Succession processes in a food web of a two autotroph–one herbivore system

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Abstract

This paper deals with the succession process of a food web model consisting of one herbivore, two autotrophs and available nutrient in the environment in a closed nutrient flux. The model provides a way of describing successional changes in the form of species replacement with increasing nutrient levels. It is shown that distinct threshold (with upper and lower) values of nutrient are required for progression of succession process. © 2000 Elsevier Science Ireland Ltd. All rights reserved.

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1. Introduction

Ecosystem changes may be caused by fluctuations in the internal population interactions or by fluctuations of the controlling factors. Such changes could be cyclical changes or directional changes from less complex to more complex communities, and can be considered as progression in succession. During progressive succession there is usually an increase in productivity of biomass, related to stability and diversity of species. Succession is a typical example of an irreversible process in ecology in which co-operation between organisms replace one another in a given region. The succession of species population may be a result of one or a combination of general factors: (i) phenotypic characteristics of species (some entering a disturbed area sooner than others and growing faster); (ii) externally imposed changes in one or more environmental parameters that favour some species over the others; (iii) changes in the environment caused by the populations themselves (see DeAngelis, 1992; Smith, 1990).

In this paper a possible succession process due to changes in the amount of nutrients will be analysed on the assumption that succession ends in the formation of a stable climatic biocenosis. Rosenzweig (1971) studied a series of predator-prey models with different prey productivities and predator functional response curves, and established the possibility of oscillatory instability un-
nder conditions of nutrient enrichment. Armstrong (1979) modelled the process of succession under gradual changes in environmental conditions, namely, increases in nutrient levels in the ecosystem, or 'eutrophication' to one-prey many-predator systems. He described a graphical approach in order to analyse changes along gradients of nutrient enrichment. Alekseev (1982) also discussed a model of Lotka–Volterra type in order to study succession and predicted simple and complex succession series obtained from the stability conditions of possible stationary states at different levels of total nutrients. Holt et al. (1994) studied a food-web model and assumed that the model is closed with respect to the limiting nutrients. It is found in their study that distinct thresholds of nutrient levels are required to support the various food-web configurations. Recently, Kesh et al. (1997) studied succession in a three species food chain model and found that distinct thresholds of nutrient levels are required to support the species of the food chain.

The succession process through species replacement with increasing nutrient level changes in autotroph species composition under temporal or spatial gradients in nutrient levels has been observed in many studies. Olsen and Willen (1980) reported on the effects of reduction in phosphorous loading to Lake Vattern in Sweden and subsequent changes in phytoplankton volume in the lake during a period of ten years. DeNoylles and O’Brien (1978) enriched experimental ponds with nitrogen, phosphorous and potassium in order to study phytoplankton succession. Davy and Bishop (1984) also investigated the effects of addition of nutrients to a Breckland grass heath. It was observed that nutrient addition caused an increase in the biomass of Festuca ovina and Koeleria macrantha, whereas the biomass of competing species such as Hieracium pilosella showed a considerable decline. DeAngelis (1992) discussed species replacement with increasing nutrient levels in an environment closed to nutrient flux.

In this paper, possible succession process as due to changes in the amount of nutrients will be analysed under the assumption that succession ends in the formation of a stable climateric biocenosis. We investigate the succession series of a food-web model comprising two autotrophs competing for a single limiting resource and grazed on by a single generalized herbivore. In the proposed model the growth of autotrophs are assumed to follow Lotka–Volterra type interactions with the available nutrients while the uptake rates of the generalized predator are taken in a general functional form. From the model study it appears that the co-existence of one autotroph with a corresponding herbivore depends on the upper and lower threshold levels of available nutrients and also on the form of the uptake function of the herbivore. If threshold levels of nutrients are further enhanced, co-existence of two autotrophs and one herbivore is possible provided an intricate relationship between uptake functions of the first and second autotroph by the herbivore is satisfied. From the model study it appears that both autotrophs cannot co-exist in the absence of the herbivore.

The organisation of the paper is as follows. In Section 2, a food-web model and mathematical preliminaries are presented. Section 3 deals with the existence of possible boundary equilibria. In Section 4, stability conditions and possible simple and complex succession series for the model are discussed. A numerical example is given in Section 5 to illustrate the results. Lastly, a discussion follows in Section 6.

2. The model and basic results

We consider here a trophic scheme of a food-web comprising two autotrophs and one herbivore with nutrient limited growth in a closed environment, whose total nutrient level \( N \) in the environment is assumed to be conserved. Let \( x_1(t), x_2(t) \) and \( y(t) \) denote equivalent biomass (or the mass of the limiting nutrient) of autotrophs and herbivore respectively and \( R_0(t) \) be the mass of the available limiting biogenic resources (nutrient) in the environment.

