NONLOCAL GENERALIZED MODELS OF PREDATOR-PREY SYSTEMS

CHRISTIAN KUEHN
Institute for Analysis and Scientific Computing
Vienna University of Technology
1040 Vienna, Austria
Max Planck Institute for the Physics of Complex Systems
01187 Dresden, Germany

THILO GROSS
Department of Engineering Mathematics
University of Bristol
Bristol BS8 1TR, United Kingdom
Max Planck Institute for the Physics of Complex Systems
01187 Dresden, Germany

(Communicated by Gail Wolkowicz)

Abstract. The method of generalized modeling has been used to analyze differential equations arising in applications. It makes minimal assumptions about the precise functional form of the differential equation and the quantitative values of the steady-states which it aims to analyze from a dynamical systems perspective. The method has been applied successfully in many different contexts, particularly in ecology and systems biology, where the key advantage is that one does not have to select a particular model but is able to provide directly applicable conclusions for sets of models simultaneously. Although many dynamical systems in mathematical biology exhibit steady-state behaviour one also wants to understand nonlocal dynamics beyond equilibrium points. In this paper we analyze predator-prey dynamical systems and extend the method of generalized models to periodic solutions. First, we adapt the equilibrium generalized modeling approach and compute the unique Floquet multiplier of the periodic solution which depends upon so-called generalized elasticity and scale functions. We prove that these functions also have to satisfy a flow on parameter (or moduli) space. Then we use Fourier analysis to provide computable conditions for stability and the moduli space flow. The final stability analysis reduces to two discrete convolutions which can be interpreted to understand when the predator-prey system is stable and what factors enhance or prohibit stable oscillatory behaviour. Finally, we provide a sampling algorithm for parameter space based on nonlinear optimization and the Fast Fourier Transform which enables us to gain a statistical understanding of the stability properties of periodic predator-prey dynamics.

2010 Mathematics Subject Classification. Primary: 34A34, 37G15; Secondary: 92D40.
Key words and phrases. Generalized models, periodic orbits, predator-prey system, Floquet theory, moduli space flow, Fourier series, discrete convolution, parameter sampling, optimization, correlation.

The first author is partially supported by an ERC Marie-Curie Re-Integration Grant.
1. **Introduction.** Predator-prey systems capturing the interaction between a predator population \( Y \) and a prey population \( X \) have been a cornerstone in mathematical biology for many decades [7, 33, 4, 6]. Examples for modeling the situation by ordinary differential equations (ODEs) are [8, 7]

\[
\begin{align*}
(LV) \quad \left\{ \begin{array}{l}
X' &= p_1X - p_2XY, \\
Y' &= p_3XY - p_4Y,
\end{array} \right. \\
(RM) \quad \left\{ \begin{array}{l}
X' &= k_1X - k_2X^2 - k_3\frac{XY}{X+Y}, \\
Y' &= k_5\frac{XY}{X+Y} - k_6Y,
\end{array} \right.
\]

where \( p_i, k_i \) are parameters and (LV) are the Lotka-Volterra equations and (RM) is the Rosenzweig-MacArthur model [33]. These two examples are the most common models of the form

\[
\begin{align*}
X' &= S(X) - G(X, Y) \\
Y' &= \alpha G(X, Y) - M(Y)
\end{align*}
\]  

(1)

where \( \alpha > 0 \) is a parameter describing biomass conversion efficiency and the functions \( S, G \) and \( M \) represent prey growth, predation, and predator mortality, respectively. Because the parameter \( \alpha \) can always be removed by scaling the variable \( Y \) and re-labelling the functions we will always assume \( \alpha = 1 \) from now on.

Generalized models [22, 35] directly work with the formulation (1) without specifying functional forms for \( S, G, M \) and without knowledge about stationary point locations, only assuming the existence of one stationary point. This step is a crucial change of the viewpoint commonly used in applied dynamical systems. In fact, by not making detailed assumptions about the functional forms the generalized modelling approach allows us to treat entire classes of model systems simultaneously.

The conclusions we obtain are still immediately applicable to biological and physical systems since the bifurcation analysis carried out will be based on a set of parameters that have interpretations in the context of the model class considered [22].

Previous works on generalized models [17, 15, 55] focused on analyzing the dynamics close to stationary states. Beyond the structure of the equations (1) this analysis requires only the assumption that steady states exist in the class of models under consideration. The central idea of generalized modeling is to parametrize all possible Jacobians that can be encountered in steady states in the class of systems under consideration. Using a specific renormalization procedure, one can define parameters that are not only easily interpretable but often also directly measurable in applications.

Applications of generalized models to ecology can be found in various contexts. In [21, 51] the stability of low-dimensional food chain networks is investigated. Chaotic dynamics in food webs is considered in [20] and enrichment is discussed in [19]. Equivalence and coarse-graining via generalized models is proposed in [23] while pattern-forming bifurcations in spatial predator-prey partial differential equations are treated in [3]. Statistical techniques for generalized modelling have been employed to reveal stabilizing factors in large food webs by sampling, and analyzing the stability, of several billion food webs [24]. We remark that this study is also a main motivation for our algorithmic approach to nonlocal generalized models in this paper developed in Section 8. The stability of producer-grazer systems is studied in [52]. Generalized models have also found applications in other branches of mathematical biology such as gene networks [15] and systems biology [50]. An elementary introduction to the concepts of generalized modes in ecology also recently appeared [54].
Let us emphasize that we do not claim that stability results from generalized models have not been observed before in some specific models; in fact, the literature on stability of planar-predator prey systems is very large. For instance, questions of local and global stability have been investigated in various predator-prey systems [16, 28, 53, 42]. We refer the reader to [52, 35] for detailed discussions regarding the relation between specific and generalized models. Furthermore, we already state that we will only be able to draw conclusions about the behaviour near a periodic orbit. Generalized models are focused on the analysis near invariant sets by their construction.

In the present paper we go beyond the previous analysis and study nonstationary dynamics in the context of generalized modeling. Our main contributions are: We extend the theory of generalized models to arbitrary periodic solutions in the context of the predator-prey system (1). The main mathematical result is that the time-periodic generalized parameters of the predator-prey model obey a system of ODEs (a flow on moduli space). Then we apply Floquet theory [9] and Fourier analysis [29] to derive analytical conditions for the solvability of the moduli space flow and prove an analytical stability formula. The stability formula for periodic solutions only depends on two constants that can be calculated via a discrete convolution. This formula is used to identify parameters and conditions that enhance the stability of predator-prey cycles. Furthermore, we develop an algorithmic approach to sample the function space of parameters by solving an auxiliary optimization problem. This algorithm yields further conclusions about stability of predator-prey cycles and will also be instrumental for future applications to larger systems.

The paper is structured as follows: In Section 2, we recall the necessary tools from steady-state generalized models, Floquet theory, and Fourier analysis. In Section 3, we calculate the generalized vector field for non-equilibrium solutions. In Section 4, we derive the flow on moduli space. In Section 5, we compute the generalized scale and elasticity functions for several specific functional forms. In Section 6, we derive algebraic conditions from the moduli space flow. In Section 7, we provide an analytical stability analysis of periodic orbits and use this result to identify which situations increase or decrease stability. In Section 8, we develop a sampling technique for generalized scale and elasticity functions based on solving an auxiliary optimization problem and the Fast Fourier Transform. We use this sampling-based approach to improve our understanding of stabilizing and destabilizing factors of the predator-prey system. In Section 9, we conclude with a brief summary and outline the large range of applications and theoretical challenges in non-equilibrium generalized models.

2. Background. In this section we introduce essential tools and techniques that will be used throughout this work and fix the notation. Below, we denote a general ordinary differential equation ODE by

$$\frac{dZ}{dt} = Z' = F(Z), \quad \text{for } Z \in \mathbb{R}^N$$

and assume always that $F$ is sufficiently smooth.

2.1. Generalized models. We start by reviewing generalized modeling [22, 35] for ODEs with equilibrium points in the context of a planar predator-prey system [23]. Such systems describe the interaction of a population of prey $X$ and a population
of predators $Y$. The prey population grows at rate $S(X)$, predation occurs at rate $G(X, Y)$ and natural mortality of the predator at rate $M(Y)$. Denoting the prey density as $X$ and predator density as $Y$ we capture the dynamics by

$$
X' = S(X) - G(X, Y),
Y' = G(X, Y) - M(Y),
$$

where $S, M \in C^r(\mathbb{R}^+, \mathbb{R}^+)$ and $G \in C^r(\mathbb{R}^+ \times \mathbb{R}^+, \mathbb{R}^+)$ are sufficiently smooth functions. Generalized modeling assumes that (3) admits at least one equilibrium point $(X, Y) = (X^*, Y^*) \in \mathbb{R}^+ \times \mathbb{R}^+$; note that for this paper we exclude the case $\mathbb{R}_0^+$ which is discussed in [35].

We normalize the equilibrium defining new coordinates

$$
x := \frac{X}{X^*} \quad \text{and} \quad y := \frac{Y}{Y^*}.
$$

This transformation moves the equilibrium to $(x, y) = (1, 1)$. The next step is to normalize the rate functions

$$
s(x) := \frac{S(X^*)}{S(X^*)}, \quad g(x, y) := \frac{G(X^*x, Y^*, y)}{G(X^*, Y^*)}, \quad m(y) := \frac{M(Y^*)y}{M(Y^*)}
$$

where the notation indicates on which term in (3) the normalized functions depend. A direct substitution of (4)-(5) into (3) gives

$$
x' = \frac{S(X^*)}{X^*} s(x) - \frac{G(X^*x, Y^*, y)}{Y^*} g(x, y),
y' = \frac{G(X^*, Y^*)}{X^*} g(x, y) - \frac{M(Y^*)y}{Y^*} m(y),
$$

where the prefactors of the form $S(X^*)/X^*$, $G(X^*, Y^*)/X^*$, etc. represent normalized fluxes in the steady state and are also called scale parameters

$$
\beta_s := \frac{S(X^*)}{X^*}, \quad \beta_1 := \frac{G(X^*, Y^*)}{X^*}, \quad \beta_2 := \frac{G(X^*, Y^*)}{Y^*}, \quad \beta_m := \frac{M(Y^*)}{Y^*}
$$

where now the subscripts indicate the dependence of the scale parameters on the respective gain and loss terms appearing in (3). Since $(x, y) = (1, 1)$ is an equilibrium point we know that the following holds:

$$
0 = \frac{S(X^*)}{Y^*} s(1) - \frac{G(X^*x, Y^*, y)}{Y^*} g(1, 1) = \beta_s - \beta_1,
0 = \frac{G(X^*, Y^*)}{Y^*} g(1, 1) - \frac{M(Y^*)y}{Y^*} m(1) = \beta_2 - \beta_m.
$$

Therefore (6) can be re-written as

$$
x' = \beta_1 (s(x) - g(x, y)),
y' = \beta_2 (g(x, y) - m(y)).
$$

The Jacobian at the equilibrium $(x, y) = (1, 1)$ is then given by

$$
J(1, 1) = \begin{pmatrix}
\beta_1 \frac{\partial_x[s(x) - g(x, y)]}{s(x)} |_{x=1} & -\beta_1 \frac{\partial_y[g(x, y)]}{g(x, y)} |_{y=1} \\
\beta_2 \frac{\partial_x[g(x, y)]}{g(x, y)} |_{x=1} & \beta_2 \frac{\partial_y[g(x, y) - m(y)]}{g(x, y) - m(y)} |_{y=1}
\end{pmatrix}
$$

where $\partial_x, \partial_y$ denote partial derivatives and we refer to the constants

$$
s_x = \partial_x(s(x)) |_{x=1}, \quad g_x = \partial_x(g(x, y)) |_{x=1}, \quad m_y = \partial_y(m(y)) |_{y=1},
g_y = \partial_y(g(x, y)) |_{x,y=1},
$$

as elasticities. The scale parameters and elasticities are also referred to as generalized parameters.
In ecological terms we can also interpret the generalized parameters $\beta_1, \beta_2, s_x, g_x, g_y, m_y$. The scale parameters are per capita gain and loss rates, or turnover rates, for prey and predator. The elasticities also have the interpretation of sensitivities [22, 35] in the steady state. The parameter $s_x$ is the sensitivity of prey growth dependent upon prey abundance. If $s_x = 0$ the prey growth is basically limited by external factors and it is insensitive to the actual prey density. Increasing $s_x$ yields higher sensitivity up to the classical value $s_x = 1$ where the prey growth depends linearly upon prey density and predation is the important limiting factor. The parameter $m_y$ is the sensitivity of the mortality of the predator and $g_x$ and $g_y$ are the sensitivities for the predation term. For even more detailed ecological interpretations see [23, 19].

