

Viability of populations in a landscape

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Abstract

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It has long been known that extinctions or wild oscillations in populations can occur when population density is too low, or when a population is confined to too small an area at high population density. This study discovers another cause of extinction. Cellular automata models of a single population in a landscape indicate that, if a population occupies an unconfined region smaller than a critical size, it can also become extinct in spite of healthy population density, the availability of suitable areas to migrate to, and the absence of competitors and predators.

1 Introduction

A crucial issue in conserving biodiversity is the relationship between the area occupied by a population and its chances of survival. Most studies that address this relationship limit themselves to populations that are strictly confined to a small area. However, both field studies (Krebs *et al.*, 1969) and theoretical models (Crowley, 1981; Solé & Valls, 1992) suggest, in the words of Krebs *et al.* (Krebs *et al.*, 1969), “that dispersal is somehow necessary for normal population regulation” (Krebs *et al.*, 1969, author’s italics).

Furthermore, simulation studies show that inter-site interactions can cause ecosystems across a landscape to behave very differently from sets of populations at a single site (Green, 1990; Taylor, 1990; Hassell *et al.*, 1991; Sabelis *et al.*, 1991; Solé & Valls, 1992). In considering species viability, then, we need to ask whether a population is viable in a landscape. Viability of a population is most often a concern when a population is both low in numbers and reduced to a small area. It is therefore important to understand the dynamics of populations under these conditions.

The above considerations lead to the following basic question, which we address in this study: if a population is not confined to an area but is free to expand, is there any connection between the initial area that it occupies and its chances of survival? We consider this question for the simplest possible system, a single species in an obstacle-free landscape.

2 The Model

2.1 What Are Cellular Automata?

As used in this paper, a cellular automaton (Wolfram, 1984) is a cartesian grid of identical cells each of which is in one of a finite number of states. At each time step, a cell’s state is updated according to a function of the states of its neighbouring cells and

itself. All cells are updated synchronously. Cellular automata are also known as coupled map lattices (Solé & Valls, 1992).

The best-known cellular automaton is John Conway’s “Game of Life” (Berlekamp *et al.*, 1982), made famous by Martin Gardner’s column in Scientific American (Gardner, 1970). In Life, each cell in the cartesian grid is in one of two states, alive or dead. At each time step, every cell’s state is updated according to a simple function of its own state and the states of its eight nearest cells.

The cellular automaton used in our model is more complicated; a cell represents an area of landscape, the cell’s state is its local population, and the function for updating a cell’s state comes from inter-cell migration and intra-cell fertility and mortality, as described below.

2.2 Why Cellular Automata?

For a model of a population in a landscape, cellular automata are better than partial differential equations because:

- Diffusion models smooth out any heterogeneity in population density (Hastings, 1990; Hogeweg & Hesper, 1981), which disagrees with several field studies (Kareiva, 1987; Krebs *et al.*, 1969; Dodd, 1959; van der Meijden, 1979) that demonstrate that population density is often heterogeneous, with local extinctions and local booms.
- Partial differential equations, when approximated numerically on a grid, consume more computer time than a corresponding cellular automaton (Gerhardt *et al.*, 1990).

2.3 Cellular Automata and Landscape Populations

Cellular automata (Wolfram, 1984) model a wide variety of complex systems. In landscape ecology, we use them to represent a landscape as a cartesian grid in which each cell corresponds to an area of the land surface (Green, 1989; Green, 1990; Hassell *et al.*,

1991). Cell states correspond to features in the landscape. Here, a cell's state is its local population of plants or animals in the area of land surface represented by that cell. The state of cell (x, y) at discrete time step t is denoted by $N_{x,y}(t)$, the (discrete) number of individuals that occupy the area that cell (x, y) represents.

Migration occurs between each cell and its 4 compass-point neighbours.

