Original Russian Text © 2019 O. I. Evstigneev, V. N. Korotkov published in Forest Science Issues Vol. 2, No. 4, pp. 1–36.

DOI 10.31509/2658-607x-202254-118

PROFESSOR OLGA V. SMIRNOVA'S SYSTEM OF VIEWS IN FOREST ECOSYSTEM ECOLOGY

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Received: 16.19.2019
Revised: 07.10.2019
Accepted: 07.10.2019

Professor Olga V. Smirnova, Doctor of Biological Sciences, is a prominent scientist in the field of plant demography, population biology, and forest ecosystem ecology. Professor Olga V. Smirnova's edifice is based on ideas about the leading role of plant and animal populations in the organization of the biogeocenotic cover. In this case, it is implied that a continuous generational turnover in edificator (keystone species) populations is necessary to maintain the species and structural diversity in communities and ensure their sustainability. This system of views was influenced by Professor Alexey A. Uranov. The development of these ideas was consistent and gradual. First, Professor Olga V. Smirnova studied the biology of different plant species life forms. Examining their individual development, with identification of ontogenetic stages, is necessary for demographic research. She then developed the theory of coenopopulations as supraorganismal systems, which can self-sustain under different conditions. Finally, she developed the doctrine of biogeocenosis as a system of interacting populations and created the concept of anthropogenic transformation of the forest cover in the Holocene. Her contributions helped researchers to understand the mechanisms of the formation of modern zonality that are due to human activity.

Keywords: *plant biological age, plant population strategy, coenopopulation, edificator, forest ecosystem ecology, modern zonality, historical ecology*

October 9, 2019 marks the anniversary of Professor Olga Vsevolodovna Smirnova, Doctor of Biological Sciences, a prominent scientist in the field of plant demography, population biology and forest ecosystem ecology (Fig. 1).

Professor Olga V. Smirnova was born to the family of intellectual workers in 1939. Her mother, Nina Nikolaevna, was a French to Russian translator, and her father, Vsevolod Mikhailovich, was an engineer. Her maternal grandfather, Nikolai A. Zhukov, graduated

Figure 3. Olga V. Smirnova. **Top left**: An expedition in Sabar, August 1979, the Middle Urals, Artinsky District, Sverdlovsk Oblast. Photo by O. G. Barinov. **Top right:** Before the trip to Sabar in 1991. Photo by M. A. Barinova. **Bottom left:** Defense of Natalia E. Bogdanova's Candidate's thesis at the Moscow State Pedagogical University, November 20, 2006. **Bottom right:** Defense of Ekaterina L. Zheleznaya's Candidate's thesis at Moscow State Pedagogical University, March 2, 2009. Photo by O. M. Zhelezny

from the Moscow Higher Vocational School of Commerce (now Financial Academy) and worked as an economist with the People's Commissariat for Foreign Affairs. Her paternal grandfather, Mikhail I. Smirnov, graduated from the Moscow Archaeological Institute in Nizhny Novgorod. He was an outstanding professional who specialized in local history and founded the Pereslavl-Zalessky Historical, Architectural and Art Museum-Reserve in 1919. Olga V. Smirnova spent her childhood in Gagarinsky Lane in the very heart of Moscow (Zhukova, 2006).

She showed interest in biology in her high school years, attending a young naturalists hobby group at the All-Russian Society for the Protection of Nature (VOOP) headed by a renowned biologist Pyotr P. Smolin. In 1963, Olga V. Smirnova graduated from the Chair in Geobotany at M. V. Lomonosov Moscow State University. In 1968, she defended her Candidate of Sciences thesis under supervision of Professor Alexey A. Uranov that was devoted to the topic "Life cycles, number and age composition of populations of the main components of oak grass cover". In 1983, she defended her Doctor of Sciences thesis devoted to the topic "Behavior of species and functional organization of grass cover of deciduous forests (a case study of plain broad-leaved forests in the European part of the USSR and linden forests of Siberia)". From 1966 to 1992, Olga V. Smirnova had been employed with the Problem-Centered Biology Laboratory (PBL) at the V. I. Lenin Moscow State Pedagogical Institute (MGPI) (Fig. 2, 3). In 1987, she published the book *Grass Cover Structure of Broad-Leaved Forests* that resulted from her Candidate's thesis and Doctor's thesis. Since September 1, 1992, Professor Olga V. Smirnova has been employed as Principal Researcher at the Center of Forest Ecology and Productivity of the Russian Academy of Sciences (CEPF RAS). From 1993 to 2008, she taught at Pushchino State University (PuschGENI) at the Department of System Ecology, founded and headed by Professor Alexander S. Komarov (Fig. 4, 5). In 1994, a collective monograph *Eastern European Broadleaf Forests*, and in 2004, a two-volume book *Eastern European Forests: History in Holocene and Contemporaneity* were published under her editorship. In 2017, Springer published a revised version of this book, *European Russian Forests: Their Current State and Features of Their History* as requested by the *Plant and Vegetation* editorial board. The fundamentals of Professor Olga V. Smirnova's research, starting with the young naturalists hobby group and to the present day, are her expeditionary studies she conducts every year (Fig. 6–8).

In 2015, Professor Olga V. Smirnova founded an international research journal, *Russian Journal of Ecosystem Ecology*. The journal covers the functioning and dynamics of ecosystems, the organization of biogeocenotic cover, and other issues of ecology. Professor Olga V. Smirnova supervised 25 successfully defended Candidate's theses (Sugorkina, 1989; Evstigneev, 1990; Argunova, 1993; Istomina, 1993; Korotkov, 1993; Nedoseko, 1993; Chumachenko, 1993; Kiseleva, 1994; Shanijazova, 1994; Barinova, 1997;

Ripa, 1997; Samohina, 1997; Sarycheva, 2000; Bobrovskaja, 2001; Braslavskaja, 2001; Turubanova, 2002; Bobrovskij, 2004; Shestakova, 2005; Bogdanova, 2006; Romanovskij, 2006; Lugovaja, 2008; Popov, 2008; Aleinikov, 2010; Zaprudina, 2012; Kharitonenkov, 2012); five of her students were awarded the degree of Doctors of Sciences (Chumachenko, 2006; Argunova, 2010; Evstigneev, 2010; Bobrovskij, 2013; Nedoseko, 2018). On December 2, 1994, she was awarded the title of Full Professor in Botany. To date, Professor Olga V. Smirnova has published over 300 works. All her publications, including an extensive reference list, are available online at http://istina.msu.ru/profile/sov1933/.

