SOIL ORGANISMS **88** (1) · April 2016 pp. 43–54

The distribution pattern of soil macrofauna at the forest-steppe ecotone of the southernmost boreal forest (Eastern Kazakhstan)

Badamdorj Bayartogtokh[1]*, Ulzhan D. Burkitbaeva[2], Kaman Ulykpan[2], Erdenechuluun Otgonjargal[1] and Asyltan Karim[2]

[1] Department of Biology, School of Arts and Sciences, National University of Mongolia, Ulaanbaatar 210646, Mongolia
[2] Department of Biology and Ecology, Faculty of Natural Sciences, Pavlodar State University, Pavlodar 140008, Republic of Kazakhstan
* Corresponding author, e-mail: bayartogtokh@num.edu.mn

Received 1 August 2015 | Accepted 10 March 2016
Published online at www.soil-organisms.de 1 April 2016 | Printed version 15 April 2016

Abstract

We determined the activity density, population density and family-level diversity of surface-active and soil-inhabiting macrofauna in the forest interior, forest edge and steppe habitats in eastern Kazakhstan, and asked whether there were differences in their assemblages that reflected the soil properties and habitat disturbance (livestock grazing). Overall abundances of the macroarthropod assemblages were similar in most study sites, being significantly different for only some groups, such as Araneae, Chilopoda, Diplopoda, Scarabaeidae and Silphidae. The population densities of soil-inhabiting animals were relatively higher in the forest interior than in the forest edge and steppe. The soil water content has little influence on the total activity density of surface-active macroarthropods or on the population density of soil-inhabiting macrofauna, but we observed significant correlations between soil water content and the activity density of a few individual groups of surface-active arthropods (Carabidae, Staphylinidae, Scarabaeidae, Silphidae). Similar relationships were observed between soil water content and the population density of some soil-inhabiting groups of macrofauna (Araneae, Chilopoda, Curculionidae). The overall activity density of surface-active macroarthropods showed a slight negative correlation with soil bulk density, but significant relationships were found for only some groups (Staphylinidae, Silphidae, Scarabaeidae). The soil bulk density showed no significant relationship with the population density of any group of the soil-inhabiting macrofauna. We could not prove an influence of grazing intensity on the soil macrofauna, because differences in grazing intensity between study sites were not significant.

Keywords Abundance | activity density | community | macroarthropods

1. Introduction

Forest floor and grassland soils at temperate and boreal latitudes harbor abundant and diverse soil faunal communities, but there are marked differences among different kinds of forests and grasslands (Huhta & Räty 2005, Striganova & Poryadina 2004). The boreal forest is one of the most intact major vegetation regions of the Central Asia, which are characterized by sharply varying local climates and aspect-controlled differences in forest types (Hall et al. 1996). As a result, the boreal forest boundary is much more irregular there than on the plains of the Central or Northern Siberia. In Central Asia, both the northern and southern boundaries of the boreal zone are not aligned at the same latitude east to west, which depends mainly on the degree of continentality of the climate (D'Arrigo & Jacoby 1993). In eastern Kazakhstan, where we performed the current research, the Siberian boreal forest reaches its southernmost limits there.

Forest-steppe ecotones feature the co-existence of trees and grasses mainly in the mountain landscapes of Central Asia, and have been used for pasture over thousands of years. Forests in this region have undergone many changes under human influence and are highly

ISSN 1864-6417

fragmented due to fire, logging and livestock breeding (Ishii & Fujita 2013, Lkhagvadorj et al. 2013). Grazing is one of the dominant land uses in Central Asia and herbivores, such as livestock have a significant influence on forest-steppe structure and condition as the result of biomass consumption, urination, defecation and soil compaction. All these processes affect the availability of water or nutrients, which in turn influences the plant community structure and soil conditions (Clapperton et al. 2002). When livestock grazing is intensified, the soil organic matter, mineralisable N and the mean diameter of water stable aggregates decrease, whereas total N and bulk density increase (Dolmaar et al. 1990, Dolmaar & Willms 1998).

Soil animals affect organic matter decomposition, both above- and below-ground, and modify the rates of carbon and nutrient fluxes from detritus pools to the soil (Wardle et al. 2004). They contribute directly to plant litter decomposition, soil formation and nutrient cycling (Beyer et al. 2011).

There is increasing concern about the long-term sustainability of intensive pastoral systems as increased livestock stocking rates can negatively affect soil chemical and physical properties (Schon et al. 2011). Grazing by livestock affects biodiversity in different ways and comparable research into the effect on arthropods shows varying trends. Soil animal diversity and abundance may decline under significant grazing pressure (Clapperton et al. 2002, Battigelli et al. 2003, Kinnear & Tongway 2004). The spatial distribution and diversity of litter dwelling arthropods and nematodes was significantly affected by livestock grazing in moist grassland (Bargett & Cook 1998), whereas Leetham & Milchunas (1985) reported only minor effects of grazing on the abundance and diversity of soil animals in the more arid short-grass steppe in North America. Nevertheless, Leetham & Milchunas (1985) suggested that differences in the quality and quantity of soil organic matter as a result of livestock grazing were likely to have affected soil arthropods. However, most studies show an increase in abundance, biomass and species richness of soil animals under reduced grazing regimes (Dennis et al. 2004, 2008).

Several studies have shown that soil and litter animals are non-randomly distributed and reported the great dependence of their abundance and diversity from the chemical, physical and ecological properties (e.g. soil water content, temperature, prey availability, plant cover etc.) of these compartments (Usher et al. 1982, Scheu & Schäfer 1998). Also, physical and chemical conditions may be different between the edge zone and interior locations of a forest (Raynor 1971, Foggo et al. 2001).

In our study, we determined the abundance and diversity on the family level of macroarthropods and other soil-inhabiting non-arthropod groups, such as earthworms and terrestrial snails (Lumbricidae and Valloniidae) under different habitat conditions and grazing intensities in the forest-steppe ecotones of eastern Kazakhstan.

We addressed the following hypotheses: 1) soil-inhabiting and ground-dwelling macrofaunal community differs among the various habitat types, i.e. the forest-interior, forest-edge and steppe; 2) livestock grazing has a significant negative effect on assemblages of both the soil-inhabiting and surface-active macrofaunas.

2. Materials and methods

2.1. Study area and sample plot selection

Field studies were conducted in the Saur Mountains in the Zaisan District, East Kazakhstan, southeast of Lake Zaisan and ca. 30 km SW of the town of Zaisan. The Saur Mountains have a length of about 110 km, with the southern end of the range reaching northwestern China; the highest elevation reaches 3,816 m a.s.l. (Mount Muz Tau). Geologically they are composed of volcanogenic deposits, shales, limestones, sandstones and granitoids (Gvozdetsky & Mikhailov 1978).

