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SYSTEMATIC STUDY OF ARID TERRITORIES

Trophic Structure of Ground-Dwelling Insects in the Coastal Zone of a Salt Lake in Southern Siberia Based on the Data of Isotopic Analysis

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Abstract—The trophic structure of a ground-dwelling insect community has been studied in the coastal zone of a salt lake in the southern forest-steppe (Novosibirsk oblast). Five contrasting habitats along a 170-m catena with an altitude drop of 1.8 m were studied. In each habitat, the soil, as well as dominant insect and plant species, were sampled: phytophages, saprophages, and predators. According to a stable-isotope analysis of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$), phytophagous insects (the locust *Epachromius pulverilentus* and carabid beetle *Dicheirotrichus desertus*) are closely connected to their food objects and hardly migrated along the catena. Saprophages (the mole cricket *Gryllotalpa unispina* and earwig *Labidura riparia*) use various food resources; some of them (mole crickets) tend to migrate between the biotopes. Predatory beetles (carabid imagoes) can be separated into three trophic guilds: (1) highly mobile active predators, including the tiger beetles *Cephalota chiloleuca* and *C. elegans*; (2) small generalist predators of *Pogonini* tribe (*Pogonus cumanus*, *P. transfuga*, *Pogonistes rufoaeneus*, and *Cardiaderus chloroticus*); and (3) relatively large consumers of soil saprophages and aquatic organisms (*Curtonotus propinquus* and *Cymindis equestris*). The trophic niche overlap of different predators is partially compensated by their confinement to different habitats.

Keywords: Baraba Steppe, saline soils, soil invertebrates, trophic network, salt lakes, spatial structure

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The climate of the central areas of the continents are becoming more arid and contrasting as a result of global changes (*Otsenochnyi doklad ob izmeneniyakh klimata*, 2008). Aridization is manifested not only in an increase in the average annual temperature or seasonal maxima, but also in the shift of long-term flooding cycles of drainless areas towards drying.

In a wide area of the inland flow on the south of the western Siberian Plain with its center in Lake Chany, there are thousands of shallow drainless lakes varying in the degree of salinization. In the exclusively flat landscape of the Baraba Steppe (the altitude drop is about 10 m on a 10-km long profile), the shoreline of these lakes is extremely mobile. There are therefore wide areas along the shores that are at times flooded and at times exposed to drying (littoral zones). Weather and seasonal fluctuations in the level of water bodies occur for several weeks or even days. They are also influenced by long-term cycles with a periodicity of 30–50 years (*Zapadnaya Sibir'*, 1963; Krivenko, 1991; Vasil'ev et al., 2005).

The ecosystems of saline lands near the shores of saltwater bodies cover more than 3000 km^2 in Novosibirsk oblast alone (Fedorov and Mordkovich, 2012). The forest-steppe zone is the northern distribution limit of saline lands in western Siberia and Eurasia as a whole. In recent years, these biocenoses have tended to expand due to lake shallowing and drying.

Extremely dynamic biogeocenoses are formed in the littoral zone of salt lakes. They are similar to the near-water ecosystems from which life arrived on land (Ponomarenko, 2013). The ~~soil cover~~ in the littoral zones of salt lakes are also very distinctive. They are formed both on land and under water. In addition, the ratio of the main elements in bottom sediments during the process of pedogenesis under aquatic conditions is significantly different from that in watershed soils and is close to ~~that aquatic~~ organisms (Pushkareva, 2013). Plants in such ecosystems are either absent or represented by a small number of specific halophilic species. The key role in ~~them~~ is played by invertebrates, which are numerous and vary in their size and way of life. They utilize ~~waterbody organic waste~~ and enhance the conversion of a soil environment from anaerobic to aerobic (Mordkovich, 1973a; Fedorov and Mordkovich, 2012).