Professor Olga V. Smirnova's views in forest biogeocenology / forest ecosystem ecology are based on ideas about interacting populations of living beings, which were shaped under the influence of her mentor, Professor Alexey A. Uranov (Shorina et al., 2014). Within the framework of said system of views, Professor Olga V. Smirnova made a significant contribution to enhancing the concepts of plant biological age and plant population strategy by developing the doctrine of coenopopopulations and biogeocenosis as a system of interacting populations, as well as to ideas about modern zonality as an anthropogenic phenomenon.

THE CONCEPT OF PLANT BIOLOGICAL AGE

Classifying plant populations into ontogenetic (age) groups constitutes the basis of population demographics studies. The works of Tikhon A. Rabotnov (1950) and his followers, including Professor Olga V. Smirnova, substantiated and developed an approach to age differentiation in individual plants based on studying the ontogeny of living organisms from birth to death. The method provides for the allocation of stages in individual plant development, or ontogenetic states that reflect the biological age of an individual plant. Professor Olga V. Smirnova studied the ontogeny of over 30 plant species growing in Eastern European forests and linden trees of Western Siberia (Table 1). She presented early descriptions of the ontogeny in three collective monographs edited by Professor Alexey A. Uranov, *Ontogenesis and Age Composition of Flowering Plant Populations* (1967), *Morphogenesis of Flowering Plants and The Structure of Their Populations* (1968) and *Age Composition of Flowering Plant Populations Due to Their Ontogenesis* (1974).

These works show that defining the ontogenetic (age) state is incomparably more important for demographic research than the analysis of numerical age. This is due to two reasons: 1) different individual plants of the same species often reach the same ontogenetic state in different numerical terms; yet, since they are at the same development stage, they play the same part in the population and in the community; 2) the time individual plants of different species and life forms take to go through the same ontogenetic states may vary. All this means that it may be more logical to associate comparative assessment of significance of plants in coenosis with not numerical age but development stage, that is, the ontogenetic state.

