

Competition, Adaptation and Biodiversity: How Fungi Support Our Biosphere

Fungi are prominent components of terrestrial ecosystems in terms of biomass and diversity, and they influence almost every aspect of terrestrial ecosystem functioning. They are the dominant decomposers of organic plant material, with direct consequences for global carbon and nutrient dynamics [9].

In this literature, based on the experimental results of fungi traits provided by Daniel S. Maynard et al., and that of fungi decomposition rate provided by Nicky Lustenhouwer et al., we discussed the decay ability of fungi community, and how environmental conditions affect it. The problem is separated into 4 parts.

Firstly, we construct the model describing the relation between the decomposition rate and hyphal extension rate, moisture tolerance for fungi isolate with straightforward linear regression fitting. The decay ability of a fungi community with respect to the community-weighted extension rate is also specified.

Secondly, we extend the traditional **Lotka-Volterra model** to multispecific case, and further adapted the equation for the fungi community incorporating hyphal extension rate and moisture tolerance.

Thirdly, we introduced **Markov chain** model to interspecific competitive biological configuration, and inferred the homeostasis of the fungi community. The attempt of applying a time discrete, state status discrete model to a continuous circumstance is bold and novel.

Finally, we build the model describing how environmental conditions affect the fungi community, and specified the relation between the range of variation of moisture in the local environment and fungi hyphal extension rate.

The models are combined together to form an intact solution for predicting the decay ability of a fungi community. Based on this, we discovered that certain combinations of fungi species can persist in corresponding climatic conditions stably, and may boost the decay ability compared with community merely consists of more combative fungi and with less biodiversity. As the environmental conditions changes, the fungi community may be affected intensively in short term, but in the perspective of long term, the fungi community will reach new homeostasis depends on the environmental conditions. In addition to this, larger biodiversity also means the community is more robust against the variability in the local environment.

Keywords: fungi, interspecific competition, biological degradation, biodiversity

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1 Introduction

1.1 Problem Background

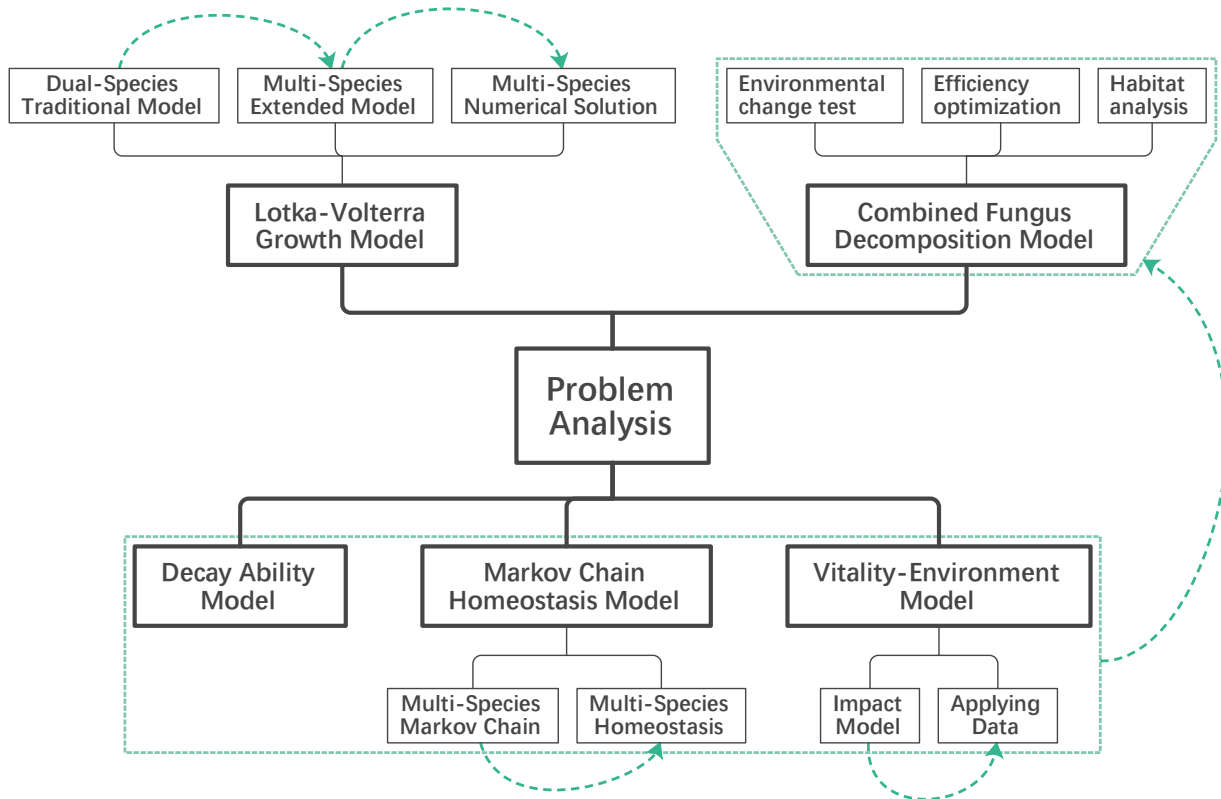
The carbon cycle describes the process of the exchange of carbon throughout the geochemical cycle of the Earth, and is a vital component for life on the planet. One key component of this part of the process is the decomposition of plant material and woody fibers. Some of the key agents in decomposing woody fibers are fungi. This problem requires the model for the the decomposition ability of fungi community.

1.2 Problem Restatement

- Describes the breakdown of ground litter and woody fibers through fungal activity in the presence of multiple species of fungi.
- Incorporate the interactions between different species of fungi, which have different growth rates and different moisture tolerances.
- Analyze model and describe the interactions between the different types of fungi, for both short and long term trends.
- Examine the sensitivity to rapid fluctuations in the environment and determine the overall impact of changing atmospheric trends.
- Include predictions about the relative advantages and disadvantages for each species and combinations of species likely to persist, and do so for different environments including arid, semi-arid, temperate, arboreal, and tropical rain forests.
- Describe how the biodiversity impacts the overall efficiency with respect to the breakdown of ground litter. Predict the importance and role of biodiversity in the presence of different degrees of variability in the local environment.

1.3 Our Work

We separated the problem into several parts, do modeling, the combined them together as shown in figure 1.

