Successional state dynamics: A novel approach to modeling nonequilibrium foodweb dynamics

C.A. Klausmeier

W. K. Kellogg Biological Station and Department of Plant Biology, Michigan State University, Hickory Corners, MI 49060, USA

ABSTRACT

Communities and ecosystems are often far from equilibrium, but our understanding of nonequilibrium dynamics has been hampered by a paucity of analytical tools. Here I describe a novel approach to modeling seasonally forced food webs, called "successional state dynamics" (SSD). It is applicable to communities where species dynamics are fast relative to the external forcing, such as plankton and other microbes, diseases, and some insect communities. The approach treats succession as a series of state transitions driven by both the internal dynamics of species interactions and external forcing. First, I motivate the approach with numerical solutions of a seasonally forced predator–prey model. Second, I describe how to set up and analyze an SSD model. Finally, I apply the techniques to three additional models of two-species interactions: resource competition (r-K selection), facilitation, and flip-flop competition (where the competitive hierarchy alternates over time). This approach allows easy and thorough exploration of how dynamics depend on the environmental forcing regime, and uncovers unexpected phenomena such as multiple stable annual trajectories and year-to-year irregularity in successional trajectories (chaos).

1. Introduction

Time is nature's way of keeping everything from happening at once.—Woody Allen

One of the most common assumptions ecologists make when analyzing dynamic models of populations, communities, and ecosystems is the assumption of equilibrium. At equilibrium, time derivatives are set to zero; in effect, everything happens at once. An equilibrium approach is sometimes appropriate, sometimes not. Its main attraction is that it greatly simplifies mathematical analysis, replacing differential equations by algebraic ones. Despite the ease of equilibrium approaches, ecologists are increasingly recognizing the importance of nonequilibrium dynamics in structuring communities (DeAngelis and Waterhouse, 1987; Chesson, 1994; Hastings, 2004).

Seasonal forcing, the regular variation of parameters over a year, is a major cause of nonequilibrium dynamics. Theoretically, it has been shown to affect the outcome of competition (Hsu, 1980; Litchman and Klausmeier, 2001) and the dynamics of epidemics (Earn et al., 2000; Stone et al., 2007) and resource–consumer (Huppert et al., 2005), predator–prey (Rinaldi et al., 1993; Scheffer et al., 1997; King and Schaffer, 1999), and food chain (Doveri et al., 1993) interactions. Seasonal forcing affects most communities. One striking and well-studied example occurs in plankton communities, where predictable species replacements are driven by a combination of external forcing and internal dynamics, a phenomenon called seasonal succession (Sommer et al., 1986; Sommer, 1989).

Progress on modeling seasonal dynamics has been hampered by a shortage of theoretical tools. The most common approach is the direct simulation of the system dynamics using numerical differential equation solvers; this is straightforward, but can be computationally expensive and does not provide general insight. More sophisticated numerical techniques are available. Floquet/Lyapunov exponents describe invasion rates in periodic/aperiodic environments (Metz et al., 1992; Klausmeier, 2008). Continuation methods allow rapid generation of bifurcation diagrams (packages: Kuznetsov and Levitin, 1996; Doedel et al., 2001; Dhooge et al., 2003; ecological examples: Doveri et al., 1993; Rinaldi et al., 1993). Harmonic balance is a numerical technique popular with engineers (e.g., Picardi, 1994) that has not been applied to ecological models. Peak-to-peak analysis is a way to understand strange attractors and can be used on time series data to forecast the size of the next population peak based on the previous one (Rinaldi and Solidoro, 1998; Candaten and Rinaldi, 2003). Beyond these computational approaches, various approximation techniques can provide analytical results that guide intuition and provide more generality than numerical techniques. Examples include the decomposition of competitive effects in a variable environment (Chesson, 1994) and transfer functions (Nisbet and Gurney, 1982; Snyder, 2007). Approximations depend on assumptions about the system and its...
forcing; these two examples assume small-amplitude temporal variation. More approximation techniques are needed, especially ones that are appropriate for vastly different forcing regimes (as in Huppert et al., 2005).

In this paper, I develop a new framework for modeling the dynamics of seasonally forced food webs, called “successional state dynamics” (SSD). The approach is an approximation based on the assumption of slow, large-amplitude environmental variation that generalizes techniques used in Litchman and Klausmeier (2001). It treats succession as a series of state transitions driven by both the internal dynamics of species interactions and external forcing. In Section 2, I motivate the approximation with numerical analysis of a seasonally forced predator–prey model. In Section 3, I describe the SSD framework and apply it to the predator–prey example. In Section 4, I apply these techniques to three more models of interspecific interaction: resource competition, facilitation, and “flip-flop” competition (where the identity of the superior competitor varies over time). In Section 5, I discuss the method’s strengths and shortcomings, highlight when it is likely to apply, and consider possible extensions. This approach will help facilitate our understanding of the dynamics of seasonally forced food webs and how nonequilibrium dynamics shape community structure.

2. A motivating example

Predator–prey interactions are one of the most widely studied types of interspecific interactions (Lotka, 1925; Volterra, 1926; Murdoch et al., 2003; Turchin, 2003). A prototypical predator–prey model is the Rosenzweig–MacArthur model

\[
\frac{dP}{dt} = rP \left( 1 - \frac{P}{K} \right) - c \frac{P}{P + kP} Z
\]

\[
\frac{dZ}{dt} = e c \frac{P}{P + kP} Z - mZ
\]

where \( P \) is the prey, \( Z \) is the predator, \( r \) is the prey maximum growth rate, \( K \) is the prey carrying capacity, \( c \) is the maximum consumption rate, \( kP \) is the half-saturation constant for consumption, \( e \) is the predator conversion efficiency, and \( mZ \) is the predator mortality rate. This model has been applied to many predator–prey systems (Murdoch et al., 2003; Turchin, 2003). Above a threshold \( K \), predators and prey coexist at a stable equilibrium until another threshold \( K \) where the equilibrium loses stability through a Hopf bifurcation, resulting in predator–prey limit cycles. I use a parameterization of this model for freshwater phytoplankton (\( P \))–zooplankton (\( Z \)) interactions (Murdoch et al., 1998), the system that originally motivated this work.

Consider this interaction in a seasonal environment, where good and bad seasons alternate. In the good season (\( \phi \) proportion of the period), the species follow (1). In the bad season (\( 1 - \phi \) proportion of the period), both species die exponentially according to

\[
\frac{dP}{dt} = \lambda_{P,0,\text{bad}} P
\]

\[
\frac{dZ}{dt} = \lambda_{Z,0,\text{bad}} Z
\]

where \( \lambda_{P,0,\text{bad}} < 0 \) and \( \lambda_{Z,0,\text{bad}} < 0 \). Overall period is \( T \). This setup caricatures the annual forcing of pelagic food webs, where many species live only during the warmer months or under stratified conditions and die off otherwise.

