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**Report**, part of Special Feature on [Ralf Yorque Memorial Competition 2001](#)

# Habitat Shape, Species Invasions, and Reserve Design: Insights from Simple Models

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## ABSTRACT

Species invasions have become a major threat to global biodiversity. We currently lack a general theory of species invasions that allows us to make useful predictions about when and where invasions will occur, whether they will be successful, and whether they will alter ecosystem function in invaded habitats. One line of enquiry in developing such a theory is to focus on the characteristics of successful invaders. A second, complementary

approach is to examine habitats of interest more closely and ask how the properties of the habitat that is being invaded affect the likelihood of invasion success. In this paper, I consider the importance of habitat shape (also termed "habitat topology" or "habitat geometry") as a variable affecting the dispersal and abundance of invasive populations. I use two well-established simulation modeling approaches, namely, a cellular automaton model and a reaction-diffusion model, to mimic species invasions in hypothetical habitats that cover a range of linear, branching, rectangular, and square shapes. The results suggest that invasions in more geometrically complex habitats will occur faster and may ultimately produce a higher abundance of the invasive species. Differences in invasion rates are not a simple consequence of differences in overall connectivity, as shown by a comparison of habitats with identical connectivities but different spatial arrangements of cells. Ultimately, if combined with other modeling approaches, these methods may be useful in generating recommendations for managers about the vulnerability of particular habitats and reserve networks to invasion.

**KEY WORDS:** cellular automaton model, colonization, connectivity, dispersal, habitat complexity, habitat geometry, habitat shape, landscape ecology, reaction-diffusion model, reserve design, reserve networks, species invasion.

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## INTRODUCTION

Human expansion of the geographical ranges of other species has become a major threat to global biological diversity. Numerous unplanned, uncontrolled experiments have shown how a wide range of invasive species including crayfish, mussels, insects, fish, birds, pathogens, and plants can affect the structure of the indigenous food web, alter key abiotic variables such as groundwater, and cause reductions in local species diversity (Parker and Reichard 1998, Parker et al. 1999). At the same time, many introductions are unsuccessful or have no effect on the structure and function of indigenous communities (Williamson and Fitter 1996). A good deal of effort has been invested in trying to understand how the intrinsic properties of invasive species such as their reproductive rates, dietary requirements, and associations with humans (Bazzaz 1986) contribute to their success or failure. Although these studies have yielded a variety of useful case studies, they have mostly failed to establish general principles to guide managers in novel instances.

Orians (1986) argues that the shift of attention away from the receiving environment to the nature of the colonizing species has contributed to the lack of progress in deriving a more general understanding of invasions. He advocates an approach that combines information about the invading organisms with information about the environments into which they are being introduced and discusses the properties of the receiving environment in terms of disturbance, biotic interactions, and temporal scale. Similarly, Parker et al. (1999) ask to what extent the impact of an invasive species is dependent on the environment into which it is introduced.

Invasions usually come as ecological surprises. Although it may not be possible to make strong predictions about the likelihood of species invasions (May 1976), we can anticipate that invasions will be more likely in some places than in others. In particular, some habitats or habitat configurations are more susceptible to invasion than others. If we can identify the general properties of habitats that make them more or less vulnerable to invasion, we need to take these properties into consideration when designing and managing conservation areas. There are many characteristics of a region that will affect the likelihood of its being successfully invaded, including:

1. geographic isolation and proximity to potential sources of invaders (MacArthur and Wilson 1967). It should be noted that habitat proximity may be natural or anthropogenic. For example, areas on transport routes or with migratory human populations will be more vulnerable to invasion;
2. the number of similar habitats in other parts of the world;
3. the productivity of the habitat and the nature of the biota currently living within it (Pacala and Roughgarden 1982);
4. the nature and frequency of relevant disturbances (Elton 1958, Hobbs and Huenneke 1992);
5. the ease with which organisms move through the habitat as determined by relevant features such as vegetation type, wind, or water flow rates;
6. historical factors affecting the local species pool such as recent extinctions and previous invasions (Allen et

- al. 1999);
- 7. the specific match of invading species to habitat; and
- 8. habitat size and shape.

These and other factors, such as the rate of increase and minimum viable population size of the invading species, will also determine how serious the consequences of the invasion are and the likelihood that the invading species can be controlled.

An important correlate of the risk associated with a particular introduction is the rate at which individuals of the invading species can multiply and disperse. In this paper, I examine the question of whether habitat shape can affect rates of colonization. Previous studies of habitat shape that focused primarily on metapopulations and dispersal between habitat fragments (Hamazaki 1996, Dunham et al. 1997) often ignored the relevance of habitat shape at smaller and larger scales. Although Major et al. (1999) found significantly higher robin (*Erithacus rubecula*) densities in larger habitat fragments and different age structures in the robin populations of large and small fragments, the scale of their analysis was such that the results must necessarily be considered in terms of between-patch rather than within-patch dispersal. As I demonstrate using two different, spatially explicit simulation methods (a cellular automaton model and a reaction-diffusion model), these processes are affected by habitat shape. The models are used to generate hypotheses about the susceptibility of different habitats to invasion. In the future, it may be possible to use this kind of approach to calibrate the relative vulnerabilities of habitat fragments and reserves to invasions.

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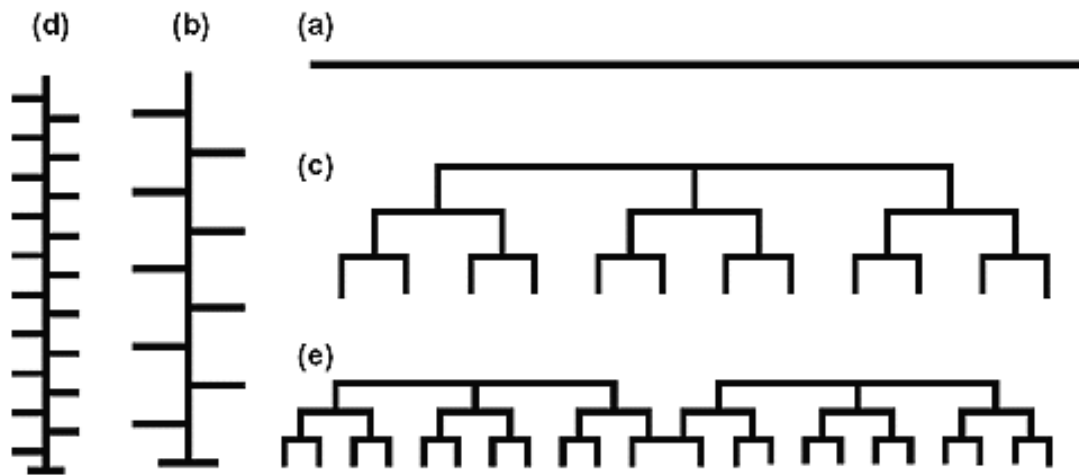
## METHODS

The spread of organisms in hypothetical habitats of different shapes was modeled using two different methods: a stochastic cellular automaton and a reaction-diffusion model. The [Matlab](#) routines for each model are provided in [Appendix 1](#). Both methods have been widely used to study invasions (Auld and Cooté 1980, Okubo 1980, Roughgarden 1986, Hengeveld 1994, Tilman and Kareiva 1997). In both instances, I kept the design of the model as simple as possible to minimize the number of parameters that might affect the outcome of the modeling exercise. All comparisons were undertaken using identical parameters and habitats of equivalent sizes (i.e., the same number of square cells) that differed only in shape.

