu_1} (e^{\mu_1} - \xi_1)^2 (e^{\mu_2} - 1) + 4 \epsilon_1 \epsilon_2 \alpha e^{-\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) \left( e^{\mu_2} - \xi_2 \right)
\]
\[
- \epsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2) - \epsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2) (\ln \rho + \alpha) + 2 \epsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + 4 \epsilon_1 \epsilon_2 \alpha e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1)^2 \mu_2 / \mu_1 + 4 \epsilon_1^2 \epsilon_2 \eta_2 e^{-2\mu_1} (e^{\mu_1} - \xi_1)^2 (e^{\mu_2} - 1),
\]
which is positive. Thus, we get the following expression for \( \bar{v} \):
\[
\bar{v} = \frac{2 \epsilon_1 e^{-\mu_1} (e^{\mu_2} - 1) \eta_1 + \epsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \epsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha)}{2 (\epsilon_1^2 e^{-2\mu_1} (e^{\mu_1} - \xi_1)(e^{\mu_2} - 1) + \epsilon_1 \eta_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1)
\]
\[
- \epsilon_1 \eta_2 e^{-\mu_1} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2) \pm \sqrt{\Delta}}{2 (\epsilon_1^2 e^{-2\mu_1} (e^{\mu_1} - \xi_1)(e^{\mu_2} - 1) + \epsilon_1 \eta_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1)}.
\]
(55)
By combining (55) with (53), we obtain
\[
\tilde{w} = \frac{\eta_2 e^{\mu_2}}{\tilde{e}_2 (e^{\mu_2} - \xi_2)} - \frac{\eta_1 e^{\mu_2}}{\tilde{e}_2 (e^{\mu_1} - \xi_1)} + \\
\frac{2 \xi_1 e^{-\mu_1} e^{\mu_2} (e^{\mu_2} - 1) \eta_1 - \xi_1 \eta_2 e^{-\mu_1} e^{\mu_2} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2)}{2 (\xi_1 \tilde{e}_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \xi_2 (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2))} + \\
\frac{\xi_2 e^{\mu_2} (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \xi_1 \tilde{e}_2 e^{-\mu_1} e^{\mu_2} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha) \pm e^{\mu_2} \sqrt{\Delta}}{2 (\xi_1 \tilde{e}_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \xi_2 (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1)}.
\]

We need to determine which of these expressions (if any) yield a positive solution. From (49), \( \tilde{u} > 0 \) if and only if \( \rho e^{\alpha - \delta (1 - e^{-\mu_1}) / \mu_1} - \tilde{w} (1 - e^{-\mu_2}) / \mu_2 - 1 > 0 \), which is equivalent to
\[
\tilde{u} (1 - e^{-\mu_1}) / \mu_1 + \tilde{w} (1 - e^{-\mu_2}) / \mu_2 < \alpha + \ln \rho.
\]

When we choose the ‘+’ sign in (55), we find
\[
\tilde{v} > \frac{2 \xi_1 e^{-\mu_1} (e^{\mu_2} - 1) \eta_1 + \xi_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \xi_1 \tilde{e}_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha) - \xi_1 \tilde{e}_2 e^{-\mu_1} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2) + \sqrt{\Delta}}{2 (\xi_1 \tilde{e}_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \xi_2 (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1)}.
\]

where
\[
\Psi = \xi_1 \tilde{e}_2 e^{-\mu_1} (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2) + \xi_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1.
\]

