


Article

Trophic Structure of the Soil-Dwelling Arthropod Communities at the Border of the Forest and the Steppe in the South of Western Siberia: Isotopic Data

Ilya I. Lyubechanskii ^{1,*} , Alexei N. Beshpalov ², Alexei V. Tiunov ³, Galina N. Azarkina ¹, Roman Yu. Dudko ¹, Lyudmila V. Salisch ² and Vyacheslav G. Mordkovich ¹

¹ Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Frunze Str. 11, Novosibirsk 630091, Russia

² Institute of Soil Science and Agrochemistry, Siberian Branch of the Russian Academy of Sciences, Lavrentiev Avenue 8/2, Novosibirsk 630090, Russia

³ A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Leninsky Prospekt 33, Moscow 119071, Russia

* Correspondence: lubech@gmail.com

Abstract: Epigeic generalist predators play a crucial role in terrestrial ecosystems, connecting above-ground and belowground food webs. Using stable isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values), we assessed the trophic niches of the two main groups of generalist predators (ground beetles (Coleoptera, Carabidae) and spiders (Arachnida: Aranei)), as well as their potential prey (phytophagous and saprophagous insects), plants, and soils in the forest, steppe, and transitional ecosystems located in the forest–steppe of southwestern Siberia. We hypothesized that (1) the trophic niche of carabids is wider than that of spiders, because some ground beetles are omnivorous, and (2) the contribution of invertebrates from the detrital food web (saprophages) to the diet of generalist predators is higher in the “detrital” forest ecosystem than in the steppe, which should be reflected in increased $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the predators in the forest. In total, 16 species of carabid and 17 species of spider were analyzed. The $\delta^{15}\text{N}$ values of ground beetles suggested a wide range of trophic niches corresponding to two or three trophic levels. Omnivorous carabids of the genera *Amara* and *Harpalus* had the minimum $\delta^{15}\text{N}$ values. The carbon isotope compositions of the ground beetles suggests that most predatory species were predominantly involved in grazing food chains. Spiders had on average increased $\delta^{15}\text{N}$ values compared to ground beetles, and a relatively narrow range of $\delta^{15}\text{N}$ values. The isotopic niche occupied by spiders hardly overlapped with the isotopic niche of carabids, which may indicate a significant difference in the range of consumed resources. Thus, our data suggest a significant difference in the trophic niches of the key generalist predators, ground beetles and spiders, which was observed both in the forest and the steppe habitats. Spiders appear to be more closely associated with detrital food webs than ground beetles. Contrary to our expectations, we did not find higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in ground-dwelling generalist predators in the forest compared to the steppe ecosystem.

Keywords: carbon; nitrogen; microarthropods; carabid beetles; spiders; ants; Carabidae; Aranei; *Formica*; *Bicolorana roeselii*; *Lymanthria dispar*; food web; Siberia



Citation: Lyubechanskii, I.I.; Beshpalov, A.N.; Tiunov, A.V.; Azarkina, G.N.; Dudko, R.Y.; Salisch, L.V.; Mordkovich, V.G. Trophic Structure of the Soil-Dwelling Arthropod Communities at the Border of the Forest and the Steppe in the South of Western Siberia: Isotopic Data. *Diversity* **2023**, *15*, 445. <https://doi.org/10.3390/d15030445>

Academic Editors: Elena N. Melekhina and Spyros Sfenthourakis

Received: 4 February 2023

Revised: 12 March 2023

Accepted: 15 March 2023

Published: 17 March 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Trophic relationships in the communities of invertebrates that inhabit the soil and its surface are extremely complex. The redundancy of their faunistic diversity, the multiplicity and ambiguity of functional groups, the significant width of the trophic niche of most species—all these factors complicate the identification of nodes and trophic links in the soil food web. This is especially true for the epigeic generalist predators inhabiting the soil

surface and litter layer, which belong to and connect both belowground and aboveground food webs [1].

Studies of the trophic relationships of organisms in ecosystems using the ratios of stable isotopes of carbon and nitrogen (stable isotope analysis) have been widely used in recent decades. The advantage of this method is that it allows one to assess the place of an animal in a trophic web not situationally, as, for example, analysis of the contents of the digestive tract, but integrated over time. The isotopic composition of nitrogen (the $^{15}\text{N}/^{14}\text{N}$ ratio, usually expressed by the $\delta^{15}\text{N}$ value) makes it possible to assess the trophic level of an organism, while the isotopic composition of carbon (the $^{13}\text{C}/^{12}\text{C}$ ratio, usually expressed as $\delta^{13}\text{C}$ value) in some cases makes it possible to refine the spectrum of its C sources. Saprophages are on average enriched in ^{13}C by 3–5‰ and in ^{15}N by 1–3‰ compared to the leaf litter. Predators are, on average, enriched in ^{13}C by about 1‰ and in ^{15}N by about 3‰ compared to saprophages [2]. In both saprophages and predators, the $\delta^{15}\text{N}$ values vary significantly [3], which indicates that saprophages and predators “in general” do not represent trophic levels, but consist of guilds, i.e., subsets of organisms, differing in resource use [2,4].

The object of our study were predaceous ground-dwelling invertebrates: ground beetles (Coleoptera, Carabidae) and spiders (Arachnida: Aranei), which play a key role in the detrital block of soil communities in the ecosystems of the temperate zone. Representatives of these taxa form complex assemblages with high species diversity and abundance. All spiders are predators, but many nonspecialized carabids are omnivores that feed largely on plant seeds [5]. However, there is no unequivocal point of view on the proportion of plant food in the diet of ground beetles [6–8].

Measurements of the isotope compositions of soil animals have generally confirmed the conclusions obtained in traditional studies of their trophic niches based on the analysis of gut contents and direct observations of feeding. Based on the results obtained in stable isotope studies, carabid beetles can be divided into three trophic guilds: “phytophages” (more precisely, “omnivores”), “consumers of saprophages”, and “generalist predators” [9]. However, this division is not strict: along with seasonal diet changes [10], strong differences in the diet have been found both between different populations and between individuals of the same population [11–13]. In the extreme conditions of the Arctic or high mountains, intraguild predation of large individuals on smaller ones can play an important role in the feeding of ground beetles [14]. For all these reasons, the trophic niches of many species overlap strongly [15], which confirms the classic view that food competition is not the main factor in the formation of ground beetle assemblages [16].

Spiders (Arachnida, Aranei) often have a less variable stable nitrogen isotopic composition than ground beetles, since they occupy closer trophic levels [17,18]. The similarity in $\delta^{13}\text{C}$ values between terrestrial spiders and springtails suggests that the latter may represent a key resource for small spiders (e.g., Linyphiidae and juvenile Lycosidae) [19,20]. For spiders, intraguild predation is also important [14,21].

The trophic structures of soil and litter invertebrate communities have been studied in sufficient detail, including via the use of stable isotope analysis. However, studies have been conducted predominantly in forest or agroecosystems (see [22], however). For open ecosystems such as meadows and steppes, the trophic structures of communities of ground invertebrates have been studied much more poorly. This is important, since the border between the forest and the steppe is quite mobile in connection with climate change in different regions. The steppe is advancing on the forest in Kazakhstan [23], and, moreover, the movement of the boundaries of the forest and treeless regions in opposite directions (including the advance of the forest on the steppe) has been observed in the neighboring mountain basins of Altai and Tyva in southern Siberia [24]. The study of the structure of the ecological communities of the ecotone between the forest and the steppe can contribute to a better understanding of these processes.

The present study was carried out in the ecotone between the forest and grassland communities of the forest–steppe biome. Forest ecosystems are often referred to as “detrital”

as opposed to open ecosystems, in which grazing food webs predominate [25]. This classification refers to the aboveground communities and it is not known to what extent it can be attributed to the inhabitants of the soil and litter. Detrital food webs are characterized by the accumulation of ^{13}C and ^{15}N [2,26]. Thus, if the forest is indeed dominated by detrital food webs, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of generalist predators that couple detrital and grazing food chains should be increased compared to those of grassland ecosystems.

The main purpose of this work was to reveal the general patterns of the trophic niches in the communities of predatory ground-dwelling arthropods in the forest, grassland, and ecotone ecosystems of the forest–steppe biome.

We addressed the following questions:

1. What is the trophic structure of the arthropod community in the “forest–edge–steppe” gradient, with special attention to ground beetles and spiders?
2. What is the difference in the trophic niches of two main groups of predatory soil macroarthropods (ground beetles and spiders)? Are the food resources consumed by spiders different from those consumed by ground beetles? We assumed that the trophic niche of ground beetles should be wider than that of spiders because of the presence of omnivorous species among ground beetles (Hypothesis 1).
3. Is the proportion of animals from the detrital food web (saprophages) higher in the diet of generalist predators in the forest ecosystem than in the steppe ecosystem? This should be reflected in higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of predators in the forest ecosystem (Hypothesis 2).

2. Materials and Methods

2.1. Brief Description of the Studied Communities of Predatory Soil-Dwelling Arthropods

The spatiotemporal structures of these communities in the studied ecosystems were studied in detail in 2007–2008 [27,28]. The taxonomic richness of spiders was 83 species from 14 families, and that of carabids was 54 species. The activity densities of representatives of both taxa were approximately equal, averaging about one individual per one pitfall trap per day. The spatial distributions of species richness and abundance in spiders and ground beetles were largely similar [29].

At the level of individual species of ground beetles and representatives of individual families of spiders, there is a distinct division into groups confined to forest and open areas. In ground beetles, specialization goes further: carabid species inhabiting grassland can be subdivided into “meadow”, “steppe”, and generalists of open spaces. Spiders do not have such a clear division; however, in the most arid and unproductive areas, species of families with relatively inactive life forms (ambushers) dominate. Apparently, the densities of ground beetles and spiders depend on the same vast and diverse group of prey, mainly inhabitants of the soil, litter layer, and litter layer surface [28,29].