The habitats of various species in such ecosystems are quite densely “packed”: there are several variants of biogeocenoses on the profile along the first hundreds of meters laid perpendicularly to the shore due to the high contrast of abiotic conditions. The spatial and temporal structure of the insect community in the littoral zone of a salt lake described in the text below was studied in detail in 2011–2012 (Fedorov and Mordkovich, 2012; Fedorov, 2013).

Our goal was to analyze the trophic structure of the community of ground-dwelling insects in the littoral zone of the salt lake. Stable-isotope analysis, which has been widely applied in recent years, was used to fulfill this purpose. The isotopic composition of nitrogen ($^{15}N/^{14}N$, commonly represented as $\delta^{15}N$) enables estimation of the trophic level of an organism, whereas the isotopic composition of carbon ($^{13}C/^{12}C$, $\delta^{13}C$) makes it possible to specify the spectrum of its food objects ~~in a number of cases~~ (Scheu and Falca, 2000; McCutchan et al., 2003; Tiunov, 2007; Goncharov and Tiunov, 2013).

We assumed that (1) predatory insects, which are relatively ~~low-~~abundant and diverse in this ecosystem (as compared to sapro– and phytophages), will constitute a competition-based community consisting of more than one guild. This type of structural organization will be indicated by differences in the diet of predators (and, accordingly, the isotopic composition) coexisting in one biotope. On the contrary, in the case of spatial separation, predators with a similar morphological structure can have the same diet (as well as isotopic composition). Furthermore, we assumed that (2) insects with higher mobility will have a wider range of $\delta^{13}C$ and $\delta^{15}N$ values and the same isotopic composition in different biotopes, whereas those with lower mobility will have a smaller range of these values and more pronounced biotopic differences.

MATERIALS AND METHODS

The material for this study was sampled on the border between the Baraba and ~~Kuludinskaya~~ forest-steppe in the southern part of Novosibirsk oblast (the south of western Siberia). Here, the winter period lasts from early November to late March; the average temperature in January is –19 to –21°C. The temperature in July is about +18–19°C with an absolute maximum of +40°C. The main amount of precipitation falls in summer; the average annual amount of precipitation is 300–350 mm. Ground waters flow close to the surface and are often salinized. Sulfate and chloride waters with a mineralization of 4–12 g/L are found (*Zapadnaya Sibir’*, 1963).

A geomorhpological profile (catena) was singled
1 out near the city of Karasuk, in the littoral zone of Lake Maloe Solenoe (53°43′ N, 77°42′ E). The altitude drop along the catena is 1.8 m; the profile is about 170 m long. The size of the lake’s water surface varies considerably: the shore ~~horizon~~ moves to a distance of tens of meters, ~~and~~ the difference between the highest and lowest levels of water is only 0.5 m. The lake was at the average level in 2011, almost dried out in 2012, and reached a high level in 2013. Five contrasting habitats along the catena were studied. They were dry during the study period. The habitats encircle the lake in the form of concentric stripes from 10 to 85 m in width. They are clearly seen in the vegetation cover and are separated from each other by sharp transitional zones of considerably smaller width (from 2 to 5 m).

Habitat 1—lacustrine-silty, sor-affected, sulfide, saline area with a width of 10-15 m during the period of investigation. Higher plants are almost absent; isolated glasswort (*Salicornia perennans* Wild.) shoots appear only toward August. Projective coverage is less than 5%.

Habitat 2—~~meadow~~, saline land with clumps of *S. perennans* mixed with *Artemisia nitrosa* Web., *Puccinellia kulundensis* Serg., *Atriplex patens* (Litv.) Iljin. Projective coverage of plants is up to 70%. This zone is up to 20 m in width.

Habitat 3—a belt of *Halocnemum strobilaceum* (Pall.) Bieb. dwarf semishrubs gradually scattered along the sor-affected saline area in a small kettle. Plants are aged 25–28 years. Soil is covered with a bright white salty crust. Projective coverage is 10–15%. The zone is about 85 m in width.

Habitat 4—a belt of dense *Atriplex verrucifera* Bieb. and *S. perennans* clumps with a projective coverage of 70%. The soil under *A. verrucifera* is meadow saline-alkali, ~~which is~~ sor-affected saline soil in the open area. The zone is about 35 m in width.

