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STRUCTURAL CHARACTERISTICS OF FOREST VEGETATION IN THE NORTHEASTERN LESSER XINGAN MOUNTAINS, CHINA

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Abstract. Importance value, ecological dominance, species diversity and community equitability were examined in 76 forest types of the Manchurian temperate forest. It was revealed that species diversity has positive relationship with species richness, total number of individuals and equitability, but it has negative relationship with ecological dominance, which in turn has positive relationship with the importance values of dominant populations, especially where the number of populations is low, and negative relationship with community equitability. In these terms sharp differences exist between community types, developmental states after logging, and vegetation zones. Specifically, ecological dominance increases and species diversity decreases in communities in order of their climatic zonation: cold temperate conifer forest → cold temperate mixed broadleaf-conifer forest → temperate conifer forest → temperate mixed broadleaf-conifer forest. While ecological dominance should decrease and species diversity should increase in the course of succession, this trend is reversed in community development after logging. This suggests a case of community retrogression.

Introduction

The characteristics of forest vegetation are interpretable on the level of community types, communities, populations and individuals. The description of these is a task for quantitative ecology. My work is concerned with structural characteristics on the community type level.

Highly relevant in this regard are works by Fisher, Corbet and Williams (1943) who first advanced the concept of species diversity, by Simpson (1949) whose probabilistic index gained wide acceptance in diversity studies, and by Margalef (1958) who adopted the entropy function of Shannon (Shannon and Weawer 1949) and made it the fundamental measure of diversity in community studies. Pielou (1975) gives a comprehensive review. Also relevant for diversity studies are related original works by Khinchin (1957), Brillouin (1962), and Rényi (1961). The base for community description was broadened with the introduction of the species importance value concept by Curtis and McIntosh (1951) and the ecological dominance concept by Simpson (1949). Peng (1987), and Wang and Peng (1989) used these concepts in their study of subtropical forests communities in southern China, and Qian (1990) applied them in his study of the Alpine Tundra vegetation in the Changbai Mountains in northern China. Quantitative structural studies in the temperate forest vegetation of China are lacking. My work contributes information in this field with focus on the forest communities of the Lesser Xingan Mountains.

Sampling method

The forest vegetation in the Lesser Xingan Mountains contains a great diversity of types. I described 76 forest types from the area (He 1990). In the sampling of these communities I used a point-centered quarter method for the tree layer (Cottam *et al.*, 1953) and the same number (16) of sampling points as Wang and Luo (1989) has used earlier in their survey of the mixed broad-leaved/Korean pine forests. I also sampled the shrub and herb layers, but in these I used two 5m x 5 m quadrats for the shrub layer and five 0.5m x 2 m quadrats for the herb layer.

Ecological indices

Importance value

Curtis and McIntosh (1951) used importance values to describe species performance in different communities in comparative terms. The importance value is a synthetic index based on a combination of relative abundance, relative cover, relative frequency, relative density, and relative dominance of species depending on the stratum in the community. The computation of importance values in the tree layer is based on

$$IV_k=\left(\frac{A_k}{\sum_{i=1}^{s}A_i}+\frac{F_k}{\sum_{i=1}^{s}F_i}+\frac{D_k}{\sum_{i=1}^{s}D_i}\right) \qquad (1)$$

In this equation, symbols A_k, F_k and D_k represent abundance, frequency and density for the kth tree population. Symbols $\sum_{i=1}^{s} A_i$, $\sum_{i=1}^{s} F_i$ and $\sum_{i=1}^{s} D_i$ represent population totals. The computation of the importance value in the shrub and herb layers is different:

$$IV_k = \left(\frac{A_k}{\sum_{i=1}^{s} A_i} + \frac{F_k}{\sum_{i=1}^{s} F_i} + \frac{D_k}{\sum_{i=1}^{s} C_i} \right) \tag{2}$$

in this A_i and F_i are similarly defined as in equation (1) and C_i is the cover value.

Diversity index

Species diversity is measurable on the community level and it reflects a structural characteristic known as entropy. It is influenced by both richness and evenness. The richer is the community in species and the more even the distribution of individuals among the species, the higher the diversity. The concepts have been presented by others (Simpson 1949, Margalef 1958, Pielou 1975, and Orlóci 1991). In this work, I use the Shannon-Wiener equation

$$D = -\sum_{i=1}^{s} p_i \log_2 p_i \tag{3}$$

in which

$$P_i = \frac{n_i}{N}$$

In equation (3) s is population number in a stand, n_i is the importance value of population i, and N is the total of the importance values of s populations. Since the log expression uses base 2, D is measured in bits.