2.2. Characteristics of the Study Area

The study site was located at the border of the Baraba and Kulunda forest–steppes in the vicinity of the village of Troitskoye, Karasuksky district, Novosibirsk region, located in the south of western Siberia. A transect about 150 m long was chosen from the center of a small forest outlier (“kolok”) to the middle of the steppe area in the northeast direction. It crossed habitats of three types (Figure 1).

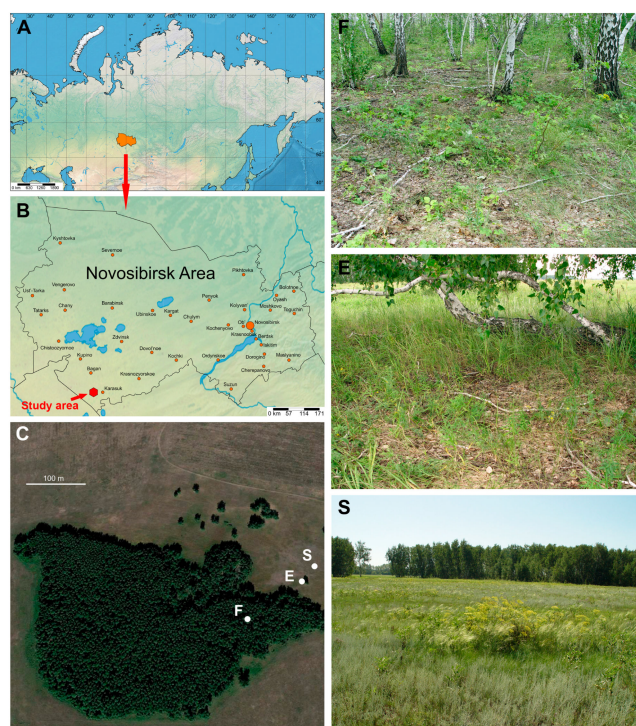


Figure 1. Geographical location of the study area. (A) Novosibirsk region, (B) location of the study site on the map of the Novosibirsk region. (C) Location of the studied habitats ((F) forest, (E) edge, (S) steppe). Scale bar—100 m. General view of habitats: (F) forest, (E) forest edge, (S) steppe. All photos were taken on 20 July 2008.

The forest (F) was a relatively low (approximately 10–12 m) stand on solodized soddy soil, formed by *Betula pendula*, *Populus tremula*, and shrubs, 200–400 m in diameter, with a total projective cover of about 100%, well-developed litter layer, and sparse ground vegetation. At the edge of the forest, the stand was sparse, becoming much denser in the middle parts. The projective cover of ground vegetation in the forest was about 30–40% at the border and only about 10% at the center (Figure 1F; 53.7127 N, 77.7071 E).

The edge of the forest, or ecotone (E) was a 30–50 m wide belt of *Calamagrostis–Peucedanum* steppe meadow on meadow-chnozem solonetz soil with individual birch trees. The richness of plants reached 35–40 species per 100 m², with representatives of steppe, meadow, and halophyte forbs and grasses (Figure 1E; 53.7135 N, 77.7080 E).

The meadow steppe (S) included two types of communities: (1) *Artemisia–Stipa–Festuca* solonetz steppe on medium-columnar and deep solonetz among the meadow steppe, with a total projective cover of 60–80%, and approximately 35 species per 100 m²; (2) Steppe meadow on ordinary chernozem with a projective cover of 80–90%, and 40–60 species per 100 m² (Figure 1S; 53.7138 N 77.7082 E). Samples and traps were evenly distributed between both types, since the size of solonetz was often small, in the order of several meters, and their boundaries had a complex shape.

We limited the study to one transect in order to minimize local spatial variations in the isotope compositions of the soil and soil animals, as occurs in the adjacent areas near saline water bodies [30].

2.3. Collection and Processing of Samples

In the three indicated habitats, soil, litter, and dominant plant and arthropod species were collected for the analysis of stable carbon and nitrogen isotopes. The composition of isotopes in the analyzed objects is given in the Table A1 in the Appendix A.

In each of the three habitats, 10 soil and litter samples were taken. Samples of the upper mineral soil layer, 5 cm in diameter, were taken to a depth of 2–3 cm. Litter samples of the same diameter included the entire depth of the litter. Samples were collected randomly

from an area of approximately 10×10 m in each habitat, at a distance of several meters from each other.

Green parts were taken from the dominant plant species in 10 replications per habitat. The collected plants were located at a distance of several meters from each other on the same areas used for collection of soils. Each replication of tree and shrub leaves (birch, aspen, wild rose) included five leaves taken from one individual plant. For herbaceous plants each replication included several leaves or stems. The collected plant parts were located at heights from a few cm (in the case of small herbs and grasses) to no more than 1 m (shrubs, trees) above the ground. The use of green parts of plants was due to their greater availability and representation throughout the season. It is known that seeds (and other “heterotrophic” parts of plants, including stems and roots) are slightly enriched in ^{13}C compared to leaves. Enrichment of seeds with ^{15}N is also often observed, but this varies in different plants. In any case, the difference between seeds and leaves is small (1–2‰) and often unreliable (for ^{13}C see [31], for ^{15}N and ^{13}C see [32]).

Arthropods were collected using pitfall traps filled with 3% acetic acid solution. Twenty traps were installed in each habitat forming a square of approximately 15 by 15 m. Traps were exposed for 30 days in total. In addition, the inhabitants of grass and shrubs were collected by entomological mowing and gathering by hand. Sampling and collection of invertebrates was carried out between 15 June and 15 July 2008. Additional collection of invertebrates was carried out in the second half of June 2014. Collected animals were kept in 70% alcohol until the identification and analysis.

In total, 10 plant species, 17 spider species, and 16 ground beetle species were analyzed. The taxonomy of ground beetles is given according to [33]. In addition to ground beetles and spiders, their potential prey and possible competitors were also collected, including phyto-, sapro-, and omnivores that dominated in the habitats. The dominant phytophages were represented by weevils (Curculionidae), *Bicolorana roeselii* grasshoppers (Tettigoniidae; they can also feed on animal food [34]), and Miridae bugs (sucking phytophages). In 2014, there was an outbreak of the gypsy moth (*Lymantria dispar*) in the forest, the caterpillars of which were also analyzed. Saprophages were represented by darkling beetles (Tenebrionidae: *Oodescelis polita*, *Blaps lethifera*) and necrophagous beetles (Silphidae: *Silpha carinata* and *Nicrophorus* spp.). In addition, polyphagous *Formica aquilonia* ants were collected and analyzed.

For stable isotope analysis, only those species that were collected in an amount of at least 5 specimens in total were used, but not more than 10 specimens of one species from one habitat were analyzed.

Soil, litter, and plant samples were dried in an oven at 50 °C for at least 48 h. Then, each sample was mixed and ground to a homogeneous powder. In insects, parts containing predominately muscle tissue were used for the analysis: the legs of large insects or the chest and head of small ones [35].

Stable isotope analysis was conducted using a Thermo Delta V Plus continuous-flow IRMS coupled with a Thermo Flash 1112 elemental analyzer (Thermo Scientific, Waltham, MA, USA) at the Joint Usage Center of the Institute of Ecology and Evolution RAS. The isotopic composition of N and C was expressed in a conventional δ -notation (in ‰) relative to the international standard (atmospheric nitrogen and VPDB, respectively). The standard deviations of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the laboratory standard (casein) were $<0.2\text{‰}$ ($n = 8$).

In total, the isotopic composition of nitrogen and carbon was determined for 450 samples. Isotopic compositions of animals in different habitats were compared using the nonparametric Kruskal–Wallis test. Post hoc tests were performed using Mann–Whitney pairwise post hoc tests. Statistical analysis was performed using the PAST 4 program [36]. The figures show the arithmetic mean with standard error.

3. Results

3.1. Soil and Litter

The soils and litters of the studied habitats turned out to be very similar in terms of ^{13}C content (for soils, $\delta^{13}\text{C}$ values were about -26.6‰ , for the litter, about -27.6‰), without significant differences between habitats (Figure 2, Table A1). Differences in the content of ^{15}N in soil (from 2.5 ± 0.2 to $3.1 \pm 0.3\text{‰}$) and litter (from -0.6 ± 0.2 to $0.1 \pm 0.4\text{‰}$) were more pronounced, but were not statistically significant (Figure 2).

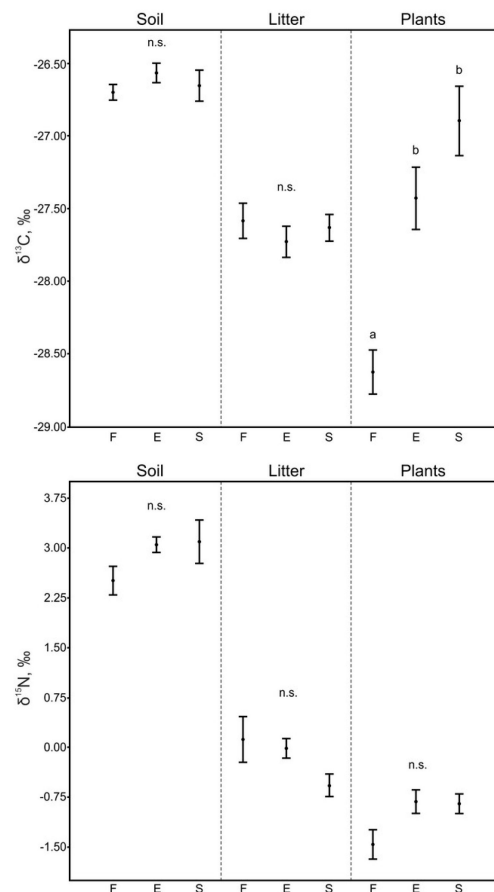


Figure 2. Mean (± 1 SE) $\delta^{13}\text{C}$ (top) and $\delta^{15}\text{N}$ (bottom) values of the soil, litter, and green parts of plants in the forest, forest edge, and steppe habitats. Significantly ($p < 0.05$) different values are indicated by different letters (a, b). n.s. – no significance. F: forest, E: edge, S: steppe.

