

# Analysis of Plant Community under Drought

## Summary

Drought is considered as a major natural hazard, and the adaptability to drought varies greatly among plant communities. In this paper, we develop a model to simulate plant community succession under drought and obtain some practical conclusions about the drought adaptation of plant communities.

First, we collect the historical precipitation in a semiarid region and fit the distribution of precipitation to a gamma distribution using **maximum likelihood estimation**. By sampling the **gamma distribution**, we simulate irregular rainfall, which is close to reality. In addition, we develop a **vitality-rainfall model** to describe the relationship between plant reproduction rate and mortality rate as functions of rainfall. The unknown parameters in the vitality-rainfall model are calibrated by taking the quantile of the gamma distribution function.

Second, we developed a reproduction-competition trade-off model to simulate plant community succession by analyzing the relationship between reproduction, mortality and competition of species. At the same time, we propose three indicators to quantitatively characterize the drought adaptation of species: species extinction rate, rate of change in total community abundance and changes in normalized Shannon-Weiner index.

Third, we use the **fourth-order Runge-Kutta method** to predict the changes of plants under various irregular weather cycles. By varying the number of species, species type and frequency and severity of droughts, we can reach the following conclusions:

- Communities need at least six species to benefit from local diversity.
- Communities with mixed perennial and annual distributions have better drought tolerance, and communities with all perennials are the least drought tolerant.
- Higher frequency and more severe droughts not only reduce the abundance of the vast majority of plants, but also make the community less stable, while lower frequency droughts enhance the community's resistance to drought.

Fourth, based on the **reproduction-competition trade-off model**, we explore the effects of habitat destruction on plant communities by changing the proportion of points within the community that are suitable for plant survival. We discover an interesting phenomenon: habitat destruction decreases the abundance of superior competitive species and even leads to their extinction. On the contrary, habitat destruction increases the abundance of inferior competitive species (even though the total survival space is reduced).

Finally, we conduct a **sensitivity analysis** on two parameters. The one is the responsiveness of plant vitality to rainfall. The other one is rainfall thresholds. Additionally, we propose suggestions to improve the long-term viability of plant communities.

**Keywords:** Plant Community Succession; Drought Adaptability; Gamma Distribution; The Reproduction-Competition Trade-off Model; Fourth-order Runge-Kutta Method

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# 1 Introduction

## 1.1 Problem Background

In recent years, global drought problem has become more and more severe, which has caused serious impact on human society and natural ecosystem. And as global climate change intensifies, the frequency and intensity of droughts are likely to increase further.

Countries around the world have devoted considerable resources to develop theories and methods to curb drought. Among all the researches, the relationship between drought adaptation and biodiversity of plant community has been one of the hottest topics. Increasing species extinction in recent years is also raising concerns about local biodiversity.

It has been proved that in many plant communities, the increase of species richness has a positive effect on drought resistance mechanism and drought adaptability of the community. To apply this effect to environmental protection or agricultural production practice, we need to understand the mechanism and detailed rules of this effect. We try to establish a model that considers irregular climate cycles, population iteration, interspecific interactions and other factors. We'll explore the number of species, type of species, frequency and severity of drought. Finally, based on the results of the research, we'll also propose practical measures and contribute our efforts to combat global drought problem.

## 1.2 Literature Review

The relationship between drought adaptability of plant communities and biodiversity has been a hot topic in the field of ecology. To obtain accurate and comprehensive conclusions, scholars have performed numerous researches on environmental conditions and plant communities modeling, using a variety of methods.

- **Regional rainfall modeling methods**

Mou, J. (2012) [1] used frequency analysis to sort and classify historical rainfall data, and then calculated the rainfall at different frequencies according to the probability distribution function. Zhang, X. et al. (2017)[2] used the extreme value distribution for local rainfall statistics. Tang, F. et al. (2020)[3] combined a meteorological model to physically simulate the formation process of rainfall. The simulation model can predict regional precipitation for a long time in the future. However, the rich and specialized experimental data required by the method are difficult to obtain.

- **Plant community modeling methods**

Shugart,H.H.(1984)[4] used the dynamic vegetation model (DGVM), which perfectly described the dynamic impact of climate on vegetation. Moorcroft,P.R. et al.(2001)[5] introduced a new type of DGVM called ecosystem demography model. However, DGVMs are too complex, which is not conducive to our modeling solution. Tilman, D. (1994)[6] proposed a reproduction-competition trade-off model. It was based on the competition of plant individuals for habitat resources, and it described the ecological niches of various species in terms of competitive hierarchies. This model is an ecological niche model with

reasonable assumptions, mathematical interpretability and good results. But it does not fully consider the limitation of environmental resource factors.

Recently, more and more researchers are using machine learning methods. Mendoza-Gonzalez,G. et al.(2019)[7] built a machine learning model to predict changes in grassland plant communities by analyzing environmental variables and species richness data. Zhang,J. et al.(2020)[8] adopted support vector machine, decision tree, random forest and other methods with relatively high prediction accuracy. Although ML models are effective, they need a large amount of reliable open-source data to support them.

Exploring the plant community drought adaptability requires quantifying regional drought intensity over time. We also need to study the effects of different drought intensity on population survival and interspecific interaction. These aspects are closely linked to regional rainfall modeling and plant community modeling. After considering the effectiveness, rationality of conditions, and ease of implementation of the above methods, we choose to carry out probabilistic modeling of regional rainfall, and introduce restrictions of water resources into the reproduction-competition trade-off model. We will provide a better method for studying the association between drought adaptation and biodiversity in plant communities.

