



Predicting fungal community dynamics driven by competition for space

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ABSTRACT

Predicting fungal community dynamics requires methods combining theory with experiments. Different elements of spatial competition influence interaction outcomes, and consequently community dynamics. Despite the literature on such elements, no theoretical study has tested the predictability of dynamics with models incorporating these elements. We aimed to develop a method for predicting dynamics, to be tested first under laboratory conditions. Six spatial competition elements were quantified for three basidiomycete species on agar. We found: constant extension; extension unaffected by other mycelia; faster replacement of younger mycelial regions; faster replacement of smaller mycelia; uniform distribution of mycelial competitive ability across the boundary with heterospecifics; and additive effects of competition. We developed a lattice model, and found that incorporation of all experimentally quantified elements was necessary for accurate prediction of dynamics. Our study provides a methodological basis for prediction of fungal dynamics, and hence of ecosystem processes in which filamentous fungi are key players.

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1. Introduction

Acquiring ecological understanding to predict and control the dynamics and function of microbial communities requires the combination of theoretical modelling and experimental hypothesis testing (Widder et al., 2016). Filamentous fungi are ideal for such integrative studies of ecological concepts and hypotheses, since multiple species can be cultured easily and rapidly, and hetero-specific or somatically incompatible basidiomycete individuals generally do not merge (Watkinson et al., 2015), facilitating the monitoring of spatiotemporal dynamics. In particular, laboratory fungal communities, under controlled conditions and complexity,

allow analysis and comprehensive quantification of key ecological processes for theoretical models. Despite the simplified characteristics of laboratory communities, ecological elements driving dynamics in the laboratory should apply to natural settings (Widder et al., 2016), improving forecasts of processes depending on fungal community structure, such as biogeochemical cycling, primary production, biocontrol, and bioremediation (Hiscox et al., 2015; Moeller and Peay, 2016; Buchkowski et al., 2017; Oliva et al., 2017; Stella et al., 2017).

The main body of a fungus is the mycelium, comprising hyphae which elongate, branch, and fuse, creating an extending network (Fricker et al., 2017). One of the main types of interaction between filamentous fungi is competition for resources in the substratum (Boddy, 2000; van der Wal et al., 2012), i.e. competition for space, which allows them subsequently to use the nutrients therein. Fungal competition for space is realised via three mechanisms according to ecological theory (Schoener, 1983; Boddy, 2000):

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preemption of unoccupied space; resource exploitation; and direct, harmful replacement after physical contact, or antagonism at a distance by production of volatile or diffusible chemicals. Different abiotic and biotic elements influence the outcomes of spatial competition (Boddy, 2000; Kennedy, 2010; Hiscox and Boddy, 2017): temperature, pH, water potential, gaseous regime, resource quality and concentration, type of substratum, invertebrate grazing, size of space occupied by mycelia, spatial configuration of mycelia, and species identity.

For controlled abiotic conditions, and in the absence of non-fungal species (e.g. bacteria or invertebrates), we have grouped empirical findings into six spatial competition elements: (1) The mycelial boundary extent into unoccupied space is commonly linear in time (Brown, 1923; Fawcett, 1925; Ryan et al., 1943; Plomley, 1959), with faster extending species preempting more space. (2) This ability to capture unoccupied space might be inhibited or enhanced by the presence of adjacent or distant mycelia (Griffith and Boddy, 1991; Heilmann-Clausen and Boddy, 2005; Evans et al., 2008; Sonnenbichler et al., 2009). (3) Following the initial extension to an unoccupied site, a mycelium increases in hyphal density at that site (Plomley, 1959; Trinci, 1969), attaining its full density and hence potential to replace or to resist replacement locally as it matures (Stahl and Christensen, 1992). (4) The ability of mycelia to replace or resist replacement is higher the greater the space they occupy (Holmer and Stenlid, 1993; White et al., 1998; Bown et al., 1999; Sturrock et al., 2002; Song et al., 2015; Hiscox et al., 2017), because local competitive ability is enhanced by translocation of resources from the whole mycelium (Jennings, 1987; Olsson, 1999; Lindahl et al., 2001). (5) A mycelium commonly has to translocate and distribute its finite resources to compete against multiple adjacent heterospecific mycelia, likely dividing its competitive ability (White et al., 1998; Bown et al., 1999; Sturrock et al., 2002; Hiscox et al., 2017). (6) Competition between multiple species might differ from pairwise species interactions in isolation, due to higher-order interactions, i.e. existence of non-additive effects of competition (Hiscox et al., 2017). These six elements appear necessary for a comprehensive view of the fungal interaction outcomes, and consequently of the dynamics.

Despite the empirical literature on these six basic elements of spatial competition, no theoretical study has tested the predictability of empirical community dynamics by a model incorporating all elements. In the earliest theoretical study of fungal interactions (Halley et al., 1994), a cellular automaton model assumed fixed replacement outcomes between species pairs, omitting any relation of replacement with mycelial age, size, and contact with multiple heterospecific mycelia. Further, no comparison between theoretical and empirical community dynamics was undertaken with this model and its later version (Halley et al., 1996), except for showing realistic spatial patterns of model mycelium fairy rings, replacement, and deadlock (in which no mycelium replaces the other). Similarly, subsequent theoretical modelling studies omitted at least one of the three elements of mycelial age, mycelial cover, and distribution of competitive ability against multiple adjacent heterospecifics, or lacked quantitative predictions of empirical community dynamics (Davidson et al., 1996a, 1996b; Bown et al., 1999; Falconer et al., 2008; Boswell, 2012; Choudhury et al., 2018).

In this study, we experimentally quantified the six basic elements of spatial competition, aiming theoretically to predict empirical dynamics in closed, dispersal-free laboratory communities of two and three species of filamentous fungi. We found all six elements were necessary for the theoretical prediction of empirical community dynamics. Our study's integrated development of a theoretical model alongside laboratory experiments

provides a methodological basis for the predictive understanding of fungal dynamics in natural communities or substrates.