This region represents the southern boundary of the Siberian boreal forest. Vegetation of the study area was dominated by alpine inter-montane meadows and relatively dry mountain steppe. Forests occur on north-facing slopes on the middle and upper parts of the mountain slopes, above an elevation of ca. 1,600 m a.s.l., and are mainly formed by Siberian larch (*Larix sibirica* Ledeb.). Lower on the north-facing slope as well as on the south-facing slope there are steppes. Annual precipitation in the study area is roughly 320 mm with a clear peak in summer. The mean July temperature is 23°C, whereas January temperatures are around -17°C (Hauck et al. 2014; http://moxnpn.ru/kazakhstan/80-saur-tarbagataj.html).

Six study sites were chosen on the northern flank of the mountain range; their geographical position and elevation are compiled in Table 1. Site selection was a non-random procedure, being based on their geographical location, topography and vegetation characteristics. The mutual distances between neighboring sites were nearly identical, all about 2–2.5 km.

Moist depressions occurring locally on the mountain slopes were deliberately avoided to improve the comparability among sites. Sites were sampled during the last three weeks of July 2011.

In each sampling site, three plots were selected (each with about 400 m^2 area). The first plot was located at the edge of the forest, covering 0–20 m area from the forest edge to its interior (hereafter referred as forest edge); the second plot was located 100 m deep in the forest to its beginning (hereafter referred as forest interior); the third plot was located in the steppe 100 m in front of the forest edge.

2.2. Sampling and processing

The samples were taken separately from non-randomly selected locations that seemed to represent the typical character of the study plot. For the collection of soil-inhabiting macrofauna (hypogaeic) 25 × 25 cm blocks of soil samples were taken (eight blocks from each plot, July 2011), to a depth of 10 cm (referred to as the density-based quadrate estimator); animals were collected by hand sorting in the field. In addition, surface-active macroarthropods (epigaeic) were collected using pitfall traps made of plastic buckets (16 cm in depth, 17 cm in aperture), each buried to its upper margin in soil. Traps were filled to 4 cm depth with water to which a few drops of detergent had been added as a wetting agent. In each plot, 25 traps were placed in quadrangular configuration, covered with a non-transparent plastic roof to avoid flooding by rain. Trapped specimens were retrieved after ca. 24 hours on the following day between 9:30 to 11:30 for five consecutive days. Animals in both types of samples were hand sorted and identified to the family level in the laboratory using a dissecting microscope. We used the term ‘activity density’ for data of surface-active animals derived from pitfall trap catches, and ‘population density’ for data of soil-inhabiting animals derived from soil quadrate sampling. Assignation of taxa to a trophic group was based on published information (e.g. Moore et al. 1988, Striganova & Poryadina 2004) and observations at the study site (Tab. 2).

At the same sampling time, soil moisture at depth of 10 cm was measured using Theta Kit, HH2 Moisture Meter (Delta-t Devices, Cambridge, England). Parallel series of soil samples were collected to determine bulk density (five samples from each plot). The soil bulk density (dry bulk density) was determined using a soil corer with 125 cm^3 volume, measured dry weight of soil samples, and calculated weight per volume. For a rough assessment of grazing intensity, the number of livestock dung droppings within each plot was counted with five replications (Tab. 1). In the study area, livestock was dominated by sheep, cattle and horses.

2.3. Data analysis

Data were tested for normal distribution with the Kolmogorov-Smirnov test using software Statistica 5.0 (StatSoft 1995). Differences in macrofaunal activity density among the sites and habitat types (forest interior, forest edge and steppe) were tested with two-way analysis of variance (ANOVA) followed by Duncan’s multiple range test. The data were *ln*-transformed prior to the analyses. Multiple linear regression was used to test for a relationship between macroarthropod activity

Table 1. Location of study sites, soil characteristics and dung density as a measure of land-use pressure (mean ± SE).

Square	Habitat*	Sites					
		1	2	3	4	5	6
Latitude (N)		47°15’851”	47°15’783”	47°15’850”	47°16’618”	47°16’991”	47°15’489”
Longitude (E)		84°54’996”	84°55’703”	84°55’491”	84°53’448”	84°053’244”	84°56’065”
Altitude, m a.s.l.		1669	1773	1748	1680	1662	1735
Soil water content, %	FI	37 ± 2.1	24 ± 2.3	27 ± 4.2	28 ± 1.3	25 ± 1.3	14 ± 0.8
	FE	36 ± 3.1	32 ± 4.9	34 ± 1.6	39 ± 3.1	18 ± 1.3	23 ± 1.2
	ST	38 ± 2.6	36 ± 2.2	30 ± 1.3	30 ± 1.4	24 ± 2.1	21 ± 1.6
Soil bulk density, g cm^{-3}	FI	78 ± 8.1	57 ± 5.1	54 ± 3.3	66 ± 6.6	87 ± 7.5	121 ± 10.1
	FE	71 ± 4.5	69 ± 7.3	57 ± 2.1	60 ± 6.1	99 ± 4.6	96 ± 8.1
	ST	85 ± 5.9	63 ± 4.6	67 ± 5.1	65 ± 7.9	140 ± 16.9	116 ± 8.8
Dung abundance, 10 m^{-2}	FI	0.8 ± 0.3	1.2 ± 0.6	2.4 ± 0.5	2.8 ± 0.6	1.4 ± 0.5	2.4 ± 0.7
	FE	3.0 ± 0.7	8.2 ± 3.6	6.0 ± 1.1	4.4 ± 0.7	8.2 ± 2.7	8.6 ± 0.5
	ST	6.6 ± 0.8	8.6 ± 2.1	22.4 ± 4.5	12.6 ± 2.1	10.8 ± 1.2	9.4 ± 2.1

*FI – forest interior; FE – forest edge; ST – steppe.

density and the measured soil properties and dung density (Tab. 1). Population densities of soil macrofauna were calculated by extrapolation from the soil samples collected. The data from all soil samples were summed and the results were transformed into numbers per square meter. Both, pitfall trap and quadrate sampling data were used for trophic guild analysis based on Duncan's multiple range test. The influence of particular factors (soil moisture, bulk density, grazing) on the activity density and population density of soil animals was analyzed by Pearson's product-moment correlation coefficient. Arithmetic means ± standard errors are presented throughout the paper, and were calculated with SAS 6.04 software (SAS Institute Inc., Cary, North Carolina, USA).

3. Results

3.1. General results

A total of 7383 individuals of soil macroinvertebrates belonging to 10 orders and 22 families was collected, 1429 of which derived from the density-based quadrate sampling (soil cores), whereas 5954 individuals were collected with the activity-based pitfall traps.

3.2. Activity density of macroarthropods derived from pitfall traps

At the order level, the two most abundant arthropod taxa in the pitfall traps were Araneae and Coleoptera, which collectively represent more than 80% of the total catch in each studied habitat (Tab. 2). Thus, there were very low activity densities of all other orders. The activity densities of Araneae, Chilopoda and Diplopoda were significantly different among some of the habitats (Fig. 1).

