Zoological Indication of Climate Change in the Central Kazakh Steppe Compared to the Middle of the 20th Century Using the Example of Carabid and Tenebrionid Beetles

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Abstract—Studies of communities of ground beetles (Carabidae) and black beetles (Tenebrionidae) were conducted in central Kazakhstan along 70° E in typical, dry, and desert steppe subzones in 1976–1978 and 2018. Parallel to that, soil-cover studies were conducted and the climate indicators of the studied areas were compared. Despite a considerable change in climate over 50 years, which has been expressed in a rise in temperatures with a simultaneous increase in precipitation, the basic features of soils have not undergone essential changes, but they keep or get strong potentials for solonetz and solonchak elementary soil processes, which are capable of drastically changing the structure of the soil cover. The generality of local fauna of carabids in 1976–1978 was 48–62% and, at the beginning of 21st century, it decreased to 16% in dry steppe and to 7% in desert steppe. In tenebrionids, which are more adapted to aridity, the faunal similarity decreased from 70–75 to 37% in the typical steppe and increased to 87% in the dry steppe. There are more "southern" subarid species in the communities and fewer relatively "northern" boreal and polyzonal species, which disappear completely in dry and desert steppes. The Tencar index that expresses the ratio of the number of individuals and species of arid tenebrionids and more humic carabids is used as an integral zoo indicator of changes in aridity of the environment. In the typical steppe, the index values are low and change little in the long-term dynamics and along the catena. However, in the dry steppe, Tencar index values increased 5 times in 2018 when compared to the middle of the 20th century and in desert steppe they grew by two orders of magnitude. The trigger for changes in the composition and structure of local communities of carabids and tenebrionids is not a change in atmospheric humidity, but a rise in average annual temperatures, which exceeded the global trend values and activated the salinization of soils, creating the conditions for the desertification of the territory and biota.

Keywords: climate changes, soil cover, carabids, tenebrionids, Carabidae, Tenebrionidae

INTRODUCTION

In the last 50 years, attention has been focused on changes in the Earth's climate and the biota parameters that are dependent on it. It is the biota that ensures the effective functioning and sustainability of ecosystems and the biosphere as a whole. In the 20th century, scientists persistently warned of phenomena such as an increase in CO_2 content in the atmosphere, the aridization of the environment, the melting of cover glaciers and permafrost, etc. (Budyko, 1980; Budyko et al., 1993). In the 21st century, the alarming predictions of climatologists and ecologists began to come true. Since the 1980s, the average annual temperature of the Earth's atmosphere has been confidently recorded to permanently rise by 0.6°C when compared with the turn of the 19–20th centuries (Houghton et al., 2001). For the period 1976–2006, the average warming

in Russia reached 1.33°C (*Otsenochnyi doklad...*, 2008). Over the past 30 years, climatic changes are characterized by a permanent increase in average annual temperatures and an increase in the amplitude and frequency of seasonal fluctuations in atmospheric circulation regimes. The important features of the coming climate are a lack of a single climate change trend and various environmental consequences (varying from aridization to humidization), depending on the geographical latitude of the area; the size of continents; the ratio of land to surrounding oceans and seas; and the macrorelief (Tishkov, 1996; Global changes..., 1999). The most significant climatic changes are expected on the vast plains of North America and Eurasia.

Global climate changes can significantly reduce the number of many organisms, especially stenobionts. It is expected that if the current trend of climatogenesis persists, this will inevitably lead to the large

restructuring of biogeocenoses by 2050. A large-scale and deep transformation, or even the complete destruction of usual habitats, is even more dangerous for modern biota (Hansky, 2010). The ongoing climate changes lead to changes in the system of geographical zones and their corresponding biomes and, at a minimum, to a shift in the range of species by 10–20 km per decade (Chen et al., 2011). The probability of such forecasts is confirmed by palynological and paleontological data that indicate the past movement of the boundaries of landscape zones from north to south by hundreds of kilometers and the emergence of new ecosystems of a large rank, up to the biome (for example, the steppe biome) (Kirikov, 1959; Zherikhin, 1993; Asworth, 2001).

The close relationship of biota at all levels of its organization with the climate and the resulting parallelism of change trends serve as the methodological basis for bio-indication and bio-diagnosis of the state of the environment (Gilyarov, 1965; Mordkovich, 1977; Rainio and Niemela, 2003). The inhabitants of the aboveground layer of biogeocenoses are the most sensitive to climate and its variability. The loose layer of the litter almost does not protect the soil surface from direct insolation, winds, precipitation, surface runoff, evaporation, and heating (which are unfavorable for living organisms). Therefore, the slightest change in the hydrothermal regime primarily affects the aboveground layer. The expressiveness of adaptations to climatic anomalies makes mesoherpetobium the most suitable object for zoological diagnostics of the state of the environment, especially in open landscapes (Mordkovich, 2014).

Carabid beetles (Coleoptera and Carabidae) are a popular object for monitoring and bio-indication studies (Rainio and Niemela, 2003; Koivula, 2011) due to their diversity and high abundance in most terrestrial ecosystems. In addition, this is one of the most faunistically studied families of insects; carabid faunas of many regions have been studied for many decades. Therefore, the study of regional faunas and carabid communities may be useful for comparison with climatic changes occurring in these areas.

The following has been shown for many carabid species:

(i) A change in the boundaries of the range (the advance of southern species to the north: (Hickling et al., 2006; Bespalov et al., 2010; Thomas, 2010; Drees et al., 2011; Aleksandrowicz, 2011; Chen et al., 2011, Ostrovskii, 2017; Dudko et al., 2018);

(ii) A shift up the slope of mountains that follows altitude belts in both Western Europe (Butterfield, 1996; Gobbi et al., 2007; Pizzolotto et al., 2014) and South America (Moret et al., 2016);

(iii) A change in the phenology and seasonal dynamics of abundance: increasingly earlier dates of the beginning of seasonal activity due to warming and its cessation at approximately the same time as before,

which has already been attributed to a reduction in the photoperiod (Pozsgai and Littlewood, 2011), or, on the contrary, a later finish of imago wintering and a later autumn activity of young individuals (Bondarenko and Zamotailov, 2013);

(iv) A decrease in the size of the beetle body and gracialization of its proportions over the past decades, which are also attributed to warming (Babin-Fenske et al., 2008; Brandmayr and Pizzolotto, 2016; Tseng et al., 2018).

Complexly organized carabid communities are sensitive to climate changes. The following has been shown for carabid communities:

(v) A decrease in the number or disappearance of short-winged species that have weak dispersal abilities and/or large sizes (Turin and den Boer, 1988);

(vi) The extinction of predatory (Voigt et al., 2003) and specialized species with the parallel invasion of generalist species (Desender et al., 2010; Clavel et al., 2011);

(vii) General impoverishment of the species composition and spectrum of ecological groups (Brooks et al., 2012; Pozsgai and Littlewood, 2014; Zamotailov et al., 2015).

Moreover, it is often difficult to distinguish the changes in the communities of herpetobiont invertebrates caused by local anthropogenic impacts, including fragmentation of habitats, from those caused by climatic changes.

Of the other beetle families, the bioindication potential is possessed by tenebrionid beetles (Coleoptera, Tenebrionidae) (Mordkovich, 1977). The studies on them are fewer in number, but it is known that some of them are also moving to the north (Sergeeva, 2014) or changing their preferred habitats from degrading steppes to trophically richer habitats in forest belts (Nabozhenko and Lebedeva, 2016).

The goal of the proposed study is to identify and evaluate the nature and degree of relationship of long-term climatic, soil, and zoological trends to a first approximation. The following tasks were solved:

(1) Analyzing the trends of changes in key climate parameters in the steppe zone of central Kazakhstan in the 21st century compared with the middle of the 20th century.

(2) Comparing the trends of the transformation of typical characteristics of the latitudinal–zonal series of steppe soils in the mentioned region for the same period, confirming or refuting their reputation as the most conservative and inert component of a biogeocenosis.

(3) Identifying the composition and structure of the animal population of similar soils in central Kazakhstan in the mid-20th century and early 21st century based on the example of herpetobium (surface carabid beetles and tenebrionid beetles) and determining the trends of change in their species com-

positions and ecological communities over the specified time.

SELECTION OF THE RESEARCH SITE

The steppe zone of central Kazakhstan was chosen as a testing ground for the joint studies of climate, soil, and zoobiota, because it represents a habitat with the widest possible range of environmental conditions in time and space. This territory is located in the depths of the giant Eurasian continent far from the oceans and, at the same time, is open for the unhindered movement of air masses in any direction. The widest range of environmental conditions, which is poorly detectable in time, is reliably established in space in the form of a system of latitudinal zones and subzones that form a gradient series that is supplemented by local gradients of conditions caused by the catena organization of space. Together they form an abiotic environment matrix that outlines the limits of variability of the steppe ecosystem, which are followed by either complete degradation or the gradual transformation of steppes into the forest-steppe landscape to the north or desert landscape to the south.

On the inland plains of central Kazakhstan, where plains alternate with areas of small hills, there are three steppe subzones:

The subzone of a typical moderately arid or arid steppe on ordinary or southern chernozems occupies an area of 24.9 million ha, including 12.9 million ha on southern chernozems (*Prirodnye usloviya...*, 1969). The vegetative cover forms an herb–fescue–feather grass stand. Its dominants are as follows: thick-sod herbs (*Stipa rubra*, *S. capillata*), thin-sod herbs (*S. lessingiana*, *Festuca pseudovina*, *Koeleria gracilis*, and *Helictotrichum desertorum*) and representatives of motley grasses (*Artemisia austriaca*, *Salvia stepposa*, *Phlomis tuberma*, etc). The projective cover of 70–80% in the arid typical steppes and grass stand height of 30–50 cm significantly impede the ground layer insolation in the steppe biogeocenosis.

The subzone of dry fescue–feather grass steppes on dark chestnut soils occupies on an area of 53.1 million ha. The dominants of the zonal vegetation are thin-sod herbs: Lessing feather grass, koeleria, desert oat grass, and fescue; motley grasses: pasture sagebrush, Austrian wormwood, and Roman wormwood; and goldilocks (*Lynosyris villosa*), pyrethrum (*Pyretrum adellifolium*), quinquefoil (*Potentilla acaulis*), Alpine saw-wort (*Saussurea salifolia*), tulip (*Tulipa* sp.), lousewort (*Pedicularis sp.*), and irises (*Iris* spp.). The projective cover of 50–60% and grass stand height of 20–30 cm weakly protect the soil surface from aggressive insolation.

The subzone of deserted semishrubby thin-sod small-herb steppes on light chestnut soils has an area of 37.5 million ha. The dominant species are the feather grass (*Stipa glareosa*), wheatgrass (Agropirum desertorum), and motley grasses: white wormwood on less saline soils and black wormwood on solonetzic and solonchak soils and pigweeds: fourwing saltbush (*Artiplex cana*) and bur grass (*Anabasis salsa*). The projective cover of 30–40% and grass stand height of 10–15 cm expose the soil surface to strong insolation.

In general, the range from the northern reaches of the steppe zone to the southern ones is characterized by an increasing amount of heat, decreasing amount of precipitation, increasing evaporation, moisture deficit, and aridization of the biota habitat (Table 1). The seasonal order of precipitation changes in the same direction: the maxima of precipitation shift from July to the spring and early summer period (*Prirodnye usloviya...*, 1969; Beresneva, 2006).

