

A Simulation Based Analysis of Fungi

Summary

Fungi are the main decomposers of woody litter in nature and play an important role in maintaining the ecological balance of nature. Many factors affect the rate of fungal decomposition, such as humidity, temperature and so on. In addition to these external factors, the interaction between various species of fungi also has a significant influence on the decomposition rate by fungi. However, the mechanism of these influencing factors is still not well understood. Therefore, it is particularly important to explore the relationship between these factors and the decomposition rate by fungi as well as the mechanism behind it.

In order to establish their quantitative relationship, we reviewed a lot of researches to find the experimental data, based on which we introduced the first-order dynamic model to unify the unit of decomposition rates. Then we carried out a multiple linear regression analysis, through which we eliminated the influence of irrelevant factors and found out the linear relationship between decomposition rate and influencing factors and the linear relationship between decomposition rate and hyphal extension rate. According to these two relationships, we established differential equations, thus deducing the function of fungal decomposition rate over time as well as the function of area covered by fungi over time. All these provide the basis for the parameter determination in the subsequent cellular automata model.

To explore the interaction mechanism between fungi, we established a complex cellular automata model with a series of rules to simulate the fungal extension which is mainly determined by extension rate and moisture tolerance. In addition, by introducing the concepts of litter/woody fiber ratio, temperature influencing factor, litter complement coefficient and so on, we established rules for litter supplementation in nature, changes in temperature and humidity in different climate zones, and different vegetation coverage, giving our model a wider range of adaptability. The parameter underwent a serious estimation and several tests before finally set, to ensure they were set in line with the actual situations. Thus, we built a cellular automata model that can simulate the extension of fungi under the interaction of multiple complex factors. The sensitivity analysis of it shows that the results of the model has strong robustness in the face of rapid changes in some environmental variates, with the ability to visualize.

In the cellular analysis, we found complex interaction between different species of fungi. We selected two different fungi for simulation analysis, and found that with the changes of environment, the relationship between them shifted from competition to cooperation. The situations under different climate zones were simulated, and it was found that a single fungus was weak combating climate changes, while multiple fungi can deal with more complex and demanding environment, which reveals how fungi interact with each other to improve the ability to cope with environmental changes as well as the importance of biodiversity in the natural ecological environment.

Notably, our models are easy to use and extend due to variable parameterization, enabling us to simulate the interaction and decomposition rate by varying fungi in almost every case.

Keywords: Cellular Automata, Multiple Regression Analysis, Quantitative, Visualization

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1 Introduction

1.1 Problem Background

The carbon cycle is an important link for the exchange, metabolism and circulation of substances in nature to maintain stability, so that carbon elements can be transformed and reused. The decomposition of plant materials and wood fibers forms part of the carbon cycle. And this decomposition process is inseparable from microorganisms, most notably fungi. Therefore, it is important to understand the decomposition by fungi.

There are many kinds of fungi. Recent scientific studies have determined the fungal traits related to decomposition rate, and it is believed that the growth rate and moisture tolerance of fungi are two key factors, but the relationship between the two is not clear yet. Since the nature is diverse and dynamic, regional differences and local environmental variability will result in differences in decomposition process by fungi by affecting their characteristics. What's more, various colony interactions also affect the overall decomposition efficiency. How to describe the decomposition of ground litters and woody fibers by fungi in the most natural terms is a problem of concern to most people.

1.2 Literature Review

The decomposition process has long been the focus of scholars in related fields, mainly studied from experimental aspect and the aspect of theoretical model to explore the influence of various factors. Here we focus on studies with modeling perspectives.

Early work about decomposition considered mostly the environmental factors. In 2005, Jari Liski *et al.* proposed carbon and decomposition model Yasso. Later in 2011, M. Tuomi *et al.* developed it and explored another two models. Though they took microbial biomass into consideration, they **failed to realize the particularity of fungi in decomposition, viewing microorganisms as a single homogeneous group** as most traditional studies did.

An outstanding work, published in 2005 by M. Corbeels *et al.*, gave a process-based model from the perspective of cycling and considered the growth of fungi. In 2014 and years later, scholars like MA Bradford and Van der Wal A. also proved its significant role. Unfortunately, they either didn't provide a specific model or the model was incomplete.

But the rivalry has been studied for years and reached a certain height. Early in 1994, John M. Halley *et al.* proposed a cellular automaton model about competition and succession in fungal communities. In 2012, X. Sun *et al.* studied community structure and preference of fungi of woody plants. In 2017, Daniel S. Maynard *et al.* found the key role of competitive network in diversity-function relationship, giving a deeper insight of competitions among fungi. And scholars have provided a competitiveness ranking based on ELO mechanism.

There are varying methods to deal with decomposition. Combining the results of early studies, we hope to **provide new solutions to the study of decomposition by fungi through more specific models and dig deeper into the meaning of biodiversity.**

1.3 Our Work

The problem requires us to simulate the decomposition of ground litter and woody fiber with a variety of fungi, describe the interactions between different species of fungi, predict the advantages and disadvantages for different combinations of species in different and changing environments, and finally conduct a biodiversity analysis according to it. Specifically, we accomplished the following tasks:

- We proposed a **multivariant linear regression decomposition model** considering varying environment and the interactions among various kinds of fungi based on their different decomposition rate, growth rate and moisture tolerance.
- We simulated through a **cellular automaton** the decomposition and competition process as well as the influence of various regional conditions and local environmental changes on fungal community, thus predicting relative advantages and disadvantages for different species and stressing the role of biodiversity in maintaining microenvironmental stability and improving decomposition effectiveness.
- We summarized our progress in what role fungi play in ecosystem.

2 Overall Preparation of Models

2.1 Problem Analysis

The variable parameterization problem requires us to build a model to describe the factors that affect the rate of fungal decomposition considering the fungal interaction. Through literature review, it's proved that the decomposition rate by fungi is mainly determined by factors as temperature, humidity, carbon content and C:N ratio. It is not difficult to obtain the relationship between the decomposition rate and these factors through multiple regression analysis of a large number of data.

As for fungal interaction, it involves quite a few factors such as temperature, humidity, fungus's own traits, etc., and the influence of the relationship between these factors is relatively complex. Therefore, to directly establish an accurate mathematical model is difficult. It's better to build a model which comprehensively takes into consideration the effects of all these factors on the basis of the principle of biology and common sense. In this paper, we introduced the cellular automata model to solve this problem.

2.2 Overall Assumptions

Asm.1 The decomposition rate has a linear relationship with the hyphal extension rate; the logarithm value of the decomposition rate is linear with the moisture tolerance of fungi (difference of each isolate's competitive ranking and their moisture niche width, both scaled to $[0, 1]$); the decomposition rate of wood depends on hyphal extension and the decomposition rate of single fungus, and the probability of hyphal extension determines its extension rate. This hypothesis is based on the findings of Nicky Lustenhouwer *et al.* (2020).

Asm.2 The decomposition of woody fibers around the world is only associated with fungi. This is because previous studies by scholars like Bradford *et al.* (2014) and Weier Kang (2008) have confirmed that the decomposition of wood, especially lignin, is mainly

completed by fungi which can explain most of the variation of decomposition rate rather than climate. To simplify the model, we assume that the decomposition of woody litters is only related to fungi.

Asm.3 All fungi follow the same set of rules for decomposition, regardless of the differences between different kinds of fungi.