Habitat 5—halomesophytic meadow on ~~meadow~~, saline-alkali soil with a well-developed (10 cm) turf horizon located on a ~~short bank near the lake~~ having a width of about 10 m. The dominant plant species are *Achnatherum splendens* (Trin.) Nevski., *Limonium coralloides* (Tausch) Lincz., *A. verrucifera*, and *A. nitrosa*. Projective coverage is about 100%.

In all habitats except 5, plant litter on the soil surface is almost totally absent. The physical and chemical properties of soils in the studied habitats are given in the table.

We analyzed the stable-isotope composition of carbon and nitrogen in the tissues of dominant insect species representing different trophic groups (phytophages, saprophages, and predators) in the model ecosystem, as well as in the plants and soil. The material for the study was collected in August 2013. In each of the five habitats, we took samples of the upper soil horizon (0–2 cm) in five replications and plants ~~dominant~~ in the projective coverage (1–4 species). ~~The plants were deprived of their~~ living vegetating parts (leaves, green parts of the stem), with five ~~plants~~ for each species under study.

Insects were captured in soil traps (plastic cups with a diameter of 65 mm, without preservative solution) set in a line, with ten traps in each line. The line

Some physical and chemical soil properties and the list of the insect species studied on the catena in the coastal zone of the salt lake Maloe Solenoe

Characteristic	Habitat				
	1	2	3	4	5
Temperature, °C*					
Minimum	11	13	12.5	12	12
Maximum	44	31.5	30	39.5	45
Average	22.8 ± 6.7	21.4 ± 3.8	20.2 ± 3.5	23.0 ± 5.7	23.9 ± 6.7
Salt allowance, % of solid*	1.8–8.1	0.6–6.5	4.1–8.5	3.6–5.6	0.5–3.0
Total of anions, mg-eq per 100 g*,	28.4–130.8	10.1–104.7	102.3–133.3	60.7–85.2	7.3–48.3
δ^{13}C soil, ‰**	–15.8 ± 0.7	–18.1 ± 3.0	–14.5 ± 1.0	–19.6 ± 0.7	–25.6 ± 0.4
δ^{15}N soil, ‰**	6.4 ± 0.6	7.2 ± 2.8	6.9 ± 1.3	8.2 ± 0.8	5.4 ± 0.4
Dominant insect species (based on the results of census by soil traps in August 2013)	**Saprophages** *Labidura riparia* **Predators:** *Cephalota elegans; Cardiaderus chloroticus*	**Saprophages:** *Gryllotalpa unispina; Labidura riparia;* **Predators:** *Cymindis equestris; Cephalota elegans;* **Mixophytophages:** *Dicheirotrichus desertus; Curtonotus propinquus*	**Saprophages:** *Labidura riparia* **Predators:** *Cymindis equestris; Pogonistes rufoaeneus; Cephalota elegans;*	**Phytophages:** *Epachromius pulverilentus;* **Saprophages:** *Grillotalpa unispina;* **Predators:** *Cephalota chiloleuca; Pogonus cumanus; Pogonus transfuga*	**Phytophages:** *Epachromius pulverilentus*

* Maximum and minimum values of three measurements in 2011 and 2012 (Fedorov and Mordkovich, 2012). ** Means and standard error, $n = 10$.

ran parallel to the shoreline and was equidistant from the habitat margins. The traps were exposed from August 1 to 21 and checked every 4–5 days. Stable-isotope analysis was carried out on ~~insects of each species. At~~ least five specimens were collected along the entire length of the catena, but no more than ten specimens per species were collected from each habitat. The list of analyzed species is given in the table.

