

Floquet theory: a useful tool for understanding nonequilibrium dynamics

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Abstract Many ecological systems experience periodic variability. Theoretical investigation of population and community dynamics in periodic environments has been hampered by the lack of mathematical tools relative to equilibrium systems. Here, I describe one such mathematical tool that has been rarely used in the ecological literature but has widespread use: Floquet theory. Floquet theory is the study of the stability of linear periodic systems in continuous time. Floquet exponents/multipliers are analogous to the eigenvalues of Jacobian matrices of equilibrium points. In this paper, I describe the general theory, then give examples to illustrate some of its uses: it defines fitness of structured populations, it can be used for invasion criteria in models of competition, and it can test the stability of limit cycle solutions. I also provide computer code to calculate Floquet exponents and multipliers.

Keywords Nonequilibrium dynamics · Floquet theory

Introduction

Populations, communities, and ecosystems vary in time, a truism obvious to natural historians (Thoreau

1854) and well-quantified by empiricists (Kratz et al. 2003). The origin of these fluctuations can be external (e.g., weather) or internal (e.g., predator–prey cycles), and the fluctuations can be random, periodic, or chaotic. Given the ubiquity of temporal variability and its potential importance for structuring ecological systems, theoreticians have been eager to incorporate its effects in ecological models (Nisbet and Gurney 1982; DeAngelis and Waterhouse 1987; Chesson 1994). Despite these efforts, we still do not have a full understanding of the effect of temporal variability on theoretical communities and ecosystems, much less real ones. Why not?

First, temporal variability is a multifaceted phenomenon with complex and idiosyncratic effects on different ecological processes. Details matter. For example, some models of competition have shown that fluctuations can increase diversity (Armstrong and McGehee 1980; Chesson 1994; Litchman and Klausmeier 2001), while others have shown that they can decrease diversity (May 1974). The effect of environmental noise has been showed to strongly depend on the spectrum of the noise (Steele and Henderson 1984; Kaitala et al. 1997).

Second, nonequilibrium dynamics are more difficult to analyze mathematically than equilibrium situations because fewer analytical tools are available. A number of analytical techniques have been applied to ecological models, but each has a limited range of applicability. For example, Chesson's decomposition of competitive effects in a stochastic environment (Chesson 1994) and Nisbet and Gurney's use of transfer functions (Nisbet and Gurney 1982) both assume small environmental fluctuations. Elsewhere, we have developed techniques that assume that environmental variability is slow compared to population dynamics (Litchman and

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Klausmeier 2001; Klausmeier in preparation). When these approximations are not valid, the typical approach to studying nonequilibrium dynamics is brute force numerical solution of the model (e.g., Grover 1991; Hastings and Powell 1991; Brassil 2006). All of these tools have their place in the theoretician's toolbox, but we could use more of them.

In this paper, I explain and illustrate one such tool: Floquet theory. Although Floquet theory has a wide range of potential uses in ecological and evolutionary modeling and is relatively easy to implement, its use in ecology has been extremely limited (Kooi and Troost 2006). The mathematics here is not novel or particularly advanced; Floquet theory is typically taught in a second course on ordinary differential equations (cf. Drazin 1992; Grimshaw 1993; Strogatz 1994). However, most ecologists do not take one, much less two, courses in differential equations. Instead, they learn modeling techniques from a course in theoretical ecology, which typically do not incorporate Floquet theory (cf. Nisbet and Gurney 1982; Yodzis 1989; Hastings 1997). Given the potential utility of Floquet theory, its lack of use indicates that it needs better advertising. Therefore, the goal of this paper is to promote the wider use of Floquet theory as a useful tool for studying the effects of temporal variability on ecological systems.

What is Floquet theory? It is the study of linear systems of differential equations with periodic coefficients. What can you do with it? You can use it for anything you would use linear stability analysis for, when dealing with a periodic system. In particular, it has three potentially important uses in ecological theory: 1) defining fitness of structured populations in periodic environments, 2) calculating invasion criteria for interacting structured populations in periodic environments, and 3) testing the stability of a limit cycle. A structured population is one that can not be modeled as a single state variable. Some different types of population structure are physiological structure (Metz and Diekmann 1986), age and stage structure (Caswell 2001), and spatial structure (Tilman and Kareiva 1997).

In the remainder of this paper, I outline the ideas behind Floquet theory. I describe a numerical method for calculating Floquet multipliers and define a Mathematica (Wolfram Research Inc. 2007) function to do this calculation. Then, I give three ecological examples of the utility of Floquet theory. First, I explore the evolution of dispersal in a two-patch metapopulation with spatiotemporal fluctuations. Second, I calculate invasion criteria in a model of competing stage-structured populations in a seasonal environment. Third, I calculate the stability of a limit cycle in a tri-trophic food

chain model (Hastings and Powell 1991). Finally, I suggest other applications of Floquet theory and describe its generalization to environments with aperiodic temporal variation (Metz et al. 1992).