There are also two cases: if \( \Psi \geq 0 \), then
\[
\tilde{v} > \frac{2 (\xi_1 e^{-\mu_1} (e^{\mu_2} - 1) \eta_1 - \xi_1 \tilde{e}_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha))}{\xi_1 e^{\mu_1} / \eta_1} = \frac{\xi_2 e^{\mu_2}}{\xi_1 (e^{\mu_1} - \xi_1)},
\]
and
\[
\tilde{w} = \frac{\eta_2 e^{\mu_2}}{\tilde{e}_2 (e^{\mu_2} - \xi_2)} - \frac{\eta_1 e^{\mu_2}}{\tilde{e}_2 (e^{\mu_1} - \xi_1)} + \frac{\xi_2 e^{\mu_2}}{\tilde{e}_2 e^{\mu_1} \tilde{v}}
\]
\[
> \frac{\eta_2 e^{\mu_2}}{\eta_1 e^{\mu_2}} - \frac{\eta_1 e^{\mu_2}}{\eta_1 e^{\mu_2}} + \frac{\eta_1 e^{\mu_2}}{\eta_1 e^{\mu_2}}
\]
\[
= \frac{\eta_2 e^{\mu_2}}{\eta_1 e^{\mu_2}},
\]
so that
\[
\tilde{u} (1 - e^{-\mu_1}) / \mu_1 + \tilde{w} (1 - e^{-\mu_2}) / \mu_2
\]
\[
> \frac{(e^{\mu_1} - 1) \eta_1}{\xi_1 \mu_1 (e^{\mu_1} - \xi_1)} + \frac{(e^{\mu_2} - 1) \eta_2}{\xi_2 \mu_2 (e^{\mu_2} - \xi_2)}
\]
\[
\geq \alpha + \ln \rho.
\]

The last inequality holds because \( \Psi \geq 0 \). However, (60) contradicts (57), thus we cannot use the ‘+’ sign in this case. If \( \Psi < 0 \), then we get
\[ \bar{v} > \varepsilon_1 e^{-\mu_2} (e^{\mu_2} - 1) \eta_1 + \varepsilon_2 e^{-\mu_2} e^{-\mu_1} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha) \\
- \varepsilon_1 e^{-\mu_2} (e^{\mu_2} - 1) \eta_2 (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2) \\
+ \varepsilon_1 e^{-\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \varepsilon_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1 \\
\]

We now want to find a lower bound of \( \bar{v}(1 - e^{-\mu_1}) / \mu_1 + \bar{w}(1 - e^{-\mu_2}) / \mu_2 \). We use the lower bounds of \( \bar{v} \) and \( \bar{w} \) and treat the three terms individually.

\[ \frac{(\ln \rho + \alpha) \varepsilon_2 e^{\mu_2} (e^{\mu_2} - 1) \eta_1 (1 - e^{-\mu_1}) / \mu_1 + \varepsilon_2 e^{\mu_2} (e^{\mu_2} - 1) \eta_2 (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1}{\varepsilon_1 e^{-\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \varepsilon_2 (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1} = \alpha + \ln \rho. \]  

(62)

\[ \frac{\varepsilon_2 e^{\mu_2} (1 - e^{-\mu_2})}{\varepsilon_2 e^{\mu_2} - \xi_2} = \frac{\varepsilon_2 e^{\mu_2} (1 - e^{-\mu_2})}{\varepsilon_2 e^{\mu_2} - \xi_2} - \frac{\varepsilon_2 e^{\mu_2} (1 - e^{-\mu_2})}{\varepsilon_2 e^{\mu_2} - \xi_2} \]  

(63)

\[ \frac{\varepsilon_2 e^{\mu_2} (1 - e^{-\mu_2})}{\varepsilon_2 e^{\mu_2} - \xi_2} = \frac{\varepsilon_2 e^{\mu_2} (1 - e^{-\mu_2})}{\varepsilon_2 e^{\mu_2} - \xi_2} \]

(64)

Hence, \( \bar{v}(1 - e^{-\mu_1}) / \mu_1 + \bar{w}(1 - e^{-\mu_2}) / \mu_2 \) is greater than the sum of (62), (63) and (64), which means

\[ \bar{v}(1 - e^{-\mu_1}) / \mu_1 + \bar{w}(1 - e^{-\mu_2}) / \mu_2 > \alpha + \ln \rho. \]

This contradicts (57), so we cannot choose the ‘+’ sign in (55). Therefore, there is at most one equilibrium \((\bar{u}, \bar{v}, \bar{w})\) satisfying \( \bar{u} > 0, \bar{v} > 0, \bar{w} > 0 \).

