Article

Dynamic Plant–Herbivore Interactions between Bison Space Use and Vegetation Heterogeneity in a Tallgrass Prairie

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Abstract: Investigations into plant–herbivore interactions are of importance for understanding grassland ecosystem dynamics. Our research quantified the effects of vegetation heterogeneity at a patch scale of 30 m on bison space use in a tallgrass prairie through the analyses of the resource utilization function. In addition, we assessed the vegetation heterogeneity associated with bison locations by comparing the patch-scale vegetation characteristics between areas with high and low bison space use through Mann–Whitney U tests. Furthermore, we simulated the interactions between bison and vegetation patches (2 × 2 m) during the early growing season for the lowland topographic positions using agent-based modeling (ABM) as a preliminary study of linking bison foraging site selection with vegetation responses to bison grazing dynamically. The bison grazing strategy in the ABM of the grassland system was adjusted to ensure consistency in the vegetation pattern variations related to bison space use between the simulation and the empirical on-the-ground observations. The results indicated the following: (1) The effects of the patch-scale vegetation heterogeneity on the bison foraging site selection varied across the seasons, which were most evident in the middle of the growing season. (2) A relatively high level of bison space use generally resulted in diverse grassland canopies with high variability and interspersion. (3) From the ABM of the grassland system, it can be implied that bison select patches with high quality and quantity at the beginning of the growing season; as the vegetation quality and quantity improve overall, the bison graze randomly. This pattern was confirmed by observations of the bison foraging site selection in our study site. The ABM proved to be valuable in exploring and elucidating the underlying mechanisms of the grassland dynamics with a native North American grazer.

Keywords: agent-based modeling; bison foraging site selection; dynamic plant–herbivore interactions; resource utilization function; vegetation heterogeneity

1. Introduction

American Bison (*Bison bison*) were once widely spread across North America and historically played a keystone role in the Great Plains until their near extirpation in the 1800s [1]. Over the past century, the recovery of bison has been pursued for ecological and conservation goals. The return of bison as a critical driver that shapes vegetation patterns and restores biodiversity in the North American prairies [2,3] has received extensive interest among ecologists and conservation organizations [4–8].

Substantial studies of the interrelationships between bison and grassland vegetation have been carried out to understand the underlying mechanisms of the large herbivore grazing system in North American tallgrass prairies [4,9–11]. Vegetation critically determines the resource availability and habitat suitability for bison in prairies. The distributions of vegetation resources affect bison foraging at different spatial scales, ranging from the

grazing activities at a fine, feeding-station scale [12] to movement patterns across landscapes [12–14]. In turn, the resulting bison landscape-level distributions and fine-scale space use further play a major role in modulating the existing grassland canopies with respect to foliar nutritional quality, plant species composition and vegetation structure [9,15,16].

Most of the previous research has quantified the interactive effects between bison distributions and vegetation pattern formation at a coarse, landscape scale that links bison movement with landscape structure over a large spatial extent [4,10,13,17]. Grassland vegetation heterogeneity has been widely investigated under a variety of static environmental factors known to shape the vegetation pattern across landscapes, such as topography, fire and grazing treatments [9,17–19]. Topography influences the composition and structure of tallgrass prairie plant communities due to the different conditions of soil depth, moisture and temperature [20]. The influence of topography on vegetation heterogeneity is more evident in the senescent season than in the early growing season [17]. Fire and grazing are historically critical components in tallgrass prairies [3,21]. Their interaction, referred to as pyric herbivory [22,23], which results in a shifting mosaic of disturbance across the landscape, has been widely used to maintain vegetation heterogeneity and sustainability in the current fire-dependent grassland systems [24].

Vegetation resource distribution with relevant static environmental factors across landscapes is a key driver for animal movement and space use. In early studies, it has been observed repeatedly that fire promotes herbivory by attracting bison toward recently burned grasslands in the growing season [3,14] due to the regrowth of vegetation after fire with a high forage quality [25,26]. In addition, bison prefer lowland topographic positions with greater soil depth, moisture and plant productivity to the dry uplands in the senescent season [3]. Recent studies in the framework of animal resource selection or resource utilization have provided quantitative information on the factors that influence bison foraging site selection. The static environmental factors have been related to bison space use through logistic or multivariate regression, from which the influence of the static environmental factors and the associated vegetation patterns at a landscape scale on bison distribution and habitat use has been evaluated [10,13].

Research into bison space use at patch scales (~1–100 m) [27,28] is less extensive than that at coarse, landscape scales—an analysis at a finer scale requires more finely resolved spatiotemporal data of the vegetation characteristics. In previous research, field data of vegetation characteristics were collected at a lower temporal sampling frequency than the data of Global Positioning System (GPS)-collared bison locations, making it difficult to relate the vegetation status or condition with animal distributions appropriately in the framework of animal resource selection or resource utilization [13]. In addition, the analysis of animal space use commonly evaluates the influence of environmental factors on animal movement and habitat use from a static perspective, in which the processes of grazing and vegetation pattern variation are not connected dynamically over a growing season, for instance.

Agent-based modeling (ABM) is potentially a suitable tool for simulating the dynamic interactions between grazers and grassland vegetation [29–32]. In the framework of ABM, a large grazer (i.e., bison) and vegetation can be simulated as autonomous agents in a computational program, and their interactive effects can be explored from a dynamic view of interactions between the agents. The key to simulations of bison and grassland vegetation dynamics by using ABM is to specify the behavioral rules for the interacting agents reasonably. Although the previous literature has provided valuable implications for establishing rules of the large herbivore grazing system at the landscape scale to simulate grassland dynamics [9,10,13,17], details of the patch-scale interactions between bison and vegetation heterogeneity remain to be clarified in tallgrass prairie ecosystems.

The principal goal of our study was to understand the dynamic interactions between bison space use and vegetation heterogeneity at patch scales in a tallgrass prairie. Our analysis focused on the burned watersheds where pyric herbivory was evident throughout the landscapes. It is clear that bison are attracted to the recently burned sites with a

high forage quality, whereas the influences of the factors within the burned watersheds, particularly vegetation resource distributions at a fine patch scale, on bison foraging decisions are unknown.