In the subzone of typical steppes, zonal soils are ordinary chernozems and southern carbonate light loamy soils. Relief depressions have meadow–chernozem and meadow soils with surface moistening. Depending on the position in the relief, salt content, compaction, clumpiness, and fracturing are manifested in soils to varying degrees. The profile of southern chernozems often contains readily soluble salts and gypsum. The depth of the upper boundary of the salt horizon is 70–100 cm; the maximum accumulation of salts is usually recorded in the second meter of the soil profile. The humus content in the upper soil horizons averages 5%, and the thickness of the humus profile can reach 1.5 m. The salinity is due to the content of exchangeable sodium in soils in the range of 4–12%. The availability of gross nitrogen and phosphorus is high, and the availability of their mobile forms is low. The availability of gross and mobile potassium is high. The proportion of solonetzes is 24.3% of all soils in the subzone of southern chernozems. Deep sodium solonetzes are formed on elevated relief elements (ridges). They are washed from water-soluble salts to a depth of more than 1 m, while carbonates and gypsum in them are localized at a depth of 50–80 cm. The content of absorbed sodium in the illuvial horizon can reach 30% of the absorbed bases. In the conditions of a shallow depression relief, solonetzes are under conditions of seasonal salinization and desalination. The solonetz horizon contains not only absorbed sodium, but also magnesium. The upper boundary of carbonates and gypsum can be localized at a depth of 15–30 cm (*Pochvennyi otchet...*, 1960; Borovskii et al., 1969; *Putevoditel' pochvennoi ekskursii*, 1974; Uspanov, 1974; Kiryushin, 1975; Borovskii, 1978; Durasov and Tazabekov, 1981; Borovskii, 1982; Titlyanova et al., 1984).

The soil properties in the subzones of dry and desert steppes are as follows: a rough structure; low profile thickness; the presence of solonetzes; high alkalinity; the presence of carbonates; a columnar, prismatic, nutty, clumpy structural organization of the illuvial horizon; and the presence of salinization, due to the nature of the parent rocks of the Kazakh Upland,

Table 1. Climatic characteristics of the flat steppes of the middle region of Eurasia in the middle of the 20th century. The values were taken from the *Guide to the Climate of the Soviet Union* (1966) (average for 1920−1965) and from the "Kazakhstan" monograph (1969)

Latitudinal steppe subzones	Meadow steppe	Typical arid steppe	Dry steppe	Deserted steppe
Zonal vegetation	Herbaceous−motley grass	Motley−feather grass vegetation	Wormwood−feather grass−fescue vegetation	Thin-sod herbaceous semishrub vegetation
Soils	Ordinary chernozem	Southern chernozem	Dark chestnut soils	Light chestnut soil
Geographical latitude	53°	52−51°	50−49°	50−49°
Study region, nearest settlement	W. Siberia	Central Kazakhstan		
	Settlement of Kara-chi	Settlement of Shortandy	Settlement of Arykty	Settlement of Barshyn
Weather station	Settlement of Chany	City of Astana Urban−type settlement of Shortandy	Settlement of Kurgaldzhin	Settlement of Staroe Barshino
Total annual precipitation (average for 50 years)	331	262	218	152
Amplitude of total precipitation, max/min, mm for 50 years (A)	250/450	122/529	104/368	88/318
Degree of amplitude of total precipitation, A/av	0.6	1.6	1.2	0.9
Evaporation, mm/year (average for 50 years)	≈300	≈500	≈700	≈800
Moisture deficit, evaporation/precipitation	0.9	1.9	3.2	5.3
Average annual temperature, °C	−0.7	1.4	1.5	3.3
Average summer temperature, °C	18	22	24	26
Sum of temperatures $T° > 10°$	1900	2100	2300	2500
Frostless period, days	110	120	123	140
R, radiation balance, kcal	24.6	31.4	31.5	37.2
Marton index	3.0	2.5	1.9	1.1

mainly loamy and alluvial−deluvial rough-structure stony deposits. The zonal soil cover is represented by dark chestnut and light chestnut soils. Along with them, meadow−chestnut soils, meadow, and meadow−marshy soils are common. There are widespread solonetzes, which develop in combination with other soils: they have a small-column structure, are solonchak and saline with a sulfate chloride salinization, and contain carbonates and gypsum. According to the composition of absorbed bases, they are sodium and sometimes magnesium. In river valleys, salt marshes develop in closed drainless hollows and lake depressions (Storozhenko, 1952; *Voprosy melioratsii…*, 1963; Borovskii et al., 1969; Durasov and Tazabekov, 1981).

MATERIALS AND METHODS

The initial climate data (annual and monthly temperatures and precipitation) for the last century were borrowed from the regularly published *Handbook on Climate of USSR* (*Spravochnik po klimatu…*, 1966) or directly from the journals of the Tselinograd (Astana, Nursultan), Kurgaldzhino (Korgalzhyn), Karaganda, Berlik, and Staroe Barshino stationary weather stations; the climate data for the 21st century were taken from the Internet resources at rp5.by ("Weather Schedule" and thermograph.ru ("Thermograph: Archived Data of Air Temperature and Rainfall"). Information on the soil microclimate for the 1970s was

obtained by the authors (soil moisture and temperature in different layers) by drying the soil samples in weighing bottles and weighing before and after drying in a thermostat; temperature measurements were carried out using Savinov thermometers.

To characterize the soils, model sections of a standard format with a description of the morphology of the soil profile and necessary laboratory and analytical support were used. To correctly compare retro- and modern results, soil classification is given according to the manual *Classification and Diagnostics of Soils of USSR* (*Klassifikatsiya i diagnostika...*, 1977).

To perform the zoological diagnostics of the state of the environment, quantitative counts of soil mesofauna were carried out. Carabid beetles (Coleoptera and Carabidae) and tenebrionid beetles (Coleoptera and Tenebrionidae) were used as reference groups that most adequately reflect the climatic and microclimatic conditions of habitats. Mesoherpetobium censuses were carried out using soil traps in 1976, 1977, 1978, and 2018 in the same reference areas located approximately along 70° E: in the typical steppe on the southern chernozem in the vicinity of the settlement of Shortandy (51°34′ N, 71°17′ E) and in the dry steppe on dark chestnut soil in the vicinity of the settlement of Arykty (50°32′ N, 70°27′ E) (Republic of Kazakhstan, Akmola Region) and in the desert steppe in the vicinity of the settlement of Barshyn (49°37′ N, 69°28′ E) (Karaganda oblast). In each area, traps were placed along the catena at eluvial, transit, and accumulative positions. At each position, traps were placed in a line of ten pieces at a distance of 1 m from each other and were exposed in late May to early June for 5−10 days in a row. For the purpose of unification, all count data are given in terms of 100 trap days. The similarity of species compositions was determined by the Jacquard coefficient. The results of counts are given in Appendix 1.

The index that reflects the ratio of the number of carabid beetles and tenebrionid beetles was proposed as an indicator of aridity for mesoherpetobium. The former, having a wide arsenal of adaptations to the aridity of the environment, symbolize progressive aridization; the latter, having only passive means of protection against dryness, are considered an indicator of the humidization of the environment (Markuzzi, 1960). We use this index in a modernized form (Mordkovich, 1977), taking into account not only the number of individuals, but also the species richness of both carabids and tenebrionids. Therefore, we considered it correct to change the name of the index to Tencar (Tenebrionidae/Carabidae). The value of the Tencar index is $(A/B)*(a/b)$, where A is the total number of tenebrionid beetles on a catena (without taking the accumulative position into account), B is the number of carabid beetles, a is the number of tenebrionid species, and b is the number of carabid species).

The species of carabid beetles noted during the study were grouped by the latitudinal component of their ranges: the species were divided into boreal, subboreal humid, subarid, and polyzonal in accordance with the methodology described in our study: (Dudko and Lyubechanskii, 2002) and its additions: (Dudko et al., 2018). The spectra of the ranges of carabid species in each habitat make it possible to determine the extent to which the species composition in a particular habitat is northern or southern.

The whole complex of studies was carried out using the catenary approach, i.e., by acquiring synchronous data not only from zonal landscapes, but also from intrazonal positions, which were previously selected and marked out (Mordkovich et al., 1985): eluvial (EL), transeluvial (transel, TR1), transeluvial—accumulative (transelac, TR2), and accumulative positions (AC). To indicate the positions, the nomenclature proposed by Glazovskaya and Gennadiev (1995) was used.

In total, climate data were processed and analyzed from 1975 to 2018 for different years, months, and periods of the growing season. We used the data of 15 soil sections and more than 1000 soil-zoological samples, which were collected over 4 years on a monthly basis from April to September.

For meteorological data, the Marton air dryness index $Ja = P/(T + 10)$ was calculated, where P is the total annual precipitation, cm, and T is the average annual temperature, °C; a more arid year has a lower index value (Bykov, 1983).

RESULTS AND DISCUSSION

Regional Anomalies of the Global Climatic Trend in the Steppe Zone of Central Kazakhstan

Until the middle of the 20th century, climate peculiarities on the plains of central Kazakhstan were usually explained by the specific effect of a narrow spur of the Siberian anticyclone, which is extended from east to west (the wind separation axis of A.I. Voeikov). A steppe biome has been formed and still exists along this spur and thanks to it (Mordkovich, 2014). In recent decades, the transport of air masses in from north to south has sharply increased, bearing cool and precipitation from the thawing North Ocean and hot dry air from the desert regions of Central Asia. As a result, the general climate trend toward warming in the steppe and desert zones of central Kazakhstan exceeds the global average values by two times (Budanov, 2016). In addition, as early as the beginning of the 21st century, the diversity of weather types and frequency of their change have sharply increased when compared with the previous century in the steppe zone of central Kazakhstan, significantly exacerbating the features of the climate that was sharply continental even without this (Beresneva, 2006).

Table 2. Climate change in the subzone of typical arid steppes on the southern chernozems of central Kazakhstan in 1970–2018 (according to the data of the weather station in the city of Astana, index 35188). Legend: A/av is the degree of amplitude of total precipitation

Climatic indicators for different years	Temperature, °C				Precipitation, mm				Marton air dryness index
	average annual $T°$	abs. max	abs. min	A/av	total annual	abs. max	abs. min	A/av	
Average long-term over the 1970s	2.5	3.6	1.2	1.1	287	321	116	0.7	2.3
Average long-term over the 1980s	3.2	4.8	1.3	1.1	305	387	266	0.4	2.3
Average long-term over the 1990s	3.2	4.5	1.6	0.9	312	411	228	0.6	2.4
Average long-term over the 2000s	4.1	5.0	3.2	0.4	332	371	248	0.4	2.3
Average long-term over the 2010s	4.1	5.3	3.4	0.4	361	494	267	0.6	2.6

We conducted an analysis of climate data in central Kazakhstan depending on year since the 1970s to date in the territory of the subzone of the typical steppes on southern chernozems, at a distance of 50 km to the south of the village of Shortandy according to measurements of the weather station in the city of Astana (Tselinograd, Nursultan). This latitudinal strip is notable for a classical sharply continental climate, which reflects the whole spectrum of states that is characteristic of the steppe zone as a whole.

The limits of variability of the radiation balance are in the range of 24.6–37.2 kcal/year, and the average annual temperature (averaged over 50 years) is from −0.7 to 3.3°C. The annual amount of precipitation varies from 88 to 529 mm, evaporation is from 300 to 800 mm/year, and moisture deficiency is from 0.9 to 5.3. Fluctuations in the degree of air dryness index (the Marton index) are possible in the range from 1.1 to 3.0 (Table 1).