Theory

Here, I largely follow Grimshaw (1993); the reader who wants more details could consult it or another differential equations text (e.g., Drazin 1992; Strogatz 1994). Consider a set of linear, homogeneous, time-periodic differential equations

$$\frac{d\mathbf{x}}{dt} = A(t)\mathbf{x} \quad (1)$$

where \mathbf{x} is a n -dimensional vector and $A(t)$ is an $n \times n$ matrix with minimal period T . Although its parameters $A(t)$ vary periodically, the solutions of Eq. 1 are typically not periodic, and despite its linearity, closed-form solutions of Eq. 1 typically cannot be found. The general solution of Eq. 1 takes the form

$$\mathbf{x}(t) = \sum_i^n c_i e^{\mu_i t} \mathbf{p}_i(t) \quad (2)$$

where c_i are constants that depend on initial conditions, $\mathbf{p}_i(t)$ are vector-valued functions with period T , and μ_i are complex numbers called characteristic or Floquet exponents. Characteristic or Floquet multipliers are related to the Floquet exponents by the relationship $\rho_i = e^{\mu_i T}$. As can be seen from Eq. 2, the solution to Eq. 1 is the sum of n periodic functions multiplied by exponentially growing or shrinking terms. The long-term behavior of the system is determined by the Floquet exponents. The zero equilibrium is stable if all Floquet exponents have negative real parts or, equivalently, all Floquet multipliers have real parts between -1 and 1 . If any Floquet exponent has a positive real part (equivalent to a Floquet multiplier with modulus greater than one), then the zero equilibrium is unstable and $\|\mathbf{x}(t)\| \rightarrow \infty$ as $t \rightarrow \infty$. Thus, Floquet exponents/multipliers can be interpreted in the same way as eigenvalues are in models with constant coefficients in continuous/discrete time, respectively; they represent the growth rate of different perturbations averaged over a cycle. Floquet exponents are rates with units time^{-1} , and Floquet multipliers are dimensionless numbers that give the period-to-period increase/decrease of the perturbation.

How can Floquet exponents/multipliers be calculated? While the eigenvalues of a matrix can be calculated analytically, Floquet exponents/multipliers typically must be calculated numerically. An efficient approach is available. Solve the matrix differential equation

$$\frac{dX}{dt} = A(t)X \quad (3)$$

over one period (from $t = 0$ to $t = T$), with the identity matrix as an initial condition ($X(0) = I$). The matrix $X(T)$ is known as a fundamental matrix (Grimshaw 1993). Floquet multipliers, ρ_i , are the eigenvalues of $X(T)$ and Floquet exponents, μ_i can be calculated as $(\log \rho_i)/T$. Code to do these calculations in Mathematica (Wolfram Research, Inc. 2007) is supplied in the [Electronic Appendix](#), which should be easily implemented in other systems.

Example 1: fitness of structured populations in periodic environments

Metz et al. (1992) showed that the general definition of fitness is given by the asymptotic exponential growth rate, which is determined by the dominant Lyapunov exponent. Floquet exponents are the special case of Lyapunov exponents applied to continuous-time periodic systems, so it follows that Floquet exponents should be useful in the evolutionary ecology of structured populations. Frequency dependence can be incorporated in a nonlinear model, calculating fitness as an invasion rate as in the next example (see also Metz et al. 1992; Kooi and Troost 2006).

Here, I give an example of the evolution of dispersal in a spatiotemporal mosaic environment. Consider a population that lives in two patches, with densities x_1 and x_2 . In each patch, the population grows or shrinks exponentially at rate $r_i(t)$ with $r_1(t) = \sin 2\pi t$ and $r_2(t) = -\sin 2\pi t$, so that the two patches change from sources ($r > 0$) to sinks ($r < 0$) perfectly out of phase with period $T = 1$. The patches are coupled by random dispersal with rate d . The model for this situation is

$$\frac{dx_1}{dt} = r_1(t)x_1 + d(x_2 - x_1)$$

$$\frac{dx_2}{dt} = r_2(t)x_2 + d(x_1 - x_2)$$

or, in the form of Eq. 1,

$$A(t) = \begin{pmatrix} r_1(t) - d & d \\ d & r_2(t) - d \end{pmatrix} \quad (4)$$

Before calculating the asymptotic population growth rate (fitness) for arbitrary d , consider two special cases.