Figure 1: Work flow of our modelling

2 Basic Assumptions and Notations

Our model is based on several approximate but reasonable assumptions. For a certain ecological configuration in restricted region, such as the decomposition process of a log dominated by fungus, it is equivalent for considering the quantity of fungus individual, biomass or population density. Therefore, our modeling is based on the population density of each species of fungus.

Since our modeling is composed of several different parts, other necessary assumptions may be found in their own sections.

Assumption 1. The vital activity of fungus community, that is, the product of metabolization, has no effect on the environment humidity and temperature.

Justification In nature circumstances, the decomposition process happens in open air, the heat and moisture produced or absorbed by fungus can be promptly carried off or replenished by the external environment, hence the local environment dominates the conditions of the growth of fungus community.

Assumption 2. The decomposition is dominated by the fungus community, and no other species

have effect on the system.

Assumption 3. The inter-species relation among the populations in the community is merely competition.

Justification Other inter-species relations such as mutualism, parasitism and predation are rarely seen among fungus. Considering only competition enables us to utilize existed models.

Table 1: Notations and definitions

Symbol	Definition
n	Total number of fungus populations in the community
x	(Relative) Biomass of the fungi isolate
D	Decomposition rate
r	Hyphal extension rate
d	Moisture niche width
c	Competitive ranking
m	Moisture tolerance
w	Environmental moisture varying range

3 Decomposition Rate with Respect to Dominant Fungi Traits

In this problem, the **hyphal extension rate** and **moisture tolerance** are the two basic dominating traits we need to consider in modeling the decay ability of the fungi community.

3.1 Decomposition rate model regarding hyphal extension rate, moisture tolerance and competitive ranking

From Figure 3 and Figure 4, it is observed that the relation between the decomposition rate and hyphal extension rate, as well as between the log transformed decomposition rate and relative moisture tolerance are approximately linear.

$$\begin{cases} D = k_1 r + b_1 \\ \ln D = k_2 m + b_2 \end{cases} \quad (3.1)$$

Note that, in 4, the x -axis variable is not exactly the moisture tolerance (moisture niche width), instead is the difference of each isolate's competitive ranking and their moisture niche width, in

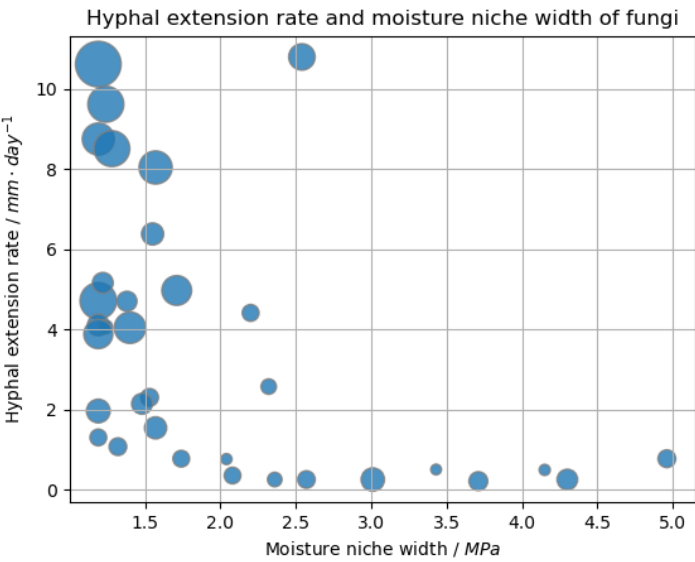


Figure 2: Hyphal extension rate and moisture niche width of the fungi, size of the bubble represents he decomposition rate of logs after 122 days of decay

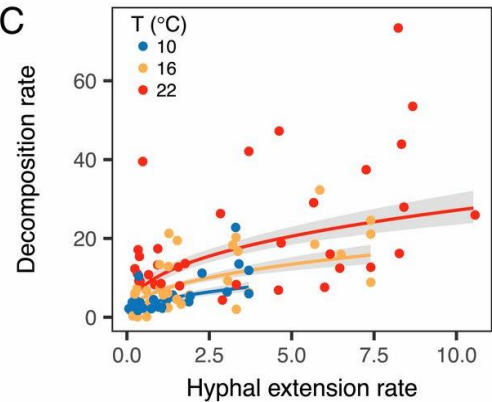


Figure 3: The relationship between the hyphal ex-
tension rate (mm/day) of various fungi and the re-
sulting wood decomposition rate (% mass loss over
122 days) at various temperatures. This figure is
adopted from [8].

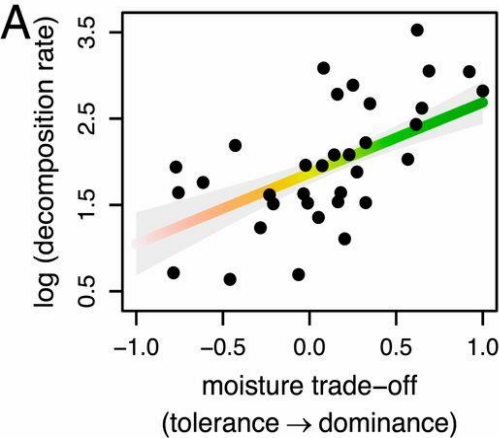


Figure 4: The relationship between the moisture
tolerance (difference of each isolate's competi-
tive ranking and their moisture niche width, both
scaled to [0,1]) of various fungi and the resulting
wood decomposition rate (% mass loss over 122
days, log transformed). This figure is adopted
from [8].

