

A measure for spatial heterogeneity of vegetation in the Center of Inner Mongolia

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Abstract

This study surveyed and analyzed the vegetation heterogeneity in the Center of Inner Mongolia (CIM) by a new method based on the beta-binomial distribution for each kind of vegetation. As many as 190 large quadrats of 5 mm × 5 mm (representing an area of 50 km × 50 km) (referred to as L-quadrats hereafter) were extracted from about an area of 475,000 km². Each L-quadrat was divided into four small quadrats (S-quadrat) of 2.5 mm × 2.5 mm (equivalent to 25 km × 25 km) and the frequency of occurrence of each type of vegetation was recorded in each small quadrat. The weighted average heterogeneity from all of the vegetations composing a landscape provides a measure at landscape level to determine the spatial intricateness of landscape composition. Our results indicated that each vegetation has its own distribution pattern and the degree of heterogeneity is different from one kind of vegetation to the other. The results proved that the beta-binomial distribution can be very useful for analyzing vegetation landscapes.

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1. Introduction

One of the most important characteristics of plant and animal communities is their spatial distribution pattern [1,2]. It is considered that heterogeneous environments lead to heterogeneous vegetation and tend to exhibit a high vegetation diversity [3]. However, the measurement of spatial heterogeneity in community/vegetation is often difficult for at least the following three reasons: (1) The spatial heterogeneity of each vegetation and vegetation diversity are highly variable and may depend on the climate, geograph-

ical conditions and human agricultural activities, etc. [4–6]. (2) Although many methods or indices can be used for estimation of heterogeneity, no single index is superior [7–9]. (3) Measurements of such indices are often difficult, tedious and tend to disturb the vegetation measured. Therefore, comparison of different communities/landscapes is usually difficult.

The heterogeneity of vegetation can be evaluated by the measurement at four levels [4,7]: (1) the spatial pattern of each vegetation composing a community; (2) the spatial pattern of the vegetation composition over the area; (3) the spatial pattern of the vegetation diversity over the area, and (4) the spatial pattern of the total biomass per unit area.

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The spatial pattern of plant communities with a short height like grasslands has been analyzed using various methods [9,10] based on the characteristics/ measurements of herbaceous plants [7,11], including the observation on the occurrence of each vegetation growing in a certain area, the aboveground biomass for each vegetation per quadrat, and frequency of each vegetation appearing per quadrat. Among these measurements, the frequency of occurrence is suitable for both vegetation comparison and community analysis because it involves easy (fastest) and non-destructive (least disturbing) measurements for sample quadrats [11]. Frequency is also most suitable for temporal studies using a permanent quadrat.

There are some methods for measuring the spatial aggregation of individuals in a biological population, such as: variance/mean ratio [12,13], Morisita's I_δ index [14,15], Kuno's C_A index [16] and Iwao and Kuno's [17] $m-m$ method [1,18,19]. However, for biological populations in which the occurrence or incidence is restricted to a binary variable such as presence or absence, these indices are not applicable [15,19,20].

Therefore, we introduce a beta-binomial distribution [21,22] method, which was used to analyze the spatial distribution of the vegetation in the Center of Inner Mongolia, using the data from the Map of China Vegetation [23] and discuss the validity and characteristics of this method in analyzing the spatial heterogeneity of vegetation.

2. Materials and methods

2.1. Study area

The study area is located in the Center of Inner Mongolia (CIM), to the northwest of Beijing, China (about 105–120°E, 37–47°N), which covers Xilinguole City, Wulanzhaibu City, and Bayannaer City (Fig. 1). The original dominant vegetation was coniferous-broadleaf deciduous forest, shrub, grassland and desert from the southeast to northwest. The annual mean air-temperature is from 7.2 °C to 9.2 °C, the monthly minimum air-temperature is from –30 °C to –11 °C in January and the monthly maximum air-temperature is from 19 °C to 26 °C in July. The annual precipitation is 50–550 mm.

2.2. Vegetation survey

Vegetation information was extracted from 1:10,000,000 Map of China Vegetation [23]. About 475,000 km² of the landscape of the study area was divided into 190 large-quadrats of 5 mm × 5 mm (50 km × 50 km) (referred to as L-quadrats hereafter). Each L-quadrat was again divided into four small-quadrats (S-quadrat) of 2.5 mm × 2.5 mm (equivalent to an area of 25 km × 25 km). In each S-quadrat, the occurrence of all the 25 vegetation types in the area was recorded (Table 1). The survey was carried out in 2005.