### 1.3 Our Work

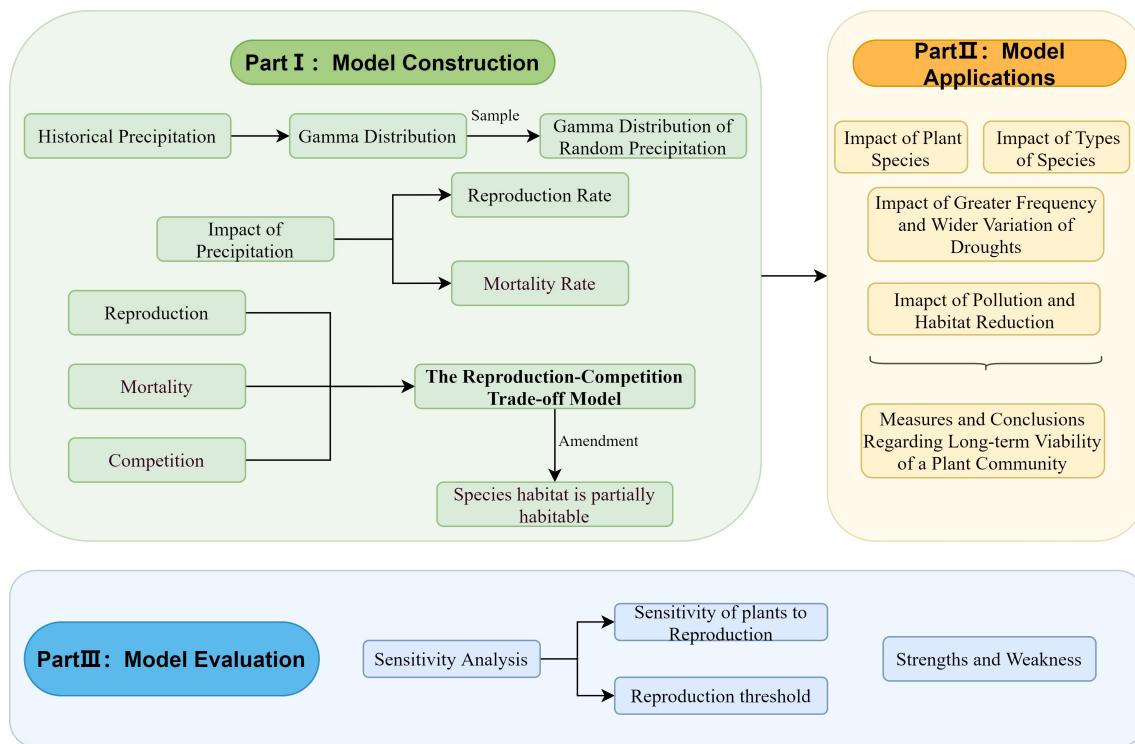


Figure 1: Our main work flow

## 2 Preparation of the models

## 2.1 Problem Analysis

Modeling the response of plant populations with different diversity to random drought conditions, first requires simulations of different degrees of drought. So Our models need to be able to quantify drought with some indicator. The variation of the indicator should have irregular frequency and amplitude changes. Then, links need to be established between drought and some characteristics of the community. Finally, We should establish a community succession model around those characteristics. The succession model should fully consider the constraints of resources and the interaction between species.

To make the weather model and community model close to reality, we should select a specific region to study in order, which makes it easy to obtain local weather and species information. The area should be exemplary and can represent the situation prevailing in drought-stricken areas around the world.

**We selected grassland plant communities in semi-arid area for specific research.** Semi-arid regions, the zone between arid and humid regions, cover 41 percent of the world's land surface and support more than 38 percent of the world's population[15]. Meanwhile, in recent years, semi-arid regions are the most seriously affected area by drought. Grassland vegetation is the most widely distributed vegetation in semi-arid region[16]. Therefore, the region we choose is representative.

So as to explore the long-term adaptability of populations to drought, our models should take longer time periods as time units and have long-term prediction capabilities.

To quantify the change of plant community over time, we need to establish an evaluation index of community survival status. Based on this, the evaluation system of drought adaptability should be proposed.

Since we're required to explore the impact of our recommendations on the environment surrounding the community, our model should also consider the impact on the soil, the atmosphere and the overall ecological cycle.

## 2.2 Global Assumptions and Justifications

Global assumptions are as follows. Some other assumptions are closely related to the model, so they are brought up during the modeling process.

- **Assumption 1: There is only interspecies interaction between plants species. And for the interaction, we only consider competition.** In the grassland zone we study, herbivory is of low intensity[9]. So predation by herbivores is negligible. In grassland plant communities, the interspecies relation between plants is mainly competition. Parasitism and epiphytism are much rarer than competition. And symbiosis mostly involves fungi or animals[10].
- **Assumption 2: In the region we study, plant species compete only for water.** Water is the main limiting factor of grassland plant communities. Moreover, as rainfall variation and drought severity intensify, the limitation effect of water continues to strengthen[11]. Comparatively, other factors such as light and nitrogen are not the main factors limiting plant growth in most semi-arid areas[12].
- **Assumption 3: In the environment of the plant community we consider, water re-**

**sources and each plant population are all evenly distributed within the community.** In a certain range, there is no obvious vertical and horizontal structure of grassland plant community. We therefore believe that: In each plant population, there is no macroscopic clustering behavior. The propagules produced by each species were also randomly dispersed throughout the habitat. In conclusion, all individuals compete for the same amount of water at the same moment.

- **Assumption 4: We define drought as "chronic lack of precipitation or significant lack of precipitation".** Drought can be defined from the perspective of meteorology, ecology and botany. To facilitate data collection and analysis, we choose the definition in meteorology: Chronic or significant lack of precipitation. Thus we use precipitation related indicators to measure the degree of drought.
- **Assumption 5: We ignore the occasion that excessive rainfall inhibits the growth of plant communities.** On the one hand, we analyze rainfall distribution in semi-arid region in subsection 3.1. The result indicates there is little chance of extremely heavy rain. On the other hand, the topic of this paper is to discuss the effects of local species diversity on drought adaptability of plant communities. So we ignore the case of excessive rainfall.
- **Assumption 6: There is no invasion of alien species.** There are too many possible outcomes from invasive species. Moreover, the situation is not common. So it is of little significance for studying the general relationship between drought adaptation and community biodiversity.

## 2.3 Notations

Symbol	Meaning
$p_i$	Abundance of species $i$ in a community at a given time
$r_i$	Natural reproduction rate of species $i$ per unit time
$m_i$	Natural mortality rate of species $i$ per unit time
$cap_i$	Competitive capability of species $i$
$V_p$	Precipitation
$V_{p0}$	Normal precipitation value
$\alpha$	Shape parameter of gamma distribution
$\beta$	Scale parameter of gamma distribution
$loc$	Position parameter of gamma distribution
$k_r$	Sensitivity of reproductive rate to rainfall
$k_m$	Sensitivity of mortality rate to rainfall
$s$	Number of species
$h$	Proportion of species-suitable living areas
$E$	Extinction rate of a species
$C_p$	Change rate of total abundance of community
$H$	Normalized Shannon-Weiner index
$C_H$	Changes in Normalized Shannon-Weiner index

### 3 Comprehensive Model of Community Succession Under Drought

#### 3.1 Probability Distribution Model of Rainfall in Semi-arid Grasslands

The weather in the semiarid zone is complex and variable, with little but not much precipitation. To simulate the irregularity of local rainfall as much as possible, we decide to construct the rainfall probability distribution model based on rainfall data of semiarid zone.

Hailar District, Hulunbuir City, Inner Mongolia Autonomous Region, China, is a typical temperate grassland semiarid zone. We obtained daily precipitation from January 1, 1952 to December 31, 2022 from the Internet [13]. We obtain annual precipitation data of Hailar District from 1952 to 2022 by summatting the daily precipitation of the same year. And the histogram of frequency distribution is demonstrated in the figure below.