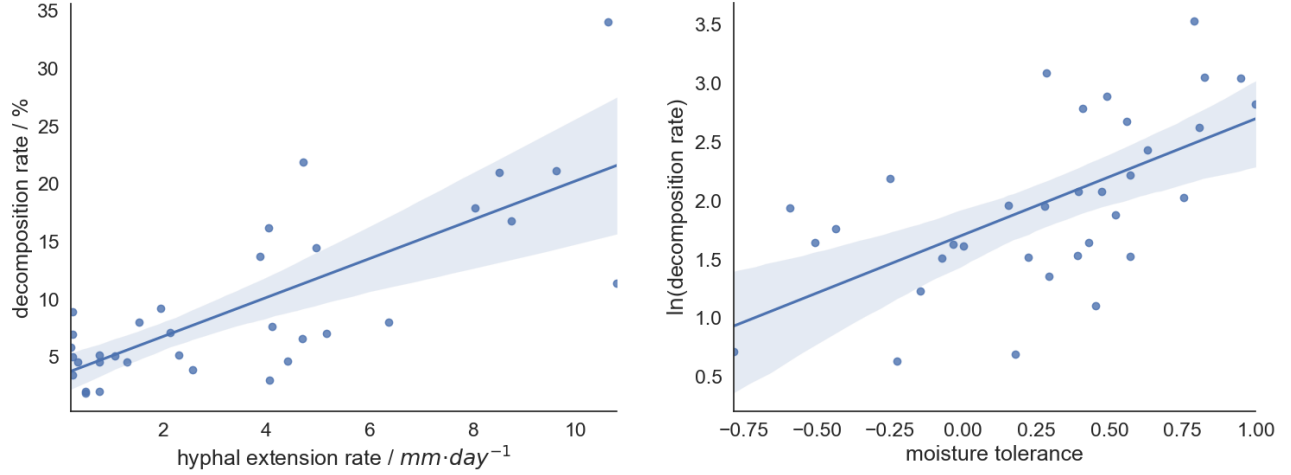


Figure 5: The relationship between the hyphal extension rate of various fungi and the resulting wood decomposition rate. The hyphal extension is commonly found in the competition behavior of rate is the geometrical average of the value tested fungi. [9] under 10, 16 and 22 Celsius in [8].

Figure 6: The relationship between the moisture tolerance and the resulting wood decomposition rate. The tolerance-dominance trade-off rate is the geometrical average of the value tested fungi. [9] under 10, 16 and 22 Celsius in [8].

Table 2: The fitted parameters for the decay ability of an isolate over a short period

k_1	b_1	k_2	b_2
1.6850	3.4082	0.5831	0.4896

range $[-1, 1]$. Hence in the model, competitive ranking c is taken into consideration. According to [9], the moisture niche width is normalized as

$$\hat{d}_i = \frac{d_i - d_{\min}}{d_{\max}}. \quad (3.2)$$

3.2 Decomposition rate data fitting for single fungus isolate

Based on the traits data of various species of fungus provided in [9], and the resulting experimental decomposition rate in [8], the fitting result is shown in table 2 and figure 1 and 6.

3.3 Extending the model to multi-species system

For multi-species case, according to 7, the decomposition of logs increases with the hyphal extension rate of the community, and is approximately characterized by a linear model with respect to the community-weighted mean extension rate. Therefore, in order to describe the decay ability of a community consists of multiple species of fungus, the relative quantity relation between of each isolate in the community is necessary.

The decay ability of a fungi community can be described quantitatively as the following expres-

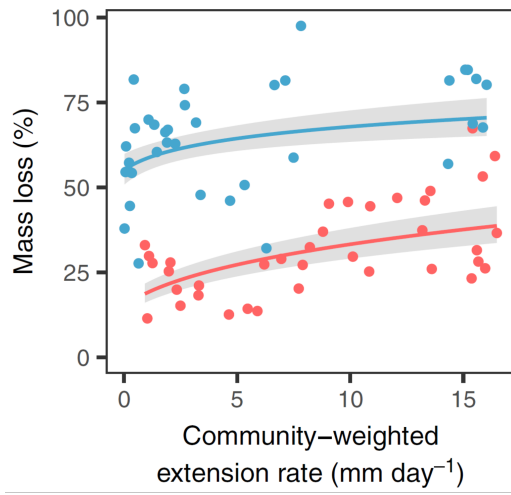


Figure 7: The decomposition of logs increases with the hyphal extension rate of the fungal community that colonized them. This figure is adopted from [8].

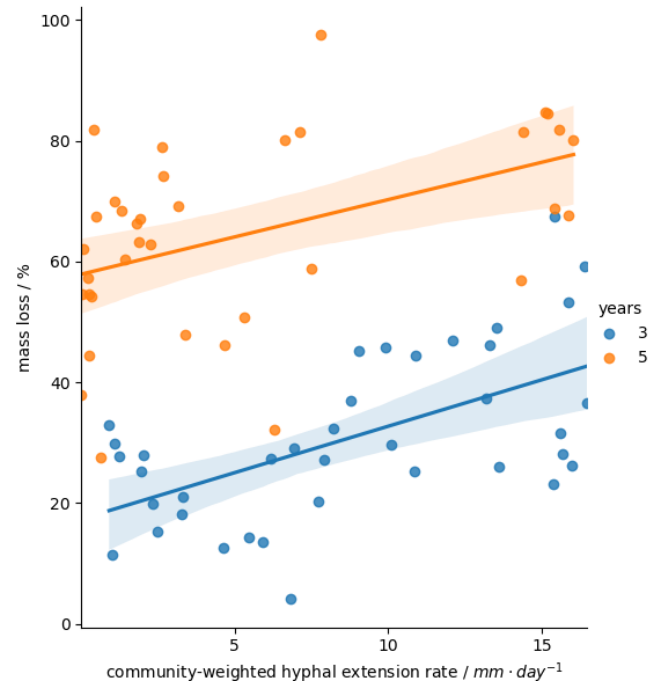


Figure 8: The mass loss rate increases with the community-weighted hyphal extension rate. The experiments are conducted on a variety of wood substrates for 3 or 5 years.

Table 3: The fitted parameters for the decay ability of a community over a long period

Years	k_3	b_3
3	1.539	17.32
5	1.237	57.87

sion.

$$D_{\text{comm}} = k_3 \bar{r} + b_3 = k_3 \frac{r_1 x_1 + \cdots + r_n x_n}{x_1 + \cdots + x_n} + b_3 = k_3 \frac{\sum_{i=1}^n r_i x_i}{\sum_{i=1}^n x_i} + b_3. \quad (3.3)$$

Research conducted in [8] presents the data obtained from experimental results on various wood substrate for 3 years or 5 years. With the data presented in [9], the coefficient is roughly determined as in 3, and the result is shown in figure 8.

For solving this model for practical prediction of the decay ability of fungi community, each x_i needs to be specified. This part is discussed in the following sections.

