



Incorporating Spatial Variation in Density Enhances the Stability of Simple Population Dynamics Models

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Simple discrete time models of population growth admit a wide variety of dynamic behaviors, including population cycles and chaos. Yet studies of natural and laboratory populations typically reveal their dynamics to be relatively stable. Many explanations for the apparent rarity of unstable or chaotic behavior in real populations have been developed, including the possible stabilizing roles of migration, refugia, abrupt density-dependence, and genetic variation in sensitivity to density. We develop a theoretical framework for incorporating random spatial variation in density into simple models of population growth, and apply this approach to two commonly used models in ecology: the Ricker and Hassell maps. We show that the incorporation of spatial density variation into both these models has a strong stabilizing influence on their dynamic behavior, and leads to their exhibiting stable point equilibria or stable limit cycles over a relatively much larger range of parameter values. We suggest that one reason why chaotic population dynamics are less common than the simple models indicate is, these models typically neglect the potentially stabilizing role of spatial variation in density.

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Introduction

Following the demonstration that even very simple first-order difference equation models of population growth can exhibit a wide range of dynamic behaviors, from stable points to chaos (May, 1974), many studies of dynamic behavior in both laboratory and wild populations of animals have been undertaken in order to assess how common complex dynamic behaviors like chaos may be in real populations (Hassell *et al.*, 1976; Thomas *et al.*, 1980; Mueller & Ayala, 1981;

Turchin & Taylor, 1992; Godfray & Grenfell, 1993; Hastings *et al.*, 1993; Dennis *et al.*, 1995; Ellner & Turchin, 1995; Stenseth *et al.*, 1996). Although some of the more recent studies do suggest that dynamic behavior other than an approach to a stable point may be more common than thought earlier, the overall impression is that unstable equilibria and chaos seem to be relatively uncommon. Broadly speaking, explanations for this apparent anomaly have, been of two kinds: evolutionary and non-evolutionary.

Evolutionary explanations are often based upon group selectionist arguments resting on the premise that populations with demographic properties resulting in severe fluctuations in numbers would tend to go extinct, and that, therefore, extant populations would be precisely

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those that happened to have relatively stable dynamics (Thomas *et al.*, 1980; Berryman & Millstein, 1989). On the other hand, many workers have also argued that, under a variety of biologically meaningful scenarios, selection at the individual level may be expected to give rise to the evolution of enhanced stability (Mueller & Ayala, 1981; Hansen, 1992; Mueller & Huynh, 1994; Doebeli & Koella, 1995; Ebenman *et al.*, 1996), although this notion is supported by very meager empirical evidence (Stokes *et al.*, 1988; but see also Mueller *et al.*, 2000; Mueller & Joshi, 2000).

Non-evolutionary explanations for the preponderance of stable populations are, if anything, more varied than evolutionary ones. The maintenance regimes typically used for laboratory populations of *Tribolium* and *Drosophila* have been shown to result in relatively stable dynamics, whereas experimental alterations to the laboratory ecology of such cultures can give rise to unstable dynamic behavior (Dennis *et al.*, 1995; Mueller & Huynh, 1994; Sheeba & Joshi, 1998; Mueller *et al.*, 2000). Incorporation of more realistic elements into simple population dynamics models can also enhance the range of parameter values permitting stable behavior. Constant levels of immigration have major stabilizing impact on the behavior of the Ricker map (Sinha & Parthasarathy, 1994). Constant emigration can, depending on the level of emigration, either cause extinction or stabilize the dynamics of the Ricker map at high intrinsic growth rates that would normally yield extinction (Sinha & Parthasarathy, 1996). Migration among groups of populations in coupled map lattice models, where subpopulation dynamics are governed by simple unidimensional maps, can also stabilize subpopulation dynamics (Doebeli, 1995; Parthasarathy & Sinha, 1995). Similarly, the existence of a minimum size, below which the population cannot fall, can also stabilize population dynamics, at least under certain conditions (Ruxton & Rohani, 1998). Ecologically, such "floors" could be a result of spatial refugia, the existence of an invulnerable age-class, or because density-dependent regulatory mechanisms set in abruptly above a certain threshold (Getz, 1996). Within-population genetic variation in sensitivity to density can also stabilize population dynamics (Doebeli & De Jong, 1999).

