Problem Chosen	2021	Team Control Number
MCM Problem A	**MCM/ICM Summary Sheet**	**2125756**

Lorem ipsum dolor sit amet, consectetuer adipiscing elit. Ut purus elit, vestibulum ut, placerat ac, adipiscing vitae, felis. Curabitur dictum gravida mauris. Nam arcu libero, nonummy eget, consectetuer id, vulputate a, magna. Donec vehicula augue eu neque. Pellentesque habitant morbi tristique senectus et netus et malesuada fames ac turpis egestas. Mauris ut leo. Cras viverra metus rhoncus sem. Nulla et lectus vestibulum urna fringilla ultrices. Phasellus eu tellus sit amet tortor gravida placerat. Integer sapien est, iaculis in, pretium quis, viverra ac, nunc. Praesent eget sem vel leo ultrices bibendum. Aenean faucibus. Morbi dolor nulla, malesuada eu, pulvinar at, mollis ac, nulla. Curabitur auctor semper nulla. Donec varius orci eget risus. Duis nibh mi, congue eu, accumsan eleifend, sagittis quis, diam. Duis eget orci sit amet orci dignissim rutrum.

Contents

List of Tables

List of Figures

1 Introduction

Decomposition by fungal and microbial communities is second only to photosynthesis in driving carbon cycling in the Earth's ecological communities [20]. While this significance is rarely understated, inner mechanisms and interactions within decomposition communities have been poory understood and treated as a 'black box' in the past by scientists studying ecosystem processes [9].

Fungi are made up of hyphae: long winding filaments enmeshed together to form a thick mat of mycelium. At the frontline of battle, hyphal tips are extending forward and branching to cover new area at a velocity dictated by the hyphal extension rate, and concurrently other hyphae are dying off or merging together [4]. Like machinery, each fungus has ideal operating conditions. Fungi native to dry or arid biomes will grow efficiently in a moisture-lacking environment when other fungi will falter. Maynard et al. (2019) defines these operating conditions by assigning temperature and moisture niche-widths to 37 studied species of fungi [32].

1.1 Competition

When fungi come into contact with each other, competitive interactions are most often observed. Tactics studied in Boddy, L. (2000) include deploying diffusable toxins, obtaining nutrients parasitically, destruction of hyphae by intentional interference, and establishing wall-like barracades to thwart attackers [11]. Most researchers, including Maynard et al. (2019) construct a competitive ranking scale based on experimental observations to encapsulate the ramifications of these complex interactions [32].

Under a constant temperature regime, previous research concludes that dominant fast-growing suppress other species which negatively impacts the overall community's efficiency. However fluctuating environmental conditions change the outcome and promote complementary growth [17]. An explanation for this is presented by Lusten-

houwer et al. (2020) suggesting a spectrum between slow-growing, stress-tolerant fungi operating in a wider environmental range than fast-growing, highly competitive fungi [36].

1.2 Substrates

Determining which fungi are present in a community depends on the organic material, or 'substrate', being broken down. In the case of fungal-mediated wood decomposition, the substrate is made up of lignocellulose polysaccarides, and the fungi involved are equipped with specialized enzymes capable of splitting linkages in the polymers to harvest usable carbohydrates. Long-term wood decomposition follows a well-studied three-phase process: the first phase is dominated by fast and opportunistic fungus claiming easily-consumable soluble sugars, followed in the second phase by consistent and dependable decomposers that degrade the holocellulose constituting 65%-85% of the material [24]. Slow and highly specialized fungi trail behind in the third phase to clean up rigid lignin polymers (15%-35%) with powerful oxidative enzymes [16]. While phase progression is an important agent governing community changes on the long-term scale, this paper will focus on only the middle phase of cellulose decomposition and will not conider lignin decomposition. [36].

1.3 Growth Model

An important step in modeling fungal communities is acknowledging separation between the growth rate and the decomposition rate of the fungus, which are influenced by different factors. Fungal growth models typically focus on the increase in overall biomass due to hyphal extension. Fungi with a greater density of hyphal tips per unit volume will grow and accrue biomass faster, as hyphae only grow from their tips. New tips are are created when hyphae branch off, while others die or fuse together via anasmotosis. Edelstein (1982) models these dynamics with the following:

$$\frac{\partial \rho}{\partial t} = nv - d \qquad (1)$$

$$\frac{\partial n}{\partial t} = -\frac{\partial nv}{\partial x} + \sigma \qquad (2)$$

Where ρ is the total hyphal density, n is the tip density, v is the hyphal extension rate, d is the hyphal death rate, and σ is the increase of tips due to branching. These equations will operate standing alone, without any other influences by enzymes or growth limitations. This allows many models to treat it as a baseplate to expand upon. Edelstein (1983) and Davidson et al. (1997) do this by considering concentrations of nutrients inside the fungi and outside in the surrounding substrate [5, 22]. Our model will likewise follow in eliminating the assumption that fungi grow over an unlimited nutrient supply. A more contemporary approach by Du et al. (2019) describes the growth of a fungus with a 3-dimensional reaction-diffusion equation based on microscopic growth mechanisms, also focusing on tip density and extension rate but with an added term to identify the proportion of tips which are actively growing [30].

1.4 Environmental Influence on Hyphal Tip Extension (v)

Environmental impacts are introduced to the decomposition model through v, the hyphal tip elongation rate. The mechanism of elongation is relatively unknown; as described in Gervais et al. (1999), "cell turgor pressure corresponds to an overpressure which allows the cell morphology, elongation, division and hence the biomass evolution" [10, 18]. In fungi, cell turgor comes from diffusion of water dictated by the water potential[1] gradients rather active transport within the cell, making it very environmentally dependent [10]. This fact justifies determining v based on environmental factors on fungal decomposition rates by varying v outside of baselines for given species

in set locations in our model. Experimental data from Maynard et al. (2019) shows the relationship between v and the environmental parameters of water potential (ψ) and temperature (T) [32].

1.5 Decomposition kinetics

Moore et al. (2015), Edelstein (1983), Moorhead et al. (2006), Parnas (1974), and Schimel et al. (2003) describe the decomposition of a certain substrate by a microbial decomposer as a function of the substrate's concentration with the Michaelis–Menton equation [3, 5, 15, 16, 25]. Thus, decompostion of carbon in a substrate is described by the following equation.

$$\frac{dC}{dt} = \frac{KBC}{K_e + C} \qquad (3)$$

Where B is the biomass of fungi, C is the amount of carbon in the system and K_e is the half-saturation coefficient. Schimel et al. (2003) and Moorhead et al. (2006) assert that decomposition levels off at a maximum rate proportional to the concentration of enzymes acting on it [15, 16]. To determine this enzyme concentration, we will make the assumption that enzyme concentration is proportional to the concentration of biomass in our system represented by r multiplied by two environmental limiting factors in $K = rS_M S_T$ [15]. This environmental factors are discussed at greater length in section 2.4.

1.6 Enzyme interactions

Enzymes produced by fungi are expelled into the surrounding substrate to autonomously break down macromolecules. Relative enzyme concentrations can be quantified by the production rates of each enzyme by a fungus. Production of enzymes is a metabolically taxing process, therefore fungi that produce enzymes which return much more usable energy and C than was put into making the enzyme, a high "return on investment",

---

[1] Water potential (ψ) describes the content of availability of moisture surrounding a fungi as dictated by the soil composition.

will be able to synthesize even more enzymes and grow rapidly [15]. Lustenhouwer et al (2020) strengthens this theory by showing through statistical analysis of 1582 various fungal isolates that fungi containing larger proportions of enzymes like acid phosphatase, which are associated with slow lignin decomposition, are demonstrated to strongly correlate with slower decomposition rates [36]. Lignin exemplifies a low return on investment, requiring powerful enzymes and greater energy input per unit C than holocellulose. But it's ultimately the fungi that have a subset of enzymes that best match their surrounding substrate which successfully grow and establish a niche. As an example, in a substrate of 70%+ lignin, the slower growing fungi with lignin enzymes normally at a disadvantage will win out over other fungi competing for a fraction of available holocellulose.