Asm.4 The rate of fungal decomposition of woody litter was independent of the species of wood. We assume that the lignin of different types of trees is not quite different from each other at the micro level since we are studying the decomposition by fungi.

Asm.5 Fungi have strong adaptability to the normal environment and strong viability. There's no external introduction or death. Predation of fungi by soil organisms is not considered as well.

Asm.6 The interactions between different species of fungi are only reflected in the consumption of resources, so we don't need to take into account other factors such as the chemical effects of fungal decomposition products on another fungus. And the clustering effect of fungi aggregation is not considered.

2.3 Notations

The following table lists the main symbols used in our models.

Table 1: Notations in this paper

Symbol	Description
A	One kind of fungi whose prototype is white-rot fungi
B	Another kind of fungi whose prototype is brown-rot fungi
C	Carbon content of woody litter
C_c	Carbon consumption rate
CI_i	The intensity of competition
D	The decomposition rate by fungi per unit area per day
D_i	The number of fungi of a particular species
E_m	Corner correction coefficient
G_r	Hyphal extension rate
H	Relative humidity
K	C:N ratio of woody litter
k	Relation constant
n_e	The number of surrounding cells without fungus
n_w	The number of surrounding cells with water
P_g	The probability of hyphal extension
R	The radius of the circular area occupied by fungi
R_i	Competitiveness ranking
r	Competitiveness factor
T	Annual mean temperature
T_s	Ambient temperature
t	The total time taken for a single fungus to complete decomposition
Δt	Unit time

2.4 Model Framework

Our modeling framework can be illustrated as shown in the figure below.

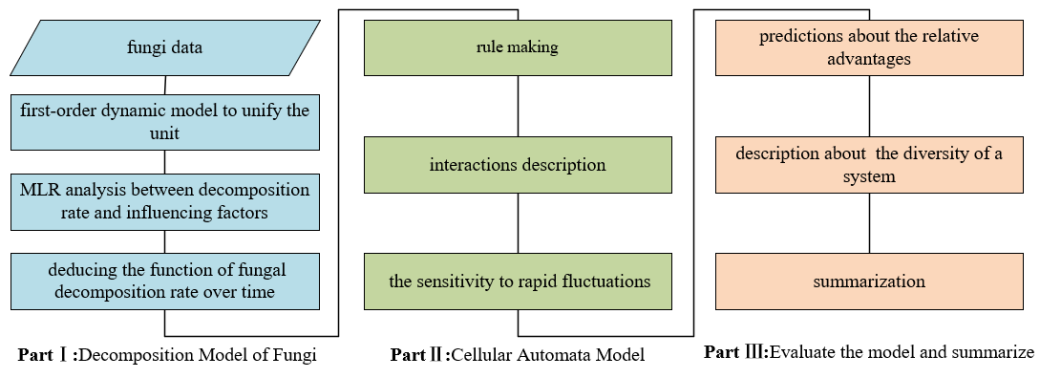


Figure 1: Overview of this work

3 Multiple Linear Regression Model

3.1 Model Overview

We reviewed a series of literature and cited two sets of reliable data to build our model based on them. We firstly used a **first-order dynamics model** to process the data to ensure the **unit unification** of different data sets. Then we built a **multiple linear regression model** and analyzed two multiple linear relationships based on the data, that is, the linear relationship between decomposition rate and factors as temperature, humidity, carbon content of litters and C:N ratio, and another between decomposition rate and hyphal extension rate and temperature. From these two relationships, we got the equation for the growth rate. Finally, the function of area covered by fungal over time and the time-based function of litter carbon content which can represent the decomposition of ground litter and woody fiber were derived by our differential equations.

In this model, we mainly studied the decomposition of litter and woody fiber by a single fungus without considering the competition between multiple fungi. Competitive relationships were taken into account in subsequent models.

3.2 Model Assumption

Asm.1 The annual variation can replace the instantaneous value of the variation. Ideally, the environment is stable over the course of investigated decomposition process by fungi, so the environment can be assumed to remain unchanged and the model can be built using annual averages.

Asm.2 The environment is assumed to be isotropic, so fungi should extend outwards in a circular shape.

Asm.3 The decomposition rate is constant. In order to simplify the model, we assume the decomposition rate will not grow faster as fungi extend (the area covered by fungi grow larger) because in nature, fungi tend to extend so quickly that are able to cover all the

woody litter nearly in a short period of time and then begin the decomposition. That's to say, we ignore the decomposition during the hyphal extension process.

Asm.4 Decomposition rate of a single fungus is only related to resource concentration which can be expressed by carbon content. That is, the process of individual fungus decomposition can be identified as the process of fungus consuming carbon.

Asm.5 The decomposition rate has the same changing trend over time at different temperatures.

3.3 Data Processing

Two sets of data are quoted. *Database I* provides the data of decomposition rate, temperature, humidity, carbon content and C:N ratio, while *Database II* provides the decomposition rate and hyphal extension rate at different temperatures.

Table 2: Data source collation

Database Number	Database Source Paper	Author
Database I	Traits drive global wood decomposition rates more than climate.	Zhenhong Hu <i>et al.</i>
Database II	A trait-based understanding of wood decomposition by fungi.	Amy E. Zanne <i>et al.</i>

Based on the model assumptions, we can introduce the **first-order dynamic model**. It holds that

$$\frac{dx}{dt} = -kx \quad (1)$$

where:

- t is the time
- $x = x(t)$ is the content of reactants in the system at time t
- the first-order derivative dx/dt is the reaction rate
- the proportionality coefficient k is the reaction rate constant ($k > 0$)
- the negative sign indicates that the content of reactants is in decay

We set the reactant content as x_0 at the initial time t_0 , then the special solution that satisfies the initial condition $x(t_0) = x_0$ is

$$x(t) = x_0 e^{-k(t-t_0)} \quad (2)$$

which shows that the reactant content in the system decays exponentially with time.

We correlated this model to the decomposition rate by fungi, using carbon content to characterize the resource concentration of litters, and then we got

$$D = -Ae^{-Bt} \quad (3)$$

which indicates that D has an exponential relationship with time.

Thus, taking day as the unit of time, we can further obtain the following two equations:

$$\begin{cases} Ae^{-B \cdot 365} = D_1 \\ Ae^{-B \cdot 122} = D_2 \end{cases} \quad (4)$$

where:

- D_1 is the average decomposition rate between 18°C and 26°C in *database I*
- D_2 is the one at 22°C in *database II*.

The reason that we decided to substitute these two average values of the decomposition rates at similar temperatures into our equation is to determine the coefficients A and B with as few errors as possible. Since it's assumed that the trend of decomposition rate over time is the same at different temperatures, we can predict the trend of decomposition rate over time at other temperatures by the one at a certain temperature.

From the equation it can be found that

$$\begin{cases} A = 0.305 \\ B = 3.053 \times 10^{-3} \end{cases} \quad (5)$$

Thus the decomposition rate with unit in days in *database II* can be obtained, that is,

$$normalized\ D_2 = initial\ D_2 \cdot e^{-B(365-122)} \quad (6)$$

It should be noted that this model aims at unifying units of data in different databases, which can well reflect the relative relationship between data from different sources. That's why we ignore the errors generated in unifying units here. However, if the model is directly used to describe the decomposition rate of fungi in nature, the error can not be ignored because we do not take everything into consideration completely in the model.