2. Materials and methods

2.1. General experimental and theoretical setting

For the experiments, we employed three strains of wood decay basidiomycetes from Cardiff University culture collection: *Vuileminia comedens* (abbreviated 'Vc' hereafter; strain VcWVJH1), *Trametes versicolor* ('Tv'; strain TvCCJH1), and *Hypholoma fasciculare* ('Hf'; strain HfDD3). The species were inoculated and cultured in 22.4 × 22.4 cm polystyrene Petri dishes (Corning®, Buckinghamshire, UK), at 15 °C in the dark, in approximately 0.5 cm thick substratum of 2% (w/v) malt agar. For inoculation, cylindrical plugs of 0.8 cm diameter were cut with a cork borer from a newly developed culture, and set with the aerial mycelium touching the new substratum. The agar plugs were removed after 2 d, to prevent any plug effects on the dynamics. Visual inspection was adequate for determining mycelial boundaries with unoccupied space and with heterospecifics, shown by re-isolation of different mycelial regions. Conspecifics fused on contact (Watkinson et al., 2015). To estimate extension and replacement rates, mycelial boundaries were drawn from the bottom of the dish at regular time intervals (Fig. 1A). Using non-parametric tests due to unknown distribution of extension and replacement rates, Monte Carlo power analysis indicated a sample size of $n = 3$ replicates of each experiment as adequate for at least 85% power to detect a pre-specified effect size, given the relatively small standard deviation of extension and replacement rates in preliminary measurements (Appendix S1). With the pre-specified effect size and $n = 3$, the non-parametric tests frequently returned the minimum p value $p = 0.1$, hence all tests were considered at significance level $\alpha = 0.1$. We provide the raw data from all experiments (Supplementary Data), and the script for our statistical analyses in R (Appendix S2; R Core Team, 2017).

For the theoretical model, a stochastic, lattice model represented the 2-dimensional mycelial boundaries from the 22.4 × 22.4 cm empirical Petri dish with a square lattice of 45 × 45 square sites in 2-dimensional space, by discretising mycelial occupancy (Appendix S1). Since the prediction of empirical community dynamics does not require accurate representation of hyphae or even mycelia, a 45 × 45 lattice was considered a satisfactory compromise between sufficient resolution and higher computational costs. The boundaries of the lattice were assumed closed, like the walls of the empirical dishes. A lattice site was either empty or occupied by one species at any moment in time. The eight lattice sites surrounding a focal site were considered as its neighbours, i.e. a Moore neighbourhood. A cluster of lattice sites connected via a Moore neighbourhood, and occupied by the same species, represented a mycelium. Given a state of the lattice at time t , two types of event could minimally change the current state at time $t + \Delta t$: an unoccupied site could become occupied by a mycelium extending from a neighbouring site (extension event); or a site occupied by one species could be replaced by another species' mycelium invading from a neighbouring site (replacement event). The model did not include mycelial withdrawal, via hyphal degeneration or recycling, because we did not observe withdrawal on the rich and homogeneously distributed substrate for the duration of our experiments. Knowing the current lattice state, and all possible events with their experimentally quantified rates of occurrence, allowed predictions about the next lattice state. We numerically simulated the temporal change in the lattice state with a rejection-free Kinetic Monte Carlo algorithm (Bortz et al., 1975; Gillespie, 1976). Given an initial lattice state at $t = 0$, the algorithm could simulate one stochastic realisation of the dynamics in continuous

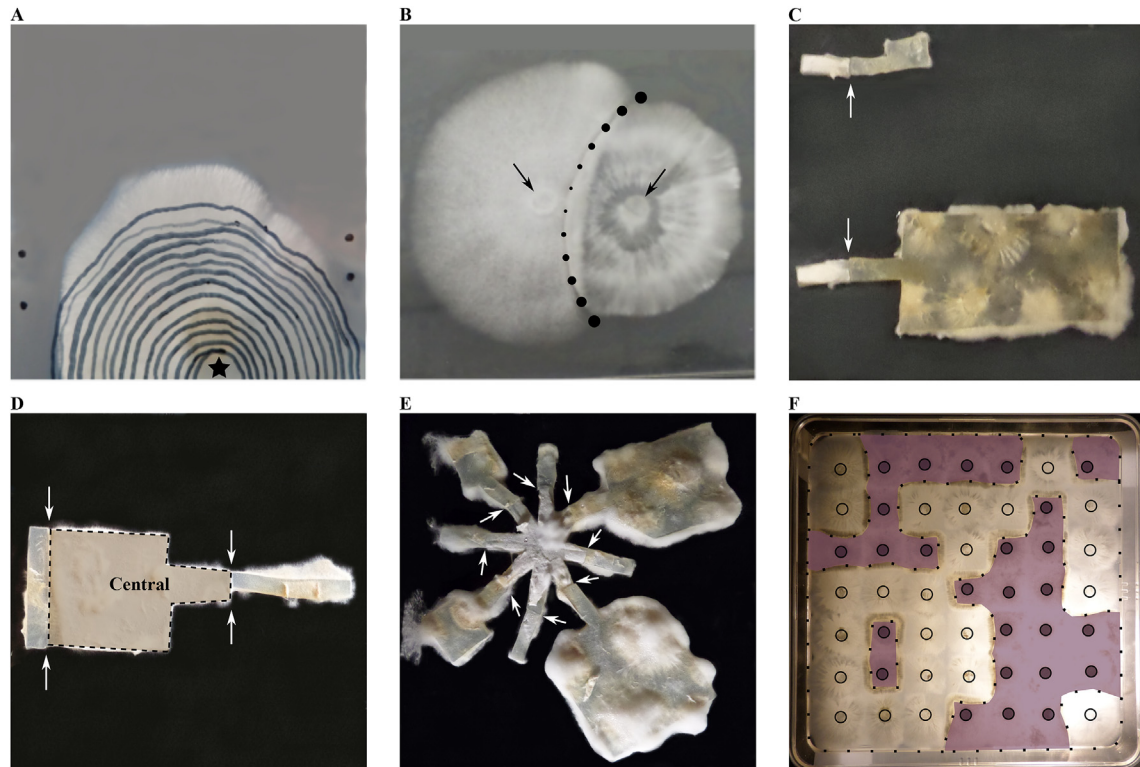


Fig. 1. The empirical system used for the main experiments. White arrows point to initial boundaries between mycelia. (A) Unconstrained mycelial extension on a Petri dish, overlaid by a transparency depicting the bottom-view mycelial boundary at regular time intervals, starting from the inoculation site (star). Dots on the dish and on the transparency were used for aligning the transparency. (B) Unconstrained mycelial extension and replacement on agar. The mycelium on the right (*Hypholoma fasciculare*) is replacing the mycelium on the left (*Vuileminia comedens*). Arrows indicate the inoculation sites. The dotted curve denotes the assumed boundary between the mycelia, with larger dots at the replaced mycelium's younger regions. (C) Pairing mature mycelia in different cover ratios, but with fixed length of boundary between the competitors (0.5 cm). (D) A pair of equally-sized mycelia of one species flanking a central mycelium of another species in two different boundary lengths (4 and 0.5 cm). (E) A central mycelium of one species, cut to provide eight boundaries of fixed length (0.5 cm), against eight heterospecific mycelia of different cover. (F) Competition on a 22.4 × 22.4 cm Petri dish, after randomly assigning the species to 49 inoculation sites (circles represent the inocula of the initial conditions), regularly configured on a square grid of 3 cm horizontal and vertical distance between inoculation site centres. In this 2-species example, mycelia have covered the dish, and replacement is observed in regions between the inoculation sites (dotted curves denote boundaries of mycelia, and the mycelia of the replaced species are shaded).

