Towards a theory of ecotone resilience: coastal vegetation on a salinity gradient

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Appendix A

1.1 The model without diffusion

$$\begin{aligned}
\frac{dN_1}{dt} &= N_1(\rho_1 f(S) - \alpha_{11}N_1 - \alpha_{12}N_2),\\
\frac{dN_2}{dt} &= N_2(\rho_2 h(S) - \alpha_{21}N_1 - \alpha_{22}N_2),\\
\frac{dS}{dt} &= \beta_0 g + \beta_1 \frac{N_2}{k+N_2} g - \epsilon S
\end{aligned} \tag{A.1}$$

with non-negative initial conditions $(N_1(0), N_2(0), S(0)) \in \mathbb{R}^3_+ = \{(x_1, x_2, x_3) \in \mathbb{R}^3 : x_1 \geq 0, x_2 \geq 0, x_3 \geq 0\}$. We have the following assumptions:

(1) $f(S) = \dfrac{\mu}{\mu+S}$ and $h(S) = 1$, where $\mu > 0$;

(2) all parameters are positive;

(3) $\alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22} > 0$.

1.2 Elementary analysis

The Jacobian matrix of (A.1) at $(N_1, N_2, S) \in \mathbb{R}^3_+$ is $J((N_1, N_2, S)) =$

$$\begin{pmatrix} (\rho_1 f(S) - \alpha_{11}N_1 - \alpha_{12}N_2) - \alpha_{11}N_1 & -\alpha_{12}N_1 & \rho_1 N_1 f'(S) \\ -\alpha_{21}N_2 & (\rho_2 h(S) - \alpha_{21}N_1 - \alpha_{22}N_2) - \alpha_{22}N_2 & \rho_2 N_2 h'(S) \\ 0 & \beta_1 kg/(k+N_2)^2 & -\epsilon \end{pmatrix}.$$

In particular, if $f(S) = \dfrac{\mu}{\mu+S}$ and $h(S) = 1$, then $J((N_1, N_2, S)) =$

$$\begin{pmatrix} (\rho_1 f(S) - \alpha_{11}N_1 - \alpha_{12}N_2) - \alpha_{11}N_1 & -\alpha_{12}N_1 & -\rho_1 N_1 f^2(S)/\mu \\ -\alpha_{21}N_2 & (\rho_2 - \alpha_{21}N_1 - \alpha_{22}N_2) - \alpha_{22}N_2 & 0 \\ 0 & \beta_1 kg/(k+N_2)^2 & -\epsilon \end{pmatrix}.$$

Using the theory of monotone dynamical systems (Smith [6]) and an approach similar to that of Jiang and Tang [3], we prove that

Theorem 1.1. *Each non-negative solution of* (A.1) *converges to an equilibrium point.*

1.3 Equilibria and their stabilities

Direct calculation yields that system (A.1) has three boundary equilibria, namely,

$$E_0 = (0, 0, \frac{\beta_0 g}{\epsilon}), E_1 = (\frac{\rho_1 \mu}{\alpha_{11}(\mu + \beta_0 g/\epsilon)}, 0, \frac{\beta_0 g}{\epsilon}) \text{ and } E_2 = (0, \frac{\rho_2}{\alpha_{22}}, (\beta_0 + \beta_1 \frac{\rho_2}{k\alpha_{22} + \rho_2})\frac{g}{\epsilon}).$$

Proposition 1.2. *Let*

$$g_1^* = \frac{\epsilon\mu\Big(\frac{\rho_1\alpha_{22}}{\rho_2\alpha_{12}} - 1\Big)(k\alpha_{22} + \rho_2)}{k\beta_0\alpha_{22} + (\beta_0 + \beta_1)\rho_2} \text{ and } g_2^* = \Big(\frac{\rho_1\alpha_{21}}{\rho_2\alpha_{11}} - 1\Big)\frac{\epsilon\mu}{\beta_0}.$$

Then

(1) *E_0 is unstable and $W^s(E_0) \cap \mathbb{R}^3_+ = \{(N_1, N_2, S) \in \mathbb{R}^3_+ : N_1 = N_2 = 0, S \geq 0\}$;*