The samples were dried in a drying chamber at a temperature of 50°C for at least 48 h. Each sample was then ground to a homogenous ~~mass~~. In insects, the body parts containing as ~~few~~ muscles as possible were used: the legs in large insects; the thorax and head in small ones (Tsurikov et al., 2015). Isotope analysis was performed with a complex of equipment consisting of a Flash 1112 elemental analyzer and a Thermo Finnigan Delta V Plus isotope mass spectrometer at the Center for Collective Use, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences. The isotopic composition of carbon and nitrogen was expressed as parts per thousand of deviation from the international standard (Vienna PeeDee Belemnite and atmospheric nitrogen, accordingly), δ (‰):

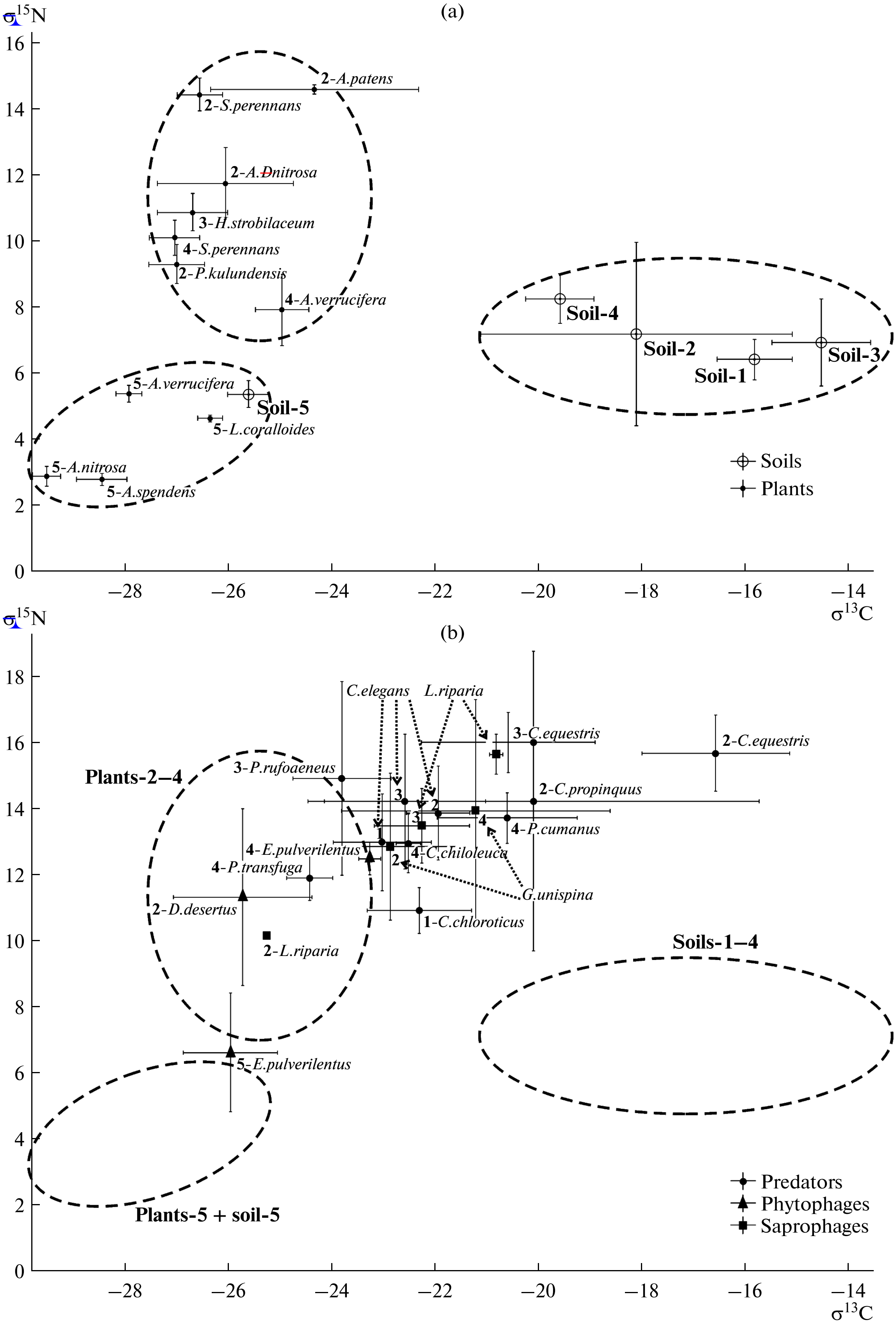
$$\delta X_{sample} = [(R_{sample}/R_{sample}) - 1] \times 1000, \quad (1)$$

