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SOIL BIOLOGY

The Role of Large Arthropods in the Development of Halomorphic Soils in the South of Siberia

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Abstract—Soil sequences along catenas crossing the peripheral parts of shallow-water drying lakes in the south of Siberia have been studied. They include the sulfidic and typical playa (sor) solonchaks (Gleyic Solonchaks), playa solonchak over the buried solonetz (Gleyic Solonchak Thapto-Solonetz)), shallow solonetz–solonchak (Salic Solonetz), and solonetzic and solonchakous chernozemic-meadow soil (Luvic Gleyic Chernozem (Sodic, Salic)). This spatial sequence also represents a series of historical stages of the development of halomorphic soils: the amphibian, hydromorphic, semihydromorphic, and automorphic–paleohydromorphic stages. During all of them, the biogenic component plays a significant role in the matter budget of halomorphic soils. The diversity, number, and functional activity of large insects and spiders are particularly important. Their total abundance in the course of transformation of the halomorphic soils decreases from several thousand to about 100 specimens/(m^2 day), whereas their species diversity increases from 17 to 45 species. Changes in the functional structure of the soil zoocenosis and its impact on the character and intensity of pedogenetic processes can be considered driving forces of the transformation of hydromorphic soils. This is ensured by the sequential alteration of the groups of invertebrates with different types of cenotic strategy and different mechanisms of adaptation to biotic and abiotic components of the soil in the course of the development of the soil zoocenosis.

Keywords: soils of periphery of the lakes, Gleyic Solonchak, Gleyic Solonchak (Thapto-Solonetz)), Salic Solonetz, Gleyic Chernozem (Natric, Salic), herpetobionts

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INTRODUCTION

Halomorphic soils are usually considered to be young soils, even relative to a generally young soil cover of the planet that was mainly shaped after the Tertiary period [30]. These young soils with short profiles attract relatively little attention in general concepts of pedogenesis and soil classifications built on the basis of well-developed zonal reference soils [9, 12].

The concepts of soil-moment and soil-memory are applicable for many soils [21]. For the halohydromorphic soils, their application seems to be particularly important. The profile of these soils is formed in a short time (from about 1 month to about 100 years or more); during this period, the soil profile composed of three–four horizons is formed under the influence of more than two elementary pedogenetic processes (EPPs). This allows us to attribute such soils to the category of developed soils [30]. It is important that these soil profiles retain the features formed at the very beginning of the subaerial pedogenesis. In these soils, the role of the living (biotic) phase in the soil development is especially significant. They are characterized by frequent alteration of characteristic EPPs owing to the mobility and efficient functioning of heterotrophic organisms.

Soil successions follow the general rules of biogeocenotic successions within the particular biomes, though they have their own specificity. Thus, Buol, Hole, and McCracken [30] noted that the changes of pedogenetic regimes result in certain succession of soils with young, mature, and old stages, each of which is characterized by its own specific properties. The concept of soil successions has also been applied and developed by Russian pedologists [6, 11].

Some authors argue that the concept of successions should only be applied to describe the chronosequence of ecosystem changes in the same place. The successions taking place in the habitats of different ages located in different may follow their own scenarios, so that the chronological regularity of succession changes derived from their study has an artificial character and might be incorrect [33]. Indeed, there is some truth in this reasoning. However, we should bear in mind that the long-term succession in a given place is never exactly repeated in nature and cannot be exactly reproduced in an experiment. It is always incomparable and unique. A succession cannot be studied in the same place, because any sampling (e.g., soil sampling) disturbs this place. Therefore, we have to use the method of spatiotemporal analogues to study successions. This method is based on the principle formulated by Vernadsky [8], who argued that spatial and temporal categories should not be considered independently Spatially separated habitats and ecosystems represent not only chorological elements of the earth surface but also different phases of the development of ecosystems typical of a give biome.

The process of initial pedogenesis was tightly related to the evolution of ancient water bodies. Because of the strong evaporation, flat topography, the absence of higher vegetation, and unconstrained erosion, such ancient water bodies on the continents were rapidly filled with continental sediments; often, they were subjected to salinization. Their ephemeral nature favored the development of an extensive "amphibian" periphery, where paleosols could be formed.

At present, the earliest fossil soils are dated back to the Precambrian time; thus, they were formed long before the appearance of terrestrial plants and most of the living invertebrates [19]. The total areas of such ecosystems with "pioneer" conditions for pedogenesis in the Archaean era (2.5–3.5 billion years ago) comprised about 10% of the modern crust [31]. Bacterial–algal mats were developed in such habitats and served as "predecessors" of soils. A considerable part of such mats perished under the layer of accumulating continental sediments. As a result, a layered "pie" with alternating layers of unoxidized charred organic matter and clayey material was formed [20]; however, it was not the soil proper as an integral bio-abiotic body.

In the Cambrian period, the first annelids and protoarthropods of the marine origin settled on land and inhabited inland water bodies. It is probable that these animals were pre-adapted to stress conditions of terrestrial life owing to the benthic habitat of their predecessors. They had relatively large sizes ensuring relative constancy of their inner media. Owing to their mobility, they could contribute to mixing of the organic and mineral layers of the protosoils. Trophic chains of the pasturing type predominating in the ecosystems were gradually replaced by the chains of detritus type, and invertebrates became an indispensable component of pedogenesis. It is important that all these changes took place long before the appearance of vascular plants.

Soil invertebrates left their tunnels in the soil and. thus, increased the soil porosity. The ancient hydromorphic protosoils with animal tunnels appeared in the Late Ordovician period [34]. The tunnels left by the animals ensured the availability of oxygen in the soil and stimulated the development of microorganisms and fungi and, later, the settling of higher plants [19, 23].

Most of the fossil soils of different geological periods have many common features; moreover, they resemble their modern analogues in the amphibiotic systems despite the radical change in the ecosystem conditions and the composition and structure of soil biota [19].

The study of such "presoils" is of great interest. There are certain prerequisites for the success: (a) the existence of the fragments of the amphibiotic biome in the natural state in the modern period, (b) the presence of the analogues of ancient phytomats and casts of dead phyto- and zoogenic organic matter on the shores of water bodies, and (c) the preservation of the leading role of invertebrates (as judged from the diversity of their taxa, number, biomass, and functional activity) representing macrofauna upon the modest role of microfauna and microflora and the virtual absence of higher vegetation [3, 17, 25, 29].