Against this unified background of the steppe climate, changes in the subzone of typical steppes in the second half of the 20th century and in the early 21st century appear as follows. The average annual air temperature (average over a decade) that was 2.4°C in the 1970s increased by almost a degree in the 1980s–1990s (3.2°C), up to 4.1°C in the 2000s and 2010s, and up to 4.6–5.3°C in the last 3 years. Given that it averaged only 1.4°C in the period from 1920 to 1970 and the limiting value of this indicator (in desert steppes) reached 5.3°C in the absence of a global warming trend, it can be asserted with certainty that there has been a permanent warming by 1.7°C in central Kazakhstan for 50 years. Since the 1970s, the average annual precipitation over a decade has also been growing continuously, but more smoothly than the average annual temperature—from 287 mm/year to 305–312 mm in 1980–1990, then to 332 mm/year in 2000–2010 and 361 mm/year in the 2010s (Table 2).

The increase in humidification that is relatively modest compared with the West Siberian plain is apparently due to the fact that humid air reaches central Kazakhstan with large losses. In addition, a significant part of moisture is accumulated by the remains of the Kazakh Upland. A relatively small, but continuous and long-term increase in annual precipitation in central Kazakhstan, which is confirmed by the decrease in aridity according to the change in the Marton index (Table 2), may be considered an anomaly in relation to the global trend of warming and aridization, which has been manifesting itself locally in the most intracontinental region in the last decade. It should be borne in mind that a slight weakening of aridity in steppes to the south can be impeded by a parallel increase in evaporation due to a significant increase in average annual temperature.

The Special Significance of Spring for Steppe Biota against the Background of Climatic Instability in the Growing Season

Climate conditions in the steppes of central Kazakhstan are generally uncomfortable for biota, because humidity and heat, which are the two main factors that limit vital activity, are in turn or simultaneously insufficient for most of the year, even in the growing season (Tables 1–3). The deficiency of one or another factor can occur in any month of the growing season.

Against this unstable background, the first third of the growing season (the period from mid-May, sometimes from April to mid-June) has the advantage of a positive effect. At this time, a rapid melting of the snow cover guarantees full moistening of the soil, regardless of the arrival or lack of summer rainfall. The invasion of warm air from the already warmed deserts located to the south provides a rapid increase in heat in spring in the steppes of central Kazakhstan to 10 or even 15–20°C, which is observed as early as from mid-May and often from April (Beresneva, 2006). Sharp and frequent changes of various weathers, which are especially characteristic for spring, provide a wide

range of environmental conditions in the steppes, while weathers of one or two types dominate in the remaining months of the growing season. The period from May to mid-June is characterized by the largest deviations of key climatic parameters from the average value for 1976−2018. Meanwhile, in the 1970s, average temperatures were higher than the norm, and in 2018 they were below the norm (Table 3).

Accordingly, it is in spring when the flowering and rapid growth of most steppe plants take place and the maxima of the diversity, abundance, and activity of dominants of the steppe fauna are observed.

In the typical steppes of central Kazakhstan for May−June during the dry years (1975−1976), the first third of the growing season accounted for 40% of total precipitation (124 mm) of the growing season; its proportion in total precipitation was 35% in wetter 1977 and 1978 and 30% in 2017, 2018.

The same trend is observed in the dry steppe subzone against a drier general background. On the southern edge of the steppe zone, the proportion of precipitation in the first third of the growing season that reached 48% in 1970 increased to 61% in 2017−2018 (Table 4).

The average temperatures of the growing season and its first third depend on the amount of precipitation, decreasing in wet years due to the heat spent on evaporation; however, a long-term trend towards an increase is observed in the subzone of typical steppes, but it is absent in other subzones. The Marton aridity index in the first third of the growing seasons does not increase in all subzones of the steppe zone from 1970 to 2017−2018, but has lower values relative to the average one for the entire growing period.

Thus, the trends of changes in key climate parameters in the first third of the growing season do not contradict the general trend that is characteristic of the growing season, being notable for more moderate temperatures and higher moistening guaranteed even in dry years due to the spring moistening of the soil with melting snow. According to the sum of climatic conditions, the first third of the growing season can be considered the most comfortable time for biota, because other periods of summer are limited in heat and/or moisture (Table 4).

Change in the State of Soil Cover in Northern and Central Kazakhstan in the 21st Century in Comparison with the 20th Century

The changes in the soil cover of northern and central Kazakhstan are most affected by the following: (a) the consequences of irrational land use (massive plowing of virgin lands, miscalculations in agricultural technology and chemicalixation, excessive pasture load, and degradation of natural pastures) and the development of erosion processes; (b) the general climate trend towards warming, which is estimated by

Table 3. Temperature and precipitation, long-term average values and values in the years of research

	Temperature		Precipitation	
	May	June	May	June
Karaganda				
Average in 1976−2018	13.3	18.9	29.7	21.7
Standard deviation	1.71	1.68	23.92	13.31
Normalized deviation in 1976	1.10	0.08	−1.20	0.09
Normalized deviation in 1977	1.68	2.34	−0.20	0.62
Normalized deviation in 1978	−0.99	0.08	−0.99	0.32
Normalized deviation in 2018	−1.92	−0.46	2.44	0.99
Astana				
Average in 1976−2018	14.0	19.8	30.6	20.7
Standard deviation	1.87	1.70	23.85	11.38
Normalized deviation in 1976	0.35	0.01	−1.03	−0.77
Normalized deviation in 1977	1.10	1.72	1.19	0.46
Normalized deviation in 1978	−1.46	0.24	−0.86	−0.59
Normalized deviation in 2018	−1.89	−0.75	1.82	−0.77

Budanov (2016) to exceed the global average values by 2 times in the steppe and desert zones of Kazakhstan, and towards a moderate increase in total annual precipitation and weakening aridization.

A significant part of the steppe soils that were intensively used in agriculture in the 1970s under the slogan of the development of virgin lands has now been removed from the agricultural fund and is in the preclimax or even climax stages of ecological-restoration succession, is used for grazing, and is often asserted to be virgin standards of the steppe landscape. Meanwhile, the intensive use of soils in agriculture against the background of the natural conditions of Kazakhstan (arid climate, open steppe nature of the terrain, and weak natural structure of the soil) contributed to the development of erosion. It was noted that by 1970 the total area of erosion-hazardous soils in the Karaganda region was 2058500 ha, including 1901500 and 157000 ha of lands areas that were hazardous in relation wind erosion and water erosion, respectively. In turn, in Tselinograd region, the total area of erosion-hazardous soils was 6204100 ha, including 4454100 and 1750000 ha of lands that were hazardous in relation to wind erosion and water erosion, respectively. Moreover, according to the data of Borovskii (1970), the eroded soils compared with noneroded soils on average contained 59% less humus, 40% less water-soluble phosphorus, and 50% less mobile potassium and had an increased average sand content and a decreased amount of physical clay.

Table 4. Climate parameters of the growing season and its first third in different years in three subzones of the steppes of central Kazakhstan

	Years		
	1975−1976	1977−1978	2017−2018
	Typical steppe		
Marton aridity index in the first third of the growing season	0.2	0.2	0.2
Average annual air T	3.0	2.8	4.9
Average annual T in the growing season	16.6	17.0	19.1
Average annual T in the first third of the growing season	14.9	15.2	16.9
$\sum$ atm. precipitation/year	235	309	257
$\sum$ atm. precipitation/growing season	124	172.7	172.5
$\sum$ atm. precipitation in the first third of the growing season	49.5 40%	61.2 35%	52.3 30%
	Dry steppe		
Marton aridity index in the first third of the growing season	0.06	0.1	0.1
Average annual air T	2.5	3.4	4.5
Average annual T in the growing season	18.6	19.6	18.5
Average annual T in the first third of the growing season	17.2	18.2	17.4
$\sum$ atm. precipitation/year	217	268	359
$\sum$ atm. precipitation/growing season	39.4	90.9	156.7
$\sum$ atm. precipitation in the first third of the growing season	17.3 44%	28 31%	37.7 24%
	Deserted steppe		
Marton aridity index in the first third of the growing season	0.1	0.1	0.2
Average annual air T	3.1	3.5	4.6
Average annual T in the growing season	18.9	17.8	19.6
Average annual T in the first third of the growing season	17.4	16.5	17.4
$\sum$ atm. precipitation/year	134	209	207
$\sum$ atm. precipitation/growing season	114	90	104
$\sum$ atm. precipitation in the first third of the growing season	42 37%	49 48%	63.5 61%
Marton aridity index during the season	0.4	0.3	0.35

Erosion provoked the development of the soil dehumification process, which is expressed in the loss of humus and deterioration of its quality, as well as a decrease in the thickness of the humus part of the soil profile. As early as 1950−1980, it was noted that the morphological structure of soils changed in the subzone of southern chernozems as a result of plowing: tongue-shaped humus structures in the upper horizons disappeared and the thickness of the humus horizon decreased. At that time, the loss of humus and gross nitrogen on arable soils was 11−15% when compared with virgin soil. In general, humus losses for the soil profile could reach 20 t/ha (more than 5% of humus reserves in the 1-m layer) (Uspanov, 1974; Titlyanova et al., 1984).

The monitoring studies of the soil cover in northern Kazakhstan that were conducted in the period 1992−2006 established (Seydalina, 2009) that the loss of humus compared to 1956 (the beginning of observations) in ordinary chernozems amounted to 12.3% in the period 1992−1996 and 21.5% in 2003−2006. Moreover, in the southern chernozems, the process of dehumification took place more intensively and the amount of humus in them decreased 18.2% by 1992−1996 and 38.2% by 2003−2006. The study by Pashkov (2006) indicates that the average annual loss of humus in the arable soil layer in northern Kazakhstan is 0.5−0.6%. Since the start of the development of virgin soil, chernozems of the North Kazakhstan Region have lost approximately 30% of humus, and chestnut soils have lost up to 40% of humus. The dehumification process also covers pasture soils. So, according to the report (Nasiev, 2015; Nasiev and Eleshev, 2014), the humus content in pasture soils of the

West Kazakhstan Region in the period 1977—2012 decreased to 51.2% of the initial content, and this was accompanied by a decrease in the thickness of the humus horizon by an average of 4 cm. Moreover, according to the data of the Uspanov Institute of Soil Science, the average decrease in the humus content on all arable lands of Kazakhstan was 20—30% (Saparov and Mamyshov, 2008).

Thus, according to modern estimates (Saparov et al., 2017), degradation phenomena have been recorded in 75% of the soil cover of Kazakhstan. At the same time, a total of approximately 30.5 million ha of agricultural land is affected by wind and water erosion. Over the past 30—50 years, the spread of highly saline soils has increased 27—30%, and now their area is 94.9 million ha.

Having left negative traces in the structure and chemistry of soils in central Kazakhstan, the agrotechnical trigger of succession, including its biota, is currently gradually weakening and affects only soils that remain in agricultural turnover. However, the climatic trigger is gaining strength. Against the background of the saturation of soils and underlying rocks with easily soluble salts that easily move along the vertical profile of soils and along the catenas with lateral and planar runoff, climate warming, combined with an increase in annual precipitation, can potentially provoke the activation of the solonchak and solonetzic elementary soil processes (ESPs), which are "dormant" or slow in the deficit of moisture and heat. The reality of this forecast is confirmed by the wide distribution of solonetzes among the steppe soils in central Kazakhstan. Their relative share in the soil cover from north to south in the steppe zone increases from 20 to 60%. Moreover, solonetzes occupy not only hydromorphic, but also automorphic relief positions, especially in the subzone of light chestnut soils. It is believed that salinization proceeded much more intensively in the past and was apparently a zonal process, which decayed more quickly and strongly in the northern subzones of the steppe and more weakly and slowly in the southern subzones due to a lack of precipitation and absence of washout as hydromorphism decreased as a result of growth in aridity. In the desert steppes subzone, solonetzes of automorphic positions are not only relics, but also modern soils formed on residual saline rocks of the Quaternary and Tertiary ages. Apparently, the solonetzic ESP was zonal in the past, and now, at least in the south of the steppe zone, it is more intensive than in the steppe zone. It is very likely that light chestnut soils are one of the stages of solonetz desolonetzization. If the existing climate trend in the center of Eurasia persists and strengthens, the change in the soil formation vector towards solonetzization can begin very soon (Neustruev, 1977).

