THE EFFECTS OF ANIMAL GRAZING ON THE MULTIPLE COEXISTENCE AND DIVERSITY OF PLANT SPECIES IN GRASSLAND COMMUNITIES

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THESIS

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草原群落における植物種の多種共存・多様性に及ぼす動物による採餌の効果

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Abstract

Grasslands are perfect examples for plant communities with extremely high species diversity. Many studies have reported that the species richness of grassland is one of the highest among plant communities in the world. In fact, some grasslands win out over tropical forests in terms of diversity on a small scale. By comparison, a small area of grassland can contain more species than that of tropical forests. Occupying one-quarter of the Earth's land area, grasslands become a vital part of the world's ecosystem. The loss of biodiversity from grassland communities may be damaging both the good and services of the ecosystem on which the human population depend. Therefore, preserving grassland's diversity is essential to maintain the ecosystem's processes.

Grazing is an important process in grasslands. In natural, seminatural, and managed grasslands, animal grazers play a significant role in regulating diversity. Extremely high grazing intensity converts grassland to bare land intensively which in turn reduces the diversity. In grassland studies, an intermediate level of grazing often results in the highest species diversity. However, why and how an increase in grazing to a certain point increases the diversity remains an open question.

A few studies have proposed hypotheses to explain this counterintuitive phenomenon, such as a tradeoff of growth and mortality between species. However, so far, we have no convincing theory to explain this unimodal response of species diversity to grazing intensity at an intermediate level. Models built by scientists tend to be limited in representing the existence of a single or a few dominant species. Using these models would be very difficult in modeling the present species diversity. Here, we present a simple model to explain the rich diversity in grasslands. We build a lattice model of a grassland community comprising multiple species with various levels of grazing. We develop a two-layer lattice model, adding

another two-dimensional lattice of grazers that randomly feed on plants. We investigate the effect of grazing in two cases, i.e., tradeoff case and opposite case, which differ in species dependence of grazing mortality. This study also explores the effect of grazing intensity on the species composition. In addition, we examine the effect of varying the dispersal rate and lattice size.

We then analyze the relationship between grazing and plant diversity in grasslands under variable intensities of grazing pressure. The highest species diversity is observed at an intermediate grazing intensity. Grazers suppress domination by the most superior species in birth rate, resulting in the coexistence of inferior species. The coexistence of species is mechanically promoted because (weak) grazing produces vacant sites available for other species. The positive correlation of birth rate and grazing rate (tradeoff case) promotes coexistence better than a negative correlation (the opposite case). However, the tradeoff is not necessary for the unimodal variation of species diversity as grazing intensity increases because the unimodality is observed in both cases. The positive and negative correlation between grazing and growth rate influences the composition of species. The unimodal grazing effect disappears with the introduction of a small amount of nongrazing natural mortality. Thus, unimodal patterns of species diversity may be limited to the case where grazers are the principal source of natural mortality.

Our model contributes new insights into understanding the species diversity in grassland communities. The model can help preserve and manage grassland areas. Adapting our model enables us to examine the other related problems on plant communities. For instance, by modifying the lattice setting, the model can be applied to terrestrial communities with predators in the system. Our results contribute to the field of ecological modeling, ecology, biodiversity especially in investigating the interaction of prey-predator in understanding species diversity of plant communities.

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Abstract

1. Introduction

1.1 Research background

a. The diversity

The diversity of life is the most exclusive and essential property of Earth. More than 9 million species, such as animals, plants, and other species, live on Earth, along with more than 7 billion people [1]. Although it is a unique feature of Earth, diversity has been a long-standing puzzle in science. Identifying and counting living species on Earth have been a never-ending work in progress [2, 3, 4]. A study by Mora et al. found that an astonishing 86% of species on land and 91% in the ocean have not been discovered and cataloged [3]. They predicted that more than 8.7 million species exist on Earth. As we all know, species on this Earth provide food, clean water, oxygen, and other infrastructure necessary for the human population. Thus, it is literally vitally important to give more attention to understanding the diversity on this planet. Many species may vanish before we discover their existence. Many species may be extinct before we know their function in the ecosystem. Many species may disappear before we reveal their potential contribution to the human being.

Extinct and endangered species are continuously reported, while scientists have continuously discovered new species [2, 3, 4, 5]. In every year, scientists keep reporting many new species from all over the world. Although knowing the number of living species is an endless work, having the list of species in our planet is essential for preserving diversity [4]. Understanding how diversity is maintained is also our essential task. Loss of biodiversity endangers the ecosystem, which indirectly threatens our existence [1]. Fortunately, and scientifically interestingly, we can still observe that high diversity is preserved in many areas around the world. Forests, grasslands and seas nurture a great many species to survive in coexistence, contributing to the preservation of biodiversity. Therefore, instead of just focusing on particular aspects of diversity, it is important to elucidate the underlying mechanism of how high diversity is preserved.

To understand diversity, we can classify species based on where they live, that is, biomes. Biomes are defined as the major communities of living organisms, classified based on primary vegetation and characterized by how species adapt to the environment [6]. There are at least four major types of biome covering our planet. Forest occupies the largest area, which covers for around one-third of the Earth's land area. Forest in tropical regions supports a variety of animal and plant species. Characterized by frequent rain, the forest maintains the highest number of species diversity on Earth [7, 8, 9, 10]. In contrast, tundra is a type of land where species are challenging to live in owing to low temperature, low precipitation, inadequate nutrients, and short growing season, [9, 11]. Desert is an extremely difficult place to inhabit. There are two types of desert, hot/dry and cold desert. In the hot and dry desert, most species must burrow to escape extremely high temperatures [9]. On the other hand, most species must burrow to keep warm from extremely low temperatures.

Grassland is the second largest area after the forest. They exist on every continent except Antarctica. Depending on where they are located, grassland areas have several different climates [9]. Characterized by dominant grasses, the areas preserve extremely high diversity. Based on species inhabited in grasslands, these areas can be classified into two types. First is a temperate grassland characterized by dominant grasses, where scattering bushes and shrub are absent typically. In contrast, tropical grassland is known for having not only grasses but also scattering trees. Grassland is located where it is neither too rainy as in the forest nor too dry as in the desert. Grasslands support a variety of species. However, diversity mechanisms on grassland studies remain unclear. Therefore, in this study, we focus on examining the diversity in grassland areas [12].

b. The grassland diversity

Grasslands occupy around one-quarter of Earth's land area, contains a remarkable plant species diversity [13]. Grasslands can win over the forest in a plant diversity competition on a small scale. In the alpine meadow of Qinghai-Tibet plateau located in the basin 3200 m in altitude, around 19 species exist in a 0.01 m^2 [14]. In Romanian grassland of Transylvanian Lowland, 43 species are recorded in a 0.1 m^2 [12]. The new world record in the Krkonoše Mountains in mountain meadow near Malá Úpa, 17 species are observed in only 0.0044 m^2 [15]. The plant species diversity is very crucial to sustain the world ecosystem. For example, Murchison falls national park in Uganda is home to a variety of wildlife species. A survey by Plumtre et al. found that 556 bird species, 144 mammal species, 51 reptile species, 28 known amphibian species, and 755 plant species live in this national park [16]. Serengeti, as another example, is very famous as one of the areas that host the Great migration. The Great Migration is the largest movement of animals on Earth. The animals migrate to do reproduction, to find food, and to survive. Serengeti show an incomparable role of grassland in preserving diversity [17, 18, 19].

c. The significance of grassland plant diversity

Studies on plant diversity have shown that an increase in plant diversity promotes benefits to the grassland ecosystem. Maintaining the species diversity of grasslands is crucial for avoiding productivity loss, affecting ecosystem processes [20, 21]. Hector et al. did a field experiment in eight European sites [20]. They simulated the effect of plant diversity loss on primary productivity. They found different results in detail at each location. However, the results revealed an overall log-linear reduction of average aboveground biomass with loss of species. Plant diversity loss showed a negative effect on productivity. An increase in plant diversity leads to an increase in grassland's productivity [22, 23]. Bradley et al. did a famous study summarized that from 44 experiments of plant richness manipulation in plant diversity on biomass production, mixtures of species produce an average 1.7 times more biomass than monocultures [22]. The result also revealed that higher plant diversity is more productive than monocultures in 79% of all experiments [22]. On the contrary, the degradation of grassland's productivity endangers the global food supply. Livestock products, such as milk and meat, are primary food sources to feed the increasing demand of the world's population [24, 25]. The meat supply from cattle, buffalo, sheep, and goats comprises almost 29% of the global meat supply [24]. An increase in diversity in grassland ecosystems also increases stability through time [26]. Tilman et al. reported that a higher number of plant species led to greater temporal stability of ecosystem production [26]. The decadal temporal stability measured in any interval of time was significantly more considerable at a higher number of plant diversity. The temporal stability tends to increase as plots grown or matured [26]. The study implies that higher plant diversity can recover better than low plant diversity. Also, plant diversity provides resistance to the grassland ecosystem to climate extreme [27]. Isbell et al. showed that biodiversity increases the ecosystem resistance for many climate events, including moderate or extreme, wet or dry, and brief or continued climate events. The study exhibited those plant communities with low diversity, 1 or 2 species, changed by 50% during climate events [27]. In contrast, plant communities with high-diversity, 16-32 species, change by only 25%. The results reported that biodiversity mainly stabilizes productivity by increasing resistance during climate events. Thus, preserving diversity is very important in grassland.

1.2 Research problem

a. Studies in grassland diversity

Previous studies attempted to explain underlying mechanisms influencing the diversity of grasslands. Some studies proposed resource partitioning in promoting diversity in grasslands [28, 29]. Sala et al. showed that resource partitioning contributes to the grassland's coexistence. They made field experiment in Patagonian steppe southern South Africa to test the resource partitioning [28]. It was observed that selective removal of grasses and shrubs affected the plant performance and the availability of soil resources. The result of the experiment confirms the hypotheses that grasses take up most of the water from the upper layer of the soil, while shrubs take up most of the water from the lower layer of the soil [28]. The study suggested that resource partitioning should be considered an important factor affecting the grassland's diversity.

Seed dispersal is also an essential factor affecting the coexistence of multiple plant species [30, 31, 32]. Using hierarchical data on species pool, Vandvik et al. quantified distances to the potential source of seed for occurring recruits in target communities [31]. With different successional histories, the dispersal contributed 29%-57% of the seedling diversity in perennial grassland [31]. This study demonstrated that seed dispersal plays a vital role in preserving diversity. Another factor that positively affects diversity is environmental heterogeneity, which exists in natural systems, including grasslands [33, 34, 35, 36, 37]. Two adjacent soil can be different in nutrient and water [37]. Tubay et al. showed that the specificity of species and sites in the environment is responsible for maintaining diversity in plant communities, including grassland [36]. However, all the studies concluded the role of niche differentiation in regulating species diversity without explicitly taking the role of grazing into account. Grazing is a ubiquitous feature in grassland. Many empirical studies indicated the essential role of grazing. To deepen our understanding of the grassland's coexistence, we focus on the grazing effect as the major target of our study.

b. Grazing in grasslands

Intermediate grazing intensity was observed to result in the highest species diversity in many natural, semi-natural, and managed grassland studies. Extreme grazing converts grassland to bare land by reducing the species diversity. However, empirical studies showed that the increase of grazing intensity increases the species diversity in some grasslands. A study by Komac et al. found that in five types of grassland communities of Andorran mountains, intermediate grazing intensity was observed to produce higher functional richness species diversity in the grassland [38]. The study also reported that grazing provides higher functional richness in most grazed communities [38]. Mu et al. compared plant species diversity and nectar production at individual and community plant levels in several grazing levels, e.g., heavily grazed, moderately grazed, lightly grazed and ungrazed in Tibetan Alpine Meadow sites [39]. The results revealed that the production of nectar was significantly higher in lightly and moderately grazed areas than in heavily and ungrazed areas at floret, individual, and community levels [39]. The results are in line with the traditional view that light and moderate grazing promote biodiversity. The results also suggest that traditional grazing is more environmentally friendly in maintaining biodiversity [39]. Niu et al. compared species richness between moderately grazed land and ungrazed land. The species richness was higher at moderately grazed, which indicates that a moderate level of grazing increases species diversity [40]. A study by Joubert et al. compared different sites in Afromontane grasslands with different levels of grazing (light, moderate, and heavy) [41]. Based on their findings, moderate grazing should be considered to maintain diversity in grassland. Besides, heavy grazing indirectly influences species richness in Inner Mongolian grassland sites [42].

Although previous empirical studies have indicated the role of intermediate grazing intensity or an increase in grazing intensity led to higher plant diversity, the explanation of how and why grazing intensity results in the highest species diversity remain an open question.

c. Vegetation modeling

In studies of modeling the coexistence of vegetation, the lottery model is recognized as one of the earliest models. The lottery model is based on a lottery mechanism in which there are no species that can consistently win. The model is applied to species coexistence such as to show environmental variability as an essential factor in promoting diversity [43, 44, 45, 46]. However, this model for species coexistence would lead to competitive exclusion for a long-time period [36]. The models can sustain only a small number of species and a more complicated model is required to accounting for multiple species. Therefore, the lottery model does not meet our requirement for examining the effects of grazing in understanding grassland’s coexistence. Besides, we also need a spatial representation in order to examine plant species coexistence [36]. Lattice models have been widely used in modeling vegetation. Incorporating the lattice and Lotka-Volterra model, Tainaka showed the coexistence mechanism of competing species [47, 48, 49, 50]. Tainaka's models exhibit that the lattice model is proper for modeling coexisting species. Kakishima et al. modified the lattice model [47, 48, 49, 50] to examine how seed disperses play its role in maintaining tree species coexistence [51]. The model represents the plant dynamics in the presence of the seed disperser and shows that animal disperser can promote the coexistence of tree species. The model of Tubay et al. is also another example of the lattice model for studying the species coexistence [36]. They incorporated the lattice and Lotka Volterra system to show that spatial heterogeneity promotes plant diversity in plant communities. Tubay et al. and Kakishima et al. were able to show coexistence of multiple species avoiding competitive exclusion over a long-time period [36, 51]. Therefore, we can examine the effects of grazing by modifying these lattice models for grassland species coexistence. In this study, we modified the previous lattice models by introducing grazing effects to examine the species diversity in grasslands.

1.3 Study purpose

Here, we introduce grazing effects into a lattice model of a grassland community to examine how species diversity is affected by grazing intensity. Following the lattice community model of Tubay et al., we develop a two-layer lattice of grassland community consisting of the plant layer and animal/grazer layer [36]. The plant layer is to show the competition of plant species. The grazer layer represents the animals that move randomly to graze on plant species. Grazing involves both the grazer and the plant layer. In nature, grazers have a high diversity in terms of body size, grazing period, preference on a plant, and herd size. It would lead to a complicated model to take account of grazer diversity. Therefore, as a canonical model, we consider the animal's preference to plant species as an important factor of the grazing process. The relationship between the grazing rate and the birth rate is also considered important for grassland species coexistence. Using our model, we examine the effects of animal grazing on grasslands and analyze the underlying mechanism of these effects on the species coexistence in grasslands. According to observations, the intermediate grazing increases the number of plant species as compared with low and high grazing intensities. The results shown below reveal a unimodal grazing effect, which disappears with the introduction of nongrazing natural mortality. We discuss the mechanism of intermediate grazing intensity to achieve the highest diversity.

2. The model backgrounds

Most terrestrial plant communities usually comprise a population of multiple species [33, 52, 53]. Natural single species community, preserving only one plant species, is rarely found in nature [33, 52, 53]. Accordingly, the coexistence of many plant species is an inherent property of plant communities. The existence of multiple plant species in the same area causes competition for resources. They usually compete for common limited resources, such as water, nutrient, and light [53, 54]. The competition for limited resources can lead to collapse of plant communities and species extinction. Previous mathematical and simulation studies proposed several model hypotheses for how species coexist.

2.1 Lotka-Volterra model

Studies with population dynamical models have shown the exclusion of other than a single species among multiple species, which is commonly referred to as the competitive exclusion principle [55, 56]. The principle stated that two species competing for a common resource cannot stably coexist and only one species survives. Most of the existing population dynamical models lead to the dominance of a single or few species. To take account of multiple species' coexistence requires a more complicated mathematical model [56]. The Lotka-Volterra model is one of the famous models in understanding the population dynamic of species. The model describes a temporal variation in population as a result of interaction between predator and prey. Mathematically, the model is described as a pair of nonlinear differential equations

$$\frac{dx}{dt} = \alpha x - \beta xy$$

$$\frac{dx}{dt} = \delta x - \gamma xy$$

where x and y denote the population numbers of the prey and predator respectively. $\alpha, \beta, \delta, \gamma$ are the parameters for the interaction of the two species. However, this model is not sufficient to understand how multiple species can coexist as we can observe in many plant species communities [33, 52, 53].

2.2 Niche differentiation

Some previous studies proposed hypotheses to allow for the coexistence of competing species in plant communities. Niche differentiation is one of the famous theories that elucidating this phenomenon. The niche theory stated that competing species could survive if they use their niche distinctively or have a different niche to prevent competition with other species [53, 57, 58, 59]. Factors promoting coexistence such as symbiosis, specific tradeoffs, and extrinsic factors are necessary to avoid extinction [33, 52, 53]. However, without such factors observed, we still can discover high diversity in forests and grasslands [37, 59, 60]. Tilman identified that environmental variation could promote the coexistence of tree species [33, 52]. Terrestrial plant communities are observed to have a very variable soil system [61]. The distinct in two soil samples usually because of litter difference in dead leaves and dead animal, derbis and so on [37]. The variation in soil affects the establishment rate of plant species. Takenaka's model demonstrated that the seedling establishment rate affects the tree species diversity [45]. Takenaka's result is in line with other leading studies of spatial heterogeneity on coexistence [43, 44, 46]. However, the previous studies adapted lottery model, maintaining only a few plant species in a shorter time frame.

2.3 Lottery model

The lottery model is first proposed by Sale in 1977 [62]. This model assumes that propagules occupy a certain site is based on a lottery in the basis of first come first served. The chance of a species establishing a vacant microsite is simply a function of the proportion of all progapules produced by that species in that year as shown in the following $L_i\ /\sum_{j=1}^{k} L_j$ where L_i and L_j is larvae or propagules of species i and other species respectively [63]. Chesson and Warner (1981) adopt this model to build a lottery competitive model [43]. One of the models is as the following:

$$P_i(t+1)=\left[1-\delta(t)\right]P_i(t)+\left[\sum_{j=1}^{k}\delta_j(t)P_j(t)\right]\left[\frac{\beta_i(t)P_i(t)}{\sum_{j=1}^{k}\beta_j(t)P_j(t)}\right]$$

where the parameters $P_i\ (t)$ denotes total proportion of homes occupied by species i at the time t, $\beta_i\ (t)$ denotes per capita net production of species during $(t,\ t+1)$ and $\delta_i\ (t)$ denote proportion of adults species i dying during $(t,\ t+1)$. $K\sum_{j=1}^{k}\delta_j\ (t)P_j$ is the total number of homes or sites available for new recruits. Recruit of species i take up the proportion of $\beta_i\ (t)P_i(t)/\ K\sum_{j=1}^{k}\beta_j\ (t)P_j$ of the space. Therefore, according the lottery model, which species to survive is based on the proportion of all species produced by the species in time t to the available sites. Thus, using a lottery model is also not satisfactory to capture the nature of the grassland's species coexistence.

