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湖北宜昌大老岭桦、栎、栗林优势种群的分布格局动态研究

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摘 要

运用方差与平均密度的比值、以 Lloyd 的平均拥挤度为指标、Morisita 的两个个体落入同一样方的概率与随机分布的比值等多种格局的分析方法，研究了位于湖北宜昌大老岭的桦、栎、栗林演替过程中，优势种群格局的动态过程。结果表明，在植物群落演替过程中的各个时期，无论是先锋种还是顶级种，都是以群集分布方式入侵样地，然后向均匀分布格局方向发展。

关键词 分布格局，演替，亮叶桦，锥栗，短柄枹栎，枹栎

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SUCCESSIONAL TREND OF DISTRIBUTIONAL PATTERN FOR POPULATION IN DALAO RIDGE, YICHANG, HUBEI PROVINCE

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Abstract Several measures, which included variance/mean ratio, Lloyd test, and Morisita, M test, were used to analyze the trend of pattern over successional pathway at Dalao Ridge, Yichang, western Hubei Province. Results showed that population rarely distributed in poisson pattern at real communities, instead it was commonly from contagious to even pattern as communities developed. After then, pioneer species disappeared, while climax species cycled from contagious to even pattern and kept stable self-regeneration.

Key words Pattern, Succession, *Betula luminifera*, *Castanea henryi*, *Quercus glandulifera* var. *brevipetiolata*, *Quercus glandulifera* var. *glanduligera*

Succession has been one of the basic conceptual frameworks in ecology. Many works dealt with its process and mechanism toward the interpretation and prediction of its pathways[1~5], which based on different hierarchical levels—— population, community, and ecosystem approach, and/or different scales—— stand, watershed, and landscape, etc. As a time-dependent process, the occurrence of succession would be a complex interplay among all ecological variables[3]. Therefore, the question was how could we summary these interactive changes, and what was the most sensitive indicator for this process.

Historically, the origin of the analysis of pattern started with numerical determination of non-randomness[6]. Pattern was defined as divergence from randomness[7] for explaining spatial arrangement of individuals on communities. Various ecological factors, biotic and abiotic, would contribute their effects to the formation of pattern[7]. So pattern might be one of the most important indicators to integrate the effects of habitats and relationship among individuals in community.

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In this paper, we address the following question: how did the distributional pattern of dominant species change during successional process?

1 STUDY SITE AND METHODS

1.1 Study site and data collection

The study was conducted out in Dalao Ridge, Yichang, western Hubei Province. For the specially subtropical habitats and subalpine biogeoclimatic factors, there has been diversity in both species and forested ecosystems[1),2)], and species from genera *Quercus*, and *Castanea* dominated in most area to form deciduous forests[3)]

The data were collected within the deciduous forests dominated by *Betula luminifera*, *Quercus glandulifera* var. *brevipetiolata*, *Quercus glandulifera* var. *glanduligera*, and *Castanea henryi*. Thirty-four quadrants (20m × 25m each) were sampled. Considered the homogeneity between and among quadrants, no large-scale natural or manmade disturbances even happened with determined by the uneven-age trees (actually size in field) and uniform composition. All trees with DBH>5cm were recorded and projected on diagrams.

1.2 Data analysis

All quadrants were divided into 5×5 square meter units by the projected diagrams, and counted the numbers of trees by species in each unit. A lot of measures had been developed for the test of departure from randomness[7,8]. In this essay, following measures were chosen to test the distributional pattern.

1.2.1 Variance/mean ratio[9] (coefficient of dispersion)

Theoretically, mean (M) should equal variance (V) when data were poisson distribution, then

>1 contagious distribution

If the ratio of variance to mean $=1$ poisson distribution

<1 even distribution

This test was symbolized by V/M in Table 1.

1.2.2 Lloyd test

An index of mean crowding (m) was proposed for the test of population pattern[10], which considered how many individuals would fall into same unit.