However, the current state of the soils in the steppe zone allows us to consider them an invariant against the background of the climatic trend that is still gaining strength. This is evidenced by almost identical descriptions of morphological profiles, which were made by different specialists on the same model sites with an interval of 50 years. They are almost identical, which is extremely rare in studies of soil scientists. Thus, the zonal types of soils in central Kazakhstan are still as follows: southern low-humus carbonate medium-thick chernozem in the subzone of typical arid steppes, dark chestnut solonetzic soil in the subzone of dry steppes, and light chestnut surface stony soil and medium-columnar steppe solonetzes in the subzone of desert steppes. A description of the current state of soils that was made in 2018 is given in Appendix 1.

Against the background of a conservative parameter such as the morphology of the vertical profile, the soil microclimate remains the most sensitive to climate. It is its changes that invertebrates, especially mesoherpetobium, quickly and adequately respond to.

The daily and seasonal monitoring of the soil microclimate on the reference catenas in three subzones of the steppes of central Kazakhstan showed that actual soil temperatures in soil layers deeper than 5 cm were comparable with the temperature of the surface air layer. In spring and early summer, they are 16—17°C in the southern chernozem of the typical steppe, decreasing down the catena. In the dark chestnut soil of the dry steppe, the temperatures of the upper soil layer increase to 20—22°C. On the surface of all steppe soils, temperatures rise by 10—11 a.m. up to 25—30°C in the chernozem and dark chestnut soil and up to 45°C in the light chestnut soil. At night, temperatures decrease in the 0—15 cm layer by 2—2.5 times.

The soil moisture of the eluvial catena positions in the 5—15 cm layer in the latitudinal zonal series of soils decreases from 23—36% in the southern chernozem to 14—21% in the dark chestnut soil and 12—20% in the light chestnut soil. Down the catenas, the soil moisture increases at the transit catena positions by 1.5—2.5 times in comparison with the eluvial ones. In the swamp—meadow soils of accumulative positions, the moisture rises to 100% in the spring, autumn, and summer after heavy rains, but it decreases to 5% in dry periods.

Thus, under the conditions of a significant climate change over 50 years that was manifested in the rise in temperature with a simultaneous increase in precipitation, the main features of soils have not undergone significant changes, but keep or get strong potentials for the activation of solonetzic or solonchak elementary soil processes that can drastically change the soil structure in the southern half of the steppe zone of Kazakhstan in a short time.
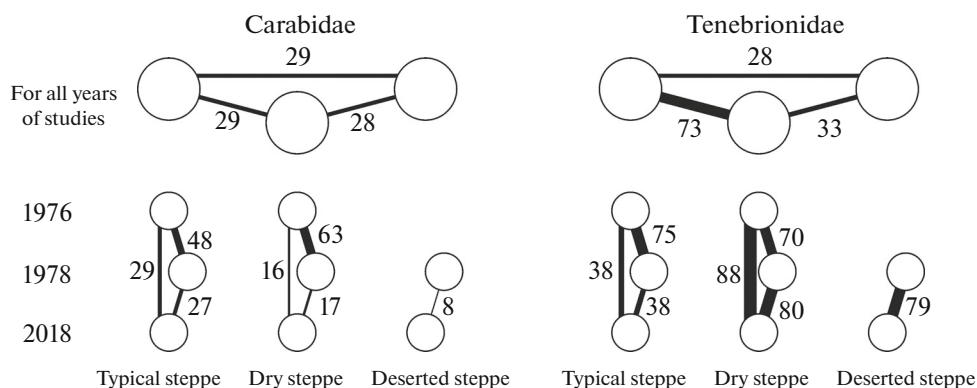
Fig. 1. Generality of local species composition of carabids and tenebrionids in the latitudinal zonal gradient of the steppes of central Kazakhstan in the mid-20th century and early 21st century according to the Jacquard index (%).In total for four years of research is given on top; interannual differences are given below.

Changes in the Faunal Parameters of the Carabid and Tenebrionid Families in the Steppes of Central Kazakhstan from the Middle of the 20th Century to the Beginning of the 21st Century

The flat steppes of central Kazakhstan at the automorphic and semihydromorphic catena positions are notable for a small set of carabid species and an even smaller variety of tenebrionids. In spring and early summer, a total of 60 and 16 species were identified in the studied areas over 4 years of research for the former and latter beetles, respectively. Taking into account hydromorphic positions, the list of carabids as a more hygrophilic group of beetles increases to 93 species, and the list of tenebrionids does not change.

The variety of carabids that is estimated by our surveys to be 41 species in the typical steppes decreases to 25 species in the subzone of dry steppes that is the next one south and remains at this level in the subzone of desert steppes. The species diversity of tenebrionids that is low in the typical and dry steppes (9−10 species) grows slightly in the desert steppes to 14 species (Appendix 2). The generality of carabid fauna and tenebrionid fauna does not fall below 28−9% and 28−33%, respectively (Fig. 1).

Significant fluctuations in local species compositions in the long-term dynamics are possible in any decade. In the 1970s, the greatest contrast was observed in 1976, when precipitation was 1.5 times less than the annual average norm over a decade, and in 1978, when precipitation was 1.5 times higher than normal. In the typical steppe, despite significant (more than between the middle of the 20th century and the beginning of the 21st century) differences in atmospheric moisture, the generality of the carabid species composition in dry 1976 and wet 1978 reached 48%. The same indicator in the dry steppe in 1976 and 1978, which were contrasting in moisture, reached 62%. The generality of tenebrionid species compositions in these

years reached 70−75% (Fig. 1). Against this background, a decrease in such a generality among carabids in 2018 to 16−17% compared with both dry 1976 and wet 1978 looks like a destructive event and, moreover, its decline to 7.7% in the desert steppes by the beginning of the 21st century compared to the 1970s seems to be a faunistic catastrophe (Fig. 1). In tenebrionids, the generality of species compositions in 2018 in comparison with the 1970s also decreased to 37% in the typical steppe and increased to 80−87% in the dry steppe. At the same time, it is noteworthy that the indices of generality of species compositions for 2018 are almost the same with respect to dry 1976 and wet 1978. This indicates that the main role for the generality of local species compositions was not played by fluctuations in atmospheric humidification, but it was most likely played by the rise in average annual temperature by the beginning of the 21st century up to 4.1°C, i.e., by 1.7 times compared with the middle of the 20th century. This conclusion is supported by the fact that the decrease in the generality of the species composition of tenebrionids that have a set of morphological and physiological adaptations to climate aridity was much less pronounced than among carabids that do not have such adaptations.

The character of long-term changes in the taxonomic structure is even more convincingly explained by the change in the ratio of carabids and tenebrionids (the Tencar index). In the years with different amount of precipitation (dry 1976 and wet 1978), the Tencar index did not vary significantly (Table 5a). The index value in the typical steppe with temperate hydrothermal conditions has increased in favor of tenebrionids for half a century from just 0.1 to 0.3. In the dry steppe with more extreme environmental conditions, the Tencar index grew from the 1970s to 2018 by more than 4 times and, in the desert steppe, it increased 12 times. An increase in the favor of tenebrionids was provided by the species of the tribes Tentyriini, Platyscelidini,

and Blaptini, which have the most advanced adaptations to aridization: a large subelytral cavity that occupies up to a third of the body volume, elytra that are fused along the juncture and laterally adherent, strong chitinization of the integument, and low level of defecation (Mordkovich, 2011).

The values of the indicated index in central Kazakhstan vary in space and time very expressively. Along the catena gradients of habitats in the typical steppe subzone, the value of the index for the communities of eluvial and transit catena positions is at an extremely low level (0.02–0.2) in both 1976 and 2018, which indicates humid climatic conditions, at least in the first third of the growing season, when melting winter moisture reserves make themselves felt. A different pattern is observed to the south. In the dry steppe subzone, the Tencar index for the community of the transit catena position, which was low in 1976 (0.5), increased 5 times in 2018, remaining unchanged at the eluvial position, but quite high in value (4.2–4.3). In the desert steppe subzone, the Tencar index for the community of the transit position increased in 2018 in the same range compared to 1976, but jumped two orders of magnitude at the eluvial position (Table 5b), indicating an increase in aridization.

The noted tendency towards change in the Tencar index can be interpreted as evidence of an increase in aridization in the steppe zone of central Kazakhstan, especially in its southern half; moreover, it is independent of the annual precipitation, which commonly fluctuates in the steppe zone. Apparently, the decisive climatic factor is the increase in the average annual temperature to values above 4°C, which enhances evaporation, stimulating the aridization of the environment. Attention is drawn by the increase in the values of the Tencar index in 2018 compared with the 1970s in the communities of the accumulative catena positions in the subzones of dry and desert steppes due to the mass immigration of xerophilic tenebrionids *T. nomas*, *B. halophila*, etc., to degrading swampy habitats. The death of these reserve habitats for steppe biota in the case of a continuing aridization trend may be incentive for the desertification of the steppe zone.

Thus, the tendencies of changes in the faunistic parameters adequately reflect the nature of the climatic trend, primarily its warming. The scale of change in the faunal parameters of tenebrionids allows them to slightly change the fauna composition within the steppe gradient. In carabids that are less adapted to aridity, a change in composition is much more significant.

Changes in the Spectrum of Arealogical Groups in Carabids at the Beginning of the 21st Century Compared with the Middle of the 20th Century

The spectra of arealogical groups in carabids regularly vary in the zonal series of steppes. In the typical steppe (Shortandy), up to six boreal species and up to

Table 5a. Changes in the Tencar index during the years with different weather in the mid-20th and early 21st centuries in different subzones of the steppes of central Kazakhstan

| Steppe subzones	Years		
	1976	1978	2018
Typical steppes	0.1	0.2	0.3
Dry steppes	0.9	0.7	3.0
Deserted steppes	No data	0.5	6.0

Table 5b. Change in the Tencar index along the catenary and latitudinal zonal gradient of the steppes at the beginning of the 21st century compared with the middle of the 20th century

Steppe zone subzones	Year	Catena positions		
		EL	TR	AC
Typical steppes	1976	0.2	0.02	0.0
	2018	0.6	0.6	0.02
Dry steppes	1976	4.3	0.5	0.07
	2018	4.2	2.3	0.5
Deserted steppes	1976	10.7	0.5	0.01
	2018	400	3.0	0.4

nine polyzonal species (30−40% of all biotope species) can be found at accumulative positions; in the dry steppe (Arykty), the number of these species decreases to two (20−30%); and in the desert steppe (Barshyn), boreal species disappear completely and the polyzonal species remain in the number of 1−2 (no more than 20%) (Fig. 2).

An increase in the proportion of boreal species (in the typical and dry steppes) and polyzonal species is also observed in moving down the catena in each natural subzone. These trends change insignificantly in 1976 and 1978.