We used the nitrogen content within the vegetation canopy to characterize the vegetation resource availability for bison given that nitrogen is an indispensable element that drives organismal growth and is an often limiting nutrient in natural ecosystems, including grasslands. The effects of the patch-scale canopy nitrogen distributions on bison space use were quantified through the animal resource utilization function (RUF) [33–35] to understand how the bison selected foraging sites within the burned grasslands across the seasons. In addition, we compared the patch-scale canopy nitrogen distributions between areas with high and low levels of bison space use to evaluate how the grazing intensity by large herbivores affected the vegetation heterogeneity within the burned watersheds. Furthermore, we simulated the interactions between the bison and vegetation patches for the lowlands during the early growing season in the framework of ABM as a preliminary study. From the quantitative analysis of the interactive effects between bison space use and vegetation heterogeneity, we established the behavioral rules for bison and vegetation patches in this fire-dependent study system. In the simulated grassland system, the processes of bison foraging site selection and vegetation responses to bison grazing were interconnected, which provided a dynamic perspective to understand the interactions between the bison foraging decisions and grassland vegetation pattern variations. Our ABM of the grassland system was useful for the dynamic simulation of bison space use and grassland vegetation heterogeneity, which had the potential to be a valuable tool for grassland resource conservation and management.

2. Methods

2.1. Study Area

Our research was conducted at Konza Prairie Biological Station (KPBS), a tallgrass prairie dominated by a continental climate near Manhattan, Kansas, USA (39°05′N, 96°35′W). The elevation of the site ranges from 331 m to 441 m. The vegetation is featured by perennial C_4 grasses (*Andropogon gerardii*, *Sorghastrum nutans*, *Bouteloua gracilis*, *Panicum virgatum* and *Schizachyrium scoparium*), interspersed with a highly diverse mixture of C_3 forbs and a few C_3 grasses [36]. KPBS is operated by the Division of Biology at Kansas State University for long-term studies on the interactive processes among fire, large herbivore grazing and grassland vegetation communities. The site is divided into more than fifty watersheds, each with a treatment combined by fire and ungulate grazing. Fire frequencies range from one to twenty years. Grazing treatments include grazing by American Bison, domestic cattle (*Bos taurus*) and non-grazing. There are ten watersheds (~1000 ha) fenced and grazed by bison, where the stocking rate is currently maintained at around 0.3 animals/ha. The sex ratio of mature female bison to mature males is around 4:1. Male bison are removed from the herd at the age of eight years old. Females may remain and stay in the herd until the age of fifteen. In this study, nine out of the ten bison-grazed watersheds were covered by the aerial imagery (Figure 1).

2.2. Data Collection and Preprocessing

Bison live in maternal herds, dominated by older females. Fourteen cow bison were randomly selected and collared with Telonics TGW-3700 GPS devices. Each collared individual was followed by another 30–40 members in the herd [10,11]. The locations of the collared individuals were recorded every 30 min in 2011.

Hyperspectral imagery with a 2 m resolution covering the study area was captured on four dates (26 May, 29 June, 2 August and 26 September 2011) using an AISA Eagle camera mounted on a Piper Warrior aircraft operated by the Center for Advanced Land Management Information Technology (CALMIT) of the University of Nebraska–Lincoln. Continuous maps of canopy nitrogen were derived from the hyperspectral aerial imagery data statistically. The empirical models used for retrieving the canopy nitrogen were devel-

oped (n = 108 and R^2 = 0.86) and validated (n = 54, R^2 = 0.92 and RMSE = 0.24 g/m^2) by using 162 field sample measurements collected during May–September in 2011 from three bison-grazed watersheds with different fire frequencies (1 year, 4 years and 20 years) [36].
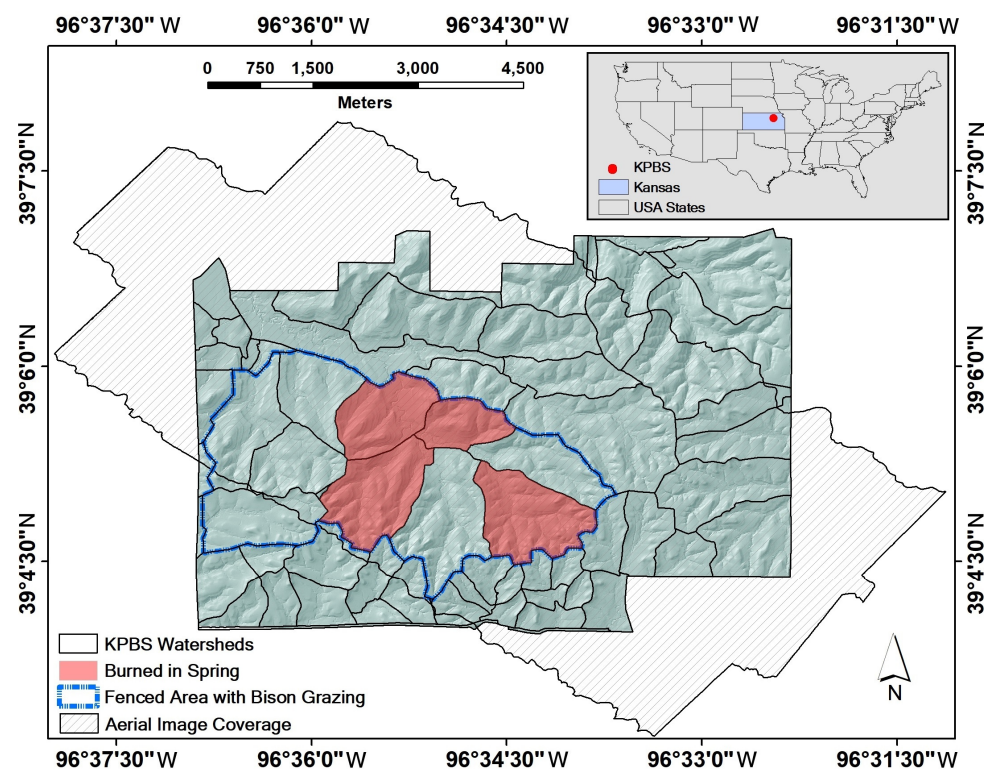

Figure 1. Study area at Konza Prairie Biological Station (KPBS), Manhattan, Kansas, USA.

The numerical values of the canopy nitrogen were classified into five levels from low to high by natural breaks (Table 1). Each level was considered a patch type. The resulting categorical maps were used to quantify the composition and spatial configuration of the patch types by using the spatial heterogeneity metrics. The retrieval of the canopy nitrogen content [36] and conversions to categorical maps [17] were completed in our previous research (Table 2).

