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ON THE INTERRELATIONS BETWEEN STRUCTURE, DYNAMICS AND EVOLUTION OF EPILITHIC LICHEN SYNUSIAE

Evolutional phenomena in communities and ecosystems have been studied insufficiently. Only little attention is paid to those phenomena even in two books of fundamental ecology by E. Odum (Одум, 1975, 1986). Nevertheless, J. M. Hall (Галл, 1984) stated that since the 50s a great number of publications on the problem have been published. The authors consider the evolutional process as coevolution of species in communities and ecosystems. In spite of a sufficient amount of theoretical papers it is not clear as yet what the expression *the evolution of communities* means. Interpretation of elementary evolutional phenomena, especially heterogeneity of populations, can be of help. As N. Timofeyev-Resovsky (Тимофеев-Ресовский, 1974) has stressed, an elementary evolutional change is not an evolution yet, but any further evolutional process is impossible without these changes.

Evolution of communities can pass in two ways — allogically, i. e. through geological and climatic changes, and autogenically, i. e. due to changes in the environment caused by the organisms' activities.

It is possible to compare, but very roughly, the evolution processes of elementary communities with group selection. Two of the most widely-known interpretations of this selection are as follows: group selection as the elimination of definite elements of a community — evolution as an elimination factor — and group selection leading to such a preservation of community properties and relations that are useful a population but not always useful for separate carriers of genetic information in a population. On the contrary — group selection eliminates or decreases to lesser frequency those properties and relations that do not stimulate the species preservation, but are selective advantages inside a population. From the point of view of population (community) dynamics it is possible to characterize an elementary evolutional phenomenon as a period of transformation of the community structure through population-genetic succession to a new state of a dynamic balance (Тимофеев-Ресовский, 1974).

The impact rate of group selection on evolution is known to be rather unclear. However, the ecosystem complexity cannot be explained apart from the level of species and an organism level. Therefore selection on the higher levels of organization of living beings should be of significance in evolution (Saunders, Но, 1976; Георгиевский, 1984).

Analyzing the epilithic lichen synusiae dynamics it is possible to distinguish some life and growth forms which may be regarded as the carriers of useful properties that enable maximum effectiveness of survival under the given conditions. Thus evolutional changes of lichen synusiae can be regarded as adaptiogenesis. Distinguishing between growth forms and life forms it is necessary for determination of various types of matter and energy exchange in synusiae and for determination of stages with various intensity of coenogenesis. Fig. 1 shows a fragment of the epilithic lichen synusiae.



Fig. 1. Epilithic lichen synusia on the glacier moraines (Polar Urals, Berg-glacier).

Material and methods

Empirical data for this work are topographical diagrams and descriptions of epilithic lichen synusiae made by J. Martin on various-age moraines on the glaciers called IGAN* and named after L. S. Berg in the Polar Urals. The synusiae descriptions and drawings were made with the help of a 20×20 cm square-grid. Species composition was marked for every species, topographical cover degree (in per cent) was estimated for every species. Topographical schemes were analysed by horizontal bands of 2 cm width. The contacts among the thalluses of epilithic lichens, mosses and sometimes flowering plants were marked on every band. *The graph of interspecies contact or the contact graph G* was applied for describing the synusiae squares on the basis of the corresponding topographical schemes (Tevet, Martin, 1986). The vertices of the contact graph *G* are the species of synusiae and every contact (in graph theory — the edge) e_{ij} is fixed, if at a pair of various species v_i and v_j there is at least one pair of a contact specimen. In respective descriptions 60 species of lichens, mosses and flowering plants are registered. These species are met in 92 synusiae squares 757 times forming 1120 pairs of species, that in their turn are described by 3232 contacts among 4371 individual thalluses.

For empirical data processing a discrete mathematical method worked out by J. T. Tevet (1987) was applied. Since the detailed presentation of the method is space-consuming let us present its basic principles that enable us to understand the further analysis and the interpretation of the results.