3.2. Plants

The $\delta^{13}\text{C}$ value gradually increased in the forest–edge–steppe series by $0.5\text{--}1.0\text{‰}$ with each step. The plants of the open habitats were significantly enriched in ^{13}C compared to the trees and shrubs of the forest. However, it should be noted that the leaves of the trees were taken from the lower parts of the crowns. In contrast, the $\delta^{15}\text{N}$ values of the dominant plants did not differ in different habitats (Figure 2).

3.3. Arthropods

3.3.1. Phytophages and Saprophages

Phytophages collected in different ecosystems did not significantly differ in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values (Figure 3). A more informative picture was obtained by depicting each specimen in a $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ isotopic biplot (Figure A1). Bugs and weevils had similar isotopic signatures ranging from -28.0 to -25.0‰ $\delta^{13}\text{C}$ and from 2.0 to 4.5‰ $\delta^{15}\text{N}$. This corresponds to the usual pattern of trophic enrichment in food chains. The grasshopper *Bicolorana roeselii* stood out quite strongly from this pattern, having a $\delta^{13}\text{C}$ value of more

than -25.0‰ and a very low content of ^{15}N ($\delta^{15}\text{N}$ not more than 1.1‰). Caterpillars of the gypsy moth *Lymantria dispar* also had relatively low $\delta^{15}\text{N}$ values, but were depleted in ^{13}C ($\delta^{13}\text{C}$ values less than -27.0‰).

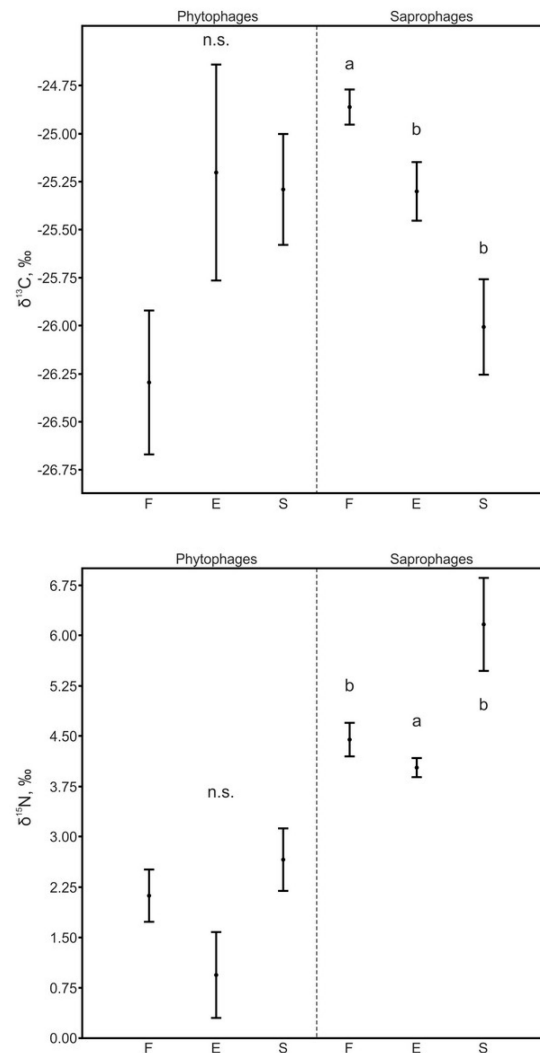


Figure 3. Mean (± 1 SE) $\delta^{13}\text{C}$ (top) and $\delta^{15}\text{N}$ (bottom) values of phytophages and saprophages in the forest, forest edge, and steppe habitats. Significantly ($p < 0.05$) different values are indicated by different letters (a, b). n.s. – no significance. F: forest, E: edge, S: steppe.

The most abundant macrosaprophagous arthropods in the studied habitats were Tenebrionidae and Silphidae beetles. They differed little from phytophages in terms of $\delta^{13}\text{C}$ values, but were significantly enriched in ^{15}N (by 2–5‰). The $\delta^{13}\text{C}$ values of saprophages decreased in the forest–edge–steppe series, while the $\delta^{15}\text{N}$ values, in contrast, were higher in the steppe than in the forest and at the forest edge (Figure 3).

The tenebrionids *Oodescelis polita* and *Blaps lethifera* formed a dense cluster in the isotopic biplot; *Blaps* were on average less enriched in ^{13}C than *Oodescelis*. Compared to darkling beetles, the silphid beetles *Silpha carinata* were enriched in ^{15}N , since they include both plant and animal remains in the diet (Figure A2). The burying beetle *Nicrophorus* differed sharply from other saprophages in having a very wide range of $\delta^{13}\text{C}$ values and a strong enrichment in $\delta^{15}\text{N}$ (Figure A2).

3.3.2. Ants

Ants (*Formica aquilonia*) were considerably enriched in ^{13}C and ^{15}N compared to phytophages. Both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of ants increased from the forest to the open habitats, with mean $\delta^{15}\text{N}$ values being significantly different at all three sites (Figure 4).

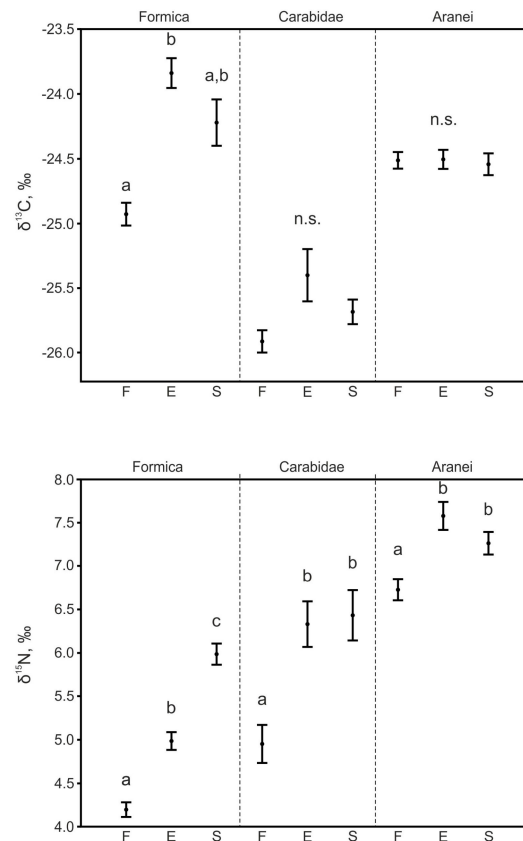


Figure 4. Mean (± 1 SE) $\delta^{13}\text{C}$ (top) and $\delta^{15}\text{N}$ (bottom) values of ants, ground beetles, and spiders in the forest, forest edge, and steppe habitats. Significantly ($p < 0.05$) different values are indicated by different letters (a, b, c). n.s. – no significance. F: forest, E: edge, S: steppe.

3.3.3. Ground Beetles

In the forest–steppe ecosystem studied, ground beetles numerically prevailed over all other taxonomic groups of macroarthropods, possibly excluding spiders (see Materials and Methods). Among ground beetles, omnivory is widespread, from mainly omnivorous representatives of the genera *Harpalus* and *Amara* to almost pure predators (*Carabus*, *Agonum*). In the studied sequence of forest–steppe habitats, 16 species of ground beetles reached a high abundance (see Table A1), and were considered in this study.

Among the ground beetles, there were no species found in all three habitats. Ground beetles of the same species collected simultaneously in two habitats (*Poecilus koyi*, *Harpalus anxius*, *Taphoxenus gigas*, *Calathus erratus*, and *Poecilus fortipes*) failed to differ in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values.

The mean $\delta^{13}\text{C}$ values of ground beetles averaged across all species collected in each habitat did not differ, although the mean $\delta^{15}\text{N}$ values increased from the forest to the open area; there was a significant differences between the forest beetles and those of the forest edge and steppe (Figure 4).

In the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ isotopic biplot, ground beetles occupied a vast area between -28.5 and -22.0 ‰ in $\delta^{13}\text{C}$ values and between 1.5 and 10.0 ‰ in $\delta^{15}\text{N}$ values (Figure A3). The isotope niche occupied by ground beetles had the shape of an almost regular triangle pointing downwards. The lower corner of the triangle was formed exclusively by representatives of the omnivorous genera *Amara* and *Harpalus*, with the lowest $\delta^{15}\text{N}$ values for the forest

beetles ($\delta^{15}\text{N}$ from 1.5 to 4.0‰). Some representatives of the genus *Amara* (*A. eurynota*, *A. bifrons*) apparently had a significant proportion of animal food in their diet and were found in the central part of the isotopic niche, along with predators. The central and upper parts of the triangle ($\delta^{15}\text{N} = 5\text{--}10\text{‰}$) were occupied by carnivorous species, although the transition zone between omnivorous and carnivorous genera was about 4‰ along the $\delta^{15}\text{N}$ axis (from 4.0 to 8.0‰). The range of $\delta^{13}\text{C}$ values in predaceous species of ground beetles was much wider than in omnivorous carabids and exceeded the corresponding range of any other taxonomic group in the studied ecosystems. The lowest $\delta^{13}\text{C}$ values were found in *Calosoma sycophanta*, a monophagous species feeding on gypsy moth caterpillars, which in turn had a very low content of ^{13}C (Figure A3). The range of $\delta^{13}\text{C}$ values of *C. sycophanta* was extremely large, suggesting that these flying beetles could arrive at the site of an outbreak of the gypsy moth from remote habitats. This behavior makes them similar to the burying beetles of the genus *Nicrophorus* described above. Furthermore, *C. sycophanta* were enriched in $\delta^{15}\text{N}$ by about 7‰ compared to gypsy moth caterpillars, which is a considerably larger value than the trophic enrichment usually observed. The highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were observed for ground beetles belonging to the genera *Poecilus*, *Calathus*, *Agonum*, and *Taphoxenus* (Figure A3), which were likely trophically linked to ^{13}C - and ^{15}N -enriched saprophages.