Communities with similar fungi of similar enzymatic makeup often see a few dominant species overwhelm the rest through competition for similar resources in the substrate, but communities of fungi with greatly differing enzymes will instead form distinct niches that partition different resources in which they are seperately able to grow. In these conditions, one dominant species faces difficulty in wiping out competitors who are individually masters of their own substrates. This effect is known as niche complementarity [17].

Research by Toljander et al. (2006) contends that environmental fluctuations further robustify a diverse community as faster growing highly competitive fungi are hindered by conditions that lapse out of their moisture niche, and slower growing stress-tolerant fungi benefit from decreased pressure by competitors. A linear regression for the moisture niche width (W_{mn}) vs competitive ranking (R_c) across 34 different fungal species studied in Maynard et al. (2019) gives $W_{mn} = 1.84R_c+2.9$, with an R^2 value of 0.227. Although the R^2 value of this regression is not particularly strong, an underlying negatively proportional relationship of the general data set is indicated. Maynard et al. (2019) provides backing for this niche distinction by applying principal component analysis to a variety of potential fungal niche-associated traits. The results of this analysis points towards a similar direction: fungal species will lean towards one of these two profiles [32].

A diverse subset fungal niches will result in a dampened and stable community will decompose the most efficiently across a range of conditions. [17]. This conclusion has signicant implications on the continuation of carbon cycling in ecosystems, as decomposers releasing carbon into the soil and atmosphere sustain a critical role in the cycle [36]

2   Model Formulation

2.1   Growth Model

In the review of various fungal growth models described in Lin et al. (2016), a specific method of modeling branching and hyphal death was found to match experimental observations in the widest variety of settings. Based on these results, for σ and d in (1) and (2) we will choose to implement the following relationships, comprising dichotomous branching, tip-hypha anastomosis, and hyphal death (or YHD).

$$\sigma = \alpha_1 * n - \mu n\rho \tag{4}$$

$$d = \gamma_1 \rho \tag{5}$$

Enzymes conducting decomposition make up a fraction of the total biomass, and the total biomass changes according to the growth rate. The total biomass B defined in (6) multiplies by maximum rate of the Michaelis-Menion equation (3) to couple growth rate with decomposition rate.

$$B = \int_{all x} \rho dx \tag{6}$$

The rate of decomposition of carbon will then be dynamically effected by the growth of the fungus contrary to the typical assumption of a static B as described by Schimel et al. (2003) [15]. Our

formulation of K which accounts for the proportion of biomass in the fungal growth containing the necessary enzyme for the carbon decomposition will change to account for this.

$$K = r * S_M * S_T * 0.04 * G \qquad (7)$$

Where r is a dimensionless parameter representing the relative abundance of one enzyme out of the total enzyme biomass of that specific fungus. The multiplication by 0.02 is a generalization that for any given species of fungus, 2% of the biomass will be relevant enzymes [16]. G is an empirically derived rate constant relating the mass of relevant enzymes to the maximum rate of the decomposition.

Limited carbon availability will also impact a fungi's growth rate. To account for this, we include a term multiplying v that can be interpreted as the available carbon for the fungi to consume for growth. The first equation in the growth model then becomes

$$\frac{\partial \rho}{\partial t} = (1 - LCI) * (10^9) * C * n * v - d \qquad (8)$$

Where LCI is the lignocellulose index[2] of a certain material and $(1 - LCI)$ is then the proportion of the substrate carbon stored in holocellulose. Multiplying by $(1 * 10^9$ is approximation to convert grams of carbon to hyphae length in mm. [citation needed for g to mm] An investigation of the effects of including the carbon term in the growth model are addressed in a later section.

So our coupled growth and decomposition models can be summarized by equations (2), (3), (6), and (8).

2.2 Defining Representative Enzymes

Maynard et al. (2019) collected data for 8 relevant enzymes and utilized a standard clustering approach to create a subset of four enzymes which best represented the effects by the fungi's enzymatic makeup on competitive interactions [32].

Our model utilizes this open-source data by normalizing the production rates of each enzyme and calculating their relative abundance as a fraction of the total enzyme biomass for that specific fungus. Interactions caused by differing rates of decomposition among different enzymes in varying environmental conditions is then represented in our model by taking the weighted sum of all contributions to the decomposition rate from any one of four enzymes in a given fungi species, represented in the following equation

$$\frac{dC_1}{dt} = c_{1,a}\frac{de_{1,a}}{dt} + c_{1,b}\frac{de_{1,d}}{dt} + c_{1,c}\frac{de_{1,c}}{dt} + c_{1,d}\frac{de_{1,d}}{dt}$$
$$(9)$$

Where $c_{1,a}$ is a enzyme breakdown efficiency coefficient for the fungal species 1 and enzyme a. Here the rate $\frac{dC_1}{dt}$ is representative of the rate of decay of the substrate by the fungi species 1. Breakdown efficiencies $c_{1,a}$ for each enzyme were derived from correlation coefficients drawn from experimentally observed data in Lustenhouwer et al. (2020) [36].

The total decomposition rate is then given by the sum of all rates over the various species of fungi.

$$\frac{dC_{tot}}{dt} = \sum_{i=1}^{n} \frac{dC_i}{dt} \qquad (10)$$

Where n is the total number of fungi being simulated. Our model simulates a system in which all 35 fungi are growing and decomposing at the same time and interacting through competition for a limited nutrient supply.

2.3 Estimating v For Various Environments

When considering a sampling of decomposition rates in various environment types, we must determine how to estimate temperate and water potentials that ground fungi would experience. In the case of determining v, this requires finding projected temperature and water potential.

Amongst existing biome classification models, Whitaker's scheme [2] is notably simple, providing

---

[2]The lignocellulose index describes the ratio of non-hydrolysable lignin to hydrolysable holocellulose in litter

a layout of biomes based on mean annual temperature and mean annual precipitation. However, modern classification of biomes has drifted away from using these traits as definitive biome identifiers [28]. These traits alone do not define all features of concern to fungal growth, such as soil composition for example. In addition, by Whitaker's scheme, we find that a given biome can have a wide range of average annual temperatures (such as arid desserts ranging from about -10 to 30 $^\circ C$) [2]. We can sample a range of temperature and moisture values to output various v and then select certain regions to profile in order to gauge potential environments where fungi can decompose and interact.

The following are the specific environments selected to represent various biomes:

Biome	Specific Environment Selected
Dessert (Arid)	Sonoran Desert, USA
Grasslands/shrublands	(Semi-Arid), central Argentina
Temperate Forest	Sal Forests, central Himalayas
Boreal Forest (Arboreal)	Pine Forests, central Himalayas
Tropical Rain Forest	Tropical Forests, Barro Colorado Island, Panama

Table 1: Specific Environments

Although water potentials can be approximated based on predictive models, the measure is best found experimentally from soil samples [29]. Single water potential and annual temperature values were selected from ranges of values experimentally determined by a variety of field studies on these environments (see: Table 2). This decision was made since we're aiming to compare discrete environmental conditions rather than create a complete span of environmental conditions.

Biome/ Environment	Temperature [$^\circ C$]	Water Potential [MPA]
Dessert (Arid)	15	-4.5
Grasslands/shrublands (Semi-Arid)	15.3	-3.2
Temperate Forest	12.49	-1.09
Boreal Forest (Arboreal)	12.49	-1.51
Tropical Rain Forest	27.5	-0.79

Table 2: Temperature & Water Potentials

Note that these are not wholly representative configurations, but rather examples to provide insight into how fungal species with specific traits may respond in discrete and distinct conditions likely to exist. We can then find v using experimental data from Maynard et al 2019 [32].**talk about continuous data technique thingy in the extra methods info sheet**

2.4 Other Responses to Temperature and Water Potential

Our growth model takes into account temperature (T) and water potential (ψ) in two more parameters: the soil temperature coefficient (S_T) and the soil temperature coefficient (S_M). Moorhead et al. (1991) provides a simple relationship between S_T

and T using the rate of increase (Q):

$$\log_{10}(S_T) = \frac{T - 25}{10} \log_{10}(Q) \qquad (11)$$

Although this equation does not take into account specific fungal response to temperature change, more recent evidence supports that this relationship is not direct, with most of the direct impact coming from moisture [34]. As the ratio of rates of decomposition given a temperature change, Q as a parameter should represent the effective output of various mechanisms influenced by temperature rather than focusing on specific mechanisms. However, for the sake of simplicity, Q has been set standard constant to a value of 2.5 [7].