Between any pair of species (vertices of graph *G*) v_i and v_j of the contact graph of synusiae a structural distance d_{ij} may be determined by the number d of contacts (edges of graph *G*) on the shortest contact chain (simple path in graph *G*) connecting these species. If there exists a contact chain between the species v_i and v_j , these species are connected. Finding the equivalence or symmetry classes of species and contacts we proceed from determining the connectivity relations r_{ij} between the species pairs by the following rule (algorithm).

CONNECTIVITY RULE determines the connectivity relations r_{ij} between all the species pairs of the contact graph *G* and presents them in the form of relation words $\pm dn_{ij}$ as follows:

(a) If species v_i and v_j are non-contactive (disadjacent vertices), the relation word is preceded by — sign, whereby

(a1) if these species are connected, it is necessary to establish the distance d_{ij} and the number n of the corresponding shortest contact chains between these species;

(a2) if these species are disconnected, then $d=\infty$ and $n=0$.

(b) If species v_i and v_j are contactive (adjacent vertices), the relation word is preceded by + sign, whereby

(b1) it is necessary to treat these species as non-contactive and establish the collateral distance d and the number n of the corresponding collateral shortest contact chains between these species;

(b2) if between these contactive species there exists no collateral contact chains, then $d=1$ and $n=0$.

$|V|^2$ -dimensional matrix whose elements are relation words is called the semantic relation matrix $S=(\pm dn_{ij})$ or *S-matrix*. If rows s, s', \dots of *S-matrix* have the identical sets of relation words $\{dn\}=\{dn'\}=\dots$ we call these rows and corresponding species semantically equivalent rows $s \sim s' \sim \dots$ and species $v \sim v' \sim \dots$.

Determination of the semantically equivalent connectivity relations sometimes requires complementary identification of dn -words (i.e. identification of the corresponding word graphs). Connectivity relation is determined by the length d and number n of the shortest chain and each link of the chain is represented by some relation word $+dn$ in

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S-matrix. Therefore, each relation word (or word graph) as a complex of contact chains can in its turn be represented by cortege complex of these relation words $\{+dn_{11}, \dots, \dots, +dn_{1d}, \dots, \dots, +dn_{n1}, \dots, \dots, +dn_{nd}\} = DN_{ij}$, where the index d is the length of a cortege and the index n the number of corteges. The differences between the cortege complexes induce the semantical differences of connectivity relations.

The possible occurrence of semantic differences between the rows (columns) $s \approx s'$ of S-matrix induce the partition into equivalence classes of rows $S_1 \cup \dots \cup S_h \cup \dots \cup S_K = S$, which, of course, coincide with the semantic equivalence classes of species $V_1 \cup \dots \cup V_h \cup \dots \cup V_K = V$.

Let the S-matrix rows and columns be arranged according to the semantic equivalence classes $S_1, \dots, S_h, \dots, S_K$. It is now possible to define the *syntactic arrangement* of this matrix as the semantic equivalence $\{s_{ih} \sim s'_{i'h'} \sim \dots\} = S_{hh'}$ of all submatrices' $S_{hh'} = S_h \cap S_{h'}$ ($h' \in [1, K]$) partial rows obtained by means of decomposing S-matrix. The syntactic arrangement is carried out by the *syntactic rule*, which, arranging the rows and columns of S-matrix according to certain features, generates new equivalence classes. This process is convergent and the matrix obtained is called *syntactic relation matrix Z* or *Z-matrix*. Z-matrix is a syntactically arranged S-matrix.

It is now possible to construct the following theorem.

Theorem 1. *The syntactic relation matrix Z represents the structural equivalence classes or symmetry classes of species (vertices) BV_h and topical as well as potential contacts (edges) classes BR_n of a graph G.*

So, in the case of any symmetry class $B_h\{v, v', \dots\} = BV_h$, its elements v, v', \dots are structurally equivalent** and occupy equal positions in the structure of the contact graph.

Structural equivalence B of the species v, v', \dots present in synusia is expressed by isomorphism $G-v \cong G-v' \cong \dots$ of the subgraph obtained by means of alternative elimination of these species.

