Linking individual behaviour to community scale patterns in fungi

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Abstract

The fungi comprise a separate kingdom of life and epitomise the indeterminate growth form. Very little is known about the factors that influence the nature of fungal diversity and the link between individual behaviour and the structure and function of fungal communities is particularly poorly understood. Here, we present a theoretical framework that is capable of elucidating this link. An individual-based model for fungal community dynamics is introduced that is developed from a physiologically based model for the fungal phenotype. The model is used to explore the role of individual interactions, the production of an external inhibitor field and the quality of the external environment on the structure and diversity of the resulting community. We show that traits relating to growth rate, autophagic behaviour and the production of inhibitors are key in influencing the success of a particular genotype in a community. The species richness increases with the amount of available resource. This is the first model of fungal community dynamics that introduces the concept of a biomass-based abundance distribution function that can be described by the log normal form which typically corresponds to communities in equilibrium. The species abundance curve is stable to changes in the relative location of innocula, although the ranked abundance of the individuals was not. We present the first attempt to identify the traits that affect the form of that curve. Future studies should examine the role of environmental heterogeneity and spore dispersal.
Keywords: fungal community dynamics, mathematical model, fungal interactions

1. Introduction

Fungi are among the most pervasive, versatile and diverse groups of organisms in terms of their manifest morphology and life cycles (Falconer *et al.* 2005). However, a quantitative understanding of fungal ecology and factors promoting fungal diversity and coexistence is limited. This is surprising as such an understanding is needed to maintain the ecosystem services that fungi support, estimated to be $33T (Costanza 1997). The main reasons for this lack of knowledge are the indeterminate nature of fungi, and their habit of being dispersed and immersed in the substratum which makes recognition of fungal individuals and their spatial extent difficult. This is further complicated by the myriad of factors that affect fungal interactions which ultimately shape community structure. These include environmental conditions such as temperature and pH, the nutritional status of colonies and the growing medium, and species combativity and inhibitor production (White 2003). Little is known regarding inhibitor production by species although it is clear that species detecting non-native chemical compound(s) results in reduced growth (Falconer *et al*. 2008), although the chemical basis of the myriad of compounds produced and how they are sensed is unclear (White & Boddy 1992).These features have presented problems, experimentally and theoretically, in measuring communities of fungi and we focus on the role of the last three factors on community structure and diversity in this paper.

Progress has been made in experimental studies of fungal diversity where the domain can be directly observed, such as leaf surfaces, forest floors and infected plants, where the numbers of spores, fruit bodies (Vogt *et al.* 1992) and lesions (Jeger 1987) can be determined via direct or indirect methods. Where isolation frequencies are a measure of relative abundance the community structure follows a log-normal distribution (Wirsel *et al.* 2005; Lussenhop 1981). In Ecology abundance distributions are a common measure of community structure and those that resemble the log-normal form appear to be ubiquitous amongst determinate systems, although their origin remains hotly debated (Pachepsky *et al*. 2000; Mutshinda *et al*. 2008; Sizling *et al*. 2009). In such systems, the abundance of an individual can be simply defined as the number of individuals at a given time. In indeterminate systems, where individuals have an unlimited lifespan and where they can grow to indefinite biomass, the definition is less clear. It has been argued that since the mycelium grows and shrinks other measures such as the size, mass, volume or area of substratum colonised may be a more useful abundance measure (Warrall 1999). This is especially true in

media where securing territory, e.g. in wood systems, is a key process for governing survival. From a theoretical perspective there are a number of existing mathematical models of fungal colony growth; see Davidson (2007) for a review. However, there are fewer models focused on studying fungal interactions of multiple species. Bown *et al.* (1999) and Halley *et al.* (1996) investigated community scale patterning as a consequence of interactions among species. These models and the accompanying data make it clear that the dynamics of the community requires a description that accounts for the effect of mycelial-scale context in the community on the outcome of individual interactions. However, as far as the authors are aware, there is no existing model of fungal growth and interactions that can do this. Ideally, such a model should also employ parameters that can, in principle, be measured directly on individuals and is scalable in terms of modelling multiple individuals. Such an approach would deliver the first theoretical ecology of indeterminate systems and so help us understand the relation between individual behaviour and community structure in fungi, and the impact of environment. The fact that such a model also predicts community function would allow us to address the question of the relationship between community structure and function in indeterminate systems, which would be of immense practical value for sustainable agricultural and forestry practices.

