

1 Environmental Impacts

1.1 Environment and Moisture Tolerance

Moisture tolerance, as the difference between competitive ranking and moisture niche width for a given fungus, takes into account the response of specific fungi to its environment. Since it is more of an established response trait rather than a dynamic response, value will not be varied based on environmental conditions, but rather used for analysis of the interactions between species.

1.2 Environmental Influence on Hyphal Tip Extension (ν)

Environmental impacts are introduced to the decomposition model through ν , the hyphal tip elongation rate. This elongation occurs at tip of the hyphae via vesicles known as Spitzenkorper, but the mechanism of this extension remains 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" [?]. In fungi, cell turgor itself is respondent to water potential gradients rather than to active transport within the cell, making it very environmentally dependent [?]. Thus, we have reason to examine environmental impacts on fungal decomposition rates by varying ν outside of baselines for given species in set locations.

This brings us to the issue of determining ν based on environmental factors. Experimental data from Maynard et al. 2019 shows the relationship between ν and the environmental parameters of water potential (ψ) and temperature (T) [?]. Water potential as a parameter will take into account both moisture content to fungi as well as the availability of that moisture as dictated by the soil composition.

1.3 Estimating ν 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 ν , this requires finding projected temperature and water potential.

Amongst existing biome classification models, Whitaker's scheme [?] is perhaps the simplest, being particularly trait-based. Whitaker's scheme provides 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 [?]. 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 °C) [?]. Thus, we can sample a range of temperature and moisture values

to output various ν 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

Although water potentials can be approximated based on predictive models, the measure is best found experimentally from soil samples [?]. Ranges for moisture potential of these environments have been found experimentally from a variety of studies is shown in the following table. Note that single water potentials and temperatures are selected for sampling, as we are aiming to compare discrete environmental conditions rather than create a complete span of environmental conditions. The following are the selected values of average annual temperatures and water potential for these biomes. If ranges are given, the average of the ranges or seasonal values is the selected value. For full ranges and data sources, see appendix TABLE ???.

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

Given these estimates, we can have a probable example combination of temperature and moisture potential in various environments. 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 ν using experimental data from Maynard et al 2019. **** (talk about continuous data technique thingy in the extra methods info sheet)

1.4 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):

$$\log_{10}(S_T) = \frac{T - 25}{10} \log_{10}(Q) \quad (1)$$

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 [?]. 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 [?].

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

$$S_M = \alpha_2 - \lambda \log_{10}(-\psi) \quad (2)$$

These two parameters help calculate the maximum growth rate by the relationship:

$$\beta = S_T S_M r \quad (3)$$

where r is the enzyme biomass ratio.

2 Niche Differentiation and Biodiversity

Although natural fungal niches are disperse, two distinct general categories of niches emerge from wide evidence: that of a more competitive and faster growing fungus and that of a slower, more resilient group. The 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, the underlying negatively proportional relationship of the general data set is indicated. This idea trade-off between competitive ranking and moisture niche width is aligned with the prevailing niche distinction to pursue opportunism or stability.

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 [?].

Decomposition of organic materials is essential to the continuation of carbon cycling, releasing carbon into the soil and atmosphere [?]. A system containing this niche configuration of fungal species that could potentially benefit two-fold. Stable slow-growing populations could serve as a basis for long-term fungal action, while the opportunist-leaning fungi could prove beneficial in continuing the fungal role in the face of a dynamic environment.

3 Analysis

3.1 Total Carbon vs Time for Specific Environments

A sampling of different environmental parameters within the model was taken as described in section X****. The results of these model runs were taken in terms of the total grams of carbon over time. Here, we see more moist soil environments lead to clearly more expedient rates of total carbon decrease and reach complete carbon 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.

3.2 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 substrate. 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.

With one set of environmental parameters, we can gain insight into how different species of fungi potentially perform relative to each other, shown in figure. In addition to an expected loose positive correlation between ν and the average contribution of a given fungi, there is a loose 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 [?].