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$$m=\frac{\sum_{i=1}^{Q}X_i(X_i-1)}{X_i}$$

if m/M >1 contagious distribution
$=1$ poisson distribution
<1 even distribution

Here Q was the number of quadrants; X_i, the number of individuals in i-th quadrat; M, the mean. This test was symbolized by m/M in Table 1.

Table 1 The distributional pattern of population in different communities*

Type of community	No. of sample	Species	N	M	V	V/M	m	m/M	$I\delta$	Type of distribution
Form. Bl	2	Bl	20	1.40	0.88	0.64	1.00	0.71	0.74	E
	3	Bl	19	2.16	1.36	0.63	1.76	0.81	0.83	E
	7	Bl	20	1.45	2.46	1.70	2.34	1.62	1.67	C
	9	Bl	18	2.72	3.86	1.42	3.06	1.12	1.15	C
	10	Bl	18	1.39	1.43	1.03	1.44	1.04	1.02	C
	12	Bl	16	1.62	1.46	0.90	1.30	0.80	0.80	E
Form. Bl-Qgb	11	Bl	20	0.70	0.64	0.92	0.57	0.82	0.88	E
	11	Qgb	20	1.45	1.94	1.34	1.72	1.19	1.23	C
Form. Qgb	16	Qgb	20	1.30	0.43	0.33	1.00	0.77	0.80	E
	17	Qgb	20	0.90	0.73	0.81	0.67	0.74	0.78	E
	18	Qgb	20	3.75	2.28	0.61	3.17	0.85	0.86	E
Form. Bl-Ch	4	Bl	20	1.00	0.84	0.84	0.80	0.80	0.84	E
	4	Ch	20	0.45	0.47	1.05	0.46	1.03	1.11	C
	14	Bl	18	0.44	0.38	0.85	0.25	0.56	0.64	E
	14	Ch	18	0.89	1.16	1.31	1.12	1.26	1.35	C
Form. Ch-Qgg	32	Ch	20	1.05	1.00	0.95	0.95	0.91	0.95	E
	32	Qgg	20	1.00	0.84	0.84	0.80	0.80	0.84	E
	22	Ch	15	0.47	0.55	1.18	0.57	1.22	1.43	C
	22	Qgg	15	0.87	1.16	1.34	0.92	1.06	1.15	C
Form. Qgg	24	Qgg	20	2.15	2.02	0.94	1.77	0.82	0.84	E
	25	Qgg	20	1.25	1.33	1.06	1.52	1.22	1.27	C
	26	Qgg	20	1.70	2.51	1.48	1.94	1.14	1.18	C

* Species and type of community: Bl. *Betula luminifea*; Qgb, *Quercus glandulifere* var. *brevipetiolata*; Qgg, *Quercus glandulifera* var. *glanduligera*; Ch, *Castanea henryi*; N, the number of samples; M, mean number of trees per unit; V, variance.

Type of distribution: E, even distribution; C, contagious distribution

1.2.3 Morisita, M test

Compared with others, Morisita, M test[11] based on the measure of diversity rather than direct comparison with poisson distribution to determine the departure from randomness. Given n individuals in i-th quadrat ($i=1,2,3$, etc.), if randomly took two individuals from $N(N=\sum_{i=1}^{Q}n_i)$, the probabilities that the two individuals fall into the same unit were:

$$I_\delta=\frac{n_i(n_i-1)}{N(N-1)}\quad\begin{array}{l}>1\text{ contagious distribution}\\ \text{if } I=1\text{ poisson distribution}\\ <1\text{ even distribution}\end{array}$$

This test was symbolized by I_δ in Table 1.

2 RESULTS AND DISCUSSION

Obviously, community succession could be considered as the flux or change of species over time series (Fig. 1), and there were many ecological charactertics in communities associated or directed this change. In the deciduous forests dominated by birch, oaks at Dalao Ridge, there were two successional pathways based on the change of four dominant species from previous papers[12,13]: Series 1, Form. *Betula luminifera* (Form. Bl) — Form. *Betula luminifera* + *Quercus glandulifera* var. *brevipetiolata* (Form. Bl-Qgb) — From. *Quercus glandulifera* var. *brevipetiolata*; Series 2, Form. *Betula luminifera* — Form. *Betula luminifera* + *Castanea henryi* — Form. *Castanea henryi* + *Quercus glandulifera* var. *glanduligera* — Form. *Quercus glandulifera* var. *glanduligera*. The distributional patterns for these four dominant species in different formations were showed in Table 1.

