Evidence for emergent behaviour in the community-scale dynamics of a fungal microcosm

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A stochastic cellular automaton for modelling the dynamics of a two-species fungal microcosm is presented. The state of each cell in the automaton depends on the state of a predefined neighbourhood via a set of conditional probabilities derived from experiments conducted on pairwise combinations of species. The model is tested by detailed comparison with larger-scale experimental microcosms. By employing different hypotheses which relate the pairwise data to the conditional probabilities in the model, the nature of the local and non-local interactions in the community is explored. The hypothesis that the large-scale dynamics are a consequence of independent interactions between species in a local neighbourhood can be excluded at the 5% significance level. The form of the interdependencies is determined and it is shown that the outcome of the interactions at the local neighbourhood-scale depends on the community-scale patterning of individuals. The dynamics of the microcosm are therefore an emergent property of the system of interacting mycelia that cannot be deduced from a study of the components in isolation.

Keywords: community dynamics; emergent behaviour; cellular automaton; stochastic model; fungal interactions

1. INTRODUCTION

The treatment of space and of spatial interactions is of fundamental importance in ecology (Levin *et al.* 1997). It has been clearly demonstrated both experimentally and theoretically that the degree to which organisms are spatially mixed greatly influences the dynamics of the system (Tilman & Kareiva 1997; Levin *et al.* 1997). However, theoretical approaches differ greatly in the way that the spatial context is treated and in particular how spatial effects are averaged (Levin 1994). Spatially discrete models (including cellular automata) are composed of individual cells that are usually arranged in a regular lattice (Ermentrout & Edelstein-Keshet 1993). Parameterized rules are chosen that determine the evolution of a cell in terms of the states of a predefined fixed neighbourhood of cells. The assumptions regarding the neighbourhood, together with the rules, encapsulate the degree of spatial mixing in the system. Consequently, at any point in time the behaviour at the neighbourhood scale is assumed to be independent of the larger-scale context. Mean-field approaches (i.e. those based on differential equations) are formulated according to the assumption that there exists some characteristic spatial

scale below which individuals in the community can be regarded to be well mixed. The resulting dynamic is then described in terms of parameters averaged over that scale. Clearly, mean-field models preclude the explicit representation of individual behaviour and the questions of the existence and determination of the characteristic mixing length are usually overlooked.

Discrimination between different assumptions regarding spatial mixing is confounded by the difficulties in obtaining independent measures of the parameters in what are usually highly nonlinear systems, and by the fact that comparison between the predicted and observed spatial behaviour is often qualitative. Under these circumstances, agreement between theory and observation is not sufficient justification for interpreting the role of spatial context in the dynamics.

The role and nature of spatial interactions is particularly controversial in fungal ecology, and this is largely due to the indeterminate nature of the organism. Studies of ecological systems are almost exclusively concerned with determinate organisms where individual size and/or mobility can be used as a basis for choosing characteristic scales for the analyses. With indeterminate organisms, the situation is complicated by the existence of a continuous hierarchy of spatial scales across which interactions might occur. In the case of the fungal community, controversy

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centres on the scales over which spatial context plays an important role in the dynamics. Fungal mycelia proliferate through the extension and branching of protoplasm-filled tubes (hyphae) and a predominant assumption is that individual hyphae (hyphal growth units) do not interact (Trinci 1978; Prosser 1994*a,b*), with both models and experiments being cited in support. In the only previous attempt to model a multi-species fungal community, Halley *et al.* (1996) assume that there is no spatial interaction between the hyphae in a mycelium and support this assumption through a qualitative comparison with data. Ritz & Crawford (1990) demonstrated the existence of spatial correlations in the distribution of hyphae that argue against spatial independence. In subsequent work (Davidson *et al.* 1996*a,b*), mean-field approaches were used to show that patterning in single and interacting fungal mycelia implied interactions might exist across a range in spatial scale.

In all the modelling studies cited above, the comparison between experiment and theory is based on qualitative descriptors rather than on quantitative measures of the spatial and temporal patterns. Furthermore, the parameters relating to the spatial dynamics are either not directly measured, or are determined from experiment under the assumption that they remain constant irrespective of the spatial context. These facts together with the controversy outlined above mean the question of the role and nature of spatial interactions in the dynamics of fungal communities remains open.