### Hypothetical habitats

Each hypothetical habitat consisted of 1600 square cells (the habitat files are available in [Appendix 2](#)). Habitat shapes ranged from a straight line 1600 cells long to a 40 x 40 grid. The network habitats ([Fig. 1](#)) imitate streams of different complexities with 0, 10, and 20 nodes, respectively. Hypothetical streams of the same length and with the same number of nodes can be constructed at different levels of complexity, depending on how many ramifications their divergences have (i.e., how hierarchical they are); I constructed both a simple and a more complex model for each of the branching streams (10 and 20 nodes). Note that the complex 10-node and 20-node networks have slightly different hierarchical arrangements.

**Fig. 1.** Different hypothetical streamlike habitats compared in the modeling exercise (these drawings are not to scale). Each habitat consists of 1600 square cells; all parts of each network are the same width. Drawing (a) represents a linear habitat with no nodes; (b), a simple design with 10 nodes; (c), a complex design with 10 nodes; (d), a simple design with 20 nodes; and (e), a complex design with 20 nodes. Note that the complex 10-node habitat (c) has a different form from that of the complex 20-node habitat (e).

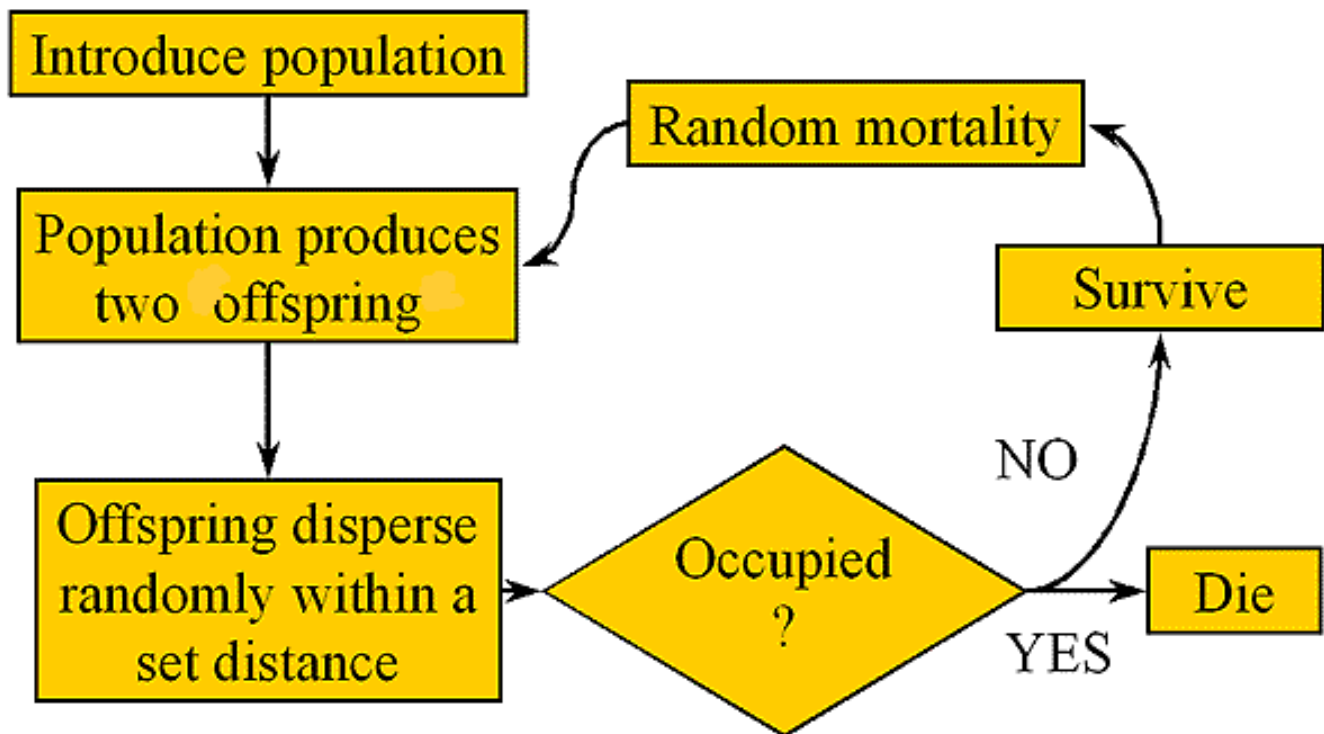


The regularly shaped habitats imitate square or rectangular terrestrial areas measuring 10 x 160, 20 x 80, and 40 x 40 cells, respectively. I did not attempt to simulate the effects of increasing the number of corners, although corner cells will obviously have a lower connectivity than do perimeter cells.

### Cellular automaton model

A thorough description of cellular automata in spatial ecology can be found in Tilman and Kareiva (1997). The model follows a simple, iterative form in which, at each time step, occupied cells can produce two offspring (these "propagules" can be thought of as subpopulations or migrating individuals). The offspring are assigned randomly to any one of the cells within a user-defined maximum dispersal distance of the parent cell (Fig. 2); this distance is set at three cell widths for all simulations. If an occupied cell (value = 1) is selected by the random function, no net change occurs; if an unoccupied cell is selected, its value changes from 0 to 1. The multiplication and dispersal processes are offset by a mortality level that ranges from 0 to 1. Mortality is imposed on each cell by selecting a uniformly distributed random number between 0 and 1; at a mortality of 0.3, for example, a cell's value will change from 1 to 0 if the random number is less than or equal to 0.3.