Ecological dominance index

Ecological dominance is dominance concentration. It is the extent to which dominance is concentrated on one or several species. Its value is maximal in a one-species community. In multispecies communities the absolute maximum dominance cannot be attained. It is interesting to note that the Simpson index (Simpson 1949) measures concentration which is in fact "dominance". The derivation of the Simpson index assumes that individuals are drown in pairs without replacement from a community of N individuals and S populations. Population sizes are N_i, i= 1, 2, 3, ..., s and the total number of individuals is $\sum_{i=1}^{s} N_i = N$. If the probability that any two individuals belong to the same population is large, then this will indicate high concentration of the community. We regard this probability as the index of concentration:

$$C'' = \sum_{i=1}^{s} \frac{N_i(N_i-1)}{N(N-1)} \tag{4}$$

C" is a parameter which has no sampling error. In practical surveys , only equation (5) is operational:

$$C' = \sum_{i=1}^{s} \frac{(n_i(n_i-1)}{N(N-1)}\} \tag{5}$$

When the n_i are large, the dominance index is approximately equal to

$$C' = \sum_{i=1}^{s} \left(\frac{n_i}{N}\right)^2 \tag{6}$$

In equations (4), (5) and (6) the definitions of s, n, and N are the same as in equation (3).

Community equitability

Equitability or evenness (Margalef 1958) is the evenness of abundance among populations. Highest diversity occurs at maximum evenness when the populations have equal representations. Therefore, equitability can be measured based upon the ratio of actual species diversity to the possible highest diversity. In these terms, based on D in equation (3) , equitability is defined by

$$J = \frac{D}{D_{max}} \tag{7}$$

where $D_{max} = \log_2 s$.

Results

I used equations (1), (2), (3), (6) and (7) to calculate importance, species diversity, ecological dominance and equitability values for 76 communities. These values and community richness, as well as total individual numbers are displayed in Tables 1, 2, 3.

Analysis and discussion

Indices

Species diversity, ecological dominance and equitability are considered:

Species diversity. Inferring from what has already been said, species diversity is a synthetic index. Species diversity is correlated with population number and equitability. The higher the population number and the higher is equitability, the greater is species diversity. For instance, in the *Carex lanceolata - Corylus mandshurica - Tilia amurensis - Populus davidiana* community (a) and in the *Oxalis acetosella - Corylus mandshurica - Abies nephrolepis - Pinus koraiensis* community (b), the population numbers, total number of individuals and community equitability are respectively 8, 2626, 67.559% and 6, 1877, 61.682%. Species diversity is 2.2029 and 1.5941. Species diversity is similar between the two communities, one having higher equitability, lower population numbers and lower numbers of individuals, and the other having lower equitability, higher population numbers and higher numbers of individuals. This peculiarity is attributed to ecological dominance. In another case, involving the *Carex campylorhina - Corylus mandshurica*

Table 1. The quantitative characteristics of organization in the tree layer of 4 typical cases in 76 forest communities. Partial list is given, but all the records are used in further analyses. Explanation of symbols: R - number of species in the community, N - total number of individuals estimated per hectar, C - dominance, D - diversity, J- evenness per cent, IV - importance value per cent. Community a: *Oxalis acetosella, Corylus mandshurica, Abies nephrolepis, Pinus koraiensis*; Community b: *Carex campylorhina, Corylus mandshurica, Abies nephrolepis, Pinus koraiensis*; Community c: *Matteuccia struthiopteris, Deutzia amurensis, Pinus koraiensis, Abies nephrolepis;* Community d: *Carex lanceolata, Corylus mandshurica, Tilia amurensis, Populus davidiana.*

Community		R	N/ha	C	D	J%	IV%
1	a	6	1877	0.4056	1.5941	61.682	52.85
2	b	7	1801	0.2949	2.1836	77.802	46.50
3	c	10	1190	0.2027	2.6527	79.884	33.30
...	...	...	...	...	...	...	...
76	d	8	2627	0.3700	2.2030	67.559	57.70

Table 2. The quantitative characteristics of organization in the shrub layer of 4 typical cases in 76 forest types. See explanations of symbols and description of communities in the caption of Table 1.