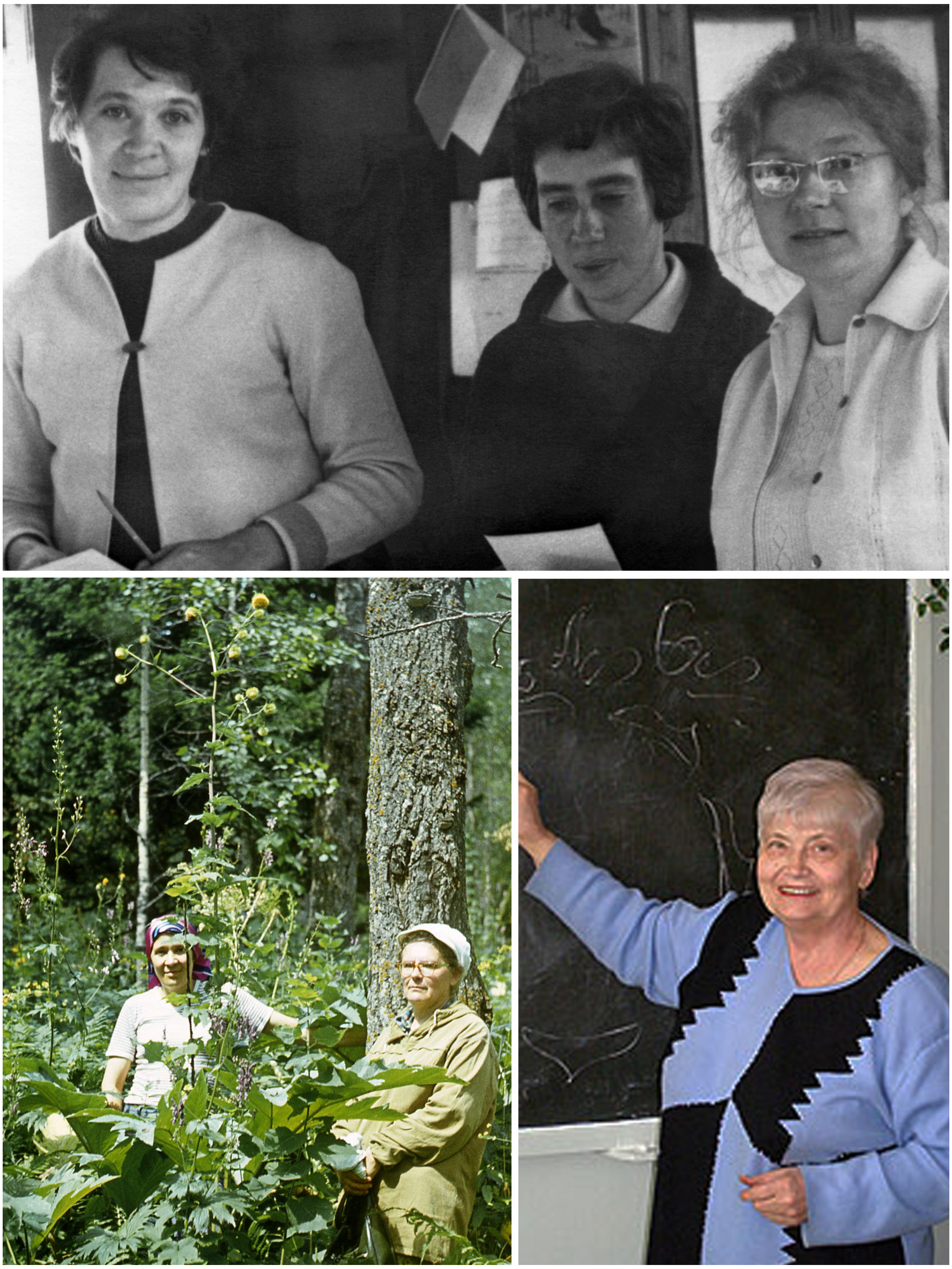

Figure 2. Professor Olga V. Smirnova's colleagues (start). **Top:** Olga V. Smirnova with Alexey A. Uranov's students — Inna M. Ermakova (Researcher at the Problem-Centered Biology Laboratory, Moscow State Pedagogical Institute) and Nina M. Grigorieva (Professor of the Chair in Botany of the Moscow State Pedagogical Institute, right), 1974. **Bottom left:** Among the tall forest herbs with Tatiana I. Serebryakova (Head of Chair in Botany at the Moscow State Pedagogical Institute from 1974 to 1986) during a trip to Salair (Guryevsky District, Kemerovo Oblast), 1982. Photo by M. A. Barinova. **Bottom right:** Aleksandra A. Chistyakova (Candidate of Biological Sciences, Full Professor at the Chair in Botany, Physiology and Plant Biochemistry, Penza State University), a co-author of Olga V. Smirnova's principal works devoted to the interacting populations in forest communities

Figure 3. Professor Olga V. Smirnova's colleagues (cont'd). **Top:** With Roman V. Popadjuk (Researcher at the Problem-Centered Biology Laboratory, Moscow State Pedagogical Institute) during an expedition to Prioksko-Terrasny Nature Reserve in 1990. Photo by M. A. Barinova. **Bottom left:** Natalia A. Toropova (Candidate of Biological Sciences, Associate Professor at the Chair in Botany, Tambov State Pedagogical Institute) in the Kanevsky Nature Reserve (Cherkasy Oblast, Ukraine), 1983. **Bottom right:** Professor Olga V. Smirnova's colleagues discussing research plans in the Laboratory of Ecosystem Modeling, Institute of Physicochemical and Biological Problems of Soil Science, RAS (Pushchino). Left: Lyudmila B. Zaugol'nova (Doctor of Biological Sciences, Principal Researcher at the Center of Forest Ecology and Productivity, RAS, Moscow), right: Larisa G. Khanina (Candidate of Biological Sciences, Associate Professor, Head of Laboratory of Computational Ecology, Institute of Mathematical Problems of Biology, RAS, Pushchino), 1999

Table 1. Ontogeny of plants studied by Professor Olga V. Smirnova

Life forms	**Plants**
Long rhizome herbs	*Aegopodium podagraria* L., *Carex pilosa* Scop., *Mercurialis perennis* L.
Short rhizome herbs	*Anemone altaica* Fisch. Ex C. A. Mey., *A. coerulea* D. C., *A. nemorosa* L., *A. ranunculoides* L., *Asarum europaeum* L., *Carex sylvatica* Huds., *Dentaria bulbifera* L., *D. quinguefolia* Bleb., *Lamium maculatum* (L.) L., *Pulmonaria obscura* Dumort., *Lathyrus vernus* (L.) Bernh., *Viola mirabilis* L.
Bulb-rhizome herbs	*Allium victorialis* L., *Erythronium sibiricum* (Fisch et Mey) Kryl.
Bulbiferous herbs	*Allium ursinum* L., *Gagea erubescens* (Bess.) Schult. & Schult. Fil., *G. granulosa* Turcz., *G. lutea* (L.) Ker-Gawl., *G. minima* (L.) Ker-Gawl., *Scilla bifolia* L., *S. sibirica* Haw, *Tulipa biebersteiniana* Schult. & Schult. Fil.
Tuberous herbs	*Corydalis bracteata* (Steph.) Pers., *C. solida* (L.) Clairv., *C. cava* (L.) Schweigg. & Koerte, *C. marschalliana* (Pall. Ex Willd.) Pers.
Litter-ground-creeping herbs	*Galeobdolon luteum* Huds., *Galium odoratum* (L.) Scop., *Stellaria holostea* L., *Viola odorata* L.
Herbs with racemose root system	*Ficaria verna* Huds.
Taproot herbs	*Alliaria petiolata* (Bieb.) Cavara & Grande
Trees	*Fagus sylvatica* L.

Note. Some of the ontogenies were researched in co-authorship; see the webpage at http://istina.msu.ru/profile/sov1933/

THE CONCEPT OF PLANT POPULATION STRATEGY

Based on the system of ideas about plant coenotypes proposed by Leonty G. Ramensky (1935) and the concept of plant strategies developed by J. Grime (1979), Professor Olga V. Smirnova substantiated a new approach to studying plant population strategies (population behavior) (Smirnova, 1980, 1987; Smirnova, Chistyakova, 1980). The essential provisions of this approach are as follows.

1. The following properties are considered as integral, phytocoenotically significant plant population strategies: competitive, phytocoenotically tolerant, and reactive. *Competitive strategy* (violent, competitive power) means the ability of species to create and control the environment in a community, as well as suppress other living organisms due to the great vitality and highly intensive environment use. *Phytocoenotically tolerant strategy* (patient, resistance, endurance in an extremely unfavorable phytocoenotic environment) means the ability of species to survive for a long time in the area occupied by other living organisms, due to the maximum lowered vitality. *Reactive strategy* (explerent, dynamism, pioneering, ruderality) means the tendency of a species to the fastest possible development of released resources in the community due to vigorous vegetative growth and significant reproductive effort.

