

Zoological Aspects of Ecological Succession on the Graded-Flat Dump of the Nazarovo Lignite Open-Cast Mine in Krasnoyarsk Krai

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Abstract—This paper presents the results of a study on the population of ground beetles (Coleoptera, Carabidae) on graded-flat dumps of the Kansk-Achinsk fuel and energy complex (KATEK) in the south of Krasnoyarsk krai in 1983–1985. In total, seven plots are examined, ranging in age from several weeks to 26 years. Abundance and species richness exhibit undulatory changes in the ground-beetle population of a sequence of unevenly aged communities. These demographic parameters have been found to be at a relatively high level in three communities, namely, pioneer (less than 1-year-old), initial (2-year-old), and medial (26 years). The three communities, which are the reference standards for the above stages, are distinguished by their own set of preferential species with a high density of populations in key habitats. Over a quarter-century succession in carabidocenosis, three types of the cenotic strategy (specific combinations of adaptive tactics) gradually replace one another in the following sequence: extreme pioneers → ruderal → stress-tolerant. The parameters of ground-beetle population succession and the order of their replacement on the graded dump are essentially different from the population of the dump with the differentiation of habitats by mesorelief. Under conditions of the gently rolling drawlike relief, the composition and structure of the 25-year-old beetle population approached the native standards of the forest-steppe biome much more closely than in the plateau conditions of the graded dump.

Keywords: Carabid beetles, open-cast mines, successions, life strategies

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INTRODUCTION

An increase in scale, pace, and diversity of anthropogenic impacts on the environment has led to biologists turning to problems of dynamic ecology, which have been the focus of attention of more than half of the biological literature published globally since the 1970s–1980s onwards (Mirkin and Naumova, 2012). Most attention has been paid to ecological successions (*Suktsessii i biologicheskii krugovorot...*, 1993; Titlyanova and Sambuu, 2016; Pormenter et al., 1987; Frouz et al., 2008). Contentious debates unfold with respect to the typology of successions; their compatibility in different taxa of biota; the dependence of the self-development of a community on ecological relationships not only inside the considered community, but also adjacent communities; the validity and practicality of analogies between chronological sequences of communities in one habitat and sequences of unevenly aged ecosystems scattered in space; and the role of abiotic trends as triggers of succession (Mordkovich, 2017; Johnson and Miyanishi, 2008; Mirkin and Naumova, 2012).

The indicated problems are difficult to observe within integral dynamics of complexly organized native ecosystems, but they become more apparent in

“reduced to lowest term” ecosystems of industrial anthropogenic dumps. The area occupied by industrially disturbed soil has been rapidly expanding, which offers ecologists a unique opportunity for experimenting with different variants of successions, unfolding in an uncommon pattern at high rates. The mentioned perspectives attract the increased attention of professionals in various fields. Even the first studies into dumps of lignite basins in Europe, North America, and Siberia generated unforeseen results, which fundamentally changed attitudes towards earlier undisputable canons of successional theory formulated by recognized scientists in the field of phytocenology as applied to native ecosystems (Grime, 1979; Clements and Shelford, 1939; Mirkin and Naumova, 2012). Pioneers—founders, initiating the succession, have proved to be not the ruderal embryophyte species, but rather the invertebrate edaphobionts (geobionts) that are adapted to passive and active phoresy, airland on the dumps during the first hours of the emergence of the latter, and form functionally effective communities long before plants become involved and established in the successions (Dunger, 1968). It was further discovered that the first ecological relationships in dump ecosystems are formed by invertebrate utilizers of mort

mass inherited from the preceding destroyed ecosystem or disseminated by wind and water from surrounding native cenoses. The activity of utilizers in the top layer of the dump substrate, which previously was an inert medium, gives rise to humification processes (0.5 mg C/year per 1 g of substrate over the initial 30 years), which soon begin to dominate over mineralization and generate conditions necessary for the germination of ruderal species seeds (*Suktsessii i biologicheskii krugovorot...*, 1993; Shugalei, 2009; Topp et al., 2001). The dump sites of the coal-mining enterprises in particular have been found to be home for ecosystems forming and sequentially replacing each other, which, though not possible in native landscapes, follow the zonal trend in their successional development. In practice, however, even after 50 years, they fail to attain the climax state typical for ecosystems of a corresponding biome (Babenko, 1982; Burykin, 1985; Dmitriyenko, 1990; *Suktsessii i biologicheskii krugovorot...*, 1993; Brandle et al., 2000).

Based on the analysis, different subpopulations of biota demonstrated different rates, pace, and even directions of the successions among different taxa of animals and plants (*Suktsessii i biologicheskii krugovorot...*, 1993). As is illustrated by multiple examples in biocenoses of coal-mining dumps, species diversity, being extremely low in the beginning of succession (from two to four species), grows with time. Moreover, species typical of the terminal successional stages emerge as early as in the first year of succession, even if there are very few of them. On the other hand, pioneer species continue to maintain dominant positions in phytocenoses aged 20–30 and even 50 years. Among living organisms, decomposers, i.e., microorganisms and protists are the ones that most promptly and effectively become involved in biotic turnover, followed by heterotroph invertebrates. The latter largely feature arthropods, i.e., springtails and beetle mites, which emerge in the dump substrate as early as the next day after piling and achieve high numbers as early as in 1 month. Subsequently, in the course of succession, numbers are growing multifold, but only on account of a few euribiont species (beetle mites *Oppiella nova*, *Tectocephus velatus*, etc.) (Babenko, 1982; Dmitriyenko, 1990; *Suktsessii i biologicheskii krugovorot...*, 1993; Stebaeva and Andrievskii, 1997).

Soil large- and medium-sized arthropods (mesofauna), contrary to popular belief, inhabit the dumps prior to not only plants, but also microarthropods, using both passive and active ways of phoresy. Mesofauna specimens employ their α -diversity potential more selectively and pointedly when compared with microarthropods. The most successful at colonizing the poor substrate of the dump are small omnivorous r-strategists well adapted to flight, either combining or alternating myceto-, algo-, zoo-, sapro-, and phytagogy. The most diverse and abundant species on the dumps include ground beetles, rove beetles, typical bugs, and spiders able to use void space or dig burrows

in the substrate (Mordkovich, 1994; Mordkovich and Kulagin, 1986; Dmitriyenko and Shaimuratova, 1986; Pormetner et al., 1987). Similar to microarthropods, mesofauna pioneer species persist in the communities of the mature and even terminal successional stages of up to 30 years of age. However, their representation in mature communities is much lower than of microarthropods (Frouz et al., 2007; Luzyanin et al., 2015).

The significant role of the mesorelief is evident from the technological standards for land revegetation. The technical preparatory stage of the reclamation entails two options for the removal of overburden during dumping: (a) the formation and subsequent keeping of drawlike topography and (b) grading and transforming the dump into a flat land largely uniform in parameters except for age of plots graded in due order year after year (Motorina, 1986).

These provisions predetermined the goal of the present research study, which is to understand in what way flattening of the drawlike rolling relief is reflected upon the parameters of biodiversity in zoedaphon, in particular, and succession.

To attain this goal, it is necessary to answer the following questions:

- (1) Whether changes in the composition and ecological structure of ground beetles are stochastic in nature or are a predictable order typical of the successions.
- (2) Providing a pattern of changes in carabidae–cenosis corresponds in its multiyear dynamics to the successional order status and how it agrees with a successional pattern of other components of industrially disturbed ecosystems.
- (3) Whether the change process in composition and structure of ground-beetle communities is reversible.
- (4) In what way changeover in species composition from the pioneer to initial and, subsequently, to medial stages of community development reflects upon the transformation of biocenotic relationships.
- (5) How a system of biocenotic relationships in the community correlates with types of life strategy, the changeover of which is traditionally considered the driving force for the succession.
- (6) Whether and how the following coincide or differ: direction, rate, and order of succession, as well as the extent of its progression on dumps with a graded-flat relief and those where a rolling topography has been preserved.

