Facilitation Systems

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Presentation Outline

• Facilitation: definition and conceptual models
• Facilitation vs. competition in a gradient of environmental stress
• The simplest model
• A real case our simple model
• Results of the model
• Other possible (and more complicated) scenarios
Facilitation

Species that positively affects another species, directly or indirectly.
Fig. 1. The Menge–Sutherland model without and with facilitation. Models predict the relative importance of predation, competition, abiotic stress and two types of facilitation (amelioration of abiotic stress and associational defenses). All models assume high levels of recruitment of the basal (prey) taxa. (a) original model; (b) inclusion of intraspecific facilitation; and (c) inclusion of interspecific facilitation. Reproduced, with permission, from [d].

Bruno et al., 2003
Salt Marshes

Physical conditions
- Waterlogged soils
- High soil salinities
Juncus gerardi

More tolerant to high salinities acts on amelioration of physical conditions:

shades the soil - limits surface evaporation and accumulation of soil salts.
Iva frutescens

Relatively intolerant to high soil salinities and waterlogged soil conditions
PHYSICAL STRESS AND POSITIVE ASSOCIATIONS AMONG MARSH PLANTS

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\textit{Juncus girardi} and \textit{Iva frutescens}
Fig. 1.—Schematic diagram of the terrestrial border of a typical New England salt marsh illustrating the major vegetation zones and physical conditions considered in this study.

Bertness & Hacker, 1994
\[ \frac{dA}{dt} = r_A * A * \left( 1 - \frac{A}{K_A} - b_{AB}B - a_A S \right) \]

- Change of species A (facilitator) abundance over time
- Exponential term of population growth
- Saturation or logistic term of population growth
- Competition effect of species B (facilitated) on species A (facilitator)
- Effect of salinity on species A (facilitator)
\[ \frac{dB}{dt} = r_B \times B \times \left(1 - \frac{B}{K_B} - b_{BA}A - a_B S\right) \]

Change of species B (facilitated abundance over time)

Exponential term of population growth for species B

Saturation or logistic term of population growth for species B

Competition effect of species A (facilitator) on species B (facilitated)

Effect of salinity on species B (facilitated)
Final salinity $S = S_0 \times e^{-\sigma A}$

Initial salinity

Effect of abundance of species A on salinity
Reducing the number of parameters. Nondimensionalization

\[
\frac{dA}{dt} = r_A A \left(1 - \frac{A}{K_A} - b_{AB} B - a_A S_0 e^{-\sigma A}\right)
\]

\[
\frac{dA'}{dt} = A' \left(1 - A' - c_{AB} B' - F_A e^{-\sigma A'}\right)
\]

\[
\frac{dB}{dt} = r_B B \left(1 - \frac{B}{K_B} - b_{BA} A - a_B S_0 e^{-\sigma A}\right)
\]

\[
\frac{dB'}{dt} = rB' \left(1 - B' - c_{BA} A' - F_B e^{-\sigma A'}\right)
\]
Looking for fixed points

Condition:

\[
\begin{align*}
\frac{dA}{dt}(A_f, B_f) = 0 & \quad \Rightarrow \quad A = 0 \lor B = \frac{(1 - A - F_A e^{-\sigma A})}{c_{AB}} \\
\frac{dB}{dt}(A_f, B_f) = 0 & \quad \Rightarrow \quad B = 0 \lor B = 1 - c_{BA} A - F_B e^{-\sigma A}
\end{align*}
\]

\[
\alpha = 1 - c_{AB}, \quad \beta = 1 - c_{AB} c_{BA}, \quad \gamma = F_A - F_B c_{AB}
\]

\(A_f\) are that \(\alpha - \beta A_f - \gamma e^{-\sigma A_f} = 0\)

Don't have analytical solution!!

Ok, we look ...

\[1 - \beta' A_f = \gamma' e^{-\sigma A_f}\]

\(\gamma' > 1\)

\[
\begin{cases}
\beta' > 0 & \exists \text{ one } A_f \neq 0 \\
\text{else} & \text{ don't } \exists \ A_f \neq 0
\end{cases}
\]

We can have:
- No solution
- One solution
How do fixed points vary with the parameters?

We can have:

- No solution
- Two solutions
Some critical cases

\[ A = A_f = 0 \rightarrow \frac{dA}{dt} = 0 \rightarrow \frac{dB}{dt} = \rho (1 - B - S_B) = 0 \quad \Leftrightarrow \quad B_f = 0, \quad B_f = 1 - S_B > 0 \]

1. If \( S_B < 1 \) \( \exists \) two fixed points

\[ B_f = 0 \text{ is instable} \]
\[ B_f = 1 - S_B \text{ is stable} \]

If \( B \) doesn't suffer too much stress, and doesn't suffer competition \( \rightarrow \) survives

2. If \( S_B > 1 \) \( \exists \) one fixed points

\[ B_f = 0 \text{ is stable} \]
\[ B_f = 1 - S_B \text{ don't } \exists \]