where X is the element (nitrogen and carbon) and R is the mole ratio of heavy and light isotopes of the corresponding element. Analytic error in the identification of the isotopic composition of nitrogen and carbon did not exceed ±0.2‰.

The mean values were ~~aligned based on~~ the Mann-Whitney test. The data in the figures are presented as mean values and standard deviation (SD). The systematics of carabids (Carabidae of the World, 2015) is provided according to the electronic catalog at http://carabidae.org/. The carabid body length is given based on the data from our measurements (averaged for five specimens).

RESULTS

Soil and plants. The values of δ^{13}C and δ^{15}N in the catena soils varied from –25.6 to –14.4 and from 5.4 to 8.4‰, respectively. The soils in positions 1 to 4 were considerably and significantly ($p < 0.05$) enriched ~~with~~ carbon and nitrogen as compared to those in the meadow (position 5) (see figure, A). The highest dis-



Isotopic signatures of soils, plants, and insects of the catena in the dry part of the salt lake. A—Soils and plants. B—Insects. Numbers near species names indicate the catena. Groups of soils and plants similar in isotopic composition are designated by ellipses.

persion for the isotopic composition of both elements was observed in position 2.

The value of $\delta^{15}N$ in plants evenly ~~reduced~~ up the catena (from position 2 to 4) and sharply ~~decreased~~ in position 5 (see figure, A). Different plant species within the same position on the catena were little different based on the isotopic composition (except position 2, where the stable-isotope signature of *P. kulundensis* is significantly different from those of wormwood (*A. nitrosa*) and chenopodiacious plants (*A. patens*, *S. perennans*)). On the contrary, plants of the same species growing in different positions of the catena were considerably different based on the nitrogen isotopic composition. Thus, *A. verrucifera* in positions 4 and 5 was different by 2.5‰, *S. perennans* in positions 2 and 4 by 4‰, and *A. nitrosa* in positions 2 and 5 by almost (see figure, A). The mean value of $\delta^{13}C$ in plant tissues on the catena varied from –29.5 to –24.5‰, generally decreasing from position 2 to position 5 (see figure, A). The dispersion of the values of $\delta^{13}C$ and $\delta^{15}N$ in plants, as in soils, was the highest in position 2 of the catena. This is probably associated with the greater diversity of the soil cover and the unstable water regime of this habitat.

Isotopic composition of nitrogen and carbon in different trophic groups. The only "true" phytophage, *Epachromius pulverilentus*, was found only in positions 4 and 5. In two neighboring biotopes, the isotopic signatures of *E. pulverilentus* are ~~reliably~~ different ($p < 0.001$ for carbon and $p < 0.01$ for nitrogen; see figure, B), which corresponds to differences in the isotopic composition of plants in the respective plots.

The isotopic signature of the mixophagous ground beetles *Dicheirotrichus desertus* is placed on the ~~graph to the left~~ of the "isotope field," among the isotopic signatures of plants growing in the position where it was found. This indicates a close relationship of *D. desertus* with ~~pasture~~ food chains. Another mixophage, *Curtonotus propinquus*, has the widest dispersion among all of the investigated animals within the catena, based on nitrogen and carbon, but with a shift of the "isotope field" to the right side, which indicates both a wide diet spectrum and the minimal ~~plant representation in it~~.

The isotopic niche of the saprophages *Gryllotalpa unispina* and *Labidura riparia* is located in the same area of the isotope field as in predators, but it is smaller in size. Saprophages are characterized by a more variable isotopic composition of carbon and nitrogen than phytophages ($\delta^{13}C$ from –25 to –21‰, $\delta^{15}N$ from 10 to 15‰), but this variability is lower than in some predators.