At the family level, a few families of beetles (Carabidae, Staphylinidae, Silphidae) were codominant in the pitfall traps, collectively forming more than 60% of the total catch (Tab. 2). Among the Coleoptera, 35%, 37% and 45% were ground beetles (Carabidae) from the steppe, forest edge and forest interior catches, respectively, whereas the rove beetles (Staphylinidae) comprise 48%, 37% and 30% of the respective total catches. Carrion beetles (Silphidae) were less often caught in the steppe habitats (2.5% of all beetles) than in the forest edge (5.7%) or the forest interior (8.5%). Activity densities of the other beetle families were very low.

The steppe plot of study site 4 was richest in surface-active macroarthropod assemblages with 600±12 catches, more than 74% of which were composed by beetles of the families Carabidae and Staphylinidae, and ground-

Table 2. Soil animal assemblages collected through pitfall trapping from different habitats in forest-steppe ecotone (sum of individuals).

Orders and families	**Number of individuals**			**% of total catch**	**Trophic guild**
	Forest-interior	Forest-edge	Steppe		
Haplotaxida: Lumbricidae	18	19	41	1.3	soil-feeder
Araneae: multiple fam.	113	306	361	13.1	predator
Chilopoda: multiple fam.	194	137	23	5.9	predator
Diplopoda: multiple fam.	57	6	13	1.3	decomposer
Homoptera: Aphididae	2	0	6	0.1	herbivore
Hemiptera: Cydnidae	4	21	43	1.1	herbivore
Coleoptera: Carabidae	660	587	496	29.3	predator
Coleoptera: Silphidae	160	121	36	5.3	decomposer
Coleoptera: Anobiidae	25	43	78	2.4	herbivore
Coleoptera: Leiodidae	15	13	7	0.6	scavenger
Coleoptera: Staphylinidae	443	584	679	28.6	predator/decomposer
Coleoptera: Scarabaeidae	43	65	19	2.1	scavenger/humivore
Coleoptera: Elateridae	1	67	5	1.2	herbivore
Coleoptera: Tenebrionidae	3	12	2	0.3	scavenger/decomposer
Coleoptera: Chrysomelidae	13	7	7	0.4	herbivore
Coleoptera: Curculionidae	19	47	38	1.7	herbivore
Other Coleoptera	94	36	56	3.1	
Diptera: Tipulidae	8	16	83	1.8	herbivore
Pulmonata: Valloniidae	0	0	2	0.03	herbivore

dwelling spiders (Araneae). Four other plots, namely the forest edge of study site 3, the forest interior of study site 5 as well as the steppe and the forest edge plots of study site 1 were characterized by relatively high macroarthropod activity densities with more than 430 ± 14 individuals per five days catch. In these plots, the above-mentioned three codominant groups represented more than 67% of the total captures. The forest interior plots of study sites 1 and 6, the steppe plots of sites 3 and 6, and the forest edge of site 4 had the lowest abundance of surface-active macroarthropods. Except for the forest edge and the forest interior of study site 6, where beetles of the family Silphidae were dominant, the representatives of the Carabidae, Staphylinidae and Araneae formed more than half of the total catches from all other study plots. Notwithstanding the dominance of these groups, representatives of the Chilopoda and Diplopoda were found on the forest edge and forest interior plots of most sites, though they occurred in low abundance. Two-way ANOVA showed that there were significant differences in the activity densities of Araneae, Chilopoda and Diplopoda between the habitat types (Tab. 3).

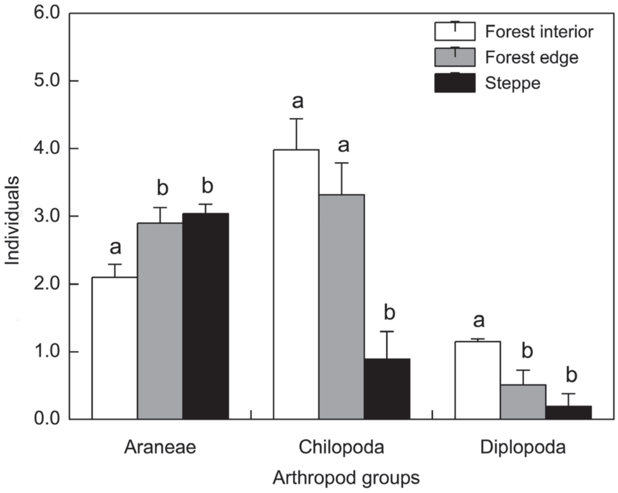

Figure 1. Activity density of selected arthropod groups (mean individuals per trap) in different habitats (forest interior, forest edge, steppe) of the forest-steppe ecotone. Within an arthropod group, means (±SE) marked with the same letter do not differ significantly (Duncan's multiple range test, $p < 0.05$, $df = 15$).

3.3. Frequency of the macroarthropod taxa in pitfall traps

The highest frequency of occurrence – expressed as the proportion of pitfall traps in which the taxon was found – was recorded for taxa belonging to Coleoptera (Carabidae, Staphylinidae, Silphidae, Anobiidae), Araneae (e.g. Lycosidae, Thomisidae, Salticidae), Chilopoda and Diplopoda. The ground-dwelling Homoptera (Aphididae) and Pulmonata (Valloniidae) showed the lowest frequencies (Fig. 2). In addition to Araneae and Coleoptera, species of Chilopoda and Diplopoda were highly frequent in the forest interior plots, whereas species of Hemiptera were most frequent in the steppe plots.

3.4. Population density of soil-inhabiting macrofauna derived from quadrate sampling

Diplopoda, Chilopoda, Carabidae, Staphylinidae, Diptera, Valloniidae and Lumbricidae showed distinctly higher densities in the forest interior than in the forest edge and steppe (Tab. 4), but the differences were significant only for Diplopoda and Valloniidae. A distinctly higher mean number of soil animals was collected from the forest interior of study site 1 and the steppe of study site 4 compared to the other plots. The forest interior of study

Table 3. Results of two-way ANOVA quantifying the effects of the habitat (forest interior, forest edge, steppe) and the site (six replicates) on the activity density of selected arthropod groups.

Orders or families	**Total (*df* = 7)**			**Habitat (*df* = 2)**		**Site (*df* = 5)**	
	R²	*F*	*P*	*F*	*P*	*F*	*P*
Araneae: multiple fam.	0.77	4.81	0.01	9.98	**0.004**	2.74	0.08
Chilopoda: multiple fam.	0.75	4.34	**0.01**	12.75	**0.002**	0.98	0.47
Diplopoda: multiple fam.	0.77	4.97	0.01	11.53	**0.002**	2.34	0.11
Coleoptera: Carabidae	0.60	2.22	0.12	1.45	0.27	2.52	0.09
Coleoptera: Silphidae	0.69	3.21	0.05	3.34	0.07	3.16	0.05
Coleoptera: Anobiidae	0.62	2.38	0. 10	2.31	0.15	2.40	0.11
Coleoptera: Staphylinidae	0.54	1.70	0.21	0.55	0.59	2.16	0.14
Coleoptera: Scarabaeidae	0.80	5.78	**0.007**	1.64	0.24	7.43	**0.004**
Coleoptera: Curculionidae	0.61	2.28	0.11	0.73	0.50	2.90	0.07
Diptera: Tipulidae	0.53	1.63	0.23	1.38	0.29	1.72	0.21
Total	**0.17**	**0.29**	**0.94**	**0.20**	**0.82**	**0.33**	**0.88**

site 1 hosted large numbers of Carabidae, Chilopoda, Lumbricidae and Valloniidae, whereas the steppe of study site 4 harbored large numbers of Formicidae, Curculionidae, Lumbricidae and larvae of Carabidae. Though ants (Formicidae) were not captured in the pitfall traps, they composed more than 37% of mean total individuals in the soil quadrate samples from steppe. The forest edge and steppe plots of the study sites 1 and 6 exhibited much lower population densities of soil animals than the other plots ($p < 0.05$).