The additional condition of structural equivalence of connectivity relations r, r', \dots (i.e. the topical and potential contacts or edges of graph G) is as follows: the corresponding identical relation words must belong to the same submatrix $\{dn = dn' = \dots\} \in Z_{hh'}$.

We will now present one more interesting theorem (Tevet, 1987).

Theorem 2. *Graphs G_a and G_b are isomorphic $G_a \cong G_b$ if and only if their syntactic relation matrices Z_a and Z_b syntactically equivalent $Z_a \approx Z_b$.*

The topographical scheme of synusia square in the early stage of coenogenesis with its contact graph G and canonical matrix Z presenting the structure of the synusia square and its symmetry classes is represented in Fig. 2.

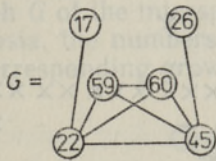
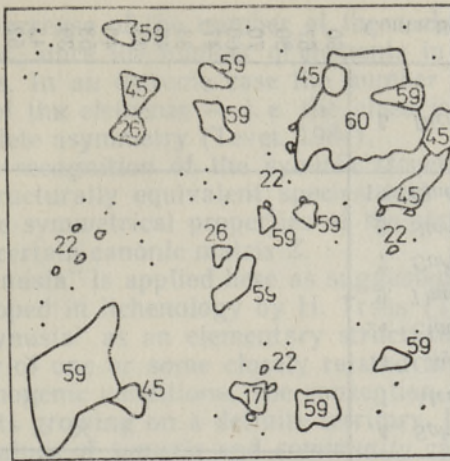
It is now easy to formulate on the basis of syntactic relation matrix Z such summary characteristics as *the structural complexity η of synusia* which is the value of a function determined by the number of species I , the number of contacts (i.e. contact pairs of species) m , the number of symmetry classes of species K and the number of contact symmetry classes N (Tevet, Martin, 1987):

$$\eta = \log_2(I \cdot m \cdot K \cdot N).$$

Roughly the following stages can be distinguished on the newly formed rocky substrate: 1) microbial films, 2) alga films, 3) crustaceous lichens layer, 4) folious lichens layer, 5) moss layer, 6) flowering plants layer and 7) multi-layered communities, varying in intensity, effectiveness of substance transformation and productivity.

In the present paper the evolution of a community is regarded as the replacement of lower growth and life forms by higher ones in the process of lichens synusia during coenogenesis within the stages of layer and storey overgrowth.

** Our concept of structural equivalence or symmetry corresponds exactly to the similarity concept ($\alpha(v) = v'$) in the graph theory and our concept of symmetry class corresponds exactly to the transitivity domain of similarity or orbit's concept.



1	1	2	2	3	3	3 classes	k
17	26	59	60	22	45	species	i
0	-3.1	-2.1	-2.1	+1.0	-2.1		17 1
	0	-2.1	-2.1	-2.1	+1.0		26 1
		0	+2.2	+2.2	+2.2		59 2
			0	+2.2	+2.2		60 2
				0	+2.2		22 3
					0		45 3

Fig. 2. Topographical scheme of the epilithic lichen synusia on early coenogenesis stage, the corresponding contact graph G and canonical Z -matrix presenting the structure and symmetry classes of the synusia. Vertices of the graph indicate the following lichen species: 59 — *Rhizocarpon geographicum* ssp. *arcticum*, 60 — *R. hochstetteri*, 17 — *Lecanora polytropa*, 45 — *Umbilicaria hyperborea*, 26 — *U. cylindrica*, 22 — *Lecanora atra*. All these lichen species belong to crustaceous and folious lichen growth form.

Discussion

A community is a discrete system where the relations between the structure and evolutionary states are of primary interest for us. We assume that these relations proceed from the structurativity principle, while the criterion of structuralization in this case is the contactivity between the species in lichen synusia.