(2) *E_1 is unstable if $g > g_2$, stable if $g < g_2$;*

(3) *E_2 is unstable if $g < g_1$, stable if $g > g_1$.*

In addition, if E_1 is unstable, then $W^s(E_1) \cap \mathbb{R}^3_+ = \{(N_1, N_2, S) \in \mathbb{R}^3_+ : N_1 > 0, S \geq 0\}$; if E_2 is unstable, then $W^s(E_2) \cap \mathbb{R}^3_+ = \{(N_1, N_2, S) \in \mathbb{R}^3_+ : N_2 > 0, S \geq 0\}$. Here $W^s(E)$ denote the stable manifold of an equilibrium E.

Proof. The Jacobian matrices at the three boundary equilibria E_0, E_1 and E_2 are

$$J(E_0) = \begin{pmatrix} \frac{\rho_1\mu}{\mu + \beta_0 g/\epsilon} & 0 & 0 \\ 0 & \rho_2 & 0 \\ 0 & \beta_1 g/k & -\epsilon \end{pmatrix},$$

$$J(E_1) = \begin{pmatrix} -\frac{\rho_1\mu}{\mu + \beta_0 g/\epsilon} & -\frac{\rho_1\alpha_{12}\mu}{\alpha_{11}(\mu + \beta_0 g/\epsilon)} & -\frac{\rho_1^2\mu^2}{\alpha_{11}(\mu + \beta_0 g/\epsilon)^3} \\ 0 & \rho_2 - \frac{\rho_1\alpha_{21}\mu}{\alpha_{11}(\mu + \beta_0 g/\epsilon)} & 0 \\ 0 & \beta_1 g/k & -\epsilon \end{pmatrix}$$

and

$$J(E_2) = \begin{pmatrix} \frac{\rho_1\mu}{\mu + \Big(\beta_0 + \beta_1\frac{\rho_2}{k\alpha_{22} + \rho_2}\Big)\frac{g}{\epsilon}} - \frac{\rho_2\alpha_{12}}{\alpha_{22}} & 0 & 0 \\ -\rho_2\alpha_{21}/\alpha_{22} & -\rho_2 & 0 \\ 0 & \beta_1 gk/(k + \rho_2/\alpha_{22})^2 & -\epsilon \end{pmatrix}.$$

The proposition is immediately proved. □

Remark 1.3. If $g_2^* \geq 0$, that is, $\frac{\rho_1\alpha_{21}}{\rho_2\alpha_{11}} - 1 \geq 0$, then $g_1^* < g_2^*$ and $\frac{\partial(g_2^* - g_1^*)}{\partial\beta_0} < 0$. In fact,

$$\alpha_{12}\alpha_{21} > \alpha_{11}\alpha_{22} \Leftrightarrow \frac{\rho_1\alpha_{21}}{\rho_2\alpha_{11}} - 1 > \frac{\rho_1\alpha_{22}}{\rho_2\alpha_{12}} - 1 \Leftrightarrow \Big(\frac{\rho_1\alpha_{21}}{\rho_2\alpha_{11}} - 1\Big)\frac{\epsilon\mu}{\beta_0} > \Big(\frac{\rho_1\alpha_{22}}{\rho_2\alpha_{12}} - 1\Big)\frac{\epsilon\mu}{\beta_0}$$

$$\Rightarrow g_2^* = \Big(\frac{\rho_1\alpha_{21}}{\rho_2\alpha_{11}} - 1\Big)\frac{\epsilon\mu}{\beta_0} > g_1^* = \frac{\epsilon\mu\Big(\frac{\rho_1\alpha_{22}}{\rho_2\alpha_{12}} - 1\Big)(k\alpha_{22}+\rho_2)}{k\beta_0\alpha_{22} + (\beta_0+\beta_1)\rho_2}$$