In fact, when we use the ‘-’ sign in (55), we find

\[ \bar{v} < \frac{2 \varepsilon_1 e^{-\mu_1} (e^{\mu_2} - 1) \eta_1 + \varepsilon_2 (1 - e^{-\mu_1}) \eta_1 \mu_2 / \mu_1 + \varepsilon_2 e^{-\mu_1} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha)}{2 (\varepsilon_1 e^{-2\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \varepsilon_2 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1)} \\
- \varepsilon_1 e^{-\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \varepsilon_1 e^{-\mu_1} (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1 \]  

(65)

where \( \Psi \) is as in (59). For \( \Psi \geq 0 \), we get

\[ \bar{v} < \frac{(e^{\mu_2} - 1) \eta_1 + \varepsilon_2 e^{\mu_2} (e^{\mu_1} - \xi_1) (\ln \rho + \alpha) - \eta_2 (e^{\mu_2} - 1) (e^{\mu_1} - \xi_1) / (e^{\mu_2} - \xi_2)}{\varepsilon_1 e^{-\mu_1} (e^{\mu_1} - \xi_1) (e^{\mu_2} - 1) + \varepsilon_2 (1 - e^{-\mu_1}) (e^{\mu_1} - \xi_1) \mu_2 / \mu_1}. \]
Using (53), we calculate
\[ \bar{v}(1 - e^{-\mu_1})/\mu_1 + \bar{w}(1 - e^{-\mu_2})/\mu_2 < \alpha + \ln \rho, \] (66)
so that \( \bar{u} > 0 \). For \( \Psi < 0 \), we calculate
\[
\bar{v} < \frac{2(\varepsilon_1 e^{-\mu_1}(e^{\mu_2} - 1)\eta_1 + \varepsilon_2(1 - e^{-\mu_1})\eta_1\mu_2/\mu_1)}{\eta_1 e^{\mu_1}} = \frac{\eta_2 e^{\mu_2}}{\varepsilon_2(e^{\mu_2} - \xi_2)}.
\]
and
\[
\bar{w} < \frac{\eta_2 e^{\mu_2}}{\varepsilon_2(e^{\mu_2} - \xi_2)}.
\]
so that
\[
\bar{v}(1 - e^{-\mu_1})/\mu_1 + \bar{w}(1 - e^{-\mu_2})/\mu_2 < \frac{(\varepsilon_1 - 1)\eta_1}{\varepsilon_1 \mu_1(e^{\mu_1} - \xi_1)} + \frac{(\varepsilon_2 - 1)\eta_2}{\varepsilon_2 \mu_2(e^{\mu_2} - \xi_2)} < \alpha + \ln \rho.
\] (67)
The last inequality holds because \( \Psi < 0 \). \( \bar{u} \) is positive, independent of the sign of \( \Psi \), with \( \bar{v} \), \( \bar{w} \) as shown in (66), (67).

Finally, we need to show that \( \bar{v} \) and \( \bar{w} \) are positive. We have that \( \bar{v} > 0 \) if and only if the following two conditions are satisfied:
(I) \[ \varepsilon_2(1 - e^{-\mu_1})\eta_1\mu_2/\mu_1 - \varepsilon_1\eta_2 e^{-\mu_1}(e^{\mu_2} - 1)(e^{\mu_1} - \xi_1)/(e^{\mu_2} - \xi_2) + 2\varepsilon_1 e^{-\mu_1}(e^{\mu_2} - 1)\eta_1 + \varepsilon_1\varepsilon_2\mu_2 e^{-\mu_1}(e^{\mu_1} - \xi_1)(\ln \rho + \alpha) > 0, \]

\[ \iff \frac{\mu_2 \varepsilon_1 e^{-\mu_1}}{e^{\mu_2} - \xi_2} \left( \frac{e^{\mu_2} - 1}{\mu_2} ((e^{\mu_2} - \xi_2)\eta_1 - (e^{\mu_1} - \xi_1)\eta_2) + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_2(\ln \rho + \alpha) \right) + \varepsilon_1 e^{-\mu_1}(e^{\mu_2} - 1)\eta_1 + \varepsilon_2(1 - e^{-\mu_1})\eta_1\mu_2/\mu_1 > 0; \]

(II) \[ \varepsilon_2\mu_2\eta_1(\ln \rho + \alpha) + \left( \frac{\eta_1}{e^{\mu_1} - \xi_1} - \frac{\eta_2}{e^{\mu_2} - \xi_2} \right) \eta_1(e^{\mu_2} - 1) - (e^{\mu_1} - \xi_1)\alpha\varepsilon_2\mu_2 > 0, \]

\[ \iff \frac{\left( e^{\mu_2} - 1 \right)}{\mu_2} \left( (e^{\mu_2} - \xi_2)\eta_1 - (e^{\mu_1} - \xi_1)\eta_2 \right) + (e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)\varepsilon_2(\ln \rho + \alpha) - (e^{\mu_1} - \xi_1)\alpha \frac{\mu_2\eta_1}{\eta_1(e^{\mu_1} - \xi_1)(e^{\mu_2} - \xi_2)} > 0. \]

Therefore (I) and (II) together are equivalent to (45).

