THE BOTANIST V. N. SUKACHEV AND THE DEVELOPMENT OF DARWIN'S IDEAS IN RUSSIA[1]

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ABSTRACT. Darwin's concepts on the struggle for existence and natural selection were widely discussed in Russian academic and public press from the second half of the nineteenth to the first quarter of the twentieth century. Apart from Darwin's interpretation of the struggle for existence and natural selection, a number of competing theories emerged. There was only one way to solve this problem. It was necessary to create experimental models that could confirm or correct Darwin's theory. This paper aims to analyze the experimental research on the struggle for existence developed by the Russian botanist V. N. Sukachev in the 1920s-50s.

KEY WORDS. Vladimir Nikolaevich Sukachev, experimental models of the struggle for existence and natural selection, evolutionary theory in Russia.

In memory of Alistar Crombie, one of the first to made experimental research on the competition among animals.

In Darwin's theory, the mechanism of natural selection consists on occasional variations, inheritance, and the struggle for existence. However, Darwin had no real evidence of how the struggle for existence leads to natural selection. In the nineteenth century no solid proofs of the Darwinian mechanism of evolution could be obtained. At that time, the struggle for existence was discussed throughout the world and especially in Russian scientific and general periodicals. In that debate three other non-Darwinian interpretations were proposed:

1. The struggle for existence was considered exclusively as a conservative factor. In this case its result is the selection of the adaptive norm of a species (S. Mivart, N. Ja. Danilevsky, L. Cuenot, L. S. Berg, etc.).

2. The result of the struggle for existence within species was the breakdown of the differentiation between individuals and even the cause leading to their total elimination (K. Nageli, P. A. Kropotkin, V. N. Lubimenko, etc.).

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3. There is no struggle for existence at all within species in nature. The struggle for existence takes place only between species, and occasionally results in the survival of a particular species. It does not trigger natural selection (Hugo de Vries).

To many biologists, these hypotheses regarding the role of the struggle of existence in evolution appeared equivalent to Darwin's own hypothesis. A certain period of time was required to test the hypotheses and to make the transition to a systematic experimental research. But, why was it required? The problem of competition in plant communities was studied in detail by F. Clements during the 1930s [3]. However, American scientists did not touch the evolutionary aspects of this problem. In 1909, F. Clements published the article "Darwin's influence upon plant geography and ecology", in which he wrote that Darwin did not add anything new in studying the problem of competition, in comparison with Lyell and Herbert (Clements 1909, 148). He stressed another aspect of Darwin's work: "An experimental ecologist without doubt follows Darwin in relation to the inheritance of acquired characters" (Clements 1909, 149). A non-Darwinian or rather pre-Darwinian tradition had prevailed in the research on plant and animal communities over a very long period (Clements and Shelford 1939, 435).

Anyhow, experiments testing Darwin's concept of the struggle for existence was the position of leading Russian zoologists and botanists. For example, Leo S. Berg denied the evolutionary role of such struggle, and V. N. Lubimenko tried to disprove Darwinism experimentally (Lubimenko, Sheglova and Bulgakova 1925).

V. N. Sukachev was a leader among botanists and Russian biologists, who studied the struggle for existence and natural selection experimentally. His teacher in science was G. F. Morozov, a forestry specialist, who implanted Darwinism in Russian forestry during the period of the 'eclipse' of Darwinism [4]. Due to his great interest to build a population biology based on Darwin's theory, Sukachev became a specialist on meadow plants, although he needed a long period of time to verify data and to obtain reliable results.

