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Ecological aspects of the evolution of modular organisms

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Summary: Fundamental traits of modular organization ensure the specific ecological features of organisms with open growth. Modular organisms function both as environment-forming and cenosis-forming objects. As a result, they form the ecological frameworks of terrestrial and marine biocenoses. The wide variety of modular plants and animals ensures the possibility of a complex and multi-level structure of such frameworks, which may be of significant size. The evolution of modular organisms had a big influence on the process of formation of various biomes and Earth's biogeocenotical cover. The formation of the main variants of herbaceous biomes was connected to the biomorphological transformation of certain groups of flowering plants. A conjugate analysis of the evolution of modular organisms and biomes will promote a deeper understanding of the fundamental role of modular living objects in ecosystems of different levels, including the biosphere.

Keywords: modular organism, evolution, ecology, population biology, plants, animals, fungi, biocenosis, biome, evolution of biomes

The interest in understanding the evolution at the planetary level is currently on the rise (Grinin et al. 2013; Yablokov et al. 2016; Savchenko et al. 2018; Bryntsev 2018; etc.). General scientific theories are being used more and more often in this process (Kirpotin 2005, 2007; Bogatykh 2006; Oleskin 2013; Bryntsev 2018; etc.). However, a more comprehensive use of the potential of general biological approaches is equally important. Among them, the concept of modular organization is worth noting (Marfenin 1999, 2018; Notov 2011, 2017, 2019; etc.). According to this theory, modular and unitary organisms are two principally different types of living organisms (Gatsuk 2008; Marfenin 1993, 2018; Notov 1999, 2005; etc.). They can be found in all the main components of biota, including plants, animals, fungi and prokaryotes (Notov 2011, 2017). Modular plants and animals form ecological frameworks of phytocenoses, coral reef ecosystems, communities of giant kelp and marine animal forests (Hallé et al. 1978; Preobrazhensky 1986; Sorokin 1990; Oldeman 1992; Marfenin 1993; Dubinsky & Stambler 2011; Schiel & Foster 2015; Rossi et al. 2017; Brandl et al. 2019; etc.). Modular organisms played a key part in the formation of the Earth's biogeocenotical cover. Their evolution was not only connected with phylocenogenesis, but in some cases ensured the emergence of new biomes. According to some points of view, "the biosphere's evolution is mainly the evolution of plant biomorphs" (Khokhryakov 1981: 158). The stages of the formation of the structural diversity of corals played an equally significant role in the evolution of marine biomes. However, a conjugate analysis of changes that occurred on different levels of the organization of living systems is still a goal for future research. Its relevance has not been fairly understood. Currently, the understanding of ecological aspects is not given enough attention in the process of researching the morphological evolution of modular organisms. Also, as a rule, in the analysis of biome evolution, the significance of structural transformations of their components is not given special consideration. The goal of this article is to draw the attention to the relevance of a targeted analysis of the ecological aspects of the evolution of modular organisms.

Materials and methods

Perceptions of ecological specifications of living organisms with open growth are relevant in understanding the connection between the evolution of modular organisms and the processes of biome transformation. Modular organisms have been analyzed from different standpoints of various branches of ecology. When studying the specifics of their relationships with the environment, scientific reviews on particulars of structure, functioning, ontogenesis and self-regulation processes in modular animals, plants and fungi have been used (White 1979; Bologova 1989; Shafranova 1990; Zhukova & Komarov 1990; Marfenin 1993, 2008, 2018; Zhukova 1995; Notov 1999, 2005; Zhmylev 2006; Zmitrovich 2006, 2010; Gatsuk 2008; Shefferson et al. 2017; Notov & Zhukova 2019; etc.).

A system analysis from the position of the functional theory of organization has been carried out by comparing modular organisms and unitary organisms with populations (Starostin 1967; Setrov 1972; Vinogray 1989, 2013; Notov 2005) (Table 1). Particulars of population life in modular organisms and displays of ontogenesis polyvariance have been analyzed (Bologova et al. 1985; Zhukova & Komarov 1990; Zhukova 1995; Notov 2005; Marfenin 2018; Notov & Zhukova 2019; etc.).