Fig. 1 illustrates the asymptotic dynamics of this model, on both arithmetic and logarithmic scales. Parts A and B show a case that leads to stable equilibrium in the unforced model (1); C and D show a case that leads to a limit cycle in the unforced model. Parts A&C represent annual forcing (\( T = 365 \text{ days} \)); parts B&D use a longer period without natural significance (\( T = 1000 \text{ days} \)) to illustrate the mathematical effect of increasing \( T \). In all cases, the dynamics have four distinct phases. (1) Prey and predators are rare, prey grow and predators die exponentially. (2) Prey are relatively constant near their carrying capacity, predators remain rare and grow exponentially. (3) Prey and predators are near the coexistence attractor of the unforced model (equilibrium [Fig. 1 A and B], or limit cycle [Fig. 1 C and D]). (4) Prey and predators die off exponentially in the bad season. Each of these phases corresponds to a stable or unstable equilibrium or limit cycle of the unforced model.

Comparing Fig. 1A with B and C with D shows that the main effects of increasing the period \( T \) are to sharpen the distinction between the four phases and to deepen the minimum densities. The relative timing of the transitions between phases appears to change little as \( T \) increases. Fig. 2 verifies this phenomenon: as \( T \to \infty \) the relative timing of each species’ appearance (defined as when a species first reaches half its maximum density) converges on a single value. When prey and predators can coexist at a stable equilibrium in the unforced model, this convergence is relatively simple (Fig. 2A). When they coexist on a limit cycle in the unforced model, the forced dynamics are more complicated, showing multiannual cycles or apparent chaos for intermediate \( T \) (Fig. 2B; see also Kuznetsov et al., 1992; Rinaldi et al., 1993). Despite this potential complexity, the timing of species’ first appearance in the mathematically convenient period of \( T = \infty \) closely predicts the timing under the ecologically relevant period of \( T = 365 \text{ days} \). This suggests that the dynamics of infinitely slowly forced food webs can provide a reasonable guide to the dynamics of food webs with realistic forcing periods. I formalize this SSD approximation below.

3. Successional state dynamics

An SSD approximation is possible for any ecological model with piecewise-periodic forcing and is based on the limit \( T \to \infty \). In this limit, the system is almost always near one of the invariant sets (equilibria, limit cycles, strange attractors) of the unforced model, punctuated by instantaneous jumps between invariant sets. These invariant sets may be stable or unstable. Each corresponds to a state where a species is either visible (those with positive density on the corresponding invariant set) or invisible (those with zero density on the corresponding invariant set). Visible species do not change in density but invisible species grow or shrink exponentially. Since populations change exponentially, it is natural to consider densities on a logarithmic scale, scaled by \( T \) so that visible densities are 0 and invisible densities are \( < 0 \) (see Appendix A for more formal justification). A state transition occurs when an exponentially growing invisible species’ scaled density reaches zero, becoming visible. Furthermore, rescale time by the forcing period \( T \) to focus on relative timing of events within a period. To distinguish between time within and between periods, let \( t = t' + T \), where \( 0 \leq t' < 1 \) denotes the time within a period and integer \( t' \) denotes the period number.

The SSD approximation results in a hybrid dynamical system that combines both continuous (scaled log densities) and discrete variables (the state of the system). Hybrid dynamical systems have been widely used in engineering (van der Schaft and Schumacher, 2000; Savkin and Evans, 2002) but have not been used in ecology. Because these SSD models represent a new class of models (a particular type of hybrid dynamical system), we must establish how to analyze them by “porting” the techniques used to analyze more familiar models to this new platform.
3.1. Model formulation

An SSD model has a number of ingredients: \( P \), the set of populations (e.g., \( P \) and \( Z \)); \( \bar{N} \), a vector of log densities of the populations, scaled by \( T \) so that 0 means visible density and <0 is invisible; \( M \), the set of externally forced modes (e.g., good and bad seasons); \( S(m) \), the set of possible states in each mode \( m \in M \) (e.g., empty set \( \emptyset \), \( \{P\} \), \( \{P, Z\} \)); \( \lambda_{p,s,m} \), the invasion rate of population \( p \) in state \( s \) and mode \( m \); \( Y_{p,s,m} \), the new state of the system should population \( p \) become visible in state \( s \) and mode \( m \) (only needed if

Fig. 1. Dynamics of the seasonally forced predator–prey model (1–2), parameterized for freshwater phytoplankton–zooplankton after Murdoch et al. (1998). \( r = 0.5 \text{ day}^{-1}, k_P = 0.16 \text{ mg C/L}, c = 1 \text{ day}^{-1}, e = 0.5, m_z = 0.29 \text{ day}^{-1}, \lambda_{p, \text{good}} = \lambda_{Z, \text{bad}} = -0.1 \text{ day}^{-1}, \phi = 0.75 \): (A) \( T = 365 \) days, \( K = 0.5 \text{ mg C/L}; \) (B) \( T = 1000 \) days, \( K = 0.5 \text{ mg C/L}; \) (C) \( T = 365 \) days, \( K = 1.0 \text{ mg C/L}; \text{ and (D) } T = 1000 \) days, \( K = 1.0 \text{ mg C/L}. \)
The SSD parameters are related to the parameters of the differential equation model (1) by

\[ \lambda_{Z,p,good} = \frac{K}{K + k_p} - m_Z > 0 \]  

(3)

The bad season parameters are the exponential death rates in (2).

An invisibility template is a useful way to visualize the structure of an SSD model. It is a directed graph with all possible states \( S \) as nodes and edges given by all possible transitions \( v \). The invisibility template for the predator–prey example is given in Fig. 3A.

3.2. Simulation

Projection of the community forward in time is the most basic analytical tool. Because exponential growth is linear on a log scale, the algorithm to simulate an SSD model is straightforward. First, calculate the timing of each potential next event. These potential next events are the transition of each invisible population to visible and externally forced mode changes. Population \( p \) can be projected to become visible after time increment \( \delta_p = -N_p/\lambda_{p,s,m} \) and the set of externally forced mode changes is \( \mathbb{X} \). Thus the next event is given by the smallest \( t + \delta_p \) or \( t \in \mathbb{X} \) greater than the current time \( t \). Let the time to the next event be \( \delta \). Second, update all population sizes according to their current growth rates, setting \( N_p(t + \delta) = N_p(t) + \delta \lambda_{p,s,m} \). Third, update the state of the system as \( s = v_{m,s,m} \) if a population became visible and as \( s = v_{m,s,m} \) if the mode changed from \( m \) to \( m' \). Update the mode if needed. Repeat this process as desired. For periodically forced models, it is often natural to simulate the model over one full period, resulting in a Poincaré map.