In 2018, the range of arealogical groups of carabid species was observed to be impoverished. In the typical steppe, boreal species disappear at the relatively dry eluvial and transit catena positions, remaining at the accumulative position. In the dry steppe, boreal species completely fall out of the carabid community of the catena. Polyzonal species behave in a similar way: in the typical steppe they disappear at the eluvial position and in the dry and desert steppes they completely disappear, even from the accumulative positions. In the desert steppe, only subarid species are found at both the eluvial and transit catena positions; some of them have an extremely southern distribution, for example, *Harpalus tenebrosus*. In the typical steppe, the fauna of accumulative landscapes is even somewhat enriched at the expense of subboreal humid species,
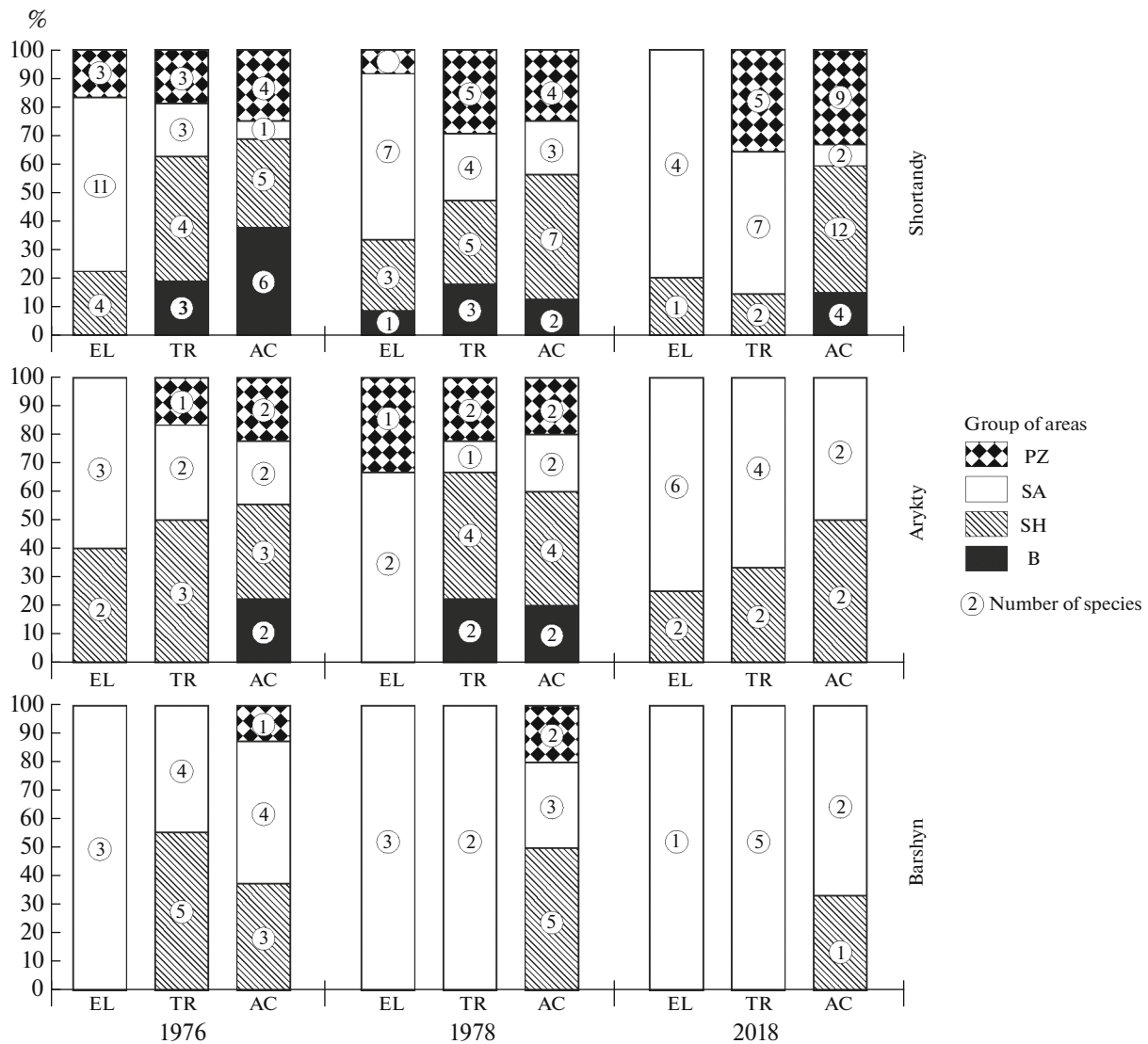
Fig. 2. Spectra of arealogical groups of carabids in the latitudinal−zonal gradient of the steppes of central Kazakhstan at different catena positions in 1976−1978 and in 2018. Legends: EL is eluvial, TR is transit, AC is accumulative catena position, B is boreal species, SH is subboreal humid species, SA is subarid species, and PZ is polyzonal species.

while in the dry and desert steppe the number of species remains at the same level or decreases (Fig. 1).

Such changes in the arealogical structure indicate a decrease in the size of populations of carabid species that have a relatively "northern" distribution (therefore, they are not included in the counts) and the general aridization of the carabidofauna.

Change in the Spectra of Adaptive Models in Carabids at the Beginning of the 21st Century Compared with the Middle of the 20th Century

The ecological structure of invertebrate communities is best reflected comparatively in the spectrum of adaptive types (ecological or functional groups, life forms, etc.) rather than in the taxonomic composition.

Attempts to single out the adaptive types of pedobiont organization that are universal for a series of large taxa have been made repeatedly (Stebaev and Kolpakov, 2003), but have not been successful due to the ambiguity of the adaptive value of even similar characters. Recognition has been gained by the types of organization, which were singled out on the basis of adaptive morphology, physiology, and behavior within individual families (for example, I.Kh. Sharova's system of life forms for carabids (1981), the distinguishing of ecological groups (Mordkovich and Lyubechanskii, 2010); for tenebrionids, these were studies by Medvedev (1959) and Mordkovich (1977)).

Focusing on the order of the quantitative distribution of beetle populations relative to the local zonal catena matrix of the environment and the confine-

Table 6. Adaptive models of tenebrionids in the steppe zone of central Kazakhstan

EL	TR	AC
Oligoxerophiles, I	Glycomesophiles, IV	Acidohygrophiles, VII
Hemixerophiles, II	Haloidomesophiles, V	Glycohygrophiles, VIII
Euxerophiles, III	Halomesophiles, VI	Halohygrophiles, IX

ment of the maximum dynamic density of imagoes over three years of research, nine types (=models) of adaptation of carabids and tenebrionids to the ecological features of the steppe environment have been identified (Table 6).

Tenebrionids in the steppes of central Kazakhstan are represented by five adaptive models. Our material does not include classes VII–VIII from Table 6. Oligoxerophiles include *Pedinus femoralis* and *Opatrum sabulosum*, which place the largest part of the population at the eluvial catena positions in the subzone of the typical steppes, where moisture deficiency manifests itself only periodically. The integument of herpetobiont imagoes of these species are moderately sclerotized. The beetles have slightly convex elytra and a slightly pronounced subelytral cavity, where the spiracles of the trachea open. Elytra do not grow together along the juncture and do not adhere laterally to tergites. The extended shanks of the forelegs make it easier to burrow into the soil in the case of an increase in temperature on its surface. An adaptation to periodic aridity is the stretching of the preimaginal phases of ontogenesis in time, in particular, the phase of oviposition. Being saprophages, oligoxerophilic tenebrionids consume more food than other adaptive models, thereby compensating for the loss of water and energy due to a very high level of defecation (Mordkovich, 2011).

Hemixerophilic tenebrionids (*Tenthyria nomas*, *Blaps halophila*, and *Platyscelis hypolithos*) place the greater part of the population at the eluvial catena positions in the dry steppe subzone. They are notable for the strong chitinization of the integument and the presence of an extensive subelytral cavity, which occupies at least 1/3 of the beetle-body volume. Elytra usually grow together along the juncture and adhere laterally to tergites, tightly closing the subelytral cavity. However, due to the use of comfortable shelters, burrowing representatives of this type of tenebrionids have large unprotected sections of the membranous surfaces of the oral cavity, which limits the presence of these species on the soil surface to twilight and night hours, when the temperature decreases. The level of food intake in hemixerophiles is lower than in mesophiles. In addition, they have to save water on defecation, reducing the mass of feces to 17% of the food eaten (Mordkovich, 2011).

Euxerophilic tenebrionids (*Anatolica lata* and *Platyscelis rugifrons*) are mainly found at the eluvial catena positions in the subzone of the desert steppes. The characterized adaptive tenebrionid model has a

large subelytral cavity with a volume of at least half of the beetle body. Elytra are irreversibly fused and adhere laterally to tergites. A small opening at the top of the elytra is tightly closed by raised pygidium, ideally isolating the vestibule of the trachea from an aggressive external environment with soil moisture dropping to 1−2%. The level of food consumption is the highest among steppe tenebrionids, and the level of defecation is the lowest. The mass of feces is only 15% of the mass of food eaten (Mordkovich, 2011).

Glycomesophilic tenebrionids (*Crypticus quisquilius* and *Opatrum riparium*) have a maximum dynamic density at the transit catena positions in the north of the steppe zone, where the deficit of humidification is weak and inconstant due to additional humidification with lateral runoff, groundwater, and moisture-retaining properties of the solonetz soil horizon (which is saturated with silt particles). Accordingly, the adaptability of the characterized species to aridity of the climate is poorly manifested. Their oral apparatus is unreliably isolated from the external environment, the subelytral cavity is weakly pronounced and poorly closed, and the integument is weakly sclerotized. On the other hand, they have kept a second pair of wings that ensures efficient and mobile migration in the event of a sharp deterioration in the state of the environment at the transit catena positions. The living conditions on solonetzes are characterized by extreme variability, which is even greater than in the zonal steppes, which is especially relevant for the hydrothermal regime and salinization. Accordingly, steppe mesophiles are characterized by the rapid passage of preimaginal phases of ontogenesis. The egg phase, larvae phase, and imago phase last only 5−6 days, 2−2.5 months, and up to 2 years, respectively. Elytra of these beetles are soft, do not grow together along the juncture, and do not adhere laterally to tergites. The mesophilia in this type of beetles is confirmed by physiological characteristics. They are notable for the lowest specific consumption of food among tenebrionids and the highest defecation values. The proportion of feces from the mass of food consumed reaches 40−47% in them.

Haloidomesophiles include tenebrionids *Gonocephalum granulatum* and *G. pygmaeum*, and halomesophiles include *Oodescelis polita* and *Platyscelis rugifrons*. Halohygrophiles are represented by two species: *Centorus filiformis* and *C. procerus*. They are confined to salted, drying swamps in relief depressions, which

Typical steppes   Dry steppes   Deserted steppes.
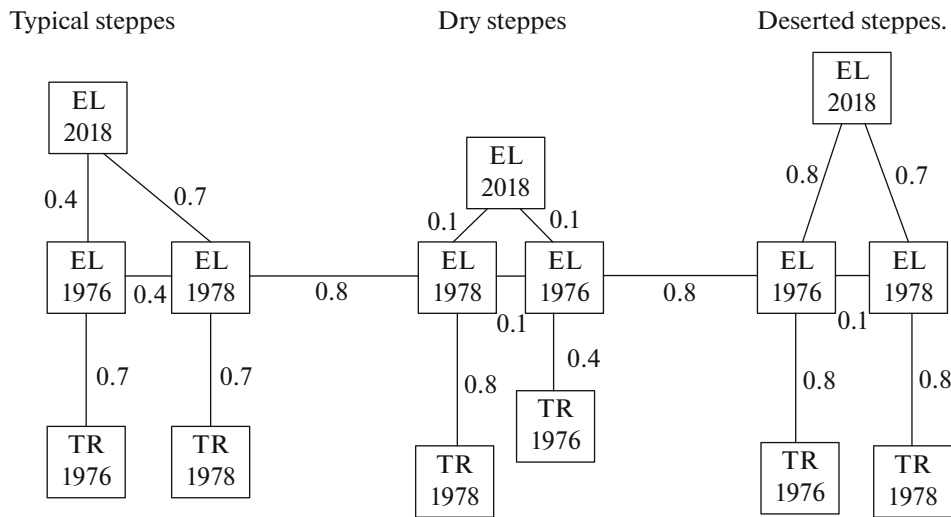
Fig. 3. Bray−Curtis difference index of the tenebrionid taxocenes in 1976, 1978, and 2018 in zonal typical, dry, and desert steppes of central Kazakhstan. Designations are the same as in Fig. 2.

turn into abundant salt marshes by the middle of summer (Table 7).