In this paper we explore the link between individual functioning and community scale behaviour for fungal systems based on previously published work detailing individual fungal growth and interactions models (Falconer *et al.* 2005; Falconer *et al.* 2008). The model has an explicit account of the physiology of the vegetative development of a fungal individual, and includes colony interactions in a spatially explicit context and so can be linked to experimentation. Important physiological processes included are nutrient absorption, 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 (Bown *et al.* 1999). Thus ultimately permitting different parts of the mycelium to expand and senesce concurrently. The model is used to generate mycelial distribution maps that emerge from fungal interactions among a community of intrinsically different individuals.

The purpose of this work is to study the effect of individual interactions and the nutritional and intrinsic properties of fungi on community development. In particular we investigate:

- the link between individual interactions and community structure
- the role of resource level in the environment and its effect on community structure,
- the impact of intrinsic inhibitor production on community structure.

For indeterminate organisms such as fungi, the community structure may be characterised by spatial maps (Fig. 1) from which we may calculate biomass abundance measures for each individual, species richness relations and, where a sufficient number of individuals have survived, abundance curves can be determined. We interpret theses maps in terms of dynamic processes underlying the organization of the community.

2. Methods

The effect of individual interactions, resource level and inhibitor production on community structure was assessed using the modelling framework of Falconer *et al.* (2008). This framework was developed to capture the minimal set of physiological processes required to reproduce the observed range in phenotypic response (Falconer *et al.* 2005). It has also been used to investigate the consequences of environmental heterogeneity for biomass distribution (Falconer *et al.* 2007). The development of this model for the individual phenotype to incorporate processes relevant to community interactions (Falconer *et al.* 2008) is based on five physiological processes**: *uptake, redistribution of biomass, remobilisation of biomass, inhibitor production, and growth*** which are known to be important for vegetative growth of fungi but have not collectively been incorporated into previous modelling frameworks. The mathematical model (Supplementary material) describes these processes and requires five state variables, described below, to be defined: non- insulated, insulated and mobile biomass; an inhibitor field; and an external resource. Figure 2 depicts the relationship between the state variables and the relevant physiological processes. The model formulation represents an individual mycelial network as biomass comprising three components. The first component is referred to as non-insulated biomass (b_n), and corresponds to the portion of hyphal biomass capable of significant uptake of external resource enabling assimilation (Cooke & Rayner 1984; Rayner *et al.* 1999; Falconer *et al.* 2005), e.g., a component of this may be active hyphal tips. The second component is referred to as insulated biomass (b_i), and corresponds to hyphal biomass where the cell wall has changed

in character such that uptake is significantly reduced creating resilient hyphae that maintain physiological integrity (Falconer *et al.* 2005; Rayner *et al.*1999). Insulated hyphae can become non-insulated under the recycling mechanism, reflecting that the configuration and properties of fungal boundaries can change Rayner et al. (1999). The third and final component of biomass is referred to as mobile biomass (n), and corresponds to biomass that is internal to the hyphae and that is being redistributed within the mycelium e.g. vesicles or internal resource. Environmental components are external resource (s) and inhibitor (i) . External resource is acquired from the environment, via ***uptake*** from insulated (λ_2) and non-insulated biomass (λ_1), and converted into mobile biomass. ***Remobilisation*** process involves biomass recycling, which is the interconversion between mobile biomass (n) and structural biomass ($b_{i \text{ and }} b_n$). Mobile biomass may be utilized to produce insulated or non-insulated biomass, at a rate determined by parameters $\alpha_{i,}$ and α_n respectively, corresponding to hyphal biomass production. Biomass (both insulated and non-insulated) may also be converted into mobile biomass (at a rate determined by parameters β_I and β_n respectively) corresponding to hyphal degradation and redistributed. ***Redistribution*** of mobile biomass is governed by a non constant diffusion coefficient (D_n), which depends on the local concentration of mobile biomass and is assumed to be redistibuted within the fungal colony. One consequence of this dependence, in conjunction with the other properties of the model, is that mobile biomass accumulates at sites where the local uptake of resource is high, e.g., at the growing margin of the colony. Accumulation of mobile biomass, e.g., vesicles, at these locations is an observed characteristic of real fungi, and facilitates the development of exploitative growth forms through the production of new hyphal tips in areas of relatively high external resource (Ritz & Crawford 1990). The production of ***inhibitor*** in the model consumes the internal resources of the colony and is represented by a reduction in local mobile biomass at a relative rate determined by the parameter, Ω, and a conversion factor χ. The inhibitor is assumed to diffuse in the external environment at a constant diffusion rate (D_i). For ***growth*** the colony expands at a rate dependent on a constant diffusion coefficient, D_b. In a given time interval, a proportion, ζ, of non-insulated biomass is converted into insulated biomass. This corresponds to extension of hyphae and the rigidification of hyphae behind tips. Growth in regions of high uptake is accelerated by a non-linear term (θ) associated with increased rate of conversion of mobile biomass into insulated and/or non insulated biomass. There is a metabolic cost associated with both recycling of biomass (γ) and inhibitor production (χ) that represents the energy required for these processes. For a fuller description of all model parameters the reader is referred to Falconer *et al.* (2008). A mathematical description of colony growth and interactions based on these physiological process results in a genotype vector (α_n, α_i, β_n, β_i, θ, λ_1, λ_2, ζ, Dn, Db, Ω, η, χ, γ) which characterise nutrient ***uptake*** (λ_1, λ_2), biomass ***redistribution and remobilisation***(α_n, α_i, β_n, β_i, θ, γ Dn,), ***inhibitor production*** (Ω, η, χ) and ***growth*** (ζ, Db) (Falconer *et al.* 2008). The equation set is provided in the electronic supplementary material. Because the vector fully characterises the phenotypic response of an individual to its environment, we refer to an individual defined by its vector as a 'genotype'.