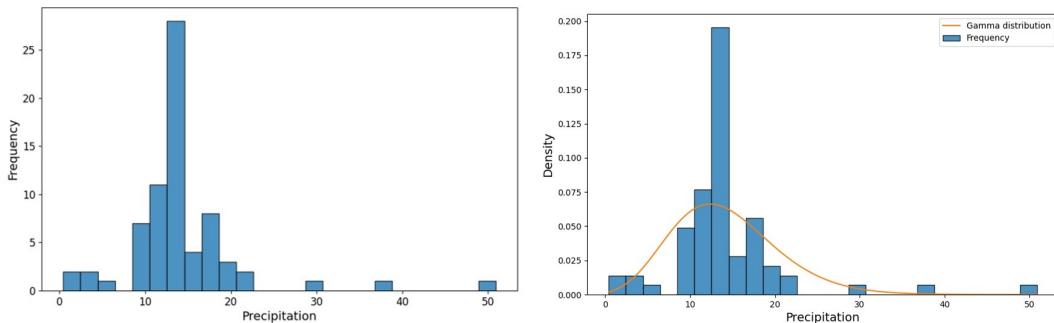


Figure 2: Histogram of precipitation frequency distribution in Hailar District

The left panel of Fig.2 shows that the annual precipitation is likely to fall between 10 and 15mm. The probability of falling below 6mm or above 18mm is small, but the extreme situation may be close to 0mm or 50mm. According to the characteristics of annual precipitation distribution in this region, we fit a gamma distribution. The shape parameter of the distribution  $\alpha = 12.018$ , the position parameter  $loc = -7.456$ , and the scale parameter  $\beta = 1.803$ . The curve of the probability density function is shown in the right panel of Fig.2.

Therefore, we can obtain annual precipitation data of the region by sampling the distribution.

#### 3.2 The Vitality-Rainfall Model

Based on global assumption 5, we do not consider the inhibition of excessive precipitation on plant communities. Under the present conditions, we believe that the reproductive rate of a plant population is positively correlated with precipitation  $V_p$ , while the mortality rate is negatively correlated with  $V_p$ , as shown in Fig. 3.

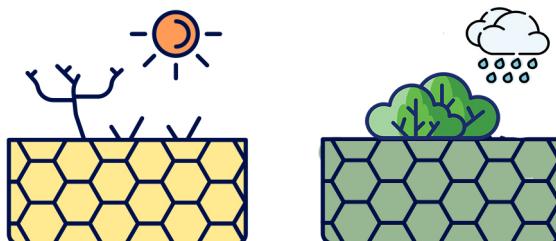


Figure 3: Effect of rainfall on plant vitality

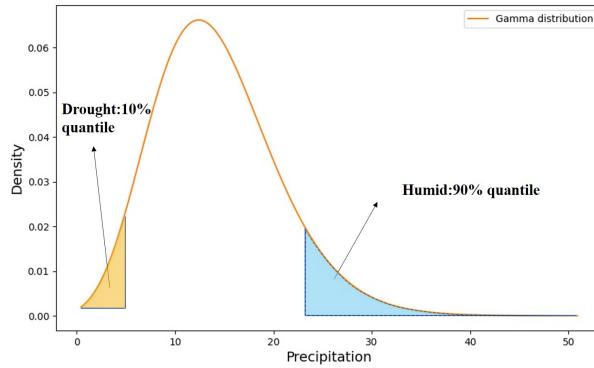


Figure 4: Evaluation of rainfall thresholds, where  $V_{p1}=6.754$  and  $V_{p2}=22.480$

Considering the different ecological characteristics of plant functional groups in grassland ecosystem, Kang L et al. divided grassland vegetation into perennial plants and therophyte[14] according to life history.

Perennial plants are common life histories in grassland vegetation, including some grasses and shrubs. They have long life cycles and complex root systems. Comparatively, therophyte usually thrives during the right season but dies quickly when conditions are harsh. They play an important role in material circulation and energy transfer in grassland ecosystem.

Since the time unit of our model is one year, we believe that the mortality rate of therophyte is 1, while that of perennial plants is within  $[0, 1]$ . And we set the reproductive rate of all plant species within the interval  $[0, +\infty]$ .

When precipitation is moderate, perennial reproductive rate, perennial mortality rate and therophyte reproductive rate do not change significantly with precipitation. So we set all those parameters to constants. However, when the precipitation is very little or very much, the change of the parameters with the precipitation is more obvious. We suppose the relationship to be linear.

Therefore, we believe that the reproductive rate  $r_i$  of perennial or therophyte species  $i$  has the following relationship with precipitation  $V_p$ :

$$r_i = \begin{cases} k_r(V_p - V_{p1}) + r_0, & V_p < V_{p1} \\ r_0, & V_{p1} < V_p < V_{p2} \\ k_r(V_p - V_{p2}) + r_0, & V_p > V_{p2} \end{cases} \quad (1)$$

where  $k_r$  and  $r_0$  are positive constants that vary with species, while  $V_{p1}$  and  $V_{p2}$  are species-independent constants.

Similarly, we believe that the mortality rate  $m_i$  of perennial species  $i$  has the following quantitative relationship with precipitation  $V_p$ :

$$m_i = \begin{cases} -k_m(V_p - V_{p1}) + m_0, & V_p < V_{p1} \\ m_0, & V_{p1} < V_p < V_{p2} \\ -k_m(V_p - V_{p2}) + m_0, & V_p > V_{p2} \end{cases} \quad (2)$$

where constant  $k_m$  and  $m_0$  are positive and species-related, while  $V_{p1}$  and  $V_{p2}$  are species - independent .

We believe that the values of  $V_{p1}$  and  $V_{p2}$  in the two formulas are the same.  $V_{p1}$  is equal to the 10% quantile of the gamma distribution in Fig.2. $V_{p2}$  is equal to the 90% quantile.  $V_{p1}$  and  $V_{p2}$  are shown in Fig.4.

### 3.3 Community Succession Model Based on Reproduction-competition Trade-off

In 3.2, we obtain the relationship between population quantity characteristics and rainfall conditions. To describe the community succession with population characteristics, and introduce the competition between species, we establish a reproduction-competition trade-off model. We first model the change rule of a single population. In the simplest case, we also reveal some important mathematical conclusions. Then the model was extended to an infinite number of species. Finally, we put together a comprehensive model of community succession.

#### 3.3.1 Model Assumption

- Assumption 1: All individuals live in a spatially structured, subdivided habitat.** Each individual in a community exists at a specific point in space. Rather than regarding the community as completely continuous and mixed up, our model treats the space occupied by each individual as a "point" according to the basic principles of niche modeling. The scale of a point is generally less than 3m.
- Assumption 2: At the early stage of succession, the natural reproductive rate and mortality rate of grassland plant communities remain constant.** Before the succession enter the competitive equilibrium stage, we consider water resources to be sufficient, and the limiting effect of water resources on plant population are ignored.