If the two patches are completely uncoupled ($d = 0$), then the growth rate in each patch varies from -1 to 1 , with an average growth rate of zero. It is well known

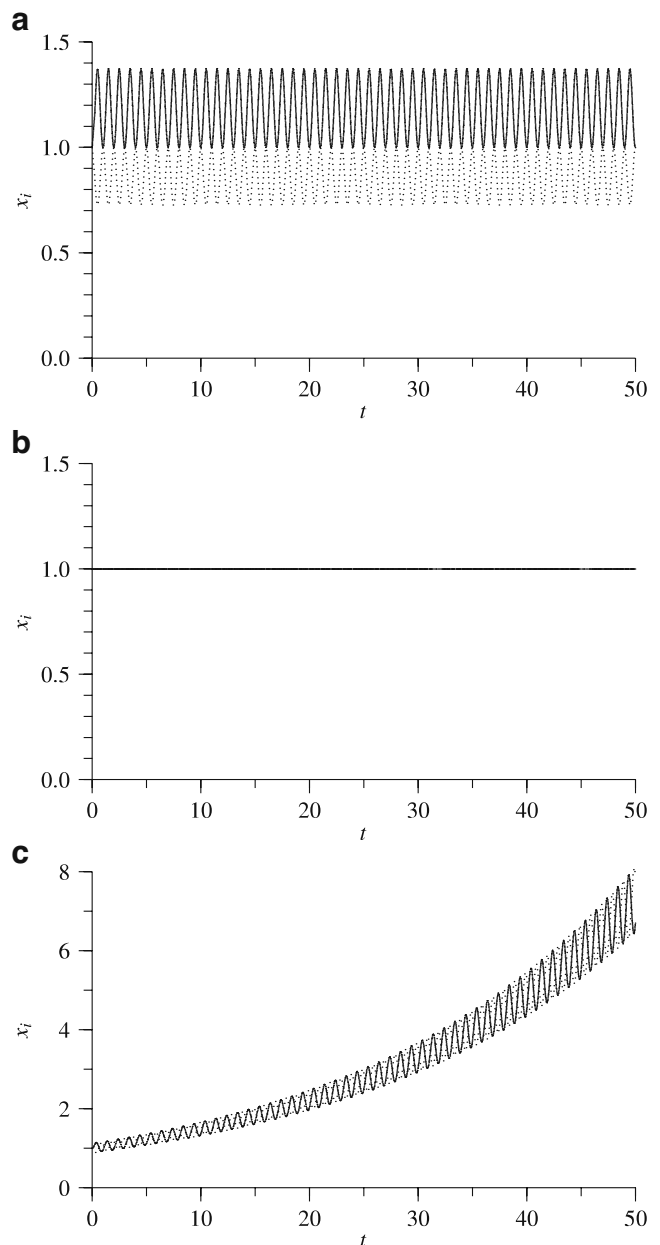


Fig. 1 Population dynamics in two patches governed by Eqs. 1 and 4 with different dispersal rates. Initial conditions: $x_1(0) = 1$, $x_2(0) = 1$. *Solid line* is density in patch 1, *dotted line* is density in patch 2. **a** $d = 0$. **b** $d = 10^4$ (effectively infinite). **c** $d = 3$

that an isolated population growing exponentially in a time-varying environment grows according to its average growth rate. Therefore, for $d = 0$, we expect no net growth or decline. A numerical solution of Eq. 1, with $A(t)$ given by Eq. 4, shows this to be correct (Fig. 1a). Each subpopulation grows during the favorable part of the period and declines the exact same amount during the unfavorable part.

If the two patches are completely well-mixed ($d = \infty$), then we expect the population to experience both patches equally, averaging growth rates over space. Because the two patches are out-of-phase, the spatial-average growth rate is $(r_1 + r_2)/2 = 0$, so we would again expect no net growth, this time without any fluctuations. Again, the numerical solution of Eqs. 1 and 4 with large d shows this to be correct (Fig. 1b).

Given the behavior of these two limiting cases and the linearity of Eq. 1, one might expect no net growth for any d . Numerical solution of Eqs. 1 and 4 shows this to be incorrect; instead, the population grows without bound (Fig. 1c). Evaluating the maximum Floquet exponent of Eq. 4 as a function of dispersal rate, d , verifies that these numerical results are correct (Fig. 2): net population growth is zero for $d = 0$ and $d = \infty$, but it is positive for intermediate d . Figure 2 shows that there is an optimal dispersal rate d that maximizes fitness; in this case, it is $d = 3.132$, which leads to a growth rate of 0.03966. Thus, even with no explicit cost of dispersal, there is an optimal dispersal rate in a spatiotemporal mosaic environment. This is a simple example of the phenomenon of inflation recently introduced by Holt and colleagues (Gonzalez and Holt 2002; Holt et al. 2003; Roy et al. 2005); it complements their work because it considers multiple patches in continuous time and with periodic variability, whereas existing work focuses on a single patch (Gonzalez and Holt 2002;

Holt et al. 2003) or stochastic variability in discrete time (Roy et al. 2005).