Also, we are going to use the insight that every power law function corresponds to an elasticity that is identical to the exponent of the power law. For example, if we assume that the mortality $M(Y)$ is a linear function $M(Y) = KY$ then we find

$$m_y = \partial_y \left( \frac{M(Y^s y)}{M(Y^s)} \right) \bigg|_{y=1} = \partial_y \left( \frac{KY^s y}{KY^s} \right) \bigg|_{y=1} = 1.$$ 

Hence we can relate the growth properties of the unspecified functions forms to the elasticities. Let us also point out that conventional models and generalized models can be related as presented in [52] for a producer-grazer system; additional explanations of this relation can be found in [35].

The stability of the equilibrium $(x, y) = (1, 1)$ can be inferred from the eigenvalues of $J(1, 1)$ and hence only depends on the generalized parameters. This admits a bifurcation analysis of all steady state models of the form (3) in generalized parameter space. Despite the large class of models that one treats simultaneously it is often easy to interpret scale parameters and elasticities in other applications as well [22]. Thereby a generalized model enables us to draw conclusions about a whole class of differential equations, for further examples see [24, 49, 44, 15].

2.2. Floquet theory. Suppose (2) has a period orbit $\gamma(t) = \gamma(t + T)$ where $T$ is the minimal period $T = \inf\{S > 0 : \gamma(t + S) = \gamma(t)\}$. Let $\Sigma$ denote a suitable $(N-1)$-dimensional transversal transversal section to $\Gamma$ and consider the associated Poincaré map $P : \Sigma \to \Sigma$. This map has a fixed point $X_\gamma \subset \Sigma$ associated to the periodic orbit $\gamma$ i.e. $P(X_\gamma) = X_\gamma$. Recall [10, 36] that the stability of $\gamma$ is determined by the $N-1$ eigenvalues (or characteristic/Floquet multipliers) $\lambda_1, \ldots, \lambda_{N-1}$ of the matrix $DP(X_\gamma)$. If $|\lambda_j| < 1$ for all $j \in \{1, \ldots, N-1\}$ then the periodic orbit is stable, if there exists $\lambda_j$ such that $|\lambda_j| > 1$ then the orbit is unstable and eigenvalues with $|\lambda_j| = 1$ signal bifurcations under parameter variation. We can study the stability of $\gamma$ by considering the non-autonomous linear variational equation

$$v' = DF(\gamma(t))v =: A(t)v$$ (12)

where $A(t)$ is periodic. An $N \times N$ matrix $M(t)$ that satisfies

$$M' = A(t)M \quad \text{with} \quad M(0) = \text{Id}$$ (13)

is called the fundamental matrix solution of (12). The constant matrix $M(T)$ is called the monodromy (or circuit) matrix. It has eigenvalues

$$1, \lambda_1, \lambda_2, \ldots, \lambda_{N-1}$$

where the trivial eigenvalue 1 is associated to the direction tangent to the periodic orbit that links the variational equation to the Poincaré map $P$. Furthermore, the
Liouville formula (see e.g. [36, p.30])

\[ \lambda_1 \lambda_2 \cdots \lambda_{N-1} = \det M(T) = \exp \left( \int_0^T \text{Tr}(A(t))dt \right) \]  

holds. An elegant explicit formula for the Floquet multiplier from (14) is only available for \( N = 2 \). In general the computation of Floquet multiplier thus requires numerical approaches, which typically start with computing the periodic solution with a suitable boundary value method such as collocation or finite differences [36, 11].

The variational equation (13) is solved on suitable sub-intervals of the periodic orbit discretization as an initial value problem to obtain \( M(T) \). The eigenvalues of \( M(T) \) are then obtained yielding the Floquet multipliers. Although, in certain circumstances, such as large multipliers, the computation can be numerically problematic [12, 39].

Let us point out that Floquet theory has not been widely applied in the context of ecology [31] although it is a standard tool in the mathematical theory of dynamical systems [10]. Klausmeier [31] suggests that “Floquet theory is a useful tool for studying the effects of temporal variability on ecological system”.

2.3. Fourier series. We briefly recall basic facts about Fourier series to fix normalization constants and notation. Assume that \( f: \mathbb{R} \to \mathbb{R} \) is \( T \)-periodic so that we can identify the domain of \( f \) as the circle \( \mathbb{R}/(T\mathbb{Z}) \cong S^1 \). We formally write the complex Fourier series \( F[f] \) of \( f \) as follows:

\[ F[f](t) = \sum_{k=-\infty}^{\infty} \hat{f}(k) \exp \left( \frac{2\pi ikt}{T} \right) \]  

where the Fourier coefficients \( \hat{f}(k) \) are

\[ \hat{f}(k) = \frac{1}{T} \int_0^T f(s) \exp \left( -\frac{2\pi iks}{T} \right) ds. \]

Observe that \( \hat{f}(k) = \overline{\hat{f}(-k)} \), where the overbar denotes complex conjugation. Further, \( \hat{f}(0) = 1/T \int_0^T f(t)dt \) is the time average of the periodic function. The convergence question \( F[f](t) \to f(t) \) is extremely intricate depending on the properties of \( f \) [56, 29]. In the following, all functions we are going to approximate by Fourier series will be in \( C^r(S^1, \mathbb{R}) \) for some sufficiently large \( r \) or even \( r = \infty \). In this case, uniform convergence is immediate. A very important practical result in this context is to control the Fourier coefficients.

Theorem 2.1 (see [29]). If \( f \in C^r(S^1, \mathbb{R}) \) then \( |\hat{f}(k)| = \mathcal{O}(k^{-r}) \) as \( |k| \to \infty \).

Theorem 2.1 is a version of the Riemann-Lebesgue Lemma for smooth functions and can provide an extremely rapid decay of the Fourier coefficients. This justifies (for the smooth case!) dropping higher-order terms \( |k| > \kappa \) for some rather small suitable \( \kappa \in \mathbb{N} \). The remaining sum is expected to be a good approximation to the original periodic function \( f \). We write

\[ F_\kappa[f](t) := \sum_{|k| \leq \kappa} \hat{f}(k) \exp \left( \frac{2\pi ikt}{T} \right) \approx f(t). \]
Another important tool in Fourier analysis we will need are convolutions. Recall that the discrete convolution of two periodic functions \( f \) and \( g \) is defined as
\[
(f * g)(n) = \sum_{k=-\infty}^{\infty} f(k)g(n-k).
\]
Obviously the convolution operator \( * \) is associative, commutative and distributive.

3. **Non-equilibrium planar predator-prey systems.** We return to the planar predator-prey system (3) from Section (2.1) given by
\[
X' = S(X) - G(X, Y), \quad Y' = G(X, Y) - M(Y).
\]  
Denote the vector field of (16) by \( F(X, Y) \). The vector field is only considered on the first (positive) quadrant \( F : \mathbb{R}^+ \times \mathbb{R}^+ \to \mathbb{R}^2 \) as predator-prey densities are assumed to be non-negative.

We want to analyze the class of vector fields (16) under the assumption that it admits a non-equilibrium orbit that is bounded as \( |t| \to \infty \). A simple, but still non-trivial and interesting choice, are so-called predator-prey limit cycles. We assume that (16) has at least one periodic orbit \( \gamma(t) = (\gamma_1(t), \gamma_2(t)) \) with period \( T \). The definition of the model implies that \( \gamma_i > 0 \) for \( i \in \{1, 2\} \) and all \( t \).

In the following, we are going to slightly extend the notation employed already in Section (2.1) by re-using names for variables and generalized parameters. As in the case of equilibria one can consider a normalizing coordinate change
\[
x := \frac{X}{\gamma_1}, \quad y := \frac{Y}{\gamma_2}
\]
which maps the periodic orbit to the point \( (x, y) = (1, 1) =: 1 \). The ODEs (16) and the product rule imply
\[
X' = x'\gamma_1 + x\gamma'_1 = x'\gamma_1 + xF_1(\gamma) = S(x\gamma_1) - G(x\gamma_1, y\gamma_2), \\
Y' = y'\gamma_2 + y\gamma'_2 = y'\gamma_2 + yF_2(\gamma) = G(x\gamma_1, y\gamma_2) - M(y\gamma_2).
\]
Therefore the new equations can be written as
\[
x' = \frac{\gamma_1}{\gamma_2} (S(x\gamma_1) - G(x\gamma_1, y\gamma_2) - xF_1(\gamma)) \\
y' = \frac{\gamma_2}{\gamma_1} (G(x\gamma_1, y\gamma_2) - M(y\gamma_2) - yF_2(\gamma))
\]  
(17)
In analogy to the equilibrium case we introduce normalized functions
\[
s(x) := \frac{S(x\gamma_1)}{S(\gamma_1)}, \quad g(x) := \frac{G(x\gamma_1, y\gamma_2)}{G(\gamma_1, \gamma_2)}, \quad m(y) := \frac{M(y\gamma_2)}{M(\gamma_2)}
\]  
(18)
where, as in Section (2.1), the notation indicates on which terms of the original model (16) the normalized functions depend. Then we define the scale parameters
\[
\beta_s(t) := \frac{S(\gamma_1(t))}{\gamma_1(t)}, \quad \beta_1(t) := \frac{G(\gamma_1(t), \gamma_2(t))}{\gamma_1(t)}, \quad \beta_2(t) := \frac{G(\gamma_1(t), \gamma_2(t))}{\gamma_2(t)}, \quad \beta_m(t) := \frac{M(\gamma_2(t))}{\gamma_2(t)}
\]  
(19)
which are now time-dependent \( T \)-periodic scale functions; subscripts indicate the dependence in the notation for the scale functions. We will often suppress the time-dependence in the notation and just write, for instance, \( \beta_s \) instead of \( \beta_s(t) \). Using
\[ x' = \beta_1[s(x) - x] - \beta_4[g(x, y) - x], \]
\[ y' = \beta_2[g(x, y) - y] - \beta_3[m(y) - y]. \]  

(20)

For applying Floquet theory we linearize (20) around the limit cycle which yields the matrix \( A(1; t) = \)
\[ \begin{pmatrix}
\frac{\partial_x(s(1) - 1)}{(\partial_x g)(1)} & -(\partial_y g)(1) \\
\frac{\partial_y g)(1)}{\partial x g)(1)} & \frac{\partial_y g)(1) - 1 - \beta_m[(\partial_x m)(1) - 1] \\
\end{pmatrix}. \]

We can re-write \( A(1; t) \) in terms of the more familiar elasticities, leading to \( A(1; t) = \)
\[ \begin{pmatrix}
\beta_1[s_x(t) - 1] - \beta_1[(\partial_x g)(1) - 1] & -g_y(t) \\
g_x(t) & \beta_2(t)[g_y(t) - 1 - \beta_m(t)m_y(t) - 1] \\
\end{pmatrix} \]

where the four time-dependent \( T \)-periodic elasticity functions are
\[ s_x(t) := (\partial_x s)(1), \quad g_x(t) := (\partial_x g)(1), \quad g_y(t) := (\partial_y g)(1), \quad m_y(t) := (\partial_y m)(1). \]

The periodicity and time-dependence becomes more apparent once we write out the detailed definitions, for example
\[ s_x(t) = (\partial_x s)(1) = \partial_x \left( \frac{S(x\gamma_1)}{S(\gamma_1)} \right) \big|_{x=1} = \frac{\gamma_1 S'(\gamma_1)}{S(\gamma_1)}. \]

The previous calculations show that we can introduce replacements for the generalized parameters for equilibrium points in the context of periodic orbits. In particular, the scale parameters and elasticities become time-dependent and periodic. For planar systems the stability of the periodic orbit is determined by computing the only non-trivial Floquet multiplier \( \lambda \). Liouville’s formula (14) implies that
\[ \lambda = \exp \left( \int_0^T \beta_x(s_x - 1) - \beta_1(g_x - 1) + \beta_2(g_y - 1) - \beta_3(m_y - 1) dt \right). \]

We can thus express the Floquet multiplier as a function depending on elasticity and scale functions. This is analogous to writing the eigenvalues of the Jacobian as functions of the generalized parameters in the equilibrium case.