The fire history records [37] and the digital elevation model (DEM) with the 2 m cell size of the study area [38] were provided by the National Science Foundation (NSF) Long-Term Ecological Research Program at KPBS (Figure 2). According to the elevation and slope data retrieved from the DEM, the study area was divided into four topographic types, including drainage bottoms, lowlands, uplands and hillslopes. The hillslopes were the transition zones between the drainage bottoms and lowlands or between the lowlands and uplands with the slope value >10° [17]. The drainage bottoms were excluded in the data analysis due to the severe encroachment by the gallery forests.

Table 1. Natural breaks of continuous canopy nitrogen values across seasons. The continuous canopy nitrogen values for each month were classified into five levels: low (L), moderately low (ML), moderate (M), moderately high (MH) and high (H).

Month	Natural Breaks of Canopy Nitrogen Values			
	L–ML	ML–M	M–MH	MH–H
May	0.83	1.36	1.82	2.27
June	1.46	1.74	2.00	2.27
August	0.50	0.90	1.28	1.71
September	0.32	0.50	0.69	0.92

Table 2. Summarization of data collection and preprocessing. Global Positioning System (GPS) data of bison locations are used for utilization distribution estimation that reflects bison space use.

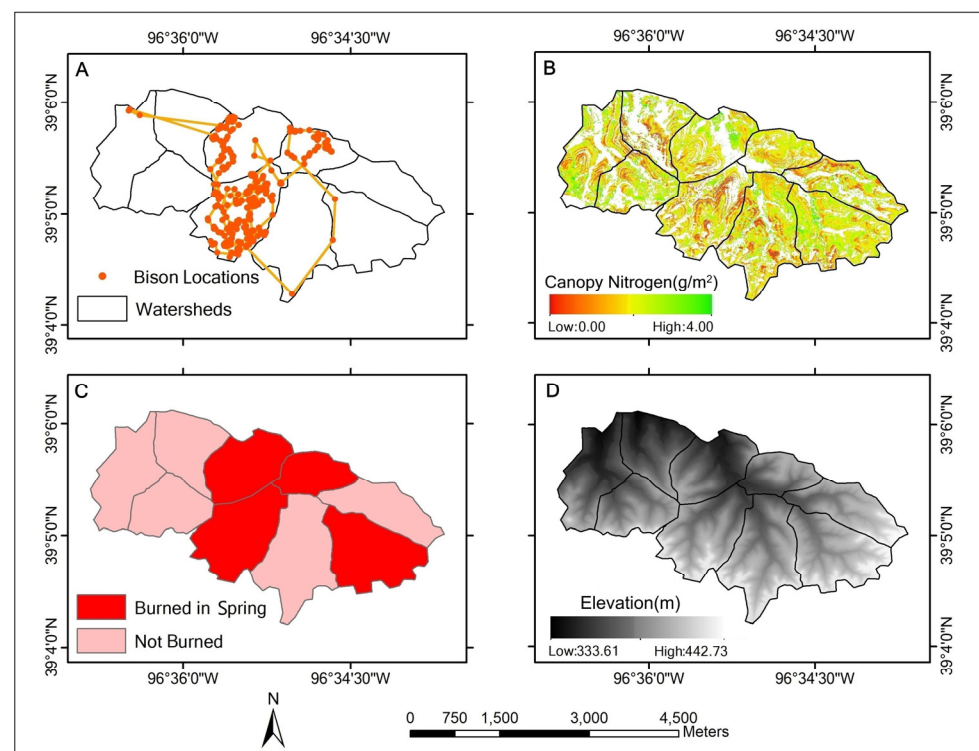| Metadata	Derived Data	Data Source
GPS locations	Bison space use	This research
Hyperspectral imagery	Continuous canopy nitrogen maps	Ling et al. [35]
	Categorical canopy nitrogen maps	Ling et al. [17]
Fire history records	Burning maps	This research
Digital elevation model	Slope	Ling et al. [17]
	Topographic position divisions	

Figure 2. Data collection for the analysis of interactions among bison, vegetation and topography. (**A**) The locations and movement trajectory of bison #026 during 27 May–2 June 2011, were shown as an example of the Global Positioning System (GPS) data that were used for the estimation of bison space use. (**B**) The spatial distribution of canopy nitrogen derived from the hyperspectral image captured on 26 May 2011, was shown as an example of the data that characterized the vegetation resource heterogeneity. (**C**) The fire treatments were operated at the watershed level. (**D**) The digital elevation model (DEM) was used to acquire topographic features.

2.3. Data Analysis

2.3.1. Assessment of Bison Space Use at a Patch Scale

Our analysis of bison space use focused on the watersheds burned in the spring of 2011. Unburned watersheds were excluded from the analysis. The influence of the fire frequency at the watershed level on bison distributions was not analyzed given that the bison foraging preference for burned grasslands was studied exhaustively in previous research [13,14].

The environmental factors related to bison space use in our analysis included topographic features and vegetation characteristics. The topographic features, including elevation and slope, were retrieved from the DEM of the study area (Table 2). The vegetation characteristics were measured within the sample patch from several perspectives, including the mean of the canopy nitrogen contents ($\bar{N}$), standard deviation of the canopy nitrogen contents (SD_N), contagion and Simpson's diversity index (SIDI) of patches with

different canopy nitrogen levels. Contagion is a metric of aggregation [39]. A higher value of contagion indicates that the patch types are more aggregated. SIDI is a metric of diversity. A higher value of SIDI indicates that the patch richness is greater, and the proportional distribution of area among patch types is more equitable. The $\overline{N}$ and SD_N were calculated from the continuous canopy nitrogen maps. The contagion and SIDI were calculated from the categorical canopy nitrogen maps in the program of Fragstats 4.2 [40].

We selected the data of the bison locations collected during the week after the capture of the aerial imagery to calculate the bison space use and investigate how the existing spatial patterns of the vegetation influenced the bison movement and habitat selection. The bison space use was modeled using the utilization distribution (UD), which calculates the probability density of the animal's relative occurrence frequency in a two-dimensional plane [41,42]. The UD estimations of the bison individuals were calculated with a 2 m resolution using the method of biased random bridge movement-based kernel density [43]. The values of the UD were scaled linearly into the range between 0 and 1. A value of the scaled UD closer to 1 indicates a higher possibility that the animal selects the foraging site.

