Differences in Spatial Heterogeneity at the Species and Community Levels in Semi-natural Grasslands under Different Grazing Intensities

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Synopsis

In this study, we aimed to clarify how the spatial heterogeneity of a semi-natural grassland community at both the community and species levels is affected by grazing intensity. We examined three pastures with different grazing intensities: light (Pasture L), medium (Pasture M) and heavy grazing (Pasture H). Heterogeneities at both levels ranged from random/low to aggregated/high. The spatial heterogeneity at the community level was high in Pasture L, and low in Pastures M and H. The differences among the spatial heterogeneities at the community level were due to most of the dominant species in Pasture L having a higher heterogeneity than those in Pastures M and H. Pasture L was composed of a mixture of many species that had high heterogeneities, but Pastures M and H were composed of both highly heterogeneous species and weakly heterogeneous species. These differences in the spatial heterogeneity at the species level can be partly explained by the propagation types (clonal or non-clonal) of the species. The results of this study suggest that grazing intensity altered species composition and the spatial heterogeneity at the species level, and as a result, when grazing intensity was heavy, the spatial heterogeneity at the community level was low.

Key words: Beta-binomial model, Clonal species, Grazing, Non-clonal species, Spatial heterogeneity.

Introduction

Vegetation of grassland is spatially heterogeneous. This spatial heterogeneity occurs as a result of the interaction of various factors. The spatial heterogeneity of grassland communities has been evaluated with respect to (1) each species composing a community\cite{18,19,22}, (2) the botanical composition over the area\cite{3}, (3) the species diversity over the area, and (4) the biomass per unit area\cite{6,7}. The first of these spatial patterns can be an important determinant of species coexistence and biodiversity\cite{20}, and may play a critical role in plant community dynamics\cite{5}. In this study, we focused on the spatial heterogeneity of each species composing a community.

Each species or population composing the community has a spatial heterogeneity or a spatial pattern (referred to as spatial heterogeneity at the species level) that ranges from low/random to high/aggregated pattern. Because each plant community is regarded as an assembly of many species, the spatial heterogeneity can also be defined for the community, and is referred to as spatial heterogeneity at the community level (Fig. 1). For example, if a plant community is composed of many species that have a high spatial heterogeneity, the community has a high spatial heterogeneity. On the other hand, if a plant community is composed of many species that have a low spatial heterogeneity, the community has a low heterogeneity. Thus, as with the spatial heterogeneity at the species level, the spatial heterogeneity at the community level ranges from low/random to high/aggregated pattern. In this paper, we define the spatial heterogeneity at the community level as the total amount of the spatial heterogeneity for each species occurring in a community (Fig. 1). Note that the spatial heterogeneity at the community level does not include the aspect of botanical composition. With this community level measure of spatial heterogeneity, we can compare the community-level spatial structure/properties among many different communities. In general, past studies have not measured spatial heterogeneities at both the species and community levels. The current method provides a unique opportunity to understand the effects of spatial heterogeneity on the structure and dynamics of a community.
A factor controlling the spatial heterogeneity at the community level is the spatial heterogeneity at the species level. The spatial heterogeneity at the species level is influenced by various factors such as seed dispersal, disturbance, and topography. In particular, the propagation type, clonal or non-clonal, may influence the spatial heterogeneity at the species level. For example, clonal species may have a high spatial heterogeneity because propagules are located near the parent. On the other hand, non-clonal species may have a low spatial heterogeneity when seeds and seedlings are placed at random. However, it is unclear how the spatial heterogeneity at the species level is affected by changes in population size of clonal and non-clonal species due to competition or disturbance.

One factor that can change the spatial heterogeneity at the species level is grazing by cattle and sheep. In grassland, grazing can alter community structure such as species diversity, biomass and species composition. The activities of cattle such as feeding, excretion of dung and urine, and trampling are spatially heterogeneous, and create environmental heterogeneity at different spatial scales. Thus, not only the propagation type, but also these effects of grazing may directly and/or indirectly alter the spatial heterogeneity at the species level. As a result, the changes of the spatial heterogeneity at the species level may lead to changes of the spatial heterogeneity at the community level.