2.4 Lattice model

Lattice model consist of points distributed over a lattice. The species dynamics in the lattice model is regulated based on assumption from biological systems such Lotka-Volterra system. Tainaka et al. is known as one of the first studies that used lattice model on species coexistence [47, 48, 49, 50]. They incorporate lattice model and Lotka Volterra system to examine the mechanism of species coexistence. The built model is also known as lattice competition system which is a discrete version of the Lotka Volterra competition model. The model only used the system of Lotka-Volterra in a discrete way.

Kakishima et al. applied multiple layers to model the coexistence of tree species given animal disperser [51]. The model represents the interaction dynamics between tree communities on one layer given the existence of disperser on the other layers. Tubay et al. used one two-dimensional lattice or layer and incorporate Lattice-Volterra system to represent the plant species competition and spatial heterogeneity of plant species' coexistence [36]. The model assigns random settlement rate over the lattice site for spatial heterogeneity. The settlement rate to represents the germination and seedling success of seed. Tubay's model maintains at least 15 species when species-specific heterogeneity is introduced in the settled plans' mortality rates [36]. Lattice model is more suitable for modeling the multiple species coexistence because this model is possible to represent many species and describe the dynamic interaction.

2.5 The contact process

In this study we also applied multiple-species contact process for overal dynamics of the model. The contact process is a stochastic process used for population growth on set of sites [64]. The occupied sites become vacant and vacant sites become occupied at certain rate. Many previous lattice models used this contact process to show the overal dynamics. For example Tubay et al. used the following multi-species contact process such that:

$$X_i + O \rightarrow X_i + X_i, \quad \text{rate: } b_i$$

$$X_i \rightarrow O, \qquad \text{rate: } d_i$$

where X_i denotes plant species and O denotes vacant sites [36]. X_i occupies vacant site O at rate b_i or birth rate. Or, X_i can become vacant site at rate d_i or mortality rate. We also used this kind of contact process for the overal dynamic of our model.

The previous models and hypotheses have not shown a multiple plant species competition given predator in the system in grassland's species coexistence. In this study, we follow and modify previous lattice models [36, 47, 48, 49, 50, 51]. We include the grazing process by introducing a grazer layer. We consider dispersal and environmental heterogeneity in the model. Our model can represent grazing, a common feature of grasslands, to fill the knowledge gap in understanding the underlying mechanism of plant species diversity in grasslands.

3. Methods

3.1 Lattice Model

The lattice model consists of lattice points distributed over lattice cells. In our model, the lattice points represent sites inhabited by plant species. Each individual is assumed to interact (compete) with their neighbors. They compete for limited resources e.g., nutrient, light, and water [36]. In this study we introduce a grazing effect due to the presence of predators. The plant species are not just competing with their neighbors but also should survive the animal grazing. Therefore, our lattice model consists of two layers, a plant layer X and a grazer layer Y (Figure 3.1a, b).

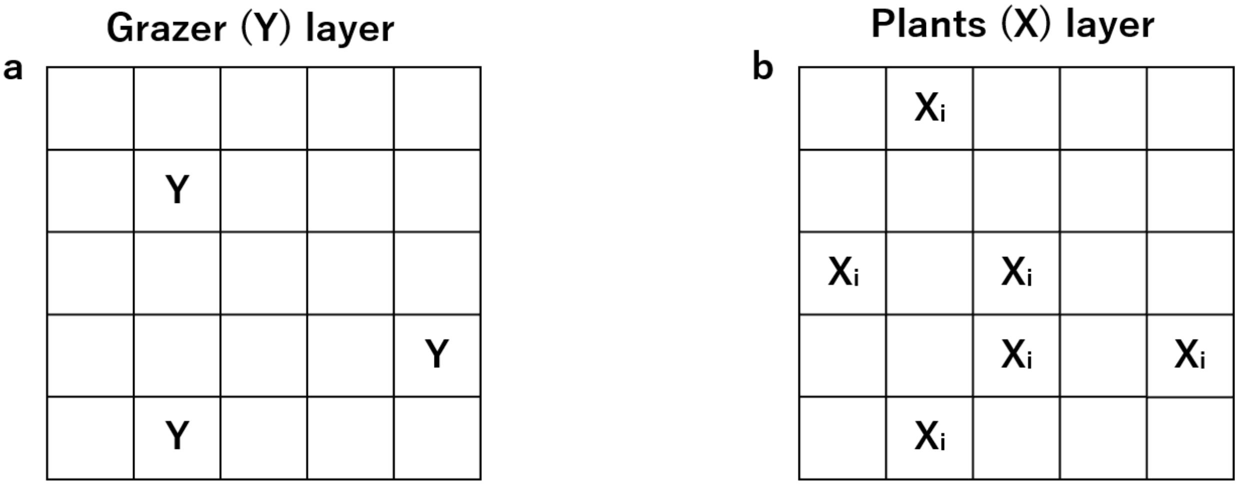

Figure 3.1 Two layers of the lattice model. (a) grazer layer Y. (b) plant layer X

Dynamics of plant species depends on the birth rate b_i, the grazing mortality g_i, and the nongrazing mortality d_i of plant species *i*. Following the lattice models of Tubay et al. [36], we consider the interaction of b_i, d_i, g_i in a modified lattice Lotka-Volterra competition model, with which we describe the grazing effect on plant species in a grassland community. The dynamics of multi-species contact process is shown by the following transitions:

$X_i + O \rightarrow X_i + X_i,$ rate: b_i

(1)

$X_i \rightarrow O,$ rate: d_i

(2)

$Y + X_i \rightarrow Y + O,$ rate: g_i.

(3)

Reproduction of plant species X_i by the birth rate (Eq. (1)) and death by nongrazing mortality (Eq. (2)) occur in the plant layer. The layer is a two-dimensional lattice (100 x100), over which plant species are distributed with density I_i. We assume that the birth rate is given by $b_i=B_i\,\varepsilon_i[m,n]$, where $\varepsilon_i[m,n]$ is a random number between 0 and 1 that denotes the specific dependence on species i and site $[m,n]$. $\varepsilon_i[m,n]$ represents the germination of the seedling success of seed on a lattice cell [36]. Each species has a unique value of $\varepsilon_i[m,n]$ on every site (from [0,0] to [100,100]). The expected birth rate (fecundity) B_i is given by $B_i = B$-0.002 (i - 1) (i=1, 2, …, 20), i.e., species 1 is strongest, and 20 is the weakest among 20 plant species. B is a basal fecundity that does not depend on plant species. The value 0.002 is a minimum variation allowed for the expected birth rate/fecundity B among all species [36].

Death by grazing (Eq. (3)) occurs in the grazer layer with the same size as in the plant layer. The grazer layer Y is the site occupied by the population of animals/grazers that move randomly to feed on plant species X_i. The animal grazers are distributed over the grazer layer with grazer density I_y. The density of grazer I_y and plant species I_i are kept constant, unless specified. The higher the grazing intensity, the higher the g_i. In the plant layer, one site can be occupied by only one plant species, or otherwise it remains vacant. In contrast, a grazer cell may represent more than one grazing animal, depending on grazing intensity.

Nongrazing mortality d_i is not considered or regarded as negligible unless otherwise stated. We consider two cases of grazing mortality g_i:

(1) Tradeoff case: $g_i = G + G'(20 - i)$

(2) Opposite case: $g_i = G + G'(i - 1)$

In the opposite case, the highest (lowest) birth rate species is the most superior (inferior) species. The grazing mortality rate is similarly constructed for the case where the highest (lowest) birth rate species is the lowest (highest) grazing mortality rate. The last case means that the most superior species is the strongest (low grazing rate) to the grazing mortality. We examined another possible mechanism that might promote diversity and exist in nature. We compare the opposite case with the trade-off case where the highest (lowest) birth rate is the highest (lowest) grazing mortality rate. The latter case represents a condition where more superior species in birth rate is preferable than less superior species. The parameter G denotes the basal grazing intensity that does not depends on species. The parameter G' is a species-dependent factor representing the animal preference on the grass or selectiveness in grazing. In the tradeoff case, a plant species with a high grazing intensity has a high birth rate. In the opposite case, the grazing intensity for plant species is strongest for the weakest among all species. Figure 3.3 shows the process of grazing in both the plant and the grazer layer.

3.2 Simulation process

We analyze the effect of grazing mortality (g_i) on the number of surviving plant species according to the following simulation procedure (Fig. 3.2):

a. Initial distributions

   (1) Assign specificity-species.

   Specificity of species *i* on every site [*m*,*n*] (B_i $\varepsilon_i[m,n]$) is distributed over the plant layer of the lattice model. Each plant species X_i has its own specificity on every site. For example, plant species 1 has ε_1 on all cells of plant layer e.g., [*0*,*0*] until [*100*,*100*] (Fig. 3.3).

   (2) X_i disposition.

   Plant species X_i is randomly distributed over the square-lattice cells of plant layer with density I_i. In this study, we set initial density I_i=0.03.

   (3) Y disposition

   Animal/ grazer cells are randomly distributed on the cell of grazer layer. We set the initial density of grazer with I_y = 0.4.

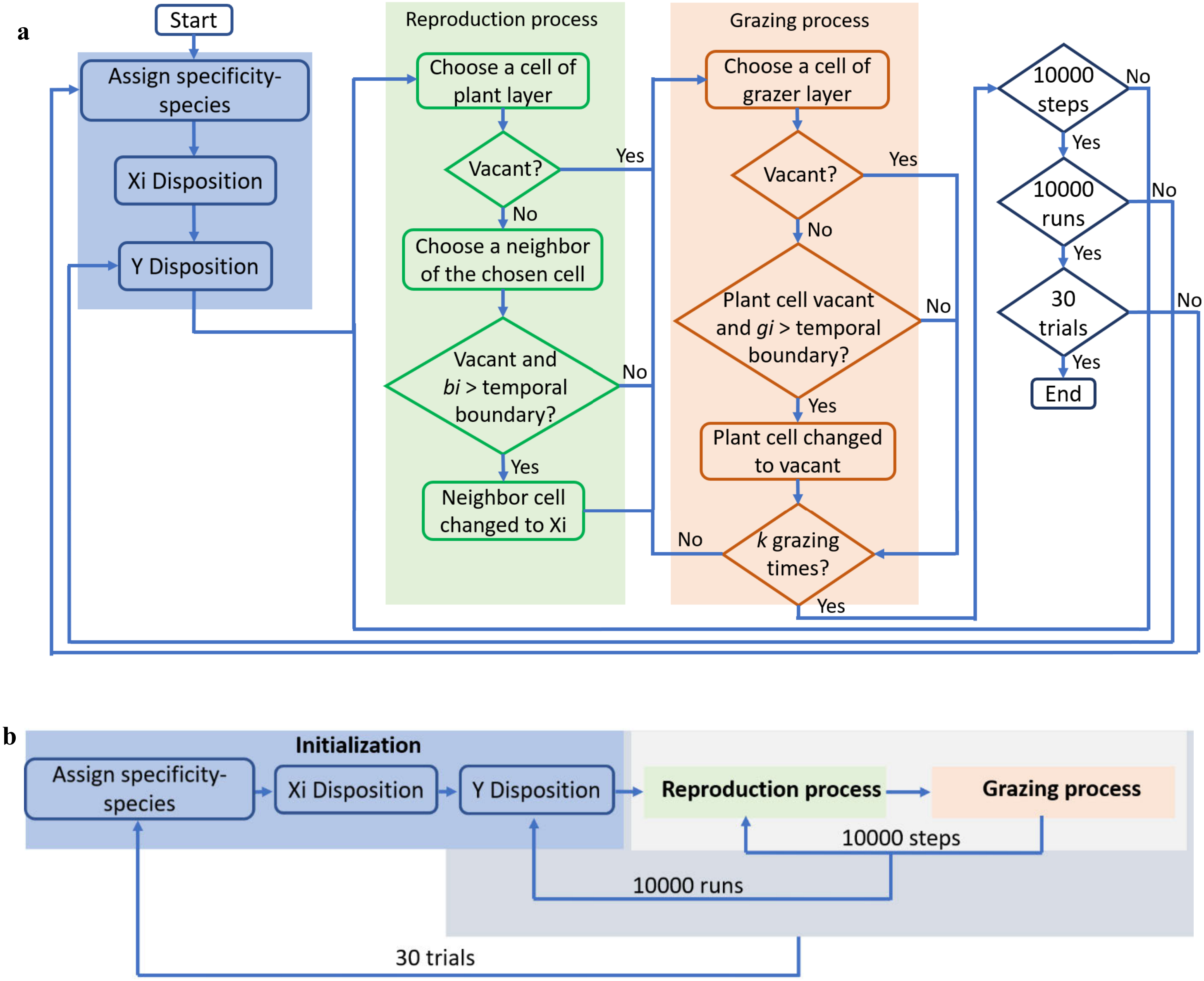

Figure 3.2 Simulation process of lattice model. (a) Simulation flowchart of the model. (b) Main processes of the lattice model.

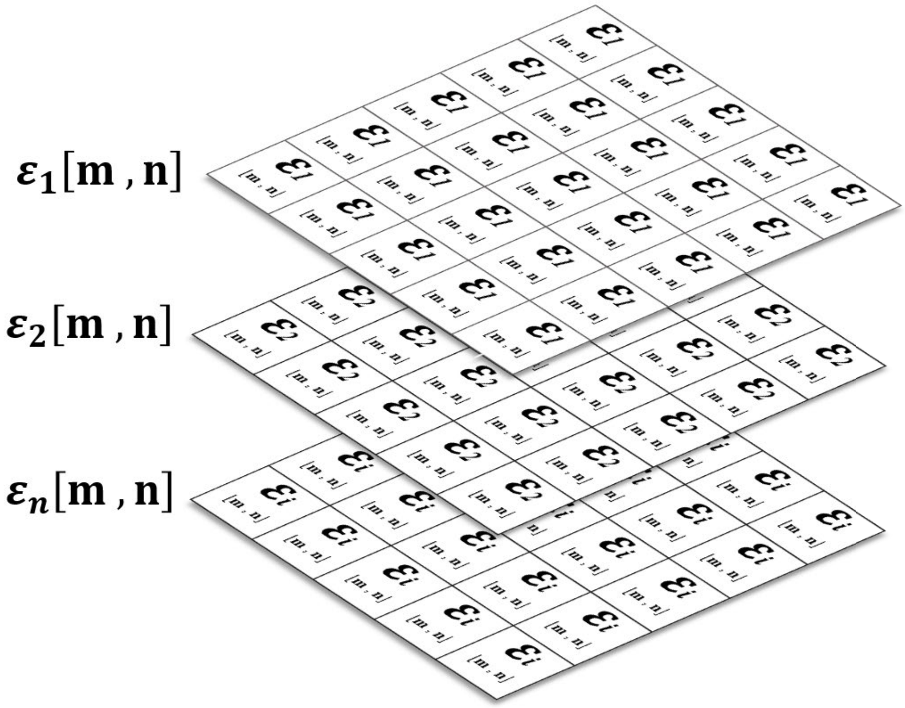

Figure 3.3 Specificity species *i* on every lattice site [*m,n*]

b. Reproduction process

The reproduction process is run in plant layer. The process is proceeded with following procedure;

(1) To choose a cell of plant layer.

First, a cell on plant layer is chosen randomly (Figs. 3.4a).

(2) To choose a neighbor of the chosen cell.

If there is plant X_i on that cell then one more cell is chosen randomly within the dispersal range of the chosen plant species X_i (Figs. 3.4b, c).

(3) Chosen neighbor cell is change to $X_{i.}$

If the second chosen cell is vacant then plant species X_i occupies the vacant cell with the rate of b_i (Fig. 3.4d).

(4) First chosen cell occupied/unoccupied.

However, if the first chosen cell is vacant then the reproduction process is ended and the process moves to grazing process, while the chosen cell remains unchanged.

(5) Chosen neighbor cell occupied/unoccupied, b_i is higher/lower than temporal boundary.

Also, if the second chosen cell is occupied by a plant species $X_{i.}$ and/ or b_i is lower than the temporal boundary then the reproduction process is ended and the process moves to grazing process, while the second chosen cell remains unchanged.

c. Grazing process

Grazing process involve both grazer layer and plant layer. The process is proceeded with the following procedure;

(1) To choose a cell of grazer layer.

First, we choose a cell randomly on the grazer layer (Figs. 3.5a, b).

(2) To choose a plant cell.

If there is a grazer or an animal Y on that cell then one cell with the same position [*m,n*] with the chosen grazer cell on the plant layer is selected (Fig. 3.5b).

(3) Plant cell changed to vacant.

If there is a plant species $X_{i.}$ on the plant layer and the rate g_i is higher to temporal boundary then that cell is grazed by grazer Y with (Fig. 3.5 d).

(4) Chosen grazer cell is unoccupied.

However, if there is no grazer/animal on the chosen cell of animal layer then the process is ended, and the cell remains unchanged. The process moves to check number of grazing time (k).

(5) Chosen plant cell unoccupied

Also, if there is no plant species X_i on the plant layer then the process is ended and the cell remains unchanged. The process moves to check the number of grazing time (k).

(6) To check the k grazing times.

If the number of grazing times is satisfied e.g., $k = 3$, then the process moves to the next step. But if number of grazing time (k) is not satisfied, then grazing process is repeated from the beginning.

d. Repetition process

(1) Reproduction and grazing process are repeated $L\times L$ and $k\times L\times L$ times, respectively. $L \times L$ refers to the number of square-lattice cell and k denotes the grazing time.

(2) 1 step in the simulation means 1-time reproduction process and k time grazing process. In addition, $L\times L$ and $k\times L\times L$ times refer to 1 run which is repeated from grazer Y distribution process.

(3) Processes in a is repeated for 30 trials. 1 trial means the process is repeated from assigning specificity species on lattice sites for 10,000 runs (Fig. 3.2).