3.5. Trophic guild analysis

In the trophic guild analysis, we included soil feeders and decomposers in scavengers as they generally feed on dead organic matter. Across the habitats, predators were more abundant in the soil samples than herbivores and scavengers, though this trend was only statistically significant for the difference between predators and herbivores (Duncan's multiple range test, $p < 0.05$).

The trophic guilds did not differ much in activity density among the habitats (Fig. 3A–C), except for the herbivores, which were less active in the forest interior than at the forest edge and in the steppe (Fig. 3A). If population densities are considered instead of activity densities, all trophic guilds tended to be more abundant in the forest interior than in the other habitats (Fig. 3D–F); in the case of predators, this tendency was statistically significant (Fig. 3E).

3.6. Effects of soil properties

The overall activity density of surface-active macroarthropods and population density of the soil macrofauna were not significantly correlated with the soil water content. However, significant relationships were observed between soil water content and some surface-active beetle families (Tab. 5). These correlations were partly positive (Staphylinidae, Carabidae) and partly negative (Scarabaeidae). Population density was significantly correlated to soil water content in Chilopoda (forest edge, positive correlations), Araneae (forest interior, positive correlations) and the Curculionidae (forest interior, negative correlation) (Tab. 6).

The overall abundance of surface-active macroarthropods as well as the soil animal population density showed no correlation with soil bulk density. Among the surface-active beetles, soil bulk density had a strong negative effect on the activity density of Staphylinidae at the forest edge, but a positive effect on the activity density of Silphidae in the forest interior as well as on the Scarabaeidae in the forest edge and steppe habitats (Tab. 5). In contrast

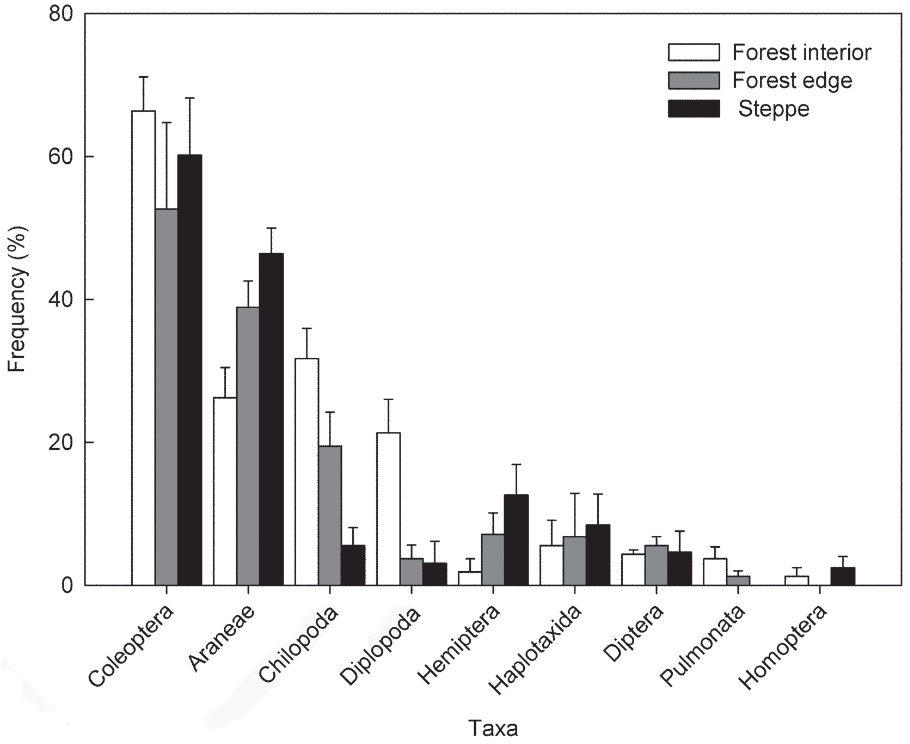

Figure 2. Frequency (percentage of occurrence) of surface-active animals collected in the forest interior, the forest edge and the steppe using pitfall traps (bars indicate standard errors).

Table 4. Population density of soil animals (derived from soil quadrate sampling) in the forest-interior, forest-edge and steppe (mean ± SE).

Orders and families	Density (individuals/m^2) Forest-interior	 Forest-edge	 Steppe
Oligochaeta: Lumbricidae	54.2 ± 6.7	38.7 ± 6.2	30.7 ± 11.0
Araneae: multiple fam.	13.3 ± 4.4	10.7 ± 5.3	10.7 ± 4.9
Chilopoda: multiple fam.	26.2 ± 7.6	8.0 ± 3.5	9.8 ± 7.1
Diplopoda: multiple fam.	20.0 ± 11.4	8.8 ± 4.0	2.8 ± 2.6
Hemiptera: Cydnidae	0	2.8 ± 2.6	4.2 ± 3.9
Hymenoptera: Formicidae	2.8 ± 2.6	10.7 ± 7.9	48.0 ± 32.7
Coleoptera: Carabidae	74.7 ± 20.1	20.5 ± 8.4	24.0 ± 12.9
Coleoptera: Staphylinidae	56.5 ± 11.6	15.5 ± 5.3	24.0 ± 10.0
Coleoptera: Scarabaeidae	0	0	5.5 ± 5.3
Coleoptera: Elateridae	0	2.8 ± 2.6	2.8 ± 2.6
Coleoptera: Tenebrionidae	13.3 ± 2.6	5.5 ± 5.3	2.8 ± 2.6
Coleoptera: Chrysomelidae	2.8 ± 2.6	5.5 ± 5.3	8.0 ± 5.4
Coleoptera: Curculionidae	10.7 ± 5.3	32 ± 9.2	26.2 ± 8.8
Other Coleoptera	24.0 ± 7.6	15.3 ± 5.5	21.3 ± 8.0
Diptera: Tipulidae	90.2 ± 55.8	35.2 ± 16.0	19.7 ± 4.3
Pulmonata: Valloniidae	25.3 ± 8.8	8.0 ± 3.5	0