The set of differential equations describing the dynamics of the model of this process is given in the form
\[
\frac{dx_1}{dt} = -\varepsilon_1 x_1 - y p_1(x_1) + \beta_1 x_1 R_o
\]

\[
\frac{dx_2}{dt} = -\varepsilon_2 x_2 - y p_2(x_2) + \beta_2 x_2 R_o
\]

\[
\frac{dy}{dt} = -\varepsilon_3 y + y(p_1(x_1) + p_2(x_2))
\]

\[
\frac{dR_o}{dt} = \varepsilon_1 x_1 + \varepsilon_2 x_2 + \varepsilon_3 y - R_o(\beta_1 x_1 + \beta_2 x_2)
\]

with \(x_i(0) = x_{i0} > 0\), \(i = 1, 2\) and \(y(0) = y_0 > 0\).

Here the uptake rates of available nutrients by autotrophs are taken in Lotka–Volterra form while response function of the generalized herbivore is taken in a general form \(p_i(x_i)\); \(i = 1, 2\). Also \(\varepsilon_1, \varepsilon_2, \varepsilon_3\) are the mortality rates and \(\beta_1, \beta_2\) the efficiency rate of utilizing the resources, which are taken to be positive.

From the (Eq. (2.1)) it follows that

\[
R_o(t) + x_1(t) + x_2(t) + y(t) = \text{Constant} = N \quad \text{(say)}
\]

Hence the model meets the conservation principle. Using conservation condition (Eq. (2.2)) for nutrient in (Eq. (2.1)), we get the following system as:

\[
\frac{d}{dt} x_1 = \beta_1 x_1(N - \lambda_1 - x_1) - \beta_1 x_2 x_1 + y(p_1(x_1) + \beta_1 x_1)
\]

\[
\frac{d}{dt} x_2 = \beta_2 x_2(N - \lambda_2 - x_2) - \beta_2 x_1 x_2 - y(p_2(x_2) + \beta_2 x_2)
\]

\[
\frac{d}{dt} R_o = y(-\varepsilon_3 + p_1(x_1) + p_2(x_2))
\]

where \(\lambda_i = \varepsilon_i / \beta_i; i = 1, 2\).

In this system \(R_o\) is not explicitly present and it resembles a two autotroph–herbivore system in which autotrophs are in competition, and the functional response of the herbivore is enhanced to the form \(p_i(x_i) + \beta_i x_i\).

### 2.1. Remark 1

From the model (Eq. (2.3)) it seems that there is indirect vertical interactions among the autotroph–herbivore levels and indirect horizontal (competitive) interactions. These indirect effects are mediated through direct interactions in a food-web of herbivores that share two autotroph in an environment which is closed with respect to limiting nutrients.

### 2.2. Hypotheses

We impose the following hypotheses on the functions \(p_i\) (for interpretation of (a) and (b) see Freedman, 1980) in order to analyze the model.

\(H1\)

(a) \(p_i: \mathbb{R}_+ \to \mathbb{R}\), and these are \(C^1\) functions.

(b) \(p_i(0) = 0, p_i'(x_i) > 0\) for \(x_i \in \mathbb{R}_+\) and

\[
\lim_{x_i \to \infty} p_i(x_i) = p_i(\infty) < + \infty
\]

(c) \(p_i(x_i) < 0\) for \(x_i < 0\);\( p_i(x_i) > 0\) for \(x_i > 0\).

(d) \(\frac{d}{dx_i} \left( \frac{p_i(x_i)}{x_i} \right) < 0\) for \(x_i \in (0, N - \lambda_i)\).

(e) \(\lambda_1 < \lambda_2\).

### 2.3. Lemma 2.1

All solutions of system (2.3) that initiate in \(\mathbb{R}_+^3\) for all initial points \((x_{10}, x_{20}, y_0)\) are eventually uniformly bounded and enter into a region \(\mathcal{B}\) defined by

\[
\mathcal{B} = \{(x_1, x_2, y) \in \mathbb{R}_+^3: 0 < x_i < C_i; 0 < x_1 + x_2 < k_2/m_3; 0 < x_1 + x_2 + y < k_2/m_2\}
\]

where

\[
C_i = N - \lambda_i, k_2 = C_i g_1(0) + C_i g_2(0) + \eta_1 + \eta_2
\]

\[
m_1 = \min[g_1(0), g_2(0)], m_2 = \min[g_1(0), g_2(0), \varepsilon_3]
\]

\[
g_i(x_i) = \beta_i(N - \lambda_i - x_i)\text{ and }\eta_i = \max_{x_i \in (0, c_i)} x_i g_i(x_i).
\]
2.4. Proof