The *structurativity principle* (Веденов, Кремьянский, 1970) is of substantial cognitive value in the studies concerning communities, since it allows to grasp a large amount of information about the object or phenomenon under investigation. On the grounds of this structurativity principle it is possible to build the investigation of the structure of separate (morphological, patterned) phenomena as well as dynamic (populational, coenogenetical, evolutionary) phenomena, or what is even more essential, the complex study of *statics and dynamics of the structures*.

The most general property of a structure is *symmetry and asymmetry* which is expressed by the *structural equivalence of its elements*. Symmetry reveals itself where there exist at least two structurally equivalent elements and increases when the number of such elements increases. Symmetry reaches its maximum if the elements form only one equivalence

class. With the increase of the number of these classes, symmetry of the synusia decreases, since the number of elements in structural equivalence classes decreases. In an extreme case the number of equivalence classes can equal that of the elements — i. e. the class is unielemental. This is the case of complete asymmetry (Tevet, 1984).

For the final recognition of the synusia structure it is important to determine its structurally equivalent species and structurally equivalent contacts (i. e. the symmetrical properties of the structure) and present it in the form of a certain canonic matrix Z .

The word "synusia" is applied here as suggested by T. Lippmaa (1933, 1939) and developed in lichenology by H. Trass (Tpac, 1964, 1966), i. e. we recognize "synusia" as an elementary structural element of the plant cover, consisting of one or some closely related life forms located under more or less homogenic conditions. The conception of *community* includes some set of plants growing on a definite territory. Under some conditions the conception values of *synusia* and *community* can coincide. We regard the term *community* as a general interpretation, not considering the classification application.

Dealing with the present empirical material it appeared to be appropriate to divide the species under consideration into four groups of life and growth forms: $l=1$ — crustaceous and folious lichens, $l=2$ — fruticose lichens, $l=3$ — mosses and $l=4$ — flowering plants. The vertices of the graph G of the interspecies contacts of synusia are the species composing synusia, the numbers of the vertices indicate the index l of the stage of the corresponding growth or life forms (Fig. 3).

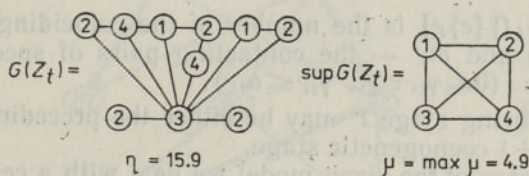


Fig. 3. Graph $G(Z_t)$ shows one state Z_t of the late coenogenetical stages of epilithic lichen synusia and supergraph $\text{sup}G(Z_t)$ of the evolutionary state $\text{sup}Z_t$ with complexity characteristics. Graph vertices are species belonging to the corresponding life or growth form ($l=1$ — crustaceous and folious lichens, $l=2$ fruticose lichens, $l=3$ — mosses, $l=4$ — flowering plants).

It is now possible to formulate the *evolutional complexity* μ of *synusia* as the value that fixes the variety and stages of growth forms

$$\mu = \log_2 \sum_{l=1} 2^l,$$

where l is the growth or life form index.

Matrix Z which pictures the structure of synusia square is simultaneously the *static model* Z of the *synusia square* that can be regarded from the *coenodynamic aspect* as the *coenogenetic state* of *synusia* Z_t within the time stage t and whose structural complexity is $\eta(t)$ and evolutionary complexity $\mu(t)$. The *evolutional state* of *synusia* $\text{sup}Z$ at time stage t can be presented as rough superstructure $\text{sup}Z$, which elements $\text{sup}(v)$ are different growth and life forms of the species in synusia and the structural links $\text{sup}(e)$ — the contacts between the species with the corresponding growth forms. Fig. 3 shows the graph $G(Z_t)$ which illustrates the state Z_t of the late coenogenetic stage of lichen synusia on the moraine and the supergraph $\text{sup}G(Z_t)$ which represents the evolutionary state $\text{sup}Z_t$ (Tevet, Martin, 1987).