$$\Rightarrow \Big(\frac{\rho_1\alpha_{21}}{\rho_2\alpha_{11}} - 1\Big)\frac{\epsilon\mu}{\beta_0} > \frac{\epsilon\mu\Big(\frac{\rho_1\alpha_{22}}{\rho_2\alpha_{12}} - 1\Big)(k\alpha_{22}+\rho_2)}{k\beta_0\alpha_{22} + (\beta_0+\beta_1)\rho_2} \times \frac{\beta_0(k\alpha_{22}+\rho_2)}{k\beta_0\alpha_{22} + (\beta_0+\beta_1)\rho_2}$$

$$\Leftrightarrow \frac{\partial g_2^*}{\partial \beta_0} = -\Big(\frac{\rho_1\alpha_{21}}{\rho_2\alpha_{11}} - 1\Big)\frac{\epsilon\mu}{\beta_0^2} < \frac{\partial g_1^*}{\partial \beta_0} = -\frac{\epsilon\mu\Big(\frac{\rho_1\alpha_{22}}{\rho_2\alpha_{12}} - 1\Big)(k\alpha_{22}+\rho_2)^2}{(k\beta_0\alpha_{22} + (\beta_0+\beta_1)\rho_2)^2}.$$

Let $K = \{(x_1, x_2, x_3) \in \mathbb{R}^3 : x_1 \geq 0, x_2 \leq 0, x_3 \leq 0\}$ and $\mathrm{Int}K = \{(x_1, x_2, x_3) \in K : x_1 > 0, x_2 < 0, x_3 < 0\}$. For $x, y \in \mathbb{R}^3_+$, we define $x \leq_K y$ if $y - x \in K$, $x <_K y$ if $y - x \in K\backslash\{0\}$, and $x \ll_K y$ if $y - x \in \mathrm{Int}K$. When $x, y \in \mathbb{R}^3_+$ and $x \leq_K (\ll_K) y$, let $[x, y]_K = \{w \in \mathbb{R}^3_+ : x \leq_K w \leq_K y\}$ ($(x, y)_K = \{w \in \mathbb{R}^3_+ : x \ll_K w \ll_K y\}$).

Remark 1.4. Note that $E_2 \leq_K E_0 \leq_K E_1$ and all orbits starting in $\mathbb{R}^3_+$ are attracted to the set $[E_2, E_1]_K$ (see [1]). The set of all positive equilibria, denoted by E^+, is a subset of $(E_2, E_1)_K$ and it is totally strongly ordered with respect to $\ll_K$, i.e., either $E^* \ll_K \tilde{E}^*$ or $\tilde{E}^* \ll_K E^*$ for any two points E^* and $\tilde{E}^*$ in E^+ satisfying $E^* \neq \tilde{E}^*$.

Theorem 1.5. *For system* (A.1)*, both E_1 and E_2 are stable if and only if there exists a positive equilibrium E^*. Moreover, it is unique and unstable when E^* exists.*

Proof. Suppose that both E_1 and E_2 are stable, then $g_1^* < g < g_2^*$.

If $E^* = (N_1^*, N_2^*, S^*)$ is a positive equilibrium of (A.1), then it satisfies the following three equations

$$\begin{aligned} &\rho_1\frac{\mu}{\mu+S} - \alpha_{11}N_1 - \alpha_{12}N_2 = 0, \\ &\rho_2 - \alpha_{21}N_1 - \alpha_{22}N_2 = 0, \\ &\beta_0 g + \beta_1\frac{N_2}{k+N_2}g - \epsilon S = 0. \end{aligned} \tag{A.2}$$

Let $\omega = \alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22} > 0$. After solving N_1 and S in terms of N_2 from the last two equations of (A.2), and substituting them into the first equation, we get

$$\rho_1\frac{\mu}{\mu + (\beta_0 g + \beta_1\frac{N_2}{k+N_2}g)/\epsilon} - \alpha_{11}\frac{\rho_2 - \alpha_{22}N_2}{\alpha_{21}} - \alpha_{12}N_2 = 0,$$

which can be simplified to a quadratic equation

$$F(N_2) \equiv AN_2^2 + BN_2 + C = 0, \tag{A.3}$$

where $A = (\beta_0 + \beta_1 + \frac{\epsilon\mu}{g})\omega > 0$, $B = (\beta_0 + \frac{\epsilon\mu}{g})k\omega + (\beta_0 + \beta_1 + \frac{\epsilon\mu}{g})\rho_2\alpha_{11} - \frac{\epsilon\mu}{g}\rho_1\alpha_{21}$ and $C = (\beta_0 + \frac{\epsilon\mu}{g})k\rho_2\alpha_{11} - \frac{\epsilon\mu}{g}k\rho_1\alpha_{21}$.

