

Comparison of ant communities (Hymenoptera: Formicidae) in different habitat types in North-Central Mongolia with special reference to their response to livestock grazing

Сравнение сообществ муравьев (Hymenoptera: Formicidae) в различных местообитаниях на севере Центральной Монголии под влиянием пастбищной нагрузки

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Key words: Hymenoptera, Formicidae, ant community, habitat type, livestock grazing, nest density, Bogdkhan Mountains, Mongolia.

Ключевые слова: Hymenoptera, Formicidae, сообщество муравьев, тип среды обитания, выпас скота, плотность гнезд, Богд-Хан-Уул, Монголия.

Abstract. We examined for the first time the effects of livestock grazing on ant species richness, structure of ant communities and nesting density in three different habitat types and natural and grazed conditions in the Bogdkhan Mountains region, North-Central Mongolia. Twenty one species of ants were recorded in the studied area. The most species rich genera were *Formica* with 8 species (38.1%) and *Myrmica* with 4 species (19%) when all the habitat types are combined. Overall, we collected 19 species (90.5%) from forest steppe, 18 species (85.7%) from steppe, and 12 species (57.1%) from meadow. Based on occurrence data, the most common species were *Formica candida*, *Myrmica kasczenkoi* and *Myrmica pisarskii*. The number of ant species in each habitat depends on the grazing condition ($F = 6.3837$, $P = 0.0217$), and interaction between grazing condition and habitats ($F = 6.6647$, $P = 0.0073$). The frequency occurrence of ants in all habitat types depends only on habitat conditions ($F = 4.4556$, $P = 0.0499$) and not on any effects of habitats ($F = 4.4207$, $P = 0.6632$) and interaction between grazing condition and habitats ($F = 0.9008$, $P = 0.4248$). In total, we counted 1173 ant nests in 23 transects. The largest number of nests (957, or 81.5%) belonged to *Formica candida*, followed by *Myrmica kasczenkoi* (46 nests, 3.9%). The lowest number of nests (1, or 0.08%) belonged to *Formica exsecta*, *Formica sanguinea* and *Leptothorax acervorum*, followed by *Formica uralensis* and *Myrmica forcipata* (2, or 0.15%). Among the six habitats, the lowest density of nests was in the grazed forest steppe (0.15 nests/m²) and the highest in the natural meadow (1.17 nests/m²). The natural (0.41 nests/m²) and grazed (0.59 nest/m²) steppes had similar nest densities. Statistically, there was no difference in the nest density between all habitat types ($F = 6.68$, $P = 0.5237$).

Резюме. Впервые проанализировано влияние пастбищной нагрузки на видовое разнообразие, структуру сообществ и плотность гнезд муравьев в трех различных типах местообитаний, в условиях отсутствия и наличия выпаса, в районе горы Богд-Хан-Уул, север Центральной Монголии. На исследуемой

территории зарегистрирован 21 вид муравьев. Наибольшее видовое разнообразие отмечено для родов *Formica* (8 видов, 38.1% всей мирмекофауны) и *Myrmica* (4 вида, 19%). В лесостепи было найдено 19 видов (90.5%), в степи 18 видов (85.7%), на луговых участках 12 видов (57.1%). Наиболее многочисленны *Formica candida*, *Myrmica kasczenkoi* и *Myrmica pisarskii*. Количество видов муравьев в каждом местообитании зависит от выпаса ($F = 6.3837$, $P = 0.0217$) и взаимосвязи между биотопом и условиями выпаса ($F = 0.9008$, $P = 0.4248$). Частота встречаемости муравьев во всех типах местообитаний зависит только от состояния биотопа ($F = 4.4556$, $P = 0.0499$), а не от каких-либо воздействий местообитания ($F = 4.4207$, $P = 0.6632$) и взаимодействия между условиями выпаса и местом обитания ($F = 0.9008$, $P = 0.4248$). На 23 трансектах было насчитано 1173 гнезда. Наибольшее количество гнезд отмечено у *Formica candida* (957, или 81.5%) и *Myrmica kasczenkoi* (46, или 3.9%), наименьшее – у *Formica exsecta*, *Formica sanguinea* и *Leptothorax acervorum* (по 1, или 0.08%) и *Formica uralensis* и *Myrmica forcipata* (по 2, или 0.15%). Самая низкая плотность гнезд была в лесостепи с выпасом (0.15 гнезд/м²), самая высокая – в нетронутых лугах (1.17 гнезд/м²). Плотность гнезд в степи на участках с выпасом и без существенно не отличалась (0.59 и 0.41 гнезд/м² соответственно). Большая разница в плотности гнезд во всех типах местообитаний статистически отсутствует ($F = 6.68$, $P = 0.5237$).

Introduction

Ants have numerous advantages over vertebrates and other arthropods in studies of landscape disturbance and species diversity. They are extremely abundant, have relatively high species richness, include many specialist species at higher trophic levels, and are responsive to changing environmental conditions [Nash et al., 2001].