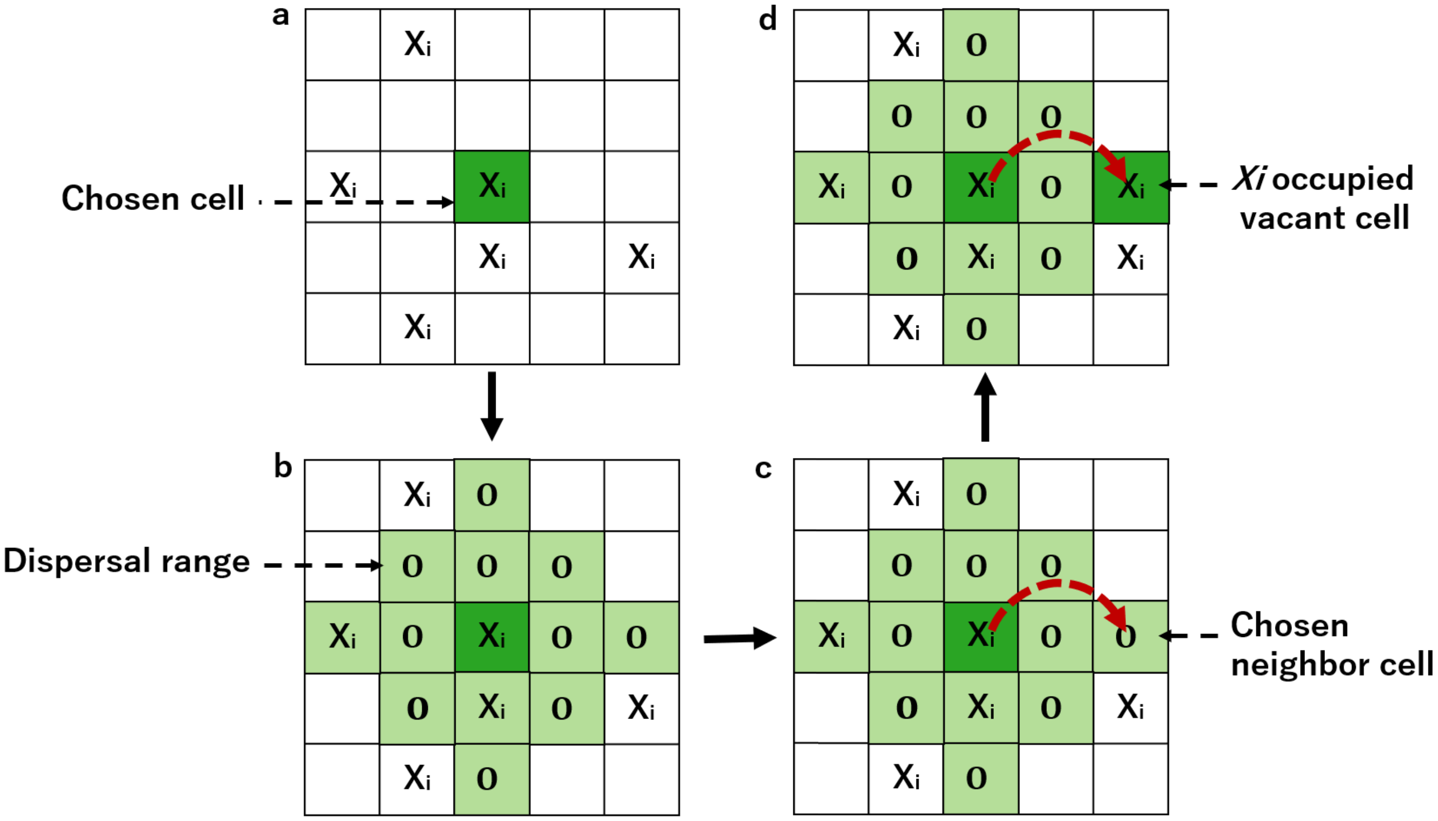

Figure 3.4 Reproduction process of the lattice model

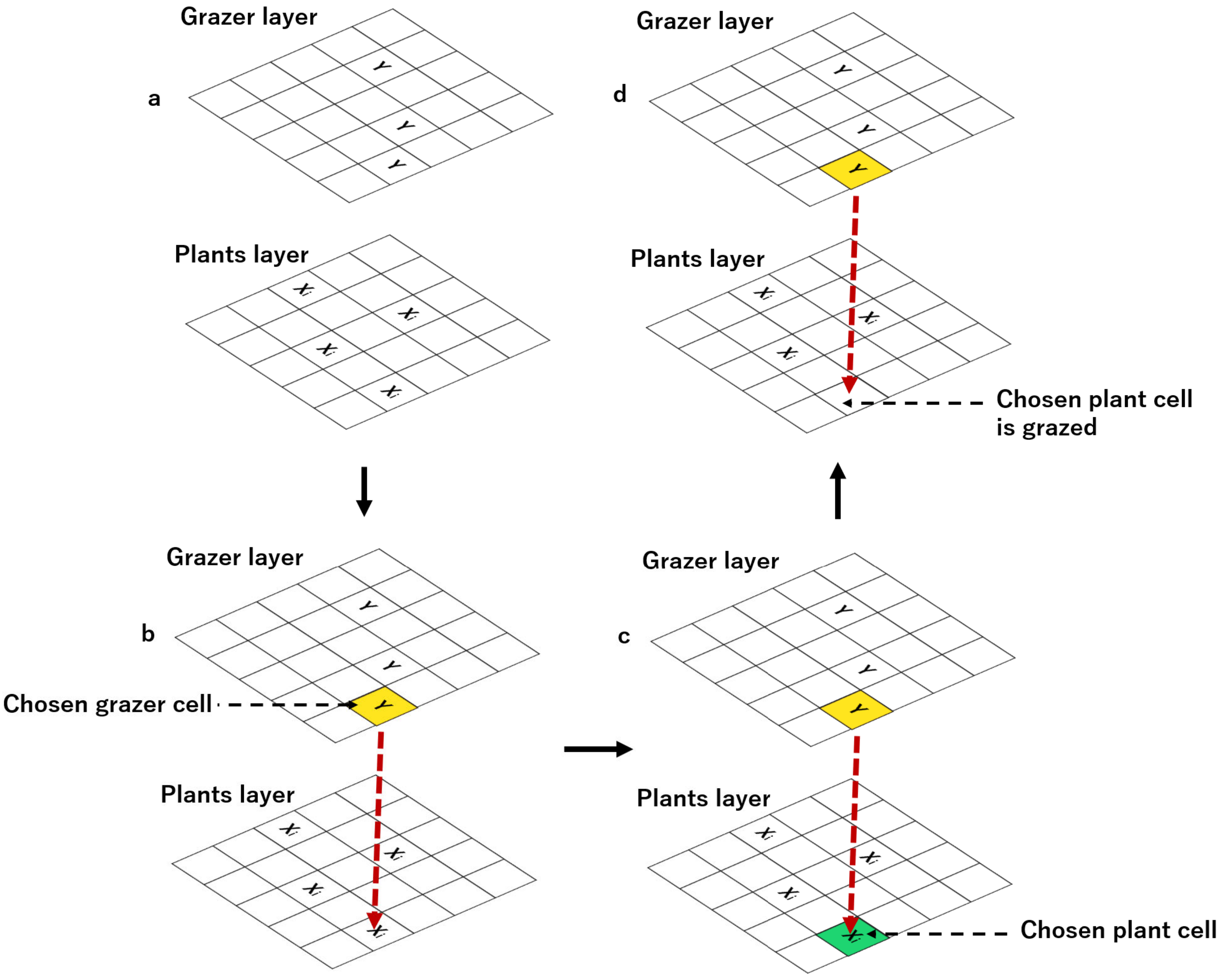

Figure 3.5 Grazing process of the lattice model.

3.2 Research tools

We mainly used two computer machines to run the simulations. The computer's specification is as the following:

a. Computer machine 1

  - Processor Intel(R) Core(TM) i7-4790K CPU @4.00 GHz 4.00 GHz.
  - RAM memory is 16 GB.
  - Operating system (OS) is Windows 10 Pro.
  - System type is 64-bit operating system, x64 based processor

b. Computer machine 2

  - Processor Intel(R) Core(TM) i7-4790K CPU @4.00 GHz 4.00 GHz
  - RAM memory is 16 GB (15.7GB usable).
  - Operating system (OS) is Windows 10 Home.
  - System type is 64-bit operating system, x64 based processor.

4. Results

4.1 The effect of species-independent factors

In an early stage of the present study, we only considered the opposite case for grazing mortality. We studied the effect of grazing period k and grazing intensity G on the number of surviving species (Figs. 4.1b, d). The number of surviving plant species responds unimodally on the grazing intensity G (Fig. 4.1b). The increase of grazing times maintains the unimodal behavior with the decrease of number of survivors. We investigated the effect of k grazing time and fecundity B on the reproduction of plant species (Figs. 4.1a, c). The coexisting species increases with the increase of fecundity B (Fig. 4.1a). The results also indicated the importance of the interspecific grazing difference G' to promote coexistence of plant species (Figs. 4.1b-d).

Previous studies show that animal grazer might tend to feed on a more dominant species, a tradeoff. We studied the effect of the tradeoff on the number of survivors (Figs. 4.2b-d). Surprisingly, more plant species can survive (Fig. 4.2b). The number of survivors is also higher given various values of fecundity B, compared to the opposite case (Fig. 4.2a). Similarly, G' is necessary for unimodality in the tradeoff case (Figs. 4.2b-d).

Proceeding the investigations, we simulated various dispersal rates and lattice sizes (Figs. 4.3a, b). The dispersal rates do not show any significant effect on the number of survivors (Fig. 4.3a). Similarly, the number of species increase proportionally with the increase of the lattice sizes (Fig. 4.3b). We examined the processing time of the simulation on each set parameter values which is also a consideration to determine the repetition of simulations (Figs. 4.4a, b). On average, high grazing maintains low density and low grazing showed a higher species density. (Figs. 4.5a, b).

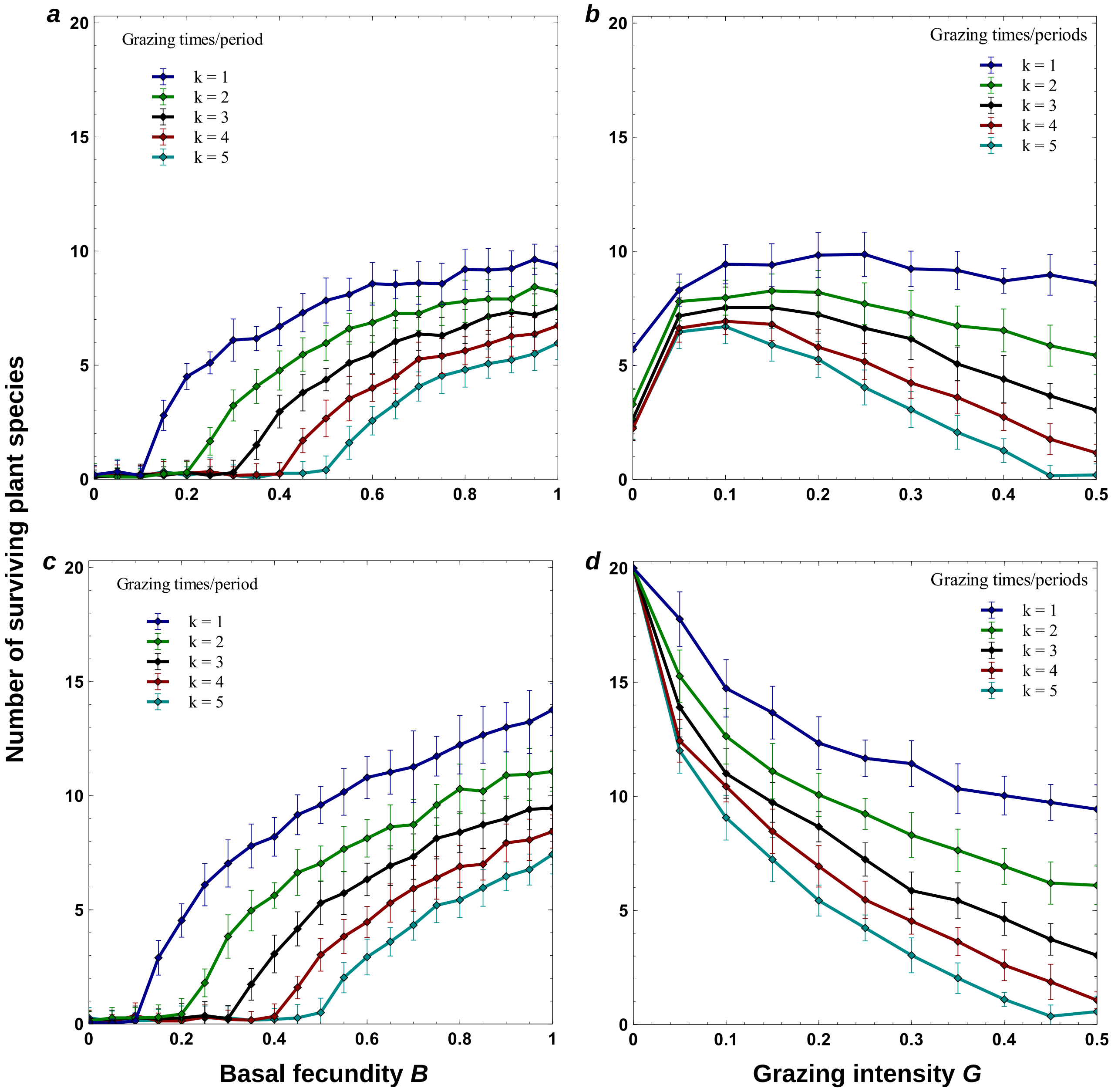

Figure 4.1 The number of surviving species as a function of the basal grazing intensity *G* or basal fecundity *B* for various values of grazing times *k*. (**a-d**) The grazing intensity increases as the initial birth rate decreases, i.e., $g_i = G + G'(i-1)$ and $B_i = B-0.002(i-1)$ for i=1, 2, …, s), indicating that inferior species are eaten more often by grazers. (**a, b**) The value of the species-dependent factor is $G' = 0.0005$. (**c, d**) The value of the species-dependent factor is $G' = 0$. (**b**) Fecundity $B = 1$. The lattice size is 100 x100. The dispersal rate is $P = 40$. The initial species density is $I_i = 0.03$ (same for all species). The density of grazer cells is $I_y = 0.4$. Error bars indicate the standard deviations.

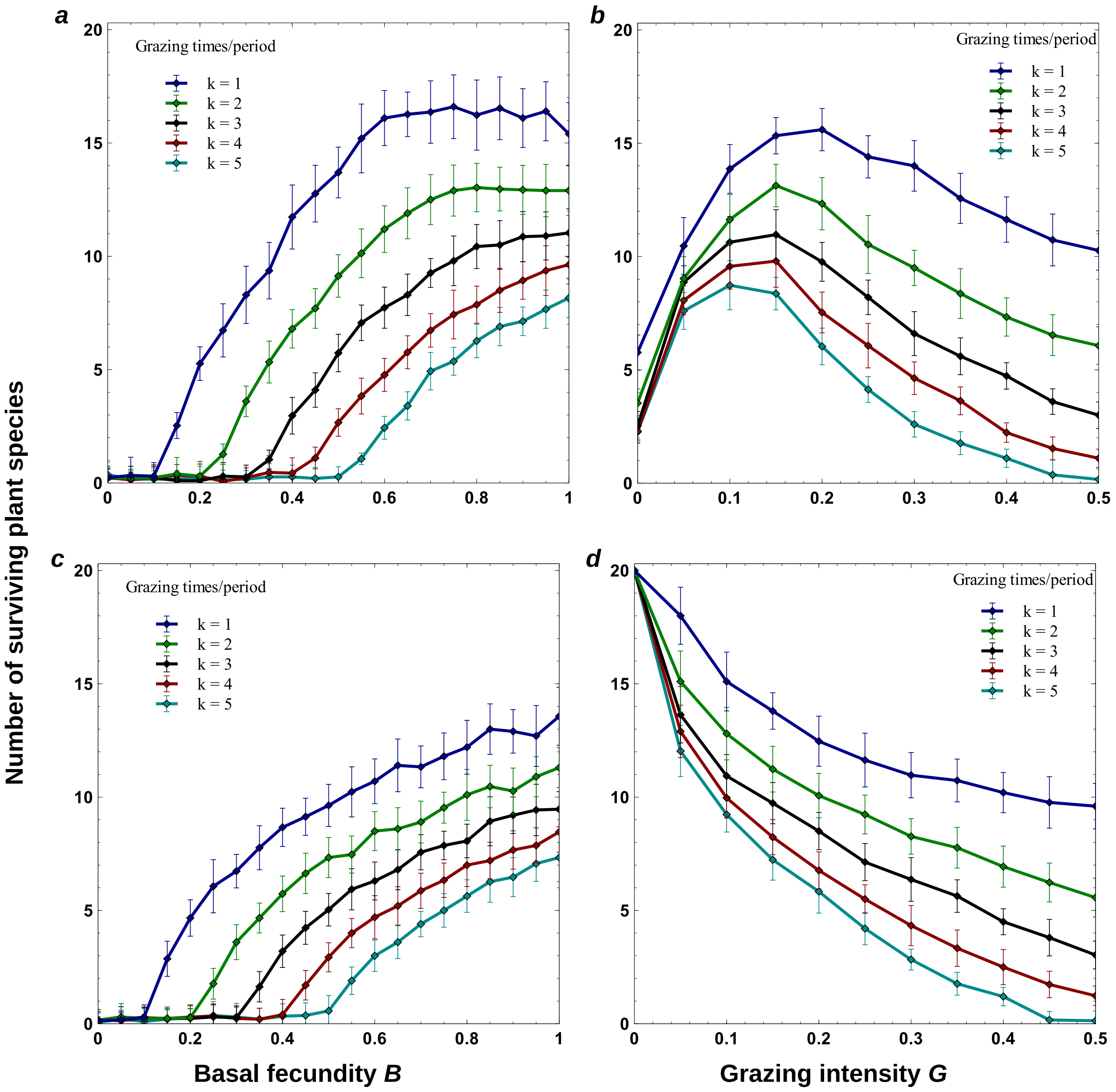

Figure 4.2 The number of surviving species as a function of the basal grazing intensity G or basal fecundity B for various values of grazing times k. (**a-d**) The grazing rate of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and $B_i = B\text{-}0.002(i\text{-}1)$ for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. (**a, b**) The value of the species-dependent factor is G' = 0.0005. (**c, d**) The value of the species-dependent factor is G' = 0. (**b**) Fecundity B = 1. The lattice size is 100 x100. The dispersal rate is P = 40. The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