Sample points were arranged every 30 m along the movement trajectory of each individual. The sample patch was determined by the circular area with a radius of 15 m centered at each sample point, within which the bison space use, topographic features and vegetation characteristics were sampled at a patch scale. The sampled bison space use was linked to the topographic features and vegetation characteristics using a multivariate regression model in the RUF [33–35,44–46], which was proposed by Marzluff et al. [47]:

$$y = \beta_0 + \beta_1 \cdot \text{Elevation} + \beta_2 \cdot \text{Slope} + \beta_3 \cdot \overline{N} + \beta_4 \cdot SD_N + \beta_5 \cdot \text{Contagion} + \beta_6 \cdot \text{SIDI} + \varepsilon$$

where y is a continuous variable denoting the scaled UD of individual bison; β_0 is the intercept; β_1 and β_2 are the regression coefficients for the elevation and slope, respectively; β_3–β_6 are the coefficients for the vegetation characteristics, namely, $\overline{N}$, SD_N, contagion and SIDI; and ε is an error in the regression model. For each environmental factor, the mean of the coefficients calculated for the bison individuals was compared with 0 using a *t*-test at the 0.05 significance level. If the mean of the coefficients is significantly different from 0, the corresponding environmental factor is statistically significant in the RUF. The negative coefficients indicate that the corresponding environmental factors are avoided by the animal. The positive coefficients indicate that the animal prefers the corresponding environmental factors. The relative importance of the environmental factors was examined by comparing the absolute values of the coefficients in the standardized RUF. We also removed the data collected from the sample patches in the hillslope zones and excluded the topographic features in the RUF to investigate the influence of vegetation characteristics on bison space use apart from the influence of topography.

2.3.2. Quantification of Patch-Scale Vegetation Heterogeneity Related to Bison Space Use

The bison locations recorded for a week before the capture of the aerial imagery were selected for the UD estimations to investigate how bison space use influenced the vegetation heterogeneity. The UD maps were calculated for the individuals and overlaid to form a summarized map of the bison space use. The summarized UD estimation was classified into three levels from low to high using natural breaks.

The influence of bison space use on vegetation heterogeneity at a patch scale was assessed by comparing the patch-scale canopy nitrogen distributions in the areas with the high and low levels of bison space use. The patch-scale canopy nitrogen distributions were quantified using the moving window method. A circular window with a radius of 15 m moved over each cell in the continuous and categorical maps of the canopy nitrogen. Within each window, the $\overline{N}$, SD_N, contagion and SIDI of the patches with different canopy nitrogen levels were calculated and assigned to the central cell to characterize the patch-scale canopy nitrogen distribution. The canopy nitrogen distribution characteristics of the cells in the areas with the high and low levels of bison space use were compared using

Mann–Whitney U tests at the 0.001 significance level [48]. The comparison analyses were conducted separately for the lowlands, hillslopes and uplands across the seasons.

2.3.3. Simulation of Bison and Vegetation Interactions

As a preliminary study on the ABM of the grassland system, we simulated the dynamic interactions between the bison foraging site selection and vegetation responses to the bison grazing in the lowland zones for a month (30 days) from May to June. The simulation was implemented in the program of NetLogo 6.3.0 [49]. The simulated grassland system consisted of two types of agents: vegetation patches and bison. The "world" of the grassland was divided into a 261 × 121 grid of tiles with a tile size of 2 m, which were set as vegetation patches with a cell size consistent with the canopy nitrogen maps. Two variables, *N* and *times*, were defined for each patch to record the canopy nitrogen value of the patch and the number of times the patch was grazed by bison, respectively.

The bison herded on the vegetation patches. In the herd of bison, a leader was set up that decided the movement directions and was followed by other members. Each individual had a possibility of grazing that was determined by the effects of the canopy nitrogen distributions on the bison foraging site selection quantified in the RUF at a spatial scale of 30 m (Figure 3). Once the individual had decided to graze, the grazing strategy determined which small patch (2 × 2 m) was selected within the search area of the individual. We set up two grazing strategies: random grazing and selective grazing. When following the random grazing strategy, each individual of the herd grazed the patch on which it was standing. When following the selective grazing strategy, each individual searched in a circular area with a certain radius around itself and grazed one of the patches with the highest *N* value. In addition to grazing, the bison also roamed on the patches. The movement distance at each time step was set according to the analysis of the bison movement trajectories.
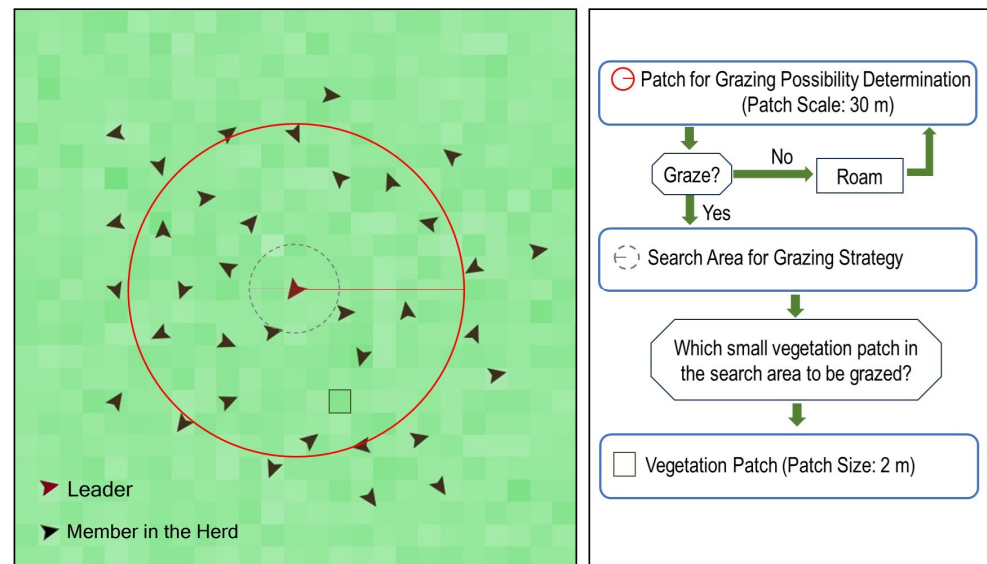

Figure 3. Various patch scales in agent-based modeling (ABM) of the grassland system. At the scale of 30 m, bison decide whether to graze according to the grazing possibility determined by the effects of canopy nitrogen distributions on bison foraging site selection quantified in the resource utilization function (RUF). The patch scale of 30 m is consistent with the size of the sample patch in the analyses of the RUF, which has a radius of 15 m. As a grazer decides to graze, a specified grazing strategy is applied, through which the grazer grazes a small vegetation patch (2 × 2 m) within its search radius. The search radius is a variable in the ABM, which can be adjusted, and it determines the scale at which the grazing strategy is applied.