The key assumptions of the model are those related to biomass redistribution namely the concentration-dependence of the mobile biomass diffusion coefficient, and the sensitivity of the switch between net immobilisation and mobilisation of mobile biomass on mobile biomass concentration (determined by θ). This allows expansion or senescence of different parts of the mycelial network and the accumulation of internal resource at the growing margin, which is a characteristic of real fungi. A full sensitivity analysis has been presented elsewhere (Falconer *et al*. 2005; Falconer *et al*. 2008).

The equations of Falconer *et al.* 2008 are discretized on a 30x30x30 3D lattice large enough for monitoring the evolution of 40 fungal individuals. They are solved using the implicit Crank Nicholson scheme with Successive Over Relaxation (Press 1992) and the boundary conditions are of von Neumann type. The spatial (h) and temporal (k) disctretisations used in the simulations were selected small enough to avoid numerical instability (Crank 1975). In this paper our focus is on the role of intrinsic properties of individuals on community structure and so we assumed that the environment was homogeneous and constant. Within this environment 40 individuals with different intrinsic properties, *i.e.*, genotypes, were randomly placed with the same inoculum biomass. Each individual has its own copy of the insulated, non insulated, mobile biomass and inhibitor state variables but all 40 individuals interact in the same environment. The parameters corresponding to the genotype vectors of the 40 individuals were also randomly selected and are provided in supplementary material. This represents the sequential and spatially random arrival of 40 spores located in the 3D volume. The subsequent growth of each individual is determined by the genotype driving

physiological processes and the interactions among individuals. The external substrate is depleted on a first come first serve process and is replenished after all individuals' uptake resource i.e. at the beginning of each computational time step. In this system resource and space are inextricably linked, and securing space means securing resources and this is exemplified in the model results. Competition for external resource will occur when mycelial boundaries overlap, however there will be competition for space from the outset. In all simulations the environment was replenished at the beginning of each computational time step with a prescribed resource amount to maintain a homogeneous and constant resource base and to represent the constant food supply in a wood environment. The metabolic costs associated with inhibitor production (χ) for all individuals was constant and equal to 0.01. The model was run until a dynamic equilibrium, defined as the state where the number and biomass abundance of fungal individuals remained constant for at least 250 computation time steps. This occurred after around 1500 computational time steps.

(a) Effect of individual interactions

To determine the effect of interactions on community structure we first simulated the growth of each genotype in isolation to determine if that individual could survive in isolation in the defined environment. Total biomass corresponds to the summation of the insulated, non insulated and mobile biomass components for each individual. A preset biomass threshold of 10e -06 was used to determine survival of a specific individual. The inoculum position for all genotypes grown in isolation is towards the centre of the environment, at position (15, 15, 15), as this limits the impact of the effects of the boundaries. In the model formulation, the growth of a single individual through the environment is deterministic and so no replicates are required. We investigated genotype survival in complex communities, where individual interactions play a role in colony survival. We randomly distributed the inoculum positions of the 40 individuals across the homogeneous environment, and simulated 39 different realisations to allow for the fact that the growth and survival of any individual may be sensitive to the mix of genotypes in a local neighbourhood. We compared survival of individuals grown in isolation and within communites, and investigated biomass abundance relations in communities of individual. The species abundance curve is used often in Ecology and is a measure of the abundance of individuals of a given species in a community. Preston (1948) developed a graphical means of comparing relative abundance where the x-axis shows the log abundance in terms of intervals and the y-axis represents the number of types within that interval.