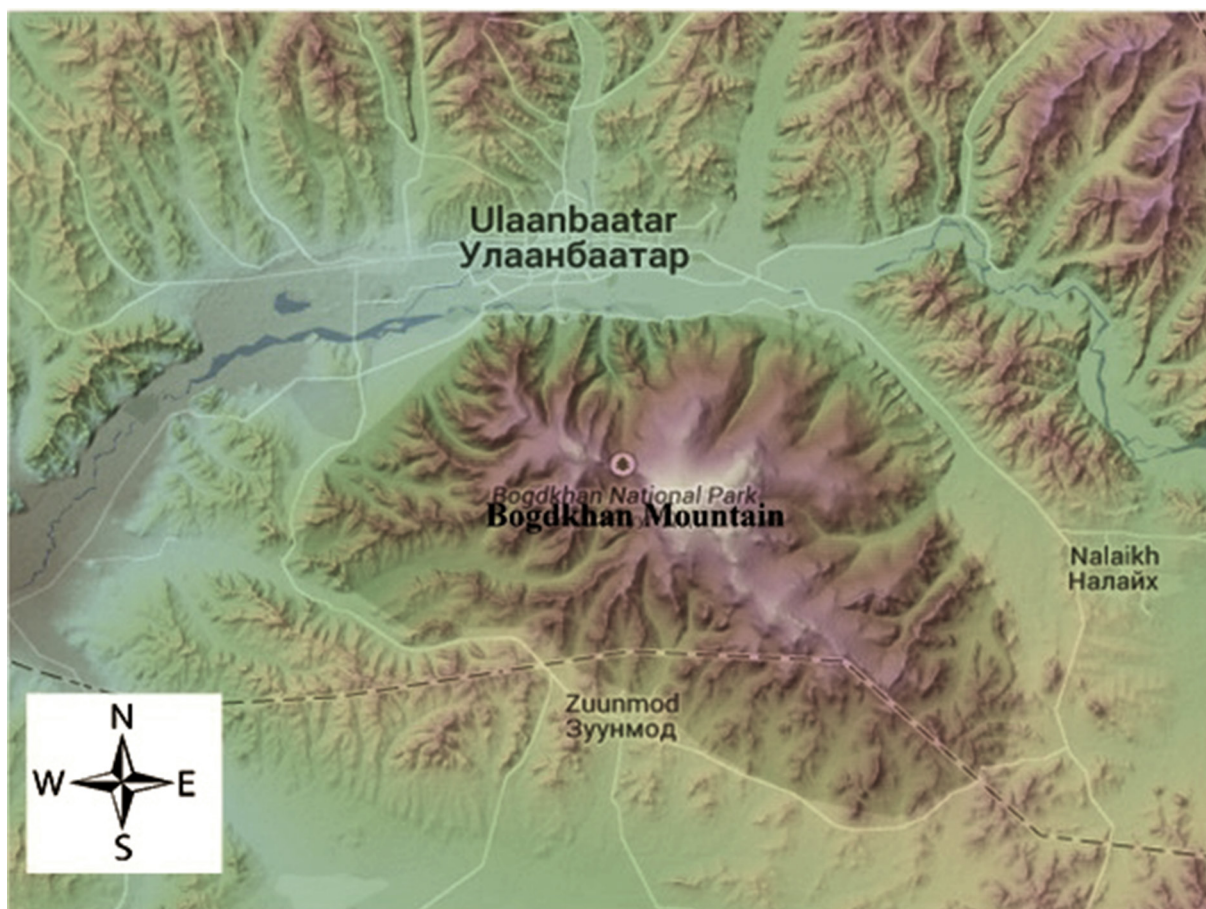


Fig.1. Map of the Bogdkhan Mountains, Mongolia.
Рис. 1. Гора Богд-Хан-Уул, Монголия.

They occur throughout the world, are easily collected, are taxonomically relatively well known, and constitute an important fraction of animal biomass in terrestrial ecosystems [Lynch et al., 1988; Hölldobler, Wilson, 1990]. On the regional and local scale, the ant species richness is sensitive to plant cover and diversity [Morrison, 1998], soil type [Peck et al., 1998], disturbance regime [Feener, Schupp 1998].

Ant communities have a number of attributes that may make them particularly useful as indicators of ecosystem change. The structure and composition of ant communities are influenced by competition, natural enemies, resource availability, habitat change, and disturbance [Hölldobler, Wilson, 1990; Bestelmeyer, Wiens, 2001; Andersen, 1997; Kaspari, Majer, 2000]. Habitat degradation and biological invasions are the two greatest threats to global biodiversity. The maintenance of species diversity in modified and natural habitats is the central focus of conservation biology [Luis et al., 2010].

A number of studies have examined the effects of different habitat disturbances on ant communities (for livestock grazing effects, see Wisdom and Whitford [1981], Bestelmeyer and Wiens [2001], Nash et al. [2001, 2004]; Luis et al. [2010]). Ant assemblages can be quantified on the scale of abundance or nest density [Bestelmeyer et al., 2000; Schlick-Steiner et al., 2006; Sagata et al., 2010].