In the early 1920s, A. P. Shennikov and V. N. Sukachev started their research program on population biology of plants, their primary task being to study the struggle for existence (Shennikov 1921, Sukachev 1925). To do so, it was necessary to study the magnitude and the conditions concerning the elimination of plants depending on the action of different biotic and abiotic factors; the selective role of small mutations, and the influence of the density of population upon individual development. An open question was: which part of a population died, and under what conditions, as the result of the struggle for existence? Darwin's statement that the struggle is most intense between individuals of the same species

had, according to Sukachev, an *a priori* character and needed to be tested within different plants (Sukachev 1925, 179). To answer the question it was necessary to study a mixed population consisting on several pure lines, closely related species, and species of different genera. Then, by comparing the intensity of elimination of plants in populations so mixed, it would be possible, Sukachev thought, to measure the intensity of the struggle for existence itself. It was especially interesting to devise such experimental models for studying the interaction of intra- and inter-species competition in the process of natural selection.

For Sukachev, it was important to use both annual and perennial plants experimentally in order to formulate a general law of such struggle within plants. He started with artificial populations of self-pollinating plants consisting in several pure lines or biotype clones, which he compared to the struggle for existence in natural populations of cross-pollinated plants. Sukachev believed that using biometric figures for the study of variability in morphological traits under different population densities was also very important. The completion of Sukachev's research program could provide valuable data on the struggle and its evolutionary meaning.

In 1924, Sukachev and his collaborators began the experimental research on such struggle using breeding nurseries of the St. Petersburg Forestry Institute and the St. Petersburg Agricultural Institute. Later experiments were continued at the Peterhoff Biological Institute of the St. Petersburg University. Sukachev studied six biotypes of dandelion (*Taraxacum officinale*) of different geographic origin and two population densities: 3 x 3 and 18 x 18 cm. It was shown that the most solid (adaptive) biotype of intraspecies competition could be the less adaptive one in inter-biotype competition.

The next stage of Sukachev's experiments was to study the reproductive abilities of the surviving biotypes. The general evolutionary meaning of such research was obvious to Sukachev: the ability to produce and maintain viable descendants was a main feature of Darwinian adaptation. That was what Sukachev meant when he wrote that it was possible to imagine a situation where one biotype preserved a large number of individuals in the struggle for existence, although very weak ones, unable to maintain their descendants, while at the same time a small number of surviving specimens of another biotype could be satisfactorily developed and fruit-bearing (Sukachev 1927, 202). Thus, Sukachev did not completely reject Lubimenko's concept of total oppression and elimination of plants under the struggle for existence. He wanted to verify this hypothesis, but his data did not confirm it. Sukachev discovered that competitive ability included survival and reproduction, although these two features did not coincide.

Sukachev's experiments with dandelions yielded not only direct experimental evidence of a struggle for existence and natural selection, but also

demonstrated how little was known about the factors of evolution acting in experimental and natural populations. He continued his experiments using another subject, warty fescue (*Festuca sulcata* Hack. Nym.) and concluded: "Till the present all that was said about the struggle for existence among plants in the process of speciation, as well as in the life of plants communities was on the basis of *a priori* statements" (Sukachev 1935, 70).

The study of inter-biotype struggle is important, according to Sukachev, since small heritable forms originated through mutation and combination, produce suitable material for new adaptive forms, separation of taxons, and improvement of organization as the results of natural selection. Sukachev elaborated in detail his next research program in 1925. He indicated, for instance, the need to investigate different biotypes of one species in competition with others (1935, 71).

In 1928, the largest fescue plants were cloned, and our scientist used this genetically pure material in his new experiments. One of Sukachev's conclusions was that the struggle for existence played a great role in the selection of biotypes during the formation of ecotypes and thus greatly influenced speciation. From this method of cloning, he was able to discover genetic differences in plants' reactions to density. Differences between plants increased with the density of population, and the increase in intraspecific competition set up rapid intraspecific differentiation. Sukachev demonstrated clearly that intraspecific competition led to natural selection in heterogenic populations, and small biotypical differences sufficed for the effectiveness of natural selection. He got good experimental evidence not only for the selective meaning of intraspecific competition, but also for the changes of adaptive value of genotypes as the result of such competition. Thus, several models of micro-evolutionary transformations were studied. Without doubt, these experiments disproved the non-Darwinian interpretations of the evolutionary meaning of the struggle for existence, at least for population densities as those used in his experiments. This was especially important as genetics and ecology were still isolated from each other at that time, and Sukachev's research showed how they could be integrated in the experimental study of evolution.