The aim of our study was to reveal the role of large invertebrates as stimulators and navigators of EPPs (solonchakous, gleyzation, sulfide-accumulative, etc.) during the first stages of the succession of halomorphic soils. We tried to differentiate pedobionts according to their ecological specialization and the impact on pedogenesis, to analyze the contribution of different components of the zoocenosis to the formation of initial porosity and the accumulation and transformation of organic matter in the newly subaerial soils and to evaluate the role of large invertebrates in the development of the upper horizons of the vertical profile of halomorphic soils.

OBJECTS AND METHODS

Southern Siberia (54°–50° N), where our studies were performed, is a region with sharply continental climate and considerable contrasts in the heat and water supply. Numerous endorheic lakes with unstable hydrological regime are developed in this region. These lakes have an extensive amphibiotic peripheral zone; the area of automorphic soils with halomorphic features is very considerable. Overall, the portion of halomorphic (salt-affected) soils in the south of Western Siberia is estimated at about 37% of the soil cover [24]. Nearly 6000 salt lakes are found in the south of the West Siberian Plain [1, 7].

The origin of salts in the Baraba Lowland confined to the deep Omsk syneclise is related to the filling of this depression with marine and continental sediments from the Middle Cretaceous to the Middle Oligocene periods. In the lowermost (105 m a.s.l.) Chany part of the Baraba Lowland, ancient salt-bearing sediments are found close to the surface. Water erosional processes acting in this area since the end of Oligocene have exposed these sediments and caused their redeposition and accumulation in the local depressions. Additional source of salts was related to their eolian transport from more arid southern regions of Kulunda and Kazakhstan [7].

Dried parts of Maloe Solenoe Lake (22 km to the southwest of the city of Karasuk in Novosibirsk oblast)

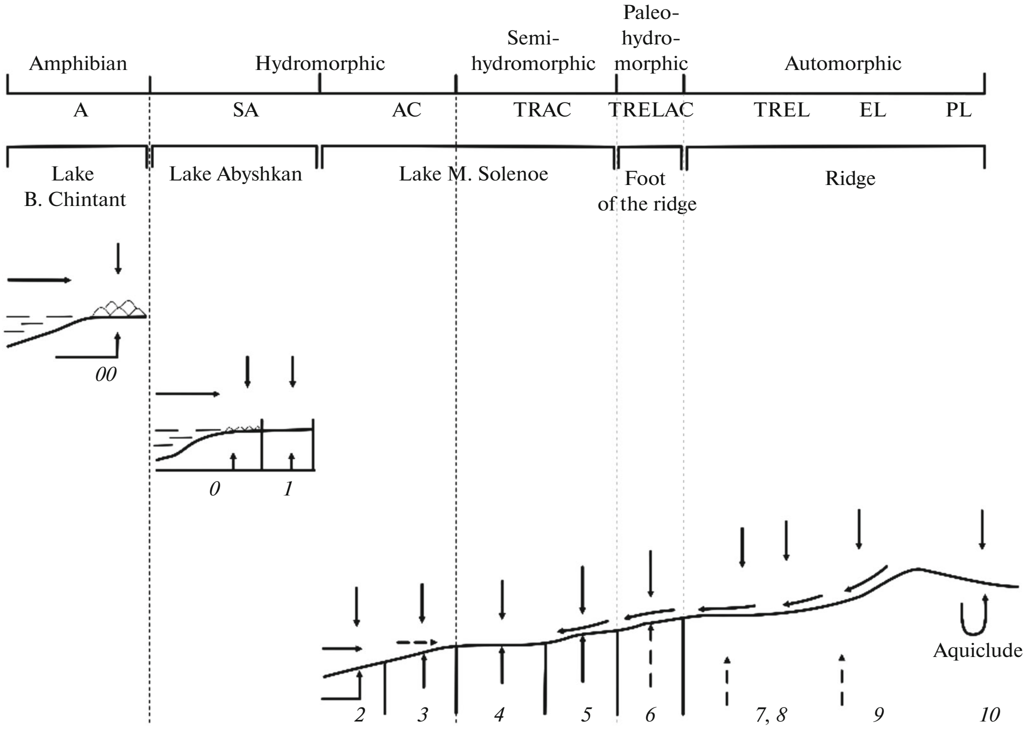

Fig. 1. Stages of the succession of halomorphic soils, their catenary positions, and types of soils and vegetation. Catenary positions: (A) amphibian (water level during waves), (SA) superaqual (alteration of drying and ponding); (AC) accumulative, (TR) transitional, (EL) eluvial, and PL (plakor, automorphic). Soils and vegetation: *00*—periodically drying lake bottom with casts of rotting algae; *0*—lacustrine sulfidic solonchak without higher plants; *1*—playa wet sulfidic solonchak without higher plants; *2*—playa crusty sulfidic solonchak with single saltworts; *3*—typical solonchak under halophytic meadow; *4*—playa solonchak over buried solonetz under *Halocnemum strobilaceum*; *5*—shallow to medium-deep solonetz–solonchak under saltbush community; *6*—solonetzic and solonchakous chernozemic-meadow soil under needlegrass herbaceous mesohalophytic meadow; *7, 8*—meadow-chernozemic soil in association with the crusty and medium-deep solonetzes under grassy–forb xerophytic meadow; *9*—ordinary chernozem under meadow feather grass herbaceous meadow; and *10*—soddy solod under aspen–birch grove.

and Abyshkan Lake (formerly, a part of Lake Chany) in the Baraba forest-steppe region and Bol'shoi Chindant Lake in the southeast of the Transbaikal region were selected as the key polygons for our study. The location of soils on different elements of mesotopography crossed by the studied catenas is shown in Fig. 1.

According to the evolutionary- genetic soil classification system by Kovda [13], the soils along the periphery of the studied lakes can be attributed to intrazonal variants of the soil-geochemical formation of alkaline and salt-affected soils. On the studied polygons, they are represented by several types reflecting the first stages of the halomorphic pedogenesis. Its major diagnostic feature is the surface solonchakous horizons containing more than 1% of soluble salts (according to the analysis of soil water extracts) in the uppermost 10 cm of the soil profile [18].

The composition of salts was determined in the soil water extracts (1 : 5). The humus content in the upper soil horizons of the soil profile studied in the area of Maloe Solenoe Lake was determined by Tyurin's method in the Institute of Soil Science and Agricultural Chemistry (Siberian Branch of the Russian Academy of Sciences) in Novosibirsk. The soil water content was measured with a TDR-100 probe at the depth of 5 cm in the midday time once per 10 days. The soil temperature at the same depth was recorded by a thermochron logger each 6 h during the entire period of the study.