Predatory insects are represented in our samples by the highest number of species inhabiting positions 1 to 4. Variations in the isotopic composition of carbon and nitrogen of predatory insects were quite significant: the values of $\delta^{13}C$ varied from –24.5 to –16.5‰, and the values of $\delta^{15}N$ from 12 to 16‰. The $\delta^{13}C$ values of most predators were shifted to a significant degree in the right part relative to plants of the catena (and slightly relative to phyto– and saprophages) and were ~~near~~ the soil $\delta^{13}C$ values (see figure, B).

Ecological differentiation of related species. The spatial ~~division~~ of species having a similar diet was demonstrated for *C. chiloleuca* and *C. elegans*. Thus, *C. elegans* was found in 2013 within positions 1 to 3, whereas *C. chiloleuca* was detected only in position 4. Their isotopic signature varies insignificantly. In 2011, having considerably higher abundance, these two species were also divided spatially: about 90% of *C. elegans* specimens were found in position 1 and almost all *C. chiloleuca* specimens occurred in position 4 (Fedorov and Mordkovich, 2012).

Trophic differentiation of ground beetles ~~included in~~ the tribe Pogonini was found: *Pogonus cumanus* and *P. transfuga*, found together in 2013 in position 4, have different dietary spectra (the differences between the isotopic signatures are ~~reliable~~; $p < 0.001$ ~~based on~~ carbon and $p < 0.01$ ~~based on~~ nitrogen). The differences in the feeding preferences of these beetles may be ~~indicated by~~ their different body sizes (*P. cumanus* is larger: body length 8.3 mm against 6.6 mm in *P. transfuga*). *Pogonistes rufoaeneus* (the smallest among all of the other Pogonini representatives under study (5.5 mm)) is spatially isolated from these species. At the same time, it occupies an intermediate position between them based on the content of heavy carbon, which may ~~indicated~~ feeding on prey involved in the diet of both species of this ~~tribe~~. *P. rufoaeneus* was registered in position 3 in 2013 and inhabited mainly position 1 in 2011; this species, in contrast to other Pogonini representatives, has two abundance maxima, in spring and summer (Fedorov, 2013). *Cardiaderus chloroticus* (7.7 mm) is spatially separated from other species (inhabited only position 1, in 2011, along with *P. rufoaeneus*) and has the lowest $\delta^{15}N$ (see figure, B).

Isotopic signatures and insect distribution along the catena. The suggestion that more mobile insects have higher dispersions of $\delta^{13}C$ and $\delta^{15}N$ and will not differ ~~based on it~~ in different positions of the catena is satisfied for the highly mobile *Cephalota elegans*, which has slightly different isotopic signatures with significant dispersion in different biotopes. This may indicate both the great diversity of their ~~victims~~ and high migration activity, compared with other ground beetles (as was also shown by the occurrence of ground beetles of this species in the largest range of habitats, position 1 to 3 of the catena) (see figure, B).

The assumption of the relation between the isotopic signature and migratory activity is consistent with the fact that specimens of the much less mobile ground beetle *Cymindis equestris* in positions 2 and 3 are clearly distinguished by the isotopic composition of carbon ($p < 0.05$). Specimens of *C. equestris* in position 2 are most enriched with heavy isotopes of both carbon and nitrogen, as compared to all investigated invertebrates. This allows *C. equestris* in position 2 to be considered a consumer of a particular group of prey that is little used by other predators: for example, insect larvae and crustaceans that feed on aquatic plant waste on the shore.

The ~~reliable~~ difference in the isotopic signatures of the phytophagous *E. pulverilentus* (~~based on~~ carbon and nitrogen, $p < 0.01$) in positions 4 and 5 of the catena is surprising, because the locust is a quite mobile insect and we expected that it would migrate between the neighboring biotopes.

