Uncertainty and predictability in population dynamics of a bitrophic ecological model: Mixed-mode oscillations, bistability and sensitivity to parameters

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1. Introduction

In Nature, every species live in a web of complex relationships with other species and tries to remain in an equilibrium state within the ecosystem. However, large fluctuations in the population densities of various species, specially, in small mammals and insects, have been reported and is a subject of interest amongst environmentalists, entomologists and conservationists. A few such examples include population fluctuations in snowshoe hares in the boreal zone of North America, vole cycles in the Northern Europe and in the boreal forest arctic-tundra of Siberia, lemming cycles in the high arctic tundra of Eurasia and North America, house mice in southeastern Australia, devastating desert locusts outbreaks in Australia, and the more benign larch budmoth cycles, which have been reconstructed from the tree rings of the host subalpine larch in the European Alps with their records dating back to more than a thousand years (see Casimir, 1962; Esper et al., 2007; Korpimäki et al., 2004; Wright, 1987 and the references therein), etc. A rapid increase in the population densities of some of these species can lead to pest outbreaks, which in turn can lead to other cumulative effects such as large scale defoliation of local forests or farming losses or damage of stored food grains. Similarly, outbreaks of vector-borne diseases may lead to epidemics. These outbreaks are
intrinsically unpredictable and often demand timely and effective responses. On the other hand, a sudden decrease in the population can bring an endangered species perilously close to an extinction. The precise mechanism behind these cycles is still an open question, but there has been a general consensus that trophic interactions or maternal effects that cause delayed negative feedback can cause such oscillations. Negative feedbacks that stem from lower trophic levels (such as host plants, prey) and/or from higher trophic levels (such as predators, diseases) are capable of producing oscillations specially if there are time lags in their effects (see Esper et al., 2007 and the references therein).

As noted earlier, the cycles of boom and bust in Nature are random and seem unpredictable. This makes it even more challenging to understand the patterns of population densities and/or predict the extreme events of outbreaks and/or collapses from field studies alone. On the other hand, even small amplitude (non-extreme events) irregular or chaotic fluctuations in population densities that may arise due to a deterministic process have been a subject of both fascination and intense debate in the ecological community. The unpredictable fluctuations in a natural population data can also be viewed as random effects due to environmental noise/and or errors in the measurement data. Documenting deterministic chaos in the wild is complicated as it is difficult to distinguish chaos from noise (Cushing et al., 2001; May, 1976). However, chaos has been documented in laboratory studies of populations of interacting species. Based on the time-series data and controlled laboratory experiments with manipulated demographic data, various nonlinear phenomena including chaos has been observed in several ecosystems (Cushing et al., 2001).

Typically an ecosystem can be divided into various trophic levels based on the size and the time needed for reproduction and growth of the individuals of each population. In almost all predator–prey interactions, the rate of production per unit biomass decreases from bottom to top along the trophic levels. For example, in the interactions between rabbits and foxes, or insects and birds, or phytoplankton and zooplankton, the lower trophic level exhibits a faster dynamics. Such time diversified predator–prey models can give us an insight to some of the features observed in the population cycles of species in the wild. Some of the studies conducted in multiple time scales ecological models include the two-trophic model involving two predators competing for their common prey (Muratori and Rinaldi, 1989; Rinaldi and Muratori, 1992; Sadhu, 2015, 2016; Sadhu and Chakraborty Thakur, 2015), the tri-trophic food chain models (Brons and Kaesan, 2010; Deng, 2001), and age-structured predator–prey models with dormancy of the predators (Kuwamura and Chiba, 2009), etc.

In this paper, we consider the model studied in Sadhu (2015, 2016) which involves two predators competing for their common prey with one of the predators (the territorial predator, say) exhibiting density dependent mortality rate, and the prey exhibiting fast dynamics, aligning with the common observation found in Nature. Typical examples would be lemmings, owls and arctic foxes, or voles, owls and weasels, or budworms and their avian predators. The model is cast into the framework of a singularly perturbed system of equations with one fast (prey dynamics) and two slow (predator dynamics) variables. As the density dependent mortality rate of the territorial predator is varied, the system exhibits a variety of rich nonlinear dynamics, including but not limited to relaxation oscillation cycles, stable and chaotic mixed mode oscillation (MMO) patterns, periodic cycles with small amplitude oscillations (SAOs), global bifurcations of limit cycles and chaos via a cascade of limit cycles bifurcations. The SAOs in our model represent the small fluctuations in the population densities of the species, whereas the relaxation oscillations or the large amplitude oscillations (LAOs) signify the periodic outbreaks and collapses corresponding to large fluctuations in the population densities. The relaxation oscillations exhibit four phases involving two distinct time scales: due to heavy predatory exploitation, the prey population quickly collapses and remains in an endemic state on a slow time scale until the predators become scarce, after which the prey quickly regenerate allowing the predators to grow slowly. The cycle repeats itself when the exploitation pressure reaches its threshold. MMO cycles on the other hand, are concatenations of SAOs and LAOs that can be regarded as a connector between these two types of limit cycles. In these cycles, the three species coexist via SAOs over an intermediate time scale, but the fast dynamics of the prey is not completely filtered out, and is periodically revealed by the burst of an LAO.

