

Ground Beetles (Coleoptera, Carabidae) and Zoodiagnostics of Ecological Succession on Technogenic Catenas of Brown Coal Dumps in the KAFEC area (Krasnoyarsk Krai)

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Abstract—The population of ground beetles on artificial catenas of dumps of brown-coal pits in Krasnoyarsk krai (dump age of one month, seven years, and 25 years) was investigated. The material was collected in the eluvial, transitional, and accumulative positions of each catena. The species diversity and activity of ground beetles after 25 years of succession in all catena positions do not reach the state of natural communities. The rate and direction of succession of the ground beetle taxocenes differed significantly depending on their relief position. The appearance of species typical of zonal forest–steppe ecosystems began after seven years of succession. In the accumulative position, succession developed more slowly than in the eluvial and transitional positions, where ruderal carabid species were gradually replaced by meadow mesophilous, and then by mesoxerophilous species. After 25 years, the taxocene of ground beetles in the accumulative position became similar not to the herb, but to the wood communities of the forest–steppe.

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INTRODUCTION

The most important reason for the reduction of biota diversity is the change in the “spatial matrix of the habitat” (Margalef, 1992; Hanski, 2010). This is facilitated by the incorporation of man-made habitats inhabited by ruderal biota of depleted composition with random cenotic organization and disordered dynamics into the landscape background of the biosphere (Parmenter and Macmahon, 1987; Dunger et al., 2001; Hendrychov et al., 2012). Coal mining, which, according to Rosstat data, from 2002 to 2013 increased by 37% (http://www.gks.ru/bgd/regl/B08_14p/Main.htm), makes a significant contribution to the distortion of the evolutionarily established system of habitats. The most negative environmental consequences result from coal mining using an open method, which is accompanied by the destruction of the natural landscape and its replacement by extensive quarries and waste dumps with the burial of natural ecosystems under the multimeter overburden. The technology of coal mining provides for land reclamation: technical, i.e., leveling or terracing of the hilly-ridge relief of dumps, and biological, i.e., artificial sowing of grass or woody plants on technozems. However, in practice, land reclamation activities are usually either carried out many years later or not at all. As a result, chaotic relief changes and the formation of surrogate ecosystems occur.

Interest in the study of biota successions on dumps, in particular, of coal enterprises, arose in the 1960s (Dunger, 1968). Data collected over half a century in different regions (mainly on brown coal dumps in East Germany, the Czech Republic, the Soviet Union, and the United States) have revealed a number of patterns of universal ecological significance. In the territories occupied by dumps, ecosystems are formed, only partly resembling the natural ones, but preserving the zonal orientation of succession development. However, they almost never reach the state of climax biogeocenoses of the corresponding biome (Burykin, 1985; Titlyanova et al., 1993).

The transformation of the basic properties of ecosystems arising on the dumps is primarily due to the state and activity of the living phase, succession changes of vegetation and invertebrates, and the intensity of the biological cycle. The soil forms more slowly than biota. The qualitative composition of the technozem exchange cations is determined primarily by the properties of the underlying rock, i.e., overburden. The process of humus accumulation dominates over mineralization, but it develops very slowly: 0.5 mg of C/g per 1 g of the substrate in the first 30 years. Later, the intensity of humus accumulation decreases five-fold. A primitive binomial soil is formed with a thin humus-accumulative horizon that lies directly on the parent rock. Artificial application of a fertile humus layer (10–20 cm) to the dump surface does not restore

the basic physicochemical properties typical of natural soils. The technozem remains a habitat with an extremely short time of formation and erasure of soil properties (Titlyanova et al., 1993; Topp et al., 2001; Shugalei, 2009). Nevertheless, the application of a fertile layer to the reclaimed surface accelerates the formation of vegetation and has a positive effect on the soil fauna (Frouz et al., 2007).

The number of species in the phytocenoses of coal mining dumps, which is extremely low initially (2–4), grows with time. However, species that are characteristic of climax stages of succession, which appear, at least once, from the first year of succession, rarely become the dominant community even after 20–30 years. But ruderal species retain dominant positions in the community not only at the pioneering stages, but also after 10 years or more. The phytocenoses do not reach the species richness of typical meadows or forests for 50 years (Brändle et al., 2000). During the succession of vegetation, the biological cycle becomes increasingly closed and the rate of exchange of total carbon and nitrogen in the ecosystem slows down (Titlyanova and Mironycheva-Tokareva, 1988).