3.3.4. Spiders

Despite a rather large number of species studied (17 species), the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of spiders was very small in comparison with other studied groups. The range of the mean $\delta^{13}\text{C}$ values of individual spiders species was only about 1‰ (from -25.0 ± 0.3 to $-24.0 \pm 0.1\text{‰}$), and approximately 2.5‰ for $\delta^{15}\text{N}$ values (from 5.7 ± 0.5 to $8.3 \pm 0.5\text{‰}$) (see Table A1). The mean $\delta^{13}\text{C}$ values of the spiders occupying different habitats did not differ. The mean $\delta^{15}\text{N}$ values of spiders were significantly ($p < 0.001$) higher at the forest edge and in the steppe than in the forest (Figure 4).

Web-building cribellate spiders (*Titanoeca quadriguttata*, *Agelena labyrinthica*) were less enriched in ^{15}N compared to other species, which could be associated with their predominant feeding on phytophages inhabiting the grass stand. Ambush spiders (*Xysticus ninni*, *Thanatus arenarius*) had average $\delta^{15}\text{N}$ values, while wandering spiders belonging to the families Lycosidae and Gnaphosidae showed both low and high levels of enrichment in ^{15}N (Figure A4).

4. Discussion

We measured the isotopic compositions of generalist predators, as well as their potential prey, plants, and soil in adjacent forest and steppe habitats. Figure 5 shows the general distribution of living and nonliving elements of the studied ecosystems in the isotopic biplot separately for the forest and steppe areas. In both ecosystems, the enrichment in heavy isotopes gradually increased from plants and litter to phytophages, saprophages, and predators. As expected, the content of ^{15}N increased by 2–5‰ per trophic level. The $\delta^{15}\text{N}$ value averaged -1.5‰ in plants, about 3.0 in phytophages, about 5.0 in saprophages, and about 7.0‰ in predators. There was also a noticeable increase in the $\delta^{13}\text{C}$ values from plants to top predators, especially in the steppe ecosystem.

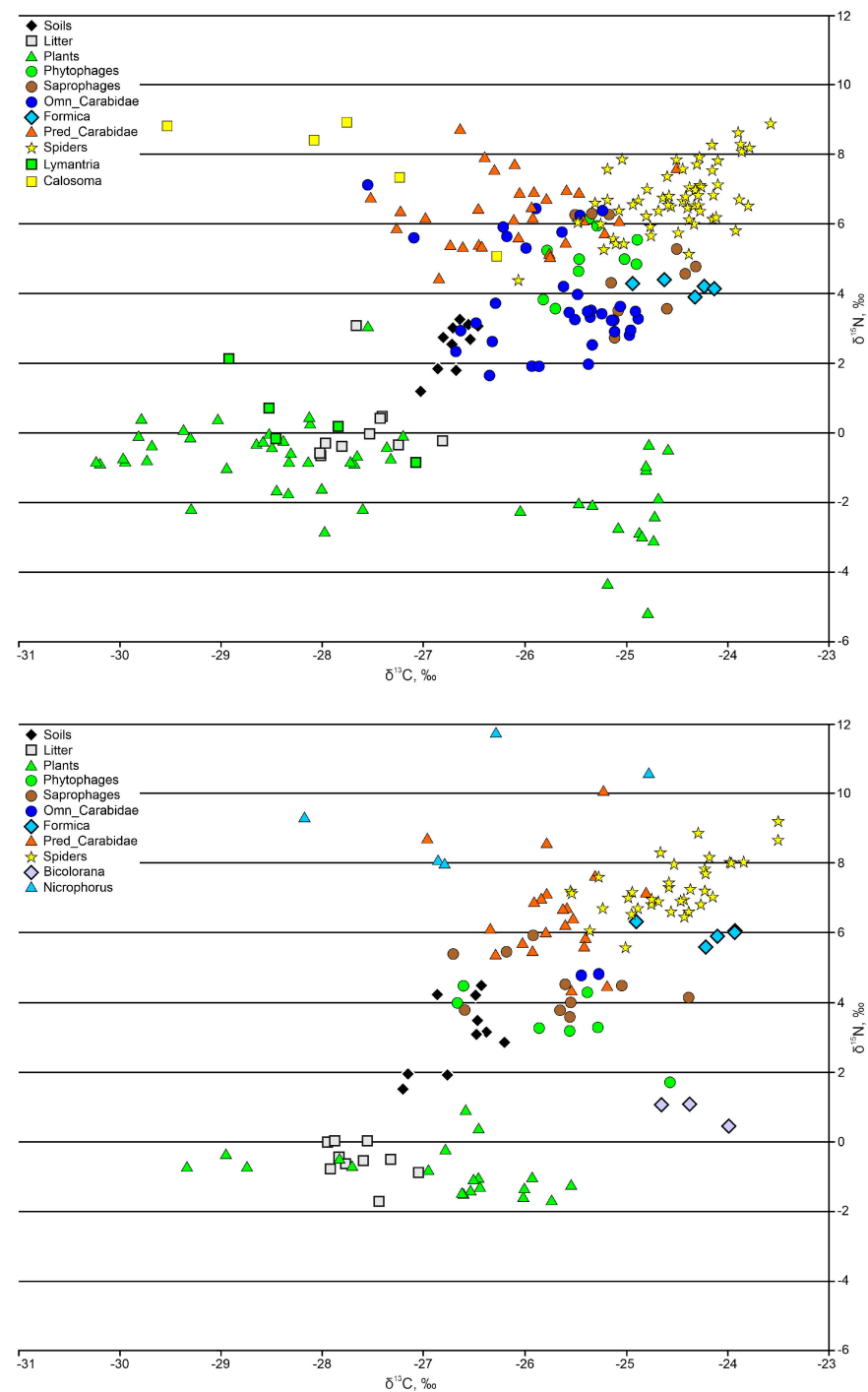


Figure 5. Isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) of soil, plants, litter, and main trophic and taxonomic groups of arthropods in the forest (above) and steppe (below) ecosystems. Each symbol represents one specimen. Omn_Carabidae: omnivorous Carabidae (*Amara* and *Harpalus*), Pred_Carabidae: predaceous Carabidae (other genera).

Plants were relatively depleted in ^{15}N ($\delta^{15}\text{N}$ values typically less than 0‰), with no significant differences in the average $\delta^{15}\text{N}$ values between habitats (Figure 2). This indicates a relatively homogenous “isotopic baseline” of the studied ecosystems. Much larger and more variable $\delta^{15}\text{N}$ values were found in plants growing in the solonchak (salina) ecosystem located 1–2 km from the studied sites, where the $\delta^{15}\text{N}$ values of the steppe vegetation at the edge of the solonchak ranged from 2 to 5‰ [30]. In terms of $\delta^{13}\text{C}$ values, plants from the steppe and ecotone habitats were similar to those described in [30], while forest plants

were, on average, depleted in ^{13}C , although the variation was very large. This is probably a consequence of the so-called canopy effect, i.e., a decrease in $\delta^{13}\text{C}$ values under conditions of shadow photosynthesis [37,38].

Most of the analyzed phytophages probably fed on the analyzed plants, and thus had $\delta^{13}\text{C}$ values similar to those of the plants (Figure 5). Against this background, the larvae of the grasshopper *Bicolorana roeselii* from the steppe habitat appear paradoxical, having a $\delta^{13}\text{C}$ value significantly higher (at the level of saprophages and predators) than its potential food objects. *Formica* ants, which largely obtain carbon from aphids' honeydew, had similar $\delta^{13}\text{C}$ values. Perhaps the grasshoppers in our ecosystem also feed heavily on aphids (aphids were reported in the diet of *B. roeselii*, for example, by [34]). However, aphids of different species and their honeydews can have variable isotopic compositions [39]; moreover, the low $\delta^{15}\text{N}$ values of grasshopper larvae suggest predominant phytophagy. Cases of low enrichment of phytophages in ^{15}N compared to food plants are known, including in aphids [40], but in general, the isotopic composition of grasshopper larvae remains mysterious and may be associated with physiological adaptations. Another unusual phenomenon was the very low $\delta^{13}\text{C}$ values of gypsy moth caterpillars feeding on birch leaves. The content of lipids with a low content of ^{13}C [2] in the tissues of the larvae was not high, as indicated by the C/N ratio similar to those of other animals (6.0 ± 0.6 , data not shown). A similarly low (less than -29.0‰) value of $\delta^{13}\text{C}$ in Lymantriidae caterpillars has already been noted [41].

Red ants (*Formica aquilonia*) were collected in all three studied ecosystems. Ants of this genus in the forest–steppe of the south of western Siberia feed their larvae mainly on invertebrates, while the basic energy source of the imagoes is the honeydew of aphids, i.e., condensed plant sap. Significant differences in the isotopic compositions of ants from different habitats suggest that ant nests occupying different habitats have strictly delimited foraging areas. This is also confirmed by the data obtained for ants at the site of our study in previous years, including with the help of isotopic analysis [39,42]. Among all predators, only ants showed pronounced differences in $\delta^{13}\text{C}$ values between forest and open areas (Figure 4), which confirms a close relationship of ants with plants, which also had increased $\delta^{13}\text{C}$ values in the open habitats (Figure 2).