In this study, we aimed to clarify how the spatial heterogeneities at both the community and species levels are affected by grazing intensity. We first examined the spatial heterogeneity at the community level between grasslands with different grazing intensities. Second, we categorized species into two groups according to their propagation type: clonal or non-clonal species (defined below), and compared changes of the spatial heterogeneity of both groups of species under different grazing intensities. Lastly, we discussed the influence of the spatial heterogeneity at the species level on the spatial heterogeneity at the community level. To survey and analyze the spatial heterogeneity of the grassland community, we adopted the beta-binomial model. A unique feature of this model is that it can estimate the spatial heterogeneity at the both community and species levels.

**Materials and Methods**

1. **History and management of grasslands**

This study was carried out at a flat semi-natural grassland grazed with cattle at the National Institute of Livestock and Grassland Science (36°55'N, 139°58'E, about 300 m asl). The grassland is divided into the following three pastures with different grazing histories. (1) Pasture L that was burnt every March from 1974 to 1994 without grazing, and has been grazed from early summer to middle autumn since 1995 each year. The area is about 0.25 ha. (2) Pasture M that was grazed from early summer to middle autumn since 1974. The area is about 0.5 ha. (3) Pasture H where four Japanese Black cows of about 450 kg body-weight have been grazed from early summer to middle autumn since 1974. The area is about 1 ha.

Pastures L, M and another neighboring pasture (0.25 ha) were incorporated into one block with about 1 ha in early spring before the grazing season in 1995. In the incorporated block, two Japanese Black cows with about 450 kg body-weight were grazed every year. The grazing intensity was about half of that in
Pasture H.

Grazing intensity is defined as the number of cattle and the number of years grazed. In Pastures L and M, the same number of cattle, two heads per ha, were grazed, but the numbers of years were different between the two pastures. Pastures L and M had been grazed for 6 and 15 years, respectively. In Pasture H, 4 heads were grazed per ha for 26 years. The annual grazing period for each pasture was about 100 days. Therefore, we regarded the ranking of historical grazing intensities as follows: L < M < H.

2. Field surveys

A 50 m-long line-transect was set in each of the three pastures. One hundred 50 cm × 50 cm quadrats (referred to as L-quadrats hereafter), which were divided into four smaller 25 cm × 25 cm quadrats (S-quadrats), were arranged along each of the line-transects. Therefore, we had 100 L-quadrats and 400 S-quadrats in each pasture. All species that occurred in each of the S-quadrat were recorded. If even a small part of a plant was contained in a given S-quadrat, the plant was considered to occur in that S-quadrat. A vegetation survey was carried out on four days in late May (May 23, 27, 30 and 31) 1998 (before grazing) in all the pastures. In 1997, the grazing intensities were 153 cow days in Pastures L and M, and 285 cow days in Pasture H.

3. Beta-binomial model

To measure the spatial heterogeneity, we used the beta-binomial model\(^1\):\(^{10}\). This method can measure two levels of spatial heterogeneity. One is for the species level; we call this "spatial heterogeneity at the species level", and represent it by \(\rho\). Another is for the community level; we call this "spatial heterogeneity at the community level", and express it by \(\rho_c\). These two indices are explained in detail later.

Here, we consider a general case in which an L-quadrat is divided into \(n\) S-quadrats. First, let the probability that a given species occurs in \(i\) S-quadrats of one L-quadrat be expressed by \(P(i)\), where \(i = 0, 1, ..., n\), and \(P(i)\) is described by the following equation:

\[
P(i) = \binom{n}{i} \frac{\beta(p-1)+i}{\beta(ho-1)+1},
\]

where \(\binom{n}{i}\) denotes the beta-function, \(p\) is the probability of occurrence of the species per S-quadrat, and \(\rho\) is the degree of spatial heterogeneity for occurrence of the species per S-quadrat. The family of beta-binomial distribution contains the binomial distribution, that is, equation 1 approaches the binomial distribution as \(\rho \rightarrow 0\).