#### 3.3.2 The Reproduction and Mortality Trade-off for Individual Species

**Model Principle** According to global assumption 3, species and resources are evenly distributed. Therefore, when we measure the survival state of a species at a certain moment, we do not consider the spatial characteristics of species, but the quantitative characteristics. According to model assumption 1, the territory of the community is subdivided into points, and the adults of each species can completely occupy a point. The competition rules are demonstrated in Fig. 5

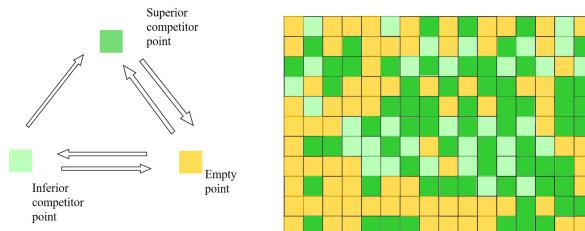


Figure 5: The structure of Reproduction-Competition Trade-off Model

So let  $p$  be the fraction of points occupied by a species. We call  $p_i$  the abundance of species  $i$ . Abundance  $p_i$  can be defined by the following equation:

$$p_i = \frac{\text{the number of points that species } i \text{ occupied at a given time}}{\text{the total number of points in the community}} \quad (3)$$

We used abundance  $p_i$ , natural reproduction rate  $r_i$  and natural mortality rate  $m_i$  to characterize the survival state of species  $i$ .

Let us now consider the simplest case, the primary succession of a monospecies community. At some moment, species  $i$  is the only species in the community. We calculate the change rate of  $p_i$  as follows:

$$\frac{dp_i}{dt} = r_i p_i (1 - p_i) - m_i p_i \quad (4)$$

In equation (4), we call  $r_i p_i (1 - p_i)$  the reproduction term, which represents the process of species  $i$  colonizing glades. It means that the growth rate of  $p_i$  caused by reproduction is proportional to these factors: the reproduction rate, the abundance and the proportion of remaining invasible points ( $1 - p$ ) at the moment. We call  $m_i p_i$  the mortality term, which describes the process by which species  $i$  dies and quits its occupied point. Mathematically, the mortality term represents the rate at which death reduces abundance. It's proportional to the mortality rate and abundance values.

Some other features of the equation also support its plausibility. We assume the monospecies community to start its succession from zero, and we ignore the limiting effect of water at the beginning of succession according to model hypothesis 2. So, let  $p_i$  be 0 at time 0. Let  $r_i$  and  $m_i$  be fixed at different values. The abundance - time graph of species  $i$  is as follows:

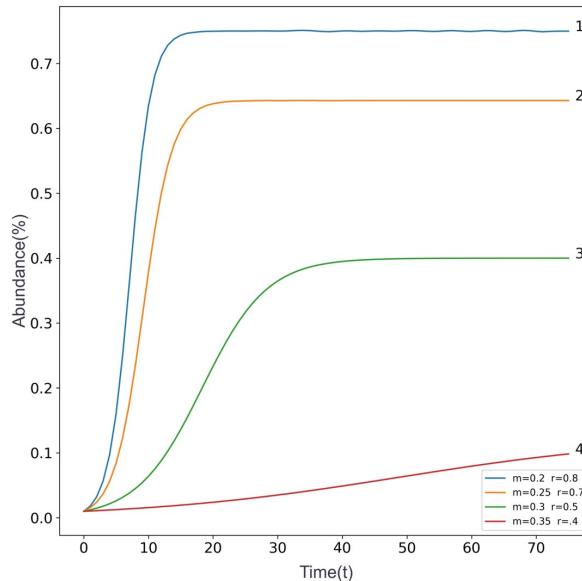


Figure 6: Succession of four species in a mutually independent community

As Fig. 6 shows, when  $r_i$  and  $m_i$  remain unchanged, the abundance of species  $i$  eventually reaches a stable value. Taking  $\frac{dp_i}{dt} = 0$  in equation 4, we solve the stable value of  $p_i$  as follows:

$$\hat{p}_i = 1 - \frac{m_i}{r_i} \quad (5)$$

This equilibrium has the following important implications:

- When water resources are sufficient at the early stage of succession, the species was not obviously limited by water. Instead, the reproduction rate and mortality rate are mainly determined by biological features of the species itself. So  $r_i$  and  $m_i$  remained constant. After the succession began, the abundance gradually increased, and when the abundance value reached  $\hat{p}_i$ , reproduction and mortality reached a balance.

It was not until after equilibrium that water resources begin to play a significant limiting role, which means  $r_i$  and  $m_i$  values begin to change with rainfall. This situation will be discussed in 3.5.

- If  $m_i > r_i$ , then  $\hat{p}_i < 0$ . In other words, even if the resource is rather abundant, species  $i$  cannot survive. Therefore, the species can't contribute to assessing the drought adaptability of the community. So when we solve the model later, we set natural mortality rate less than the natural reproduction rate for all species.

### 3.3.3 The Reproduction - competition Trade-off for Multiple Species

**Model Principle** Based on global assumption 1, we only consider the competition between plant populations. When two species are present at the same point, the superior competitor always replaces the inferior competitor, but the inferior competitor can neither invade nor displace the superior competitor from a single point.

First, we consider a community composed of two species. According to the above theory, if we assume that species  $i$  is the superior competitor and species  $j$  is the inferior competitor. We list the following equation set:

$$\begin{cases} \frac{dp_i}{dt} = r_i p_i (1 - p_i) - m_i p_i \\ \frac{dp_j}{dt} = r_j p_j (1 - p_i - p_j) - m_j p_j - r_i p_i p_j \end{cases} \quad (6)$$

where  $p_i, p_j, r_i, r_j, m_i, m_j$  respectively represent the abundance, reproductive rate and mortality of species  $i$  and  $j$  at a certain moment.

Competition is mainly in the equation for species  $j$ . Compared to the case of individual species, in the reproduction term of species  $j$ , the factor changed from  $(1 - p_j)$  to  $(1 - p_i - p_j)$ . Moreover, a term  $-r_i p_i p_j$  is added.

These changes indicate that, not only the colonization space of the inferior species is squeezed, but also its living space may be directly invaded by the superior species. Compared to species  $j$ , the formula for species  $i$  is exactly the same as equation (4), which means the superior species is completely unaffected by the superior species.

Next, we extend equation  $x$  and  $x$  to the competition of an infinite number of species. We rank the competitiveness of species from worst to best:

$$cap_1 < cap_2 < \dots < cap_i \dots < cap_{n-1} < cap_n \quad (7)$$

Then the equation of abundance change rate for the species  $i$  is:

$$\frac{dp_i}{dt} = r_i p_i (1 - \sum_{j=1}^i p_j) - m_i p_i - (\sum_{j=1}^{i-1} r_j p_j p_i) \quad (8)$$

The factors that affect the dynamics of each population can be divided into internal factors and external factors. For internal factors, we consider reproduction and death. For external factors, we only consider superior species occupying inferior ones.