We attribute the wide variation in $\delta^{13}\text{C}$ values of the burying beetles (*Nicrophorus* sp.) to the fact that these strong fliers could originate from different places where their larvae fed on the corpses of higher animals that differed significantly in isotope composition [43]. Consuming the bodies of animals, mainly small mammals, *Nicrophorus* was also enriched with ^{15}N ; therefore, it was characterized by high concentrations of ^{15}N , similar to those of higher predators.

The $\delta^{15}\text{N}$ values of carabids suggest a wide range of trophic niches corresponding to two or three trophic levels. This is consistent with other studies [15]. Seed-eating omnivores of the genera *Amara* and *Harpalus* had the minimum values of $\delta^{15}\text{N}$, and a greater diversity and abundance of these groups was observed in the forest compared to the steppe area. Most predatory carabids had relatively low $\delta^{13}\text{C}$ values (Figure 5), indicating feeding on phytophages. This was especially true for *Calosoma sycophanta*. For this species, the highest enrichment in ^{15}N compared to the prey was also found. This may have been due to its extremely high food activity (this beetle is able to prey on more than 30 caterpillars per day) and very high metabolic rate, which is also favored by diurnal activity. Low enrichment of ground beetles in ^{13}C suggests that ground beetles (with the exception of individual specimens of *Poecilus fortipes*, *Calathus erratus*, *Agonum gracilipes*, and some others) are predominantly involved in the grazing food chains.

In contrast, spiders had increased $\delta^{13}\text{C}$ values compared to ground beetles, and a relatively narrow range of $\delta^{15}\text{N}$ values. Previously, a much wider variability in $\delta^{15}\text{N}$ values was shown for terrestrial spiders [18,44]. This may be because we collected spiders with pitfall traps, and this limited the set of life forms of spiders available for the stable isotope analysis. In our study, the area occupied by spiders in the isotopic biplot (Figures 5 and A4) almost did not intersect with the area occupied by ground beetles in either the forest or the steppe areas, which may indicate a significant difference in the range of consumed

resources. In particular, high $\delta^{13}\text{C}$ values indicated a closer relationship between spiders and detrital food chains, which are characterized by the enrichment in ^{13}C (so-called detrital shift [2]). It has been shown that closely related species of spiders clearly share their ecological niches, existing in the same habitat [45]. In our case, we had only a slight separation between representatives of different life forms (such as ambushers, stray spiders, and net builders). Therefore, we assume that many species of spiders, representatives of the same life form, draw their food source from a single numerous and diverse group of prey, mainly saprophages.

Comparison of the isotopic niches of ground beetles and spiders generally confirmed our Hypothesis 1, especially for the forest ecosystem. With a somewhat lower species diversity, ground beetles occupied between two and three trophic levels, primarily due to the presence of omnivores (*Amara* and *Harpalus*), while ground spiders occupied not more than two trophic levels. Moreover, our data suggest that phytophages are the main food of carnivorous ground beetles, while spiders have more saprophages in their diet.

Differences in the isotopic composition between different types of habitat were similar in ground beetles and spiders. They were expressed as an increase in the mean $\delta^{15}\text{N}$ values in open habitats compared to forest (Figure 4), although no difference was found in the isotopic compositions of soil and litter (Figure 2). The increased content of ^{15}N in the food web of grassland compared to woodland was previously noted by Crotty et al. [22], but no mechanistic explanation has been proposed. We assumed that the higher activity and abundance of saprophages in the “detrital” forest ecosystem would be reflected in increased $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of generalist predators (Hypothesis 2). However, no significant differences in the $\delta^{13}\text{C}$ values between predators from different habitats were found, and the $\delta^{15}\text{N}$ values, on the contrary, were increased in the steppe compared to the forest. In the case of ground beetles, the relatively low $\delta^{15}\text{N}$ values in the forest can be explained by the high proportion of omnivorous species (Figure A3). However, an increase in the $\delta^{15}\text{N}$ values of spiders in open habitats forced us to reject Hypothesis 2. Increased ^{15}N contents in spiders have several reasons, including features of the dominant types of mycorrhiza [46] and variations in the average length of food chains [47]; however, the available data are insufficient to explain the pattern observed.

Thus, we showed a significant difference in the trophic niches of the key generalist predators, ground beetles and spiders, which was observed both in forest and steppe habitats. Spiders appear to be more closely associated with detrital food webs than ground beetles. Contrary to our expectations, we did not find higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in ground-dwelling generalist predators in the “detrital” forest ecosystem compared to the steppe ecosystem.

Author Contributions: Conceptualization, I.I.L., A.V.T. and V.G.M.; Data curation, A.N.B., A.V.T. and R.Y.D.; Formal analysis, I.I.L. and A.V.T.; Funding acquisition, V.G.M.; Investigation, I.I.L., A.N.B., A.V.T., G.N.A., R.Y.D. and L.V.S.; Methodology, I.I.L., A.V.T. and V.G.M.; Project administration, I.I.L.; Resources, V.G.M.; Software, R.Y.D.; Supervision, A.V.T. and V.G.M.; Validation, A.N.B., A.V.T. and G.N.A.; Visualization, G.N.A. and R.Y.D.; Writing—original draft, I.I.L. and A.V.T.; Writing—review and editing, I.I.L., A.N.B., G.N.A., R.Y.D., L.V.S. and V.G.M. All authors have read and agreed to the published version of the manuscript.

Funding: This study was supported by the Federal Fundamental Scientific Research Program 2021–2025. Institute of Systematics and Ecology of Animals: projects no. 122011800263-6 (I.I.L., V.G.M.) and 1021051703269-9-1.6.12 (G.N.A., R.Y.D.). Institute of Soil Science and Agrochemistry: project no. 121031700309-1 (L.V.S. and A.N.B.). Stable isotope analysis and the work of Alexei Tiunov were partially supported by a grant from the Russian Science Foundation (project No 22-14-00363).

Institutional Review Board Statement: Ethical review and approval were waived for this study due to the study concerned exclusively invertebrates not included in any lists of animals subject to protection.

Informed Consent Statement: Not applicable.

Data Availability Statement: In the A.N. Severtsov Institute of Ecology and Evolution is currently creating a public repository of data on the content of stable isotopes C and N, where we plan to place our data.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, ‰) of soil, plant litter, green parts of the most abundant plant species, and arthropods in the forest (F), ecotone (E), and steppe (S) ecosystems. Mean values \pm 1SE are given.

	^{13}C			^{15}N		
	F	E	S	F	E	S
Soil	-26.70 ± 0.05 $n = 10$	-26.56 ± 0.07 $n = 10$	-26.65 ± 0.11 $n = 10$	2.51 ± 0.22 $n = 10$	3.05 ± 0.12 $n = 10$	3.10 ± 0.33 $n = 10$
Plant litter	-27.58 ± 0.12 $n = 10$	-27.73 ± 0.11 $n = 10$	-27.63 ± 0.09 $n = 10$	0.12 ± 0.35 $n = 10$	-0.01 ± 0.15 $n = 10$	-0.57 ± 0.17 $n = 10$
Plants						
<i>Betula pendula</i>	-29.40 ± 0.21 $n = 10$	-	-	-0.88 ± 0.22 $n = 10$	-	-
<i>Populus tremula</i>	-28.83 ± 0.28 $n = 10$	-	-	-0.90 ± 0.30 $n = 10$	-	-
<i>Rosa majalis</i>	-28.10 ± 0.15 $n = 10$	-	-	-1.50 ± 0.34 $n = 10$	-	-
<i>Rubus saxatilis</i>	-27.70 ± 0.13 $n = 5$	-	-	-3.68 ± 0.47 $n = 5$	-	-
<i>Peucedanum morisoni</i>	-	-27.83 ± 0.30 $n = 10$	-	-	0.09 ± 0.27 $n = 10$	-
Gramineae	-	-27.59 ± 0.29 $n = 10$	-	-	-1.12 ± 0.23 $n = 10$	-
<i>Pedicularis</i> sp.	-	-28.20 ± 0.26 $n = 5$	-	-	-1.24 ± 0.36 $n = 5$	-
<i>Glycyrrhiza glabra</i>	-	-25.54 ± 0.25 $n = 5$	-25.85 ± 0.09 $n = 5$	-	-1.59 ± 0.11 $n = 5$	-1.35 ± 0.11 $n = 5$
<i>Stipa pennata</i>	-	-	-26.60 ± 0.05 $n = 10$	-	-	-0.73 ± 0.26 $n = 10$
Miscellaneous herbs	-	-	-28.52 ± 0.32 $n = 5$	-	-	-0.58 ± 0.07 $n = 5$
Phytophages						
Heteroptera, Miridae	-	-	-25.32 ± 0.22 $n = 5$	-	-	3.12 ± 0.41 $n = 5$
Coleoptera, Curculionidae	-25.52 ± 0.17 $n = 5$	-26.86 ± 0.78 $n = 3$	-26.63 ± 0.03 $n = 2$	2.85 ± 0.34 $n = 5$	2.98 ± 0.59 $n = 3$	4.21 ± 0.26 $n = 2$
Lepidoptera, <i>Lymantria dispar</i> , larva	-28.16 ± 0.32 $n = 5$	-	-	0.38 ± 0.50 $n = 5$	-	-
Omnivores						
Orthoptera, <i>Bicolorana roeselii</i> , larva	-	-24.21 ± 0.19 $n = 5$	-24.34 ± 0.19 $n = 3$	-	-0.29 ± 0.22 $n = 5$	0.86 ± 0.20 $n = 3$
Hymenoptera, <i>Formica aquilonia</i>	-24.93 ± 0.09 $n = 5$	-23.84 ± 0.11 $n = 5$	-24.22 ± 0.18 $n = 5$	4.20 ± 0.08 $n = 5$	4.99 ± 0.10 $n = 5$	5.98 ± 0.12 $n = 5$

Table A1. Cont.

