

Modelling fungal colonies and communities: challenges and opportunities

Ruth E. Falconer^{1*}, James L. Bown², Eilidh McAdam¹, Paco Perez-Reche³, Adam T. Sampson², Jan van den Bulcke⁴ and Nia A. White¹

¹SIMBIOS Centre, University of Abertay Dundee, DD1 1HG, Dundee Scotland UK; corresponding author e-mail: r.falconer@abertay.ac.uk

²Institute for Arts, Media and Computer Games, University of Abertay Dundee, DD1 1HG, Dundee Scotland UK

³Department of Chemistry, University of Cambridge, Lensfield Road, Cambridge, CB2 1EW, UK

⁴Laboratory of Wood Technology, Department of Forest and Water Management, Ghent University and UGCT, University Ghent Centre for X-ray Tomography, Ghent University, Coupure Links 653, BE-9000 Gent, Belgium

Abstract: This contribution, based on a Special Interest Group session held during IMC9, focuses on physiological based models of filamentous fungal colony growth and interactions. Fungi are known to be an important component of ecosystems, in terms of colony dynamics and interactions within and between trophic levels. We outline some of the essential components necessary to develop a fungal ecology: a mechanistic model of fungal colony growth and interactions, where observed behaviour can be linked to underlying function; a model of how fungi can cooperate at larger scales; and novel techniques for both exploring quantitatively the scales at which fungi operate; and addressing the computational challenges arising from this highly detailed quantification. We also propose a novel application area for fungi which may provide alternate routes for supporting scientific study of colony behaviour. This synthesis offers new potential to explore fungal community dynamics and the impact on ecosystem functioning.

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INTRODUCTION

Fungi are a central component of the biosphere, essential for the growth of over 90 % of all vascular plants (Allen 1993), play an essential role in ecosystem services (Boumans 2002) and it is estimated that there may be as many as 1.5 million species of fungi globally (Hawksworth 1991). Fungi can impact on the outcome of plants and their enemies (Bennett *et al.* 2006) and are a life support network for most plants (Bardgett *et al.* 2006). Van der Heijden *et al.* (1995) stress the importance of understanding the structure and function of fungal communities is an important contributor to the maintenance of plant biodiversity. Development of such a fungal ecology requires an understanding of the spatio-temporal growth and interaction dynamics both within fungal communities and between fungi and plant systems. We therefore propose that an essential step in understanding the ecology of fungi is to combine: (1) a physiologically-based model of fungal community dynamics, capturing colony growth and interactions, in heterogeneous environments; (2) non-destructive quantification of community growth patterns through instrumentation; (3) models linking fungal communities to plant systems; and (4) next-generation computational approaches to simulate complex systems at scales consistent with that instrumentation. Here, we report on a Special Interest Group meeting held during IMC9 that

considered this agenda and the four components needed to progress our understanding of fungal ecology. Additionally the Group considered the notion of fungi as a biological metaphor for complex management problems.

MODELLING FUNGAL COMMUNITY DYNAMICS

In Falconer *et al.* (2005, 2007, 2008) we demonstrated the use of a physiologically-based model to explore the factors that influence the nature of fungal community diversity and the link between individual behaviour and the structure and function of fungal communities. The model is individual-based and incorporates the essential physiological processes of nutrient absorption, within colony biomass transport and recycling, inhibitor production and growth, and these occur differentially within a single mycelium as a consequence of local and non-local context. This differential behaviour permits different parts of the mycelium to expand and senesce concurrently. This framework was developed to capture the minimal set of physiological processes required to reproduce the observed range in phenotypic response in real colonies: uptake, redistribution of biomass, remobilisation of biomass, and growth which are known to be important for vegetative growth of fungi but have not collectively been incorporated

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into previous modelling frameworks (Falconer *et al.* 2005). We have also investigated the consequences of environmental heterogeneity for biomass distribution (Falconer *et al.* 2007), identifying which trait sets allowed individuals to persist in given environmental contexts. The model has been used to explore the effect of different soil management strategies on fungal invasion and interactions (Fig. 1; Kravchenko *et al.* 2010). The enhancement of this model to incorporate inhibitor production that impacts inter-colony interactions is described in Falconer *et al.* (2008). The model was used to generate mycelial distribution maps that emerge from fungal interactions among a community of intrinsically different individuals (Falconer *et al.* 2010). This is the first attempt to model (physiologically) the dynamics of a fungal community in terms of a fungal ecology. We introduced the concept of a biomass-based abundance distribution function, described the form of that curve, and made the first attempt to identify the traits that affect the form of that curve. Ongoing developments are to apply the model to soil systems to understand the effect of physical and chemical processes on fungal diversity. It has been shown by experiments that the fungal colony exhibits a remarkably complex cooperative behaviour (Ritz 1995, Hughes & Boddy 1996), and a linked experimental-theoretical approach by Bown *et al.* (1999) demonstrated that community scale dynamics are a consequence of non-independent local interactions. In our development of fungal ecology, we must also consider such cooperation, and here we consider as an example fungal pathogen invasion.