3.4 Model Construct

3.4.1 Decomposition Rate Functions

Before constructing the linear relationship and fitting the parameters, we observed the scatter plot and then eliminated many irrelevant items such as the annual average precipitation, and finally established four linear related factors, namely temperature, humidity, wood carbon content and C:N ratio.

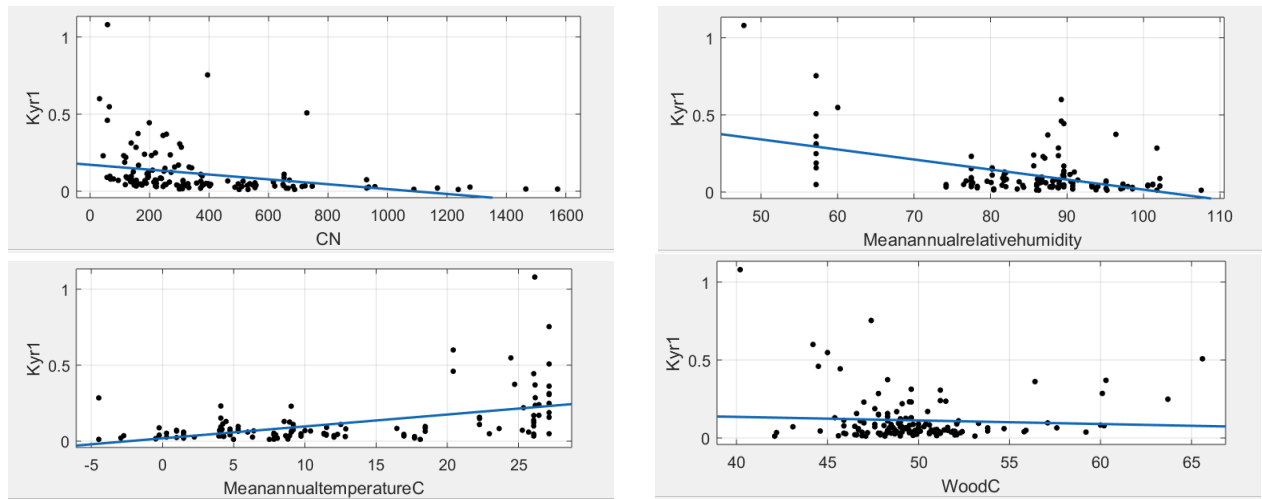


Figure 2: Scatter plot of the four factors

Set the linear equation as $D = aH + bT + cC + dK + e$, and through data fitting we can get their value as shown in the table 3, and we can thus simplify the formula as:

$$D = aH + bT + cC + e \quad (7)$$

Table 3: Quaternary linear regression results

	Correlated Coefficient Value	Sig.
Temperature	0.005	.000**
Humidity	-0.005	.000**
Carbon Content	-0.006	.038*
C:N Ratio	0.000	.006**
Constant	0.765	.000**

Note. ANOVA p = .000**

According to the data of Nicky Lustenhouwer *et al.*, linear regression analysis of decomposition rate and hyphal extension rate and temperature was conducted to obtain their linear expression, and the units of each coefficient were determined by dimensional analysis:

$$D = fT + gG_r + h \quad (8)$$

where the value of coefficients are as follows.

Table 4: Binary linear regression results

	Correlated Coefficient Value	Sig.
Extension rate	1.172	.000**
Temperature	0.378	.000**
Temperature	-6.635	.035*

Note. ANOVA p = .000**

With the simultaneous equations (7) (8), we got

$$G_r = \frac{aH + (b - f)T + cC + e - h}{g} \quad (9)$$

where the value of coefficients have been given above.

The goodness-of-fit test and the significance test both show that the two linear relation equations fit well and the results are significant.

3.4.2 Differential Equations for Decomposition

Previous studies have shown that carbon content is an important factor to measure the decomposition of woody litter. In this model, we measured the decomposition of woody litter by carbon content, and the decomposition rate was positively correlated with the consumption rate of carbon content. We assumed that $C_c = \alpha d$, where α is the proportional coefficient which can be measured by experiment.

From that, we got

$$\frac{dC}{dt} = -C_c \quad (10)$$

$$\frac{dR}{dt} = G_r \quad (11)$$

where R is the radius of the circular region occupied by fungi.

3.5 Result

From the differential equations, it could be obtained that

$$C = e^{(-At) + \frac{A}{B}} \quad (12)$$

where A and B were two unknown coefficients.

Substituting the above results into Equation (5), we got

$$R = Mt + N \int C(t)dt \quad (13)$$

Thus,

$$R(t) = (M + \frac{A}{B})t + \frac{1 - e^{-At}}{A} \quad (14)$$

where

$$\begin{cases} A = \alpha \cdot c \\ B = -\alpha(aH + bT + e) \\ M = [aH + (b - f)T + e - h]/g \\ N = c/g \end{cases} \quad (15)$$

From this, we derived the extension rate of fungi under different humidity, temperature and carbon content as well as the decomposition rate by fungi as a function of time.

4 Cellular Automaton Model

In the previous multiple linear regression model, we have constructed two linear relations and obtained the coefficients through data fitting, describing the decomposition process of single fungi greatly. Based on the real data of some climate zones, these coefficients will be applied in the following cellular automaton model which focuses mainly on the interactions between fungi, helping us to set the initial value after some initialization process.

4.1 Model Assumption

Cellular automaton is a grid dynamics model with discrete time, space and state. According to some local rules, each cell evolves in discrete time dimension. The fungal decomposition process can be considered as a discrete problem when considered in the unit of days, so the model is a periodic cellular automata model.

We made the following assumptions to simulate the reality as much as possible.

Asm.1 During the decomposition, fungi will extend their hyphae around with certain probabilities, while they themselves will stay in the original position.

Asm.2 Litter is only divided into two categories with varying degrees of moisture, in this case specifically woody fiber and other ground litter.

Asm.3 The time and priority of woody fiber and other ground litter decomposition by different kinds of fungi are different, and the probabilities of hyphal extension to the adjacent environment are also different.

Asm.4 The factors that determine the extension probability of hyphae are mainly humidity, temperature, competition ability and soil resources.

Asm.5 Different species of fungi are in competition and cannot coexist in the same position.

Asm.6 The external environment factors such as temperature will only change the extension rate of fungi but won't affect the decomposition rate of any single fungus. This is because this model focuses on revealing the interactions between fungi, giving the extension rate much higher priority than the single decomposition rate.

4.2 Model Construction

4.2.1 Model Principle

- In cellular automata, a cell is the basic unit. And cells can store state information.
- Each cell has three states at the woody litter level, that is, woody-fiber-containing, other-ground-litter-containing and empty.
- Each cell has three states at the fungal level, that is, A-present, B-present, and empty.
- Each cell has two states at the water level, that is, water-containing and non-water-containing.
- The states of cells at litter level and water level are independent of each other.
- The state of each cell at the next moment is determined by its own state and the state of surrounding cells at the current moment according to certain rules.
- From the assumption of linear relation, the relation is obtained as

$$\log(\text{wood decomposition rate}) \propto (1 + H - r) \quad (16)$$

$$\text{wood decomposition rate} \propto P_g \cdot \frac{1}{t} \quad (17)$$

$$G_r \propto \text{wood decomposition rate}, G_r \propto P_g \rightarrow G_r \propto \frac{1}{t}, P_g \cdot t = \text{constant} \quad (18)$$

4.2.2 The Rules

1. Hyphal extension

- All species of fungi can only extend their hyphae to neighboring cells in unit time. During this unit time, the extended hyphae are in a state of growth, but after this unit time, they are treated as fungi and follow all the decomposition rules.
- The fungi extend around according to their own growth probability P_g .