Fig. 4 illustrates this algorithm for the predator–prey example. In Fig. 4A, the growth of each population is projected. Looking at the invasion rates and next states:

\[ \lambda_{Z,p,good} > 0, \quad v_{Z,p,good} = \{ P \} \]
\[ \lambda_{Z,bad} < 0 \]

Mode switches and next states:

\[ t = 0 : \quad m = good, \quad v_{good,bad} = 0 \]
\[ t = \phi : \quad m = bad, \quad v_{bad,good} = 0, \quad \forall s \in S(\text{good}) \]

The SSD ingredients can be derived from a periodically forced differential equation model. \( S(m) \) corresponds to the invariant sets (equilibria, limit cycles, strange attractors) of the unforced model in mode \( m \). \( \lambda_{p,s,m} \) is given by the invasion rate when rare of population \( p \) in state \( s \) and mode \( m \). This is the average per capita growth rate of the invading population at the invariant set corresponding to state \( s \). \( v_{p,s,m} \) is the invariant set reached when population \( p \) successfully invades state \( s \) in mode \( m \). Alternatively, an SSD model might be created without reference to a differential equation model, based on either empirically determined invasion rates and state transitions or a priori assumptions.

The SSD model for the predator–prey example is

\[ \lambda_{Z,p,good} > 0, \quad v_{Z,p,good} = \{ P \} \]
\[ \lambda_{Z,bad} < 0 \]

Mode switches and next states:

\[ t = 0 : \quad m = good, \quad v_{good,bad} = 0 \]
\[ t = \phi : \quad m = bad, \quad v_{bad,good} = 0, \quad \forall s \in S(\text{good}) \]

The SSD parameters are related to the parameters of the differential equation model (1) by

\[ \lambda_{Z,p,good} = \frac{K}{K + k_p} - m_Z > 0 \]  

(3)

The bad season parameters are the exponential death rates in (2).

An invisibility template is a useful way to visualize the structure of an SSD model. It is a directed graph with all possible states \( S \) as nodes and edges given by all possible transitions \( v \). The invisibility template for the predator–prey example is given in Fig. 3A.

3.2. Simulation

Projection of the community forward in time is the most basic analytical tool. Because exponential growth is linear on a log scale, the algorithm to simulate an SSD model is straightforward. First, calculate the timing of each potential next event. These potential next events are the transition of each invisible population to visible and externally forced mode changes. Population \( p \) can be projected to become visible after time increment \( \delta_p = -N_p/\lambda_{p,s,m} \) and the set of externally forced mode changes is \( \mathbb{X} \). Thus the next event is given by the smallest \( t + \delta_p \) or \( t \in \mathbb{X} \) greater than the current time \( t \). Let the time to the next event be \( \delta \). Second, update all population sizes according to their current growth rates, setting \( N_p(t + \delta) = N_p(t) + \delta \lambda_{p,s,m} \). Third, update the state of the system as \( s = v_{p,s,m} \) if a population became visible and as \( s = v_{m,s,m} \) if the mode changed from \( m \) to \( m' \). Update the mode if needed. Repeat this process as desired. For periodically forced models, it is often natural to simulate the model over one full period, resulting in a Poincaré map.

Fig. 4 illustrates this algorithm for the predator–prey example. In Fig. 4A, the growth of each population is projected. Looking at

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>( P )</td>
<td>Set of populations</td>
</tr>
<tr>
<td>( M )</td>
<td>Set of modes</td>
</tr>
<tr>
<td>( S(m) )</td>
<td>Set of states in mode ( m )</td>
</tr>
<tr>
<td>( N = (N_1, N_2, \ldots) )</td>
<td>Log densities of populations ( i ) scaled by ( T )</td>
</tr>
<tr>
<td>( \lambda_{p,s,m} )</td>
<td>Invasion rate of population ( p ) in state ( s ) and mode ( m )</td>
</tr>
<tr>
<td>( v_{p,s,m} )</td>
<td>New state when population ( p ) becomes visible in state ( s ) and mode ( m )</td>
</tr>
<tr>
<td>( \mathbb{X} )</td>
<td>Set of mode switches, each consisting of a time and a new mode</td>
</tr>
<tr>
<td>( v_{m,s,m} )</td>
<td>New state in mode ( m ) when switching from old mode ( m ) and old state ( s )</td>
</tr>
<tr>
<td>( t = t + \delta )</td>
<td>Time</td>
</tr>
<tr>
<td>( \delta )</td>
<td>Time step in simulation algorithm</td>
</tr>
<tr>
<td>( \tau )</td>
<td>An annual trajectory</td>
</tr>
<tr>
<td>( \delta_{\text{transition}} )</td>
<td>Time of a transition</td>
</tr>
<tr>
<td>( \lambda_{p,\tau} )</td>
<td>Invasion rate of population ( p ) averaged over trajectory ( \tau )</td>
</tr>
<tr>
<td>( A )</td>
<td>Eigenvalues of annual map</td>
</tr>
</tbody>
</table>

Table 1: Summary of notation used.
the x-axis shows that the next event is P becoming visible. In Fig. 4B, the state has been updated from 0 to (P) at time \( t_0 \rightarrow |P| \), and again the growth of each population is projected with new state-dependent growth rates. The next event is Z becoming visible, which is shown in Fig. 4C at time \( t_1 \rightarrow |Z| \). The only transition possible once both species are visible is the mode change from the good to the bad season at \( t = \phi \), after which each species declines until the mode change back from the bad to the good season at \( t = 1 \) (Fig. 4D). These steps can be repeated ad infinitum to project the populations further ahead in time.

3.3. Find annual trajectories

An annual trajectory is one that ends in the same state as it began one period ago. Annual trajectories are analogous to equilibria in a nonforced model, and therefore may or may not be dynamically stable, an issue treated in Sections 3.5 and 3.6. An annual trajectory is defined as an ordered set of \( n \) state/mode pairs:

\[
\tau = \{ |s_1, m_1| \rightarrow |s_2, m_2| \rightarrow \cdots \rightarrow |s_n, m_n| \} \tag{4}
\]

Annual trajectories make closed loops in the invasibility template. In the predator–prey example (Fig. 3A), there are three possible annual trajectories:

- [None] = \{[0, good] \rightarrow [0, bad]\}
- [P only] = \{[0, good] \rightarrow [P], [good] \rightarrow [0, bad]\}
- [P & Z coexist] = \{[0, good] \rightarrow [P], [good] \rightarrow [P,Z], [good] \rightarrow [0, bad]\} \tag{5}

3.4. Solve for transition times

Having identified the possible annual trajectories, the next step is to solve for the times of the state transitions in each trajectory. To do so, use the fact that for each species present in a trajectory, the net change in log population density must be zero for each interval during which that species is invisible. Due to the linearity of exponential growth on a log scale, the change in log density in a state is given by the growth rate \( \lambda_{p,s,m} \) multiplied by the time spent in that state \( \phi_{s,m} \). This results in a system of linear equations, with an equal number of equations and unknowns (the timings), which can be easily solved. A consistency criterion is that the order of timings must match that implied by the trajectory.