4. The moduli space flow. In analogy to the generalized exploration of local dynamics, the stability of the limit cycle can be studied by assuming plausible values for the generalized parameters (here, scale and elasticity functions). The value of generalized models lies in their ability to cover the whole range of possibilities that are plausible in the system. For an unbiased analysis it is essential that we consider only those values of parameters that are consistent with the set up of the system. For instance, in case of equilibrium generalized models we must demand that the parameter values which we assume do not preclude the existence of an equilibrium solution in the class of systems. Likewise, only those scale and elasticity functions should be considered which are mutually consistent and thus could arise in at least one example system in the class of models under consideration. To understand this problem we briefly go back to the equilibrium scenario (see Section 2.1). Suppose we just choose a set of generalized parameters
\[ \beta_1 = \beta_1^*, \quad \beta_2 = \beta_2^*, \quad s_x = s_x^*, \quad g_x = g_x^*, \quad g_y = g_y^*, \quad m_y = m_y^*, \]

(22)

where we assume that all parameters are positive. One natural question is if there exist specific functions \( S, G \) and \( M \) that lead to the generalized parameters (22).
Proposition 4.1. Suppose (22) are given positive generalized parameters. Then there exist functions $S$, $G$, $M$ and an equilibrium $(X, Y) = (X^*, Y^*)$ for (3) so that (7) and (11) hold i.e. there exists a differential equation of the form (3) that has the given set of generalized parameters.

Proof. Pick $M(Y) = p_1 Y^{m_y}$ for some $p_1 \in \mathbb{R}^+$ then $m_y = \partial_y(M(Y^*)/M(Y^*))|_{y=1} = m_y^*$. Similarly we pick $S(X) = p_2 X^{s_x^*}$ and obtain $s_x = s_x^*$. Using a slight modification of this approach we define $G(X, Y) = X^{g_x^*}Y^{g_y^*}$ and get $g_y = g_y^*$ as well as $g_y = g_y^*$. We also must have $\beta_s = \beta_1 = \beta_1^*$ and $\beta_m = \beta_2 = \beta_2^*$ which translates into the conditions

\[
\beta_1 \begin{cases} \text{(C1)} & p_1(X^*)^{s_x-1} = (X^*)^{g_x-1}(Y^*)^{g_y}, \\
\text{(C2)} & p_2(Y^*)^{m_y-1} = (X^*)^{g_x}(Y^*)^{g_y-1}. 
\end{cases}
\]

We can always choose $p_1$ and $p_2$ to satisfy (C2) and (C4). Then we can use $X^*$ and $Y^*$ to satisfy (C1) and (C3). The result follows. □

For non-equilibrium systems the situation is different since one has to ask whether a whole set of given functions

\[
\beta_s(t), \beta_m(t), \beta_1(t), \beta_2(t), s_x(t), g_x(t), g_y(t), m_y(t),
\]

can potentially arise from a system of the form (16).

Theorem 4.2. Suppose we are given elasticity functions $s_x$, $m_y$, $g_x$ and $g_y$ then the scale functions have to satisfy the following set of ODEs

\[
\begin{align*}
\beta_s' &= \beta_s(\beta_s - \beta_2)(s_x - 1), \\
\beta_m' &= \beta_m(\beta_2 - \beta_m)(m_y - 1), \\
\beta_1' &= \beta_1((\beta_s - \beta_1)g_x - (\beta_s - \beta_1) + (\beta_2 - \beta_m)g_y), \\
\beta_2' &= \beta_2((\beta_2 - \beta_m)g_y - (\beta_2 - \beta_m) + (\beta_s - \beta_1)g_x).
\end{align*}
\]

Proof. We start by deriving the equation for $\beta_s$. We know that $\beta_s = S(\gamma_1)/\gamma_1$ and direct differentiation with respect to time via the quotient and chain rules gives

\[
\beta_s' = \frac{\gamma_1 \gamma_1' S'(\gamma_1) - S(\gamma_1) \gamma_1'}{(\gamma_1)^2} = \frac{\gamma_1 \gamma_1' S'(\gamma_1)S(\gamma_1) - S(\gamma_1) \gamma_1'}{(\gamma_1)^2} - \frac{\gamma_1 \gamma_1'}{\gamma_1}
\]

Noting that $s_x = \gamma_1 S'(\gamma_1)/S(\gamma_1)$ and using the definition of $\beta_s$ the equation transforms to

\[
\beta_s' = \frac{s_x \gamma_1' S(\gamma_1) - S(\gamma_1) \gamma_1'}{(\gamma_1)^2} = \frac{s_x \gamma_1' \beta_s}{\gamma_1} - \frac{\beta_s \gamma_1'}{\gamma_1} = \beta_s(s_x - 1) \frac{\gamma_1'}{\gamma_1}.
\]

Since $(\gamma_1, \gamma_2)$ is a trajectory of (16) we must have $\gamma_1' = S(\gamma_1) - G(\gamma_1, \gamma_2)$. This implies upon substitution into (24) that

\[
\beta_s' = \beta_s(s_x - 1) \frac{S(\gamma_1) - G(\gamma_1, \gamma_2)}{\gamma_1} = \beta_s(s_x - 1)(\beta_s - \beta_1)
\]
which is the first equation in (23). The calculation for $\beta''_m$ is similar. For $\beta'_1$ we find

$$
\beta'_1 = \frac{\gamma_1 G_x(\gamma_1, \gamma_2)\gamma'_1 + G_y(\gamma_1, \gamma_2)\gamma'_2 - \gamma'_1 G(\gamma_1, \gamma_2)}{(\gamma_1)^2}
$$

$$
= \frac{\gamma_1 G_x(\gamma_1, \gamma_2)\gamma'_1}{G(\gamma_1, \gamma_2)\gamma_1^2} + \frac{\gamma_1 G_y(\gamma_1, \gamma_2)\gamma'_2}{G(\gamma_1, \gamma_2)\gamma_2} - \frac{\gamma'_1 G(\gamma_1, \gamma_2)}{(\gamma_1)^2}
$$

$$
= g_x \beta_1 \frac{\gamma'_1}{\gamma_1} + g_y \beta_1 \frac{\gamma'_2}{\gamma_2} - \beta_1 \frac{\gamma'_1}{\gamma_1}
$$

$$
= \beta_1 (g_x (\beta_s - \beta_1) + g_y (\beta_2 - \beta_m) - (\beta_s - \beta_1))
$$

The calculation for $\beta'_2$ is similar to the one for $\beta'_1$.

The main conclusion is that the elasticities and scale functions which parameterize the ODE (20) satisfy an ODE themselves. Because one often uses the terms “parameters” and “moduli” interchangeably, Theorem 4.2 implies that the time-dependent parameters of generalized models generate a flow on moduli space.

**Remark.** The term “moduli space” is most commonly used in algebraic geometry which, broadly speaking, is the study of solutions of algebraic equations [26, 27]. The solutions form algebraic varieties (e.g., curves). Often suitable parametrized families of algebraic varieties again have the structure of an algebraic variety, where the latter object is the moduli space of parametrized families. The study of the geometry of moduli spaces has also been transported into different branches of physics such as quantum field theory [1]. In dynamical systems theory, a classical moduli space argument is made in the renormalization analysis of parametrized families one-dimensional maps [25], where the renormalization transformation can be viewed as a map generating a dynamical system on moduli space. A very similar situation occurs for billiard dynamics where the so-called Teichmüller flow on the space of lattices appears [47, 40].

We note that the positive quadrant is an invariant set for (23) which means that this property lifts from the predator-prey family of vector fields to the moduli space. From Theorem 4.2 we can immediately infer a necessary condition for the existence of a generalized model with given elasticities.

**Corollary 4.3.** Suppose $s_x$, $m_y$, $g_x$ and $g_y$ are given $T$-periodic elasticity functions with minimal period $T$. If (23) has no $T$-periodic solutions then there exists no generalized model of the form (16) for the given elasticities.

Observe that for the equilibrium case the conditions $\beta_1 = \beta_s$ and $\beta_2 = \beta_m$ give $\beta'_s = \beta'_m = \beta'_1 = \beta'_2 = 0$ consistent with steady state generalized modeling. It is also interesting to ask what happens if we do not specify the elasticities. Taking the idea of deriving a differential equation one step further we consider

$$
s_x = \frac{\gamma_1 S'(\gamma_1)}{S(\gamma_1)} \Rightarrow s'_x = S(\gamma_1)\frac{\gamma_1 S'(\gamma_1) + \gamma_1 \gamma'_1 S''(\gamma_1)}{S(\gamma_1)^2} - \gamma_1 S'\gamma'_1 S'(\gamma_1)
$$

Applying similar substitutions as in the proof of Theorem 4.2 we obtain

$$
s'_x = \frac{S(\gamma_1)\gamma_1 S'(\gamma_1) + \gamma_1 \gamma'_1 S''(\gamma_1)}{S(\gamma_1)^2} - \frac{\gamma'_1}{\gamma_1}s_x = s_x \left(\frac{1}{\beta_s} (\beta_s - \beta_1) + \frac{1}{\beta_s} S''(\gamma_1)\right).
$$
also occurs in the context of moment closure for networks \cite{30,18} and for moment equations of stochastic differential equations \cite{48,14}.