A model based on the study of the empiric material and imitating coenogenesis is designed to investigate the interrelation between the

structure of a community and its evolutionary state. For that purpose the following attributes are formed: 1) topographical descriptions of the synusia squares are transformed by applying the corresponding rules into Z-matrices which represent the states of coenogenesis $\{Z_t\}$; 2) assuming that in conditions free from anthropogenic impact the coenogenesis duration time should largely correlate with the increase of synusia cover, we divide according to the cover degree the quantity of states $\{Z_t\}$ into *coenogenesis stages* $\{c_t\}$. In case of the present empirical material it appeared appropriate to differentiate the following stages: $0 < c_t \leq 0.05$; $0.05 < c_t \leq 0.1$; $0.1 < c_t \leq 0.17$; $0.17 < c_t \leq 0.6$; $0.6 < c_t \leq 0.7$; $0.7 < c_t \leq 0.8$; $0.8 < c_t \leq 0.87$; $0.87 < c_t \leq 0.95$; $0.95 < c_t \leq 1.0$, $t \in T$.

3) For imitating the possible succession it is necessary to estimate for each coenogenesis stage Z_t its nearest neighbour $Z_{t'}$ at the next coenogenesis stage by means of determining the maximum values of the *coefficients of the succession* $\max \alpha_{tt'}$ and $\max \gamma_{tt'}$.

$$a) \quad \alpha_{tt'} = \frac{2 \text{ card } [\{v\}_t \cap \{v\}_{t'}]}{I_t + I_{t'}};$$

where $\text{card } [\{v\}_t \cap \{v\}_{t'}]$ is the number of the coinciding species of states Z_t and $Z_{t'}$; and I_t and $I_{t'}$ — the number of species in these states ($0 \leq \alpha_{tt'} < 1$).

$$b) \quad \gamma_{tt'} = \frac{2 \text{ card } [\{e\}_t \cap \{e\}_{t'}]}{m_t + m_{t'}}$$

where $\text{card } [\{e\}_t \cap \{e\}_{t'}]$ is the number of the coinciding contact pairs of species, and m_t and $m_{t'}$ — the contacting pairs of species in the corresponding states ($0 \leq \gamma_{tt'} \leq 1$; $\gamma_{tt'} \leq \alpha_{tt'}$).

The neighbouring stage t' may be either the preceding $t' = t - 1$ or the following $t' = t + 1$ coenogenetic stage.

Thus in the case of the given model we deal with a certain *system with the output function* $y_t = \lambda(Z_t)$ which determines the output values of each state in every coenogenetic stage $t \in T$ in the form of structural and evolutionary complexity of the synusia $y \in \{\eta, \mu\}$.

Synusiae on one and the same coenogenetic stage c_t , arranged in sequence by the increase of structural complexity η and evolutionary complexity μ represent *ecological series of synusiae*. Consequently from the point of view of coenogenesis the ecological series can be considered as *static series* which embrace a definite number of *synusiae of various complexity*. A set of ecological series arranged in sequence according to the coenogenetic stage c_t presents a dynamic partition of ecological series — *dynamic classification*. There is a *succession function* $Z_{t'} = \varphi(Z_t, c_{tt'})$, its values being the states $Z_{t'} \in \{Z\}$ where synusia appears to be on the coenogenetic stage $t' \in T$ if on the previous stage it was in the state Z_t and in the process of the increase of covering $c_{t'} = c_t + \Delta c_{tt'}$ a certain change $\varphi: Z_t \rightarrow Z_{t'}$ occurs preserving a different invariant $Z_{tt'} = Z_t \cap Z_{t'} \neq 0$ of the synusia structure.

Thus in spite of the fact that our empiric material is extensive we are able to model a *dynamic process of successionism — coenogenesis* — by applying the coefficients of succession $\max \alpha_{tt'}$, $\max \gamma_{tt'}$ and the succession function φ .

Fig. 4 presents the graphs $G(Z_t)$ and $G(Z_{t'})$ that illustrates two subsequent states of coenogenesis imitation model.