Livestock grazing is one of the most extensive forms

of land use. Approximately 26% of the earth's land surface [Carlos, Steinfeld, 1996], 70% of land in the 11 western United States, 67% of land in Kazakhstan and 82% (129,294 mill. ha) of land in Mongolia are used primarily for grazing [Review..., 2009]. Around 70% of pasture land in Mongolia has been degraded by overgrazing, mining, climate change, and desertification [Tuvshintogtokh, Ariungrel, 2013].

We examined the effects of livestock grazing on species composition, structure and nesting density in ant communities in six different habitat types/conditions in the Bogdkhan Mountains region, North-Central Mongolia. It is postulated that the ant species richness would decline as a function of rangeland worsening, and that the abundance of some species or functional groups would consistently respond positively or negatively to the change in rangeland condition.

Material and methods

Study area. The Bogdkhan Mountains are located in North-Central Mongolia, constituting the southern part of the Khentii Mountain Range, which lies between forest steppe and steppe, and also forms the southern border of larch forest. This mountain range is regarded as typical of northern regions of Mongolia characterized by the cold winter, cool summer and sharp continental climatic



Figs 2–7. Transects in the Bogdkhan Mountains (2–5) and ants attracted to a sugar baits (6–7).

2 – natural forest steppe; 3 – grazed forest steppe; 4 – grazed steppe; 5 – grazed meadow; 6 – *Formica manchu* workers; 7 – *Formica candida* and *Myrmica kasznenkoi* workers.

Рис. 2–7. Трансекты на Богд-Хан-Уул (2–5) и муравьи на сахарных приманках (6–7).

2 – нетронутая лесостепь; 3 – лесостепь с выпасом; 4 – степь с выпасом; 5 – луг с выпасом; 6 – *Formica manchu*, рабочие; 7 – *Formica candida* и *Myrmica kasznenkoi*, рабочие.

features. Four vegetation subzones are found in this area, i.e., alpine taiga, alpine forest, forest steppe and arid steppe. Also, some mountain riversides have generated patch meadows. The annual mean air temperature ranges from -2.5°C to -3.1°C , and precipitation 200–300 mm at the meteorological station in Ulaanbaatar. More than 80% of precipitation fall between May and September. In the coldest month, January, the mean air temperature is -19°C to -24°C , and in the warmest month, July, it is $+14.5^{\circ}\text{C}$ to $+16.8^{\circ}\text{C}$. The territory of Bogdkhaan Mountains covers 41.6 thousand ha and the average elevation is 1580 m above the sea level. The present survey was carried out in the

valleys of Hurhree, Shajinhurh, Turhurh, Huht and Turgen in and around the Bogdkhan Mountains (Fig. 1).

Data collection. In total, 23 transects were established in 3 types of vegetation and in natural and grazed conditions (Figs 2–7): natural steppe ($n = 3$), grazed steppe ($n = 7$), natural and grazed forest steppe ($n = 3$ for each), natural meadow ($n = 3$), and grazed meadow ($n = 4$), from June to September in 2007, 2008 and 2009 (in total 6 habitat types). Each transect (belt) was $2\text{ m} \times 50\text{ m}$, and was divided into 25 quadrats ($2\text{ m} \times 2\text{ m}$), totalling to 575 quadrats. We sampled ants with 3 types of bait (powdered cheese, honey, sesame seeds). Baits of the 3 kinds were randomly placed

directly on the soil in each quadrat (in total 75 baits per transect). For honey baits we used square pieces of cotton (2 cm × 5 cm) soaked with 40% honey.

This is a technique similar to those used to measure ant richness and activity in a variety of habitats and locations [Perfecto, Vandermeer, 2002]. We started to check the baits approximately 20 minutes after placing them, recorded the ants present at baits, and collected some individuals of each species for later identification. Also, we recorded ants not attracted to the baits, but found within quadrats. Ant nests were located and counted within quadrats. Generally there were many entrance holes of presumably the same nests on the ground surface. We estimated the nest numbers within quadrats observing ant behaviour.

Ants sampled were identified to species with keys in Radchenko [2005], Radchenko and Elmes [2010], Kupyanskaya [1995], and other literature.

Data analysis. The ant species richness was estimated for each transect using Chao 2 index in the software package EstimateS [Colwell, 2006]. Comparisons of the number of species and the number of nests among different habitat types were conducted with StatView 5.0.1 (1992–1998, SAS Institute Inc.) and also used two-way ANOVA (JMP 5.0 1992–1998, SAS Institute Inc.). The number (proportion) of quadrats with ants of each species and the number of nests per transect (100 m²) were used to evaluate the frequency of each species. These results were compared between the habitat types and between the natural and

grazed conditions. In two-way ANOVA, DF is the degree of freedom; F Ratio (Fisher test ratio) is the Model Mean Square divided by the Error Mean Square; Prob > F (p) is the probability value of the Fisher test.

Species composition and richness between transects were analyzed based on the species frequency data using CANOCO 4.56 (1997–2009, Cajo J.F. ter Braak and Petr Smilauer).