(b) Effect of resource level

We studied the effect of resource level on community structure and diversity using one realisation as the model is deterministic and preliminary investigations demonstrated that the resulting species richness is not sensitive to the distribution of inoculum positions. Therefore, one realisation of a community, i.e. the same 40 individuals with a particular set of initial inoculum locations, was constructed. We varied the amount of resource available in all computational cells whilst maintaining a homogeneous 3D environment in order to isolate the effect of resource availability on community structure. In particular, using 3 runs we investigated community structure with low (1) medium (10) and high resource (100) levels.

(c) Effect of inhibitor production

We further explored colony interactions in simulation by investigating the effect of inhibitor production on community structure. Here, we compared the community structure of 40 individuals with and without inhibitor production capability in an environment where each computational cell has an intermediate external resource quantity (10). The first 40 genotypes are created by sampling from a uniform distribution and have the capacity to produce inhibitor. From this set we produce a second set of 40 types by fixing the inhibitor production trait of each individual to zero ($\Omega = 0$) but keeping the other traits unchanged, thus creating the corresponding non inhibitor producing community. Again since the model is deterministic and species richness is not sensitive to the distribution of inoculum positions (see results below) one realisation of a community (the same 40 individuals with known initial spatial locations) was constructed and the role of inhibitor production on community development was assessed by comparing the species richness for communities with and without the capacity for inhibitor production.

3. Results

(a) Effect of individual interactions

19 of the 40 individuals had biomass abundances greater than the preset threshold (10e-6) when grown in isolation whilst only 10 individuals survived when grown within the community. The 21 that did not survive when grown in isolation either had traits for high turnover into mobile biomass (corresponding to autophagic

capabilities i.e. the controlled recycling of nutrients inside an intact plasma membrane) or low uptake and growth. When the same individuals are grown in a community a further 9 individuals die due to competition effects and the individual's inability to secure its spatial territory. Competition is mainly for space and it is only when mycelial boundaries overlap that there will be competition for nutrients.

The simulation experiment was repeated for the same 40 genotypes, but with random initial inoculation points to average out the effect of neighbourhood dynamics. Figure 3 illustrates a sample biomass abundance distribution with a normal curve fitted at computational time (t) =1500. Here the x-axis represents log biomass abundance and the y-axis corresponds to the number of individuals that can be allocated to that interval. In each replicate, the individuals that survived were the same and so species richness was not sensitive to spatial locations. However the ranked abundances of individuals varied across runs. The resulting abundance distribution was of log-normal form for all 39 replicates based on a Sharpio – Wilk normality test (preferred test when mean and standard deviation are estimated from the sample itself). The lowest p value was found to be ($p = 0.272 > 0.05$).

(b) Effect of resource level

For the same community as in (a), as resource quantity increases so does the number of coexisting individuals. For low, medium and high resource level 2, 10 and 30 individuals coexist respectively. Figure 4 shows species richness as a function of computational time (time) for three resource levels. The resource quantity affects the species richness and also the rate at which individuals die out in the early stages of the simulation. The less resource available the harder it is for the less competitive individuals to survive and these die out at a faster rate.

(c) Effect of inhibitor field

For the same community as in (a) we determined the effect of inhibitor production on the community. Figure 5 shows the effect of inhibitor production on species richness. Inhibitor production supports more fungal diversity despite a metabolic cost (χ=0.01) associated with the process and this is due to maintenance of exclusive zones as a result of inhibitor production. In the non-inhibitor producing community the number of individuals decreased much more rapidly than the inhibitor producing community, and took longer to reach dynamic equilibrium, 1250 computational time steps compared with 1050. The species richness is 10 and 3 fungal colonies for the communities with and without inhibitor production respectively.