When thinking about the density of real populations, it is often useful to visualize space as being a lattice comprising of sites that can be either occupied or vacant (Auerbach & Shmida, 1987), a view that directly leads to a distinction being drawn between the mean density of a population and the local density actually experienced by an individual (Lloyd, 1967). Clearly, the important factor in determining the level at which density-dependent regulatory mechanisms operate will, in this case, be the local density, which is likely to be highly variable unless the spatial distribution of individuals is absolutely uniform. Consequently, analyses of lattice models that do not take local density into account are likely to yield misleading results (Matsuda *et al.*, 1992; Harada & Iwasa, 1994). In this paper, we develop an approach to incorporate random spatial variation in density into two commonly used simple models of population growth, the Ricker & Hassell maps (Ricker, 1954; Hassell *et al.*, 1976), and show that the stability properties of these models are greatly altered by incorporation of spatial variation in density.

The Model

Before developing the modified versions of the Ricker & Hassell maps, we briefly discuss the motivation and rationale for the specific form in which we incorporate spatial variation in density into these population dynamics models. Consider a population such that its habitat consists of n patches (or area, or volume, as the case may be). Further, let the total number of individuals be mn , so that the mean number of individuals per patch is m , with no restriction on how many individuals a patch may accommodate; the only assumption made is that the distribution of individuals among the patches is random. It follows, then, that the probability that a patch is occupied by k individuals equals $((mn)!(n-1)!^{mn-k})/((k)!(mn-k)!(n)^{mn})$, from which, letting $n \rightarrow \infty$, we obtain the Poisson distribution,

$$P[m, i] = \frac{e^{-m} m^i}{(i)!}. \quad (1)$$

The Poisson distribution gives the probability of i individuals being present in one patch, given

that the mean number is m individuals per patch. When dealing with models of density-dependent growth, however, we require a continuous version of the Poisson distribution because the variable to be distributed, the population density x , is continuous. For a more intuitive perspective, imagine a population distributed over a large area. The global density can be estimated by dividing the total number of individuals by the total number of patches. One could envisage doing the same to calculate local densities, which are the ultimate quantities we are interested in. However, as population size gets smaller, it becomes increasingly difficult to make accurate estimates of local densities because the number of individuals likely to be occupying a patch decreases dramatically with patch size. Ultimately, we are faced with local densities as quantities defined on point areas (volumes), which clearly cannot be estimated directly. One way out of this problem is to assume that local density is a random variable, with the mean equal to the global density. This assumption permits estimation of the local density of the population as a function defined at every point in the habitat, from which the density function over any region can be obtained by integration.

In order to incorporate spatial variation into population dynamics models in the manner described above, we assume that the population be randomly distributed spatially at every generation. This may appear to be an unduly restrictive and unnatural assumption. We note, however, that in the framework we develop here, the population dynamic models are to be applied to point local densities. On such a small spatial scale, some amount of micro-spatial migration will inevitably occur even in sessile organisms (through propagule dispersal), and it is not unreasonable to assume that migration at this fine spatial scale will be essentially random.

