A model for spatial conflict

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SUMMARY

Two species compete for territory along their mutual boundary. The species are fairly matched and the result of conflict is the invasion by one of the species of territory held by the other. A simple stochastic model for this process is described and rules are given for the calculation, as a function of time, of the probabilities that individual territories and groups of territories are held by a single species. Asymptotic results are given for the pattern of territories held by a single species, and here a remarkable distinction is seen between the cases of one-dimensional and two-dimensional competition and the case of three-dimensional competition. The process of invasion is contrasted with two relatively benign processes, that in which an exchange of territories is arranged and that in which a spatial alternation of species may be beneficial to the community. The implications of the long-term behaviour of such processes are discussed. It is suggested further that, under certain ideal conditions, it may be possible to estimate the duration of a spatial struggle for life by observing at some time the configuration of territories held by each species.

Some key words: Struggle for life; Spatial processes; Competition of species; Discrete diffusion; Invasion.

1. INTRODUCTION

The development of models for the competitive acquisition of territory by two opposing species gives rise to problems of considerable evolutionary and mathematical interest. Data will be of the binary form, zero or one, depending on who occupies a particular site. With a presumption of eventual stationarity, the recent papers of Dobrushin (1968), Spitzer (1971), Bartlett (1972), Besag (1972) and an unpublished paper of Hammersley & Clifford are relevant. The behaviour at intermediate times is described in principle by Bartlett's spatial-temporal processes (1971), but explicit solutions are generally not known.

We consider the case where conflict takes place only along the frontier, victory and defeat resulting in the acquisition and loss of territory.

Our exploratory work presupposes that occupiable positions are situated at points on a rectangular lattice in 1, 2, 3 or higher dimensions. A further specification is that the chance of a particular position being overrun depends only on the disposition of the enemy in the immediate neighbourhood. The case in which the rate of invasion is an exponential function of the number of enemy neighbours has been treated analytically by Bartlett (1971) but it should be noted that the model violates our requirement that changes should only take place along the frontier. When the rate of invasion is a linear function this requirement can be met but the analysis has proved to be difficult (Eden, 1961; Williams & Bjerknes, 1972).

These difficulties may be overcome in the case of fair competition. Furthermore, a swapping process may be introduced in which confrontations are resolved by the exchange of territory. In our approach this process is contrasted with the invasion process and the processes are shown to be related. We have chosen to reproduce the original method of analysis which argued *via* an intermediate spatial Poisson process, as we feel it may be of heuristic value, not least in providing insight into the generalization of our results to arbitrary lattices and graphs.

2. INDIVIDUAL COLOURS

$2 \cdot 1$. The swapping process

Throughout we refer to members of the opposing species as black and white cells. In the one-dimensional case each integral point on a line is occupied either by a black or white cell and the following process occurs in time. In any small interval of time $(t, t+\tau)$ the probability of adjacent black and white cells swapping positions is $\tau + o(\tau)$. To consider how the configuration develops, we consider the following representation.

In the plane with the original line of cells along one axis and continuous time along the other, points are thrown down randomly with unit density. We now envisage that the line of black and white cells sweeps forward in time and that swapping of adjacent cells take place at every instant when a random point intercedes between them. Note that if a random point passes between two white cells as the line moves across the plane then swapping occurs but the pattern of colours remains unchanged. It is clear that the probability that adjacent black and white cells swap position in any time interval is the same in both representations, and with respect to the development of the pattern of colours the processes are stochastically identical. If we wish to determine the colour of the cell which will occupy a certain position x_0 at some time t_0 then since the colour of a cell does not change we merely need to trace the history of the positions of the cell, using the second process until we can determine the colour from the original configuration. Since the points in the plane determine a unique path back to some position in the original configuration and each path is a realization of a unit step symmetric random walk in continuous time with rate two we have

LEMMA 1. In a swapping process on the lattice of integers, the probability of the position n being occupied at time t by the cell originally at k is the probability that the unit step symmetric random walk in continuous time with rate 2, starting at k, is at n at time t.

As a consequence we have the following:

THEOREM 1. In a swapping process, if A is the set of positions initially occupied by black cells, then at time t_0 the probability that a position x_0 is occupied by a black cell is the probability that a random walk starting from x_0 at time t = 0 takes one of the values in the set A at time $t = t_0$.