In the predator–prey example, there are two nontrivial trajectories: [P only] and [P & Z coexist]. In the [P only] trajectory, there is one unknown, \( t_0 \rightarrow |P| \). In this trajectory, P is invisible from the end of the good season \( t = \phi \) until \( t_0 \rightarrow |P| \) in the next period. Thus, \( \lambda_{p,0,0,|bad|} (1 - \phi) + \lambda_{p,0,|good|t_0 \rightarrow |P|} = 0 \) can be solved to find

\[
t_0 \rightarrow |P| = \frac{-(1 - \phi)\lambda_{p,0,|bad|}}{\lambda_{p,0,|good|}} \tag{6}
\]

The consistency criteria are \( 0 \leq t_0 \rightarrow |P| \leq \phi \).

In the [P & Z coexist] trajectory, there are two unknowns, \( t_1 \rightarrow |P| \) and \( t_1 \rightarrow |P,Z| \) and two equations, one for each species. They are

\[
\lambda_{p,0,|bad|} (1 - \phi) + \lambda_{p,0,|good|t_1 \rightarrow |P,Z|} = 0
\]

Fig. 3. Invasibility templates for models investigated in this paper: (A) seasonal predator–prey; (B) seasonal resource competition; (C) seasonal facilitation; and (D) “flip-flop” competition.

Fig. 4. Simulation of an SSD model using predator–prey example. Gray lines represent projections used to determine the next event when a population reaches log zero density (visibility).
\[ \lambda_{Z_0,\text{bad}}(1 - \phi) + \lambda_{Z_0,\text{good}} t_{0} \rightarrow (P) + \lambda_{Z_1,P_0,\text{good}} (t_{1} \rightarrow (P), Z \rightarrow t_{0} \rightarrow (P)) = 0 \]  

and can be solved for the timings

\[ t_{0} \rightarrow (P) = \frac{-(1 - \phi)\lambda_{P_0,\text{bad}}}{\lambda_{P_0,\text{good}}} \]  
\[ t_{1} \rightarrow (P), Z = -\frac{(1 - \phi)(\lambda_{P_0,\text{good}} \lambda_{Z_0,\text{bad}} - \lambda_{P_0,\text{bad}} \lambda_{Z_0,\text{good}} + \lambda_{P_0,\text{bad}} \lambda_{Z_1,P_0,\text{good}})}{\lambda_{P_0,\text{good}} \lambda_{Z_1,P_0,\text{good}}} \]

The consistency criteria for this trajectory are \( 0 \leq t_{0} \rightarrow (P) \leq t_{1} \rightarrow (P), Z \leq \phi \). Notice that the timing of the \( 0 \rightarrow (P) \) transition is the same in both the [P only] and the [P&Z coexist] trajectories; this means that predators have no effect on the timing of the prey appearance.

### 3.5. Invasion criteria

The invasion rate of a species when rare is an important quantity in analyzing community models (Armstrong and McGehee, 1980). In a periodic SSD model, the growth rate of a rare species must be averaged over one period. Define \( \lambda_{p,\tau} \) as the invasion rate of species \( p \) invading trajectory \( \tau \). It is simply the average of the growth rate of species \( p \) in all states \( \tau \), weighted by the time spent in each state.

\[ \lambda_{p,\tau} = \sum_{i,m \in \tau} \lambda_{p,i,m} \delta_{i,m} \]

Invasion criteria can be used to determine critical \( \phi \) values for each species to persist in the predator–prey example. The critical \( \phi \) for \( P \) is determined by when it can invade the [None] trajectory.

\[ \lambda_{P,\text{None}} = \phi \lambda_{P_0,\text{good}} + (1 - \phi) \lambda_{P_0,\text{bad}} \]

To find the minimum \( \phi \) that allows \( P \) to persist by itself, we set \( \lambda_{P,\text{None}} = 0 \) and solve for \( \phi_{\text{crit},P} \):

\[ \phi_{\text{crit},P} = \frac{\lambda_{P_0,\text{bad}}}{\lambda_{P_0,\text{good}}} \]

Z's growth rate is negative in both \([0,\text{good}]\) and \([0,\text{bad}]\), so \( Z \) cannot invade the empty trajectory [None]. The invasion rate of predators \( Z \) into the prey-only trajectory [P only] is the sum of its growth rates in each state, weighted by the time spent in those states.

\[ \lambda_{Z,\text{[P only]}} = \lambda_{Z_0,\text{good}} \cdot t_{0} \rightarrow (P) + \lambda_{Z_1,P_0,\text{good}} (\phi - t_{0} \rightarrow (P)) + \lambda_{Z_0,\text{bad}} (1 - \phi) \]

where \( t_{0} \rightarrow (P) \) is given by Eq. (7). The critical \( \phi \) for the predator's invasion into a monoculture of prey is found by setting \( \lambda_{Z,\text{[P only]}} = 0 \) and solving for \( \phi_{\text{crit},Z} \):

\[ \phi_{\text{crit},Z} = \frac{\lambda_{Z_0,\text{bad}} \lambda_{P_0,\text{good}} - \lambda_{Z_1,P_0,\text{good}} \lambda_{P_0,\text{bad}} + \lambda_{Z_0,\text{good}} \lambda_{P_0,\text{bad}}}{\lambda_{Z_0,\text{bad}} \lambda_{P_0,\text{good}} - \lambda_{Z_1,P_0,\text{good}} \lambda_{P_0,\text{bad}} + \lambda_{Z_0,\text{good}} \lambda_{P_0,\text{bad}} + \lambda_{Z_1,P_0,\text{good}} \lambda_{P_0,\text{bad}}} \]

### 3.6. Stability analysis

To test the dynamical stability of an annual trajectory, use the simulation algorithm (Section 3.2) to calculate a stroboscopic (Poincaré) map that advances the scaled log populations one period:

\[ \hat{N}(t+1) = f(\hat{N}(t)) \]

Given the linearity of growth, this can typically be done analytically. Stability of the annual trajectory is equivalent to the stability of this map, which is determined by the eigenvalues \( \Lambda \) of the Jacobian matrix

\[
J = \begin{pmatrix}
\frac{\partial N_1(t+1)}{\partial N_1(t)} & \cdots & \frac{\partial N_1(t+1)}{\partial N_1(t)} \\
\vdots & \ddots & \vdots \\
\frac{\partial N_N(t+1)}{\partial N_1(t)} & \cdots & \frac{\partial N_N(t+1)}{\partial N_N(t)}
\end{pmatrix}
\]

Because the stroboscopic map is a discrete-time system, all eigenvalues must have magnitude less than one for the annual trajectory to be stable.