5. \textbf{Specific functions.} To get a better understanding of the stability of non-equilibrium generalized models and the flow on moduli space we proceed to calculate the generalized elasticity and scale functions for several well-known predator-prey models. All the model parameters \(k_l\) (for \(l \in \mathbb{N}\)) we are going to use below are positive due to modeling considerations. We start with the growth of the prey \(S(X)\). Typical choices are

\[
\begin{align*}
S(X) &= k_1 X, \quad \text{(linear growth)}, \tag{24} \\
S(X) &= k_1 X^p, \quad \text{(power growth)}, \\
S(X) &= k_1 X - k_2 X^2, \quad \text{(logistic growth)}, \\
S(X) &= k_1 X(k_2 - X)(X - k_3), \quad \text{(strong Allee effect), } 0 < k_2 < k_3.
\end{align*}
\]

We start by looking at linear growth. We find

\[
\beta_s = \frac{S(\gamma_1)}{\gamma_1} = k_1, \quad s_x = \partial_x \left( \frac{S(x \gamma_1)}{S(\gamma_1)} \right) \bigg|_{x=1} = 1.
\]

For estimating the impact of linear growth on stability we consider the formula \eqref{21} and view it as a product of exponentials. The term involving \(\beta_s\) and \(s_x\) is

\[
\exp \left( \int_0^T \beta_s [s_x - 1] dt \right). \tag{25}
\]

Therefore, a linear prey growth does not contribute to the non-trivial Floquet multiplier because \(s_x = 1\) and \(\exp(\int_0^T 0 dt) = 1\). Different types of polynomial growth with a single term can be treated analogously since for \(S(X) = k_1 X^p\) we find

\[
\beta_s = \frac{S(\gamma_1)}{\gamma_1} = k_1 \gamma_1^{p-1}, \quad s_x = \partial_x \left( \frac{S(x \gamma_1)}{S(\gamma_1)} \right) \bigg|_{x=1} = p.
\]

where the elasticity function coincides with the result for equilibrium generalized models. This allows us to write

\[
\beta_s [s_x - 1] = k_1 \gamma_1^{p-1} [p - 1].
\]

Considering \eqref{25} we find that increasing \(p\) increases the Floquet multiplier and therefore has always a destabilizing effect, whereas decreasing \(p\) has a stabilizing effect. For logistic growth we obtain

\[
\beta_s = \frac{S(\gamma_1)}{\gamma_1} = k_1 - k_2 \gamma_1, \quad s_x = \partial_x \left( \frac{S(x \gamma_1)}{S(\gamma_1)} \right) \bigg|_{x=1} = 2 + \frac{k_1}{-k_1 + k_2 \gamma_1}.
\]

This implies

\[
\beta_s [s_x - 1] = (k_1 - k_2 \gamma_1) \left[ 2 + \frac{k_1}{-k_1 + k_2 \gamma_1} - 1 \right] = -k_2 \gamma_1. \tag{26}
\]

Considering \eqref{25} again we find

\[
\exp \left( \int_0^T \beta_s [s_x - 1] dt \right) = \exp \left( \int_0^T -k_2 \gamma_1 dt \right) = \exp \left( -k_2 \int_0^T \gamma_1 dt \right)
\]
where the integral is positive because $k_2 > 0$. This means that increasing $k_2$ or increasing $\int_0^T \gamma_1(t) dt$ will promote stability as the Floquet multiplier will move closer to 0. For logistic growth increasing $k_2$ corresponds to decreasing the carrying capacity $k_1/k_2$ of the population. This can be interpreted as a manifestation of the paradox of enrichment [45, 19] which captures the observation that increasing the carrying capacity generally has a destabilizing effect on attractors observed in ecological models. Furthermore, the expression obtained for logistic growth permits discussion of the contribution of the shape of the limit cycle to stability. For $t \in [\delta_1, T - \delta_2]$, where $\delta_{1,2} > 0$ are small, we find that

$$0 < \gamma_1(t) \ll 1 \quad (27)$$

which implies that the integral $\int_0^T \gamma_1(t) dt$ is small as well. In this case the limit cycle is only weakly stable (or weakly hyperbolic). It is well-known that noise effects can lead to large spreading of possible system states [34] in regimes of weak hyperbolicity which leads to a high extinction probability. Therefore limit cycles where the number of prey is extremely small for long times are not expected to be a basis for a stable ecological system.

For the functional form of growth with strong Allee effect from equation (24) we find

$$\beta_s[sx - 1] = k_1(k_2 - \gamma_1)(\gamma_1 - k_3) \left[ 1 + \gamma_1 \left( \frac{1}{\gamma_1 - k_2} + \frac{1}{\gamma_1 + k_3} \right) - 1 \right] = k_1\gamma_1(k_2 + k_3 - 2\gamma_1). \quad (28)$$

Considering the contribution of this term to the Floquet multiplier yields

$$\exp \left( \int_0^T \beta_s[sx - 1] dt \right) = \exp \left( \int_0^T k_1\gamma_1(k_2 + k_3 - 2\gamma_1) dt \right) = \exp \left( \int_0^T k_1\gamma_1(k_2 + k_3) dt - \int_0^T k_12\gamma_1^2 dt \right).$$

Increasing $k_2$ and/or $k_3$ will decrease stability. This is natural as these parameters represent the threshold to growth and the carrying capacity, providing another example for the paradox of enrichment.

Note that the shape of the limit cycle can influence stability. In particular, the same conclusion to assumption (27) holds. The de-stabilization effect for long periods of low prey density even enters quadratically in the term $\int_0^T k_12\gamma_1^2 dt$. This confirms the intuitive conclusion that imposing a threshold to growth is a de-stabilizing factor for non-equilibrium systems when the prey density is small.

We proceed to consider the mortality of the predator. A very common functional form used in a large number of models is so-called density independent (linear) mortality

$$M(Y) = k_1Y \Rightarrow \beta_m[m_y - 1] = k_1[m_y - 1] = k_1[1 - 1] = 0.$$

Therefore, a linear mortality elasticity coefficient $m_y$ has no effect on the stability of the periodic solution.

The interaction term between prey and predator is usually the most complicated and debated choice for the model. Some common choices are considered in Table 1. The observation that $\beta_2[g_y - 1]$ vanishes for all functions considered in Table 1, can
be directly linked to the ecological assumption that predators hunt independently of each other. The functions that are therefore used in practice are generally linear in the density of predators and the impact of predator dependence on stability vanishes. The same assumption cannot generally be made for prey dependence of predation, leading to more complex expressions for the impact on stability.

Therefore, we are going to make the assumptions of “linear dependence of predation on predator density” and “linear dependence of predator mortality on predator density” given by

\[ g_y = 1 \quad \text{and} \quad m_y = 1 \]  

(29) from now on. Regarding the Floquet multiplier formula (21) the assumptions (29) simplify the situation to investigating

\[ \lambda = \exp \left( \int_0^T \beta_s (s_x - 1) - \beta_1 (g_x - 1) \, dt \right). \]

(30)

The influence of \( g_x \) and \( \beta_1 \) on stability is not obvious since there is a non-trivial interaction with the shape of the limit cycle. The flow on moduli space given by (23) simplifies to

\[ \begin{align*}
\beta_s' &= \beta_s (\beta_s - \beta_1) (s_x - 1), \\
\beta_1' &= \beta_1 ((\beta_s - \beta_1) g_x - (\beta_s - \beta_1) + (\beta_2 - \beta_m)), \\
\beta_2' &= \beta_2 (\beta_s - \beta_1) g_x, \\
\beta_m' &= 0,
\end{align*} \]

(31)

where we can view \( \beta_m \) as a parameter and simply drop the last equation.
Figure 1. Dynamics in a specific example. (a) Stable periodic orbit $\gamma(t)$ of (32) (solid black) and two other trajectories (dashed magenta) with initial conditions marked by stars; the parameters are given in (33). Five points (black dots) are shown on the limit cycle for orientation purposes which are equally spaced over one period. (b) Scale functions in moduli space (black) for $\gamma$ solving (31); a trajectory (solid magenta) with slightly perturbed initial conditions is also shown where the same elasticities as for the periodic orbit were used for numerical integration. (c) Time series of $\beta_s(t)$ for part (b). (d) Time series $\gamma_1$ (solid black) and $\gamma_2$ (dashed black). (e) Scale functions associated to $\gamma$: $\beta_s(t)$ (red), $\beta_m(t)$ (green), $\beta_1(t)$ (blue) and $\beta_2(t)$ (cyan). (f) Elasticity function associated to $\gamma$: $s_x(t)$ (red), $g_x(t)$ (blue) and $g_y(t)$ (green); note that $m_y = 1 = g_y$.

Example 5.1. For gaining an intuitive understanding one can consider the flow on the moduli space in a specific example. The combination of logistic prey growth, Holling-type-II interaction and linear predator mortality gives us the Rosenzweig-MacArthur predator-prey model that can produce periodic solutions

$$
X' = k_1 X - k_2 X^2 - k_3 \frac{XY}{X+k_4}, \\
Y' = k_3 \frac{XY}{X+k_4} - k_5 Y,
$$

(32)

where we use the parameters

$$
k_1 = 2, \quad k_2 = 0.5, \quad k_3 = 1, \quad k_4 = 1, \quad k_5 = 0.5.
$$

(33)

Figure 1 shows that integrating a slightly perturbed initial condition trajectory does seem to diverge from the exact periodic solution in moduli space. Furthermore, even for a classical planar predator-prey system, the scale and elasticity functions are quite complicated for non-equilibrium solutions. In fact, prescribing the elasticities is much more difficult than just picking a set of fixed parameters for equilibrium generalized models.
To verify the necessary condition from Corollary 4.3 for periodic solutions we must ask for solvability of the boundary value problem (BVP)
\[
\begin{align*}
\beta_s & = \beta_s(\beta_s - \beta_1)(s_x - 1), \\
\beta_1 & = \beta_1((\beta_s - \beta_1)g_x - (\beta_s - \beta_1) + (\beta_2 - k_3)), \\
\beta_2 & = \beta_2(\beta_s - \beta_1)g_x, \\
\beta(0) & = \beta(T) \text{ for } T > 0,
\end{align*}
\]
where \(\beta(t) := (\beta_s(t), \beta_1(t), \beta_2(t))\). It is well-known that BVPs have one, many or no solutions [2]. Furthermore determining solvability conditions is usually not easy and even using numerical methods may be dangerous; for example, if a numerical algorithm fails to provide a solution to (34) this may just be due to the numerical problems that can arise when solving BVPs [2].

Let us point out that the results we have discussed in this section are independent of the rest of the manuscript. A generalized analysis can be carried out without ever specifying explicit functional forms. However, we felt that it is good to see how the two approaches relate and which additional assumptions on the scale and elasticity functions one might want to impose due to modelling considerations imposed by the predator-prey application context. In fact, our generalized modelling results obtained throughout this manuscript can always be mapped to any specific predator-prey model as explained in [52] for the stationary case. The logic for the stationary case of mapping bifurcation diagrams carries over to the limit cycle context [52, 35].

6. Fourier decomposition. The previous discussion of specific functions motivates the need for a more concrete version of the moduli space conditions (34) and of the Floquet multiplier (30). The natural step is to use a decomposition of the periodic functions into Fourier series; see Section 2.3. Using discrete convolution we can easily re-write the problem (34) on moduli space.

Proposition 6.1. Suppose we are given \(T\)-periodic elasticity functions \(s_x, m_y, g_x\) and \(g_y\). Then the Fourier coefficients of periodic scale functions have to satisfy the following set of algebraic equations
\[
\begin{align*}
\frac{2\pi i}{T}\beta_s(k) & = [\beta_s * (\beta_s - \beta_1) * (s_x - 1)](k), \\
\frac{2\pi i}{T}\beta_m(k) & = [\beta_m * (\beta_2 - \beta_m) * (g_x - 1)](k), \\
\frac{2\pi i}{T}\beta_1(k) & = [\beta_1 * ((\beta_s - \beta_1) * \hat{g}_x + (\beta_2 - \beta_m) * g_y - (\beta_s - \beta_1))]\beta_1)(k), \\
\frac{2\pi i}{T}\beta_2(k) & = [\beta_2 * ((\beta_s - \beta_1) * \hat{g}_x + (\beta_2 - \beta_m) * g_y - (\beta_2 - \beta_m))]\beta_2)(k),
\end{align*}
\]
for all \(k \in \mathbb{Z}\) where we have also used the notation \(\hat{1}(0) = 1\) and \(\hat{1}(k) = 0\) for \(k \neq 0\) and employed the obvious definition for addition of infinite sequences.