By assumption (H1), both of the autotrophs are limited by their carrying capacities, and so from
(Eq. (2.3))
\[ x_i \leq x_i \beta_i(N - \lambda_i - x_i) = x_i g_i(x_i); \ i = 1, 2. \]

By the usual comparison theorem (Hale, 1969), we have
\[ x_i < C_i = N - \lambda_i \]

Let us define, \( S_i(t) = x_i(t) + x_2(t) \). The time derivative along a solution of the system is
\[
\dot{S} = x_i g_i(x_i) + x_2 g_2(x_2) - (\beta_1 + \beta_2) x_1 x_2 \\
- y(p_1(x_1) + \beta_1 x_1) - y(p_2(x_2) + \beta_2 x_2) \\
\leq x_i g_i(x_i) + x_2 g_2(x_2) \\
= - (x_i g_i(0) + x_2 g_2(0)) + x_1 g_2(0) + x_2 g_2(0) \\
+ x_i g_i(x_i) + x_2 g_2(x_2)
\]
or,
\[
\dot{S} \leq -m_1(x_1 + x_2) + C_1 g_1(0) + C_2 g_2(0) + \eta_1 + \eta_2
\]
Therefore,
\[ \dot{S} + m_1 S < k_2, \text{ where } k_2 = C_1 g_1(0) + C_2 g_2(0) + \eta_1 + \eta_2 \]

Applying a theorem on differential inequalities (Birkhoff and Rota, 1982), we obtain
\[ 0 \leq S_1 \leq (k_2/m_1) + e^{-m_1 S_1} x_i(0, x_2(0)). \]

As \( t \to \infty \), \( 0 < S_1 < k_2/m_1 \).

Define \( S_2(t) = x_1(t) + x_2(t) + y. \) Then
\[
\dot{S}_2 = \dot{x}_1 + x_2 + \dot{y} \\
\leq x_i g_i(x_i) + x_2 g_2(x_2) - \epsilon_0 y \\
= - (x_i g_i(0) + x_2 g_2(0)) + x_1 g_2(0) \\
+ x_2 g_2(0) + x_1 g_i(x_i) + x_2 g_2(x_2).
\]

Therefore,
\[
\dot{S}_2 \leq -m_2(x_1 + x_2 + y) + C_1 g_1(0) \\
+ C_2 g_2(0) + \eta_1 + \eta_2,
\]
or \( \dot{S}_2 + m_2 S_2 < k_2 \) and \( 0 < S_2 < k_2/m_2 \) as \( t \to \infty \).

Hence system (2.3) is dissipative with the asymptotic bound \( k_2/m_2 \). Thus there is a compact neighbourhood \( B \subset \mathbb{R}_+^2 \) such that for sufficiently large \( T = T(x_{0}\mu_0) \), \( x(t) \in B \) for all \( t > T \), where \( x(t) = \{x_1(t), x_2(t), y(t)\} \) is a solution of (2.3) that initiates in \( \mathbb{R}_+^3 \). This completes the proof of the lemma.

3. Existence of possible boundary equilibria

In system (2.3), when all species are absent, the trivial equilibrium \( E_0(0, 0, 0) \) always exists. The existence of other boundary equilibria depends critically on the amount of total nutrient \( N \) in the environment. The axial equilibria \( E_i(N \lambda_1, 0, 0) \) and \( E_2(N \lambda_2, 0, 0) \) exist provided \( N > \lambda_1 \) and \( N > \lambda_2 \), respectively. We now investigate the interior equilibrium in the positive \( x_1 \) \& \( y \) plane. Here isolines are \( \dot{x}_1 = 0 \), or \( y = F_i(x_i; N) \) where
\[
F_i(x_i; N) = \frac{\beta_i(N \lambda_1 - x_i)}{p_i(x_i)/x_i + \beta_i}
\]  
and \( \dot{y} = 0 \) is the vertical line \( x_1 = \mu_1 \), where \( \mu_1 \) is finite.

From (Eq. (3.1)), \( F_i(N \lambda_1; N) = 0 \) and
\[
F_1(0; N) = \lim_{x_1 \to 0^+} F_i(x_1; N) = \frac{\beta(N \lambda_1)}{p_1(0) + \beta_1} > 0
\]

a possible configuration of the autotroph isolines is given in Fig. 1.

