Consider model with positive dilution rate D and positive input nutrient concentration S^0. Denote the nutrient, cooperator and cheater by S, X_1, and X_2 respectively. The cooperator distributes its energy over three functions: $q_1(e)$ is the fraction of nutrient uptake allocated towards enzyme production which is dependent on the amount of enzyme available, q_2 is the fraction of nutrient uptake allocated to ostracism which depends on the quantity of cheaters present, and q_3 is the remaining nutrient uptake allocated towards growth. The parameters $q_1(e), q_2(X_2) \in [0,1)$ and $q_1 + q_2 + q_3 = 1$, that is, the sum of these functions is necessarily equal to all of the energy available. Thus, we can eliminate q_3 from the system, and represent the fraction of energy spent on growth as $1 - q_1(e) - q_2(X_2)$, which is assumed to be positive. Ostracism will occur at positive rate $\Sigma(q_2)$. The per capita uptake rates of cooperator and cheater are assumed to be the same given by $\frac{F(S,E)}{\gamma}$, where γ is the yield constant in the conversion of nutrient to new biomass. η_E denote the efficiency of the conversion of nutrient to the public good.
This leads to the following model:

$$\dot{S} = D(S^0 - S) - \frac{1}{\gamma}F(S,E)(X_1 + X_2) \tag{1}$$

$$\dot{E} = \eta_E q_1(E) X_1 F(S,E) - DE \tag{2}$$

$$\dot{X}_1 = X_1((1 - q_1(E) - q_2(X_2))F(S,E) - D) \tag{3}$$

$$\dot{X}_2 = X_2(F(S,E) - D) - \Sigma(q_2(X_2))X_1) \tag{4}$$

N1: assume the per capita uptake rate function $F(S,E)$ is non-negative and twice continuously differentiable and satisfies the following assumptions:

$$F(0,E) = F(S,0) = 0,$$

$$F(S,E) > 0 \text{ when } S > 0 \text{ and } E > 0,$$

$$\frac{\partial F}{\partial S}(S,E) > 0 \text{ and } \frac{\partial F}{\partial E}(S,E) > 0 \text{ when } S > 0 \text{ and } E > 0.$$

These assumptions imply there is no nutrient uptake when nutrient or public good are absent, that there is nutrient uptake when both are present, and that with increased levels of nutrient or public good there is also an increase in uptake rates.

N2: assume that the cost of ostracism function $q_2(X_2) \in [0,1)$ is non-decreasing, that is, either constant or monotonically increasing. Additionally assume that it satisfies $q_2(0) = 0$. Assume further that the rate of ostracism, $\sigma(q_2(x_2))$ is monotonically increasing, that is, more energy spent on ostracism results in an increase in ostracism. Moreover, $\sigma(0) = 0$.

N3: Further assume that the fraction of nutrient uptake spent on producing enzyme is dependent upon the amount of enzyme present in the environment. That is, $q_1(e)$ will be a decreasing function and $q_1(0) > 0$.

These assumptions imply that there is a cost to ostracize only when cheaters are present and that the ostracism rate is 0 when no cheaters are present. Additionally, that if the environment is saturated with nutrient, the cooperator will produce less of it and when there is a lack of enzyme present the cooperator will produce more of it.

We can then scale out the conversion factors γ, η_E, η_T by setting $s = S, e = \frac{E}{\eta_E \gamma}, s^0 = S^0, x_i = \frac{x_i}{\gamma}, d = D, f(s,e) = F(s, \eta_E \gamma e)$.

We can also set $\sigma(q_2(x_2)) = \frac{\Sigma}{X_2}(q_2(x_2))$

This leads to the scaled system:

$$\dot{s} = d(s^0 - s) - (x_1 + x_2)f(s, e) \tag{5}$$

$$\dot{e} = q_1(e)x_1 f(s, e) - de \tag{6}$$

$$\dot{x_1} = x_1((1 - q_1(e) - q_2(x_2))f(s, e) - d) \tag{7}$$

$$\dot{x_2} = x_2(f(s, e) - d - x_1\sigma(q_2(x_2))) \tag{8}$$

Note that $f(s, e) \geq 0 \forall s \geq 0, e \geq 0$. Additionally, $f(0, e) = f(s, 0) = 0 \forall s \geq 0, e \geq 0$ and $\frac{\partial f}{\partial s} \geq 0$ and $\frac{\partial f}{\partial e} \geq 0$.

This model is well-posed in the following sense that (5)-(8) is dissipative.

let $m = s + e + x_1 + x_2,$, then

$$\dot{m} = d(s^0 - m) - q_2(x_2)x_1 f(s, e) - x_1\sigma(q_2(x_2)) \leq d(s^0 - m),$$

and hence $\lim_{\tau\to+\infty} \sup m(\tau) \leq s^0$, implying that (5)-(8) is dissipative.