Of all living organisms, heterotrophs become involved in the biological circulation of dumps faster than others (Dunger, 2008). Microarthropods (springtails, oribatid mites) appear in the substrate of dumps in the first days after dumping. Their number and diversity increase multifold with the age of the dumps (Babenko, 1982; Stebaeva and Andrievskii, 1997). The data on the structure and dynamics of the population of macroarthropods (mesofauna) are much more limited. Unlike the protozoans, microarthropods, and juvenile spider individuals that fall into dumps by passive wind transport, macroarthropods penetrate into the dumps actively. The most diverse and abundantly represented in the dumps are beetles, mainly staphylinids and ground beetles (Mordkovich and Kulagin, 1986; Dmitrienko and Shaimuratova, 1986; Mordkovich, 1994). It is assumed that omnivorous species are the most successful colonists (Parmenter and Macmachon, 1987). The high species diversity of beetles on reclaimed lands may be due to the diversity of habitats arising from the hilly-ridged relief of the dump. These micro-habitats can serve as a refuge for rare species, sometimes reaching high abundance there (Brändle et al., 2000). As dumps overgrow, the total number of beetles may experience significant fluctuations against the background of a gradual decrease in the degree of dominance of ruderal species (Frouz et al., 2008; Luzyanin et al., 2015). However, the general patterns of the dynamics of the beetle taxocene on reclaimed lands remain poorly studied and the features of beetle communities in the first days and weeks after the appearance of a dump are completely unexplored.

Ground beetles (Carabidae) were chosen as a model group, because this group of beetles is charac-

terized by a high level of species richness and abundance and a wide range of environmental preferences. In addition, it is the most numerous component of the zoedaphon, confined to the soil surface and its upper horizon, and therefore the most accessible to study.

The study polygon was the dumps of the brown coal mines of KAFEC located within the Achinsk-Bogotol, Chulym-Yenisei, and Kansk basins of the Middle Siberian Plateau. Land rehabilitation at KAFEC began in 1973. This process includes several successive stages. The first stage is the removal of “overburden,” i.e., the rocks overlying coal seams, the offloading and dumping of the rock of which leads to the formation of the dump. The dumps are artificial hills of light and medium loams mixed with aleurolite rubble, 15–25 m high, alternating with depressions of relief between them. Physiologically, the terrain resembles the natural ridge-hollow relief of the forest-steppe latitude zone of Siberia. The second stage (reclamation) involves leveling the relief and forming a plakor raised above the rest of the terrain. At subsequent stages of reclamation, a 25- to 50-cm layer of natural soil is poured over the parent rock. The final stage is biological rehabilitation, i.e., natural or accelerated regeneration of the vegetation cover on dumps.

In the 1980s and early 1990s, on the KAFEC territory, a large team of biologists and soil scientists under the guidance of A.A. Titlyanova conducted comprehensive studies of the biodiversity and the biotic circulation, in which one of the authors of this paper was a participant. The results of these works were presented in the collective monograph “Successions and the Biological Cycle” (Titlyanova et al., 1993). For various reasons, materials on macroarthropods were not included in it. This gap, although very late, is partly filled in by this article.

The aim of this work is to study the succession of the taxocene of ground beetles and to assess the impact of hilly ridge terrain and catena organization of habitats on the α - and β -diversity parameters in the dumps of coal mining, as well as to obtain answers to the following questions:

How different are the composition and variety of ground beetles in the technogenic ecosystems of the Kansk-Achinsk fuel and energy complex (KAFEC) from those in the natural ecosystems of the “parent” forest-steppe biome?

Does the organization of communities of ground beetles on technogenic dumps show signs of classical ecological succession or is it an arbitrary fluctuation of the diversity and abundance of randomly introduced species?

Does the taxocene development of ground beetles attain a state characteristic of the climax stages of ecological succession in the forest steppe? Does the 20-year period prescribed by the technological standards of planned recultivation (Motorina, 1986) suffice?

How do the direction, speed, and order of succession shifts differ on different elements of the technogenic relief and on dumps of different ages?

MATERIALS AND METHODS

Studies of the soil population were carried out in the summer of 1986 in naturally overgrown dumps one month, seven years, and 25 years of age, located inside a quarry on the territory of the Nazarovo coal mine, 10 km southwest of the town of Nazarovo, Krasnoyarsk krai. Within each dump, a chain of habitats was considered: eluvial positions at the top of each hill, transitional positions on the slope and accumulative ones in the depression between the hills. A total of nine habitats in the dumps were examined. The selected ages of the dumps correspond to the conditional stages of leveling of the artificial relief and overgrowing of the substrate, first with ruderal and then with characteristic vegetation of natural meadows of the surrounding zonal forest–steppe landscape.