Figure 4. Field trips. **Top left:** Summer field trip with 2nd-year undergraduate students of the Moscow State Pedagogical Institute in 1977 with Olga V. Smirnova (Candidate of Sciences, left) and Marina P. Solovyova (Associate Professor, Candidate of Sciences, second right) in Tellermanovskoe Forestry (Voronezh Oblast). **Top right:** Winter field trip with Master's students of the Pushchino State University in Central Forest Nature Reserve, 1994: Konstantin V. Belyakov (Master's student, left), Olga V. Smirnova, Mikhail S. Romanov (Master's student, right). Photo by M. A. Barinova. **Bottom left:** Fall field trip with 1st-year Master's students of the Pushchino State University in Kaluzhskiye Zaseki Nature Reserve, 1996. **Left to right:** Vladimir N. Korotkov (Candidate of Sciences, Senior Researcher at the All-Russian Research Center for Forest Resources), Oksana Sinotova (Master's student), Marina Mishchenko (Master''s student), Larisa Tarasova (Master's student), Maxim V. Bobrovskij (Senior Lecturer). Sitting, left to right: Aleksandr Kuritsyn (Master's student), Vladimir Timofeev (Master's student), Aleksandra Agafonova (postgraduate student), Olga V. Smirnova, Alexey Egorov (Master's student). **Bottom right:** Fall field trip with 1st-year Master's students of the Pushchino State University in Russky Sever National Park, 2005. Left to right: Alexey Aleinikov, Maxim Kharitonenkov, Olga V. Smirnova, Ekaterina Kobozeva, Vladimir Shanin, Alexey Gornov. Photo by M. V. Bobrovskij

According to said definitions, a plant population strategy means the ability of species to dominate or occupy a subordinate position in a community, which resulted from a long evolution in preagricultural climax coenoses undisturbed by humans. The described population strategies reflect the phytocoenotic potencies of a species. The real-life ranking of a species in a particular coenosis makes up its phytocoenotic position. Phytocoenotic potencies and phytocoenotic positions may be expected to overlap completely in climax communities in the preagricultural age. Real-life position of a species in modern communities differ significantly from its role in climax coenoses, since the communities structure has been fundamentally transformed by humans.

2. Integral properties (competitive, phytocoenotically tolerant, reactive) are inherent in every species but expressed to various degrees. Species that are predominantly competitive are violent, species that are predominantly tolerant are patient, and species that are predominantly ruderal are explerent. Aside from groups of species characterized by these three strategy types (behavior), following J. Grime (1979), Professor Olga V. Smirnova identified the groups of species that occupy an intermediate position.

3. Investigation of a plant strategy is based on investigation of biological properties of a species. This assumes a differentiated approach to studying biological (behavior) and ecosystem properties of a species. Knowing the ecosystem properties, one could reveal the requirements of a species to environment resources, whereas studying biological properties could help to define the method and nature of how to use said resources. In other words, plant ecosystem properties determine the species composition in a community, whereas biological properties determine the predominant or subordinate role of the species in the community. This approach to identifying types of plant behavior differs significantly from the methods of studying the coenotypes proposed by Leonty G. Ramensky (1935) and plant strategies developed by J. Grime (1979). Thus, Ramensky's patient plants (or Grime's stress-tolerant plants) are allocated based on ecosystem properties of species, while violent (competitive) plants and explerent (reactive) plants are allocated based on biological properties.

4. The history of studying phytocoenotic potencies in plants shows that it is not possible to single out any standalone, independent feature that would determine the type of plant behavior in its entirety. At the same time, each type of plant behavior is characterized by a set of particular (differential) properties, which are specific manifestations of competitive, tolerant and reactive strategy.

5. It may be advisable to analyze the types of behavior in plants of relative life forms occupying the same space-time niche and belonging to the same trophic level, i. e. the same synusia (Smirnova, 1987). This is determined by the fact that the types of a single synusia are characterized by similar impact on the environment and play a similar role in the community. Moreover, the biological originality of a given species is most fully manifested if we investigate the entire historically formed set of species at the same time. In temperate forests, synusias

of trees, shrubs, summer broadleaf herbs, and early spring ephemeroids are usually considered as such (Eastern European ..., 1994).

Based on these provisions and a detailed study of the biological plant properties, Professor Olga V. Smirnova developed a classification of plant species by strategy (behavior) type in the synusias of spring ephemeroids and summer broadleaf herbs (Smirnova, 1987). This approach was successfully implemented when studying the types of strategy of trees and shrubs in Eastern European forests (Smirnova, Chistyakova, 1980; Evstigneev, 2004, 2010; Evstigneev, Didenko, 2004). Below is an example of a plant classification by type of behavior in the synusia of summer broadleaf herbs (Smirnova, 1987).

Type I. Competitive species (violent).

Group 1 — vegetatively mobile: *Aegopodium podagraria* L., *Convallaria majalis* L., *Carex pilosa* Scop., *Mercurialis perennis* L.

Type II. Tolerant species (patient).

Group 1 — vegetatively slightly mobile: *Asarum europaeum* L., *Carex digitata* L., *C. rhizina* Blytt ex Lindbl., *Paris quadrifolia* L., *Polygonatum multiflorum* (L.) All., *Pulmonaria obscura* Dumort., *Viola mirabilis* L.

Group 2 — vegetatively immobile: *Brachypodium sylvaticum* (Huds.) Beauv., *Bromopsis benekenii* (Lange) Holub, *Carex sylvatica* Huds., *Campanula latifolia* L., *C. rapunculoides L.*, *C. trachelium* L., *Dactylis glomerata* L., *Festuca gigantea* (L.) Vill., *F. sylvatica* L., *Geum urbanum* L., *Melica nutans* L., *Lathyrus vernus* (L.) Bernh., *Poa nemoralis* L., *Ranunculus cassubicus* L., *Scrophularia nodosa* L., *Scutellaria altissima* L.

Type III. Reactive species (explerent).

Subtype 1: competitive reactive species. Group 1 — vegetatively mobile: *Ajuga genevensis* L., *A. reptans* L., *Galeobdolon luteum* Huds., *Milium effusum* L., *Viola odorata* L. Group 2 — vegetatively immobile: *Lamium maculatum* (L.) L.

Subtype 2: Actually reactive. Group 1. Vegetatively mobile: *Galium odoratum* (L.) Scop., *Glechoma hederacea* L., *Stachys sylvatica* L., *Stellaria holostea* L., *Urtica dioica* L. Group 2: vegetatively immobile: *Alliaria petiolata* (Bieb.) Cavara & Grande, *Chaerophyllum temulum* L., *Geranium robertianum* L., *Torilis japonica* (Houtt.) DC.