Once the patch was grazed, *N* decreased by a certain amount, and *times* increased by 1. The *N* values also increased by a certain amount continuously at each time step, as the

vegetation was growing in the spring. The grazed patches were set to have a higher growth rate than the ungrazed patches due to the overcompensation of the vegetation in response to herbivory [50]. The decrease in the N value due to the bison grazing and the growth rate of N were set according to the quantification of the vegetation heterogeneity related to the bison space use.

We set 48 time steps a day in the simulation, consistent with the temporal resolution of the bison location data. There were a total of 1440 time steps for the 30 days in the simulation. At each time step, the bison followed the rules of "grazing" and "roaming"; the vegetation patches were grazed and grew. We quantified the patch-scale canopy nitrogen distributions by the measurements of the $\overline{N}$, SD_N, contagion and SIDI at the initial and final states. The variable *times* was used to calculate the bison space use during the last 7 days (the last 336 time steps) through the analysis of the kernel density. The resulting map of the bison space use was classified into three levels from low to high. The canopy nitrogen characteristics at the final state were compared between the areas with the high and low levels of bison space use by using Mann–Whitney U tests at the 0.001 significance level. We adjusted the settings and variables of the model until the simulated canopy nitrogen characteristics were similar to the empirical on-the-ground observations.

3. Results

3.1. Assessment of Bison Space Use at a Patch Scale

The analyses of the RUF showed that the effects of the topographic features and vegetation characteristics on the bison space use varied across the seasons (Table 3). For the topographic features, elevation was not statistically significant in May and September, whereas it had significant coefficients greater than 0 in June and August. Slope was a significant factor with negative coefficients throughout the seasons, and it had the greatest absolute values of the standardized coefficients in all the months except for August.

For the vegetation characteristics, the $\overline{N}$ was insignificant except that in August it had a negative coefficient significantly different from 0. The SD_N was statistically significant with negative coefficients over the seasons. The contagion and SIDI were significant in June–September with positive coefficients. SIDI had greater absolute values of the standardized coefficients than contagion, indicating that SIDI was a more important factor than contagion in bison foraging site selection and resource utilization.

Table 3. The coefficients of topographic features and vegetation characteristics determined for resource utilization functions (RUF) of 14 bison individuals across seasons. Bold font indicates a significant predictor of bison space use.

	Unstandardized RUF			Standardized RUF		
	$\overline{\beta}$	SE	$p\ (\overline{\beta} = 0)$	$\overline{\beta}$	SE	$p\ (\overline{\beta} = 0)$
May						
Intercept	−0.0258	0.3433	0.9413	0.3774	0.0206	0.0000
Elevation	0.0012	0.0008	0.1666	0.0161	0.0110	0.1667
Slope	**−0.0054**	**0.0018**	**0.0090**	**−0.0238**	**0.0077**	**0.0089**
$\overline{N}$	−0.0234	0.0258	0.3799	−0.0092	0.0098	0.3645
SD_N	**−0.2042**	**0.0599**	**0.0047**	**−0.0192**	**0.0054**	**0.0035**
Contagion	0.0004	0.0004	0.3565	0.0046	0.0045	0.3342
SIDI	0.1056	0.0712	0.1620	0.0139	0.0091	0.1509
June						
Intercept	−0.5474	0.2396	0.0398	0.2846	0.0275	0.0000
Elevation	**0.0016**	**0.0006**	**0.0162**	**0.0235**	**0.0079**	**0.0110**
Slope	**−0.0123**	**0.0010**	**0.0000**	**−0.0558**	**0.0041**	**0.0000**
$\overline{N}$	−0.0328	0.0175	0.0837	−0.0065	0.0034	0.0763
SD_N	**−0.7865**	**0.1233**	**0.0000**	**−0.0377**	**0.0060**	**0.0000**
Contagion	**0.0022**	**0.0004**	**0.0001**	**0.0142**	**0.0025**	**0.0001**
SIDI	**0.7143**	**0.0828**	**0.0000**	**0.0462**	**0.0057**	**0.0000**

Table 3. *Cont.*

	Unstandardized RUF			Standardized RUF		
	$\overline{\beta}$	SE	$p\,(\overline{\beta} = 0)$	$\overline{\beta}$	SE	$p\,(\overline{\beta} = 0)$
August						
Intercept	−0.2536	0.1980	0.2226	0.2736	0.0189	0.0000
Elevation	**0.0013**	**0.0005**	**0.0296**	**0.0216**	**0.0088**	**0.0287**
Slope	**−0.0061**	**0.0019**	**0.0060**	**−0.0287**	**0.0087**	**0.0057**
$\overline{N}$	**−0.0437**	**0.0183**	**0.0328**	**−0.0152**	**0.0063**	**0.0319**
SD_N	**−0.3401**	**0.0956**	**0.0035**	**−0.0326**	**0.0091**	**0.0034**
Contagion	**0.0012**	**0.0004**	**0.0065**	**0.0139**	**0.0043**	**0.0066**
SIDI	**0.2479**	**0.0839**	**0.0112**	**0.0364**	**0.0124**	**0.0116**
September						
Intercept	0.1492	0.1679	0.3919	0.2366	0.0172	0.0000
Elevation	0.0000	0.0004	0.9940	−0.0004	0.0062	0.9527
Slope	**−0.0109**	**0.0019**	**0.0001**	**−0.0515**	**0.0088**	**0.0001**
$\overline{N}$	0.0165	0.0473	0.7337	0.0024	0.0077	0.7564
SD_N	**−0.8085**	**0.2462**	**0.0065**	**−0.0360**	**0.0108**	**0.0059**
Contagion	**0.0014**	**0.0003**	**0.0006**	**0.0116**	**0.0025**	**0.0006**
SIDI	**0.3986**	**0.0992**	**0.0017**	**0.0349**	**0.0088**	**0.0018**

$\overline{\beta}$ is the mean of the coefficients calculated from bison individuals; SE is the standard error. $p\,(\overline{\beta} = 0)$ is the p value of the *t*-test; if $p\,(\overline{\beta} = 0) < 0.05$, $\overline{\beta}$ of the environmental factor is significantly different from 0.