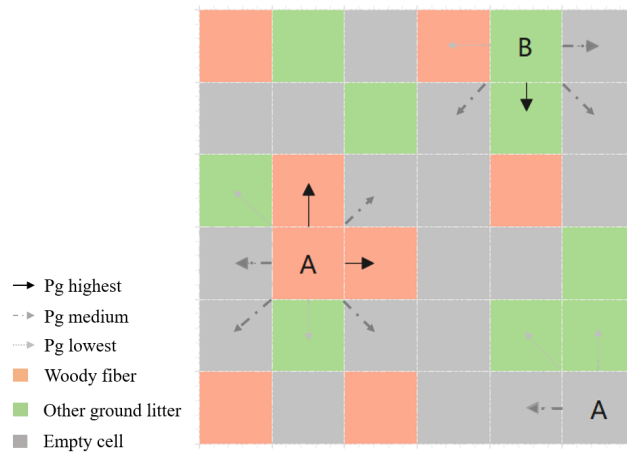


Figure 3: Schematic diagram of extension

2. Initialization

The initialization requires allocation of woody fiber, other ground litter and moisture with certain ratios, which are set according to different environments.

The initial value of the extension probabilities of different species of fungi is determined by the water status of surrounding cells and fungal moisture niche width.

3. Humidity

Assuming that there are n_w cells with water around the fungi cell and the humidity is expressed as H , then $H = \frac{n_w}{8}$, which scales to $[0, 1]$.

Humidity affects the probability of hyphal extension probability in initialization since each species of fungi has its own moisture niche width which is highly related to the extension rate and since that humidity has a linear relationship with decomposition rate. Setting the specific value of possibilities requires the coefficients from multiple linear regress model and a large amount of local data. And since we have the relation that

$$\log(P_g \cdot \frac{1}{t}) = k \cdot (1 + \frac{n_w}{8} - r) \quad (19)$$

the possibilities of any two fungus should follow that

$$\frac{P_{gi}}{P_{gj}} = \frac{t_i}{t_j} e^{\frac{k}{8}(n_{wi}-n_{wj})-k(r_i-r_j)} \quad (20)$$

For example, in our simulation, we set it according to previous results as follows:

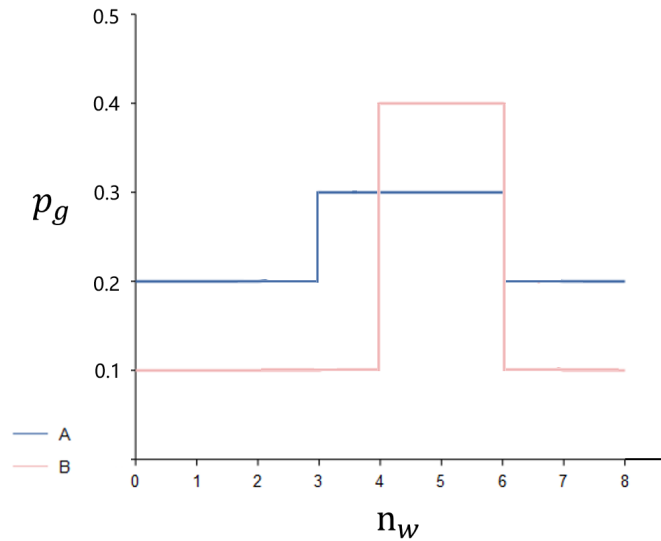


Figure 4: Effect of humidity on hyphal extension

4. Location correctness

In reality, under the condition of sufficient resources, fungi grow approximately equidistant in all directions, presenting a circle, while the cell is distributed in a rectangle shape. Thus, the corner correction coefficient are set and will affect the extension possibility as:

$$E_m = \frac{\text{Euclidean Distance}}{\text{Manhattan Distance}} \quad (21)$$

$$P_g = E_m \cdot P_g \quad (22)$$

5. Decomposition and dominance

It takes some time for fungi to decompose. We made this time a constant, with the value determined according to the actual time proved in literature. It is expressed as $n\Delta t$, where Δt is the basic time unit and n is determined by the traits of certain fungi to decompose things.

When a fungus finishes decomposition thus the cell has neither lignin nor cellulose, then it will transform into a dormant state after staying for Δt to simulate the resource shortage in reality. If the cell itself is empty and it does not need to decompose, then the fungus will also become dormant after staying for Δt . When a fungus is in dormant state, the cell is absolutely in empty state.

Vividly, the decomposition rule of the cellular automata can be expressed as follows. The value is set on the basis of their competitiveness ranking, moisture niche width and the previous linear relations and has been normalized. It is set specially for our simulation later, but can be changed according to different cases.

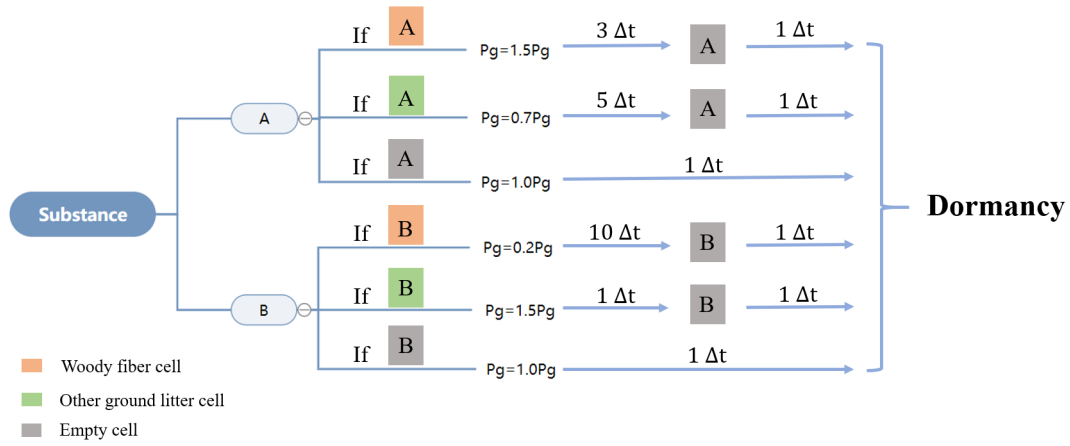


Figure 5: Fungal decomposition rules for woody litter

6. Temperature

Temperature changes the probability of hyphal extension around. According to the research results of Kirschbaum(2000), the standard temperature is set as $30^{\circ}C$, then

$$P_g = P_g \cdot e^{\frac{3.90(T_s - 30)}{T_s + 31.79}} \quad (23)$$

where T_s is the current ambient temperature.