time, generating the next lattice state and its time of appearance at each repetition of the following main steps (C++ code in [Appendix S3](#)):

1. Calculate the rate of each possible extension and replacement event, according to the experimentally characterised elements of spatial competition (described in the following section), and the model parameters estimated from the experiments ([Appendix S1](#)).
2. Calculate the sum, R , of the rates from step 1. The next event will be realised after an inter-event time Δt , randomly drawn from an exponential distribution with parameter $\lambda = R$ (fewer and slower events lead to longer inter-event times on average). Increment current time t by Δt .
3. Select randomly one of the events from step 1, with probability weighted by its rate (a faster event has greater probability of occurring next). Realise the event.

Steps 1–3 were repeated until t exceeded a specified time limit, or until no event was possible ($R = 0$). We additionally implemented a parameter for the smoothness of mycelial boundaries ([Appendix S1](#)), to resemble smooth empirical boundaries ([Fig. 1A,B,F](#)). Our 'noise reduction' method created square or diamond-like mycelia instead of the desired disk-like mycelia. This increased 'anisotropy' with decreased noise is known from other models of cluster growth on a square lattice ([Meakin, 1988](#)). A proposed way for reducing

anisotropy is by using a Moore neighbourhood with altered rates towards the diagonal neighbours ([Meakin, 1998](#)). This is the reason our model included diagonal neighbours with the Moore neighbourhood (rather than, e.g., the Von Neumann neighbourhood with only the four nearest neighbours), and why extension and replacement rates towards diagonal neighbours were half of the rates towards horizontal and vertical neighbours ([Appendix S1](#)). Another proposed way of reducing anisotropy is with a hexagonal lattice ([Meakin, 1998](#)), but we preferred a square lattice for its better representation of the square empirical Petri dish. To check the applicability of our method to a different setting though, we tested the model's predictions from a hexagonal lattice ([Appendix S1](#) for details, and [Appendix S3](#) for code). We note here that this did not alter our main results or conclusions.

2.2. The six elements of spatial competition

To develop a corresponding, realistic theoretical model, a series of experiments were designed for providing measurements on six spatial competition elements, with extension and replacement rates as response variables. The chosen six elements of spatial competition, which build up from the extension of single mycelia to the replacement in the presence of all three species, were:

1. Extension rate in relation to mycelial size, shape, position and age. How does a single mycelium extend?

2. Extension rate in the presence of other mycelia. How does a mycelium extend in the presence of homospecific or heterospecific mycelia?
3. Replacement rate in relation to the age of mycelial regions. How is a mycelium replaced by another mycelium across its boundary which has regions of different age, and hence different hyphal density?
4. Replacement rate in relation to mycelial cover. How is a mature mycelium replaced by another mature mycelium given their cover ratio?
5. Replacement rate against multiple adjacent heterospecifics. How does a mycelium replace or is replaced when flanked by two mycelia of another species?
6. Additive or non-additive effects of competition. How does a mycelium replace or is replaced when interacting with both other species?

We limited this first attempt to biotic predictor variables: mycelial size, shape, position and age for Element 1; presence of other mycelia for Element 2; age of replaced mycelial regions for Element 3; mycelial cover for Element 4; length of boundary with heterospecifics for Element 5; and presence of both other species for Element 6. Thus, we did not experimentally measure, or explicitly incorporate into the model, any kind of abiotic predictor variables, e.g. resource quality or concentration.

2.2.1. Element 1: extension rate in relation to mycelial size, shape, position and age

In the experiment for mycelial size, each species was inoculated at the centre of the 22.4 × 22.4 cm dishes. We measured the extent of the boundary over time, taking the mean extent from the inoculation site to four orthogonal directions of unconstrained extension. Similarly, we measured extent over time for empirical mycelia: at dish corners, for the effect of position; at 0.8 cm wide strips of substratum, for the effect of mycelial shape; and from pieces of aged culture that we attached next to 0.5 cm wide strips of unoccupied substratum, for the effect of age. We hypothesised that mean extension rate of each species is independent of mycelial size, shape, position and age (tested with Kruskal–Wallis one-way analysis of variance). Note that we limited this study to higher-level predictor variables (mycelial size, shape, position and age), omitting other underlying predictor variables, such as hyphal density. For example, when considering the replacement rate in relation to the age of mycelial regions (Element 3, below), we assumed that denser mycelial regions would be replaced faster, but we measured age of mycelial regions as a surrogate predictor variable for hyphal density.

The lattice model mycelia of each species included local extension rates from occupied lattice sites to neighbouring unoccupied sites (probability of local extension per day, d^{-1}). Local extension rate in the model (d^{-1}) was determined from the rate of extent of empirical mycelium boundary in the experiments ($cm d^{-1}$) (Appendix S1).

2.2.2. Element 2: extension rate in the presence of other mycelia

We experimentally inoculated two mycelia of the same or different species at various positions and distances from each other on the dish. We measured three extension rates of each mycelium across the line passing through the inoculation sites of the mycelia: towards the other mycelium; away (side of the colony opposite the other mycelium) prior to contact; and away after contact. These three extension rates were compared with each other using a Friedman rank-sum test, and with the fungus growing alone on dishes, using a Wilcoxon rank-sum test (two-sided).

2.2.3. Element 3: replacement rate in relation to the age of mycelial regions

For this experiment, we assumed that a very young and sparse mycelial region would impose little resistance to a replacing mycelium, being replaced as fast as unoccupied space was captured. This replacement rate was expected to decrease where the mycelium being replaced was older. We measured the replacement rate at a snapshot of time across the boundary between two mycelia because the age of the replaced mycelium decreases at the mycelium margin (Fig. 1B; and Appendix S1).

To incorporate this relation into the lattice model, the age of each lattice site's occupancy was monitored. A site's occupancy age increased by each new inter-event time Δt , and age was set to zero whenever occupancy changed.