	¹³ C			¹⁵ N		
	F	E	S	F	E	S
Omnivorous carabids						
<i>Amara brunnea</i>	−25.19 ± 0.07 n = 10	-	-	3.29 ± 0.07 n = 10	-	-
<i>Amara communis</i>	−25.71 ± 0.19 n = 10	-	-	2.81 ± 0.20 n = 10	-	-
<i>Amara eurynota</i>	−25.68 ± 0.17 n = 5	-	-	6.07 ± 0.16 n = 5	-	-
<i>Amara bifrons</i>	−26.62 ± 0.30 n = 5	−26.84 ± 0.11 n = 3	-	5.51 ± 0.55 n = 5	5.23 ± 0.35 n = 3	-
<i>Harpalus cisteloides</i>	−25.91 ± 0.28 n = 2	−26.02 ± 0.20 n = 5	-	2.71 ± 0.50 n = 2	5.31 ± 0.73 n = 5	-
<i>Harpalus anxius</i>	-	−25.60 ± 0.21 n = 3	−25.35 ± 0.08 n = 2	-	4.01 ± 0.24 n = 3	4.78 ± 0.03 n = 2
Saprophages						
Coleoptera, Tenebrionidae: <i>Oodescelis polita</i>	−24.91 ± 0.13 n = 10	−24.86 ± 0.18 n = 5	−25.68 ± 0.25 n = 5	3.65 ± 0.33 n = 10	4.42 ± 0.22 n = 5	3.90 ± 0.15 n = 5
Coleoptera, Tenebrionidae: <i>Blaps lethifera</i>	-	−25.81 ± 0.28 n = 5	−25.76 ± 0.39 n = 5	-	3.76 ± 0.37 n = 5	5.06 ± 0.33 n = 5
Coleoptera, Silphidae: <i>Silpha carinata</i>	−24.46 ± 0.15 n = 5	-	-	5.50 ± 0.25 n = 5	-	-
Coleoptera, Silphidae: <i>Nicrophorus</i> sp.	−26.58 ± 0.55 n = 5	-	-	9.54 ± 0.73 n = 5	-	-
Predaceous carabids						
<i>Pterostichus oblongopunctatus</i>	−26.16 ± 0.11 n = 10	-	-	6.39 ± 0.36 n = 10	-	-
<i>Agonum gracilipes</i>	−26.15 ± 0.49 n = 5	−23.60 ± 1.57 n = 2	-	7.15 ± 0.47 n = 5	7.13 ± 0.89 n = 2	-
<i>Carabus marginalis</i>	−26.82 ± 0.28 n = 5	-	-	5.61 ± 0.36 n = 5	-	-
<i>Calathus erratus</i>	−25.65 ± 0.25 n = 5	−25.02 ± 0.21 n = 5	-	6.07 ± 0.26 n = 5	6.99 ± 0.67 n = 5	-
<i>Cymindis angularis</i>	−25.92 ± 0.22 n = 5	−26.44 n = 1	-	6.31 ± 0.27 n = 5	5.18 n = 1	-
<i>Poecilus fortipes</i>	-	−24.99 ± 7.31 n = 10	−25.53 ± 0.22 n = 5	-	0.40 ± 0.20 n = 10	6.83 ± 0.31 n = 5
<i>Poecilus koyi</i>	-	−25.49 ± 0.43 n = 2	−25.80 ± 0.09 n = 8	-	6.58 ± 0.92 n = 2	6.52 ± 0.42 n = 8
<i>Taphoxenus gigas</i>	-	−25.88 n = 1	−25.91 ± 0.54 n = 3	-	7.78 n = 1	8.42 ± 1.07 n = 3
<i>Syntomus truncatellus</i>	-	-	−25.65 ± 0.20 n = 5	-	-	5.38 ± 0.2 n = 5
<i>Calosoma sycophanta</i>	−27.77 ± 0.53 n = 5	-	-	7.70 ± 0.72 n = 5	-	-

Table A1. Cont.

	¹³ C			¹⁵ N		
	F	E	S	F	E	S
Predators: Spiders						
<i>Alopecosa aculeata</i>	−24.27 ± 0.13 n = 8	-	-	6.25 ± 0.17 n = 8	-	-
<i>Alopecosa sulzeri</i>	−24.59 ± 0.20 n = 10	−24.15 ± 0.19 n = 4	−24.44 ± 0.25 n = 5	6.87 ± 0.31 n = 10	7.93 ± 0.34 n = 4	7.22 ± 0.49 n = 5
<i>Alopecosa cuneata</i>	-	−24.23 ± 0.19 n = 5	-	-	6.94 ± 0.28 n = 5	-
<i>Alopecosa cursor</i>	-	-	−24.34 ± 0.05 n = 5	-	-	7.18 ± 0.16 n = 5
<i>Alopecosa taeniata</i>	−24.28 ± 0.05 n = 5	-	-	6.48 ± 0.10 n = 5	-	-
<i>Pardosa lugubris</i>	−24.60 ± 0.10 n = 10	-	-	6.67 ± 0.16 n = 10	-	-
<i>Pardosa schenkeli</i>	-	-	−24.84 ± 0.23 n = 5	-	-	6.72 ± 0.44 n = 5
<i>Xerolycosa miniata</i>	-	−24.77 ± 0.10 n = 10	−24.70 ± 0.18 n = 5	-	7.50 ± 0.35 n = 10	7.22 ± 0.29 n = 5
<i>Trochosa terricola</i>	−24.04 ± 0.10 n = 5	-	-	7.73 ± 0.28 n = 5	-	-
<i>Berlandina cinerea</i>	-	-	−23.97 ± 0.15 n = 5	-	-	8.04 ± 0.36 n = 5
<i>Gnaphosa leporina</i>	-	−24.37 ± 0.15 n = 5	-	-	8.27 ± 0.48 n = 5	-
<i>Haplodrassus signifer</i>	-	−24.55 ± 0.19 n = 5	-	-	7.87 ± 0.23 n = 5	-
<i>Zelotes apricorum</i>	−24.32 ± 0.24 n = 5	-	-	7.88 ± 0.27 n = 5	-	-
<i>Zelotes subterreaneus</i>	−24.80 ± 0.17 n = 5	-	-	7.14 ± 0.32 n = 5	-	-
<i>Agelena labyrinthica</i>	−25.04 ± 0.30 n = 5	-	-	5.67 ± 0.45 n = 5	-	-
<i>Titanoeca quadriguttata</i>	−24.66 ± 0.13 n = 5	−24.68 ± 0.23 n = 3	-	6.10 ± 0.46 n = 5	6.83 ± 0.18 n = 3	-
<i>Thanatus arenarius</i>	-	-	−24.84 ± 0.25 n = 5	-	-	7.69 ± 0.22 n = 5
<i>Xysticus ninnii</i>	-	-	−24.68 ± 0.23 n = 5	-	-	6.80 ± 0.13 n = 5

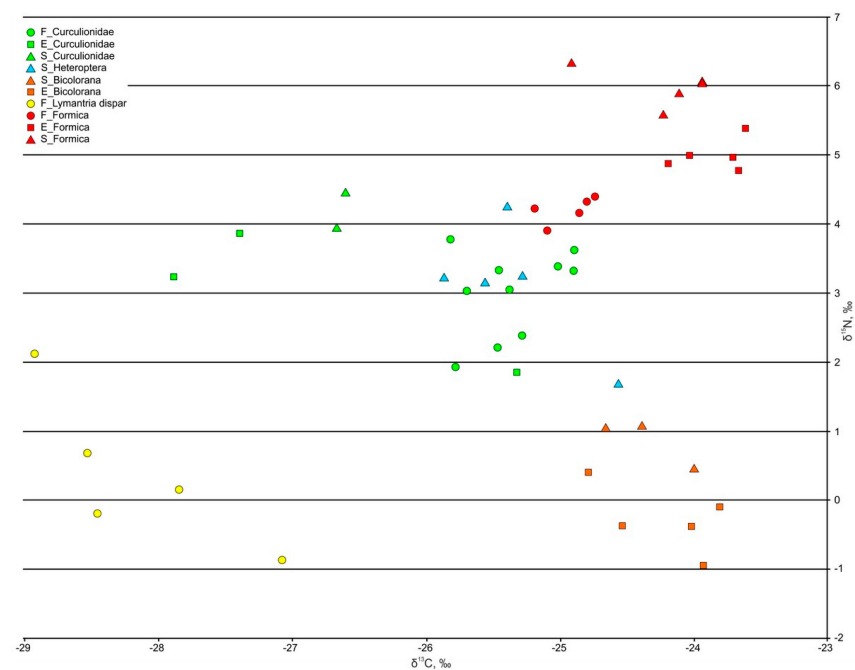


Figure A1. Distribution of phytophagous insects and ants of the studied ecosystems in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ isotopic biplot. Each symbol shows one specimen. F: forest (circles), E: edge (squares), S: steppe (triangles).