The kind of continuous density function we discussed in the preceding paragraphs can be obtained by letting $i \rightarrow \infty$ in eqn (1), and applying Stirling's formula

$$\lim_{n \rightarrow \infty} \frac{(n)!}{(\sqrt{2n\pi})(n/e)^n} = 1,$$

to yield

$$P[m, y] = \frac{e^{-m}(me/y)^y}{\sqrt{2\pi y}}, \quad (2)$$

where y is the averaging parameter. This means that while the expected (average) value of the random variable is m , it can actually take values ranging from 0 to ∞ , and the probability that it takes the value y is given by $P[m, y]$. Simple models of population dynamics are typically of the form $dx/dt = f(x)$, for continuous time models, and $x_{t+1} = g(x_t)$ for discrete time models, where x is the population density. What is typically meant by that is that x is the average population density over the entire population range space, and that the whole population exhibits dynamical behaviour governed by this single average value. Incorporating random spatial variation in density as represented by eqn (2) into such simple models would yield equations of the form

$$dx/dt = \sum_y n_y f(y), \quad (3a)$$

$$x_{t+1} = \sum_y n_y f(y) \quad (3b)$$

where n_y is the population size in the patch y , for all patches y , since y is the space-averaging parameter. Since we do not know this number in each patch *a priori*, we use an appropriate probability distribution estimate of the number of patches with a particular population size n_y . On normalizing, this becomes a probability density function $P[m, y]$ with the reasonable assumption made that the distribution depends on the overall average density m . Then we let the patch size go to zero, since this would enable us to obtain a truly local, indeed point-wise, definition of local population density.

It could be argued that the function thus obtained is a mere mathematical artifact and has no biological significance. However, it should be noted that the number of individuals per non-zero area patch can be obtained simply by integrating the equation over a suitable range. This representation of the system is, thus, a finer

representation than the original one we started off with, in which the population was divided into patches. Without losing accuracy, we have gained the advantage of mathematical tractability.

Carrying out the limiting process described above yields equations of the form

$$\frac{dx}{dt} = \int_{y=0+}^{y=\infty} P[x, y] f(y) dy, \quad (4a)$$

$$x_{t+1} = \int_{y=0+}^{y=\infty} P[x_t, y] g(y) dy \quad (4b)$$

for continuous and discrete time, respectively. It should be noted here that the integrals on the RHS of eqns (4a) and (4b) will typically return the original functions $f(x)$, $g(x)$, only for models of exponential growth wherein $f(x) = cx$ (c constant). Clearly, in models incorporating some

density-dependent feedback terms, each patch will follow its own density-dependent growth rate, and the various density-dependent functions will not average out across patches to match the growth rate determined by the average density of the population. In eqns (4a) and (4b), the integrating procedure assumes a random (Poisson) distribution of the population density among patches in every generation, and then deterministically calculates the growth in the population.

We applied this integration procedure to two widely used simple discrete time population dynamic models, namely the Ricker & Hassell maps, in order to examine how the stability properties of these models may be affected by incorporating spatial variation in density. The standard form of the Ricker map, with population density scaled by carrying capacity, is