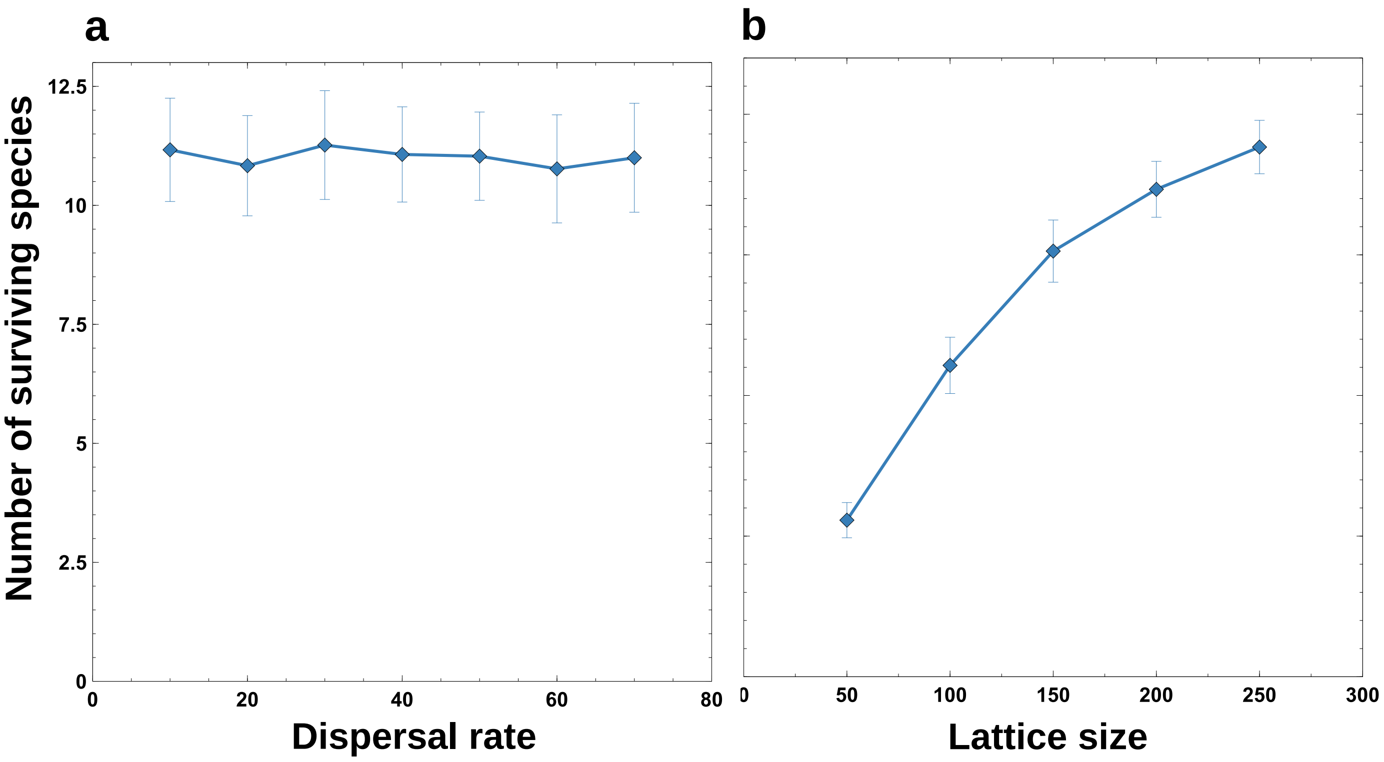

Figure 4.3. The effects of dispersal range and lattice size on the number of surviving species in a grassland community under grazing. (**a-d**) The grazing rate of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and B_i = B-0.002(i-1) for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. The birth rate is B_i = B-0.002(i-1), where B = 1. (**a-d**) G' = 0.0005, G = 0.15. The lattice size is 100 x100 for (**a**). The dispersal rate is P = 40 for (**b**). The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

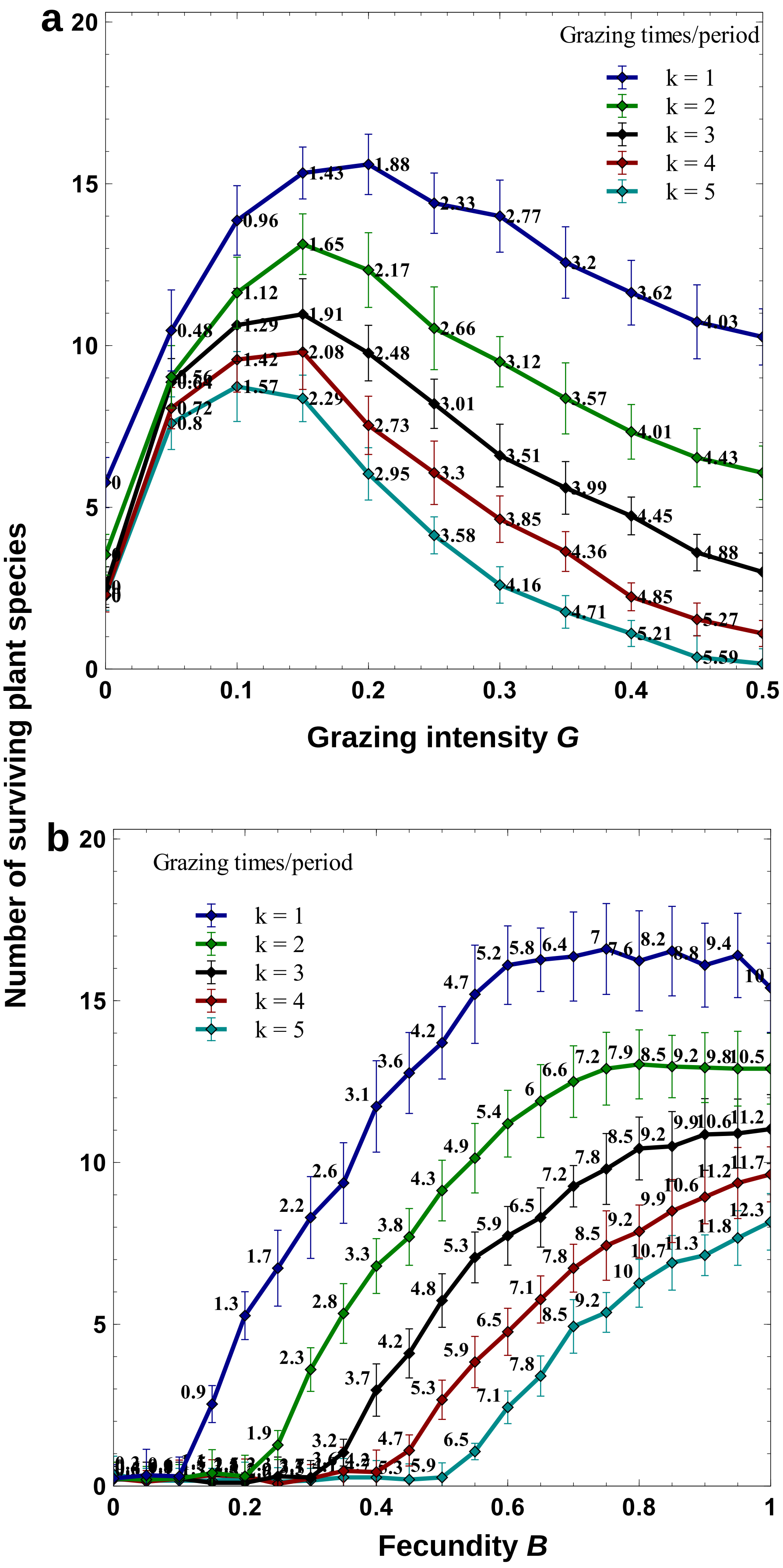
a
b
Number of surviving plant species
Grazing times/period
k = 1
k = 2
k = 3
k = 4
k = 5
Grazing intensity G
Fecundity B
0
5
10
15
20
0.1
0.2
0.3
0.4
0.5
0.6
0.8
1
0.48
0.96
1.43
1.88
2.33
2.77
3.2
3.62
4.03
0.56
1.12
1.65
2.17
2.66
3.12
3.57
4.01
4.43
0.64
1.29
1.91
2.48
3.01
3.51
3.99
4.45
4.88
0.72
1.42
2.08
2.73
3.3
3.85
4.36
4.85
5.27
0.8
1.57
2.29
2.95
3.58
4.16
4.71
5.21
5.59
0.9
1.3
1.7
2.2
2.6
3.1
3.6
4.2
4.7
5.2
5.8
6.4
7
7.6
8.2
8.8
9.4
10
1.9
2.3
2.8
3.3
3.8
4.3
4.9
5.4
6
6.6
7.2
7.9
8.5
9.2
9.8
10.5
3.2
3.7
4.2
4.8
5.3
5.9
6.5
7.2
7.8
8.5
9.2
9.9
10.6
11.2
4.7
5.3
5.9
6.5
7.1
7.8
8.5
9.2
9.9
10.6
11.2
11.7
5.9
6.5
7.1
7.8
8.5
9.2
10
10.7
11.3
11.8
12.3

Figure 4.4 The processing time of the number of surviving species as a function of the basal grazing intensity *G* or basal fecundity *B* for various values of grazing times *k*. The label of each point shows the processing time (in hours) from the beginning of simulation e.g. $G = 0$. (**a, b**) The grazing rate of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and $B_i = B\text{-}0.002(i\text{-}1)$ for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. (**a, b**) The value of the species-dependent factor is $G' = 0.0005$. (**a, b**) The value of the species-dependent factor is $G' = 0.0005$. (**b**) Fecundity $B = 1$. The lattice size is 100 x100. The dispersal rate is $P = 40$. The initial species density is $I_i = 0.03$ (same for all species). The density of grazer cells is $I_y = 0.4$. Error bars indicate the standard deviations.

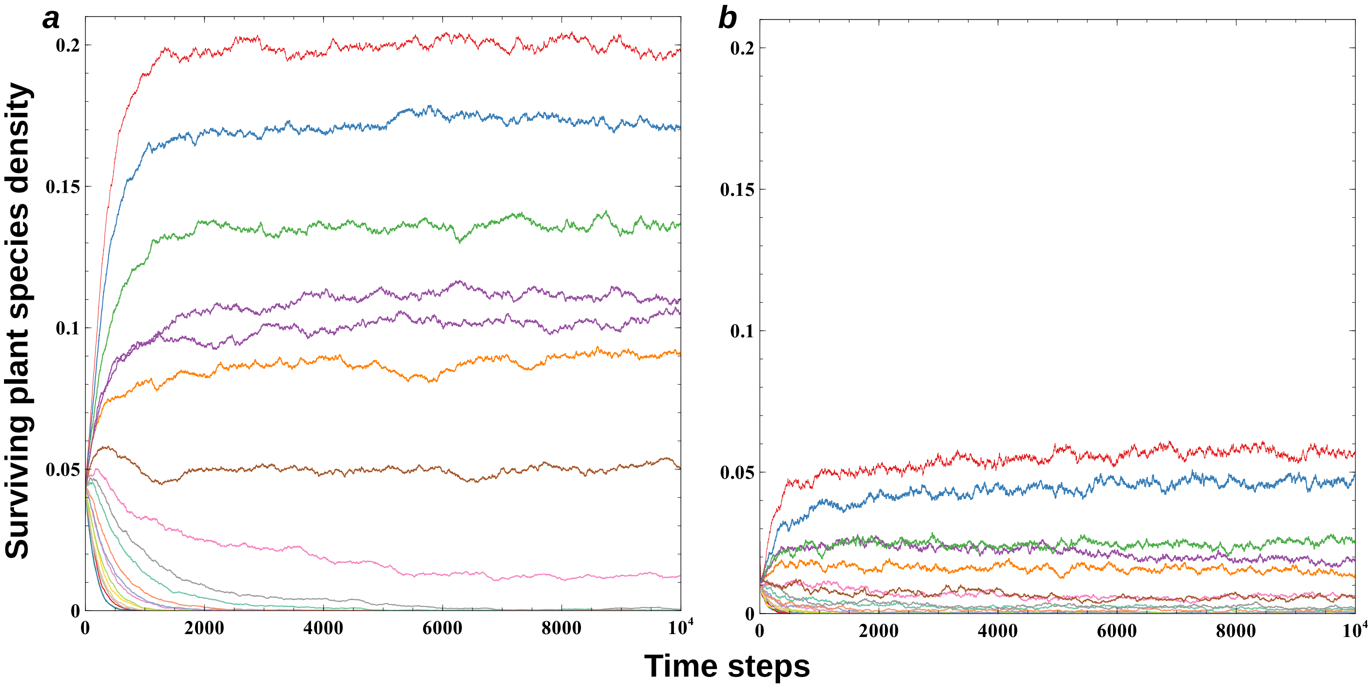

Figure 4.5 Temporal dynamic of surviving plant species density. (**a, b**) The grazing intensity increases as the initial birth rate decreases, i.e., $g_i = G + G'(i-1)$ and $B_i = B\text{-}0.002(i\text{-}1)$ for i=1, 2, …, s), indicating that inferior species are eaten more often by grazers. (**a, b**) The value of the species-dependent factor is G' = 0.0005. (**a**) The value of the species-dependent factor is G = 0.05. (**b**) The value of the species-dependent factor is G = 0.5 (**b**) Fecundity B = 1. The lattice size is 100 x100. The dispersal rate is P = 40. The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

4.2 The effect of species-dependent factors

We simulate a lattice grassland model with 20 plant species under various levels of grazing intensity (*G*) without nongrazing natural mortality, i.e., $d_i = 0$ (Figs. 4.6, 4.7, 4.8, 4.13). The temporal dynamics exhibit large fluctuations in the number of individuals of each species over a long period of time (Figs. 4.6a, 4.7a, and 4.8a). In contrast, this number is fairly stable over a short timescale (Figs. 4.6b, 4.7b, and 4.8b). Based on the short-term temporal dynamics (Figs. 4.6b, 4.7b and 4.8b) and snapshots of the plant distributions (Figs. 4.6c, 4.7c and 4.8c), the number of surviving plant species is highest at an intermediate grazing intensity (*G*). At the low grazing intensity, the number of survivors is higher than high grazing intensity (Figs. 4.6c, 4.8c).

To test the effect of grazing on species coexistence, we vary the basal grazing intensity *G* to examine the effects of grazing (Figs. 4.9, 4.18, 4.19, 4.20, Table 4.1). The number of species is highest at an intermediate grazing intensity (*G*) for a given fecundity *B* and interspecific grazing difference G' (Fig. 4.9, 4.17b, c, e, f). The interspecific grazing difference G' is the difference in animal preference or selectiveness in grazing, e.g., palatable herbs or unpalatable grass. For example, grass species is more preferred than herbs for animal grazers. To examine the effects of a tradeoff between birth rate and grazing intensity, we consider the following opposite relations between the species-specific expected birth rate B_i and grazing rate g_i: (1) the tradeoff case: species with a high B_i have a high g_i (grazing is subject to a tradeoff) and (2) the opposite case: species with a high B_i have a low g_i. In both cases, the number of surviving species exhibits unimodal behavior in response to the grazing intensity *G*. The number of coexisting species at peak diversity is larger under the first case (with the tradeoff) than under the second case (the opposite) (Fig. 4.9).

If there is no interspecific grazing difference ($G' = 0$), then the number of surviving species decreases monotonically with an increase in the grazing intensity G (Figs. 4.17a, d, 4.18a, 4.19a, c, e, 4.20a). However, if a slight difference (e.g., $G' = 0.0005$) is introduced, then the number of species responds unimodally (Figs. 4.9, 4.17b, c, e, f, 4.18b, 4.19b, f, 4.20b). Interestingly, the peak height (the number of surviving species) decreases as the interspecific grazing difference G' is further increased (differences in colored lines in Figs. 4.9, 4.18b, c). The number of coexisting species decreases as the density of grazer cells I_y increases (Figs. 4.10a-c, 4.19a, c, e). However, the unimodal behavior is preserved as long as the density of grazer cells is kept constant (Figs. 410d-f, 4.19b, d, f, 4.20b). Natural mortality d_i (i.e., $d_i = 0.1$) also suppresses the unimodal behavior (Fig. 4.10f).

To understand the effect of grazing on population density, we examine the composition of surviving species (Figs. 4.11, 4.12). In the first (tradeoff) case, the species with the lowest grazing rate dominates at a low grazing intensity (Fig. 4.6c), and that with the highest birth rate dominates at a high grazing intensity (Fig. 4.8c), while various species survive at low densities at an intermediate grazing intensity (Fig. 4.7c). In contrast to the second case (opposite to the tradeoff case) (Figs. 4.13, 4.14), however, the results of the first case (with the tradeoff) reveal a large fluctuation when the grazing intensity G is high (Figs. 4.11, 4.12). Here, which species survive depends on the simulation run (Figs. 4. 11c, d, 4.12 c, d). In any case, the results converge, and monotonic behavior is recovered as G' decreases to zero (Figs. 4.17 a, d). Accordingly, the results indicate that the species dependence of grazing G' is important for unimodality but the tradeoff between the birth rate and grazing intensity is not essential.