LINKING FUNGAL COMMUNITIES TO PLANT SYSTEMS

In Perez-Reche *et al.* (2010), we used probabilistic models to determine how cooperation at the individual scale led to epidemic spread at the community scale. To investigate this

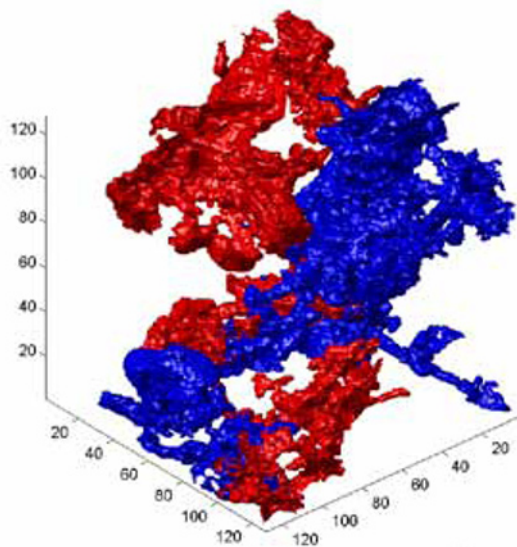


Fig. 1. Effect of soil structure on fungal invasions and interactions for a single soil management practice. Blue and red isosurfaces correspond to the two boundaries of different fungal species.

phenomenon we constructed a model of fungal invasion that is spatially explicit and considers heterogeneous, discrete resource distribution. In general, the transmission of the fungus from a colonised donor host (d) to a healthy recipient host (r) does not only depend on the d - r pair but it is influenced by the environment of the d - r pair. On the one hand, the rate of transmission of the pathogen may be enhanced (constructive synergy) if the fungus is using resources from several colonised hosts. On the other hand, the rate can be diminished (interfering synergy) because of several factors arising from the competition between different parts of the colony. We have addressed the question of whether synergistic effects occurring at the individual scale play an important role in epidemics spreading at the community-scale. We have also investigated the effect of synergy on properties such as the foraging strategy followed by the pathogen, the probability of epidemic invasion, and the efficiency of invasion. The approach is based on an extension of a spatial model for SIR (susceptible-infected-removed) processes (Grassberger 1983) to incorporate synergistic effects in the transmission rate between pairs of hosts depending on the number of infected neighbours to the pair. Analysis of the model by means of numerical simulations has shown that synergy at the host level has non-trivial consequences at the population level. The foraging strategy of the pathogen changes from being explorative for interfering synergy to being exploitative for constructive synergy. The invasion in the exploitative regime is temporally more efficient, i.e., it is quicker, than invasion using an explorative strategy. However, explorative epidemics are spatially more efficient than exploitative epidemics because they can lead to invasion by infecting fewer hosts. The modelling carried out so far is based on simple assumption such as equal intrinsic infectivity and susceptibility for all the hosts in the population. Extensions of the model to account for heterogeneity in transmission of infection and perhaps other factors will be essential to provide quantitative predictions for possibly invasive epidemics in real populations. While it is possible to validate models of infection spread because the domain may be directly observed, such as in infected plants where the number of lesions can be determined *via* direct or indirect methods (Jeger 1987), this is much more challenging for opaque soil and wood systems. For these systems, in order to obtain the experimental data for model calibration and validation information regarding the spatial distribution and biomass amounts is required. One technique that has been used to determine the physical architecture of the soil and wood systems is X-ray Computed Tomography and progress is being made in quantifying and visualising fungal biomass *in situ*.

NON-DESTRUCTIVE QUANTIFICATION OF COMMUNITY GROWTH PATTERNS

X-ray computed tomography enables a non-destructive view of the internal structure of an object and is therefore an extremely valuable technique in many research fields. The continuously improving performance of equipment,

