Nonspreading Solutions and Patch Formation in An Integro-Difference Model With a Strong Allee Effect and Overcompensation

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1 Nonspreading Solutions and Patch Formation in an
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3 and Overcompensation

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Abstract

Previous work involving integro-difference equations of a single species in a homogeneous environment has emphasized spreading behaviour in unbounded habitats. We show that under suitable conditions, a simple scalar integro-difference equation incorporating a strong Allee effect and overcompensation can produce solutions where the population persists in an essentially bounded domain without spread despite the homogeneity of the environment. These solutions are robust in that they occupy a region of full measure in the parameter space. We develop bifurcation diagrams showing various patterns of nonspreading solutions from stable equilibria, period two, to chaos. We show that from a relatively uniform initial density with small stochastic perturbations a population consisting of multiple isolated patches can emerge. In ecological terms this work suggests a novel endogenous mechanism for the creation of patch boundaries.

Key words. Integro-difference equation, Allee effect, Overcompensation, Nonspreading solution.

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2 Introduction

As spatial ecology has developed, a great variety of mathematical modeling approaches have been used to study questions at various levels of complexity. Integro-difference equations, which feature a continuous space but discrete time formulation, have proven especially useful for studying questions about population-level processes and species interactions. For example, integro-difference models have been used to predict changes in gene frequency [33, 34, 35, 45, 51], and characterize species' spatial dynamics [18, 19, 20, 21, 24, 25, 26, 31, 39]. Because integro-difference equations often admit traveling wave solutions of various kinds, a primary focus in many of these studies has been spatial spread (e.g., expansion of a population or a

favorable allele). Examples include scenarios in which population fronts can expand spatially in an accelerating fashion [27] and cases where one or more species can (or cannot) outrun the pace of environmental change [22, 30, 53].

Here, we adopt a very different perspective in that we use an integro-difference formulation to study non-spreading solutions. Roughly speaking, a nonspreading solution is a solution which persists in a virtually bounded domain for all generations without expanding its spatial range. Such a solution describes ‘invasion pinning’ that has been investigated for coupled ordinary differential systems in a discrete (patch) environment (see Keitt et al. [23] and references therein). Similar results can emerge for partial differential equations when the focus is on gap-crossing ability in heterogeneous landscapes, leading to ‘geographic range margins’ beyond which the species cannot spread [13].

As we discuss below, non-spreading solutions hinge on the existence of so-called Allee effects and overcompensation in the population dynamics of the spatially distributed species. An Allee effect arises when the per-capita birth rate increases as a function of population density when population density is small. Overcompensation is said to occur when high population densities result in a net decrease in offspring production. Allee effects may occur via a great many biological mechanisms [1, 2, 4, 5, 6, 9, 10, 11, 12, 17, 32, 37, 42, 46], and they have been studied in connection with integro-difference equations in the context of spatial spread [28, 50]. A special kind of Allee effect, termed a strong Allee effect, occurs when there is a critical population density below which extinction occurs. Mating failure, which can arise through mechanisms like pollen limitation and reproductive asynchrony [6, 17], has been linked to strong Allee effects in diverse biological systems. For example, in evergreen bagworms (*Thyridopteryx ephemeraeformis*), the intensity of a strong Allee effect arising from mating failure is a function of climate, and this spatial variation leads to a hard geographic boundary for the species [36, 43].

We consider the spatial-temporal dynamics of populations governed by the integro-difference equation

$$u_{n+1}(x) = \int_{-\infty}^{\infty} k(x-y) g(u_n(y)) dy, \quad (1)$$

where $u_n(x)$ is the density of individuals at point x and time n , $g(u)$ describes density dependent fecundity, and $k(x-y)$ is the dispersal function, which depends upon the distance $|y-x|$ between the location of birth y and the location of settlement x . Model (1) describes that individuals at location y generate $g(u_n(y))$ offspring and then die and these offspring disperse to location x with the probability $k(x-y)$. We will assume that $g(1) = 1$, so that the population has an equilibrium at the carrying capacity $u_n(x) \equiv 1$, and that $k(x)$ decays at least exponentially fast near $\pm\infty$ so that the probability that an individual travels a very long distance is small.