Community		R	N/ha	C	D	J%	IV%
1	a	5	54	0.2779	2.0807	89.611	44.31
2	b	6	22	0.2101	2.41999	93.616	34.52
3	c	8	98	0.1394	2.9799	97.333	15.31
...	...	...	...	...	...	...	...
76	d	5	26	0.2476	2.1485	92.532	36.04

Table 3. The quantitative characteristics of organization in the herb layer of 4 typical cases in 76 forest communities. See explanations of symbols and description of communities in the caption of Table 1.

Community		R	N/ha	C	D	J%	IV%
1	a	20	57	0.0874	3.9080	90.423	19.96
2	b	16	41	0.0898	3.7200	87.593	32.62
3	c	9	105	0.1791	2.7765	97.333	15.31
...	...	...	...	...	...	...	...
76	d	24	35	0.0726	4.2538	92.800	19.29

- *Abies nephrolepis - Pinus koraiensis* community (c), the population number, total number of individuals and community equitability are 7, 1801, 77.082. The equitability of community (c) is higher then that of community (a), but both communities have very similar species diversity, 2.1836 and 2.2029. Obviously, these communities have different ecological dominance, 0.3705 in community (a) and 0.2949 in community (c).

Ecological dominance. Temperate forest communities have well-defined tree, shrub and herb layers, but the tree populations are the key factors. Frequently in the case of trees, there are few populations, yet they control the energy flow and affect the internal environment of other species in the community. Species capable of exerting such a control are the ecological dominant species (Odum 1971, Peng 1987). According to inferences based on the equation of dominance (6), magnitude can be assigned to different populations. Monodominance implies high ecological dominance. For instance, there is high ecological dominance in the tree layer of a secondary birch forest, poplar forest, and larch forest with index values as high as 0.32. Oligodominance implies low ecological dominance in the community, such as in the broad-leaf/Korean pine forests where the dominance index is as low as 0.18. In general, dominance declines as the species numbers increase. The subtropical evergreen broad-leaved forests are examples where the dominance index can be as low as 0.12 or even less. Because of low species numbers in the Lesser Xingan Mountains, there is a positive cor-

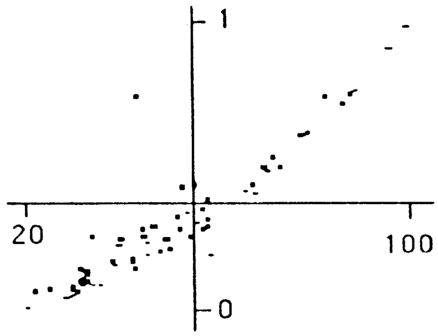

Figure 1. Joint scatter of importance value (horizontal axis) and ecological dominance (vertical axis) in the sample of 76 forest types described from the Lesser Xingan Mountains.

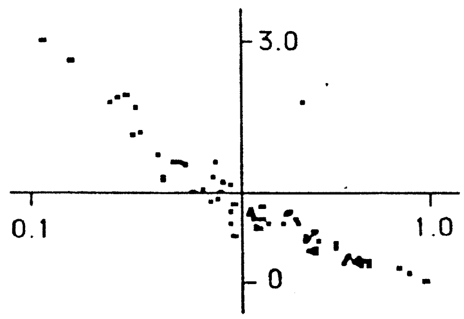

Figure 2. Joint scatter of ecological dominance (horizontal axis) and diversity (vertical axis) in the sample of 76 forest types described from the Lesser Xingan Mountains.

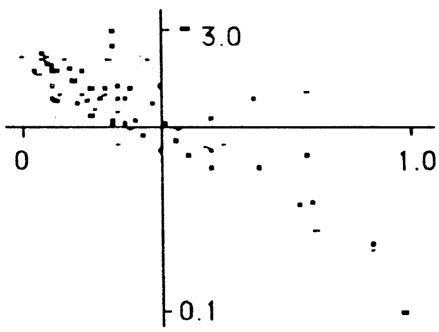

Figure 3. Joint scatter of equitability (horizontal axis) and ecological dominance (vertical axis) in the sample of 76 forest types from the Lesser Xingan Mountains.2.

relation between ecological dominance and the importance value of the dominant populations. (Fig. 1). Obviously, the higher the importance value of dominant species, the greater the role that they play in the community. Interestingly, there is a negative correlation between species diversity and ecological dominance (Fig. 2), suggesting that dominance does not generate stability.

Community equitability. Equitability and ecological dominance are two complementary characteristics of the community. When ecological dominance is high, equitabiliy is low (Table 1, Fig. 3).