7. Competition

- Different species of fungi cannot exist at the same cell at any time, that is, the hyphae will not extend to the occupied cell.
- Different species of fungi have different competitive abilities. For one, if its competitiveness rank is R_i and there are n species, then its competitiveness factor $r = \frac{R_i}{\sum_1^n R_i}$, which scales to $[0, 1]$. Thus, the relationship in the model can be expressed as:

$$\log(P_g \cdot \frac{1}{t}) = k \cdot (1 + \frac{n_w}{8} - \frac{R_i}{\sum_1^n R_i}) \quad (24)$$

$$P_g = t e^{k(1 + \frac{n_w}{8} - \frac{R_i}{\sum_1^n R_i})} \quad (25)$$

- In consideration of the interaction of interspecific competition and population competition, if n_e represents the number of cells that are not occupied by any fungus around a single cell, then P_g is corrected as:

$$P_g = [2 - (\frac{n_e}{8})^2] \cdot P_g \quad (26)$$

- When the cell is in empty state, it will change to the woody fiber or other ground litter state with a certain probability in the next unit time, which simulates the constant supplement of litter in reality. The probability is variable in different environments.

- When a dormant cell is again converted to woody fiber or other ground litter, the cell may be occupied by one of a variety of fungi and the decomposition process will be repeated as described above. The probability of occupation is proportional to the intensity of competition which is expressed as

$$CI_i = \sum_{j=1}^{n_i} \frac{k_j \cdot N_j}{K_i \cdot N_i \cdot L_{ij}} \quad (27)$$

where n_i is the number of those fungal species participating in the competition, N is the number of fungi, L_{ij} is the distance between competing fungi A and B, and k_i is an experimental constant.

4.3 Simulation

In the case of multiple species of fungi, we took two species as an example and chose white-rot fungi and brown-rot fungi as prototype. The specific algorithm steps of all simulations are similar:

- Step 1** Initialize the cellular automata. All the cells are initially empty. Then allocate lignin, cellulose, and water according to the proportion and probability.
- Step 2** The initial extension probabilities of the two species of fungi are determined by water content.
- Step 3** According to the litter state of the cell, the extension probabilities of the hyphae change and the decomposition begins.
- Step 4** During the decomposition process, the cells in the empty state will transform into litter state according to the probabilities, and all the cells will have transformation in the level of water state according to probability.
- Step 5** The fungi extend or become dormant according to the rules during the decomposition process. If there are competitions or changes in environmental factors, the probability of hyphal extension will change.

5 Interaction Result

To describe the interaction between different fungi vividly, we plot the number of fungi A and fungi B over time in the absence of a resource supply and we changed the water distribution in the middle of the process to find out the competition mechanism.

We found that at the beginning, the resources were abundant, and the number of fungi A increased much faster than that of fungi B because fungi A was more competitive. When we changed the water distribution, their relative advantage changed due to their different moisture tolerance, so fungi B grew faster and occupied more area than fungi A. But without the supplement of organic matter, both species of fungi eventually tended to be dormant.

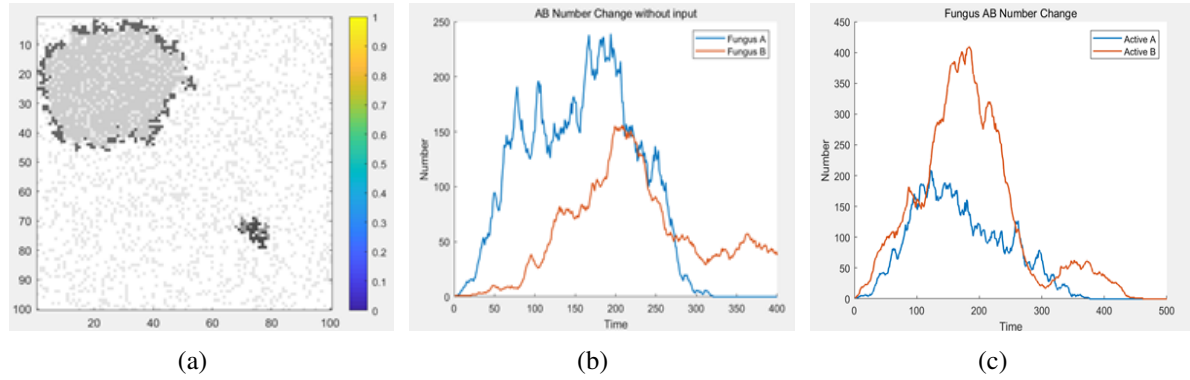


Figure 6: (a)The extension area of both fungi (b)The number of both fungi over time (c)The active number of both fungi over time

From the perspective of competition intensity, we can find that in the early stage, the space was sufficient and the competition intensity was relatively small. Both the number of fungi A and B showed an increasing trend. But in the long run the competition intensity increased as can be seen from the figure. In addition, the extension rate of fungi A and B both slowed down. The number of active fungi B even decreased.

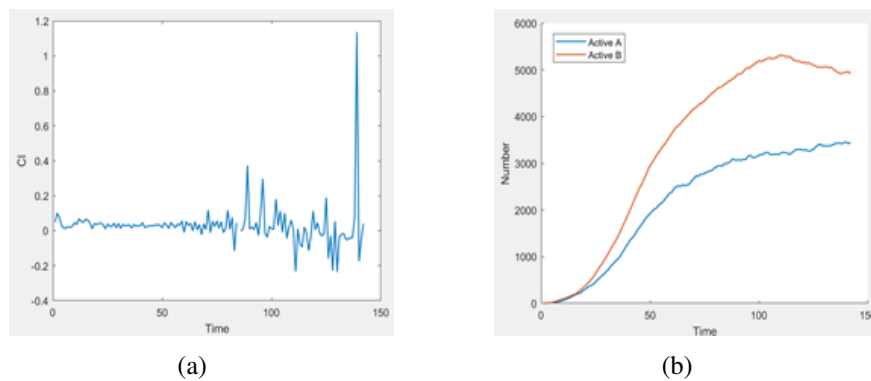


Figure 7: (a)Competition intensity over time (b)The number of both fungi over time

If there is competition, there must be some kind of fungi to take advantage. Thus we introduced the concept of dominance degree, which is a measure of the comprehensive situation of the population at a certain time. It is expressed as

$$d_i = (n_i, D_i, t) \quad (28)$$

where n_i is the proportion of the number of living fungi, D_i is the extension rate D_i , t is time. And abiotic factors influence dominance by influencing n_i, D_i .

Thus we have our quantitative comparative advantage model. Introducing dominance degree in the cellular automata model, we analyzed from the extension process and dominance degree. In the early stage with the same initial number, fungi A extended rapidly and had the dominance degree significantly higher than fungi B. But due to the interaction of fungi in the face of limited resources, fungi B had higher dominance degree in the later period of time.

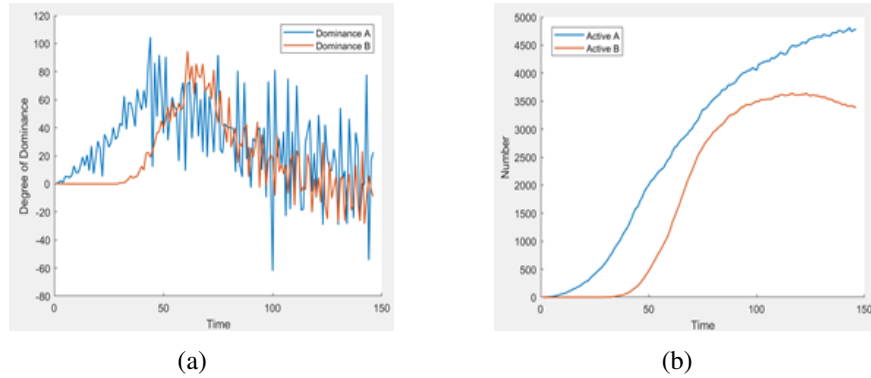


Figure 8: (a) Dominance degree over time (b) The number of both fungi over time

To predict the relative advantages and disadvantages for each species and combinations of species, we adjusted the parameters of the model to simulate five different environment types and performed simulation under these environment types, in addition to the simulation and comparison of fungal extension under the same conditions. It should be noticed that the litter supplement were taken into consideration here.