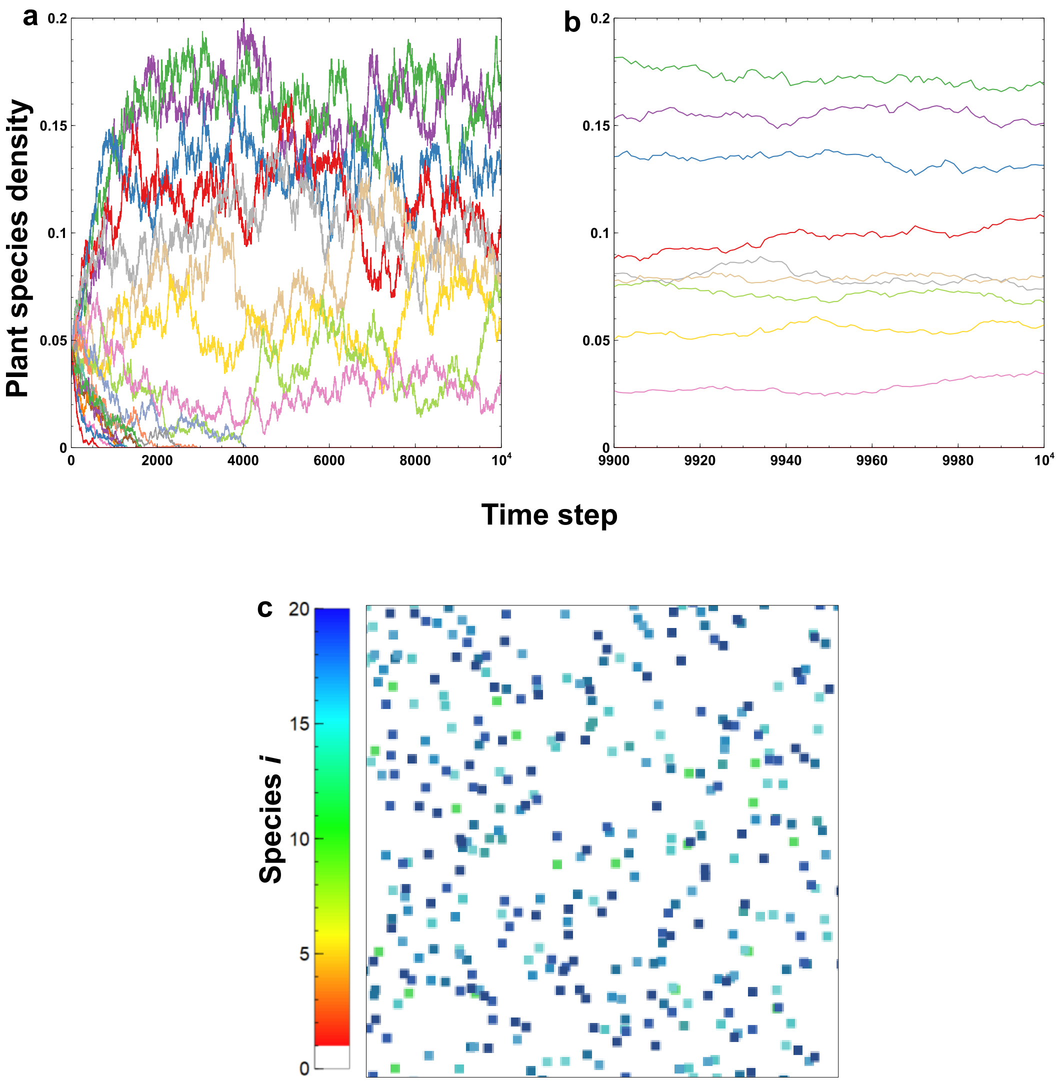

Figure 4.6 The temporal dynamics of species density and a snapshot of the final density composition at low grazing rate *G*= 0.05. (**a-c**) The grazing intensity of a species decreases as the initial birth rate decreases, i.e., $g_i = G + G'(20 - i)$ and B_i = *B*-0.002(*i*-1) for *i*=1, 2, …, *s*), indicating a tradeoff between the birth rate and grazing intensity of a species. (**a**) Temporal dynamics for 10000 steps. (**b**) Temporal dynamics of the last one hundred steps. (**c**) A snapshot of the final surviving species composition. The value of the species-dependent factor is *G*' = 0.0005. The lattice size is 100 x100. The dispersal rate is *P* = 40. The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

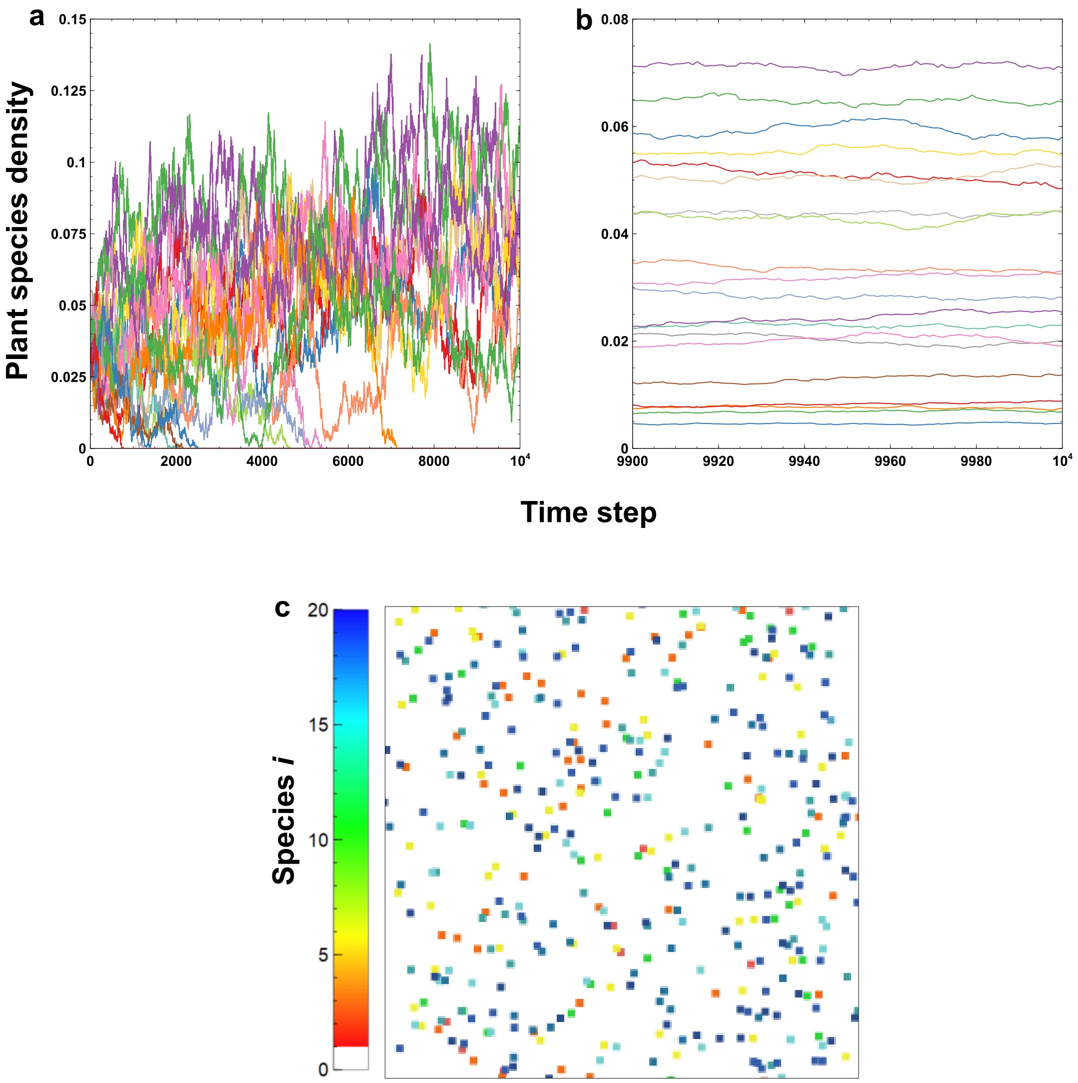

Figure 4.7 The temporal dynamics of species density and a snapshot of the final density composition at intermediate grazing rate G= 0.15. (**a-c**) The grazing intensity of a species decreases as the initial birth rate decreases, i.e., $g_i = G + G'(20-i)$ and $B_i = B\text{-}0.002(i\text{-}1)$ for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. **a**) Temporal dynamics for 10000 steps. (**b**) Temporal dynamics of the last one hundred steps. (**c**) A snapshot of the final surviving species composition. The value of the species-dependent factor is G' = 0.0005. The lattice size is 100 x100. The dispersal rate is P = 40. The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

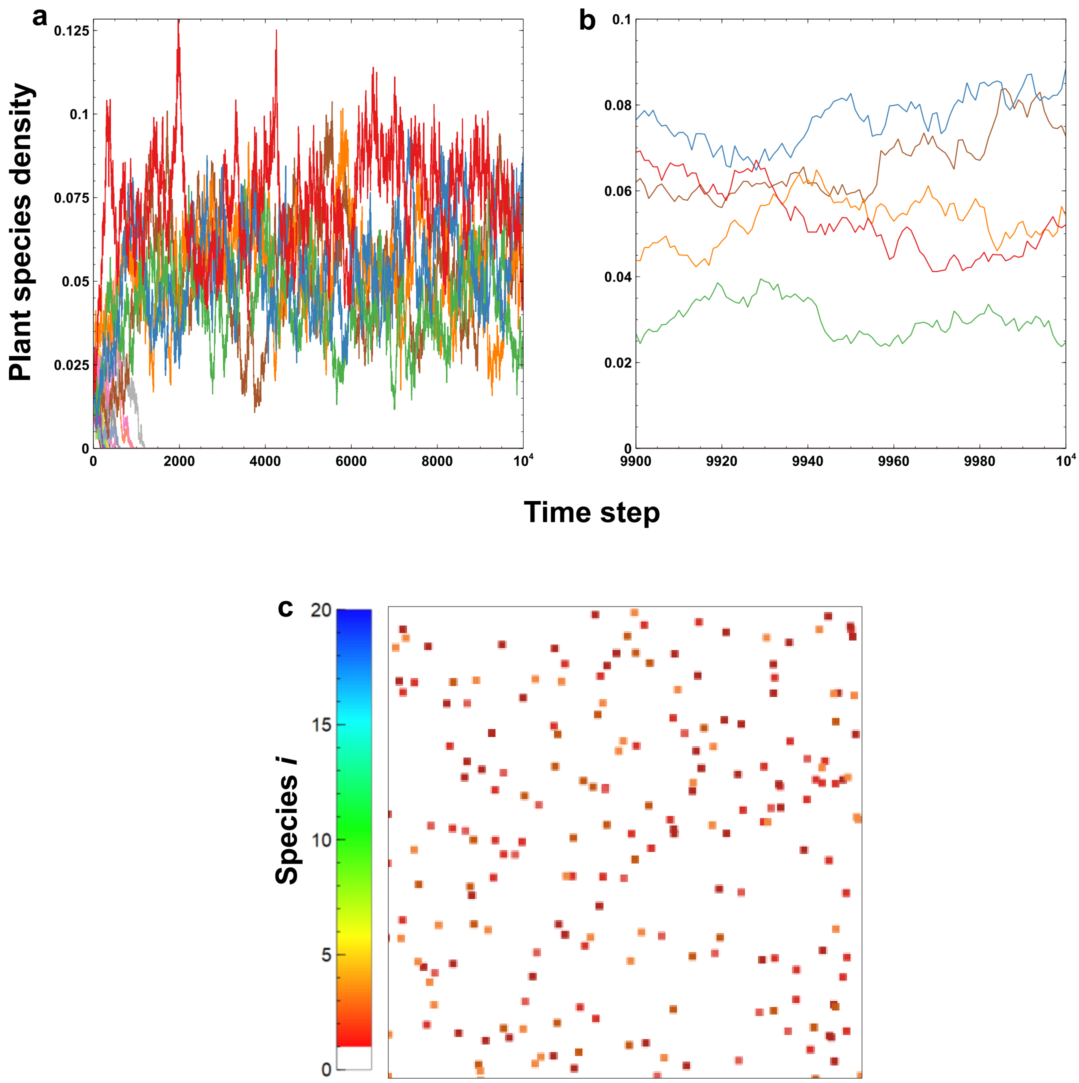

Figure 4.8 The temporal dynamics of species density and a snapshot of the final density composition at high grazing rate G= 0.4. (**a-c**) The grazing intensity of a species decreases as the initial birth rate decreases, i.e., $g_i = G + G'(20-i)$ and B_i = B-0.002(i-1) for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. (**a**) Temporal dynamics for 10000 steps. (**b**) Temporal dynamics of the last one hundred steps. (**c**) A snapshot of the final surviving species composition. The value of the species-dependent factor is G' = 0.0005. The lattice size is 100 x100. The dispersal rate is P = 40. The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

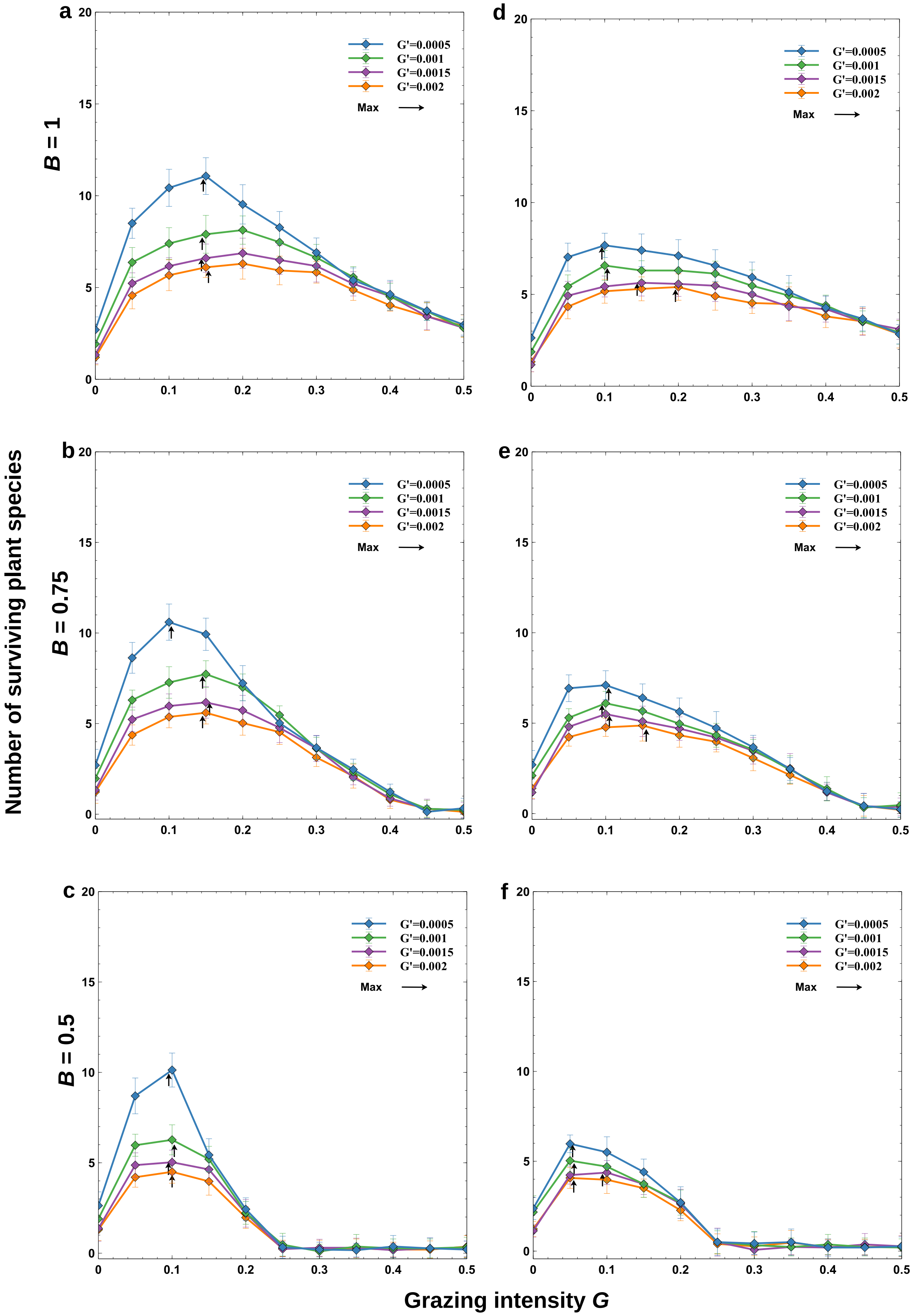
a
b
c
d
e
f
B = 1
B = 0.75
B = 0.5
Number of surviving plant species
Grazing intensity G
G'=0.0005
G'=0.001
G'=0.0015
G'=0.002
Max
0
5
10
15
20
0
0.1
0.2
0.3
0.4
0.5

Figure 4.9 The number of surviving species as a function of the basal grazing intensity *G* for various values of interspecific grazing differences (*G'*). Three different values of the basal birth rate are shown: (**a, d**) *B*= 1; (**b, e**) *B*= 0.75; and (c, **f**) *B*= 0.5. (**a-c**) The grazing intensity of a species decreases as the initial birth rate decreases, i.e., $g_i = G + G'(20 - i)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. (**d-f**) The grazing intensity increases as the initial birth rate decreases, i.e., $g_i = G + G'(i - 1)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating that inferior species are eaten more often by grazers. The value of the species-dependent factor is $G' = 0.0005$. The lattice size is 100 x100. The dispersal rate is $P = 40$. The initial species density is $I_i = 0.03$ (same for all species). The density of grazer cells is $I_y = 0.4$. Error bars indicate the standard deviations.

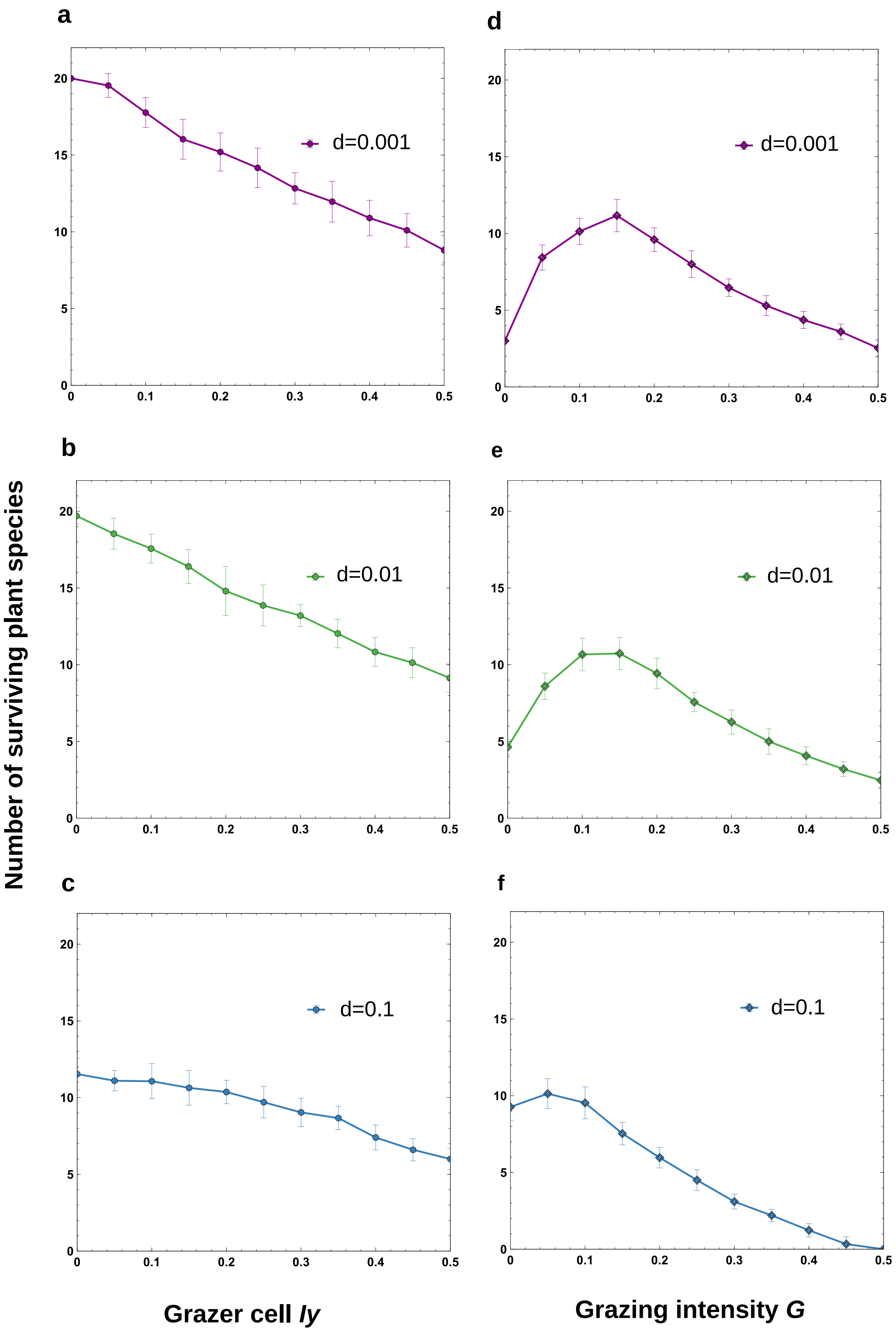
a
b
c
d
e
f
d=0.001
d=0.01
d=0.1
d=0.001
d=0.01
d=0.1
0
5
10
15
20
0
0.1
0.2
0.3
0.4
0.5
Number of surviving plant species
Grazer cell *ly*
Grazing intensity *G*

Figure 4.10 The effects of the animal density I_y on the number of surviving species under various basal grazing intensities (G) and natural mortalities (d_i). (**a-c**) The grazing intensity of a species decreases as the fecundity decreases, i.e., $g_i = G + G'(20 - i)$ and $B_i = B-0.002(i-1)$ for $i=1, 2, \ldots, s$), indicating a tradeoff between the birth rate and grazing intensity of a species. (**a-c**) $G' = 0.0005$. The lattice size is 100 x100. (**a-c**) The grazing intensity is 0.15. The dispersal rate is $P = 40$. The initial species density is $I_i = 0.03$ (same for all species). (**d-f**) The density of grazer cells is $I_y = 0.4$. Error bars indicate the standard deviations.