The results of the analyses focusing on the vegetation characteristics by excluding the topographic features in the RUF (Table 4) showed that the SD_N was the only significant factor that had a negative coefficient in May. In June and August, all the vegetation characteristics were significant. The SD_N and SIDI were of greater importance than the $\overline{N}$ and contagion. In September, all the vegetation characteristics were significant except for the $\overline{N}$. The main difference between the results of the analyses including and excluding the topographic features was that the $\overline{N}$ became a significant factor in June when the topographic features were excluded.

Table 4. The coefficients of vegetation characteristics determined for resource utilization functions (RUF) of 14 bison individuals across seasons. Bold font indicates a significant predictor of bison space use.

	Unstandardized RUF			Standardized RUF		
	$\overline{\beta}$	SE	$p\,(\overline{\beta} = 0)$	$\overline{\beta}$	SE	$p\,(\overline{\beta} = 0)$
May						
Intercept	0.3118	0.0757	0.0012	0.3795	0.0190	0.0000
$\overline{N}$	0.0370	0.0311	0.2556	0.0093	0.0087	0.3037
SD_N	**−0.2517**	**0.0698**	**0.0032**	**−0.0229**	**0.0066**	**0.0041**
Contagion	0.0008	0.0006	0.2061	0.0080	0.0063	0.2273
SIDI	0.0884	0.1045	0.4128	0.0090	0.0117	0.4578
June						
Intercept	0.1144	0.0803	0.1780	0.3196	0.0249	0.0000
$\overline{N}$	**−0.1087**	**0.0273**	**0.0016**	**−0.0218**	**0.0054**	**0.0014**
SD_N	**−0.8781**	**0.1587**	**0.0001**	**−0.0424**	**0.0078**	**0.0001**
Contagion	**0.0022**	**0.0006**	**0.0037**	**0.0144**	**0.0041**	**0.0038**
SIDI	**0.8274**	**0.1217**	**0.0000**	**0.0533**	**0.0080**	**0.0000**
August						
Intercept	0.2808	0.0398	0.0000	0.2940	0.0199	0.0000
$\overline{N}$	**−0.0612**	**0.0186**	**0.0059**	**−0.0213**	**0.0066**	**0.0068**
SD_N	**−0.5124**	**0.1035**	**0.0003**	**−0.0467**	**0.0094**	**0.0003**
Contagion	**0.0013**	**0.0004**	**0.0057**	**0.0152**	**0.0047**	**0.0068**
SIDI	**0.2958**	**0.0685**	**0.0008**	**0.0466**	**0.0111**	**0.0010**

Table 4. *Cont.*

	Unstandardized RUF			Standardized RUF		
	$\overline{\beta}$	SE	$p\ (\overline{\beta} = 0)$	$\overline{\beta}$	SE	$p\ (\overline{\beta} = 0)$
September						
Intercept	0.1014	0.0756	0.2043	0.2723	0.0193	0.0000
$\overline{N}$	−0.0301	0.0619	0.6358	−0.0055	0.0106	0.6132
SD_N	**−0.9790**	**0.3188**	**0.0097**	**−0.0414**	**0.0133**	**0.0089**
Contagion	**0.0013**	**0.0004**	**0.0031**	**0.0103**	**0.0027**	**0.0026**
SIDI	**0.4903**	**0.1214**	**0.0016**	**0.0387**	**0.0094**	**0.0014**

$\overline{\beta}$ is the mean of the coefficients calculated from bison individuals; SE is the standard error. $p\ (\overline{\beta} = 0)$ is the p value of the t-test; if $p\ (\overline{\beta} = 0) < 0.05$, $\overline{\beta}$ of the environmental factor is significantly different from 0.

3.2. Quantification of Patch-Scale Vegetation Heterogeneity Related to Bison Space Use

The comparison analyses performed by using the Mann–Whitney U tests (Figure 4) showed that the differences in the vegetation characteristics between the areas with the high and low levels of bison space use were statistically significant at the 0.001 level in most cases, except for the differences in contagion for the lowlands ($p = 0.0168$) and hillslopes ($p = 0.3178$) in August and for the uplands in September ($p = 0.1939$). In general, the areas with the high level of bison space use had lower values of $\overline{N}$ and contagion and higher values of SD_N and SIDI than the areas with the low level of bison space use. There were a few exceptions, particularly in the upland zones. For example, the uplands with the high level of bison space use had lower values of SIDI than the uplands with the low level of bison space use in May, August and September.
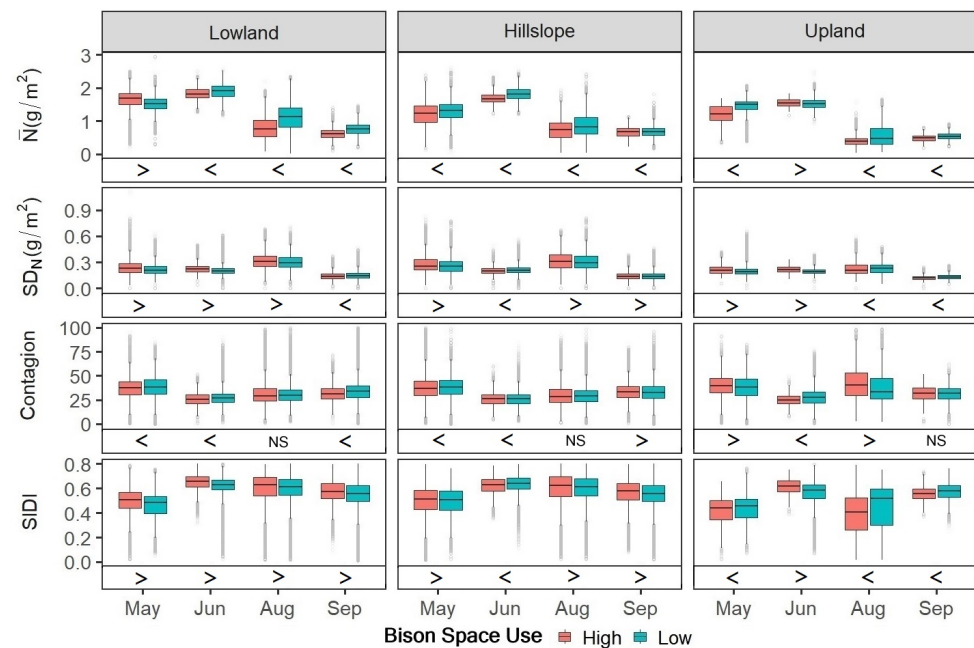