Water potential also relates to a constant, S_M, in a simple equation described in Moorhead et al. (1991) using α_2 and λ:

$$S_M = \alpha_2 - \lambda \log_{10}(-\psi) \qquad (12)$$

2.5 Assumptions

Further assumptions made in the formulation of our model that have not yet been discussed are largely simplifications that are not relevant to any significant or interesting discussion. An itemized list of these assumptions is provided below.

2.5.1 Growth

- Growth occurs in a 1-dimensional space

- Neglecting effects from direct interactions between fungi

- Neglecting effects from N limitation

- Litter is not added to or removed from the carbon pool by forces external of the fungi

- LCI is 0.291 and remains constant over time

- Dynamics regarding the rate of nutrient absorption and transport of metabolites within the mycelium are ignored or simplified *more specific

- Ignoring other growth traits

- Substrate use efficiency (SUE) is 1

- Hyphal death rate γ_1 remains constant regardless of environmental fluctuations

- 100% of living hyphal tips are active

- No biomass created by a fungus will be geometrically isolated from the substrate

- Neglecting effects due to spacial limitations and phyiscal obstructions

2.5.2 Decomposition Kinetics

- Neglecting effects due to enzymes not included in the model

- Production of enzymes increases proportionally with biomass

- For any species of fungus, 2% of the biomass will be relevant enzymes

- Relative proportions of enzymes will stay constant regardless of environmental fluctuations

- Neglecting effects on decomposition rate due to changing metabolic rate of the fungi

2.5.3 Temperature/Moisture effects

- Turgor is a function of water potential

- Fungal decomposition occurs in surface soil (0-30 cm)

- Experimental data for average water potentials in specific biomes/environments are representative of the conditions of those environments

- Temperature and moisture are the only environmental parameters of significance to the model

- Rate of increase of temperature Q remains constant regardless of environmental fluctuations

- Soil moisture potential is effectively equivalent to that found in ground litter and wood fibers

3 Parameter selection and representative result

We created a representative run of the coupled growth and decomposition model to select realistic values for the parameterts, with some values found by consulting literature. An overview of the parameter selection for this representative run can be seen in Table 3, however several parameters are worth some discussion.

3.1 Growth model parameters

Two main parameters were studied for their effect on the growth model's result: the branching rate and the hyphal death rate. These parameters were not agreed upon in literature so values were selected from a pool of possible valus depending on their effect on the model to converge on the most likely realistic output.

Most results of the growth model were comprised of traveling wave solutions, converging to a uniform distribution in both space and time. This can be thought of as a convergence to the maximum growth of the fungus into its total space. The branching rate (α_1) was found to increase the hyphal density in the end behavior of the solution, with the ending density increasing as α_1 increases. The hyphal death rate (γ_1) was found to increase the oscillations in time and larger γ_1 values would increase the oscillations and the time to reach a given end-behavior. Many papers (Edelstein (1982), Lin et al. (2016), Schnepf et al. (2007), Du et al. (2019)) discussing the values of these parameters were concerned more with short-term dynamics in perfectly ideal conditions [4, 19, 27, 30]. The purposes of this paper is the assess the longterm decomposition rates under variable conditions, so parameters that could predict long-term behavior, comparable to long term decomposition dynamics described in Moorhead et al. (2000), Moorhead et al. (2006), and Moorhead et al. (1991) were selected [7, 13, 16].

3.2 Decomposition parameters

The value for G represents a rate constant relating the concentration of relevant enzymes to the maximum rate of carbon decomposition. Formulation for S_M and S_T come from Moorhead et al. (1991) which uses a simpler equation to describe the reaction dynamics for decomposition of carbon [7]. Our model adds complexity to this so we based this parameter on agreement with other more similar models and experimental data. The most important conclusion drawn for G was in selecting a timescale of decomposition to be comparable with that of Lustenhouwer et al. (2019) [36].

3.3 Representative results

We ran the coupled growth and decomposition model using parameters summarized in Table 3 to obtain a representative result. In the growth model, ρ was found to exhibit travelling wave dispersion throughout space, as similarly shown in Mimura et al. (2000) and Edelstein (1982) [4, 12]. As a consequence of only running the simulation for a timespan of three years, the decrease in carbon over time looks fairly linear, with slight fluctuations likely due to the fluctuating fungal biomass densities over time.

In the first initial runs, no coupling term defining a limited nutrient availability was present in the growth equations. This eliminated the effects of decreasing concentration of carbon as the growth model assumed an abundance of nutrients was present. Under short time scales this could be a perfectly valid assumption, as short time scales tended to show little overall decrease in the concentration of holocellulose carbon. However the

consequences seen from introducing this term in the growth equations become more apparent as longer time scales are considered. These effects can be seen in our results. The outcome for overall biomass of the communitty was mostly unaffected other than replacing decaying oscillations towards a steady state with a somewhat constantly increasing biomass overtime with a decaying slope.

Overall, including the nutrient availability term in the growth equation captures more of the fundamental interaction that this paper is concerned with (that of decomposing wood and ground litter rather than free-growing fungi), so it remained present for further analysis.
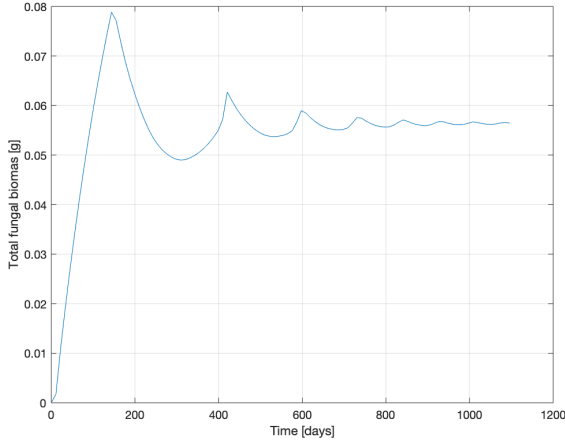
(a) Growth independent of carbon concentration.
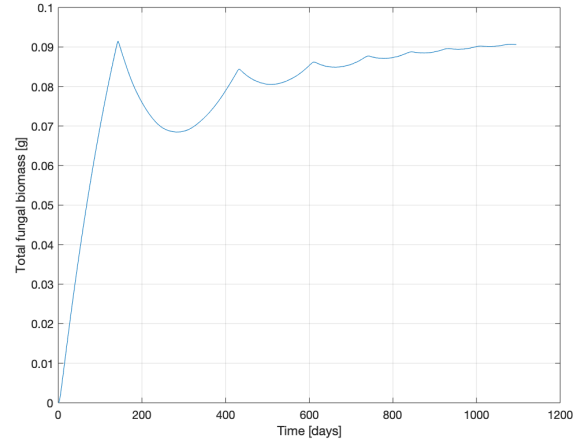
(b) Growth rate proportional to available carbon