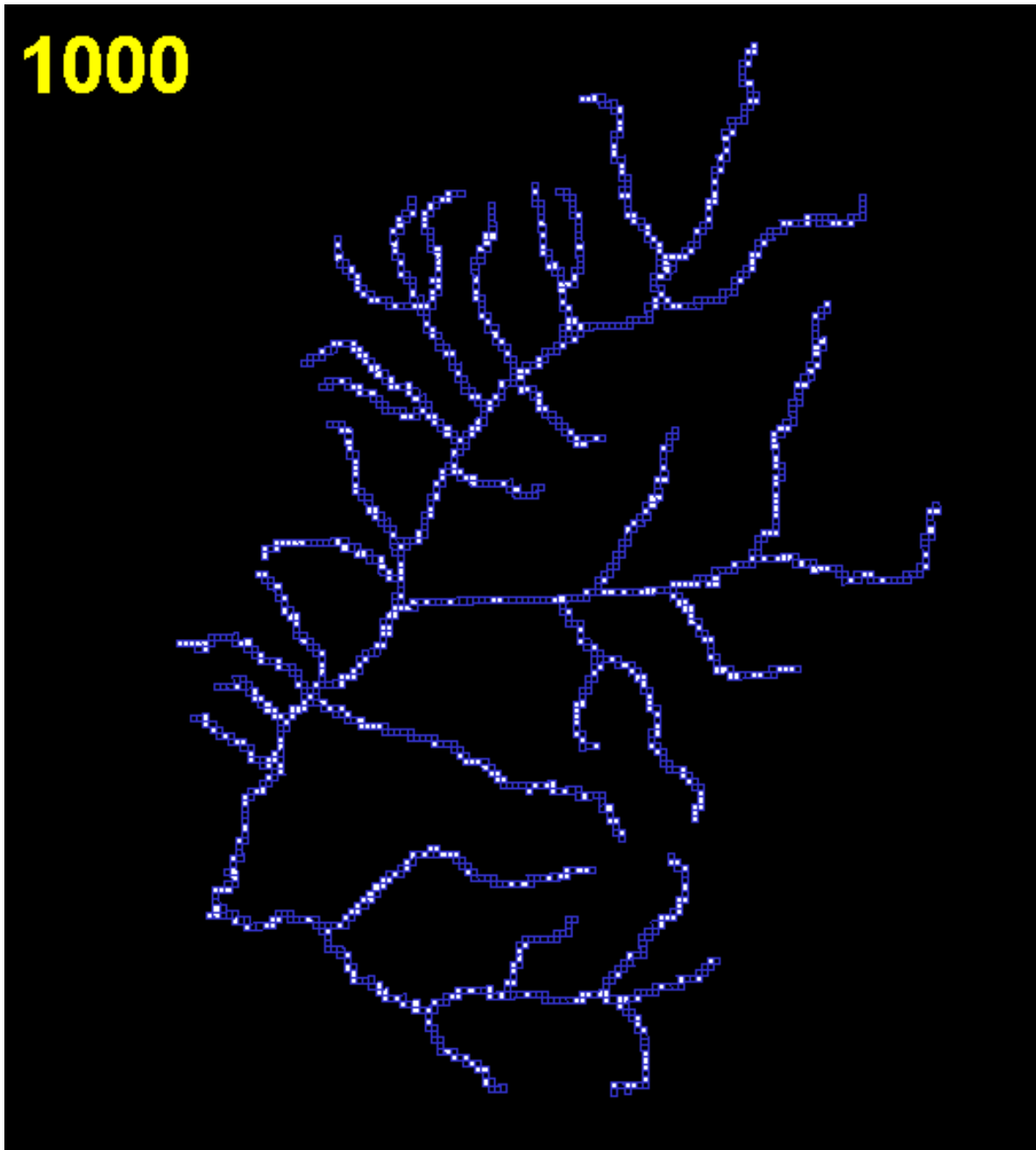
**Fig. 2.** A flow chart showing the processes that occur within the cellular automaton model. The introduced population produces two propagules or offspring that disperse randomly within a set distance. If they land in an occupied cell, they die; if they land in an unoccupied cell, they survive. All occupied cells then undergo random mortality before the cycle repeats itself.



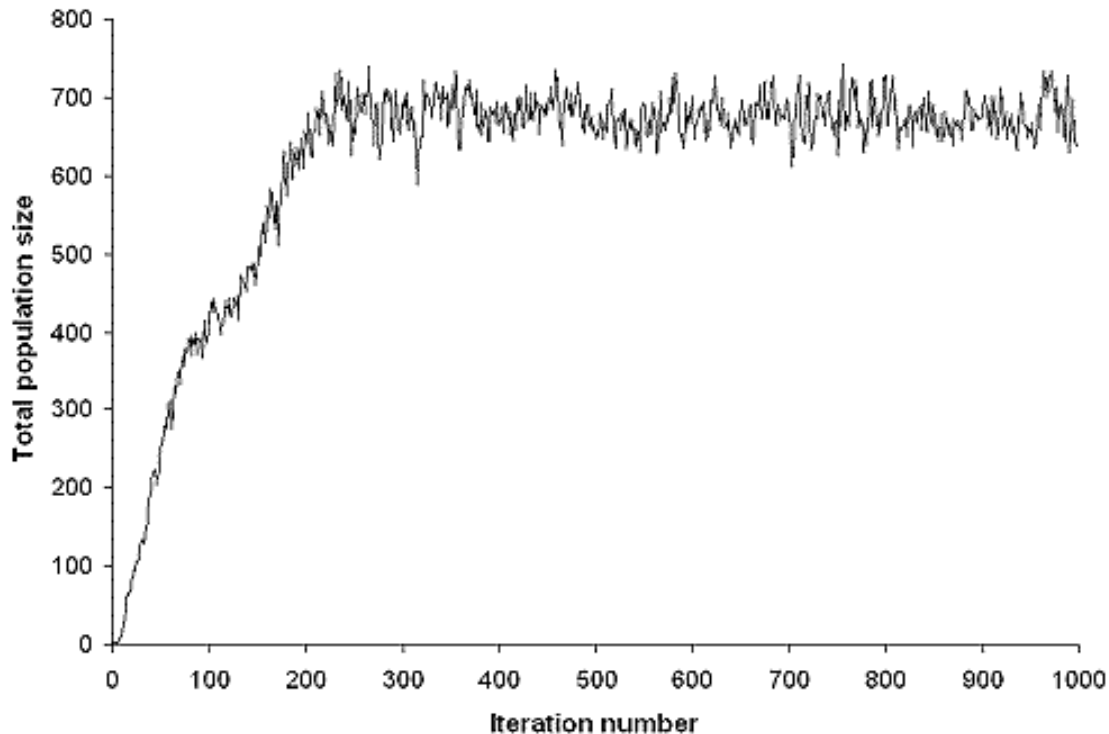
Individual simulations were continued for 5000 iterations, by which time each simulation had reached equilibrium. Because the model is stochastic, it does not produce the same answer every time; although it approaches similar equilibrium densities, these may differ depending on random fluctuations. I used multiple replicates of each set of conditions to establish general trends. The program reports which cells are occupied at each iteration and the total number of cells occupied, which serves as a surrogate for metapopulation density. I initially explored the consequences of varying mortality rates using 20 replicates of each set of conditions. These simulations suggested that shape effects were more likely at higher mortality rates. I then ran 100 replicates in each hypothetical habitat type at a mortality of 0.3. These simulations included five stream habitat types (simple with 0 nodes and simple or complex with 10 or 20 nodes) and three grid habitat types (40 x 40, 20 x 80, and 10 x 160 cells, respectively).

For each hypothetical habitat, I considered the rate at which the simulation reached equilibrium and the total carrying capacity of each cell. The data were summarized using the total number of occupied cells at each time step. To determine an equilibrium value for cellular automaton simulations, I took the mean of the last 500 iterations. Time to equilibrium was defined as the time that elapsed before the total number of occupied cells first exceeded this mean value. A typical sequence of colonization through a real stream network in Wisconsin is shown in [Figs. 3](#) and [4](#).

**Fig. 3.** Animated time series simulating colonization of a real stream habitat in Wisconsin by a hypothetical invasive species, as modeled using the cellular automaton model. The number in the upper left corner indicates the number of iterations at which the observation was made. The blue grid outlines habitat cells, and white shading indicates cell occupancy.



**Fig. 4.** Plot showing the total size of the metapopulation of the real stream over time. As can be seen by watching [Fig. 3](#), the species has reached all parts of the stream network by iteration 250; after this there is little net change in abundance, although the occupancies of different cells vary.



## Reaction-diffusion model

Roughgarden (1986) stated that the theory of the rate of spread of an invasion "... is quite robust, has been empirically tested, and is about as reliable as theory gets." The theory to which she was referring originated with Fisher's (1937) population-genetic model for the spread of a favorable mutation and was first brought into a specifically ecological context by Skellam (1951). The central prediction, i.e., that the square root of the area occupied by the invading species grows linearly with time, follows from the coupling of a diffusion model with exponential population growth to produce a reaction-diffusion model. Although classical reaction-diffusion models have some shortcomings when applied to real data, because their assumption of a normal rather than a leptokurtic dispersal curve may result in the underestimation of the rate of spread of the invading population (Kot et al. 1996), this inaccuracy is irrelevant to the conclusions of this paper.