4 Competition Model of the Growth of Fungi Community

4.1 Traditional Lotka-Volterra model for dual-species system

In the early twentieth century, Alfred Lotka and Vito Volterra simultaneously derived a model that described how competition affects population growth from the perspective of differential equations, which is now known as the Lotka-Volterra, or LV model. [1]

First, for single population, if the resources are sufficient enough, the population size, or similarly, density, is expected to grow in the form of

$$\frac{dx_1}{dt} = r_1 x_1. \quad (4.1)$$

In which, the intrinsic rate of increase r is the per capita growth rate that could potentially be realized by a fungus population. However, unlimited growth is impossible in reality, environment itself has retardant effect on the population. Take the bounded carrying capacity into consideration, obtains

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1} \right). \quad (4.2)$$

The extra term places a limit on exponential growth, and the resulting equation represents the logistic growth.

In a dual-species system, the resistance against the growth of one population comes not only from the environment, but also another specie. It is natural that, when specie 2 has larger population density, specie 1 will be in face of larger competitive pressure, and similar for species 2. Such notion

is also capable for intra-specie competition. Combining the inter-species and intr-specie competition into (4.2), obtains the differential equations set

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{\alpha_{11}x_1 + \alpha_{12}x_2}{K_1} \right) \\ \frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{\alpha_{22}x_2 + \alpha_{21}x_1}{K_2} \right) \end{cases} \quad (4.3)$$

Which is the model for dual-species competition. Note that, neither Lotka nor Volterra explained this equation from the perspective of ecology, it is Tilman who made a convincing interpretation. His resource-based model included resources requirement, consumption and supply, which is concise and rigorous but not the topic of this literature. [13]

4.2 Extended Lotka-Volterra model for multi-species

Based on LV model, we extended (4.3) to a multi-species system with n various populations.

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{\sum_{j=1}^n \alpha_{1j} x_j}{K_1} \right) \\ \dots \\ \frac{dx_i}{dt} = r_i x_i \left(1 - \frac{\sum_{j=1}^n \alpha_{ij} x_j}{K_i} \right) \\ \dots \\ \frac{dx_n}{dt} = r_n x_n \left(1 - \frac{\sum_{j=1}^n \alpha_{nj} x_j}{K_n} \right) \end{cases} \quad (4.4)$$

The equations set can be simplified with matrix differential equations as

$$\frac{d\mathbf{x}}{dt} = \mathbf{r} \cdot \mathbf{x} \left[\mathbf{1} - (\mathbf{A}\mathbf{x}) \cdot \hat{\mathbf{K}} \right]. \quad (4.5)$$

In which the matrix $\hat{\mathbf{K}}$ is the element-wise reciprocal of \mathbf{K} , that is, $\hat{\mathbf{K}}_{ij} \mathbf{K}_{ij} = 1$.

The growth process of fungus community considering competition is characterized by this first-order linear ordinary differential equations group, with n unknown functions. Note that while the analytical can be difficult to be found, we can still figure out the development of the system using computer numerically.

4.3 Adaptive Lotka-Volterra model for fungi community

As shown in (4.5), a significant drawback of LV model is that, in total $n^2 + n$ extra defined parameters, symbolizing the stress exerted from each specie onto each another and the carrying

capacity of the environment for each specie are needed. It would be impractical for our model if such amount of factors without support from experimental result need to be considered.

Assumption 4. The stress from other species of fungi can be characterized by the ratio of the product of relative moisture tolerance and biomass of the two species, and normalized with an exponential function. **Justification** The relative moisture tolerance is defined as the difference of each isolate's competitive ranking and their moisture niche width, indicating the significant tolerance-dominance trade-off property in the competition of fungi. While incorporating the effect of multiple species, the form of the differential equations are roughly consistent with LV model.

Considering features of various types of fungi with available data, and the compatibility to the composition rate model constructed, traditional LV model in dual-species case is redefined to adapt the fungi community circumstances as follows.

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \exp \left(1 - \frac{m_1 x_1}{m_1 x_1} \cdot \frac{m_2 x_2}{m_1 x_1} \right) \\ \frac{dx_2}{dt} = r_2 x_2 \exp \left(1 - \frac{m_1 x_1}{m_2 x_2} \cdot \frac{m_2 x_2}{m_2 x_2} \right) \end{cases} \quad (4.6)$$

When extended to multiple species, we have

$$\begin{cases} \frac{dx_1}{dt} = r_1 x_1 \exp \left(1 - \frac{m_1 x_1}{m_1 x_1} \dots \frac{m_n x_n}{m_1 x_1} \right) \\ \dots \\ \frac{dx_i}{dt} = r_i x_i \exp \left(1 - \frac{m_1 x_1}{m_i x_i} \dots \frac{m_j x_j}{m_i x_i} \dots \frac{m_n x_n}{m_i x_i} \right) \\ \dots \\ \frac{dx_n}{dt} = r_n x_n \exp \left(1 - \frac{m_1 x_1}{m_n x_n} \dots \frac{m_n x_n}{m_n x_n} \right). \end{cases} \quad (4.7)$$

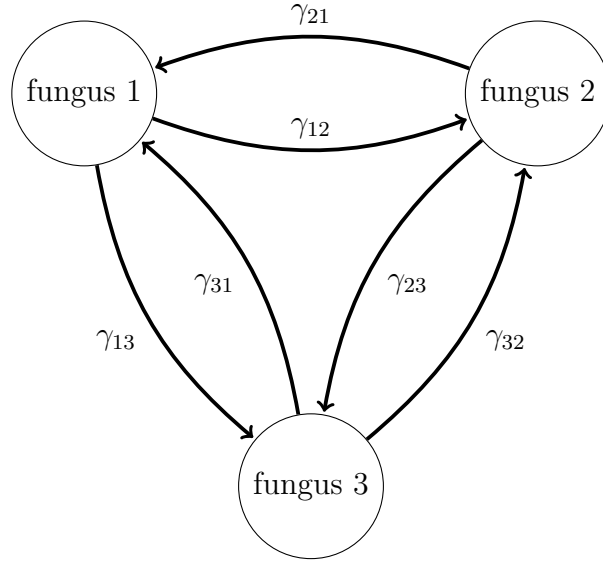
Or simply expressed as

$$\frac{dx_i}{dt} = r_i x_i \exp \left(1 - \frac{\prod_{j=1}^n m_j}{m_i^n} \cdot \frac{\prod_{j=1}^n x_j}{x_i^n} \right). \quad (4.8)$$

5 Homeostasis of the Community with Markov Chain Model

5.1 Feasibility of utilizing Markov chain model in fungus community

Since it is presumably impractical for finding the symbolic solution of the LV model, Markov chain model is introduced for predicting the stable state, that is, the relatively static composition of the fungus populations density in the community.