Arthropods in the soils studied in the area of Bol'shoi Chindant Lake were manually collected from the samples of the casts on the soil surface; overall, 40 soil samples of 0.0625 m^2 in area from five biotopes were analyzed in 1965. In the area of Maloe Solenoe Lake, the species composition and number of herpetobionts (animals dwelling on the soil surface) was studied by the method of soil traps—cups inserted into the soil flush with the soil surface. The accounting of trapped animals was performed from the end of May to the end of August in 2011–2012. In addition, the number of burrows (per square meter) left by burrowing invertebrates on the soil surface was counted several times per season; the depth and length of their horizontal tunnels that could be traced from the soil surface were measured.

The results of detailed studies of the animal population were published earlier: for Lake Bol'shoi Chindant, in [17, 25]; for Maloe Solenoe Lake, in [3, 27, 28]. The

Table 1. The system of cenotic strategies and adaptive tactics of halobiont arthropods

Adaptive tactics	State of halomorphic pedogenesis			
	amphibian	hydromorphic	semihydromorphic	paleohydromorphic
	cenotic strategies			
	utilization (U)	ruderal (R)	stress-Tolerant (ST)	competitive (C)
Topic	Amphibionts	Solonchakous	Solonetzic	Glycobionts
Trophic	Omnivore	Polyphagy	Polyphagy	Oligophagy
Fabric	Destruction of the environment	Engineering	Structuring of cenosis	Dispersion in the environment
Phoric	Force majeure (invasion)	Ordered roaming	Temporal occupation	Long-term colonization
Demographic	r-selection	rK-selection	Kr-selection	K-selection
Resulting cenotic effect	"Clearing" of perished ecosystem; regress	Creation of the elements of a new ecosystem	Vectorized progress of the ecosystem	Circularity of the biotic turnover

species diversity and abundance of the animal population at these sites were used as the main parameters. The trophic structure of insects studied in the soil catena at Maloe Solenoe Lake with the use of the method of stable isotopes was described in [14]. The species composition of ground beetles was determined with the use of an online catalogue (www.carabidae.org). The statistical treatment included the comparison of the mean values of the numbers of species in different biotopes with the use of the Mann–Whitney criterion.

The major terms and concepts of succession have been developed by geobotanists [5, 15]. In essence, ecosystem succession implies changes in the structure and functioning of an ecosystem owing to a regular alteration of the organisms with different types of life strategy.

One of the popular classifications of the types of life strategy is the system developed by Ramenskii and Grime [16]. Its key categories include three types of strategy: ruderal, stress-tolerant, and competitive. With respect to the invertebrates, the fourth type of strategy can be specified. We suggest that it might be referred to as the utilization strategy. This is the strategy of organisms specializing in the enhanced utilization of considerable accumulations of dead organic mass (mortmass, e.g., manure, leaf litter, fallen trees, etc.) in the ecosystems.

With respect to plants, classical works on the theory of successions suggested the analysis of a demographic criterion as the result of action of different forms of natural selection: r-strategy and K-strategy. However, this criterion is insufficient to characterize cenotic relationships of invertebrates. From our point of view, each strategy is developed as an integral manifestation of complementary tactic responses of the particular biological species. Therefore, such a strategy can be named a "cenotic strategy."

The typology of adaptive tactics can be built on the basis of the proposals by Beklemishev [2] about the types of symphysiological relationships of invertebrates in an ecosystem. Four types of such relationships are distinguished: trophic, fabric (based on the character of substrate use), phoric (based on the distribution patterns in space), and topic (according to the confinement of populations to the particular habitats).

Trophic tactics are a classical object of the study. However, the belonging of particular species of invertebrates to the given trophic level is still unknown for many species and requires further studies. Data on the spectrum of food objects for different animal species are even less complete. To solve these problems, the method of stable isotopes [10] can be applied together with classical methods of studying animal diets [22]. The analysis of isotopic records for model species of halobiont insects with uncertain trophic preferences makes it possible to distinguish between at least three different variants of the trophic tactic (Table 1).

Fabric tactics are typical of all the arthropods, though they can be differently manifested. For example, amphibiont utilizers concentrated in the casts actually "eat their own house" and, thus, destroy the perished ecosystem. Arthropods with the ruderal cenotic strategy are active ecosystem engineers. Often, they do not have physiological adaptation to anaerobic, chemically aggressive water-saturated media. So, they build tunnels, burrows, and chambers with suitable conditions for their dwelling. The cenotic strategy of competitors is in agreement with the fabric tactic of diffuse distribution in the substrate. Mull humus of the chernozemic-meadow soil favors the realization of this tactic.

Phoric tactics may also be different. Thus, the force majeure tactic is typical of utilizers, regular nomadism is typical of ruderal species, temporal occupation tac-

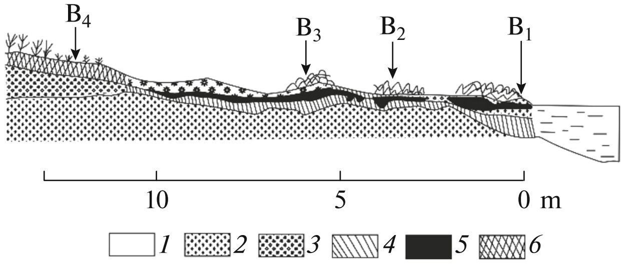

Fig. 2. Soil profile at the water level of Lake Bol'shoi Chindant: (*1*) casts, (*2*) sand, (*3*) sand with sulfides, (*4*) gleyed layer, (*5*) sulfidic layer, and (*6*) sod layer. B1–B4 are the "rolls" of casts.

tic is typical of stress-tolerators, and continuous colonization tactic is typical of competitors.

Topic tactics are aimed at choosing the particular habitats in the discretely organized space. The major preferred biotope can be used to determine the type of cenotic strategy of a given species of invertebrates. Preferred biotopes are those biotopes, the number of specimens in which is considerable greater than the number of specimens in other biotopes.

RESULTS AND DISCUSSION

General characterization of animal population of the studied polygons. Overall, 165 insect species have been identified on the studied polygons. The greatest species diversity and abundance were found for the orders of Coleoptera, Hemiptera, Dermaptera, Orthoptera, Diptera, and Hymenoptera. The total abundance of insects varied between the particular habitats and changed within the summer season from tens to thousands of specimens per 1 m^2 of catching area per day. Representatives of the subphylum Chelicerata (spiders) were second in abundance after Insecta. Overall, 50 species of spiders were identified, and their abundance reached 214 specimens/(m^2 day).