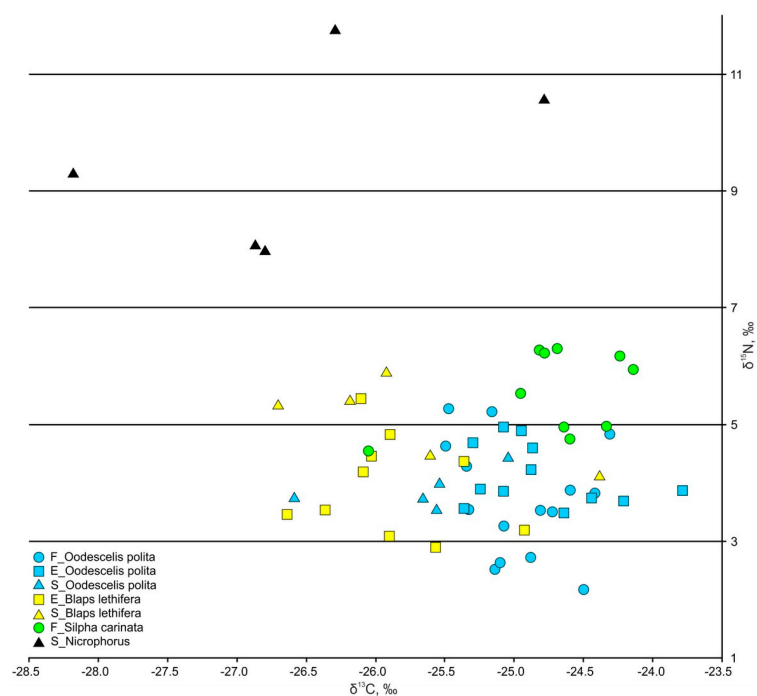


Figure A2. Distribution of saprophagous and necrophagous insects of the studied ecosystems in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ isotopic biplot. Each symbol shows one specimen. F: forest (circles), E: edge (squares), S: steppe (triangles).

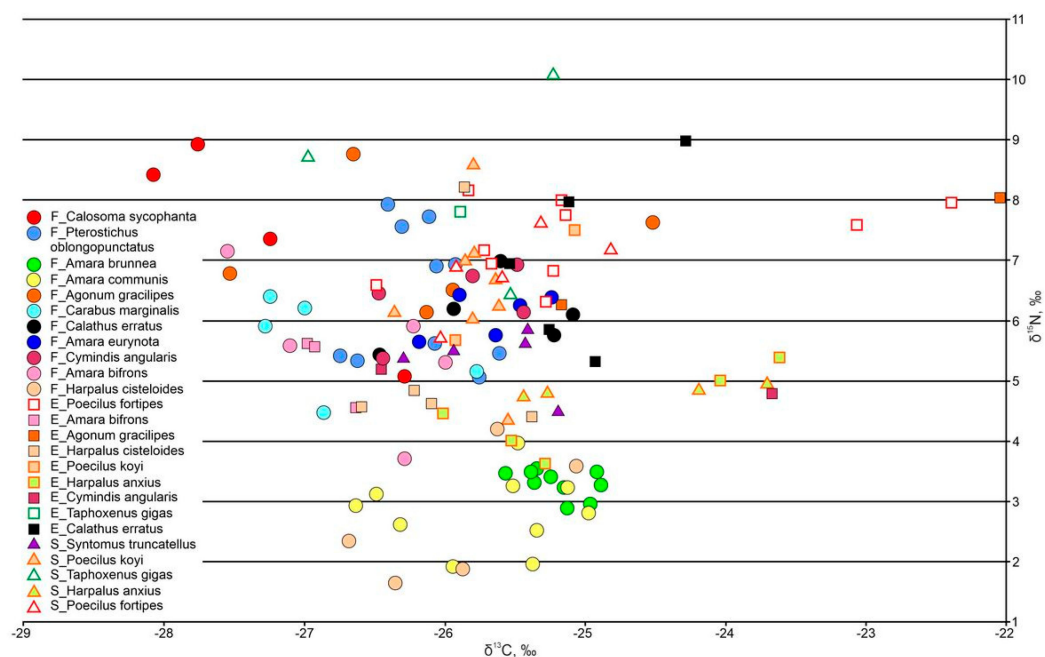


Figure A3. Distribution of carabid beetles of the studied ecosystems in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ isotopic biplot. Each symbol shows one specimen. F: forest (circles), E: edge (squares), S: steppe (triangles).

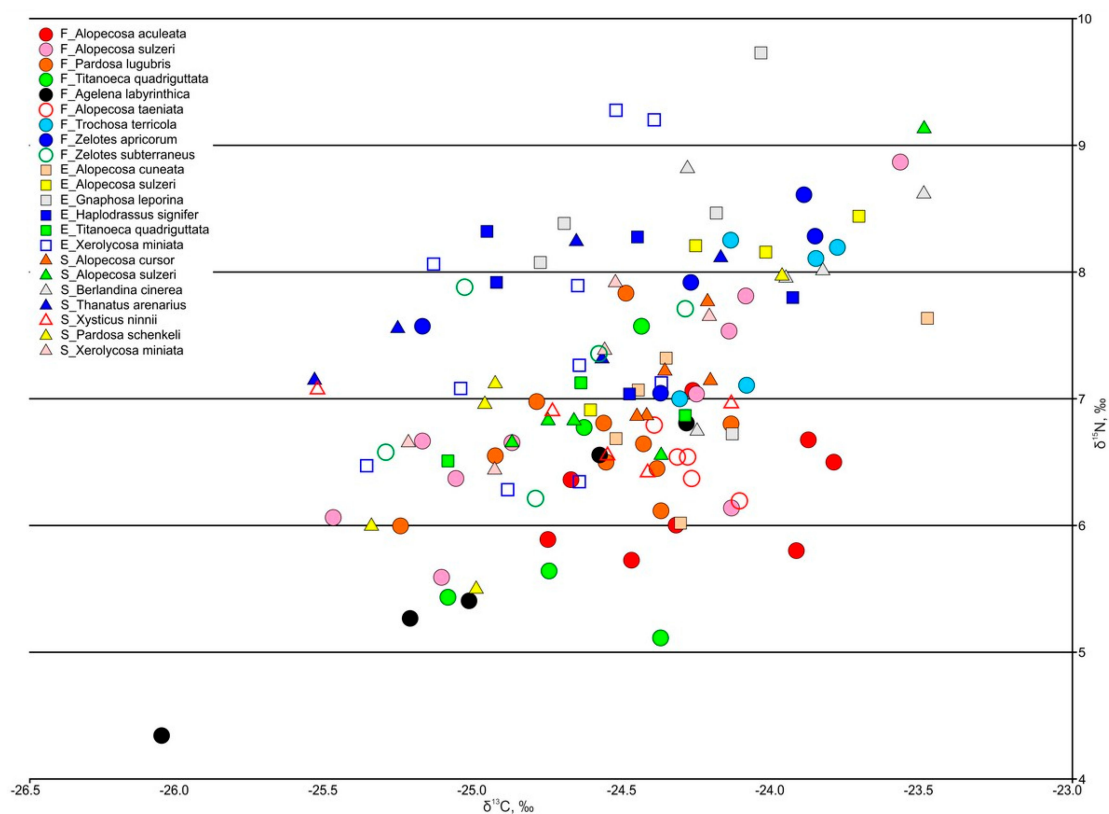


Figure A4. Distribution of spiders of the studied ecosystems in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ isotopic biplot. Each symbol shows one specimen. F: forest (circles), E: edge (squares), S: steppe (triangles).