Precipitation erodes friable loam dumps, displaces the thin fractions of the substrate down in the profile, and enriches reduced terrain elements with them. At the same time, there is an increase in the rubble content of the summit substrate and especially of the hill slopes. By seven years, the height of the hill has decreased from 25 to 22 m, and by the age of 25 years, to 20 m. The slope steepness decreases from the original 40° to 35° in seven years and to 30° in 25 years. The removal of aleurite from the top and the slope of the hill causes a decrease in the absorptive capacity in the initial period of soil formation and inhibits its development, whereas in the depressions of the terrain, it is the reverse (Titlyanova et al., 1993). The profile of the dump can be considered a technogenic catena, which is in the process of active formation, but already with differentiation of positions into eluvial, transitional, and accumulative.

During the period of mesofauna accounting, the temperature of the upper 5 cm of soil was measured using Savinov's soil thermometers and the moisture content of soil samples by weighing and subsequent drying. The temperature difference in the different positions of the catena was minimal (2–4°C) on the 7-year-old dump, and on the 25-year-old one, it increased to 10°C. The habitats of the accumulative positions of the dumps of one month of age turned out to be the coolest, while the habitats of the eluvial positions on the dumps of any age, but especially the 25-year-old one, were the warmest (Table 1). The soil moisture increased from top to bottom along the slopes of dumps of any age (1.5 times on the 7-year-old and four times on the 25-year-old dumps). The differences in the hydrothermal regime of soils in the eluvial and transitional positions were minimal in the first seven years of succession and doubled in the catena of 25 years of age (Table 1).

The tendency of formation and accumulation of humus corresponded to the direction of change of the vegetative cover. The concentration of organic carbon (C_{org}) and its stock in the substrate of dumps is two orders of magnitude less than in native forest–steppe soils. The accumulation of humus increases with the age of the dump in all positions, and in the accumulative position of the 25-year-old dump, it reaches values close to natural meadow soils (Table 1) (Titlyanova et al., 1993). The stock of phytomass also increases with the age of the dumps. The total number of species of higher plants on the 7-year-old dump is 66 and on the 25-year-old, 79. In its eluvial and transitional positions, there are associations of tall weeds with a huge biomass and high projective cover. A primitive grass and rush community is formed in the overmoistened accumulative positions of the 7-year-old dump. On the 25-year-old dump, all three positions of the relief differ by the composition of the dominants. A community richer in meadow grasses is formed in the accumulative position of the 25-year-old dump.

As a control for comparison with the dumps, two typical natural landscapes of the Central Siberian forest–steppe were selected in their surroundings: a steppe meadow in the eluvial–transitional position of a natural catena with meadow chernozem soil and forb and graminoid mesoxerophytic vegetation (*Stipa pennata*, *Poa pratensis*, *Onobrychis arenaria*, *Potentilla longifolia*, *Artemisia commutata*) and a clay–pebble beach in the floodplain of the Chulym River with hardly any higher vegetation.

In the habitats studied, ground beetles accounted for 80–90% of the total species richness and abundance of macroarthropods. The ground beetles were accounted for using the method of soil traps (plastic cups with a diameter of 6.5 cm). The censuses were performed by ten traps in each biotope over five days during the summer maximum of ground beetle activity (July 21–27, 1986).

For each biotope, the Menhinick's species richness index was calculated. Its value is <1, corresponding to low species diversity with a high abundance of the pronounced dominant, and can be a sign of the primitive organization of a community that is in the pioneering stage of succession. For a community of a forest–steppe biome at the middle stage of development, values of Menhinick's index equaling 1–2 are characteristic, and for climax communities, even higher values (Mordkovich, 2017). Using cluster analysis, we studied the similarity of the populations of ground beetles in the studied biotopes. The binary (Simpson's coefficient) and quantitative similarity coefficients (Dice index) were calculated. Clusters were constructed using the unweighted pair group method with the arithmetic mean (UPGMA) with the calculation of bootstrap coefficients ($n = 1000$). The calculations were performed using the PAST V.2.17 program (Hammer et al., 2001).

Table 1. Ecological characteristics of technogenic ecosystems of the KAFEC Nazarovo coal mine dumps (Tityanova et al., 1993)