2.4 Local Population Dynamics

The local population dynamics within each cell is based on the discrete logistic equation for a single population, which applies to a wide range of population models and works best for species that reproduce seasonally:

$$N(t+1) = rN(t) \left(1 - \frac{N(t)}{K}\right) \quad (1)$$

where $r \geq 0$ denotes the reproduction rate and K is the maximum possible local population.

In order to treat the effects of fertility and mortality separately, we re-write equation 1 in the form:

$$N(t+1) = N(t) + (1-r)N(t) + \left(-\frac{r}{K}\right)N(t)^2 \quad (2)$$

Here, $(1-r)$ controls fertility, and mortality can be independently controlled by the term $\left(-\frac{r}{K}\right)$. We relabel these to give:-

$$N(t+1) = N(t) + \alpha N(t) + \beta N(t)^2 \quad (3)$$

Here, fertility $\alpha = r - 1$ and mortality $\beta = -\frac{r}{K} = -\frac{1+\alpha}{K}$. The important assumption we make here is that β incorporates mortality in the population, rather than simply a change in fertility.

Note that $N_{eq} = -\frac{\alpha}{\beta}$ is the equilibrium population size. If the initial population equals the equilibrium population, $N(0) = N_{eq}$, then it is static for all time, $N(t) = N_{eq}$ for all $t > 0$.

2.5 Migration

To allow migration between adjacent cells on the grid we need to add a migration term to equation 3. We choose the discretised diffusion operator ∂^2 between a cell (x, y) and its four compass-point neighbours (Solé & Valls, 1992), defined as:

$$\partial^2 N_{x,y} = N_{x,y-1} + N_{x,y+1} + N_{x+1,y} + N_{x-1,y} - 4N_{x,y} \quad (4)$$

Adding this to equation 3 gives the behaviour of cell (x, y) at time step t :

$$N_{x,y}(t+1) = N_{x,y}(t) + \alpha N_{x,y}(t) + \beta N_{x,y}(t)^2 + \gamma \partial^2 N_{x,y}(t) \quad (5)$$

Here $\gamma < 1$ is the per-step migration parameter, i.e., the fraction of a cell's population that is prepared to migrate.

We make no attempt to define the exact scale of the grid used here. In principle, the model can represent any scale, because $\beta = -\frac{r}{K} = -\frac{1+\alpha}{K}$ takes into account a cell's maximum population K , whatever that may be. A small maximum population per cell implies fine resolution where each cell represents a small area. A higher maximum per-cell population implies a larger scale where each cell represents a larger area that could contain more individuals.

The dispersal rate γ adjusts the scale. A larger dispersal rate can model a species that moves more rapidly, or else it can model the same species at a finer scale. That is, if cells represent a smaller area, then movement at the same rate carries individuals over cell boundaries more often, so increasing the migration rate γ has the effect of making cells represent a smaller area.

If one lowers the migration rate too far, to see the problem at an unrealistically large scale where each cell represents a huge area, then the effects of spatial distribution are modelled too coarsely and the model would make unrealistic predictions. The values of migration rate γ which gives rise to the interesting results below are high enough to avoid this unrealistic effect.

Finally, populations in the real-world are never negative, but models like equation 5 can violate this condition for some parameter values (Solé & Valls, 1992). The usual solution to this

problem (Crowley, 1981; Solé & Valls, 1992) is to use the Heaviside operator $H(z)$, which satisfies: $H(z) = z$ for $z > 0$, and $H(z) = 0$ otherwise.

The full system of difference equations is therefore:

$$N_{x,y}(t+1) = H \left(N_{x,y}(t) + \alpha N_{x,y}(t) + \beta N_{x,y}(t)^2 + \gamma \partial^2 N_{x,y}(t) \right) \quad (6)$$

For the values of fertility ($\alpha < 0.3$) used here, the logistic equation behaves in a non-chaotic manner. However, as each cell on the grid interacts with its neighbours (as described below), this tells us little about the whole system due to undecidability and computational irreducibility in cellular automata (Wolfram, 1985; Darwen, 1992). Suffice to say that in nearly all cellular automata (including the most famous example, Conway's Game of Life (Berlekamp *et al.*, 1982)), the local dynamics alone don't offer simple predictions about the global dynamics. For example, in a very similar but much smaller (10×10 cells) model (Solé & Valls, 1992), chaos was present for values of fertility for which chaos was not present in the single logistic equation (Solé & Valls, 1992); i.e., chaos is more widely present over a wider range of parameters in the cellular automaton than in the single logistic equation.