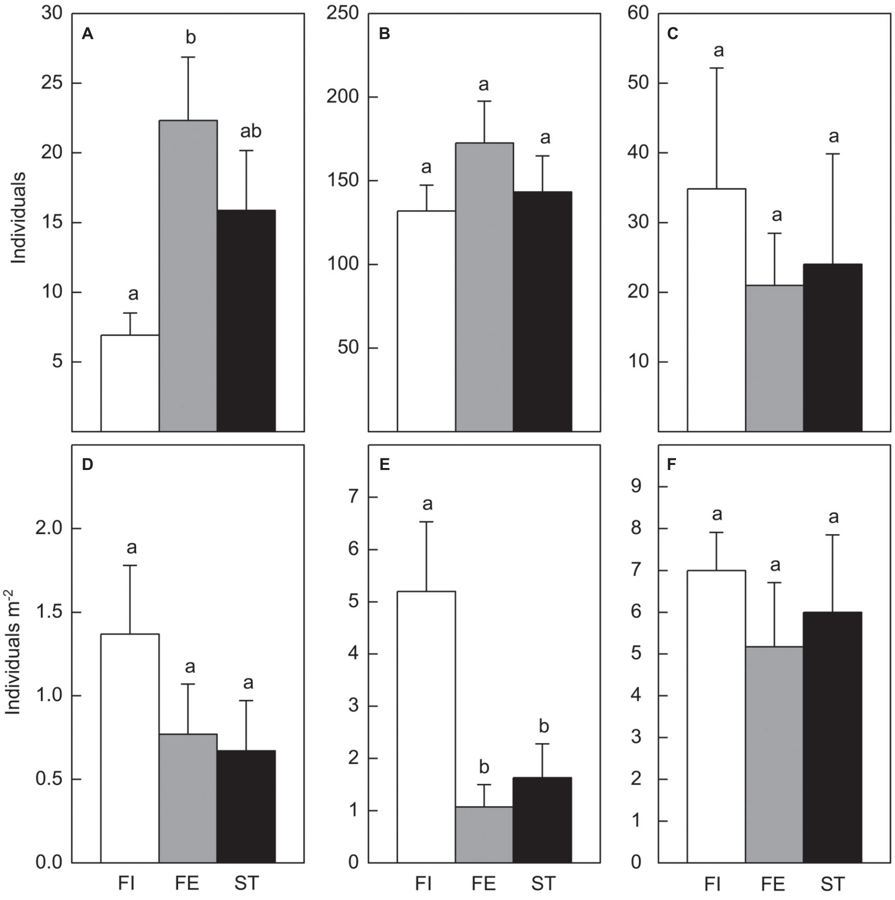

Figure 3. (**A–C**) Mean activity density (individuals per trap, **A–C**) and mean population density (individuals per m^2, **D–F**) of trophic guilds [herbivores (**A**, **D**), predators (**B**, **E**) and scavengers (**C**, **F**)] in the different habitat types [forest interior (FI), forest edge (FE), steppe (ST)] of the forest-steppe ecotone. Within a trophic guild, means (±SE) marked with the same letter do not differ significantly (Duncan's multiple range test, $p < 0.05$, $df = 15$).

to activity densities, soil bulk density had no significant relationship with population density of any group of soil-inhabiting macrofauna (Tab. 6).

3.7. Effects of grazing

The livestock dung density (used as a measure of grazing intensity) did not significantly differ among the habitats or the individual study sites. The activity densities of surface-active arthropods (Staphylinidae, Carabidae and total) significantly decreased with increasing dung density in the forest-edge (Tab. 5). The population density of the Chilopoda in the forest edge had a strong negative correlation with dung density, whereas the density of the Carabidae significantly increased with dung density in the steppe (Tab. 6).

Multiple regression analysis showed the occurrence of combined effects of soil water content, soil bulk density and dung density on the activity densities of some groups of macroarthropods (e.g. Scarabaeidae, Silphidae, Staphylinidae, Chilopoda, Diplopoda and larvae of Diptera) (Tab. 7).

4. Discussion

The community of surface active arthropods in our study site has a few abundant taxa at both the order and family levels, such as Araneae (e.g. Lycosidae, Thomisidae and Salticidae) and Coleoptera (Carabidae, Staphylinidae and Silphidae). Similar community patterns were found in other semiarid and arid regions (Bromham et al. 1999, Seymour & Dean 1999, Cheli et al. 2009). Furthermore, there were some moderately abundant groups (Chilopoda, Cydnidae, Scarabaeidae, Curculionidae, Anobiidae, Leiodidae), and a rather large proportion of 'rare' taxa (Valloniidae, Aphididae, Dermestidae, Tenebrionidae, Chrysomelidae, Histeridae), for which very few individuals were caught through pitfall traps.

In comparison to their relatively low frequency of capture in pitfall traps, the true soil-inhabiting groups, such as earthworms (Lumbricidae), millipedes (Diplopoda), snails (Valloniidae) and larvae of different flies (Diptera) were abundantly represented in the soil quadrate samples, which was to be expected because of their cryptic nature and underground lifestyle habits. The population density of soil-inhabiting animals, such as ground beetles (Carabidae), rove beetles (Staphylinidae) and millipedes (Diplopoda), was significantly higher in most forest interior and steppe plots than in the forest edge. Thus our hypothesis 1, suggesting a difference of community of soil-inhabiting and surface-active macroinvertebrates in various habitat types could be partly verified. It is well known that the diversity and abundance of soil animal communities are influenced by vegetation, soil properties, food resources, and tree stand density (Scheu et al. 2003, Huhta & Räty 2005, Napierała et al. 2009). Among these factors, the vegetation structure usually provides the habitat template for the assembly of surface-active arthropods in multitrophic communities by offering shelter, food resources, oviposition microsites and refuge against predators (Dennis et al. 1998, Seymor & Dean 1999). In the Saur Mountains, the diversity of vascular plants influences specifically the assemblages of surface-active macroarthropods (Hauck et al. 2014), as demonstrated by Dennis et al. (2001) and Cole et al. (2005) in other areas.

Although we expected significant effects of soil properties (water contents and bulk density) on the assemblages of both soil-inhabiting and surface-active macrofauna, this was observed only for few groups, such as Staphylinidae, Carabidae, Scarabaeidae, Chilopoda, Diplopoda, Araneae and larvae of Diptera. Thus, our results are consistent with those of Vannier (1971), Villani & Wright (1990) and Huhta & Hänninen (2001) in that some groups of soil animals might not suffer from low soil moisture under field conditions; in the above-mentioned studies, the moisture regimes were not critical for soil arthropods. It should be noted here that soil water content fluctuates frequently depending on precipitation, but there was no rainfall during the three weeks of our field survey.

The overall activity density of surface-active arthropods showed negative correlations with soil bulk density. We suppose that the soil bulk density affects even the surface-active arthropods as they use soils for temporary inhabiting, sheltering, food resources, oviposition etc. However, the activity-densities of a few other groups, such as the Silphidae in the forest interior, the Scarabaeidae at the forest edge and in the steppe, showed significant positive correlations with soil bulk density. Surprisingly, there were no significant relationships between the population density of soil-inhabiting animals and the soil bulk density. Thus, the soil bulk density has only little influence on the both surface-active and soil-inhabiting macrofauna (except for Silphidae and Scarabaeidae), and it might be explained that this soil property is less important as demonstrated by Hossain et al. (2002) and Birkhofer et al. (2012) in other areas. Additionally, Villani & Wright (1990) noted that the primary soil textural units may not completely explain the activities of macroscopic soil organisms.