Scientific reviews of the structure and evolution of biocenoses, whose ecological framework has been created by various groups of modular organisms, have been studied (McCloskey 1970; Hallé et al. 1978; Preobrazhensky 1986; Sorokin 1990; Zherikhin 2003; Dubinsky & Stambler 2011; Strömberg 2011; Schiel & Foster 2015; Rossi et al. 2017; Wilson et al. 2017; Brandl et al. 2019; etc.). We have analyzed works which discussed the role of modular components of terrestrial and marine biocenoses in the formation of biogeochemical cycles of the biosphere (Khokhryakov 1981; Vacchi et al. 2017; Drake & Ivarsson 2018; Lu & Hedin 2019; McLaughlin et al. 2019; Steidinger et al. 2019; etc.). Special attention has been given to publications that consider the connection between processes of structural evolution with the transformation of biomes and biogeocenotical cover (Serebryakova 1971; Khokhryakov 1981; Gamalei 2015; Rossi et al. 2017; Lu & Hedin 2019; Starko et al. 2019; etc.). Works on co-evolution of various biomes components and the role of fungi in strengthening functional connections in phytocenoses have been analyzed (Karatygin 1993; Rossi et al. 2017; Savinov 2017; Ivarsson et al. 2020; etc.). Materials on the specifics of structural evolution of various groups of modular organisms have been consolidated (Serebryakova 1971; Khokhryakov 1981; Kuznetsova 1986; Meyen 1988; Marfenin 1993; Marfenin & Kosevich 2004; Sánchez 2004; Zmitrovich 2006, 2010, 2017; Notov 2015, 2016, 2017, 2019; Niklas 2016; etc.).

Results and discussion

Ecological specifics of modular organisms

Organism, population and environment. Fundamental specifics of modular organization precondition the particulars of organisms with open growth from the standpoints of all the main branches of ecology – autecology, demecology (ecology of populations) and synecology. These specific traits are connected, interdependent and linked to ways of functioning, self-regulation and distinctness of the ontogenesis of modular organisms. Some traits that reflect the interaction with the environment and the position of modular organisms in biocenoses have been considered in separate studies (Marfenin 1993, 2008, 2018; Notov 2005; etc.).

Table 1. Some system characteristics of populations, unitary and modular organisms: differences in forms of reliability have been considered in separate works (Starostin 1967; Notov 2005).

Traits	Unitary organism	Modular organism	Population
STRUCTURE			
Features of structural units (SU) (elements)	*heteronomous*	*homonomous*	
	inequality *irreplaceability*	*equality* *replaceability*	
	unrepeatability in time	*repeatability*	
	low level of autonomy	relative *autonomy*	
Number of same-type SU	*uniqueness* of SU or *certainty* of their number	*plurality* of SU and *uncertainty* of their number	
Strength of connection between SU	*strong* functional connections	*weaker* functional connections	
	mandatory *physical continuity*	*physical continuity* or *discreteness* of ramets after clone formation	*discreteness* of SU lack of physical connection
FUNCTIONING			
Specifics of SU interaction	*mutualistic* relationships are dominant	*competitive* relationships are often	
Reliability mechanisms	‘*warm*’ reliability, functional plasticity	‘*cold*’ reliability, structural and functional *redundancy*	
Regulation mechanisms	*centralized regulation*	regulation of the intensity of functioning through *changing the number* of forming SU	
DEVELOPMENT			
Specifics of growth processes	*growth* within the given system is *limited* *determinacy* of sizes	*unrestricted growth* within the given system *indeterminacy* of sizes	
Specific of SU morphogenesis	*simultaneous* appearance of SU	*different age* of structural elements	
Level of development determinacy	*big* development determinacy	*polyvariance* of development amount of dynamics of SU depend on environment	
	life span is more definite	life span is *undetermined*	

Due to unlimited growth in modular organisms, size and age restrictions are easily overcome; plasticity of shapes and a wide variability of the sizes of adult organisms is seen (Marfenin 2018). As a result of active lifelong morphogenesis, the plasticity (polyvariance) of ontogenesis of modular organisms reaches a high level. Developmental pathways (trajectories) are highly diverse (Zhukova 1995; Notov & Zhukova 2019). Common variations include the ‘loss’ of certain ontogenetic states, disturbance of their sequence and variation in the degree of ontogenesis completeness. During ontogenesis, the life form may often change and the organism may lose its integrity and be divided into parts (particulated) to form daughter individuals. In one of the latest versions of the classification of ontogenesis polyvariance, 7 supertypes and 11 types of polyvariance have been distinguished (Notov & Zhukova 2019).