We can estimate the two parameters contained in equation 1, \(p\) and \(\rho\), from the following equations:

\[
p = \frac{k}{nN},
\]

and

\[
\rho = \frac{1}{n-1} \left[ \frac{V_0}{V_k} - 1 \right].
\]

where \(k\) denotes the observed total number of S-quadrats containing the species, \(N\) is the number of L-quadrats, \(V_0\) is the variance of observed frequency distribution between the L-quadrats, and \(V_k\) is the variance under the random distribution (binomial distribution): \(V_k = np(1-p)\). The parameter value of occurrence, \(p\), ranges between 0 and 1. If \(p = 0\), the species occurs in no S-quadrats, and if \(p = 1\), the species occurs in all S-quadrats. The parameter value of species heterogeneity, \(\rho\), ranges between \(-n-1\) and 1. Note that when \(p \rightarrow 1, \rho \rightarrow 0\). The spatial heterogeneity is determined based on the following rule: (1) if the occurrence randomly distributes between L-quadrats, \(\rho\) takes a value of 0. (2) If the occurrence distributes more heterogeneously between L-quadrats than would be expected in the random case, \(\rho\) takes a larger value than 0, and the higher the degree of heterogeneity, the larger value \(\rho\) takes. (3) If the occurrence is more regularly distributed than would be expected in the random case, \(\rho\) takes a negative value, and the lower the degree of heterogeneity, the smaller value \(\rho\) takes.

Using the above-mentioned two parameters of the beta-binomial series, an index describing heterogeneity at the community level, \(\rho_c\), is defined for s species:

\[
\rho_c = \frac{\sum p_i \rho_i}{\sum p_i}.
\]

The spatial heterogeneity at the community level is determined based on the same rule as used for the \(\rho\)-value for a single species. This \(\rho_c\)-value has the following characteristics: (1) the value is more strongly influenced by species with high \(p\)-values compared with those with low \(p\)-values, and (2) in a community with a small \(\rho_c\), the species composing the community form small, finely intricate patches with each other, but in a community with a large \(\rho_c\), the species form exclusive, large patches.

Equation 3 can be divided into two or more terms. For example, it can be divided into two terms, in which one corresponds to the clonal species group and the other corresponds to the non-clonal species group:

\[
\rho_c = T_c + T_n
\]

where \(T_c\) represents the subtotal of the terms for clonal species, and \(T_n\) is the subtotal of the terms for non-clonal species.

4. Data analyses

We analyzed field data using the beta-binomial model with \(n = 4\) (number of S-quadrats in each L-
and N = 100 (the number of L-quadrats on each line-transect). To investigate the goodness-of-fit of the beta-binomial series to the actual data for all species, the $\chi^2$ test was used where the null hypothesis ($H_0$) is: the frequency of occurrence of a given species between S-quadrats follows a random (binomial) distribution. A rejection of $H_0$ indicates that the frequency follows either a more heterogeneous spatial pattern or a more regular pattern than would be expected in a random pattern.

We compared spatial heterogeneities at the community level, $\rho_s$, between the three pastures. Species were categorized as either clonal or non-clonal one. Clonal species were those that propagating by horizontal growth, that is, runners, tussocks, slant, ascendent or decumbent stems, and lianas. Species without these traits were considered as non-clonal species. We compared $p$- and $\rho$-values for each group between grazing intensities, and for some clonal species between grazing intensities.

**Results**

1. **Overview**

The total number of species that occurred in the three pastures were 54, 50 and 45 in Pastures L, M and H, respectively (Table 1). The three most dominant species were *Potentilla freyniana* Bornm., *Pteridium aquilinum* Kuhl var. *latuscalum* Underw. ex Hell and *Liriope minor* Makino in Pasture L, *Zoysia japonica* Steud., *P. freyniana* and *Hydrocotyle sibthorpioides* Lam. in Pasture M, and *Z. japonica*, *Ixeris dentata* Nakai and *Anthoxanthum odoratum* L. in Pasture H. In Pasture L, all five of the dominant species were clonal, but in both Pastures M and H, two of the five dominant species were non-clonal. Under heavy grazing intensity, *Z. japonica* dominated and the $p$-value attained 1, that is, *Z. japonica* appeared at all S-quadrats.