COROLLARY. For the one-dimensional rectangular lattice with $A = \{0, 1, 2, ...\}$ the probability that any given position is occupied by a black cell at time t tends to $\frac{1}{3}$ as $t \to \infty$.

We have only considered the one-dimensional case in detail, but it is clear, from the representation used, that the theorem, with the appropriate random walk, is true for arbitrary graphs. Thus, for an arbitrary set of positions, it will be necessary to decide which pairs of positions will be able to swap cells. This will determine the arcs of a graph and the random points will be thrown down on the product space formed by the arcs of the graph and the time dimension. We define the *d*-dimensional rectangular lattice to be the graph of all positions having integer co-ordinates, with arcs joining every pair of nearest neighbours.

If A, the set of positions initially black, is arbitrary, then the asymptotic probability that

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a given position is black is given by the limit as $t \to \infty$ of the probability that at time t the random walk lies in A. Since this raises the question of the existence of such asymptotic probabilities we will state without proof the following result. In order for such a limit to exist in the case of a d-dimensional rectangular lattice it is necessary and sufficient that in the initial configuration of black and white positions the proportion of black positions in an increasingly large d-dimensional sphere should have a limit. The two limits are then identical.

$2 \cdot 2$. The invasion process

In the invasion process a pair of adjacent black and white cells do not swap, but either cell may generate a new cell of the same colour; the neighbour is then eliminated and replaced by the newly born cell. Thus a black-white combination may become either black-black or white-white. The process is fair if both these events occur at a unit Poisson rate.

Our representation is essentially the same as before in that points are thrown down randomly in the product space formed by the arcs of the lattice and the time dimension. The difference is that the points have density two, and that, if at some time s, say, there is a random point between two positions, then both positions become of one colour, namely, the colour of the cell at the position nearer the point immediately prior to s; of course, this may result in no apparent change in the pattern of colours. Again we observe that with regard to the development of patterns of colours we have two equivalent processes. The random walk taken to determine the probability of a particular position being occupied by a black cell is much the same, except in that a jump along an arc of the lattice is made only if a random point is found more than half way along that arc. Because the points have been thrown down with density two the random walk has the same probabilities as that in the swapping case. We proceed straight to

THEOBEM 2. Starting from the same initial configuration, the probabilities that a certain position will be occupied by a black cell in a swapping process and a fair invasion process are equal.

The Corollary to Theorem 1 is obvious in the invasion case, for if all the black cells are together initially, then interaction can only take place at the black-white interface, which moves, therefore, backwards and forwards as a random walk.

3. JOINT COLOURING

$3 \cdot 1$. The invasion process

Although the probabilities for individual cells being black or white are the same for the two processes, we should not expect the resulting patterns to look similar. For example, in the case where the initial configuration is a solid block of black cells facing a solid block of white cells, mixing occurs immediately in the swapping process, but in the invasion process it can only occur by a relatively slow process of encirclement. It is simple to see what happens in the invasion process. If we are attempting to determine the colour of the cell in a certain position at a certain time by retracing its random walk in our representation, then each time an invasion occurs it is equivalent to that random walk joining another; that is, prior to this event their history is the same. Thus if we consider any pair of positions, if their random walks have met at some previous time, then the cells occupying the positions must have the same ancestor and so have the same colour. Since in one and two dimensions a random walk visits every point infinitely often we may state:

THEOBEM 3. For an invasion process on the one- or two-dimensional rectangular lattice, the probability that any finite set of positions will be occupied by cells of the same colour tends to 1 with increasing time.

This means that if initially the black and white cells are mixed, as time proceeds larger and larger areas are 'controlled' by cells of the same colour with the same ancestor. This theorem does not therefore depend on their being only two types of cell, for even if we start with an infinite variety of cells, any two of which have equal chance of invading each other when in adjacent positions, it still follows that as time proceeds any finite set of positions will tend to have the same ancestor.

But we do not expect there to be ultimate victory in any sector, for let us consider the simplest case in which initially all the black cells and all the white cells are together, in either one or two dimensions. At any stage in the evolution there is a point or line beyond which all the cells are white, say, and considering the further evolution beyond this stage, we see that the probability of any position being white is at least the probability that the random walk from that position reaches into the all-white sector at some time, and that this latter probability is 1.