2.3. Model and analysis

Every vegetation type in the area was studied. If the vegetation is not very heterogeneous over the area, the distribution of the occurrence of vegetation i may follow a random pattern, which means that the number of S-quadrats containing vegetation i per L-quadrat follows a binomial distribution. Let each L-quadrat be divided into n (≥ 2) S-quadrats with an equal area, and π be the probability that vegetation i occurs in any individual S-quadrat (π is a constant over the area), the probability that vegetation i occurs in j ($j = 0, 1, 2, \dots, n$) of the n S-quadrats within an L-quadrat can be expressed by a binomial series with the parameters n and π .

In a landscape that is influenced by climate, geographical conditions and human agricultural activities, the vegetation may exhibit a spatially heterogeneous distribution. Then, it is assumed that π changes continuously from site to site in the landscape following a beta distribution. So the beta density of π can be expressed by the equation: $\pi_i^{\alpha(i)-1} (1 - \pi_i)^{\beta(i)-1} / B[\alpha(i), \beta(i)]$, where $B[\alpha(i), \beta(i)]$ indicates the beta function, and $\alpha(i) = p(1/\rho - 1)$ and $\beta = (1 - p)(1/\rho - 1)$ are parameters of the distribution if the spatial heterogeneity is expressed for vegetation i by ρ_i and the overall probability of occurrence of vegetation i per S-quadrat by p_i .

The derived distribution, referred to as a beta binomial distribution, is given by the following equation [19,20,22]

$$P(0) = \beta_i(\beta_i + 1) \cdots (\beta_i + n - 1) / \{(\alpha_i + \beta_i) \times (\alpha_i + \beta_i + 1) \cdots (\alpha_i + \beta_i + n - 1)\}$$

$$P(j) = P(j - 1)(n - j + 1)(\alpha_i + j - 1) / \{(\beta_i + n - j)j\} \quad \text{for } j = 1, 2, \dots, n$$

where $\alpha_i = p_i(1/\rho_i - 1)$, $\beta_i = q_i(1/\rho_i - 1)$, $0 \leq p_i \leq 1$, $1/(n - 1) \leq \rho_i \leq 1$, $q_i = 1 - p_i$ and n is the number of S-quadrats contained in each L-quadrat ($n = 4$ in this study).

The parameter ρ is the correlation coefficient between n S-quadrats in an L-quadrat, which can be used as an index to describe the spatial heterogeneity of the vegetation [20]. A high ρ value indicates a high heterogeneity in the occurrence of vegetation i between n L-quadrats (in this study $n = 190$), and $\rho = 0$ indicates a random pattern (i.e. the occurrence of vegetation i follows a binomial distribution). The mean μ_i and variance σ_i^2 of the beta-binomial distribution for vegetation i are given by

$$\mu_i = np_i, \quad \text{and} \quad \sigma_i^2 = np_i q_i \{1 + \rho_i(n - 1)\}$$

Let the sample mean and sample variance of the frequency distribution for vegetation i be expressed by m_i and s_i^2 , respectively. The estimated value of p_i and ρ_i are expressed using m_i and s_i^2 by the following equations: $p_i = m_i/n$ and $\rho_i = s_i^2 / \{(n - 1)m_i(1 - m_i/n)\} - 1/(n - 1)$.

The community average ρ_c for s vegetation is defined by:

$$\rho_c = \left(\sum_{i=1}^s p_i \rho_i \right) / \left(\sum_{i=1}^s p_i \right)$$