Hence the unique interior equilibrium
\[
E_{1i}\left(\mu_1, 0, \frac{\beta_i(N \lambda_1 - \mu_1)}{p_i(\mu_1)} + \beta_1\right)
\]
exists in the \( x_1 \) \& \( y \) plane provided
\[
N > \lambda_1 + \mu_1
\]
4. Stability of equilibria

We denote by $\Omega^+(E)$ and $\Omega^-(E)$ as the local stable and unstable manifolds respectively, of equilibrium $E$. Let $x \in \mathbb{R}_+^1$, and let $\Omega(x)$ be the omega-limit set of the orbit through $x$.

Local stability properties of the feasible boundary equilibria are obtained by computing the variational matrix $V(x)$ of system (2.3) about these equilibria. The variational matrix of (Eq. (2.3)) is given by

$$V(x) = V(x_1, x_2, y) =$$

$$\begin{bmatrix}
H_1(x_1, x_2, y) & -\beta_1x_1 & -p_1(x_1) + \beta_1x_1 \\
-\lambda_1 & -x_2\beta_2 & -p_2(x_2) + \beta_2x_2 \\
\lambda_1 & -x_1\beta_1 & p_1(x_1)
\end{bmatrix}$$

where

$$H_1(x_1, x_2, y) = \beta_1(N - \lambda_1) - 2\beta_1x_1 - \beta_1x_2 - y(p_1(x_1) + \beta_1)$$

and

$$H_2(x_1, x_2, y) = \beta_2(N - \lambda_2) - 2\beta_2x_1 - 2\beta_2x_2 - y(p_2(x_2) + \beta_2).$$

Evaluating $V$ at different equilibria, we get their local stability properties.

4.1. Case 4.1: $N < \lambda_1 < \lambda_2$

$E_0$ is a sink (i.e. $E_0$ is saturated). No organism can live in the environment.

4.2. Case 4.2: $\lambda_1 < N < \lambda_2$

$E_0$ and $E_1$ exists and no other boundary equilibria are feasible. $E_0$ is a hyperbolic saddle point (or equivalently non-saturated). It has along each of the $y$-axis and $x_2$-axis a non-empty one dimensional (local) stable manifold.

The flows along the $x_1$ and $x_2$ axes are away from $E_0$ and approach $E_1$. $E_1$ is stable or unstable (locally) along the $y$-direction according as $-\epsilon_1 + p_1(N - \lambda_1) < 0$, i.e. $N < \lambda_1 + \mu_1$. So $E_1$ is unstable along $y$-direction and $y$ always increases (as its invasion parameter $-\epsilon_1 + p_1(N - \lambda_1) > 0$) at the axial equilibrium $E_1$ if $N > \lambda_1 + \mu_1$.

Hence $E_1$ becomes a saturated equilibrium for

$$\lambda_1 < N < \lambda_1 + \mu_1 < \lambda_2$$

$E_1$ becomes non-saturated for

$$\lambda_1 < \lambda_1 + \mu_1 < N < \lambda_2.$$  (4.3)

We now have the following result.

4.3. Theorem 4.1

Suppose that $\lambda_1 < N < \lambda_1 + \mu_1 < \lambda_2$. Then any solution of system (2.3) with $x_1(0) > 0$, $y(0) > 0$ satisfies
\[
\lim_{t \to \infty} x_i(t) = N - \dot{\lambda}_i, \quad \lim_{t \to \infty} x_3(t) = 0
\]
\[
\lim_{t \to \infty} y(t) = 0 \quad \text{and} \quad \lim_{t \to \infty} R_0(t) = \dot{\lambda}_1.
\]

### 4.4. Proof

Under the assumption of Theorem 4.1, it follows that \( E_1 \) is a saturated equilibrium. Thus it is a local attractor and autotroph \( x_3 \) cannot survive since \( \dot{x} < 0 \) for \( N < \lambda_2 \). Hence by the Butler–McGehee lemma (Freedman and Waltman, 1984) it follows that \( E_0 \) is not the \( \omega \)-limit set and hence all orbits with positive initial condition converge to the equilibrium \( E_1 \). From the conservation condition (2.2), it also follows that

\[
\lim_{t \to \infty} R_0(t) = \dot{\lambda}_1
\]

### 4.5. Case 4.3: \( \lambda_1 + \mu_1 < \lambda_2 < N < \lambda_2 + \mu_2 \)

Under this assumption, \( E_0 \), \( E_1 \), \( E_2 \), \( E_{13} \) are possible boundary equilibria. From the variational matrix, \( E_0 \) is non-saturated. It has along each of the \( x_i \)-axes a non-empty one-dimensional (local) unstable manifold. The flows along the \( x_i \) and \( x_3 \)-axes are away from \( E_0 \) and approach \( E_1 \) and \( E_2 \) respectively. \( E_1 \) is unstable along the \( y \)-direction since \( N > \lambda_1 + \mu_1 \). When \( N < \lambda_2 + \mu_2 \), \( E_2 \) has a non-empty one-dimensional (local) stable manifold in the \( x_2-y \) plane. Hence \( E_2 \) is non-saturated.