3.2. The swapping process

We consider the joint distribution of the colours of a set of n cells occupying positions $H = \{h_1, \ldots, h_n\}$ on a *d*-dimensional rectangular lattice at some time t. We wish to show that the colours are *asymptotically independent*; that is, for large t the probability of a joint colouring tends to the product of the marginal probabilities for the individual colours. Our approach is to look at the random walks proceeding backwards in time from the positions H. These walks behave exactly as n independent random walks when they are apart, but when any two occupy adjacent positions they swap positions at a unit rate, and thus the rate at which at least one move occurs is less. Let $\mathbf{X}(t) = \{X_1(t), \ldots, X_n(t)\}$ be the position of the n swapping random walks at some time t. Let

$$S = \bigcup_{i \in I} \{ (x_1, ..., x_n) : ||x_i - x_j|| = 1 \},\$$

where x_i is a point on the *d*-dimensional lattice, and $||x_i - x_j||$ denotes the distance between the points x_i and x_j . Outside of the set *S* the process $\mathbf{X}(t)$ behaves as a vector of positions of *n* independent random walks in *d* dimensions.

Let us consider the two processes X(t) and Y(t), and let them move forward in time, constrained in such a way that when $X(t) \notin S$ they make the same displacements. Further, Y(t)moves freely as a random walk when $X(t) \in S$. It is clear that Y(t) has the distribution of a random walk. They differ in what occurs while $X(t) \in S$. Let us call the time spent in S, $\tau(t)$; then we will show first that $E\{\tau(t)\} = O(\sqrt{t})$. Consider

$$\operatorname{pr} \{ \mathbf{X}(t) \in S \} = \operatorname{pr} \{ \bigcup_{i,j} (\|X_i(t) - X_j(t)\| = 1) \} \leq \sum_{i,j} \operatorname{pr} \{ \|X_i(t) - X_j(t)\| = 1 \}$$

$$\leq \sum_{i,j} \sum_{k=1}^{d} \operatorname{pr} \{ |X_i^k(t) - X_j^k(t)| \leq 1 \} \leq n^2 d \operatorname{pr} \{ |X_i^k(t) - X_j^k(t)| \leq 1 \}$$

where $X_j^k(t)$ is the kth element of the d-dimensional random variable $X_j(t)$. Thus $E\{\tau(t)\}$ is no larger than the product of n^3d and the expected time spent by $Z(t) = |X_i^k(t) - X_j^k(t)|$ in the set of states (0, 1). We compare Z(t) with |W(t)|, the absolute value of a unit step symmetric

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random walk in continuous time with rate four. The two processes are subject to the same transition probabilities for all transitions other than that from state 1 to 0. For this transition the process Z(t) moves to zero at a rate no larger than |W(t)|; thus sojourns of Z(t) in the set (0, 1) are not stochastically longer than sojourns of the process |W(t)|. Since the expected time spent by W(t) in (0, 1) is known to be $O(\sqrt{t})$ we have the desired result. Now, since each element of the matrix of the displacements made by both X(t) and Y(t) always has mean 0 and variance ≤ 1 , and displacements occur at a rate bounded above and below, the difference between X(t) and Y(t) is a random variable $\epsilon(t)$ whose elements have variance $O(\sqrt{t})$. Thus

$$\frac{\mathbf{Y}(t)}{\sqrt{t}} = \frac{\mathbf{X}(t)}{\sqrt{t}} + \frac{\boldsymbol{\epsilon}(t)}{\sqrt{t}},$$

where $\epsilon(t)/\sqrt{t}$ is a matrix of elements each of which converges in probability to zero. If the initial coloration of the *d*-dimensional lattice is black in a region *R* (and white in its complement \overline{R}) which is scale independent, that is, in polar co-ordinates does not depend on the radius, then we must show that $\operatorname{pr} \{\mathbf{X}(t) \in \mathbb{R}^m \overline{\mathbb{R}^{n-m}}\}$ is asymptotically

$$\prod_{i=1}^{m} \operatorname{pr} \left\{ X_{i}(t) \in R \right\} \prod_{i=m+1}^{n} \operatorname{pr} \left\{ X_{i}(t) \in \overline{R} \right\}.$$

This follows from the asymptotic equivalence of $Y(t)/\sqrt{t}$ and $X(t)/\sqrt{t}$, since

$$\operatorname{pr} \{ \mathbf{X}(t) \in \mathbb{R}^m \overline{\mathbb{R}^{n-m}} \} = \operatorname{pr} \{ \mathbf{X}(t) / \sqrt{t} \in \mathbb{R}^m \overline{\mathbb{R}^{n-m}} \},$$

and similarly for Y(t). We thus have:

THEOREM 4. For a swapping process on the d-dimensional rectangular lattice, if the initial coloration is black in a scale independent region, then the colours at any finite set of positions are asymptotically independent.