The particulars mentioned above define the activity forms and strategies of engagement with the environment that are different from those of unitary organisms (Marfenin 1993, 2018; Notov 2005; Savinov 2015). The abilities of slowly occupying the territory through growth and ingrowing into the environment (Marfenin 2018) 'divide' the environment and its transformation is manifested.

Modular organisms are highly interesting objects of population ecology. From the point of view of system organization, they are very similar to populations (Table 1). On the other hand, their population life is very specific (Zhukova 1995; etc.). Modular organisms and populations are weakly determined systems with decentralized self-regulation (Notov 2005; Marfenin 2018; etc.). Their similarity involves all the main aspects of organization – structure, functioning and development (Table 1). Modular organisms and populations have the ability to reproduce the elements they consist of numerous times throughout their lifespan. Constant formation of new elements does not only maintain integrity, but is also aimed at development. Elements of a modular organism or of a population are homonomous, functionally equal, interchangeable and relatively autonomous. Regulation of the compared systems is always decentralized (Notov 2005; Marfenin 2018; etc.). It is carried out through changing the intensity of element formation (morphogenetic activeness or rate of reproduction accordingly) and their number. Development, functioning and regulation of modular objects and populations are connected to changes in their structure and composition. New elements are created in the course of development and functioning; distinctive connections are formed between them. As opposed to modular organisms, unitary organisms are systems with strong connections between heteronomous, unique and irreplaceable elements (Table 1).

The similarity between modular organisms and populations is seen even through a more superficial view. It is not surprising that different researchers have tried to see modular plants as a colony or a meta-population many times, and considered modular animals to be a conglomerate of connected individuals (see White 1979; Marfenin 1993; etc.). 'Demographic' approaches are often used in describing plant structure by characterizing the number of structural elements of different ranks (Bologova et al. 1985; Bologova 1989; etc.). The possibility of competitive relationships between parts of a modular organism attests to their similarity to populations. They can be seen, for example, in dying and shedding of branches in *Pinus sylvestris* L. that are shadowed by upper elements of the canopy (Notov & Zhukova 2015). The dynamics of dying processes in elements of tussock have been described in detail using the example of *Dactylis glomerata* L. (Bologova 1989). In places of chronic food deficits in modular animals, zooids are dissolved and nutrients are transported to other parts of the colonial organism (Marfenin 1993, 2018). Similarity with populations is strengthened in partition and formation of clones. In this case, not only the functional, but also the physical connection between parts of the organism is lost. Ramets created in this process are virtually indistinguishable from similar looking individuals of seminal origin. Ramet aggregates live and function like a population. In this context, there are certain problems in using terms like 'organism' or 'individual' with respect to modular organisms (Gatsuk 2008). Clone formation is highly prevalent in plants and fungi. A similar separation of elements of colonial organisms has been noted in hydroid polyps, where the central part of the colony is destroyed (Marfenin 1993, 2018; etc.).

Some modular objects may be similar to cenotic level systems. Among them, for example, there are lichens, which are symbiotic associations that consist of organisms belonging to different kingdoms of living beings. Since the integrity of such associations is close to that of an organism, it is traditional to use approaches that are used for studying biological species, they are given binary names, populations are outlined and their structure is described. The widespread occurrence of complex life cycles with the change of generations leads to the fact that in individual development, a modular organism often serves as several independent bionts. They hold isolated ecological niches and perform different functions in biocenoses (Notov 2011, 2018). Each one forms its own system of interconnections.