Similarly, \( \bar{w} > 0 \) if and only if two conditions are met:
(III) \[ \varepsilon_1\varepsilon_2\mu_2 e^{-\mu_1} e^{\mu_2}(e^{\mu_1} - \xi_1)(\ln \rho + \alpha) + \varepsilon_1\eta_2 e^{-\mu_1} e^{\mu_2}(e^{\mu_2} - 1)(e^{\mu_1} - \xi_1)/(e^{\mu_2} - \xi_2) - \varepsilon_2(1 - e^{-\mu_1})\varepsilon_2\eta_1\mu_2/\mu_1 + 2\varepsilon_2\eta_2 e^{\mu_2}(1 - e^{-\mu_1})(e^{\mu_1} - \xi_1)\mu_2/(e^{\mu_2} - \xi_2)/\mu_1 > 0, \]

\[ \iff \]
bifurcations that lead to qualitatively different behavior. The stability of the semi-trivial and the coexistence equilibria as well as the different equilibrium exists. In the next section, we use numerical methods to determine the values (within the model constraints and also constraining ε₁ = ε₂ and ξ₁ = ξ₂). We calculate the Jacobian matrix and use the Jury method to determine the stability of the unique positive impulsive orbit in the hybrid system. The close-up in Figure 1 (right plot) illustrates how both consumer densities decrease during a season and increase with the birth pulse at the beginning of the summer. The resource decreases at the beginning of each summer but increases toward the end when the consumer populations are lower. The resource decreases from the end of one summer to the beginning of the next.

In Figure 2, we illustrate conditions (39) and (45) when parameters µ₁ and η₁ vary. The shaded region indicates the parameter range for which the unique positive equilibrium exists. In the next section, we use numerical methods to determine the stability of the semi-trivial and the coexistence equilibria as well as the different bifurcations that lead to qualitatively different behavior.

4. Stability analysis, bifurcations and numerical simulations. In the previous section, we found conditions for a coexistence steady state for the induced discrete-time system, or, equivalently, for an impulsive periodic orbit of period one in the hybrid system. In this section, we study the stability of steady states of the induced discrete-time system and the possible bifurcations that arise when the stability changes. We calculate the Jacobian matrix and use the Jury method to determine the stability of the unique positive impulsive orbit in the hybrid system. The close-up in Figure 1 (right plot) illustrates how both consumer densities decrease during a season and increase with the birth pulse at the beginning of the summer. The resource decreases at the beginning of each summer but increases toward the end when the consumer populations are lower. The resource decreases from the end of one summer to the beginning of the next.

In Figure 2, we illustrate conditions (39) and (45) when parameters µ₁ and η₁ vary. The shaded region indicates the parameter range for which the unique positive equilibrium exists. In the next section, we use numerical methods to determine the stability of the semi-trivial and the coexistence equilibria as well as the different bifurcations that lead to qualitatively different behavior.
Figure 1. Illustration of the unique positive impulsive periodic orbit, corresponding to the unique positive steady state of the discrete map. Parameter values are: $\mu_1 = 0.7$, $\mu_2 = 0.3813$, $\eta_1 = 10$, $\eta_2 = 7.5811$, $\varepsilon_1 = \varepsilon_2 = 0.8711$, $\xi_1 = \xi_2 = 0.2941$, $\alpha = 5.3063$, $\rho = 0.8324$.