For the case that small populations grow (i.e., $g'(0) > 1$), the reproduction function $g(u)$ exhibits no Allee effect (i.e., $g(u) \leq g'(0)u$), and $g(u)$ may or may not produce overcompensation (i.e.,

$g(u)$ decreases for u past a certain population density), the population will spread at a constant asymptotic spreading speed that can be characterized as the slowest speed of a class of traveling waves (Weinberger [52], Li et al. [29]). In this case, the wave is pulled by the leading edge of invasion. When the reproduction function produces overcompensation, oscillations are generated in the population density behind the wave front (Li et al. [29]). Constant spreading speed also occurs if $g(u)$ exhibits a strong Allee effect (i.e., $g'(0) < 1$) and $g(u)$ is increasing (i.e., there is no overcompensation). In this case, the spreading speed is the unique speed of traveling waves connecting zero and the carrying capacity (Lui [35]), and the sign of the wave speed is the same as that of $\int_0^1 [g(u) - u] du$ (Wang et al [50]). If $\int_0^1 [g(u) - u] du > 0$, the traveling wave moves forward, if $\int_0^1 [g(u) - u] du < 0$, the traveling wave moves backward, and if $\int_0^1 [g(u) - u] du = 0$ the traveling wave is stationary. The wave speed depends on the forward pushing force developed by the high-density populations above the Allee threshold behind wave front as well as the backward pulling force generated by the lower-density populations below the Allee threshold along the leading edge of invasion.

Fluctuating invasion speeds can be generated by a strong Allee effect and strong overcompensation (Sullivan et al. [48]). Strong overcompensation in general produces large spatiotemporal variation in density behind the invasion front and thus, variation in the strength of the push, leading to oscillating spreading speeds. As pointed out in [48], where the population density is smaller than the Allee threshold along the leading edge of the invasion, the population declines before the next time step. Populations above the Allee threshold will grow until they surpass the overcompensation threshold. If the overcompensation is strong enough they will return from a high level to a low level resulting in cyclical variability in the pushing strength of the wave.

In this paper we further study the effects of a combination of a strong Allee effect and strong overcompensation. We will show that such a combination can produce biologically meaningful robust nonspreading solutions in solid regions of the parameter space for (1). We will demonstrate the existence of robust nonspreading solutions with a variety of spatiotemporal patterns. One of our novel findings is the existence of non-spreading solutions that oscillate in both density and spatial range. Here in the long run, the oscillating forward pushing force developed by overcompensation is balanced by the backward pulling force from populations below the Allee threshold, leading to persisting nonspreading solutions. It should be pointed out that, as discussed above, for the case of no overcompensation, there exists a traveling wave with zero speed if $\int_0^1 [g(u) - u] du = 0$; however this condition is not robust and is not satisfied with a slight change of model parameters. It is surprising to note that simple scalar integro-difference equations designed as a modelling tool to investigate spatial spread of populations possess biologically meaningful solutions that actually do not spread in a homogeneous continuous environment. One consequence of the existence of nonspreading solutions concentrated on effectively bounded domains is the formation of multiple population ‘patches’ separated from each other in space. This will be also explored in the present paper.

3 Non-Spatial Model

We will model growth using the two parameter function presented by Vortcamp et al. [49]. In this growth function a represents the Allee threshold and r represents a parameter controlling the strength of over-compensation. By appropriate scaling of u the carrying capacity can be assumed to be 1. The growth function used in model (1) is then

$$g_{a,r}(u) := u \exp \left(r(1-u) \left(\frac{u}{a} - 1 \right) \right).$$

Increasing r for fixed a increases the maximum value of $g_{a,r}(u)$ and accordingly increases the magnitude of the derivative at the equilibria $u = a$ and $u = 1$ (Supplementary Materials, Fig. 8). We see that decreasing a for fixed r , increases the maximum value of $g_{a,r}(u)$. It can also be seen that in this parametrization the shape of $g_{a,r}(u)$ is more sensitive to the parameter a than r .

Essential extinction is said to occur when the image of the maximum value of $g_{a,r}(u)$ is mapped below the Allee threshold [44]. This region in parameter space is indicated in green in Fig. 4(a). It is known that for monotone growth functions with an Allee effect that the sign of population spread is indicated by the sign $\int_0^1 [g_{a,r}(u) - u] du$ [50]. While this is not necessarily true for non-monotone functions, we can still interpret the negativity of the integral as an indication of overall weak growth. The region in parameter space with weak growth is indicated in blue in Fig. 4(a).

