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Population structure of biogeocenoses of south tundra, their productivity and stability

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Biogeocenoses of the southern tundra are formed by elements of different faunistic and floristic origin and different degrees of adaptation to extreme life conditions. This determines the sharp fluctuations in the productivity of tundra communities in time and space. In areas with favourable soil, hydrological and microclimatic conditions, "southern" elements of fauna and flora form stable populations, and typical tundra animals and plants give maximum productivity. Such areas, veritable oases in tundra, must not be considered as unimportant exceptions against the background of the low biological productivity of the subarctic. Their study provides a possibility of evaluating the potential biological productivity of tundra communities, as realised under unfavourable climatic conditions.

Direct observations show that such oases form during the short growing season a herbage of heterogeneous associations, the biomass of which is commensurate with that of rich meadows in southern zones. The maximum biological productivity of populations of voles in southern tundra is comparable with the maximum productivity of populations of related species in any landscape zone. Calculations show that the productivity of populations of a large number of groups of insects (primarily = Diptera) exceeds that in the majority of southern biomes. Productivity of flourishing reindeer herds is quite commensurate with the maximum productivity of saiga (Saiga tatarica) herds in steppes. Even species usually considered as alien elements in tundra fauna sometimes realize maximum biological productivity. Taking into consideration the short period of plant growth, the slightly longer period of animal reproduction and the low temperature of air, water and soil, which lowers the growth rate and development of many organisms, we come to a paradoxical conclusion: the potential productivity of all trophic levels of southern tundra is commensurate with the productivity of southern biomes. The study of the laws which determine the high potential productivity of southern tundra, realised only in rare cases, must aid the formation of a theory of wildlife management for northern communities.

Terrestrial and fresh water communities are more closely combined ecologically than in the majority of other biomes. Low relief, rapid rises of water level in rivers, marked variation of the water level in lakes, rapid and complete drying out of even relatively large ponds in the process of thawing of permafrost, and high soil humidity all create peculiar temporary ecosystems. Side by side with the development of typical tundra lakes and swamps arise temporary reservoirs covering typical terrestrial plant associations. In some areas such temporary ponds cover up to 30 per cent of the surface. The biological productivity of hydrobionts is exceptionally high, and for this reason the formation of such reservoirs opens the richest source of nutrition for many species of animal. At the same time, reservoirs of the type described enrich soil with organic matter, and promote the development of rich terrestrial plant associations. The reservoirs in southern tundra bring about increases in productivity of terrestrial ecosystems; dry tundra becomes lifeless.

The poverty of the majority of ecosystems, the limited number of dominant species forming the basis of biological production, the relative homogeneity of landscape, facilitating migration of animals, all these factors lower the pressure of consumers on vegetation. Under these conditions the main mechanisms of population dynamics for the majority of species are the density-dependent factors and the direct influence of climatic factors on animal numbers, which sharply increases. In southern tundra, with its richer (in comparison with High Arctic) fauna and flora, typical population cycles of dominant species are constantly broken. This often leads to a change in the faunistic structure of dominant communities. This, as will be appreciated, leads to a synchronization of the population cycles of a large number of species of common faunistic origin. Consequently, not only separate species but whole trophic levels as well, may disappear over immense areas.

Boundaries between landscapes where the life takes place are only boundaries between prevailing types of biogeocenoses but not climatic boundaries, the areas of synchronization of life-cycles of dominant species often do not coincide with the zone boundaries. Therefore, in some years in the fauna of southern tundra, the typical arctic elements prevail, while in others the northern forms of widely distributed species do so. Since the part played in tundra ecosystems by these groups of animals is essentially different, the course of the basic biocenotic processes differs essentially in different years. On the other hand, this lowers to an even greater degree the general biocenotic activity of southern tundra as a whole, but increase the energy flow in individual regions of the biome.