4. Discussion

The results confirm that colony interactions are fundamental in shaping community structure. The community model demonstrates both primary and secondary resource capture. Initially individuals must secure space and this is achieved via relatively high growth rates which was a characteristic of the surviving individuals in the numerical simulations. Subsequently, the individuals must maintain their spatial extent. None of the individuals with autophagic capabilities, the controlled recycling of nutrients inside the hypha, persisted in a community as these individuals do not defend their territory against competitors. These two characteristics of competition account for the main differences between the community and isolated individual results.

The results also demonstrate that higher resource levels support more diversity. This is consistent with experimental work where competition was reduced as a consequence of increased availability of resource. The work of Holmer and Stenlid (1996) investigated the outcome of competitive interactions among wood decaying fungi and found that a constant input of uncolonised woody debris reduced competition and led to a richer community compared with situations where resources were lacking. Other experimental studies supporting the link between increased resource availability and fungal diversity are Carney *et al.* (2004) and Waldrop *et al.* (2006). The results also indicate that maintenance of an exclusive spatial domain fosters coexistence and this is reflected in recent experimental work. Six and Bleiker (2009) showed that despite an overlap in resource niches two fungal symbionts of the mountain pine beetle, *Grosmannia clavigera* and *Ophiostoma montium*, coexisted. While these fungi share the same resources within a tree, field studies demonstrated that these species can coexist by maintaining exclusive areas. This is recognised as a trade off between competitive ability and predator invulnerability by Chase and Knietel (2004). In our result predator

invulnerability is exhibited by rapid growth and avoidance via inhibitor production allowing maintenance of an exclusive area space. These invulnerability traits then inhibit the stronger competitor's ability to gather resources which, ultimately reduces competitive ability. This is consistent with previous studies where it was noted that simple avoidance behaviours foster coexistence (Mimura 1991). Inhibitor production may promote diversity in a physically homogeneous environment but this may not be true for more complex media such as soils where the physical architecture of soil creates disconnected regions creating a physical barrier that in itself promotes avoidance.

Future directions in our community structure investigations include the representation of a soil-like environment through which resources are distributed heterogeneously and fungal interactions are impacted by the physical environment. In a complex environment the antagonistic mechanisms in the tortuous environment may not be beneficial in promoting coexistence and this can be tested via simulation. We can explore the adopted strategies of different subsets of genotypes and how these are affected by environmental context. Other processes such as traits relating to spore production and dispersal, and interconnections among microenvironmental sites (Falconer *et al*. 2006) may affect coexistence. Given the simplistic nature of the model, its usefulness in investigating the link between process and pattern has been demonstrated. Our modelling framework provides a representation of fungal colony interactions that integrates physiological processes of uptake, redistribution of biomass, remobilisation of biomass, inhibitor production and growth of fungal colonies. Moreover, the framework facilitates interactions among individual colonies in space over time. Here we have shown that our results reflect patterns observed in real systems, and since our model is process based we are able to link individual processes to community scale patterns. Such modelling is likely to prove invaluable in efforts to understand the ecology of fungi in complex environments.