Since $g < g_2^*$ implies $C < 0$, (A.3) has exactly one positive root, N_2^*. To establish the existence of E^*, we need verify the positivity of

$$N_1^* = (\rho_2 - \alpha_{22}N_2^*)/\alpha_{21} \text{ and } S^* = (\beta_0 g + \beta_1 \frac{N_2^*}{k + N_2^*} g)/\epsilon,$$

respectively. Obviously, it suffices to show that $N_2^* < \rho_2/\alpha_{22}$ or $F(\rho_2/\alpha_{22}) > 0$. In fact,

$$\begin{aligned}
&F(\frac{\rho_2}{\alpha_{22}}) = A(\frac{\rho_2}{\alpha_{22}})^2 + B\frac{\rho_2}{\alpha_{22}} + C \\
=&(\beta_0 + \beta_1 + \frac{\epsilon\mu}{g})(\omega\frac{\rho_2^2}{\alpha_{22}^2} + \rho_2\alpha_{11}\frac{\rho_2}{\alpha_{22}}) + (\beta_0 + \frac{\epsilon\mu}{g})(k\omega\frac{\rho_2}{\alpha_{22}} + k\rho_2\alpha_{11}) - \frac{\epsilon\mu}{g}(\rho_1\alpha_{21}\frac{\rho_2}{\alpha_{22}} + k\rho_1\alpha_{21}) \\
=&(\beta_0 + \beta_1 + \frac{\epsilon\mu}{g})\frac{\rho_2^2}{\alpha_{22}^2}(\omega + \alpha_{11}\alpha_{22}) + (\beta_0 + \frac{\epsilon\mu}{g})k\frac{\rho_2}{\alpha_{22}}(\omega + \alpha_{11}\alpha_{22}) - \frac{\epsilon\mu}{g}\rho_1\alpha_{21}(\frac{\rho_2}{\alpha_{22}} + k) \\
=&(\beta_0 + \beta_1 + \frac{\epsilon\mu}{g})\frac{\rho_2^2}{\alpha_{22}^2}\alpha_{12}\alpha_{21} + (\beta_0 + \frac{\epsilon\mu}{g})k\frac{\rho_2}{\alpha_{22}}\alpha_{12}\alpha_{21} - \frac{\epsilon\mu}{g}\rho_1\alpha_{21}(\frac{\rho_2}{\alpha_{22}} + k) \\
=&(\beta_0 + \beta_1)\frac{\rho_2^2}{\alpha_{22}^2}\alpha_{12}\alpha_{21} + \beta_0 k\frac{\rho_2}{\alpha_{22}}\alpha_{12}\alpha_{21} - \frac{\epsilon\mu}{g}\big(\rho_1\alpha_{21}(\frac{\rho_2}{\alpha_{22}} + k) - \frac{\rho_2^2}{\alpha_{22}^2}\alpha_{12}\alpha_{21} - k\frac{\rho_2}{\alpha_{22}}\alpha_{12}\alpha_{21}\big) \\
=&(\beta_0 + \beta_1)\frac{\rho_2^2}{\alpha_{22}^2}\alpha_{12}\alpha_{21} + \beta_0 k\frac{\rho_2}{\alpha_{22}}\alpha_{12}\alpha_{21} - \frac{\epsilon\mu}{g}(\rho_2 + k\alpha_{22})(\frac{\rho_1\alpha_{22}}{\rho_2\alpha_{12}} - 1)\frac{\rho_2}{\alpha_{22}^2}\alpha_{12}\alpha_{21} > 0
\end{aligned}$$

is equivalent to $g > g_1^*$. Thus the proof of the necessity is complete.