Proof. To complete the proof we only have to recall another basic fact from Fourier analysis. For two \(T\)-periodic functions \(f, g\) we have
\[
f(t)g(t) = \sum_{k=-\infty}^{\infty} \sum_{m=-\infty}^{\infty} \hat{f}(k)\hat{g}(m) e^{\frac{2\pi i (k + m) t}{T}} = \sum_{n=-\infty}^{\infty} \sum_{k=-\infty}^{\infty} \hat{f}(k)\hat{g}(n - k) e^{\frac{2\pi i n t}{T}} = \sum_{n=-\infty}^{\infty} (\hat{f} * \hat{g})(n) e^{\frac{2\pi i n t}{T}}
\]
This formula for Fourier coefficients of products of functions yields the right-hand side of equation (35) as a direct consequence of Theorem 4.2. The left-hand side
of equation (35) follows from direct differentiation which is allowed since all our periodic functions are assumed to be sufficiently smooth; see Section 2.3.

Fig. 2. Absolute value of the first nine Fourier coefficients ($|k| \leq 4$) associated to the stable periodic orbit $\gamma(t)$ of (32); the parameters are given in (33). The coefficients of the phase space coordinates as well as the generalized elasticity and scale functions are shown.

Since (35) is an infinite set of algebraic equations it may look like we have not considerably simplified the problem of finding scale functions that are consistent with prescribed elasticities. However, the rapid decay of Fourier coefficients provided by Theorem 2.1 allows us to approximate the solution of (35) by focusing on the first few harmonics with $|k| \leq \kappa \ll \infty$.

Example 6.2 (Example 5.1 continued). Just for illustration purposes we look a the Fourier coefficients of generalized scale and elasticity functions in an example. Figure 2 shows the results for the Rosenzweig-MacArthur model from Section 5 with $\kappa = 4$. We can clearly see that the Fourier coefficients decay very rapidly; it is also interesting to observe that $\hat{s}_x(k)$ is bimodal for logistic growth whereas the other coefficients show a uni-modal distribution for the first few harmonics. For the Rosenzweig-MacArthur model the algebraic relations (35) on the Fourier coefficients become

\[
\begin{align*}
2\pi ik \hat{\beta}_s(k) &= [\hat{\beta}_s * (\hat{\beta}_s - \hat{\beta}_1) * (\hat{s}_x - \hat{1})](k), \\
2\pi ik \hat{\beta}_1(k) &= [\hat{\beta}_1 * ((\hat{s}_x - \hat{\beta}_1) * \hat{g}_x + (\hat{\beta}_2 - \hat{\beta}_m) - (\hat{s}_x - \hat{\beta}_1))](k), \\
2\pi ik \hat{\beta}_2(k) &= [\hat{\beta}_2 * ((\hat{s}_x - \hat{\beta}_1) * \hat{g}_x)](k).
\end{align*}
\]

(36)

Figure 3 shows the values of the Fourier coefficients for the Rosenzweig-MacArthur example where we see that the algebraic conditions (36) are satisfied as proven in Proposition 6.1. Furthermore, it is evident that due to the convolution a wider support $\kappa_M$ is necessary i.e. the algebraic equations (35) must be satisfied for $|k| \leq \kappa_M$ where $\kappa_M > \kappa$ and $\kappa$ is our truncation for the Fourier coefficients of the phase space periodic orbit.
Figure 3. Absolute value of the first seventeen Fourier coefficients ($|k| \leq 17$) for the left-hand and right-hand sides of the algebraic conditions (36); parameter values used are given in (33). The black coefficients (lines shifted slightly left) are the coefficients of the derivatives $\hat{\beta}'_s$, $\hat{\beta}'_1$ and $\hat{\beta}'_2$ and the green coefficients (dashed lines shifted slightly right) are associated to the periodic functions on the right-hand side of (36). The agreement of the two sets of coefficients is clearly visible.

7. **Stability analysis.** For gaining a better understanding of stability we can also use the Fourier series approach to re-express the Floquet multiplier (30) given by

$$
\lambda = \exp \left( \int_0^T \beta_s(s_x - 1) - \beta_1(g_x - 1) + \beta_2(g_y - 1) - \beta_m(m_y - 1) dt \right). \tag{37}
$$

The next results shows how the different Fourier coefficients enter in formula (37).

**Theorem 7.1.** For the non-equilibrium generalized predator-prey model with $g_y = 1 = m_y$ the single Floquet multiplier of a $T$-periodic orbit is given by

$$
\lambda = \exp \left( T \left( \frac{[\hat{\beta}'_s * (\hat{s}_x - 1)](0)}{=; C_1} - \frac{[\hat{\beta}_1 * (\hat{g}_x - 1)](0)}{=; C_2} \right) \right) = \exp(T(C_1 - C_2)) \tag{38}
$$

i.e. whether $|\lambda| > 1$ or $|\lambda| < 1$ depends only on the difference of two zeroth-order Fourier coefficients $C_1$ and $C_2$ that arise from two discrete convolutions.

**Remark.** Before we prove (7.1), we point out that the result is very general and reveals a deep structural property for the stability of periodic predator-prey systems. Only a lowest-order convolution between a canonical set of measured functions along the limit cycle, i.e. between the scale and elasticity functions, determines the stability of the ecological system. Proposition 7.2 below is going to refine this result further by giving an explicit dependence upon averages and higher-order harmonics. These dependencies could never be proven within the framework of a specific model as classical parameter-dependent specific models would lead to myriads of possibilities how the multiplier $\lambda$ depends on system parameters.
Proof. We start by looking at the first summand in integral in (37) which gives
\[
\int_0^T \beta_x(s_x - 1) dt = \int_0^T \sum_{k = -\infty}^{\infty} [\hat{\beta}_x * (\hat{s}_x - \hat{1})](k) e^{2\pi i k t / T} dt
\]
\[
= \sum_{k = -\infty}^{\infty} [\hat{\beta}_x * (\hat{s}_x - \hat{1})](k) \int_0^T e^{2\pi i k t / T} dt
\]
\[
= \begin{cases} 
0 & \text{for } k \neq 0 \\
T [\hat{\beta}_x * (\hat{s}_x - \hat{1})](0) & \text{for } k = 0
\end{cases}
\]
where the last step follows from the fact that \( \int_0^T e^{2\pi i k t / T} dt = 0 \) for \( k \neq 0 \). From this calculation we find \( C_1 \) and in a similar way also \( C_2 \). Using the two factors \( C_{1,2} \) and \( m_y = 1 = g_x \) in (37) the result (38) follows. Since \( T > 0 \) the modulus \( |\lambda| \) only depends on the difference of \( C_1 \) and \( C_2 \); if \( C_1 - C_2 > 0 \) then \( |\lambda| > 1 \) and if \( C_1 - C_2 < 0 \) we obtain \( |\lambda| < 1 \). \( \square \)

Before we consider in more detail the dependency of stability on \( C_1 \) and \( C_2 \) we briefly investigate the influence of the period \( T \). If \( T \gg 1 \) then the period amplifies stability and instability. For example, when \( C_1 - C_2 > 0 \) then a long period moves the multiplier even further away from \( |\lambda| = 1 \) and trajectories near the unstable periodic orbit will escape very quickly. On the other hand, if \( C_1 - C_2 < 0 \) and \( |\lambda| < 1 \) then a very large period \( T \) moves the multiplier even closer to the super-attracting case \( 0 \leq |\lambda| < 1 \). A very short period \( 0 < T < 1 \) has the effect of moving the multiplier very close to \( |\lambda| \approx 1 \). This means that when the periodic orbit is unstable, it will take a very long time to escape from it. The last effect can be interpreted as inducing meta-stability i.e. when the period of the predator-prey cycle is short then the predator-prey system stays near a metastable state for a long time although it is eventually unstable. This could lead to the conjecture that fast oscillations could be beneficial to survival for predator-prey populations during periods when external parameters entering \( C_1 \) and \( C_2 \) drive the system, potentially only temporarily, to a state where \( |\lambda| > 1 \).

We want to understand how the Fourier coefficients of \( \beta_x, \beta_1, s_x \) and \( g_x \) influence \( C_1 \) and \( C_2 \).

**Proposition 7.2.** The two constants \( C_{1,2} \) are given by
\[
C_1 = \hat{\beta}_s(0)(\hat{s}_x(0) - 1) + 2 \sum_{k=1}^{\infty} (\text{Re}[\hat{\beta}_s(k)]\text{Re}[\hat{s}_x(k)] + |\text{Im}[\hat{\beta}_s(k)]| |\text{Im}[\hat{s}_x(k)]|)
\]
\[
C_2 = \hat{\beta}_1(0)(\hat{g}_x(0) - 1) + 2 \sum_{k=1}^{\infty} (\text{Re}[\hat{\beta}_1(k)]\text{Re}[\hat{g}_x(k)] + |\text{Im}[\hat{\beta}_1(k)]| |\text{Im}[\hat{g}_x(k)]|)
\]

**Proof.** Given two sequences \( \{\hat{f}(k)\}_{k=-\infty}^{\infty} \) and \( \{\hat{g}(k)\}_{k=-\infty}^{\infty} \) of Fourier coefficients for two real-valued functions a direct calculation yields
\[
(\hat{f} * \hat{g})(0) = \sum_{k=-\infty}^{\infty} \hat{f}(k)\hat{g}(-k)
\]
\[
= \hat{f}(0)\hat{g}(0) + \sum_{k>0} \hat{f}(-k)\hat{g}(k) + \sum_{k>0} \hat{f}(k)\hat{g}(-k)
\]
\[
= \hat{f}(0)\hat{g}(0) + \sum_{k>0} \hat{f}(k)\hat{g}(k) + \sum_{k>0} \hat{f}(k)\bar{\hat{g}(k)}
\]
where we have used $\hat{f}(-k) = \overline{\hat{f}(k)}$ and the real-valuedness $\bar{f} = f$, $\bar{g} = g$ in the last step. Next, observe that

$$\bar{f}(k)\hat{g}(k) + \hat{f}(k)\bar{g}(k) = 2(\text{Re}[\hat{f}(k)]\text{Re}[\bar{g}(k)] + \text{Im}[\hat{f}(k)]\text{Im}[\bar{g}(k)]).$$

Now the formulas (39)-(40) follow immediately as $\hat{\beta}_s(t)$, $\hat{\beta}_1(t)$, $s_x(t)$ and $g_x(t)$ are all real-valued.