Typical combinations of adaptive tactics characteristic of the corresponding cenotic strategies are listed in Table 1. Their analysis is given below.

Stages of succession of halomorphic soils and the role of large invertebrates in them. Five consecutive stages in the development of halomorphic soils can be distinguished: the amphibian, hydromorphic, semihydromorphic, paleohydromorphic, and automorphic stages [13].

The amphibian stage is most distinctly manifested in the superaqual soil of the catena on the shore of Lake Bol'shoi Chindant subjected to incomplete drying during the dry season. At the boundary between water and terrestrial habitats, dead organic mass (mortmass) of aquatic and, partly, terrestrial vegetation is deposited; it also includes larval skins, eggs, and dead bodies of arthropods. Being mixed with sand, this mass forms small rollers of 1–5 cm in thickness and dozens of centimeters in width. The soil under such rollers is formed under the impact of groundwater coming up to the surface and periodical splashes of lake water. The water is of the carbonate–chloride–sulfate composition with the salinity of about 21 g/L and with the strongly alkaline reaction (pH 8.6–9). Salt efflorescence of the soil surface mainly consists of sulfates. The specific microflora ensures the reduction of sulfates. Oxygen is spent for oxidation of the organic mass, which leads to the reduction of sulfur and the formation of pyrite (FeS) insoluble in water; it accumulates immediately under the rollers (casts) forming the black layer of 3–5 cm in thickness (Fig. 2). Below, a horizon saturated with ferrous iron (because of the absence of free oxygen) is formed; its thickness is up to 7 cm. Under this bluish gleyed horizon, the layer of yellowish sand saturated with soluble sulfates, chlorides, and soda is found [17, 25]. Thus, three EPPs can be distinguished in such formations: solonchakous, gleyzation, and sulfide accumulation. Their action leads to the development of a "layered pie" very similar in its appearance to the soil profile. This specific substrate is characterized by the positive (accumulative) balance of substances with the major role of the mechanical accumulation of organic detritus; the geochemical mechanisms of the accumulation of substances are also significant. The biogenic accumulation has an impulse character. Its products cannot be incorporated into the vertical profile to form separate horizons. Some of these products are washed off back into the lake, and other products are utilized in situ to activate the processes of the accumulation of sulfides and gleyzation.

Along with sulfate reducers and other microorganisms, large arthropods with the utilization cenotic strategy (Table 2) also serve as the agents of biogenic accumulation.

The topic tactic of utilizers is characterized by their concentration in places of ecological catastrophes with inevitable lethal end for the ecosystem. In our case, such situations are typical of the water border, where the casts of organic matter are occupied by arthropods from the adjacent temporal recreation places (shores of neighboring lakes, manure and compost heaps near cattle farms, etc.). Imago and larvae of Diptera (Stratyomyidae, Ephydridae, Syrphidae, Tendipedidae; semiaquatic and terrestrial beetles from the families of water-lovers, trailers, and staphylinides; bugs from the families Saldidae and Coreidae; etc.).

All these animals are true masters of the force majeure tactic of sudden raid. This is favored by the presence of well-developed wings and flight, as well as smell, which allows them to find the right place from the specific smell of hydrogen sulfide.

Table 2. Composition and structure of soil arthropods during the amphibian stage of the succession of halomorphic soils in the drying zone of Lake Bol'shoi Chindant (manual sorting of the casts and upper 5-cm-thick soil layer), spec. /m^2 ± error of the mean

Taxon	Casts differentiated according to the degree of decomposition of the mortmass				
	1	2	3	4	5
INSECTA: Diptera					
Tendipedidae, l.	1048 ± 397	16 ± 4	0	0	0
Heleidae, l.	1600 ± 338	512 ± 76	8 ± 3	0	0
Stratyomiidae, l.	0	18 ± 4	0	0	0
Brachycera Cyclorrhapha, l.	0	28 ± 7	20 ± 4	50 ± 5	32 ± 12
Ephydridae, l.	0	0	136 ± 7	0	0
Dolichopodidae, l.	0	4 ± 2	8 ± 3	12 ± 7	56 ± 11
Tabanidae, l.	0	0	8 ± 3	0	0
Coleoptera					
Hydrophilidae					
Cercyon melanocephalus, l.	120 ± 27	48 ± 23	12 ± 3	12 ± 7	4 ± 4
C. melanocephalus, im.	24 ± 5	576 ± 86	44 ± 5	36 ± 3	54 ± 14
C. analis, im.	0	28 ± 6	16 ± 4	0	2 ± 2
C. analis, l.	0	4 ± 3	80 ± 5	156 ± 11	32 ± 5
Dryopidae	6328 ± 570	7068 ± 1066	452 ± 46	10 ± 8	76 ± 7
Heteroceridae					
Heterocerus paralellus, im.	0	0	4 ± 3	2 ± 2	4 ± 3
H. paralellus, l.	96 ± 11	20 ± 5	156 ± 28	0	16 ± 6
Malachidae					
Malachius bipustulatus, l.	0	4 ± 3	320 ± 17	0	0
Carabidae					
Bembidion infuscatum, im.	0	10 ± 4	24 ± 11	8 ± 4	4 ± 3
Dyschirius pusillum, im.	0	0	12 ± 10	8 ± 4	8 ± 4
B. dentellum, im.	0	0	20 ± 8	8 ± 3	4 ± 4
Pogonus luridipennis, im.	0	0	12 ± 10	4 ± 3	4 ± 3
B. andreae, im.	0	0	20 ± 4	16 ± 7	4 ± 4
P. iridipennis, im.	0	4 ± 3	4 ± 4	24 ± 4	4 ± 3
D. nitidus, im.	0	0	0	2 ± 2	0
Dyschirius sp., im.	0	0	10 ± 6	30 ± 7	4 ± 3
B. latiplaga, im.	8 ± 3	8 ± 3	28 ± 6	4 ± 3	0
P. meridionalis, im.	0	0	0	8 ± 4	8 ± 3
P. punctulatus, im.	0	0	0	4 ± 3	4 ± 4
Amara marcida, im.	0	0	0	0	5 ± 3
Staphylinidae	0	64 ± 23 (2 species)	248 ± 54 (4 species)	12 ± 5 (2 species)	38 ± 9 (2 species)
Heteroptera					
Chiloxanthus pilosus im., l.	8 ± 3	48 ± 7	84 ± 12	50 ± 12	32 ± 7
Halosalda lateralis im., l.	0	8 ± 8	400 ± 40	290 ± 33	246 ± 26
Peritrechius convivus im., l.	0	16 ± 4	4 ± 4	0	0
ARANEI	0	60 ± 12 (2 species)	204 ± 32 (4 species)	40 ± 19 (2 species)	28 ± 4 (2 species)
Total species	8	23	32	22	25
Ind./m^2	9230 ± 715	8544 ± 1015	2334 ± 55	786 ± 42	669 ± 30

l.—Larvae; im.—imago; 1—fresh casts; 2, 3, 4—casts with the decreasing content of mortmass as dependent on the age; and 5—mortmass particles mixed with sand.