Figure 1: Fungal biomass of coupled growth and decomposition kinetics model

4 Analysis

4.1 Total Carbon vs Time for Specific Environments

A sampling of different environmental parameters within the model was taken as described in section 2.3. The results of these model runs were taken in terms of the total grams of carbon over time, shown in Figure . Here, we see more moist soil environments lead to clearly more expedient rates of total carbon decrease and reach complete carbon decomposition decomposition quicker in our model. The rain forest environment exceeds the other environmental profiles, effectively completing decomposition in under 1640 days (roughly 4.5 years. On this time scale of roughly 5 years individual biomes will exhibit negligible changes in environmental parameters. But biomes in a given area can change in non-negligible ways over longer time scales. We can consider these long term changes as the effective transition between different biomes and thus different overall performance, as assessed by the model. Therefore, difference in performance between different environments can be roughly equated to the change in performance under long term environmental fluctuations.
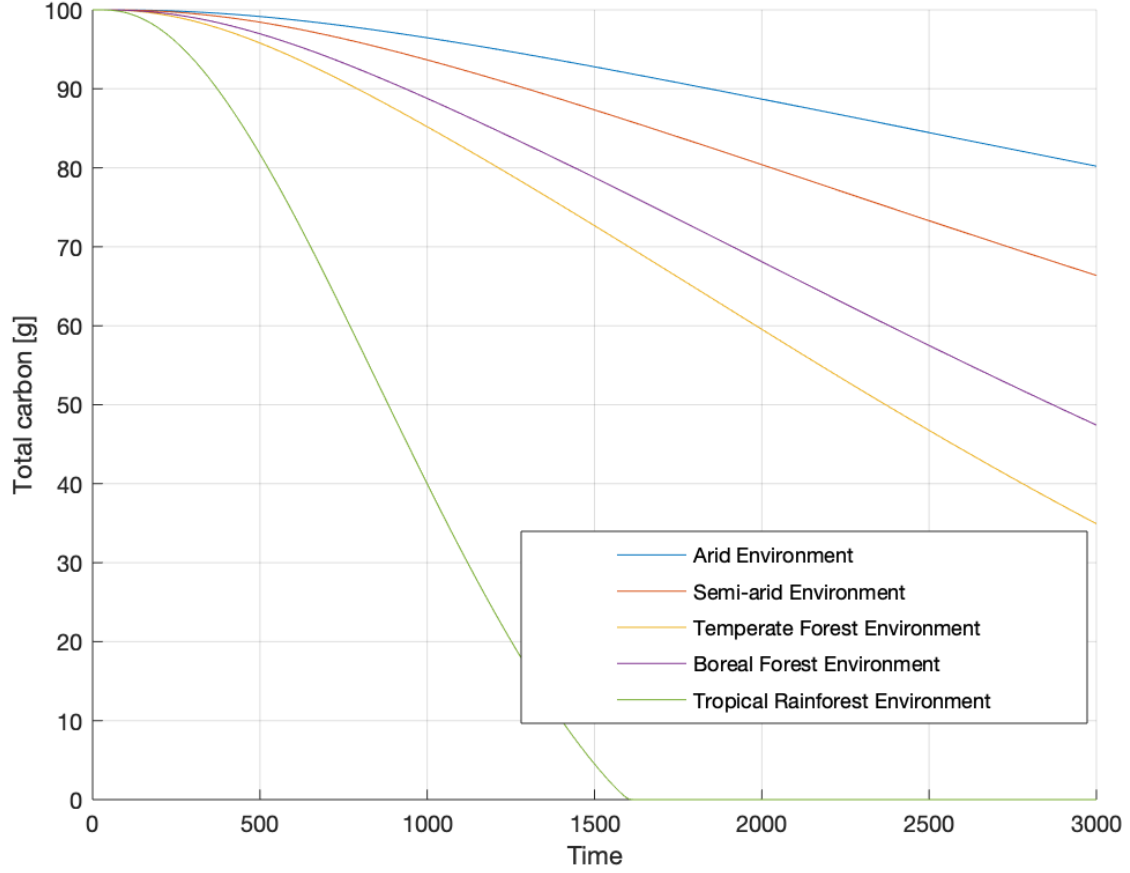
Figure 2: Total carbon in the substrate for five representative sampled environmental parameters.

4.2 ν vs Average Contribution to Substrate Decay

Using the decomposition model, average contribution to substrate decay and the tip elongation rate ν can be found for each fungal species for a given environmental configuration.

The contribution of a particular fungi over time is taken to be the absolute value of the decrease in total carbon caused by all enzymes of the specific fungi in question divided by the total initial carbon of the substraight. As described in the model formulation, these decreases are calculated independently and summed together to calculate the total carbon decrease. The average contribution is then calculated as $C_{avg} = \frac{\int C_{cont}\,dt}{\delta t}$ where C_{cont} is the contribution of the enzyme in question and δt is the total change in time.
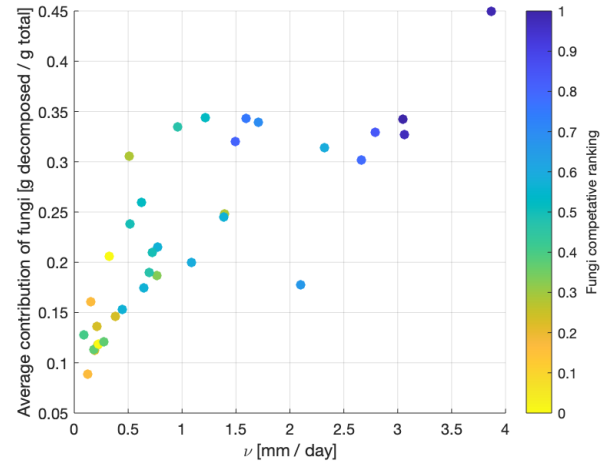

Figure 3: Average total decomposition contribution for specific fungi compared to hyphal extension rate. Coloring indicates competitive ranking coefficient.

With one set of environmental parameters, we

9

can gain insight into how different species of fungi potentially perform relative to each other, show in Figure 4.2. In addition to an expected loose positive correlation between ν and the average contribution of a given fungi, these is a lose correlation of higher fungi competitive ranking with greater ν and greater average contribution. This suggests that the fungi that are more 'active' in our model,

with the largest performance dependence on ν, are also the most competitive. Competitive ranking has a higher correlation with ν, indicating that in our model growth rate may be more sensitive to ν in competitive circumstances. This aligns with established trends of the primary 2 fungal niches [32].
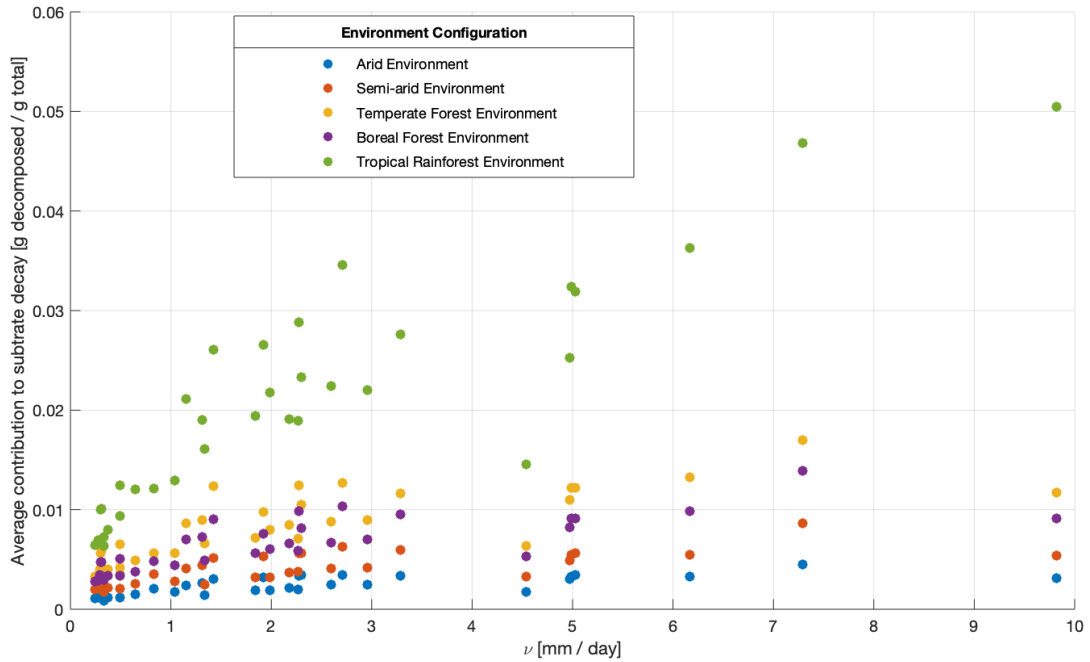

Figure 4: Average total decomposition contribution for specific fungi compared to hyphal extension rate. Coloring indicates values chosen for environmental parameters.