2.2.4. Element 4: replacement rate in relation to mycelial cover

We experimentally focused on mycelial cover, which is the area covered by a mycelium's boundary, viewed from underneath the dish. We measured replacement rates in pairs of heterospecific mycelia of different cover ratios (Fig. 1C), cut from mature cultures in shapes that limited the boundary to a fixed width (0.5 cm). Maturity of mycelial cultures was inferred from the experimental relations obtained for Element 3, i.e. when the effect of mycelial age on replacement was diminished. The cut pieces were paired in contact with each other on empty dishes without medium. Replacement rate was estimated from the distance that the replacement front had moved 2 d after the mycelium of the replacing species was noted entering its opponent's territory. Additionally, to test if only the cover ratio matters, rather than the absolute cover, pairings were set up with the following Hf/Vc and Tv/Vc basic cover ratios (expressed as absolute cover in cm^2/cm^2 within parentheses): 1/1 (1/1, 2/2 and 4/4); 4/1 (4/1, 8/2 and 16/4); and 16/1 (16/1, 32/2 and 64/4). We did not set up pairings for Hf/Tv (or Tv/Hf) because in preliminary investigations Hf (Tv) deadlocked with Tv (Hf) at the maximum Hf/Tv (Tv/Hf) 256/1 cover ratio, and thus they were also expected to deadlock in any other, smaller cover ratio. Kruskal–Wallis one-way analysis of variance was used to test differences between the three different absolute cover ratios of each basic ratio.

To incorporate this relation into the model, we measured the sizes of all model mycelia during simulations (Martín-Herrero, 2004). Mycelium size was the number of lattice sites occupied by the same species, and connected via a Moore neighbourhood.

2.2.5. Element 5: replacement rate against multiple adjacent heterospecifics

We experimentally set a central mycelium of one species, 18 cm^2 cover, against two competitor mycelia of another species, both 2 cm^2 cover, but one with 0.5 cm wide boundary (narrow competitor), and the other with 4 cm (wide competitor) (as in Fig. 1D). We hypothesised that the observed replacement rates were as if the central mycelium: (1) retained its full cover-related competitive ability against both competitors (expected replacement rates as in paired mature mycelia of 18/2 central/wide, and 18/2 central/narrow competitor cover ratio from Element 4); (2) divided equally to each competitor (replacement rates as from 9/2 central/wide, and 9/2 central/narrow cover ratios); or (3) divided proportionally to the length of boundary with each competitor (replacement rates as from 16/2 central/wide, and 2/2 central/narrow cover ratios; the 16 and 2 cm^2 division of the central mycelium cover is proportional to the 4 and 0.5 cm wide and narrow boundary lengths, respectively). We compared expected with observed replacement rates at both boundaries with the Wilcoxon rank-sum test (two-sided). Additionally, we paired mycelia as in Element 4 but on 4 cm wide boundaries with the following

mycelium cover ratios (absolute cover in cm^2/cm^2): 2/4, 2/2, and 4/2 for Hf/Vc; and 2/2, 4/2, and 8/2 for Tv/Vc. We tested if replacement rates on 4 cm wide boundaries for each cover ratio were as in the 0.5 cm boundaries for Element 4 (two-sided Wilcoxon rank-sum test).

In the lattice model, we were measuring the length of each mycelium's boundary with heterospecifics during the simulations. This heterospecific boundary length was the number of a mycelium's neighbouring lattice sites occupied by other species.

2.2.6. Element 6: additive or non-additive effects of competition

We experimentally set a central mycelium of one species (8 cm^2 cover) against mycelia of both other species (two mycelia of 1 cm^2 and two of 16 cm^2 from each other species, with a 0.5 cm wide boundary; similarly to Fig. 1E). If there were additive effects of competition, the observed replacement rates in these 3-species settings would not be different from the replacement rates expected from paired mature mycelia for Element 4, after considering how the central mycelium is divided to the eight competitors according to the results for Element 5. For each replicate, the observed replacement rate was the mean from the two boundaries with the same-cover and same-species competitors (compared to expected rate with two-sided Wilcoxon rank-sum test).

2.3. Lattice model prediction of community dynamics

To determine how close the predictions from the lattice model were to actual dynamics of empirical communities, we prepared four experimental test cases: a 3-species community, and three 2-species communities (all paired combinations of three species). For these experimental test cases, we assigned a species at each of 49 inoculation sites regularly distributed on the $22.4 \times 22.4 \text{ cm}$ Petri dish (Fig. 1F). To compare with the theoretical model's predictions of species relative cover, the mycelial boundary drawings were processed with ImageJ (Rasband, 2016), to discretise dish space to 45×45 occupancy sites on a square lattice (Appendix S1; Java code ImageJ plugin in Appendix S4).

We compared the communities developing in the experimental matrix of species on agar, with the same layout of species in the lattice model. In particular, we ran the model with the same initial conditions as in the discretised 3- and 2-species empirical communities, after incorporating all six elements of spatial competition from the experiments (this was also done on a hexagonal lattice; Appendix S1 for details, and Appendix S3 for code). Similarly, the model was run with elements of spatial competition simplified, to test if all elements were necessary for the prediction of empirical community dynamics. We quantified the goodness-of-fit of model's predictions to empirical dynamics with the mean sum of squared differences, D , between the empirical relative cover of each species s , at each time point t of measurement ($E_{s,t}$), and the model relative cover in each of the n simulation runs for each test case, for the same species s , at the same time point t ($M_{n,s,t}$):

$$D = (1/n) \sum_n \sum_s \sum_t (E_{s,t} - M_{n,s,t})^2.$$

3. Results

3.1. The six elements of spatial competition

The experimentally quantified forms of the six elements of spatial competition incorporated into our theoretical lattice model are summarised in Fig. 2.