The environment types and corresponding environment parameters are shown in the following table.

Table 5: The environment types and corresponding parameters

Environment	Moisture	Temperature	Litter supplement
Arid	0.1	0.7	0.04
Semi-arid	0.3	0.7	0.06
Temperate	0.5	0.3	0.10
Arboreal	0.6	0.2	0.15
Tropical rain forests	0.8	0.8	0.20

We show the results in arid areas below.

In arid areas, both fungi A and fungi B could survive well in the case of existing alone, and the number of fungi B eventually stabilized at about 5000, while fungi A at about 2500. When fungi A and fungi B coexisted, then fungi B suffered a sharp decrease in number and even found it difficult to survive because of the existence of fungi A, while A was not greatly affected. In addition, the fluctuation range of the number of fungi A in the face of coexistence was significantly smaller than that of fungi A alone, which meant that the population number of fungi A was more stable.

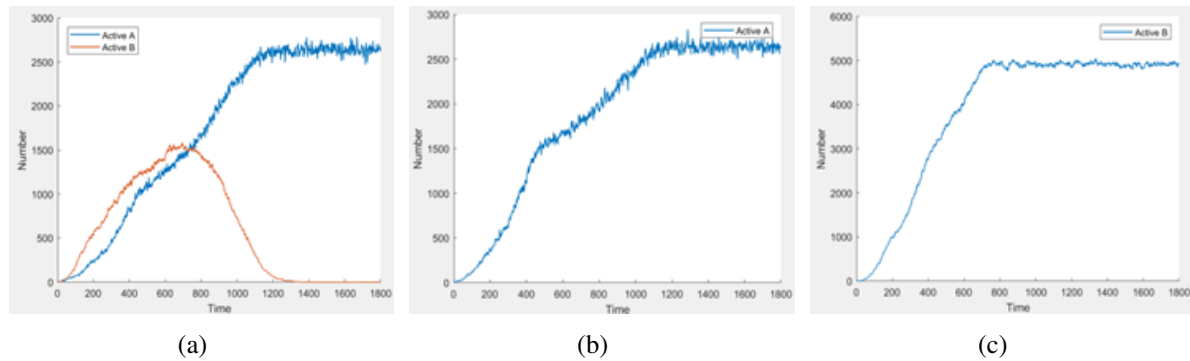


Figure 9: (a)The number of active fungi A and B when both present (b)The number of fungi A if there is no other fungi (c)The number of fungi B if there is no other fungi

A similar analysis of the other four cases (see Appendix for the results) lead us to the following conclusion:

- In the same environment, fungi extend faster when they exist alone. showing a disadvantage if coexist. But if the extension rate is relatively similar in the separate existence, it is less likely to show obvious advantages or disadvantages in the simultaneous existence.
- In the harsh environment, the fluctuation of the number of both fungi is smaller when coexisting than that in the single existence, thus the population is more stable. But when resources become sufficient, the quantity of fungi A and fungi B will fluctuate much more in coexistence than when they exist alone.
- Counting the total number of all fungi in the model, we find that when the environment is harsh, the number of fungi A and fungi B in coexistence is smaller than that of fungi A and fungi B alone. However, when the environment is improved, the number of fungi A and fungi B in coexistence gets closer and closer to that if exist alone. In other words, when the environment is harsh, the coexistence of multiple fungi will reduce the overall decomposition efficiency, while when the environment is suitable, this effect will gradually diminish.

6 Importance of Biodiversity

From the third conclusion above we can see that biodiversity won't matter much to the overall decomposition rate when the environment is more suitable for fungal extension (since all kinds of fungi can extend rapidly), thus improving the waste decomposition efficiency by biodiversity. As for the environment that is not so suitable, in order to improve the overall efficiency of litter decomposition, efforts should be made to try to reduce the number of fungal species to reduce the influence of interspecific competitions. There's need and importance to note that fungal species should not be too few in harsh environments. That's because from the second conclusion above, it is suggested that competition among multiple species helps to reduce fungal population fluctuations and improves the ability to respond to environmental mutations, though it will decrease overall decomposition efficiency to some extent. Therefore, the most appropriate level of biodiversity must be determined in the context of both.

7 Sensitivity Analysis

We conducted a model analysis to observe the sensitivity and adaptability of our model to the mutant environment in the face of rapid fluctuations.

1. Rainfall

Weather factors such as rainfall can cause a sudden rise in ground moisture. We simulated this by suddenly improving the possibility that a cell transformed to water-containing state. Since the soil has good drainage, this state of high water content will not last long time. So after some time(here $100\Delta t$), we set it back as the original level.

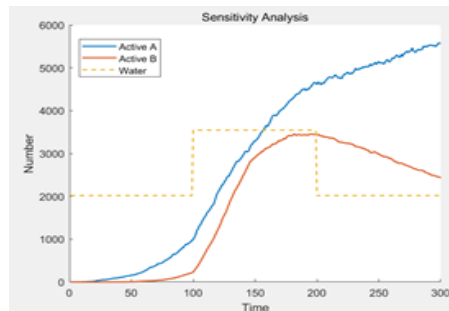


Figure 10: The number of fungi over time

It can be seen that when there was a sudden rise in moisture, the extension rate of both fungi A and B increased rapidly, and when the moisture regained back to the initial conditions, the rates both slowed down, with even drops in the rate of fungi B. This means that both fungi A and B will grow faster with more appropriate moisture conditions after rainfall, but this will also lead to the rapid of resources consumption. That's why there is an obvious slowdown at the end of the precipitation.

2. Litter

In reality, litter such as falling tree branches fall is constantly replenished, or it may be kicked away by animals running by, i.e., litter may mutate. We simulate these cases in our model. First, some cells that were empty were replenished by litter at some point($t = 150$) and converted to wood fiber or other ground litter. Then, at some point($t = 250$), the litter suddenly disappears and some cells became empty.

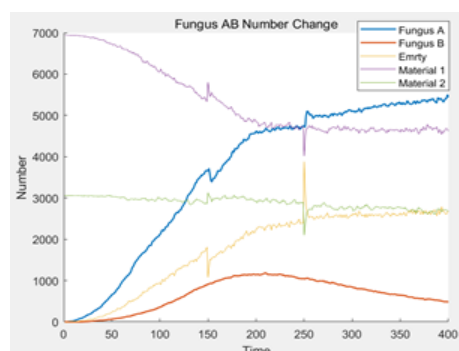


Figure 11: The number of fungi over time with mutant changes in litter

It can be seen that our model is very sensitive to the environmental change, since there is an obvious inflection point on the curve. The number of all the fungi rose sharply when litter increased, while the curve fell sharply when litter suddenly disappeared. But in the long term, this does not affect the steady population of fungi. This shows that our model is both sensitive and stable, and the obtained results are robust.