MATERIALS AND METHODS

The study area where research was conducted is located on a site of KATEK (the Kansk–Achinsk Fuel and Energy Complex). The plots were arranged on an external dump, i.e., outside the boundaries of open pits where coal is extracted, of the Nazarovskii open-cast mine, 10 km south of the town of Nazarovo in

Table 1. Ecological conditions in unevenly aged habitats without human intervention on a graded-flat dump of Nazarovskii lignite open-cast mine of KATEK

| Environmental parameters | Habitat no. | | | | | | |
|---|------------------------|---|---|--|---|---|---|
| | 0 | 1 | 2 | 3 | 4 | 5 | 26 |
| Dates recorded | Aug. 1–30, 1983 | June–Aug., 1984 | June–Aug., 1984 | June–Aug., 1985 | June–Aug., 1984 | June–Aug., 1985 | June–Aug., 1984 |
| Relative age of habitat | 1–30 days | 1 year | 2 years | 3 years | 4 years | 5 years | 26 years |
| Amount of summer precipitation, mm | 224 | 253 | 253 | 261 | 253 | 261 | 253 |
| Soil moisture, % 0–5 cm, June 26, 1984 | 15.9 | 19.6 | 19.5 | 19.9 | 22.3 | 24.5 | 30.7 |
| C _{org} , depth 0–5 cm, %, June 1984 | 0.11 | 0.13 | 0.16 | 0.17 | 0.29 | 0.50 | 7.63 |
| Overall phytomass stock, g/m ² , July 1984 | Mort mass appr. 500 | 207 | 569 | 1600 | 1335 | 2173 | 2604 |
| Vegetation cover, % | 0 | 30 | 90 | 90 | 70 | 80 | 90 |
| Number of plant species | 0 | 14 | 34 | 40 | 45 | 48 | 60 |
| Plant dominance in the order of decreasing significance | No plants | <i>Melilotus albus</i> <i>Trifolium pratense</i> <i>Cirsium setosum</i> | <i>C. setosum</i> <i>M. albus</i> <i>Elytrigia rep- ens</i> <i>T. pratense</i> | <i>Agrostis gigantea</i> <i>M. albus</i> <i>Artemisia annua</i> <i>C. setosum</i> <i>T. pratense</i> | <i>A. gigantea</i> <i>M. albus</i> <i>Trifolium pratense</i> <i>C. setosum</i> <i>Poa pratensis</i> | <i>E. repens</i> <i>A. gigantea</i> <i>P. pratensis</i> <i>T. pratense</i> | <i>E. repens</i> <i>P. pratensis</i> <i>A. gigantea</i> <i>T. repens</i> |

The numerical order of habitats corresponds to their absolute age from the moment of their technical revegetation (site planning). Data on mort mass of the destroyed cenosis no. 0 are provided according to (*Suktsessii i biologicheskii krugovorot...*, 1993).

Krasnoyarsk krai. The examined dump was piled during the period from 1954 to 1972 to the Chertovo Lake floodplain, which was an oxbow lake of the Chulym River.

Biological revegetation of the dump continued for 20 years without human intervention through passive and active phoresy in microflora, protists, plants, and animals from the surrounding landscapes and agrocenoses of the forest-steppe biome.

From 1958 to 1983, the rolling relief of the dump was graded and transformed into a flat raised plain stripped of the diverse habitats and biocenoses that had established over 25 years of the revegetation. The first series of planning was attempted in 1958 (habitat no. 26), but soon cut short. Subsequent grading did not embrace the entire area of the dump, but was rather done on a step-by-step basis from year to year. During this process, another six habitats were identified, which differed in age starting from the moment of planning, but shared the same positions in manmade terrain (*plakor*), were underlain by the same rock (quaternary loam with admixed sandstone, broken siltstone rocks, and fine-grain lignite), and received equal mean precipitation amount per growing season (220–260 mm) with the equal sum of summer temperatures in the 5-cm-thick ground layer (Table 1).

Thus, the observed spatial sequence of habitats and their biocenoses can be reasonably considered a near-perfect successional chronological sequence. The described succession was deemed secondary (*Suktsessii i biologicheskii krugovorot...*, 1993).

Habitat Description

The research was conducted in 1983–1985. The numerical order of the habitats and associated communities correspond to their absolute age starting from the moment the relief was smoothed. Brief comparative descriptions of the habitats are presented in Table 1.

Habitat no. 0 was revegetated at the end of summer of 1983. With the absolute age of 15 days by the time of the examination, it featured a bare loam deprived of live vegetation, but with fragments of the 30-year-old long-fallow meadow mort mass.

Habitat no. 3 is basically the same site as no. 2, but a year later (in 1985). The same holds for habitats 4 and 5.

Habitat no. 26 is the oldest in the considered land-fill (graded in 1958). With the absolute age of 26 years old by the time of the examination, it is a procenosis dissimilar to the zonal meadow or meadow-steppe cenoses based on most parameters (*Suktsessii i biolog-*

icheskii krugovorot..., 1993; Titlaynova et al., 1988); in regards to the phytomass stock, it nearly has achieved a level of zonal upland meadows (av. 2604 and 2800 g/m²). Soil moisture in top layer and C_{org} content on the plot is on par with native meadow soils and forest-steppe chernozems (*Suktsessii i biologicheskii krugovorot...*, 1993).

Thus, the described chronological sequence of ecosystems displays a pronounced gradual increase in the plant α -diversity from 0 to 60 species, in the cover from 0 to 90%, and phytomass stock from 207 to 2604 g/m². Against the ongoing dominance of common clover over the entire recorded period, the orderly replacement of dominant species was reported at each stage of development, specifically, for ruderal forbs by rhizomatous plants and subsequently by sod-forming grass. At the age of 26, the common clover is substituted by the white clover. As succession progresses, soil moisture rises from 15.9 to 30.7%, while C_{org} increases from 0.11 to 7.7%. This trend indicates the improvement of habitat-condition comfort level for zoedaphon with time (Table 1).

Zoological material was collected over the period from 1983 to 1985 monthly from June to August in all aforementioned described habitats using the conventional pitfall trap method. The latter employed flower pots 10 cm in diameter and 12 cm in depth without the use of preservatives and water, which artificially improves the trapping capacity of the method. The traps were dug into the soil flush with its surface in tens on each habitat spaced 1 m apart in three rows and were exposed every month for 5 consecutive days. Data from the three summer months were summarized for each habitat. The resultant data was rated for as 50 trap days (10 traps \times 5 days).

Additionally, we determined the Menhinick's diversity index and the Bray–Curtis index of dissimilarity. The latter involved multidimensional scaling. The calculations were performed using the PAST software (Hammer et al., 2001).

RESULTS

Mesofauna on the dump was found to be largely composed of ground beetle imagines, whose population numbered hundreds of individuals per record unit. In the total population, they accounted for 96% in the newborn community, 70–80% in middle-aged community, and 60–65% in the terminal community. The overall diversity of ground beetles included 46 species, which exceeds the species diversity in other arthropods on the dump five- to eightfold. In addition to ground beetles, the studied landfill featured rove beetles (Staphylinidae), antlike beetles (Anthicidae), and true or snout weevils (Curculionidae), as well as bugs in the families of Saldidae and Lygaeidae, stone centipedes (Lithobiidae), spiders (Araneae), and harvestmen (Opiliones). Ground beetles proved to be the object most suited for solving the set objectives, inas-

much as the present research is based on the comparison principle. The distribution of their population across the habitats is shown in Table 2.

The population of ground beetles from newly born habitat no. 0 started forming in the next few hours after the dump grading. As for the former inhabitants of the destroyed carabidae-cenosis, only occasional specimens were detected, including *Bembidion properans*, *Microlestes minutulus*, and *Synuchus vivalis*, whose numbers had peaked at several dozens and hundreds per record unit at this same location as recently as a few days earlier. Because of the reduction in their population to minimum due to grading, the aforementioned species should be classified as atavistic elements in the newly forming community. At the same time, *B. femoratum* and *B. quadrimaculatum*, the number of which totaled 466 individuals per 50 trap-days (t-d) as early as in 2 weeks, undoubtedly can be called pioneers. Based on their physiological characteristics, the beetles could not have reproduced on-site on such a scale over such a short period. They air landed from the neighboring native and anthropogenic ecosystems where their population density is high (Mordkovich, 1970). Two to 3 weeks later, *Amara fulva* and *Poecilus curpeus* joined the above, but with a population an order of magnitude smaller than in *Bembidion*. Total species richness amounted to only nine species in the pioneer community by the end of the first month, while being accompanied by an extraordinary high population size.