Example 2: invasion criteria for interacting structured populations

Invasion criteria are a powerful tool for analyzing pairwise competitive interactions (Armstrong and McGehee 1980). Each species is grown in monoculture, then the other species is introduced at low density and its invasion rate is calculated. If species one invades species two, but not vice versa, then we say species one outcompetes species two. If the reverse is true, species two outcompetes species one. If each species can invade a monoculture of the other, then we say the two species coexist, and if neither species can invade a monoculture of the other, then the system exhibits founder control. Complications can arise in systems with multiple attractors (Namba and Takahashi 1993; Mylius and Diekmann 2001), but invasion criteria have found widespread use in studying real and apparent competition (e.g., Armstrong and McGehee 1980; Chesson 1994; Grover and Holt 1998; Litchman and Klausmeier 2001). Invasion criteria are so popular because they focus on the linear stability of monoculture attractors, which eliminates the need to solve for a coexistence attractor. This is analytically and computationally more tractable. Because Floquet theory is the appropriate measure of linear stability in periodic structured population, it has a natural role in applying invasion criteria in these cases.

Here, we give an example of the use of Floquet theory in calculating invasion criteria, using the case of competition of stage-structured populations in a seasonal environment. This lets us look at how life-history trade-offs can permit coexistence in a nonequilibrium system with competition for a single limiting resource.

Each species i has two stages: juvenile ($N_{J,i}$) and adult ($N_{A,i}$). We assume the environment has two distinct phases: a good season (proportion ϕ of the time), where reproduction is possible, and a bad season (proportion $1 - \phi$ of the time), where reproduction is impossible. These seasons alternate with period T . We have previously used such a piecewise forcing regime in a model of competition of unstructured populations (Litchman and Klausmeier 2001). In both seasons, juveniles mature into adults at rate m_i and juveniles and adults have density-independent mortality rates $d_{J,i}$ and $d_{A,i}$, respectively. In the good season, adults give birth to juveniles at rate $f_i(R)$, which depends on the concentration of resource R through a

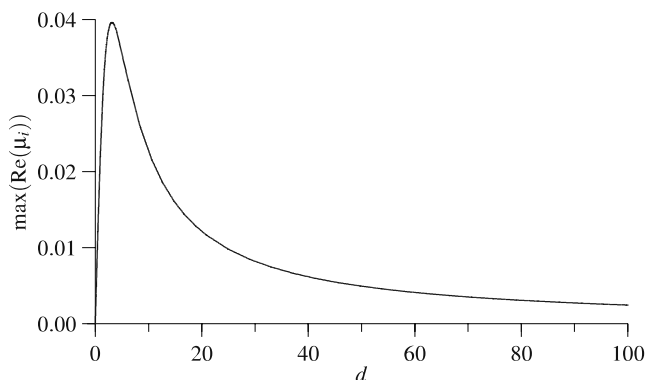


Fig. 2 Dominant Floquet exponent as a function of dispersal rate, d . Fitness is maximized at an intermediate $d = 3.132$

type-II functional response, $f_i(R) = b_{max,i}R/(R + K_i)$. The resource is treated algebraically, with $R = R_{tot} - \sum(N_{J,i} + N_{A,i})$. During the bad season, reproduction ceases. Taken together, these assumptions result in the following model:

$$\begin{aligned} \frac{dN_{J,i}}{dt} &= \begin{cases} f_i(R)N_{A,i} - m_iN_{J,i} - d_{J,i}N_{J,i}, & t \in [iT, (i + \phi)T] \\ -m_iN_{J,i} - d_{J,i}N_{J,i}, & t \in [(i + \phi)T, (i + 1)T] \end{cases} \\ \frac{dN_{A,i}}{dt} &= m_iN_{J,i} - d_{A,i}N_{A,i} \\ R &= R_{tot} - \sum(N_{J,i} + N_{A,i}) \end{aligned} \tag{5}$$

Because this is a model of pure resource competition for a single limiting resource, in the absence of environmental forcing, the competitive exclusion principle holds (Levin 1970), with the winner of competition the species with lowest break-even resource level R^* (Tilman 1982). This model is similar to the single-species structured resource competition model of Revilla (2000) but includes interspecific competition in addition to intraspecific competition.