In the southern subarctic, contrary to generally accepted ideas, the efficiency of energy utilisation in every succeeding link of trophic levels decreases markedly. But this becomes apparent only when large areas are considered over a long period of time. In some parts of the tundra, a highly complete utilisation of plant biomass by consumers and biomass of herbivorous animals by predators may be observed. Since in different years the life conditions in different parts of the tundra change, to varying degrees and not rarely in different directions, the focal point of high biocenotic activity (a marked increase in energy flow) constantly moves from one place to another, and as a whole the biomass of all trophic levels is utilised to an insignificant degree. A constant transfer of populations takes place, and migration of animals from places of temporary concentration to places of "ecological vacuum" become a general rule. In this situation, the well-known ecological mechanisms lead to an increase of biological potential in certain species, and to the prevention of the development of morpho-physiologically specific local forms. The evolutionary consequence of this process is the rapid evolution of species as a single entity over wide territories and the relatively slow increase in species diversity in northern ecosystems. On the other hand, since the reaction of different species to similar alterations of life conditions, does not coincide in a large number of cases, the distribution of focal points of increasing concentration even of ecologically related species frequently fails to coincide. A break-down of ecological relations occurs, and the general productivity of an ecosystem falls dramatically. Similar mechanisms sharply limit the possibility of the permanent influence (during many years) of dominant species of animal on the vegetation (an important exception is the domestic reindeer). The years of high consumer pressure on producers alternate with years of "rest" for the vegetation. This is the basis of the optimal conditions for interaction of different trophic levels: the negative role of animals in the development of plant cover is reduced to a minimum, while their positive role sharply increases. The activity of animals under conditions of weakened activity of decomposers determines to a considerable degree the rate of return to the soil of organic substances which contain dying parts of plants; the improved aeration of soil and the increase in the rate of thawing out of permafrost, bring about essential changes in vegetation and seed production of plants, thus determining the species composition of plant communities. A positive correlation exists between the productivity of organisms of different trophic levels. This becomes apparent from the investigation of large areas of southern tundra by means of permanent investigations over a long period of time.

The totality of processes described above determines the most important characteristic of the ecological structure of the southern tundra: the local rise in biological productivity, commensurate with the highest productivity of southern biomes, against a background of the generally extremely low productivity of the biome as a whole. The level of organisation of tundra communities as a system (from the cybernetic point of view) is low. Therefore an alteration in trophic levels or an alteration of population structure of dominant species, does not change significantly the functioning of the biogeocenoses as an ecological entity. Subarctic biogeocenoses, as ecosystems subject to natural fluctuations of the highest degree, can resist maximum alteration without collapsing and without much change.

It is generally known that tundra biogeocenoses concern the youngest natural complexes, being formed under extreme life conditions. The adaptation to these conditions demands the radical transformation of many ecological and morpho-physiological characteristics of animals and plants. The process of formation and development of tundra ecosystems is going on at present. In southern tundra it is proceeding more intensively, as a result of the relatively mild conditions (as compared with the High Arctic), and the proximity of southern biomes leads to the constant penetration northwards of more southerly faunal and floral elements. Some of these transgress the boundary of the forest tundra and by accomodation to the climatic conditions are gradually drawn into typically arctic communities. The final stage of this process is illustrated by Microtus oeconomus, and the initial stage, by Arvicola terrestris. There is an impression that we are witnessing the most important evolutionary event: a new stage in the formation of tundra biogeocenoses. The progressive adaptation of forest and steppe forms to arctic life conditions is taking place now, and the coevolution of northern animals and plants is in progress. The result of this coevolution is the coordination of life cycles of individual species and subdivisions of biogeocenoses. In an ideal biological complex the fluctuations in life conditions must show simultaneous effects on the members of the community. Otherwise any deviation from the average of many years leads to a breakdown in the interrelationships between organisms, and would lead to ecological chaos. The results of our 12 years' investigations in Jamal tundra demonstrate that the southern tundra is almost ideal for investigating the correlation between the evolution of organisms and the evolution of ecosystems. The solution of this problem will provide the theoretical basis for wildlife management.