Zonation

The study site has a clearly defined zonation pattern of vegetation with altitude from temperate to cold temperate climates. This zonation is modified by temperature inversion which is responsible for the intrazonal vegetation. The latter is a low altitude variant of vegetation from high altitude climates. The vegetation types in Table 4, abundant in the study site, are listed according to zonation from cold to temperate climate.

The intrazonal cold temperate conifer forest has high ecological dominance and low species diversity, typical of monodominant communities. The zonal temperate mixed deciduous/conifer forest is relatively rich in species which have low importance values. This community has also low ecological dominance and high species diversity. The vegetation type which lies bet-

Table 4. The quantitative characteristics of organization in the tree layer in forest communities. The arrangement is according to climatic zonation. See explanations of symbols and description of communities in the caption of Table 1.

Vegetation type	R	N/ha	C	D	J%	IV%
Cold temperate conifer forest	5.89	2213	0.3679	1.8224	76.416	49.55
Cold temperate mixed broadleaf-conifer forest	5.57	2341	0.3429	1.9111	81.710	45.01
Temperate conifer forest	8.20	1183	0.3220	2.0421	67.454	45.73
Temperate mixed broadleaf conifer forest	8.00	2147	0.2656	2.2335	84.158	40.67

Table 5. The quantitative characteristics of organization in the tree layer of seral communities in broad-leaf/Korean pine forest after logging. See explanations of symbols and description of communities in the caption of Table 1.

Developmental stage	R	N/h	C	D	J%	IV%
Betula costata - Pinus koraiensis community	8	2166	0.1837	2.7123	98.455	32.20
Mixed broadleaf forest community	10	2059	0.1939	2.6917	82.446	30.24
Populus davidiana - Betula platyphylla community	6	2745	0.3617	1.9043	71.974	52.85
Quercus mongolica forest community	5	3187	0.4872	1.4286	61.491	61.63

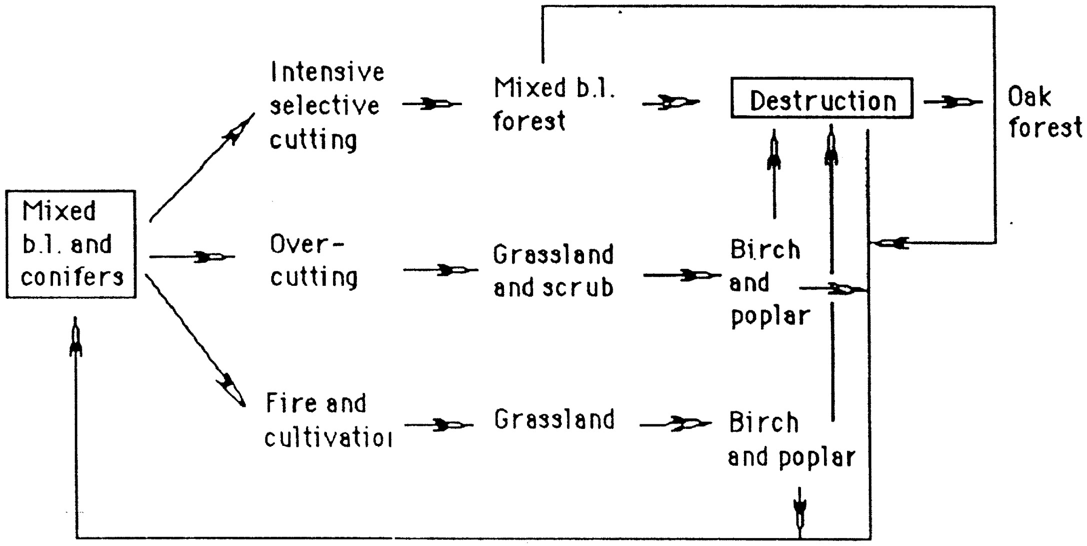

Figure 4. Pathways in community dynamics after logging in a broad-leaf/ Korean pine forest. The structural characteristics of the tree layer in the different seral stages are included in Table 5.

ween these two types have index values that are also intermediate.

Secondary dynamics

Temporal changes in the quantitative indices cannot be observed directly, but can be inferred analytically. The characteristics of the different seral communities are shown in Fig. 4 and Table 5. It can be seen that ecological dominance and species number change in such a way that ecological dominance increases while species diversity and equitability decrease. These indicate retrogression.

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