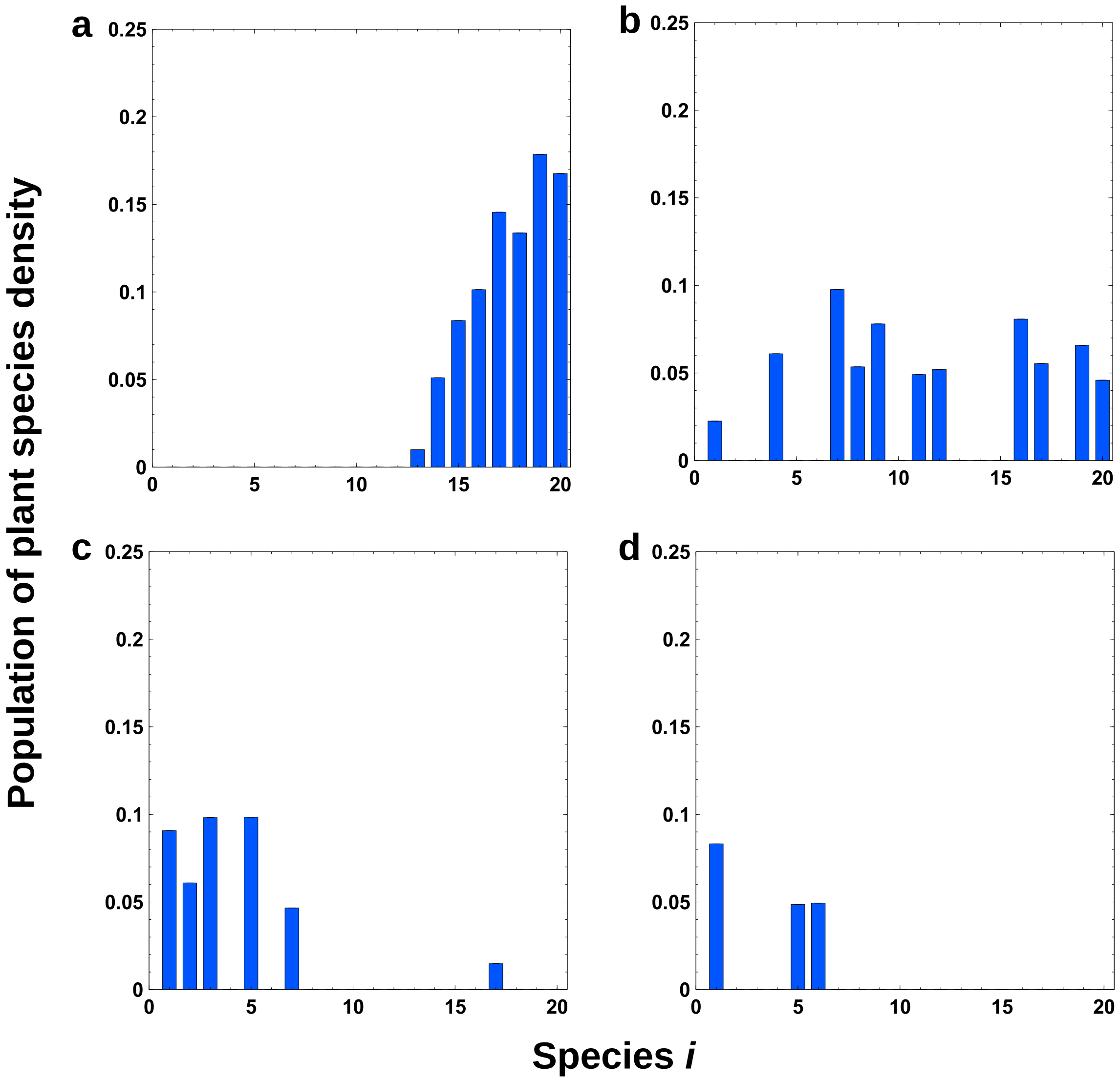

Figure 4.11 Population densities of species with respect to the basal grazing intensity *G* for the tradeoff case. (**a-d**) The grazing intensity of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and $B_i = B\text{-}0.002(i\text{-}1)$ for i=1, 2, …, *s*), indicating a tradeoff between the birth rate and grazing intensity of a species. (**a-d**) The result of a single run. (**e-h**) The average of 30 runs. The basal grazing rates are (**a**) *G*= 0.05, (**b**) *G*= 0.1, (**c**) *G* = 0.3, and (**d**) *G* = 0.5. The parameters are as follows: interspecific grazing difference, *G'* = 0.0005; basal fecundity, *B*= 1; initial species density, I_i = 0.03 (for all species); density of grazer cells, I_y = 0.4; and dispersal rate, *P* = 40. The lattice size is 100 x100.

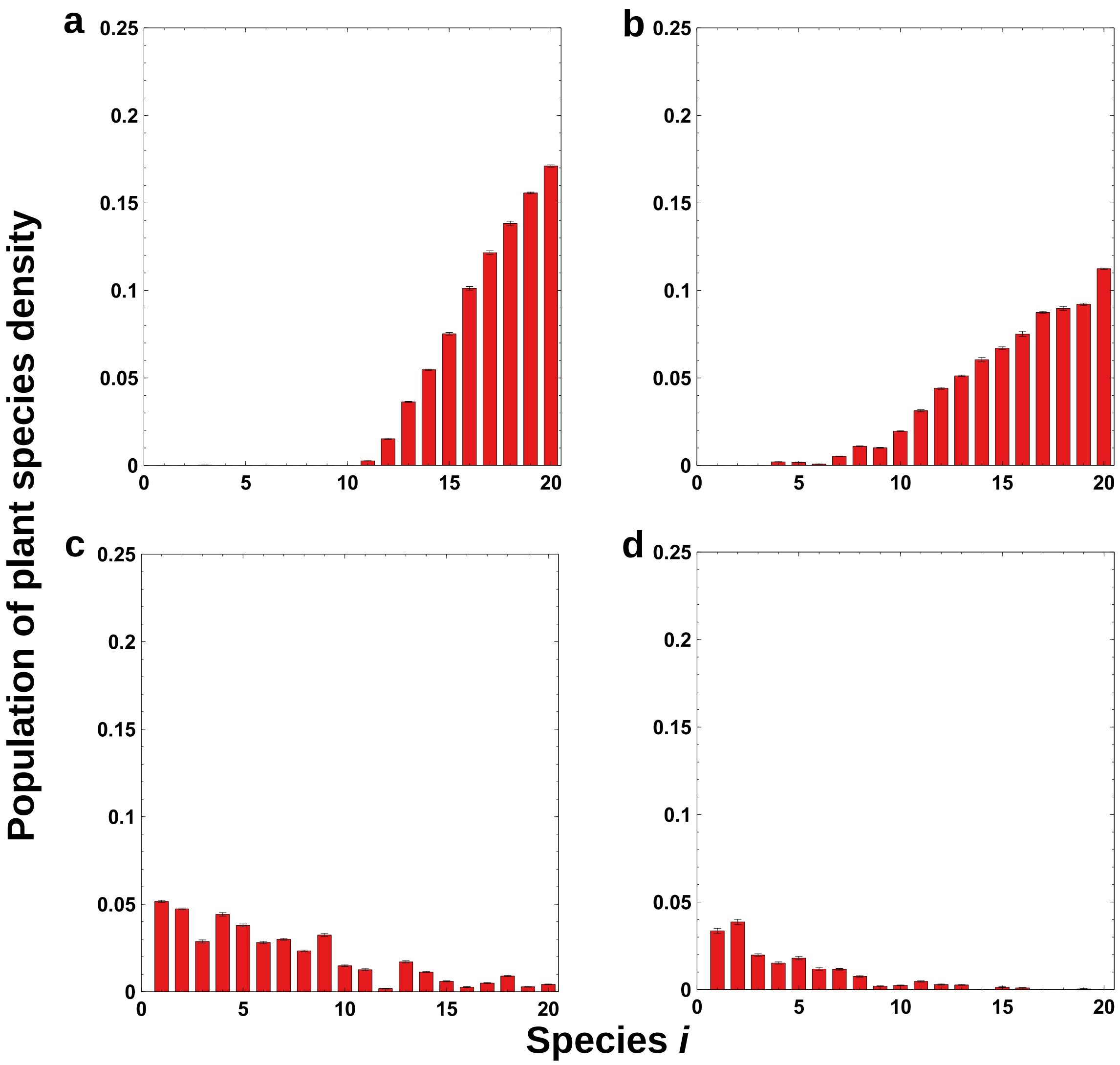

Figure 4.12 Population densities of species with respect to the basal grazing intensity *G* for the tradeoff case. (**a-d**) The grazing intensity of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and B_i = B-0.002(i-1) for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. (**a-d**) The average result of 30 runs. The basal grazing rates are (**a**) G= 0.05, (**b**) G= 0.1, (**c**) G = 0.3, and (**d**) G = 0.5. The parameters are as follows: interspecific grazing difference, G' = 0.0005; basal fecundity, B= 1; initial species density, I_i = 0.03 (for all species); density of grazer cells, I_y = 0.4; and dispersal rate, P = 40. The lattice size is 100 x100.

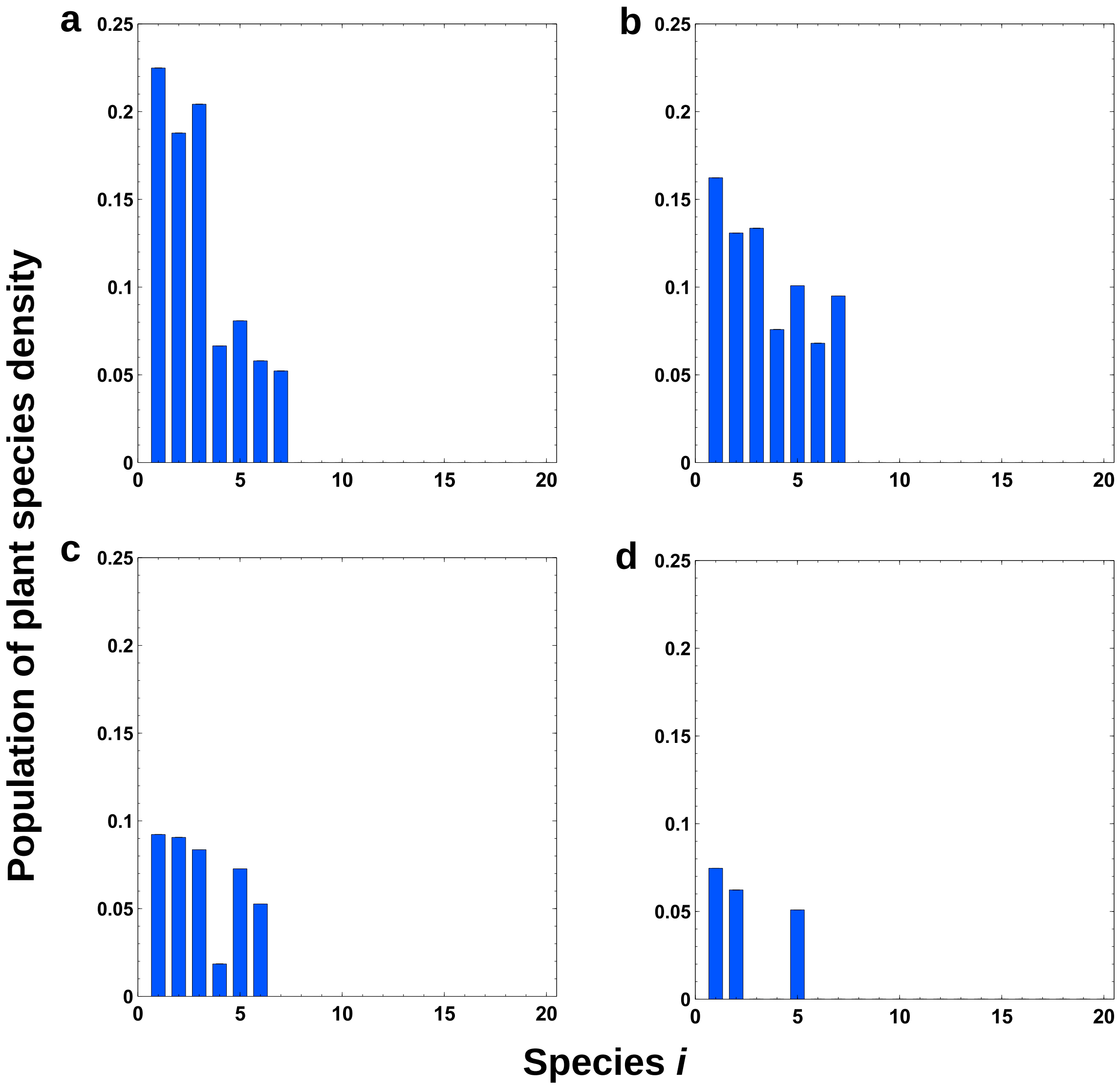

Figure 4.13 Population densities of species with respect to the basal grazing intensity G for the opposite case. (**a-d**) The grazing intensity decreases as the fecundity increases, i.e., $g_i = G + G'(i-1)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating that inferior species are eaten more often by grazers. (**a-d**) The result of a single run. The basal grazing rates are (**a**) G= 0.05, (**b**) G= 0.1, (**c**) G = 0.3, and (**d**) G = 0.5. The parameters are as follows: interspecific grazing difference, G' = 0.0005; basal fecundity, B= 1; initial species density, I_i = 0.03 (for all species); density of grazer cells, I_y = 0.4; and dispersal rate, P = 40. The lattice size is 100 x100.

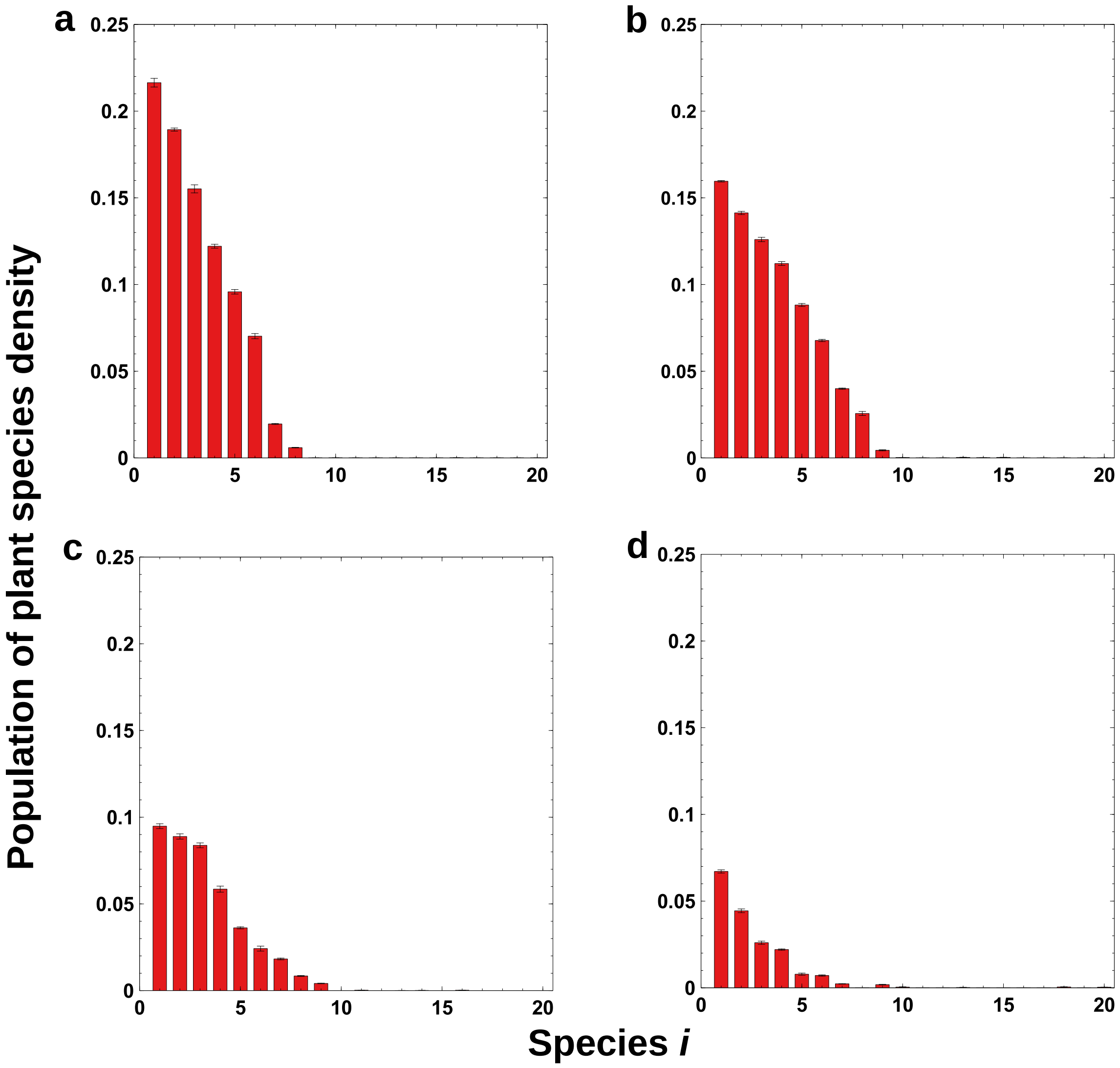

Figure 4.14 Population densities of species with respect to the basal grazing intensity *G* for the opposite case. (**a-d**) The grazing intensity decreases as the fecundity increases, i.e., $g_i = G + G'(i-1)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating that inferior species are eaten more often by grazers. (**a-d**) The average result of 30 runs. The basal grazing rates are (**a**) G= 0.05, (**b**) G= 0.1, (**c**) G = 0.3, and (**d**) G = 0.5. The parameters are as follows: interspecific grazing difference, G' = 0.0005; basal fecundity, B= 1; initial species density, I_i = 0.03 (for all species); density of grazer cells, I_y = 0.4; and dispersal rate, P = 40. The lattice size is 100 x100.