4 Dispersal Kernel

It is long been known that the shape of the dispersal kernel, particularly its kurtosis, can have a profound influence on the the spreading dynamics in an integro-difference equation [27]. To model dispersal with varying kurtosis we will use the generalized Gaussian distribution centered at the origin with standard deviation 1. Spatial coordinates can trivially be rescaled to satisfy that the standard deviation is 1 without altering the dynamics of the integro-difference equation. The kurtosis of the distribution is controlled by the parameter $\eta > 0$. The probability density function used in model (1) for dispersal is then

$$k_\eta(x) = C \exp\left(-\left|\frac{x}{S}\right|^\eta\right)$$

$$\text{where } C = \sqrt{\frac{\Gamma\left(\frac{3+\eta}{\eta}\right)}{12 \Gamma\left(\frac{1+\eta}{\eta}\right)^3}}$$

$$\text{and } S = \sqrt{\frac{3 \Gamma\left(\frac{1+\eta}{\eta}\right)}{\Gamma\left(\frac{3+\eta}{\eta}\right)}}$$

Where $\Gamma(\dots)$ refers to the gamma function.

135

136 Kurtosis, which is defined as the ratio of the fourth moment to the square of the second, gives a
 137 measure of the “fatness” of the tail of the distribution. Leptokurtic distributions ($0 < \eta < 2$) can
 138 be thought of as having most individuals disperse very small distances with a few individuals
 139 dispersing extreme distances in such a way the standard deviation remains fixed. Conversely,
 140 platykurtic distributions ($\eta > 2$) can be thought of as most individuals dispersing about the
 141 same distance. When $\eta = 1, 2$, and ∞ , the commonly used Laplace, Gaussian and Uniform
 142 distribution are recovered as is shown in Fig. 9 in the Supplementary Materials.

143 5 Spatial Model

The spatial model is specified by model (1) with the definitions of $g_{a,r}(u)$ and $k_\eta(x)$ previously outlined. The initial data is specified by

$$u_0(x) = \begin{cases} p_0 \cos\left(\frac{\pi}{w_0}x\right) & |x| < \frac{w_0}{2} \\ 0 & \text{otherwise,} \end{cases}$$

144 where p_0 is the maximum density and w_0 is the width of the support. The solution set $\{u_n(x)\}_{n=0}^\infty$
 145 is thus fully specified by the 5 parameters a, r, η, p_0, w_0 together with model (1).

146

147 To numerically generate the solution set we uniformly discretize space using a step size $\delta =$
 148 0.005 and use *conv* in Matlab to compute the accelerated convolution. We use the symmetry of
 149 $u_n(x)$ about $x = 0$ to further accelerate calculations. Both the vector representing $k(x)$ and $u_n(x)$
 150 are clipped where they fall below 10^{-5} . It should be noted that this clipping of $k(x)$ only very
 151 minorly effects the computed value 0th, 2nd and 4th order moments provided $\eta \gtrsim 0.5$.

6 Non-Spreading Solutions

In contrast to integro-difference equations with Allee or over-compensation effects considered separately [29, 35, 50], we are able to find solid regions of parameter space with solutions where the population persists but is effectively confined to a limited region of space. As a demonstration, in Fig. 1 we see an example of a solution converging to a stable equilibrium where the population is effectively limited to $-4 \leq x \leq 4$. More complex behavior such as period 2 and non-periodic non-spreading solutions can be observed as well (Supplementary Material Fig. 10, 11). It should be noted that throughout this paper, we define domain size to be the distance from the left most point where $u_t(x) = a$ to the rightmost point where $u_t(x) = a$.

Figure 1: Solution with parameters $a = 0.62$, $r = 8$, $\eta = 5$, $p_0 = 0.9$, $w_0 = 4$. In part (a) the blue curve is $u_0(x)$, and the gray curves are the transients u_1 through u_{15} and the black is u_{16} through u_{100} . In (b) we see the domain size converging to that of the stable equilibrium.

6.1 Parameter Bifurcations for Non-spreading Solutions

Below we present parameter bifurcation diagrams centered on the parameter set $a = 0.61$, $r = 8$, $\eta = 5$, $p_0 = 1$, $w_0 = 6$. The bifurcations around this set of parameters are typical of those made for other choices. The x-axis is the bifurcation parameter, and the y-axis is the domain size of the density curve $u_n(x)$. Only the domain size of iterations 200-400 are plotted.

In Fig. 2 we see a period doubling bifurcation in the parameter a . For values of a between .603 and .64 we see a single period 1 solution emerges; for values between 0.58 and 0.603 a period 2 solution emerges; and for values approximately between 0.575 and 0.58 chaotic dynamics occur. Extinction occurs for small and large values of a , and it can be seen regions of extinction are intermingled with non-spreading solutions for a between 0.58 and 0.6.