Conversely, suppose that there is a positive equilibrium $E^* = (N_1^*, N_2^*, S^*)$. From the first two equations of (A.2), we can solve N_1 and N_2 in terms of S, i.e.,

$$N_1^* = (\rho_2\alpha_{12} - \rho_1 h(S^*)\alpha_{22})/\omega > 0 \text{ and } N_2^* = (\rho_1 h(S^*)\alpha_{21} - \rho_2\alpha_{11})/\omega > 0,$$

which imply that $\frac{\rho_2\alpha_{11}}{\rho_1\alpha_{21}} < f(S^*) < \frac{\rho_2\alpha_{12}}{\rho_1\alpha_{22}}$. Note that $E^* \in (E_2, E_1)_K$ and therefore $S_1 \equiv \frac{\beta_0 g}{\epsilon} < S^* < S_2 \equiv (\beta_0 + \beta_1\frac{\rho_2}{k\alpha_{22} + \rho_2})\frac{g}{\epsilon}$, then $f(S_2) < f(S^*) < f(S_1)$. Hence $f(S_2) < \frac{\rho_2\alpha_{12}}{\rho_1\alpha_{22}}$ and $f(S_1) > \frac{\rho_2\alpha_{11}}{\rho_1\alpha_{21}}$ which mean that both E_1 and E_2 are stable.

When E^* exists, the Jacobian matrix of (A.1) at $E^* = (N_1^*, N_2^*, S^*)$ is

$$J(E^*) = \begin{pmatrix} -\alpha_{11}N_1^* & -\alpha_{12}N_1^* & -\rho_1 N_1^* f^2(S^*)/\mu \\ -\alpha_{21}N_2^* & -\alpha_{22}N_2^* & 0 \\ 0 & \beta_1 kg/(k + N_2^*)^2 & -\epsilon \end{pmatrix}$$

and its determinant $\det(J(E^*)) > \epsilon(\alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22})N_1^*N_2^* = \epsilon\omega N_1^*N_2^* > 0$. Therefore, E^* must have a positive eigenvalue and it is unstable. By the theory of connecting orbits in [2], system (A.1) can have at most one positive equilibrium. Otherwise, there must exist a further positive equilibrium which contradicts to (A.3). □

Remark 1.6. From (A.3), we can obtain an explicit expression for the positive equilibrium when it exists. Since $\mathrm{tr}(J(E^*)) = -(\alpha_{11}N_1^* + \alpha_{22}N_2^* + \epsilon) < 0$, $J(E^*)$ has one positive eigenvalue and two eigenvalues with negative real parts. Therefore, the stable manifold $W^s(E^*)$ of E^* is a two-dimensional smooth surface which separates $\mathrm{Int}\mathbb{R}_+^3$ into two parts: the lower one in the order $\leq_K$ is the basin of attraction for E_2 and the upper one is the basin of attraction for E_1.

Remark 1.7. In case there is no positive equilibrium, either E_1 or E_2 is globally globally asymptotically stable in $\text{Int}\mathbb{R}^3_+$. More precisely, if $g > \max\{g_1^*, g_2^*\}$, then E_2 is globally asymptotically stable in $\text{Int}\mathbb{R}^3_+$; if $g < \min\{g_1^*, g_2^*\}$, then E_1 is globally asymptotically stable in $\text{Int}\mathbb{R}^3_+$. The scenario $g_2^* < g < g_1^*$ is impossible, if otherwise, this means that $g_2^* < 0 < g_1^* \Leftrightarrow \dfrac{\rho_1\alpha_{21}}{\rho_2\alpha_{11}} < 1 < \dfrac{\rho_1\alpha_{22}}{\rho_2\alpha_{12}}$ which contradicts to the assumption $\alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22} > 0$. Thus the dynamical behavior of system (A.1) is consistent with the competition exclusion principle in two-species Lotka-Volterra competition model.