The trophic tactic of different ruderal arthropods is usually represented by the indiscriminative myxophagy (omnivore feeding).

The fabric tactic of utilizers is primitive, but highly efficient. Their numerous individuals are concentrated in the substrate of organic casts on the soil surface. During the summer, they literally eat their own biotope dooming themselves to the inevitable death or exodus to another suitable place. The ephemeral nature of the preferred habitat and its destruction predetermine the demographic tactic of r-selection.

The cenotic effect from all these activities is the development of gleyzation. Gleyzation is well developed during the amphibian stage of the succession. This process may take place upon the continuous and plentiful inflow of energy into the system [4]. Mobile humic compounds getting into the soil from the organic casts after their decomposition by bacteria and by the larvae and imago of arthropods serve as the major source of energy. Imago of arthropods also contribute to the mechanical destruction of organic debris and to their biochemical transformation in their digestive tract to the state of prohumic substances [22]. These prohumic substances enter the newly forming soil with animal feces. Taking into account large sizes, high abundance, high reproduction capacity of the animals, their huge biomass reaching 200–300 g/m^2, and their feces (up to 40% of the total zoomass per day), arthropods–utilizers can considered one of the most important agents of the transformation of halomorphic soils during the amphibian stage. As a result of their activity, by the end of summer, the casts of organic material disappear, and the soil under them acquires of mosaic pattern with alternation of the gleyed mottles and inclusions of jarosite.

The hydromorphic stage is represented by the soils forming for 1–3 years on the completely dried bottom of Maloe Solenoe Lake. Their characteristics are given in Table 3.

Hydromorphic habitats occupy accumulative positions in the catenas. In contrast to the amphibian stage with the pendulum-type oscillation of the water/terrestrial conditions, the hydromorphic stage is characterized by a sudden and prolonged conversion of a typically water system into the terrestrial system. The soil of the dried lake bottom is saturated with salts, and their evaporative concentration in the upper horizon takes place. Under hot and dry summer weather, salts can be transported by wind to considerable distances. The bodies of typical water inhabitants accumulate on the soil surface in the form of organic detritus. In several days, all the organic matter accumulated on the bottom of the lake is transformed into detritus. Being mixed with salts, it forms a bio-abiotic film on the surface of the dried bottom similar to that on the surface of desert takyrs. In several weeks, the dried crust exfoliates from the soil and is subjected to polygonal cracking. Cracks continue deep into the soil. We argue that the functional significance of this process deserves its separate identification as the takyric EPP. Owing to it, the soil becomes dissected by cracks and fissures ensuring the penetration of free oxygen into the previously anaerobic soil mass. The unstable FeS compound is destroyed along the walls of cracks and under the surface crust. The appearing hydrogen sulfide serves as an odor signal, which attracts terrestrial arthropods–utilizers with corresponding sensor adaptation.

The hydromorphic stage of the succession proceeds virtually without the mechanical accumulation of substances and with distinct contribution of geochemical and biogenic processes to the matter budget, though, initially, it begins without participation of higher plants. The soils are characterized by a steady decrease in the water content from 100 to about 70%, the rise in temperature of the surface layer by 0.5–2°C, and the decrease in the content of soluble salts in the upper 5 cm by about an order of magnitude in comparison with the amphibian stage of the succession. As a rule, the soils of the hydromorphic stage form a series of variants somewhat differing in their age and properties (positions *0*, *1*, *2*, *3*; Fig. 1). A distinctive feature of positions *1* and *2* is the absence of higher plants. In position *2,* single saltworts appear by the fall of the first year of the bottom drying. Continuous covers of saltworts, halophytic grasses, and forbs appear on the next year, provided that no new ponding of the dried bottom takes place. In such a short period, the activation and then hampering of the EPPs of sulfide accumulation and gleyzation take place. The corresponding soil horizons appear and then become subjected to degradation. By the end of the hydromorphic stage, the solonchakous EPPs becomes weaker, whereas the soddy meadow EPPs becomes is developed.

In the absence of higher plants, weak development of microflora, and a relatively small role of mechanical processes, the major role in this transformation belongs to large soil arthropods, mainly insects and spiders [17, 27, 28] (Table 4).

Their number is dynamic and averages about 200 specimens/(m^2 day), which is significantly smaller than that during the amphibian stage of the succession. However, the ratio of zoomass to the mass of organic detritus at the hydromorphic stage is much narrower than that during the amphibian stage (1 : 3 and 1 : 100, respectively). Animals–utilizers remain the major inhabitants of the dried bottom; in particular, these are *Cephalota elegans* beetles. According to the isotopic analysis, ground beetles *Pogonistes rufoaeneus, Cephalota elegans,* and *Cymindis equestris* act as obligate zoophages; the former two species feed themselves with amphibionts, and the third species prefers terrestrial preys [14]. However, their way of feeding is an extraintestinal digestion, which allows us to partially qualify such predators as detritophages. Other insects are characterized by the high variability of isotopic "signatures" for nitrogen and carbon, which may

Table 3. Characteristics of the topsoil (0–5 cm) layer in the coastal catena of Maloe Solenoe Lake