Figure 2. The existence range of the positive equilibrium with respect to parameters $\mu_1$ and $\eta_1$. The upper boundary curve corresponds to condition (39), while the lower curve corresponds to (45). Parameters are as in Figure 1, unless otherwise noted.

conditions to determine stability. Since an explicit treatment of the Jury conditions is impossible in most cases, we illustrate the stability boundaries numerically. We present simulations of our system that confirm and illustrate the possible bifurcations. To analyze the stability of steady states, we linearize the system and write the Jacobian matrix as

$$J = \begin{bmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{bmatrix}.$$

For the $(0,0,0)$ equilibrium, we find $J_{11} = \rho e^\alpha$, $J_{22} = \xi_1 e^{-\mu_1}$, $J_{33} = \xi_2 e^{-\mu_2}$, and all other elements are equal to 0. Hence, the eigenvalues of the Jacobian matrix are $\rho e^\alpha$, $\xi_1 e^{-\mu_1}$ and $\xi_2 e^{-\mu_2}$. Since $\xi_i \leq 1$, $(0,0,0)$ is unstable if and only if $\rho e^\alpha > 1$. And in this case, the resource-only equilibrium exists.
The eigenvalues of Jacobian matrix at the resource-only equilibrium \((\frac{\rho^\alpha-1}{\alpha}, 0, 0)\) are
\[
\begin{align*}
\lambda_1 &= \frac{1}{\rho^\alpha - 1} \xi_1 e^{-\mu_1} + \frac{\eta_1 (\ln \rho + \alpha)}{\alpha e^{\mu_1}}, \\
\lambda_2 &= \frac{\eta_2 (\ln \rho + \alpha)}{\alpha e^{\mu_2}},
\end{align*}
\]
Therefore, \((\frac{\rho^\alpha-1}{\alpha}, 0, 0)\) is unstable if \(\eta_1 (\ln \rho + \alpha) > (e^{\mu_1} - \xi_1)\alpha\) or \(\eta_2 (\ln \rho + \alpha) > (e^{\mu_2} - \xi_2)\alpha\). These conditions are precisely the conditions for the existence of a semi-trivial steady state in which exactly one of the consumers is present alongside the resource; see proposition 3 and corollary 1. There are two aspects of stability of the semi-trivial state \((\bar{u}, \bar{v}, 0)\), say: stability within the (invariant) \(u-v\) plane and stability with respect to perturbations in the \(w\) direction. We studied the latter in the context of mutual invasibility. It turns out that understanding the stability behavior of the \((\bar{u}, \bar{v}, 0)\) state within the \(u-v\) plane is helpful to understand the behavior of the full system. A detailed analysis of the \(u-v\) system with linear consumer reproduction (using a slightly different but equivalent model formulation) was given in [23]. We briefly outline the corresponding analysis with nonlinear consumer reproduction here.

4.1. **Stability of the semi-trivial state.** The elements of the \(2 \times 2\) Jacobian for the semi-trivial equilibrium \((\bar{u}, \bar{v}, 0)\) within the \(u-v\) plane are given by
\[
\begin{align*}
J_{11} &= \frac{1}{\rho^\alpha - 1} \xi_1 e^{-\mu_1} + \frac{\eta_1 (\ln \rho + \alpha)}{\alpha e^{\mu_1}}, \\
J_{12} &= -\bar{u}(1 - e^{-\mu_1})/\mu_1 + \frac{\alpha \bar{u}^2 \int_0^1 (1 - e^{-\mu_1 \tau}) e^{\alpha \tau - \bar{v}(1 - e^{-\mu_1 \tau})/\mu_1} d\tau}{\rho \mu_1 e^{\alpha \bar{v}(1 - e^{-\mu_1})/\mu_1}}, \\
J_{21} &= -\bar{v}(1 - e^{-\mu_1})/\mu_1 + \frac{\alpha \eta_1 \bar{v} e^{-\mu_1} (\rho e^{\alpha \bar{v}(1 - e^{-\mu_1})/\mu_1} - 1)}{\rho \mu_1 e^{\alpha \bar{v}(1 - e^{-\mu_1})/\mu_1} (\alpha + \varepsilon_1 \bar{v} e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1))^2}, \\
J_{22} &= \xi_1 e^{-\mu_1} + \frac{\alpha (1 - e^{-\mu_1}) \xi_1}{\alpha + \varepsilon_1 \bar{v} e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1)} - \frac{\alpha \eta_1 \bar{u} e^{-\mu_1} \int_0^1 (1 - e^{-\mu_1 \tau}) e^{\alpha \tau - \bar{v}(1 - e^{-\mu_1 \tau})/\mu_1} d\tau}{\mu_1 (\rho^\alpha - 1) / \mu_1 (\alpha + \varepsilon_1 \bar{v} e^{-\mu_1} (\ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1})/\mu_1))^2}.
\end{align*}
\]
In the case of two dimensions, the Jury conditions for the stability of an equilibrium are
\[
1 - \text{tr} J + \det J > 0, \\
1 + \text{tr} J + \det J > 0, \\
1 - \det J > 0.
\]
The semi-trivial state can be stable or unstable in the \(u-v\) plane. It can lose stability in a flip bifurcation if the second of these inequalities is an equality, which leads to two-cycles, or in a Hopf bifurcation (Naimark–Sacker) if the third of these conditions is an equality, which leads to regular oscillations. We illustrate the stability boundaries for those cases in Figure 3.