Professor Olga V. Smirnova showed that defining phytocoenotic potencies in plants makes it possible to understand some features in the organization of climax coenoses which differed in maximum species diversity (Smirnova, Chistyakova, 1980; Smirnova, 1983, 1987). Competitive plant species constituted a stable basis for every synusia, for they were predominant in number and biomass, involved the largest portion of matter and energy in the community, significantly changed the coenotic environment, and executed the function of edificators. Tolerant plant species, having an extremely low vitality level, used resources that could not be occupied by competitively powerful plants. Reactive plant species “roamed around” from one disturbance to another and “patched the holes” that occasionally occurred in the community in areas where individuals died in populations of edificators. Species with different strategy (behavior) types act as complementary formations, thanks to which the community resources are used most efficiently.

THE THEORY OF COENOPOPULATIONS

The team at the Problem-Centered Biology Laboratory at the Moscow State Pedagogical Institute where Professor Olga V. Smirnova was employed at the time, published four outstanding books on plant demography, *Plant Coenopopulations (Basic Concepts and Structure*) (1976), *Plant Coenopopulations* (*Development and Relationships*) (1977), *Dynamics of Plant Coenopopulations* (1985), and *Plant Coenopopulations* (*Essays on Population Biology*) (1988). The books are based on ideas of plant biological age. These monographs present the concept apparatus and propose a system of methods in plant population biology. Having summarized her long-term studies at the Problem-Centered Biology Laboratory and Chair in Botany at the Moscow State Pedagogical Institute, Professor Olga V. Smirnova, in collaboration with Lyudmila B. Zaugol'nova, developed the ideas of characteristic ontogenetic spectrum (COS) and elementary demographic unit (EDU).

COS is a full-membered ontogenetic spectrum with a certain ratio of ontogenetic group number, which allows for a continuous generational turnover. This spectrum is due to the plant biological properties: 1) total duration of ontogeny and individual age states; 2) rate of development in individuals having various ontogenetic states; 3) methods of population self-sustainment; 4) intensity and frequency of inspermation and elimination; 5) ability to create a soil reserve of seeds or other vegetative rudiments; 6) area of resource consumption by individuals at different stages of ontogeny (Zaugol'nova, 1994; Zaugol'nova, Smirnova, 1978; Smirnova, 1987; Zaugol'nova et al., 1992; Eastern European ..., 1994, 2004). At first, in the framework of studies conducted by said researchers, COS was considered synonymous with "basic ontogenetic spectrum". However, the authors later limited the concept of the basic ontogenetic spectrum with the modal one, obtained by averaging data on several coenopopulations belonging to one community variant (Smirnova et al., 1993; Zaugol'nova, 1994).

COS reflects the dynamically stable (definitive) coenopopulation state to which it returns from deviations caused by external influences. The real ontogenetic spectrum is most consistent with the COS in undisturbed (climax) communities. In human-transformed coenoses, the ontogenetic spectrum of a population generally deviates from COS to varying degrees (Coenopopopulations..., 1976; Smirnova et al., 1987, 1989, 1990, 1991, 1992; Eastern European ..., 1994).

Professor Olga V. Smirnova showed that plants have three types of characteristic ontogenetic spectra (Smirnova, 1987; Eastern European ..., 1994). *The first type is left-sided spectrum*, with the maximum falling on pregenerative individuals. It is found in trees, monocarpic and oligocarpic tap-root herbs, bulbous, tuber-bulbous, and tuberous geophytes. These plants actively propagate by seed and/or deep rejuvenated vegetative rudiments. *The second type is a centered spectrum*: the largest number of individuals are located on middle-aged generative plants. It is characteristic of tap-rooted, long- and short-rhizomed herbs, sod grasses, and semi-shrubs. They have a weakly expressed aging period, propagate by seed or have a mixed propagation type, their vegetative reproduction is not accompanied by deep rejuvenation. *The third type is a bimodal spectrum* with two maxima: one in young individuals, and the other in mature or old generative individuals. This type is described in dense and loose sod grasses, tap-rooted and short-rhizomed herbs, in semi-shrubs. These plants have a significant life expectancy with a well-defined period of aging, their active propagation by seed is combined with vegetative reproduction with no deep rejuvenation.

EDU is a population unit, which is a set of individuals of different ages of the same species, necessary and sufficient to ensure sustainable generational turnover in the minimum allowable area. Important EDU characteristics include: 1) minimum number of individuals which allows for a continuous generational turnover; 2) minimum space necessary for a steady flow of generations; 3) lifetime of one generation (Smirnova et al., 1989; Zaugol'nova et al., 1993). EDU of different types are arranged in continuous series by values of each of the listed features (Table 2).

Table 2. Some parameters of elementary demographic units (EDU) in plants growing in broad-leaved forests (Smirnova et al., 1992)

Type	Lifetime of a single generation, years	Minimum space, sq. m
Quercus robur L.	350	4.20×10^5
Fraxinus excelsior L.	250	1.30×10^5
Tilia cordata Mill.	180	2.70×10^4
Acer platanoides L.	180	1.80×10^4
Carpinus betulus L.	120	1.20×10^4
Corylus avellana L.	80	2.50×10^3
Lathyrus vernus (L.) Bernh.	20	1.00×10^0
Corydalis solida (L.) Clairv.	10	0.25×10^0
Geranium robertianum L.	1	1.00×10^0