The ground beetle population of habitat no. 1 combines species typical of both the initial and 2-year-old communities. Among the dump pioneers, only *B. quadrimaculatum* remains dominant (200 ind./50 t-d), as opposed to *B. femoratum*, whose numbers rapidly decline (Table 2). Numbers of subdominant *A. fulva* and *P. cupreus* persist at a moderate level. At the same time, diverse (though low in numbers) ground-beetle species occur, which will attain the maximum abundance further down the road, i.e., in the second-year community (*Asaphidion pallipes*, *Notiophilus aquaticus*, *Amara apricaria*, *Curtonotus aulicus*, *C. convexiusculus*, *Harpalus rufipes*, *H. affinis*, *P. lepidus*, *B. properans*, *P. versicolor*, *Calathus melanocephalus*, *M. minutulus*, *Clivina fessor*, and *Pseudophonus griseus*). Due to them, the total species richness of ground beetles leaps 2.6-fold up to 23 species in the 1-year-old community when compared with the preceding pioneer community. The emergence of multiple newcomers with modest population numbers does not, however, compensate for the loss in summed abundance of the population from 497 to 336 ind./50 t-d, resulting from a sharp drop in numbers of pioneer species *B. femoratum*.

The ground-beetle population from habitat no. 2 demonstrates a qualitative shift in composition and structure of the 2-year-old carabidae-cenosis. The population of *B. quadrimaculatum* has grown 1.2-fold. It remains dominant (232 ind./50 t-d), notwithstand-

Table 2. Population size and distribution of ground-beetle species across habitats of different age and their topic and successional preferences, ind./50 t-d; 3 summer months summed

| Ground-beetle species | Ecogroup | Habitat | | | | | | |
|--|----------|------------|------------|-----------|-----------|-----------|-----------|------------|
| | | no. 0 | no. 1 | no. 2 | no. 3 | no. 4 | no. 5 | no. 26 |
| <i>Bembidion femoratum</i> Strum | E | 269 | 9 | 2 | — | — | — | — |
| <i>B. quadrimaculatum</i> (L.) | HM | 197 | 200 | 232 | 74 | 64 | 49 | 18 |
| <i>B. properans</i> (Steph.) | MSX | 2 | 27 | 35 | 57 | 44 | 85 | 155 |
| <i>B. gilvipes</i> Strum | DM | — | — | — | — | 41 | 31 | 38 |
| <i>Asaphidion pallipes</i> Duft. | HM | — | 3 | 18 | 14 | — | — | — |
| <i>Clivina fossor</i> (L.) | HM | — | 2 | — | — | 19 | 8 | 26 |
| <i>Trechus secalis</i> (Payk.) | DM | 1 | 3 | 3 | 1 | 3 | 2 | — |
| <i>Leistus terminatus</i> (Panz.) | DM | — | — | 5 | 2 | — | — | — |
| <i>Notiophilus aquaticus</i> (L.) | HM | — | 6 | 44 | 6 | — | — | — |
| <i>N. palustris</i> (Duft.) | DM | — | — | — | — | 1 | 2 | 3 |
| <i>Loricera pilicornis</i> F. | DM | — | — | 7 | — | — | — | — |
| <i>Amara fulva</i> (O.F. Mull.) | HM | 16 | 14 | 23 | 14 | — | — | — |
| <i>A. apricaria</i> (Payk.) | HM | — | 7 | 20 | 1 | — | — | — |
| <i>A. bifrons</i> (Gyll.) | HM | — | 14 | 15 | 10 | — | 1 | 3 |
| <i>A. tibialis</i> (Payk.) | HM | 3 | — | 17 | 7 | — | 5 | 4 |
| <i>Curtonotus aulicus</i> (Panz.) | HM | — | 7 | 11 | — | 2 | 1 | — |
| <i>C. convexiusculus</i> (Marsh.) | HM | — | 1 | 70 | — | — | — | — |
| <i>A. equestris</i> (Duft.) | HM | — | — | — | — | 25 | 20 | 25 |
| <i>A. similata</i> (Gyll.) | DM | — | — | — | — | 5 | 4 | 12 |
| <i>A. majuscula</i> (Chaud.) | DM | — | — | — | — | — | — | 2 |
| <i>A. ingenua</i> (Duft.) | HM | — | — | 5 | — | — | — | — |
| <i>A. spreata</i> Dej. | HM | — | — | 9 | — | — | — | — |
| <i>A. ovata</i> (F.) | HM | — | 3 | — | — | — | — | — |
| <i>A. aenea</i> (De Geer) | HM | — | — | 1 | 1 | — | — | — |
| <i>Sericoda quadripunctata</i> (De Geer) | DM | — | 2 | 3 | — | — | — | — |
| <i>A. gracilipes</i> (Duft.) | DM | — | — | — | — | — | — | 1 |
| <i>Anisodactylus signatus</i> (Panz.) | HM | — | — | 3 | 2 | — | — | — |
| <i>Harpalus rufipes</i> (De Geer) | HM | — | 6 | 61 | 13 | 9 | 14 | 10 |
| <i>Harpalus griseus</i> (Panz.) | HM | — | 1 | — | — | — | 5 | 5 |
| <i>Harpalus affinis</i> (Schrank) | HM | — | 5 | 10 | 5 | 4 | 2 | 3 |
| <i>H. distinguendus</i> (Duft.) | HM | — | — | 9 | — | 4 | 4 | 5 |
| <i>H. rubripes</i> (Duft.) | MSX | — | — | 2 | — | 8 | 5 | 13 |
| <i>H. latus</i> (L.) | DM | — | — | — | — | 4 | — | 20 |
| <i>H. modestus</i> Dej. | MSX | — | — | — | — | — | 2 | 2 |
| <i>H. zabroides</i> Dej. | MSX | — | — | — | — | — | — | 2 |
| <i>Pterostichus niger</i> (Schall.) | DM | — | 3 | — | — | — | — | — |
| <i>Poecilus cupreus</i> (L.) | E | 6 | 4 | — | — | — | — | — |
| <i>P. lepidus</i> (Leske) | HM | — | 5 | 13 | 2 | — | — | — |
| <i>P. versicolor</i> (Strum) | DM | — | 6 | 3 | — | 16 | 15 | 24 |
| <i>P. fortipes</i> (Chaud.) | MSX | — | — | — | — | 14 | 23 | 22 |
| <i>P. punctulatus</i> (Schall.) | MSX | — | — | — | — | — | — | 3 |
| <i>Calathus melanocephalus</i> L. | DM | — | 6 | 15 | 10 | 18 | 17 | 24 |
| <i>C. erratus</i> (C.R. Sahlb.) | HM | — | — | — | 2 | 8 | 12 | 14 |
| <i>Synuchus vivalis</i> (Ill.) | DM | 1 | — | — | 15 | 32 | 21 | 38 |
| <i>Microlestes minutulus</i> (Goeze) | MSX | 2 | 2 | 3 | 15 | 14 | 16 | 40 |

Quantitatively preferred habitats are set in bold. Numerical order of habitat corresponds to the relative age from the moment of dump planning.

Legend: herbaceous meadow mesophiles (HM), dendro-meadow mesophiles (DM), meadow-steppe semixerophiles (MSX), and ephemeral extreme species (E).

ing the considerable growth in population of the species that have already been detected in the preceding successional stage (*A. pallipes*, *N. aquaticus*, *A. apricaria*, *A. tibialis*, and *C. convexiusculus* (70 ind./50 t-d) and *H. rufipes* (61 ind./50 t-d in particular). As a result, summed abundance and species richness of ground beetle at the 2-year-old stage of the carabidae-cenosis development approached the maximum value of 639 ind./50 t-d and 27 species in the studied series of the chronological communities.

The ground-beetle population from habitat no. 3 in the third year of succession is characterized by the next (in a series of communities) decline in summed abundance from 639 to 252 ind./50 t-d and species richness from 27 to 19 species when compared with the 2-year-old community. Pioneer *B. femoratum* and *P. Cupreus* entirely dropped out from the composition. The population of *B. quadrimaculatum* shrunk by a factor of 3.1 compared with the 2-year-old and by a factor of 2.7 compared with the 1-year- and month-old communities. Population sizes of the subdominants from the preceding 2-year-old community also reduced from 44 to 6 ind./50 t-d in *N. aquaticus*, from 70 to 0 in *C. convexiusculus*, from 20 to 1 in *A. apricaria*, from 13 to 2 in *P. lepidus*, and from 61 to 13 ind./50 t-d in *H. rufipes*. A slight increase in the number of individuals in species characteristic of the older communities (*B. properans* from 34 to 56 and *S. vivalis* to 15 ind./50 t-d) failed to compensate for the reduction in summed abundance and species richness of the population of the third year of succession.