A comparative analysis of 27 tenebrionid communities in the steppe zone of central Kazakhstan (three natural subzones with three catena positions for three years of research) according to the spectra of adaptive models shows that these spectra, in comparison with the indicators of the total number and diversity of species, do not change randomly, but in direct proportion to the change in the aridity of the environment from north to south from one steppe subzone to another, along catenas and in time. Moreover, the Bray−Curtis difference index values at eluvial positions in different steppe subzones reach values which are close to the maximum (0.7−0.8) (Fig. 3). The differences in the spectra at the eluvial and transit catena positions in all three steppe subzones are just as great. However, the differences in the spectra of the communities at the eluvial position in dry 1976 and wet 1978 unexpectedly turned out to be low (0.4 in the subzone of the typical steppes) and minimal in the subzones of the dry (0.1) and desert steppes (0.1).

Even more expressive are the changes in the ecological structure of tenebrionid communities at the beginning of the 21st century compared with the middle of the 20th century, which are observed in the

Table 7. Ecological species ordination of tenebrionids relative to the zonal catenary matrix of habitats in central Kazakhstan. Average dynamic density over 3 years of research, ind./100 trap days

Steppe subzone	*B. halophila*			*Platyscelis* sp.			*A. lata*			*T. nomas*			*P. femoratum*		
	EL	TR	AC	EL	TR	AC	EL	TR	AC	EL	TR	AC	EL	TR	AC
Typical steppe	2	2	–	–	–	–	–	–	–	6	2	–	9	7	–
Dry steppe	41	3	2	–	–	–	–	–	–	287	70	21	9	1	–
Desert steppe	19	7	–	85	2	–	61	7	–	31	11	–	6	7	–
	O. sabulosum			*O. polita*			*P. hypolithos*			*P. rugifrons*			*C. filiformis*		
Typical steppe	36	14	1	–	–	–	1	–	–	–	–	–	–	–	–
Dry steppe	3	3	1	3	4	–	3	–	–	–	–	–	–	–	–
Desert steppe	–	5	–	–	41	–	–	–	–	–	4	–	–	3	3
	C. procerus			*G. granulatum*			*G. pygmaeum*			*C. quisquilius*			*O. riparium*		
Typical steppe	–	–	–	11	39	1	–	–	–	1	5	–	1	39	2
Dry steppe	–	–	–	9	131	42	2	8	3	1	3	2	–	–	–
Desert steppe	–	3	7	–	–	–	–	–	–	–	–	–	–	–	–

extreme south of the steppe zone of central Kazakhstan. In the desert steppe subzone, the index of the difference in the spectra of adaptive tenebrionid models increases compared with other steppe subzones, reaching a value of 0.8, which is close to the maximum. However, these differences are ensured by no means by desert euxerophiles, which dominated the population in the 1970s, but by oligoxerophiles. An increase in their numbers brought closer the zonal tenebrionid taxocenes of the desert and dry steppes in 2018, which adequately reflects the climatic situation in central Kazakhstan that is anomalous with respect to global aridization.

In general, the analysis of carabid and tenebrionid communities suggests a significant restructuring of the zoedaphon contingent in the steppes of central Kazakhstan in favor of carabids and permits this phenomenon to be considered an integral part of the progressive aridization of the territory.

CONCLUSIONS

The global trend of climate warming and aridization is abnormal in the steppe zone of central Kazakhstan. Compared with the middle of the last century, the average annual temperatures of the surface air layer were recorded to increase by 1.6°C (more than 1.5 times) in the last decade of the 21st century. Moreover, the annual precipitation is not decreasing, but increasing, even in the extreme south of the steppe zone. Since most of the precipitation occurs there in winter and the first part of the growing season, aridization is most pronounced in the middle of summer, when surface air temperatures rise from 18−23°C in May to 40−42°C in July, evaporation increases, and the moisture content of the upper soil layer drops to 1.5−2%.

An increase in humidification in spring and evaporation in summer promotes the activation of the solonetzic process in steppe soils, which was previously inhibited under the conditions of acute moisture deficiency. Pulling easily soluble salts up the soil profile turns the middle solonetzes into crustal ones and converts meadow−marshy soils in relief depressions into solonchaks.

The climatic trends are most adequately followed by large invertebrates that live in the most extreme tier of biogeocenosis—on the soil surface, and they include tenebrionids and carabids, which make up 60−80% of the species composition and population of soil beetles. The generality of local carabid fauna in dry 1976 and wet 1978, which was 48−62%, decreased at the beginning of the 21st century to 16% in the dry steppe and 7% in the desert steppe. In tenebrionids that are more adapted to aridity, the generality of faunas decreased from 70−75% to 37% in the typical steppe and increased to 87% in the dry steppe. Meanwhile, the values of the generality index for the local

faunas of the 1970s and 2018 turned out to be the same in relation to both the dry and wet years of the last century. It follows from this that the trigger for a change in the composition of local faunas is not a change in atmospheric moisture, but a rise in average annual temperatures that has exceeded the average values for the global trend.

Relatively "northern" boreal and polyzonal species become fewer in communities and more "southern" subarid species become more numerous. In the typical steppe, the northern species are still present at the relatively moist accumulative and transit catena positions; in the dry and desert steppes, they completely disappear.

The Tencar index was used as an integral zoo indicator of changes in the aridity of the environment, expressing the ratio of the number of individuals and species of arid tenebrionids and more humid carabids. In the typical steppe, which is more or less provided with precipitation at a relatively low level of evaporation, the values of the Tencar index are not high and vary in seasonal, long-term dynamics and insignificantly along catenas. However, in the dry steppe the values of the Tencar index increased 5 times in 2018 when compared to the middle of the last century, and in the desert steppe they grew by two orders of magnitude. In 2018, the values of the Tencar index in the south of the steppe zone increased even in the communities of accumulative catena positions due to the active and massive migration of oligoxerophilic tenebrionids there. The tendency towards a change in the Tencar index indicates an increase in aridization in the south of the steppe zone of central Kazakhstan regardless of the fluctuation of precipitation, which was usual for the steppe zone at all times, but under the influence of the increase in average annual temperature by 1.6°C, evaporation, and the activated salinization of soils, creating the preconditions for the desertification of the territory and biota due to special properties.

The nature of the change in the ecological structure of the mesoherpetobiont communities in the early 21st century compared with the middle of the 20th century reflects the spectrum of adaptive organization models (AM) of tenebrionids. It is typologized mainly by the nature of the quantitative distribution of populations in the zonal catenary habitat system in the steppe zone of central Kazakhstan, with the use of morphophysiological adaptive criteria. The comparative analysis of the tenebrionid communities of the steppe zone of Kazakhstan by AM spectra has shown that the greatest differences for tenebrionids in dry 1976 and wet 1978 (the Bray−Curtis difference index was 0.1−0.4) increased to 0.7−0.8 in 2018. However, the growth of differences is not ensured by semidesert euxerophiles, which dominated the structure of the tenebrionid population in the middle of the 20th century, but by more tolerant oligo- and hemixerophiles.

Soil sections in the zonal series of steppe soils of central Kazakhstan, which were observed in 2018

Catena position	Coordinates	Soil	Horizons, cm	Description
				Kazakhstan, Akmola Region, environs of the settlement of Shortandy. Virgin steppe site
EL	51.56608° N 71.28065° E	Southern carbonate deeply solonetzic medium-thick chernozem	Adk (0—12)	Light loamy, dry, dark gray, powdery, intertwined with roots of steppe vegetation, loose, soil effervesces from HCl
			Ak (12—43)	Light loamy, fresh, dark gray, slightly lumpy, loose, soil effervesces from HCl
			AVk (43—76)	Light loamy, fresh, gray-brown, tongue-shaped humus streaks on a brown background, compacted, lumpy—nutty prismatic, slightly sticky, soil effervesces from HCl
			Vk (76—103)	Light loamy, fresh, yellowish brown with gray spots of humus, prismatic, dense, soil effervesces from HCl
			Sks (103—...)	Light loamy, fresh, brownish with a whitish tint, structureless, less dense than horizon B, gypsum in the form of small grains, soil effervesces from HCl
TR1	51.56540° N 71.28464° E	Meadow chernozem solonetzic soil	Ad (0—9)	Light loamy, dry, dark gray, powdery, intertwined with roots of steppe vegetation, loose, soil does not effervesce from HCl
			Ak (9—37)	Light loamy, fresh, dark gray, lumpy—nutty, compacted, abundant with plant roots, soil effervesces from HCl
			AVk (37—74)	Light loamy, fresh, uneven grayish brown color due to tongue-shaped humus streaks on a yellowish brown background, lumpy—nutty, carbonate structures in the form of veins along the pores and root passages, compacted, soil effervesces from HCl
			Vk (74—102)	Light loamy, fresh, yellowish brown, prismatic, small dark spots of approximately 0.5—1 mm in size (possibly manganese structures), compacted, soil effervesces from HCl
			Sks (102—...)	Light loamy, fresh, brownish with a whitish tint, gypsum in the form of grains, loose, structureless, soil effervesces from HCl
TR2	51.56681° N 71.29067° E	Deeply carbonate solonetz	Adk (0—7)	Medium loamy, dry, light gray, powdery, loose, intertwined with roots of steppe vegetation, soil effervesces from HCl
			Ak (7—30)	Medium loamy, fresh, spotty brownish gray, slightly lumpy powdery, slightly compacted, rich in carbonates in the form of lines and tubes along root passages, soil effervesces from HCl
			V1k (30—54)	Heavy loamy, fresh, grayish brown, richly colored with humus, nutty—prismatic, abundant with carbonates in the form of lines and tubes along the passages of plant roots, sticky, compacted, soil effervesces from HCl
			V2k (54—77)	Heavy loamy, moist, yellowish brown with humic streaks, sticky, lumpy—prismatic, abundant with carbonates in the form of lines and tubes along the passages of plant roots, compacted, soil effervesces from HCl

Catena position	Coordinates	Soil	Horizons, cm	Description
AC	51.56628° N 71.29117° E	Alluvial meadow-marshy soil	Vks (77—95)	Heavy loamy, moist, light brown, prismatic, spots of gypsum, spots of humus are found along the facets of individual structures, stickiness is barely noticeable, carbonates in the form of impregnation, compacted, soil effervesces from HCl
			Adg (0—21)	A lot of undecomposed organic matter (approximately 40—50%), the mineral part is light loamy, very loose, moist, black with a brown tint and bluish tint, the structure of the mineral part is lumpy, soil does not effervesce from HCl
			Ag (21—79)	Light loamy, very loose, black with a bluish tint, wet, loosely lumpy, abundant with plant roots, bright brown spots, soil does not effervesce from HCl
			Bg (79—...)	Medium loamy, wet, lumpy grainy, black with a brownish tint, slightly compacted, soil does not effervesce from HCl