However, as this is a deterministic cellular automaton with a finite number of states, any run will ultimately end in a fixed state or a finite limit cycle (Green, 1993). This is because each cell can be in a finite number of states, and there are a finite number of cells, giving a finite number of combinations that the model can be in. After enough time steps have passed, the model will return to a combination of states it has already been in, forming a finite limit cycle.

2.6 Boundary conditions

Endangered species usually occur as isolated populations, so we will let a population initially occupy a small area (10×10 cells or less) at the centre of the 128×128 cell model. If the population expands to the edge, we will take that to mean that the popu-

lation is viable. We may also assume that the population is not augmented by immigrants from outside the model.

Thus, the boundary conditions have no effect on the results. So without loss of generality, we will use absorbing boundaries in our model, where anything that migrates “off the edge” of the matrix disappears from the model.

2.7 Initial conditions

For the initial distribution, we select a small square sub-matrix in the centre of the 128×128 matrix of cells. Each cell in this sub-matrix is initialized with population $N_{x,y}(0) = -\frac{1}{\beta}$, which is greater than the equilibrium population for a single cell $N_{eq} = -\frac{\alpha}{\beta}$ for the values of α we will use. This assumption guarantees that the initial population density is high enough to avoid complications caused by low population density. Each cell outside the square sub-matrix is initialized to zero population.

2.8 Implementation

The model is written in CM-FORTRAN and runs on the Australian National University’s CM-2 Connection Machine super-computer. It is implemented as a 128×128 matrix of cells. Each cell’s state (or population) $N_{x,y}$ can take a value between 0 and 200, i.e., the maximum local population is $K = 200$. The model is strictly deterministic.

3 Results

At the beginning of a run, the population expands to occupy the nearest empty cells — a cell is occupied if its population is greater than zero. Figure 1 shows three sample runs, and demonstrates the three long-term outcomes:

1. small patches shrink and disappear;
2. medium-sized patches neither expand nor shrink, and their size is constant or oscillates between two sizes;

3. large patches expand indefinitely.

A large number of runs indicated that if a population was still expanding after the first 200 time steps, then it would keep expanding until the whole matrix was occupied. Thus only 200 time steps were executed for each set of variables, with exceptions handled as follows. If the proportion of occupied cells after 200 time steps was:

1. zero or constant for the 5 most recent time steps, then this value (zero or constant) was taken as the final number of occupied cells;
2. still increasing for the 5 most recent time steps, then the entire matrix was taken as the final number of occupied cells;
3. neither constant nor increasing for the 5 most recent steps, then the simulation continued until all cells were occupied, or empty, or the number of occupied cells stayed at a constant level.

Figure 2 shows that the system undergoes a critical change when the diffusion parameter γ is high enough:

- For high γ the population usually expands to occupy the entire grid, and the population is viable. This is the high plateau of Figure 2.
- For lower γ , the result depends on the size of the area initially occupied. If the initial population is small then the population dies out. For larger initial areas, expansion stops at a small fraction of the available area, and does not expand to the edge of the 128×128 cell matrix. This is the low floor of Figure 2, that gradually slopes up at the left-hand corner.
- Between the high plateau and the low floor of Figure 2 there is sharp transition between these regions of expansion and stagnation/extinction.

Sharp transitions like this have been demonstrated for many landscape phenomena (Green, 1990; Green, 1993).