The ground-beetle populations of habitats nos. 4 and 5 proved to be very similar to each other, resulting from the quantitative dominance of the same species typical of the medial successional stage in the native forest-steppe landscape.

Despite reaching the absolute age of four to five years, both communities preserve similarity features with the population of the initial successional stage largely on account of *B. quadrimaculatum*, whose numbers remain rather high (49–64 ind./50 t-d). Notwithstanding, its dominance is outcrossed by the more euribiont *B. properans* (44–85 ind./50 t-d) and newly occurred *B. gilvipes*. Subdominant positions in the 4- and 5-year-old community are taken by *C. fossor*, *A. equestris*, *P. versicolor*, *P. fortipes*, *C. melanocephalus*, *C. erratus*, *S. vivalis*, and *M. minutulus*. Total species richness largely remained at 3-year-old level, while the summed population abundance continued to increase (1.4-fold to 336–344 ind./50 t-d).

The ground-beetle population from habitat no. 26 was little or no different in species composition from the 4- to 5-year-old community, despite what it should seem to be a considerable age of 26 years. The gain in total species richness (up to 26 species) was to some extent ensured by the least numerous species, namely *Agonum gracilipes*, *H. modestus*, *H. zabrioides*, *P. punctulatus*, and *A. majuscula* typical of the climax

“steppified” meadow and wooded meadow (“park–forest”) communities of their native Siberian forest steppe (Mordkovich and Volkovintser, 1974; Lyubchanskii and Bespalov, 2011). A significant part of the overall abundance of individuals was contributed by species typical of the native forest steppe, such as 155 ind./50 t-d of *P. properans*, 26 of *C. fossor*, 25 of *A. equestris*, 38 of *B. gilvipes*, 22 of *P. fortipes*, 40 of *M. minutulus*, 20 of *H. latus*, 13 of *H. rubripes*, 24 of *P. versicolor*, 38 of *S. nivalis*, and 24 ind./50 t-d of *C. melanocephalus* (Mordkovich and Volkovintser, 1974). In the community that reached the age of 26 years, overall species richness of ground beetles amounts to 26 species, which ensures another step-up in overall population abundance up to 512 ind./50 t-d or, in other words, a 1.5 increase compared to the 5-year-old community (Table 2). Notwithstanding, it is considerably lower than in adjoining native meadows and wood meadows of Siberian forest steppe (Lyubchanskii and Bespalov, 2011).

We compared populations of the examined biotopes and repeats. As was revealed by the Ochiai coefficient, habitat no. 0 is markedly different from all the others. A high degree of similarity is recorded in the population of the same biotope in different years (nos. 2 and 3 and nos. 4 and 5). Biotopes, except for no. 0, were grouped in accordance with their successional age, that is, one group was formed by biotopes nos. 1, 2, and 3 and another group included biotopes nos. 4, 5, and 26. Figure 1 illustrates results of multidimensional scaling.

DISCUSSION

A study of the pattern of succession in invertebrate animals on the rolling topography of the KATEK dump has shown that, after 25 years, diversity parameters do not achieve equivalence with the native forest-steppe communities across all sites of anthropogenic catenae. The rate and direction of succession in zoocenosis considerably differ depending on the topographic position of surrogate cenosis. Compared to native ones, the eluvial and transitional positions of industrially disturbed catenae feature frequent backsliding to primitive successional stages. Species typical of zonal forest-steppe ecosystems occasionally occur as late as in the seventh year from the start of succession. Accumulative positions of the dump are characterized by a slower but more orderly succession than in other positions, which, in contrast to the soil and phytocenosis, develops not toward the meadow herbage, but rather forest zoocenoses, whose features become apparent by the 25th year of development (Mordkovich and Lyubchanskii, 2019).

A markedly different ecological situation arises on graded dumps, where the evolution of emerging biota composition occurs without the participation of the catena gradient, which promotes an increase in species richness and diversity. Moreover, compared

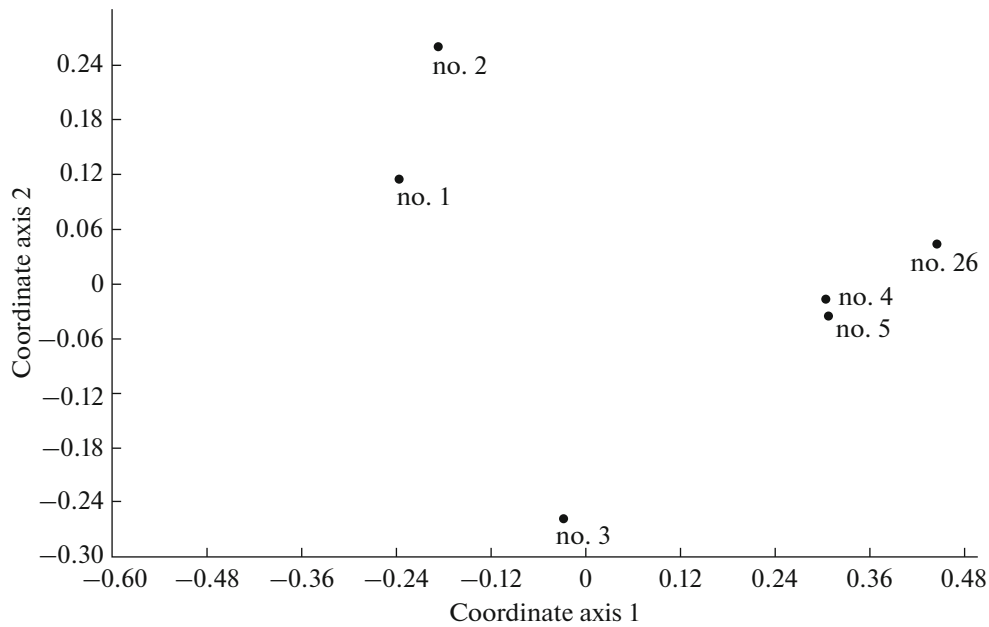


Fig 1. Distribution of carabidocenoses at multidimensional scaling (the Bray–Curtis index). Point numbers reflect age of carabidocenoses in years.

with the other destroyed catena positions, the *plakor* provides for the most inert regime of change in the ecological environment and the delayed regime of biotic turnover.

System of Ecological Relationships in Biota

The findings offer the possibility to assess characteristics of change in parameters of ground-beetle diversity within a chronological sequence of industrially disturbed ecosystems both at the population–species and cenotic levels of life organization and provide insight into the content of the succession as a process of optimizing a system of ecological relationships between different components of ecosystem in approaching the zonal optimum.

In his classification of ecological relationships, Beklemishev (1970) identified four types reflecting the different aspects of relationships in an ecosystem, namely, topic, trophic, phoric, and fabric interactions. In pursuit of the specific objectives, the analysis of the author was exclusively confined to the indicated relationships, first, between different elements of biota; second, at organismic and population–species levels of its organization; and, third, without considering the ecological niche. Notwithstanding, the proposed system of relationships does not semantically exclude the broad interpretation, including a biogeocenotic level of organization.

In this case, topic relationships can be assessed not just as the compatibility between different species in one habitat, but also based on the selective attitude of species towards particular habitats and the formation

of steady-state compositions of species that are characterized by similar ecological requirements with respect to particular environmental conditions. A broad interpretation of trophic relationships is understood not only as organisms using each other, but represents a system of preferences in a choice of prey items and diets under different habitat conditions. Phoric interactions are not limited to some organisms using others as transportation mean, but additionally embrace the biota ability for migration and distribution, using for this purpose the adaptive capacities of their own organisms and capabilities of the environment for the dispersal of local populations across the most suitable conditions. Fabric interactions similarly extend beyond the organisms using each other for building material, shelter, and breeding ground and additionally include the capability of biota to actively transform the habitat in the favorable direction or passively yet effectively utilize the latter to satisfy its needs. To complete the above set of the interactions, it is necessary to add at least one more type of relationships, demographic, between the number of species and number of individuals in each species within the boundaries of the specific community in the particular environmental conditions.