In this paper we explore the spatial interactions in a simple fungal microcosm containing two species. In particular we test the hypothesis that the dynamics can be explained by independent spatially localized interactions. Experimental microcosms are arranged with contrasting spatial patterns ranging in the degree of patchiness in the configuration of species. A key aspect of the interaction between mycelia is the variation in possible outcomes between replicated systems (White *et al.* 1998). This is suggestive of an underlying sensitivity which argues against the use of purely deterministic rules to describe the behaviour. Therefore a stochastic cellular automaton is developed and used to link data relating the local-scale interactions between mycelia to the larger-scale dynamics of the fungal microcosms.

2. EXPERIMENTAL SYSTEM

The microcosm used in all experiments was based on that described by Ritz (1995). Square tiles of 2% (w/v) malt extract agar (MEA) (10 mm × 10 mm, 3 mm in depth) were arranged in prescribed configurations in sterile Petri dishes. In order to prevent significant movement of extracellular diffusibles that may complicate the interpretation of observed spatial effects, 2 mm air gaps were introduced between the tiles. The time taken for hyphae to cross the air gap is an order of magnitude smaller than the time to cross a tile, and there was no apparent effect of air gaps on the growth of the mycelia. The centrepiece of each tile was then inoculated with a core of pre-grown fungal mycelium. The fungal species used are implicated in wood decay and were isolated from wooden components of the Frigate Unicorn, the oldest British-built warship still afloat (White *et al.* 1996) in

Dundee, Scotland, UK. They have been identified as *Coniophora marmorata* (a cord-forming basidiomycete), and a *Paecilomyces variotii* strain. These are referred to as species Cm and species Pv, respectively, hereafter. The spatial patterns of tiles used comprised simple pairwise challenges to calibrate the model, and 36 tile arrays (6 × 6 tessellations) with differing initial spatial configurations of species to validate the model; see also White *et al.* (1998). The Petri dishes containing the tiles were sealed with Parafilm and incubated in plastic bags containing moist tissue paper (to maintain a relatively high humidity) at 15 °C. After incubation periods of 8 and 12 days (for 6 × 6 tessellations), and 4, 6, 7, 8, 10 and 12 days (for paired tiles), fungal occupancy of individual tiles was assessed by dividing each tile into equally sized quadrants and placing each of these onto fresh 2% MEA. These plates were then inspected for an outgrowth of fungal species after three to four days and the presence of particular species confirmed by observation (the mycelia were visually distinguishable; where there was any uncertainty, subcultures were paired against known isolates in a further interaction plate). At each time point there were ten replicates of the paired tiles and five replicates of the 6 × 6 tessellations.

3. MODELLING APPROACH

The cellular automaton used in this study is a five-cell neighbourhood in two dimensions as defined by Von Neumann (1966). The rule defining the state at time $t + 1$, of a given cell (i, j) in the two-dimensional lattice a at a time t is

$$a_{t+1}(i, j) = \phi_t[a_t(i, j), a_t(i, j + 1), a_t(i, j - 1), a_t(i + 1, j), a_t(i - 1, j)].$$

In this study the function ϕ_t is required to be stochastic and temporal in nature.

Our choice of the size of the tiles used in the experiments imposes a characteristic scale on our analysis of the system. Although the introduction of such scales is implicit or explicit in all modelling approaches, as the discussion in §1 makes clear, it is essential to understand the influence that the choice of scale may have on the interpretation of spatial interactions. Therefore we followed two approaches. The first assumed that detail below the scale of the tile was unimportant and the model was parameterized, run and validated at the characteristic scale of the tile. The second approach assumed that detail below the scale of the tile was important and the model was parameterized and run at the quarter-tile scale, the output was averaged over the whole-tile scale, and the results compared with the microcosm experiment at the whole-tile scale. Subsequent analysis showed that the first approach produced results that were inconsistent with the observed behaviour, suggesting that spatial details below the scale of the tile were important in the description of the dynamics. Therefore we proceeded with the second approach.