3.1.1. Element 1: extension rate in relation to mycelial size, shape, position and age

Under all four experimental settings (empirical mycelia at dish

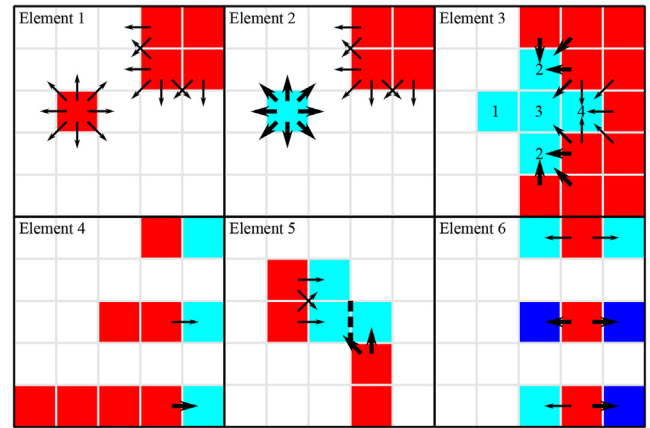


Fig. 2. The experimentally quantified elements of spatial competition incorporated into the theoretical lattice model. A blank square lattice site is unoccupied space; a cluster of same-colour/shading sites connected via a Moore neighbourhood is a mycelium of a species; and a wider arrow symbolises faster extension, or replacement of a heterospecific mycelium. Element 1: mycelial extension rate was constant, independent of mycelial size, shape, position or age. Element 2: mycelial extension was not influenced by the presence of other mycelia. Element 3: younger mycelial regions were replaced faster (a larger number indicates an older 'hypothetical' age). Element 4: relatively larger mycelial cover increased the ability to replace or resist replacement. Element 5: a central mycelium distributed its competitive ability to multiple competitors proportionally to the length of the boundary with each competitor (central mycelium's division of cover indicated with the dashed line segment). Element 6: replacement rates from 2-species settings were conserved in 3-species settings, i.e. additive effects of competition.

centres, at dish corners, on substratum strips, and aged mycelia), the boundary extent increased linearly in time (e.g. in Fig. 3A, until the mycelium started reaching the dish walls at approximately $t = 20 \text{ d}$). Thus, we could calculate mean rates of empirical boundary extent from the slopes of the linear extent–time relationships. We found no differences in mean extension rates between the four settings ($p > 0.1$; Kruskal–Wallis test).

For the lattice model, we assumed that the rate of boundary extent of Hf was 0.14 cm d^{-1} , of Tv was 0.39 cm d^{-1} , and of Vc was 0.2 cm d^{-1} . The extent and relative cover over time in model mycelia were in agreement with the empirical dynamics (Fig. 3A).

3.1.2. Element 2: extension rate in the presence of other mycelia

In this experiment, no significant differences were found between mycelial extension rates towards, away pre-contact, and away post-contact for each species (Fig. 3B; $p > 0.1$; Friedman test). Colony extension rates in the presence of other empirical mycelia were as if mycelia were alone on the dish (Fig. 3B; $p > 0.1$ for all comparisons with no other mycelium on the dish, except $p = 0.1$ for Hf towards Vc, and away from Tv pre- and post-contact; Wilcoxon test).

3.1.3. Element 3: replacement rate in relation to the age of mycelial regions

In this experiment, young mycelial regions at the periphery of Vc were replaced as fast as unoccupied space was captured by Hf and Tv (Fig. 4A,C). Replacement rates decreased across the boundary, from the Vc mycelial margins until the 4–8 d old Vc mycelial regions.

For the lattice model, we assumed that 0 d old Vc mycelium was replaced at the mean extension rates of Hf and Tv, and replacement rates decreased linearly until 6 d old Vc mycelial regions. For older Vc regions (Fig. 4A,C), replacement rates were according to the mean replacement rate obtained by the paired mature mycelia setting of the next Element 4.

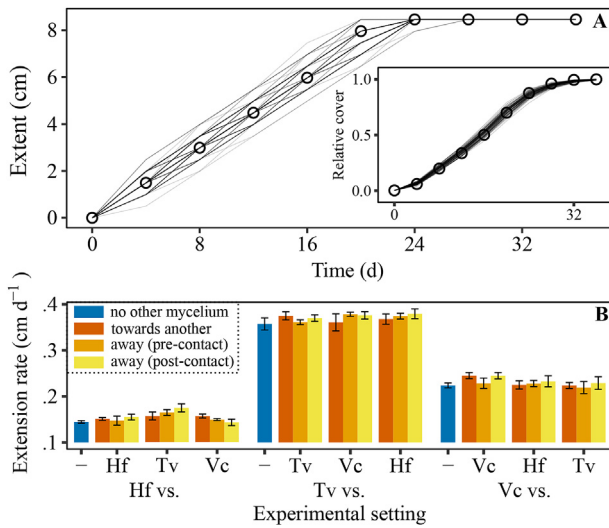


Fig. 3. Extension to unoccupied space (for Elements 1 and 2). (A) An example of three Tv mycelia closely inoculated at the dish centre, fusing to form a single mycelium which extended unconstrained until it reached the dish walls, covering the whole dish (relative cover dynamics in inset). Circles represent extent of the empirical mycelium boundary towards a specific direction, and lines represent $n = 100$ theoretical trajectories from the lattice model with the same initial conditions as in the empirical dish, measuring the extent towards the same direction. Model dynamics at the time points of empirical measurements were linearly interpolated from the exponentially distributed inter-event model times (Appendix S3). (B) Mean extension rate of mycelia towards, and away from other mycelia before and after making contact ($n = 3$ or $n = 4$; error bars show ± 1 standard error).

3.1.4. Element 4: replacement rate in relation to mycelial cover

In the experiment with the paired mature mycelia of different cover ratios, there was deadlock at 1/256 Hf/Vc (1/1 Tv/Vc) cover ratio, and Hf (Tv) started to replace Vc at 1/128 Hf/Vc (2/1 Tv/Vc) cover ratio (Fig. 4B,D). The replacement rate increased linearly with the logarithm of cover ratio, and became as fast as the mean extension rate of Hf in unoccupied space at around 64/1 Hf/Vc cover ratio (when Tv was replacing, it did not attain a maximum replacement rate equal to its extension rate against Vc in our maximum 256/1 Tv/Vc cover ratio setting). In the second experiment, replacement rates were unaffected by the absolute cover in the cover ratios tested experimentally ($p > 0.1$ in the three absolute cover ratios of each basic cover ratio; Kruskal–Wallis test).

Consequently, the model incorporated the lin–log relations from Fig. 4B,D for the replacement rate of Vc by Hf (r_{Hf}) and Tv (r_{Tv}):

$$r_{Hf} = a_{Hf} \log_2 \left(\frac{C_{Hf}}{C_{Vc}} \right) + b_{Hf}, \quad (1)$$

$$r_{Tv} = a_{Tv} \log_2 \left(\frac{C_{Tv}}{C_{Vc}} \right) + b_{Tv}, \quad (2)$$

where C_X is the cover of a species X mycelium (Hf, Tv or Vc), $a_{Hf} = 0.0093 \text{ cm d}^{-1}$ and $a_{Tv} = 0.024 \text{ cm d}^{-1}$ are the slopes, and $b_{Hf} = 0.078 \text{ cm d}^{-1}$ and $b_{Tv} = 0 \text{ cm d}^{-1}$ are the intercepts.