Change of Demographic Relationships in Ground-Beetle Taxocene with the Age of the Communities

The summed abundance of ground beetles changes in an undulating manner, in contrast to its permanent increase in microarthropods (Babenko, 1982; Dmitrienko, 1990) between the pioneer and terminal suc-

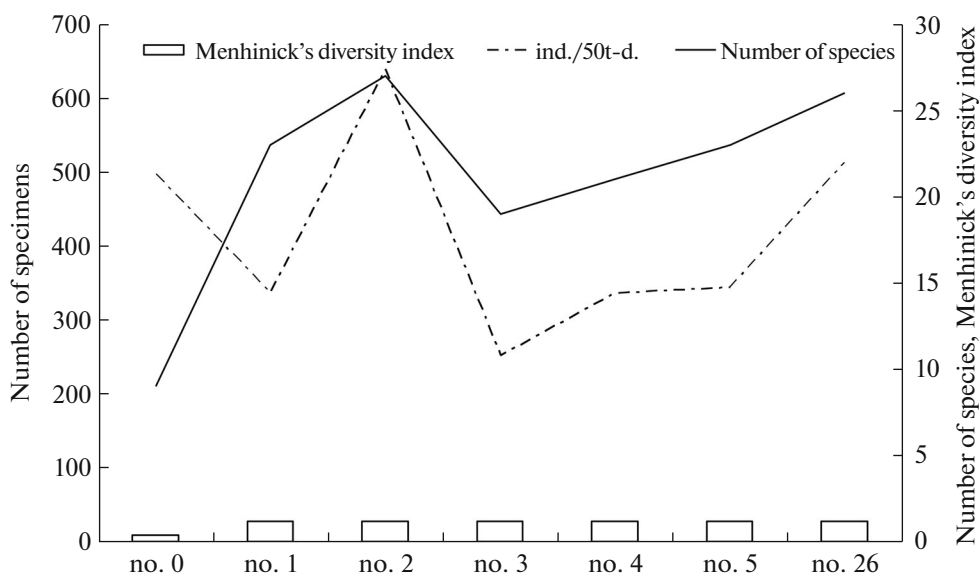


Fig. 2. Change of demographic relationships in ground-beetle taxocene with age.

cessional stages in the considered series of unevenly aged communities. Among the seven studied communities, three are distinguished by high abundance at a level of ≈ 500 ind./50 t-d, namely, 0, 2-year-old, and 26-year-old communities.

The first upturn in ground-beetle population occurs in the beginning of succession during the first weeks after dump preparation (Fig. 2). The sudden spurt is generated by two species in the family *Bembidion*. Both species are organisms that evolve tending to an increase in expenditures for reproduction rather than sustaining the life of the adult organism (r selection) (Pianka, 1981). Despite this and a similarity between habitus *B. femoratum* and *B. quadrimaculatum*, their demographic tactics unfold in a different way as succession progresses. It precisely matches the proper r-strategy in *B. femoratum*, the population of which, after the burst in at the start, declined by a factor of 30 as early as the next year and dropped to a minimum level in the second year. The species entirely disappeared from the carabidocenosis composition in the third year of succession. A different type of behavior in the aged series is exhibited by *B. quadrimaculatum*, which, after the strong irruption, along with *B. femoratum* at the start of succession, on the other hand, continues to maintain a high level of abundance and dominant positions in communities over the next 5 years and onward to the age of 26. The explanation for the ephemerality of one and longevity of another habitually similar species apparently lies in other types of ecological relationships.

The next upturn in the summed abundance of ground beetles is ensured not by two, but ten ground-beetle species, among which, in addition to the noted *B. quadrimaculatum*, a prominent role is played by

Notiophilus aquaticus, *Harpalus rufipes*, *Curtonotus convexusculus*, and *Amara fulva* in the second-year community. This second upsurge in abundance is followed by the decline by 50% and more (by a factor of 2.5–2), which is concluded with new upturn at 26 at the earliest. This third time irruption is generated by 15 species (Fig. 2).

The trend of species richness disagrees with the trend of the abundance of individuals in that the former is distinguished by the minimal diversity at the start of succession, growth to 27 species in the second-year community followed by a moderate decline by the fourth year of succession, and a subsequent insignificant (up to 26 species) increase by the 26th year of succession.

Thus, as the age of the dump grows, number of species occupying it increases; the density of their populations declines; and the strength of interspecific competition and likelihood of the competitive exclusion increases, which is perfectly in line with the ideal equilibrium model (Mac-Arthur and Wilson, 1967) formulated for recent ocean islands.

Menhinick's diversity index, reflecting equilibrium between the number of species and individuals in the community (Magurran, 1988), characteristically exhibits minimal values (0.4) in the conditions of the environment brought to the lowest terms at the beginning of succession. However, as early as in a year, the Menhinick's diversity index climbs to values near 1.2, reflecting the stressor state of habitat conditions. It normally attains higher levels (2.3–2.6) in the stable competitively balanced climax communities of the meadow steppe of the Siberian forest steppe (Mordkovich and Volkovintser, 1974; Lyubechanskii and Besspalov, 2011). This state, however, has not been

attained by ground beetle taxocene of the graded dump (Fig. 2).

Change in Topic Relationships in Ground Beetle Taxocene with Community Age

Markedly, three blocks of communities stand out based on specific features of the species composition assessed using the Bray–Curtis index among the examined series of seven communities aged from 0 to 26 years. First is a stand-alone “infantile” community no. 0, emerging straight after the dump grading at the place of destroyed fallow–meadow cenosis; second is a block of young communities of 1 to 3 years of age; and third is a block of mature communities of ages ranging from 4 and 5 to 26 years old (Fig. 1). The first coordinate in the multidimensional scaling graph is essentially temporal, while the second reflects the population size of carabidocenosis.

Inside each block, the population is differentiated by the presence of preferential species, which are especially abundant in one particular community. Preferential species are strongly marked in pioneer community no. 0 with a preference coefficient—the ratio of dynamic density in the preferred habitat to the total number of specimens in this entire series of habitats—of 96% for *B. femoratum*. Another dominant species from this community manifests itself as a preferential species in community no. 2. The latter is outstanding in terms of the preferential advantage in the block of young communities nos. 1, 2, and 3, thus leaving no preferential species for communities nos. 1 and 3, which can be ranked as transitional compared with key community no. 2, where 20 out of 27 species are considered preferential. Among them, the highest levels of preference are attributed to *C. convexiusculus* (99%), *N. aquaticus* (78%), *A. apricaria* (74%), *A. fulva* (65%), *C. aulicus* (61%), *P. lepidus* (65%), and *Ps. rufipes* (54%). Block of communities nos. 4, 5, and 26 compares to the foregoing in terms of the number of preferential species, which attain the greatest dynamic density of local populations in community no. 26, namely, *B. properans* (with a preference coefficient of 38%), *B. gilvipes* (35%), *A. equestris* (36%), *P. fortipes* (37%), *C. melanocephalus* (27%), *C. erratus* (39%), *P. versicolor* (36%), *Clivina fossor* (49%), *Microlestes minutulus* (43%), and *Synuchus vivalis* (36%).

The order of preferential species replacement in communities of the succession series clearly marks the differentiation of ground beetle taxocene as the succession progresses, which helps divide the communities into key ones with preferential species present and transitional communities without them and determine the successional stages, but it does not shed light on the ecological essence of the succession. The latter is determined by the ecological-biotope reference standard for preferential species developed by them over the course of long evolution, adequately and in actual fact occurring in a zonal catena matrix of specific hab-

itats, which are regularly distributed over a system of coordinates preset by latitudinal zonal and catenal ecological gradients of environment. The pattern of species population distribution in a coordinate system of habitats of the Siberian forest-steppe zone indicates combinations of species based on their response to limiting environmental factors such as heat availability, moisture, and land cover (Lyubechanskii and Mordkovich, 1997). From a large pool of distribution types, the KATEK site features topoecological assemblages of herbaceous meadow mesophiles (HM), dendro-meadow mesophiles (DM), and meadow-steppe semixerophiles (MSX) (Table 2). In the native habitat system of the Siberian forest-steppe zone, the preferences include mesophytic meadows in the first, moderately moist sparse small-leaved isolated forest stands or groves on watershed divides in the second, and meadow steppes and dry “steppificated” meadows in the third. One stand-alone category is comprised of ephemeral extreme environment species (E), which prefer marsh meadows with highly variable hydrothermal and hydrochemical conditions in the steppe zone or occur nonselectively in the forest-steppe zone, extensively including agrocenoses.