### 3.4 Drought Adaptation Indicators

To quantitatively represent the changes of plant communities under irregular drought cycles, we propose three indicators to characterize the community's drought adaptation:

- **Species extinction rate**

$$E = \frac{s_0 - s_1}{s_0} \quad (9)$$

where  $s_1$  is the number of species present in the community after experiencing drought weather and  $s_0$  is the number of species present in the community when it is stable.

- **Total abundance change rate**

$$C_p = \frac{\sum_{i=1}^s p_i^* - \sum_{i=1}^s p_i}{\sum_{i=1}^s p_i} \quad (10)$$

where  $\sum_{i=1}^s p_i^*$  is the total abundance of the community after experiencing drought weather and  $\sum_{i=1}^s p_i$  is the total abundance of the community when it is stable.

- **Changes in Normalized Shannon-Weiner index** Normalized Shannon-Weiner index ( $H$ ) is commonly used in ecology to describe species diversity[17]. A higher Normalized Shannon-Weiner index indicates greater ecological diversity and richness within the community.

$$H = \frac{-\sum p_i \times \ln(p_i)}{\ln(s)} \quad (11)$$

where  $p_i$  is the abundance of each species and  $s$  is the number of species.

$$C_H = H^* - H \quad (12)$$

where  $H^*$  and  $H$  represent the normalized Shannon-Weiner index of the community under drought conditions and at equilibrium, respectively.

### 3.5 Model Summary

According to the conclusion in section 3.3.3, rainfall and weather cycles do not play a limiting role for the community, until the species within the community reach equilibrium. Therefore, we divided the succession process of plant community under drought condition into two stages:

- **Stage 1: Initial succession to community stability.** In the early stage of succession, when water resources are sufficient, reproduction rate and mortality rate do not change with rainfall. That is,  $r_i$  and  $m_i$  were fixed, and only the reproduction-competition trade-off model in section 3.3 was involved in this stage.

- **Stage 2: Drought impact stage.** It is assumed that the water resources during this stage are scarce and the reproduction rate and death rate of species will vary with rainfall. The relations of these factors are described by the model in section 3.2. Therefore, it is necessary to combine the two models in 3.2 and 3.3 in this stage:

$$\frac{dp_i}{dt} = r_i p_i \left(1 - \sum_{j=1}^i p_j\right) - m_i p_i - \left(\sum_{j=1}^{i-1} r_j p_j p_i\right) \quad (13)$$

$$r_i = \begin{cases} k_r(V_p - V_{p1}) + r_0, & V_p < V_{p1} \\ r_0, & V_{p1} < V_p < V_{p2} \\ k_r(V_p - V_{p2}) + r_0, & V_p > V_{p2} \end{cases} \quad (14)$$

$$m_i = \begin{cases} -k_m(V_p - V_{p1}) + m_0, & V_p < V_{p1} \\ m_0, & V_{p1} < V_p < V_{p2} \\ -k_m(V_p - V_{p2}) + m_0, & V_p > V_{p2} \end{cases} \quad (15)$$

## 4 Model Simulation Results and Conclusions

### 4.1 The simulation Algorithm

The simulation of the above model is essentially a process of solving differential equations. We use the fourth-order Runge-Kutta method for solving to obtain a more accurate and stable solution. To simulate various irregular weather cycles, we sample the rainfall gamma distribution curve we obtained in 3.1. The detailed algorithm is as follows:

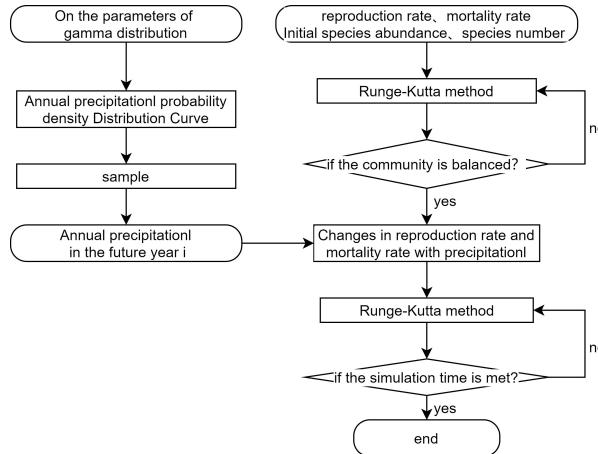


Figure 7: Topographic map of the 2021 Olympic Time Trial course

- **Step0:** Set the initial conditions of the differential equation. Namely, the reproduction rate  $r_i$ , mortality rate  $m_i$ , competitiveness  $cap_i$ , the initial abundance  $p_i^0$  of each species, and the number of species  $s$ . Then we use the Fourth-order Runge-Kutta method to simulate  $p_i$  changing with time  $t$  until the equilibrium was reached between the species.

- **Step1:** Input the parameters of the gamma distribution curve to obtain the probability density curve of annual rainfall, and then get the average annual rainfall in the T-year through sampling.
- **Step2:** Based on each abundance value under the equilibrium state established in Step 0, the species' reproductive and mortality rates start to change with rainfall. The fourth-order Runge-Kutta method continues to be used to simulate the variation of each abundance over time  $t$  under various irregular weather cycles.

## 4.2 Impact of Species Numbers

To explore the mechanism of how several species affects the plant community, in this section, we set each reproduction rate to 0.8. And for each species, we change the mortality rate according to its competitiveness. Then we simulated the succession process of different communities, with the number of species from 2 to 18.

The competitiveness level from high to low is 1, 2..... $s$ . So 1 represents the most competitive species and  $s$  the least competitive. (In the following discussion, we keep using the same way of sorting). Part of the results are shown in Fig.8

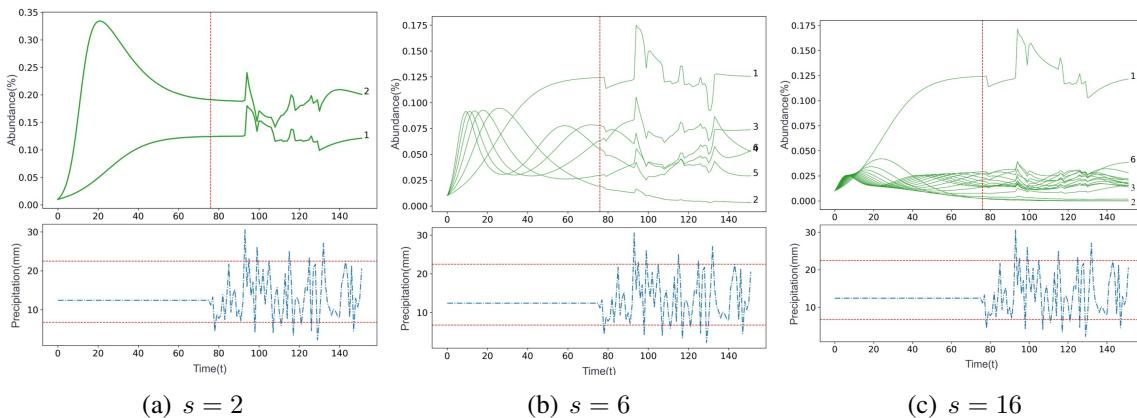


Figure 8: Dynamics of competition among multiple species

where species 1 is the best competitor, and all species have identical reproduction rate ( $r = 0.8$ ), but different mortality rate( $m_i = 0.7 - 0.5 \times \frac{1}{S} \times i$ ,  $S$  is the number of species). All species had initial abundances of 0.01 and the gamma distribution is sampled with the same parameters.