Parameters	Dump age*											
	1 month (0)			7 years (66)			25 years (79)					
	EL	TR	AC	EL	TR	AC	EL	TR	AC	EL	TR	AC
Communities	Single plants			Weeds	Weeds	Grasses and rush	Grasses	Forbs, legumes, and grasses	Legumes, grasses, and sedge			
Dominant species	<i>Tussilago farfara</i> , <i>Artemisia vulgaris</i> , <i>Cirsium setosum</i>			<i>T. farfara</i> , <i>A. vulgaris</i> , <i>C. setosum</i> , <i>Elytrigia repens</i>	<i>Typha angustifolia</i> , <i>E. repens</i> , <i>T. farfara</i> , <i>C. setosum</i>	<i>E. repens</i> , <i>Poa pratensis</i> , <i>Calamagrostis epygeios</i>	<i>E. repens</i> , <i>Equisetum pratense</i> , <i>Trifolium pratense</i> , <i>Achillea millefolium</i>	<i>Carex capitata</i> , <i>P. pratensis</i> , <i>C. epygeios</i> , <i>T. pratense</i>				
Phytomass, g/m ²	0	0	0	1337	1006	1098	2339	1848	2860			
Soil temperature (0–10 cm), °C	23.5	20.5	19	27.5	26	25	30.7	28	20.6			
Soil humidity (0–10 cm), %	14.1	13.3	25.2	18.7	18.4	28.1	8.9	18.8	36.4			
C _{org} content, %	0.11	–	0.33	0.75	0.38	1.38	3.58	5.50	8.02			
C _{org} , g/m ²	71	–	213	435	225	825	1790	2200	3208			

(*) The parentheses give the number of species of vascular plants. (EL) Eluvial, (TR) transitional, and (AC) accumulative positions of the catena. The soil temperature and humidity are given for the time of sample collection (July 1986).

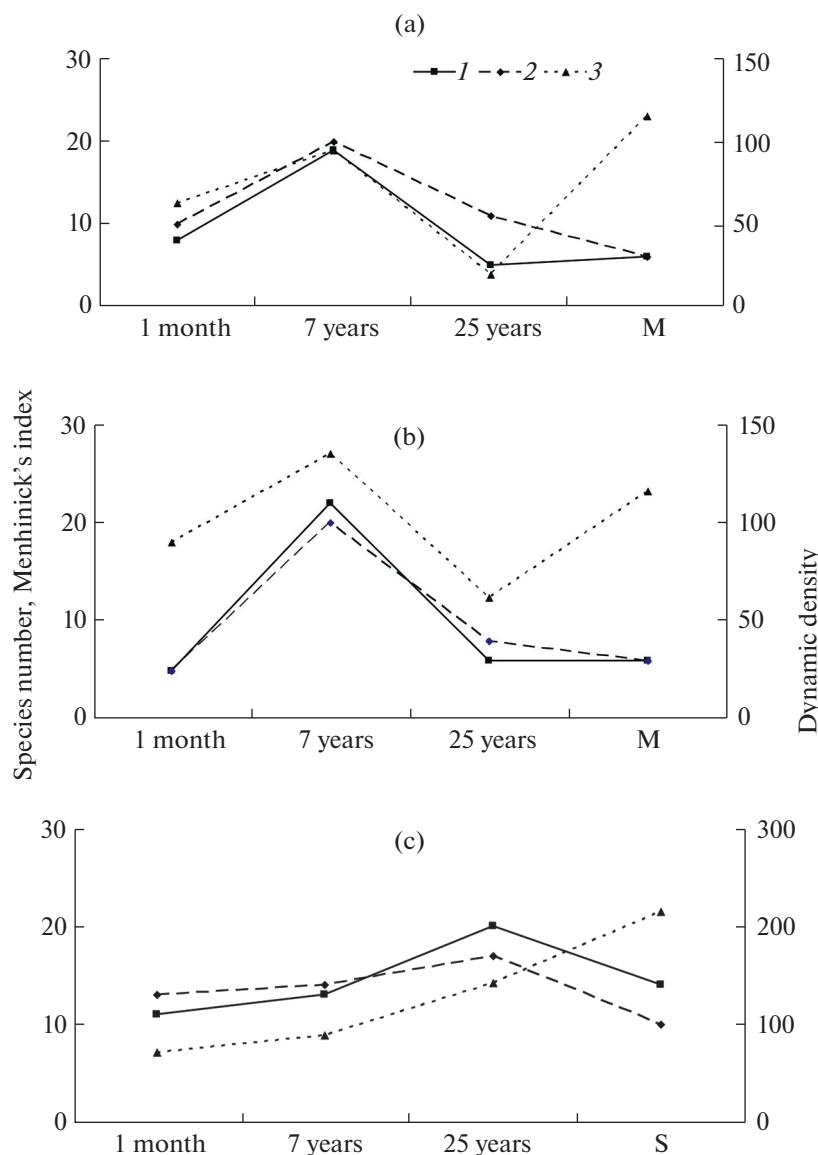


Fig. 1. Change of species richness and dynamic density of ground beetles in the course of succession in the different positions of artificial catenas and in natural habitats. (a) Eluvial, (b) transitional, and (c) accumulative positions of a catena, (M) steppified meadow; (S) shallows. (1) Number of species, (2) dynamic density, ind./50 t.d., (3) Menhinick's index multiplied by 10.