Figure 9: A Markov chain diagram containing 3 fungi species

Assumption 5. Once the community component is stabilized, if possible, the population density of each fungi specie interchange in a rate proportional to its own population density, the coefficient is a constant. **Justification** Though the Markov chain model is based on discrete time and state space, since the stable state is all we concerned in this attempt, we can still utilize such notion.

5.2 Constructing Markov chain for fungus community

Consider a given time interval T , and the population density of each fungus species at time t is denoted as $\mathbf{x}(t) = [x_1(t), x_2(t), \dots, x_n(t)]^T$. In the evolution process of the community, at each time interval, a specific percentage of fungi i is remained, and others can be considered as transformed into population density of other species of fungus.

For a simple dual-species system, such transition relation can be expressed as

$$\begin{cases} x_1(t+T) = \gamma_{11}x_1(t) + \gamma_{21}x_2(t) \\ x_2(t+T) = \gamma_{22}x_2(t) + \gamma_{12}x_1(t) \end{cases} \quad (5.1)$$

More generally, in an n -species community, the system is characterized by

$$\begin{cases} x_1(t+T) = \gamma_{11}x_1(t) + \cdots + \gamma_{n1}x_n(t) \\ \cdots \\ x_i(t+T) = \sum_{j=1}^n \gamma_{ij}x_j \\ \cdots \\ x_n(t+T) = \gamma_{n1}x_1(t) + \cdots + \gamma_{nn}x_n(t). \end{cases} \quad (5.2)$$

Which can be further simplified with matrix notation.

$$\mathbf{x}(t+T) = \mathbf{x}(t)\mathbf{Y}. \quad (5.3)$$

In which, the matrix $\mathbf{Y}_{n \times n}$ is defined to be the transition matrix of the system, with element γ_{ij} denoting the transition rate from fungus specie i to j .

$$\mathbf{Y} = \begin{bmatrix} \gamma_{11} & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & \ddots & & \vdots \\ \vdots & & \ddots & \vdots \\ \gamma_{n1} & \cdots & \cdots & \gamma_{nn} \end{bmatrix} \quad (5.4)$$

Note that the transition rate in the biological configuration considerably differs from that in stochastic process. In a typical Markov chain model, each element in the transition matrix represents a certain probability of transition or decision towards another state. To implement this model in a continuous mathematical configuration, adjustments must be and evidently can be made to the definition of the population density x_i itself, ensuring that a unit of population density of different species of fungus takes up the same amount of resources in the system. With such adjustment, it is guaranteed that, for each element and row of the transition matrix, we have

$$\begin{cases} \mathbf{Y}_{ij} \in [0, 1], \quad i, j \in \{1, 2, \cdots, n\} \\ \sum_{j=1}^n \mathbf{Y}_{ij} = 1, \quad i \in \{1, 2, \cdots, n\}. \end{cases} \quad (5.5)$$

In addition, though during the growth process of the populations, and in macroscopic view the early stage of the decomposition, the transition matrix may not satisfy condition (5.5), and the sum of the rows could possibly even vary with time, it is shown that the final homeostasis is only related to the transition matrix after the community enters Markov process.

Table 4: The four species chosen in verifying the model

Specie	Competitive Ranking	Hyphal Extension Rate
Phlebia acerina MR4280 B9G	1	8.75
Phlebiopsis flavidoalba FP150451 A8G	0.9864	10.8
Armillaria gallica HHB12551 C6C	0	0.49
Armillaria tabescens TJV93 261 A1E	0	1.07

5.3 Incorporate hyphal extension rate and moisture tolerance

To model the system of fungi community, the transition matrix is further specified as follows in order to incorporate traits we concerned.

$$\gamma_{ij} = \text{Softmax} \left(1 - \frac{r_i}{r_j} \right) = \frac{e^{1-r_i/r_j}}{\sum_{k=1}^n e^{1-r_i/r_k}} = \frac{e^{-r_i/r_j}}{\sum_{k=1}^n e^{-r_i/r_k}}. \quad (5.6)$$

In which the Softmax is for normalizing the data. The hyphal extension rate is a significant trait characterizing the **combative ability** of fungus, the ratio represents at what rate a fungus will be replaced another fungus isolate. It can be easily verified that, definition (5.6) is normalized for keeping consistent with prerequisite (5.5).

The final homeostasis can be expressed simply as

$$\pi = \mathbf{x}(0) \lim_{n \rightarrow \infty} \mathbf{Y}^n. \quad (5.7)$$

5.4 The homeostasis of the system

In a Markov process, the final homeostasis is only related to the transition matrix as shown in (5.7), but cannot be explicitly expressed. We postulate a quad-species fungi community, among them two in the top and two in the bottom of the competitive ranking, to visualize and verify this model.

The traits value of the four fungi is shown in table 4, and the transition matrix is

$$\begin{bmatrix} 0.45253 & 0.54712 & 0.00000 & 0.00035 \\ 0.44167 & 0.55827 & 0.00000 & 0.00006 \\ 0.32586 & 0.32935 & 0.12678 & 0.21801 \\ 0.38964 & 0.39879 & 0.04959 & 0.16198 \end{bmatrix}$$

As the iteration proceeds, the system reached the homeostasis gradually, and dominant species substitute weaker species completely in the end.

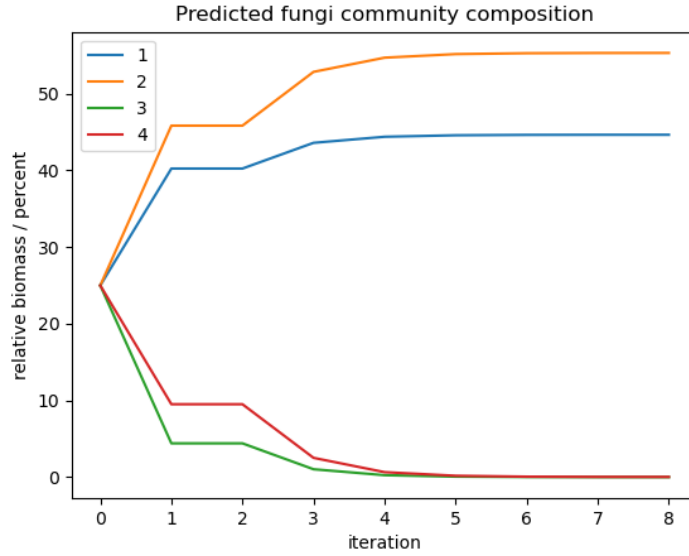


Figure 10: The community composition of a quad-species system, after several iteration, the relative biomass reaches homeostasis. 1 - *Phlebia acerina*, 2 - *Phlebiopsis flavidoalba*, 3 - *Armillaria gallica*, 4 - *Armillaria tabescens*

6 Environmental Effect on the Decay Ability of the Community

The purpose of this section, is to describe the environment affect the decomposition ability of a fungi community.