A *series of successional states* $Z_{t_1} \rightarrow Z_{t_2} \rightarrow Z_{t_3} \rightarrow \dots$ is a dynamic series. A set of dynamic series of synusia forms a dynamic model that imitates coenogenesis. 92 states of this model are divided among $T = 9$ genesis

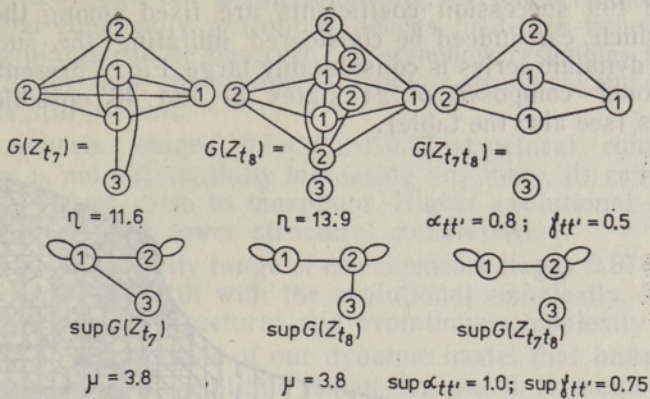


Fig. 4. Two subsequent states $G(Z_{t_i})$ and $G(Z_{t_s})$ of coenogenesis imitation model. The subgraph $G(Z_{t_i,t_s})$ illustrates their succession invariant. The supergraphs $\text{sup}G(Z_{t_i})$ and $\text{sup}G(Z_{t_s})$ expressing their evolutionary state together with the corresponding numerical characteristics.

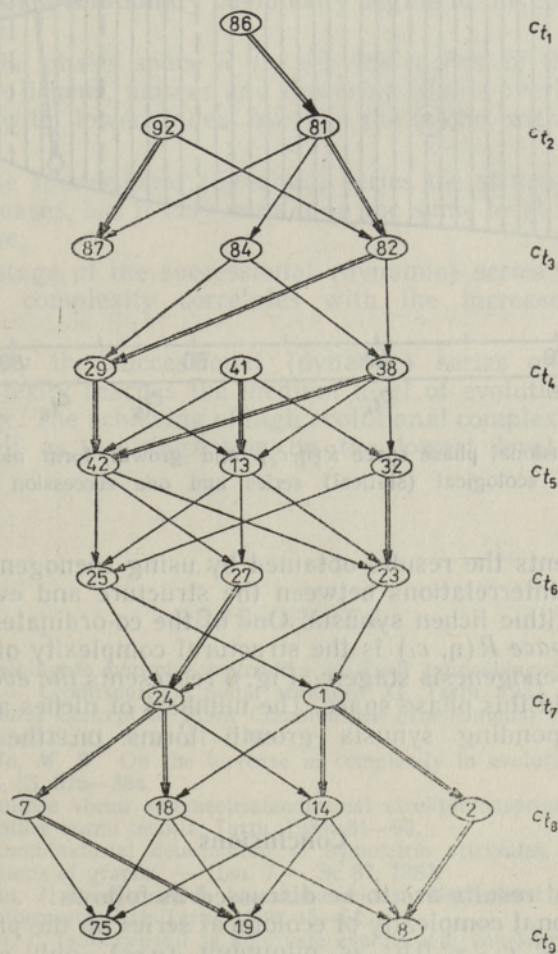


Fig. 5. Fragment of the dynamic model of coenogenesis includes 24 states Z_t and 46 probable successions of elements (wide arrows indicate the most probable successions ways). The number in the circle indicates the number of synusia.

stages and 199 succession coefficients are fixed among the state pairs, most of which can indeed be considered imitating the succession. The amount of dynamic series is considerably large. Fig. 5 presents a fragment of this model composed of 24 states Z_t and 46 possible elementary successions (see also the table).