RESULTS

In all the artificial and natural habitats studied, 56 species of ground beetles were identified, the total dynamic density of which varied in different biotopes from a few to >100 ind./50 trap days (t.d.). Just a month after the rock was dumped, the species diversity of ground beetles in the eluvial and transitional positions of the catena in the absence of higher vegetation reached 5–8 species, and the dynamic density was 63–90 ind./50 t.d. (Fig. 1). In the accumulative position of the catena, on the border with the temporary reservoir, the diversity of ground beetles reached 11 species, and the dynamic density was 72 ind./50 t.d. The only dominant in the eluvial and transitional positions was

Amara fulva. The accumulative position was dominated by the same species, but with the addition of subdominant *Bembidion semipunctatum* and *Nebria livida*.

On the 7-year-old dump, overgrown with tall thick weeds by this time, the species diversity of ground beetles slightly increased in the accumulative position, 2.4 times in the eluvial position, and 4.4 times in the transitional one, compared to the fresh dump (Fig. 1). A change of dominants took place. In the eluvial and transitional positions of the catena, along with *A. fulva*, which continued to play the leading role, *Bembidion femoratum*, *B. quadrimaculatum*, *Curtonotus convexiusculus*, *C. aulicus*, and *Acupalpus meridianus* occupied equal positions. In the accumulative

position community, *Bembidion semipunctatum* maintained the dominant position, a significant number of *B. quadrimaculatum*, *B. lunatum*, and *Asaphidion pallipes* appeared along with it.

At the 25th year of succession, when graminoid and forb meadow vegetation took hold in the eluvial and transitional positions of the catena, lower species diversity (5–6) and dynamic density (up to 19 specimens/50 t.d.) of ground beetles were observed (Fig. 1). *Calathus erratus*, *Amara equestris*, and *Poecilus fortipes* became dominant. In the accumulative position of the artificial catena, by the age of 25, a hygrophyte meadow with sedge and reed was formed. The species diversity of ground beetles was 1.5 times higher, and the dynamic density was 1.6 times higher than on the 7-year-old dump. *Pterostichus niger*, *Trechus secalis*, *Carabus violaceus*, *C. henningi*, and *C. regalis* were dominant.

The course of succession in the eluvial and transitional positions of the dumps was very similar up to 25 years. Even at the monthly stage of succession, the values of Menhinick's index ranged from 0.5 to 1, and by the 7th year, they reached 2, which indicates a rapid pace of succession development in the KAFEC habitats. However, by the 25th year, the complexity of the taxocene of ground beetles decreased again (Menhinick's index was 0.8–1).

The succession of the population of ground beetles from the accumulative position of the catena proceeded more consistently. Here, Menhinick's index slowly but continuously increased from 1.3 to 1.7 from the monthly stage to the 7-year stage and further to the 25-year stage.

In the control biotopes (steppe meadow for eluvial and transitional positions and river shoal for the accumulative one), the number of species and the dynamic density of ground beetles were lower and the Menhinick index was higher than at the intermediate stages of succession on the dumps (Fig. 1).

Cluster analysis of the population of ground beetles of the studied catena positions showed that all biotopes were divided into two parts: "old" biotopes (25 years), together with the natural biotope of steppe meadows and "young" biotopes (one month, seven years), along with the constantly updated biotope of river shoals. The similarity of the dumps to the "reference" biotopes was small, which may indicate four independent clusters (Fig. 2). The studied biotopes are grouped mainly by the degree of closeness in the succession age. The eluvial and transitional positions are more similar to each other (and with high bootstrap values) than the accumulative ones. A tree constructed from the values of the Simpson coefficient, which takes into account only the presence or absence of a species, is characterized by a high level of similarity in