Soil characteristics	Catenary position				
	2	3	4	5	6
Soil temperature (June 17–August 22, 2011) °C					
minimum	11	13	12.5	12	12
maximum	44	31.5	30	39.5	45
mean	22.8 ± 6.74	21.4 ± 3.80	20.2 ± 3.47	23.0 ± 5.74	23.9 ± 6.65
Relative water content, % of the total soil water capacity	100	100	100	100	15–100 (40)
Groundwater level, m	0.05–0.3	0.1–0.3	0.5–0.9	0.5–0.9	>2
Humic acids, % of C_{org}, June 2011	15.4	35.1	33.0	37.2	40.5
August 2011	17.6	29.7	21.2	30.0	32.8
C_{org}, % of soil					
June 2011	1.1	0.77	0.91	2.9	2.54
August 2011	0.34	0.37	0.66	2.83	2.56
C in soil (bulk elemental analysis) in August 2013, %	0.82 ± 0.41	1.6 ± 0.81	1.4 ± 0.44	2 ± 0.19	5.48 ± 1.37
Sum of salts, % (per air-dried sample)					
June 2011	8.14	6.47	8.46	3.55	1.23
August 2011	4.96	0.63	6.69	5.59	0.46
Composition of salts, cmol/kg (June 2011)					
CO_3^{2-}	0	0	0	0	0
HCO_3^-	0.8	0.72	0.72	0.76	0.72
Cl^-	70	64	60	48.5	8.9
SO_4^{2-}	60	40.0	72.6	11.4	9.8
Ca^{2+}	8	10	12.5	6	5.55
Mg^{2+}	24.5	13.5	21	13	3.25
$Na^+ + K^+$	98.3	81.2	99.8	41.7	10.6
Sum of cations	130.8	104.7	133.3	60.7	19.4
Composition of salts, cmol/kg (August 2011)					
CO_3^{2-}	0.04	0	0	0	0
HCO_3^-	0.56	0.4	0.76	1	0.84
Cl^-	42.3	5.6	35.5	60.8	3.8
SO_4^{2-}	37.1	4.1	66.0	23.5	2.6
Ca^{2+}	4	1.7	3.9	11	1.76
Mg^{2+}	17.5	1.98	12.1	21.3	1.14
$Na^+ + K^+$	58.5	6.4	86.3	52.9	4.4
Sum of cations	80.0	10.1	102.3	85.2	7.3

Catenary position: 2—playa sulfidic solonchak (Gleyic Solonchak), 3—typical solonchak (Gleyic Solonchak), 4—solonchak over buried solonetz (Gleyic Solonchak (Thapto-Solonetz)), 5—shallow to medium-deep solonetz–solonchak (Salic Solonetz), 6—solonetzic solonchakous meadow-chernozemic soil (Luvic Gleyic Chernozem (Sodic. Endosalic)).

Table 4. Numbers of dominant species of arthropods at different stages of the succession of halohydromorphic soils in the drying zone of Maloe Solenoe Lake, specimens/(m^2/day), ± error of the mean

Parameter		Succession stage					
		1	2	3	4	5	6
Total number of specimens		359.2 ± 132.4	324.1 ± 150.6	185.1 ± 86.3	77.3 ± 44.8	115.8 ± 59.7	84.9 ± 48.1
Total number of species		17	16	42	32	40	41
U	*Cariodioderus chlorotichus*	**255 ± 74.5**	**187 ± 76.9**	0	0	0	0
U	*Pogonistes rufoaeneus*	**38.8 ± 12.1**	**35.4 ± 7.4**	5.6 ± 3.1	2.9 ± 1.7	0	0
R	*Gryllotalpa unispina*	3.8 ± 2.5	12.1 ± 5.3	**35.3 ± 6.5**	5.2 ± 2.6	0	0
U	*Cephalota elegans*	**20 ± 13.3**	**29 ± 15.6**	2 ± 1.4	1.5 ± 1	0.8 ± 0.8	0
U	*Labidura riparia*	**24 ± 14.5**	**40.6 ± 3**	16 ± 7.5	0.8 ± 0.8	1.4 ± 0.9	0
R	*Cymindis equestris*	2.1 ± 1.4	6 ± 4.1	**40.5 ± 12.1**	12.7 ± 5.5	5.6 ± 3	0
R	*Daptus vittatus*	0	3.5 ± 2.6	**24.9 ± 11.2**	2.1 ± 1.6	0	0
ST	*Pogonistes convexcollis*	0	0	3.9 ± 1.7	**10 ± 3.6**	**7.6 ± 3.2**	0
ST	*Epachromius pilverilentus*	0	0	2.4 ± 1.9	2.1 ± 1.1	**9.7 ± 4.1**	1.5 ± 1
ST	*Pogonus meridionalis*	0	0	0	**10 ± 3.6**	0	0
ST	*Cephalota chiloleuca*	0	0	0	0	**22.2 ± 7.3**	0
ST	*Modicogryllus frontalis*	0	0	0	0	**9.6 ± 3.6**	2.9 ± 1.4
ST	*Curtonotus propinquus*	0	0	0	0	**8.2 ± 2.8**	2.9 ± 1.7
C	*Poecilus fortipes*	0	0	0	0	2.8 ± 1.5	**8.5 ± 2.9**
C	*Calathus erratus*	0	0	0	0	0	**3.9 ± 1.5**
	Aranei in total (according to [28])	6.4	7.3	20.8	24.8	23.9	34.2

Succession stages: (1–2) amphibian, (3) hydromorphic, (4–5) semihydromorphic, and (6) paleohydromorphic. Cenotic strategies: U—utilizers, R—ruderal species, ST—stress-tolerant species, and C—competitive species. Preferential biotopes for given species are shown in bold.

attest to their polyphage nature [14]. This trophic tactic is in line with the utilization cenotic strategy. By the fall, utilizers give way to ruderals—engineers. Ground beetles of the *Dyschirius* are the first to penetrate under the takyric crust and create a dense network of subhorizontal tunnels there. This air reservoir becomes occupied by other small arthropods (staphyllinides, ground beetles of the genera *Bembidion, Pogonus, Cardiaderus,* etc.). Then, they penetrate deeper into the soil along numerous biogenic and abiogenic fissures. Oxidation of unstable FeS and Fe_3O_4 takes place along the fissures, and their walls acquire ocherous color. At the same time, the main mass of the soil inside the polygons remains under anaerobic conditions until the beetles from the Heteroceridae family start their work. They appear in position *1* in two—three weeks. Imago of these beetles create vertical burrows of 4–5 mm in diameter to the depth of 7–15 cm; they lay eggs into lateral extensions of such burrows. They keep organic detritus in these side channels for further larvae. The soil thrown out from the burrows is a loose substrate with granular structure; the content of chlorides and sulfates of Na^+ and K^+ in such casts reaches 8.3% in comparison with about 3.1% in the surrounding soil mass beyond the burrows. The density of the burrows left by these beetles on the dried bottom of Lake Abyshkan may reach 110 spec./m^2. The air-dry mass of a single cast is about 8.5 g; however. the total mass of such casts reaches 935 g/m^2. The soil crust saturated with salts is gradually subjected to degradation and wind erosion; gradually, it becomes scattered over the entire playa surface. As animal casts on the soil surface are also saturated with animal metabolites, we can suppose that this factor plays an important role in the formation of salt crusts with organic matter within the entire playa surface. The network of burrows left by *Heterocerus fenestratus* can play a significant role in the further cracking of the soil.