It is well known that grazing by large herbivores alters physical and chemical properties of soils (Harrison & Bardgett 2008), but it depends on the grazing intensity.

Table 5. Pearson correlation coefficients for the relationship of the activity density of selected beetle groups with dung density, soil bulk density and soil moisture (numbers in bold are significant values and the *p* value is in brackets).

Orders and families	**Forest interior**			**Forest edge**			**Steppe**		
	Dung density	Soil density	Soil moisture	Dung density	Soil density	Soil moisture	Dung density	Soil density	Soil moisture
Coleoptera: Scarabaeidae	-0.03 (0.97)	0.61 (0.20)	-0.46 (0.36)	0.71 (0.12)	**0.95** **(0.004)**	**-0.95** **(0.004)**	0.05 (0.93)	**0.91** **(0.01)**	**-0.86** **(0.03)**
Coleoptera: Silphidae	0.31 (0.55)	**0.89** **(0.02)**	**-0.84** **(0.04)**	0.45 (0.37)	0.62 (0.19)	-0.45 (0.37)	-0.61 (0.20)	-0.20 (0.70)	0.18 (0.74)
Coleoptera: Staphylinidae	0.15 (0.78)	-0.61 (0.20)	-0.06 (0.91)	**-0.82** **(0.05)**	**-0.82** **(0.05)**	**0.84** **(0.04)**	-0.27 (0.60)	-0.33 (0.52)	0.79 (0.06)
Coleoptera: Carabidae	-0.03 (0.96)	-0.06 (0.92)	0.03 (0.96)	**-0.92** **(0.009)**	-0.74 (0.09)	**0.85** **(0.03)**	0.008 (0.99)	0.40 (0.44)	-0.27 (0.62)
Total	0.17 (0.75)	0.46 (0.36)	-0.77 (0.07)	**-0.82** **(0.05)**	**-0.88** **(0.02)**	**0.91** **(0.01)**	-0.26 (0.62)	0.22 (0.68)	0.28 (0.59)

Note: Groups without significant correlations are not included in the table (Chilopoda, Diplopoda, Diptera, Araneae, Curculionidae and Anobiidae).

Table 6. Pearson correlation coefficients for the relationship of population density of the selected arthropod groups with dung density, soil bulk density and soil moisture (numbers in bold are significant values and the *p* value is in brackets).

Orders and families	**Forest interior**			**Forest edge**			**Steppe**		
	Dung density	Soil density	Soil moisture	Dung density	Soil density	Soil moisture	Dung density	Soil density	Soil moisture
Araneae: multiple fam.	-0.17 (0.74)	-0.54 (0.28)	**0.81** **(0.05)**	-0.15 (0.78)	-0.57 (0.24)	0.34 (0.52)	0.58 (0.23)	-0.62 (0.19)	0.36 (0.48)
Chilopoda: multiple fam.	-0.50 (0.31)	-0.56 (0.25)	0.29 (0.58)	**-0.91** **(0.01)**	-0.76 (0.08)	**0.82** **(0.05)**	-0.44 (0.38)	-0.14 (0.79)	0.62 (0.19)
Coleoptera: Carabidae	0.40 (0.43)	-0.36 (0.49)	0.35 (0.49)	-0.02 (0.97)	-0.68 (0.14)	0.40 (0.43)	**0.88** **(0.02)**	-0.69 (0.13)	0.21 (0.68)
Coleoptera: Curculionidae	0.42 (0.41)	0.63 (0.18)	**-0.82** **(0.05)**	0.14 (0.80)	-0.51 (0.30)	0.22 (0.68)	-0.25 (0.63)	-0.29 (0.58)	0.25 (0.64)

Note: Groups without significant correlations are not included in the table (Lumbricidae, Diptera, Staphylinidae and total).

Table 7. Results of multiple regression analysis quantifying the effects of the dung density, soil bulk density and soil moisture on the activity density of selected arthropod groups (numbers in bold are significant values).

Orders or families	**Dung density/ soil moisture**		**Dung density/ soil density**		**Soil density/ soil moisture**	
	R²	*P*	R²	*P*	R²	*P*
Araneae: multiple fam.	0.31	0.06	0.30	0.07	0.13	0.34
Chilopoda: multiple fam.	0.34	**0.05**	0.43	**0.01**	0.23	0.14
Diplopoda: multiple fam.	0.42	**0.02**	0.22	0.15	0.28	0.08
Coleoptera: Carabidae	0.14	0.32	0.11	0.42	0.04	0.74
Coleoptera: Anobiidae	0.11	0.43	0.11	0.43	0.004	0.97
Coleoptera: Staphylinidae	0.38	**0.03**	0.15	0.29	0.38	**0.03**
Coleoptera: Scarabaeidae	0.44	**0.01**	0.30	0.07	0.47	**0.009**
Coleoptera: Silphidae	0.40	**0.02**	0.27	0.97	0.35	**0.04**
Coleoptera: Curculionidae	0.04	0.73	0.05	0.71	0.05	0.66
Diptera: Tipulidae	0.06	0.62	0.37	**0.03**	0.42	**0.02**

Grazing, through its impact on vegetation, as well as the thickness and the quality of the litter layer could be key factors determining macrofaunal communities (Rosén & Bakker 2005, Bardgett et al. 2005). We expected, therefore, certain effects of grazing on soil macrofaunal community, but due to our experimental design we were unable to prove these effects as there was no significant difference of grazing intensities among the study sites. Thus, our hypothesis 2 could not be tested by this study.

For some groups of arthropods, especially obligate coprophiles and certain small predators, dung is an essential substrate (Lenoir & Lennartsson 2010). Thus, we observed partly opposing trends of changes in the activity density of surface-active arthropods and the population density of soil-inhabiting animals in the forest-steppe ecotones of the Saur Mountains. In general, livestock grazing influences plant community structure, soil quality, health and, with it, the populations as well as diversity of soil biota (Clapperton et al. 2002, Bayartogtokh & Otgonjargal 2009, Numa et al. 2010, Lkhagva et al. 2013). Zahn et al. (2007) found higher species richness and frequencies of surface-active arthropods (ground beetles, rove beetles, spiders) in grazed than ungrazed grassland areas, due to the habitat mosaic created by the livestock (cattle). Moreover, Bardgett et al. (1998) and Dombos (2001) revealed that the abundance of some groups of soil animals increased with grazing pressure. Bromham et al. (1999) revealed the highest total invertebrate catches in the pasture, but the lowest ones in ungrazed woodland, and Seymour & Dean (1999) found higher abundance of ground-dwelling invertebrates at the heavily grazed areas. This pattern was largely attributable to the most common orders, particularly Hymenoptera (ants), Araneae and Coleoptera. Roberts & Morton (1985) reported that some beetles, such as Scarabaeidae biomass peaked in intermediate grazing intensity.