It is well-known that species exhibit a range of ecological strategies, some of which are selected for in equilibrium conditions (K -strategies) and some of which are selected for during times of abundant resources (r -strategies) (MacArthur and Wilson 1967). In a nonequilibrium environment, species with these two strategies may coexist if there is a trade-off between maximum growth rate (r -strategy) and competitive ability as measured by R^* (K -strategy) (Koch 1974; Armstrong and McGehee 1980; Grover 1990; Litchman and Klausmeier 2001). In a nonstructured population, this trade-off is attained only if the functional responses of two species cross. In structured populations, there are more mechanisms that can set up an r - K trade-off. For example, in a model of variable internal nutrient stores, Grover showed that maximum nutrient uptake rate, maximum growth rate, and nutrient storage ability could each trade-off with equilibrium competitive ability (Grover 1991).

In our model, we assume both species have the same functional response to the resource but differ in their life-history parameters. Species one is a K -selected species, with a slow rate of maturation from juvenile to adult ($m_1 = 0.01$) but an efficient use of resources to make new offspring ($Y_1 = 20$); species two is an r -selected species, with a fast maturation rate ($m_2 = 10$)

and inefficient resource use ($Y_2 = 1$). All other parameters are set equal between species.

To show that these species do possess an r - K trade-off, we will show that species one is a superior equilibrium resource competitor but that species two grows faster under low-density, nutrient-rich conditions. Equilibrium competitive ability is measured by the break-even resource level, R^* (Tilman 1982). We compute R^* for each species by setting $dN_{J,i}/dt = 0$ and $dN_{A,i}/dt = 0$ and numerically solving for R . We find that $R_1^* = 0.00582$ and $R_2^* = 0.0112$, so species one is the superior competitor at equilibrium. The growth rate of species i under low-density conditions is given by the largest eigenvalue, $\lambda_{i,\phi,good}$, of the stage-transition matrix with $R = R_{tot}$. That matrix is

$$\begin{pmatrix} -m_i - d_{J,i} & f_i(R_{tot}) \\ m_i & -d_{A,i} \end{pmatrix} \tag{6}$$

When $R_{tot} = 1$, we find $\lambda_{1,\phi,good} = 0.321$ and $\lambda_{2,\phi,good} = 0.739$, so that species two grows faster in a low-density environment. Therefore, these species exhibit an r - K trade-off and have the potential to coexist in some nonequilibrium environments.

To see if the species do coexist in some nonequilibrium environments, we numerically solve the model Eq. 5. Figure 3 shows the total population sizes and the proportion adults for both species after a stable limit cycle has been reached. Figure 3a uses a shorter period for the environmental forcing ($T = 300$) compared to Fig. 3b ($T = 10000$), resulting in smoother dynamics. In both cases, the two species coexist over the cycle.

We calculate invasion criteria using Floquet theory to summarize the outcome of competition as a function of ϕ and T (Fig. 4). Because there are four possible attractors (no species persists, 1 outcompetes 2, 2 outcompetes 1, and 1 and 2 coexist), we need two types of calculations: first, whether a species can invade the empty system, and second, whether a species can invade a monoculture of the other.

Whether a species can persist by itself is determined by the dominant Floquet multiplier of the periodic matrix corresponding to invasion of the empty system,

$$A_{inv}(t) = \begin{cases} A_{inv,good}, & t \in [0, \phi T] \\ A_{inv,bad}, & t \in [\phi T, T] \end{cases} \tag{7}$$

where

$$A_{inv,good} = \begin{pmatrix} -m_{inv} - d_{J,inv} & f_{inv}(R_{tot}) \\ m_{inv} & -d_{A,inv} \end{pmatrix} \tag{8}$$