2. **Fitting Beta-binomial distribution**

The goodness-of-fit of the beta-binomial series to the observed frequency data was tested using the $\chi^2$ test (Table 2). We could not test all species because the frequencies of occurrence were not sufficient for some species. In Pastures L and M, the numbers of species with sufficient frequency for the statistical test were 13 and 9, respectively. These species were not significant only for the beta-binomial distribution. In pasture H, the number of species to be statistically tested was seven. Five of seven species were not significant for the beta-binomial distribution ($P>0.05$), and the other two species were not significant both for the beta-binomial distribution and the binomial distribution. These results are summarized as follows: the observed frequency distributions fitted well to the beta-binomial or binomial distribution.

3. **Spatial heterogeneity at community and species levels**

The $\rho_s$ - values in Pasture L (0.3581) was higher than the values in Pasture M (0.3126) and Pasture H (0.3185).

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**Table 1. Outline of the three pastures with different grazing intensities.**

<table>
<thead>
<tr>
<th>Grazing intensity</th>
<th>Pasture L</th>
<th>Pasture M</th>
<th>Pasture H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of species occurred</td>
<td>54</td>
<td>50</td>
<td>45</td>
</tr>
<tr>
<td>Spatial heterogeneity at community level, $\rho_s$</td>
<td>0.3581</td>
<td>0.3126</td>
<td>0.3185</td>
</tr>
<tr>
<td>Dominant species</td>
<td><em>Potentilla freyniana</em></td>
<td><em>Zoysia japonica</em></td>
<td><em>Z. japonica</em></td>
</tr>
<tr>
<td></td>
<td><em>Pteridium aquilinum</em></td>
<td><em>P. freyniana</em></td>
<td><em>Ixeris dentata</em></td>
</tr>
<tr>
<td></td>
<td><em>Liriope minor</em></td>
<td><em>Hydrocotyle sibthorpioides</em></td>
<td><em>Anthoxanthum odoratum</em></td>
</tr>
<tr>
<td></td>
<td><em>Arundinella hirta</em></td>
<td><em>I. dentata</em></td>
<td><em>Poa siberica</em></td>
</tr>
<tr>
<td></td>
<td><em>Z. japonica</em></td>
<td><em>L. cuneata</em></td>
<td><em>P. japonica</em></td>
</tr>
</tbody>
</table>

a) Non-clonal species.

**Table 2. Fits to binomial and/or beta-binomial distributions.**

<table>
<thead>
<tr>
<th>No. species occurred</th>
<th>No. species testable</th>
<th>Fit to binomial only</th>
<th>Fit to beta-binomial only</th>
<th>Fit to both</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pasture L</td>
<td>54</td>
<td>13</td>
<td>0</td>
<td>13</td>
</tr>
<tr>
<td>Pasture M</td>
<td>50</td>
<td>9</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>Pasture H</td>
<td>45</td>
<td>7</td>
<td>0</td>
<td>5</td>
</tr>
</tbody>
</table>

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(Table 1). The $\rho$-values were calculated using all species that occurred in each pasture. This result indicates that the species occurring in Pasture L formed a higher spatial heterogeneity than those of Pastures M and H on average.