Ecologically, an MMO orbit indicates the adaptability of a species to prolong its successive cycles of outbreaks and collapses. As observed in most outbreak events, the return time of the successive outbreak does not have a fixed periodicity, but follows an irregular pattern (see Fig. 5 in Esper et al., 2007 for the larch budmoth dynamics). Annual defoliation data collected by Virginia Department of Forestry spanning 1953–2014 Asaro and Chamberlin (2015) suggests that the population densities of gypsy moth (Lymantria dispar L.) and fall cankerworm (Alsophila pometaria Harris) seem to exhibit chaotic MMO cycles. More examples of such MMO cycles with mixed signatures can be drawn from the data pertaining to Australian locust outbreaks between 1934–2011 Casimir (1962) and Wright (1987) obtained from the Australian Plague Locust Commission Bulletin (1977–2011). The data measuring the intensities of the outbreaks suggests that the population of locusts exhibits a wide range of fluctuations varying from small to intermediate to large depending on other external factors such as rainfall, etc. The irregularities in these outbreak events can be explained to some extent by the simple model that we consider in this paper. In our model, the return time of an outbreak event can be anticipated from the occurrence of local minima in the predator populations while the prey population is in the endemic state (corresponding to one of the slow phases in an LAO cycle). An MMO orbit can exhibit different numbers of SAOs in between successive LAO peaks, and hence the return time of an outbreak event can be effectively read off from the time series of such an orbit. Thus the system of equations considered in this paper cannot only model the events of outbreaks and collapses, but can also be used to predict the occurrence of such events. Moreover, we understand that external effects of either local climate change or loss of habitat can impact relevant activities such as food consumption patterns, reproduction habits, etc., and in our model they can be incorporated by adding fluctuations (small variations) in the ecological parameters chosen (birth rates, carrying capacities, death rates, etc.). Changes in long term patterns due to sudden rapid changes in the climate is observed in the larch budmoth population (Esper et al., 2007). Minor changes in even one of the parameters used in our model can lead to such dramatic changes in the patterns of the population densities of the prey. In this paper, we will show some numerical results that elucidate the sensitivity of the system to initial conditions and parameters. It is worth mentioning that understanding the distinction between stochastic and deterministic dynamics gives us an insight of apparently irregular dynamics occurring in the wild. As Hastings et al. (1993) mentioned in their work that if fluctuations in population sizes are driven by some deterministic factors, and if those factors are understood, then it allows predictions of the dynamics over a short time scale. Management decisions are feasible in these situations. In this paper, we explain the mechanisms behind the irregular fluctuations in the population sizes driven by deterministic factors in our
model in an attempt to understand the dynamics occurring in a natural population.

The paper is organized as follows. In Section 2, we introduce the ecological model and rescale the parameters to transform the model into a non-dimensional system. Preliminary analysis and background information about geometric singular perturbation is given in Section 3 which provides us a framework for understanding the dynamics of the subsystems and the full-system in Sections 4 and 5, respectively. The mechanism of occurrence of MMOs is presented in Section 6. Numerical simulations exhibiting various nonlinear dynamics phenomena, bistability and the sensitivity of the system to parameters and initial conditions is presented in Section 7. We conclude the paper with a discussion in Section 8.

2. The model

The ecological model that we consider is a system of three coupled nonlinear differential equations of the form:

\[
\begin{align*}
\frac{dX}{dt} &= rX \left(1 - \frac{X}{K}\right) - \frac{p_1 XY}{H_1 + X} - \frac{p_2 XZ}{H_2 + X} \\
\frac{dY}{dt} &= b_t p_1 XY - d_t Y \\
\frac{dZ}{dt} &= b_t p_2 XZ - d_t Z - sZ^2
\end{align*}
\]

(1)

under the initial conditions

\[X(0) = X_0 > 0, \quad Y(0) = Y_0 > 0, \quad Z(0) = Z_0 > 0,\]

(2)

where \(X\) represents the population density of the prey and \(Y, Z\) represent the densities of the predators. The parameters \(r\) and \(K\) represent the intrinsic growth rate and the carrying capacity of the prey, \(p_1\) and \(p_2\) are the maximum per-capita predation rate of \(Y, H_1\) is the semi-saturation constant at which the predator's predation rate is half of its maximum \((p_1/2)\), \(d_t\) is the death rate of the predators, \(d_t\) is the per-capita growth rate of \(Y\), and \(X\) is the per-capita natural death rate of \(Y\). The other parameters \(p_2, d_{t2}, d_t, H_2, H_1\) are defined analogously for \(Z\). The parameter \(s\) measures the density dependent mortality rate in the class of which can be interpreted to be the result of intraspecific competition for resources.

Ruan et al. (2007) studied model (1) and showed that two competitors, exhibiting Holling II functional response with a density dependent mortality in one of the predators, can coexist upon the same prey. In the absence of density dependent mortality, it was shown in Hsu et al. (1978) and Muratori and Rinaldi (1989) that two competitors can coexist only via a locally attracting periodic orbit. Hence if \(s = 0\) in system (1), then there exists no positive equilibrium state and thus the system is only weakly persistent. However, when \(s > 0\), Ruan et al. (2007) showed the existence of a positive steady state (which is also globally attracting) thus ruling out the principle of competitive exclusion Hek (2010) and proving that system (1) is permanent. With the following change of variables and parameters:

\[
\begin{align*}
t_1 &= r t, \quad x = \frac{X}{K}, \quad y = \frac{p_1 Y}{rK}, \quad z = \frac{p_2 Z}{rK}, \quad \xi_1 = \frac{b_t p_1}{r}, \quad \xi_2 = \frac{b_t p_2}{r}, \\
n &= \frac{H_1}{K}, \quad \beta_2 = \frac{H_2}{K}, \quad c = \frac{d_t}{b_t p_1}, \quad d = \frac{d_t}{b_t p_2}, \quad h = s z_0, \quad h = \frac{s Z_0}{b_t p_2},
\end{align*}
\]

where \(Z_0 = \frac{rK}{p_2}\), system (1) takes the following dimensionless form:

\[
\begin{align*}
x &= x \left(1 - x - \frac{y}{\beta_1 + x} - \frac{z}{\beta_2 + x}\right) \\
y &= \xi_1 y \left(\frac{d}{\beta_1 + x} - c\right) \\
z &= \xi_2 z \left(\frac{d}{\beta_2 + x} - d - h x\right)
\end{align*}
\]

(3)

where \(h = \frac{s Z_0}{b_t p_2}\). Similar scaling variables were first considered in a three-trophic food chain model by Deng (2001). We will assume the following conditions on the parameters:

(A) The maximum per capita growth rate of the prey is much larger than the per capita growth rates of the predators, i.e. \(b_t p_1 < r\) and \(b_t p_2 < r\), thus yielding \(0 < \xi_1, \xi_2 < 1\). This is usually observed in situations when the prey exhibits a high growth rate, and in comparison, the predators have lower conversion efficiencies (Hek, 2010; Rinaldi and Muratori, 1992). Common examples may include worms and their avian predators or rabbits vs coyotes and foxes. Typically in mammals, growth and reproduction rates tend to be greater in small species than in large ones. Terrestrial animals commonly exhibit a rather low production to assimilation ratio of approximately 1–2%, thus enabling our model (3) to represent such ecosystems (Evans, 2006). For simplicity, we will assume in our model that \(\xi_1 = \xi_2 = \xi\) (say).