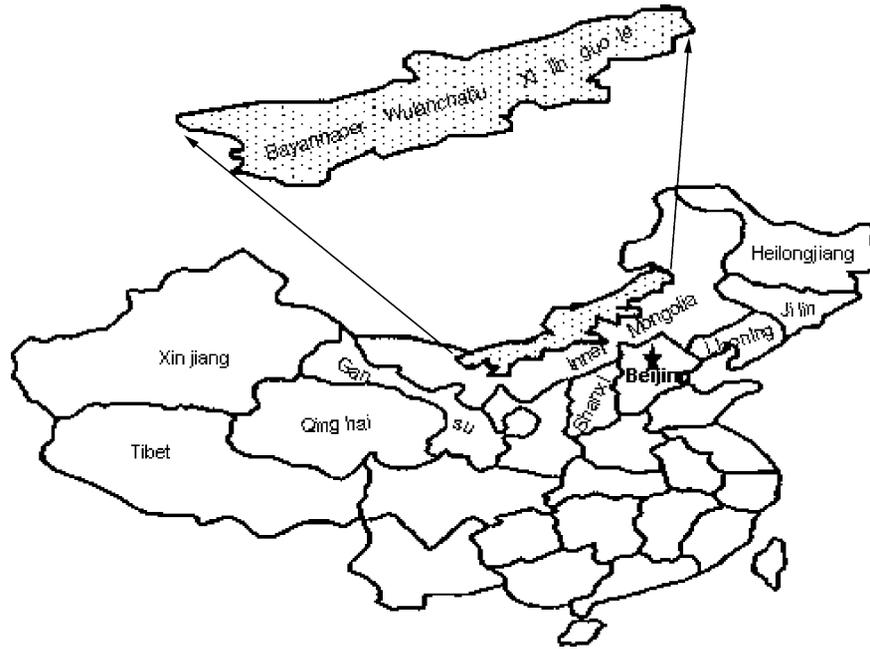


Fig. 1. The study area—the Center of Inner Mongolia (dotted area).

Table 1
Vegetation types in the Center of Inner Mongolia (CIM)

+	++	Vegetation type
V ₁	V _{14a}	Deciduous oak forest (a) <i>Quercus mongolica</i> (including <i>Ostyopsis</i> and <i>Lespedeza</i>)
V ₂	V _{14b}	Deciduous oak forest (b) <i>Quercus liaotungensis</i> and <i>Quercus</i> sp.
V ₃	V ₁₅	Mountainous forest of poplars (<i>Populus</i>) and birches (<i>Betula</i>)
V ₄	V ₂₈	Shrub of <i>Ostyopsis daridiana</i> and <i>Spiraea hailarensis</i>
V ₅	V ₃₀	Desert of shrub and semi-shrub
V ₆	V ₃₇	Grassland of <i>Fillifolium sibiricum</i> , <i>Stipa baicalensis</i> , <i>Festuco ovina</i> and <i>Aneurolepidium chinense</i>
V ₇	V ₃₈	Grassland of <i>Aneurolepidium chinense</i> , <i>Stipa glareosa</i> and forbs
V ₈	V ₃₉	Grassland of <i>Aneurolepidium</i> sp., <i>Stipa bungeana</i> and forbs
V ₉	V ₄₀	Grassland of <i>Stipa grandis</i> and Grassland of <i>Stipa grandis</i> — <i>Aneurolepidium chinense</i>
V ₁₀	V ₄₁	Grassland of <i>Stipa krylovii</i> and Grassland of <i>Cleistogenes squarrosa</i> — <i>Stipa krylovii</i>
V ₁₁	V ₄₃	Grassland of <i>Stipa bungeana</i> — <i>Stipa breviflora</i> , and grassland of <i>Artemisia frigida</i> — <i>Thymus mongolicus</i>
V ₁₂	V ₄₄	Grassland of thick small grasses (<i>Agropyron cristatum</i> and <i>Cleistogenes squarrosa</i>)
V ₁₃	V ₄₅	Grassland of <i>Stipa gobica</i>
V ₁₄	V ₄₆	Grassland of <i>Stipa breviflora</i> , <i>Cleistogenes squarrosa</i> and <i>Anaphalis</i> sp.
V ₁₅	V ₄₇	Grassland of <i>Stipa glareosa</i> and small semi-shrub
V ₁₆	V _{51b}	Desert of <i>Haloxyylon ammodendrom</i>
V ₁₇	V ₅₂	Gravel desert of <i>Ephedra przewalskii</i> , <i>Zygophyllum xanthoxylon</i> and <i>Nitraria sphaerocarpa</i>
V ₁₈	V ₅₃	Gravel desert of <i>Caragana tibetica</i>
V ₁₉	V ₅₄	Gravel desert of <i>Potaninia mongolica</i> and <i>Ammopiptanthus mongolica</i>
V ₂₀	V ₅₅	Desert of <i>Artemisia sphaerocephalla</i> and <i>Artemisia ordosica</i>
V ₂₁	V ₅₉	Gravel desert of <i>Reaumuria soongorica</i>
V ₂₂	V ₆₆	Meadow on river rapids
V ₂₃	V ₆₇	Salt meadow
V ₂₄	V _{70a}	Annual crop and cold-resistant economic crop (Songnen flatland type)
V ₂₅	V _{70b}	Annual crop and cold-resistant economic crop (Inner Mongolia-Gansu-Xinjiang type)

+, Used in this study.