rapidly increasing computing power, and faster algorithms for reconstruction and data processing make large volume scanning at high resolutions feasible. The state-of-the-art equipment at the UGCT (Centre for X-ray Tomography at Ghent University) is highly flexible, with in-house developed software for scanner control, sample reconstruction, analysis, and visualisation. This set-up allows scanning with a resolution of 0.2 mm for samples of 37 cm in diameter down to approximately 400 nm for objects about the size of a splinter. As such, apart from visualisation, 3D quantitative information can be retrieved from objects with a broad range of sizes. Sub-micron resolution scanning should enable the visualisation of fungal hyphae and by using time-lapse tomography the growth of these tubular structures could be monitored (van den Bulcke *et al.* 2009). The latter procedure however has associated challenges. First, fungal growth can interfere with scanning during moderately long scan times. Second, with lab-based X-ray sources, polychromatic X-rays, scattering, fluorescence and noise disturb the ideal acquisition (Vidal *et al.* 2005). Third, at sub-micron resolution phase contrast emerges especially at sharp edges, complicating thresholding and segmentation. Fourth, tube shift during long scans at sub-micron resolution can reduce image quality. Fifth, hyphal tubes are hollow thin-walled structures, as such having a very low X-ray attenuation. A drastic solution to some of the problems is the use of synchrotron radiation, having a monochromatic X-ray bundle, allowing faster scanning with less heating of the samples, but access to such facilities is a major bottleneck. Especially the available beam time is limited and as such this is not an option for long-running experiments, of the order of days to weeks, and for repeated experiments. Many of the aforementioned problems are handled at the UGCT facility. Post-processing can contribute to the enhancement of image quality; the phase contrast phenomenon can be solved using dedicated filtering (Boone *et al.* 2009, De

Witte *et al.* 2009); and tube shift can be counteracted with correction software. Proper scanning and processing can result in the visualization of fungal hyphae as illustrated in Fig. 2, obtained after scanning of a piece of *Pinus sylvestris* subjected to white-rot. In order to study pigmented species with rather large hyphal structures, such as *Aureobasidium pullulans* (van den Bulcke *et al.* 2008), visualization is easier due to X-ray interference of the pigment. Apart from individual hypha tracking, processing of X-ray volumes should enable the quantification of the effects of material degradation on different spatial scales, which might be an important concept to implement a degradation monitoring system. With the existing scanners, frequent scanning and quantification of degradation or hyphal biomass on a larger spatial scale will be a very valuable tool for non-destructive time-lapse analysis. Advanced algorithms implementing X-ray physics during reconstruction will increase image quality, whereas more advanced image processing code will improve quantitative results. The field of X-ray tomography, both hardware and software, is rapidly evolving and therefore is promising for in situ fungal monitoring and quantification in wood and perhaps soil systems in the near future, in addition to other modalities such as confocal laser microscopy (Hickey *et al.* 2005) and magnetic resonance imaging (Müller *et al.* 2002).

NEXT-GENERATION COMPUTATIONAL APPROACHES

Our ability to exploit the experimental advantages described above is currently constrained by the limited scales at which existing simulation technologies are able to operate. For example, in spite of data at larger scales, in Falconer *et al.* (2010) we use a domain size for the soil/fungal interactions of approx 1 cm³ with a voxel resolution of 30 microns; for predictions to be useful we need to work at, at the very

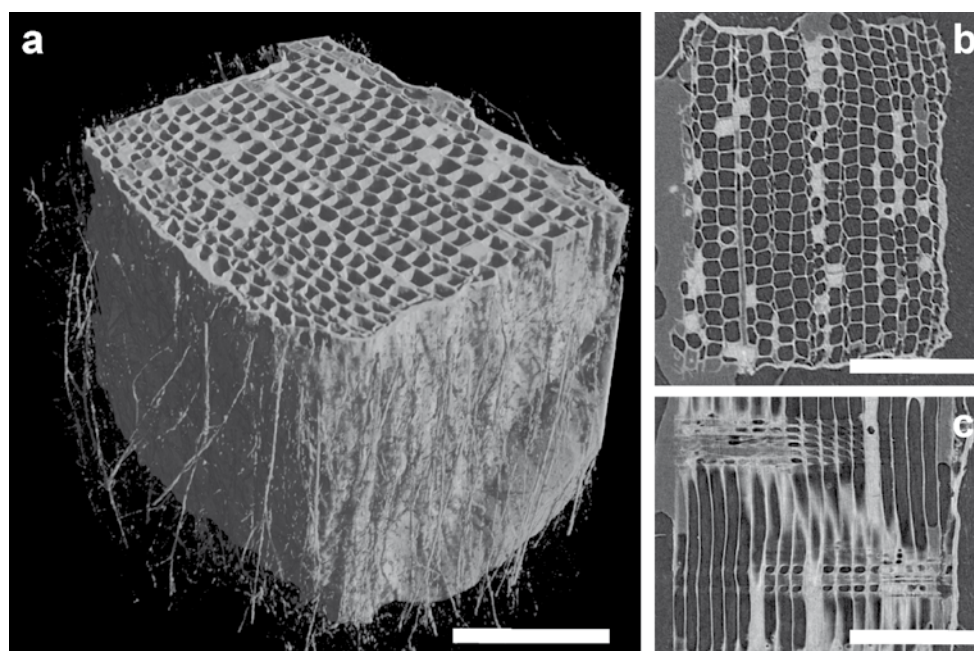


Fig. 2. (a) Three dimensional rendering of hyphal tubes of a white rot fungus winding around a small piece of *Pinus sylvestris* in contact with malt extract agar (filling some cell lumina). (b) Cross-sectional and (c) longitudinal view illustrating the high anatomical detail. Bar = 200 µm; voxel size 0.79 µm.

