Current Challenges for Mathematical Modelling of Cyclic Populations
BIRS 15frg202

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Nov 8, 2015 – Nov 15, 2015

1 Overview

The 8 members of the focussed research group met with the express purpose of writing a paper based on the successful 2013 BIRS 5-day workshop of the same title (BIRS 13w5151). During the Focussed Research Group, we submitted a paper proposal to Ecology Letters, a widely-read and high impact journal, which was accepted. It is therefore to this journal that we have submitted our paper (submission date: February 5th, 2016).

The paper is co-authored by virtually all of the attendees of the 2013 workshop, which include both mathematicians and ecologists. The goal of the original workshop was to look for mathematical innovation at the interface of theory and data. This interdisciplinary approach naturally carried over into the writing of the paper, which is thus a document that marries both mathematical and ecological points of view. From a mathematical perspective, the paper achieves two very important goals. First, the paper contains a wealth of information on cyclic population dynamics and models thereof, gathered in one place, that will serve as an invaluable resource to mathematicians interested in developing new theory. Second, as a publication in the journal Ecology, the paper will receive a wide readership within the theoretical ecology community. Consequently, the mathematical aspects of the paper will have the widest possible impact among ecologists, thus creating bridges between mathematicians and ecologists.

The following report is a summary of some of the highlights of the paper.

2 Abstract

Population cycling is a widespread phenomenon in ecology, observed across taxa in both lab and field conditions. Despite the theoretical and practical relevance of population cycles to our appreciation of ecological dynamics, both the mechanisms underlying such phenomena and their consequences for whole ecosystems remain incompletely understood. Our paper reviews recent theoretical work in this area. We explore how cycle loss or gain arises from environmental changes, as well as links between population cycles and eco-evolutionary dynamics, spatial synchrony, biodiversity maintenance, and from a management perspective,

the control of outbreaks. In particular, we emphasise the importance of stochasticity in modulating or creating cyclic behaviour, and suggest that future developments in the field will need to be intrinsically tied to a stochastic point of view.

3 Introduction

Almost a century after the publication of Elton's seminal paper on population cycles [1], we now understand and can recognize many different causes of oscillatory behavior [2, 12]. While the many successes in the study of population cycles warrant celebration, empirical research continues to reveal areas where our knowledge is far from complete. In our paper, we review how the interplay between data and mathematical theory has led and continues to lead to new insights into the mechanisms behind, and consequences of, cyclic population dynamics.

Although many populations show annual cycles driven by cyclic weather patterns, we focus here on sustained oscillations in population abundance that are not a mere reflection of seasonality. In particular, we highlight cases where connecting observation to theory has proven particularly challenging. For example, the observation that cycle amplitudes of many populations decrease along North-South gradients in the Northern Hemisphere has puzzled ecologists for decades [3]. Earlier mechanistic models suggested that this pattern is due to a geographical gradient in the predator community with a stabilizing influence of generalist predators in the South [4, 5]. However, several alternative explanations are possible, including changes in seasonality and prey life history [3, 6], partly because generalist predators do not always have a stabilising effect in model communities [7] and partly because spatial patterns are not clear-cut [6]. Recent mechanistic modeling shows that incorporating well-documented seasonal changes in prey fecundity can explain these patterns [8]. This example illustrates how empirical work guided theoretical development and how the use of varied assumptions in theoretical studies broadened our understanding of how and why population cycles arise.

Apart from uncertainties regarding the mechanisms causing population cycles, understanding the effects of cycles on ecosystems poses its own challenges. These effects can be rather dramatic as cyclic populations can be momentarily very abundant, and such highly fluctuating communities may play a role in biodiversity maintenance [9]. Furthermore, many open questions remain on the response of cycling populations to environmental changes [10] and, reciprocally, the control of pest outbreaks [11]. Understanding the ecosystem-level consequences of cycles is particularly important for populations that historically cycled but have recently become non-cyclic, and vice versa.