I used a simple form of reaction-diffusion model known as Fisher's equation. A full outline of mathematical and programming methods for diffusion models can be found in Press et al. (1992). Reaction-diffusion models have two parts: a diffusion term and a reaction term. Diffusion and reaction occur separately. The reaction term in this instance was a simple logistic population increase:

$$N_{t+1} = N_t + rN_t(1 - (N_t/K)) \quad (1)$$

where  $N_t$  is the population size at time  $t$ ,  $r$  is the intrinsic rate of increase, and  $K$  is the carrying capacity (Tilman and Kareiva 1997). I did not include stochastic mortality in the population model. The population parameter  $r$  was set at 0.5, and  $K$  remained at 500 individuals per cell for all simulations.

The diffusion term used a multidimensional form of the diffusion equation (Press et al. 1992), which in one space dimension is

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left( D \frac{\partial u}{\partial x} \right) \quad (2)$$

where  $D$  is the diffusion coefficient,  $t$  is time,  $u$  is the population size in a given cell, and  $x$  is the distance over which diffusion takes place. This equation can be differenced in various ways, the simplest of which (in a single dimension) is

$$(u_j^{n+1} - u_j^n) / \Delta t = D(u_{j+1}^n - 2u_j^n + u_{j-1}^n) / (\Delta x)^2 \quad (3)$$

where  $D$  is the diffusion coefficient,  $u_j$  is the population size at time  $t$ ,  $u_{j+1}$  and  $u_{j-1}$  indicate population sizes in neighbouring cells,  $n$  is the current iteration,  $t$  is the time step, and  $x$  is the distance over which diffusion takes place. I used this form of the equation because of its computational speed, which is important for simulations this large. Its main drawback is that it is only stable for parameter combinations such that

$$2D\Delta t / (\Delta x)^2 \leq 1. \quad (4)$$

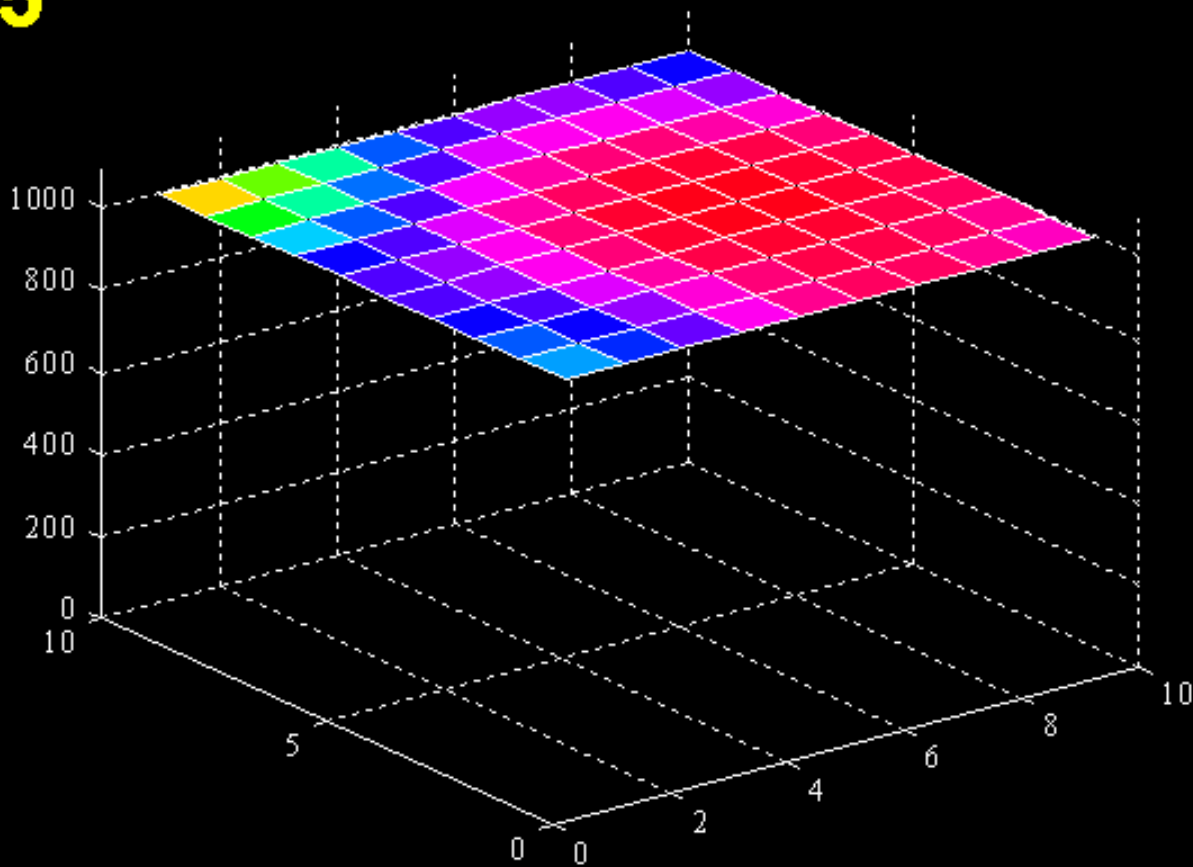
All the simulations used unit habitat cells and a time step of 1, but, because each cell had up to four neighbours, the value of the diffusion coefficient ( $D$ ) was constrained to less than 0.25.

For each cell, the model considers how many neighbors it has and uses the appropriate diffusion term (i.e., for one, two, three, or four neighbors). Neighboring cells in the reaction-diffusion model are defined as those that share two corners; dispersal was permitted only between immediate neighbors. If run to equilibrium, the model will fill all available habitat to carrying capacity (Fig. 5).

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**Fig. 5.** Animated time series simulating colonization of a 10 x 10-degree grid by a hypothetical invasive species, as modeled using a reaction-diffusion process. A population of 100 individuals is introduced at the centre of the grid, and logistic population increase, coupled with diffusion, occurs until the population reaches carrying capacity. The number in the upper left corner indicates the iteration number. The colors correspond to the values of individual cells along a gradient from red through blue and green to yellow and back to red; cells are reshaded at each iteration.