Although \( B \) doesn't have competition, the stress is hard \( \rightarrow \) dies
Some critical cases

\[ B = B_f = 0 \rightarrow \frac{dB}{dt} = 0 \rightarrow \frac{dA}{dt} = A(1 - A - S_A e^{-\sigma A}) = 0 \quad \iff \quad A_f = 0 \quad \text{and some} \quad A_f > 0 \]

If \( A \) doesn't suffer too much stress, and doesn't suffer competition

\[ S_A < 1 \quad \exists \quad \begin{cases} 
A_f = 0 \text{ is instable} \\
\exists \quad A_f \in (0,1) \text{ is stable}
\end{cases} \]

With a high self-facilitation, \( A \) can survive if it has already large numbers

\[ S_A > 1 \quad \exists \quad \begin{cases} 
A_f = 0 \text{ is stable} \\
A_f > 0 \text{ don't } \exists \text{ if } \sigma \text{ is small} \\
\exists \text{ two } A_f \in (0,1) \text{ if } \sigma \text{ is large.} \\
\text{One stable, the other instable.}
\end{cases} \]
Temporal variation of both species and salinity when, at equilibrium, both co-exist.
Temporal variation of both species and salinity when, at equilibrium, both co-exist.

\[ S_0 = 2.00, \quad A_0 = 0.10, \quad B_0 = 0.50 \]
\[ K_A = 1.00, \quad K_B = 0.50 \]
\[ r_A = 0.10, \quad r_B = 0.10 \]
\[ \beta_{AB} = 4.50, \quad \beta_{BA} = 0.70 \]
\[ \sigma_A = 0.10, \quad \sigma_B = 0.50 \]
Temporal variation of both species and salinity when, at equilibrium, species B goes extinct.
Variation of abundance of both species with respect to salinity.

**Variation of abundance of both species with respect to salinity.**

- **Species A**
- **Species B (with facilitation)**
- **Control for species B**

### Parameters

- $A_0 = 0.1$, $B_0 = 0.1$
- $K_A = 1.0$, $K_B = 1.0$
- $r_A = 0.1$, $r_B = 0.1$
- $\beta_{AB} = 1.1$, $\beta_{BA} = 0.7$
- $\sigma_A = 0.1$, $\sigma_B = 0.5$
Conditions of facilitation (treat - control > 0),
competition (treat - control < 0) and no difference (treat
- control = 0) with respect to a gradient of salinity and
competition of B on A. Beta_{ab}: 0.68
Conditions of facilitation (treat - control > 0), competition (treat - control < 0) and no difference (treat - control = 0) with respect to a gradient of salinity and competition of A on B. Beta \( \beta_{ba} \): 1.2
Conditions of facilitation (treat - control < 0), competition (treat - control > 0) and no difference (treat - control = 0) with respect to a gradient of competition of A-B and B-A.
Real world example sustaining our model!

<table>
<thead>
<tr>
<th>Sp. A</th>
<th>Stress level 0</th>
<th>Stress level 1</th>
<th>Stress level 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without B</td>
<td>900</td>
<td>300</td>
<td>300</td>
</tr>
<tr>
<td>With B</td>
<td>500</td>
<td>700</td>
<td>600</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sp. B</th>
<th>Competition ( - - )</th>
<th>Facilitation ( + + )</th>
<th>Facilitation ( + + )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A</td>
<td>750</td>
<td>200</td>
<td>150,2</td>
</tr>
<tr>
<td>With A</td>
<td>125</td>
<td>350</td>
<td>300</td>
</tr>
</tbody>
</table>

Bertness & Hacker, 1994

SOIL SALINITY

[Graph showing soil salinity with and without neighbors]
Other scenarios...

Auto-facilitation of the facilitated

Why does it matter biologically?
The diagram illustrates the succession of plant life over time. Starting with Annual Plants and Perennial Plants and Grasses, the area progresses through Shrubs, Softwood Trees - Pines, and finally Hardwood Trees. The arrow labeled "Time" indicates the direction of progression from one stage to the next.
\[ S = S_0 \cdot e^{-s(A + \frac{1}{2}B)} \]

\[
\frac{dA}{dt} = r_A \cdot A \cdot \left(1 - \frac{A}{K_A} - b_{AB} - a_A S\right) \\
\frac{dB}{dt} = r_B \cdot B \cdot \left(1 - \frac{B}{K_B} - b_{BA} - a_B S\right)
\]
This is what we had in the previous model:

There are clear stable points.
And this is what I ended up with:

UNTRUE!
Another snapshot time:

Population at time $t = 4000$
Population at time 400

Competitive exclusion
Plain competition: \( A \) is excluded
Population at time 400

- Competitive exclusion
- Competition/facilitation
\[ B \text{ needs } A, \text{ both are stable} \]
Population at time 400

- Competitive exclusion
- Ecological succession!
- Successive oscillations
- Competition/facilitation

[Graph showing population trends over environmental stress, with marked points for competitive exclusion and ecological succession]
Looking for the bifurcation

$T = 400$

$T = 4000$
Converges fast to stability

Oscillating at very low frequency and high amplitude