(B) The parameters \(c\) and \(d\) satisfy the inequality \(0 < c, d < 1\), which implies that the growth rates of the predators are greater than their death rates. This is a default assumption otherwise the predators would die out faster than they could reproduce even at their maximum reproduction rate.

(C) The parameters \(\beta_1\) and \(\beta_2\) are dimensionless semi-saturation constants measured against the prey's carrying capacity. We will assume that both the predating species are efficient as predators, and hence they will reach the half of their maximum predation rates before the prey population reaches its carrying capacity. This in turn yields that \(0 < \beta_1, \beta_2 < 1\).

Under the assumptions (A)–(C), system (3) transforms to a singular perturbed system of equations with two time scales, where the prey exhibits fast dynamics and the predators exhibit slow dynamics.

Remark 2.1.

- (i) The dimensionless quantity \(Z_0\) measures the predation capacity of \(Z\). In other words, at this capacity \(Z\) can consume \(p_2Z_0\) number of preys which equals the prey's reproduction capacity, \(rK\).
- (ii) The parameter \(h\) measures the ratio of the intraspecific competition (in \(Z\)) when \(Z\) is at its maximum predation capacity to its maximum growth rate. In this context, we will use \(h\) to measure the intensity of the intraspecific competition.
- (iii) Non-dimensionalizing model (1) in the way done in this paper leads to a natural way of incorporating two different time-scales in the system. Moreover, it is easier to interpret the assumption \(0 < \xi_1, \xi_2 < 1\) in terms of the original parameters (see Hek, 2010 in reference to the food chain model considered by Deng, 2001).
- (iv) It is to be noted that in biochemical ecosystems under batch or chemostat environments, the conversion efficiencies of predators are in general not too small (approximately around 0.1). In such situations the predator–prey interactions can be modeled by multiplying the growth rates as well as the maximum ingestion rates of the predators by a small parameter.
3. The geometric singular perturbation approach

In this section, we provide a preliminary analysis of system (3) which reads as

\[
\begin{align*}
\dot{x} &= x \left(1 - x - \frac{y}{p_1 + x} - \frac{z}{p_2 + x}\right) := xu(x, y, z) \\
\dot{y} &= \zeta y \left(\frac{x}{p_1 + x} - \frac{x}{y} - \frac{v}{u} \frac{y}{x} \frac{z}{y} \frac{z}{x}\right) := \zeta yv(x, y, z) \\
\dot{z} &= \zeta z \left(\frac{x}{p_2 + x} - \frac{d - h z}{w}\right) := \zeta zw(x, y, z),
\end{align*}
\]

where \(u, v, \) and \(w\) are the nontrivial \(x, y, \) and \(z\)-nullclines, respectively. On rescaling \(t_1\) by \(t\), where \(t = \zeta t_1\), system (4) can be reformulated as

\[
\begin{align*}
\dot{x} &= xu(x, y, z) \\
\dot{y} &= yv(x, y, z) \\
\dot{z} &= zw(x, y, z) 
\end{align*}
\]

where \(-\frac{d}{\zeta}\). Systems (4) and (5) are referred to as the fast-system and the slow-system, respectively. The time scales \(t_1\) and \(t\) are referred to as the fast and slow times, respectively. The parameter \(\zeta\) can be regarded as the separation of time scales. We will use geometrical singular perturbation theory to analyze system (5) (or equivalently system (4)). The foundation of such geometric approach to analyze systems with a clear separation in time scales was given by Fenichel (1979).

As \(\zeta \to 0\) the trajectories of (4) during fast epochs approach to the solutions of the “layer equations” given by

\[
\begin{align*}
\dot{x} &= xu(x, y, z) \\
\dot{y} &= yv(x, y, z) \\
\dot{z} &= zw(x, y, z) 
\end{align*}
\]

On the other hand, during slow epochs trajectories of (5) converge to the solutions of the “reduced problem” given by

\[
\begin{align*}
0 &= xu(x, y, z) \\
\dot{y} &= yv(x, y, z) \\
\dot{z} &= zw(x, y, z) 
\end{align*}
\]

The fast and slow subsystems (6) and (7) can be used to understand and study the dynamics of the full system (3) or (4) (see Sadhu, 2015, 2016 for details).

The algebraic equation in (7) defines the critical manifold

\[
\mathcal{M} = \{(x, y, z) : x = 0 \text{ or } u(x, y, z) = 0\} := T \cup S,
\]

where \(T = \{(0, y, z) : y, z \geq 0\} \) and \(S = \{(x, y, z) : u(x, y, z) = 0\}\). The critical manifold \(\mathcal{M}\) is the nullsurface of the fast system. It consists of two normally attracting sheets \(S^0\) and \(T^0\), and two repelling sheets \(S^\prime\) and \(T^\prime\), separated by two fold curves \(F^+\) and \(F^-\) (see Fig. 2(A)). The curve \(F^+\) is defined to be the intersection of \(T\) with \(S\). Note that reduced flow is restricted to the plane \(x = 0\) or to the surface \(S^\prime = \{x, y, z) : u(x, y, z) = 0\}.\) We will use the implicit function theorem, the surface \(S^\prime\) can be locally written as a graph of \(z = \phi(x, y)\), i.e. \(u(x, y, \phi(x, y)) = 0\). Differentiating \(u(x, y, z) = 0\) implicitly with respect to time gives us the relationship \(u_x + u_y + u_z = 0\). Thus, the reduced flow (7) restricted to \(S\), where \(S\) is considered as the graph of \(z = \phi(x, y)\) reads as

\[
\begin{align*}
-\frac{u_x}{y} &= \left(\begin{array}{c}
0 \\
u_x yv + u_z w
\end{array}\right)_{\phi(x, y)} \\
\quad \Rightarrow (1 - \frac{d - h z}{w})\frac{d}{\zeta} = \zeta zw(x, y, z)
\end{align*}
\]

System (8) has singularities when \(u_x = 0\). Such points are located on the fold curve \(F^-\). Hence standard existence and uniqueness results do not hold. Different solutions can approach the same point on \(\mathcal{F}\) in finite time. Note that the reduced flow is directed towards the fold (or away from it). On rescaling the time by the factor \(-u_x\), (8) transforms to the desingularized system

\[
\begin{align*}
\dot{x} &= u_x yv + u_z w \\
\dot{y} &= u_x yv
\end{align*}
\]