Results were also viewed under 5 different sets of environmental conditions (water potential and temperature), each corresponding to a different biome, shown in Figure . The results show that the correlation between ν and fungi contribution changes with environmental parameters. We find that in general, environments with a higher moisture potential lead to greater contributions overall and a greater contribution sensitivity to ν in our model. Our model agrees with the notion of water potential serving as an important limiting factor to the decomposition ability of individual fungi. These results can be interpreted as moisture po-

tential and temperature limiting the effectiveness of faster-growing fungi.

Species of fungi with a generally higher competitive advantage (corresponding to points with a higher ν and higher contribution) are much more adversely affected by changes in environmental conditions than points with a generally lower competitive advantage. These species with a higher competitive advantage would then have a smaller moisture niche width (environmental changes affect them more adversely). This relationship implies that species in this niche would have a lower moisture tolerance, compared with species of less

competitive advantage and less sensitivity to ψ.

4.3 Short-Term Environmental Fluctuations

Realistically, the external environment dictates environmental conditions of the system both in short time scales (year fluctuations for example) and long time scales. Due to the time scales of our model, the effects of very fast fluctuations (due to outside forces) on the scale of days are not considered as relative changes in the model's state have negligible changes on the order of a day. Thus we define our short term fluctuations to be roughly seasonal as this dictates the majority of local environmental variability. To study the effects of these short time scale fluctuations, we choose to implement an abstracted yearly moisture cycle, specifically that of the temperate forest environment. The cycle oscillates between the average yearly maximum and minimum values of ψ twice a year, creating a rough yearly pattern of ψ and thus ν for a given fungi from experimental data [14][32]. Note that this moisture model is limited in assuming one period oscillation between a maximum and a minimum yearly, neglecting the reality of oscillating between local minimum in summer and winter and locate maximums in fall and spring. To incorporate this into the model, ν and ψ were dynamically allocated over time based on the oscillatory behavior shown in Figure 4.3.

Due to time limitations and scarce data on the parameters over these yearly oscillations, only two species of fungi were simulated. A comparison of their respective decomposition contributions with that of similar environmental conditions but static ν and ψ is shown in Figure 4.3. There is no noteworthy new oscillatory motion seen in these results. There is also seen to be a slight increase in the effectiveness of both fungi in the oscillatory case. The interpretation of this increase can be that for time scales on the order of a year, the positives affect of increasing ν is greater than that of the negative affect of decreasing ν by the same amount.

This would lead us to believe that faster oscillations of ν will generally have a positive net impact on the decomposition. The frequency limits of this principle would require further investigation.
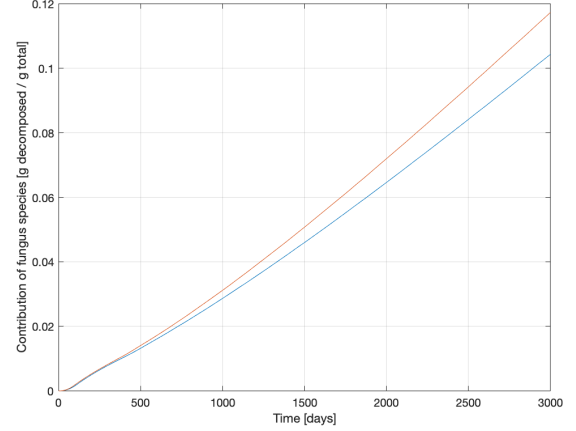
Figure 5: Contribution of two fungi species with yearly environmental fluctuations.
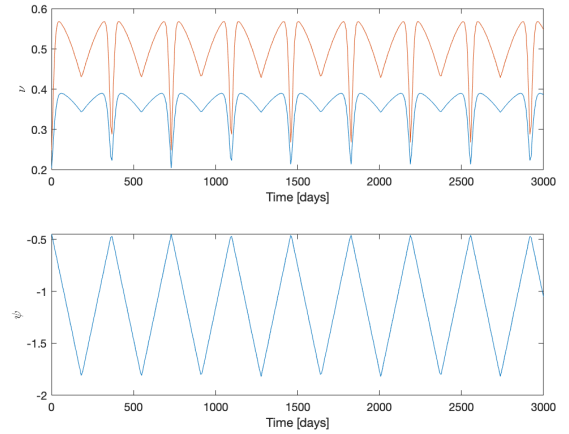

Figure 6: Environmental parameters for figure above over time.

Distribution of relative concentration of fungi

The model allows us to adjust the relative concentrations of each fungi species being simulated. In the model, this is represented with a set of $0 < c_i \leq 1$ such that $\sum c_i = 1$. Each one of these c_i multiplies the rates of hyphal density increase and

boundary/initial conditions in the growth model. With this metric, the relative concentrations of different fungi species are forced to satisfy the conditions $B_i/B_{tot} = c_i$ where B_i is the biomass of the 'i'th fungi species. This is an unrealistic constraint, as the relative concentrations of different fungal species should fluctuate with time as the different species of fungi grow at varying rates. But for the purpose of assessing the effect of biodiversity on the overall decomposition of the substraight, concentration fluctuation would add unneeded complexity to the analysis.

This analysis also considers the competitive rankings of the different fungi species [32]. The ranking-distribution coefficient, a is then defined to be

$$a = \sum_{i=1}^{n} c_i * R_i \qquad (13)$$

Where R_i s the competitive ranking for the 'i'th fungi species. The ranking-distribution coefficient can be though of as a dot-product in n-dimensional space (where n is the number of various fungi species being simulated). So a will be highest when the n-dimensional vectors "line-up" in the sense that the distribution of fungi species is closest to the distribution of competitive rankings.

To study the effects of a on the system overall, sample c values had to be chosen. Due to a lack of literature results on simple, constant fungi distributions, arbitrary Gaussian distributions spread out over the different species of fungi were chosen. Because we are mainly concerned with the relation of any given distribution to the competitive rankings, the functions can be viewed as arbitrary or random distributions (because the ordering of fungal species in our Gaussian distribution has no physical meaning). The total carbon in the subtrate over time in the model runs using these various distributions is shown in Figure 4.3.
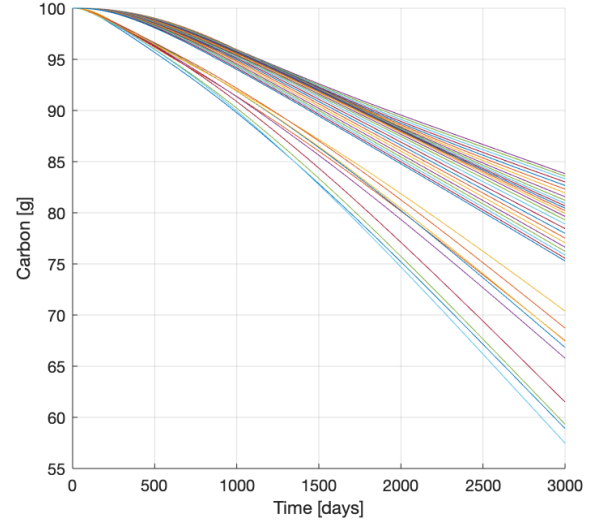

Figure 7: Total carbon in substrate for sampled fungi species distributions.

To assess the overall effectiveness of a single species distribution, the average carbon decrease over the whole interval was found via the equation $C_{avg} = \int (C_0 - C)dt/(\delta t)$ where C_0 is our initial amount of carbon and δt is the total time change over which the carbon decreases. The results of comparing this average carbon decomposed to the a value for the species distribution in question is seen in Figure . Several interesting qualitative behaviors arise from the this comparison. Firstly, there is a clear smooth trend between a and the average carbon decomposed up to approximately $a = 0.65$. At this point the smooth trend completely vanishes and the data points appear to be randomly distributed in the area. We hypothesize that this critical value of a could be representative of a bifurcation point; however further analysis on the dynamics of these coupled systems interacting would need to be done to investigate this hypothesis further. Additionally we notice that at this critical point, the average carbon decomposed tends to grow significantly. The physical interpretation of this critical point is deeply related to the effectiveness of the competitive rankings as they relate to a biologically diverse system. The results show that beyond a certain point, distributing the biodiversity more closely to the competitive rankings

12

does not have any noticeable effect on the overall effectiveness of the system.