Thus, modular organisms create an organizational continuum, in which living beings of various similarities to populations, or in some cases with mutually connected components of cenoses, can be found. The boundary between organismal and supraorganismal levels is not always clear-cut (Notov 2011; Zeleev 2011; etc.). At the same time, different ways of increasing activeness in relation to the environment are implemented at each level. Open growth and plasticity of individual development of modular organisms shape their high resistance to environmental effects, ensure their 'ingrowth' into the environment, their ability to 'divide' and transform it (Marfenin 1993, 2018; Notov 2005). The effectiveness of interaction with the environment can be increased due to the formation of vegetatively mobile forms, polycentric and acentric biomorphs (Smirnova et al. 2002; Komarov et al. 2003; Savinykh & Cheryomushkina 2015; etc.). Activeness at the populational level is increased by the large heterogeneity of individuals and high polyvariance of their ontogenesis (Zhukova & Komarov 1990; Zhukova 1995; Notov & Zhukova 2019; etc.). Additional, and sometimes fundamental, factors of increasing population size are often vegetative (asexual) reproduction and the ability to form agamic clones as well as complex life cycles (Marfenin 1993, 2018; Notov 2011; etc.).

Modular organisms in biogeocenoses. Fundamental features of modular organization and the noted traits of population's life result in the environment-forming and cenosis-forming role of modular living beings. Open (unlimited) growth, which ensures the potential of a very long lifespan, promotes the implementation of the framework function in biocenoses. It is most clearly seen in phytocenoses of trees and reef-forming corals. By 'dividing' the environment, they significantly increase the amount of ecological niches. Because of lignified and suberificated tissues and skeletal elements, modular plants and animals continue to structure the frameworks of biogeocenoses even after death. Environment-forming (transformative) activity of modular organisms can reach significant levels due to their contribution to the process of generating soil and peat cover as well as coral reef zones (Khokhryakov 1981; Sorokin 1990; Bakhnov 2002; Dubinsky & Stambler 2011; Monson 2014; Zanella et al. 2018; Brandl et al. 2019; etc.).

The cenosis-forming role of modular plants and animals is manifested by the fact that the dynamic of ontogenetic and spatial structure of their cenopopulations ensures the formation and support of the structure and system of connections that are typical for that particular biogeocenosis. Ecological frameworks of terrestrial and marine communities have a complicated composition, various sizes and are quite dynamic (McCloskey 1970; Sorokin 1990; Dubinsky & Stambler 2011; Monson 2014; Schiel & Foster 2015; Rossi et al. 2017; Brandl et al. 2019; etc.). Dominants and edificators play an important system-forming role (Smirnova & Bobrovskii 2001; Notov & Zhukova 2015; Schiel & Foster 2015; Rossi et al. 2017; Omelko et al. 2018; etc.). The dynamics of key species populations have cenosis-transforming value. It ensures the succession of biocenoses (Hallé et al. 1978; Smirnova et al. 2011; etc.).

The wholeness of ecological frameworks of biocenoses grows significantly due to the integrative function of symbiotic associations, which modular organisms form. Symbiotic plant and mycorrhiza-forming fungi systems have reached incredibly high levels of complexity and connectedness. They unite a significant part of the components of terrestrial phytocenoses into a consolidated geosymbiosis (Savinov 2015, 2017; etc.). As a result, two different groups of modular organisms play a role in the formation of the ecological frameworks of the phytocenoses; the cenosis-forming function of modular fungi is implemented. An important role can be played by lichenized fungi (lichens) – symbiotic associations that are similar to organisms in their level of integrity. Other components of the symbiotic systems that are formed by plants are equally important (Lu & Hedin 2019; Steidinger et al. 2019; etc.). The cenosis-forming function of the symbioses of marine modular animals is evident (Rossi et al. 2017; Brandl et al. 2019; etc.).