In the predator–prey example, the [P&Z coexist] trajectory is always stable when it is feasible. Because both species are visible at \( t = \phi \), \( N_p(\phi) = 0 \) and \( N_z(\phi) = 0 \), so a small change in densities at \( t = 0 \) has no effect on densities at \( t = 1 \). This makes the Jacobian matrix

\[
J = \begin{pmatrix}
0 & 0 \\
\frac{\partial N_p(t+1)}{\partial N_p(t)} & \frac{\partial N_p(t+1)}{\partial N_p(t)} \\
\vdots & \ddots & \vdots \\
\frac{\partial N_N(t+1)}{\partial N_N(t)} & \cdots & \frac{\partial N_N(t+1)}{\partial N_N(t)}
\end{pmatrix}
\]

which has eigenvalues \( \Lambda = 0, 0 \). This indicates that the trajectory is as stable as possible, because any small perturbation is completely eliminated in one period as long as the linear approximation holds. Not all models share this property, however (see section 4, More examples).

### 3.7. Summary of predator–prey example

The preceding results give us a comprehensive overview of the dynamics of the seasonal predator–prey model, summarized in Fig. 5 as a function of length of the good season, \( \phi \). As \( \phi \) increases, the stable trajectory changes from [None] to [P only] to [P&Z coexist]. As \( \phi \) increases, both species appear earlier in the good season.

---

**Fig. 5.** Annual cycles of seasonal predator–prey food web. The black region indicates the bad season. Parameter values: \( \lambda_{P_0,\text{good}} = 1.2 \), \( \lambda_{Z_0,\text{good}} = -1 \), \( \lambda_{Z_0,\text{bad}} = 2 \), \( \lambda_{P,\text{bad}} = -0.8 \), \( \lambda_{Z_0,\text{bad}} = -1 \). Critical \( \phi \)'s: \( \phi_{\text{crit},P} = 0.455 \), \( \phi_{\text{crit},Z} = 0.636 \).
4. More examples

The techniques described in Section 3 are applicable to any community model without immigration (Appendix A). Here I apply them to three more two-species interactions: seasonal resource competition, seasonal facilitation, and flip-flop competition (where the identity of the superior competitor varies periodically). Aside from their importance as common interspecific interactions, these scenarios illustrate various aspects of the general theory.

4.1. Resource competition

In general, two species competing for a single limiting resource cannot coexist at equilibrium; the species with the lowest break-even resource level, termed $R^*$, excludes the other (Tilman, 1982). However, in a nonequilibrium environment, there is the potential for coexistence of a good equilibrium competitor and species that can grow fast when resource levels are high (Armstrong and McGehee, 1980; Grover, 1990; Litchman and Klausmeier, 2001).

Here we consider resource competition in a seasonal environment of alternating good ($P_1$) and bad ($P_2$) seasons, as in the predator–prey model above. If species $P_1$ is the superior equilibrium competitor and species $P_2$ is the fast grower, this situation can be defined by the following SSD model.

**Populations:**
$P = \{P_1, P_2\}$

**Modes:**
$M = \{\text{good, bad}\}$

**States:**
$\Sigma(\text{good}) = \{0, \{P_1\}, \{P_2\}\}$
$\Sigma(\text{bad}) = \{0\}$

**Invasion rates and next states:**
$\dot{\lambda}_{P_i, \{P_j\}=0, \text{good}} > 0$, $v_{P_i, \{P_j\}=0, \text{good}} = \{P_1\}$
$\dot{\lambda}_{P_i, \{P_j\}=0, \text{good}} < 0$, $v_{P_i, \{P_j\}=0, \text{good}} = \{P_2\}$

**Mode switches and next states:**
$t = 0$ if $m = \text{good}$, $v_{\text{good}, \text{bad}} = 0$
$t = \phi$ if $m = \text{bad}$, $v_{\text{good}, \text{bad}} = 0, \forall \phi \in \Sigma(\text{good})$

The model is summarized in Fig. 3B.

A prototypical model of resource competition is the Monod model

$$\frac{dP_i}{dt} = \frac{R_i}{R + K_i} P_i - m_i P_i, \quad i = 1, 2$$

$$\frac{dR}{dt} = a(R_{\text{in}} - R) - \sum \frac{\mu_i R_i}{R + K_i}$$

In this case, $R_i = m_i K_i / (\mu_i - m_i)$, and the SSD parameters are related to the parameters of the Monod model by

$$\dot{\lambda}_{P_i, \text{good}} = \frac{\mu_i R_i}{R + K_i} - m_i \approx \mu_i - m_i \quad \text{when } R_{\text{in}} \gg K_i$$

$$\dot{\lambda}_{P_i, \{P_j\}=0, \text{good}} = \frac{\mu_i R_j}{R_j + K_i} - m_i$$

The bad season parameters are the exponential death rates in the bad season, not necessarily $m_i$ if species have resting stages.

Possible annual trajectories are

- [None] = \{0, good\} \rightarrow \{0, bad\}
- [P_1 only] = \{0, good\} \rightarrow \{P_1, good\} \rightarrow \{0, bad\}
- [P_2 only] = \{0, good\} \rightarrow \{P_2, good\} \rightarrow \{0, bad\}
- [P_1&P_2 coexist] = \{0, good\} \rightarrow \{P_1, good\} \rightarrow \{P_2, good\} \rightarrow \{0, bad\}

$$A_{P_1, [\text{none}]} = \phi \dot{\lambda}_{P_1, \text{good}} + (1 - \phi) \dot{\lambda}_{P_1, \text{bad}}$$

To find the minimum $\phi$ that allows species $i$ to persist by itself, we set $A_{P_i, [\text{none}]} = 0$ and solve for $\phi_{\text{crit}, P_1}$:

$$\phi_{\text{crit}, P_1} = \frac{\dot{\lambda}_{P_1, \text{good}}}{\dot{\lambda}_{P_1, \text{bad}} - \dot{\lambda}_{P_1, \text{good}}}$$

Timing of the transition $0 \rightarrow \{P_i\}$ for the single species trajectories

$$t_{\text{spec}, \{P_i\}} = -\frac{1 - \phi}{\phi_{\text{crit}, P_1}}$$

The invasion rate of species $P_1$ into the [None] trajectory is

$$A_{P_i, [\text{none}]} = \phi \dot{\lambda}_{P_i, \text{good}} - \phi(t_{\text{spec}, \{P_i\}}) \dot{\lambda}_{P_i, \text{bad}}(1 - \phi)$$

where $t_{\text{spec}, \{P_i\}}$ is given by Eq. (23). The critical $\phi$ for invasion of species $i$ into a monoculture of species $j$ is found by setting $A_{P_i, [\text{none}]} = 0$ and solving for $\phi_{\text{crit}, P_i, j}$:

$$\phi_{\text{crit}, P_i, j} = \frac{\dot{\lambda}_{P_i, \text{good}} + \dot{\lambda}_{P_i, \{P_j\}=0, \text{good}} \dot{\lambda}_{P_j, \text{bad}}}{\dot{\lambda}_{P_i, \text{good}} - \dot{\lambda}_{P_i, \{P_j\}=0, \text{good}} \dot{\lambda}_{P_j, \text{bad}}}$$

One can solve for the timing of the transitions

$$0 \rightarrow \{P_i\} \text{ good} \text{ and } \{P_i\} \text{ bad} \rightarrow \{P_1\} \text{ good} \text{ in the } [P_1, P_2] \text{ coexist} \text{ trajectory}$$

by setting the algebraic expressions to be equal to the time spent in those states.

$$A_{P_i, [\text{none}]} = 0$$

The 0 eigenvalue will not cause instability. The other eigenvalue is always nonnegative based on the signs of the invasion rates $\dot{\lambda}$. Therefore, the only way the $[P_1, P_2] \text{ coexist}$ trajectory could be unstable is if the second eigenvalue were greater than one, in which case the trajectory would be a saddle. If so, the outcome is founder control: whichever species established first excludes the other. It is well-established that seasonal forcing can allow a fast growing species and a superior equilibrium competitor to coexist, but the possibility of founder control is a novel finding.