Results

Diversity of ants. Twenty one species of ant were recorded in the study sites (Table 1). Five of them occurred in all the vegetation types, i.e., forest steppe, steppe and meadow: *Camponotus saxatilis* Ruzsky, 1895, *Formica candida* Smith, 1878, *Formica manchu* Wheeler, 1929, *Myrmica kasczenkoi* Ruzsky, 1905, and *Myrmica pisarskii* Radchenko, 1994. However, only two, *Formica candida* and *Myrmica kasczenkoi*, were found in all 6 habitat types. Nine species were found only in 1 habitat type: *Formica pisarskii* Dlussky, 1964, *Lasius przewalskii* Ruzsky, 1915 and *Temnothorax nassanowi* (Ruzsky, 1895) in natural steppe, *Formica uralensis* Ruzsky, 1895 and *Proformica kaszabi* Dlussky, 1969 in disturbed steppe, *Formica kozlovi* Dlussky, 1965 in natural forest steppe, *Formica sanguinea* Latreille, 1798 and *Formica lemani* Bondroit, 1917 in disturbed forest steppe, *Formica exsecta* Nylander, 1846 in disturbed meadow. The most species rich genera

Table 1. Frequency of occurrences of ant species in all habitat types.
Таблица 1. Частота встречаемости видов муравьев во всех местообитаниях.

№	Name of species Вид	Forest steppe / Лесостепь		Steppe / Степь		Meadow / Луг		Total Всего
		natural нетронутая	grazed с выпасом	natural нетронутая	grazed с выпасом	natural нетронутый	grazed с выпасом	
1	<i>Camponotus sachalinensis</i>	9	28	1	0	0	0	38
2	<i>Camponotus saxatilis</i>	0	3	5	0	2	1	11
3	<i>Coptoformica exsecta</i>	0	0	0	0	0	1	1
4	<i>Formica candida</i>	156	16	52	410	351	140	1125
5	<i>Formica exsecta</i>	0	0	0	0	0	3	3
6	<i>Formica kozlovi</i>	2	0	0	0	0	0	2
7	<i>Formica lemani</i>	0	26	0	0	0	0	26
8	<i>Formica manchu</i>	38	0	0	3	4	0	45
9	<i>Formica pisarskii</i>	0	0	7	0	0	0	7
10	<i>Formica sanguinea</i>	0	1	0	0	0	0	1
11	<i>Formica uralensis</i>	0	0	0	2	0	0	2
12	<i>Lasius gebaueri</i>	0	1	59	0	0	0	60
13	<i>Lasius przewalskii</i>	0	0	20	0	0	0	20
14	<i>Leptothorax acervorum</i>	2	0	1	0	0	0	3
15	<i>Leptothorax muscorum</i>	1	6	4	0	0	0	11
16	<i>Myrmica angulinodis</i>	7	4	20	0	0	0	31
17	<i>Myrmica forcipata</i>	0	0	3	0	0	6	9
18	<i>Myrmica kasczenkoi</i>	9	4	18	25	14	5	75
19	<i>Myrmica pisarskii</i>	19	1	29	0	14	1	64
20	<i>Proformica kaszabi</i>	0	0	0	13	0	0	13
21	<i>Temnothorax nassanowi</i>	0	0	4	0	0	0	4
	Total occurrences	243	90	223	453	385	157	1551
	Occurrences per transect	81	30	74.3	64.7	128.3	39.3	
	Total species richness	9	10	13	5	5	6	48

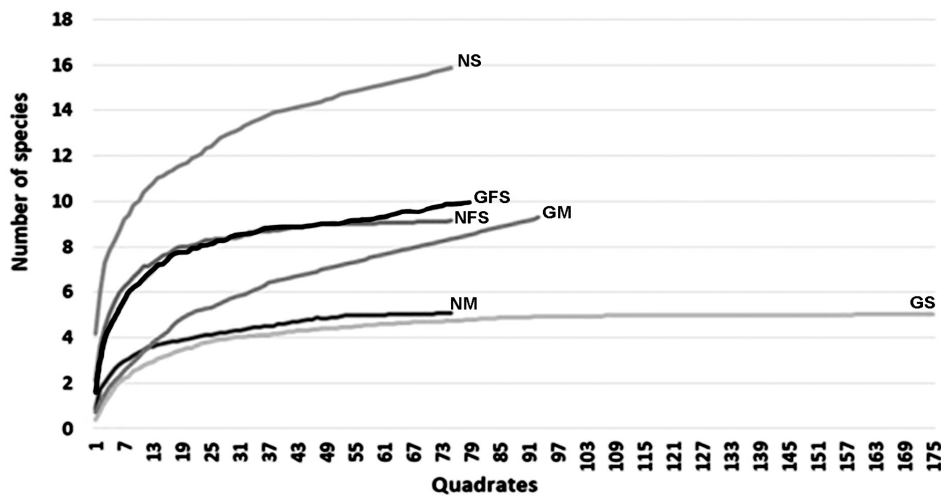


Fig. 8. Ant species abundance curves in all habitats: NFS – natural forest steppe; GFS – grazed forest steppe; NS – natural steppe; GS – grazed steppe; NM – natural meadow; GM – grazed meadow.