The blue boundary for existence of the equilibrium corresponds to a transcritical bifurcation, which occurs if the first of the Jury conditions is an equality; the red stability boundary corresponds to a Hopf bifurcation; the black stability boundary corresponds to a flip bifurcation.
4.2. Stability of the coexistence state. The elements of the Jacobian matrix for the positive equilibrium \((\bar{u}, \bar{v}, \bar{w})\) are

\[
J_{11} = \frac{1}{\rho \mu \mu_1 \mu_2 \mu_3 \mu_4 \mu_5}, \\
J_{12} = -\bar{u}(1 - e^{-\mu_1})/\mu_1 + \frac{\alpha_{2} \int_{0}^{1} (1 - e^{-\mu_1}) e^{\alpha_{2} \bar{v}(1 - e^{-\mu_1})} / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2 d \tau}{\rho_{1} \mu_{1} \mu_{2} \alpha_{2} \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}, \\
J_{13} = -\bar{u}(1 - e^{-\mu_2})/\mu_2 + \frac{\alpha_{2} \int_{0}^{1} (1 - e^{-\mu_2}) e^{\alpha_{2} \bar{v}(1 - e^{-\mu_1})} / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2 d \tau}{\rho_{2} \mu_{2} \alpha_{2} \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}, \\
J_{21} = \frac{\alpha_{1} \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}{\rho_{1} \mu_{1} \mu_{2} \alpha_{1} \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}, \\
J_{22} = \frac{\alpha_{1} \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}{\rho_{1} \mu_{1} \mu_{2} \alpha_{1} \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}(\alpha + \bar{\varepsilon}_{1} \bar{v}(1 - e^{-\mu_1}) / \mu_2)^{2}, \\
J_{23} = \frac{\alpha_{1} \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}{\rho_{1} \mu_{1} \mu_{2} \alpha_{1} \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}(\alpha + \bar{\varepsilon}_{1} \bar{v}(1 - e^{-\mu_1}) / \mu_2)^{2}, \\
J_{31} = \frac{\alpha_{2} \bar{w}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}{\rho_{2} \mu_{2} \alpha_{2} \bar{w}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}(\alpha + \bar{\varepsilon}_{2} \bar{w}(1 - e^{-\mu_2}) / \mu_2)^{2}, \\
J_{32} = \frac{\alpha_{2} \bar{w}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}{\rho_{2} \mu_{2} \alpha_{2} \bar{w}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}(\alpha + \bar{\varepsilon}_{2} \bar{w}(1 - e^{-\mu_2}) / \mu_2)^{2}, \\
J_{33} = \frac{\alpha_{2} \bar{w}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}{\rho_{2} \mu_{2} \alpha_{2} \bar{w}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2}(\alpha + \bar{\varepsilon}_{2} \bar{w}(1 - e^{-\mu_2}) / \mu_2)^{2},
\]

where \(\varphi = \ln \rho + \alpha - \bar{v}(1 - e^{-\mu_1}) / \mu_1 - \bar{w}(1 - e^{-\mu_2}) / \mu_2\).
For a $3 \times 3$ matrix $J$, let $J_k$ be the $2 \times 2$ matrix obtained from $J$ by deleting row $k$ and column $k$, and define the numbers
\[ e_1 = -\text{tr}J, \quad e_2 = \sum_{k=1}^{3} \det J_k, \quad e_3 = -\det J. \]
Then the positive equilibrium is asymptotically stable if
\[ 1 + e_1 + e_2 + e_3 > 0, \]
\[ 1 - e_1 + e_2 - e_3 > 0, \]
\[ |e_2 - e_1 e_3| < 1 - e_3^2, \]
while the equilibrium is unstable if any of the inequalities is reversed [20]. The explicit Jury conditions for our model are too complicated to yield insights. Instead, we visualize the region of stability numerically.