We applied the algorithm in 4.1 to solve the model. The drought adaptability indicators of each community are listed in the following chart:

Species Num	2	4	6	8	10	12	14
Extinction rate	0.000	0.000	0.000	0.131	0.102	0.082	0.141
Rate of change of total abundance	-0.022	0.071	0.104	0.032	0.013	0.035	-0.029
Changes in Shannon-Weiner index	-0.836	-0.608	-0.542	-0.503	-0.486	-0.462	-0.451

## Conclusion:

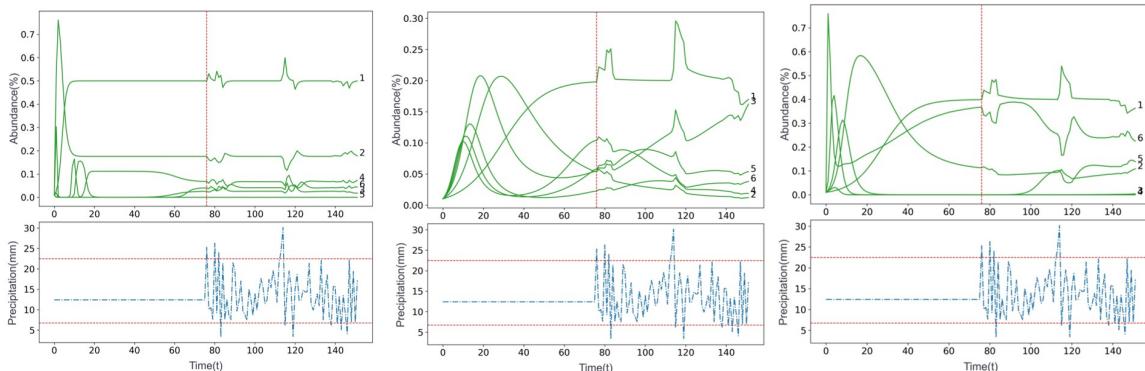
- In various irregular weather cycles, the abundance of each species presents a fluctuation change. The fluctuation change makes species with less abundance more prone to extinction.
- It can be found that Changes in Normalized Shannon - Weiner index increased gradually, indicating the increased community drought adaptability. The total abundance of the community (the sum of the abundance of all species) increased first and then decreased. When  $s=6$ , the index reaches its maximum. Therefore, we believe that at least 6 species are needed for a community to benefit from localized biodiversity. As shown in Fig.8, when the number of species increases, the abundance of superior competitors almost stays around 0.12, while the abundance of other inferior competitors will gradually decrease or even become extinct.

In conclusion, increasing number of species can improve the richness and drought adaptability of community to some extent. This conclusion also explains that herdsmen use perennial grasses, herbages, shrubs, and other plants for planting and replanting, to enhance the drought resistance of grassland.

### 4.3 Impact of Species Type

Based on the above analysis, we set the number of species to 6 in this section, and only changed the composition types of species in the following way:

- All therophyte
- All perennial plants
- Mixed therophyte and perennial plants



- (a) All therophyte  $m_i = 1$  for  $i = 1, \dots, 6$ ,  $r_i = m_i = 1, \dots, 6$ , the value of  $m_i$  decreases as  $i$  increases. Normalized Shannon-Weiner index is 0.659
- (b) All therophyte  $r_i = 0.5$  for  $i = 1, \dots, 6$ ,  $m_i = 1, \dots, 6$ , the value of  $m_i$  decreases as  $i$  increases. Normalized Shannon-Weiner index is 0.4, 0.3, 0.2, 0.15, 0.1, 0.05
- (c) Mixed therophyte and perennial plants. Perennials are 2 +  $25 \times \frac{1}{s} \times i$ ,  $s$  is the number of species. Normalized Shannon-Weiner index is 0.4, 0.3, 0.2, 0.15, 0.1, 0.05. Therophytes are 0.561, so the values of  $m_i$  are 0.2, 0.2, 0.2, 0.1, 0.1, 0.05. Normalized Shannon-Weiner index is 0.2, 0.2, 0.2, 0.1, 0.1, 0.05

Figure 9: Dynamics of competition among multiple species

### Conclusion:

- Based on Fig.9, even if a species is the least competitive, as long as it has a high reproduction rate, it can also occupy much living space in a biological community, which is similar to the "weeds" in a community.
- Normalized Shannon-Weiner index shows that mixed perennial and annual communities have the best drought adaptability, while all-perennial communities are the weakest. This also explains why plants such as trees and shrubs are hard to find in semi-arid regions.

#### 4.4 Impact of the Frequency and Severity of Droughts

We explored the effects of drought frequency and severity by adjusting the distribution of annual precipitation.

In 3.1, the annual precipitation distribution we fit is the gamma distribution. Its mean  $\mu = \alpha\beta$  and variance  $\sigma^2 = \alpha\beta^2$ . When we reduce the value of  $\beta$ , the mean  $\mu$  and variance  $\sigma$  will both be smaller. As a result, the distribution will be more concentrated and its mean will decrease. Then, the probability of sampling a smaller value will increase. That is to say, the frequency and severity of drought will also increase. On the contrary, when we increase beta, the situation is completely reversed.

Therefore, we can control the frequency and severity of drought by changing the scale parameters of the gamma distribution. In this section,  $\alpha = 12.022$ ,  $loc = -7.46$ . We set  $\beta=1.10$ , 1.4, and 1.7 respectively for simulation. The results we get are shown in Fig.10.