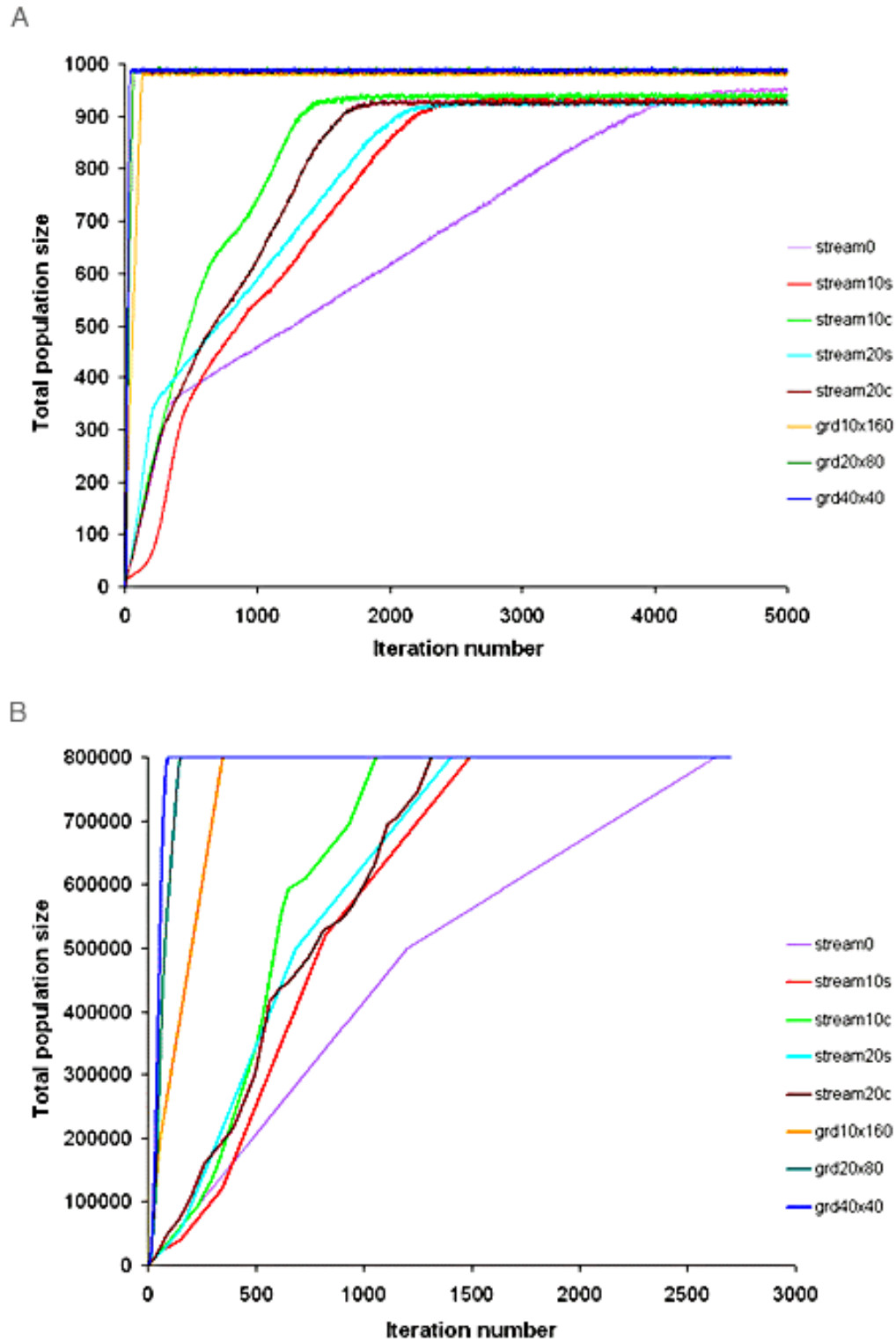
**55**

The reaction-diffusion model was run in the same hypothetical habitats as the cellular automaton model. In each instance, 100 individuals were introduced into a single cell, and the simulation continued until all the cells in the habitat had reached carrying capacity. The change in total abundance over time was then plotted to give the rate at which the invasive metapopulation increased. Because this model has no stochastic terms, multiple simulations under the same conditions were not necessary. Because there was no mortality term, the final carrying capacity of each habitat was identical.

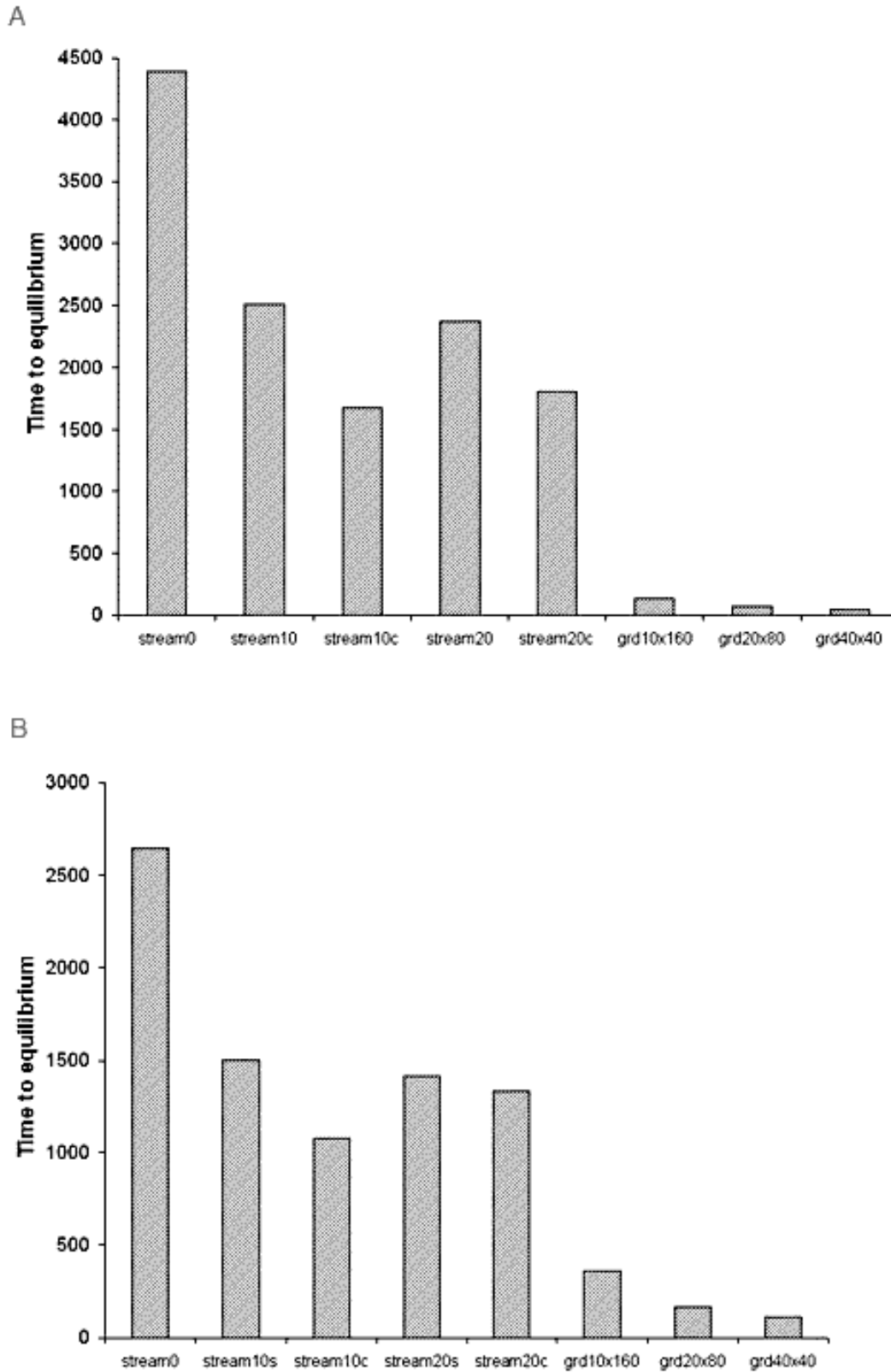
## RESULTS

For both the cellular automaton and the reaction-diffusion models, different hypothetical habitats (Fig. 1) were colonized at different rates (Figs. 6 and 7). The populations in the two-dimensional grids were the first to reach equilibrium, followed by those in the branching networks; the linear system was the slowest to be invaded in each instance. The more hierarchically arranged networks were colonized more quickly than the networks with a less nested form but the same number of nodes.

**Fig. 6.** Rates of occupancy of different hypothetical habitats under the cellular automaton model (A) and the reaction-diffusion model (B). In each graph, stream $N$  denotes a branching habitat with  $N$  nodes that can be either simple (s) or complex (c), and grdxxy denotes a square or rectangular habitat with sides of length  $x$  and  $y$ .