There are several possible scenarios for the stability behavior of the positive equilibrium, depending on parameter values. With parameters chosen as in Figure 2, the positive equilibrium is stable whenever it exists. The positive equilibrium may become unstable in a Naimark–Sacker bifurcation, for example when we decrease $\varepsilon_i$, see Figures 4 and 5. It may also become unstable in a flip bifurcation, for example when we increase $\alpha$, see Figures 6 and 7. Or it may be unstable whenever it exists, for example when we decrease $\varepsilon_i$ even further, see Figures 8 and 9.

More precisely, in Figures 4, 6 and 8, the positive equilibrium exists between the blue curves, which correspond to conditions (39) and (45) from the analysis in Section 3. They also correspond to the first inequality in the Jury conditions (70) being an equality, so that one eigenvalue is equal to unity. Hence, the coexistence state emerges in a transcritical bifurcation from a semitrivial state. The red curve corresponds to the last of the Jury conditions being an equality. There is a pair of complex conjugate eigenvalues on the unit circle, so that a Naimark–Sacker bifurcation occurs. Finally, the black curve corresponds to an eigenvalue of $-1$, when the second Jury condition is an equality and a flip bifurcation occurs.

Figures 5, 7 and 9 show orbit diagrams corresponding to fixing parameter $\eta_1$ in bifurcation diagrams 4, 6 and 8, respectively. We ran simulations until transients had died out and plotted the density of the three species for two thousand generations. In Figure 5, we see that only consumer species $v$ is present in the oscillations when $\mu_1 \in (0.2, 0.4)$ is small. As $\mu_1$ increases, the coexistence state emerges, but since it is unstable, all species now cycle. When $\mu_1$ crosses the red bifurcation curve, the oscillations cease and the coexistence equilibrium becomes stable. When $\mu_1$ increases further, the coexistence state vanishes and only consumer $w$ is present at a steady state.

Figures 6 and 7 present a similar scenario but with a two-cycle and a flip bifurcation replacing the oscillations and Naimark–Sacker bifurcation. Figures 8 and 9 also present a similar scenario. Here all species could coexist and oscillate when the positive equilibrium exists but is unstable. Figure 9 shows a small window of phase-locking near $\mu_1 = 0.6$, where the invariant curves collapse to an oscillation between finitely many points. The same behavior appears between only two species near $\mu_1 = 0.4$. This phenomenon is quite common in discrete dynamics; see e.g. [11, 14, 25].

Comparing Figures 2, 4 and 8, we see that the parameter region where the positive coexistence state exists decreases as $\varepsilon_i$ decrease. In the limit, when $\varepsilon_i = 0$, we have the case of linear consumer reproduction, and we already know from Section
there is generically no positive coexistence state. In our particular examples, the coexistence state also loses stability in some or all of the parameter range where it exists as $\varepsilon_i$ decreases. This is not necessarily the case. The coexistence state may remain stable as $\varepsilon_i$ decreases, depending on the other parameter values (plots not shown). Comparing Figures 4 and 6, flip bifurcations are more likely when the resource growth rate $\alpha$ is bigger, as in the case of one resource and one consumer in [23].

![Figure 4. Bifurcation diagram with respect to parameters $\mu_1$ and $\eta_1$. Other parameters are as in Figure 2, except $\varepsilon_1 = \varepsilon_2 = 0.5307$.](image)

4.3. The effect of season length on stability. We now apply our model to explore how a change of the summer season length, $T$, could affect the dynamics of consumer–resource systems. For an explicit dependence of $T$, we return to the original, unscaled model. We simulate its dynamics for a range of values of $T$ while keeping all other parameters fixed. The plot in Figure 10 shows that no species can survive when the summer season length is too short, which seems intuitively obvious. As the summer becomes long enough, first the resource can persist, then one of the consumers, and eventually both for the parameters chosen. All the bifurcations are transcritical bifurcations.