This leads to two possibilities beyond the critical point for the system. One possibility is that optimum biodiversity is based on more complex dynamics than the competitive rankings can assess. The other possibility is that the system behaves in a chaotic or random nature beyond this critical point and no clear metric of biodiversity could be correlated to the effectiveness of a given distribution.
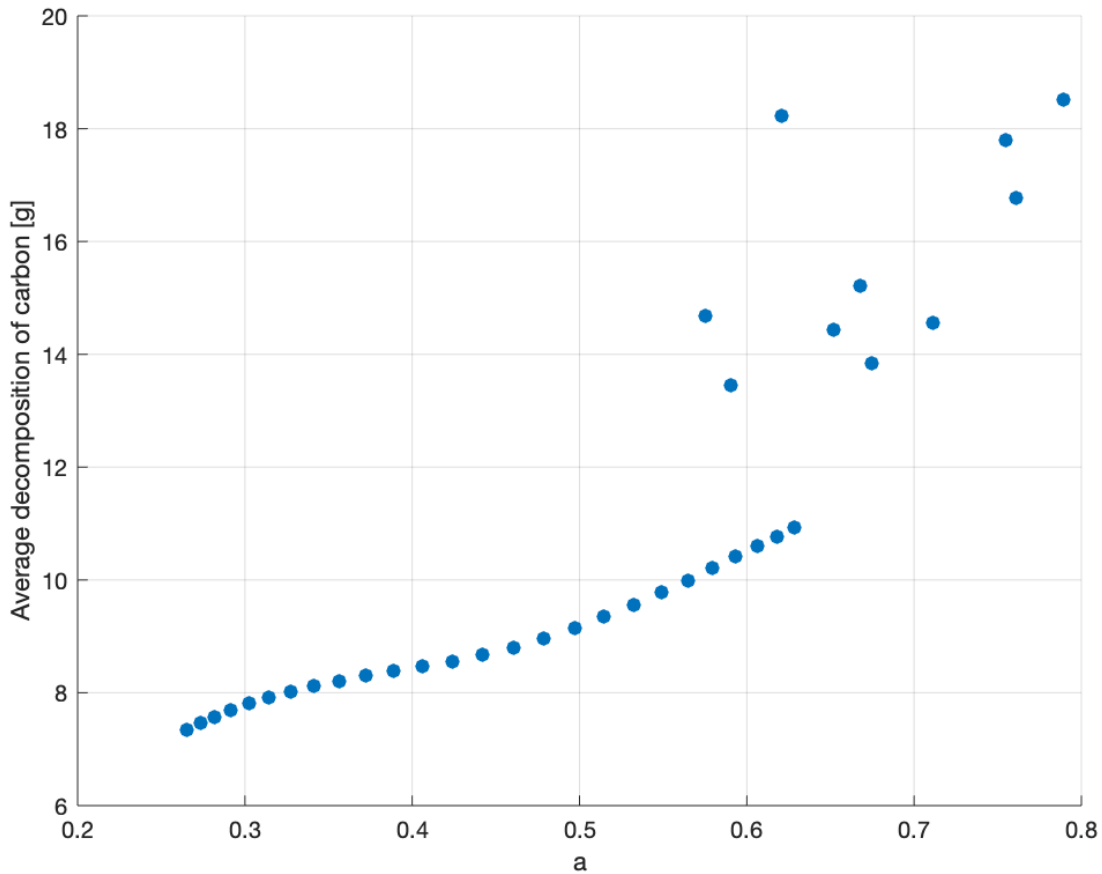

Figure 8: Average total decomposition as seen in Figure 4.3 plotted against ranking distribution coefficient for a certain species distribution.

5 Limitations

5.1 Growth Coupling

The coupling between our growth model and our decomposition kinetics model was scarsely found in literature. Instead, literature would in some cases adopt a simpler mechanism to describe fungi growth to match decomposition kinetics of equal complexity to our model, or would in other cases implement a more complex mechanism for fungi nutrient uptake while neglecting much of the complexity from interactions between fungi and with the larger environment. This resulted in a lack of applicable parameters from literature to choose from for our coupled model, for which we decided either to pull parameter values from simpler models described above or to empirically derive our parameters by fitting the model output to other reasonable outputs (as was done with the parameter G).

13

5.2 Decomposition kinetics

In our comparison of different methods for coupling the growth equation to the decomposition kinetics, there are some unrealistic disagreements between the early behavior of each growth model; mainly that of a slight increase in the first maximum biomass reached by the carbon limiting growth model. Expected behavior would exhibit less biomass gained over time when the nutrient level is limited. This result is likely a consequence of bad parameter choices derived with imperfect methods described above or a failure to incorporate a more realistic relationship between the decomposed carbon pool and available carbon pool from which the fungi supplement their own nutrient supply.

The Michaelis-Menten dynamics we implemented often considers enzyme concentration to be proportional to the maximum rate of the reaction. Taking this concentration to be proportional to total fungal biomass in some set region of space does not account for the concentration of enzymes becoming saturated as the fungi spread farther out through space. A more realistic incorporation of this idea into the model would need to address the geometric complexities involved in examining only one region of a much larger fungi growth. Even further unpackaging of these dynamics would account for fungal growth into areas that do not have physical access to the carbon being decomposed. At this point, a simplified one-dimensional growth model would not suffice.

The effect of considering biomass proportional to concentration would be seen in the longer term behavior of the model, as the fungi growth becomes limited. We may expect to see more complex dynamics transitioning between the "unbounded" fungi growth and the steady-state behavior of fungi growth. Thus, the largest area of error for our results resulting from this assumption is likely in the area of time transitioning unbounded growth and steady-state behavior.

Values for our parameter, K_e were difficult to find in the literature, as the dynamics of the four enzymes considered were not agreed upon in literature. Additionally, cellobiohydrolase was sometimes found to follow different dynamics than the Michaelis-Menten equation [26]. To obtain a more accurate value for this parameter, a study of the model's overall sensitivity to varying K_e should be conducted. A more accurate representation of fungi interactions would include a larger subset of enzymes and account for more distinctive differences in decomposition dynamics between various enzymes. But any study of alternative decomposition kinetics between enzymes was not done due to time limitations.

5.3 Direct Interactions

It was discussed in literature that there are competitive direct interactions observed between fungi growing in the same environment by various mechanisms [11]. Our model ignored the effects of these direct interactions and instead focused on indirect interactions via competition for the same nutrients source. While some effects from offensive skirmishes between fungi are typically taken to be negligible by literature other than an increase in metabolic rate, the effects from competitve fungi obstructing the growth to others due to space-limitations would likely be non-negligible. Essentially, our simulation only considered fungi competing for food, when in reality, they compete for food and space.

Further review would need to be done to assess the space-limitations inherited by environments other than open ground litter which does not pose obvious obstructions to fungi growth. This assumption of negligible spacial-limitations would not apply in the case of geometric isolation of particular fungi. Moreover, geometric access by fungi to the substraight is another complexity that would need to be addressed in a higher-dimensional growth model.

5.4 Environmental Fluctuations

The environmental conditions were analyzed for short term and long term fluctuation (short term being yearly cycles and long term being overall biome transitions over time). Our analysis found that oscillating environmental conditions showed slightly improved decomposition rates for two species of fungi, but additional studies involving a more diverse subset of species of fungi that might reveal niche complementarity were not studied due to time limitations.

In this analysis, only the effects from varying ψ were studied. Realistic environmental fluctuations would see both T and ψ fluctuating simultaneously, but for the purpose of studying the general effect of oscillating environmental conditions, this can be taken as a representative result. Future studies of the model's response to fluctuating environmental conditions could include a study of the system's response to a continuum of frequencies for environmental fluctuations, as well as studying the effects of fluctuating multiple environmental conditions simultaneously.