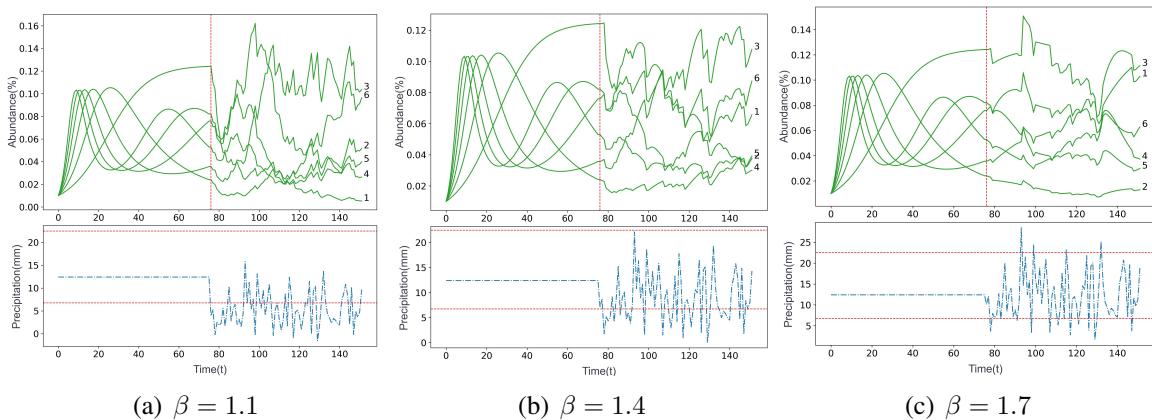


Figure 10: Dynamics of competition among multiple species

#### Conclusion:

- When the frequency and severity of drought increase, the abundance of superior species in the original competition gradually decrease. Superior species gradually lose their competitiveness.
- A certain degree of drought can moderately reduce the competitiveness of dominant species, thereby increasing the competitiveness of relatively inferior species. This results in a more average abundance distribution over species. To a certain extent, biodiversity increases. The above analysis suggests that increasing species richness is one of the ways plant communities can resist drought.

- Very severe droughts can reduce the competitiveness and abundance of most species. Only a few species keep their abundance. This shows that the drought is beyond the range plant communities can adapt to, which is the reason why extremely dry areas have so few species.

In addition, we take  $\beta = 2.0$  to reduce the drought frequency. Other parameters are the same as those in 4.2. The indicators of each community about drought adaptability are in the following table:

By comparing the table in 4.2, it can be found that if droughts are less frequent, the increase in species number will significantly improve the richness and diversity of species, and further enhance the drought resistance ability of the community.

The number of species	2	4	6	8	10	12	14
Species extinction rate	0.000	0.000	0.000	0.125	0.100	0.167	0.143
Total abundance change rate	-0.020	-0.083	-0.065	-0.030	0.009	0.013	0.000
Changes in Normalized Shannon-Weiner index	-0.005	-0.050	-0.040	0.005	0.019	0.034	0.019

## 4.5 Impact of Pollution and Habitat Reduction

### 4.5.1 Model Correction

In section 3.3, we believed that all points in the community were suitable for survival. To explore the impact of habitat destruction on the community, we set the proportion of points suitable for plant survival in the community as  $h$  ( $h$  is between 0 and 1). When  $h=1$ , the habitat was considered to have no damage. The smaller the  $h$ , the more severe the habitat damage.

The corrected reproduction-competition trade-off model is:

$$\frac{dp_i}{dt} = r_i p_i (h - \sum_{j=1}^i p_j) - m_i p_i - (\sum_{j=1}^{i-1} r_j p_j p_i) \quad (16)$$

### 4.5.2 Analysis of Results

We take  $h = 1$ ,  $h = 0.8$  and  $h = 0.6$  respectively. Fig. 11 demonstrates our results.

#### Conclusion:

Habitat destruction or pollution will reduce the amount of living space, which is occupied by superior competitive species, or even lead the species to extinction. But space for the inferior species will increase (even if the total amount of living space decreases). This conclusion can be applied to agricultural production: In farmland ecosystems, if soil gets polluted, it may cause weeds (less competitive species) to occupy more space, or even replace crops (more competitive species).

## 4.6 Measures to Improve Long-term Viability and Other Influences

We believe that the following measures can be taken to ensure the long-term viability of a plant community:

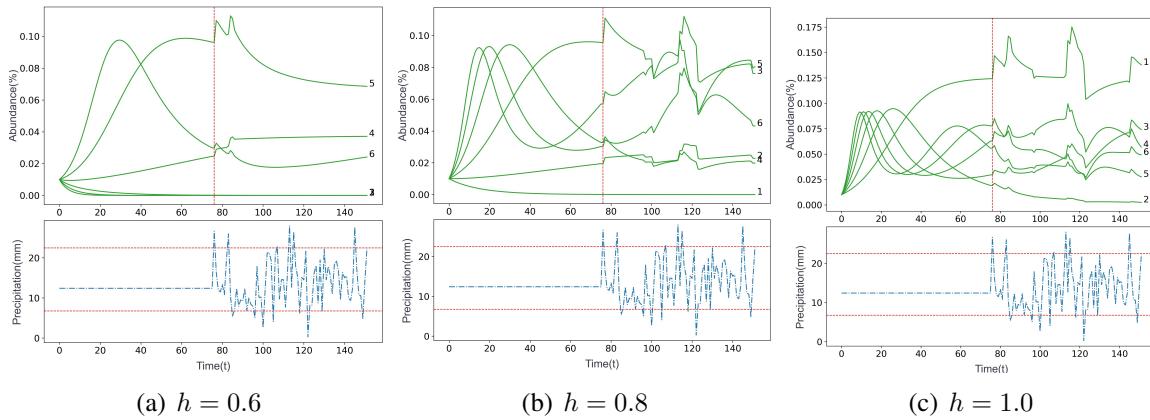


Figure 11: Dynamics of competition among multiple species

- **Plant multiple drought-resistant plant species and pay attention to reasonable combinations.** Based on the conclusions of Section 4.2 and Section 4.3, annual and perennial plants can be mixed. For example, in grassland areas, herders can use perennial grasses, forages, and shrubs for planting and replenishment to enhance the grassland's drought resistance.
- **Reasonable use of water resources.** Based on the conclusions of Section 4.3, the lack of rain or irregular rainfall is the main cause of drought. Reasonable use of water resources, such as rainwater collection and irrigation, can ensure that plants can obtain sufficient water in the absence of rainfall.
- **Protect habitats.** Based on the conclusions of Section 4.5, avoiding excessive development, reducing human interference, and avoiding a reduction in the living space occupied by superior competitive species.

At the same time, the above measures also have many positive impacts on the larger environment, as follows:

- Our measures improve the hydrological cycle. Plant transpiration can release water into the atmosphere, while plant roots can increase soil permeability and water retention, thus reducing the frequency and severity of droughts.
- Our measures improve soil quality and stability. Plant roots can grip the soil and maintain its stability, reducing soil erosion. Meanwhile, the different growth patterns and life history characteristics of different plants can also improve soil fertility.

## 5 Sensitivity Analysis

There are several variable parameters in the model, such as: reproduction rate  $r$ , mortality rate  $m$ , parameters of gamma distribution  $\alpha, \beta, loc$ , proportion of species-suitable living areas  $h$ . In Section 4, we have analyzed the influence of the above parameters on the stability of the model. Therefore, sensitivity analysis mainly focuses on the sensitivity of reproductive rate of species to rainfall  $k_r$ , the sensitivity of mortality rate of species to rainfall  $k_m$  and the threshold

of rainfall  $V_{p1}, V_{p2}$ . It is assumed that plant reproductive rate and mortality are equally sensitive to rainfall, so  $k_r$  and  $k_m$  are identically expressed by  $k$ .