The set of equilibrium points of (9) that do not lie on the fold curve \(F^+\) (i.e. for which \(u_x \neq 0\) are known as ordinary singularities. On the other hand, equilibrium points of (9) that lie on \(F^+\) are termed as folded singularities. The folded singularities can be classified as folded nodes or folded saddles or folded foci or degenerate folded nodes depending on the signs of the eigenvalues of the linearized matrix of (9) evaluated at these points. Two types of bifurcation of the folded node can occur when one of the eigenvalues of the linearized desingularized system corresponding to (9) pass through zero. They are called folded saddle node bifurcation points of types I and II (Desroches et al., 2012). Points on \(F^+\) for which \(u_x yv + u_z w = 0\) are called “jump points” and they satisfy the “normal switching condition” (Brons et al., 2006). At these points, solutions exit into relaxation after reaching \(F^+\) giving rise to relaxation dynamics (see Fig. 2 in Sadhu, 2016). On the other hand, points of \(F^-\) where the normal switching condition is violated can give rise to canards. The curve \(F^-\) will be referred to as a regular fold.

4. Analysis of the subsystems

4.1. The \(xz\) subsystem

In the absence of the predator \(y\), system (5) reduces to

\[
\begin{align*}
\dot{x} &= xu(x, 0, z) \\
\dot{z} &= zw(x, 0, z)
\end{align*}
\]

System (10) is the singularly perturbed Bazykin’s model Bazykin (1998) which admits existence of multiple equilibria and multiple limit cycles, Hopf, homoclinic and Bagdanov Takens bifurcations (Sadhu, 2016) for a two-parameter bifurcation diagram of (10). For more detailed analysis, see Kuznetsov (1988). The Hopf bifurcation is singular (i.e. the imaginary parts of the eigenvalues of the linearized system go to \(\infty\) as \(\zeta \to 0\)). The first Lyapunov coefficient \(l_0\) is calculated to be (see Sadhu, 2016 for details)

\[
l_0 = \frac{1 - d - \beta_1 - \beta_2}{2 \sqrt{\beta_2 (1 - \beta_2)}} \sqrt{\frac{\beta_2 (1 + \beta_2)}{1 - \beta_2}} \left(\frac{1 - \beta_2}{8 (1 - \beta_2)}\right).
\]

System (10) also exhibits a canard explosion at \(O(\zeta)\) away from the Hopf point. The canard explosion refers to a sudden increase in the size of the limit cycles over an extremely narrow interval (see Fig. 5 in Sadhu, 2016). The size of the periodic orbit grows rapidly from diameter \(O(1)\) away from the Hopf point.
4.2. The xy subsystem

In the absence of the territorial predator z, the two-dimensional subsystem reads as

\[
\begin{aligned}
\dot{z} &= x u(x, y, 0) \\
y &= y v(x, y, 0)
\end{aligned}
\]  

(11)

System (11) is the well-known singular perturbed Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963) and has been studied in several papers including but not limited to Hek (2010), Muratori and Rinaldi (1989) and Rinaldi and Muratori (1992). We omit the analysis here.

5. Analysis of the full system

We will analyze system (5) in this section. We note that (5) has equilibrium points located at \( E_0 = (0, 0, 0) \), \( E_1 = (1, 0, 0) \), \( E_2 = (\frac{c\beta_1}{1-c}, \frac{c\beta_1}{1-c} - \frac{c^2}{1-c} \frac{c\beta_1}{1-c}, 0) \), \( E_3 = (x_3, 0, z_3) \), where \( x_3 \) and \( z_3 \) are solutions of the equations

\[
z_3 = (1-x_3)(\beta_2 + x_3), \quad z_3 = \frac{1}{c} \left( \frac{x_3}{\beta_2 + x_3} - d \right).
\]  

(12)

It is clear that the equilibria \( E_0 \) and \( E_1 \) exist without any restrictions. The equilibrium \( E_2 \) exists if \( 1 - c - c\beta_1 > 0 \). Note that (12) leads to a cubic equation in \( x_3 \), namely

\[
h(\beta_2 + x_3)^2(1-x_3) - (1-d)x_3 + d\beta_2 = 0.
\]  

(13)

which can have one, two or real positive roots depending on the parameters.

Throughout this paper, we will choose the parameter values in such a way that \( E_3 \) exists uniquely.

Additionally, system (5) admits an interior equilibrium point \( E^* = (x^*, y^*, z^*) \), where

\[
x^* = \frac{c\beta_1}{1-c}, \quad y^* = \beta_1 \left[ 1 - c - c\beta_1 + \frac{d\beta_2(1-c)}{h(c\beta_1 + (1-c)\beta_2)} \right],
\]  

(14)

\[
z^* = \frac{c\beta_1}{1-c} \left( 1 - d - \frac{d\beta_2(1-c)}{h(c\beta_1 + (1-c)\beta_2)} \right),
\]  

(15)

provided that

\[
c\beta_1(1-d) - d\beta_2(1-c) > 0 \quad \text{and} \quad \frac{1-c-c\beta_1}{(1-c)^2} > \frac{c\beta_1(1-d) - d\beta_2(1-c)}{h(c\beta_1 + (1-c)\beta_2)^2}.
\]  

(16)

hold. Also, we assume that

\[
\beta_1(1-c) - (1-c)^2 > 0.
\]  

(17)

Treating \( \beta_1, \beta_2, c, d \) as fixed parameters, we define a constant \( h^* \) by

\[
\begin{aligned}
\dot{h} &= (1-c)^2(\beta_1 - \beta_2)(c\beta_1 - d\beta_2) \\
&= (c\beta_1 + (1-c)\beta_2)^2(c\beta_1 + 1-c - c\beta_1 - c-1).
\end{aligned}
\]  

(18)

Under the assumptions (16) and (17), keeping \( \beta_1, \beta_2, c, d \) fixed and varying \( h \), the interior equilibrium point \( E^* \) undergoes a Hopf bifurcation at some \( h = h^* + O(\zeta) \) as \( \zeta \to 0 \) (see Sadhu, 2016 for details). The local stability of \( E^* \) is given by Proposition A.1 in Appendix A.