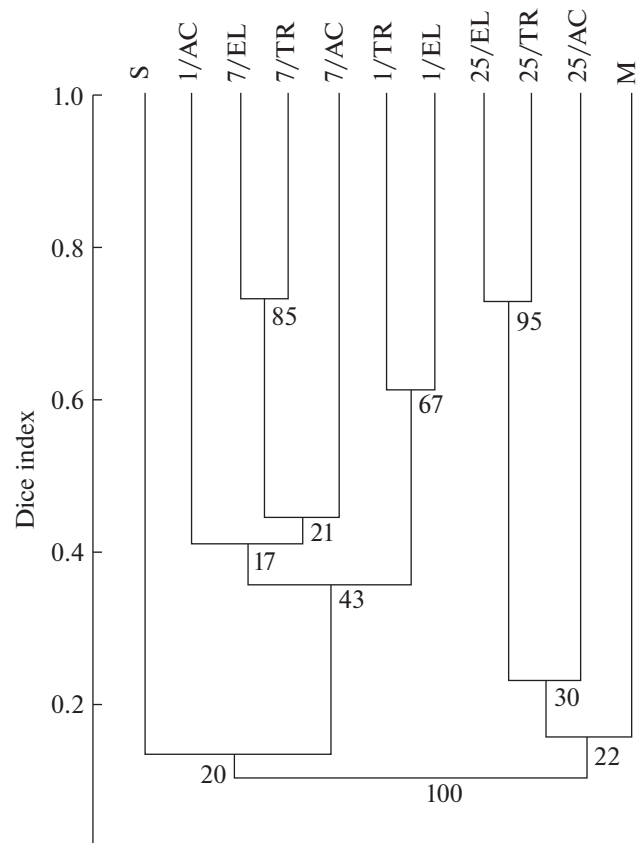


Fig. 2. Similarity of the ground beetle population of the KAFEC Nazarovo coal mine dumps according to the Dice index. Bootstrap coefficients are given at the graph nodes ($n = 1000$). (1) Dump age of one month, (7) dump age of seven years, (25) dump age of 25 years, (M) steppified meadow, (S) shallows. (EL) Eluvial, (TR) transitional, and (AC) accumulative positions of the catena.

the positions in the "young" dumps. The eluvial positions between themselves, as well as the transitional ones, have a similarity of 100% at low bootstrap coefficients (51–60).

When studying the distribution of the dominant species of ground beetles by the positions of different age catenas, we were able to identify species the numbers of which were significantly higher in some biotopes. The dynamic density of *A. fulva* reached 78 ind./50 t.d. in the transitional position of the fresh dump, *B. semipunctatum* was abundant in the accumulative position of the fresh and seven-year-old dump (19 and 40 ind./50 t.d., respectively), as well as in the shallows (38 ind./50 t.d.). *C. convexiusculus* was characteristic of the transitional position of the seven-year-old dump, and *C. erratus*, of the 25-year-old dump (62 and ind./50 t.d., respectively). These species can be considered as indicators of the corresponding stages of succession and the geomorphological position of the biotope.

DISCUSSION

A comparison of the results obtained with the available data on springtails and oribatid mites reveals a fundamental difference in the trends of diversity of micro- and macroarthropods as the dumps age.

The occupation of dumps of one month of age by oribatids and collembolans initially occurs due to a few species, the number of which is small. However, later, the abundance of some of them (the oribatid mites *Opiella nova*, *Tectocephus velatus*) grows unevenly, making them the dominant community (Babenko, 1982; Dmitrienko, 1990; Titlyanova et al., 1993; Stebaeva and Andrievskii, 1997; Bogorodskaya et al., 2010). In a four-year-old dump, the recovery of the invertebrate complex occurs more slowly. The community is dominated by springtails and predatory mites (Bogorodskaya et al., 2010). The third stage of microarthropod succession is observed in dumps of seven to ten years of age. It is characterized by a transition to a multispecific community while maintaining the dominance of all the same ruderals as in the previous stages of succession. In even older dumps (20–30 years old), the species richness increases several times, but the number of species is unstable; ruderal species still dominate (Titlyanova et al., 1993; Wanner and Dunger, 2002).

Thus, the microarthropods with their passive phoresis and the need to develop directly in the substrate of a fresh dump are characterized by a consistent increase in species diversity and abundance over 25–30 years. However, no complete equivalence with the composition and structure of the population of any of the zonal communities of the forest–steppe (meadow, meadow–steppe, or park–forest) is observed (Babenko, 1982; Titlyanova et al., 1993; Frouz et al., 2008; Hendriková et al., 2012).

Successions of populations of ground beetles, representing the category of macroarthropods, occur differently. In populating a dump in the first hours after the dumping, imagoes of beetles massively invade the dump from the surrounding ecosystems and without delay are included in the biological circulation of the fresh dumps. This is facilitated by the migration, which is, unlike that of microarthropods, carried out with the help of special adaptations (developed wings, chemoreception for wet earth, limbs adapted for movement not only on a flat surface, but also in a loose substrate), and also polyphagy. A high number of ground beetles is observed on the middle-aged dump, while on the 25-year-old dump, it decreases. Among microarthropods, even after 25 years, eurybiont species dominate in the composition of the population of dumps, as well as on young dumps; in ground

beetles, stenobionts of the natural forest–steppe are among the dominants.