4. Invasion in higher dimensions

The situation for a three-dimensional invasion process will not be the same as for the one- and two-dimensional cases because two independent random walks in three dimensions do not meet with certainty. Let us consider an invasion process on the *d*-dimensional rectangular lattice of integers in which all the black cells are initially in a region A and the white cells are initially in \overline{A} . We assume that the set A is such that the limiting probability that a particular position will be occupied by a black cell exists and equals p. We consider two positions x_1 and x_2 on the lattice and determine the asymptotic probability that the cells at these positions are of the same colour, that is, the probability that the random walks $\{X_1(t), X_2(t)\} = \mathbf{X}(t)$, starting from x_1 and x_2 , have met plus the joint probability that they have not and the walks are either in $A \times A$ or $\overline{A} \times \overline{A}$. For s < t, let E(s, t) be the event that the random walks meet for the first time in the time interval (s, t); then

$$\operatorname{pr} \{\mathbf{X}(t) \in A \times A\} = \operatorname{pr} \{\mathbf{X}(t) \in A \times A; E(0,s)\} + \operatorname{pr} \{\mathbf{X}(t) \in A \times A; E(s,t)\} + \operatorname{pr} \{\mathbf{X}(t) \in A \times A; \overline{E}(0,t)\}.$$

Denoting the terms in this expression by $p_1(t)$, $p_2(t)$, $p_3(t)$ and $p_4(t)$, we have as $t \to \infty$ $\lim p_1(t) = p^2$ and, for fixed s, $\lim p_2(t) = p^2 m(0,s)$, where $m(s,t) = pr\{E(s,t)\}$. Also $\lim p_3(t) \le m(s,\infty)$; thus for all s

$$p^{2}\{1-m(0,s)\} \ge \lim_{t\to\infty} p_{4}(t) \ge p^{2}\{1-m(0,s)\}-m(s,\infty).$$

Now m(0, s) is the probability that the unit step symmetric random walk $X_1(t) - X_2(t)$, starting from the initial position $x_1 - x_2$, will pass through the origin before time s. We will write $\lim m(0, s) = \pi(x_1 - x_2)$, and since $\lim m(s, \infty) = 0$ we have $\lim p_4(t) = p^2\{1 - \pi(x_1 - x_2)\}$. In a similar fashion it follows that $\operatorname{pr} \{\mathbf{X}(t) \in \overline{A} \times \overline{A}; \overline{E}(0, t)\} \rightarrow q^2\{1 - \pi(x_1 - x_2)\}$ as $t \to \infty$, where p = 1 - q. Thus the probability that the two positions x_1 and x_2 have cells of the same colour at time t, which equals $\operatorname{pr} \{E(0, t)\} + \operatorname{pr} \{\mathbf{X}(t) \in \overline{A} \times \overline{A}; \overline{E}(0, t)\} + \operatorname{pr} \{\mathbf{X}(t) \in A \times A; \overline{E}(0, t)\}$, converges to $p^2 + 2pq\pi(x_1 - x_2) + q^2$ as $t \to \infty$.

In one and two dimensions for an arbitrary displacement $\pi(x_1 - x_2) = 1$, and we conclude, in agreement with Theorem 3, that the probability an arbitrary pair of positions will be occupied by cells of the same colour tends to 1 as time increases. In higher dimensions $\pi(x_1 - x_2) < 1$. In three dimensions approximate values for $\pi(x_1 - x_2)$ have been calculated by McCrae & Whipple (1940). A more precise determination of $\pi(1, 0, 0)$ is given by Spitzer (1964, p. 103). To 9 decimal places $\pi(1, 0, 0)$ is given as 0.340537330. Taking $\pi(1, 0, 0) \approx 0.34$ with an initial set of black positions $A = \{(x, y, z) : x \ge 0\}$, so that $p = \frac{1}{2}$, we have that in three dimensions the probability that two adjacent cells are of the same colour is approximately $\frac{1}{2} + \frac{1}{2}(0.34) = 0.67$. This probability will obviously tend to a half as we consider more widely separated cells; the tables of McCrae & Whipple suggest that this tendency will be rapid. Thus there are no empires in a three-dimensional invasion process.