In Fig. 3 we show the bifurcation for η , which is the parameter controlling the kurtosis of

172 dispersal. We see extinction occurs for leptokurtic dispersal ($\eta < 2$), period 2 solutions occur
 173 for η slightly higher than 2 and less than 4, and a period 1 equilibrium for highly platykurtic
 174 dispersal when $\eta > 4$.

175 Bifurcation diagrams for r , p_0 and w_0 can be viewed in Fig. 12, 13, 14 in the Supplementary
 176 Materials.

Figure 2: Bifurcation diagram for parameter a with $r = 8$, $\eta = 5$, $p_0 = 1$, $w_0 = 6$.

177 6.2 Classification Map of Parameter Space for Non-spreading Solutions

178 The non-spreading solutions exist along a fairly narrow band in parameter space centered around
 179 the curve where $\int_0^1 [g_{a,r}(u) - u] du = 0$ (see Fig. 4). As was previously mentioned, the maximum
 180 value of $g_{a,r}(u)$ is highly sensitive to the parameter a and the narrowness of the region might be
 181 considered an artifact of the parametrization.

182 To numerically classify the parameter space, we divided the region of the $a - r$ plane depicted
 183 in Fig. 4(b) into a 100×100 grid. For the values of a , r on the grid, iterations are computed
 184 using $\eta = 5$, $p_0 = 1$, $w_0 = 6$. The following are used as criteria for classification:

- 185 • If the max value of $u_n(x) < a$ the solution is classified as extinction (gray).
- 186 • If the domain size (see 4.1 for definition) exceeds 24 in less than 500 iterations, the solu-
 187 tion is classified as spreading (yellow).
- 188 • If periodicity is detected or the domain size fails to exceed 24 in 500 iterations the solution
 189 is classified as non-spreading (blue).

Figure 3: Bifurcation diagram for parameter η with $a = 0.61$, $r = 8$, $p_0 = 1$, $w_0 = 6$. Note that the scale on the x -axis is logarithmic.

In Fig. 5 we examine the dependence on initial conditions by varying the parameters w_0 and p_0 in model (1). Predictably extinctions occur if the support of the initial domain is too small (small w_0), or if the initial density is too small (small p_0). We see a single non-spreading solution (blue region of Fig. 5) emerges fairly robustly for values of w_0 not extremely small or large compared to the patch size, and p_0 above the Allee threshold but not too high above the carrying capacity.

For very large values of w_0 multiple isolated patches, which are essentially copies of a single patch such as is shown in Fig.1, can emerge as the solution. In Fig. 5 we see that for large w_0 and p_0 , two patches will emerge. This can be attributed to the intermediate population densities which produce the maximum amount of offspring being located at opposing ends of the initial distribution. An equilibrium two-patch density curve is shown in Fig. 6. The resultant equilibrium is qualitatively similar for all red areas in Fig. 5, although the spacing between patches may differ.

6.3 Patch Formation with a Stochastic Initial Condition

We wish to simulate a spatially stochastic initial condition with spatial correlation length of L_{scale} . L_{scale} can be considered as the length whereby statistical correlations in density diminish to insignificant levels. To generate this initial condition we use that the value of $u_0(x)$ is an independent identically distributed random variable uniformly distributed on $[0.8, 1.2]$ for x -values that are multiples of L_{scale} . For values of x that are not multiples of L_{scale} , values are linearly in-

(a) The growth parameter space showing regions of low growth (blue), and essential extinction (green).

(b) A color map classifying the behavior of model (1) in a, r parameter space. Dark blue regions are non-spreading solutions, and yellow are spreading solutions. The solid red curve is where $\int_0^1 (g(u) - u) du = 0$.

Figure 4: In sub-figure (a) the region in the black dashed box is shown in detail in sub-figure (b). The other parameter values used in (b) are $\eta = 5$, $p_0 = 1$, $w_0 = 6$.

208 interpolated from the control points $(nL_{\text{scale}}, u_0(nL_{\text{scale}}))$. We limit our study to parameter values
 209 $a = .61$, $r = 8$, $\eta = 5$.

210 To study the effects of L_{scale} on patch formation we:

- 211 • Used a domain of length 500 initiated as described above.

Figure 5: Initial condition parameters resulting in a single patch are shown in blue. Red represents parameters giving rise to two patches. Gray represents parameters resulting in extinction. Values used for other parameters are $a = .61$, $r = 8$, $\eta = 5$.