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

3.3 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 [?][?]. 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 local 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 oscillating-psi-nu). 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 oscillating2nonoscillating-psi-contribution). There is no note-worthy 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.

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 [?]. The ranking-distribution coefficient, a is then defined to be

$$a = \sum_{i=1}^n c_i * R_i \quad (4)$$

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 results of model runs using these various distributions is shown in (figure carbon-decrease-fungi-distribution). 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 a-competative-distribution-coef-to-avg-Clost). 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 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.

4 Model Parameters

Here are the model parameters for the coupled decomposition and growth model for *Armillaria gallica* located at 30.465247 degrees latitude and -89.040298 degree longitude secreting cellobiohydrolase to decompose hardwood holocellulose [?] [?]:

Parameter	Symbol	Value	Units	Source and Specification
Half-Saturation constant ¹	K_e	7	$\frac{g_{enzyme}}{L_{litter}}$	[?] Enzyme
Holocellulose carbon ²	$1 - LCI^3$	0.709	N/A	[?]
Hyphal tip elongation rate	ν	0.250	$\frac{mm}{day}$	[?] Species, ψ , T
Temperature	T	25	$^{\circ}C$	[?] Specie's habitat
Water potential	ψ	-0.5	MPa	[?]
Enzyme biomass ratio ⁴	r	0.437	$\frac{g}{g}$	[?] Species
Hyphal death rate	γ_1	0.15	day^{-1}	[?]
Anastomosis coefficient	μ	0.3	$\frac{mm}{day}$	[?]
Branching rate	α_1	1.2372	day^{-1}	[?]
Intercept of S_M function ⁵	α_2	0.311	N/A	[?]
Slope of S_M function	λ	0.345	N/A	[?]
Soil moisture coefficient	S_M	0.4149	N/A	[?] ψ
Soil temperature coefficient	S_T	1	N/A	[?] T
Rate of Increase	Q	2.5	$^{\circ}C$	[?] T
Rate constant ⁶	G	10	$g * mm^{-1} * day^{-1}$	[?] ⁷

5 Appendix Tables

Environment Temperature Data:

Biome/ Environment	Average Annual Temperature [$^{\circ}C$]	Selected Value [$^{\circ}C$]
Dessert (Arid)	10 to 20 [?]	15
Grasslands/shrublands (Semi-Arid)	15.3 [?]	15.3
Temperate Forest	-1.42 to 26.39 [?]	12.49
Boreal Forest (Arboreal)	-1.42 to 26.39 [?]	12.49
Tropical Rain Forest	23 to 32 [?]	27.5

Environment Water Potential Data:

¹Also called Michaelis Constant.

²We assume that all carbon compounds excluding lignin are holocellulose.

³Where LCI is the lignocellulose index.

⁴Proportion of specific enzyme biomass to total enzyme biomass.

⁵The intercept of soil moisture effect on decay rate.

⁶Proportionality constant between maximum rate of decomposition and enzyme biomass.

⁷Emprically derived.

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

Environmental Parameter Table:

Parameter	Symbol	Value	Units	Source and Specification
Half-Saturation constants ⁹	K_e	-	mM	Enzyme
	K_e - Phenol oxidase	0.89	mM	[?]
	K_e - Phosphatase	0.94	mM	[?]
	K_e - Peroxidase	0.7475	mM	[?]
	K_e - Cellobiohydrolase	13.90	mM	[?]
Hyphal tip elongation rate	$\nu(T, \psi)$	Various	$\frac{mm}{day}$	[?] Species, ψ , T
Soil moisture coefficient	S_M	$S_M = \alpha_2 - \lambda \log_{10}(-\psi)$	N/A	[?] ψ
Soil temperature coefficient	S_T	$\log_{10}(S_T) = \frac{T-25}{10} \log_{10}(Q)$	N/A	[?] T

⁸Measurements taken November through January at 100 cm soil depth.

⁹Also called Michaelis Constant.