Fig. 6 summarizes the dynamics of the seasonal resource competition food web as a function of length of the good season, $\phi$. In Fig. 6A, as $\phi$ increases, the stable trajectory changes from [None] to [P_2 wins] to [P_1&P_2 coexist] to [P_1 wins]. This is essentially the same pattern found in Litchman and Klausmeier (2001), where the good equilibrium competitor dominated for long good seasons, the fast grower dominated for short good seasons, and the two coexisted in between. In contrast, in Fig. 6B, intermediate $\phi$ values result in founder control, where either $P_1$ or $P_2$ wins depending on initial conditions.
Facilitation is one of the three generalized mechanisms of succession suggested by Connell and Slatyer (1977). In it, only early successional species can establish after a major disturbance. Once established, they make the environment more favorable for later successional species. With $P_1$ as the late successional species and $P_2$ as early successional species, this interaction can be modeled in the SSD framework as follows.

### Populations:

$P = \{P_1, P_2\}$

### Modes:

$M = \{\text{good, bad}\}$

### States:

$\mathbb{S}(\text{good}) = \{\emptyset, \{P_1\}, \{P_2\}\}$

$\mathbb{S}(\text{bad}) = \{\emptyset\}$

### Invasion rates and next states:

- $\lambda_{P_1, \text{good}} < 0$
- $\lambda_{P_2, \text{good}} > 0$, $v_{P_2, \text{good}} = P_2$
- $\lambda_{P_1, \text{bad}} > 0$, $v_{P_1, \text{bad}} = P_1$
- $\lambda_{P_2, \text{bad}} < 0$
- $\lambda_{P_1, \text{bad}} < 0$
- $\lambda_{P_2, \text{bad}} < 0$

### Modeswitches and next states:

$t = 0 : m = \text{good}, v_{\text{good}, \text{bad}} = 0$

$t = \phi : m = \text{bad}, v_{\text{bad, good}} = 0, \forall s \in \mathbb{S}(\text{good})$

The model is summarized in Fig. 3C. The model is almost identical to that of resource-competition, with the exception that the equilibrium species $P_1$ cannot invade the empty system in the facilitation model ($\lambda_{P_2, \text{good}} < 0$).

A prototypical model of facilitation is a variation of the resource-competition model, where species 1 requires biomass (of either species) to grow

\[
\frac{dP_1}{dt} = \frac{\mu_1 R}{R + K_1} P_1 + \frac{P_1 + P_2}{K_2} P_1 - m_1 P_1
\]

\[
\frac{dP_2}{dt} = \frac{\mu_2 R}{R + K_2} P_2 - m_2 P_2
\]

\[R = R_{in} - P_1 - P_2\]

### Possible annual trajectories are

$[\text{None}] = \{(\emptyset, \text{good}) \rightarrow (\emptyset, \text{bad})\}$

### Annual cycles of the facilitation model of succession. Species 1 is the late-successional species, species 2 is the early-successional species. The black region indicates the bad season. Parameter values: $\lambda_{P_1, \text{good}} = -0.5$, $\lambda_{P_1, \text{bad}} = 1.2$, $\lambda_{P_2, \text{good}} = -0.3$, $\lambda_{P_2, \text{bad}} = \lambda_{P_1, \text{bad}} = -1$. Critical $\phi$'s: $\phi_{\text{crit,} P_1} = 0.455$, $\phi_{\text{crit,} P_2} = 0.888$. 

---

Fig. 6. Annual cycles of seasonal resource competition food web. Species 1 is the superior equilibrium competitor, species 2 is the fast grower. The black region indicates the bad season: (A) case with stable coexistence. Parameter values: $\lambda_{P_1, \text{good}} = 0.8$, $\lambda_{P_1, \text{bad}} = 1.2$, $\lambda_{P_2, \text{good}} = 0.4$, $\lambda_{P_2, \text{bad}} = 0.4$, $\lambda_{P_1, \text{bad}} = \lambda_{P_2, \text{bad}} = 0.1$. Critical $\phi$'s: $\phi_{\text{crit,} P_1} = 0.455$, $\phi_{\text{crit,} P_2} = 0.556$, $\phi_{\text{crit,} P_1, P_2} = 0.625$, $\phi_{\text{crit,} P_1, P_2} = 0.714$. Dominant eigenvalue of annual map on coexistence trajectory: $\lambda = 0.333$. (B) Case with founder control. Parameter values: $\lambda_{P_1, \text{good}} = 1.0$, $\lambda_{P_2, \text{good}} = 1.5$, $\lambda_{P_1, \text{bad}} = 0.0233$, $\lambda_{P_2, \text{bad}} = -0.0556$, $\lambda_{P_1, \text{bad}} = \lambda_{P_2, \text{bad}} = -0.1$. Critical $\phi$'s: $\phi_{\text{crit,} P_1} = 0.0625$, $\phi_{\text{crit,} P_2} = 0.0909$, $\phi_{\text{crit,} P_1, P_2} = 0.6$, $\phi_{\text{crit,} P_1, P_2} = 0.5$. Dominant eigenvalue of annual map on coexistence trajectory: $\lambda = 1.556$.
[(28)]

Except for the nonexistence of the \([P_1 \text{ alone}]\) trajectory, all calculations of timings, invasion rates, critical \(\phi\)'s, and stability criterion are identical to the resource-competition model above. There are two essential differences between the facilitation and the resource-competition model. First, \(P_1\) does not dominate as \(\phi \to 1\), because it cannot invade the empty system following the bad season, but must wait for \(P_2\) to condition the environment (Fig. 7).