The Hopf bifurcation is said to be singular since the linearized center manifold system has a pair of singular eigenvalues \( \lambda(h, \zeta) \) at the Hopf bifurcation point \( h^* \) that is

\[
\lambda(h, \zeta) = \alpha(h, \zeta) + i\beta(h, \zeta)
\]  

so that \( \alpha(h, \zeta) = 0 \), \( \alpha(h, \zeta) \neq 0 \) with \( \beta(h, \zeta) \to \infty \) as \( \zeta \to 0 \) on the slow time scale and \( \alpha(h, \zeta) \neq 0 \) with \( \beta(h, \zeta) \to 0 \) as \( \zeta \to 0 \) on the fast time scale (Guckenheimer, 2008). The first Lyapunov coefficient \( l \) can be explicitly computed (see Eq. (19) in Sadhu, 2016). It can be shown that the speed of crossing the imaginary axis at the Hopf parameter point is nonzero, and hence by the Hopf bifurcation Theorem (Guckenheimer and Holmes, 1983), a family of periodic orbits bifurcate from \( E^* \) at \( h = 1 \cdot \mathcal{I} \), where the periodic orbits are small in size (exhibiting SAOs) and stable at their birth and grow as \( h \) decreases below \( h \), eventually growing into relaxation oscillations (LAOs) (Fig. 1). Depending on the parameter values, in the transition regime from small amplitude oscillations to relaxation oscillations, the small amplitude limit cycles may lose their stabilities and exhibit combinations of small and large amplitude oscillations, which are termed as mixed-mode oscillations.

6. Mixed mode oscillations

Mixed mode oscillations (MMOs) are defined as complex oscillatory patterns consisting of one or more small amplitude oscillations (SAOs) followed by large excursions of relaxation type, commonly known as large amplitude oscillations (LAOs). In the phase space, an MMO orbit can be viewed as a concatenation of SAOs that were born as a consequence of the singular Hopf bifurcation, and LAOs, which commonly occur in slow-fast systems due to the presence of “jump points” on the fold curves. MMOs are commonly denoted by \( (l_1^{+}, c_1^{+}) \), attributed to their time series, where each pair \( l_1^{+} \) denotes a segment of the MMO comprised of \( l_1 \) large oscillations, followed by \( c_1 \) small oscillations (see Figs. 6 and 7). Several distinct mechanisms from dynamical systems and bifurcation theory have been used to explain the mechanism of MMOs (see Desroches et al., 2012; Kuehn, 2011 and the references therein).

In systems with one fast and two slow variables, where the critical manifold is S-shaped, MMOs can occur when the desingularized system (9) admits a folded node equilibrium, and the full system admits the existence of a global return mechanism typically in the form of a relaxation cycle induced by the critical manifold. In Brons et al. (2006) (Theorem 2.1), sufficient conditions have been stated that ensure the existence of MMOs with signature \( 1^+ \) in systems with one fast and two slow variables.

It can be checked that system (5) meets all the conditions of Theorem 2.1 in Brons et al. (2006). In fact, the critical manifold \( \mathcal{M} \) has two attracting sheets \( S^+ \) and \( T^+ \) and two repelling sheets \( S^- \) and \( T^- \) separated by two fold curves \( F^+ \) and \( F^- \) (see Fig. 2(A) and Section 3). For suitable parameter values, (9) admits folded node singularities. At a folded node singularity, the requirement is that the eigenvalues \( \lambda_{S}, \lambda_{W} \) of the linearization of (9) satisfy the condition \( \lambda_{S} < \lambda_{W} < 0 \). The perturbation of the eigendirections corresponding to \( \lambda_{S}, \lambda_{W} \) gives rise to primary canards, known as the strong canard and the weak canard, respectively. The singular funnel refers to the region bounded by the strong canard and the fold curve \( F^- \). If a trajectory gets trapped in the singular funnel, it experiences some delay due to the rotational properties of the weak canard until it jumps to the other attracting sheet of the manifold \( T^- \). As shown in Fig. 2(B), there exists a return map \( \Pi : \Sigma^+ \to \Sigma^- \), where \( \Sigma^+ \) is a cross-section orthogonal to the x-axis away from the fold \( F^- \) such that for small \( z \), all trajectories that are projected into \( S^+ \) (a perturbation of the slow manifold \( S' \)) onto a neighborhood of the funnel intersects with \( \Sigma^- \). The map \( \Pi \) can be decomposed as \( \Pi = \Pi_{G} \circ \Pi_{L} \), where \( \Pi_{G} : \Sigma^+ \to \Sigma^- \) defines the local map near the fold and \( \Pi_{L} : \Sigma^+ \to \Sigma^- \) defines the global return map. The ratio of the eigenvalues \( \lambda_{S}/\lambda_{W} \) gives an estimate on the number of small oscillations that can occur in an \( 1^+ \) MMO pattern Desroches et al. (2012) and Kuehn (2011).

The folded singularities are equilibria of system (9) that lie on the fold curve \( F^- \), i.e., more precisely, the folded singularities
satisfy the equation

\[
\frac{y}{\beta_1 + x} + z \left( \frac{x}{\beta_1 + x} - c \right) + \frac{z}{\beta_2 + x} \left( \frac{x}{\beta_2 + x} - d - h \right) = 0, \quad (19)
\]

where \((x, y, z) \in \mathcal{F}^+\). In particular when \(\beta_1 \neq \beta_2\), from (19) it follows that the folded singularities are determined by the positive roots of the equation

\[
(1 - \beta_2 - 2x)(x(1 - c) - c\beta_1) + (2x + \beta_1 - 1)(x(1 - d) - d\beta_2) - h(\beta_2 + x)^3(2x + \beta_1 - 1)^2 = 0,
\]

where \(\frac{1 - \max(\beta_1, \beta_2)}{2} \leq x \leq \frac{1 - \min(\beta_1, \beta_2)}{2}\).
The interior equilibrium $E^* = (x^*, y^*, \phi(x^*, y^*))$ is a folded singularity if and only if it lies on the fold curve $F^+$. It follows from Proposition A.2 in Appendix A that this occurs when $h = h^*$, where $h^*$ is given by (18). At $h = h^*$, a transcritical bifurcation occurs, where $(x^*, y^*)$ interchanges its stability with a folded singularity. This is also termed as a saddle-node bifurcation of type II, where the center manifold corresponding to the zero eigenvalue of the folded node is transversal to the fold curve (Szmolyan and Wechselberger, 2001).