In practice, we never use the infinite sum formulas from Proposition 7.2 but truncate them at a finite order. Using the explicit formulas for $C_1$ and $C_2$ we can directly draw several conclusions regarding periodic solutions depending on generalized scale and elasticity functions (recall: we still use $g_y = 1 = m_y$). If all Fourier coefficients of higher-order $k \geq 1$ are small, then stability of periodic solutions is dominated by the terms

$$C_1 \approx \hat{\beta}_s(0)(\hat{s}_x(0) - 1) \quad \text{and} \quad C_2 \approx \hat{\beta}_1(0)(\hat{g}_x(0) - 1).$$

Since the scale functions are always positive the time averages of the elasticity functions $\bar{s}_x(0)$ and $\bar{g}_x(0)$ determine the signs of $C_1$ and $C_2$. Therefore, average sub-linear elasticity $\bar{s}_x(0) < 1$ and average super-linear conversion $\bar{g}_x(0) > 1$ enhance stability. In ecological terms $0 \leq \bar{s}_x(0) < 1$ means that, on average, the prey growth should be limited by external factors and $\bar{s}_x(0) > 1$ means that, on average, the predation rate should be sensitive to prey abundance; see also [23] for an interpretation of the generalized parameters for the equilibrium case. Both conditions make intuitive sense: if the prey grows without external limitation then solutions may be expected to diverge from a periodic solution and become unbounded while insensitivity of predation to prey growth could potentially drive a system to extinction. Of course, also the inverse relationships hold so that $\bar{s}_x(0) > 1$ and $\bar{g}_x(0) < 1$ act towards de-stabilization. In this context, the scale functions act as amplifiers. For example, if $C_1 < 0$ and $C_2 > 0$ then a large average growth rate $\bar{\beta}_s(0) \gg 1$ and a large conversion rate $\bar{\beta}_1(0) \gg 1$ will enhance stability even more since the Floquet multiplier moves closer to the super-attracting regime $\lambda \approx 0$. In this case, initial conditions will be attracted much quicker to a stable limit cycle. If

$$\hat{\beta}_s(0)(\bar{s}_x(0) - 1) - \hat{\beta}_1(0)(\bar{g}_x(0) - 1) \approx 0 \quad \text{i.e.} \quad \hat{\beta}_s(0)(\bar{s}_x(0) - 1) \approx \hat{\beta}_1(0)(\bar{g}_x(0) - 1)$$

the leading-order terms between growth and predation balance and the stability properties are dominated by higher-order harmonics. The leading-order terms also become irrelevant for elasticity functions which average close to one

$$\bar{s}_x(0) \approx 1 \quad \text{and} \quad \bar{g}_x(0) \approx 1.$$

In this scenario we have to focus on the relations between the higher-order Fourier coefficients of $\beta_s$ and $s_x$ as well as $\beta_1$ and $g_x$. Let us assume for simplicity that $\bar{s}_x(0) = 1 = \bar{g}_x(0)$. Then stability enhancing conditions are

$$C_1 = \sum_{k=1}^{\infty} (\text{Re}[\hat{\beta}_s(k)]\text{Re}[\bar{s}_x(k)] + \text{Im}[\hat{\beta}_s(k)]\text{Im}[\bar{s}_x(k)]) < 0,$$

$$C_2 = \sum_{k=1}^{\infty} (\text{Re}[\hat{\beta}_1(k)]\text{Re}[\bar{g}_x(k)] + \text{Im}[\hat{\beta}_1(k)]\text{Im}[\bar{g}_x(k)]) > 0.$$

Figure 4 depicts several different situations in the complex plane for the first two higher-order harmonics of $\hat{\beta}_s(k)$ and $\hat{s}_x(k)$ ($k = 1, 2$). In Figure 4(a) the first two
Figure 4. Illustration how the location of Fourier coefficients for generalized elasticity and scale functions influence stability. Here we focus on the first two higher-order harmonics (first coefficient = solid line, second coefficient = dashed line) of $\beta_s(t)$ (red) and $s_x(t)$ (blue) which influence the term $C_1$ in Theorem 7.1. (a) $\pi$-phase shift gives $C_1 < 0$. (b) Small phase shift gives $C_1 > 0$. (c) Competition between first- and second-order harmonics.

higher-harmonics are in “anti-phase” so that the angles between the coefficients are separated by $\pi$. This means that

$$\text{Re}[\hat{\beta}_s(k)]\text{Re}[\hat{s}_x(k)] < 0 \quad \text{and} \quad \text{Im}[\hat{\beta}_s(k)]\text{Im}[\hat{s}_x(k)] < 0$$

for $k = 1, 2$. In such a situation, we expect that $C_1 < 0$ by disregarding higher orders so that stability is enhanced.

Figure 4(b) shows the situation where there is only a small phase difference between the coefficients (“in-phase”) which gives

$$\text{Re}[\hat{\beta}_s(k)]\text{Re}[\hat{s}_x(k)] > 0 \quad \text{and} \quad \text{Im}[\hat{\beta}_s(k)]\text{Im}[\hat{s}_x(k)] > 0.$$ 

There is also a possible situation where a competition between the different order harmonics arises as illustrated in Figure 4(c). We can now also give an ecological interpretation of these conditions. Stability $C_1 < 0$ is enhanced if $s_x(t)$ and $\beta_s(t)$ oscillate with a phase separation near $\pi$ which means that a period of high sensitivity of prey abundance should coincide with a period of low prey growth and vice versa. Note that these conditions also make sense intuitively and suggest that prey growth is most efficient if there is a small number of prey and there are no limiting factors from the environment. Similar considerations also apply to the stability enhancing condition $C_2 > 0$. A small phase separation between $\beta_1(t)$ and $g_x(t)$ increases stability of the predator-prey limit cycle. Observe that $g_x(t)$ can be interpreted as the dependence of predation on prey abundance and $\beta_1(t)$ as a predation rate (normalized by the total number of prey) [23]; the stability conditions mean that a high predation rate should coincide with a high dependence of predation on prey abundance. In other words, if the dominating factor to prey abundance is predation then it is good for the predator to hunt a lot to increase stability of the limit cycle.

It is also very important to notice, as already indicated briefly in Section 5, that once the dependence of the Floquet multiplier on parameters is classified by the generalized parameters, we can also draw conclusions about the extinction probability for stochastic predator-prey models with additive noise. To see this, let us point out that the extension to stochastic differential equations for generalized models is
discussed in [35] and the results carry over immediately to the nonlocal context for additive noise; this is a direct consequence of the Itô formula. The classical argument for extinction of species in periodic predator-prey systems is that a stochastic perturbation can lead to large deviations ending in the zero population level [33]. The crucial point is that with a very small Floquet multiplier $|\lambda| \ll 1$, deviations only occur on very long time scales as the invariant set, i.e. the periodic orbit is strongly attracting. For details on stochastic escape from hyperbolic invariant sets see e.g. [13, 5]. All our results on the influence of generalized parameters also apply. For example, superlinear conversion and sublinear elasticity for the predator make extinction less likely. However, it is also important to point out that these conclusions are relative with respect to the local behaviour i.e. how likely it is to escape from a vicinity of the periodic orbit so that we can only predict the trend of the probability under parameter variation (increase or decrease) but not the precise magnitude.

Note that although some conclusions stated above seem to be “obvious” in an ecological context, it is by no means clear how to prove them. That they can be obtained by an analysis of nonlocal generalized models underlines the applicability of the approach. It is absolutely crucial to notice that we have given a description of stability in predator-prey systems under a very small number of assumptions. For example, the results apply to systems for any conversion function and any predator-prey growth function. Usually the choice of these functional forms is highly debated and often difficult to justify from available data.

8. Sampling. Recall that due to Proposition 4.1 it was straightforward for equilibrium generalized models to choose a set of generalized parameters, just random sampling produces a set of parameters that is consistent with at least one specific model. Random sampling of generalized parameters has been exploited to correlate different aspects of the dynamical system to stability [44, 49]. For non-equilibrium systems we must certainly check the necessary condition from Corollary 4.3. For simplicity we will always choose $T = 1$ and assume $g_y = 1 = m_y$.

The following algorithm allows sampling of elasticity and scale functions:

(A1) Choose a truncation order $\kappa_M$ for the algebraic system (36) so that the necessary condition reads

$$0 = -2\pi i k \hat{\beta}_s(k) + [\hat{\beta}_s * (\hat{\beta}_s - \hat{\beta}_1) * (\hat{s}_x - 1)](k) =: c_s(k),$$

$$0 = -2\pi i k \hat{\beta}_1(k) + [\hat{\beta}_1 * (\hat{\beta}_s - \hat{\beta}_1) * \hat{g}_x + (\hat{\beta}_2 - \hat{\beta}_m) - (\hat{\beta}_s - \hat{\beta}_1)](k) =: c_1(k),$$

$$0 = -2\pi i k \hat{\beta}_2(k) + [\hat{\beta}_2 * (\hat{\beta}_s - \hat{\beta}_1) * \hat{g}_x](k) =: c_2(k),$$

for $|k| \leq \kappa_M$.

(A2) Define a new variable that collects all the Fourier coefficient values for $\beta_s$, $\beta_1$, $\beta_2$, $\beta_m$, $s_x$ and $g_x$

$$X := (\hat{\beta}_s(0), \hat{\beta}_s(1), \ldots, \hat{\beta}_s(\kappa_m), \hat{\beta}_1(0), \ldots, \hat{\beta}_1(\kappa_m), \ldots) \in C^{6(\kappa_M+1)} \cong R^{12(\kappa_M+1)}$$

where $x$ contains all the information about the scale and elasticity functions since the negative index coefficients can be obtained by complex conjugation.

(A3) Define a function

$$F(X) := \|\text{Re}(c_s)\|^2 + \|\text{Re}(c_1)\|^2 + \|\text{Re}(c_2)\|^2 + \|\text{Im}(c_s)\|^2 + \|\text{Im}(c_1)\|^2 + \|\text{Im}(c_2)\|^2$$

where we view $c_s$, $c_1$ and $c_2$ as vectors of dimension $2\kappa_M + 1$ and real and imaginary parts are applied component-wise.
Observe that $F(X_0) = 0$ if and only if the Fourier coefficients encoded in $X_0$ satisfy the algebraic equations in (A1). Therefore we can attempt to solve the following optimization problem

$$X_m := \min\{F(X) : X \in \mathbb{R}^{12(\kappa_M+1)}\}$$

with a random initial condition, say $x = x_l$.

Solving the optimization problem for different random initial conditions is expected to yield different values for $X_m$ that solve the algebraic constraint in (A1). This means that we get a set of Fourier coefficients $\{X_m(l)\}_{l=1}^L$ where $L$ denotes the sample size and the index $l \in \mathbb{N}$ indicates the dependence on the initial condition.

The main technical difficulty of the algorithm (A1)-(A4) is that it involves the solution of the optimization problem (41). This is computationally much more expensive than the direct random sampling for equilibrium generalized models. It is known [43] that the main computational cost in optimization is often given by the difficulty of the function evaluations of $F(x)$. For our case, this seems to be the case since we have to compute several discrete convolutions to evaluate $F(x)$. However, the convolution computation is inexpensive due to the Fast Fourier Transform [32].