Figure 4. Comparisons of the patch-scale (30 m) vegetation characteristics between areas with the high and low levels of bison space use across seasons. The patch-scale vegetation characteristics were measured from four perspectives: the mean of canopy nitrogen contents ($\overline{N}$), standard deviation of canopy nitrogen contents (SD_N), contagion and Simpson's diversity index (SIDI) of patches with different canopy nitrogen levels. The comparisons were conducted separately for lowlands, hillslopes and uplands. >: the value in areas with high-level bison space use was significantly greater than that in areas with low-level bison space use. <: the value in areas with high-level bison space use was significantly lower than that in areas with low-level bison space use. NS: the difference between areas with high-level and low-level bison space use was not significant.

3.3. Simulation of Bison and Vegetation Interactions

The grassland dynamics in the lowlands during the 30 days from May to June were simulated by using ABM (Figure 5A). We parameterized the model until the simulated canopy nitrogen distributions (Figure 6) were comparable with the observations (Figure 4), through which the settings and variables of the model were determined finally.
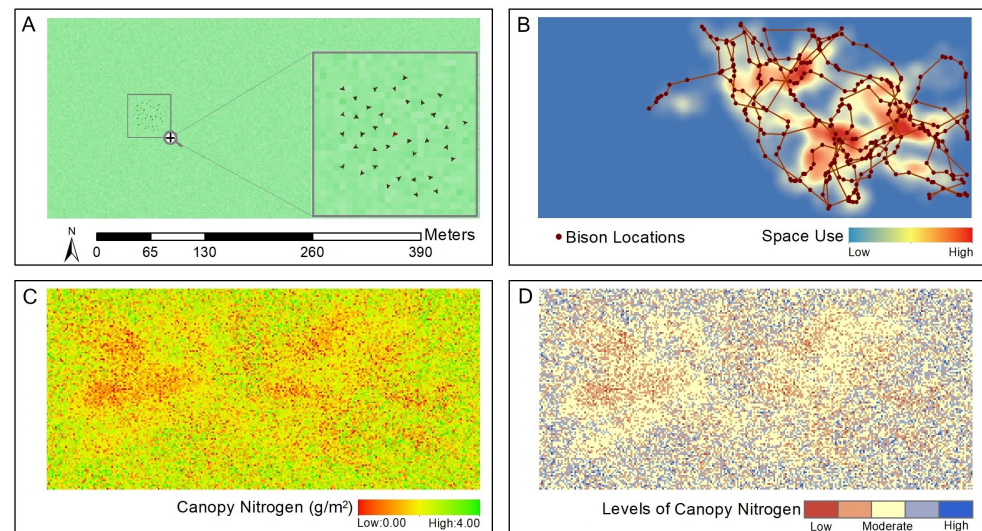

Figure 5. Simulations of dynamic interactions between bison and grassland vegetation by agent-based modeling (ABM). (**A**) The grassland "world" consisted of bison and vegetation patches; bison herded on the grassland. (**B**) Data of bison movement and space use during the last 7 days (the last 336 time steps) were related to (**C**) the output continuous and (**D**) categorical maps of canopy nitrogen for analyzing how bison grazing intensity affected vegetation heterogeneity.

Figure 6. Comparisons of the vegetation characteristics, namely, the mean of canopy nitrogen contents ($\overline{N}$), standard deviation of canopy nitrogen contents (SD_N), contagion and Simpson's diversity index (SIDI) of patches with different canopy nitrogen levels, between the initial and final state in the simulated grassland system. From the final output of canopy nitrogen map, the vegetation characteristics were compared between areas with the high and low levels of bison space use.

For the vegetation patches, initially, N = *random-normal* 1.6 0.2 (in NetLogo, *random-normal* 1.6 0.2 reported a random floating-point number drawn from a normal distribution having a mean of 1.6 and a standard deviation of 0.2); *times* = 0. If the patch was grazed by bison, N decreased by $\Delta N = 0.29 \times$ the possibility of grazing, and *times* increased by 1. For the ungrazed patch in the growing season, N increased by $\Delta N = $ (*random-normal* 0.39 0.2)$/1440 \times 0.85$; the growth rate for the grazed patch was 10% higher than that for the ungrazed patch given the overcompensation of vegetation.

For bison, the herd size of the bison was set to 35 individuals; the separation distance between the individuals was not less than 2 patches (4 m); and the search radius for the selective grazing was set to 2 patches, which simulated the bison foraging decisions made within a scale of 8 m. The possibility of grazing = $0.4449 - 0.2474 \times SD_N$, which was determined at a patch scale of 30 m by the analysis of the RUF with the only significant

factor SD_N in May. During the first 15 days (the first 720 time steps), the selective grazing strategy was applied; the random grazing strategy was applied for the rest of time. When roaming over the grassland, the movement distance = (*random-exponential* 55.8)/8 patches (in NetLogo, *random-exponential* 55.8 reported a random floating-point number drawn from an exponential distribution having a mean of 55.8).

From the output data of the simulation (Figure 5), we quantified the canopy nitrogen characteristics. The results (Figure 6) showed that from the initial state in May to the final state in June, the $\overline{N}$ and SIDI increased, whereas the SD_N and contagion decreased. A higher level of bison space use resulted in lower values of $\overline{N}$ and contagion and higher values of SD_N and SIDI. The results of the simulation were similar to the observed data, which validated the rationality of the model.