7. Transitions from SAO cycles to LAO cycles: sensitivity to parameters and initial conditions

In this section, we show numerical results pertaining to the analysis of system (5), using MATLAB (details provided in Remark A.3 in Appendix A), detailing the sensitivity of the system to parameters as well as to initial conditions during the transition from an SAO cycle to an LAO cycle. Note that system (5) has six independent ecological parameters, namely $\zeta, \beta_1, \beta_2, c, d$ and $h$. We primarily concentrate on the variation of one of the system parameters, namely $h$, which is associated to the density dependent mortality rate of the territorial predator due to the intraspecific competition for resources. We will assume that conditions (16) and (17) hold and that $h < h^*$, where $h^*$ is given by Eq. (18). We will show that the routes taken by the system on its transition from an SAO orbit to an LAO orbit can depend on the other parameters too. For example, the nature of the system can change dramatically if we slightly change the normalized per capita natural death rate $d$ of the territorial predator. The system can exhibit strong hysteresis (see Figs. 3 and 4) for $d = 0.3$ without the formation of MMOs or it can lead to the existence of orbits exhibiting MMOs (see Fig. 5), but without any hysteresis effect for...
d = 0.17, during its transition route from the SAOs dynamics to the LAOs dynamics. We elucidate the details in the following subsections. Even though the nature of the system is completely different in the two cases, in both cases we find strong sensitivity to the bifurcating parameter h and the phenomenon of bistability occurs for a certain range of h.

7.1. Transition from SAO cycles to LAO cycles via MMOs: sensitivity to the bifurcating parameter h

System (5) can be extremely sensitive to parameters. A small variation in one of the ecological parameters may altogether vary the structure as is evident from the orbital diagram shown in Fig. 5. Keeping the other parameter values fixed as in Fig. 5, and varying h, we note that the system may exhibit a variety of dynamics ranging from a small amplitude limit cycle to mixed mode oscillation patterns to relaxation oscillations. At h ≈ 2.6413, a supercritical singular Hopf bifurcation of the coexistence equilibrium point occurs, giving birth to a stable limit cycle which represents small periodic fluctuations of the populations. As h is gradually decreased, this limit cycle, with single periodicity, remains stable until about h ≈ 2.2679 where a period-doubling bifurcation of limit cycles occurs. Following a cascade of period-doubling bifurcations, the system reaches a chaotic state. Note that this period doubling route to chaos occurs over a very narrow interval of h. As h is further decreased, a saddle-node bifurcation of limit cycles occurs at h ≈ 2.25873 to render the bifurcated SAO orbits unstable, giving birth to a stable MMO pattern with signature 1^3. Fig. 7 shows a stable 1^3 MMO orbit and a chaotic attractor born as a result of a cascade of period doubling bifurcations of an SAO orbit. The transition from this chaotic attractor to a stable 1^3 MMO pattern occurs within an extremely small variation in h. The chaotic attractor does not exhibit relaxation oscillations, hence the populations at this state do not go through the extreme events of outbreaks and collapses.

It is noted that as h decreases and moves further away from the Hopf bifurcation value, the amplitudes of the limit cycles exhibiting small oscillations grow slowly, until a saddle node bifurcation of limit cycles occurs, following which a jump discontinuity in the amplitude of the oscillations occurs as shown in Figs. 5 and 7. At h ≈ 2.25872, a stable 1^3 MMO orbit exists. Since the global return loop of an MMO orbit is a reminiscent of an LAO orbit, the system now admits outbreaks and crashes with a periodicity of four units.

Subsequently the system remains in this stable 1^3 MMO state until this limit cycle goes through a transition to another stable MMO limit cycle of signature 1^2 via a combination of a reverse period doubling route (sometimes also referred to as “period halving” route) to chaos and a saddle node bifurcation of limit cycles. In reducing h, the system goes through similar transitions to form a sequence of stable MMOs: 1^3 → 1^2 → 1^1 → 2^1 → 1^0, where 1^0 represents an LAO orbit. This sequence is called a Farey sequence (Maselko and Swinney, 1986). In the transition process, the system also exhibits sensitivity to parameters (see Fig. 6). As shown in Fig. 5(A), we find that the regions of h that lead to stable MMO patterns are separated by narrow regions of chaotic MMOs.

On the other hand, reading the orbital diagram from left to right in Fig. 5(A), we note that for relatively smaller values of h, we find relaxation oscillations which represent periodic outbreaks and collapses with periodicity one. This limit cycle goes through a period doubling route to chaos with increasing h, again over a very narrow interval and then the system stabilizes to a stable MMO pattern with signature 2^1. The system remains in this state until again at some increasing value of h, the 2^1 limit cycle goes through another period doubling route to chaos over a very narrow interval and stabilizes to an MMO limit cycle of type 1^1. This repeats until the parameter value reaches the regime where MMOs no longer exist and the system only allows small oscillations limit cycles. To elucidate the sensitivity to the parameters, a zoomed version of the bifurcation diagram in Fig. 5(B) is shown to study the details of the transition from a stable 1^2 MMO pattern to a stable 1^3 MMO pattern. Sensitivity to the parameter in this transition regime is demonstrated through Fig. 6, where we show the 3-D phase space limit cycles (asymptotic attractor) and their corresponding time series. From Fig. 6(A) and (B), it follows that at h = 2.22634, the system admits a chaotic attractor which comprises of mixed signatures of types 1^2, 1^1 and 1^0. On the other hand for a very minute change in the mortality rate, i.e. at h = 2.22635, we find a very stable 1^1 MMO pattern as seen in Fig. 6(C) and (D).

7.2. Bistability: sensitivity to the bifurcating parameter h and initial conditions

For certain parameter values, system (5) exhibits bistability as shown in Figs. 3(B) and 8. We find the existence of at least two different kinds of bistabilities in our system. Fig. 8 shows that depending on the initial population densities, the three species can either get attracted to an 1^1 MMO orbit or to a chaotic MMO orbit.