$$x_{t+1} = x_t e^{r(1-x_t)}. \quad (5)$$

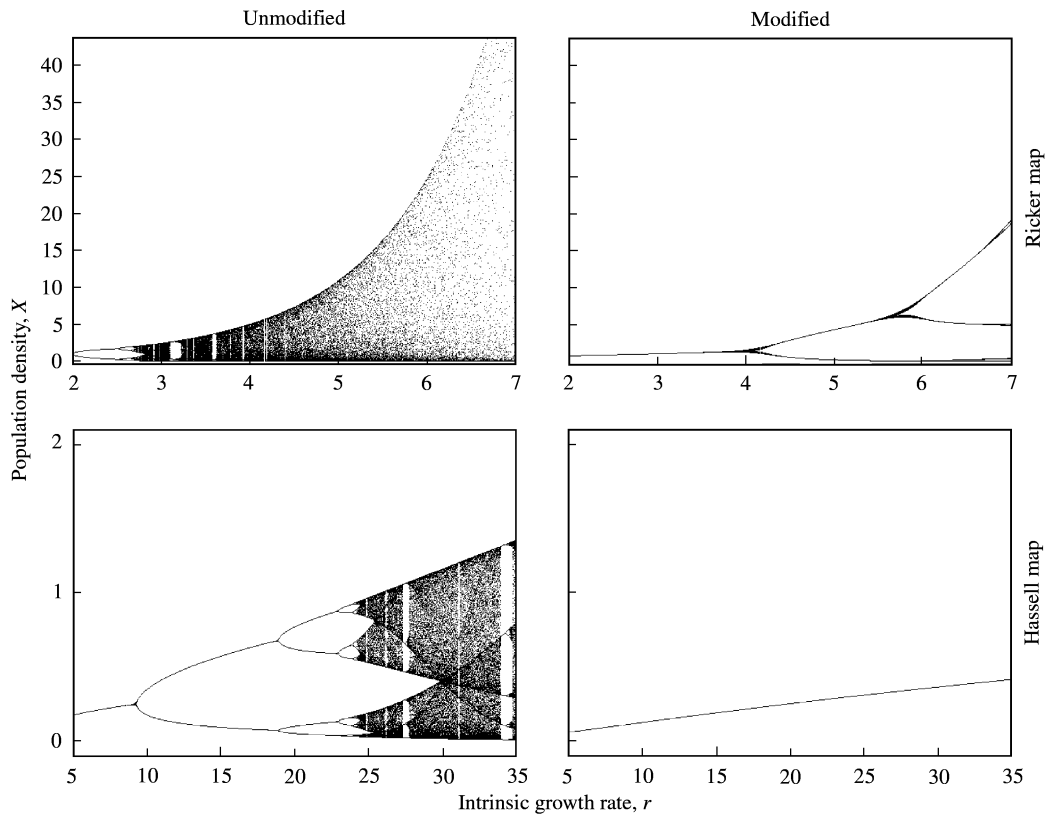


FIG. 1. Bifurcation diagrams depicting the stabilizing effect of incorporating random spatial variation in density into the Ricker and Hassell maps. The unmodified Ricker and Hassell plots were obtained by iterating eqns (5) and (7), respectively, and plotting the 125th–400th to 400th iterates, and the modified versions by doing the same with eqns (6) and (8). All functions were integrated linearly with a step size of 0.01. The value of γ for simulations of the modified and unmodified Hassell map was fixed at 10.

When the random spatial variation in density is incorporated into the Ricker map, we obtain

$$x_{t+1} = \int_{y=0+}^{y=\infty} \frac{1}{\sqrt{2\pi y}} \left(\frac{ex_t}{y}\right)^y ye^{r(1-y)} dy, \quad (6)$$

which is henceforth referred to as the modified Ricker map. Similarly, the Hassell map, with population density scaled by carrying capacity, can be represented by

$$x_{t+1} = \frac{rx_t}{(1+x_t)^y}, \quad (7)$$

and upon incorporating random spatial variation in density into the Hassell map, we obtain

$$x_{t+1} = \int_{y=0+}^{y=\infty} \frac{1}{\sqrt{2\pi y}} \left(\frac{ex_t}{y}\right)^y \frac{ry}{(1+y)^y} dy, \quad (8)$$

which is henceforth referred to as the modified Hassell map. We examined the behavior of the unmodified and modified Ricker & Hassell maps by simulating the dynamics of populations following these models across a range of parameter values. All programs were written in Borland Turbo C and implemented on a Pentium machine.

Results and Discussion

In their unmodified form, both the Ricker and Hassell maps exhibit a period doubling route to chaos, with the Hassell map tending to show stable behavior (point equilibria or stable cycles) over a relatively greater range of parameter values (Fig. 1). In general, the bifurcations in the case of the Hassell map are less violent than in the case of the Ricker map, because the latter, being governed by the exponential function, is highly sensitive to small changes around zero. Since eqn (5) is of the form $x_{t+1} = x_t e^{r(1-x_t)}$, even