3.1.5. Element 5: replacement rate against multiple adjacent heterospecifics

In this experiment, the central mycelium of 18 cm^2 cover appeared to divide its competitive ability proportionally to the length of boundary with each of the smaller competitors of 2 cm^2 cover (Fig. 5A). With the 4/0.5 cm wide/narrow boundary length ratio, the flanking competitor from the wide boundary realised an eight times larger central mycelium than the flanking competitor

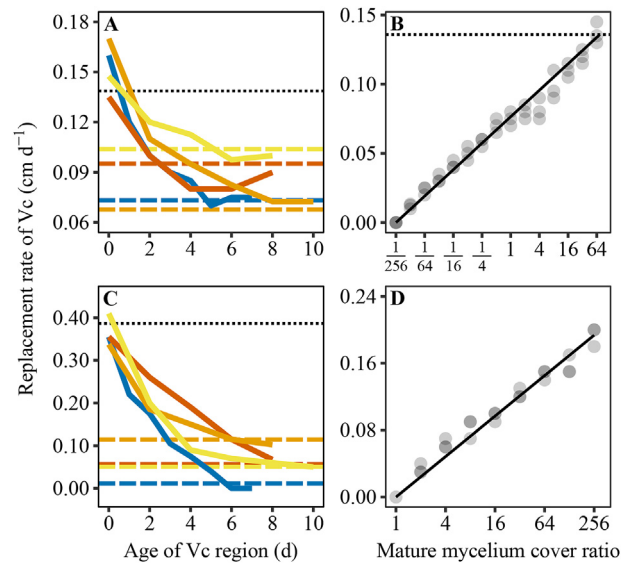


Fig. 4. Replacement in relation to the age of the replaced mycelial region, and in relation to mycelial cover (for Elements 3 and 4). (A and C) Replacement rate in the different mycelial regions across the boundary between four pairs of Hf–Vc and Tv–Vc mycelia, respectively (as in Fig. 1B, for Element 3); each curve is for a different pair, with a same-colour/shading dashed horizontal line indicating the replacement rate expected from mature mycelia of the pair's cover ratio, according to panels B and D. (B and D) Replacement rate of Vc, given the Hf/Vc and Tv/Vc mature mycelium cover ratio, respectively (as in Fig. 1C, for Element 4); the dotted points are semitransparent; lines denote the lin–log relations of Eqns. (1) and (2) incorporated into our lattice model ($n = 3$ for each cover ratio); and note that the Hf–Tv combination was not included because the two species deadlocked upon contact (i.e. there was no replacement). In any panel, dotted horizontal lines indicate the estimated mean extension rate of the replacing species into unoccupied space.

from the narrow boundary ($p > 0.1$ for the difference between observed replacement rates and expected from the $4/0.5 = 8/1$ division of the 18 cm^2 central mycelium; Wilcoxon test). In the experimental comparisons between two mature mycelia with the same cover ratio, heterospecific boundary length did not have an effect on replacement rates ($p > 0.1$ for the three cover ratios; Wilcoxon test).

The proportional distribution of cover-related competitive ability was implemented in the model by adding the ratio L_{XY}/L_X to Eqns. (1) and (2), where L_{XY} is the length of the common boundary between two mycelia of species X and Y, and L_X is the total length of boundary with heterospecifics of the species X mycelium. Thus, the lin–log relations of Eqns. (1) and (2) from Element 4 became:

$$r_{Hf} = a_{Hf} \log_2 \left(\frac{C_{Hf} \frac{L_{HfVc}}{L_{Hf}}}{C_{Vc} \frac{L_{HfVc}}{L_{Vc}}} \right) + b_{Hf} = a_{Hf} \log_2 \left(\frac{C_{Hf}/L_{Hf}}{C_{Vc}/L_{Vc}} \right) + b_{Hf}, \quad (3)$$

$$r_{Tv} = a_{Tv} \log_2 \left(\frac{C_{Tv} \frac{L_{TvVc}}{L_{Tv}}}{C_{Vc} \frac{L_{TvVc}}{L_{Vc}}} \right) + b_{Tv} = a_{Tv} \log_2 \left(\frac{C_{Tv}/L_{Tv}}{C_{Vc}/L_{Vc}} \right) + b_{Tv}. \quad (4)$$

3.1.6. Element 6: additive or non-additive effects of competition

There was no experimental evidence of non-additive effects of competition (Fig. 5B). In the 3-species setting, assuming from the results of Element 5 that the central mycelium was divided equally between the eight competitors (due to the equal heterospecific boundary lengths), the observed replacement rates were not different from those expected from the 2-species settings of paired

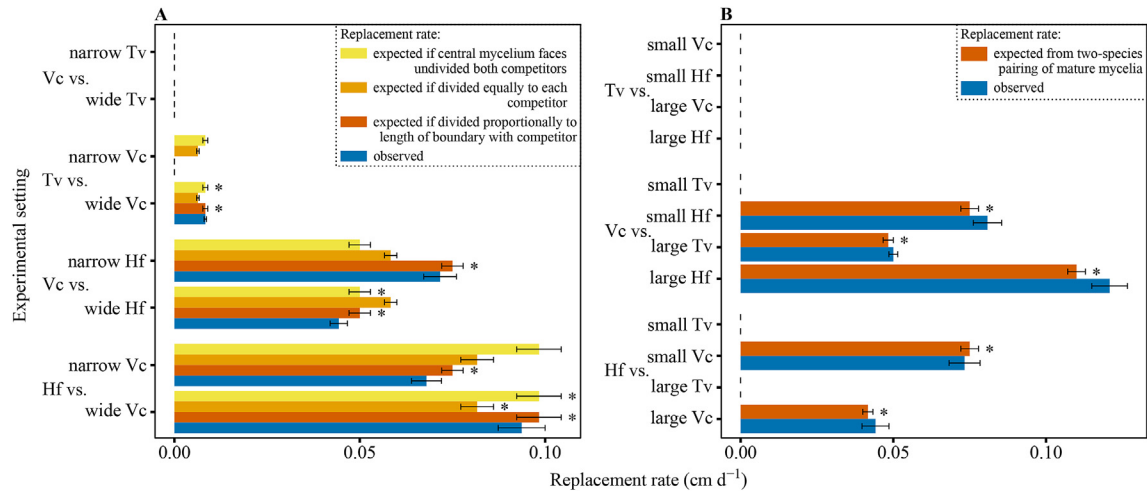


Fig. 5. Replacement against multiple adjacent competitors, and against multiple species (for Elements 5 and 6). In both panels, replacement rates refer to Hf and Tv replacing Vc. (A) Replacement rates observed in one central mycelium against two competitors of another species with different boundary lengths (as in Fig. 1D, for Element 5), compared to replacement rates expected from 2-species pairings (Fig. 4B,D). (B) Replacement rates observed in 3-species settings of a central mycelium of one species against mycelia of the other two species with two different mycelial covers (as in Fig. 1E, for Element 6), compared to replacement rates expected from 2-species pairings (Fig. 4B,D). Bars denote mean replacement rate (± 1 standard error). An asterisk indicates no significant difference between expected and observed replacement rates ($p > 0.1$ with Wilcoxon rank-sum test; $n = 3$ in all settings).