Fig. 5. A 1-parameter orbital diagram in h of system (5) detailing the transition from SAOs to LAOs via MMOs. The other parameter values considered are ζ = 0.01, β1 = 0.5, β2 = 0.25, c = 0.38, and d = 0.17. The black dots (red) represent the local maxima (minima) of x. A Hopf bifurcation occurs at h = 2.6413 (not shown here), where a small periodic orbit (0^3) is born. The 0^3 periodic orbit goes through a period-doubling route to chaos and then stabilizes into a 1^3 MMO pattern, which then later loses stability and stabilizes into a 1^1 MMO pattern. The 1^1 orbit undergoes a series of reverse period-doubling and saddle-node bifurcations and stabilizes into a 2^1 MMO pattern which finally transforms to a relaxation oscillation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Note that in this case, all the ecological parameters are kept the same. Thus the system, at these parameter values, admits two basins of attraction, leading to the phenomenon of bistability. Numerical evidence also shows that the parameter regime over which this phenomenon of bistability occurs is very narrow. Hence in this situation, the three species may either eventually undergo outbreaks and collapses with a periodicity of two units (corresponding to the 1^1 cycle), or may prolong the time period between successive outbreaks and collapses without maintaining a fixed periodicity (corresponding to the chaotic MMO orbit). Moreover we note that the nature of the oscillations are different for the two attractors. The chaotic attractor is weakly chaotic as determined by the value of the positive Lyapunov exponent (see Fig. 8(F)). The time series is aperiodic, but the variations in the peaks across any two cycles is nominal, and thus the chaotic attractor seems to visit a limited region in the 3-D phase space.

As mentioned earlier, the transition path from an SAO cycle to an LAO cycle is not necessarily the same. For certain parameter values, we find that the transition from SAOs to LAOs is possible without the formation of MMOs, but the system exhibits strong hysteresis (and hence admits bistability) in the transition route as seen in Fig. 3. The system admits two stable and one unstable limit cycles in the hysteresis regime. One of the stable limit cycles exhibits SAOs and the other exhibits LAOs, while the unstable limit cycle displays oscillations of intermediate size amplitude. Away from the hysteresis region, the system admits a unique attractor (in this case it is either an SAO orbit or an LAO orbit). This leads to a hysteretic loop, standard in many branches of natural phenomena. The turning points of the hysteresis curve correspond to saddle node bifurcations of limit cycles (see Fig. 3(B)). For a minor change in the parameter value chosen close to the turning points, the asymptotic behavior of the population densities will be remarkably distinct. In other words, the species that were coexisting through the mechanism of a cyclic behavior without experiencing the extreme events of outbreaks and collapses will go through the extreme events or vice versa for a small variation in h near the turning points. Within the hysteresis regime, the population densities can also switch from one state to another as shown in Fig. 4, regardless of their initial densities. This kind of behavior is commonly known as “long term transient dynamics” (Morozov et al., 2016). The transient dynamics demonstrates the existence of two different limit cycles in the system, namely an SAO cycle and an LAO cycle, and a transition from one state to the other signifies an ecological regime change. The time when this regime shift occurs is a function of the bifurcating parameter (as seen in Fig. 4 for h = 1.5378 and 1.5381). It is crucial to understand the hysteresis regime in Fig. 3 as it is desirable for the three species to coexist exhibiting small fluctuations, than to undergo extremes of periodic outbreaks and collapses. Again we note than the parameter regimes over which this phenomenon of hysteresis occurs is very narrow and hence renders the system to extreme sensitivity to parameters.
In this paper, we have shown that two predators competing for their common prey with the assumption that the predators’ dynamics are slower than that of the prey can exhibit a wide variety of rich dynamics. Keeping all the parameters constant, except for the density dependent mortality rate of the territorial predator, we showed that under some conditions on the parameters, the three species coexist in an equilibrium state at a higher mortality rate of the territorial predator. However, as the mortality rate is decreased, the species coexist via small amplitude limit cycles which eventually grow into relaxation orbits. The small amplitude oscillations signify the small fluctuations in the densities of the three species while the large amplitude oscillations represent the sudden outbreak and crashes in the population density of the prey. The route taken during the transition from the SAOs to the LAOs depend on the other parameters as well. In one case, during the transition from SAOs to LAOs the system demonstrates the existence of mixed mode states which are the concatenations of SAOs and LAOs. The MMOs ecologically signify the adaptability of the species to prolong their cyclic sequences of outbreaks and collapses. In this transition process, the system can exhibit an extreme sensitivity to $h$, and thus any small change in the mortality rate can lead to uncertainties in predicting the long term behavior of the system. In another case, the system shows hysteresis, without going through the MMO state, and allows the existence of two different attractors simultaneously. This is termed as bistability. For parameter values leading to MMO orbits, the system can have multiple basins of attractions, thus again leading to multistability of the system.

The mathematical signatures that results from this deterministic model, can also be ecologically significant. For example, Fig. 7(A) represents a chaotic SAO attractor (where the original single period limit cycle exhibiting SAOs has been rendered

![Fig. 7 System (5) exhibiting sensitivity to the parameter $h$. The other parameter values considered are same as in Fig. 5. (E) and (F) represents the dynamics of the two largest Lyapunov exponents of the attractors (A) and (B), respectively. The presence of a positive Lyapunov exponent ($>0.12$) in (E) suggests that the attractor (A) is chaotic. State (A) is ecologically desirable as it prevents the populations to go through the extreme events of outbreaks and/or crashes. The initial scaled population densities considered are $x = 0.14$, $y = 0.1$, and $z = 0.15$.](image)
unstable) which is ecologically more stable and desirable, since this state prevents the populations from sudden outbreaks and crashes. With a minor change in the parameter value (in this case, at the sixth decimal place in the value of \( h \)), the species can undergo periodic outbreaks and collapses, and even though the corresponding limit cycle is stable, the ecological system is rendered to extremes of population densities and can have detrimental effects in general (can lead to pest outbreaks, disease transmissions, large scale defoliation, loss of farming, damage of stored food grains, etc.). Thus relatively larger values of \( h \), which measures the strength of intraspecific competition in \( z \), is ecologically more viable as it keeps a check on the exploitation pressure on the prey, leading the three species with a higher probability of co-existence by preventing the prey to go through an endemic state. Also note that an MMO pattern with a signature of the form \( 1^1 \) extends the time between two successive outbreaks, where \( s \) serves as a regulator. In other words, the frequency between two consecutive outbreaks is proportional to \( 1/s \). Chaotic mixed mode oscillations on the other hand fails to predict the occurrence of the next outbreak event. As shown in Fig. 6, a minor change in the parameter value can lead to a chaotic MMO from a stable MMO pattern, again representing the uncertainties in predictability of long term solutions.