3. Temperature

To determine the overall impact of changing atmospheric trends to assess the impact of variation of local weather patterns, we introduced the temperature factor in our rules. Here we used for simulation the temperature data which increased with the year of Afghanistan obtained from literature to show its advantages.

One of the advantages of our model lies in the introduction of temperature factor. As can be seen from the comparison in the figures below, the introduction of temperature factor made the model more sensitive to the rise of temperature. With the rise of temperature, the extension probability of fungi increased and the coverage area expanded, while the overall trend remained stable, showing a combination of sensitivity and robustness.

It can be seen that our model has good robustness for the environment of rapid fluctuations.

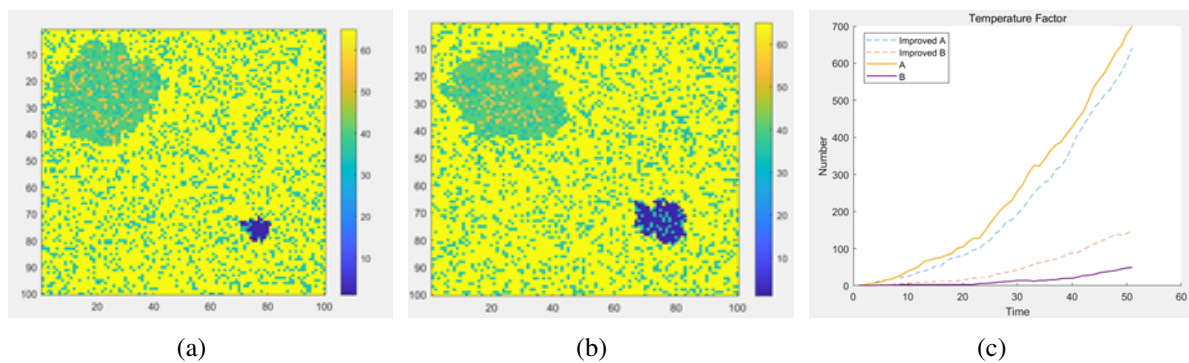


Figure 12: Subfigure (a) is the covered area without temperature factor; subfigure (b) is the covered area with temperature factor; subfigure (c) is the comparisons of the number of fungi over time with and without temperature factor.

8 Strengths and Weaknesses

8.1 Strengths

- All values in the models are determined according to real research data, so the models are close to reality to the greatest extent.
- We adopted two models, which respectively reflect the advantages of quantization and visualization and complement each other.
- In the cellular automata model, we tried our best to simulate the reality, taking into account many influencing factors and the results of the model have a strong realistic reference.
- Cellular automaton model reveals the mechanism of interaction between fungi well, and the simulation results are in good agreement with the real situation.
- Our models can be extended to the decomposition process by multiple species of fungi, providing a reference for the follow-up research.

- Our model has good environmental adaptability. By inputting the local environmental parameters into the multiple linear regression model, we can obtain results which can be used to determine the initial value of the cellular automata, thus simulating the fungal decomposition and competition process under any environmental conditions.

8.2 Weaknesses

- The competition relationship is simplified into a mutually exclusive mode, but in practice, the competition states of fungi are varied, depending on environmental conditions such as resource state, carbon and nitrogen content, respiration, etc., and fungi may exist in a symbiotic state.
- We didn't quantify the interactions and diversity in this model.
- Model assumptions have been simplified and may not match some real cases.
- We ignored the role of other microorganisms in the environment.

8.3 Promotions

We tried to figure out a more accurate relationship between the parameters in the model and real data about the environment, but with time limited, we just gave a roughly corresponding relation and the coefficients, and there was no in-depth analysis of the relationship between some variables. For example, we focused more on establishing relationship between P_g and the environmental variable, thus failed in digging into the relationship between Δt and the environment. What's more, although our model could simulate the coexistence of more species of fungi, we only simulated two species here. So next, we will improve the estimation of parameters in our model to make it closer to the actual situation, and we'll analyze the situation in the presence of more species of fungi to further explore the importance of biodiversity.

9 Conclusion

In this paper, a multiple linear regression analysis was used to analyze the existing data, and the function of fungal extension rate and decomposition rate was obtained, which provided a basis for parameter setting of the subsequent model. In order to further explore interactions between different species of fungi, we established the cellular automaton model with a series of set rules to optimize it. We also established a series of sub models for parameters estimation, making our model reproduce the actual circumstances of the fungal extension to the greatest extent. In the end, the data got from the simulation was analyzed, showing the complex interaction between different species of fungi in the face of changing environment. Thus we forecast the importance of biodiversity in different environment, and provided a direction for improving the degradation efficiency of microbial waste in different areas.

Article

Fungi are a kind of eukaryotes which are different from animals and plants. They are widely distributed on the earth's surface. Whether in mountains, forests or plains, there are fungi. Fungi propagate through spores, and the reproductive hyphae extend at an extremely rapid rate. Fungi are a wide variety of species. There are over tens of thousands of known species, which is a broad field of research for people.



Fungi have a strong ability to decompose and they play a vital role in the natural cycle. The decomposition of wood is largely dependent on the decomposition by fungi, making fungi an important part in maintaining the carbon balance of nature.

Recently, we have obtained an approximately multiple linear relationship between the decomposition rate and three factors as temperature, humidity and carbon content of organic matter through the analysis and fitting of a large number of data. In addition, Nic Lustenhouwer *et al.* also proved a linear relationship between the logarithmic value of the decomposition rate and hyphal extension rate. Based on these two linear relationship equations, we derived the function of fungal community's radius over time as

$$R(t) = \left(M + \frac{A}{B}\right) \cdot t + \frac{1 - e^{-At}}{A}$$

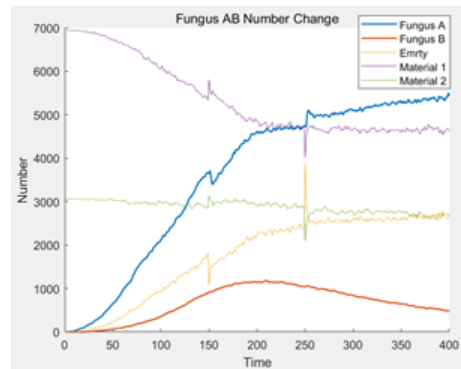
and the function of carbon content over time during decomposition process by fungi as

$$C = e^{-At + \frac{A}{B}}$$

where A, B, M are all constant.

Notably, fungi seldom appear alone in nature. There are often dozens of fungi in the same soil. They interact with each other and jointly maintain the dynamic balance of the ecosystem. The mechanism behind this balance is usually extremely complex. Beside the interaction between environmental factors and fungi, there are also complex interactions between fungi themselves. Recently, we have revealed this secret interaction mechanism through our **cellular automaton model**. By setting a series of rules, we simulated in a computer the dynamic extension process of two species of fungi with different traits. Here are a few of our findings:

Firstly, when the organic matter in the soil deviates from the original concentration, fungi will immediately answer with a mutation in its number which fluctuates accordingly, making the change of soil organic matter return to the original trend after a period of time. And the number of fungi will also return to normal after the short fluctuation. Here we raised and lowered the concentration of organic content respectively when $t = 150$ and $t = 250$ and simulation results are shown in the figure.