Since in this literature, moisture tolerance is the only trait of fungi concerned related to environment, we focus on how environment interact with this property.

6.1 Environmental impact on the hyphal extension rate

Moisture tolerance is defined as the difference of each isolate's competitive ranking and their moisture niche width. Competitive ranking can be obtained through pair wise competition experiment, and won't be affect by environment conditions since it is a relative ranking relation between species. Moisture niche width is the immediate property representing how tolerant a specie can be against varying environmental moisture condition, which is defined as the difference between the maximum and minimum moisture levels in which half of a fungal community can maintain its fastest growth rate.

According to (3.1), the hyphal extension rate and moisture niche width are implicitly related, and can be quantified as

$$k_2(c - d) + b_2 = \ln k_1 r \Rightarrow r = \frac{1}{k_1} \exp[k_2(c - d) + b_2]. \quad (6.1)$$

Assumption 6. The hyphal extension rate of fungi community is affected by the moisture range of the environment. When the humidity in the environment fluctuates in a remarkable range, the growth of fungi is depressed. **Justification** In this model, the community can be treated as a whole,

since moisture tolerance only has to do with the niche width, not the optimal moisture condition. The optimal moisture condition and the moisture niche can be varied a lot in a fungi community for different species, but the global trend with respect to the change of environment can be predicted in such assumption.

Define the moisture range in a certain environment as w , then the hyphal extension rate expression can be expressed as

$$\hat{r} = \frac{1}{k_1} \exp[k_2(c - d) + b_2] \cdot \frac{d}{w + d}. \quad (6.2)$$

The meaning of the extra factor in the equation is, if the environmental moisture width is exactly zero, then the hyphal extension rate of the community is considered as being right in the optimal moisture width of the system as a whole. Otherwise, if the environmental moisture width is equal to the feature moisture niche width of the community, then the hyphal extension rate is halved, which is consistent with the definition of niche width.

In addition, if the initial hyphal extension rate in a certain condition is available and denoted as r_0 , we can predict the same trait in other environment as

$$\hat{r} = \frac{d}{w + d} r_0. \quad (6.3)$$

6.2 Applying the data in various climates

After collecting and processing climate property data, we can obtain the moisture width of different climate, then apply these data to the model.

7 Combined Model of the Decay Ability Regarding Environment

In this section, the decay ability model, the growth model describing the composition of the fungi community, and the environmental factors are combined to determine the behaviors of the fungi community in breakdown process.

7.1 Combining the models

In (3.3), replace the hyphal extension rate with (6.3), obtains

$$\hat{D}_{\text{comm}} = k_3 \frac{\sum_{i=1}^n \hat{r}_i}{x} \sum_{i=1}^n x_i = k_3 \frac{\sum_{i=1}^n \frac{d_i r_i x_i}{w + d_i}}{\sum_{i=1}^n x_i}. \quad (7.1)$$

In (4.8), conduct the same substitution, obtains

$$\frac{dx_i}{dt} = \frac{d_i r_i}{w + d_i} x_i \exp \left(1 - \frac{\prod_{j=1}^n m_j}{m_i^n} \cdot \frac{\prod_{j=1}^n x_j}{x_i^n} \right). \quad (7.2)$$

Also, the transition matrix redefined in (5.6) is again transformed into

$$\hat{\gamma}_{ij} = \frac{e^{-\hat{r}_i/\hat{r}_j}}{\sum_{k=1}^n e^{-\hat{r}_i/\hat{r}_k}} = \frac{\exp \left(-\frac{d_i r_i}{w + d_i} \Big/ \frac{d_j r_j}{w + d_j} \right)}{\sum_{k=1}^n \exp \left(-\frac{d_i r_i}{w + d_i} \Big/ \frac{d_k r_k}{w + d_k} \right)}. \quad (7.3)$$

Equation (7.1) determines the ability of a fungi community to decompose ground litter and woody fibers. In which, r_i , d_i are the traits of the fungus, w is determined by the environmental condition, k_3 is a coefficient and is determined in data fitting as shown in 3. x_i is the only unknown variable representing the biomass of different species of fungus, and can be inferred numerically through (7.2), in which m_i is the trait owned by fungus.

7.2 Solution of the model at different climatic conditions

Since a explicit analytical solution cannot be attained from (7.2), yet from model defined in section 5, we choose all 34 fungi species with available traits data from [], and evaluate their behaviors under different climatic conditions. For the purpose of brevity, Markov chain model is chosen.

According to the test, we find that, some combinations of fungi species are able to persist stably. Such combinations varies for different climates. In general, fungi community with larger biodiversity behaves more efficient in decomposing ground litter and woody fibers.

Moreover, when environmental conditions change, in short term the community might be influenced intensively. However, in the long term, the community will again reach a new homeostasis, which is more adaptive to the new environment.

