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Introduction

Understanding the role of environmental variation in population and community dynamics

This special issue of Theoretical Population Biology brings together a series of articles examining various aspects of environmental variation in population and community dynamics. Most natural environments are physically highly variable, and in response, birth rates, death rates, and other vital rates of populations, vary greatly in time and space. Yet the dominant focus in theoretical models of population and community dynamics has not been on how populations change in response to the physical environment, but on how populations depend on their own population densities or the population densities of other organisms.

Although it has long been recognized that temporal fluctuations in the physical environment are a major driver of population fluctuations, there has been scant theoretical attention to predicting the characteristics of the resultant population fluctuations. Instead, major attention has been given to the potential for, and properties of, population fluctuations driven solely by species interactions and single-species density-dependent feedback loops. There has been a fascination with endogenously driven cycling, and with the endogenously driven fluctuations termed deterministic chaos.

In the new field of spatial ecology, the dominant focus has been on homogeneous space in which spatial variation in population density results from an interaction between deterministic features of population dynamics and demographic stochasticity. In the older but increasingly active area of metapopulation and metacommunity theory, the emphasis has been on space that is patchily habitable, but otherwise physically homogeneous.

In some cases, ignoring variation in the physical environment is seen as the first step, or as adequate for mean tendencies. In other cases, there has been a fascination with the origin of spatial and temporal population patterns when the physical environment provides no pattern or template that could explain them. It is easy to understand the intellectual interest in pattern that arises with no template, but given the pervasive nature of variation in the physical environment, one must ask, Is this theoretical emphasis the most useful for truly understanding nature? Would it not be more useful to focus more on how physical environmental variation is translated into patterns exhibited by organisms?

In fact there is growing theoretical interest in understanding how pattern in the physical environment interacts with biology to yield the patterns that organisms show. Such patterns are not restricted to patterns of population variation in time and space in response to environmental variation, but include also patterns of population growth, persistence, stability, and coexistence on large spatial or temporal scales as functions of environmental variation on smaller scales. Many researchers appreciate that it is time to for the next step in which the role of physical environmental variation is a focus in theoretical models. There is also a growing realization that the details of how population and community patterns are affected by physical environmental pattern are every bit as fascinating as the details of endogenously generated pattern. Theoretical evidence to date suggests that many population and community patterns represent intricate interactions between biology and variation in the physical environment. Such interactions are not only important for understanding nature but are also intellectually rich. This special issue of Theoretical Population Biology has been put together to display some of this richness and to demonstrate new techniques that are making this fascinating area broadly accessible.

The first three articles expand the ranges of techniques and models available for studying the effects of environmental heterogeneity. Bolker extends his spatial moment equations to include spatial heterogeneity in the physical environment, and demonstrates positive effects of environmental heterogeneity on population viability. Thomson and Ellner extend, to environmentally heterogeneous contexts, their pair-edge approach for understanding the persistence and spatial spread of invading organisms. In the process, they demonstrate major effects of environmental heterogeneity on the speed with which an invading organism spreads across a landscape. Hanski and Heino work with a metapopulation model that includes a variety of effects of heterogeneity in space, and consider simultaneous ecological and evolutionary dynamics. Their model is strongly grounded in a particular empirical system, a

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butterfly metapopulation, where environmental features are relative abundances of host plants, patch area, and connectivity with other patches.

The next two articles focus on the role of the structure of environmental variation on population dynamics. Kinezaki et al. examine invasion of an organism in a two-dimensional landscape in which the physical environment varies regularly in one dimension. They demonstrate that the shape and speed of the invasion front vary greatly with the magnitude and spatial scale of environmental variation. Haccou and Vatutin are also interested in invasions, but they focus on establishment of a local population, not spatial spread, and the variation in question is temporal environmental variation structured by temporal correlations, which they demonstrate have major effects on the likelihood that an invader will establish.

Holt et al. also investigate the effects of the temporal structuring of environmental variation but for mean population densities in the specific case of a sink habitat where an organism must rely on immigration for persistence. Holt et al. demonstrate that variation in the per capita growth rate increases mean density in a sink habitat to a degree dependent on the temporal correlation of growth-rate fluctuations. Exhibited explicitly here is an important theme repeated in many investigations of environmental variation: Nonlinear relationships between critical variables interact with environmental variation to determine the effect that environmental variation has on the question of interest.

The next three articles focus on species coexistence in variable environments. These articles could be characterized as investigations of spatial and temporal niche differentiation, but they elucidate important details by which such differentiation promotes species coexistence. Dewi and Chesson examine temporal niches in the lottery model and show how the introduction of age structure affects coexistence and the long-term growth rates of invaders. Using a class of models of recruitment variation that includes the lottery model, Chesson takes up the question of how coexistence mechanisms involving temporal fluctuations can be quantified and tested. Muko and Iwasa use a spatial version of the lottery model to demonstrate that limited dispersal greatly enhances the effectiveness by which spatial variation in competitive dominance promotes species coexistence.

The final two articles are investigations of how temporal environmental variation is translated into population fluctuations in multispecies systems. Ripa and Ives demonstrate important interactive effects between the correlation structure of environment fluctuations and the nature of species interactions. They provide simple techniques for understanding these effects. Pascual and Mazzega examine the rich interplay between nonlinear population dynamics and temporal environmental variability in a predator-prey model. They show that the resulting population dynamics can look like chaos, as defined for noisy systems, and emphasize the care necessary for interpreting the nature of the fluctuations seen in short time series of population densities.

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