We used Python to plot the curve pf abundances of species, with sensitivity  $k$  ranging from 0.02 to 0.03.

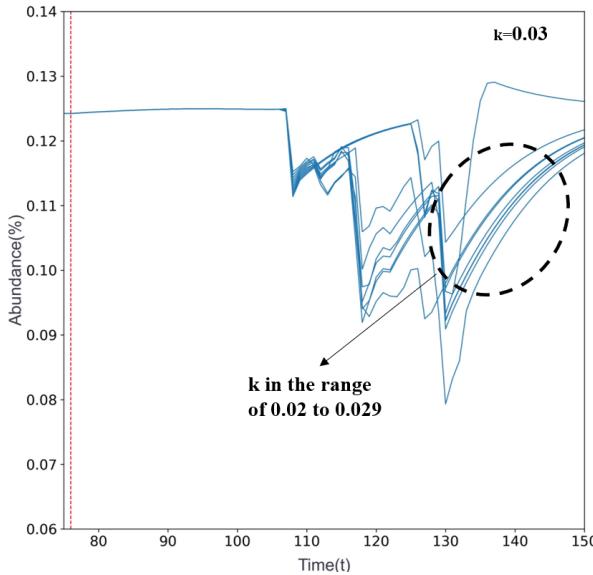


Figure 12:  $k$  within the range of 0.2 to 0.3

As shown in Fig.12, when  $k$  is within the range of (0.020,0.029), each abundance curve shows a similar fluctuation trend. Therefore, the model is stable for  $k$ , and small deviation of  $k$  will not bring great error to model results.

Fig.13 depicts the variation curve of species abundance within the deviation range of  $\pm 3\%$  of rainfall threshold.

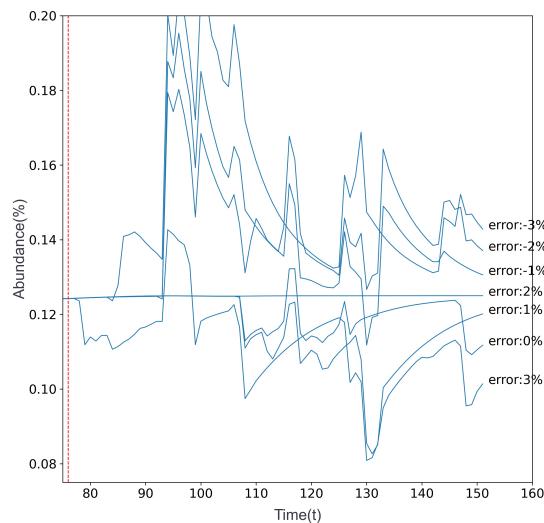


Figure 13: Rainfall threshold within  $\pm 3\%$  error

In the figure, species abundance changes have large fluctuations, especially when the rainfall

threshold is within the range of -1% -3%. Therefore, the model is sensitive to rainfall threshold. It is reasonable to select thresholds based on quantiles of historical rainfall data distribution.

## 6 Strengths and Weaknesses

### 6.1 Strengths

- **Based on mature theory.**

Our model is based on mature theories. For example, the colonization-competition trade-off model belongs to niche models. This kind of model has been developed for decades and has a solid theoretical foundation and wide application.

- **Close to reality.**

First of all, when simulating drought conditions, the model does not simply reduce precipitation but changes the parameters of the precipitation probability distribution, which can better reflect the randomness of local precipitation in the real world.

Second, there are enough parameters in the model to fully consider and describe various factors in real community succession. In the process of solving the model, we also carefully select the values of these parameters and strive to make the model as close to the actual situation as possible.

- **Universality.**

Our model uses a general probability distribution model to simulate precipitation. It also adopts a niche model that is applicable to most grassland ecosystems and is not limited to factors, such as specific plant species. As long as the detailed conditions are slightly modified, it can be applied to all kinds of grassland areas.

- **High Application Value.**

Semi-arid grassland region accounts for a high proportion of land area around the world. With a large population, the area is very sensitive to arid climate, and is the world's main drought disaster area. Our model has a certain significance for solving the problems of grassland degradation, soil erosion and so on.

### 6.2 Weaknesses

- The model does not take into account the effects of animal and microbial populations on plants. Animals feed on and pollinate plants, and some microbes live in symbiosis with plants and change soil composition. These factors are not a major constraint on plant communities in the case we studied, but may play a dominant role in other grassland areas.
- The comprehensiveness of the solution needs to be improved. Different species have different reproductive and mortality rates, as well as different sensitivity to rainfall. There are numerous combinations of these parameters, but a part of them is not considered in Section 4.

### 6.3 Conclusion

This paper analyzes in detail the relationship between drought adaptability and the number of species in a plant community. Before introducing our model, we analyze the characteristics and distribution of historical rainfall data and propose the Vitality-Rainfall Model, the Reproduction-Competition Trade-off Model, and quantitative indicators for characterizing the drought adaptation of communities.

To explore the process of species succession in the community, we use the Fourth-order Runge-Kutta method to solve the differential equations and obtain the change curve of species abundance over time. By changing the number and type of species, frequency and severity of droughts, and habitat area destruction, we have a clearer understanding of the long-term survival of plants in arid areas. And we have also obtained some interesting conclusions. For instance, increasing the number of species can improve the richness and drought adaptability of the community to some extent, but it can also lead to an increase in the extinction rate of species. What's more, communities with mixed distributions of perennial and annual plants have better drought resistance.

Finally, based on the above conclusions, we provide suggestions on how to improve the long-term viability of a plant community, and perform sensitivity analyses on plant reproductive and mortality rates, as well as rainfall threshold values. The analysis demonstrates the robustness of our model and the rationality of its parameters.

## 7 Model Extension and Furthur Discussion

### 7.1 Model Extension

Our model has great extension value and universality. It's a comprehensive model of community succession under the influence of irregular drought. Our model applies to semi-arid regions around the world. The model can be used to simulate the succession of plant communities in another area just by modifying the rainfall probability distribution sub-model, namely fitting precipitation data or other climatic data in that specific area.

Meanwhile, the competition and reproduction of other organisms, such as animals and microorganisms can also be considered in the model, to establish the succession model of the whole biological community under the change of environmental factors.

### 7.2 Furthur Discussion

We believe that our model could be improved in the following ways:

In 3.2, we argued that the reproduction rate  $r$  of all plants and the mortality rate  $m$  of perennial plants were almost constant when the precipitation was moderate. And they had a linear relationship with precipitation when the precipitation was relatively more or less. In practice, however,  $r$  and  $m$  of the same species vary with precipitation at different rates under drier or wetter conditions. Therefore when  $V_p < V_{p1}$  and  $V_p > V_{p2}$ , we can set  $k_r$  and  $k_m$  to be different, as a refinement of the model.

Additionally, the relationship between  $r$ ,  $m$  and rainfall is not smooth, which is inconsistent with the facts. The relationship can be constructed as a smooth functional relationship to improve the model.

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