The variational matrix at \( (E_{13}) \) is

\[
V(E_{13}) = \begin{bmatrix}
a_{11} & -a_{12} & a_{13} \\
0 & a_{22} & 0 \\
a_{31} & a_{32} & 0
\end{bmatrix}
\]

where,

\[
a_{11} = \beta_1(N - \dot{\lambda}_1 - 2\mu_1) - \frac{\beta_1(N - \dot{\lambda}_1 - \mu_1)}{p_1(\mu_1) + \beta_1}(p'_1(\mu_1) + \beta_1)
\]
\[
a_{12} = \mu_1 \beta_1, \quad a_{13} = p_1(\mu_1) + \beta_1 \mu_1,
\]
\[
a_{22} = \beta_2(R - \dot{\lambda}_2 - 2\mu_1) - (p'_2(0) + \beta_2)
\]
\[
a_{31} = p'_1(\mu_1) \frac{\beta_1(N - \dot{\lambda}_1 - \mu_1)}{p_1(\mu_1) + \beta_1}
\]
\[
a_{32} = p'_2(0) \frac{\beta_1(N - \dot{\lambda}_1 - \mu_1)}{p_1(\mu_1) + \beta_1}
\]

The eigenvalues of \( V(E_{13}) \) are the roots of the characteristic equation

\[
(\lambda - a_{22})(\lambda^2 - a_{11}\lambda + a_{31}a_{13}) = 0.
\]

All eigenvalues are negative or have negative real parts if

\[
a_{22} < 0 \quad \text{and} \quad a_{11} < 0.
\]

If \( a_{22} < 0 \) then

\[
N(1 - M_1) < (\lambda_1 + \mu_1)(1 - M_1) + \mu_1,
\]

or

\[
N < \lambda_1 + \mu_1 + \frac{\mu_1}{1 - M_1}
\]

(4.4)

where

\[
M_1 = \frac{p'_1(\mu_1) + \beta_1}{p_1(\mu_1) + \beta_1} < 1 \quad \text{by H1 (d)}
\]

Again, if \( a_{22} < 0 \) then

\[
N < \lambda_1 + \mu_1 + \frac{\lambda_2 - \lambda_1}{1 - L_1}
\]

(4.5)

where \( L_1 = \frac{\beta_1}{\beta_2}(\frac{p'_2(0) + \beta_2}{p_2(\mu_1) + \beta_2}) \)

If \( \beta_1 < \beta_2 \) and

\[
\frac{p_2(\mu_1)}{\mu_1} > \frac{\beta_1}{\beta_2}p'_2(0),
\]

then \( L_1 < 1 \).

Hence \( E_{13} \) is a local attractor in \( \mathbb{R}^{3+} \), provided (i) \( \dot{\lambda}_1 + \mu_1 < \dot{\lambda}_2 < N < \min \)

\[
\left( \lambda_1 + \mu_1 + \frac{\mu_1}{1 - M_1}, \lambda_1 + \mu_1 + \frac{\lambda_2 - \lambda_1}{1 - L_1}, \lambda_2 + \mu_2 \right)
\]

and (ii)

\[
\frac{p_2(\mu_1)}{\mu_1} > \max \left( p'(\mu_1), \frac{\beta_1}{\beta_2}p'_2(0) \right), \beta_1 < \beta_2
\]

(4.7)

We next show that \( E_{13} \) is a global attractor in \( x_1-y \) plane. From (3.2) we have,

\[
N < \min \left( \lambda_1 + \mu_1 + \frac{\lambda_2 - \lambda_1}{1 - L_1}, \lambda_2 + \mu_2 \right)
\]