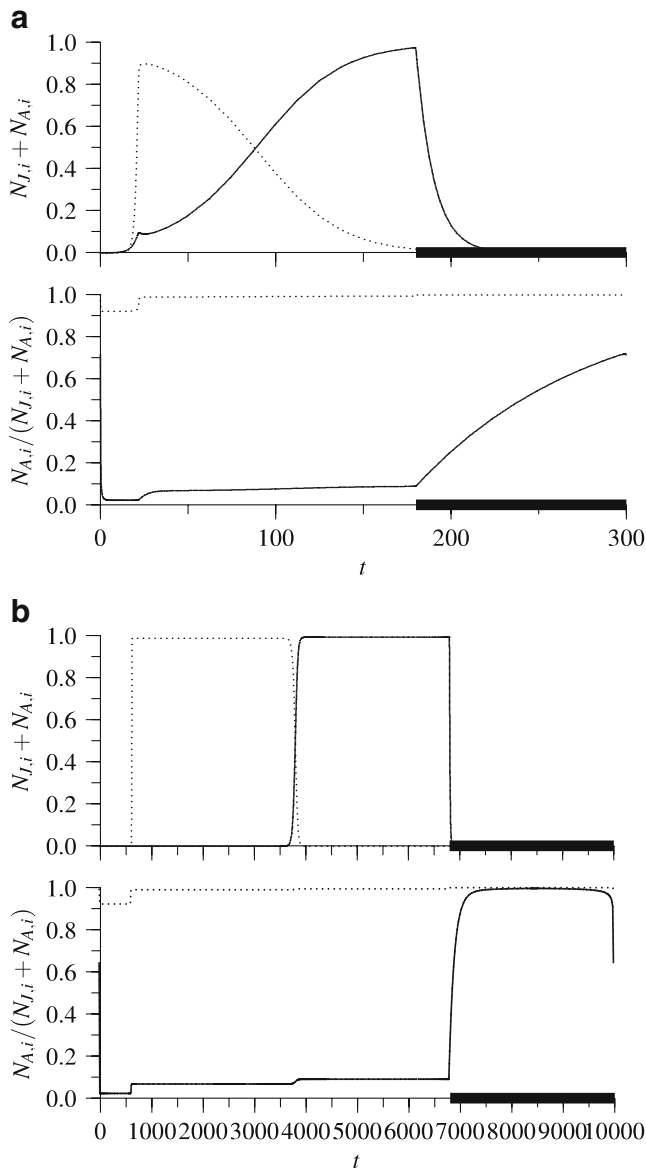


Fig. 3 Asymptotic dynamics of competition between a *K*-selected (species 1, *solid line*) and an *r*-selected (species 2, *dotted line*) species in a seasonal environment. **a** $\phi = 0.6$ and $T = 300$. **b** $\phi = 0.68$ and $T = 10000$. *Black bars* denote the “bad” season

and

$$A_{inv,bad} = \begin{pmatrix} -m_{inv} - d_{J,inv} & 0 \\ m_{inv} & -d_{A,inv} \end{pmatrix} \quad (9)$$

Because $A_{inv}(t)$ is a piecewise-constant matrix, we can compute the fundamental matrix $X(t)$ using the matrix exponential (Gökçek 2004). The fundamental matrix is

$$X(t) = \exp((1 - \phi)T A_{inv,bad}) \exp(\phi T A_{inv,good}), \quad (10)$$

whose eigenvalues are the Floquet multipliers corresponding to invasion into the empty system and can be

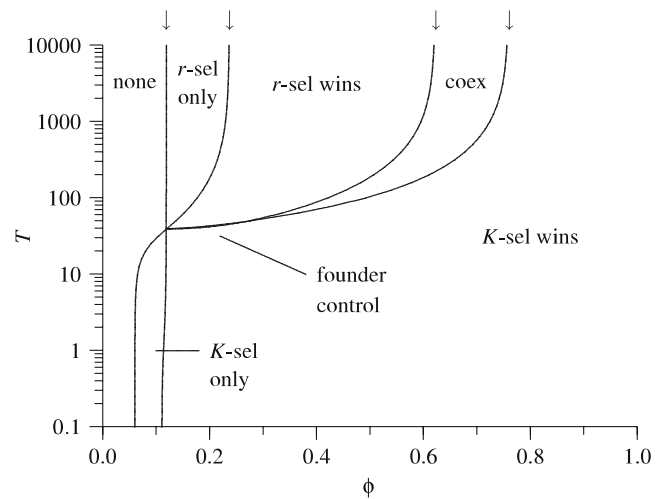


Fig. 4 Outcome of competition between a *K*-selected (species 1) and an *r*-selected species (species 2) in a seasonal environment with period T and ϕ proportion “good” season, as determined by invasion criteria using Floquet theory. *Arrows* on the top denote values for these boundaries when $T \rightarrow \infty$ determined with a slow fluctuation approximation

easily calculated numerically (see [Electronic Appendix](#)). When the dominant Floquet multiplier is greater than one, $\max(\text{Re}(\rho)) > 1$, the species can persist in monoculture. The critical ϕ that allows growth for a given T can be found numerically using Newton’s method (see [Electronic Appendix](#)). This approach gives the two leftmost lines in Fig. 4.

To determine whether a species can invade a monoculture of the other species, we first find the limit cycle solution of the resident species alone then calculate the Floquet multipliers of the matrix corresponding to the invader’s growth when rare. Here,

$$A_{good,inv} = \begin{pmatrix} -m_{inv} - d_{J,inv} & f_{inv}(R_{res}(t)) \\ m_{inv} & -d_{A,inv} \end{pmatrix} \quad (11)$$

where “inv” denotes invader and “res” denotes resident and $R_{res}(t)$ is determined from the monoculture limit cycle of the resident, which must be determined by numerically integrating a single-species version of Eq. 5. $A_{bad,inv}$ is the same as above. Again, the critical ϕ is where $\max(\text{Re}(\rho)) = 1$, which gives the two right lines bounding the coexistence region in Fig. 4.