In situations in which both invasion and swapping occurs, the invasion determines the asymptotic appearance.

5. Alternation processes

In the invasion process, we have in mind a type of interaction between two species in which competition results in the invasion by one of the species of territory held by the other. For such territory we may suppose, in general, that rather than being completely destroyed the losing species may exist in a suppressed form. One might, in a crude way, view the class struggle in any country in such a light, aided by the international forces of capitalism or socialism.

In contrast, it is possible that the presence of a neighbour of the same species is a disadvantage, since two members of the same species struggling to survive need the same resources. One thinks of the way in which growing trees kill each other off in the struggle for light or for nutrients. In a less extreme situation it may be that when the same species is in the ascendant in two neighbouring territories there will be a tendency for the species to be suppressed in one of the two territories. This sort of effect may also be found in anti-ferromagnetism, where, in a pair of adjacent domains, one of the pair may reverse its direction of magnetism in order that they should be differently aligned. We should naturally expect the resulting patterns to look very different from those of a swapping process or an invasion process, there being a strong tendency for the species to alternate.

We shall call such processes 'alternation processes', and in terms of black and white cells it means that the colour combinations BB and WW for adjacent pairs may become BW or WB with equal probability. We will show that this process may be studied by means of a related invasion process. Consider an initial configuration of black and white cells on the one-dimensional rectangular lattice, and let C be the list of colours associated with each integer on the lattice. Let C^* be the same as C on even integers and the reverse colour on odd integers. The development of C using an alternation process is then essentially the same as that of C^* using an invasion process. We thus have as a direct parallel to Theorem 1:

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THEOREM 5. For an alternation process starting from an initial configuration C at time 0, the probability that the colour at an even position is black at time t equals the probability that it would be black at time t in an invasion process with initial configuration C^* at time 0. A similar result holds for the odd positions being white.

This is simply generalized to *n* dimensions when we define C^* to have the same colour as *C* on all points (x_1, \ldots, x_d) of the *d*-dimensional lattice such that $\sum x_i$ is even (and the reverse colour elsewhere). Following from Theorem 3 we have:

THEOBEM 6. For an alternation process in one and two dimensions the probability that any finite region is occupied by alternate black and white cells at time t tends to 1 as $t \rightarrow \infty$.

In three dimensions this is not the case, and from the results in 4 we conclude that the probability that a pair of neighbours have different colours is approximately 0.67.

6. CONCLUSION

We have tended to concentrate on asymptotic results, merely stating the form of results for finite time. At least for pairs of positions, the probabilities of joint colorations are not difficult to compute as a function of time. This raises the possibility of estimating the duration of a spatial struggle for life by analysis of the pattern of territories held. The requirements would be for the species to compete for well-defined territories and for the initial configuration to be known. We envisage two types of initial configuration, that in which two species meet for the first time along a well-defined boundary such as the formation of a land link, and that in which two species formerly perfectly intermingled are forced into conflict by a sudden change in the environment. In the first case it is the degree of penetration into opposing territory which is important; in the second case we would study the proportion of adjacent cells which are the same colour.

Lastly, we observe a feature of these processes that is frequently a difference between biological and physical sciences, or perhaps more accurately between macroscopic and microscopic theories. The configurations in the swapping process become more random as time goes by, whereas in the invasion and mixing processes they become more highly ordered. The swapping process is conserving and time-reversible, and for any two configurations C_1 and C_2 the probability of passing from C_1 to C_2 in time t is the same as that of passing from C_2 to C_1 . Since, using the natural measure, almost all configurations are random, it is not surprising that as time goes by the configurations become more random. The invasion and alternation processes, however, are not time reversible and do not obey conservation laws, they represent the power of living things to reproduce themselves and order the world. Thus, although in statistical mechanics we have the thermodynamical principle of the increase of entropy, we do not, for living things, see such statistical laws of increasing randomness.

We should note that, in general, provided the invasion is fair, it is unnecessarily restrictive to assume that the rates of invasion for all neighbouring pairs of positions are the same. Thus certain invasion paths may be more frequently used than others. We are grateful to Dr J. Green, Liverpool University, for pointing this out.

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