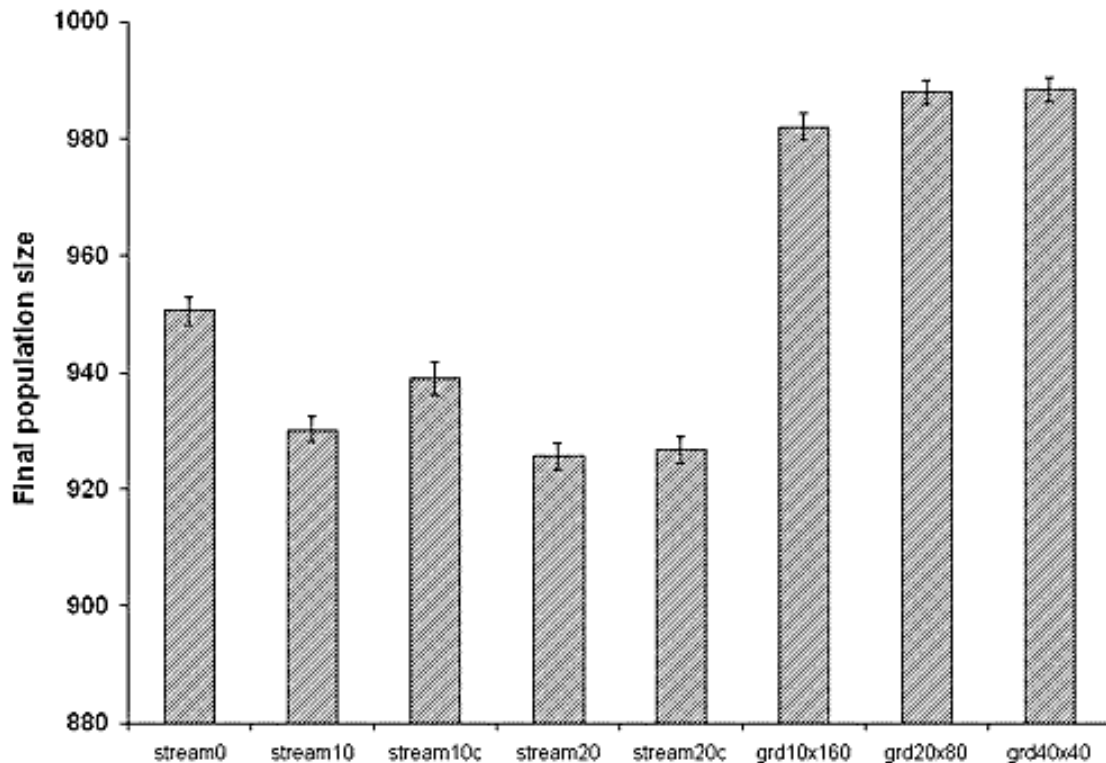


**Fig. 7.** Bar charts showing the differences in time to equilibrium for different hypothetical habitats under each model. Chart A results from the cellular automaton model at a mortality of 0.3; B, from the reaction-diffusion model with a population parameter of 0.5 and a carrying capacity of 500. Please see [Fig. 6](#) for an explanation of the captions on the x axes.



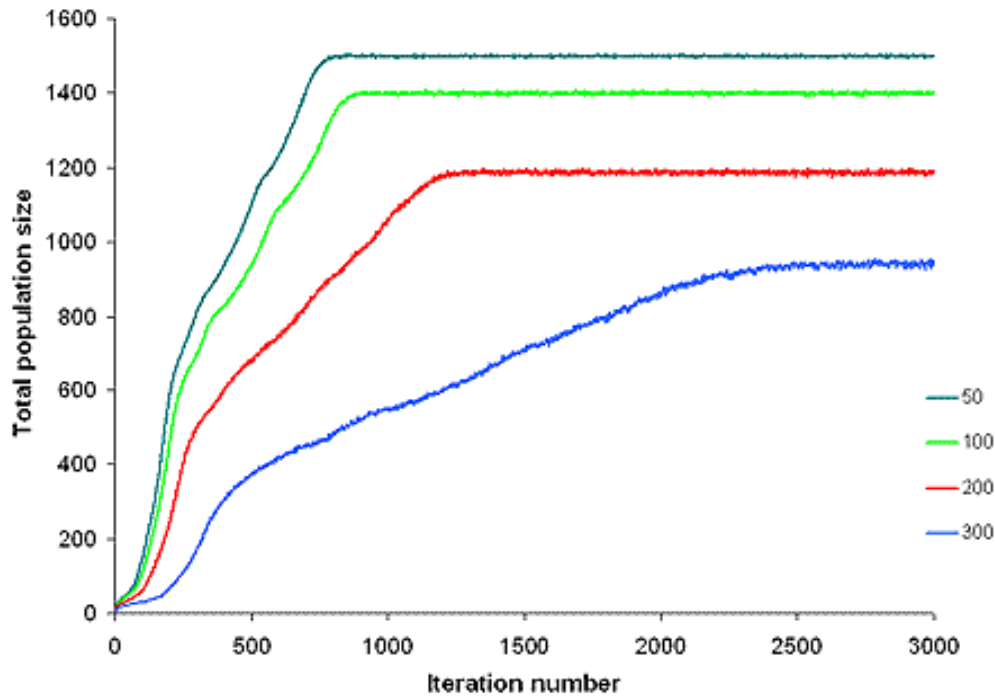
The influence of habitat shape on population processes will clearly be less pronounced for populations that have shorter generation times, move farther or faster, or have higher fecundity. As one might expect, the lower mortality rates in the cellular automaton model resulted in more similar colonization rates (Fig. 8).

**Fig. 8.** Equilibrium abundances attained in hypothetical habitats by the cellular automaton model. The error bars indicate  $\pm$  one standard deviation in the values of the last 500 iterations (each of these values is an average of 100 simulations). Please see Fig. 6 for an explanation of the captions on the x axis.



Interestingly, the final abundance of metapopulations from the cellular automaton model (as measured by the mean and standard deviation of the last 500 iterations) was significantly different between habitats (Fig. 9). In general, habitats that were colonized more quickly achieved higher eventual abundances of invaders. A test for correlation between time to equilibrium and eventual abundance yielded Kendall's Tau = -0.571 with a significance of  $p = 0.048$  ( $n = 8$ ). This result was influenced by the unexpectedly high abundance of individuals in the linear system; with this observation removed from the analysis, the value of Kendall's Tau increased to -0.81 ( $p = 0.007$ ,  $n = 7$ ).

**Fig. 9.** Times to equilibrium, expressed as number of time steps, in the 10-node stream network under different mortality conditions. When the random mortality term is set to 0.05, the population occupies its habitat more quickly and reaches a higher carrying capacity than at a mortality of 0.3.



## DISCUSSION

The results suggest unequivocally that habitat shape is an important determinant of the rate at which an invading population can fill available space. Although these models ignore many real-world factors, they serve as a useful heuristic from which to generate hypotheses. Both modeling methods have been applied successfully in real-world situations (Okubo 1980, Levin 1992, Tilman and Kareiva 1997) and yielded the same intuitively obvious conclusion. Habitats that have a more complex topology allow organisms to move through them at a faster rate, colonize unoccupied spaces more rapidly, and reach carrying capacity more quickly. Consequently, they are more likely than identical habitats of different topologies to be successfully invaded by an introduced species that is well suited to local conditions. The differences in the rates at which organisms can move within and between habitats may in turn create differences in the age structure of populations, depending on which life stages disperse more (Major et al. 1999), and the ultimate size of the population, depending on the local disturbance regime and how quickly empty habitats are recolonized.

