Revisiting the logistic map: A closer look at the dynamics of a classic chaotic population model with ecologically realistic spatial structure and dispersal

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ABSTRACT

There is an ongoing debate about the applicability of chaotic and nonlinear models to ecological systems. Initial introduction of chaotic population models to the ecological literature was largely theoretical in nature and difficult to apply to real-world systems. Here, we build upon and expand prior work by performing an in-depth examination of the dynamical complexities of a spatially explicit chaotic population, within an ecologically applicable modeling framework. We pair a classic chaotic growth model (the logistic map) with explicit dispersal length scale and shape via a Gaussian dispersal kernel. Spatio-temporal heterogeneity is incorporated by applying stochastic perturbations throughout the spatial domain. We witness a variety of population dynamics dependent on the growth rate, dispersal distance, and domain size. Dispersal serves to eliminate chaotic population behavior for many of the parameter combinations tested. The model displays extreme sensitivity to changes in growth rate, dispersal distance, or domain size, but is robust to low-level stochastic population perturbations. Large and temporally consistent perturbations can lead to a change in population dynamics. Frequent switching occurs between chaotic/non-chaotic behaviors as dispersal distance, domain size, or growth rate increases. Small changes in these parameters are easy to imagine in real populations, and understanding or anticipating the abrupt resulting shifts in population dynamics is important for population management and conservation.

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1. Introduction

Although the chaotic systems literature has grown over the past several decades, the bulk of it resides in the physical sciences (e.g. fluid dynamics) and is neither written for, nor read by ecologists. Early conceptual papers introduced chaotic concepts to the ecological literature (e.g., May, 1973; May, 1976; Schaffer, 1985; Hastings, 1993; Hastings et al., 1993) but computational limitations at the time restricted such research to simple models that are difficult to apply to real populations. Here, we revisit and build upon these earlier models by performing a closer examination of a chaotic population within an ecologically applicable framework. We create a chaotic growth-dispersal model with an explicit 1-dimensional spatial component, and detail dynamics for a large parameter space, examine the fractal-like boundaries between differing population dynamics regimes, and add stochastic elements to simulate spatio-temporal heterogeneity and observe the interactions between chaotic dynamics and stochasticity. In this way we add to the ecologists' chaotic toolbox by detailing the spectrum of behaviors possible for such a system. Incorporating enough ecologically realistic components insures that the model dynamics can be compared to the dynamics of real populations.

Chaos has been detected in many and diverse biological systems, such as the spread of infectious disease (Sugihara and May, 1990), marine environments (Glaser et al., 2014), and plant growth dynamics (Billings et al., 2015). These studies focus on detection of chaos as a way to understand system stability and future behavior. There are few examples of directly modeled

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nonlinear populations, but Cushing et al. (2003) provide a thorough analysis of the nonlinear dynamics of the flour beetle, with both a nonlinear population model and actual experimental data to verify the model. We envision our model as a stepping stone for further direct applications of nonlinear models to real populations, as our generalized model provides a mechanism for deeper understanding of the full range of dynamics present in a chaotic population, as well as a means of understanding the biological cause of behavioral changes in a population as ecologically relevant parameters change.

For example, harvesting of cod affects both the growth rate and dispersal of the population along its entire range. For cod in the Gulf of Maine, surplus production models illustrate how growth rates first increase (due to density dependence) to compensate for increased harvesting, and then decrease if the population is overfished. In heavily depleted, and therefore likely chaotic conditions (Glaser et al., 2014), the effects of this variability on cod dispersal (and, thus, availability to the fishery) are poorly understood and can result in management failures (NEFSC 55th SAW, 2013). For this reason, a better method for understanding changes in movement and dispersal in chaotic populations is essential to sustainable management.

The earliest introduction of chaotic population models to the ecological literature focused on zero-dimensional (zero spatial dimension, one-dimensional phase space) single-species models (May, 1973, 1976). Subsequent models added spatial dimension in the form of discrete patches, where a certain percentage of the population in one patch disperses to the adjacent patch(es) with each iteration of the model (Hastings, 1993; Kaneko, 1984; Willeboordse, 2003; White and White, 2005). When enough patches are incorporated, the model simulates a growth and diffusive dispersal system. However, such models employ numerical diffusion as a dispersal mechanism, which permits limited diffusion per iteration/generation, as the coupling strength parameter must remain small for the validity of the system (Kaneko, 1989). A subset of the literature expands the diffusive range by exploring globally coupled patches (Kaneko, 1992; Solé et al., 1992; Willeboordse, 2003, 2002), but these are limited to an even smaller portion of the population diffusing into neighboring patches, and each patch receives a uniform proportion of the population regardless of its proximity to the parent patch. Additionally, such models largely employ periodic boundary conditions, an ecologically unrealistic feature (Aiken and Navarrete, 2014).