For each pasture, the $p$-values and $\rho$-values are plotted for all species that occurred in Fig. 2. The most dominant species in Pasture L were clonal species such as *P. freyniana* (Poire), *P. aquilinum* (Pta), *L. minor* (Lm), *Arundinella hirta* C. Tanaka (Arh) and *Z. japonica* (Zoj) (Fig. 2 A). These clonal species exhibited high $p$- and $\rho$-values. In particular, *P. freyniana* (Poire), the most dominant species, had a high spatial heterogeneity ($\rho=0.5532$). Non-clonal species such as *Lespedeza cuneata* G. Don (Lec) and *Cirsium japonicum* DC. (Cij) in Pasture L had low values for both $p$ and $\rho$. In Pasture M, the dominant species included both clonal and non-clonal plants (Fig. 2 B). The clonal species except for *Z. japonica* (Zoj) exhibited high $\rho$-values. The non-clonal species that were dominant in Pasture M took high $\rho$-values, but the $\rho$-values were low. The most dominant species in Pasture M, *Z. japonica* (Zoj), had a low heterogeneity ($\rho=0$). In Pasture H, as in Pasture M, the dominant species were composed of both clonal species (*A. odoratum* Ano), *P. aquilinum* (Pta) and *L. minor* (Lm) and non-clonal species (*I. dentata* (Isd) and *Polygara japonica* Houtt (Poji)) (Fig. 2 C). *Z. japonica* (Zoj), the most dominant species in Pasture H, had a low heterogeneity ($\rho=0$). In Pasture H, the non-clonal species tended to be much more dominant than those in Pastures L and M (e.g., *I. dentata* (Isd) was ranked at the second dominance as shown in Fig. 2 C). But the non-clonal species exhibited low $\rho$-values (low spatial heterogeneity). In each of the pastures, both the clonal and non-clonal species with $p$-value$\leq0.2$ had widely dispersed $\rho$-values (Fig. 2).

Some plants among clonal species had its own

![Diagram](image-url)

**Fig. 2.** Relationship between the occurrence and the spatial heterogeneity of individual species at Pasture L (A), Pasture M (B) and Pasture H (C). Each plot shows a single species that is clonal (●) or non-clonal (○), and is denoted by the abbreviated name for the species with $p>0.2$ or $\rho>0.2$.

relationship between $p$ and $\rho$ for various grazing intensities (Fig. 2). For example, $P$. freyniana (Pofre) was dominant ($\rho = 0.8075$) and exhibited a high spatial heterogeneity ($\rho = 0.5532$) in Pasture L. In Pasture H, $P$. freyniana (Pofre) had a $p$-value of 0.0475 (low occurrence) and a $\rho$-value of 0.1763 (low spatial heterogeneity). In contrast to $P$. freyniana (Pofre), A. odoratum (Ano) was dominant and exhibited a high spatial heterogeneity in Pasture H, and had a low dominance ($p = 0.0025$) and a low spatial heterogeneity ($\rho = 0.0008$) in Pasture L. Unlike two species, $L$. minor (Lim) had relatively constant $p$- and $\rho$-values in the three pastures.

The differences in spatial heterogeneity at the community level were caused by the spatial heterogeneity at the species level of clonal plants (Fig. 3). The spatial heterogeneity at the species level of clonal plants decreased in Pastures M and H compared with Pasture L. For the spatial heterogeneity at the species level of non-clonal plants, there were only small differences among the three pastures. For the clonal plants, the contribution of $T_c$ in Pasture L was larger than that in Pastures M and H. The difference in contribution between Pasture L and Pastures M and H depended on $Z$. japonica (the most dominant species in Pastures M and H). Contribution of $Z$. japonica in $\rho$ was 0.05 in Pasture L. In Pastures M and H, the contributions of $Z$. japonica were 0.

**Discussion**

The purpose of this study was to clarify how the spatial heterogeneity at both the community and species levels is affected by grazing intensity in semi-natural grassland communities. The spatial heterogeneities at the community level were different between pastures (Table I). The spatial heterogeneity at the community level was high under light grazing intensity, while it was low under medium and heavy grazing intensities (Table I).

One possible reason for the difference in spatial heterogeneities at the community level was the differences in spatial heterogeneity of the most dominant species (Table I and Fig. 2). In Pasture L, the most dominant species, $P$. freyniana, showed a high $\rho$-value (0.5532) (Table I and Fig. 2A). In Pastures M and H, however, $Z$. japonica, the most dominant species, showed a low $\rho$-value (0) (Table I and Figs. 2B and 2C). The decrease in the $\rho$-values of $Z$. japonica in Pastures M and H caused a decline of the spatial heterogeneity at the community level (Fig. 3). This indicates that the most dominant species strongly affected the spatial heterogeneity at the community level.