DISCUSSION

The dispersion of the isotopic composition of carbon and nitrogen in the soil was higher in positions 1 to 4 than in position 5; it was especially high in position 2. This probably reflects the unstable hydrological regime of soil in the lower catena positions. The enrichment of the soil with ^{13}C is evidence in favor of the hydromorphic origin of soils in the lower areas of the catena, ~~because~~ "aquatic subsidy" ~~occurs in them~~ (Walters et al., 2008).

Despite the flat landscape of the studied catena, the conditions for the existence of invertebrates ~~on it~~ do not change gradually. The saline meadow located upwards in position 5 is currently not the ~~littoral~~ ecosystem of the littoral zone (it probably was one in the past, 50–100 years ago, because it bears geomorphological resemblance to the coastal steep at a much higher level of the lake surface), being dramatically different from almost all of the other four based on all indicators. The essential specific features are observed in position 2, which is located near the edge of the recent highest water stand on the poorly ~~seen bank~~ and disappears in some places of the shore. It has relatively more favorable abiotic conditions as compared with the adjacent positions (a lower daily temperature ~~difference~~, ~~less considerable~~ salinity; see the table), which has a positive influence on its vegetation and animal populations. Position 3 is very flat and leveled, due to which salts gradually accumulate every spring. This allows a sarzasan population—a desert, halophytic community common in southward areas that grows in Novosibrsk oblast in the extreme northern border of its habitat—to survive here (*Zelenaya kniga Sibiri*, 1996).

The studied insects inhabiting the catena belong to four trophic groups: phytophages, saprophages, predators, and mixophages. *Epachromius pulverilentus* is the only phytophage. The mole cricket *Gryllotalpa unispina* and earwig *Labidura riparia* are saprophages. Some carabids (*Dicheirotrichus desertus*, *Curtonotus propinquus*) (Sharova, 1981; Coll and Guershon, 2002) commonly have vegetative food objects in their diet (these two species were considered as mixophages). All other dominant carabid species were considered to be predators.

Almost all of the insect species under study, which are dominant in the coastal zone, are adapted to flying, which is used in case of unfavorable conditions. However, *C. chiloleuca* and *C. elegans* are the only species that use ~~it~~ when searching for food. Other insects studied in this work have a daily radius of foraging activity of only several meters (Bespalov and Lyubechanskii, 2011).

The number of direct trophic chains found during the study was very small. They were revealed only in phytophages, which are definitely connected with plants growing in the habitats of these insects. Both species of phytophagous insects~~, which are significantly~~ abundant on the catena (the generalist phytophage *Epachromius pulverilentus* and specific consumer of grain seeds *Dicheirotrichus desertus*) are probably not inclined to migrate ~~to~~ long distances, because the isotopic composition of carbon and nitrogen in acridoids inhabiting different positions of the catena is ~~reliably~~ different, and *D. desertus* turned out to be a stenotopic species and was registered only in position 2. In 2011, this species was also found in position 4, where *P. kulundensis* grows (Fedorov and Mordkovich, 2012). It is well known that harpalins feed on grain seeds (Kataev, 2011). In the "isotope space," *D. desertus* is placed near other phytophages and is close to its feeding plant (*Puccinellia kulundensis*).

The prey of predatory ground beetles remained "behind the scene," because they cannot be captured by soil traps and should be ~~recorded~~ with specific methods. The majority of prey are probably small soil saprophages. The high values of $\delta^{13}C$ demonstrate that the community of predatory, ground-dwelling invertebrates in the coastal zone, on the whole, gets energy from detrital ~~networks~~ (Korobushkin et al., 2014). Ground beetles near the water (*Cephalota elegans*, *Cardiaderus chloroticus*, and *Cymindis equestris*) can feed on aquatic animals, in which the isotopic signature of aquatic plants was shown (Korobushkin, 2014) and was especially pronounced in the latter species.