mature mycelia for Element 4 in Fig. 4B,D ($p > 0.1$; Wilcoxon test).

3.2. Lattice model prediction of community dynamics

With all six experimentally quantified elements incorporated, the lattice model could accurately predict the dynamics of the 3- and 2-species empirical communities, with almost all the relative cover measurements from the empirical dishes falling inside the lattice model's 95% prediction intervals (Fig. 6). Additionally, model dishes visually resembled empirical dishes in the spatial configurations and shapes of the mycelia (e.g. Fig. 6 insets). Our model exhibited a similar ability to predict dynamics when run on a hexagonal lattice (Appendix S1). The lattice model could not achieve better predictions upon incorporation of a simplified form for one or more of the Elements 3–5 which empirically had more involved form (Table 1).

4. Discussion

The aim of this study was the development of a comprehensive method to experimentally quantify and theoretically predict fungal community dynamics, to be initially tested under simpler laboratory settings. We focused on six basic elements of spatial competition between mycelia, in accordance with previous empirical findings and ecological theory (Schoener, 1983; Boddy, 2000). All elements were necessary for the prediction of empirical community dynamics. Three elements had simple form, and a more involved form was necessary for the rest (Fig. 2). Although the laboratory settings differ from natural ones, many of the elements investigated should be transferable to more realistic conditions in future studies (Widder et al., 2016), building understanding of ecological aspects, and improving the reliability of community-dependent ecosystem models such as decomposition models (McGuire and Treseder, 2010; van der Wal et al., 2012). The accurate predictions of the theoretical model, after parameterising it with our experimental results, was a first validation of the proposed methodology based on six spatial competition elements.

Larger preemption of space from faster extending mycelia can be a significant element of spatial competition in natural settings, especially between mycelia which deadlock after contact. For

example, Tv deadlocked with Hf in our study, and Tv was able to capture more space in the Hf–Tv empirical community given the similar initial relative cover, more likely because Tv extended faster than Hf, although other factors could have contributed, such as the initial dish wall proximity and the initial aggregation of each species (Fig. 6C). Such preemption competition for space has not been investigated in fungal community dynamics, although it is recognised and well-studied in other taxa, e.g. plants (Craine, 2005). Further, modification of extension rates has to be quantified for better prediction of empirical community dynamics, despite the absence of long- or short-range inhibitory or stimulatory effects between our three species (Fig. 3B), and commonly in other fungi (Evans et al., 2008).

We found decreasing replacement rates with the age of Vc mycelium regions (Fig. 4A,C). Replacement rates depended on the age of the replaced mycelium as we initially hypothesised, and not on the replacing mycelium which has the same age across its invading boundary (Appendix S1). The results for Element 3 are hence in agreement with previous studies about mycelia becoming locally denser with time (Plomley, 1959; Trinci, 1969), attaining their full density and competitive ability as they mature (Stahl and Christensen, 1992).

We have presented, for the first time, quantitative relations of replacement rate with mature mycelium cover ratio for Element 4. Until now, the only quantitative study on the effect of mycelial cover had been that of Holmer and Stenlid (1993), but replacement rates were not measurable with their experimental setup. The lin–log relations recorded in our study indicate constraints in the enhancement of competitive ability. It would be interesting to investigate the relations displayed in more natural settings, and the proximate and evolutionary reasons for their emergence, e.g. of any transportation constraints in the mycelial network (Fricker et al., 2017).

To our knowledge, the present study is the first to address quantitatively the way fungal mycelia commonly have to face multiple adjacent competitors (Element 5). Element 5 has been theoretically considered in animal territoriality (Adams, 1998), but not in fungal community models (Halley et al., 1994, 1996; Davidson et al., 1996a, 1996b; Bown et al., 1999; Falconer et al., 2008; Boswell, 2012; Choudhury et al., 2018). Two recent