Arguably the best known cause of population cycles is the delayed negative feedback loop between a specialist predator and its prey [13, 12]. Historically, predator-prey theory has had a central role in the study of population cycles. Hence, we begin our review with this basic paradigm, and use it to subsequently introduce alternative causes of cycles. The basic structure of most predator-prey models is a set of differential equations for the prey density, N, and the predator density, P:

$$\frac{dN}{dt} = \underbrace{f(N)}_{\substack{\text{prey}\\\text{pop. growth}}} - \underbrace{g(N,P)}_{\substack{\text{functional}\\\text{response}}} P \tag{1}$$

$$\frac{dP}{dt} = \underbrace{E(g(N,P))}_{\substack{\text{numerical}\\\text{response}}} P - \underbrace{\mu P}_{\substack{\text{predator}\\\text{death}}} . \tag{2}$$

Here, g is the so-called functional response, which describes prey consumption rates as a function of prey and predator densities, E is the numerical response, which describes the conversion of consumed prey into predator population growth, and μ is the predator's per capita death rate. For certain functions E and g, sustained predator-prey oscillations are possible. These oscillations emerge because temporary increases in the prey population support a growing number of predators until over-predation causes both populations to crash, initiating a new cycle.

In our review, we emphasize successes that come from integrating iterative gains made in empirical and theoretical ecology, using modeling approaches that relax classical assumptions made in eqns (1)-(2) to yield novel insights. When discussing causes of populations cycles, we make a distinction between so-called qualitative and quantitative causes. We define qualitative causes as structural features of the dynamical system (e.g., predators, parasites) whose presence allows cycles to exist through a delayed negative feedback loop. On the other hand, quantitative features are quantifiable properties such as physiological or life history traits (e.g., high prey fecundity, saturating predator functional response), that make the system more or less prone to exhibit sustained oscillations.

4 Summary

The paper follows with a discussion of work on the snowshoe hare cycles, higher-dimensional systems including food webs and large communities, age or stage structure and maturation delays, interactions between evolution and population cycles, the role of stochasticity, and the problems of cycle gain and loss as well as ecosystem function and management, especially under global change.

Our paper synthesises recent research and promising avenues for modeling population cycles. Because some of the best-studied cycles involve consumer-resource interactions, we chose this mechanism as a starting point. However, our paper points out that cycles can often be influenced, or even originate, from processes other than the popular time-delayed negative feedback between consumers and resources [13]. More than two interacting species may sometimes be necessary for cycling to develop, as in some tritrophic systems or in non-transitive competition networks. Conversely, stage structure in a single species can induce additional delays leading to cycling [2]. Furthermore, random environmental forcing may induce quasi-periodic cycles in otherwise damped systems, or cause irregular fluctuations between alternative stable states. Cyclic patterns can also be altered by eco-evolutionary dynamics or age and food web structure. These examples illustrate the broad perspective that must be taken in studying the causality of population cycles.

The richness and intricacy of recent empirical observations point to a multitude of challenges in our theoretical understanding of population cycles. These challenges suggest several important directions for mathematical modeling. First, cyclic populations are embedded into large communities that can both affect cycles in non-intuitive ways and be affected by an abundant cyclic species (e.g., altered coexistence mechanisms). Therefore, analysis of multi-dimensional ecological time series and high-dimensional dynamical models are needed to understand cycles in their broader ecosystem-level context.

Second, consideration of behavioral responses, demographic structure and short-term evolution in individual species will be needed in order to explain cyclic population dynamics with greater accuracy. All of these factors can be influenced by environmental perturbations that are generally neither white noise nor purely periodic, but a mixture of both. Future mechanistic models for cyclic populations will therefore likely be demographically structured (perhaps down to the individual level), statistically fitted to rich data sets, and forced by stochastic environmental variation.

Third, spatial or temporal changes in cyclicity, and ways to control such changes, are vibrant areas of research. Much might be learned about mechanisms behind cycling by trying to both explain the variation in population dynamics of cyclic species and, in models or laboratory systems, control such dynamics.

Ecological modeling is not yet at the stage where it can forecast the response of cyclic populations to environmental changes in the field, except in a few cases, but a constant feedback between theory and empirical research will certainly help us move forward in that direction.

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