In a month, these beetles in position *2* are replaced by *Daptus* beetles. The density of the vertical burrows of the latter in the soil studied at Lake Abyshkan reaches 90 spec. /m^2; at Maloe Solenoe Lake, it is somewhat lower. Under the salt crust, horizontal tunnels in the soil are also made by *Labidura riparia* reaching the density of 3–41 spec./(m^2 day). These ruderal burrowing species ensure degradation of the sulfidic horizon of the solonchak and the formation of a system of tunnels increasing the soil porosity by 30–50%.

The formation of a typical solonchak in place of the former lake bottom takes place on the next year. It marks the end of the hydromorphic stage (provided that the lake level remains low). At the stage of solonchak, the role of ruderal animals is still very important. Small arthropods preserved in the solonchak (e.g., *Dicheirotrichus* beetles) are complemented with large arthropods of several centimeters in length. The most considerable burrowing is performed by *Gryllotalpa unispina*, by *Broscus* and *Scarites* ground beetles, and by some spiders. The range of their topic preferences is extended to 3–5 habitats. Their phoric tactics are not limited to migration in the environment to different places; they actively move inside the soil. One large mole cricket loosens the soil within a 3-cm-wide strip to a depth of 5–7 cm; it completely tills the area of about 3 m^2 per day. Taking into account the density of mole crickets (up to 35 spec./(m^2 day), their burrowing activity can be considered an important factor in stimulating the washing regime in a typical solonchak and, as a consequence, reducing the amount of soluble salts by twofold as compared with that in the sulfide solonchak. The soil loosened by mole crickets and other ruderal animals is also densely fertilized with their feces stimulating the microbial activity and humus accumulation processes. Thus, the activity of mole crickets and other ruderal arthropods favors the removal of soluble salts and aeration of the soil and activates humification processes.

In total, **the cenotic activity** of ruderal arthropods during the hydromorphic stage of the succession turns the perished water ecosystem into the subaerial terrestrial ecosystem with true normally developed soils, in which at least three different EPPs are active being regulated by the activity of the arthropods.

The semihydromorphic stage was most distinctly manifested within the trans-accumulative position of the catena on the shore of Maloe Solenoe Lake. Both biotopes (*4* and *5*) were marked by the high variability in their hydrothermic conditions and salt and water regimes of the soils. Sharp fluctuations in the limiting factors resulted in the formation of soils with the reputation of "two-faced Janus" owing to the rivalry of solonetzic and solonchakous EPPs. In the years with low water level in the lakes, the soils of the trans-accumulative position are developed under conditions of the percolative soil water regime. The salts are leached off with lateral and vertical flows from the upper part of the soil profile. In 30–50 years, a morphologically distinct solonetzic and a thin soddy horizon are formed in the soil profile. The appearance of vascular plants (mainly, *Atriplex patens*) with the high projective cover (up to 80% in position *5*) contributes to the accumulation of humus. However, at the beginning of this stage (position *4*), the solonchakous (salinization) process is still active between the shrubs of *Halocnemum strobilaceum* and *Atriplex*; it is manifested on about 90% of the surface in position *4* and 15% in position *5*. In the periods of high water level in the lakes, the solonetzic process is stopped. The ascending migration of strongly mineral groundwater takes place and soluble salts form salt efflorescence of the soil surface. This may be favored by the water uptake by the roots of edifying shrubs. In the case of the long period of such an inversive (solonchakous) development, *Atriplex* is replaced by *Halocnemum,* which is more tolerant toward salinization and waterlogging. Salt efflorescence on the surface actually bury the solonetzic horizon for a long time [26].

The appearance of higher plants sharply increases the biogenic accumulation of matter against the background of the vividly displayed geochemical and attenuating mechanical components of the matter budget of the halomorphic pedogenesis. A characteristic feature of this stage is the substitution of vascular plants for invertebrates as the dominant factors of the biogenic accumulation of substances. The number and biomass of arthropods at this stage are 2.5 to 3.5 times lower than during the previous stage; at the same time, their species diversity increases up to 42 species [27]. The two-sided nature of the soils allows the successful existence of the animals with the stress-tolerant cenotic strategy.

As the sum of salts in the soil between the *Halocnemum* and *Atriplex* shrubs does not decrease (moreover, it increases up to the level of a typical sor (playa) solonchak because of the location of position *4* in a microdepression), both ecosystems of the semihydromorphic stage acquire the external features and functioning typical of true deserts. The portion of stress-tolerant species reaches 51% of the total number of species in habitat *4* and 75% in habitat *5* (Fig. 3); it is reliably higher than that in the other studied positions. With respect to their trophic status, such species are either obligate zoophages (five species of ground beetles from the tribe Pogonini, *Cymindis equestris*, *Cephalota* genus, etc.), or variophages (ground beetles of the *Broscus* and *Curtonotus* genera; crickets of the *Modicogryllus* genus). Burrowing activity is virtually impossible in the fluffy salt layer on the surface and in the dense substrate of the solonetzic horizon. Therefore, there are virtually no stress-tolerant species of arthropods equipped with the tools for burrowing. Instead, they are replaced by species with a constriction in the middle of their bodies making it possible for them to bend and enter narrow fissures typical of the solonetzes and channels left by the roots of edifying shrubs. The phoric tactic of stress-tolerators is to temporally occupy the soil with preservation of adaptations for immediate evacuation upon the extreme ecological situation, which is not infrequent at this stage of the succession.

The cenotic effect from the activity of stress-tolerators is manifested by the inclusion of their consortia as basic elements of the structural arrangement of the

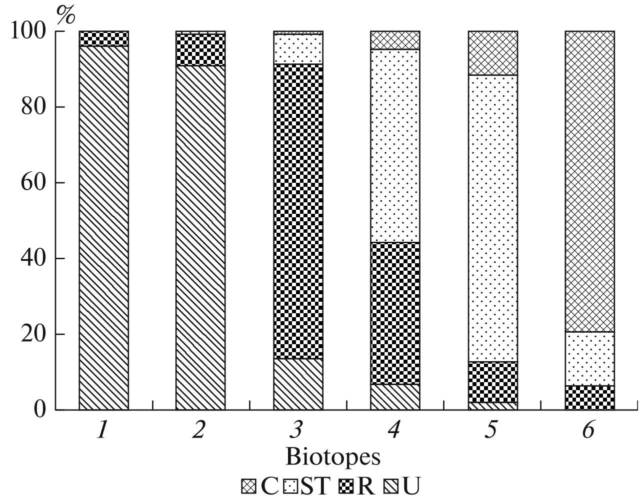

Fig. 3. Relationships between the numbers of representatives of different cenotic strategies along the coastal catena at Maloe Solenoe Lake: U—utilizers, R—ruderal species, ST—salt-tolerant species, and C—competitive species.

ecosystem that should guarantee its further long-term directed development.