Evolution of modular organisms and Earth's biogeocenotic cover

Genesis of biomes and evolution of the biosphere. A complex hierarchy of evolutionary processes of different levels and directions was created as a result of the formation of Earth's biogeocenotic cover. Genesis of biomes was connected to the emergence of global biogeochemical cycles and to the evolution of the soil cover (Khokhryakov 1981; Bakhnov 2002; Zavarzin 2015; Drake & Ivarsson 2018; Zanella et al. 2018; Lu & Hedin 2019; McLaughlin et al. 2019; etc.). The formation of the diversity of modular organisms was of significant influence at various stages of biosphere evolution and its components (Khokhryakov 1981; McLaughlin et l. 2019; etc.). However, there are very few works, in which processes of evolutionary transformation of separate groups of modular plants and animals are matched with the genesis of certain biome types (Serebryakova 1971; Sánchez 2004; Gamalei 2015; Starko et al. 2019; etc.).

The role of modular plants and animals. Modular plants played an important role in the genesis of all types of terrestrial biomes (Meyen 1987; Eskov 2008; Niklas 2016; McElwain 2018; etc.). Let's consider some examples that may be interesting from the point of view of correlated evolution of various plant groups and biomes. Significant increase of structural and taxonomical diversity of Paleozoic vascular plants coincided with the emergence of carboniferous forests, which became the first type of tropical forest biomes. Growth processes and speed of transpiration of trees from carboniferous forests were comparable with similar traits of modern angiospermous tropical trees, even though they were different from the traits of modern vascular spore plants (Wilson et al. 2017). The analysis of fossilized trees' structure led to the identification of 8 architectural models that appear in modern trees (Hallé et al. 1978). The next stage of significant increase in plant diversity and complexity of structure of tropical forest biomes was connected with the emergence of flowering plants. 21 architectural models have been described in angiospermous trees. Architectural diversity grew as a result of sophistication of available forms by means of fixing reiteration processes in the developmental algorithm (Hallé et al. 1978). Modern tropical forests are multi-layered polydominant associations with a very complex vertical structure (Eskov 2008), in which a wide spectrum of various biomorphs is displayed.

Progressive evolution of flowering plants amidst global climate and hydrology changes ensured the emergence and differentiation of herbaceous biomes, which significantly transformed Earth's vegetative cover (Eskov 2008; Strömberg 2011). Biomorphological transformations of Tertiary herbaceous plants happened as a result of adaptation to hot and cold plains. Their physiological adaptation was connected with structural changes at the anatomical and morphological levels (Serebryakova 1971; Gamalei 2015; etc.). Gramineous plants played a special role in the formation of grass biomes. Their active distribution in open environments promoted the transformation of non-rosette shoots into rosette-forming ones, as well as the emergence cespitose life form. Cespitose plants turned out to be the most adapted to biocenoses of forestless areas with large grazing mammals (Serebryakova 1971; Zherikhin 2003; Strömberg 2011; etc.). Formation of grass biomes is a unique model for studying the complex connection of evolutionary processes at different levels of structural organization of living beings and components of the environment. Many stages of biosystems' transformation, which happened during global climate changes, are connected and mutually dependent. The formation of grass biomes was mediated by the mass tendency to form rosette-forming cespitose forms in gramineous plants. However, these biomorphological transformations appeared under the influence of the emerging coevolutionary connections between plants and grazing mammals.

Pertaining to other groups of modular plants and animals, there have been attempts to connect the taxonomical evolution of certain systematic groups and transformation processes of marine biomes (Rossi et al. 2017; Starko et al. 2019; etc.).

Coevolution of fungi and plants. The formation of the hyphal system was of great importance in fungi evolution (Karatygin 1993; Zmitrovich 2006, 2010; Ivarsson et al. 2020). The emergence of this type of structure ensured the shift toward modular organization, promoted the formation of structural diversity of fungi and the implementation of their integrative function in biocenoses (Karatygin 1993; Zmitrovich 2006, 2010; Notov 2011, 2017). Coevolution of fungi and plants began at the first stages of capture of terrestrial environments and had a certain impact on changing the general habitus and architectonics of vascular plants as well as on the structural evolution of fungi (Karatygin 1993; Zmitrovich 2010). Mycorrhizal symbiosis was already present in the Devonian period. As the biocenotic cover of land developed, this symbiosis became a factor of strengthening integrational connections in the process of biome formation (Savinov 2017). In modern phytocenoses, symbiotic connections with mycorrhizal fungi unite much of the autotrophic plants into a complex integrated system – geosymbiosis (Savinov 2015, 2017; etc.). Due to the emergence of geosymbiosis, the cenosis-forming and environment-forming functions of modular plants could be carried out (Savinov 2017; Lu & Hedin 2019; Steidinger et al. 2019; etc.).