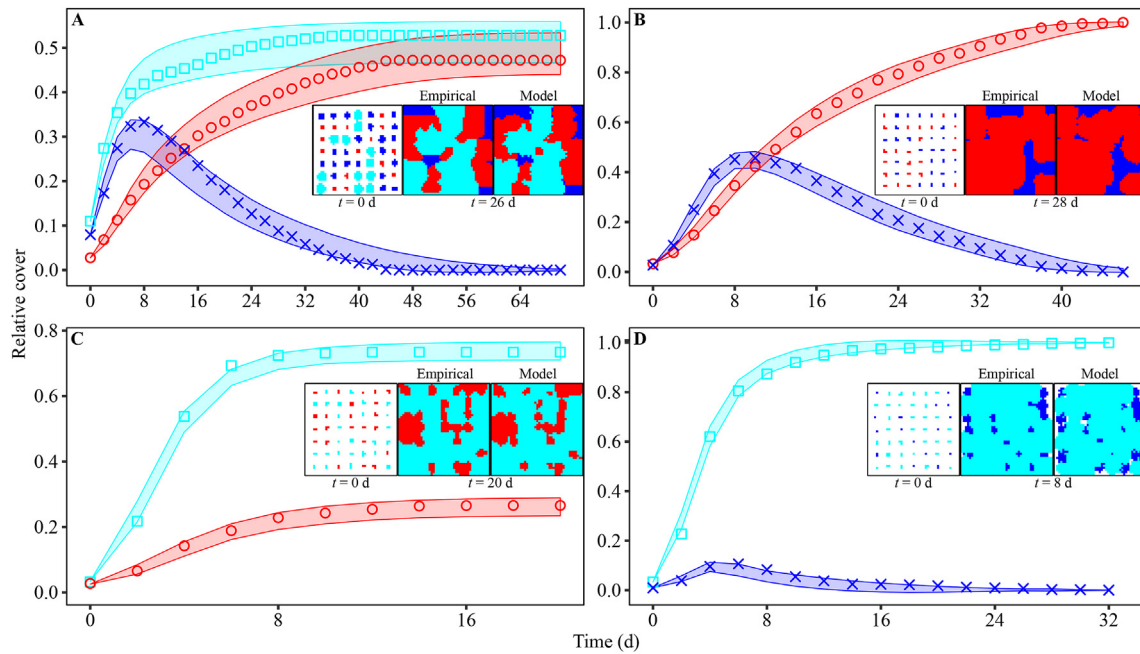


Fig. 6. Lattice model predictions of 3-species (A) and 2-species (B–D) empirical community dynamics. The data points show the empirical relative cover of each species over time, and the coloured/shaded regions show the 95% prediction intervals from $n = 100$ trajectories of the lattice model incorporating all six experimentally quantified elements of spatial competition. Insets show the common initial configuration of the empirical and model closed-boundary dish, and the empirical dish with one realisation of the model dish at the indicated time. Colour–point (of each species): red–circle (Hf), cyan–square (Tv), and blue– \times (Vc). Model relative cover at the time points of empirical measurements was linearly interpolated from the exponentially distributed inter-event model times (Appendix S3).

Table 1
Goodness-of-fit of theoretical model's prediction compared to empirical community dynamics.^a

Elements simplified ^b	Community ^c		
	Hf–Tv–Vc	Hf–Vc	Tv–Vc
None	0.063	0.019	0.011
3	0.82	0.087	0.08
4	1.13	0.11	0.92
5	0.3	0.025	0.017
3 and 4	1.34	0.16	0.94
4 and 5	1.79	0.049	0.94
3 and 5	0.37	0.2	0.012
3, 4 and 5	1.81	0.14	0.94

^a The empirical dynamics were of species relative cover (shown as points in Fig. 6). Goodness-of-fit: mean sum of squared differences between empirical dynamics and $n = 100$ model trajectories (analysis in Appendix S2). Best fit for each community is given in bold.

^b See Appendix S3 for implementation. None: all elements included in the model as experimentally quantified, with no simplification. Element 3: simplified for no effect of age of mycelial region (replacement as between mature mycelia). Element 4: simplified for no effect of mycelial cover ratio (replacement as in 1/1 cover ratio). Element 5: simplified for no distribution of competitive ability among multiple adjacent competitors (replacement as mycelia were facing undivided each competitor).

^c The Hf–Tv community is not included because the two species deadlocked upon contact, hence simplification was impossible for Elements 3–5.

experimental studies on fungi have investigated the effect of species relative position on interaction outcomes (Hiscox et al., 2017; O'Leary et al., 2018), but without testing for non-additive effects of competition due to 3-species interactions (Element 6 here), and without quantifying outcomes across different mycelium size ratios (Element 4). Quantification of Element 5 in our methodology is allowed by setting one mycelium of one species flanked by two mycelia of only one other species, to avoid any non-additive effects of competition, and by first quantifying the relation of replacement rate with mature mycelium cover ratio (for obtaining expected

rates to be compared with observed ones; Fig. 5A). With the final, simplified Eqns. (3) and (4), the experimentally observed division of a mycelium X to adjacent heterospecifics proportionally to the length of boundary with each can be equivalently expressed as uniform distribution of competitive ability across the boundary (C_X/L_X). The simplified Eqns. (3) and (4) can additionally explain the results concerning the lack of experimental effect of the boundary length on replacement rate between two adjacent mycelia: since there is only one heterospecific boundary in a pair of X and Y adjacent mycelia, the total heterospecific boundary length of both is $L_X = L_Y$, cancelling out in Eqns. (3) and (4). Does this 'strategy' of uninformative distribution of competitive ability across the boundary with heterospecifics appear in natural settings as well? Investigating further the selective advantages in specific strategies of distributing the competitive ability among multiple competitors could be an interesting research direction in fungi, and in studies of other 'territorial' taxa (Kress, 2012; Song et al., 2013; Adams, 2016).

For Element 6, this study did not find any changes in replacement rates when all three species interact simultaneously (Fig. 5B). Studies on interactions between multiple fungal species have recently appeared (Hiscox et al., 2017), but their conclusions must be interpreted in light of the results we have presented here. For example, Hiscox et al. (2017) reported that the addition of a third species destabilises the outcomes from pairwise interactions. However, they did not disentangle the effect of mycelial size (Element 4 here), and of heterospecific boundary size (Element 5), from the effect of higher-order interactions. The comprehensive methodology followed in the present study enabled the quantification of higher-order interactions of Element 6, after quantifying Elements 4 and 5.

The use of a theoretical model was necessary for the study of community dynamics. We could rapidly compute all the experimentally obtained event rates, and hence the lattice state transitions, at large enough spatial and temporal scales, and in the complex community structures resembling natural communities

(Fig. 6 insets; Coates and Rayner, 1985; Chapela et al., 1988). Moreover, building a theoretical model allowed testing of the key elements involved in the emergent community dynamics. We did not model any physiological or other mechanisms, because we did not measure any, although some surrogate variables were connected mechanistically to extension and replacement, e.g. the size of space occupied by a mycelium (Holmer and Stenlid, 1993). The model can be extended to three dimensions by introducing the extra neighbours in a 3-dimensional lattice, for testing the predictability of fungal community dynamics ultimately in natural substrata, e.g. in wood. Lastly, other elements of spatial competition can be added to the lattice model depending on the study system, simulating realistic conditions of natural variability in temperature, substratum quality, and other abiotic and biotic elements (Boddy, 2000; Kennedy, 2010; Hiscox and Boddy, 2017).

In conclusion, this study highlighted all six elements of fungal competition as being crucial for the accurate prediction of community dynamics. Some elements have been quantitatively addressed for the first time with our experiments, and we hope they will encourage further investigations in natural settings. Other elements of spatial competition can be added to the theoretical model, simulating realistic conditions of natural variability or complexity. This study is a first step towards accurate prediction of community dynamics via understanding of spatial competition elements underlying interactions and dynamics, with the ultimate aim of predicting processes in which fungi play key roles in different ecosystems.

Author contributions

DAK developed and ran the laboratory experiments and lattice model, analysed the data, and wrote the first draft of the manuscript. All authors contributed to the development and analysis of the experiments and model, and to the writing of the manuscript.

Conflicts of interest

The authors declare that they have no conflict of interest.

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Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.funeco.2019.04.003>.

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