The correlations found between distributions of fungi species and overall performance of the system in the static environmental conditions of the Arid climate biome is poorly understood and would require further investigation or numerical fitting to be studied in more detail. The change occurring at the critical point may also be a result of numerical error in approximate solution to the differential equations being solved (although there is no other indication that this is the case). Further analysis of this correlation could include assessment of this correlation in different biomes and in oscillating environmental conditions.

6 Conclusion

Advantages of certain species were taken into account via their relative concentrations of different enzymes as well as in their dependence of ν on temperature and moisture. These advantages were found to have a positive correlation with the contribution of different species to the overall decomposition. However, this exact relationship is unclear from the data. The competitive ranking of different fungi species was found to correlate to a higher sensitivity on ν in relation to the species' contribution to decomposition. Distributions according to these rankings in our model were found to positively impact overall system performance up to a critical point, where the trend dissolves completely. The presence of short term environmental fluctuations were found to have a slight positive impact on performance for a small sample of fungi species simulated. Long term environmental fluctuations, in the form of transforming overall biomes, indicates that overall fungi decomposition productivity should generally decrease as more arid conditions with less available moisture are approached.

The dynamics of different biodiversity distributions is complex, resulting in limited scope of certain descriptive values, such as competitive ranking, in capturing the full efficiency of the system. For a given species, an increase in hyphal extensional rate corresponds to different relative increases in efficiency based on environmental conditions as well as the species' sensitivity to those conditions. Generally, increasing ν has a greater affect for species with a lower moisture tolerance in an optimal environment and a lesser affect for species with a lower moisture tolerance in a suboptimal environment. Additionally, the results would imply that species with a lower moisture tolerance would perform significantly worse under long term fluctuations compared with species of a higher moisture tolerance, which would perform only slightly worse. The effect of short term fluctuations on species with a lower moisture tolerance would require further study to discern.

A   Model Parameters

Here are the model parameters for the coupled growth and decomposition model for Armillaria gallica located at 30.465247 degrees latitude and -89.040298 degree longitude secreting cellobiohydrolase (Cel7A) to decompose hardwood holocellulose [23, 32]:

Parameter	Symbol	Value	Units	Source and Specification
Half-Saturation constant [3]	K_e	7	$\frac{g_{enzyme}}{L_{litter}}$	[23] Enzyme
Holocellulose carbon [4]	$1 - LCI$[5]	0.709	N/A	[24]
Hyphal tip elongation rate	ν	0.250	$\frac{mm}{day}$	[32] Species, ψ, T
Temperature	T	25	$°C$	[32] Specie's habitat
Water potential	ψ	-0.5	MPa	[32]
Enzyme biomass ratio [6]	r	0.437	$\frac{g}{g}$	[32] Species
Hyphal death rate	γ_1	0.15	day^{-1}	[19]
Anastomosis coefficent	μ	0.3	$\frac{mm}{day}$	[27]
Branching rate	α_1	1.2372	day^{-1}	[30]
Intercept of S_M function [7]	α_2	0.311	N/A	[7]
Slope of S_M function	λ	0.345	N/A	[7]
Soil moisture coefficient	S_M	0.4149	N/A	[7] ψ
Soil temperature coefficient	S_T	1	N/A	[7] T
Rate of Increase	Q	2.5	$°C$	[7] T
Rate constant [8]	G	10	$g * mm^{-1} * day{-1}$	[36][9]

Table 3: Model Parameters

B   Appendix Tables

Biome/ Environment	Average Annual Temperature [$°C$]	Selected Value [$°C$]
Dessert (Arid)	10 to 20 [**Davey2007**]	15
Grasslands/shrublands (Semi-Arid)	15.3 [8]	15.3
Temperate Forest	-1.42 to 26.39 [35]	12.49
Boreal Forest (Arboreal)	-1.42 to 26.39 [35]	12.49
Tropical Rain Forest	23 to 32 [33]	27.5

Table 4: Environment Temperature Data

---

[3]Also called Michaelis Constant.

[4]We assume that all carbon compounds excluding lignin are holocellulose.

[5]Where LCI is the lignocellulose index.

[6]Proportion of specific enzyme biomass to total enzyme biomass.

[7]The intercept of soil moisture effect on decay rate.

[8]Proportionality constant between maximum rate of decomposition and enzyme biomass.

[9]Emprically derived.

Biome/ Environment	Water Potential Range [MPa]	Selected Value [MPa]
Dessert (Arid)	-4.0 to -5.0 MPa [6]	-4.5 MPa
Grasslands/shrublands (Semi-Arid)	-1.4 to -5.0 [10] [8]	-3.2 MPa
Temperate Forest	-0.44 (Fall), -1.19 (Winter), -0.58 (Spring), -1.42 (Early Summer), -1.81 (Summer) [14]	-1.09 MPa
Boreal Forest (Arboreal)	-0.83 (Fall), -1.20 (Winter), -0.55 (Spring), -1.61 (Early Summer), -3.36 (Summer) [14]	-1.51 MPa
Tropical Rain Forest	-1.57 MPa to 0.00 MPa [31]	-0.79

Table 5: Environment Water Potential Data

Parameter	Symbol	Value	Units	Source and Specification
Half-Saturation constants [11]	K_e	-	mM	Enzyme
K_e - Phenol oxidase		0.89	mM	[22]
K_e - Phosphatase		0.94	mM	[21]
K_e - Peroxidase		0.7475	mM	[1]
K_e - Cellobiohydrolase		13.90	mM	[26]
Hyphal tip elongation rate	$v(T, \psi)$	Various	$\frac{mm}{day}$	[32] Species, ψ, T
Soil moisture coefficient	S_M	$S_M = \alpha_2 - \lambda \log_{10}(-\psi)$	N/A	[7] ψ
Soil temperature coefficient	S_T	$\log_{10}(S_T) = \frac{T-25}{10} \log_{10}(Q)$	N/A	[7] T

Table 6: Environmental & Parameter Table
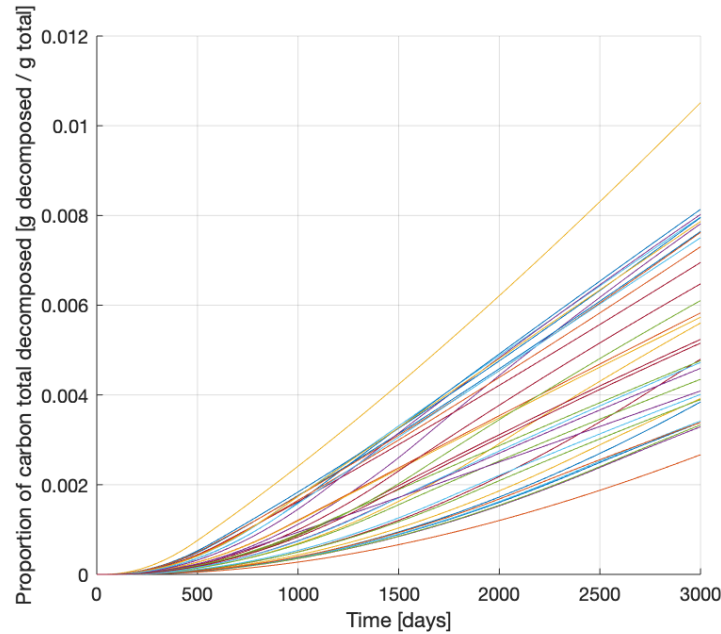
C Appendix Figures

Figure 9: Decomposition contribution of 35 simulated fungi in static arid environmental conditions.