Hence \( a_{22} < 0 \) means \( \dot{\lambda}_2 \) decreases and \( E_{13} \) becomes a saturated equilibrium. If possible, let \( \Gamma_1 \)
be any periodic orbit around $E_{13}$ in $x_1-y$ plane. Then

$$
\Delta = - \oint_{x_1} \text{div} (\hat{x}, \hat{y}) \, dt
$$

$$
= \oint_{x_1} \left[ \{\beta_i x_i(p_i(x_1) + \beta_i x_i) \right.
+ (\beta_i x_i(N - \lambda_i - x_i))p_i'(x_1) - x_i p_i'(x_1)) \}
+ \frac{d}{dt}(\ln(p_i(x_1) + \beta_i x_1)) \right] dt
$$

$$
\oint_{x_1} (p_i(x_1) + \beta_i x_1) F_{13} (x_1; N) \, dt < 0.
$$

where

$$
F_{13} (x_1; N) = \frac{(-\beta_i x_i(p_i(x_1) + \beta_i x_i) + (\beta_i x_i(N - \lambda_i - x_i))p_i'(x_1) - x_i p_i'(x_1))}{(p_i(x_1) + \beta_i x_1)^2}
$$

by H1 (d).

Hence $\Delta < 0$. So, by the Poincare Bendixson theorem (Conway and Smoller, 1986) any periodic orbit is stable. However $E_{13}$ is locally stable in the $x_1 - y$ plane, a contradiction. Hence under (4.6) and (4.7), there is no periodic orbit around $E_{13}$ in the positive $x_1 - y$ plane.

4.6. Remark 2

Let the isocline of autotroph $x_1$ and the isocline of herbivore $y$ intersect at $E(\mu, y)$ (see Fig. 1) where $H_m < y < H_M$; $H_m$ and $H_M$ being the global minimum and global maximum values of $F_{13}(x_1; N)$. Now we have following two possibilities:

1. If $a_{22} < 0$, $a_{11} > 0$, one eigenvalue is positive and two are negative. Hence $E_{13}$ is locally unstable in $x_1-y$ plane but stable along the $x_2$ direction.

2. If $a_{22} > 0$, $a_{11} < 0$, then also $E_{13}$ is locally stable in $x_1-y$ plane and unstable along the $x_2$ direction.

In (i) $a_{22} < 0$ and $a_{11} > 0 \Rightarrow \lambda_i + \mu_i + \frac{\mu_i}{1-M_i} < N < \lambda_i + \mu_i + \frac{\lambda_2 - \lambda_1}{1-L}$. Hence $E_{13}$ is unstable in the $x_1 - y$ plane provided $(\lambda_i + \mu_i) < \max (\lambda_2, \lambda_i + \mu_i + \frac{\mu_i}{1-M_i}) < N < \min (\lambda_i + \mu_i + \frac{\lambda_2 - \lambda_1}{1-L}, \lambda_2 + \mu_2)$.

Therefore, $F_{13} > 0$ and $E_{13}$ becomes locally unstable in $x_1 - y$ plane. Hence by the Poincare–Bendixson theorem (Conway and Smoller, 1986) there may exist at least one limit cycle around $E_{13}$.

If $N = \lambda_i + \mu_i + (\mu_i/(1-M_i))$, then the real part of the eigenvalues of $E_{13}$ become zero and there exists Hopf-bifurcating small amplitude periodic solutions around $E_{13}$.

In (2) $a_{22} > 0$, $a_{11} < 0 \Rightarrow \lambda_i + \mu_i + \frac{\lambda_2 - \lambda_1}{1-L} < N < \lambda_i + \mu_i + \frac{\mu_i}{1-M_i}$. Hence $E_{13}$ is stable in the $x_1 - y$ plane and unstable along the $x_2$-direction provided $(\lambda_i + \mu_i) < \max (\lambda_2, \mu_i + \frac{\lambda_2 - \lambda_1}{1-L} < N < \min (\lambda_2 + \mu_2, \lambda_i + \mu_i + \frac{\mu_i}{1-M_i})$.

Therefore, $E_{13}$ is a global attractor under conditions (4.7) and its invasion parameter is negative for all $t > 0$. Since the system (2.3) is dissipative (by Lemma 2.1), we get the following result.

4.7. Theorem 4.2

Let (H1), Lemma 2.1 and conditions (4.7) hold. Then boundary equilibrium $E_{13}$ attracts all solutions of (2.3) with $x_2(0) > 0$, that is

$$
\lim_{t \to \infty} x_1(t) = \mu_i, \quad \lim_{t \to \infty} x_2(t) = 0
$$

$$
\lim_{t \to \infty} y(t) = \frac{\beta_1(N - \lambda_i - \mu_i)}{p_i(\mu_i) \mu_i + \beta_1}
$$

4.8. Case 4.4: $N > \max (\lambda_i + \mu_i, \lambda_2 + \mu_2)$

Then boundary equilibria $E_0, E_1, E_2, E_{13}, E_{23}$ all exist. We shall now investigate the conditions for uniform persistence of the system (2.3). To derive conditions for uniform persistence of the system, we need other assumptions, namely

(H2) There exist no periodic orbit on $x_1 - y$ plane and $x_2 - y$ plane for the system (2.3).