8 Analysis

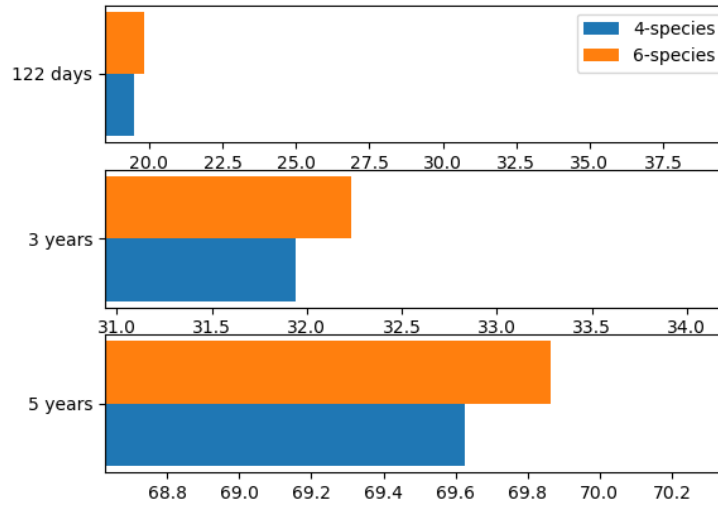
8.1 Breakdown Efficiency and Biodiversity

Consider 4 most combative species with top competitive ranking, and other 2 weaker species that are less combative and ranked in the middle, the species are shown in table 5. The comparison is made between fungi community consists of 4 species and of all 6 species.

Prediction as shown in figure 11 suggests that, when relatively weaker species are added into the community, the resulting decomposition efficiency is increased at a certain rate. Such effect

Table 5: The four species chosen in verifying the model

Specie	Competitive Ranking	Hyphal Extension Rate	Moisture Niche Width
Phlebia acerina MR4280 B9G	1	8.75	1.19
Phlebiopsis flavidoalba FP150451 A8G	0.9864	10.8	2.54
Phlebia acerina DR60 A8A	0.9726	8.51	1.28
Merulius tremellosus FP150849 C3F	0.8383	9.62	1.24
Phellinus robiniae FP135708 A10G	0.5199	2.3	1.53
Phellinus hartigii DMR94 44 A10E	0.4932	1.54	1.57

Figure 11: The decomposition rate after a certain time of decay of 4-species and 6-species community. The two extra fungi species are weaker, meaning less competitive in pair wise test.

becomes more significant when the experiment period extends longer. This result indicate that, biodiversity among the fungi community is positively related to the overall efficiency of a system with respect to the breakdown of ground litter and woody fibers.

8.2 Sensitivity Analysis

In our first model expressed (3.1), for the relation between decay ability and hyphal extension rate and moisture tolerance, with one-at-a-time method, presented great robustness. The environmental effect model is also robust against the varying of parameters or fungi properties. However, other parts of our work, especially Markov chain model and adaptive LV model are described implicitly through transition matrix or differential equations group, their robustness remains unknown unless tested massively through statistical measures.

8.3 Strengths and Weaknesses

The strengths and weaknesses of our model are both evident. For the strengths, our model

- Extended the Lotka-Volterra model to multi-species cases, proposed the corresponding mathematical description. LV-model plays a significant role in ecological competition, but there not enough researches covering the multi-species condition. More the this, we also derived an adaptive form of LV model for fungi community based on the configuration of this problem.
- Implemented the notion of Markov chain process, to describe the homeostasis of the fungi community. The implementation of a discrete time, discrete state space model in a continuous problem is a bold attempt. Such concept offers brevity and convenience of calculation in our model.
- Incorporate the varying range of moisture as the affecting environmental factor, consider the fungi community as entirety, which also keeps consistent with the assumption that only the moisture niche width is taking effect.
- Also, in many other cases, the community is considered as an entirety, which provides remarkable integrity, convenience and consistency.

As for the weaknesses, our model

- Ignored other detailed traits of fungi such as optimal moisture and temperature, some of them plays relatively important role in certain cases.
- Utilized implicit mathematical language to describe models, hence symbolical solutions cannot be found, and the intrinsic working principle remains uncertain.
- Took some assumptions that are less convincing and might even be incorrect.

9 Conclusions

In conclusion, hyphal extension rate and moisture tolerance are positively related to the decay ability of a fungi isolate as well as the community. In a fungi community, the decay ability is determined by its community-weighted hyphal extension rate. The composition of a fungi community in homeostasis can be inferred from Markov chain model or solving adaptive LV-model.

Environmental conditions have affect on the composition of the community, hence alters the decay ability. The larger the varying range of local environmental condition is, the slower the decomposition becomes. Certain species combinations may suitably persis in corresponding climate. In general, biodiversity is positively related to the decay ability. In short term, the fluctuation of environmental conditions may affect the fungi community intensively, however, in long term, the community will reach a new homeostasis.

Competition, Adaptation and Biodiversity: How Fungi Support Our Biosphere

Fungi are everywhere in the world, not just on a rotten orange, or in yeast essential bread and cake. Fungi together with a series of other microbes plays an important role in the biosphere, know as the **decomposers**. The normal functionality of biosphere requires both sustained energy and material flow, and the latter one consists of not only essential organic chemical compound such as amino acids and glucose, but also inorganic carbon dioxide. Such material flow is also called the **carbon cycle**.



Figure 1: Fungi in pair wise competition test. This figure is adopted from “Consistent trade-offs in fungal trait expression across broad spatial scales” by Daniel S. Maynard et al.

In carbon cycle, the **producers**, mainly the green plants, are responsible for the fixation of carbon, namely transforming the carbon in carbon dioxide into fixed carbon in organic matter through chemosynthesis, of which the most commonly known one is photosynthesis. Then, the **consumers** utilize these material for vital activities, some carbon transformed into again into the carbon dioxide, some maintain in consumers.

What would these carbon go? Can they go back to the atmosphere? This is where decomposers play a role. Decomposers decompose the cadavers and excrements, function as the bridge in the carbon cycle. Note that, one of the most important features of carbon cycle is that it was global, the beef, egg and milk consumptions in the US might be related to the depletion of Brazilian rain forests, which is why carbon cycle is significant to us all and more and more researchers are interested in this topic.

As an important category in decomposers, fungi are outstanding participants in the decay process, especially when dealing with ground litter and woody fibers. A recent research presented the mechanism of decay efficiency for fungi community. The decay ability is positively related to the hyphal extension rate and moisture tolerance of a fungus isolate. However, as for a fungi community, the thing is getting more complicated.

