MCM 2021 (Madison's Workspace/ Writing)

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):

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

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:

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

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

$$\beta = S_T S_M r \tag{3}$$

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 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 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. Aside from indicating an expected positive correlation between ν and contribution, 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. This corroborates with various findings, that find soil moisture as a particularly influential environmental factor, influencing elongation through pressure gradients and testing of tolerance [**?**] [**?**].

3.2 Total Carbon vs Time for Specific Environments

Similarly, a sampling of different environmental parameters within the decomposition model demonstrates the decrease of total carbon in a fungal-waste system over time. Here, we see more moist soil environments lead to clearly more expedient rates of carbon total carbon decrease and reach total decomposition quicker in our model. Again in the model, the rain forest environment exceeds the other environmental profiles, effectively completing decomposition in under 1640 days (roughly 4.5 years.

3.3 Average Contribution vs ν with Competitive Rankings

With one set of environmental parameters, we can gain insight into how different species of fungi potentially interact relative to each other. In addition to an expected lose 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 growth rates and proportions, are also the most competitive. Competitive ranking has a higher correlation with $/nu$, indicating that in our model growth rate may be more significant than proportion when it comes to competitive circumstances. This aligns with established trends of the primary 2 fungal niches [**?**].

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 (Cel7A) 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 coefficent	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:

[1] Also called Michaelis Constant.
[2] We assume that all carbon compounds excluding lignin are holocellulose.
[3] Where LCI is the lignocellulose index.
[4] Proportion of specific enzyme biomass to total enzyme biomass.
[5] The intercept of soil moisture effect on decay rate.
[6] Proportionality constant between maximum rate of decomposition and enzyme biomass.
[7] Emprically 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

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