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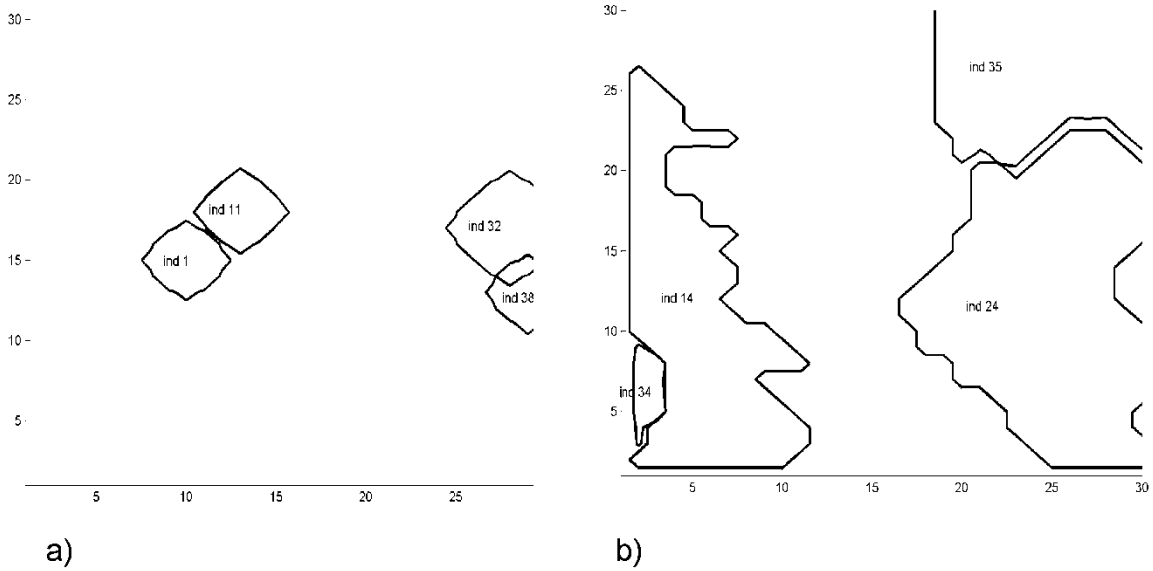
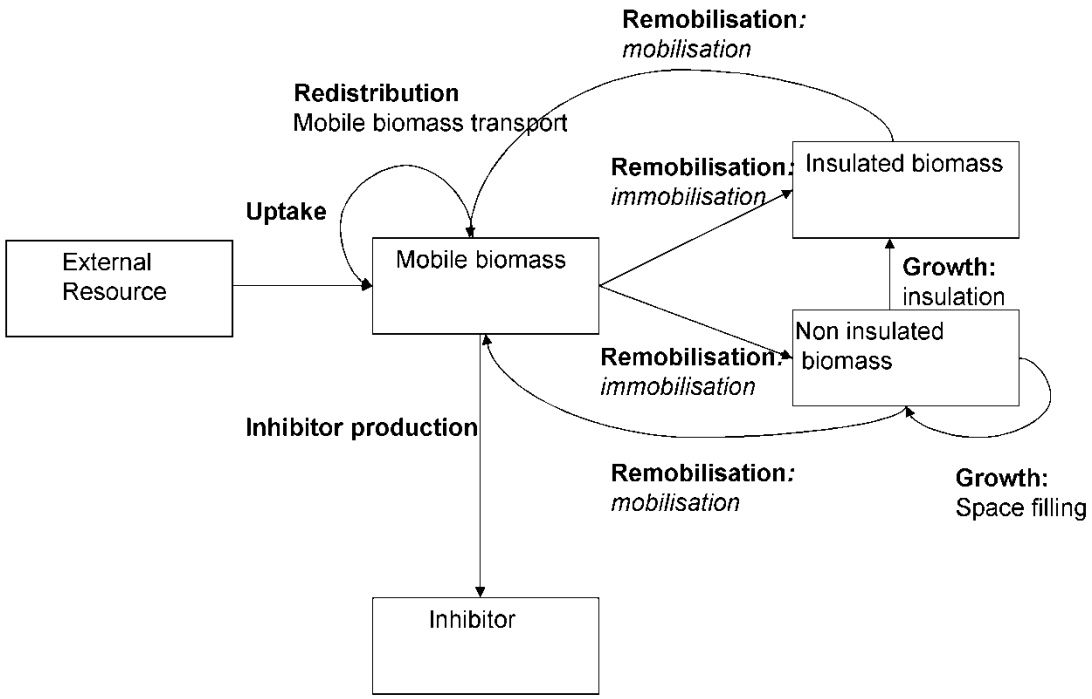


Figure 1. 2D mycelial contour map representing a 2D slice at z = 24 through the 3D volume at a) unscaled computational time t = 1 and b) unscaled computational time t =1500, with a contour value of 0.1. Each boundary corresponds to the mycelial boundaries of an individual colony which is labelled showing the initial and resultant boundaries occupied at the beginning and end of the simulation. As can be seen the individuals that were present at computational time t=1 (1, 11, 32 and 35) have been replaced by individuals (14, 24, 34 and 35) at computational time t=1500. The outcomes of competition can also be interpreted from these maps by overlapping boundaries and unoccupied areas.