Figure 5. Chair in System Ecology at the Training Center for Mathematical Biology of the Pushchino State University. **Top:** After Master's thesis defense, July 1998. Sitting, left to right: Vitaly E. Reif (Master), Elena P. Sarycheva (postgraduate student), Andrey M. Tsyplyanovsky (postgraduate student), Sergey S. Bykhovets (Senior Lecturer). Standing (first row, left to right): Oksana A. Sinotova (Master), Galina E. Rubashko (Master), Elena S. Esipova (Master), Elena G. Didenko (Master), Irina F. Medvedeva (Head of Education Department), Valentina S. (Laboratory Assistant), Svetlana A. Turubanova (Master), Larisa G. Khanina (Candidate of Sciences, Associate Professor). Standing (second row, left to right): Vadim N. Pavlov (Doctor of Biology, Professor, Chairman of the State Examination Board), Maria M. Palenova (Candidate of Biological Sciences, Associate Professor), Alexander S. Komarov (Candidate of Biological Sciences, Associate Professor, Head of Chair), Olga V. Smirnova (Doctor of Biology, Full Professor), Anna V. Manukyants (Master), Vladimir V. Timofeev (Master), Maxim V. Bobrovskij (Senior Lecturer). **Bottom left:** Professor Olga V. Smirnova's speech at the defense of Master's theses on June 18, 2007. **Bottom right:** Olga V. Smirnova and Natalia A. Leonova (Candidate of Biological Sciences, Associate Professor at the Chair in Botany, Physiology and Plant Biochemistry of the Penza State University) after a research seminar on October 11, 1996 at the Chair in System Ecology

Figure 6. Expeditions (start). **Left:** Olga V. Smirnova in the test area next to a wych elm, 1979. Sabar, Middle Urals, Artinsky District, Sverdlovsk Oblast. Photo by O. G. Barinov. **Top:** Before the trip to Sabar in 1991. Left to right: Svetlana I. Ripa (postgraduate student, Chair in Botany of the Moscow State Pedagogical Institute), Tatyana O. Yanitskaya (employee at the Chair in Higher Plants of the Moscow State University), Oleg G. Barinov (postgraduate student in Chemistry of the Moscow State Pedagogical Institute), Vladimir N. Korotkov (Researcher at the Laboratory of Nature Conservation Research Institute), Olga V. Smirnova (Doctor of Biological Sciences, Senior Researcher at the Moscow State Pedagogical Institute). Photo by M. A. Barinova. **Bottom:** Olga V. Smirnova on an all-terrain vehicle in Gorno-Khadytinsky Nature Reserve (Yamalo-Nenets Autonomous Okrug), 1999. Photo by M. V. Bobrovskij

Figure 7. Expeditions (cont'd 1). **Top left:** Olga V. Smirnova in Voronezh Nature Reserve, 1974, studying the structure of the grass cover in broad-leaved forests. **Top right:** Olga V. Smirnova next to a Korean pine in Ussurisky Nature Reserve (Far East), 2008. Photo by V. N. Korotkov. **Bottom:** Exploring the river bottom of the Podkamennaya Tunguska, July 2006. Evenkiysky District, Krasnoyarsk Krai, central area of Central Siberian Plateau. Olga V. Smirnova and Maxim V. Bobrovskij (Candidate of Biological Sciences, Associate Professor at the Chair in System Ecology, Pushchino State University)

Figure 8. Expeditions (cont'd 2). **Left:** Olga V. Smirnova next to a rowan tree in Visimsky State Nature Biosphere Reserve, May 2019. Photo by A. P. Geraskina. **Top:** In the Pechora-Ilych Nature Reserve, August 2003. Left to right: Olga V. Smirnova, Elena Chernenkova, Sergey Pautov (Omsk State Technical University employee), Maxim Bobrovskij (Senior Lecturer at the Pushchino State University). Photo by V. N. Korotkov. **Bottom:** In the protected area of the Visimsky Nature Reserve during the study of a unique coniferous/broad-leaved forest populated with small-leaved linden and wych elm, May 2019. Left to right: Anna P. Geraskina (Candidate of Biological Sciences, Zoologist at the Center of Forest Ecology and Productivity, RAS), Rustam Z. Sibgatullin (Geobotanist at the nature reserve), Natalia V. Belyaeva (Phenologist at the nature reserve), Denis S. Shilov (Florist at the nature reserve), Olga V. Smirnova. Photo by V. N. Korotkov

The idea of EDU allowed Professor Olga V. Smirnova to propose a deeper definition of an important concept in forest ecology, namely the edificator (Smirnova, 1998; Smirnova, Toropova, 2008). This category includes species with the largest EDU and population mosaics existing for a long time. They include the largest portion of matter and energy in the cycles of generational turnover. Edificators belong to powerful environment converters. Populations of edificators with spontaneous development may transform a habitat to the greatest extent: they can change the hydrology, temperature, and lighting regime of a community, create micro- and mesorelief, and transform the soil cover. The intrinsic heterogeneity of the edificator EDU habitat allows for the coexistence of ecologically and biologically diverse species with smaller EDUs, and also maintains a high biodiversity level. The concept of edificator is synonymous with those of keystone species and ecosystem engineer. In the forest zone, edificators include species of various trophic groups and systematic positions: for example, large trees, needle- and leaf-eating in- sects, and tree-destroying fungi; river beavers join them in floodplain communities.

THE CONCEPT OF BIOGEOCENOSIS AS A SYSTEM OF INTERACTING POPULATIONS

Professor Olga V. Smirnova has been actively developing an idea of the structure and dynamics of undisturbed (climax) forest biogeocoenoses that existed in the preagricultural age with no human intervention (East European ..., 1994, 2004; Smirnova et al., 1988, 1989, 1990; Smirnova, 1998, 2000; Smirnova, Toropova, 2008). This understanding is based on a population view of the community and biogeocenotic cover. According to the concept of biogeocenosis as a system of interacting populations, the forest cover should be considered a hierarchy of population units in species of different trophic groups. The population life of edificators unites this multiscale mosaic into communities. Population mosaics of keystone species create an environment suitable for sustainable life of populations of many subordinate species and determine the maximum species diversity in communities.