Рис. 8. Кривые численности видов муравьев во всех местообитаниях: NFS – нетронутая лесостепь; GFS – лесостепь с выпасом; NS – нетронутая степь; GS – степь с выпасом; NM – нетронутый луг; GM – луг с выпасом.

were *Formica* Linnaeus, 1758 with 8 species (38.1%) and *Myrmica* Latreille, 1804 with 4 species (19%) when all the habitat types are combined. Overall, we collected 19 species (90.5%) from forest steppe, 18 species (85.7%) from steppe, and 12 species (57.1%) from meadow.

Based on occurrence data, the most common species were *Formica candida*, *Myrmica kasczenkoi* and *Myrmica pisarskii*.

Species richness estimates calculated by EstimateS for all habitat types ranged from 5 to 16 (Fig. 8). The analysis showed that species accumulation curves are almost saturated for most of the habitats. However, in natural steppe and grazed meadow the number of species is still rising. According to the species estimator Chao 2, we found 70 to 100% of the estimated numbers have been already sampled.

Natural habitats generally had larger numbers of species, and grazed steppe had the smallest number (total 5 species; mean 1.5 species) among all 6 habitat types that is remarkably smaller than natural steppe (total 13 species; mean 6.6) (Fig. 9). The mean numbers of species in the remaining 4 habitats were similar, varying between 3–5 species.

The number of ant species in each habitat depends on the grazing condition ($F = 6.3837$, $P = 0.0217$), and interaction between grazing condition and habitats ($F = 6.6647$, $P = 0.0073$) (Table 2).

The occurrence of ants (total frequency of ants of

all species) in all habitat types depends only on habitat conditions ($F = 4.4556$, $P = 0.0499$) and not any effects of habitats ($F = 4.4207$, $P = 0.6632$) and interaction between grazing conditions and habitats ($F = 0.9008$, $P = 0.4248$) (Table 3).

Comparison of dominant species among different habitat types. Abundance was measured by the number of quadrats (frequency) in which individual of each species was sampled or observed for each habitat type (Table 1). Generally *Formica candida* was the dominant species in all habitats with grazing by livestock animals. But ant occurrence and nest density studies show this species was more dominant in grazed steppe and natural meadow habitats. *Myrmica kasczenkoi* was subdominant, next to *Formica candida*, in the grazed steppe and natural meadow. In natural forest steppe, *F. manchu* was dominant, followed by *Myrmica pisarskii*. Also *M. pisarskii* was a dominant species in all natural habitats. *Lasius gebaueri* Seifert, 1992 and *L. przewalskii* were dominant in the natural steppe habitat. *Myrmica kasczenkoi* and *M. forcipata* Karavaiev, 1931 were subdominant in the grazed meadow habitat.

Formica candida and *Myrmica kasczenkoi* mainly dig nests in the soil under stones and livestock dung in all habitat types, but *F. candida* often constructs small soil mounds. *Camponotus sachalinensis* Forel, 1904, *Formica sanguinea* and *F. lemami* nests are built in the soil, under stones and logs partly in the soil in the grazed forest steppe. *Formica uralensis* builds medium-sized mounds with

Table 2. Factors affecting the number of species.

Таблица 2. Факторы, влияющие на количество видов.

Source / Ресурс	DF	Sum of Squares / Сумма квадратов	F Ratio	Prob > F
Habitats / Местообитания	2	9.81394	1.9529	0.1724
Condition / Условие	1	16.039737	6.3837	0.0217
Habitats* conditions / Условия* местообитаний	2	33.491359	6.6647	0.0073
Error / Ошибка	17	42.71429		

Note. * – indicating interaction of habitats and conditions.

Примечание. * – индикация взаимодействия местообитания и условий.

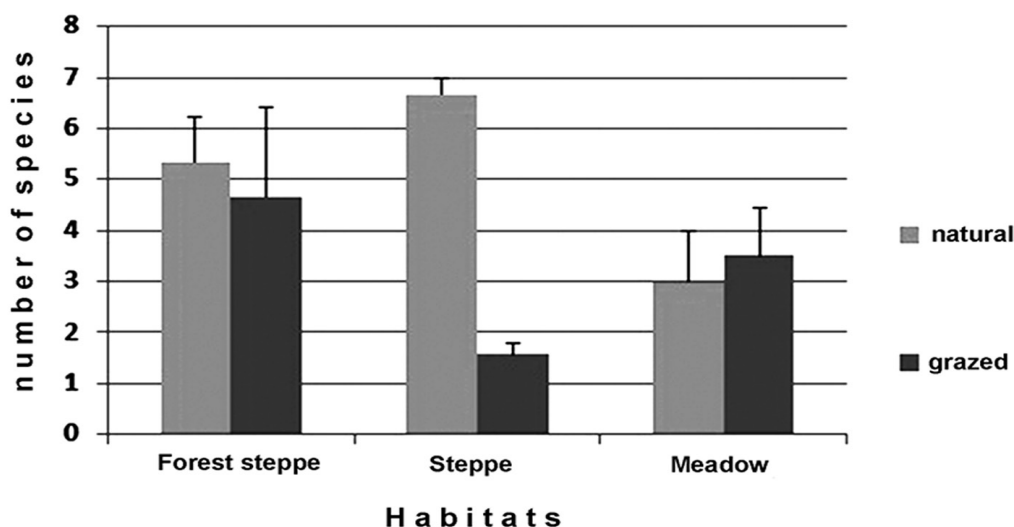


Fig. 9. Mean number of ant species for all habitats. Error bar line indicates ± 1 standard error.