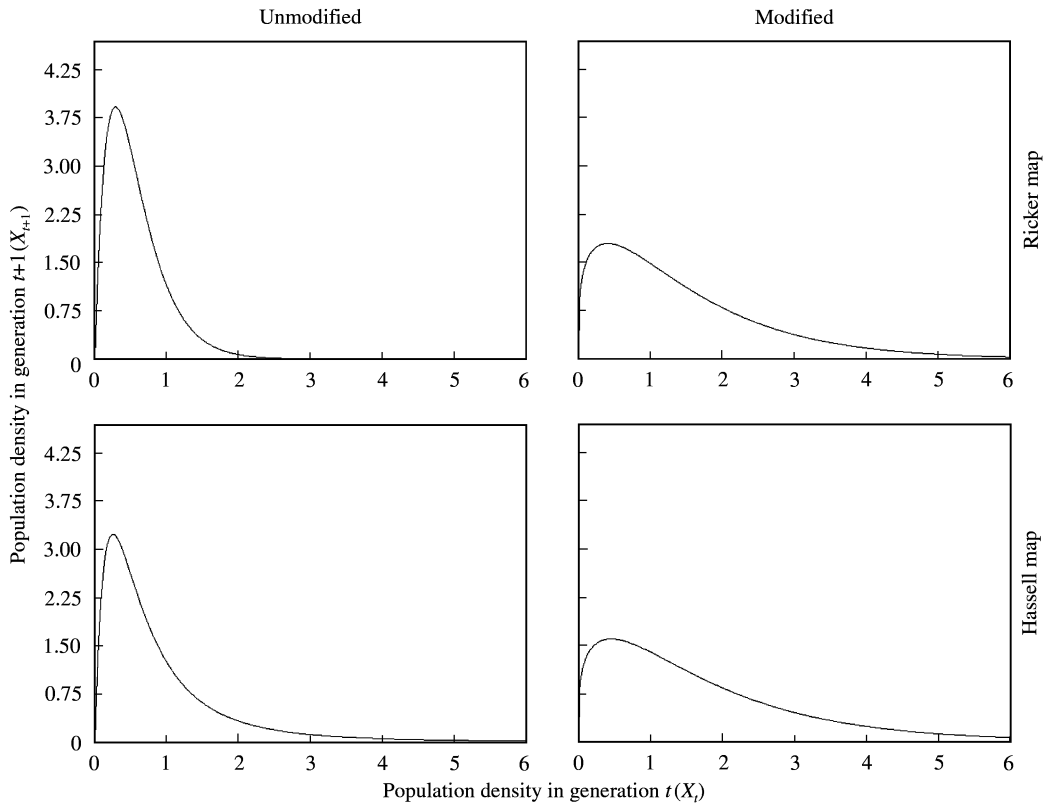


FIG. 2. Plots of the relationship between population densities at successive generations, depicting the stabilizing effect of incorporating random spatial variation in density into the Ricker and Hassell maps. All details are as in Fig. 1.

if x_t is small but not too close to zero, x_{t+1} can be very large for large values of r .

More interestingly, both the Hassell and Ricker maps tend to exhibit greater stability over a larger range of r values in their modified form, when the spatial distribution averaging process is factored in Fig. 1. Essentially, the averaging process tends to flatten out the successive generation density graph for both models (Fig. 2), resulting in a smaller negative slope to the right of the inflection point and, thus, to increased stability. The modified Hassell map, in particular, exhibits a stable point equilibrium for a wide range of r values (Fig. 1), and this enhanced stability is clearly reflected in the relatively smaller negative slope to the right of the inflection point in the successive generation density plot for the modified Hassell map (Fig. 2). Intuitively, this increased stability can be viewed as being due to the fact that severe reductions in local population growth rates in regions of locally very high density, will tend to be compensated for by higher growth rates in regions of local low density, coupled with a random redistribution of local (point) densities each generation.

Overall, it is clear that incorporating random spatial variation in local density into the commonly used Ricker and Hassell maps has a major stabilizing influence on the dynamics of these models, especially in the case of the Hassell map. It may be that one of the reasons we do not see chaotic behavior in real biological populations as often as we might expect based on studying simple population growth models is the models do not incorporate spatial variation in population density, even though such variation is likely to be the norm in natural populations.

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