Phytogenic mosaicism in undisturbed forests results from the population life of edificator trees. In forests, the population life of trees creates a mosaic of lighting, water and soil regimes. This mosaic results from gaps in tree canopy that occur due to aging and death of one or several trees growing nearby. The death of a tree and associated soil perturbation determine the development of wind-soil complexes. At the same time, it builds a specific dumping microrelief, including hills, depressions, and coarse woody debris (Bobrovskij, 2004, 2013). Heterogeneous gap-like environment and wind-soil complexes, created as a result of generation flows in edificator tree populations, determines the presence of the maximum possible set of subordinate species of plants, animals, fungi, and representatives of other kingdoms in undisturbed forests. Having studied said mosaicism, Professor Olga V. Smirnova and her students created a new system of understanding forest ecology, the gap paradigm (Korotkov, 1991, 1993; Smirnova, 1998; Assessment ..., 2000).

Professor Olga V. Smirnova convincingly shows that mosaicism caused by vitality of animal phytophages is as characteristic a feature of forest landscapes as phytogenic one (Smirnova et al., 1993; Eastern European …, 1994, 2004). Zoogenic mosaicism in preagricultural forests resulted from population life of animal edificators. In undisturbed European forests, these animals included: 1) large herd ungulates (bison, auroch, tarpan, etc.); 2) leaf- and needle-eating insects; 3) beavers. Large herd ungulates that destroyed young trees, shrubs, and grasses, as well as compacted and cherished the soil, created zoogenic glades with meadow, forest margin, and meadow-steppe flora. By destroying leaves and needles, insects increase the illumination on the grass cover surface and the temperature of the air and soil, enrich the soil with nitrogen and other minerals, and also contribute to an increase in number of light-loving and nitrophilic types of herbs. Beavers, by building dams on streams and small rivers, create ponds and lowland swamps, increase species diversity and the number of related plant and animal species. By destroying trees and shrubs in the coastal strip, beavers form glades with light-loving flora and fauna.

Professor Olga V. Smirnova shows that strong anthropogenic impact, destroying the population mosaic, breaks the cycles of generational turnover in keystone species. As a result, the development of communities becomes unidirectional, or succession, before the natural mosaic is restored. Understanding biogeocenosis as a system of interacting populations and a quantitative assessment of population parameters of principal coenosis builders make it possible to reconstruct the potential structure of biogeocenotic cover in an area, quantify the degree of disturbance in communities and their complexes, as well as to streamline existing succession systems.

THE CONCEPT OF ANTHROPOGENIC TRANSFORMATION OF THE FOREST COVER IN THE HOLOCENE

Despite the large number of works devoted to anthropogenic transformation of the forest cover in the Holocene, the paradigm of climate migration still prevails in domestic science. Summarizing historical and paleontological data, Professor Olga V. Smirnova proposed a new, “anthropic” system of views that defines human impact as the essential factor in biogeocoenotic cover transformation in the Holocene (Smirnova, Bobrovskij, 2000; Smirnova et al., 2001a, 2001b, 2006, 2013; Turubanova, 2002; Smirnova, Turubanova, 2003; Haritonenkov, 2012; Smirnova, Toropova, 2016; Kalyakin et al., 2016; Smirnova, Toropova, 2016; Smirnova et al., 2018). This new paradigm can be described as follows.

Written sources indicate that, over the recent 1–2 millennia, the diversity of life on Earth has been rapidly decreasing due to anthropogenic transformation. However, paleontological studies show that significant transformations on the Russian Plain and throughout Northern Eurasia date back much earlier. The first man-made environmental crisis in said area occurred 22–18 thousand years ago. It was caused by extermination of crucial edificators of late Pleistocene — that is, mammoths, woolly rhinoceros, giant deer, and other animals. They used to edify the composition and structure of plants and animals at that time. Herbs, primarily grasses, growing on meadow-steppe glades and forest margins were their primary source of nutrition. Meadow-steppe communities alternated with small clusters of trees. At the same time, palynology studies show that coniferous and broad-leaved tree species used to inhabit the entire Russian Plain in the Pleistocene. The soils of cryogenic savannah with a layer of permafrost underneath are chemically similar to modern chernozem soils. Their productivity throughout Northern Eurasia was so great that it allowed for sustainable existence of huge herds of giant phytophages and their retinue. Paleozoologists call this feature "the paradox of prehistoric pastures". It was in cryogenic savannahs of the late Pleistocene (Upper or Final Paleolithic) that the sites of mammoth hunters with highly-developed farming and culture were found.

Over the recent 10.000–7.000 years, there has been a general climate warming, which coincided with gradual destruction of keystone species of giant and large animals of the mammoth complex as a result of hunting. The degradation of the mammoth complex, which began in the late Pleistocene, led to woody plants strengthening their role. The pastures the mammoths and their companions used to graze were then inhabited by trees. The first trees appeared by volatile seeds and a rapid generational turnover: that were birch, willow, aspen, and pine trees. They were followed by dark coniferous (spruce, fir) and broad-leaved (oak, linden, maple, ash, beech, hornbeam, etc.) trees. The near extinction of the giants and largest phytophages in the mammoth complex, combined with warming, marked the beginning of development of a forest belt in the early Holocene at the site of former Pleistocene cryogenic savannahs.

At the beginning of the Middle Holocene (7.000–2.500 years ago), the forest belt was almost completely developed on the Russian plain with broad-leaved and dark coniferous trees being predominant species; it occupied the space from the northern to southern seas. Within the forest belt, due to transforming activity of bisons, aurochs, tarpans, the saiga and other animals, zoogenic glades with meadow and steppe plants occurred constantly. Beavers built settlements with wetlands along small watercourses. As a result, the biogeocenotic cover of the Middle Holocene was a set of forest-meadow-bog complexes, created and regulated by keystone species, that is, large herd ungulates, beavers, and trees.

Since the mid-Middle Holocene occurred the production economy as the most powerful factor of biogeocenotic cover impact (agriculture, cattle breeding, smelting). The osteological material of this time includes a greatly reduced ratio of bones of wild ungulates (bison, auroch, tarpan, etc.) and increased ratio of livestock bones, whereas pollen of cultivated grasses appeared in the spore-pollen spectra. The production economy changed the biogeocenotic cover structure fundamentally. First of all, large herd ungulates and beavers disappeared not only due to hunting, but also due to the radical transformation of their habitats under the influence of slash-and-burn agriculture, logging and other harvesting trades. With the destruction of keystone animal species, the ratio of natural meadow-steppe ecosystems decreased, and that of forest ecosystems increased. As a result, the life of light-loving tree species (primarily oak and pine), as well as all light-loving plant species of other life forms, and many animal species that had previously inhabited zoogenic glades, became possible only in anthropogenic habitats. For example, pioneer tree species regenerated mainly on abandoned arable land.