Рис. 9. Среднее число видов муравьев для всех местообитаний. Линия ошибок показывает стандартное отклонение ± 1 .

plant material and *F. exsecta* constructs mounds with tiny plant material. *Proformica mongolica* nests in the soil in the grazed steppe, and *Myrmica forcipata* nests are built in the soil in the grazed meadow. *Leptothorax acervorum* (Fabricius, 1793) nests in soil in the natural forest steppe. *Lasius gebaueri*, *L. przewalsii* and *Temnothorax nassonowi* nests are built in soil and under stones in the natural steppe. *Leptothorax muscorum* (Nylander, 1846) nests are in soil in the grazed and natural forest steppe.

Nest density. In total, we counted 1173 ant nests in 23 transects (Table 4). The largest number of nests (957, or 81.5%) belonged to *Formica candida*, followed by *Myrmica kasczenkoi* (46 nests, 3.9%). The lowest number of nests (1, or 0.08%) belonged to *Formica exsecta*, *Formica sanguinea* and *Leptothorax acervorum*, followed by *Formica uralensis* and *Myrmica forcipata* (2, or 0.15%).

Among the six habitats, the lowest density of nests was in the grazed forest steppe (0.15 nests/m²) and the highest in the natural meadow (1.17 nests/m²). The natural (0.41 nests/m²) and grazed (0.59 nest/m²) steppes had similar nest densities (but differed in the number of species, Table 1). Statistically, there was no difference in the nest density between all habitat types ($F = 6.68$, $P = 0.5237$).

The highest mean number of ant nests per transect (116.6) was in the natural meadow and the lowest (15) was in the grazed forest steppe habitat types. The mean numbers of nests in the natural (59.5) and grazed steppe (41.3) were

similar. But in the natural (44.6) and grazed forest steppe (14.6) the mean numbers of nests were different.

On the other hand the number of nests does not depend on habitats ($F = 1.0222$, $P = 0.3809$) or grazing conditions ($F = 2.2325$, $P = 1.1535$), and also their interactions do not affect the number of nests ($F = 2.0559$, $P = 0.1586$) (Table 5). The slice test for meadow habitat only shows that ant nest number depends on the habitat condition ($F = 5.1762$, $P = 0.03613$) (Table 6). But the number of ant nests in other habitats does not depend on condition and habitat types.

The scores of principal component analysis of species for natural steppe and grazed forest steppe differed significantly from all other habitats and were randomly distributed and showed no grouping (Fig. 11). It means natural steppe and grazed forest steppe had not similar species composition. The cluster analysis showed that ant communities cannot be grouped according to habitat types. However, the natural and grazed meadow habitats are always grouped into the same cluster.

Discussion

Up to now the Mongolian ants have been studied mainly on the taxonomy and distribution [e.g., Dlussky, Pisarski, 1970; Pfeiffer et al., 2007; Aibek, Yamane, 2010;

Table 3. Factors affecting the occurrence (frequency) of ants.

Таблица 3. Факторы, влияющие на частоту встречаемости муравьев.

Source / Ресурс	DF	Sum of Squares / Сумма квадратов	F Ratio	Prob > F
Habitats/ Местообитания	2	2562.145	0.4207	0.6632
Condition / Условие	1	13567.408	4.4556	0.0499
Habitats*condition / Условия* местообитаний	2	5486.113	0.9008	0.4248
Error / Ошибка	17	51765.512		

Note. * – indicating interaction of habitats and conditions.

Примечание. * – индикация взаимодействия местообитания и условий.

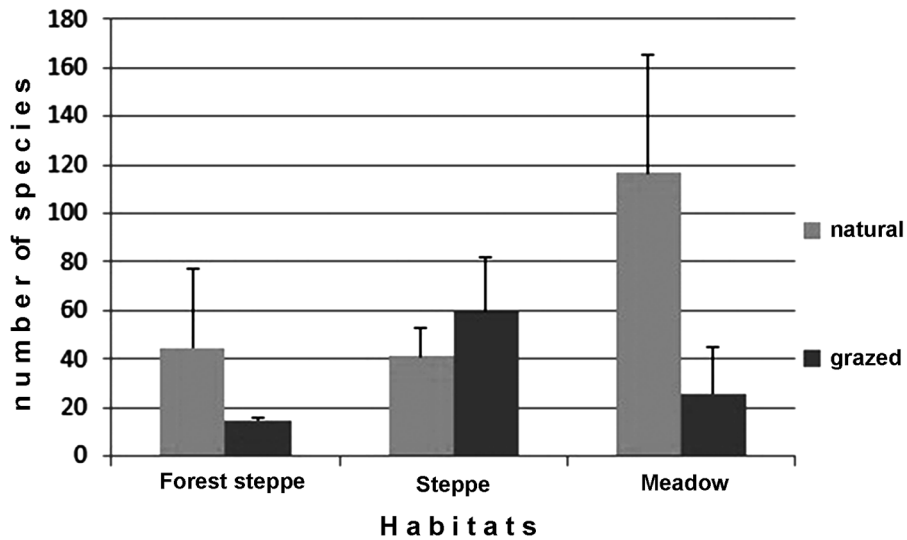


Fig. 10. Mean number of ant nests per transect for all habitat types. Error bar line indicates ± 1 standard error.