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407 **Figure 2.** Schematic diagram showing relationship between physiological processes and state variables of
408 the model. The square boxes represent state variables and the labelled arrows depict processes that cause
409 state transitions or updates.
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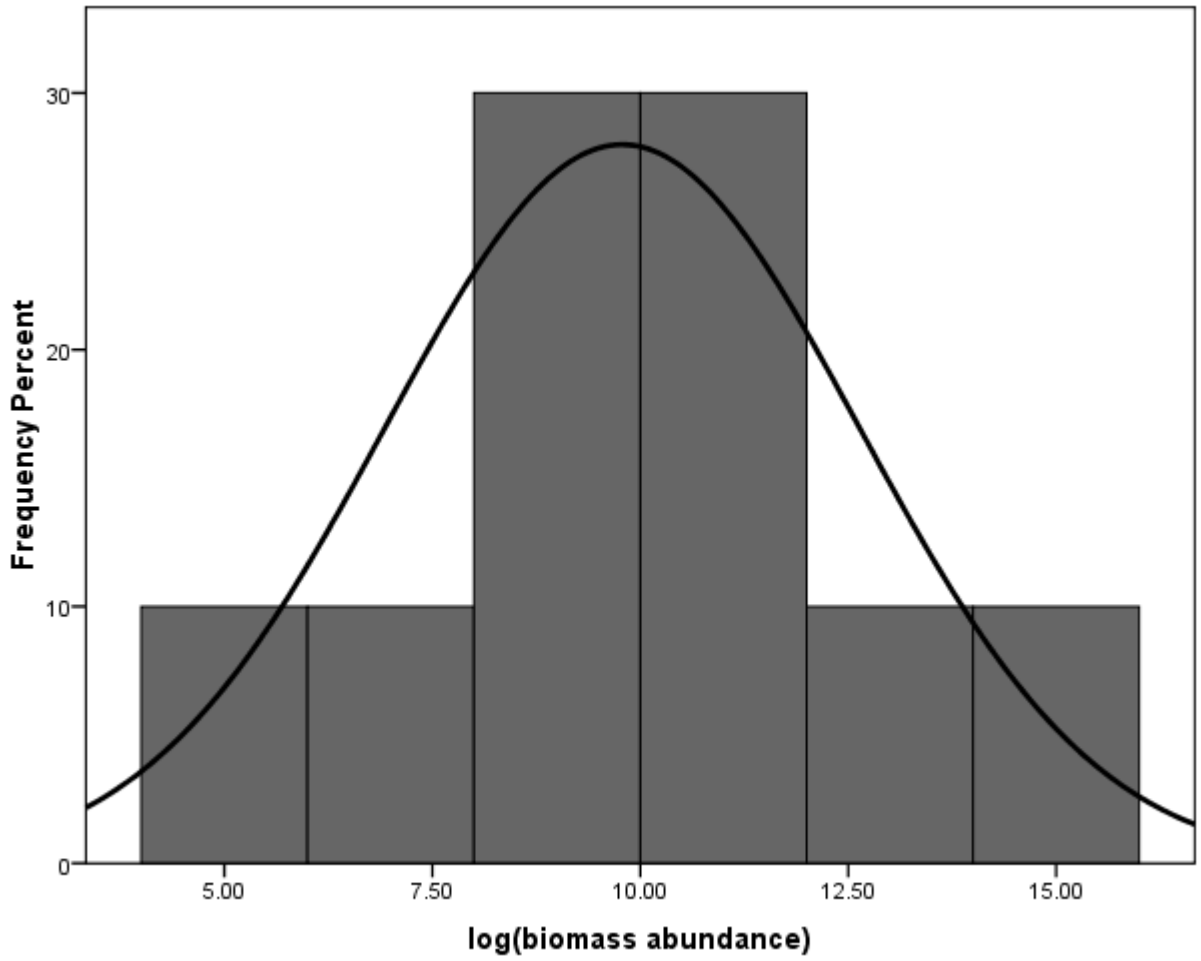

Figure 3. A sample biomass abundance plot, log transformed, superimposed with the best fit normal distribution