(H3) There exist no homoclinic orbits or other closed invariant set connected to each other in a closed chain for the system (2.3).
Let us consider an average Lyapunov function of the form (see Hofbauer, 1981; Hutson and Vickers, 1983).

\[ p(x) = p(x_1, x_2, y) = x_{11} x_{22} y, \quad s_i > 0 \]

Then in Int B, we get

\[ \psi(x) = \frac{\dot{p}(x)}{p(x)} = s_1 \beta_1 (N - \lambda_1 - x_1) - \beta_1 x_2 \\
- y(p_1(x_1) + \beta_1) \\
+ s_2 \beta_2 (N - \lambda_2 - x_2) - \beta_2 x_1 \\
- y(p_2(x_2) + \beta_2) \\
+ s_3 (-\epsilon_1 + p_1(x_1) + p_3(x_3)). \]

\( E_{13} \) is globally asymptotically stable in \( x_1 - y \) plane by conditions (4.7), and there is no periodic solutions around it. Hence by (H1), (H2) and (H3), the \( \omega \)-limit set of every orbit on boundary B consists of fixed points. So uniform persistence of the system (2.3) holds if \( \psi \) is positive at \( E_0, E_1, E_2, E_{13}, E_{23} \). To show this we have to make suitable choices of \( s_1, s_2, s_3 > 0 \) such that the following inequalities are satisfied.

\[ \psi(E_0): s_1 \beta_1 (N - \lambda_1) + s_2 \beta_2 (N - \lambda_2) - s_3 \epsilon_3 > 0 \]
\[ \psi(E_1): - s_2 (\lambda_2 - \lambda_1) + s_3 (-\epsilon_2 + p_1(N - \lambda_1)) > 0 \]
\[ \psi(E_2): s_1 (\lambda_2 - \lambda_1) + s_3 (-\epsilon_2 + p_3(N - \lambda_2)) > 0 \]

(4.8)

\[ \psi(E_{13}): s_2 \beta_2 (N - \lambda_2 - \mu_2) - \frac{\beta_1 (N - \lambda_1)}{\mu_1} + \frac{\beta_2 (p_1(0) + \beta_1)}{\mu_2} > 0 \]
\[ \psi(E_{23}): s_1 \beta_1 (N - \lambda_1 - \mu_2) - \frac{\beta_2 (N - \lambda_2 - \mu_2)}{\mu_2} + \frac{\beta_2 (p_2(0) + \beta_2)}{\mu_2} > 0 \]

(4.9)

\( \psi(E_2) \) is always positive, by proper choices of \( s_1, s_2 \) and \( s_3 \), it is easy to see that \( \psi(E_0) \) and \( \psi(E_1) \) are positive. Also \( \psi(E_{13}) > 0 \) and \( \psi(E_{23}) > 0 \), provided

\[ \max \left( \lambda_1 + \mu_1 + \frac{u_1}{1 - M_1}, \lambda_1 + \mu_1 + \frac{\lambda_2 - \lambda_1}{1 - L_1}, \lambda_2 + \mu_2 \right) \]

\[ < N < \left( \frac{\lambda_2 + \mu_2 + \lambda_2 - \lambda_1}{L_2 - 1} \right) \]

where, \( 0 < L_1 < 1 \) and \( L_2 = \frac{\beta_2}{\beta_1} + \frac{p_1'(0)/\beta_1}{p_3(\mu_2)\mu_2 + \beta_2} > 1 \)

Also \( \psi(E_2) > 0 \) since \( N > \lambda_2 + \mu_2 \). Hence we have the following result.

4.9. Theorem 4.3

Let (H1), (H2), (H3), Lemma 2.1 and conditions (4.7) hold, and if

1. \( \frac{\beta_2 p_1'(0)}{\beta_1} > \frac{\mu_2}{\mu_2} \)
2. \( \max \left( \lambda_1 + \mu_1 + \frac{u_1}{1 - M_1}, \lambda_1 + \mu_1 + \frac{\lambda_2 - \lambda_1}{1 - L_1}, \lambda_2 + \mu_2 \right) < N < \left( \frac{\lambda_2 + \mu_2 + \lambda_2 - \lambda_1}{L_2 - 1} \right) \)

then the system (2.3) is uniformly persistent.

4.10. Remark 3

If we reverse the condition of H1(e), then we get similar results by changing the suffix of all previous results as discussed from Case 4.1 to 4.4.