Secondly, fungi are very sensitive to environmental changes in the short term. When confronted with sudden changes in environmental factors such as sudden rain, cold wave and so on, their total number and competition intensity will all be affected, but all of these will return to normal and stable state during the long term, which reflects the environmental adaptability of fungi and makes the fungal decomposition persistent and stable.

Thirdly, fungal diversity has different manifestations in different environments. Through the comparative analysis of the simulation results, we found that in the harsh environment, fungal diversity would reduce the fluctuation of the total number of fungi, making the colony more stable, while in the more suitable environment it's the opposite.

Finally, for the decomposition efficiency, fungal diversity will reduce the overall decomposition efficiency under harsh conditions, but with the improvement of the environment, this effect will gradually disappear because with an adequate supply of litter and the proper growing conditions, each fungus can extend rapidly.

Traditional studies have often treated the decomposition process of microorganisms as one by a single population without noticing the hidden but significant role of fungi in it. Here we selected the phototypes of the two species of fungi in our model with different decomposing capacities and preference for woody fibers and other ground litter, which allows them to play different roles in different environments despite interspecific competition. As the main decomposers of litter and wood, fungi do play an important role. Unfortunately, relevant studies are still insufficient and incomplete and we look forward to your further exploration and discovery on the basis of our model and our findings.

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Appendices

All the following figures are presented as:

- (a) The number of active fungi A and B when both present
- (b) The number of fungi A if there is no other fungi
- (c) The number of fungi B if there is no other fungi

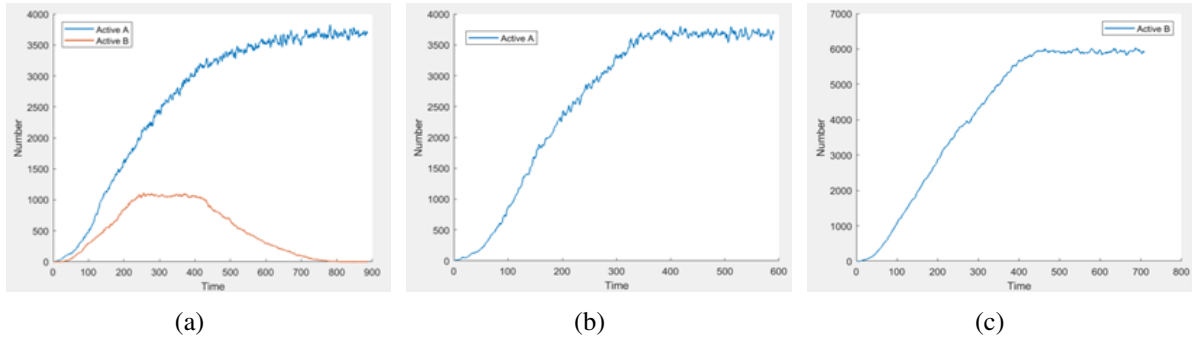


Figure 13: Simulations in semi-arid zones.

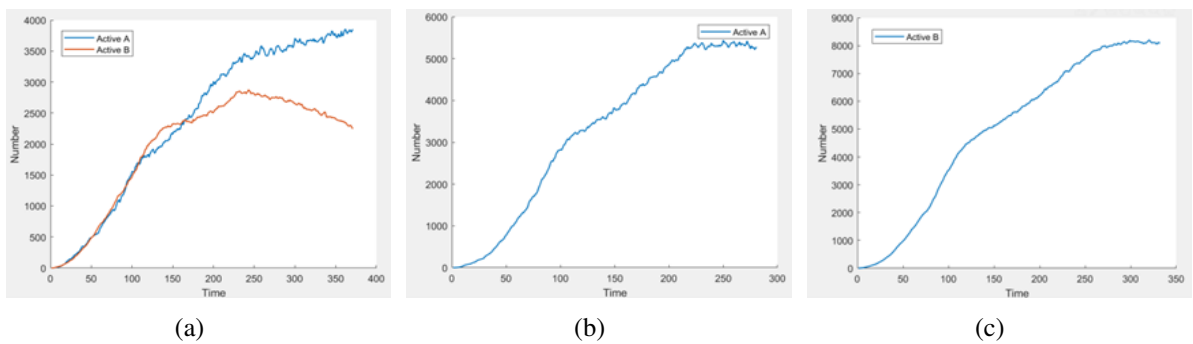


Figure 14: Simulations in temperate zones

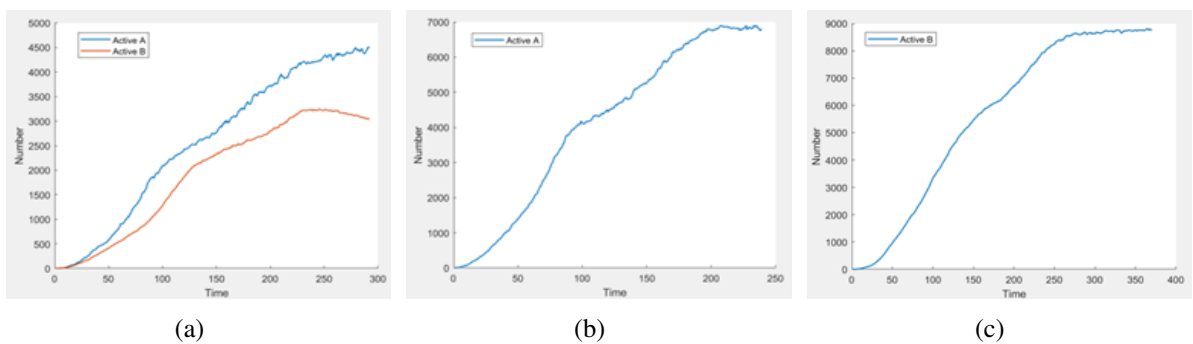


Figure 15: Simulations in arboreal zones

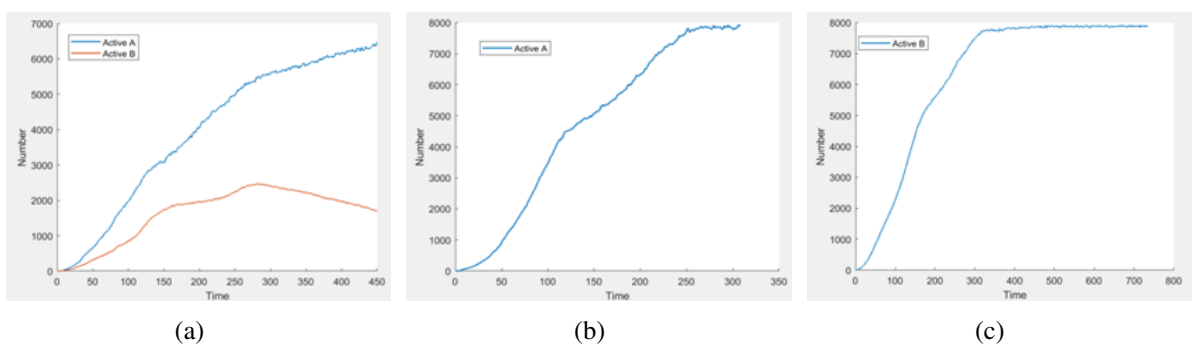


Figure 16: Simulations in tropical rain forests