As a first step in the analysis, we characterized the independent challenges between species using pairings of tiles as described above. In a two-species interaction (assuming no empty cells) there are three possible states:

Figure 1. The arrangement of tiles in (a) tessellation 1, (b) tessellation 2, and (c) tessellation 3. Arrangement (a) has a patch size of nine with 12 Cm–Pv interfaces; arrangement (b) has a patch size of three with 36 Cm–Pv interfaces; arrangement (c) has a patch size of one with 60 Cm–Pv interfaces.

state α (i.e. the cell contains only species α); state β (i.e. the cell contains only species β); state $\alpha\beta$ (otherwise). The time evolution of the system is governed by state transition probabilities, $p(x|\alpha, \beta, t)$, defined to be the probability of obtaining state x given a cell in state α is challenged by a cell in state β for a time t . The values of the probabilities are derived from the pairwise challenges in the following way. The tiles belonging to all replicates corresponding to a particular time point were quartered and the state of each quarter was individually assessed. The value of $p(x|\alpha, \beta, t)$ was set equal to the fraction of quarters that changed from state α to state x during the time interval t . Since the experiments are necessarily snapshots at the sampled time points (4, 6, 7, 8, 10 and 12 days), linear interpolation was used to provide values at intervening times (i.e. for days 5, 9 and 11).

These values for $p(x|\alpha, \beta, t)$ are used in the automaton where each cell represents a quarter-tile in the real system. The model produces an outcome in the form of a lattice of states representing occupancy of tiles as α (if all quarters are in state α), β (if all quarters are in state β), and $\alpha\beta$ (otherwise) at each discrete time step. The lattice is subsequently characterized in terms of 6×6 state transitions with respect to the initial configuration, where $\alpha \rightarrow \alpha$ denotes no state change, $\alpha \rightarrow \beta$ denotes a change in state from α to β and $\alpha \rightarrow \alpha\beta$ denotes a change in state from α to the mixed state $\alpha\beta$. Since we are averaging over scales below the scale of the tile, we ignore spatial information relating to the relative location of the different quarter-tile states. For example, if any three out of the four quarter-tiles are in state α and the fourth is in state β , then the tile is defined to be in the mixed state $\alpha\beta$. The large-scale biological validation experiments are similarly spatially averaged and characterized, and the predictions made by the model are thus compared with the actual outcomes of the biological system.

To test our hypothesis, we make various assumptions about how the set of $p(x|\alpha, \beta, t)$ are implicated in the dynamics of the microcosm community. The first assumption, which we will subsequently refer to as case A, is that the nearest-neighbour challenges are independent. Therefore, if a cell simultaneously contains two species, each one interacts as if the other were not present. For example, the probability that a cell containing species α changes to containing species β when challenged by n neighbourhood cells containing species β for a time, t , is

$$1 - (1 - p(\beta|\alpha, \beta, t))^n. \quad (1)$$

The next simplest assumption, case B, is that the outcome of a five-neighbourhood challenge can be expressed as a weighted sum of the probabilities of the

pairwise challenges. Thus, we define $p(x|f_\alpha, f_\beta, t)$ to be the probability of outcome x after time t in a five-cell neighbourhood where the subject cell is in state α , and f_α and f_β are the frequencies of the states α and β in the neighbourhood, respectively. The general form of the relation between $p(x|f_\alpha, f_\beta, t)$ and $p(x|\alpha, \beta, t)$ is given by

$$p(x|f_\alpha, f_\beta, t) = \frac{(f_\alpha - \delta)^v p(x|\alpha, \alpha, t) + f_\beta^w p(x|\alpha, \beta, t)}{(f_\alpha - \delta)^v + f_\beta^w}, \quad (2)$$

where δ , v and w are constants. Strictly, if we ignore the subject cell in the weighting then $\delta = 1$. However, for the purpose of subsequent analysis we leave δ as a parameter.

Figure 1 shows the 6×6 layouts (termed ‘tessellation 1’, ‘tessellation 2’ and ‘tessellation 3’) used in the validation experiments. These arrangements were specifically designed to investigate the influence of large-scale patterning in the distribution of species on the dynamics of the community. The size of the same-species patches progressively decreases from tessellation 1 to tessellation 3, and therefore the number of inter-species interfaces progressively increases.