The paleohydromorphic stage was studied within the transeluvial part of the catena on the shore of Maloe Solenoe Lake (position *6* with a solonetzic and solonchakous chernozemic-meadow soil) characterized by the active development of humus accumulation of the meadow type. In contrast to hydromorphic soils, this soil is characterized by higher temperatures in the upper horizon. In the period of our studies, the soil water content varied from 15 to 40%, but it never was as high at that at the lower positions in the catena. The organic carbon content in the soddy soil layer at this stage reached 2.5%, or twice as high as that during the previous succession stage; the content of humic acids reached 37% of C_{org}. The pool of soluble salts decreased by 8–18 times in comparison with the hydromorphic soils and by 3.5 times in comparison with the semihydromorphic soil. Anions Cl^- and SO_4^{2-}, and cations Na^+ and K^+ were still present in the composition of salts, but the portion of HCO_3^- and Ca^{2+} increased considerably.

Direct impact of invertebrates on the chemical composition of salts is well known. For example, ants bring carbonate minerals onto the soil surface during the construction of their underground tunnels. As shown by Frouz with coauthors, the calcium content increases in the soil near ant hills [32].

The species diversity of vegetation during the terminal stage of the succession increases by several times in comparison with the previous stage. The portion of halophytic plants decreases to several percent of the total projective cover. The presence of sod mats of *Achnatherum splendens* can be considered an indication of the active desolonetzization of the soil. The biogenic accumulation of substances predominates over the geochemical and mechanical accumulation. Among the biogenic agents, the role of large invertebrates is smaller than the role of vascular plants. The dominance of the latter (they cover up to 95% of the surface) results in the increased production of difficultly decomposable cellulose and lignin, so that the organic matter is sequestered in the soil. The biological turnover typical of herbaceous ecosystems is formed. Food webs of the pasturing type predominate over detrital food webs. As a result, living conditions favor the development of arthropods–K-strategists competing for resources. Their portion in the animal population of the soil increases up to 87% of the total number of specimens (Fig. 3). Obligate phytophages (*Epachromius pulverilentus*) or the species combining predation and phytophagy (ground beetles of the *Harpalus, Poecilus,* and *Amara* genera) predominate in the community. In this case, phytophagy can be considered an element of competitive cenotic strategy. The fabric tactic includes the diffusive distribution of specimens, which is favored by the homogeneity of the soddy soil horizon. Species-competitors are characterized by the long-term colonization supported by the stability of the taxonomic composition and density of the population of arthropods. However, their density is minimal in the sequence of halomorphic soils (about 100 spec./(m^2 day). At the same time, their species diversity reaches its maximum (more than 45 species) owing to multiple and diverse ecological niches.

The resulting **cenotic effect** during the final stage of the halomorphic soil succession is manifested by the establishment of the biological turnover and pedogenesis typical of the forest-steppe biome. The role of invertebrates in the transformation of the soil mass and its organic components is by far smaller than the role of plants. At the same time, animals indirectly stimulate pedogenesis via their feces that are especially abundant for phytophages owing to the low coefficient of nutrient assimilation.

CONCLUSIONS

Soil sequences along catenas across peripheral parts of the depressions with shallow-water drying salt lakes in the south of Siberia can be also considered the series of stages of the historical development of halomorphic soils: the amphibian, hydromorphic, semihydromorphic, and automorphic–paleohydromorphic stages. During the initial stages of halopedogenesis, a considerable role in the matter budget belongs to the biogenic components against the background of a relatively weak contribution of the mechanical and geochemical components. At the same time, the activity of microflora at these stages is low, and vascular plants are absent or are present in small amounts, whereas the species diversity, number, and functional activity of large invertebrates (particularly, insects and spiders) are high. Their total abundance in the course of the succession of halomorphic soils decreases from several thousand to about 100 spec./(m^2 day), but the species diversity increases from 17 to 45 species. However, an important driving force of the soil formation is the sequential replacement of cenotic strategies and adaptive tactics of invertebrates in their interaction with the bio-abiotic environment rather than the changes in the composition and number of species and their abundance.

The amphibian stage of halopedogenesis is ensured by the invertebrates with the utilization strategy dwelling in the casts of organic detritus from the lake on the soil surface. As myxophages, these animals "eat their own house" and supply the underlying anaerobic substrate with energy sources ensuring energy-consuming EPPs of the accumulation of sulfides and gleyzation.

During the next hydromorphic solonchakous stage of the succession, the invertebrates–utilizers are replaced by the invertebrates with the ruderal cenotic strategy. They withstand the extreme environment due to their capacity to vary feeding traits, to use several habitats (from the single habitat typical of the utilizers to three–four different habitats), to migrate, and to improve their habitats via engineering activity, i.e., via digging burrows in the soil. Along with the physical fissuring and cracking processes, the burrowing activity of invertebrates at this stage increases the soil porosity by many times, which ensures aeration of the previously anaerobic soil, favors the development of vascular plants, and provides for the enhanced humus accumulation. The work of ruderal species of arthropods results in attenuation of the accumulation of sulfides and gleyzation, hampering of salinization (solonchakous) process, and degradation of the corresponding horizons in the soil profile.

During the semihydromorphic solonchakous–solonetzic stage of halopedogenesis, ruderal species with their mobile responses to stress are replaced by the stress-tolerant invertebrates. Their adaptive tactics make it possible to survive and withstand the action of stress without migration; they form consortia with plants–edifiers that appear at this stage of the soil transformation. Invertebrates in symbiotic relationships with the plants exert powerful influence on the soils. Finally, during the paleohydromorphic stage of halopedogenesis, invertebrates with the competitive cenotic strategy become the dominant species in the soil zoocenosis. They tend to the diffuse distribution in the soddy soil horizons and occupy relatively narrow ecological niches. The direct influence of such competitors on the soil is relatively small in comparison with the influence of vascular plants. However, metabolic products of these animals dispersed in the soil become the centers of microbial activity and, thus, regulate humus accumulation processes.

Taking into account the important role of invertebrates ensuring the high rate and degree of transformation of substances in halomorphic soils on the drying bottoms of salt lakes and the directed trend of this transformation, we may consider this process an ecological succession and analyze it with the use of the concepts and terms of the succession theory.

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