Relatively “independent” from humans remained the ecosystems of “shadow” coniferous/broad-leaved forests; their spontaneous development is possible even now under a natural reserve regime. However, only part of the region’s natural flora and fauna can sustainably exist in these communities. Ecosystems representing the “fragments” of mid-Holocene forest-meadow-bog complexes have been preserved in the modern forest cover of the Russian Plain only as a small number of refugiums, untouched by strong anthropogenic transformation of recent centuries.

It is from the late mid-Holocene that it becomes fundamentally impossible to restore the potential (former) biogeocenotic cover in a spontaneous mode, since, on the one hand, the populations of keystone animal species (large herd ungulates and beavers) have greatly decreased in number, and, on the other hand, humans have become the most powerful environment transforming force. Human activity began to determine the existence of certain subordinate plant and animal species.

By the late mid-Holocene, forest burning for the slash-and-burn agriculture cycle pushed the southern border of the forest belt to the north. The spread of nomadic cattle breeding in the south of the Russian Plain resulted in the formation of steppe and semi-desert-steppe zones. These events were a major step towards modern zonality and probably had a significant impact on changes in the macroclimate of Eurasia in its entirety. They maybe were a reason for the growing climate instability in the second half of the Holocene.

From Iron Age to early Middle Ages (2.500–500 years ago), the northern borders of the ranges of broad-leaved tree species significantly retreated to the south, mainly due to slash-and-burn agriculture, which marked the beginning of the modern taiga — a forest strip where said tree species do not exist. At the same time, specific pyrogenic forests with predominance of *Pinus sylvestris* developed on the sandy soils of the forest belt. Slash-and-burn, and then cross-bed and arable agriculture, forest grazing, gathering litter and coarse woody debris as well as other kinds of forest use resulted in soil cover degradation in large areas. Forest burning on the northern border was the reason why the tundra zone developed from the forest tundra and northern taiga in the late Holocene.

In general, the production economy of the mid- and late Holocene divided the unified forest-meadow-bog complex into two groups: 1) ecosystems capable of supporting themselves with spontaneous development ("shadow" forests), which formed the forest belt itself; 2) ecosystems that require constant anthropogenic impact for life (floodplain and land meadows, meadow steppes, forests of pioneer tree species). At the same time, there was a final step in formation of anthropogenic zonality — under human impact, the unified forest belt on the Russian Plain divided into coniferous, coniferous/broad-leaved and broad-leaved forests.

CONCLUSION

Professor Olga V. Smirnova's edifice is based on ideas about the leading role of plant and animal populations in the organization of the biogeocenotic cover. In this case, it is implied that a continuous generational turnover in edificator (keystone species) populations is necessary to maintain the species and structural diversity in communities and ensure their sustainability. This system of views was influenced by Professor Alexey A. Uranov. The development of these ideas was consistent and gradual. First, Professor Olga V. Smirnova studied the biology of different plant species life forms. Examining their individual development, with identification of ontogenetic stages, is necessary for demographic research. She then developed the theory of coenopopulations as supraorganismal systems, which can self-sustain under different conditions. Finally, she developed the doctrine of biogeocenosis as a system of interacting populations and created the concept of anthropogenic transformation of the forest cover in the Holocene. Her contributions helped researchers to understand the mechanisms of the formation of modern zonality that are due to human activity.

We would like to congratulate Professor Olga V. Smirnova on her anniversary! We wish her a long life full of success in her new creative endeavors, vigor, energy, and good health! Her colleagues and students, as well as *Forest Science Issues* editorial board, join the congratulation.

ACKNOWLEDGMENTS

The authors thank Oleg G. Barinov, Maria A. Barinova, Maxim V. Bobrovskij, Natalia N. Bogomolova, Alexey V. Gornov, Elena S. Esipova, Ekaterina L. Zheleznaya, Ekaterina A. Kobozeva, Svetlana I. Ripa, Mikhail S. Romanov, Andrey M. Romanovskij, Elena P. Sarycheva, Nikolay S. Smirnov and Larisa G. Khanina for their help in preparing this article.

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СИСТЕМА ВЗГЛЯДОВ О. В. СМИРНОВОЙ В ЛЕСНОЙ БИОГЕОЦЕНОЛОГИИ

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Поступила в редакцию: 16.09.2019
После рецензирования: 07.10.2019
Принята к печати: 07.10.2019

О. В. Смирнова — профессор, доктор биологических наук, крупный ученый в области демографии растений, популяционной биологии и лесной биогеоценологии. Система взглядов О. В. Смирновой построена на представлениях о ведущей роли популяций растений и животных в организации биогеоценотического покрова. При этом подразумевается, что непрерывный оборот поколений в популяциях эдификаторов (ключевых видов) — необходимое условие для поддержания видового и структурного разнообразия сообществ, а также для обеспечения их устойчивости. Эта система взглядов сформировалась под влиянием идей профессора А. А. Уранова. Развитие этих представлений было последовательным и постепенным. Сначала О. В. Смирнова изучает биологию видов растений разных жизненных форм, их индивидуальное развитие, в котором выделяет онтогенетические состояния, необходимые для демографических исследований, затем — разрабатывает теорию ценопопуляций как надорганизменных систем, способных к самоподдержанию в различных условиях, и, наконец, — развивает учение популяционной организации биогеоценозов и создает концепцию антропогенной трансформации лесного покрова в голоцене. Все это помогает понять механизмы формирования современной зональности, которые обусловлены деятельностью человека.

Key words: *биологический возраст растений, популяционная стратегия растений, ценопопуляция, эдификатор, лесная биогеоценология, современная зональность, историческая экология*

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