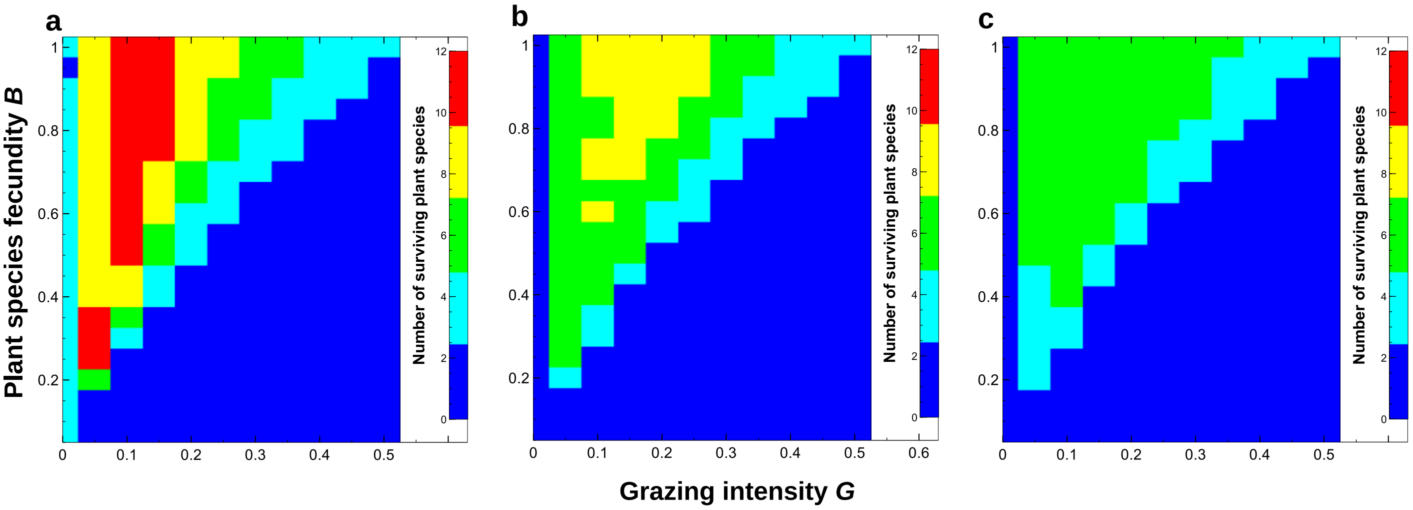

Figure 4.15 The average number of surviving species as a function of the basal grazing intensity *G* and basal fecundity *B* for three values of interspecific grazing differences (*G′*). (**a-c**) The grazing intensity of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, *s*), indicating a tradeoff between the birth rate and grazing intensity of a species. The values of interspecific grazing differences are (**a**) *G*'= 0.0005, (**b**) *G*'= 0.001, and (**c**) *G*'= 0.0015. The lattice size is 100 x100. The dispersal rate is P= 40. The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4.

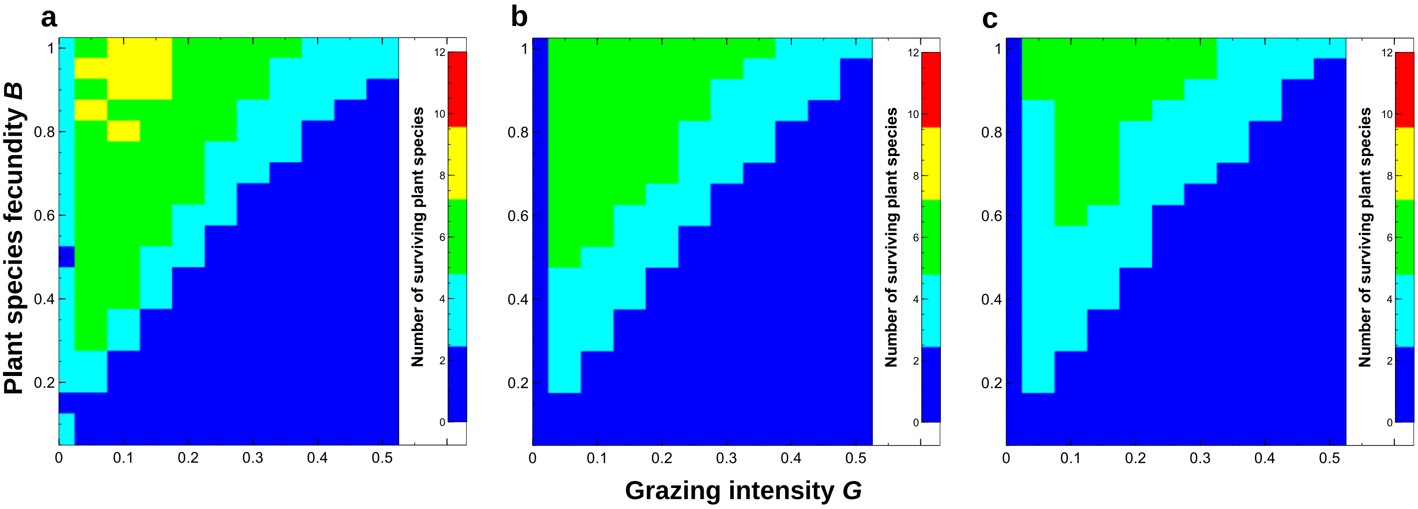

Figure 4.16 The average number of surviving species as a function of the basal grazing intensity *G* and basal fecundity *B* for three values of interspecific grazing differences (*G′*). (**a-c**) The grazing rate decreases as the fecundity increases, i.e., $g_i = G + G'(i-1)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating that inferior species are eaten more often by grazers. The values of interspecific grazing differences are (**a**) *G*'= 0.0005, (**b**) *G*'= 0.001, and (**c**) *G*'= 0.0015. The lattice size is 100 x100. The dispersal rate is P= 40. The initial species density is $I_i = 0.03$ (same for all species). The density of grazer cells is $I_y = 0.4$.

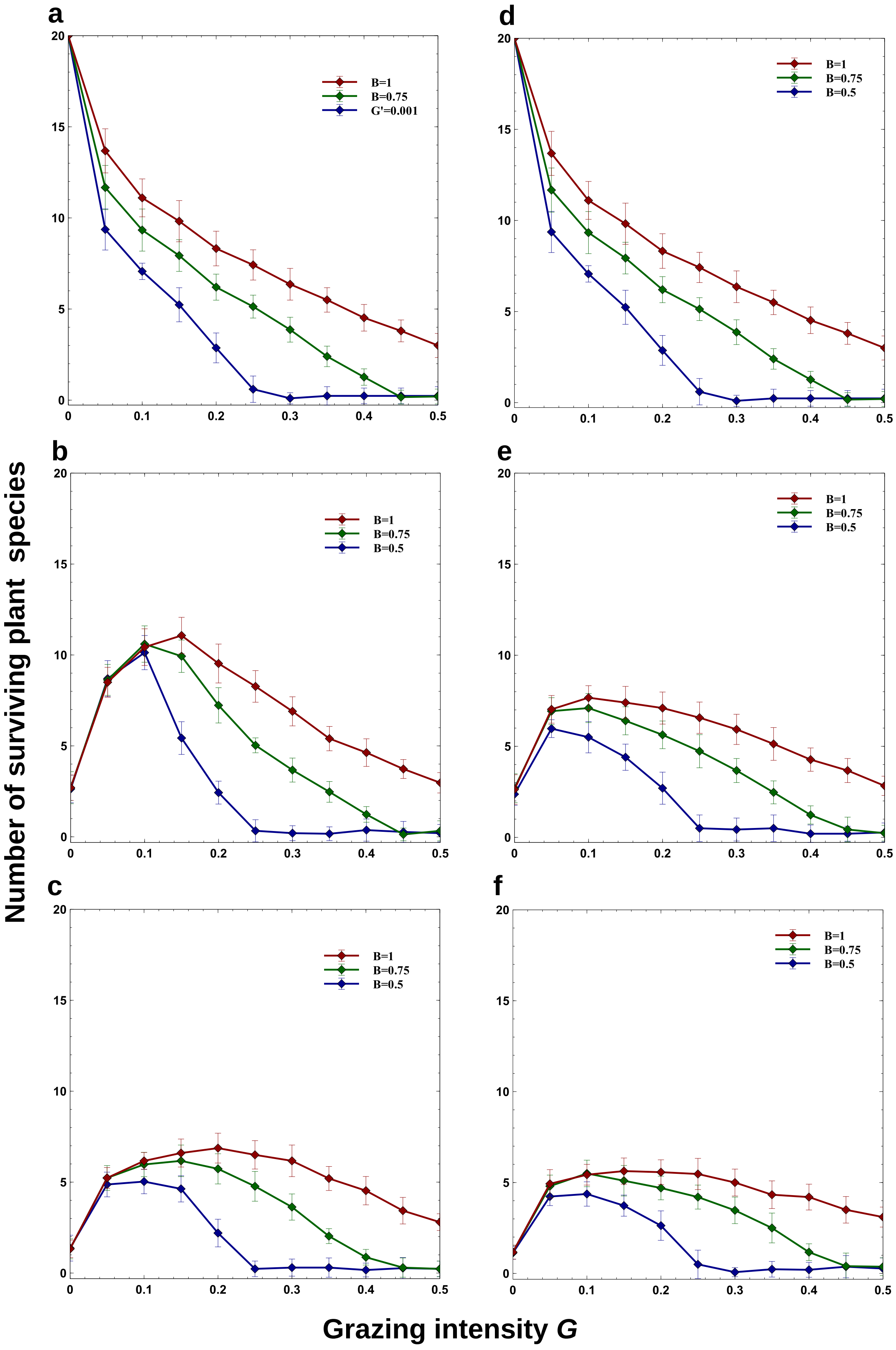a
B=1
B=0.75
G'=0.001
d
B=1
B=0.75
B=0.5
b
B=1
B=0.75
B=0.5
e
B=1
B=0.75
B=0.5
c
B=1
B=0.75
B=0.5
f
B=1
B=0.75
B=0.5
0
5
10
15
20
0
0.1
0.2
0.3
0.4
0.5
Number of surviving plant species
Grazing intensity G

Figure 4.17 The number of surviving species as a function of the basal grazing intensity *G* for various values of the basal birth rate B with G' = 0. (**a-c**) The grazing intensity of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. (**d-f**) The grazing intensity decreases as the fecundity increases, i.e., $g_i = G + G'(i - 1)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating that inferior species are eaten more often by grazers. The differences in the interspecific grazing rate are (**a, d**) G'= 0, (**b, d**) G'= 0.0005, and (**c, f**) G'= 0.0015. The lattice size is 100 x100. The dispersal rate is P = 40. The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

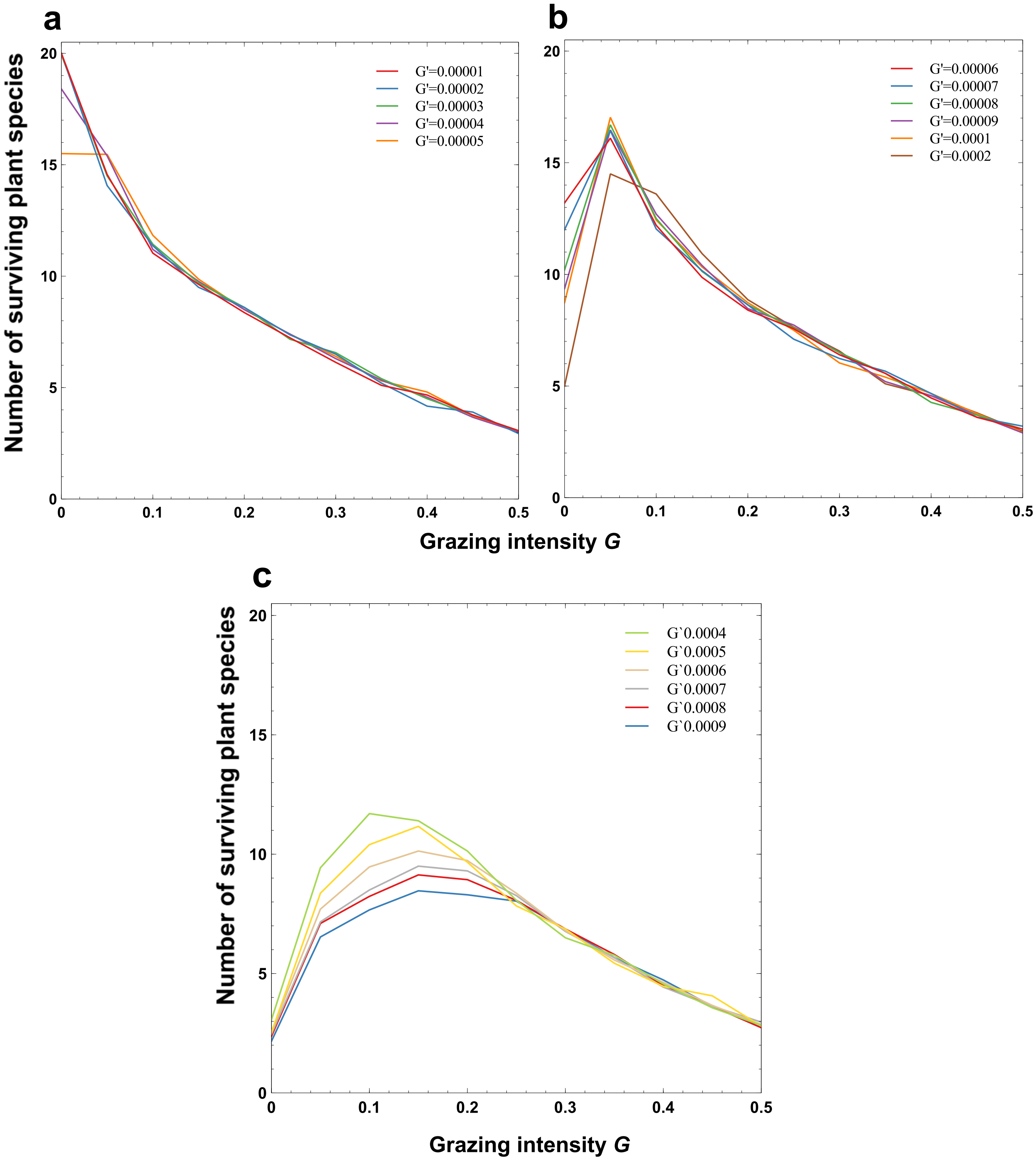
a
Number of surviving plant species
20
15
10
5
0
G'=0.00001
G'=0.00002
G'=0.00003
G'=0.00004
G'=0.00005
b
G'=0.00006
G'=0.00007
G'=0.00008
G'=0.00009
G'=0.0001
G'=0.0002
0
0.1
0.2
0.3
0.4
0.5
Grazing intensity G
c
G`0.0004
G`0.0005
G`0.0006
G`0.0007
G`0.0008
G`0.0009
Number of surviving plant species
Grazing intensity G

Figure 4.18 The effect of the interspecific grazing difference value G' on the number of surviving species. (**a-c**) The grazing intensity of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and B_i = B-0.002(i-1) for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. (**a-c**) G = 0.15. The lattice size is 100 x100. The dispersal rate is P = 40. The initial species density is I_i = 0.03 (same for all species). The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

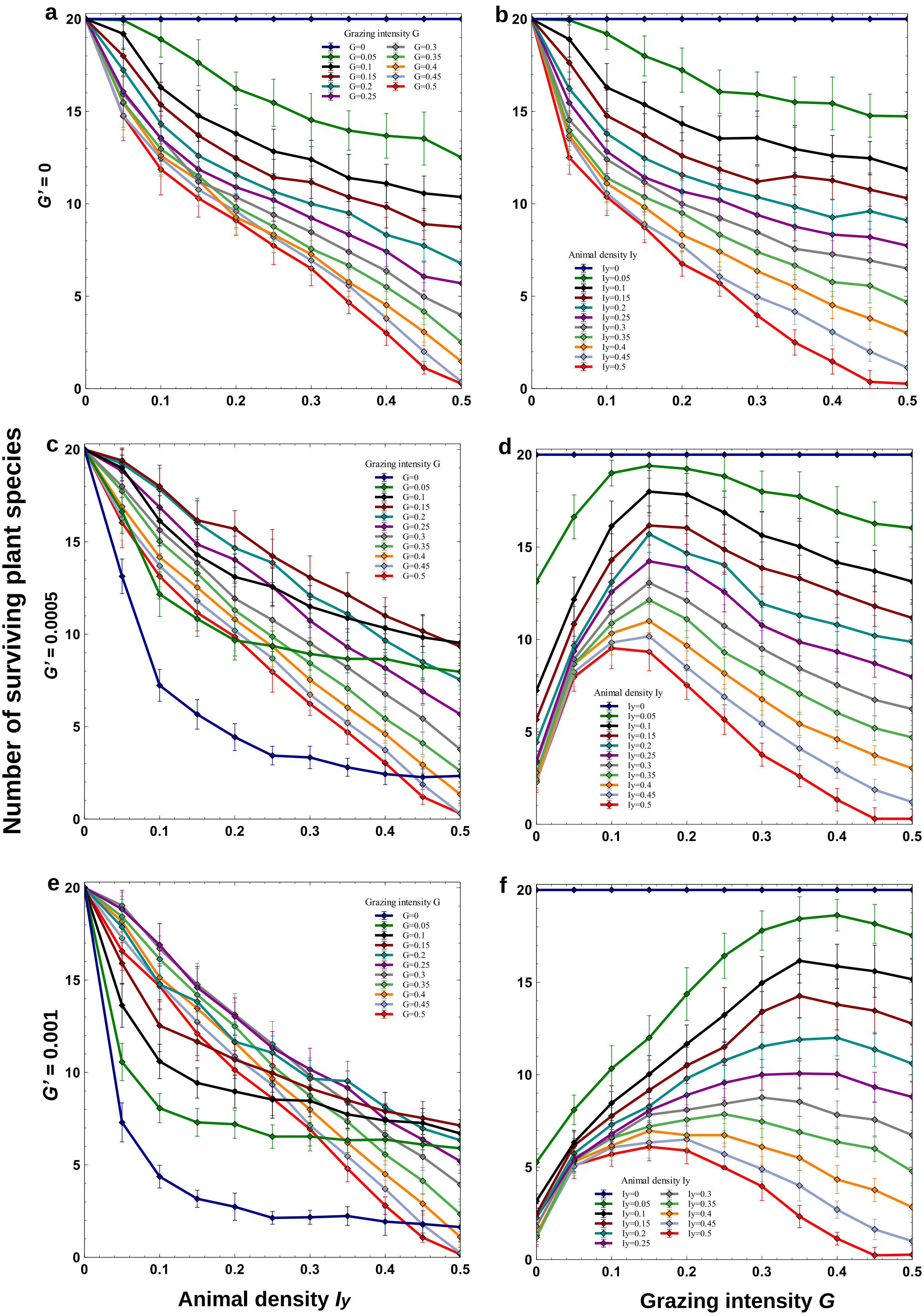
a
b
c
d
e
f
Number of surviving plant species
G’ = 0
G’ = 0.0005
G’ = 0.001
Animal density Iy
Grazing intensity G
Grazing intensity G
G=0
G=0.05
G=0.1
G=0.15
G=0.2
G=0.25
G=0.3
G=0.35
G=0.4
G=0.45
G=0.5
Animal density Iy
Iy=0
Iy=0.05
Iy=0.1
Iy=0.15
Iy=0.2
Iy=0.25
Iy=0.3
Iy=0.35
Iy=0.4
Iy=0.45
Iy=0.5
0
5
10
15
20
0
0.1
0.2
0.3
0.4
0.5

Figure 4.19 The effect of the animal density I_y, basal grazing rate G, and interspecific grazing difference G' on the number of surviving species. (**a-f**) The grazing intensity of a species increases as the fecundity increases, i.e., $g_i = G + G'(20 - i)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. The differences in the interspecific grazing rate are (**a-b**) $G' = 0$ (**c-d**) $G' = 0.0005$ (**e-f**) $G' = 0.001$. The lattice size is 100 x100. The dispersal rate is $P = 40$. The initial species density is $I_i = 0.03$ (same for all species). Error bars indicate the standard deviations.