++, From the China Vegetation Map.

The goodness-of-fit of the frequency distributions of vegetation which appeared at CIM to the beta-binomial and binomial distributions had been tested by deviance analysis previously [24]. The null hypothesis in the statisti-

cal test was that beta-binomial distribution and/or the binomial distribution fits the observed frequency distribution of the occurrence of a vegetation.

Shannon-Wiener's index [25], *H*, was calculated by:

$$H = - \sum_{i=1}^s (P_i) (\log_{10} P_i)$$

3. Results

3.1. Beta-binomial distribution

Table 2 lists the observed and estimated frequencies of beta-binomial distribution for $i = 0, 1, 2, 3, 4$ for the 25 dominant vegetations we studied. Based on the deviance analysis shown in this table, the following three conclusions could be made: (1) the beta-binomial distribution with three parameters fitted better than the binomial distribution with two parameters; (2) the binomial distribution did not fit the frequency distribution for all the vegetations, and (3) the beta-binomial distribution fitted all the observed frequency distributions well.

The p and ρ values are shown in Table 2. From the table we can see that V_9 , V_{10} and V_{13} have a frequency of >0.2 per L-quadrat on average; V_{10} , V_9 , V_{13} and V_{21} have high ρ values; V_1 , V_2 and V_{24} have rather low values. The relationship between the overall mean occurrence of the species present in an S-quadrat, and the estimated correlation coefficient, is depicted in Fig. 2. In the areas with low occurrence, ρ seems to vary over a wide range without a specific tendency. The weighted average of heterogeneity, ρ_c , is 0.7052, and the vegetation diversity index is 1.70984.

3.2. Vegetation categorized by occurrence and spatial heterogeneity

On the basis of occurrence and spatial heterogeneity of each vegetation shown in Table 2 and Fig. 2, the vegetation landscape can be divided into seven categories: Group I (V_9 , V_{10} and V_{13}) exhibited a high heterogeneity and high occurrence pattern (>0.2 per L-quadrat on the average), and V_9 is the most common vegetation in this landscape. Group II (V_5 , V_6 , V_{11} , V_{21} and V_{25}) exhibited a high heterogeneity and medium occurrence pattern. Group III (V_7 , V_8 , V_{14} , V_{15} , V_{17} and V_{20}) exhibited a high heterogeneity and low occurrence pattern. Group IV (V_3 , V_4 , V_{12} and V_{22}) exhibited a medium heterogeneity and low occurrence pattern. Group V (V_{23}) was salt meadow, showing a distinctive distribution pattern of medium heterogeneity and occurrence. Group VI (V_{16} , V_{18} and V_{19}) exhibited a low heterogeneity and occurrence pattern. Group VII (V_1 , V_2 and V_{24}) exhibited both low heterogeneity and low occurrence.

4. Discussion

4.1. Model evaluation

The concept of beta-binomial distribution was theoretically developed by Skellam [22]. This distribution is part of a family of generalized hypergeometric distributions [26]. It was introduced into the field of human epidemiology and

plant ecology in the 1950s, and was used to describe changes in the spatial pattern of the number of rice plants infected with yellow dwarf disease virus [27,28]. Recently it was applied to epidemiology in various kinds of crops to represent the number of infested or infected host plants in a unit area [19,20,29–31]. The present approach follows the one adopted in the study by Kemp and Kemp [28] who used pins instead of square quadrats. In a sown grassland in Japan, it was found that the beta-binomial distribution can express the spatial heterogeneity of plants [21,28,32].