Based on an analysis of the population structure in the context of topo-ecological relationships, the specific characteristic of the pioneer community is exclusively determined by extremophiles and *B. femoratum* in particular. Young communities of the initial successional stage, no. 2 in particular, are distinguished by the key role of herbaceous meadow mesophiles (81–86% individuals in the community). The latter continue to maintain their leading positions (52%) in population structure of community no. 3, while concurrently and increasingly significance is being shifted to dendro-meadow mesophiles *C. melanocephalus* and *S. vivalis* (20.6%) and meadow-steppe semixerophiles *M. minutulus* and *B. properans* (27%). In the medial successional stage, community no. 4 is intermediate between communities nos. 3 and 5 based on the topoecological structure. Communities nos. 5 and particularly 26 see topoecoassemblages of meadow-steppe semixerophiles *B. properans*, *M. minutulus*, *H. rubripes*, and *P. fortipes* taking center stage (38–46%). The share of dendro-meadow mesophiles is expanding to 32% (*B. gilvipes*, *H. latus*, *P. versicolor*, *C. melanocephalus*, and *S. vivalis*) (Table 3). However, when compared with the native communities of the meadow steppe (Mordkovich and Volkovintser, 1974; Lyubechanskii and Bespalov, 2011), community no. 26 was found to have made it only halfway in the course of its successional development toward the climax over a quarter-century (the share of the title meadow steppe-specific species in it amounts to as little as 46%, while 87% is required for the standard).

The change in ground-beetle trophic relationships in the considered chronological series of unevenly aged communities resolves itself into combining (in the population structure) the subpopulations (contin-

Table 3. Spectra of ground-beetle topoecological assemblages in a series of unevenly aged communities of the graded dump, %

| Topo-ecological assemblages | Habitats | | | | | | | |
|-------------------------------|----------|-------|-------|-------|-------|-------|--------|--------|
| | no. 0 | no. 1 | no. 2 | no. 3 | no. 4 | no. 5 | no. 26 | climax |
| Extreme species | 95 | 3.3 | 0.3 | 0 | 0 | 0 | 0 | 0 |
| Herbaceous meadow mesophiles | 4.2 | 81.5 | 85.9 | 52 | 40 | 35.2 | 22 | 9.2 |
| Dendro-meadow mesophiles | 0.4 | 6 | 7.6 | 20.6 | 35.7 | 26.7 | 31.6 | 1.4 |
| Meadow-steppe semi-xerophiles | 0.4 | 8.6 | 6.2 | 27.4 | 24.1 | 38.1 | 46.4 | 86.7 |
| Steppe xerophiles | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.7 |
| ρ (%) | 0.91 | 0.06 | 0.34 | 0.15 | 0.14 | 0.13 | 0.43 | |

Data on the climax community is presented according to (Lyubechanskii and Bespalov, 2011).

Table 4. Change in ground-beetle trophic interactions in a series of unevenly aged communities on industrial anthropogenic dump at KATEK, %

| Ground-beetle trophotypes | Habitat | | | | | | | |
|---|---------|-------|-------|-------|-------|-------|--------|--------|
| | no. 0 | no. 1 | no. 2 | no. 3 | no. 4 | no. 5 | no. 26 | climax |
| Obligate oligo-zoophages | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Obligate poly-zoophages | 96 | 76 | 56 | 68 | 56 | 56 | 55 | 8 |
| Mixophages (phytozoophages) | 3 | 17 | 40 | 21 | 18 | 18 | 21 | 21 |
| Variophages (phyto-sapro-zoo-phytophages) | 1 | 7 | 4 | 11 | 26 | 26 | 24 | 71 |
| Σ individuals in community | 100% | 100% | 100% | 100% | 100% | 100% | 100% | 100% |

Data on the climax community is presented according to (Lyubechanskii and Bespalov, 2011).

gents) of obligate poly-zoophages (Cicindelini, Carabini, Lebiini, Bembidiini, Trehini, Notiophilini, Nebriini, Agonini, Loricerini, and Clivinini); mixophages that combine or alternate zoophagy and phytophagy during ontogenesis (Amarini, Harpalini, and Anisodactylini); and variophages with an even broader spectrum of alternation between zoo-, phyto-, and saprophagy (Pterostichini and Sphodrini). The diet typology and its correspondence to particular genera and species have been oriented by us toward the scheme of Sharova (1981) with minor modifications resulting from our experience. Thus, in addition to a concept of *mixophagy*, it appears appropriate to use *variaphagy* as suggested by the data available with respect to a change in the quantitative proportion of plant and animal matter in guts of ground beetle genera *Pterostichus*, *Poecilus*, *Calathus*, and *Synuchus* from different biotopes as spring progresses and heads into the fall (Skuhravy, 1959; Inyaeva, 1965; Soboleva-Dokuchaeva, 1975). Table 4 details the change pattern in the trophic structure of unevenly aged communities.

Two *Bembidion* species occupy the leading positions in ground-beetle taxocene at the start of succession (within the first month). Their morphological, physiological, and behavioral features (long pointed mandibles and interstitial digestion) unequivocally indicate predation, though not exclusive of zoosaprophagy. Diet items of the micropredators include

microarthropods, nematodes, and small mesofauna species that concurrently emerge on the freshly scalped dump.

Against the overwhelming majority of obligate poly-zoophages, accounting for 96% of ground-beetle population, as early as the next month after grading, the dump becomes a home for phytozoophagous ground beetles *Amara fulva* (3% of population), which alternate between zoo- and phytophagy and focus on mort mass from the preceding fallow or on seed and vegetative part of plants transported from external sources by wind (Table 4).

At the initial successional stage represented by a block of communities nos. 1, 2, and 3, trophic population structure preserves the dominance of small obligate poly-zoophages, which are especially abundant in transitional communities nos. 1 and 2. In parallel, a share of mixo-phyto-zoophages expands notwithstanding, including *H. rufipes*, *C. convexiusculus*, *A. apricaria*, *A. tibialis*, *H. affinis*, and *H. distinguendus*, in particular. The gain in share of this species, especially in key community no. 2 up to 40%, correlates with the vigorous growth of vascular ruderal plants, featuring a large amount of aboveground phytomass, which ensures a massive addition of litterfall to a litter layer to form comfort conditions for herpetobionts.

Poly-zoophages continue to keep the lead in population structure at the medial successional stage (communities nos. 4, 5, and 26), though more modestly

compared to what was observed at the previous stages (56 vs. 76%) (Table 4). Phytozoophages experience a 50% decrease compared with community no. 2 (Table 4). They are replaced by a growing population of the broad-spectrum variaphages (*Poecilus*, *Calathus*, and *Synuchus*), which is in line with the increased species richness in plants and invertebrates. All three communities of the third successional stage display a remarkable similarity in trophic structure of the population of communities. Such uniformity may be regarded as a long-standing deceleration of carabidocenosis in the stagnant condition far from the climax native standards of the forest steppe, where the share of obligate poly-zoophages is an insignificant 8%. With that, the climax cenosis has numerous micropredators replaced by large predators (*Carabus*, *Calosoma*, and *Cicindela*). In addition, as the weight of phytozoophages in the climax native community of meadow steppe decreases, they give way to an increasing share of variaphages (up to 71%), alternating their diet from season to season (*P. fortipes*, *C. erratus*, and *P. sericeus*) (Lyubechanskii and Bepalov, 2011). Thus, over 26 years, the trophic structure of ground-beetle taxocene on the dump falls short of approaching a state characterizing the climax standards of forest-steppe landscapes (Table 4).

Fabric interactions of ground beetles with other invertebrate animals manifest themselves rather weakly. Notwithstanding, the selective use of particular soil properties for utilitarian purposes, such as dwelling, refuge, transport corridor, and plane for locomotion, is substantively reflected in the morphology and behavior of ground beetles and their imagines in particular. The following forms are distinguished in ground beetles based on the pattern and degree of interactions with particular soil properties and horizons: (a) above the soil, which use the soil surface for travelling but dig vertical tunnels at the larval phase; (b) exploiters of soil pore space, cracks, and crevices along large roots; and (c) forms actively digging their ways in soil (Sharova, 1981).

As for the population structure of the examined series of unevenly aged communities on an industrial anthropogenic dump at all successional stages over the 25 years, the leadership was kept by the ground-beetle pore-exploiters of micro- (body length 3–7 mm) and medium (8–20 mm) sizes adequate to the loose top layer of the dump ground. The species that are pronouncedly adapted to active digging (*Clivina fossor*) emerge as the soil compaction advances and more plants roots evolve, starting at the fourth year of succession, and gradually bring up the dynamic density of their populations to 26 ind./50 t-d in the 26-year-old community (Table 2).