5. Example

In model (2.3), we take \( \beta_1 = 1, \beta_2 = 2, \lambda_1 = 1/2, \lambda_2 = 2, \epsilon_3 = 1/3, \)

\[ p_1(x_1) = \frac{x_1}{x_1^2 + x_1 + 1} \text{ and } p_2(x_2) = \frac{x_2}{2(x_2^2 + x_2 + 1)}. \]

then

\[ \frac{dx_1}{dt} = x_1(N - 1/2 - x_1) - x_1 x_2 - x_1 y \left( \frac{1}{x_1^2 + x_1 + 1} \right) \]

\[ \frac{dx_2}{dt} = 2x_2(N - 2 - x_2) - 2x_1 x_2 - x_2 y \left( \frac{1}{2(x_2^2 + x_2 + 1) + 2} \right) \]

\[ \frac{dy}{dt} = y \left( -\frac{1}{3} \frac{x_1}{x_1^2 + 1} + \frac{x_2}{2(x_2^2 + x_2 + 1)} \right) \]
It is easy to see that all the hypothesis of (H1) are satisfied. All solutions of (5.1) which initiate in \( R^1_+ \) will enter the confined convex set \( B \) defined by
\[
B = \{ (x_1, x_2, y) \in R^3_+ : 0 \leq x_1 \leq N - 1/2; \\
0 \leq x_2 \leq N - 2; \\
0 < x_1 + x_2 < k_2/m_1; 0 \leq x_1 + x_2 + y \leq k_2/m_2 \},
\]
where \( k_2 = (60N^2 - 180N + 165)/16 \), \( m_1 = N - 1/2 \) and \( m_2 = 1/3 \).
1. If \( 0.5 < N < 1.5 \), then all solutions of (5.1) initiating in \( R^1_+ \) will converge to the equilibrium \((N - 1/2, 0, 0)\) and \( R_0 = 1/2 \) as \( t \to \infty \).
2. If \( 1.5 < N < 5.5 \), then all solutions of (5.1) which initiate in \( R^1_+ \) converge to \((1, 0, (3N/4 - 9/8)) \) and \( R_0 = N/4 + 1/8 \).
3. If \( 5.5 < N < 26.458 \), then the system (5.1) is uniformly persistent.
4. If \( N > 26.458 \), then either of the autotrophs competing for the same limiting nutrient will go to extinction.

6. Conclusions

Successional changes can be explained utilizing population dynamics, especially competition, regeneration, mortality and by physiology and life history strategies. Species composition over time is determined by the development and response to competition. The replacement of species by other species results in part from interspecific competition which permits one group to suppress the other. Thus the succession comes about as the relative availability of resources changes through time. Community composition changes along the gradient as the availability of limiting resources changes and the species reach an equilibrium with this availability. In doing so, they lower the available resources to a point at which other species can not invade.

From the present study, it follows that if \( N \in (\lambda_1, \lambda_1 + \mu_1) \) where \( \lambda_1 + \mu_1 < \lambda_2 \) then autotroph \( x_1 \) exists for all future time but no other autotroph and its herbivore can survive. This is the first stage of succession.

The second stage of succession involving co-existence of the first autotroph \( x_1 \) and its herbivore becomes successful, provided the total nutrient \( N \) is further enhanced and lies in the threshold
\[
\left( \lambda_1 + \mu_1, \lambda_1 + \min \left( \frac{\mu_1}{1 - M_1}, \frac{\lambda_2 - \lambda_1}{1 - L_1} \right) \right)
\]
and the specific uptake rate for autotroph \( x_1 \) satisfies the condition
\[
\frac{p_1(\mu_1)}{\mu_1} > \max \left( \frac{p_1'(\mu_1), \beta_1}{\beta_2}, \frac{p_2'(0)}{\mu_2} \right)
\]
In this case autotroph \( x_2 \) can not grow in the environment.

The last phase of succession in which two autotrophs and a generalized herbivore co-exist is attained provided \( N \) is further enhanced and lies within the threshold
\[
\left( \lambda_1 + \mu_1 + \frac{\lambda_2 - \lambda_1}{1 - L_1}, \lambda_1 + \mu_1 + \frac{\mu_1}{1 - M_1} \right),
\]
where
\[
\frac{p_1(\mu_1)}{\mu_1} > \frac{\beta_1}{\beta_2} p_1'(0) \text{ and } \frac{\beta_2}{\beta_1} p_2'(0) > \frac{p_2'(\mu_2)}{\mu_2}
\]
This dynamics does not follow the usual succession series of its states from pioneer to climax (stable), but this study does gives conditions on the resources for one to study the introduction of species to form a food chain/web.

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