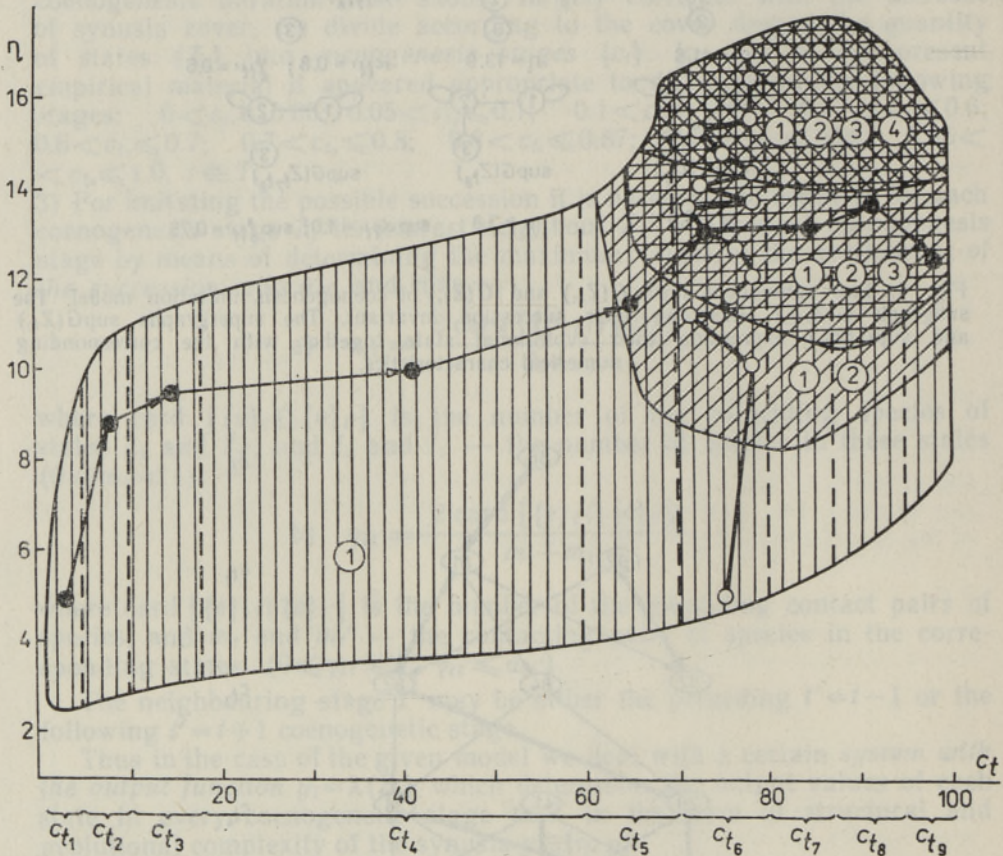


Fig. 6. Two-dimensional phase space $R(\eta, c_t)$ and growth form niches in this space. Circles mark one ecological (statical) series and one succession (dynamic) series.

Fig. 6 presents the results obtained by using coenogenesis model that illustrates the interrelations between the structure and evolutionary process of the epilithic lichen synusia. One of the co-ordinates of two-dimensional *phase space* $R(\eta, c_t)$ is the structural complexity of synusia η and the other the coenogenesis stage c_t . Fig. 6 represents *the evolutionary niches of the synusia* in this phase space. The numbers of niches are the indices l of the corresponding synusia growth forms on the corresponding coordinates.

Conclusions

The obtained results are to be discussed as follows:

The evolutionary complexity of ecological series on the primary stages of coenogenesis $0 < c_{t_{1-4}} \leq 0.6$ is minimum ($\mu=1$, only crustaceous and folious lichens can be observed) though the structural complexity of the ecological series on the genesis stage $0.05 < c_{t_2} \leq 0.1$ is considerably high.

The maximum structural complexity of the ecological series on coeno-

genesis stage $0.6 < c_{ts} \leq 0.7$ is still increasing, its complex synusia possess high evolutionary complexity μ (folioous lichens, fruticose lichens, mosses and flowering plants can be observed), it somehow resembles the "evolutional leap". At the same time synusiae with low structural and evolutionary complexity are still present.