Kazakhstan, Akmola Region, environs of the settlement of Arykty. Lake depression

Catena position	Coordinates	Soil	Horizons, cm	Description
EL	50.54415° N 70.46271° E	Dark chestnut solonetzic soil	Ak (0—17)	Light loamy, fresh, powdery, brownish gray, loose, rounded sand grains of white and brown color, plant roots, upper 8 cm are strongly intertwined with plant roots, soil effervesces from HCl from the depth of 5 cm
			V1k (17—32)	Medium loamy, fresh, brownish gray, rounded sand grains of white and brown color, compacted, lumpy—prismatic, small plant roots, soil effervesces from HCl
			V2k (32—70)	Heavy loamy, fresh, nutty—prismatic, very dense, vertical cracks with streaks of humus, abundantly saturated with carbonates (the section wall becomes white upon drying), rounded sand grains of white and brown color, small plant roots, soil effervesces from HCl
			V3k (70—78)	Light loamy, fresh, light brown, indistinctly prismatic, compacted, rounded sand grains of white and brown color, saturated with carbonates, soil effervesces from HCl
			S1ks (78—101)	Light loamy, fresh, brown, structureless, slightly compacted upon drying, single spots of gypsum, rounded sand grains of white and brown color, soil effervesces from HCl
			S2ks (101—124)	Light loamy, fresh, brown, structureless, slightly compacted upon drying, gypsum accumulations in the form of spots and spherical (ball-shaped) formations, rounded sand grains of white and brown color, soil effervesces from HCl
			S3ks (124—...)	Light loamy, fresh, brown, structureless, loose, accumulations of gypsum in the form of spots, carbonates in the form of impregnation, rounded sand grains of white and brown color, soil effervesces from HCl

Catena position	Coordinates	Soil	Horizons, cm	Description
TR1	50. 54271° N 70.46065° E	Meadow–chestnut solonetzic saline soil	Ak (0–20)	Light loamy, dry, loose, upper 2 cm are abundantly intertwined with plant roots, brownish gray, lumpy–powdery, rounded sand grains of white and brown color, soil effervesces from HCl from the depth of 5 cm
			V1k (20–51)	Light loamy, fresh, whitish brown, streaks of humus, lumpy–nutty, carbonates in the form of impregnation, rounded sand grains of white and brown color, small plant roots, compacted, soil effervesces from HCl
			V2skg (51–89)	Medium loamy, fresh, compacted, whitish brown (due to salts and gypsum), nutty–prismatic, rounded sand grains of white and brown color, gypsum accumulations in the form of spots and tubes, salt crystals abundantly appear on the section wall upon drying, individual small roots, carbonates along pores and root passages in the form of small tubes, soil effervesces from HCl
			S1kg (89–124)	Lightly loamy, fresh, brown, rounded sand grains of white and brown color, sand grains are glued together by clay material into conglomerates, salt crystals abundantly appear on the section wall upon drying, structureless, sticky, streaked with small black dots of 0.3–0.5 mm (possibly manganese structures), there are no gypsum structures, soil effervesces from HCl
			S2k (124–...)	Light loamy, sticky, structureless, fresh, brown, rounded sand grains of white and brown color, the horizon contains a layer of sand mixed with loam, there are no gypsum structures, soil effervesces from HCl
TR2	50.54246° N 70.46014° E	Crustal saline solonetz	Ak (0–2)	Light loamy, gray, dry, powdery, intertwined with roots of steppe vegetation, loose, rounded sand grains of white and brown color, soil effervesces from HCl
			V1k (2–18)	Heavy loamy, brownish gray, compacted, nutty–columnar, plant roots, rounded sand grains of white and brown color, carbonates in the form of spots, dry, soil effervesces from HCl
			V2ksg (18–100)	Heavy loamy, wet, brown, sticky, grained, gypsum in the form of spots and tubes, rusty spots, the section wall is covered with salt crystals upon drying, rounded sand grains of white and brown color, loose, soil effervesces from HCl
AC	50.54190° N 70.45928° E	Shor solonchak	Crust (0–2)	Heavy loamy, gray, wet, loose, wall saltpeters, structureless, plastic, sticky, soil effervesces from HCl
			Skg (2–40)	Heavy loamy, brown, wet, loose, wall saltpeters, structureless, plastic, sticky, soil effervesces from HCl

Catena position	Coordinates	Soil	Horizons, cm	Description
		Kazakhstan. Karaganda Region, environs of the settlement of Barshino. Lake depression		
EL	49.62547° N 69.47282° E	Light-chestnut surface—stony soil	A (0—13)	Sandy loam, medium stony, fresh, light gray-brown, slightly compacted, lumpy powdery fine earth, plant roots, soil does not effervesce from HCl
			V (13—30)	Sandy loam, very stony, brown, denser than the previous one, the amount of solid structures increases sharply, the fine earth is organized into a lumpy—nutty structure, soil does not effervesce from HCl
TR1	49.62322° N 69.47160° E	Meadow chestnut surface—stony soil	Ad (0—5)	Sandy loam, intertwined with roots of steppe vegetation (approximately 40—50% of the horizon), fresh, gray, lumpy powdery fine earth, compacted by roots, there is no skeleton, soil does not effervesce from HCl
			A (5—14)	Sandy loam, fresh, gray, lumpy powdery fine earth, many plant roots, slightly compacted, there is no skeleton, soil does not effervesce from HCl
			AV (14—32)	Sandy loam, medium stony, fresh, brown, plant roots, fresh, lumpy fine earth, slightly compacted, soil does not effervesce from HCl
			VS (32—45)	Sandy loam, very stony, fresh, whitish brown, loosely lumpy fine earth, denser than the previous one, single plant roots, soil does not effervesce from HCl
TR2	49.62237° N 69.47198° E	Crustal surface—stony solonetz	A (0—3)	Sandy loam, slightly stony, dry, gray, lumpy powdery fine earth, a small amount of plant roots, soil does not effervesce from HCl
			V (3—12)	Sandy loam, slightly stony, fresh, grayish brown, columnar, many plant roots, dense, soil does not effervesce from HCl
			Sk (12—36)	Sandy loam, medium stony, structureless fine earth, fresh, brownish brown, single plant roots, less dense than the overlying horizon, soil effervesces from HCl
			Dk (36—...)	Rocky crimson mass mixed with fine earth of the same color, a small amount of small dead plant roots, soil effervesces from HCl
TR3	49.62034° N 39.47446° E	Crustal surface—stony solonetz	A (0—4)	Sandy loam, medium stony, fresh, cracking crust on the surface, loose, powdery fine earth, gray-brown, there are many plant roots, but they do not form turf, soil does not effervesce from HCl
			V (4—30)	Clayey, medium-stony, very dense, lumpy, brownish brown, fresh, dead plant roots, soil does not effervesce from HCl
AC	49.61977° N 69.47681° E	Shor solonchak	Ks (0—1)	Salt crust, soil effervesces from HCl
			Sgkg (1—30)	Clayey, brown, structureless, wet, plant roots are found in the upper part of the horizon, salt crystals appear on the section wall upon drying, soil effervesces from HCl

Spring population of carabids and tenebrionids on the steppe catenas of central Kazakhstan in 1976–78 and in 2018 (the sum of specimens per 100 trap days). Legends: EL is eluvial, TR is transit, AC is accumulative catena position; L is the latitudinal group of ranges: B is boreal, SH is subboreal humid, SA is subarid, PZ is polyzonal.

A. Subzone of the typical arid steppe, Shortandy

		1976			1978			2018		
	Beetle species	positions								
		EL	TR	AC	EL	TR	AC	EL	TR	AC
L	**Carabidae**									
B	Agonum fuliginosum	–	–	3	–	–	–	–	–	3
PZ	Agonum thoreyi	–	–	–	–	–	–	–	–	3
B	Agonum viduum	–	–	–	–	–	–	–	–	5
PZ	Amara aenea	2	–	–	–	1	–	–	–	–
B	Amara infima	–	–	–	3	–	–	–	–	–
SA	Amara pastica	1	–	–	–	–	–	–	–	–
B	Amara plebeja	–	–	1	–	–	–	–	–	–
SH	Amara tibialis	–	18	1	–	14	5	–	–	–
PZ	Anisodactylus binotatus	–	–	–	–	–	–	–	–	3
SH	Badister unipustulatus	–	1	–	–	–	5	–	–	–
SA	Bembidion varium	–	–	–	–	–	–	–	–	3
SH	Bembidion biguttatum	–	–	–	–	–	–	–	–	8
B	Bembidion humerale	–	–	11	–	–	–	–	–	–
SH	Bembidion minimum	–	–	–	–	–	–	–	–	5
SH	Bembidion octomaculatum	–	–	35	–	–	30	–	–	–
SA	Bembidion pallidiveste (?)	–	–	6	–	–	9	–	–	–
PZ	Bembidion properans	1	144	2	–	–	4	–	5	–
PZ	Bembidion quadrimaculatum	–	1	–	–	3	–	–	–	–
SH	Bembidion quadripustulatum	–	–	–	–	–	–	–	–	3
B	Bembidion transparens	–	1	41	–	10	6	–	–	–
SH	Bradycellus caucasicus	–	–	60	–	–	7	–	–	–
B	Calosoma investigator	–	–	–	–	2	–	–	–	–
SH	Carabus clathratus	–	–	1	–	–	–	–	–	8
SA	Carabus cribellatus	4	3	–	3	–	–	–	3	–
SA	Carabus estreicheri	1	–	–	–	–	–	–	–	–
PZ	Carabus granulatus	–	–	–	–	–	–	–	–	5
B	Chlaenius nigricornis	–	1	6	–	3	–	–	–	10
SA	Chlaenius spoliatus	–	–	–	–	–	–	–	–	10
PZ	Chlaenius tristis	–	–	–	–	–	–	–	–	5
PZ	Clivina fossor	–	–	–	–	–	–	–	–	5
SH	Curtonotus aulicus	–	–	–	–	–	–	–	–	15
SH	Curthonotus castaneus	–	–	–	–	–	–	–	3	–
SH	Curtonotus convexiusculus	–	–	–	2	–	–	–	–	–
SH	Cymindis angularis	1	–	–	–	2	–	–	–	–
SA	Cymindis lateralis	1	–	–	–	–	–	–	–	–
SA	Dyschiriodes rufipes	3	2	–	28	3	–	–	–	–
–	Dyschiriodes sp.	–	–	–	–	–	–	–	2	–
SH	Elaphrus cupreus	–	–	–	–	–	–	–	–	10
SA	Harpalus amplicollis	5	–	–	3	–	–	–	2	–
SA	Harpalus anxius	–	–	–	–	5	5	–	5	–
SA	Harpalus calathoides	1	–	–	5	2	–	–	–	–
PZ	Harpalus distinguendus	–	–	–	–	2	–	–	–	–
SA	Harpalus modestus	1	–	–	–	–	–	–	–	–