Improvements upon the numerical diffusion models were made when the diffusive dispersal mechanisms were replaced with dispersal kernels (e.g. Ruxton and Doebeli, 1996; Doebeli and Ruxton, 1998; Saravia et al., 2000; Labra et al., 2003). The kernels provide a more realistic dispersal scenario than discretized diffusion, as the dispersal distance is easily changed, and neighboring discrete locations generally receive a larger percentage of neighboring populations than far away locations.

Many of the aforementioned models share a common model of growth: the logistic map. The logistic map represents one of the simplest difference equations with chaotic dynamics, popularized by Robert May (1976) as a discretization of the logistic equation:

$$p_{n+1} = ap_n(1 - p_n),$$

where a is the growth parameter, n is the discrete time index, and p is a dimensionless population (in May's model, for p outside of the range $0 < p < 1$ solutions will diverge and therefore lose physical meaning). There is no spatial structure in this model. This "classic logistic map" can represent an organism that reproduces in discrete generations with no overlap (e.g., annual plants, some anadromous fish, some benthic invertebrates, and many insect populations). An array of complicated population dynamics result

from this equation, depending on the growth parameter. For $1 < a < 3$ the population reaches steady state after the initial growth period. As a increases, the population experiences a period doubling bifurcation cascade until eventually descending into chaos. Doubling begins for $a \approx 3$ and the onset of chaos begins for $a \approx 3.57$ (May, 1976). Beyond the beginning of chaos, the logistic map has pockets of periodicity at special values of $3.57 < a < 4$, e.g., $a = 3.835$ exhibits a period-3 population cycle (Strogatz, 1994). The equation has some ecologically impractical constraints, such as population extinction for $a > 4$ and $p > 1$ (May, 1976).

A family of similarly simplistic models exhibit great dynamical complexity (see May and Oster, 1976), and the Ricker model displays qualitatively indistinguishable dynamics to the logistic map (e.g., Andersen, 1991). Indeed, the bifurcation diagrams for the two models look incredibly similar. Besides displaying chaotic dynamics over a particular parameter range, these models exhibit other interesting dynamical behaviors, such as long periods of transience (e.g. Hastings and Higgins, 1994; Saravia et al., 2000; Labra et al., 2003).

Our model starts with the classic logistic map as one of the simplest models of growth. We employ a normalized Gaussian kernel as the dispersal mechanism, which is a more flexible and ecologically applicable dispersal framework than discretized diffusion (and dispersal kernels have a long and established history of use in the ecological modeling literature, e.g., Chesson and Lee, 2005). The dispersal kernel has several advantages, such as decoupling the scale and length of dispersal distance from the spacing of discrete patches, as well as providing a mechanism to easily change the dispersal distance.

Gaussian kernels are found in seed dispersal models (e.g., Clark et al., 1999), planktonic dispersal models (e.g., Byers and Pringle, 2006), and myriad other ecological models. Generally, diffusive-type dispersal effectively models the random dispersal of offspring away from parents. As the number of random movements away from the parent increases, the shape of these random movements forms a Gaussian. This is called the "random walk" model, and is appropriate for small animals such as insects (Skellam, 1951). Diffusive-type spread also applies to animals moving over favorable terrain over multiple generations (Krebs, 2009; Pielou, 1979), or immobile species transported by wind or water (Okubo, 1980).

Although diffusive-type dispersal is a useful simplification, there exist many alternative dispersal mechanisms, e.g., non-Gaussian kernels (Kot et al., 1996; Chesson and Lee, 2005; Pringle et al., 2009) and asymmetrical advective dispersal (Okubo, 1980; Byers and Pringle, 2006; Lutscher et al., 2010); these will be included in our future work. However, for this paper, we start with the simplest case and limit ourselves to the symmetrical dispersal-only model. Additionally, we chose to work in a one-dimensional domain, which is an applicable simplification for certain environments, including edge communities bounded by two distinct habitats such as riparian, littoral or coastal areas.

We test ecologically relevant absorbing (dissipative) boundary conditions, and these boundary conditions serve as the basis for the bulk of our ecological analysis. We additionally test periodic boundary conditions to provide deeper insight and as an illustrative comparison with previous literature and with the classic logistic map. However, these boundaries are not ecologically useful in most real-world systems, as opposite ends of a domain are neither correlated nor connected. Furthermore, periodic boundaries cannot serve as a proxy for an infinite domain. An infinite domain naturally explores the limit of small dispersal (with respect to domain size). Because our dispersal distance expresses length relative to domain size, larger dispersal distances would effectively model the biologically implausible case of infinite dispersal. Boundaries in which 5% of the population survives over the boundary edge and