The variations in colonization rates among different hypothetical habitats are not a simple consequence of differing degrees of connectivity. Although connectivity is undoubtedly important, the difference in colonization rates between hypothetical networks with identical connectivities but different spatial arrangements (such as the simple and complex networks with 10 nodes) shows that the precise arrangement of cells relative to one another is also important for processes related to dispersal. A more important metric, but one that is harder to quantify, is how branching or hierarchical the system is. Once an increasing population has split into two subpopulations at a node, it then increases at twice the previous rate. Faster colonization is facilitated by habitat configurations that split the population more frequently per unit area. Arrangements with more nodes are colonized more rapidly, but the position of these nodes relative to one another is also important. In real aquatic systems, this implies that more complex river networks will be more vulnerable to invasion than simpler ones; in the terrestrial context, reserve arrangements or the manner in which habitats are fragmented will be a correlate of their susceptibility to invasion.

The current focus in the design of reserves and reserve networks is primarily on proximity and connectivity. The connection of protected areas by corridors (Simberloff et al. 1992, Collinge 2000, Mortberg and Wallentinus 2000) needs to be carefully thought out, particularly in regions where species invasions are common. Increasing the connectivity of reserves will not necessarily be beneficial to the cause of conservation. Habitats that are more complex may be more vulnerable to the spread of invaders, parasites, and pathogens. On the positive side, they may also be more resilient to external perturbations because areas from which organisms are eliminated will be filled more quickly. The results of this study suggest that dispersal and population abundance will be influenced not only by the number of corridors but also by how hierarchical the resulting system is. In aquatic systems, where branching is more obvious, control of invasive species may be made more efficient by taking habitat complexity and topology into account; managers will need to move more rapidly to contain invasive species in habitats with complex topologies, where they will spread more quickly and attain higher abundances, than in simpler catchments where the spread of the species is likely to be slower and the final impact smaller. Similarly, it may be easier to fragment complex habitats deliberately without loss of functionality by breaking key connections, thus limiting the spread of invaders through the system.

Adequate tests of these predictions are likely to be difficult in real situations, where differences in the local environment between habitat fragments may obscure shape effects. The model world differs from the real world in many ways, most importantly in the simplifying assumptions that the models make about habitat homogeneity and constant rates of movement. Stream environments will probably be less homogeneous within highly branching networks than within relatively linear systems because of differences in the rates of change in stream size. In addition, the number of tributaries feeding into a stream is affected by superficial geomorphology, which also affects biotic communities. Large differences in tributary ramifications are unlikely to occur in highly similar habitats. Real-world populations typically show considerable variation in mortality rates; abiotic disturbances, human interventions, and biotic factors such as competition and predation are seldom constant in time or space. Similarly, animals typically disperse more at certain times of the year than at others. The best test systems will probably be those involving hardy, ubiquitous invaders that move along stream networks or riparian corridors; possible study species include crayfish and rabbits.

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## SPECULATION

As with other explicitly spatial phenomena, the relative differences generated by shape effects are likely to depend on scale. In real-world situations where there is a choice between different reserve designs, this kind of simulation approach may provide some valuable insights into the likely success of invasions and reintroductions. Dispersal and reproduction models that more closely imitate the spread of real animals in real habitats need to be developed and tested in real and hypothetical reserves of different designs. We can envisage that most reserve designs will be a compromise between risk and security, with smaller reserves being more vulnerable to disruption and larger reserves more robust. Conversely, control of invasive species will be more difficult in larger areas. Given more information on the vulnerability of habitats to invasion, it may be possible at some point to calculate an optimal or minimum reserve size, shape, and connectivity for individual species to balance internally and externally driven processes. In the meantime, the most secure long-term strategy is probably to maintain reserves of different sizes and shapes (including some very isolated areas) and monitor them closely.

The shape-dependency of dispersal and reproduction processes over large areas and long time scales may also have important consequences for evolutionary processes such as speciation and extinction. Speciation is more likely in habitats where genetic isolation is more readily achieved. It stands to reason that the likelihood of an isolating event would be higher in longer, thinner habitats with fewer connections. Extinctions may also be more likely in less complex habitats; for example, the effects of global warming on cold-water fish species may be more evident in high-altitude streams that have fewer branches.

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## RESPONSES TO THIS ARTICLE

Responses to this article are invited. If accepted for publication, your response will be hyperlinked to the article.

To submit a comment, follow [this link](#). To read comments already accepted, follow [this link](#).

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## APPENDIX 1

[Append1.zip](#) contains [Matlab](#) version 5.3 routines for both of the models that are presented in this paper. The files are in ASCII text format. Use the links below to view the files online.

### *The cellular automaton model*

[Cellaut.m](#) contains matlab code for the cellular automaton model. It is currently set to run 20 iterations, each of 5000 steps, under the given conditions.

### *The reaction-diffusion model*

This program consists of six separate .m files. [Diffuse.m](#) is the master routine. [Diffuse1.m to Diffuse4.m](#) are diffusion routines that are called by Diffuse.m for cells with one to four neighbours. [Reproduce.m](#) contains the logistic population increase term. This model provides a framework into which any set of coordinates can be read. It requires that parameter restrictions are observed (as outlined in the methods section) and that the distance between cells is unity. Grids based on real coordinates can easily be reformatted to give unit coordinate spacing; simply subtract the minimum x and y coordinates and divide by the inter-cell distance. If this is done in a spreadsheet, keeping the key of matching coordinate pairs, the results can readily be matched to the original coordinates and plotted in 'real' space. Note that dispersal can only occur between adjacent cells; there is no long-distance dispersal to unconnected habitat patches. In both cases you will need to change the working directory (from which input files are read, and to which the results file is sent) by altering the line 'cd d:\myfolder' to 'cd yourworkingdiskdrive:\yourfolderofchoice'. (e.g. change 'd:\myfolder' to d:\models\diffusion'). You may also need to add your folder to Matlab's directory using the 'set path' option in the Matlab command window.

### *cellaut.m*

```
% Cellular automaton model - stochastic dispersal, reproduction and mortality  
% Written by Graeme Cumming, November 2000
```

```
% set the working directory for your own machine  
cd e:\cellaut2
```

```
% these commands read in x,y coords from file myfile.txt  
fid = fopen('stream0.txt','r');  
[xcoord,ycoord] = textread('stream0.txt','%f %f');  
status = fclose(fid);  
count = size(xcoord);
```

```
% initialise the variables for the program  
cell = zeros(count);  
cell2 = zeros(count);  
cell(500) = 1; %starting value  
dispdist = 3; %dispersal distance in m  
inc = 2; %number of 'offspring' per iteration
```

```

mortality = 300; %death rate / 1000
area = ceil (3.141592654*(dispdist^2)); %max possible number of neighbours
neighbour = zeros (count,area);

reps = 5000;

%first we write a matrix containing identifiers of all cells in dispersal range
for x = 1:count
    match = 1;
    for i = 1:count
        distance = sqrt(((xcoord(x)-xcoord(i))^2)+((ycoord(x)-ycoord(i))^2));
        if distance <= dispdist
            match = match + 1;
            neighbour(x,1) = neighbour(x,1)+1;
            neighbour(x,match) = i;
        end;
    end;
end;

%now begins the main loop of the program

for z = 1:100

cell = zeros (count);
cell2 = zeros (count);
cell (500) = 1;
results = zeros (10000,1);

for r = 1:reps

%disperse
for j = 1:count
    if cell(j) == 1
        cell2(j) = 1;
        for m = 1:inc
            rnum = rand * neighbour(j,1);
            p = ceil(rnum);
            if p==1
                p = 2;
            end;
            plusone_id = neighbour(j,p);
            cell2(plusone_id) = 1;
        end;
    end;
end;

cell = cell2;
cell2 = zeros (count);

for k = 1:count
    if round(rand*1000) < mortality
        cell(k) = 0;
    end;
end;

%results
tally = sum(cell);