![Histogram of the 5·63587 Fourier coefficients for βs obtained from the optimization of (41) with uniformly sampled initial conditions (42). The columns show the five different real numbers with their observed number on the vertical axes. The first row shows coefficients associated to a stable Floquet multiplier and the second row those with an unstable Floquet multiplier. Observe that the number of stable coefficients is substantially larger than the number of unstable ones.](image)

Now we want to demonstrate that the algorithm can be used for a sampling analysis of stability similar to the one used in [24]. It is very important to note that the strategy employed in [24] was crucial to reveal intrinsic stabilizing factors of large food webs. Without generalized models it is very difficult to sample large classes of all available food models and calculate the dynamic stability. In particular, a fast systematic sampling and a fast evaluation of stability provide key tools to consider several billions of food webs. The fast algorithm we presented above precisely provides the analog for periodic solutions. Hence it extends another key strength of generalized models from steady states to the nonlocal case.
Let us point out that here we do not attempt a full detailed statistical analysis of the predator-prey model but that we only aim at a proof-of-principle. We solved (41) for 110000 initial conditions for \( \kappa_M = 2 \) using a standard algorithm for nonlinear optimization [41, 38]. Each sequence of Fourier coefficients in the initial condition consists of five real numbers e.g.

\[
\hat{\beta}_s(0), \text{Re}(\hat{\beta}_s(1)), \text{Im}(\hat{\beta}_s(1)), \text{Re}(\hat{\beta}_s(2)), \text{Im}(\hat{\beta}_s(2)),
\]

which were sampled uniformly and independently from the interval \([0, 1.5]\). We discarded all solutions of the optimization algorithm that did not satisfy the positivity condition

\[
\hat{\beta}_s(0) > 0, \quad \hat{\beta}_1(0) > 0, \quad \hat{\beta}_2(0) > 0, \quad \hat{\beta}_m(0) > 0.
\]

which is required by the definition of the scale functions and the invariance of the positive quadrant for the moduli space flow. The 63587 remaining solutions \( x_m(l) \) satisfied the optimization problem (and therefore the moduli space flow) at least up to a tolerance of \( 10^{-4} \) i.e. \( |x_m(l)| < 10^{-4} \) for all \( l \); the average value was \( \mathbb{E}[x_m(l)] \approx 1.73 \cdot 10^{-6} \). We have also calculated the single Floquet multiplier \( \lambda_l \) associated to each solution using Proposition 7.2.

| \( \hat{\beta}_s(k) \) | \( \hat{\beta}_s(0) \) | Re(\( \hat{\beta}_s(1) \)) | Im(\( \hat{\beta}_s(1) \)) | Re(\( \hat{\beta}_s(2) \)) | Im(\( \hat{\beta}_s(2) \)) |
|----------------------|--------------------|----------------|----------------|----------------|----------------|
| mean (stable)        | 1.6021             | 0.2207         | 0.5635         | -0.0117        | -0.1205        |
| variance (stable)    | 0.8840             | 0.3226         | 0.4000         | 0.1009         | 0.1202         |
| mean (unstable)      | 1.4409             | 0.1936         | 0.3963         | -0.0232        | -0.0591        |
| variance (unstable)  | 0.9129             | 0.2863         | 0.3409         | 0.1014         | 0.1381         |

| \( \hat{\beta}_1(k) \) | \( \hat{\beta}_1(0) \) | Re(\( \hat{\beta}_1(1) \)) | Im(\( \hat{\beta}_1(1) \)) | Re(\( \hat{\beta}_1(2) \)) | Im(\( \hat{\beta}_1(2) \)) |
|----------------------|--------------------|----------------|----------------|----------------|----------------|
| mean (stable)        | 1.3187             | 0.3275         | 0.3219         | 0.0157         | 0.2875         |
| variance (stable)    | 0.6755             | 0.3050         | 0.2431         | 0.1502         | 0.1226         |
| mean (unstable)      | 1.4502             | 0.1778         | 0.3445         | -0.0686        | 0.2649         |
| variance (unstable)  | 0.7578             | 0.3213         | 0.2796         | 0.1679         | 0.1344         |

| \( \hat{\beta}_2(k) \) | \( \hat{\beta}_2(0) \) | Re(\( \hat{\beta}_2(1) \)) | Im(\( \hat{\beta}_2(1) \)) | Re(\( \hat{\beta}_2(2) \)) | Im(\( \hat{\beta}_2(2) \)) |
|----------------------|--------------------|----------------|----------------|----------------|----------------|
| mean (stable)        | 2.0800             | 0.4823         | 0.5761         | -0.0583        | 0.2164         |
| variance (stable)    | 1.8865             | 0.6716         | 0.7486         | 0.2135         | 0.2970         |
| mean (unstable)      | 1.8914             | 0.3399         | 0.3835         | -0.0375        | 0.0592         |
| variance (unstable)  | 1.8228             | 0.5437         | 0.5892         | 0.1593         | 0.2070         |

| \( \hat{\beta}_m(k) \) | \( \hat{\beta}_m(0) \) | Re(\( \hat{\beta}_m(1) \)) | Im(\( \hat{\beta}_m(1) \)) | Re(\( \hat{\beta}_m(2) \)) | Im(\( \hat{\beta}_m(2) \)) |
|----------------------|--------------------|----------------|----------------|----------------|----------------|
| mean (stable)        | 1.6184             | 0.9865         | 0.4756         | 1.7548         | 0.4965         |
| variance (stable)    | 1.5568             | 2.2090         | 2.3338         | 2.9748         | 3.1220         |
| mean (unstable)      | 1.7736             | 1.0465         | 0.6171         | 1.7885         | 0.7635         |
| variance (unstable)  | 1.5189             | 2.2642         | 2.7503         | 2.9247         | 3.4595         |

| \( \hat{\beta}_s(k) \) | \( \hat{\beta}_s(0) \) | Re(\( \hat{\beta}_s(1) \)) | Im(\( \hat{\beta}_s(1) \)) | Re(\( \hat{\beta}_s(2) \)) | Im(\( \hat{\beta}_s(2) \)) |
|----------------------|--------------------|----------------|----------------|----------------|----------------|
| mean (stable)        | 1.5988             | 1.6598         | 1.6699         | 1.6222         | 0.5934         |
| variance (stable)    | 2.2079             | 2.8519         | 2.2995         | 2.4361         | 3.1797         |
| mean (unstable)      | 2.5967             | 1.5343         | 1.9850         | 1.5559         | 1.2697         |
| variance (unstable)  | 3.7412             | 3.0413         | 3.5637         | 2.7521         | 2.9364         |

| \( \hat{\beta}_s(k) \) | \( \hat{\beta}_s(0) \) | Re(\( \hat{\beta}_s(1) \)) | Im(\( \hat{\beta}_s(1) \)) | Re(\( \hat{\beta}_s(2) \)) | Im(\( \hat{\beta}_s(2) \)) |
|----------------------|--------------------|----------------|----------------|----------------|----------------|
| mean (stable)        | 2.7354             | 1.9742         | 2.4564         | 0.9165         | 1.3490         |
| variance (stable)    | 4.3300             | 3.6009         | 3.4094         | 2.9125         | 2.6612         |
| mean (unstable)      | 4.7877             | 1.6774         | 1.8789         | 1.2302         | 1.1109         |
| variance (unstable)  | 2.3056             | 3.4147         | 3.4502         | 3.5286         | 3.1522         |

**TABLE 2.** Mean and variance for the Fourier coefficients obtained from optimization (solution of the moduli space flow). Coefficients associated to stable and unstable Floquet multipliers are considered separately.
Figure 5 shows some of the output of the computation. We plot the Fourier coefficients associated to the scale function $\beta_s$. The top row in Figure 5 corresponds to coefficients with stable periodic orbit ($|\lambda| < 1$) and the bottom row to coefficients with an unstable periodic orbit ($|\lambda| > 1$). We see that, despite the initial uniform sampling, the results for each coefficient of $\beta_s$ closely resemble normal distributions. The same observation also applies for the other scale and elasticity functions. In total we find that 37873 solutions associated to a stable multiplier and 25714 unstable ones. From this discrepancy one may either conjecture that the moduli space flow constraint could bias the ecological system towards stability or that our choice of initial uniform random sampling over a particular region in parameter space causes the bias towards stability.

In Table 2 we list mean and variance for each coefficient. Several observations can be made based on Table 2. The scale functions $\beta_2$ and $\beta_m$ have a much bigger variance than $\beta_s$ and $\beta_1$. This could indicate that the prey growth rate and the prey-per-capita predation rate have to obey much smaller ranges in ecological systems compared to the predator-per-capita rates describing consumption and mortality. It is also interesting that the mortality rate $\beta_m$ allows for much larger amplitude higher-order harmonics whereas e.g. $|\hat{\beta}_s(2)|$ is always comparatively small. The elasticities show no consistent variance decay towards higher-order harmonics although the coefficients themselves seem to decay. From the ecological perspective this suggest that predator-prey systems may exhibit a wide diversity in terms of sensitivities $s_x$ and $g_x$.

To understand how the different coefficients relate to stability we calculate the Pearson correlation coefficient. For two vectors of observations $\{a_l\}$ and $\{b_l\}$ it is defined as

$$r(a, b) := \frac{\sum_l(a_l - \mathbb{E}[a])(b_l - \mathbb{E}[b])}{\sqrt{\sum_l(a_l - \mathbb{E}[a])^2 \sum_l(b_l - \mathbb{E}[b])^2}}.$$

Figure 6 shows $r(a, \lambda_l)$ where $a$ is a sequence of real or imaginary parts of the Fourier coefficients e.g. $\{a_l\} = \{\text{Re}(\hat{\beta}_s(i(k)))\}$. One important conclusion to draw from the correlation coefficients is that although a Fourier coefficient does not appear in the stability formula for the Floquet multiplier it may still correlate positively or negatively with stability. For example, $\hat{\beta}_2(1)$ and $\hat{\beta}_2(2)$ show a negative correlation with Floquet multiplier. This effect can be caused by the fact that the scale and elasticity functions are not independent i.e. they are related via the moduli space flow.

It is very important to observe that we can recover conclusions, which we found already analytically in Section 7, from the statistical analysis. For example, the coefficient $\hat{g}_x(0)$ correlates negatively with stability which means that decreasing it increases the Floquet multiplier and acts towards destabilization. This is precisely the result we have already obtained analytically in Section 7. Let us point out again that the basic statistical analysis we have provided is incomplete but that it definitely does show that the proposed sampling techniques based on the FFT, optimization and correlations can help to understand stability of periodic solutions.

9. Conclusions & outlook. In this paper we have extended the method of generalized modeling from equilibrium to non-equilibrium systems. This extension has been achieved in the context of a classical predator-prey system with periodic solutions. We proved that the generalized elasticity and scale functions satisfy a flow on moduli space (Theorem 4.2). The Jacobian $A(t)$ of the system has to be analyzed
using Floquet theory. Stability depends only on two coefficients which can be calculated via discrete convolutions (Theorem 7.1). Using the two coefficients we have identified which generalized parameters stabilize or de-stabilize predator-prey limit cycles. In the last part of the paper, we suggested a practical sampling algorithm that uses optimization methods to find elasticity and scale functions that satisfy the (algebraic) moduli space flow. During our analysis we have also obtained several ecological conclusions about arbitrary predator-prey models that can be written in the generalized form (3).

Since this paper presents the first step from steady-state to limit cycle generalized models there are many possible directions to extend theory and applications of the method. Any outlook in this direction will be incomplete but we are going to sketch a few ideas that could be useful for future work. The first natural question is whether we can extend to limit cycles in $N$-dimensional systems for $N > 2$. In [35] generalizations to $\mathbb{R}^N$ in the steady state context have been carried out. The procedure from Section 3 (except Liouville’s formula) can be extended in the same way as for the steady state case. Unfortunately, the notation becomes a bit cumbersome with many different indices to keep track of the various scale and elasticity functions. Therefore we decided against presenting Section 3 for $\mathbb{R}^N$ as we want to keep this first step as accessible as possible. The second key point would be to prove an analogue of Theorem 4.2 for the $N$-dimensional case. Although this requires additional work let us point out that all the methods in the proof are available in any dimension. Also the Fourier analysis in Proposition 6.1 can still be applied to a larger system. The main difference in $\mathbb{R}^N$ is that we have to compute the Floquet multipliers numerically since Liouville’s formula only provides the product of the eigenvalues.
Another important step would be to look at bifurcations and bifurcation-detection in $\mathbb{R}^N$. In $\mathbb{R}^2$ we only considered the fold bifurcation of limit cycles as an instability mechanism when the single Floquet multiplier passes through $1$; period-doubling, Neimark-Sacker, and many other bifurcations are already excluded due to the restriction to $\mathbb{R}^2$. Hence this issue must be addressed in future work for $\mathbb{R}^N$.