Sukachev's work of 1927 was translated into German, which immediately attracted the attention of his western colleagues. J. B. S. Haldane and J. Huxley considered Sukachev's experiments as the best evidence of natural selection. Dobzhansky in his famous book *Genetics and the Origin of Species* devoted a paragraph to Sukachev and cited the original Russian texts [5].

Sukachev's program helped to create a whole school of plant population biologists (V. B. Sochava, L. I. Uspenskaya, E. A. Smirnova, V. P. Kushnirenko; see Gall 1976, 73-89). Theoretical results followed, and a

selectionist meaning of intraspecific competition was established. Many data showed that adaptive transformations of populations took place. Thus, H. De Vries and L. S. Berg's concepts were falsified; those concepts denied the reality of intraspecific competition and considered the struggle for existence as only a conservative factor of evolution. The role of small differences between species in interspecific competition was also demonstrated.

Even so, the idea of massive oppression and elimination of plants due to overpopulation was still alive. Darwinism met serious difficulties in interpreting data on the depression of perennial plants under high densities of population. It was not easy to explain why there was no massive elimination or massive sterilization among many annual plants under such high densities. That was why Sukachev used annual and perennial plants under different densities in his experiments. He demonstrated that an intense struggle for existence had different effects on the individual development of annual and perennial plants. Among annuals, individual development speeded up; in perennials, the process slow down (Sukachev 1941). Our author concluded that both reactions are adaptive. If changes in individual development enhance reproduction, such changes, the result of natural selection, are adaptive. It is better for annual plants to accelerate the reproductive cycle well in advance of unfavorable conditions. It is better for perennial plants under conditions of overpopulation to slow down their development in order to survive unfavorable conditions (Sukachev 1941, 754). Evidence for this rule emerged when plants were sown in an open space where they developed normally and finished their cycle by fruiting.

It can be said that Sukachev clearly demonstrated the weakness of the views of botanists like V. N. Lubimenko, who tried to disprove Darwin's notions of the struggle for existence and natural selection experimentally. The slowing down of perennial plants under overpopulation was not "a total oppression", but rather a complex adaptive reaction that appeared as the result of natural selection. This adaptation results from a special evolutionary mechanism protecting populations against the most dangerous consequences of overpopulation.

These conclusions of Sukachev were practically unnoticed within Russia and beyond, possibly because they were published in the first days of the Russian war against Germany in 1941, or because T. D. Lysenko's influence in Soviet biology was growing. Lysenko was an opponent not only of Darwin's idea of the role of intraspecific competition in evolution, but also of its very reality.

Sukachev was one of the first who used experimental methods to study the co-action of intraspecific and interspecific competition in the process of natural selection (Sukachev 1959). In his experiments on willows he

developed models that allowed him to study differences between biotypes for interspecific and intraspecific competition and adaptability. He showed that the adaptive value of genotypes could change depending on the density of population and on the type of co-action between plants, whether intra- or interspecific.

Sukachev was a real paladin for Darwinism. From 1946 onwards, he struggled continuously with Lysenko who opposed Darwin's views on intraspecific competition. Sukachev published a whole series of articles critical to seudoscience. When genetics was on the edge of extinction in the USSR, Sukachev was a leader in the fight to save it. In the 1950s he was a chief editor of *Botanicheskii Zhournal* (The Botanical Journal) and *Bulletenya MOIP* (The Bulletin of the Moscow Society of Naturalists), publications that favored the protection and development of Darwinism in the Soviet Union.

NOTES

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3 Clements and Weaver 1924; Clements, Weaver and Hanson 1929.