The appearance of lichens, a symbiosis between fungi and algae, was of equal significance to the evolution of terrestrial biomes. This symbiosis significantly increased the structural diversity of lichenized fungi. Lichenization promoted the significant diversification of complex branching fruticose forms (Notov 2014; etc.). Fruticose lichens often became typical components of surface covers. Lichen and moss-and-lichen associations became the basis for the appearance of specific tundra biomes under extreme conditions.

Prospects of future research. The comments above do not only highlight the important role of various groups of modular living beings in the evolution of Earth's biogeocenotic cover. They also show the possibility of identifying key trends of structural and taxonomic evolution of modular organisms that have provided the formation of certain biomes. Examples of such trends are the appearance of rosette-forming shoots and cespitose forms among gramineous plants, realization of additional ways of increasing architectural diversity of arboreous flowering plants and the appearance of fruticose and orthotropic lichen forms. This analysis allows us to understand the mechanisms of biome evolution at different levels of structural organization, to establish their connections and mutual dependency as well as connections with global climate changes.

Further research in this regard should be based on the understanding of evolutionary specifics of modular organisms, their populations, life strategies in biogeocenosis and ways of interacting with its components. When analyzing paths and means of evolutionary transformation of biomes and biomorphological evolution, it is reasonable to pay special attention to changes that are connected to the ecological specifics of modular organisms. For example, revealing mechanisms of formation of polycentric biomorphs and wider spectra of ontogenesis polyvariance as well as the connections of these spectra with polyvariance of biocenosis (Zhukova & Notov 2018; Notov & Zhukova 2019; etc.). An ecological aspect of specific modes of structural evolution in modular organisms is of special interest. For example, the appearance of new types of polycentric biomorphs and the strengthening of polyvariance of development in populations can be considered one of the results of homeotic transformations of plants (Notov 2015; Zhmylev et al. 2019; etc.).

Research of biomorphological evolution should be done from the position that an organism's life form is one of the elements of biocenosis structure. Understanding plant's habitus as an important characteristic of a population goes as far back as classical studies of plant geography (Humboldt & Bonpland 1807). However, it still does not have a decent representation in biomorphologist's research. In this regard, the morphological-geometrical approach is of importance (Kirpotin 2005, 2007). The analysis of architectural models is a universal method for describing the structure of a modular organism (Hallé et al. 1978; Dauget 1991; Oldeman 1992; etc.). Its applicability to coral colonies has been strongly indicated (Dauget 1991).

The idea that the ecomorphological continuum is a habitat of phylema should be considered (Arefyev 2009, 2010; Zmitrovich 2017). Presently, our understandings of mycocenosis and mycocenology are being formed. They are aimed toward a fuller understanding of fungi roles in biocenoses (Storozhenko 2012). The symbiotic approach (the symbiotic paradigm) to biome analyzing should become the basis for studying ecosystems (Savinov 2015, 2017; etc.). It has a more full and in-depth conception of the system of connections and particulars of biocenosis organization (Savinov 2015, 2017; etc.). Geosymbiosis plays the main integrative function in terrestrial ecosystems. A detailed analysis of its structure is an important task for future research.

Conclusion

Fundamental specifics of modular organization precondition the specificity of living organisms with open growth from the position of all main branches of ecology. Modular organisms have different levels of similarity to populations, and the boundary between the organismal and supraorganismal levels is not always clear-cut. Modular organisms in biocenoses have an important environment-forming and cenosis-forming function. They played an important role in the genesis of many types of terrestrial and marine biomes as well as in the formation of geochemical cycles.

A conjugate analysis of the evolution of various groups of modular organisms and biomes will allow researchers to consider the processes of biodiversity at a qualitatively different level. It will promote a deeper understanding of the fundamental role of modular living beings in ecosystems of different levels, including the biosphere.

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