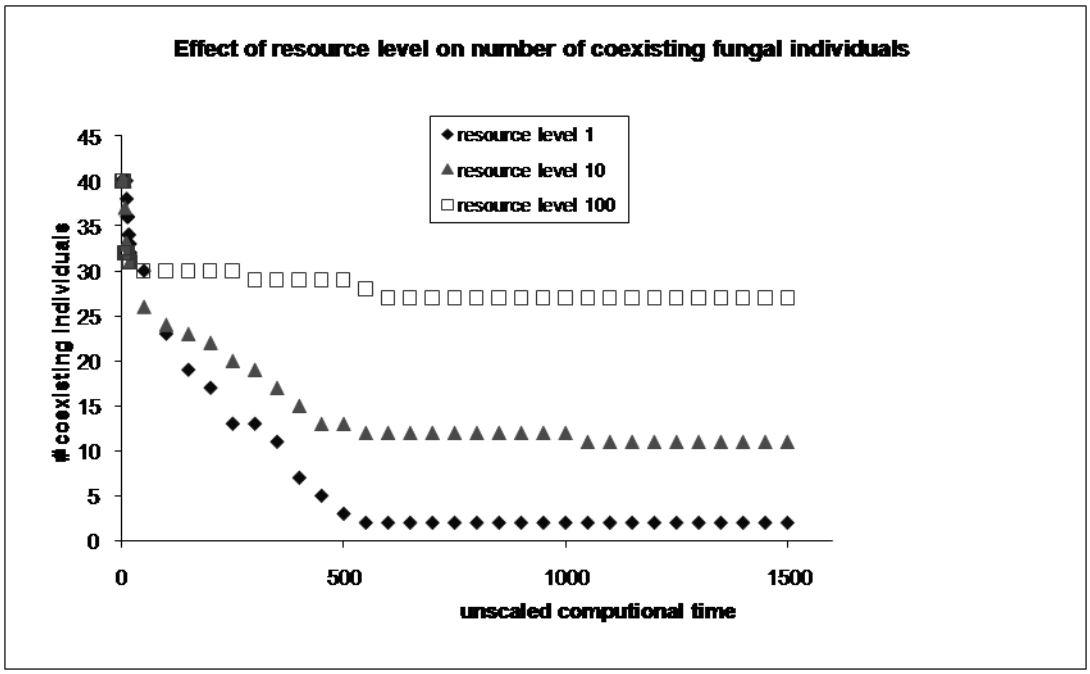

Figure 4. Effect of resource level on number of individuals (y axis) the environment can support over computational time (x axis). Each trend line represents an environment with a resource level of 1 (diamond), 10 (triangle), 100 (square).

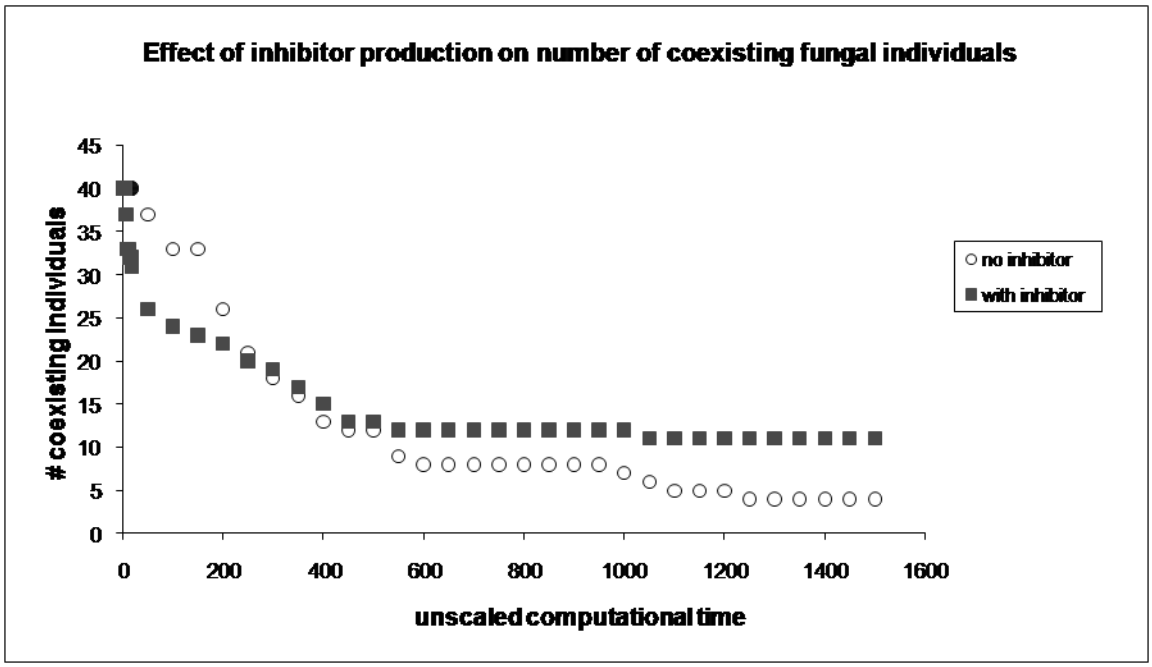

Figure 5. Effect of inhibitor production on number of coexisting individuals (y axis) in communities with and without inhibitor production over computational time (x axis). Each trend line represents a community with (square trend line) and without (circle trend line) inhibitor production.