	Beetle species	1976			1978			2018		
		positions								
		EL	TR	AC	EL	TR	AC	EL	TR	AC
SA	Harpalus politus	–	–	–	3	–	–	–	2	–
SA	Harpalus pusillus (?)	1	–	–	–	–	–	–	–	–
SH	Harpalus smaragdinus	–	1	–	–	–	–	–	8	–
SA	Harpalus subcylindricus	–	–	–	–	–	–	–	3	–
SH	Harpalus tardus	1	–	–	–	–	–	–	–	–
SA*	Harpalus tenebrosus	–	–	–	2	–	–	–	–	–
SA	Microlestes fissuralis	–	–	–	–	–	–	3	–	–
SA	Microlestes maurus	–	–	–	–	–	–	–	10	–
PZ	Microlestes minutulus	33	81	22	25	130	85	–	15	–
SH	Oodes helopioides	–	–	–	–	–	–	–	–	18
SH	Oxypselaphus obscurus	–	–	–	–	–	–	–	–	5
SH	Poecilus cupreus	–	2	29	–	–	4	–	–	3
SH	Poecilus punctulatus	–	18	–	–	2	1	–	–	–
SA	Poecilus sericeus	5	1	–	2	–	–	13	5	–
SA	Poecilus subcoeruleus	–	–	–	–	2	–	–	–	–
PZ	Poecilus versicolor	–	–	–	–	2	4	–	3	–
SA	Pseudotaphoxenus rufitarsis	–	–	–	–	–	–	3	–	–
SH	Pterostichus anthracinus	–	–	–	–	–	–	–	–	25
SH	Pterostichus gracilis	–	–	–	–	–	–	–	–	8
SH	Pterostichus macer	1	5	–	5	16	–	–	–	–
B	Pterostichus minor	–	3	26	–	–	10	–	–	7
PZ	Pterostichus niger	–	–	4	–	–	–	–	3	5
PZ	Pterostichus nigrita	–	–	3	–	–	–	–	–	30
PZ	Pterostichus strenuus	–	–	–	–	–	2	–	–	3
SH	Pterostichus vernalis	–	–	–	–	–	5	–	–	3
PZ	Stenolophus mixtus	–	–	–	–	–	–	–	–	5
SA	Microlestes plagiatus	–	–	–	–	–	10	–	–	–
SH	Syntomus truncatellus	2	17	–	45	13	–	3	–	–
SA	Taphoxenus gigas	1	–	–	–	–	–	3	–	–
	Total number of Carabidae species	**65**	**299**	**251**	**126**	**212**	**192**	**25**	**69**	**213**
	Total number of Carabidae individuals	**18**	**16**	**16**	**12**	**17**	**16**	**5**	**14**	**27**
	Menhinick's index	**2.2**	**0.9**	**1.0**	**1.1**	**1.2**	**1.2**	**1.0**	**1.7**	**1.8**
	Tenebrionidae									
	Blaps halophila	3	5	–	3	2	–	–	–	–
	Blaps lethifera	2	–	–	–	1	–	–	–	–
	Centorus procerus moldaviensis									1
	Crypticus quisquilius	3	–	–	–	15	–	–	–	–
	Gonocephalum granulatum pusillum	12	2	–	16	8	2	5	107	–
	Opatrum riparium	–	36	–	3	82	5	–	–	–
	Opatrum sabulosum	11	–	–	96	18	2	–	23	–
	Pedinus femoralis	6	–	–	17	2	–	5	18	–
	Platyscelis hypolitha	–	–	–	2	–	–	–	–	–
	Tentyria nomas	2	–	–	–	–	–	15	5	–
	Total number of Tenebrionidae species	**7**	**3**	**–**	**6**	**7**	**3**	**3**	**4**	**–**
	Total number of Tenebrionidae individuals	**39**	**43**	**–**	**137**	**198**	**9**	**25**	**153**	**–**
	Menhinick's index	**1.1**	**0.5**	**–**	**0.5**	**0.6**	**1.0**	**0.6**	**0.3**	**–**

B. Dry steppe, Arykty

	Beetle species	1976			1978			2018		
		positions								
		EL	TR	AC	EL	TR	AC	EL	TR	AC
L	**Carabidae**									
B	Amara infima	–	–	–	–	7	–	–	–	–
B	Amara littorea	–	–	4	–	–	6	–	–	–
SA	Amara pastica	4	–	–	–	–	–	–	–	–
SH	Amara tibialis	–	–	–	–	14	3	–	–	–
SA	Brachinus hamatus	–	–	–	–	–	3	–	47	40
SH	Broscus semistriatus	–	–	–	–	–	–	–	3	5
SH	Calosoma auropunctatum	–	6	–	–	–	–	–	–	–
SH	Calosoma denticolle	10	–	–	–	–	–	–	–	–
SH	Carabus clathratus	–	10	6	–	3	5	–	–	–
SA	Corsyra fusula	–	–	–	–	–	–	20	–	–
SA	Harpalus anxius	–	–	–	–	–	–	–	3	–
PZ	Harpalus distinguendus	–	–	–	–	8	–	–	–	–
SA	Harpalus sarmaticus	–	–	–	–	–	–	7	–	–
SH	Harpalus smaragdinus	–	–	–	–	–	–	10	–	–
SA	Harpalus subcylindricus	–	–	–	–	–	–	3	–	–
PZ	Microlestes minutulus	–	70	34	6	328	208	–	–	–
SA	Microlestes plagiatus	–	10	6	–	–	–	–	–	–
SA	Microlestes schroederi	–	–	–	–	–	–	7	–	–
SH	Poecilus cupreus	–	–	58	–	–	6	–	–	–
SH	Poecilus punctulatus	–	–	–	–	10	–	–	–	–
SA	Poecilus sericeus	36	–	–	18	–	–	30	7	3
SA	Poecilus subcoeruleus	–	16	6	–	33	3	–	–	–
SH	Pterostichus macer	1	62	60	–	20	23	–	–	–
B	Pterostichus minor	–	–	4	–	7	15	–	–	–
PZ	Pterostichus nigrita	–	–	6	–	–	3	–	–	–
SH	Syntomus truncatellus	–	–	–	–	–	–	3	30	3
SA	Taphoxenus gigas	16	–	–	3	–	–	10	7	–
	Total number of Carabidae species	**4**	**6**	**9**	**3**	**9**	**10**	**8**	**6**	**4**
	Total number of Carabidae individuals	**60**	**174**	**184**	**27**	**430**	**275**	**9**	**97**	**51**
	Menhinick's index	**0.5**	**0.5**	**0.7**	**0.6**	**0.4**	**0.6**	**0.8**	**0.6**	**0.6**
	Tenebrionidae									
	Blaps halophila	40	–	–	52	–	–	30	10	7
	Blaps lethifera	–	–	–	–	–	–	27	3	–
	Centorus rufipes									1
	Crypticus quisquilius	–	3	5	2	5	2	–	–	–
	Gonocephalum granulatum pusillum	–	3	–	26	382	125	–	7	–
	Gonocephalum pygmaeum	7	25	10	–	–	–	–	–	–
	Oodescelis polita	–	5	–	5	3	–	3	3	–
	Opatrum riparium	–	–	–	–	–	–	–	–	–
	Opatrum sabulosum	–	–	–	10	6	3	–	3	–
	Pedinus femoralis	6	–	–	–	–	–	20	3	–
	Platyscelis hypolitha	–	–	–	6	–	–	3	–	–
	Tentyria nomas	234	47	17	167	10	3	460	153	44
	Total number of Tenebrionidae species	**4**	**6**	**3**	**7**	**5**	**4**	**6**	**7**	**2**
	Total number of Tenebrionidae individuals	287	83	32	268	406	133	543	182	51
	Menhinick's index	**0.2**	**0.7**	**0.5**	**0.4**	**0.3**	**0.3**	**0.3**	**0.5**	**0.3**

C. Deserted steppe, Barshyn (Barshino)

	Beetle species	1976			1978			2018		
		positions								
		EL	TR	AC	EL	TR	AC	EL	TR	AC
L	**Carabidae**									
SH	Agonum viridicupreum	–	–	30	–	–	8	–	–	–
–	Amara (Bradytus) sp.	–	6	–	–	–	–	–	–	–
SA	Bembidion pallidiveste (?)	–	–	–	–	–	10	–	–	–
SA	Brachinus hamatus	–	–	200	–	–	–	–	–	–
SH	Calosoma auropunctatum	–	–	6	–	–	8	–	–	–
SH	Calosoma denticolle	–	6	–	–	–	–	–	–	4
SA	Carabus bessarabicus	–	–	6	–	16	–	–	8	–
SA	Chlaenius spoliatus	–	–	30	–	–	–	–	–	–
PZ	Chlaenius tristis	–	–	–	–	–	30	–	–	–
SH	Curtonotus convexiusculus	–	10	–	–	–	–	–	–	–
SA	Cymindis lateralis	–	10	60	–	–	–	–	–	–
SA*	Cymindis violacea (?)	30	–	–	4	–	–	–	–	–
SH	Elaphrus cupreus	–	–	–	–	–	60	–	–	–
SA	Harpalus dispar splendens	–	–	–	–	–	–	–	–	8
SA	Harpalus salinus	14	–	–	16	–	–	–	–	–
SH	Harpalus smaragdinus	–	4	–	–	–	–	–	–	–
SA	Harpalus steveni	–	12	–	–	–	–	–	–	–
SA	Microlestes maurus	–	–	–	–	–	–	–	4	–
PZ	Microlestes minutulus	–	–	80	–	–	10	–	–	–
SA	Microlestes plagiatus	–	–	–	–	–	84	–	–	–
SH	Ophonus rufibarbis	–	6	–	–	–	–	–	–	–
SA	Poecilus crenuliger	–	–	–	–	–	–	–	20	–
SH	Poecilus cupreus	–	–	–	–	–	50	–	–	–
SA	Poecilus laevicollis	–	–	–	–	–	–	–	–	8
SA	Poecilus sericeus	–	–	–	–	–	–	–	12	–
SA	Poecilus subcoeruleus	–	70	–	–	58	392	–	–	–
SA	Pseudotaphoxenus tillesii	–	6	–	–	–	–	–	–	–
SH	Pterostichus macer	–	6	24	–	–	16	–	–	–
SA	Taphoxenus gigas	4	–	–	8	–	–	1	4	–
	Total number of Carabidae species	**3**	**10**	**8**	**3**	**2**	**10**	**1**	**5**	**3**
	Total number of Carabidae individuals	**48**	**136**	**436**	**28**	**74**	**668**	**1**	**48**	**20**
	Menhinick's index	**0.4**	**0.9**	**0.4**	**0.6**	**0.2**	**0.4**	**1.0**	**0.7**	**0.7**
	Tenebrionidae									
	Anatolica lata	5	6	–	124	–	–	4	16	–
	Blaps halophila	14	–	–	26	8	–	16	12	24
	Blaps lethifera	–	–	–	–	–	–	8	12	–
	Centorus calcaroides intermedius									1
	Centorus filiformis	–	–	–	–	8	–	–	–	–
	Centorus procerus	–	10	6	–	–	16	–	–	–
	Oodescelis polita	–	70	–	–	50	–	–	4	–
	Opatrium sabulosum	–	–	–	–	8	–	–	8	–
	Pedinus femoralis	10	6	–	8	8	–	–	8	–
	Platyscelis rugifrons	–	–	–	–	–	–	–	12	–
	Platyscelis sp.	200	6	–	54	–	–	–	–	–
	Tentyria nomas	30	6	–	50	8	–	72	20	–
	Total number of Tenebrionidae species	**5**	**6**	**1**	**5**	**6**	**1**	**4**	**8**	**2**
	Total number of Tenebrionidae individuals	**308**	**104**	**6**	**262**	**90**	**16**	**100**	**92**	**24**
	Menhinick's index	**0.3**	**0.6**	**0.4**	**0.3**	**0.6**	**0.2**	**0.4**	**0.8**	**0.2**

* With the transition to the arid group of species.

COMPLIANCE WITH ETHICAL STANDARDS

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

Statement on the welfare of animals. This article does not contain any studies involving animals performed by any of the authors.

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