The good fit to beta-binomial distribution obtained in this study indicates that the vegetations were distributed according to a heterogeneous spatial pattern such as a patchy pattern. V_1 , V_2 and V_{24} with low ρ values also fitted the beta-binomial distribution well, comparing with the results of species heterogeneity [21,33]. In the landscape we surveyed, the beta-binomial distribution was proved to be a good model for describing the spatial heterogeneity of vegetation, because the null hypothesis in deviance analysis was statistically accepted.

Variance/mean ratio is an index used widely to evaluate spatial patterns of biological populations [7,18]. This index is not valid for occurrence data expressed by presence or absence, but valid only for individuals like aphids which can increase to infinite numbers on a plant or in a quadrat. According to Shiyomi and Yoshimura [21], $\sigma_L^2 / \{\mu_L(1 - \mu_L/n)\}$ is a version of the variance/mean ratio for the presence/absence or occurrence/non-occurrence data. Estimated $\sigma_L^2 / \{\mu_L(1 - \mu_L/n)\}$ for the presence data takes the same value as that for absence data. Under the assumption of the beta-binomial distribution of occurrence, the following relationship is held: $\sigma_L^2 / \{\mu_L(1 - \mu_L/n)\} = (n - 1)\rho$. Then, ρ takes the same value for both the presence and the absence data.

Any index of spatial heterogeneity or aggregation is, in principle, sensitive to the quadrat size. The current index, ρ , will depend on the quadrat size, too, although in this study this problem was not examined. By measuring the spatial heterogeneity for each vegetation using different quadrat sizes, the characteristics of the spatial pattern of a vegetation may be depicted.

This experimental and statistical method can be widely and easily applied to studies on vegetation map, remote vegetation map and plant community with short height. It is especially suitable for vegetation diagnosis.

4.2. Spatial heterogeneity of the study area

For almost all of the vegetations in the landscape we surveyed, the beta-binomial distribution fitted very well, unlike the binomial distribution (Table 2). This fact indicates that each type of vegetation is distributed heterogeneously, although the degree of heterogeneity is different from vegetation to vegetation.

Generally all the grassland vegetations show a high heterogeneity. The three kinds of grasslands, *Stipa grandis* and *Aneurolepidium chinense* (V_9), *Stipa krylovii*, *Cleistogenes*

Table 2

Fitting of the beta-binomial distribution with the frequency distribution of 25 vegetation types and estimated parameters (values outside and inside parentheses indicate observed and estimated frequency values, respectively)