Zahn et al. (2007) found that the invertebrate species richness and frequencies benefited from low intensity grazing. They concluded that low-density grazing by cattle can increase habitat diversity even in small areas and thus enhance invertebrate richness. At low livestock densities, grazing is assumed to favor species diversity by the creation of diverse habitats (Eligsen et al. 1997, van Wingerden et al. 1992). In contrast, high grazing pressure reduces arthropod richness, as the structural diversity decreases (Bell et al. 2001, Dennis et al. 1997, Gibson et al. 1992, Kruess & Tscharntke 2002).

In the case of our study, a higher resolution of taxonomic study may be needed to determine if the differences in response to disturbance are due to the presence of different species, an effect masked by broad ordinal classification. Therefore, our future work will focus on explaining such responses by examining associations between soil animal species belonging to certain groups and quantifiable treatment effects among the study plots.

5. Acknowledgements

We are grateful to the staff of the Forestry Agency of the Zaisan District, East Kazakhstan Province for giving permissions for field work and their kind assistance. Thanks are also due to R. A. Norton, State University of New York, Syracuse, USA, M. Hauck, Georg August University, Göttingen, Germany for reading the manuscript and valuable discussions. This research was supported by the Volkswagen Foundation in the scope of the project ‘Forest regeneration and biodiversity at the forest-steppe border of the Altai and Khangai Mountains under contrasting developments of livestock numbers in Kazakhstan and Mongolia’, performed by the researchers from the Georg August University of Germany, the National University of Mongolia, and Pavlodar State University, Kazakhstan. Thanks are also due to the anonymous reviewers for their critical reading of the manuscript, and the authors are also grateful to Ricarda Lehmitz, for her thorough review and editorial suggestions, which considerably improved this article.

6. References

Bardgett, R. D. & R. Cook (1998): Functional aspects of soil animal diversity in agricultural grasslands. – Applied Soil Ecology **10**: 263–276.

Bardgett, R. D., D. A. Warlde, & G. W. Yeates (1998): Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. – Soil Biology and Biochemistry **30**: 1867–1878.

Bardgett, R. D., W. Bowman, R. Kaufmann & S. Schmidt (2005): A temporal approach to linking aboveground and belowground ecology. – Trends in Ecology & Evolution **20**: 634–641.

Battigelli, J. P., G. S. McIntyre, K. Broersma & M. Krzic (2003): Impact of cattle grazing on prostigmatid mite densities in grassland soils of southern interior British Columbia. – Canadian Journal of Soil Science **83**: 533–535.

Bayartogtokh, B. & E. Otgonjargal (2009): Assemblages of coprophilous beetles (Insecta: Coleoptera) in the pastureland of Central Mongolia. – Mongolian Journal of Biological Sciences **7**: 19–27.

Bell, L., R. Philip, C. P. Wheater & W. R. Cullen (2001): The implications of grassland and heathland management for the conservation of spider communities: a review. – Journal of Zoology **255**: 377–387.

Beyer, S., A. Kinnear, L. B. Hutley, K. McGuinness & K. Gibb (2011): Assessing the relationship between fire and grazing on soil characteristics and mite communities in a semi-arid savanna of northern Australia. – Pedobiologia **54**: 195–200.

Bromham, L., M. Cardillo, A. F. Bennett & M. A. Elgar (1999): Effects of stock grazing on the ground invertebrate fauna of woodland remnants. – Australian Journal of Ecology **24**: 199–207.

Birkhofer, K., I. Schöning, F. Alt, N. Herold, B. Klarner, M. Maraun, S. Marhan, Y. Oelmann, T. Wubet, A. Yurkov, D. Begerow, D. Berner, F. Buscot, R. Daniel, T. Diekötter, R. B. Ehnes, G. Erdmann, C. Fischer, B. Foesel, J. Groh, J. Gutknecht, E. Kandeler, C. Lang, G. Lohaus, A. Meyer, H. Nacke, A. Näther, J. Overmann, A. Polle, M. M., Pollierer, S. Scheu, M. Schloter, E. Schulze, W. Schulze, J. Weinert, W. W. Weisser, V. Wolters & M. Schrumpf (2012): General relationships between abiotic soil properties and soil biota across spatial scales and different land-use types. – PLoS ONE, **7**: e43292. doi:10.1371/journal.pone.0043292

Cheli, H. C., J. C. Corley, O. Bruzzone, M. del Brío, F. Martínez, N. M. Román & I. Ríos (2009): The ground-dwelling arthropod community of Peninsula Valdes in Patagonia, Argentina. – Journal of Insect Science **10**: 1–16. http://insectscience.org/10.50

Clapperton, M. J., D. A. Kanashiro & M. Behan-Pelletier (2002): Changes in abundance and diversity of microarthropods associated with Fescue prairie grazing regimes. – Pedobiologia **46**: 496–511.

Cole, L. J., D. I. MacCracken, I. S. Downie, P. Dennis, G. N. Foster, T. Waterhouse, K. J. Murphy, A. L. Griffin & M. P. Kennedy (2005): Comparing the effects of farming practices on ground beetle (Coleoptera: Carabidae) and spider (Araneae) assemblages of Scottish farmland. – Biodiversity and Conservation **14**: 441–460.

D'Arrigo, R. D. & G. C. Jacoby (1993): Secular trends in high northern latitude temperature reconstructions based on tree rings. – Climatic Change **25**:163–177.

Dennis, P., M. P. Young & C. Bentley (2001): The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpiones of *Nardus stricta* grassland in upland Scotland. – Agriculture, Ecosystems and Environment **86**: 39–57.

Dennis, P., M. R. Young & I. J. Gordon (1998): Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. – Ecological Entomology **23**: 253–264.

Dennis, P., M. R. Young, C. L. Howard & I. J. Gordon (1997): The response of epigeal beetles (Col.: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands. – Journal of Applied Ecology **34**: 433–443.

Dennis, P., J. Doering, J. A. Stockan, J. R. Jones, M. E. Rees, J. E. Vale & A. R. Sibbald (2004): Consequences for biodiversity of reducing inputs to upland temperate pastures: effects on beetles (Coleoptera) of cessation of nitrogen fertilizer application and reductions in stocking rates of sheep. – Grass and Forage Science **59**: 121–135.

Dennis, P., J. Skartviet, D. I. McCracken, R. J. Pakeman, K. Beaton, A. Kunaver, & D. M. Evans (2008): The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. – Journal of Applied Ecology **45**: 279–287.

Dombos, M. (2001): Collembola of loess grassland: effects of grazing and landscape on community composition. – Soil Biology and Biochemistry **33**: 2037–2045.

Dolmaar, J. F., S. Smoliak & W. D. Willms (1990): Distribution of nitrogen fractions in grazed and ungrazed fescue grassland Ah horizons. – Journal of Range Management **43**: 6–9.

Dolmaar, J. F. & W. D. Willms (1998): Effects of forty-four years of grazing on fescue grassland soils. – Journal of Range Management **51**: 122–126.

Eligsen, H., B. Beinlich & H. Plachter (1997): Effects of large scale cattle grazing on populations of *Coenonumpha glyceron* and *Lasiommata megera* (Lepidoptera: Satyridae). – Journal of Insect Conservation 1: 13–23.