Phoric relationships. For transportation, ground beetles use apt abiotic components of the environment (in a broader sense of phoresy) between aerial and underground layers of biocenosis. In the majority of

ground beetles, the second pair of wings is not well-developed or can be used selectively or as a last resource (Kryzhanovskii, 1983). Ground beetles inhabiting the dumps, which are similar to island ecosystems, generally have and actively employ a second pair of wings to air land from external environments and for species-composition interchange among communities of different ages.

Legs are a huge help for spatial movements in ground beetles. Several phoric types have been identified in the beetles based on their adaptation for dispersal (Mordkovich, 1970; Sharova, 1981). The first are very long-legged, with remarkable tibia (longer than femur) of the hind and middle pairs of legs, e.g., *Cicindela*, *Nebria*, *Carabus*, and *Calosoma*. For brevity, we will refer to them as “runners,” capable of long-distance movement at high speeds; the second include forms with midsize and short legs and remarkable tibia on hind legs only, which are notionally defined by us as “walkers” (Harpalini, Pterostichini, Sphodrini, Lebiini, and Amarini) travelling short distance with average speed; and the third are the short-legged forms with femur longer than tibia for all three pairs of legs, which either move slowly and not far (*Clivina* and *Dyschirius*) or fast and jerkily, but over a short distance (*Bembidion*, *Asaphidion*, and *Notiophilus*).

Species of the third phoric type keep the dominance in this series of unevenly aged communities of the dump throughout the entire duration of succession. The first type is almost entirely missing from the graded dump in contrast to the dumps with a differentiated relief (Mordkovich and Lyubechanskii, own observations). As succession progresses, considerable changes in the structure largely occur in the second phoric type, which, though not represented very well at the start (5% of population), peaks at 50% of population at the initial and furthermore at the medial successional stage. That said, the 26-year-old carabidocenosis of the graded dumps still fails to approach the structural condition of the climax meadow-steppe native community, where a share of walkers is close to 90%.

Life Strategies of Carabidocenosis as Ecological-Interaction Toolset

According to the classical postulates, the driving force for succession originates from internal contradictions in community, resulting in the sequential replacement of biological species, featuring different types of life strategies (Mirkin and Naumova, 2012), namely, ruderal, stress-tolerant, and competitive (Ramenskii, 1938; Grime, 1979). With that, a semantically extensive concept of strategy is restrictively substantiated based on demographic criteria (r and K selections) and imaginative descriptions of species ability to live together amicably. In addition to the narrowed interpretation of the concept of strategy, the adjective “life” is equally elusive.

Considering the finding discussed in the previous sections of the present article, it appears reasonable to perceive compatibility and cooperation strategies of biota as categories of cenotic rather than population—species organization levels during different successional stages, which are essentially determined by a system of adaptive tactics subordinate to strategies. It also appears reasonable to define these strategies more specifically as *cenotic* rather than “life.”

Provided we assume this approach to the three classical variants of cenotic (life) strategies (R, ruderal; ST, stress tolerant; and C, competitive), it is necessary to additionally introduce at least one more, the extreme (E), which is the most effective at the starting successional phase in delicate habitats of marine sublittoral, floors of desiccating shallow lakes, and mountain screes, as well as newly formed industrial anthropogenic overburden dumps featuring the extremely unstable and temporally poorly predictable conditions of the environment during the first days or weeks of their occurrence.

In the graded dump conditions, extreme strategies are demonstrated by the preferential species of the abruptly scalped dump in the first weeks of its existence. In contrast to the ruderal, maximum energy expenditures in these ground beetles goes toward the large-scale air landing from the external environment or urgent evacuation from an extreme habitat when the limiting factors change beyond the threshold levels, rather than to the onsite reproduction. In trophic terms, extreme species are tied with the mort mass left behind from the preceding scalped cenosis, as well as with other extreme species that attack a newly formed dump by means of active and passive phoresy concurrently with ground beetles.

As the carabidocenosis progresses, as early as less than a year, extreme pioneers give way in the community to ruderals, which rapidly occupy preferential positions and take over the habitat through reproducing at unprecedented rate. Ruderal ground beetles use a type of diet combining zoo- and phytophagy to the extent of feeding on flowers in equivalent proportion to phytomass abundance formed by lush tall-grown and dense weeds. Stress-tolerant species with a wide range of demographic, topic, trophic, and other biocenotic tactics begin to replace the ruderal species in carabidocenosis from the fourth or fifth year of succession onward and achieve maximum success in the 26-year-old community. Over a quarter century of succession, the carabidocenosis structure is still a long way from achieving the climax stage even having been evolving towards the climaxes of forest-steppe biome. In the 26-year-old dump community, the share of ground beetles preferential for the native meadow-steppe community of the Siberian forest steppe accounts for as little as 46%, which is just 50% of what is appropriate for the forest-steppe zone climax; even

among the former, species with the competitive cenotic strategy are very low in number.

CONCLUSIONS

(1) In a series of unevenly aged ecosystems of graded dump, changes in composition and structure of the ground-beetle population occur in a certain order rather than chaotically.

(2) This order contains elements shared by most successional trends in other components of biota, but additionally distinguished by development patterns unique to ground beetles.

(3) The ground-beetle population size and species richness changes in an undulatory fashion. Three communities, namely, pioneers less than a year old, initial 2 years in age, and medial of 26 years, tend to exhibit rather high levels of demographic parameters. They correspond to three key stages in carabidocenosis.

(4) The three communities standard for the forenamed stages are each distinguished by their own set of preferential species with an increased density of population in key habitats in contrast to others, which lack character and belong to transitional.

(5) It is not only a set of species (including preferential) and population proportion that change from the pioneer stage of community self-development (no. 0) through initial (communities nos. 1, 2, and 3) further to medial (communities nos. 4, 5, and 26), but primarily a system of biocenotic relationships.

(6) Particular combinations of ecological interactions tend to form integral categories of biocenotic relationships, i.e., life strategies, which should be more appropriately called cenotic, inasmuch as they exclusively manifest themselves at the corresponding level of life organization. Based on the analysis of our findings, it appears reasonable to supplement three traditionally assumed types of life (cenotic) strategies i.e., ruderal (R), stress-tolerant (ST), and competitive (C), with the extreme (E) type.

(7) Over a quarter century of succession in carabidocenosis, the three types of cenotic strategy (specific combinations of adaptive tactics) are gradually replaced in the following sequence: extreme pioneers → ruderal → stress-tolerant. Bearers of competitive strategy, even if they emerge at the 26-year stage, occur incidentally and, therefore, do not in any significant way affect the ecosystem functioning.

(8) Parameters of succession in ground beetle taxocene and order of their replacement on graded dump, occupying a geomorphological position analogous to the natural *plakor*, fundamentally differ from those in the population of the dump with differentiation of habitats by mesorelief. Over 25 years, the composition and structure of ground beetles in the rolling relief conditions approached the native standards of forest-steppe biome much closer than in *plakor* conditions of graded-flat dump. In addition, communities of habi-

tats differing in relief develop in different directions, that is, toward the meadow-steppe standards in eluvial and transitional positions and toward wooded meadow (“park–forest”) communities in accumulative positions of catenae.

In the *plakor* conditions of graded dump, communities make no progress between the age of 4 and 26, while combining a marginally equal proportion of herbaceous-meadow, dendro-meadow, and meadow-steppe semixerophiles in its composition and structure.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