As the duration of the summer increases, the duration of the winter decreases. It is therefore reasonable to assume that the parameters that describe overwintering survival of resource and consumer also change with $T$. For a simple scenario, we assume that only the duration but not the severity of the winter season changes. Then the survival rates should increase as the duration of the winter decreases. We model this effect heuristically and simplistically by setting $\rho = \xi_i = e^{-\omega(1-T)}$ for some fixed value $\omega > 0$. The results are plotted in Figure 11. The overall qualitative behavior is somewhat similar to that in Figure 10, but some differences are possible. In one case, the density of the first consumer (red) continues to grow for a while when the second consumer (black) first appears. In the other case, the density of the first consumer (red) decreases immediately when the second consumer (black) appears. Eventually the first consumer goes extinct while the second consumer and the resource cycle after a Naimark–Sacker bifurcation.

5. Discussion. In this work, we studied the dynamics of two consumer species that exploit a single common limiting resource. The study of exploitation dynamics
in continuous-time models has, of course, a long history in mathematical ecology [2, 12, 13, 18] with the competitive exclusion principle as one of its hallmark results [3, 10]. Our study differs from these earlier works in that we take some aspects of seasonal changes during a year into account. More specifically, reproduction of the consumers is pulsed, which represents a single annual reproduction event that many species in temperate climates exhibit. The resource replenishes continuously throughout the consumers’ growing season, but may experience decline between
two growing seasons. This behavior is again typical for temperate climates. Our model is an extension and slight variation of the model by Pachepsky et al [23], who considered a single consumer. Related models exist for chemostat dynamics, but these controlled microbial systems differ in several respects from macro-ecological systems; for example, microbial growth can be considered continuous, and only the resource replenishment is considered pulsed [5, 7, 32, 36].
We solved the differential equations that describe the dynamics during the growing season and substituted the solution into the difference equations that represent the between-season events to obtain a discrete map from one year to the next. We then analyzed the equilibria of this discrete-time system. For linear consumer reproduction, we proved that there is no coexistence steady state in general. Hence,
we recovered the competitive exclusion principle for our model. However, for non-linear consumer reproduction, we proved the existence and uniqueness of a positive equilibrium under conditions (39) and (45); in fact, we gave an explicit, albeit complicated, expression for the coexistence state. Furthermore, we found that the sufficient conditions for instability of the semi-trivial equilibria are also the necessary and sufficient conditions for the existence of the positive equilibrium. This result is related to the principle that “mutual invasion implies coexistence” but the situation in our model is more complicated, because the coexistence point is not necessarily stable when it exists.

We analyzed stability of the coexistence state via the Jury conditions and visualized the results in several bifurcation diagrams. We also simulated the original semi-discrete (or hybrid) model to confirm the analytical results and illustrate the dynamical behavior. We found that the coexistence equilibrium (as well as the semi-trivial equilibria with only a single consumer present) may undergo a flip bifurcation to two-cycles or a Naimark–Sacker bifurcation to regular oscillations. In additional preliminary numerical explorations (no plots shown), we found secondary bifurcations and more complex behavior in our model, which can be expected because of the discrete-time nature of the equations. A detailed study of this complex behavior is the subject of our ongoing research.

While several fully discrete models for two-species competition exist [1, 15, 16], our semi-discrete approach has the advantage that we can study the potential effects of a changing climate on the dynamics. We chose the season length as a bifurcation parameter and showed how the dynamics can change as a result.

Two other, related questions are part of our ongoing research on this topic. One is whether the two consumers will coexist whenever the coexistence equilibrium exists. Our simulations seem to indicate that this is the case: even when the equilibrium is unstable, both consumers remain in the system but their densities fluctuate. The other is whether the two consumers may coexist (with their densities fluctuating) even when the coexistence state does not exist. Numerical simulations for the case of linear consumer reproduction indicate that this is the case; see Figure 12. Even though we proved that there is no coexistence state with linear consumer reproduction (see proposition 2), the two consumers coexist in a two-cycle for the

![Figure 11. Three species densities with different summer length. ρ, ξ₁, ξ₂ increasing in T with ω = 0.7, other parameters are as in Figure 10, except δ₁ = δ₂ = 0.0711 in right plot.](image)
parameter values chosen. It is also interesting to study coexistence mechanisms in semi-discrete models for 3 and more consumer species on a single resource.

![Figure 12](image)

**Figure 12.** Three species coexist with linear reproduction. Parameters are $\mu_1 = 0.7$, $\mu_2 = 0.5378$, $\eta_1 = 5.9$, $\eta_2 = 7.2284$, $\xi_1 = 0.6681$, $\xi_2 = 0.1788$, $\alpha = 55.0495$, $\rho = 0.9599$.

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