On coenogenesis stages $0.7 < c_{ts} \leq 0.87$ structural complexity of ecologic series is not substantially increasing any more, its range is large and it reaches values close to maximum. Higher evolutionary complexity is achieved already with lower structural complexity.

The structural complexity range of coenogenesis stages $0.87 < c_{ts} \leq 1.0$ is narrowed correlating still with the evolutionary complexity. The role of the synusiae with lower structural and evolutionary complexity decreases.

As a result of the analysis of our dynamic model that imitates coenogenetical processes in the epilithic lichen synusia it is possible to state the following:

1) elementary evolutionary changes may appear on the coenogenesis stage $c_t > 0.6$ when cover degree is more than 60% and these changes are related to high structural complexity of synusiae;

2) the average structural complexity of the ecological (statical) series increases till it attains the stage $0.6 < c_{ts} \leq 0.7$ and stabilizes then. Starting from this stage the evolutionary complexity begins to increase having been minimum before;

3) in the synusia phase space $R(\eta, c_t)$ the niches of the crustaceous, folioous, fruticose lichens, mosses and flowering plants overlap each other: certain niches with lower index overlap the niche with higher index completely;

4) in case of the successional (dynamic) series the structural complexity η probably increases, but it may remain on the same level for a long time or even decrease;

5) on the last stage of the successional (dynamic) series the increase of the evolutionary complexity correlates with the increase of structural complexity;

6) most probably the successional (dynamic) series on high level of structural complexity reaches the medium level of evolutionary complexity on the final stage. The achieving of high evolutionary complexity is much less probable as well as the stagnation on the lowest level of evolutionary complexity.

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EPILITSETE SAMBLIKUSÜNUUSIDE STRUKTUURI, DÜNAAMIKA JA EVOLUTSIOONI VAHEKORRAST

Artiklis on analüüsitud Polaar-Uurali jääliustike moreenide epiliitset samblikukatet. Samblikusünuusi kirjeldamiseks on kasutatud liikidevaheliste suhete (kontaktide) graafe, mille alusel on määratud vastavate sünuusiruutude kui sünuusi dünaamiliste seisundite staatilised karakteristikud, mis iseloomustavad sünuuside struktuuri ja evolutsiooni keerukust. Võimalike seisunditevaheliste suksessioonide imiteerimiseks on postuleeritud suksessioonifunktsioon, mille abil on leitud igale seisundile tema võimalikud järglased.

Kasutatud empiirilise materjali põhjal on sellise mudeli abil muu hulgas näidatud, kuidas samblikusünuusi keerukus korreleerub evolutsioneeruvusega. Seisundite faasiruumis kattuvad koorik-, leht- ja põõsassamblike ning sammalde ja õistaimede nišid sellisel, et iga madala kasvu- või eluvormi indeksiga nišš hõlmab kõrgema indeksiga niši.

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О СООТНОШЕНИИ СТРУКТУРЫ, ДИНАМИКИ И ЭВОЛЮЦИИ ЭПИЛИТНЫХ ЛИШАЙНИКОВЫХ СИНУЗИИ

Анализируются показатели структуры эпилитных синузий, описанные по разновозрастным моренам ледников Полярного Урала. Для представления лишайниковых синузий используются графы межвидовых отношений (контактов) и на их основе определяются статические характеристики — структурная и эволюционная сложности. Для имитации динамики и сукцессии между синузийными квадратами, рассматриваемых в качестве состояний синузий, постулируется т. н. сукцессионная функция, при помощи которой выявляются для каждого состояния его возможные преемники.

При помощи такой модели показано, как коррелируется сложность лишайниковых сообществ с эволюционируемостью, и как ниши накипных, листоватых и кустистых лишайников, а также мхов и цветковых растений в фазовом пространстве сообществ перекрываются таким образом, чтобы ниша с индексом более низкой формы роста охватывала нишу с более высоким индексом.