```



```
results(r,1) = tally;
```

```
if tally==0
    break
end;
```

```
disp (r);
```

```
end;
%^ ends the main loop
```

```
if z == 1
    final = results;
end;
if z > 1
    final = cat(2,final,results);
end;
```

```
end;
```

```
save ('results1.txt','final','-ascii');
```

*diffuse.m*

```
% Program Diffuse
% Written by Graeme Cumming, October 2000
```

```
% Program aim is to provide a general reaction-diffusion modelling framework
% Coordinates of study system are read in from a text file 'coords'
% A matrix 'proxim' is then written that holds the number of adjacent cells
% and which cells are adjacent, for each cell
```

```
% Diffusion occurs in one of three ways depending on # adjacent cells
%     1 adjacent cell: simple exchange
%     2 adjacent cells: reaction-diffusion in one plane
%     3 adjacent cells: r-d between 3 peripheral and one central cells
%     4 adjacent cells: two dimensional r-d
```

```
% After diffusion is completed for each cell, populations increase
% Population increase is determined by a logistic growth equation
```

```
% start by setting the home directory
cd e:\diffusn\streams\
```

```
% these commands read in x,y coords from columns in file tlake1.txt
fid = fopen ('stream0.txt','r');
[xcoord,ycoord] = textread ('stream0.txt','%f %f');
status = fclose (fid);
count = size (xcoord);
% the coordinate data are now in two vectors, 'xcoord' and 'ycoord'
% 'count' holds the number of coordinates
```

```
global adjacent
    adjacent = zeros (count,5);
% reserve space for number of and identifiers of adjacent cells
global current;
    current = zeros (count);
```

```

% the vector 'current' holds current n for each cell at time t
global cplus1;
    cplus1 = zeros (count);
% 'cplus1' holds n for each cell at time step t+1
global D;
    D = 0.1;
% D is the diffusion coefficient
% for the current diffuse2 it must be <= .5
global cellwidth;
cellwidth = 1;
% the real-world width of the cells, which are presumed to be squares

% now to calculate the proximity key
for j = 1:count
    adjacent(j,1) = 0;
    for i = 1:count
        distance = sqrt(((xcoord(i)-xcoord(j))^2)+((ycoord(i)-ycoord(j))^2));
        if distance == cellwidth
            adjacent(j,1) = adjacent(j,1) + 1;
            celltofill = adjacent(j,1) + 1;
            adjacent(j,celltofill) = i;
        end;
    end;
end;
% the 5 x count matrix has number of neighbours and up to 4 cell identifiers
% for each cell in the analysis

% seed the 500th cell with 100 individuals
current(500) = 100;

% next, the main diffusion loop

iterations = 3000;
step = 1;
%results = current;
num = 1;
results = zeros (count);

for k = 1:iterations
% number of diffusion iterations

% the following calls different diffusion routines
for j = 1:count
    switch (adjacent(j,1))
        case (1)
            diffuse1 (j);
        case (2)
            diffuse2 (j);
        case (3)
            diffuse3 (j);
        case (4)
            diffuse4 (j);
        otherwise
            disp ('ERROR - not finding neighbours');
    end;
    reproduce (j);
end;

```

```
current = cplus1;
```

```
% save the results every n steps
if k/step == floor(k/step)
    % results = cat(2,results,cplus1);
    results(num) = sum(cplus1);
    num = num+1;
end;
```

```
disp (k)
```

```
if k/3000 == floor(k/3000)
    save ('results1.txt','results','-ascii');
end;
```

```
end;
```

*diffuse1.m to diffuse4.m*

```
diffuse1.m
function [diff1] = diffuse1(j)
```

```
% diffusion into the end-cell
```

```
global cplus1;
global adjacent;
global current;
global D;
global cellwidth;
```

```
neighbour = adjacent(j,2);
unj = current(neighbour);
% unj is the current value of the cell next to the end-point
```

```
endcell = current(j);
```

```
if endcell <= unj
    cplus1(j) = endcell + (unj-endcell)/2;
end;
```

```
if endcell > unj
    cplus1(j) = endcell - (endcell-unj)/2;
end;
```

```
diffuse2.m
function [diff2] = diffuse2(j)
```

```
global cplus1;
global current;
global adjacent;
global D;
global cellwidth;
```

```
unj = current(j);
currnt1 = adjacent(j,2);
```

```
unjplus1 = current (currnt1);
currnt2 = adjacent (j,3);
unjminus1 = current (currnt2);
```

```
RHS = (((unjplus1 - (2*unj) + unjminus1))/(cellwidth^2))*D;
% cellwidth = delta x
```

```
cplus1(j) = RHS + unj;
```

*diffuse3.m*

```
function [diff3] = diffuse3(j)
```

```
global cplus1;
global current;
global adjacent;
global D;
global cellwidth;
```

```
unj = current(j);
```

```
c1 = adjacent(j,2);
c2 = adjacent(j,3);
c3 = adjacent(j,4);
```

```
% c1-c3 are the identifiers of the 3 neighbouring cells
```

```
currnt1 = current(c1);
currnt2 = current(c2);
currnt3 = current(c3);
```

```
% currnt1-currnt3 are the values of the 3 neighbouring cells
```

```
RHS = (((currnt1 - (3*unj) + currnt2 + currnt3))/(cellwidth^2))*D;
```

```
% cellwidth = delta x = 1; delta t is 1
% the flow is now three-way
```

```
cplus1(j) = RHS + unj;
```

*diffuse4.m*

```
function [diff4] = diffuse4(j)
```

```
global cplus1;
global current;
global adjacent;
global D;
global cellwidth;
```

```
unj = current(j);
```

```
c1 = adjacent(j,2);
c2 = adjacent(j,3);
c3 = adjacent(j,4);
c4 = adjacent(j,5);
```

% c1-c4 are the identifiers of the 4 neighbouring cells

```
currnt1 = current(c1);  
currnt2 = current(c2);  
currnt3 = current(c3);  
currnt4 = current(c4);
```

% currnt1-currnt4 are the values of the 4 neighbouring cells

```
RHS = (((currnt1 - (4*unj) + currnt2 + currnt3 + currnt4))/(cellwidth^2))*D;
```

```
% cellwidth = delta x = 1; delta t is also 1  
% the flow is now four-way
```

```
cplus1(j) = RHS + unj;
```

*reproduce.m*

```
function [shithappens] = reproduce (j)
```

% exponential population increase

```
global cplus1;
```

```
N = cplus1(j);  
r = .5;  
K = 500;
```

```
babies = r*N*(1-(N/K));
```

```
%fate = rand;  
% fate is a random number between 0 and 1  
% corpses = ((fate/1)*N)/2;  
% a random proportion of the population, not exceeding 50%, dies at every iteration
```

```
corpses = 0;
```

```
cplus1(j) = cplus1(j) + babies - corpses;
```

---

## APPENDIX 2

[Append2.zip](#) contains the hypothetical habitat files used in the analysis. Each pair of (x,y) coordinates specifies the centre of a habitat cell. The files are in ASCII text format; PC users can open them through Excel or view them directly in Notepad.

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grd10x160  
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2 1
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