Figure 3 shows how much initial area is needed to guarantee the population's expansion into the empty space. The migration

parameter γ and fertility parameter α in Figure 3 both come from equation 6. The z -axis represents the smallest initial area that supports an expanding population (z is the side of the initially occupied square sub-matrix in the centre of the 128×128 cell landscape) that is just large enough to allow indefinite population growth. In Figure 3:

- A z -value of 1 indicates that a population will expand indefinitely from just 1 cell in the grid.
- A z -value of $n > 1$ indicates that a population will expand indefinitely if it starts in a square of side n cells, but not if it starts from a square with side $n - 1$ cells or smaller.

As described above, we observed that a population that does not expand to fill all the available area either dies out completely or stops expanding at a fraction of the available area.

4 Discussion

Figure 2 implies that a population's viability can depend on the geographic area it occupies, independently of other factors. Extinction can occur if a species occupies too small an area, even if the species is:

- surrounded by empty, habitable land and is free to expand;
- without competitors or predators;
- at a reasonable population density, with neither overcrowding nor sparseness.

Figure 2 agrees with other models (Crowley, 1981; Hassell *et al.*, 1991; Solé & Valls, 1992), and with studies of biodiversity on isolated islands (May, 1981), that greater area prevents extinction. However, those previous studies considered a population confined to a small area. Our study is unique in that a population is not confined, and is free to expand out of the small area it initially occupies. While Figure 2 shows that a population's initial area affects its survival, the question that this paper addresses is this:

what is the minimum area that a population must occupy in order to expand into the space available? How much area ensures growth?

Figure 3 answers this question. The migration parameter γ and the fertility parameter α are both from equation 5. The z -axis represents the minimum area that supports an expanding population (it is the side of the initially-occupied square sub-matrix).

We may summarize Figure 3 as follows:

- High fertility with low migration rates will expand, even from a single cell on the grid.
- Low fertility, at any migration rate, requires a larger initial area to expand.
- Surprisingly, a too-high migration rate also requires a larger initial area to expand, even with high fertility.

The relevance of the above results depends on the validity of the model's underlying assumptions. In particular, the model represents both time and space discretely. Discrete time steps accurately represent seasonally reproducing species, which include many plant and animal species. The discrete, cartesian grid used by this cellular automaton allows the heterogeneous population distribution exhibited by many species.

The sharp transition in dynamics (from extinction to expansion) is typical of critical phenomena. Criticality has now been demonstrated for many landscape phenomena (Green, 1990; Hassell *et al.*, 1991; Green, 1993). The characteristic features of such processes include sharp, systematic changes in behaviour and the three phases noted here — extinction, transition, and expansion. An important feature of such systems is that the transition zone tends to be chaotic (Green, 1993). The occurrence of chaos in the present system may explain the variability in behaviour observed for many combinations of parameters that lie near the “phase changes”. Variability of this kind would not otherwise occur in a deterministic system such as this model.

The model's results are clearly relevant to a number of issues in conservation.

Foremost is the warning that any population is potentially endangered if it does not occupy a large enough area, as shown by figures 1 and 2. Extinction occurs in the model despite the availability of suitable space, the absence of predators, and the lack of any other cause of extinction. This means that extinction is possible even in large empty reserves where the species concerned is well protected.

Putting this phenomenon to good use, one way to control a pest species might be to eradicate the species in strips so as to divide its occupied area into small, non-viable patches which will die out separately. This is a variation on the “fence effect”, where a species (such as field mice (Krebs *et al.*, 1969)) suffers a population collapse if it occupies an area which is too small. Our model suggests this may also happen to an isolated but unfenced population if its migration rate and fertility are small enough.

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List of Figures

Figure 1: The model runs on a 128×128 matrix of cells. A cell is dark if occupied, and white if empty. Each row of this diagram shows a particular run of the model, with pictures taken during the course of that row's run:

Top Row: In this run, isolated patches are too small to persist. Although larger patches persist for some time, they are gradually shrinking and extinction eventually occurs (top right-hand box).