References

1. Scheu, S. Plants and generalist predators as links between the below-ground and above-ground system. *Basic Appl. Ecol.* **2001**, *2*, 3–13. [\[CrossRef\]](#)
2. Potapov, A.M.; Tiunov, A.V.; Scheu, S. Uncovering trophic positions and food resources of soil animals using bulk natural stable isotope composition. *Biol. Rev.* **2019**, *94*, 37–59. [\[CrossRef\]](#) [\[PubMed\]](#)
3. Korobushkin, D.I.; Gongalsky, K.B.; Tiunov, A.V. Isotopic niche ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) of soil macrofauna in temperate forests. *Rapid Commun. Mass Spectrom.* **2014**, *28*, 1303–1311. [\[CrossRef\]](#)
4. Oelbermann, K.; Scheu, S. Trophic guilds of generalist feeders in soil animal communities as indicated by stable isotope analysis ($^{15}\text{N}/^{14}\text{N}$). *Bull. Entomol. Res.* **2010**, *100*, 511–520. [\[CrossRef\]](#)
5. Talarico, F.; Giglio, A.; Pizzolotto, R.; Brandmayr, P. A synthesis of feeding habits and reproduction rhythm in Italian seed-feeding ground beetles (Coleoptera: Carabidae). *Eur. J. Entomol.* **2016**, *113*, 325–336. [\[CrossRef\]](#)
6. Thiele, H.U. *Carabid Beetles in Their Environments*; Springer: Berlin/Heidelberg, Germany, 1977.
7. Mader, V.; Diehl, E.; Wolters, V.; Birkhofer, K. Agri-environmental schemes affect the trophic niche size and diet of common carabid species in agricultural landscapes. *Ecol. Entomol.* **2018**, *43*, 823–835. [\[CrossRef\]](#)
8. Lundgren, J.G. *Relationships of Natural Enemies and Non-Prey Foods*; Springer International: Dordrecht, The Netherlands, 2009.
9. Zalewski, M.; Dudek, D.; Godeau, J.-F.; Maruszkiewicz, M. Stable isotopic research on ground beetles. Review of methods Baltic. *J. Coleopterol.* **2012**, *12*, 91–98.
10. Okuzaki, Y.; Tayasu, I.; Okuda, N.; Sota, T. Stable isotope analysis indicates trophic differences among forest floor carabids in Japan. *Entomol. Exp. Appl.* **2010**, *135*, 263–270. [\[CrossRef\]](#)
11. Ikeda, H.; Kubota, K.; Kagawa, A.; Sota, T. Diverse diet compositions among harpaline ground beetle species revealed by mixing model analyses of stable isotope ratios. *Ecol. Entomol.* **2010**, *35*, 307–316. [\[CrossRef\]](#)
12. Sasakawa, K.; Ikeda, H.; Kubota, T. Feeding ecology of granivorous carabid larvae: A stable isotope analysis. *J. Appl. Entomol.* **2010**, *134*, 116–122. [\[CrossRef\]](#)
13. Zalewski, M.; Dudek-Godeau, D.; Godeau, J.-F.; Kujawa, K.; Sienkiewicz, P.; Tiunov, A.V.; Ulrich, W. Trophic generalism at the population level in ground beetles (Coleoptera: Carabidae). *Can. Entomol.* **2016**, *148*, 284–293. [\[CrossRef\]](#)
14. Raso, D.; Sint, D.; Mayer, R.; Plangg, S.; Recheis, T.; Brunner, S.; Kaufmann, R.; Traugott, M. Intraguild predation in pioneer predator communities of alpine glacier forelands. *Mol. Ecol.* **2014**, *23*, 3744–3754. [\[CrossRef\]](#) [\[PubMed\]](#)
15. Zalewski, M.; Dudek, D.; Tiunov, A.V.; Godeau, J.-F.; Okuzaki, Y.; Ikeda, H.; Sienkiewicz, P.; Ulrich, W. High niche overlap in the stable isotope space of ground beetles. *Ann. Zool. Fennici.* **2014**, *51*, 301–312. [\[CrossRef\]](#)
16. Den Boer, P.J. Exclusion or coexistence and the taxonomic or ecological relationship between species. *Neth. J. Zool.* **1980**, *30*, 278–306. [\[CrossRef\]](#)
17. Girard, J.; Baril, A.; Mineau, P.; Fahrig, L. Carbon and nitrogen stable isotope ratios differ among invertebrates from field crops, forage crops, and non-cropped land uses. *Ecoscience* **2011**, *18*, 98–109. [\[CrossRef\]](#)
18. Zuev, A.; Heidemann, K.; Leonov, V.; Schaefer, I.; Scheu, S.; Tanasevitch, A.; Tiunov, A.; Tsurikov, S.; Potapov, A. Different groups of ground-dwelling spiders share similar trophic niches in temperate forests. *Ecol. Entomol.* **2020**, *45*, 1346–1356. [\[CrossRef\]](#)
19. McNabb, D.N.; Halaj, J.; Wise, D.H. Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: A stable isotope analysis. *Pedobiologia* **2001**, *45*, 289–297. [\[CrossRef\]](#)
20. Wise, D.H.; Moldenhauer, D.M.; Halaj, J. Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecol. Appl.* **2006**, *16*, 865–876. [\[CrossRef\]](#)
21. Berman, D.I.; Mordkovich, V.G. Entomological features of the polar steppes of Yakutia Bulletin of Moscow Society of Naturalists. *Biol. Ser.* **1979**, *84*, 39–45.
22. Crotty, F.V.; Blackshaw, R.P.; Adl, S.M.; Inger, R.; Murray, P.J. Divergence of feeding channels within the soil food web determined by ecosystem type. *Ecol. Evol.* **2014**, *4*, 1–13. [\[CrossRef\]](#)
23. Mordkovich, V.G.; Khudyaev, S.A.; Dudko, R.Y.; Lyubchanskii, I.I. 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. *Contemp. Probl. Ecol.* **2020**, *13*, 443–468. [\[CrossRef\]](#)
24. Mordkovich, V.G.; Dudko, R.J.; Khudyaev, S.A.; Lyubchanskii, I.I. Changes in the Ground Beetle and Darkling Beetle Communities (Coleoptera: Carabidae, Tenebrionidae) in the Mountain Hollows of the Tuva and Altai Republics over 60 Years: A Trend or a Fluctuation? *Contemp. Probl. Ecol.* **2022**, *15*, 579–596. [\[CrossRef\]](#)
25. Odum, E.P. *Basic Ecology*; W.B. Saunders: Philadelphia, PA, USA, 1983.
26. Hyodo, F.; Kohzu, A.; Tayasu, I. Linking aboveground and belowground food webs through carbon and nitrogen stable isotope analyses. *Ecol. Res.* **2010**, *25*, 745–756. [\[CrossRef\]](#)
27. Lyubchanskii, I.I. Carabid beetles community of the typical habitats in southern forest-steppe (West Siberia). *Euroasian Entomol. J.* **2009**, *8*, 315–318.
28. Lyubchanskii, I.I.; Bepalov, A.N. Spatial Heterogeneity of a Ground Beetle (Coleoptera, Carabidae) Population along a Forest-Steppe Transect: Local Level of Consideration. *Contemp. Probl. Ecol.* **2011**, *4*, 388–395. [\[CrossRef\]](#)
29. Lyubchanskii, I.I.; Azarkina, G.N. Ecological Structure of the West Siberian Forest-Steppe Spider Community (Arachnida, Araneae) and Its Comparison with the Ground-Beetle (Coleoptera, Carabidae) Community. *Contemp. Probl. Ecol.* **2017**, *10*, 164–177. [\[CrossRef\]](#)

30. Lyubechanskii, I.I.; Dudko, R.Y.; Tiunov, A.V.; Mordkovich, V.G. Trophic Structure of Ground-Dwelling Insects in the Coastal Zone of a Salt Lake in Southern Siberia Based on the Data of Isotopic Analysis. *Arid. Ecosyst.* **2015**, *5*, 222–229. [\[CrossRef\]](#)
31. Cernusak, L.A.; Tcherkez, G.; Keitel, C.; Cornwell, W.K.; Santiago, L.S.; Knoch, A.; M Barbour, M.M.; Williams, D.G.; Reich, P.B.; Ellsworth, D.S.; et al. Why are non-photosynthetic tissues generally ^{13}C enriched compared with leaves in C3 plants? Review and synthesis of current hypotheses. *Funct. Plant Biol.* **2009**, *36*, 199–213. [\[CrossRef\]](#)
32. Codron, J.; Codron, D.; Lee-Thorp, J.A.; Sponheimer, M.; Bond, W.J.; de Ruiter, D.; Grant, R. Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from an African savanna. *J. Archaeol. Sci.* **2005**, *32*, 1757–1772. [\[CrossRef\]](#)
33. Lorenz, W. *Systematic List of Extant Ground Beetles of the World (Coleoptera «Geadephaga»: Trachypachidae and Carabidae, inc. Paussinae, Cicindelinae, Rhysodinae)*, 2nd ed.; Lorenz: Tutzing, Germany, 2005.
34. Marshall, J.A.; Haes, E.C.M. *Grasshoppers and Allied Insects of Great Britain and Ireland*; Harley Books: Colchester, UK, 1988.
35. Tsurikov, S.M.; Goncharov, A.A.; Tiunov, A.V. Intra-body variation and ontogenetic changes in the isotopic composition ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) of beetles (Coleoptera). *Entomol. Rev.* **2015**, *95*, 326–333. [\[CrossRef\]](#)
36. Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **2001**, *4*, 9.
37. Brooks, J.R.; Flanagan, L.B.; Buchmann, N.; Ehleringer, J.R. Carbon isotope composition of boreal plants: Functional grouping of life forms. *Oecologia* **1997**, *110*, 301–311. [\[CrossRef\]](#) [\[PubMed\]](#)
38. Tiunov, A.V. Stable isotopes of carbon and nitrogen in soil ecological studies. *Biol. Bull.* **2007**, *34*, 395–407. [\[CrossRef\]](#)
39. Iakovlev, I.K.; Novgorodova, T.A.; Tiunov, A.V.; Reznikova, Z.I. Trophic position and seasonal changes in the diet of the red wood ant *Formica aquilonia* as indicated by stable isotope analysis. *Ecol. Entomol.* **2017**, *42*, 263–272. [\[CrossRef\]](#)
40. Wilson, A.C.C.; Sternberg, L.d.S.L.; Hurley, K.B. Aphids alter host-plant nitrogen isotope fractionation. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 10220–10224. [\[CrossRef\]](#)
41. Rozanova, O.L.; Tsurikov, S.M.; Krivosheina, M.G.; Tanasevitch, A.V.; Fedorenko, D.N.; Leonov, V.D.; Timokhov, A.V.; Tiunov, A.V.; Semenina, E.E. The isotopic signature of the “arthropod rain” in a temperate forest. *Sci. Rep.* **2022**, *12*, 321. [\[CrossRef\]](#) [\[PubMed\]](#)
42. Reznikova, Z.I. *Mezhvidovye Otnosheniya u Muraviev [Interspecific Interactions of Ants]*; Nauka: Novosibirsk, USSR, 1983.
43. Bennett, P.M.; Hobson, K.A. Trophic structure of a boreal forest arthropod community revealed by stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analyses. *Entomol. Sci.* **2009**, *12*, 17–24. [\[CrossRef\]](#)
44. Kudrin, A.A.; Tsurikov, S.M.; Tiunov, A.V. Trophic position of microbivorous and predatory soil nematodes in a boreal forest as indicated by stable isotope analysis. *Soil Biol. Biochem.* **2015**, *86*, 193–200. [\[CrossRef\]](#)
45. Kennedy, S.; Lim, J.Y.; Clavel, J.; Krehenwinkel, H.; Gillespie, R.G. Spider webs, stable isotopes and molecular gut content analysis: Multiple lines of evidence support trophic niche differentiation in a community of Hawaiian spiders. *Funct. Ecol.* **2019**, *33*, 1722–1733. [\[CrossRef\]](#)
46. Mayor, J.R.; Schuur, E.A.; Henkel, T.W. Elucidating the nutritional dynamics of fungi using stable isotopes. *Ecol. Lett.* **2009**, *12*, 171–183. [\[CrossRef\]](#)
47. Post, D.M. The long and short of food-chain length. *Trends Ecol. Evol.* **2002**, *17*, 269–277. [\[CrossRef\]](#)

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.