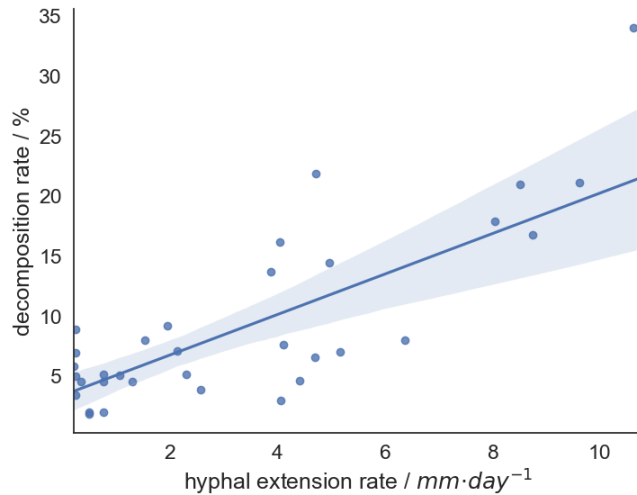


Figure 2: The relationship between the hyphal extension rate of various fungi and the resulting wood decomposition rate. The hyphal extension rate is the geometrical average of the value tested under 10, 16 and 22 Celsius.

The composition of the fungi community can be predicted by the famous Lotka-Volterra model as shown in (*), which indicates that in a multi-species system, each species would exert stress on other species. Tilman interprets that, the intrinsic mechanism is the limitation of certain resources. Generally, the fungus which grows slower, can better tolerate a wide range of environmental conditions. Therefore, some most competitive fungi may attain huge superiority at the start, and replace the less combative fungi completely. Sometime, more tolerant fungi might be able to endure the oppression and gain dominance in the later stages. Such feature determines that, some combinations of fungi may be able to persist and reach a dynamic homeostasis. It is apparent that, these combinations may vary with environmental conditions, you may do your own experiments in the laboratory to find out the “recipe”.

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{\sum_{j=1}^n \alpha_{ij} x_j}{K_i} \right) \quad (*)$$

Another interesting fact is that, when less competitive species of fungi are introduced to the community, the decay ability of the fungi community may be boosted instead of decreased. This phenomenon can be explained as, different species are preponderant in decomposing at different stages. A large varieties of species, namely the **biodiversity**, enables the possibility of various combinations. Such combination is relevant to the climatic conditions, resulting unique biodiversity in different geographical areas. Biodiversity also makes the community more variability in face of the variability in local environment.

The global carbon cycle integrates whole biosphere all together, with inconspicuous fungi as a crucial part in it. It is our shared responsibility to restrict carbon emission and protect biodiversity. Biodiversity provides efficiency and robustness to our biosphere. Hope next time you could feel less disgusted when seeing a rotten apple, it might be fungi answering their call!

References

- [1] Mira-Cristiana Anisiu. Lotka, volterra and their model. *Didáctica matemática*, 32:9–17, 2014.
- [2] Jianhai Bao, Xuerong Mao, Geroqe Yin, and Chenggui Yuan. Competitive lotka–volterra population dynamics with jumps. *Nonlinear Analysis: Theory, Methods & Applications*, 74(17):6601–6616, 2011.
- [3] KC Burns and PJ Lester. Competition and coexistence in model populations. 2008.
- [4] Maica Krizna A Gavina, Takeru Tahara, Kei-ichi Tainaka, Hiromu Ito, Satoru Morita, Genki Ichinose, Takuya Okabe, Tatsuya Togashi, Takashi Nagatani, and Jin Yoshimura. Multi-species coexistence in lotka-volterra competitive systems with crowding effects. *Scientific reports*, 8(1):1–8, 2018.
- [5] Jef Huisman and Franz J Weissing. Fundamental unpredictability in multispecies competition. *The American Naturalist*, 157(5):488–494, 2001.
- [6] Alfred J Lotka. Analytical note on certain rhythmic relations in organic systems. *Proceedings of the National Academy of Sciences*, 6(7):410–415, 1920.
- [7] ALFRED J LOTKA. Fluctuations in the abundance of a species considered mathematically. *Nature*, 119(2983):12–12, 1927.
- [8] Nicky Lustenhouwer, Daniel S Maynard, Mark A Bradford, Daniel L Lindner, Brad Oberle, Amy E Zanne, and Thomas W Crowther. A trait-based understanding of wood decomposition by fungi. *Proceedings of the National Academy of Sciences*, 117(21):11551–11558, 2020.
- [9] Daniel S Maynard, Mark A Bradford, Kristofer R Covey, Daniel Lindner, Jessie Glaeser, Douglas A Talbert, Paul Joshua Tinker, Donald M Walker, and Thomas W Crowther. Consistent trade-offs in fungal trait expression across broad spatial scales. *Nature microbiology*, 4(5):846–853, 2019.
- [10] Daniel S Maynard, Mark A Bradford, Daniel L Lindner, Linda TA van Diepen, Serita D Frey, Jessie A Glaeser, and Thomas W Crowther. Diversity begets diversity in competition for space. *Nature ecology & evolution*, 1(6):1–8, 2017.
- [11] Daniel S Maynard, Thomas W Crowther, and Mark A Bradford. Fungal interactions reduce carbon use efficiency. *Ecology letters*, 20(8):1034–1042, 2017.
- [12] TS Sadasivan. competition in fungi. In *Proceedings of the Indian Academy of Sciences-Section B*, volume 10, pages 1–26. Springer India, 1939.
- [13] D Tilman. Resource competition and community structure. *Monographs in population biology*, 17:1—296, 1982.
- [14] Chao Zhu and G Yin. On competitive lotka–volterra model in random environments. *Journal of Mathematical Analysis and Applications*, 357(1):154–170, 2009.

Appendices

A Source Code

The source code for Markov chain model.

```
1 import numpy as np
2
3
4 def cal_trans(r) -> np.array:
5     trans = np.zeros([len(r)] * 2)
6     for i in range(len(r)):
7         row = [- r[i] / e for e in r]
8         trans[i] = softmax(np.array(row))
9     return trans
10
11
12 class Markov():
13     def __init__(self, trans, init=None) -> None:
14         self.init = init
15         self.trans = trans
16
17     def run(self, times):
18         p = self.trans
19         for i in range(times - 1):
20             p = p @ self.trans
21         return self.init @ p
22
23
24 def dist(r):
25     init = np.array([100] * len(r))
26     markov = Markov(cal_trans(r), init)
27     return markov.run(100) / (100 * len(r))
```

B Fungi Traits Data

The decomposition rate data from [8], can be retrieved at Supplementary Information for A trait-based understanding of wood decomposition by fungi.

The other fungi traits data from [9], can be retrieved at [dsmaynard/fungal_biogeography](https://github.com/dsmaynard/fungal_biogeography).