[10]Measurements taken November through January at 100 cm soil depth.
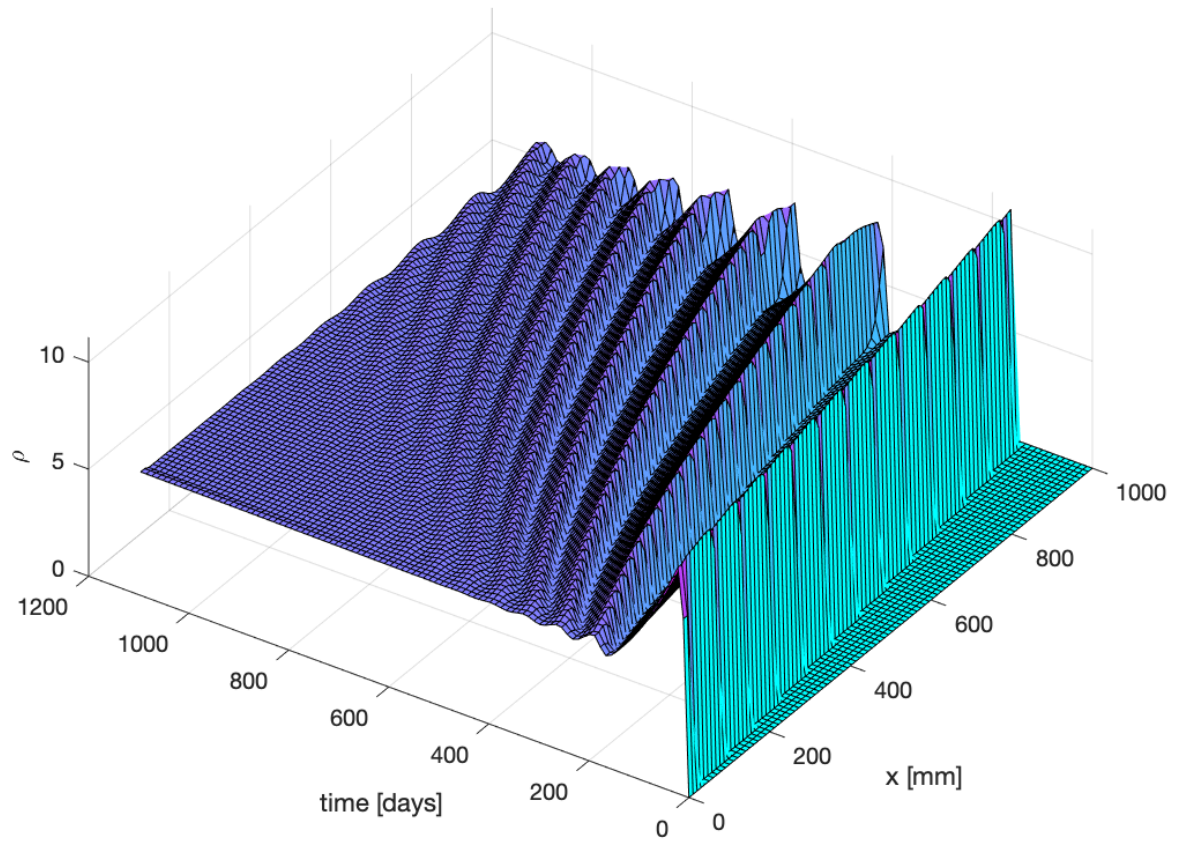[11]Also called Michaelis Constant.

Figure 10: Hyphal density in time and space for non carbon-limited growth model.

References

[1] B. Chance, *Journal of Biological Chemistry* **1943**, *151*, 553–577.

[2] R. Whittaker, *Communities and ecosystems*, Macmillan, **1970**.

[3] H. Parnas, *Soil Biology and Biochemistry* **1975**, *7*, 161–169.

[4] L. Edelstein, *Journal of Theoretical Biology* **1982**, *98*, 679–701.

[5] L. Edelstein, L. Segel, *Journal of Theoretical Biology* **1983**, *104*, 187–210.

[6] E. T. Nilsen, M. R. Sharifi, P. W. Rundel, W. M. Jarrell, R. A. Virginia, *Ecology* **1983**, *64*, 1381–1393.

[7] D. L. Moorhead, J. F. Reynolds, *Ecological Modelling* **1991**, *56*, 197–219.

[8] D. Peláez, R. Distel, R. Bóo, O. Elia, M. Mayor, *Journal of Arid Environments* **1994**, *27*, 71–78.

[9] O. AndreÂna, J. Balandreaub in, **1999**.

[10] P. Gervais, C. Abadie, P. Molin, *Journal of Scientific & Industrial Research* **1999**, *58*, 671–677.

[11] L. Boddy, *FEMS Microbiology Ecology* **2000**, *31*, 185–194.

[12] M. Mimura, H. Sakaguchi, M. Matsushita, *Physica A: Statistical Mechanics and its Applications* **2000**, *282*, 283–303.

[13] D. L. Moorhead, R. L. Sinsabaugh, *Applied Soil Ecology* **2000**, *14*, 71–79.

[14] D. B. Zobel, S. C. Garkoti, S. P. Singh, A. Tewari, C. M. S. Negi, *Current Science* **2001**, *80*, 774–779.

[15] J. P. Schimel, M. N. Weintraub, *Soil Biology and Biochemistry* **2003**, *35*, 549–563.

[16] D. L. Moorhead, R. L. Sinsabaugh, *Ecological Monographs* **2006**, *76*, 151–174.

[17] Y. Toljander, B. Lindahl, L. Holmer, N. Högberg, *Oecologia* **2006**, *148*, 625–31.

[18] G. Steinberg, *Eukaryotic Cell* **2007**, *6*, 351–360.

[19] A. Schnepf, T. Roose, P. Schweiger, *Journal of The Royal Society Interface* **2008**, *5*, 773–784.

[20] K. L. McGuire, K. K. Treseder, *Soil Biology and Biochemistry* **2010**, *42*, 529–535.

[21] P. Nannipieri, L. Giagnoni, L. Landi, G. Renella in, **2011**, pp. 215–243.

[22] E. A. Davidson, S. Samanta, S. S. Caramori, K. Savage, *Global Change Biology* **2012**, *18*, 371–384.

[23] J. Kari, J. Olsen, K. Borch, N. Cruys-Bagger, K. Jensen, P. Westh, *The Journal of biological chemistry* **2014**, *289*, 32459–32468.

[24] F. Segato, A. R. L. Damásio, R. C. de Lucas, F. M. Squina, R. A. Prade, *Microbiology and Molecular Biology Reviews* **2014**, *78*, 588–613.

[25] J. A. M. Moore, J. Jiang, W. M. Post, A. T. Classen, *Ecosphere* **2015**, *6*, art29.

[26] B. S. Razavi, E. Blagodatskaya, Y. Kuzyakov, *Frontiers in microbiology* **2015**, *6*, 1126–1126.

[27] X. Lin, G. Terejanu, S. Shrestha, S. Banerjee, A. Chanda, *Journal of Theoretical Biology* **2016**, *398*, 85–95.

[28] L. Mucina, *Biome: evolution of a crucial ecological and biogeographical concept*, New Phytologist, **2018**.

[29] F. Z. Abkenar, A. Rasoulzadeh, A. Asghari, *Bragantia* **2019**, *78*, 119–130.

[30] H. Du, T.-B.-T. Tran, P. Perré, *Journal of Theoretical Biology* **2019**, *470*, 90–100.

[31] S. J. Kupers, B. M. J. Engelbrecht, A. Hernández, S. J. Wright, C. Wirth, N. Rüger, *Journal of Ecology* **2019**, *107*, 860–874.

[32] D. S. Maynard, M. A. Bradford, K. R. Covey, D. Lindner, J. Glaeser, D. A. Talbert, P. J. Tinker, D. M. Walker, T. W. Crowther, *Nature Microbiology* **2019**, *4*, 846–853.

[33] S. Paton, Barro Colorado Island, ClearingTemperature, manual, **2019**.

[34] A. Petraglia, C. Cacciatori, S. Chelli, G. Fenu, G. Calderisi, D. Gargano, T. Abeli, S. Orsenigo, M. Carbognani, *Plant and Soil* **2019**, *435*, 187–200.

[35] S. N. Zaz, S. A. Romshoo, R. T. Krishnamoorthy, Y. Viswanadhapalli, *Atmospheric Chemistry and Physics* **2019**, *19*, 15–37.

[36] N. Lustenhouwer, D. S. Maynard, M. A. Bradford, D. L. Lindner, B. Oberle, A. E. Zanne, T. W. Crowther, *Proceedings of the National Academy of Sciences* **2020**, *117*, 11551–11558.