Рис. 10. Среднее количество муравейников на трансекту для всех типов местообитаний. Линия ошибок показывает стандартное отклонение ± 1 .

Yamane, Aibek, 2012; Bayartogtokh et al., 2014] except of Pfeiffer et al. [2003], who studied the ant community structure along an ecological gradient from steppe to desert in Mongolia. The present study is the first intensive survey to compare the ant community among different vegetation types and to clarify the effect of livestock grazing on ant communities in the same area.

Different patterns were observed in species accumulation curves between 3 vegetation types according to conditions (natural or grazed). Although in most of the habitat types the ant species number seemed saturated

during our survey, in natural steppe and grazed meadow the species number was still rising (Fig. 8). For the natural steppe this is reasonable because of its complex dimensional structure (grasses are tall and dense) and warmer condition during summer. However, for the grazed meadow the reason is not clear.

In steppe vegetation the species number was much higher in natural condition than in grazed condition (Fig. 9). This is consistent with the results of Andersen [1997], King et al. [1998], Majer and Nichols [1998] that ant communities in disturbed habitats have lower

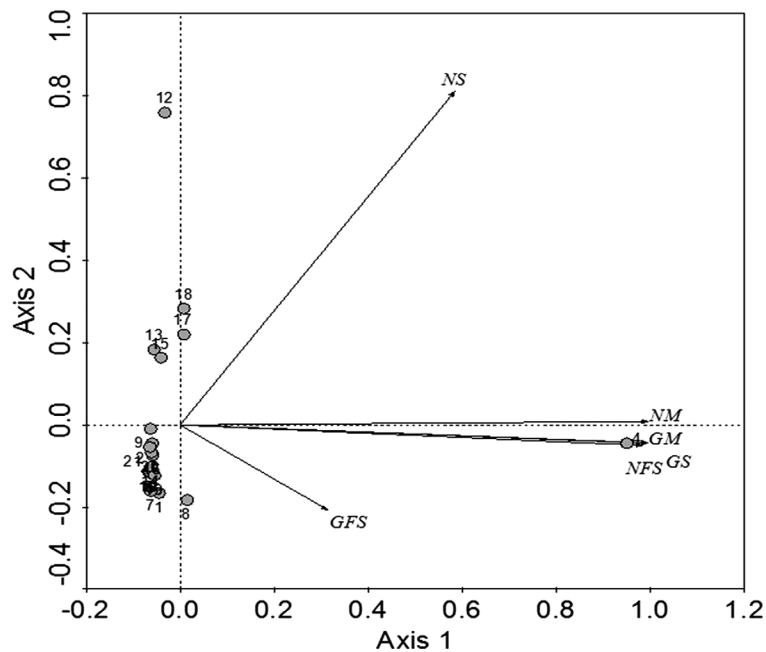


Fig. 11. Principal component analysis (PCA) plots of samples for 6 habitats and scores of all 21 species. NFS – natural forest steppe; GFS – grazed forest steppe; NS – natural steppe; GS – grazed steppe; NM – natural meadow; GM – grazed meadow.

Рис. 11. Результаты метода главных компонент (PCA) для участков образцов шести местообитаний и оценки 21 вида найденных муравьев. NFS – нетронутая лесостепь; GFS – лесостепь с выпасом; NS – нетронутая степь; GS – степь с выпасом; NM – нетронутый луг; GM – луг с выпасом.

Table 4. Total number of nests per habitat type.
Таблица 4. Общее количество гнезд в каждом типе местообитания.

№	Name of species Вид	Forest steppe / Лесостепь		Steppe / Степь		Meadow / Луг		Total Всего
		natural нетронутая	grazed с выпасом	natural нетронутая	grazed с выпасом	natural нетронутый	grazed с выпасом	
1	<i>Camponotus sachalinensis</i>	0	12	0	0	0	0	12
2	<i>Camponotus saxatilis</i>	0	2	2	0	0	0	4
3	<i>Formica candida</i>	104	12	33	384	326	98	957
4	<i>Formica exsecta</i>	0	0	0	0	0	1	1
5	<i>Formica lemani</i>	0	4	0	0	0	0	4
6	<i>Formica manchu</i>	12	0	0	3	1	0	16
7	<i>Formica sanguinea</i>	0	1	0	0	0	0	1
8	<i>Formica uralensis</i>	0	0	0	2	0	0	2
9	<i>Lasius gebaueri</i>	0	1	37	0	0	0	38
10	<i>Lasius distinguendus</i>	0	0	18	0	0	0	18
11	<i>Leptothorax acervorum</i>	1	0	0	0	0	0	1
12	<i>Leptothorax muscorum</i>	1	6	0	0	0	0	7
13	<i>Myrmica angulinodis</i>	2	2	13	0	0	0	17
14	<i>Myrmica forcipata</i>	0	0	0	0	0	2	2
15	<i>Myrmica kasczenkoi</i>	5	4	7	15	12	3	46
16	<i>Myrmica pisarskii</i>	9	0	12	0	11	0	32
17	<i>Proformica mongolica</i>	0	0	0	13	0	0	13
18	<i>Temnothorax nassonovi</i>	0	0	2	0	0	0	2
	Total number of nests	134	44	124	417	350	104	1173
	Density of nest (nest/m ²)	0.45	0.15	0.41	0.59	1.17	0.26	