One can also try to consider non-equilibrium systems beyond periodic orbits. For example, suppose a homoclinic orbit

$$
\gamma = \gamma(t) : \mathbb{R} \to (\mathbb{R}^2)^+, \quad \gamma(t) = (X^*, Y^*), \quad \text{as } |t| \to \infty
$$

for (16) exists where $(X^*, Y^*)$ is a positive steady state. Formulating a generalized model starting from (16) up to (20) works as for limit cycles. Theorem 4.2 also applies, as periodicity is not used. We have to replace the periodic boundary conditions in (34) with $\beta(\pm \infty) = \beta^*$, where $\beta^*$ is a vector of generalized scale parameters at $(X^*, Y^*)$. Fourier analysis cannot be applied directly and also the bifurcation-detection for homoclinic orbits for generalized models requires more work.

Carrying out this additional work it seems important to consider how steady-state and non-local generalized models link up i.e. what happens when a bifurcation involves a steady state as well as a non-local orbit. In this regard, it is reassuring that the limit cycle case we have developed reduces to classical steady-state generalized models when the minimal period is $T = 0$; in fact, Theorem 4.2 is trivially satisfied as it just implies that the scale functions are constants due to the conditions $\beta_s = \beta_1$ and $\beta_m = \beta_2$ from (8). Also a comparison between non-local generalized models and classical models with given functional forms, as carried out in [52] for the steady-state case, would be extremely helpful.

Other open problems are further extensions with a view towards ecological applications. Steady-state generalized models have been used to investigate issues such as enrichment [19], pattern-formation [3], large food web stability [24], producer-grazer systems [52] and omnivory [54]. What happens in the limit cycle context with these studies is again a wide-open problem. Also investigating the case of multiple steady states further, similar to the discussion for the saddle-node bifurcation in [52] in the steady-state context, would be interesting and relates to recent work [37] that uses generalized models for predicting critical transitions [46, 34].

Acknowledgments. We would like to thank an anonymous referee whose comments helped to improve the manuscript.

REFERENCES

[1] L. Andrianopoli, M. Bertolini, A. Ceresole, R. D’Auria, S. Ferrara, P. Fré and T. Magri, $N = 2$ supergravity and $N = 2$ super Yang-Mills theory on general scalar manifolds: Symplectic covariance gaugings and the momentum map, J. Geom. Phys., 23 (1997), 111–189.

[2] U. M. Ascher, R. M. M. Mattheij and R. D. Russell, “Numerical Solution of Boundary Value Problems for Ordinary Differential Equations,” Classics in Applied Mathematics, 13, SIAM, Philadelphia, PA, 1995.

[3] M. Baumann, T. Gross and U. Feudel, Instabilities in spatially extended predator-prey systems: Spatio-temporal patterns in the neighbourhood of Turing-Hopf bifurcations, J. Theor. Bio., 245 (2007), 220–229.

[4] A. D. Bazykin, “Nonlinear Dynamics of Interacting Populations,” Edited and with a foreword by Alexander I. Khibnik and Bernd Krauskopf, World Scientific Series on Nonlinear Science, Series A: Monographs and Treatises, 11, World Scientific Publishing Co., Inc., River Edge, NJ, 1998.
[5] N. Berglund and B. Gentz, “Noise-Induced Phenomena in Slow-Fast Dynamical Systems. A Sample-Paths Approach,” Probability and its Applications (New York), Springer-Verlag London, Ltd., London, 2006.
[6] A. A. Berryman, The origins and evolution of predator-prey theory, Ecol., 73 (1992), 1530–1535.
[7] F. Brauer and C. Castillo-Chávez, “Mathematical Models in Population Biology and Epidemiology,” Texts in Applied Mathematics, 40, Springer-Verlag, New York, 2001.
[8] M. Braun, “Differential Equations and their Applications,” Hochschultext, Springer-Verlag, Berlin-New York, 1979.
[9] C. Chicone, Inertial and slow manifolds for delay differential equations, J. Diff. Eqs., 190 (2003), 364–406.
[10] C. Chicone, “Ordinary Differential Equations with Applications,” Second edition, Texts in Applied Mathematics, 34, Springer-Verlag, New York, 2006.
[11] E. J. Doedel, A. Champneys, F. Dercole, T. Fairgrieve, Y. Kuznetsov, B. Olde- man, H. Paffenroth, B. Sandstede, X. Wang and C. Zhang, Auto 2007p: Continuation and bifurcation software for ordinary differential equations (with homcont), http://cmvl.cs.concordia.ca/auto, 2007.
[12] T. F. Fairgrieve and A. D. Jepson, O. K. Floquet multipliers, SIAM J. Numer. Anal., 28 (1991), 1446–1462.
[13] M. I. Freidlin and A. D. Wentzell, “Random Perturbations of Dynamical Systems,” Second edition, Grundlehren der Mathematischen Wissenschaften [Fundamental Principles of Mathematical Sciences], 260, Springer-Verlag, New York, 1998.
[14] C. Gardiner, “Stochastic Methods. A Handbook for the Natural and Social Sciences,” Fourth edition, Springer Series in Synergetics, Springer-Verlag, Berlin, 2009.
[15] E. Gehrmann and B. Drossel, Boolean versus continuous dynamics on simple two-gene modules, Phys. Rev. E (3), 82 (2010), 046120, 9 pp.
[16] B. S. Goh, Global stability in two species interactions, J. Math. Biol., 3 (1976), 313–318.
[17] T. Gross, M. Baermann, U. Feudel and B. Blasius, Generalized models - a new tool for the investigation of ecological systems, in “Complex Population Dynamics: Nonlinear Modeling in Ecology, Epidemiology and Genetics” (eds. B. Blasius, J. Kurths, and L. Stone), World Scientific, Singapore, (2006), 21–48.
[18] T. Gross, C. J. Dommar D’Lima and B. Blasius, Epidemic dynamics on an adaptive network, Phys. Rev. Lett., 96 (2006), 208701.
[19] T. Gross, W. Ebenhöh and U. Feudel, Enrichment and foodchain stability: The impact of different functional forms, J. Theor. Bio., 227 (2004), 349–358.
[20] T. Gross, W. Ebenhöh and U. Feudel, Long food chains are in general chaotic, Oikos, 109 (2005), 133–155.
[21] T. Gross and U. Feudel, Analytical search for bifurcation surfaces in parameter space, Physica D, 195 (2004), 292–302.
[22] T. Gross and U. Feudel, Generalized models as an universal approach to the analysis of nonlinear dynamical systems, Phys. Rev. E, 73 (2006), 016205–14.
[23] T. Gross and U. Feudel, Local dynamical equivalence of certain food webs, Ocean Dynamics, 59 (2009), 417–427.
[24] T. Gross, L. Rudolf, S. A. Levin and U. Dieckmann, Generalized models reveal stabilizing factors in food webs, Science, 325 (2009), 747–750.
[25] J. Guckenheimer and P. Holmes, “Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields,” Applied Mathematical Sciences, 42, Springer-Verlag, New York, 1983.
[26] Joe Harris, “Algebraic Geometry. A First Course,” Graduate Texts in Mathematics, 133, Springer-Verlag, New York, 1992.
[27] Robin Hartshorne, “Algebraic Geometry,” Graduate Texts in Mathematics, No. 52, Springer-Verlag, New York-Heidelberg, 1977.
[28] A. Hastings, Global stability of two-species systems, J. Math. Biol., 5 (1977/78), 399–403.
[29] Y. Katznelson, “An Introduction to Harmonic Analysis,” Third edition, Cambridge Mathematical Library, Cambridge University Press, Cambridge, 2004.
[30] M. J. Keeling, D. A. Rand and A. J. Morris, Correlation models for childhood epidemics, Proc. R. Soc. B, 264 (1997), 1149–1156.
[31] C. A. Klausmeier, Floquet theory: A useful tool for understanding nonequilibrium dynamics, Theor. Ecol., 1 (2008), 153–161.
[32] T. W. Körner, “Fourier Analysis,” CUP, 1989.
[33] M. Kot, “Elements of Mathematical Ecology,” CUP, 2003.
[34] C. Kuehn, *A mathematical framework for critical transitions: Normal forms, variance and applications*, submitted, arXiv:1101.2908, 1–46, 2011.
[35] C. Kuehn, S. Siegmund and T. Gross, *On the analysis of evolution equations via generalized models*, accepted, IMAJ Appl. Math., arXiv:1012.4340, 2012.
[36] Yu. A. Kuznetsov, “Elements of Applied Bifurcation Theory,” Third edition, Applied Mathematical Sciences, 112, Springer-Verlag, New York, 2004.
[37] S. J. Lade and T. Gross, *Early warning signals for critical transitions: A generalized modeling approach*, PLoS Comp. Biol., 8 (2012), e1002360–6.
[38] J. C. Lagarias, J. A. Reeds, M. H. Wright and P. E. Wright, *Convergence properties of the Nelder-Mead simplex method in low dimensions*, SIAM J. Optim., 9 (1998), 112–147.
[39] K. Lust, *Improved numerical Floquet multipliers*, Int. J. Bif. Chaos Appl. Sci. Engrg., 11 (2001), 2389–2410.
[40] H. Masur and S. Tabachnikov, *Rational billiards and flat structures*, in “Handbook of Dynamical Systems” (eds. B. Hasselblatt and A. Katok), Vol. 1A, North Holland, Amsterdam (2002), 1015–1090.
[41] The MathWorks, Matlab 2010b, 2010. (with Control and Optimization Toolboxes).
[42] S. M. Moghadas and M. E. Alexander, *Dynamics of a generalized Gauss-type predator-prey model with a seasonal functional response*, Chaos, Solitons and Fractals, 23 (2005), 55–65.
[43] J. Nocedal and S. J. Wright, “Numerical Optimization,” Springer Series in Operations Research, Springer-Verlag, New York, 1999.
[44] E. Reznik and D. Segré, *On the stability of metabolic cycles*, J. Theor. Biol., 266 (2010), 536–549.
[45] M. L. Rosenzweig, *Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time*, Science, 171 (1971), 385–387.
[46] M. Scheffer, J. Bascompte, W. A. Brock, V. Brovkhin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara, *Early-warning signals for critical transitions*, Nature, 461 (2009), 53–59.
[47] J. Smillie, *Introduction to rational billiards*, MSRI Workshop on Geometric Group Theory, 2007. Available from: http://ww.math.cornell.edu/~vogtmann/MSRI/index.html.
[48] L. Socha, “Linearization Methods for Stochastic Dynamic Systems,” Lecture Notes in Physics, 730, Springer, Berlin, 2008.
[49] R. Steuer, T. Gross, J. Selbig and B. Blasius, *Structural kinetic modeling of metabolic networks*, Proc. Natl. Acad. Sci., 103 (2006), 11868–11873.
[50] R. Steuer, A. Nunes Nesi, A. R. Fernie, T. Gross, B. Blasius and J. Selbig, *From structure to dynamics of metabolic pathways*, Bioinformatics, 23 (2007), 1378–1385.
[51] D. Stiefs, T. Gross, R. Steuer and U. Feudel, *Computation and visualization of bifurcation surfaces*, Int. J. Bif. Chaos, 18 (2008), 2191–2206.
[52] D. Stiefs, G. A. K. van Voorn, B. W. Kooi, U. Feudel and T. Gross, *Food quality in producer-grazer models*, Am. Nat., 176 (2010), 367–380.
[53] G. S. K. Wolkowicz, *Bifurcation analysis of a predator-prey system involving group defence*, SIAM J. Appl. Math., 48 (1988), 592–606.
[54] J. D. Yeakel, D. Stiefs, M. Novak and T. Gross, *Generalized modeling of ecological population dynamics*, Theor. Ecol., 4 (2011), 179–194.
[55] M. Zumsande, D. Stiefs, S. Siegmund and T. Gross, *General analysis of mathematical models for bone remodeling*, Bone, 48 (2011), 910–917.

Received February 2012; revised April 2012.

E-mail address: ck274@cornell.edu
E-mail address: thilo2gross@gmail.com