The order, rate, and direction of differentiation of the ground beetle population depend not only on the age of the dump, but also on its position in the relief (Fig. 2). In the eluvial and transitional positions that become warmer and drier year by year, the ruderals (*B. femoratum* and *A. fulva*), completely dominating on the monthly dump, are replaced with meadow mesophiles on the seven-year-old dump (*B. quadrimaculatum*, *C. convexiusculus*, *C. aulicus*, and *A. meridianus*). On the 25-year-old, the dump where soil moisture in the eluvial and transitional positions is halved compared to that in the monthly dump (Table 1), the mesoxerophilous species characteristic of meadows in the natural landscapes of the Siberian forest–steppe seize the dominant positions in the ground beetles population (Mordkovich and Lyubechansky, 2010): *C. erratus*, *A. equestris*, *P. fortipes*, *Harpalus nigratarsis*, and *H. modestus*. In the accumulative positions, where the soil becomes wetter with age (Table 1), amphibian species (*Nebria livida* and *B. semipunctatum*), which occurred along the edge of a temporary reservoir of a month's age, on the seven-year-old dump replaced meadow hygrophiles *A. pallipes* and *B. lunatum* and meadow mesophiles *C. aulicus*, *C. convexiusculus*, and *Clivina fossor* (Table 2).

The appearance of single specimens of the forest species (according to their topical preferences) in the accumulative position of the seven-year-old dump, seemingly an accident, turns into a trend on the 25-year-old dump, when forest and forest edge species become dominant in the ground beetle population (*T. secalis*, *C. violaceus*, *C. henningi*, and *C. regalis*) (Mordkovich and Lyubechanskii, 2010), although there are no signs of afforestation in the soil or in the vegetation cover (Titlyanova et al., 1993). Thus, the forest taxocene of ground beetles develops earlier than the corresponding vegetation appears, and one can see the difference between the succession on the dumps and the one taking place in the natural biocenoses of the forest–steppe. Apparently, it is necessary to recognize ground beetles as forerunners of some, as yet unidentified, processes and properties that predict the appearance of a forest-type ecosystem in the habitat in the near future.

The change in ground beetles species with different topical preferences is determined by the fundamental restructuring of the structural and functional organization of the communities forming on the dumps. The greatest contribution to this process is made by cenophile species with a high abundance and clearly differentiating the geomorphological positions and stages of succession.

Table 2. Distribution of ground beetles in the studied KAFEC habitats (ind./50 t.d.)

Species	Catena position									Compared habitats		N
	1/EL	1/TR	1/AC	7/EL	7/TR	7/AC	25/EL	25/TR	25/AC	M	S	
<i>Acupalpus meridianus</i>	0	0	0	14	8	0	0	0	0	0	0	22
<i>Agonum ericeti</i>	0	0	0	0	1	3	0	0	5	0	0	9
<i>A. gracilipes</i>	0	0	0	0	1	0	0	0	0	0	0	1
<i>A. livens</i>	0	0	0	0	0	0	0	0	1	0	0	1
<i>Amara apricaria</i>	7	6	1	1	1	0	0	0	0	0	0	16
<i>A. bifrons</i>	0	0	0	1	1	0	0	0	0	0	0	2
<i>A. communis</i>	0	0	0	0	0	0	0	0	5	0	0	5
<i>A. equestris</i>	0	0	0	1	3	0	1	13	0	0	0	18
<i>A. fulva</i>	40	78	31	10	17	0	0	0	0	0	0	176
<i>A. ovata</i>	0	0	1	1	0	0	0	0	0	0	0	2
<i>A. parvicollis</i>	0	0	0	0	0	0	0	0	0	0	3	3
<i>A. spreta</i>	0	0	0	0	0	0	0	0	0	3	0	3
<i>A. tibialis</i>	0	0	0	0	0	0	0	0	0	3	0	3
<i>Anisodactylus signatus</i>	0	0	0	1	1	2	0	0	0	0	0	4
<i>Asaphidion pallipes</i>	0	0	1	0	1	6	0	0	0	0	0	8
<i>Bembidion articulatum</i>	0	0	0	0	0	0	0	0	0	0	4	4
<i>B. femoratum</i>	10	2	0	5	11	0	0	0	0	0	0	28
<i>B. litorale</i>	0	0	0	0	0	0	0	0	0	0	55	55
<i>B. lunatum</i>	0	0	3	0	2	4	0	0	0	0	0	9
<i>B. properans</i>	0	0	0	0	0	0	0	0	0	8	0	8
<i>B. quadrimaculatum</i>	2	0	2	17	8	10	0	0	0	3	1	43
<i>B. semipunctatum</i>	0	0	19	0	0	40	0	0	0	0	38	97
<i>B. striatum</i>	0	0	0	0	0	0	0	0	0	0	46	46
<i>Calathus erratus</i>	0	0	0	0	0	0	2	24	6	0	0	32
<i>Cal. melanocephalus</i>	1	0	0	2	2	4	0	0	5	0	0	14
<i>Cal. micropterus</i>	0	0	0	0	0	2	0	0	0	0	0	2
<i>Carabus aeruginosus</i>	0	0	0	0	0	0	0	0	3	0	0	3
<i>C. henningi</i>	0	0	0	0	0	0	0	0	5	0	0	5
<i>C. regalis</i>	0	0	0	0	0	0	0	0	7	0	0	7
<i>C. violaceus</i>	0	0	0	0	0	0	0	0	8	0	0	8
<i>Chlaenius nigricornis</i>	0	0	0	0	0	0	0	0	0	0	3	3
<i>Clivina fossor</i>	0	0	1	3	0	2	0	0	3	0	8	17
<i>Curtonotus aulicus</i>	0	0	0	9	4	0	0	0	1	0	0	14
<i>Cur. convexinsculus</i>	1	2	0	15	62	4	0	0	0	0	0	84
<i>Dyschirius obscurus</i>	0	0	0	0	0	0	0	0	0	0	24	24
<i>Dyschirius sp.</i>	0	0	0	0	0	0	0	0	0	0	5	5
<i>Elaphrus riparius</i>	0	0	0	0	0	0	0	0	0	0	6	6
<i>Harpalus affinis</i>	0	0	1	4	4	0	0	0	0	0	0	9
<i>H. distinguendus</i>	0	0	0	0	1	0	0	0	0	0	0	1
<i>H. modestus</i>	0	0	0	0	0	0	1	0	0	0	0	1
<i>H. nigrans</i>	0	0	0	0	0	0	7	1	0	0	0	8
<i>H. rubripes</i>	0	0	0	2	1	4	0	1	3	0	0	11
<i>H. rufipes</i>	0	0	0	0	2	0	0	1	6	0	0	9