species diversity. Our direct observations showed that the grazed steppe was characterized by very poor plant species richness, simple dimensional structure and much drier soil that is exposed (for plant diversity, see Fujita and Amartuvshin [2013], Tuvshintogtokh and Ariungrel [2013]). All this should prevent the survival of many ant species. On the other hand, in other vegetation types the species number did not significantly differ according to the condition (natural or grazed). Grazed steppe had a higher density of ant nests than any other habitat types. This high density was mainly supported by one species, *Formica candida*, other species being very rare in both total occurrence and nest density. According to the species saturation curves, the grazed meadow can be expected to harbor a rich ant fauna, but it may not be true because only *F. candida* super-dominated other species that may be represented by just chance occurrences.

The natural forest steppe had a slightly higher species number than the grazed steppe. It had a slightly smaller species number and lower nest density than natural steppe. However, both the natural steppe and natural forest steppe harbored the richest ant diversity if the species number, total occurrence and nest density are considered

in combination. Furthermore, the principal component analysis showed that the natural steppe had a particular ant species composition and community compared with other habitat types. This means the protection of the natural steppe is most important in maintaining a rich ant fauna in North-Central Mongolia.

It is interesting that in terms of nest density there was no significant statistical difference between the two steppe habitat conditions. The nest density is even relatively high in the grazed steppe even if species diversity is poor. Although at present it is difficult to estimate the biomass of ants in each habitat type, it can be mentioned that even if the habitat condition deteriorates ants continue to retain a substantial biomass. However, for the other two vegetation types, the nest density was higher in natural condition than in grazed condition (Fig. 10). Contrary to the general expectation, the observed nest densities in the natural forest steppe and natural steppe were not very high. This might be true, but the detection of nests in natural condition is not so easy because of dense vegetation cover. We should have a better methodology to estimate the biomass of ants in such habitats.

Table 5. Factors affecting the number of nests.
Таблица 5. Факторы, влияющие на количество гнезд.

Source / Ресурс	DF	Sum of Squares / Сумма квадратов	F Ratio	Prob > F
Habitats / Местообитания	2	5566.04	1.0222	0.3809
Condition / Условие	1	6077.9	2.2325	0.1535
Habitats*condition / Условия* местообитаний	2	11194.481	2.0559	0.1586
Error / Ошибка	17	46282.381		

Note. * – indicating interaction of habitats and conditions.

Примечание. * – индикация взаимодействия местообитания и условий.

Table 6. Number of nests in the meadow habitats.
Таблица 6. Количество гнезд в луговых местообитаниях.

Sum of Squares / Сумма квадратов	14092.19
Numerator DF / Числитель DF	1
Denominator DF / Знаменатель DF	17
F Ratio	5.176208
Prob > F	0.036134

In terms of the frequency of occurrences, *Formica candida* was the dominant species in all habitat types, followed by *Myrmica kasczenkoi* and *M. pisarskii* that were found in all or in most of the habitat types. These 3 species are supposed to have a broader range of adaptability than other ant species, and will survive considerable habitat change. It is not clear that these species simply use degraded condition effectively or they actually drive out other species in particular conditions.

It is also observed that the most of the ant species coexist well, except the only aggressive species *Lasius gebaueri* that does not allow other species to construct their nests within its vicinity (authors' unpublished data). We do not know at present the resource partitioning among the species concerned since the food preference of each species is not precisely documented. At least some larger species seemed to tolerate smaller species at baits. Direct observations on species interaction are needed in the field to reveal the mechanism of the coexistence of particular species.

In conclusion, the effect of livestock grazing is not negligible on ant species richness and ant community. Since most of species seem to tolerate other species living close to each other, the decrease in species richness should be accelerated mainly by habitat degradation. The change in important food (other arthropods and plants) should be evaluated through habitat change for further understanding of ant community change. Although we did not find any alien ant species in the study sites, the ant fauna should be monitored with regular intervals to find out any factors that potentially decrease ant diversity.

Acknowledgements

We would like to thank graduated students of the National University of Mongolia, Ms. Jargalsaikhan Purevdelger and Tserensambuu Ulzii for their great help in data collecting. Discussion with Prof. Badamdorj Bayartogtokh, Prof. Martin Pfeiffer (National University of Mongolia) and Prof. Takao Itioka (Kyoto University, Japan) was very helpful. We also would like to thank The Japan Society for the Promotion of Science for financial support of this research during four years from 2007 (MECS-10731).

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