A slight change in the ecological parameter \( d \), can change the nature of the system and sometimes can lead to a hysteresis loop as shown in Fig. 3. Here the system can also go through a sharp transition from LAOs to SAOs (see Fig. 4) and for ecological considerations, it would be desirable to keep the system in the SAO state. There have been examples of restoration of ecological properties via human intervention, the reintroduction of wolves in the Yellowstone national park being one of the examples. We hope that these kinds of studies will help in identifying different regimes of ecological extremes and suggest possible ways to prevent large scale outbreaks or crashes. It is interesting to note that the simple three-species-two-trophic model considered in this paper can reproduce several natural ecological phenomena such as the

![Fig. 8. System (5) exhibiting bistability at the parameter value \( h = 1.87 \). The other parameter values considered are \( \zeta = 0.1, \beta_1 = 0.5, \beta_2 = 0.15, c = 0.4, \) and \( d = 0.2 \). In (A) the attractor is an MMO orbit with signature \( 1^1 \), while (B) is a chaotic attractor with the largest Lyapunov exponent being positive (\( >0.016 \)) as shown in (F). Depending on the initial densities, the prey population can exhibit periodic outbreaks and collapses interspersed with small fluctuations in their densities with a periodicity of two units, or may exhibit aperiodic outbreaks and collapses. In (A), the initial conditions considered: \( (0.014, 0.1, 0.15) \), while in (B), the initial conditions considered: \( (0.013, 0.1, 0.15) \).](image-url)
dynamics of outbreaks and crashes, variations in the periodicity between the extreme outbreak events and also shows the extreme sensitivity of the system to both its ecological parameters and initial conditions. We note that the sensitivity to initial conditions in the regime exhibiting bistability as shown in Fig. 8 is intrinsically different from the regime where the system exhibits sensitivity to initial conditions due to the presence of a chaotic attractor (Fig. 6(A)). In the former case, keeping all the ecological parameters fixed, the system admits more than one attractor and the nature of the attractors are significantly different, while in the latter case, the system admits a global chaotic attractor. More investigations of some variations of this model are being undertaken, for example, introduction of scavengers in the ecosystem, consideration of environmental variations in the ecological parameters leading to a system of stochastic differential equations (Sadhu, 2016), etc. More complex signatures of MMOs with a variety of rich dynamics including existence of chaotic attractors and stronger bistability phenomenon (coexistence of chaotic SAOs and strongly modulated MMOs) have been observed in a two-trophic ecological model with two predators, one being a preying scavenger, competing for their common prey (Sadhu and Chakraborty Thakur, 2015). Other possible extensions to this study that are being undertaken are to investigate the spatial variations in the distribution of the populations densities.

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Appendix A

Remark A.2. The expression for $u_a(x^*, y^*, z^*)$ is given by

$$
\frac{u_a(x^*, y^*, z^*)}{\beta_1} = \frac{1}{(1 - c) - (1 - c)} \left( \frac{h x^*}{h} - 1 \right).
$$

Hence, under assumption (17), it follows that for $h > h^*$, $u_a(x^*, y^*, z^*) < 0$, whereas for $h < h^*$, $u_a(x^*, y^*, z^*) > 0$.

Proposition A.1. Keeping $\beta_1$, $\beta_2$, c, d fixed, under the assumptions (16) and (17), the interior equilibrium point $E^*$ is locally asymptotically stable if $f \geq h x^*$ for all $\xi > 0$, and unstable if $h < h^*$, provided $\xi > 0$ is sufficiently small. Moreover, system (5) undergoes a singular Hopf bifurcation at $h = h^*$ or $O(\xi)$ at a distance $O(\xi)$ away from the fold curve $F^*$.

The proof can be found in Sadhu (2016).

Proposition A.2. Keeping $\beta_1$, $\beta_2$, c and d fixed, and under the assumptions (16) and (17), the equilibrium point $E^*$ is asymptotically stable for $h > h^*$ and a saddle for $h < h^*$ of (9). At $h = h^*$, $E^*$ transforms to a folded singularity.

Proof. The Jacobian of (9) evaluated at $E^*$ is

$$
M = \begin{pmatrix}
-\frac{h y^* x^*}{(\beta_1 + x^*)^2} & \frac{h x^* y^*}{(\beta_2 + x^*)^2} & 0 \\
\frac{h x^* y^*}{(\beta_1 + x^*)^2} & -\frac{h x^* y^*}{(\beta_2 + x^*)^2} & 0 \\
0 & 0 & 0
\end{pmatrix}.
$$

Note that

$$
\det(M) = -u_a(x^*, y^*, z^*) \frac{h y^* x^*}{(\beta_1 + x^*)^2} \frac{h x^* y^*}{(\beta_2 + x^*)^2}.
$$

Hence it follows that if $u_a(x^*, y^*, z^*) < 0$ (i.e. when $h > h^*$), then both the eigenvalues of $M$ have negative real parts which implies that $(x^*, y^*)$ is locally asymptotically stable, whereas if $u_a(x^*, y^*, z^*) > 0$ (i.e. when $h < h^*$), then $(x^*, y^*)$ is a saddle. If $u_a(x^*, y^*, z^*) = 0$, then the equilibrium point of the full system (5) lies on the fold curve $F^*$ and hence is a folded singularity of the desingularized system (9). At this parameter value, the eigenvalues of $M$ are 0 and

$$
0 - \frac{h y^* x^*}{(\beta_1 + x^*)^2} \frac{h x^* y^*}{(\beta_2 + x^*)^2}.
$$

Note that $(x^*, y^*)$ changes its stability (from a stable node to a saddle with decreasing $h$) when it crosses the fold curve, i.e. when $h = h^*$, where $h^*$ is defined as in (18). □

Remark A.3. Most of the numerical simulations in this paper were done in MATLAB. We used classical ODE45 solver to numerically solve system (5). We iterated the trajectories for a time span of [0, 2000] and the last 60%, 7.5% and 25% of the trajectories were retained to generate Figs. 6–8, respectively. The relative and the absolute error tolerance were chosen to be $10^{-9}$ and $10^{-12}$, respectively.

References


Sadhu, S., 2016. Stochasticity Induced Mixed-Mode Oscillations and Distribution of Recurrent Outbreaks in an Ecosystem under review.