Vegetation	V ₁	V ₂	V ₃	V ₄	V ₅
Frequency					
0	187(187)	189(189)	176(174.74)	176(174.74)	140(140.64)
1	3(2.98)	1(0.99)	3(6.41)	3(6.41)	12(12.49)
2	0(0.01)	0(0.00)	6(3.56)	6(3.56)	13(8.58)
3	0(0.00)	0(0.00)	3(2.70)	3(2.70)	4(8.80)
4	0(0.00)	0(0.00)	2(2.59)	2(2.59)	21(19.49)
B → Bb	0.0200***	-0.0013***	36.9992***	36.9992***	7.7124***
B	0.0358***	0.0039***	40.8272***	40.8272***	13.1128***
Bb	0.0157	0.0053	3.8279	3.8279	5.4004*
Mean	0.0158	0.0053	0.1684	0.1684	0.7053
Variance	0.0156	0.0053	0.4265	0.4265	1.8069
p	0.0039	0.0013	0.0421	0.0421	0.1763
ρ	-0.0022	0.0004	0.5479	0.5479	0.7035
Vegetation	V ₆	V ₇	V ₈	V ₉	V ₁₀
Frequency					
0	157(155.35)	180(179.19)	187(186.67)	113(113.02)	139(139.54)
1	5(10.27)	2(3.61)	0(1.12)	9(11.31)	5(5.37)
2	12(6.69)	2(2.21)	2(0.68)	14(8.46)	7(3.95)
3	5(6.40)	4(1.98)	0(0.61)	6(10.07)	2(4.48)
4	11(11.29)	2(3.01)	1(0.93)	48(47.14)	37(36.30)
B → Bb	26.4916***	41.5206***	5.4594***	161.6899***	96.3186***
B	33.5926***	44.3660***	10.6022***	167.1648***	100.4324***
Bb	7.1009*	2.8454	5.1428	5.4749*	4.1138
Mean	0.4632	0.1368	0.0421	1.3000	0.9105
Variance	1.2341	0.3939	0.1252	2.9942	2.5687
p	0.1158	0.0342	0.0105	0.3250	0.2276
ρ	0.6711	0.6601	0.6684	0.8041	0.8842
Vegetation	V ₁₁	V ₁₂	V ₁₃	V ₁₄	V ₁₅
Frequency					
0	159(157.90)	179(178.03)	135(133.65)	179(178.69)	181(180.47)
1	4(8.25)	2(4.77)	6(10.56)	2(3.33)	2(3.43)
2	11(5.52)	5(2.72)	12(7.59)	4(2.11)	3(2.04)
3	3(5.63)	2(2.16)	8(8.55)	1(2.03)	2(1.75)
4	13(12.71)	2(2.33)	29(29.65)	4(3.84)	2(2.31)
B → Bb	15.9367***	28.1204***	73.1157***	5.9557***	22.8848***
B	24.3397***	31.7843***	77.6944***	8.5570***	24.0659***
Bb	8.4030*	3.6639	4.5787	2.6014	1.1811
Mean	0.4579	0.1368	0.8947	0.1526	0.1158
Variance	1.2866	0.3621	2.3169	0.4581	0.3251
p	0.1145	0.0342	0.2237	0.0382	0.0289
ρ	0.7243	0.5800	0.7785	0.7067	0.6306
Vegetation	V ₁₆	V ₁₇	V ₁₈	V ₁₉	V ₂₀
Frequency					
0	185(184.64)	182(181.23)	180(178.33)	182(181.43)	177(176.29)
1	3(4.06)	1(2.71)	3(7.83)	4(5.49)	3(4.57)
2	2(1.00)	2(1.69)	7(2.62)	3(2.0)	3(2.81)
3	0(0.25)	3(1.59)	0(0.96)	1(0.82)	4(2.52)
4	0(0.04)	2(2.79)	0(0.26)	0(0.27)	3(3.81)
B → Bb	9.4228***	34.5639***	27.4857***	23.5430***	34.9992***
B	11.1010***	37.2794***	38.8478***	25.0118***	36.5519***
Bb	1.6782	2.7155	11.3621*	1.4687	1.5527
Mean	0.0368	0.1158	0.0895	0.0684	0.1737
Variance	0.0568	0.3463	0.1560	0.1276	0.4935

(continued on next page)

Table 2 (continued)

Vegetation	V ₁₆	V ₁₇	V ₁₈	V ₁₉	V ₂₀
<i>p</i>	0.0092	0.0289	0.0224	0.0171	0.0434
ρ	0.1857	0.6933	0.2610	0.2990	0.6567
Vegetation	V ₂₁	V ₂₂	V ₂₃	V ₂₄	V ₂₅
Frequency					
0	165(165.19)	178(177.62)	154(145.94)	188(188.01)	150(150.48)
1	6(5.56)	4(5.19)	11(23.79)	2(1.99)	11(10.59)
2	3(3.78)	4(2.88)	14(11.39)	0(0.01)	8(7.10)
3	5(4.03)	2(2.19)	7(6.08)	0(0.00)	6(7.12)
4	11(11.45)	2(2.12)	4(2.79)	0(0.00)	15(14.71)
B → Bb	18.1394***	20.0567***	36.0353***	0.0053***	12.7288***
B	18.5803***	20.7672***	46.2317***	0.0159***	13.0459***
Bb	0.4409	0.7105	10.1965*	0.0105	0.3170
Mean	0.3737	0.1368	0.4000	0.0105	0.5526
Variance	1.1242	0.3515	0.7285	0.0105	1.4761
<i>p</i>	0.0934	0.0342	0.1000	0.0026	0.1382
ρ	0.7728	0.5533	0.3412	-0.0009	0.6997

B → Bb, deviance for testing the effect of change from binomial to beta-binomial model; B, deviance for testing binomial fit; Bb, deviance for testing beta-binomial fit; *p*, overall occurrence in an S-quadrat; ρ , correlation coefficient between four S-quadrats in L-quadrats. * and ***, significant at 5% and 0.1% levels, respectively, in the χ^2 test.