Figure 6: The two-patch equilibrium population density curve for $a = .61$, $r = 8$, $\eta = 5$, $p_0 = 1.3$, $w_0 = 17$.

- Iterated until a fixed point condition was met.
- Counted the number of patches formed by integrating the total population and dividing by the population of a single patch.
- For values of $L_{\text{scale}} = 0.01, 0.05, \dots, 50, 100$, twenty trials were completed for each value.
- 90% confidence intervals are computed using the assumption of normality (Student T distribution). It should be noted that the sample standard deviation for patch formation was

about 3 patches relatively independent of L_{scale} .

The length scale of a single patch is ~ 8 (see Fig.1). As patches cannot overlap, the maximum possible density of patch formation is $\sim \frac{1}{8}$. In Fig.15 we give the density of patch formation ($\#$ of patches formed/500) as a ratio to this maximum theoretical value.

We see that for about 3 orders of magnitude, $0.1 < L_{\text{scale}} < 10$, the density of patch formation saturates at around 25% of the maximum possible density. The reason it does not come closer to 100% appears to be that slight overlap of patches usually results in both patches annihilating. For large values of L_{scale} efficiency of patch formation drops, presumably due to the mild gradients causing the dynamics to be similar to the spatially uniform case where essential-extinction results. Finally, for L_{scale} much less than the scale of the dispersal distance ($\sigma^2 = 1$) we see the efficiency of patch formation again drops. Since dispersal sharply drops the amplitude of the Fourier components with wavenumber much greater than the dispersal length, we see the 1st generation will be an almost constant density whose value will be the average of $g(u)$ over $0.8 < u < 1.2$. Thus again the non-spatial dynamics will be dominant.

Figure 7: Typical plots of initial conditions (blue) and resulting patch formation (red) at short, intermediate, and long length scales.

7 Discussion

In this paper we studied non-spreading solutions for the integro-difference equation (1) where the growth function $g(u)$ exhibits a strong Allee effect and overcompensation. The non-spreading solutions take forms of stable equilibrium solutions vanishing at $\pm\infty$ and solutions oscillating in densities and spatial ranges. Such nonspreading solutions exist in a solid region in the parameter space. In a large habitat, patch formation can be developed with each patch essentially formed by a non-spreading solution. Our results show that single species model (1) with constant parameters can have very rich nonspreading population dynamics.

Both a strong Allee effect and overcompensation in population growth are necessary to produce biologically meaningful nonspreading solutions. Overcompensation generates a forward pushing force from populations above the Allee threshold. Likewise, a backward pulling force is created from populations below the Allee threshold. Nonspreading solutions emerge when there is a balance between the forward pushing and backwards pulling forces. The existence of oscillating non-spreading solutions is due to a forward pushing force derived by variation in density behind the population distribution front. In the absence of overcompensation, model (1) with a strong Allee effect can have a non-spreading solution if and only if $\int_0^1 [g(u) - u] du = 0$, so that such a solution exists only in a region with measure zero in the parameter space, and thus it is not robust. However, as indicated in the bifurcation diagram Figure 13, with both a strong Allee effect and overcompensation, there is a solid parameter region (blue) in which non-spreading solutions exist. In this region, $\int_0^1 [g(u) - u] du$ can be greater than 0, less than 0, or 0. The bifurcation diagram Fig. 2 shows various patterns of nonspreading solutions from steady states, period two, to chaos when a varies while other are fixed. It should be noted that η , the kurtosis of the dispersal kernel, and initial data also play important roles in developing nonspreading solutions. In Fig. 3, there is no nontrivial nonspreading solutions for $\eta < 2$, period 2 nontrivial solutions exists on a relatively small interval near $\eta = 2$, and for relatively large η there is a stable nonspreading equilibrium. In Fig. 13 and 14, nonspreading solutions depend on the amplitudes and support of initial data. In addition to the growth function used within this paper, the PhD Thesis of Otto [41] demonstrates that nonspreading solutions can form with a variety of other forms of growth function.

Nonspreading solutions provide a basis for the development of patch formation. For a large habitat, separate patches can emerge from perturbations in a relatively constant population, with each patch basically a nonspreading solution as is demonstrated in Fig. 7. Patch formation is weakly sensitive to the length scale of correlations in the initial distribution as shown in the Supplementary Materials Fig. 15, with patch formation being favored by length scales on the order of the dispersal distance. Correlation lengths much larger or smaller than the dispersal distance result in inefficient patch formation.