4. RESULTS

Biological interactions were analysed for the 6×6 layouts (figure 1). The observed state transition data for these experiments, expressed as means of the replicates, are shown in tables 1, 2 and 3. Note that the transitions Cm $\rightarrow$ Pv and Cm $\rightarrow$ CmPv were never observed and thus have zero frequency, and hence are assumed to have zero probability. Similarly, Cm $\rightarrow$ Cm was always observed and thus is assumed to have unitary probability. These trivial transitions are omitted from the tables for the sake of clarity. The computer models were run and the outcomes observed at eight (simulated) days and 12 (simulated) days for the three 6×6 configurations (tessellations 1, 2 and 3) using the calibration data from the 2×1 experiments. One thousand runs of each tessellation, providing sufficient output for testing the model against the biological data at the 5% significance level (Marriott 1979), were undertaken and ranked. The means and central 95% confidence intervals for each state-transition category are also shown in tables 1, 2 and 3 (assuming $v=1$ and $w=0$). Whilst only the data from the final investigation are presented, other results were assessed in a similar manner.

The models were run for each of the three tessellations under case A assumptions. The predicted outcomes disagreed with the results of the biological experiments for all tessellations, i.e. not all the observed state transition data were within the central 95% confidence

Table 1. *Results of the comparison between model output and the experimental microcosm for tessellation 1*

(The table shows the observed transition data corresponding to the number of each type of transition averaged over the five replicate experiments at day 8 and day 12. For comparison, the number of transitions of each type averaged over 1000 realizations of the simulation are shown for values of $\delta = 0, 0.15, 0.9$ (see text). Numbers in brackets represent the 95% confidence interval derived from the simulations, and the emboldened transition data denote the optimal fit to the observed data. The values of v and w were constant for each run: $v = 1$; $w = 0$.)

state transition categories			Pv→Pv	Pv→Cm	Pv→CmPv
observed state transition data		day 8	8.6	0	9.4
		day 12	0.4	14	3.6
mean and central 95% confidence interval of predicted state transition data					
(Lower, Upper)	$\delta = 0$	day 8	9.37 (7, 13)	0.09 (0, 1)	8.06 (5, 11)
		day 12	2.79 (0, 4)	7.13 (4, 12)	8.07 (4, 11)
	$\delta = 0.15$	day 8	9.69 (7, 12)	0.11 (0, 1)	8.2 (5, 11)
		day 12	2.43 (0, 6)	8.03 (3, 11)	7.54 (4, 12)
	$\delta = 0.9$	day 8	8.86 (6, 12)	0.26 (0, 2)	8.88 (6, 12)
		day 12	1.33 (0, 4)	11.4 (7, 16)	5.24 (2, 9)

Table 2. *Results of the comparison between model output and the experimental microcosm for tessellation 2*

(See caption to table 1 for details.)

state transition categories			Pv→Pv	Pv→Cm	Pv→CmPv
observed state transition data		day 8	0.4	9.2	8.4
		day 12	0	16.58	1.42
mean and central 95% confidence interval of predicted state transition data					
(Lower, Upper)	$\delta = 0$	day 8	0.34 (0,2)	6.22 (3, 11)	11.43 (7, 15)
		day 12	0 (0, 0)	17.16 (15, 18)	0.83 (0, 3)
	$\delta = 0.15$	day 8	0.23 (0, 1)	7.35 (3, 12)	10.42 (6, 15)
day 12		0 (0, 0)	17.5 (16, 18)	0.5 (0, 2)	
	$\delta = 0.9$	day 8	0.08 (0, 1)	12.18 (8, 16)	5.79 (2,10)
		day 12	0 (0, 0)	17.98 (18, 18)	0.02 (0, 0)

Table 3. *Results of the comparison between model output and the experimental microcosm for tessellation 3*

(See caption to table 1 for details.)

state transition categories			P _V →P _V	P _V →C _m	P _V →C _m P _V
observed state transition data		day 8	0.2	1	16.8
		day 12	0	15.8	2.2
mean and central 95% confidence interval of predicted state transition data					
(Lower, Upper)	$\delta = 0$	day 8	0.88 (0, 3)	0.69 (0, 3)	16.42 (14, 18)
		day 12	0 (0, 0)	15.57 (14, 18)	2.43 (0, 5)
	$\delta = 0.15$	day 8	0.67 (0, 3)	0.94 (0, 3)	16.39 (14, 18)
		day 12	0 (0, 0)	16.64 (14, 18)	1.36 (0, 4)
	$\delta = 0.9$	day 8	0.33 (0, 2)	2.67 (0, 6)	15 (12, 18)
		day 12	0 (0, 0)	17.92 (17, 18)	0.07 (0, 1)

intervals. This demonstrates the important result that the dynamics of these fungal communities do not result from independent challenges from nearest neighbours.