1 Case 1: Cooperators Only

First consider the case where $x_2 = 0$, that is, cheaters are not present. In this case, there is no ostracism occurring, thus by **N2**, $q_2(x_2) = 0$. Then (5)-(8) is transformed into the system:

$$\dot{s} = d(s^0 - s) - (x_1)f(s, e) \tag{9}$$

$$\dot{e} = q_1(e)x_1 f(s, e) - de \tag{10}$$

$$\dot{x_1} = x_1((1 - q_1(e))f(s, e) - d) \tag{11}$$

Transforming the state of the system from (s, e, x_1) to (m, e, x_1) where

$$m = s + e + x_1,$$

we get:

$$\begin{aligned}
\dot{m} &= d(s^0 - m) \\
\dot{e} &= q_1(e)x_1 f(m - e - x_1, e) - de \\
\dot{x_1} &= x_1((1 - q_1(e))f(m - e - x_1, e) - d),
\end{aligned}$$

from which it follows as $\tau \to +\infty$, $m(\tau) \to s^0$. Hence the dynamics are understood by considering the following system:

$$\dot{e} = q_1(e)x_1 f(s^0 - e - x_1, e) - de \tag{12}$$

$$\dot{x_1} = x_1((1 - q_1(e))f(s^0 - e - x_1, e) - d) \tag{13}$$

The steady states, which will be represented of the form $\{e, x_1\}$, can be found by finding solutions to (12) -(13).

Note that when $x_1 = 0$, $\dot{e} = -de- \to 0$, thus we get the washout stead state $W = \{0, 0\}$.

From (12) -(13), we get

$$f(s^0 - e - x_1, e) = \frac{d}{q_1(e)x_1}e = \frac{d}{1 - q_1(e)}.$$

Solving this, we get

$$x_1 = \frac{1 - q_1(e)}{q_1(e)}e.$$

Replacing x_1 in our system with this value gives us a function with just one parameter, e.

Let $f(s^0 - \frac{1}{q_1(e)}e, e) = h(e)$, and let $\frac{d}{1-q_1(e)} = k(e)$, then solutions to (12) -(13) will occur when $h(e) = k(e)$.

Since $\frac{e}{q_1(e)}$ is unbounded, increasing, and 0 when $e = 0$, there exists some e^0 such that $\frac{e^0}{q_1(e^0)} = s^0$. Thus, we only consider values of e such that $0 < \frac{e}{q_1(e)} < s^0$.

Notice that **N1** implies that $h(0) = h(s^0) = 0$ and that $h(e) > 0$ when $0 < e < q_1(e)s^0$.

When the function $h(e)$ is strictly concave down (i.e. $h''(e) < 0$ for $0 < e < q_1(e)s^0$), and the equation $k(e) = \frac{d}{1-q_1(e)}$ is sufficiently small, then there will be two positive solutions.

Note that functions of the form $f(s, e)$ can be rewritten as a product of a function of s and e respectively, i.e., $f(s, e) = f_1(s)f_2(e)$. Then $f(s, e) = h(e) = f_1(s^0 - \frac{e}{q_1(e)})f_2(e)$.

For $h''(e) < 0$, it is necessary and sufficient that $g''(e) = \frac{-e}{q_1(e)} < 0$.

Some examples of functions which satisfy this condition are:

1) $q_1(E) = e^{-E}$ and thus $g(E) = -Ee^E$. Here, $g''(E) = -2e^E - Ee^E < 0$.

2) $q_1(E) = \frac{1}{1+E^2}$. Then $g(E) = \frac{-E}{q+E^2}$ and $g''(E) = \frac{-2E^3+6E}{(E^2+1)^3} < 0$.

N3 Assume $g''(e) < 0$ and $k(e) = \frac{d}{1-q_1(e)}$ is sufficiently small. Then it follows, $h''(e) < 0$. Thus, there are two positive solutions e^* and e^{**}, where $0 < e^* < e^{**} < q_1(e)s^0$, such that $h(e) = k(e)$.

Thus (12)-(13) has three steady states. $W = \{0, 0, 0, 0\}$, $R^* = \{e^*, \frac{1-q_1(e^*)}{q_1(e^*)}e^*\}$, $R^{**} = \{e^{**}, \frac{1-q_1(e^{**})}{q_1(e^{**})}e^{**}\}$.

Next we will determine stability of R^* and R^{**}. The linearization of system

(12)-(13) is given by:

$$J = \begin{bmatrix} x_1 \frac{dq_1(e)}{de} f + x_1 q_1(e) \frac{\partial f}{\partial e} - d & q_1(e) f \\ x_1((1 - q_1(e)) \frac{\partial f}{\partial e} - f \frac{dq_1(e)}{de}) & (1 - q_1(e)) f - d \end{bmatrix}$$

where the argument (s, e) is suppressed on $f(s, e)$ to ease notation.

Considering the