Foggo, A., C. M. P. Ozanne, M. R. Speight & C. Hambler (2001): Edge effects and tropical forest canopy invertebrates. – Plant Ecology **153**: 347–359.

Gibson, C. W. D., C. Hambler & V. K. Brown (1992): Changes in spider (Araneae) assemblages in relation to succession and grazing management. – Journal of Applied Ecology **29**: 132–142.

Gvozdetsky, N. A. & N. I. Mukhailov (1978): Physical geography of USSR. Asian Part, third ed. – Mysl' Publishing, Moscow: 572 pp. (in Russian)

Hall, F. G., P. J. Sellers & D. L. Williams (1996): Initial results from the boreal ecosystem-atmosphere experiment, BOREAS. – Silva Fennica **30**:109–121.

Harrison, K. A. & R. D. Bardgett (2008): Impacts of grazing and browsing by large herbivores on soil and soil biological properties. – In: Gordon, I. J. & H. H. T. Prins, (eds.): The ecology of browsing and grazing. – Springer: 201–216.

Hauck, M., Ch. Dulamsuren, B. Bayartogtokh, K. Ulykpan, U. D. Burkitbaeva, E. Otgonjargal, S. V. Titov, T. Enkhbayar, A. K. Sundetpaev, U. Beket & Ch. Leuschner (2014): Relationships between the diversity patterns of vascular plants, lichens and invertebrates in the Central Asian forest-steppe ecotone. – Biodiversity and Conservation **23**: 1105–1117.

Hossain, M. Z., M. H. K. Choudhury, M. F. Hossain & Q. K. Alam (2002): Effects of ecological agriculture on soil properties and arthropod diversity in rice-based cropping systems in floodplain areas in Bangladesh. – Biological Agriculture and Horticulture **20**: 215–227.

Huhta, V. & S. Hänninen (2001): Effects of temperature and moisture fluctuations on an experimental soil microarthropod community. – Pedobiologia **45**: 279–286.

Huhta, V. & M. Räty (2005): Soil animal communities of planted birch stands in central Finland. – Silva Fennica **39**: 5–19.

Ishii, R. & N. Fujita (2013): A possible future picture of Mongolian forest-steppe vegetation under climate change and increasing livestock: results from a new vegetation transition model at the topographic scale. – In: Yamamura, N., N. Fujita & A. Maekawa (eds): The Mongolian Ecosystem Network: Environmental Issues under Climate and Social Changes. – Springer, Tokyo: 65–82.

Kinnear, A. & D. J. Tongway (2004): Grazing impacts on soil mites of semi-arid chenopod shrublands in Western Australia. – Journal of Arid Environments **56**: 63–82.

Kruess, A. & T. Tscharntke (2002): Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. – Conservation Biology **16**: 1570–1580.

Leetham, J. W. & D. G. Milchunas (1985): The composition and distribution of soil microarthropods in the shortgrass steppe in relation to soil water, root biomass, and grazing by cattle. – Pedobiologia **28**: 311–325.

Lenoir, L. & T. Lennartsson (2010): Effects of timing of grazing on arthropod communities in semi-natural grasslands. – Journal of Insect Science **10**: 1–24.

Lkhagva, A., B. Boldgiv, C. E. Goulden, O. Yadamsuren & W. K. Lauenroth (2013): Effects of grazing on plant community structure and aboveground net primary production of semiarid boreal steppe of northern Mongolia. – Grassland Science **59**: 135–145.

Lkhagvadorj, D., M. Hauck, Ch. Dulamsuren & J. Tsogtbaatar (2013): Pastoral nomadism in the forest-steppe of the Mongolian Altai under a changing economy and a warming climate. – Journal of Arid Environments **88**: 82–89.

Moore, J. S., D. E. Walter & H. W. Hunt (1988): Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. – Annual Review of Entomology **33**: 419–439.

Napierała, A., J. Bloszyk & J. Bruin (2009): Communities of uropodine mites (Acari: Mesostigmata) in selected oak-hornbeam forests of the Wielkopolska region (Poland). – Experimental and Applied Acarology **49**: 289–295.

Numa, C., C. Rueda, J. R. Verdú & E. Galante (2010): Influence of grazing activities on species diversity of dung beetles in Mediterranean pastures. – Options Méditerranéennes **92**: 277–280.

Roberts, R. J. & R. Morton (1985): Biomass of larval Scarabaeidae (Coleoptera) in relation to grazing pressures in temperate, sown pastures. – Journal of Applied Ecology **22**: 863–874.

Raynor, G. S. (1971): Wind and temperature structure in a coniferous forest and a contiguous field. – Forest Science **17**: 351–363.

Rosén, E. & J. P. Bakker (2005): Effects of agri-environment schemes on scrub clearance, livestock grazing and plant diversity in a low-intensity farming system on Oland, Sweden.– Basic and Applied Ecology **6**: 195–204.

Scheu, S., D. Albers, J. Alphei, R. Buryn, U. Klages, S. Migge, C. Platner & J.-A. Salamon (2003): The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forces. – Oikos **101**: 225–238.

Scheu, S. & M. Schäfer (1998): Bottom-up control of the soil macrofauna community in a beechwood on limestone: manipulation of food resources. – Ecology **79**: 1573-1585.

Schon, N. L., A. D. Mackay & M. A. Minor (2011): Soil fauna in sheep-grazed hill pastures under organic and conventional livestock management and in an adjacent ungrazed pasture. – Pedobiologia **54**: 161–168.

Seymour, C. L. & W. R. J. Dean (1999): Grazing effects on invertebrates in arid rangelands. – Journal of Arid Enironments **43**: 267–286.

StatSoft (1995): Statistica for Windows. – StatSoft, Tulsa, OK.

Striganova, B. R. & N. M. Poryadina (2004): Communities of soil animals in boreal forests of western Siberia. – KMK Scientific Press, Moscow: 233 pp. (in Russian)

Usher, M. B., R. G. Booth & K. E. Sparkes (1982): A review progress in understanding the organization of communities of soil arthropods. – Pedobiologia **23**: 126-144.

Vannier, G. (1971): Les fourmis, prédateurs permanents de certains types de collemboles. – Revue D Ecologie et de Biologie du Sol (8): 119–132.

Villani, M. G. & R. J. Wright (1990): Environmental influences on soil macroarthropod behavior in agricultural systems. – Annual Review of Entomology 35, 249–269.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setala, W. H. van der Putten & D. H. Wall (2004): Ecological linkages between aboveground and belowground biota. – Science **304**: 1629–1633.

Wingerden, W. K. R. E., A. R. Kreveld & W. Bongers (1992): Analysis of species composition and abundance of grasshoppers in natural and fertilized grassland. – Journal of Applied Entomology **113**: 138–152.

Zahn, A., A. Juen, A. Traugott & A. Lang (2007): Low density cattle grazing enhances arthropod diversity of abandoned wetland. – Applied Ecology and Environmental Research 5: 73–86.