Models were also run for each of the three tessellations under case B assumptions. The constants v and w were allowed to vary independently from zero to two in increments of 0.1 with $\delta = 1$ (the subject cell is therefore not included in the weighting of $p(x|\alpha, \alpha, t)$). Models having non-zero values for w were inconsistent with the experimental results, i.e. not all the observed state transition data were within the central 95% confidence intervals.

Models with parameter values $v = 1$ and $w = 0$ performed best, in terms of the number of observed state transition data within the central 95% confidence intervals, in all tessellations. In particular, a good agreement with the results of tessellation 1 was obtained, in the sense that all observed state transition data were within the central 95% confidence intervals.

In order to understand the poorer agreement with the experiments conducted in tessellation 2 and tessellation 3, the effect of large-scale patterning on the local interactions was considered. This was investigated by modifying

the value of the parameter δ in equation (2). Values of δ of less than one effectively weaken the challenge of Cm on Pv relative to the situation encountered in tessellation 1. In this search, δ was allowed to vary from zero to one in increments of 0.05. It was found that the optimal value of δ (i.e. the value such that all the observed state transition data lay within the 95% confidence interval and were closest to the observed mean) depended on the nature of the large scale patterning in the tessellations. For tessellation 1 the optimum δ value was 0.9; for tessellation 2 the optimum δ value was 0.15; for tessellation 3 the optimum δ value was zero. For comparative purposes the means and central 95% confidence intervals for each tessellation for each of the three δ values noted are provided in tables 1, 2 and 3.

5. DISCUSSION

The simplest model assumes that the dynamics of the communities are a result of independent challenges from species in a predefined local neighbourhood. Comparison with the results from the experimental microcosms showed we could exclude this hypothesis at the 5% significance level.

The next simplest model assumes that the challenges are not independent, and that the probability relating to the change in state of the subject can be written as a weighted sum of the probabilities relating to the independent challenges. The weightings express the assumption that the strength of the challenge from an individual cell in the neighbourhood depends on the number and species types in the rest of the local (five-cell) neighbourhood. This model is parameterized by two weighting factors, v and w , and an additional parameter δ . The values for these parameters are determined by comparison with experiment and yield insight into the nature and scales of interaction between individuals in the microcosm community.

The parameter, w , represents the weighting applied to the frequency of the species β within the neighbourhood of a subject cell of species α . Comparison with the experimental results from the microcosm show that the optimal models for all tessellations require $w=0$, indicating that only the presence or absence of species β in the neighbourhood is of significance for the dynamics.

The parameter, v , represents the weighting applied to the frequency of the species α within the neighbourhood of a subject cell of species α . Comparison with the microcosm results shows that the optimal models for all tessellations require $v=1$, indicating that the number of subject-cell species in the neighbourhood is important for the dynamics.

Whilst the values of v and w are consistent with the experimental results for all tessellations, δ varies across tessellations. Furthermore, this variation reveals a relation between the value of δ and the large-scale spatial arrangement of species in the corresponding tessellation. More precisely, as the same-species patch size increases, the value of δ increases. As noted earlier, species Cm is a known cord-former suggesting that initially isolated mycelia may undergo a process of anastomosis or hyphal networking (Rayner *et al.* 1994; Rayner 1996), effectively resulting in a scale change in species Cm. The trend of

the value of δ with degree of patchiness represents a strengthening of the combative nature of species Cm in large patches.

Since the large-scale patterning of the community changes with time, we would expect that δ would also be time dependent. Our data are not inconsistent with this, but we were unable to detect a statistically significant time dependency. The fact that we were able to model the dynamics using a constant value for δ that depends only on the initial state of the microcosm, may reflect the relatively slow rate at which the system loses its 'memory' of previous states.

From these results we can conclude that the community-scale dynamics of the microcosm are a consequence of non-independent local interactions, and that the nature of these interactions is modified by the community-scale features of the system. This behaviour may be a consequence of anastomosis leading to translocation of resources from sites of low combative stress to interaction fronts where antagonistic or defence responses increase metabolic demand. This combination of scale effects greatly complicates understanding of the large-scale behaviour of microcosms, and precludes the extrapolation of results from experiments conducted out of the spatial context of the community. Instead, the results strongly suggest that most progress will be made by studying the dynamics at the community level, acknowledging the influence on the dynamics of emergent behaviour resulting from cooperative strategies.

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