For large periods, population dynamics become step-like (Fig. 3b). Elsewhere, we have developed approximate analytical techniques for studying competition in an alternating environment in this limit of slow fluctuations (Litchman and Klausmeier 2001; Klausmeier in preparation). That slow fluctuation approximation can also be applied to this stage-structured model as follows. Let $\lambda_{i,\theta,good}$ denote the dominant eigenvalue of the matrix corresponding to species i invading the

empty system in the good season, $\lambda_{i,\{j\},\text{good}}$ denote the dominant eigenvalue of the matrix corresponding to species i invading species j at equilibrium in the good season, and $\lambda_{i,\emptyset,\text{bad}}$ denote the dominant eigenvalue of the matrix corresponding to species i declining in the bad season. The critical ϕ for persistence of species i by itself is

$$\phi = \frac{\lambda_{i,\emptyset,\text{bad}}}{\lambda_{i,\emptyset,\text{bad}} - \lambda_{i,\emptyset,\text{good}}} \tag{12}$$

and the critical ϕ for invasion of species i into a monoculture of species j is

$$\phi = \frac{(\lambda_{i,\emptyset,\text{bad}}\lambda_{j,\emptyset,\text{good}} - \lambda_{i,\emptyset,\text{good}}\lambda_{j,\emptyset,\text{bad}} + \lambda_{i,\{j\},\text{good}}\lambda_{j,\emptyset,\text{bad}})}{(\lambda_{i,\emptyset,\text{bad}}\lambda_{j,\emptyset,\text{good}} - \lambda_{i,\{j\},\text{good}}\lambda_{j,\emptyset,\text{good}} - \lambda_{i,\emptyset,\text{good}}\lambda_{j,\emptyset,\text{bad}} + \lambda_{i,\{j\},\text{good}}\lambda_{j,\emptyset,\text{bad}})} \tag{13}$$

(Klausmeier in preparation). For the parameters used here, the critical ϕ values for persistence in monoculture are $\phi_1 = 0.2373$ and $\phi_2 = 0.1192$, and the critical ϕ values for coexistence are $\phi_1 = 0.6231$ and $\phi_2 = 0.7606$ (see [Electronic Appendix](#)). These values are noted with arrows in Fig. 4, where they can be seen to agree with the numerical results generated with Floquet theory as the period $T \rightarrow \infty$.

This example shows that coexistence of an r - and a K -selected species is possible if there is a life-history-mediated trade-off between maximum growth rate and competitive ability, even if both species share the same functional response. Unlike the nonstructured population model we previously studied (Litchman and Klausmeier 2001), there is no switch in competitive dominance for small periods. Instead, the K -selected species dominates for all ϕ for small T . There is also a small region of parameter space where founder control occurs (Fig. 4).

Example 3: Stability of a limit cycle

The most common use of Floquet theory is to test the stability of a limit cycle solution. This is useful in understanding how dynamics depend on parameter values. Here, we illustrate this use on a classic model of a three-species food chain that is known to have limit cycle solutions that can become unstable as model parameters are changed (Hastings and Powell 1991; Kuznetsov and Rinaldi 1996).

The Hastings–Powell food chain model consists of three species (basal x , intermediate predator y , and top predator z). The basal species grows logistically, every resource–consumer pair is coupled by a type-

II functional response, and the intermediate and top predators experience density-independent mortality (Hastings and Powell 1991). The resultant nondimensionalized model is

$$\frac{dx}{dt} = x(1 - x) - \frac{a_1x}{1 + b_1x}y = f_1 \tag{14}$$

$$\frac{dy}{dt} = \frac{a_1x}{1 + b_1x}y - \frac{a_2y}{1 + b_2y}z - d_1y = f_2 \tag{15}$$

$$\frac{dz}{dt} = \frac{a_2y}{1 + b_2y}z - d_2z = f_3 \tag{16}$$

(Hastings and Powell 1991).

Following Hastings and Powell (1991), we focus on the nondimensional parameter b_1 . Using brute force numerical solution of the model, Hastings and Powell showed that, as b_1 increased from 2.25 to 2.4, the model undergoes the period-doubling route to chaos (Fig. 4c in Hastings and Powell 1991, our Fig. 5a, b). Here, we investigate the first period doubling using Floquet theory.