The spatial heterogeneity at the species level is related to the propagation type i.e., clonal or non-clonal (Fig. 2). Clonal species except for $Z$. japonica exhibited a high spatial heterogeneity when the $p$-values for these species were high. On the other hand, non-clonal species exhibited a low spatial heterogeneity even when the $p$-value was high. The spatial heterogeneities of clonal and non-clonal species did not change irrespective of grazing intensities except for $Z$. japonica (Fig. 2). Undoubtedly, the propagation type is one of the major factors controlling the spatial heterogeneity at the species level. This fact implies that, if a species can have a high occurrence, the propagation type of the species determines the spatial pattern of the species.

When the frequency of occurrence was low, however, the relationship between the propagation type and the spatial heterogeneity at the species level was not clear. When the $p$-value was low, $p$-values exhibited a large variation among species regardless of clonal or non-clonal species (Fig. 2). This fact implies that the estimated $p$-value under a small $p$ is not precise and/or is controlled strongly by chance. But the $p$-value may also change due to ecological principles. For example, immediately after an invasion of a new species to a grassland community, the species may show a low occurrence and a low spatial heterogeneity even if the invader is a clonal species. Also, an aggregation of seeds and seedlings may lead to a high spatial heterogeneity even if the invader is a non-clonal species.

Among clonal species, the frequencies of occurrence and the spatial heterogeneity at the species level for some species differed between the pastures. In Pasture L, $P$. freyniana had a dominant and high spatial heterogeneity. $P$. freyniana in Pasture H had a low occurrence and a low spatial heterogeneity. $A$. odoratum was dominant and had a high spatial heterogeneity in Pasture H. In Pasture L, the species

![Graph](image_url)
showed a low dominance and had a low spatial heterogeneity. Compared with these two species, L. minor differed little in occurrence and heterogeneity between the three pastures with different grazing intensities. This result shows that each species had a different response to the activities of cattle such as feeding, excretion and trampling, which created different environments in soil fertility and light conditions.

In this study, we found that p, is an appropriate index for measuring the spatial heterogeneities of grassland communities. Moreover, this index can be used to investigate relationships between the spatial heterogeneity at the community level and the species diversity and productivity.

The spatial heterogeneity at both the community and species levels, however, depends on the scale of the quadrat. For example, if different scales of L- and S-quadrats are used, the spatial heterogeneity at both the community and species levels would change. Grazing creates environmental heterogeneity at different spatial scales120, and the spatial heterogeneity at the species level may have a different spatial response between plant species. Thus, to detect the scale of the spatial heterogeneity in a grassland community grazed by cattle and sheep, one should use quadrats with various scales. Various effective methods have been suggested in previous studies1115. Focusing on the spatial heterogeneity at the community level will help to increase our understanding of the role of spatial structure in plant communities.

Acknowledgments

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References

要旨
安住泰輔・塩見正雄・高橋繁男（2003）：異なった放牧圧における半自然草地の枝生の空間的不均一性の差異。日本誌49,101-108。
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本研究では、放牧圧に対する草地群落の空間的不均一性の差異を明らかにするために、枝の空間的不均一性と群落の空間的不均一性の2つの観点から調査、解析した。放牧圧の異なる3つの草地を比較すると、群落の不均一性は弱放牧区で最も高く、中、強放牧区では低かった。この群落の不均一性の違いは優占種の不均一性の違いを反映していた。優占種は、弱放牧区では不均一性の高い種から、中、強放牧区では不均一性の高い種と低い種の両方から構成されていた。種の空間的不均一性は繁殖様式（栄養繁殖と種子繁殖）を考慮することによっていくつかの優占種は説明できたが、出現頻度の低い種は他の要因が強く作用している可能性が示唆された。

キーワード：空間的不均一性、クローナル植物、ノンクローナル植物、ベータ2項分布モデル、放牧。