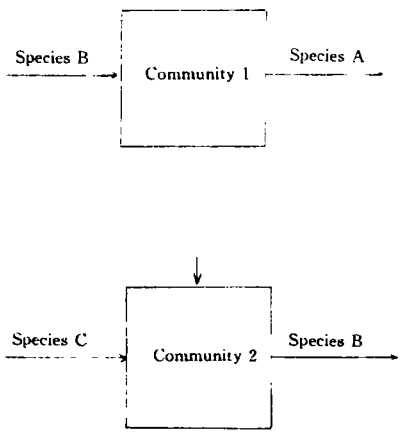

Fig. 1 The diagram showing the relationship between flux of species and community dynamics

As showed in Table 1, a distinct trend from contagious to even distribution could be figured out from the changes of pattern during succession. *Betula luminifera*, a pioneer species in this area, could occur in three communities. However, its pattern might be both contagious and/or even distribution in the same or different communities. In Form. Bl, it was contagious and even distribution at different stages. At the early sapling stage in quadrat 7, 9 and 10 (about 25-year-old), it was contagious. As time being, it tended evenness in quardrat 2, 3, and 12 (about 40-year-old). Therefore, the results represented the time series model of pattern from contagious to even distribution within the same community. Moreover, its patterns trended as other species invaded the site. *Castanea henryi* was a transitional species, which meant it was neither pioneer nor climax species in the successional pathway. It was contagious distribution as individuals invaded site, and both contagious and even distribution occurred as they entered later community Form. Ch-Qgg in the successional pathways until it disappeared from the site. As the climax species, both oak species invaded site with contagious pattern, and tended evenness at the climax and kept stable regeneration. Moreover, the cycle from contagious to even pattern could happen again for the self regeneration in their dominant climax.

Theoretically, if habitat was homogeneous, species would distribute randomly over landscape with poisson pattern. However, this homogeneity rarely happened in real communities, and there must have some difference between two growth units for individual identifying, so species tended to clustering in their preferred habitat and formed bell-shape distribution in one environmental gradient[7,14]. No much work tried to explore the mechanisms of pattern formation, but it seemed reasonable to explain it by some internal and/or external factors on different scales and sequences. The external factors would include temperatrue, humidity, nutrients, etc., which might happen at the beginning of individual invasion and determine whether or not the species existed in the special habitat. While the others, such as species secretion, competition etc. might have their effects after the establishment of individuals, and they would be the primary force to drive pattern development.

In this paper, we would say these factors (may be part of them) might be responsible for the dynamics of pattern. For the suitable habitat in Dalao Ridge, four species could sequentially occur and establish themselves in site and select their suitable habitats in contagious pattern. It was probably from competition and site modification[3,5] which would make pioneer species disappear and climax species tend evenness and keep stable regeneration. Based on these, we could figure out the general model for the distributional trend of pattern during succession: pioneer species invaded site in contagious distribution from the combined effects of microhabitat (*e. g.* gap) and seed resources, then it became evenness and disappeared from the site because of competition and resource limitation. Climax species had the same trend at the beginning, but it cycled from contagious to even distribution again and again and kept stable self-regeneration instead of disappear.

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摘 要

运用方差与平均密度的比值、以 Lloyd 的平均拥挤度为指标、Morisita 的两个个体落入同一样方的概率与随机分布的比值等多种格局的分析方法，研究了位于湖北宜昌大老岭的桦、栎、栗林演替过程中，优势种群格局的动态过程。结果表明，在植物群落演替过程中的各个时期，无论是先锋种还是顶级种，都是以群集分布方式入侵样地，然后向均匀分布格局方向发展。

关键词 分布格局，演替，亮叶桦，锥栗，短柄枹栎，枹栎