It can be argued that most members of this community are labile ~~based on their feeding objects~~. The insects probably switch to a resource that is available "here and now," rather than actively migrating along the ecosystem in search of a particular food object. This is indicated by the isotopic signatures of *Cymindis equestris* and *Epachromius pulverilentus*, which are reliably different among the biotopes. Migrations to neighboring biotopes are important for *Cephalota elegans*, which move freely between positions 1 to 3, and probably for *Gryllotalpa unispina*, which makes multimeter tunnels in the studied biocenosis and flies in many cases. In more mobile species, the "~~dispersion~~ area" of the isotopic composition of nitrogen and carbon (the product of ~~dispersions for~~ $\delta^{13}C$ and $\delta^{15}N$) is several times higher than in the majority of stenotopic species.

On the other hand, the higher dispersion of $\delta^{13}C$ and $\delta^{15}N$ values in some species (primarily in the mixophagous ground beetle *Curtinotus propinquus*) can be related to the wide range of consumed resources. What is more, different specimens of the same species must have consumed different food objects.

Based on the observations of V.G. Mordkovich, such species as *Cymindis equestris* "detach" large contingents of imagoes from initial position 2 as the lake dries into emerging areas of sor (position 1). Here, due to the ability to breed during the ~~larger part of~~ season, females lay new eggs. As a result, from the margin to the center of the lake ~~kettle~~, several larval cohorts are formed; they have different ages and geochemical environments for development (Mordkovich, 1973b). The differences in the isotopic signatures of larvae from different cohorts are probably transferred to new generations of imagoes, which hatch in different terms on different sor areas. This mechanism can be also involved in forming the wide dispersion of the isotopic composition in different parts of the metapopulation of the same species.

Although the insect community on the catena was studied during a period that was far from the abundance peak, our results suggest a certain degree of competitive structure. This was indicated by the spatial isolation of two species, *C. chiloleuca* and *C. elegans*, which have a similar ~~trophism~~, and the separation of four carabid species of the Pogonini tribe based on either preferred food objects or habitats, and, in the case of *Pogonistes rufoaeneus*, on the periods of seasonal activity. Ground beetles coexisting on the catena in the same biotope should feed on different resources. This is additionally simplified by the size-based differentiation of related Pogonini species, which forces them to use different food objects. A similar size-based differentiation that reduces competition among ground beetles was found in tiger beetles (Pearson and Mury, 1979).

CONCLUSIONS

Therefore, the insect community of the studied catena is split into three trophic groups (phytophages, saprophages, and predators). The group of predators is, in turn, divided into three ~~clear~~ guilds.

(1) Highly mobile predatory epibionts (*C. chiloleuca* and *C. elegans*). These beetles fly when hunting and find prey using their eyes. They have a similar isotope signature and are spatially isolated on the catena.

(2) Small generalist predators (four species of ground beetles of the Pogonini tribe: *Pogonus cumanus*, *P. transfuga*, *Pogonistes rufoaeneus*, and *Cardiaderus chloroticus*). Ground beetles of the Pogonini tribe belong to another life form (~~ground litter~~ soil hiding stratobionts), have a smaller size, and hunt differently from tiger beetles. Within ~~the limits of~~ this guild, a division based on trophism, preferred catena position, or seasonal activity peak is observed.

(3) Relatively large consumers of soil saprophages and aquatic dwellers (two surface ~~ground litter~~ species of different tribes: *Curtonotus propinquus* and *Cymindis equestris*). These two species are very different based on the isotopic composition of carbon and nitrogen and are enriched to the maximum level with heavy isotopes of both elements.

Significant migration between the catena positions was registered only for some species. On the whole, our data suggest a quite labile feeding behavior (and, accordingly, wide overlapping of the trophic niches) in most predatory ground beetles. A similar conclusion was derived by M. Zalewski et al., who studied the isotopic composition of ground beetles in the forest-meadow community of the temperate zone (Zalewski et al., 2014). It is probable that the trophic niche overlap of different predators in the studied biotopes is partially compensated by their confinement to different habitats, but this suggestion is provisional due to the small volume of analyzed material.

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