REFERENCES

- Babenko, A.B., Dynamics of soil microarthropods during overgrowing of technogenic dumps, *Zool. Zh.*, 1982, vol. 61, no. 12, pp. 1815–1825.
- Beklemishev, V.N., *Biotsenologicheskie osnovy sravnitel'noi parazitologii* (Biocenotic Principles of Comparative Parasitology), Moscow: Nauka, 1970.
- Biologicheskaya produktivnost' travyanykh ekosistem. Geograficheskie zakonomernosti i ekologicheskie osobennosti* (Biological Productivity of Herbaceous Ecosystems: Geographic Pattern and Ecological Features), Novosibirsk: Nauka, 1988.
- Brändle, M., Durka, W., and Altmöös, M., Diversity of surface dwelling beetle assemblages in open-cast lignite mines in Central Germany, *Biodiversity Conserv.*, 2000, vol. 9, pp. 1297–1311.
- Burykin, A.M., Theory of recultivation of technogenic landscapes, in *Rekul'tivatsiya zemel', narushennykh gornymi rabotami na KMA* (Recultivation of Lands Disturbed by Mining Works in Kursk Magnetic Anomaly), Voronezh: Voronezh. S-kh. Inst., 1985, pp. 3–11.
- Clements, F.E. and Schelford, V.E., *Bio-Ecology*, New York: Wiley, 1939.
- Dmitrienko, V.K., Dynamics of invertebrate communities in the soils of industrial dumps of the western zone of the Kansk-Achinsk fuel and energy complex used for forest growing, in *Sovremnnoe sostoyanie biotsenozov zony KATEKa* (Modern Status of Biocenoses of the Kansk-Achinsk Fuel and Energy Complex Zone), Leningrad: Gidrometeoizdat, 1990, pp. 186–197.
- Dmitrienko, V.K. and Shaimuratova, N.S., The structure of complexes of pedobionts on recultivated lands in the western part of Kansk-Achinsk Fuel and Energy Complex, *Geogr. Prirod. Resur.*, 1986, no. 4, pp. 81–85.
- Dunger, W., Die Entwicklung der Bodenfauna auf rekultivierten Kippen und Halden des Braunkohlentagebaues, *Abh. Ber. Naturkundemus. Gorlitz*, 1968, vol. 43, no. 2.
- Frouz, J., Pižl, V., and Tajovský, K., The effect of earthworms and other saprophagous macrofauna on soil microstructure in reclaimed and un-reclaimed post-mining sites in Central Europe, *Eur. J. Soil Biol.*, 2007, vol. 43, suppl. 1, pp. S184–S189.
- Frouz, J., Prach, K., Pižl, V., Háněl, L., Starý, J., Tajovský, K., Materna, J., Balík, V., Kalčík, J., and Řehouňková, K., Interactions between soil development, vegetation and soil fauna during spontaneous succession in post mining sites, *Eur. J. Soil Biol.*, 2008, vol. 44, pp. 109–121.
- Grime, J.P., *Plant Strategies and Vegetation Process*, Chichester: Wiley, 1979.
- Hammer, O., Harper, D.A.T., and Ryan, P.D., PAST: Paleontological statistics software package for education and data analysis, *Palaeontol. Electron.*, 2001, vol. 4, no. 1. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- Inyaeva, Z.I., Ground beetles on crop field, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow, 1965.
- Johnson, E.A., and Miyanischi, K., Testing the assumptions of chronosequences in succession, *Ecol. Lett.*, 2008, vol. 11, pp. 419–431. <https://doi.org/10.1111/j.146100248.2008.01173.x>
- Kryzhanovskii, O.L., *Fauna SSSR. Zhestkokrylye. Tom 1. Vyp. 2. Chast' 1. Zhuki podotryada Adephaga* (Fauna of USSR: Coleoptera, Vol. 1, No. 2, Part 1: Beetles of Suborder Adephaga), Leningrad: Akad. Nauk SSSR, 1983.
- Luzyanin, S.L., Dudko, R.Yu., Bespalov, A.N., and Eremeeva, N.I., Biodiversity of carabids (Coleoptera, Carabidae) on coal mining dumps of Kuzbass region, Kemerovo oblast, Russia, *Evraziatskii Entomol. Zh.*, 2015, vol. 14, no. 5, pp. 455–467.
- Lyubechanskii, I.I. and Bespalov, A.N., Spatial heterogeneity of a ground beetle (Coleoptera, Carabidae) population along a forest-steppe transect: local level of consideration, *Contemp. Probl. Ecol.*, 2011, vol. 4, no. 4, pp. 388–395.
- Lyubechanskii, I.I. and Mordkovich, V.G., Ecological classification of terrestrial animals by the example of ground beetles of the West Siberian Plain, *Sib. Ekol. Zh.*, 1997, no. 6, pp. 597–608.
- MacArthur, R.H. and Wilson, E.O., *The Theory of Island Biogeography*, Princeton: Princeton Univ. Press, 1967.
- Magurran, A.E., *Ecological Diversity and Its Measurement*, Princeton: Princeton Univ. Press, 1988.
- Mirkin, B.M. and Naumova, L.G., *Sovremennoe sostoyanie osnovnykh kontseptsii nauki o rastitel'nosti* (Modern Status of General Concepts of Vegetation Science), Ufa: Gilem, 2012.
- Mordkovich, V.G., Herpetobium of the depression steppes of the south of Siberia by the example of ground and dark beetles, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow: Inst. Evol. Morphol. Ecol. Anim., 1970.
- Mordkovich, V.G., Zoological successions on young technogenic catens and the principle of space-time analogues, *Izv. Ross. Akad. Nauk, Ser. Biol.*, 1994, no. 3, pp. 446–452.

- Mordkovich, V.G., Interconnectedness between ecological successions and catenary arrangement of space, *Zh. Obshch. Biol.*, 2017, vol. 78, no. 2, pp. 32–46.
- Mordkovich, V.G. and Kulagin, O.E., Composition of ground beetles and diagnostics of technogenic ecosystems of Kuzbass, *Izv. Sib. Otd., Akad. Nauk SSSR, Ser. Biol.*, 1986, no. 2, pp. 86–92.
- Mordkovich, V.G. and Lyubchanskii, I.I., Ground beetles (Coleoptera, Carabidae) and zoological diagnostics of ecological succession on technogenic catenas of brown-coal dumps of Kansk-Achinsk Fuel and Energy Complex (Krasnoyarsk krai), *Izv. Ross. Akad. Nauk, Ser. Biol.*, 2019, no. 5, (in press).
- Mordkovich, V.G. and Volkovintser, V.V., Soil fauna, in *Struktura, funkcionirovanie i evolyutsiya sistemy biogeotsenozov Baraby. Chast' 1. Biogeotsenozy i ikh komponenty* (Structure, Functions, and Evolution of the Biogeocenoses of Baraba Region, Part 1: Biogeocenotic Components), Kovalev, R.V., Ed., Novosibirsk: Nauka, 1974, pp. 18–21.
- Motorina, L.V., Natural recovery of biogeocenoses and Recultivation of lands disturbed by open mining of minerals, in *Obshchie problemy biogeotsenologii* (General Problems in Biogeocenology), Moscow: Nauka, 1986, vol. 2, pp. 44–46.
- Pianka, E.R., *Evolutionary Ecology*, New York: Harper and Row, 1978, 2nd ed.
- Pormenter, R.R. and Macmahon, J.A., Early successional patterns of arthropod recolonization on reclaimed strip mines in southwestern Wyoming: the ground-dwelling beetle fauna (Coleoptera), *Environ. Entomol.*, 1987, vol. 16, pp. 168–177.
- Ramenskii, L.G., *Vvedenie v kompleksnoe pochvenno-geobotanicheskoe issledovanie zemel'* (Introduction into Complex Soil-Geobotanical Study of Lands), Moscow: Sel'khozgiz, 1938.
- Sharova, I.Kh., *Zhiznennye formy zhuzhelits* (Life Forms of Ground Beetles), Moscow: Nauka, 1981.
- Shugalei, L.S., Resistance of soils of forest-steppe and southern taiga of Central Siberia to external impacts, *Vestn. Krasn. Gos. Agrar. Univ.*, 2009, no. 9, pp. 66–77.
- Skuhřavý, V., Příspěvek k bionomii polních střevlkovitých (Coleoptera, Carabidae), *Rozpr. Cesk. Akad. Ved, Rada Mat. Prir. Ved.*, 1959, vol. 69, no. 2, pp. 1–64.
- Soboleva-Dokuchaeva, I.I., Serological determination of the role of ground beetles (Coleoptera, Carabidae) in agrobiocenosis, *Zh. Obshch. Biol.*, 1975, vol. 36, no. 5, pp. 749–761.
- Stebaeva, S.K. and Andrievskii, V.S., Collembolans (Collembola) and oribatid mites on brown-coal dumps of Siberia (Krasnoyarsk krai), *Zool. Zh.*, 1997, vol. 76, no. 9, pp. 1004–1015.
- Suktsessii i biologicheskii krugovorot* (Successions and Biological Cycle), Kurachev, V.M., Ed., Novosibirsk: Nauka, 1993.
- Titlyanova, A.A. and Sambuu, A.D., *Suktsessii v travyanykh ekosistemakh* (Successions in Herbaceous Ecosystems), Novosibirsk: Sib. Otd., Ross. Akad. Nauk, 2016.
- Topp, W., Simon, M., Kautz, G., Dworschak, U., Nicolini, F., and Prückner, S., Soil fauna of a reclaimed lignite open-cast mine of the Rhineland: improvement of soil quality by surface pattern, *Ecol. Eng.*, 2001, vol. 17, pp. 307–322.

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