The second difference concerns the stability of the \([P_1 \& P_2 \text{ coexist}]\) trajectory. The eigenvalues of the annual map on this trajectory are

\[
A = 0, \quad \frac{\lambda_{P_1,P_2,\text{good}} - \lambda_{P_1,0,\text{good}} \lambda_{P_2,P_1,\text{good}}}{\lambda_{P_1,0,\text{good}} \lambda_{P_2,0,\text{good}}} \tag{29}
\]

as in the resource competition model. However, the second eigenvalue can now be \(< -1\), which indicates an instability of the annual cycle where perturbations grow and alternate in sign (Strogatz, 1994). Typically this leads to a period-doubling bifurcation which results in a two-cycle, and this is often followed by more period-doubling bifurcations as the parameter is varied further, leading to chaos (Strogatz, 1994). This model apparently does not follow the period-doubling route to chaos (Fig. 8), but instead gives rise to irregular dynamics immediately at the bifurcation point where \(A = -1\) \((\lambda_{P_2,P_1,\text{good}} \approx -0.343)\). I conjecture this represents

---

**Fig. 8.** Effect of \(\lambda_{P_2,P_1,\text{good}}\) on dynamics in the facilitation model of succession: (A) timing of appearances of \(P_1\) (black) and \(P_2\) (gray) over 2000 periods after a 10,000 period warmup to eliminate transients and (B–I) 40 periods of dynamics following a 10,000 period warmup for varying \(\lambda_{P_2,P_1,\text{good}}\).
the phenomenon of “instant chaos” found in other piecewise-linear models (Yoshida et al., 1983; May, 1985; Ohnishi and Inaba, 1994). The phenomenon of “instant chaos” occurs only in the SSD limit of $T \to \infty$; for finite periods chaos occurs after a period-doubling cascade (see online Appendix for details). Regardless of the mathematical details of the bifurcation, the ecological meaning is clear (Fig. 8). For $A > -1$ the system shows regular annual cycles. For $A < -1$, the system never settles into a regular annual cycle, but shows increasingly irregular dynamics as $\lambda_{P_1}(P_1)_{\text{good}}$ decreases. Inspection of the eigenvalues in Eq. (29) shows that decreasing $\lambda_{P_1}(P_1)_{\text{good}}$, $\lambda_{P_1}(P_1)_{\text{better}}$, and $\lambda_{P_2}(P_1)_{\text{good}}$ all tend to destabilize the annual cycle by making $A$ more negative. Interestingly, the length of the good season $\phi$ does not enter into this calculation, and therefore has no effect on stability.

4.3. Flip-flop competition

The models above all consist of a good season followed by a bad season where all species die off to near zero densities. Instead consider the scenario where two species compete for single limiting nutrient but the identity of the superior competitor changes seasonally. An SSD model describing this scenario is

| Populations: | $P = \{P_1, P_2\}$ |
| Modes: | $M = \{P_1 -\text{wins}, P_2 -\text{wins}\}$ |
| States: | $\{(P_1, P_2)\}$ |

Invasion rates and next states:

- $\lambda_{P_1}(0, 0)_{\text{wins}} > 0$, $\lambda_{P_2}(0, 0)_{\text{wins}} = \{P_1\}$
- $\lambda_{P_1}(0, 0)_{\text{wins}} > 0$, $\lambda_{P_2}(0, 0)_{\text{wins}} = \{P_2\}$
- $\lambda_{P_1}(P_1, P_2)_{\text{wins}} > 0$, $\lambda_{P_1}(P_1, P_2)_{\text{wins}} = \{P_1\}$
- $\lambda_{P_2}(P_1, P_2)_{\text{wins}} < 0$
- $\lambda_{P_1}(P_2, P_1)_{\text{wins}} > 0$, $\lambda_{P_1}(P_2, P_1)_{\text{wins}} = \{P_2\}$
- $\lambda_{P_2}(P_2, P_1)_{\text{wins}} > 0$, $\lambda_{P_2}(P_2, P_1)_{\text{wins}} = \{P_2\}$
- $\lambda_{P_1}(P_1, P_2)_{\text{wins}} < 0$

Mode switches and next states:

$$t = 0: m = P_1 -\text{wins}, V_{P_1 -\text{wins}}, s_{P_2 -\text{wins}} = S$$

$$t = \phi: m = P_2 -\text{wins}, V_{P_2 -\text{wins}}, s_{P_1 -\text{wins}} = S$$

The model is summarized in Fig. 3D.

Possible annual trajectories are

- [None] = $\{(0, P_1 -\text{wins}) \to (0, P_1 -\text{wins})\}$
- $[P_1 \text{ only}] = \{[(P_1), P_1 -\text{wins}) \to (P_1, P_2 -\text{wins})\}$
- $[P_2 \text{ only}] = \{[(P_2), P_1 -\text{wins}) \to (P_2, P_2 -\text{wins})\}$
- $[P_1 \& P_2 \text{ coexist}] = \{[(P_2), P_1 -\text{wins}) \to ([P_1], P_1 -\text{wins}) \to (P_1, P_2 -\text{wins}) \to (P_2, P_2 -\text{wins})\}$

The invasion rate of species $P_i$ into the [None] trajectory is

$$A_{P_i, [\text{None}]} = \phi \lambda_{P_i}(0, 0)_{\text{wins}} + (1 - \phi) \lambda_{P_i}(0, 0)_{\text{wins}}$$

Since we assume that both species can survive in monoculture in each season, the [None] trajectory is unstable and can be invaded by both species for any $\phi$. Because both species can persist in both seasons, the only events in the monoculture trajectories are the externally forced mode switches at $t = 0$ and $t = \phi$.

5. Discussion

In this paper I describe a new mathematical framework for modeling the successional dynamics of periodically forced food webs. Instead of focusing on population numbers, this approach
treats species as either common ("visible") or exponentially rare ("invisible"). This coarse-graining simplification enables the food web dynamics to be thought of as a succession of states, with transitions driven by both internal dynamics and external forcing.

There are three main reasons to study a SSD model instead of a nonautonomous system of differential equations. (1) **Analytical results:** Analytical results are easier to obtain in SSD models. Analytical results allow for more general understanding of the model's behavior than numerical results. (2) **Numerical speed:** SSD models are much faster to simulate than the stiff systems of differential equations they result from. (3) **Alignment with observational data:** Empirical studies often focus on what species are dominant and the timing of species appearances (Sommer et al., 1986; Sommer, 1989). The SSD approach works directly in these currencies. As Segel (1972) put it:

Simplification of a given set of equations may make it possible to avoid large machine calculations or massive analytic work and still to obtain a useful answer. Even if the equations can be solved exactly without undue effort, simplified equations may yield a sufficiently accurate solution whose features are more readily apparent than those of the exact solution. Drastic simplification may allow rapid solution and immediate determination of whether one is on the right track.

I apply this approach to four interspecific interactions: seasonal predator–prey, seasonal resource-competition, seasonal facilitation, and "flip-flop" competition. In each case, the successional trajectory depends on the duration of the externally imposed seasons (Figs. 5–7 and 9). Two dynamical phenomena more complicated than unique annual cycles can occur: seasonal resource competition and flip-flop competition can result in alternative annual cycles (Fig. 6B) and seasonal facilitation can result in successional patterns that vary irregularly from year-to-year (Fig. 8). Because the approach is general, it can be readily applied to any model of interacting species.