Before we can study the stability of the limit cycle solution, first we have to locate it, which we must do numerically. We must locate one point on the limit

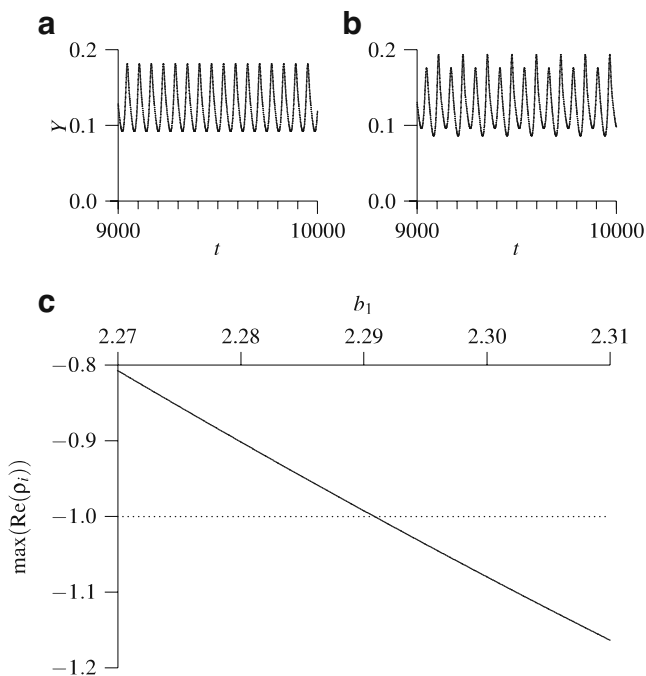


Fig. 5 Stability of a limit cycle solution in the Hastings and Powell (1991) food chain model. Parameters are: $a_1 = 5.0$, $a_2 = 0.1$, $b_2 = 2.0$, $d_1 = 0.4$, and $d_2 = 0.01$. **a–b** Dynamics of y . **a** A limit cycle with $b_1 = 2.28$. **b** A period-doubled limit cycle with $b_1 = 2.3$. **c** Dominant Floquet multiplier of the limit cycle as a function of b_1 . Around $b_1 = 2.291$, there is a period-doubling bifurcation

cycle, as well as its period T , such that $x(t + T) = x(t)$, $y(t + T) = y(t)$, and $z(t + T) = z(t)$. We do this using Newton's method through Mathematica's FindRoot command (see [Electronic Appendix](#)).

Once the limit cycle is in hand, we test its stability by asking if small perturbations away from the limit cycle grow or shrink over a complete period. This corresponds to finding the stability of the periodic system obtained by linearizing the full model Eq. 10 around the limit cycle (Grimshaw 1993). Define the Jacobian matrix of Eq. 10 as

$$J(t) = \begin{pmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} & \frac{\partial f_1}{\partial z} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} & \frac{\partial f_2}{\partial z} \\ \frac{\partial f_3}{\partial x} & \frac{\partial f_3}{\partial y} & \frac{\partial f_3}{\partial z} \end{pmatrix}_{(x(t), y(t), z(t))_{\text{limit cycle}}} \quad (17)$$

The Floquet multipliers of $J(t)$ determine the stability of the limit cycle. Figure 5c shows that the dominant Floquet multiplier of $J(t)$ as b_1 is increased from 2.28 to 2.32. Near $b_1 = 2.291$, the dominant Floquet multiplier passes through -1 , signifying a period-doubling bifurcation of the limit cycle. This corroborates the brute force numerical analysis of Hastings and Powell (1991).

Discussion

The three examples in this paper demonstrate that Floquet theory is a versatile tool for studying the ecology and evolution of periodic systems. Floquet theory defines fitness in periodic environments, can calculate invasion criteria for competing species, and can be used to test the stability of limit cycle solutions. Given these diverse uses and the ubiquity of both structured populations and periodic systems in nature, Floquet theory should be a useful addition to theoreticians' toolboxes. Although Floquet theory is a linear theory, nonlinear models can be linearized near limit cycle solutions to enable the use of Floquet theory.

An alternative way to compute Floquet exponents and multipliers is to use numerical continuation software such as AUTO (Doedel et al. 2001), XPPAUT (Ermentrout 2002), CONTENT (Kuznetsov and Levitin 1996), or MATCONT (Dhooge et al. 2003). These programs provide powerful environments for analyzing the behavior of nonlinear dynamical systems. See van Coller (1997) for an ecological introduction to continuation software.

Floquet theory deals with continuous-time systems. The theory of periodic discrete-time systems is closely analogous (Caswell 2001, chapter 13). In that case,

one can multiply the T transition matrices together to determine how a perturbation changes over a period, which is similar to finding the fundamental matrix.

One limitation of Floquet theory is that it applies only to periodic systems. Although many systems experience periodic forcing, others experience stochastic or chaotic forcing. In these cases, the more general Lyapunov exponents described by Metz et al. (1992) play the role of Floquet exponents (see also Ferriere and Gatto 1995). Conceptually similar to Floquet exponents (and therefore to eigenvalues of the Jacobian matrix associated with an equilibrium point), Lyapunov exponents are more challenging to compute numerically because, instead of calculating how a perturbation grows or shrinks over one period, this must be done in the limit at $T \rightarrow \infty$. For a practical algorithm for this in continuous systems, see Wolf et al. (1985).

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