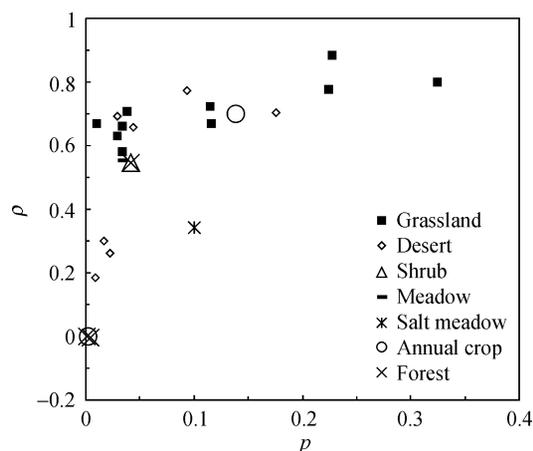


Fig. 2. Relationship between frequency of occurrence in an S-quadrat, *p* and ρ values for spatial heterogeneity in the CIM vegetation.

squarrosa (V₁₀) and *Stipa gobica* (V₁₃), exhibited a very high heterogeneity and occurrence (Fig. 2), and distinguishingly dominated the Center of Inner Mongolia. The vegetation formed distinctive patches even though their occurrences were low. The deciduous oak forest of *Quercus mongolica* (V₁), *Quercus liaotungensis* (V₂) and the annual crop and cold-resistant economic crop (Songnen flatland type, V₂₄), which exhibited a low heterogeneity and with occurrence near zero, showed that the *Quercus* forest was a rare vegetation and should be protected urgently, and the rare Songnen flatland economic crop type should be managed by specific agricultural model. In the areas with a small *p* in Fig. 1, the ρ values exhibited a large variation among vegetations. This implies a distinguishable heterogeneity (ρ) hierarchy in small or same *p*. Mountainous forest of poplars (*populus*) and birches (*Betula*) (V₃), shrub of

Ostyopsis daridiana and *Spiraea hailarensis* (V₄), grassland of *Aneurolepidium chinense*, *Stipa glareosa* and forbs (V₇), *Aneurolepidium* sp., *Stipa bungeana* and forbs (V₈), *Agropyron cristatum* and *Cleistogenes squarrosa* (V₁₂), *Stipa breviflora*, *Cleistogenes squarrosa* and *Anaphalis* sp. (V₁₄), *Stipa glareosa* and small semi-shrub (V₁₅), the desert of *Ephedra przewalskii*, *Zygophyllum xanthoxylon* and *Nitraria sphaerocarpha* (V₁₇), *Artemisia sphaerocephalla* and *Artemisia ordosica* (V₂₀), meadow on river rapids (V₂₂) and annual crop and cold-resistant economic crop (Inner Mongolia-Gansu-Xinjiang type) (V₂₅) distributed in the small scale. The desert of *Haloxylon ammodendrom* (V₁₆), gravel desert of *Caragana tibetica* (V₁₈), *Potaninia mongolica* and *Ammopiptanthus mongolica* (V₁₉), which exhibited similar low heterogeneity and occurrence, showed some small patches in the V₂₀ and V₂₁ covered area.

The weighted average of the landscape heterogeneity, ρ_c , was 0.705154. Comparing with 0.4473 for a temperate mixed seeding pasture in Japan [21] and 0.2146–0.2245 for a natural pasture in Heilongjiang Province of northern China [33], the heterogeneity of vegetation in our study area was higher than species diversity.

4.3. Relationship between the frequency of occurrence and spatial heterogeneity

The spatial heterogeneity of each vegetation and vegetation diversity are highly variable and may depend on the climate, geographical conditions and human agricultural activities [5,6]. With similar climate, better geographical conditions and less human agricultural activities, a vegetation landscape may be highly uniform. The reverse may result in a low occurrence in vegetation landscape. Rare vegetation exhibited a low heterogeneity/random and low

occurrence pattern while dominant vegetation exhibited a high heterogeneity/aggregated and high occurrence pattern. The degenerating vegetation exhibited a high heterogeneity and a low occurrence pattern. The degenerative succession of vegetation first decreased in occurrence and then decreased in heterogeneity. In many vegetation landscapes, spatial heterogeneity is often characterized in relation to the vegetation-specific traits. Therefore, the functional mechanisms of vegetation landscape heterogeneity should be evaluated in terms of the dynamic changes of vegetation heterogeneity.

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