We also found that growth parameters giving rise to essential extinction in the non-spatial model, can actually experience population spread and population growth in the spatial model. This is consistent with Vortkamp et al.[49], who using a spatially discrete 2-patch model demonstrated that essential extinction could be stabilized due to out of phase rescue effect. We will save further investigation of this phenomena for future work.

Our result on non-spreading solutions contrasts with that of Sullivan et al. [48]. Working on (1) with a truncated Ricker's function for population growth, they found that fluctuating spreading speeds can occur as a result of a combination of a strong Allee effect and overcompensation. The scaled growth function $g(u)$ given by (1) with the carrying capacity 1 has two parameters describing the Allee threshold and strength of overcompensation, respectively. If the carrying

capacity of the truncated Ricker's function is scaled to 1, there is no parameter controlling the strength of overcompensation. Therefore the growth function used in this paper is more flexible than the truncated Ricker's function considered in [48]. Observe that in Figure 4, there also exists a solid region (green) where spreading solutions exist. Depending on the parameters, model (1) possesses spreading and nonspreading dynamics as well as extinction.

The fact that a single mathematical equation can admit such qualitatively divergent output as spreading solutions, non-spreading solutions, and extinction is intriguing. The possibility of non-spreading solutions is particularly interesting because it suggests a new way to connect the widely employed modeling framework of integro-difference equations to a completely different purpose: the origin and maintenance of ecological boundaries. The factors influencing the location and maintenance of species' spatial distributions, whether patch boundaries on small scales or geographic range boundaries on larger scales, have been the subject of intense interest by ecologists for decades [3, 16, 47]. The specific biological mechanisms leading to the existence of such boundaries are diverse, but often reflect an interplay between local population dynamics and dispersal. Such dynamics could be related to the oscillating wave fronts observed with this model (Supplementary Materials, Fig. 10, 11). For example, repeated processes of invasions and extinctions appear to be important for the maintenance of species' patch boundaries in mixed conifer-hardwood forests [15]. Likewise, Allee effects can contribute to the existence of geographic range boundaries in some insect systems with short dispersal distances [36, 43].

Identifying the existence of non-spreading solutions in integro-difference equations opens up several additional lines of inquiry for this modeling framework. One such possibility would involve investigations of how large contiguous populations collapse into small patches, either on evolutionary timescales [38] or in connection with the persistence of relictual populations in conservation biology [7, 8]. Likewise, future research could examine non-spreading solutions for integro-difference equations operating on a landscape gradient (e.g., temperature, rainfall) that influences population growth rate. Such studies would provide a vehicle for investigating the interplay between biological and environmental processes that can jointly influence the origin and maintenance of geographic range boundaries [16], including the possibility of patchy population structure at geographic range margins [3, 14]. Overall, the existence of non-spreading solutions in integro-difference equations suggests the emergence of a welcome new tool for studying diverse phenomena in spatial ecology.

8 Supplementary Materials

Figure 8: The graph of $g_{a,r}(u)$ and $y = u$ line for various values of a and r .

Figure 9: Generalized Gaussian distributions with standard deviation=1 for various values of η .

(a) density curves

(b) domain size

Figure 10: Solution with parameters $a = 0.585$, $r = 8$, $\eta = 5$, $p_0 = 0.9$, $w_0 = 4$. In part (a) the blue curve is $u_0(x)$, the gray curves are the transients u_1 through u_{16} , the red are the odd indexed iterations u_{17} through u_{99} , and the black are the even indexed iterations u_{18} through u_{100} . In (b) we see the domain size oscillating with period 2.

Figure 11: Solution with parameters $a = 0.57865$, $r = 8$, $\eta = 5$, $p_0 = 0.9$, $w_0 = 4$. In (a) the blue curve is $u_0(x)$, the multicolored curves are u_{100} through u_{200} . In (b) we see aperiodic oscillations in the domain size.

Figure 12: Bifurcation diagram for parameter r with $a = 0.61$, $\eta = 5$, $p_0 = 1$, $w_0 = 6$.

Figure 13: Bifurcation diagram for parameter p_0 with $a = 0.61$, $r = 8$, $\eta = 5$, $w_0 = 6$.

Figure 14: Bifurcation diagram for parameter w_0 with $a = 0.61$, $r = 8$, $\eta = 5$, $p_0 = 1$.

Figure 15: The mean density of patch formation relative to the maximum possible patch density as a function of the correlation length scale of the stochastic initial condition. The black bars are the 90% confidence intervals. Note the x -scale is logarithmic.

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