1.4 The model with diffusion

Now, we develop a spatial model for the interaction between salt-tolerant and salt-intolerant vegetation types by including species diffusion and salt distribution. Thus, we have the following reaction-diffusion equations (Murray [5]),

$$
\begin{aligned}
\frac{\partial N_1}{\partial t} &= N_1(\rho_1 f(S) - \alpha_{11}N_1 - \alpha_{12}N_2) + D_1\frac{\partial^2 N_1}{\partial z^2} \text{ in } (0, L) \times (0, \infty),\\
\frac{\partial N_2}{\partial t} &= N_2(\rho_2 h(S) - \alpha_{21}N_1 - \alpha_{22}N_2) + D_2\frac{\partial^2 N_2}{\partial z^2} \text{ in } (0, L) \times (0, \infty),\\
\frac{\partial S}{\partial t} &= \beta_0 g(z) + \beta_1\frac{N_2}{k + N_2}g(z) - \epsilon S + D_S\frac{\partial^2 S}{\partial z^2} \text{ in } (0, L) \times (0, \infty),\\
\frac{\partial N_1}{\partial n} &= \frac{\partial N_2}{\partial n} = \frac{\partial S}{\partial n} = 0 \text{ on } \{0, L\} \times (0, \infty),
\end{aligned}
\tag{A.4}
$$

with nonnegative initial conditions. Here $N_1(z,t), N_2(z,t)$ and $S(z,t)$ are the population density/concentration of N_1, N_2 and S in altitude z at time t. The diffusion rates D_1, D_2 and D_S are assumed to be positive constants and $g(z)$ is a positive decreasing function of z.

For mathematical tractability, we discretize (A.4) to a two-patch model

$$
\begin{aligned}
\frac{dN_1}{dt} &= N_1(\rho_1 f(S) - \alpha_{11}N_1 - \alpha_{12}N_2) + D_1(\bar{N}_1 - N_1),\\
\frac{dN_2}{dt} &= N_2(\rho_2 h(S) - \alpha_{21}N_1 - \alpha_{22}N_2) + D_2(\bar{N}_2 - N_2),\\
\frac{dS}{dt} &= \beta_0 g + \beta_1\frac{N_2}{k + N_2}g - \epsilon S + D_S(\bar{S} - S),\\
\frac{d\bar{N}_1}{dt} &= \bar{N}_1(\rho_1 f(\bar{S}) - \alpha_{11}\bar{N}_1 - \alpha_{12}\bar{N}_2) + D_1(N_1 - \bar{N}_1),\\
\frac{d\bar{N}_2}{dt} &= \bar{N}_2(\rho_2 h(\bar{S}) - \alpha_{21}\bar{N}_1 - \alpha_{22}\bar{N}_2) + D_2(N_2 - \bar{N}_2),\\
\frac{d\bar{S}}{dt} &= \beta_0\bar{g} + \beta_1\frac{\bar{N}_2}{k + \bar{N}_2}\bar{g} - \epsilon\bar{S} + D_S(S - \bar{S}),
\end{aligned}
\tag{A.5}
$$

with nonnegative initial conditions. We assume that $\alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22} > 0$ and $g_1^* < g, \bar{g} < g_2^*$.

¿From above analysis, we know each isolated patch has four equilibria, i.e., E_0 (unstable), E_1 (stable), E_2 (stable), E^* (unstable) for patch 1 and $\bar{E}_0$ (unstable), $\bar{E}_1$ (stable), $\bar{E}_2$ (stable), $\bar{E}^*$ (unstable) for patch 2. Moreover, almost all orbits converges to either E_1 or E_2 in patch

1, and $\bar{E}_1$ or $\bar{E}_2$ in patch 2. The system (A.5) admits two stable equilibria $(E_1, \bar{E}_2)$ and $(E_2, \bar{E}_1)$ when the two patches are disconnected.

Similar to Levin [4], for small diffusion rates D_1, D_2 and D_S, the equilibria $(E_1, \bar{E}_2)$ and $(E_2, \bar{E}_1)$ do not disappear but move slightly off the boundary. By a perturbation theorem [4], $(E_1, \bar{E}_2)$ and $(E_2, \bar{E}_1)$ remain stable for sufficiently small diffusion rates. When the diffusion rates are high, the two patches model are approximate to a single patch model, thus coexistence is again impossible. These indicate that it is possible that one species persists in one patch to exclude the other and regime shifts still present for system with diffusion.

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