Table 2. (Contd.)

Species	Catena position									Compared habitats		N
	1/EL	1/TR	1/AC	7/EL	7/TR	7/AC	25/EL	25/TR	25/AC	M	S	
<i>Loricera pilicornis</i>	0	0	0	0	0	2	0	0	0	0	0	2
<i>Microlestes minutulus</i>	1	0	0	2	0	0	0	0	0	0	0	3
<i>Nebria gyllenhali</i>	0	0	0	0	0	0	0	0	0	0	5	5
<i>N. livida</i>	0	0	11	0	0	0	0	0	0	0	13	24
<i>Poecilus cupreus</i>	0	2	1	0	1	0	0	0	0	0	0	4
<i>P. fortipes</i>	0	0	0	2	1	0	8	22	6	48	0	87
<i>P. versicolor</i>	0	0	0	1	2	0	0	0	9	0	0	12
<i>Pterostichus eximus</i>	0	0	0	0	0	0	0	0	0	53	0	53
<i>Pt. melanarius</i>	0	0	0	0	0	0	0	0	6	1	0	7
<i>Pt. minor</i>	0	0	0	0	0	0	0	0	1	0	0	1
<i>Pt. niger</i>	0	0	0	0	0	0	0	0	44	0	6	50
<i>Synuchus vivalis</i>	1	0	0	4	0	4	0	0	3	0	0	12
<i>Trechus secalis</i>	0	0	0	0	0	0	0	0	15	0	0	15
Total individuals in catena	63	90	72	95	135	87	19	62	142	119	217	1101

(1) Dump age of one month, (7) dump age of seven years, (25) dump age of 25 years, (M) steppified meadow, (S) shallows. (EL) Eluvial, (TR) transitional, and (AC) accumulative positions of the catena. (N) The total number of individuals of one species.

CONCLUSIONS

Over time, the differentiation of environmental conditions in the different positions of dump relief, negligible at one month of age, gradually increases. The catena type of organization of dumps and fractional differentiation of the environment in space and time form a multitude of habitats of macroarthropods.

The speed and direction of the taxocene succession of ground beetles differ significantly depending on the position of cenoses in the relief. In the eluvial and transitional positions of technogenic catenas, separate species characteristic of the zonal ecosystems of the forest–steppe appear seven years after the beginning of the succession. The conditions in the accumulative positions change the most rapidly and in the direction the most comfortable for soil invertebrates. The succession develops consistently, but more slowly than in the eluvial and transitional positions. The species diversity and dynamic density of ground beetles after 25 years of succession in all positions of a technogenic catena do not become identical with natural communities. In 25 years, a ground beetle taxocene in the accumulative position acquires similarity not with the herb, but with woody communities of the forest–steppe, in contrast to phytocenosis and the soil.

The characterized patterns of change in the taxocene population of ground beetles, consistent in time and space, can collectively qualify as ecological successions, as they approach a state close to climax states of natural forest–steppe communities. However, this

process does not require 12–18 years, adopted today as the standard time for reclamation, but much more. According to our data, 25 years is not sufficient for this.

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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.

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