The SSD approach developed here rests on two critical assumptions. First, it assumes that the community growth dynamics are significantly faster than the external forcing (Fig. 2), so that species can be considered either visible or invisible. Second, it assumes that species can recover from low densities without facing extinction due to demographic stochasticity or reaching a population size of less than one individual. A simple rule-of-thumb test for whether demographic stochasticity is a concern is to define a minimum viable population as one organism. After the SSD rescaling of population densities so that visible is zero and time so that a period runs from 0 to 1, this minimum viable population is \(-\log \frac{n}{T}\) where \(n\) is a typical visible population size. This could be compared against the scaled density at the end of a "bad" season, \(-\lambda_{bad}(1-\phi)\), or against the minimum scaled density across a whole period. If there is any doubt about the applicability to a particular system, the results derived using the SSD approach can be compared to numerical simulations of traditional differential equation models.

As with all approximations, these assumptions render the approach appropriate for some communities and inappropriate for others. It is most applicable to taxa that are fast-growing relative to variation in the environment and those that achieve high population densities. The system which inspired this approach, plankton undergoing seasonal succession (Sommer et al., 1986; Sommer, 1989), fits both assumptions, with characteristic generation times 100 times greater than the forcing period and population densities on the order of 10^5 individuals per ml, large enough to prevent stochastic extinction (Litchman and Klausmeier, 2001). Our laboratory experiments further validate the approach (Steiner et al., 2009). Other microbial communities likely match these assumptions as may some insects and diseases. Phytoplankton are responsible for 50% of the earth's primary production; other microbes play key roles in global biogeochemical cycles and are responsible for diseases of humans, animals, and plants. Therefore, this approach is valid for systems of widespread importance. Because a key parameter in these models is the length of the growing season, this approach should prove useful in determining the effect of climate change on community structure and the timing of species blooms.

Further work and extensions to the approach are possible. First, the SSD approximation could be more derived with more mathematical rigor than in Appendix A. Second, a refined approximation that accounts for differences in densities in different states (e.g., prey with and without predator) may extend the range of periods over which the approximation is good and allow for a finite period correction. Third, populations should be very susceptible to immigration when invisible. A generalization that considers this could yield important implications for understanding metacommunity dynamics and ecosystem management. Fourth, a generalization to structured populations would be useful. In this case, invasion rates should be given by eigenvalues, Floquet or Lyapunov exponents from vector-valued analogs of (A7) when invading stable, periodic, or aperiodic states, respectively. Finally, the approach could be generalized to include stochastic forcing, where the length of each season is a random variable. This would allow exploration of the interplay of externally driven and internally generated variability in driving succession.

**Acknowledgments**

I thank Elena Litchman and countless other colleagues for useful discussions on this topic, and Mary Anne Evans, Jarad Mellard, and three anonymous reviewers for comments on this manuscript. This research was supported by NSF Grant DEB-0610532 and a grant from the James S. McDonnell Foundation. This is contribution # 1546 of the Kellogg Biological Station.

**Appendix A. Deriving SSD model from ODEs**

Consider a model with \(N \geq 1\) species without immigration and \(\sigma \geq 0\) other variables (including species with immigration). Species \(i\) has density \(n_i\) and per capita growth rate \(g_i\), where \(g_i\) is bounded as \(n_i \rightarrow 0\). Other variable \(i\) has value \(\sigma_i\) and absolute growth rate \(f_i\). Let \(x = (n_1, n_2, \ldots, n_N, \sigma_1, \sigma_2, \ldots, \sigma_r)\) denote the state of the system. Dynamics are given by

\[
\frac{dn_i}{dt} = n_i g_i(x) \tag{A.1}
\]

\[
\frac{d\sigma_i}{dt} = f_i(x) \tag{A.2}
\]

The growth rates are piecewise-defined periodic functions of time with period \(T\) that cycle among a set of \(M\) modes, \(M = \{m_1, m_2, \ldots, m_M\}\) so that

\[
f_i = \begin{cases} f_{i,m_1} & 0 \leq \text{mod} (t/T, 1) < t_{m_1} \\ f_{i,m_2} & t_{m_1} \leq \text{mod} (t/T, 1) < t_{m_2} \\ \vdots \\ f_{i,m_M} & t_{m_{M-1}} \leq \text{mod} (t/T, 1) < 1 \end{cases} \tag{A.3}
\]

\[
g_i = \begin{cases} g_{i,m_1} & 0 \leq \text{mod} (t/T, 1) < t_{m_1} \\ g_{i,m_2} & t_{m_1} \leq \text{mod}(t/T, 1) < t_{m_2} \\ \vdots \\ g_{i,m_M} & t_{m_{M-1}} \leq \text{mod} (t/T, 1) < 1 \end{cases} \tag{A.4}
\]
Rescale time by the period by letting $\tilde{t} = t/T$ and define

$$N_i = \frac{\ln n_i}{T}. \quad (A.5)$$

$$\frac{1}{T} \frac{dn_i}{dt} = n_i g_i(\tilde{x}) \quad (A.6)$$

In the limit of large periods,

$$\lim_{\tilde{t} \rightarrow \infty} \frac{1}{T} \frac{dn_i}{dt} = 0 = n_i \tilde{g}_i(\tilde{x}) \quad (A.7)$$

$$\lim_{\tilde{t} \rightarrow \infty} \frac{1}{T} \frac{d\tilde{y}_i}{dt} = 0 = \tilde{f}_i(\tilde{x}) \quad (A.8)$$

where $\tilde{f}_i = (1/\epsilon) \int_{-\infty}^{\infty} f_i$ and $\tilde{g}_i = (1/\epsilon) \int_{-\infty}^{\infty} g_i$ for small $\epsilon$ (Sanders et al., 2007). We apply this averaging to allow for limit cycles and chaotic attractors. Therefore, the system is almost always near a limit set as $T \rightarrow \infty$. For the “other” variables, Eq. (A.8) implies $\tilde{f}_i(\tilde{x}) \approx 0$. For the species, Eq. (A.7) implies that either $n_i \approx 0$ or $\tilde{g}_i \approx 0$. If $n_i \approx 0$, we consider species $i$ to be invisible; in this case, $\tilde{g}_i \approx 0$, $N_i \approx 0$ and $dn_i/dt \approx 0$. If $n_i \approx 0$, we consider species $i$ to be visible; in this case, $N_i \approx 0$ and $d\tilde{y}_i/dt = \tilde{g}_i(\tilde{x})$. A transition occurs when previously invisible species becomes visible ($N_i \approx 0$). States of the system correspond to all the solutions of (A.7–8) and invasion rates are given by $\tilde{g}_i(\tilde{x})$ for each species $i$, given state $\tilde{x}$.

In the main text I drop the $\tilde{}$ from time $t$ for ease of notation.

Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version at 10.1016/j.jtbi.2009.10.018.

References