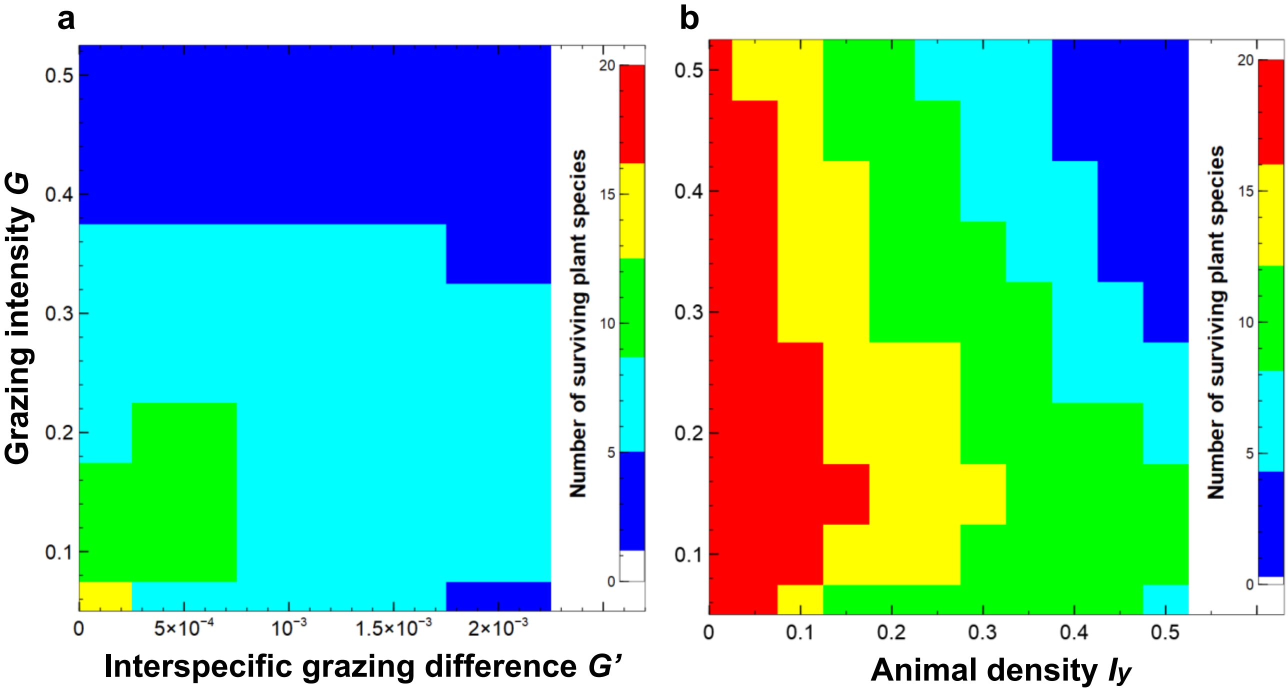

Figure 4.20 The effect of the animal density I_y, basal grazing rate G, and interspecific grazing difference G' on the number of surviving species. (**a-b**) The grazing intensity of a species increases as the fecundity increases, i.e., $g_i = G + G'(20-i)$ and $B_i = B$-0.002(i-1) for i=1, 2, …, s), indicating a tradeoff between the birth rate and grazing intensity of a species. (**b**) G' = 0.0005. The lattice size is 100 x100. The dispersal rate is P = 40. The initial species density is I_i = 0.03 (same for all species). (**a**) The density of grazer cells is I_y = 0.4. Error bars indicate the standard deviations.

Table 4.1 Number of surviving species based on the grazing intensity G and interspecific grazing difference G'. The grazing intensity of a species increases as the fecundity increases, i.e., $g_i = G + G'(20-i)$ and $B_i = B-0.002(i-1)$ for $i=1, 2, \ldots, s$), indicating a tradeoff between the birth rate and grazing intensity of a species. The lattice size is 100 x100. The dispersal rate is P= 40. The initial species density is $I_i = 0.03$ (same for all species). The density of grazer cells is $I_y = 0.4$.

G’ **G**	**0**	**0.05**	**0.1**	**0.15**	**0.2**	**0.25**	**0.3**	**0.35**	**0.4**	**0.45**	**0.5**
0.00001	20.00	14.57	11.03	9.63	8.37	7.23	6.13	5.10	4.67	3.77	3.07
0.00002	20.00	14.07	11.37	9.50	8.60	7.37	6.50	5.20	4.17	3.90	2.93
0.00003	19.93	14.50	11.43	9.70	8.60	7.17	6.57	5.40	4.50	3.77	3.07
0.00004	18.40	15.40	11.20	9.77	8.50	7.40	6.30	5.33	4.57	3.67	3.00
0.00005	15.50	15.47	11.83	9.87	8.50	7.40	6.40	5.30	4.80	3.73	3.03
0.00006	13.20	16.10	12.20	9.87	8.40	7.57	6.40	5.57	4.47	3.60	3.07
0.00007	12.00	16.43	12.03	10.17	8.63	7.10	6.23	5.67	4.67	3.60	3.20
0.00008	10.20	16.70	12.50	10.13	8.63	7.60	6.50	5.57	4.27	3.70	3.07
0.00009	9.37	16.47	12.70	10.40	8.47	7.73	6.50	5.20	4.57	3.70	2.90
0.0001	8.73	17.03	12.43	10.33	8.73	7.50	6.03	5.40	4.67	3.77	2.93
0.0002	5.00	14.50	13.60	10.93	8.87	7.63	6.57	5.10	4.57	3.80	2.97
0.0003	3.80	11.33	13.50	11.70	9.33	7.70	6.53	5.33	4.50	3.70	3.13
0.0004	3.07	9.43	11.70	11.40	10.13	8.07	6.50	5.77	4.57	3.57	2.83
0.0005	2.53	8.37	10.40	11.17	9.67	7.83	6.87	5.43	4.47	4.07	2.80
0.0006	2.57	7.70	9.47	10.13	9.73	8.37	6.80	5.57	4.63	3.67	2.87
0.0007	2.47	7.17	8.50	9.50	9.30	8.27	6.77	5.67	4.43	3.63	2.97
0.0008	2.37	7.10	8.23	9.13	8.93	8.07	6.87	5.80	4.50	3.63	2.73
0.0009	2.17	6.53	7.67	8.47	8.30	8.03	6.87	5.67	4.73	3.63	2.73

5. Discussion

In the present thesis, it is shown that our model simulation is able to reproduce the empirical observation of species diversity maintained by grazing animals. This thesis presents the first possible mechanism to explain the enhancement of species diversity by grazing. Our result confirms that the coexistence of plant species is possible under grazing in grasslands (Figs. 4.6, 4.7, 4.8). The results reveal unimodality in which the peak species diversity occurs at an intermediate grazing intensity (Fig. 4.9). When there is a tradeoff between the birth rate and grazing rate, the number of coexisting species is large (more than 10 species) (Figs. 4.9a-c). Therefore, this tradeoff promotes coexistence by balancing competitiveness among all plant species. We also test the case in which the grazing rate is negatively correlated with the birth rate. Surprisingly, unimodality in response to grazing intensity is still observed (Figs. 4.9d-f). In this case, the intermediate grazing rate allows less superior species to persist by occupying the new vacant sites produced by grazers (Figs. 4.13b, 4.14b), while it is not strong enough to exclude them (as in Figs. 4.13d, 4.14d). Thus, the coexistence of species is mechanically promoted because (weak) grazing produces vacant sites available for other species. The number and composition of coexisting species vary depending on simulation runs (Figs. 4.11a-d, 4.13a-d), while on average they are determined by the birth rate and grazing mortality rate (Figs. 4.12a-d, 4.14a-d). The tradeoff between the birth rate and grazing rate is not necessary for the unimodality in response to grazing intensity.

According to the presented results, species coexistence ceases to be maintained if natural mortality caused by other factors is introduced (Figs. 4.10d-f, 4.17a, d, and 4.18). Therefore, an increase in diversity due to grazing does not occur when grazing is not the principal source of mortality in grasslands, i.e., when the nongrazing mortality is not negligible. This prediction should be tested empirically in future field studies. The interspecific grazing difference G' also plays an important role in the promotion of coexistence. If the difference is absent or very minute, then the promotion of coexistence by grazing disappears (Fig. 4.18a vs Figs. 4.18b, 4.18c).

It should be remarked that the composition of surviving species depends on how the birth rate varies compared to the variation of grazing mortality (Figs. 4.11, 4.12, 4.13, 4.14). In the tradeoff case, inferior species (with low birth rates) exclude superior species (with high birth rates) (Figs. 4.9a-c). In the opposite case, superior species dominate the grassland (Figs. 4.9d-f). The composition of surviving species is highly variable in the tradeoff case but stable in the opposite case (Figs. 4.11, 4.12, 4.13, 4.14). These results should be verified empirically in managed grasslands. Furthermore, the current simplified assumptions about grazing rate g_i may be modified explicitly to include the behavior of grazing animals, e.g., the frequency dependence in food-plant selection.

The effects of herbivores on plant diversity in grasslands have been analyzed by using empirical data [65, 66, 67]. The proposed grazing model integrated with a microhabitat locality model [36] should be sufficient as a canonical model with which to investigate the functional mechanisms of herbivore grazing effects mathematically. In terms of maintaining and increasing diversity, our results are in line with those of some empirical studies [14, 38-42, 68-73]. For example, Komac et al. stated that maintaining an adequate grazing intensity (avoiding both abandonment and overgrazing) is necessary to preserve diversity in grasslands [38]. Mu et al. also found that light and moderate grazing promote plant biodiversity [39]. In addition, Chen et al. showed that heavy grazing has an indirect influence on biodiversity [42]. Furthermore, Chen et al. based on empirical observation inferred that grazing type and vegetation structure that affect spatial variation are the reasons for the high species richness in the Qinghai alpine meadow [14]. The two reasons are in line with our models and results.

In a grassland where grazing is not the only main mortality factors, intermediate grazing intensity is also necessary to maintain diversity. Joubert et al. found that coupling fire disturbance and moderate grazing can maintain plant diversity [41]. They measured the species richness was significantly higher at recently burned grassland and coupled with moderate grazing intensity. Their results conform to our model (Figure 4.10) that in grassland where nongrazing mortality is not negligible, the unimodality is still maintained when nongrazing mortality is kept at a low rate or in nature grazing has sufficient time to increase diversity after the burning. Collin et al. also revealed that grazing even reverses the loss of diversity caused by frequent burning [68]. They also showed that in two long-term field experiments, diversity decreased on burned and fertilized treatments, while grazing preserved diversity under the same conditions. The studies imply that grazing naturally maintains plant diversity in various conditions.

The studies on herbivore in grasslands are in line with our result that, for example, trade-off cases where animal grazers prefer dominant plant species, resulting in higher plant diversity [65, 66, 73]. Animal grazer Assemblages, including large herbivores, animals with weight > 30kg increased plant diversity at higher productivity of grassland areas [65]. Usually, large animals tend to feed on dominant plant species. The preferred grasses decreased significantly under heavy grazing (large animal grazer) but increased without grazing [73]. However, when light (a small number of grazers) and moderate (moderate number of grazers) grazing is introduced, the proportion of less dominant species increased.

As for an example of the field experiment, Hasbagan et al. measured the species diversity in under four grazing levels [no grazing, light(2.4 sheep units ha–1), moderate (3.6 sheep units ha–1), and heavy (6.0 sheep units ha–1) grazing] in 5 years (2006–2010) grassland in Qinghai-Tibetan Plateau. They measured the number of species to determine the species richness on the plot objects. They found that moderate grazing enhanced the species diversity higher than light and heavy, and twice higher than without grazing [73]. This study is in line with our result that the number of less superior species increases under moderate grazing intensity, whereas preferred species tend to decrease, depends on grazing intensity or assemblage of animal grazer in nature [65, 66, 67]. Studies by McNaughton, known for his work in Serengeti, also found that the moderate grazing stimulated productivity up to twice higher than in ungrazed plots [17]. Animal grazing increases the overall productivity of grassland by invoking the recovery action in grass species more than that without grazing [18]. The grazing increases the productivity of plant species even after the loss by grazing.

In principle, the numerical values of the parameters may be evaluated from empirical data of the birth and death rates of coexisting plant species. However, in practice, it has yet to be done because each grassland ecosystem is uniquely complex in a substantial manner. In a grassland community consisting of more than ten species, the birth and death rates of each species is almost impossible to trace over time. The only available data are the number of species (species diversity) and the covers of each species at time in a community [14, 37]. One possible approach to test the current simulation results is the use of an experimental pasture where the number of grass species are limited to 10 to 20 species [54]., but surrounded by natural grasslands with many more species. We divide the experimental plot into several plots with different density of grazing. In this approach, we may be able to test directly the effects of animal grazing on plant species diversity. We may be able to test if low level of grazing will increase the number of plant species. Note here the new species should have invaded from the surrounding natural grasslands. Recently a similar approach has been taken to show that grazing enhances species richness [74]. However, the direct empirical demonstration of the current simulation results is still very difficult. Thus, the empirical proof of this model is a future problem of grassland ecosystems.

Moreover, by modifying the lattice setting, the current model can be applied to other terrestrial communities while considering predators. However, this mechanism of grazer or predator effects should be directly verified using empirical data in the future.

We should also note that this grazing model presents similar results with the intermediate disturbance models [34, 43, 44, 75,76]. In these models, there may be several specific underlying mechanisms promoting coexistence. Intermediate disturbance hypotheses stated that disturbances such as fire, flood, and even deforestation by humans might promote diversity if they occur at the intermediate level. Qualitatively the current grazing model appears to conform to these models. Because our model also achieves the highest diversity at the intermediate level of grazing. However, whether the current model is considered as one such specific mechanism or not is a future issue.

6. Conclusion

The study presented in this dissertation is a significant contribution to elucidate the actual grazing behavior of grasslands in the area of ecological fields. Scientists had performed many empirical studies to test the effect grazing for decades. However, no convincing explanation was provided for the unimodal response of grazing. We believe that it would take decades or even hundreds of years to verify the grazing mechanism experimentally. Owing to the vast area covering one-quarter of the Earth's land area, various conditions of the environment, and many other complicated factors changing through time, it appears almost impossible to examine grazing effect to conclude a universal understanding of the plant species coexistence in grasslands. Therefore, we conduct the research to verify the effect of grazing on species coexistence using mathematical and simulation methods. Simulations studies have been advanced with the development of technology. The recent computer technology allows for more realistic and accurate simulations.

We used a lattice model to analyze how grazing influences the grassland's diversity. Our model revealed that the coexistence of multiple species is possible with the existence of grazers. The results exhibit that intermediate grazing intensity causes the peak of unimodality, which signifies the highest number of surviving plant species. The animal grazers produce vacant sites in which inferior species can inhabit. Grazing also moderates the competitiveness to feed on more palatable dominant plant species. This is shown to occur in the tradeoff case. We also test the opposite case that the dominant species is more unpalatable for grazers. The result still maintains coexistence with a smaller number of survivors. The coexisting species depends on the interspecific relationship between birth rate and grazing mortality rate. In the tradeoff case, the surviving species is inconsistent with the grazing effect. Inferior species dominate at a low grazing rate while superior species do at a high grazing rate. However, both superior and inferior species coexist at the intermediate grazing rate. In the opposite case, superior species dominate at all grazing intensities. Introduction of nongrazing mortality leads to elimination of the promotion of coexistence. Moreover, an increase in diversity does not occur when grazing is not the primary mortality source. The seed dispersal of plant species is also an important factor, while the range of dispersal does not significantly affect the promotion of diversity.

This research provides the first possible mechanism that explains the grazing effect in grassland species coexistence. The model can be extended to consider other parameters capturing other essential features of grasslands. The specific dependence of species and lattice sites can be modified to represent a more realistic grassland's dynamics. The assemblages of grazers are also possible to be incorporated in the model. In our model, the grazer's appetite properties are assigned specific values depending on plant species. A new parameter can be defined to test the effect of grazer's diversity on grassland's coexistence. The model can also include factors such as climate change and disturbances. Furthermore, this model can be modified for other plant communities with the existence of predators.

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