Middle Row: In this run, some isolated patches are large enough to persist, but not large enough to expand. Smaller patches shrink and die out.

Bottom Row: Some patches that persist without expanding, and larger patches expand indefinitely.

Conclusion: small area can destroy the long-term viability of a population, even though the population is free to expand into unoccupied space.

Figure 2: This shows what proportion of cells are occupied after a long time, starting from a square sub-matrix of occupied cells in the centre of the model. The x -axis measures the migration parameter γ , and the y -axis represents the population's initial area (actually, the side of the occupied square sub-matrix in the 128×128 matrix of cells). The z -axis measures the proportion of cells occupied after a long time passes; 1 represents filling all available space, 0 represents extinction, and intermediate values represent a stagnant population that doesn't expand despite available empty space surrounding it. Note the sharp transition between expansion and stagnation/extinction.

Figure 3: The relationship between the migration parameter γ (x -axis), the fertility constant α (y -axis) (both from equation 5), and the minimum initial area needed for the population to fill the available space (z -axis) (or more precisely, the side of the initially-occupied square sub-matrix in the centre of the model). A value of 1 for z indicates that the population will expand indefinitely from a single cell in the grid. A larger value of z means the population requires a larger area to ensure expansion, below which it stagnates or dies out.

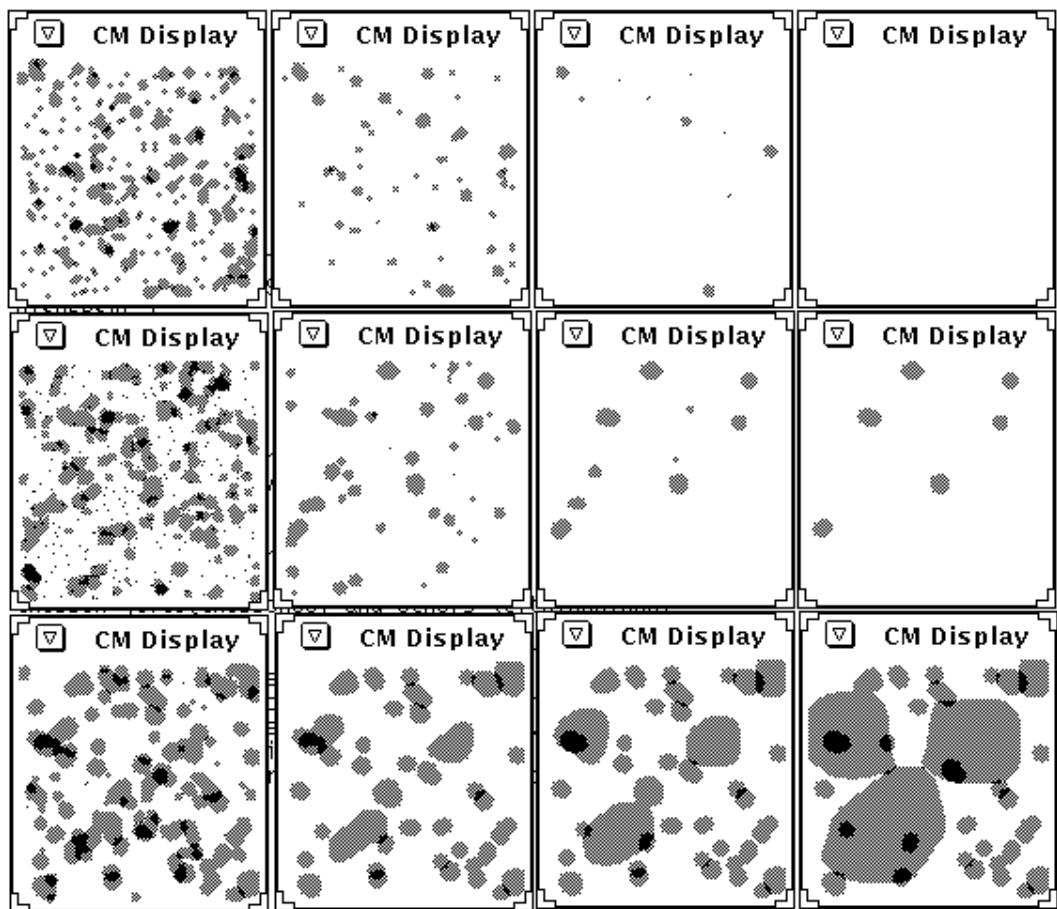


Figure 1: Authors: P. J. Darwen and D. G. Green

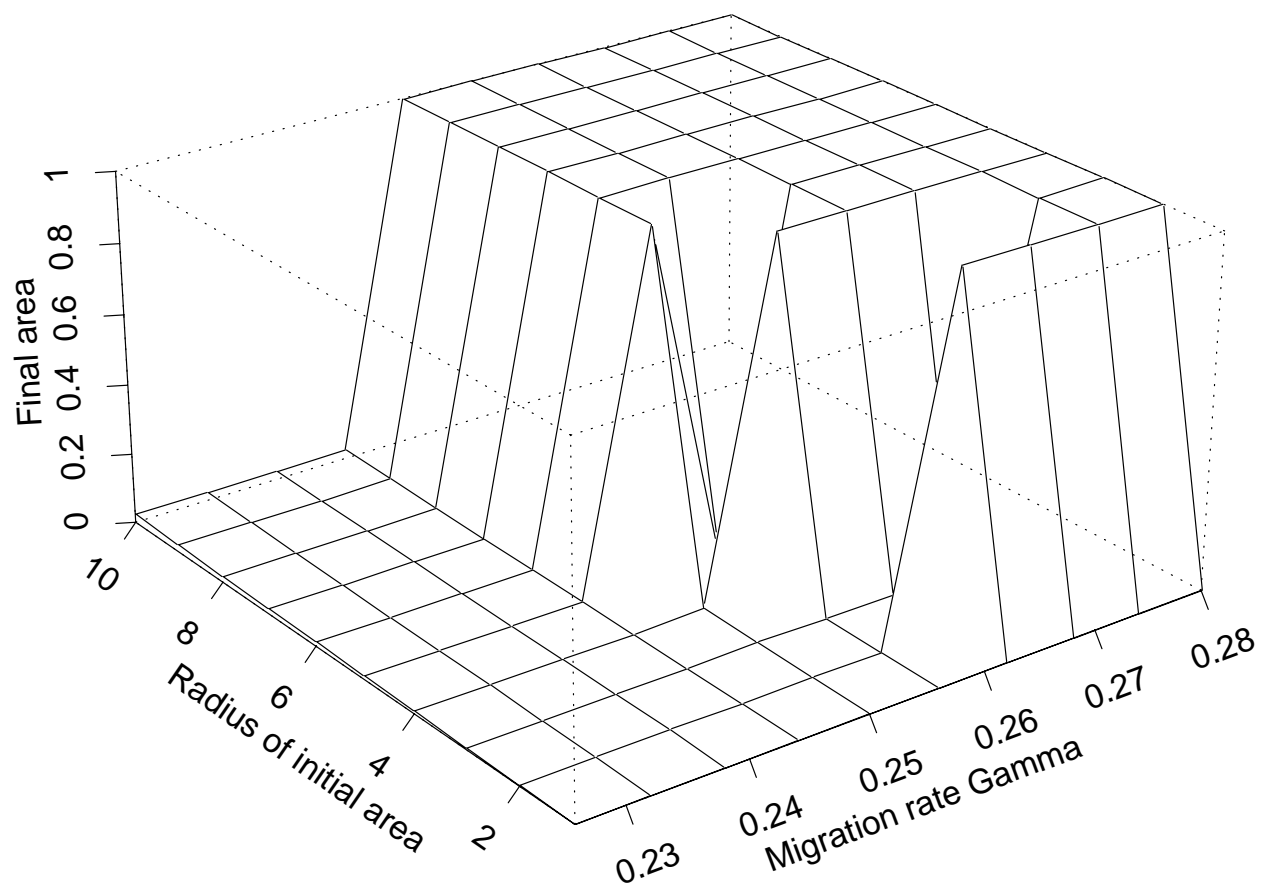


Figure 2: Authors: P. J. Darwen and D. G. Green

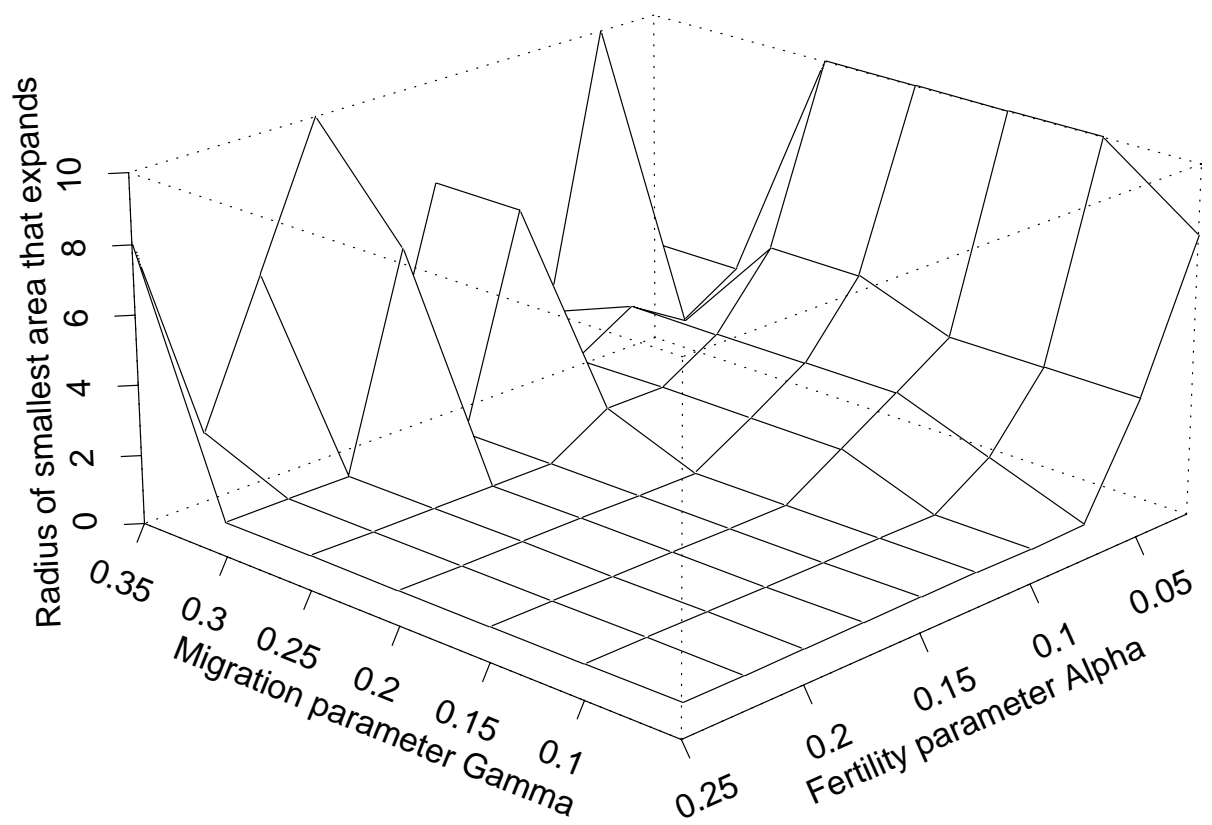


Figure 3: Authors: P. J. Darwen and D. G. Green