In the model, bison foraging decisions at two patch scales were simulated: 30 m (determining whether to graze) and 8 m (determining which patch within the search radius to be grazed). At the scale of 30 m, the bison foraging site selection was determined by the SD_N of the grassland patch according to the analysis of the RUF throughout the simulation. At the scale of 8 m, the settings of the bison grazing strategies were found to have an influence on the vegetation heterogeneity. When the bison followed the selective grazing strategy, the SD_N decreased constantly. When the bison followed the random grazing strategy, the SD_N increased over time. The selective grazing strategy was required to generate decreased values of SD_N from May to June, whereas the random grazing strategy was required to generate the grasslands having higher values of SD_N in areas with high-level bison space use than areas with low-level bison space use. We attempted to use a mixed strategy with a 15% probability of selective grazing and an 85% probability of random grazing for each time step. The resulting grasslands in this way showed seasonal variations in the canopy nitrogen characteristics similar to the observations, in which the $\overline{N}$ and SIDI increased, whereas the SD_N and contagion decreased from May to June. However, the grasslands of the simulation had lower SD_N and SIDI in areas with the higher level of bison space use, contrary to the observations. We adjusted the mixed strategy, in which the selective grazing strategy was followed by the bison for the first 720 time steps, and the random grazing strategy was followed by the bison for the rest of time. With the adjusted mixed strategy, the variations in the canopy nitrogen characteristics of the simulated grasslands were consistent with the observed vegetation pattern variations.

4. Discussion

Our analysis revealed that topographic features were important factors affecting bison foraging site selection and habitat use. The bison always avoided the hillslopes and preferred elevated sites in the middle of the growing season. These findings were consistent with the previous literature on tallgrass prairies [10,13]. Further, our research quantified the influence of the patch-scale canopy nitrogen characteristics on bison space use across the seasons. In the early growing season, the bison avoided the grasslands with great variability in the canopy nitrogen contents. In the middle of the growing season, the bison tended to select the grasslands within which the patch types were highly aggregated and evenly proportioned. Meanwhile, the bison avoided the grasslands within which the canopy nitrogen contents were generally at high levels with great variability. In the late growing season, the influence of the canopy nitrogen contents was not significant. It was implied that bison preferred uniform grassland patches with low variability at the beginning of the growing season [10,13]. In the middle of the growing season, the grassland vegetation became more diverse given that bison grazing decreased the dominance by C_4 grasses and increased the abundance of forbs [2]. The vegetation heterogeneity appeared to have more evident effects on the bison space use. In addition, the avoidance of high canopy nitrogen contents (i.e., remaining green vegetation) was found at this phenological stage when the high-level canopy nitrogen contents were mixed with more mature vegetation patches. This finding may be explained by the forage maturation hypothesis [51], which proposes that bison select low-to-moderate forage biomass (i.e., available regrowth) to

maximize energy intake as the forage quality declines with plant maturation. The analysis, which focused on the vegetation characteristics by excluding the topographic features in the RUF, had similar results to the analysis that included the topographic features, indicating that the effects of the vegetation characteristics on bison space use were almost consistent across the different topographic positions. The models determined by the RUF including the topographic features and vegetation characteristics were expected to be feasible for the prediction of bison distributions throughout the tallgrass prairie topography within the burned watersheds.

The comparison analyses of the vegetation characteristics between the areas with the high and low levels of bison space use extended our previous research on vegetation heterogeneity at the watershed scale [17] by providing detailed information on the patch-scale canopy nitrogen distributions associated with bison grazing intensity. A general tendency was found that higher levels of bison space use resulted in grasslands having lower levels of canopy nitrogen contents with greater variability, within which the patch types were more disaggregated with more equitable proportions. These quantitative analyses of vegetation heterogeneity were essential for simulating the grassland dynamics using ABM and validating the simulation.

In the ABM of the grassland system, the bison foraging decisions at a scale of 8 m determined by the grazing strategy were found to be influential in vegetation pattern formation. The selective grazing strategy resulted in low variability in the canopy nitrogen contents and highly aggregated patch types. The random grazing strategy resulted in high variability in the canopy nitrogen contents and disaggregated patch types with equitable proportions. With a mixed strategy, in which the selective grazing strategy was used in the beginning for a while and then the random grazing strategy was applied for the rest of the time, the simulation had optimal results that were consistent with the observations. This mixed strategy provided a possible explanation for the dynamic interactions between the bison foraging decisions at patch scales and the vegetation heterogeneity. At the beginning of the growing season, the grassland vegetation was particularly immature with a generally low quantity. The bison selected vegetation resources with a relatively high quality and quantity, resulting in highly uniform canopies. As the vegetation grew, the forage quality and quantity improved overall. The vegetation patch randomly selected by the bison probably satisfied the requirements of the bison. Therefore, the bison appeared to follow the random grazing strategy when palatable vegetation patches were uniformly distributed in the early growing season. This pattern matches observations of bison foraging site selection across the growing season in this enclosure [11,12]. As the bison kept grazing randomly, the uniform grasslands became diverse with interspersed patch types in the middle of the growing season. The ABM of the grassland system had proven to be useful for the simulation of the bison space use and vegetation heterogeneity. Further, through adjusting the settings of the behavioral rules and parameterizing the model, how the bison and vegetation patches affected each other could be explored, which provided a visual and computational tool for understanding the underlying mechanisms of interactions between bison foraging site selection and vegetation pattern variation.

5. Conclusions and Future Outlook

Our research quantified the interactive effects between bison space use and vegetation heterogeneity at a patch scale (30 m), which extended previous research at the landscape level [13,17]. It was found that the effects of the patch-scale vegetation resource distributions on bison foraging site selection were most evident in the middle of the growing season. Particularly, the observed avoidance of mature vegetation with high canopy nitrogen may be explained by the forage maturation hypothesis [51]. Bison space use was found to have a significant influence on the patch-scale vegetation heterogeneity. There was a general tendency that higher levels of bison space use resulted in more diverse grassland canopies with higher variability and more interspersed patch types. These quantitative analyses provided useful information for simulations of grassland dynamics. From the simulation

of the dynamic interactions between the bison and vegetation pattern variation in the early growing season by using ABM, we proposed a mixed strategy of selective grazing and random grazing for bison, which may explain how bison foraging decisions at a fine patch scale (8 m) shaped vegetation patterns from uniformity to diversity.

Our research is a precursor to simulations of grassland dynamics through ABM, which proves the feasibility of ABM to simulate ungulate space use and vegetation pattern variation. Moreover, ABM provides a useful tool for exploring mechanisms that underlie grassland structure and function, including the interplay between ungulate grazing and vegetation resource heterogeneity. In the future study, we will develop the model of a grassland system by importing the actual data of topographic features and vegetation characteristics, which are expected to provide practical implications for grassland resource conservation and management.

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