4 Morozov 1912; see also Gall 1976.

5 Sukachev 1928; Haldane 1932, 89-91; Huxley 1942, 120; Dobzhansky 1937, 92-93.

REFERENCES

Clements, Frederic (1909), "Darwin's influence upon plant geography and ecology," *American Naturalist* 53.507: 148-49.
Clements, Frederic and John Weaver (1924), *Experimental Vegetation*, Washington: Carnegie Institute.
Clements, Frederic, John Weaver and H. Hanson (1929), *Plant Competition: An Analysis of Community Function,* Washington: Carnegie Institute.
Clements, Frederic and Victor Shelford (1939), *Bio-ecology*, New York: Wiley.
Dobzhansky, Theodosius (1937), *Genetics and the Origin of Species*, New York: Columbia University Press.
Gall, Yakov M. (1976), *Borba za sushchestvovanie kak faktor evolyutsii* (The struggle for existence as a factor of evolution), Leningrad: Nauka.
Haldane, John B. S. (1932), *The Causes of Evolution*, London: Longman, Green and Co.
Huxley, Julian Sorell (1942), *Evolution: The Modern Synthesis*, London: George Allen and Unwin.
Lubimenko, Vladimir. N., Olga A. Sheglova and Zinaida P. Bulgakova (1925), 'Opyty nad sorevnovaniem za mesto u rastenii' (Experiments on competition for space in plants), *Zhurnal russkogo botanicheskogo obschestva* (Journal of the Russian Botanical Society) 10. 3-4: 293-338.
Morozov, Georgii F. (1912), *Uchenie o lese* (Forest Theory), St. Petersburg: [n. pub.].
Shennikov, Alexandr P. (1921), 'Fitosotsiologiya i opytnye pitomniki' (Phytosociology and experimental nurseries), *Zhurnal petrogradskogo agronomicheskogo obshchestva* (Journal of Petrograd Agronomic Society) 3-4: 34-45.
Sukachev, Vladimir N. (1925), 'Eksperimental'naya fitosotsiologiya i ee zadachi' (Experimental phytosociology and its tasks), *Zapiski leningradskogo sel'skokhozyaistvennogo instituta* (Proceedings of Leningrad Institute of Agriculture) 2: 174-86.
Sukachev, Vladimir N. (1927), 'K Voprosu o bor'be za sushchestvovanie mezhdu biotipami odnogo i togo zha vida' (On the struggle for existence between biotypes of the same species), *Ubilei. Sbornik posvyaschennii I. P. Borodinu* (Jubilee Collected Works Devoted to I. P. Borodin), Leningrad: Russkoe botanicheskoe obshchestvo, p. 202.
Sukachev Vladimir N. (1928), 'Einige experimentelle Untersuchungen über den Kampf ums Dasein zwischen Biotypen derselben Art', *Zeitschrift für induktive Abstammung und Vererbungslehre* 47. 1: 54–74.
Sukachev, Vladimir N. (1935), 'Opyt eksperimental'nogo izucheniya mezhbiotipnoi bor'by za sushestvovanie u rastenii' (Experimental study of inter-biotypic struggle for existence in plants), *Trudy petergofskogo biologicheskogo instituta leningradskogo universiteta* (Proceedings of the Peterhof Biological Institute at Leningrad University) 15: 70, 71.
Sukachev, Vladimir N. (1941), 'Vliyanii intensivnosti bor'by za sushchestvovanie mezhdu rasteniyami na ikh razvitie' (On the influence of the struggle for existence between plants on their development), *Doklady AN SSSR* (Proceedings of AS USSR) 30.8: 752-55.
Sukachev, Vladimir N. (1959), 'Novye dannye po eksperimental'nomu izucheniyu vzaimootnoshenii rastenii' (New data on experimental study of plant relations), *Bulleten MOIP. Otdel biol.* (Bulletin of the Moscow Society of Naturalists: Biology Section) vol. 64. 4: 35-40.