least, core scale (10 cm³). We need simulations to operate at realistic scales in order to accurately reproduce the observed, often emergent behaviours we wish to study. Emergent behaviours are often scale-dependent, a simulation that includes only a restricted region of the system may demonstrate different emergent behaviours, and we may not know in advance what scale is appropriate. One approach to scaling up simulations is to simplify the underlying model, for example the homogenisation approach proposed by Roose & Schnepf (2008), where the environmental heterogeneity is carefully coarse-grained, and by model reduction, for example Gibbons *et al.* (2009), where stripping out unnecessary model components reduces computational demands. Both raise considerable difficulties. In each case, simplification requires identification of the important model components, which are unlikely to be obvious in a complex system. An alternative approach is to increase the computational power available to the simulation by taking advantage of multicore CPUs, GPUs and clusters. Parallelisation is widely regarded as an experts-only programming problem, and one that is strongly tied to the particular computational platform in use. However, complex biological systems simulation is a problem with an inherently high degree of concurrency in the natural system: a complex system fundamentally consists of a large number of independent, but interacting, agents and processes. Most approaches to parallel programming focus on highly regular numerical problems, and make building such a simulation difficult. Simulation becomes much more straightforward with the use of concurrent programming techniques, in which the concurrent activities in a system and their relationships are specified, and the execution of those activities in the most efficient manner across the available resources is managed automatically by software. With careful design, a simulation built this way can be truly scalable, meaning that its complexity can be increased in a near-linear fashion by dividing it across more computational resources. This approach has become particularly interesting with the rise of grid and cloud computing: researchers can now gain access as required for a short period of time to a very large number of nodes upon which to execute their simulation, rather than relying upon in-house resources. Using cloud resources, we can potentially scale up by a few orders of magnitude. Approaches to scalability and validation in complex systems simulation are currently being investigated by CoSMoS (www.cosmos-research.org), drawing on expertise in modelling, highly-dependable software engineering and concurrent programming to develop and document reusable techniques for complex systems modelling and simulation. CoSMoS techniques for parallel, distributed simulation of agent-based spatial models have been successfully applied to problems including those in the fields of immunology (*in-silico* experimentation with lymphocyte migration (Andrews *et al.* 2008) and granuloma formation (Flügge *et al.* 2009)) and mycology (scaling up of the Falconer *et al.* 2005 model, in preparation).

FUNGI AS A METAPHOR

Fungal colonies are a highly successful organism, demonstrating pervasive growth through harsh environments. They achieve this through their capacity to operate in a decentralised manner, reacting locally to changes in context while interoperating at the colony scale and with other organisms. Fungi have the capacity to recycle biomass, effecting dynamic reallocation of investment, capitalise on fluxes in available resource and self-heal. These properties make them attractive metaphors for managing large, complex, distributed artificial networks. Other researchers have used other biological metaphors for similar problems. For example, ant colonies have been used as a metaphor for telecommunication routing algorithms. Typically, stigmergic pheromone trails are used to profile rates of flow of ants and other network traffic and the local strength of the trail is coupled to the values in local routing tables (e.g. Di Caro & Dorigo 1998). Similarly, in the field of artificial immune systems, the properties of the immune system have been used to inspire solutions in the areas of anomaly detection and data mining (Timmis *et al.* 2008). We have been exploring the potential for fungi as a metaphor for protecting society's critical infrastructures. Modern societies are heavily dependent upon a number of critical infrastructure networks that allow our societies to function, including water, power and transportation. These networks are open to failure through a range of processes including shortage of essential resources, breakdowns at key nodes and surges in demand and this means that effective management of such networks is challenging (Schulman *et al.* 2004). Bebbler *et al.* (2007) recognise that understanding how fungi grow may inform the design of man-made networks and through image analysis, have characterised fungal colony growth patterns in terms of nodes and edges of a graph. They show that fungal colonies are efficient transport networks that are robust to damage and react to local variation in resource. In order to translate the concept into a working solution, we have developed a graph-based implementation of Falconer *et al.* (2005). We are now exploring the capacity of our model to provide robust and resilient management solutions to resource limitations, node failures, and demand surges.

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