

Diversity and biogeography of ants in Mongolia (Hymenoptera: Formicidae)

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ABSTRACT. Information on the biogeographical composition and spatial distribution patterns of ant assemblages in Mongolia is relatively scarce. In this study we investigated species richness, spatial distribution and biogeographical composition of the Mongolian ant fauna and recorded a total of 71 species belonging to 17 genera and three subfamilies. Genus and species richness of ants is lower in Mongolia than in most surrounding geopolitical regions. Using published literature as well as our own data we examined how ant species richness was related to phytogeographical elements. The major part of the Mongolian ant fauna is associated with the mountain taiga and forest-steppe ecosystems. A few ant species belong to the arid steppe, semi-desert and desert ecosystems. We observed no significant correlation between species richness of ants and land area size of phytogeographical regions; however, species richness of ants and plants in various phytogeographical regions showed a significant positive correlation. We did not detect strong differentiation of ant species along the elevational gradients of the country as most of the species were recorded in a wide range of elevations, but mid-elevational altitudes (1000 – 2000 m a.s.l.) showed the greatest diversity of ants. Regarding the biogeographical composition, species with wide geographical distributions, i.e. Transpalearctic species together with Eastern Palearctic, Central and East Asian elements, comprise a large proportion of the ant fauna in Mongolia. The ant fauna of Mongolia does not differ significantly from that of neighbouring regions, and the majority of species occurring in this country probably originated in neighbouring areas to the west, north and east.

Keywords: Formicidae, area size, biogeography, distribution, diversity, elevation, Mongolia

INTRODUCTION

Ants are common, almost ubiquitous insects in Mongolia, and they can be found in all ecosystems and main terrestrial habitats. However, the ant fauna of Mongolia is still incompletely known.

Mocsáry & Szépligeti (1901) and Ruzsky (1903, 1915) published the pioneer works on the Mongolian ants, based on material from the southern Gobi and northern forested areas. However, the exact locality of some historical records from southern and northern Mongolia is

unclear, because these places are now in China or Russia, and difficult to access. For instance, Hølgersen (1943) recorded *Myrmica rubra* (Linnaeus, 1758) from the place named as Sajan, Sistikem, but Wetterer & Radchenko (2011) revealed that the actual name of this place is Systyg Khem of the Sayan Mountains (in Siberia), which is located in the Russian Republic of Tuva. Another example is Stitz (1934), who reported five species, namely *Formica clara* Forel, 1886, *F. picea* Nylander, 1846, *Lasius alienus* (Foerster 1850), *Tapinoma geei* Wheeler, 1927 and *T. orthocephalum* Stitz, 1934 from south and southwestern Mongolia, without giving exact names of the collection localities. Two of the above-mentioned species, *T. geei* and *L. alienus*, have not yet been confirmed in Mongolia. It is possible that the collection sites are located in Inner Mongolia, China.

Actual research on ants in Mongolia is considered to have commenced in the mid 1960s with Dlussky (Dlussky 1965). Later, Pisarski (1969a, b), Dlussky & Pisarski (1970), Pisarski & Krzysztofiak (1981) and Radchenko (1994a) published extensive works and recorded more than 50 species for the country. However, this number required some amending to reflect the taxonomic status and actual occurrence of some species in Mongolia. Therefore, Radchenko (1994a, b, 1995, 1997, 2005) and Seifert (2000, 2002, 2004) provided additional information on the ants of Mongolia, and were concerned with the taxonomic resolution of the species. Pfeiffer *et al.* (2003) completed the first comprehensive study on ant communities in Mongolia examining the distribution patterns of ants along an ecological gradient from steppe to desert, assessing the impact of climatic parameters and the influence of vegetation on community structure and species diversity of ants. Later, Aibek *et al.* (2006) reported 17 species from Mt Bogdkhan in north-central Mongolia along with information on nesting habits of each species. They reviewed the ant species list recorded in this mountain area, and made comments on status and earlier records of some of those species.

Summarising the literature sources as well as their unpublished records, a checklist of ants in Mongolia was published by Pfeiffer *et al.* (2007), which reported 68 species from 17

genera, with new records of six species. They excluded several species from the checklist due to improbable occurrence or incorrect identification. Subsequently, Yamane & Aibek (2007) published a short note on ants of Mongolia that included all species also included in Pfeiffer *et al.* (2007).

Later studies focused on certain systematic groups, rather than on documentation of overall faunal diversity. Thus, Aibek & Yamane (2009) reviewed the genus *Camponotus* in Mongolia, and recorded five species along with a new finding of two species, *C. aterrimus* Emery, 1895 and *C. (Tanaemyrmex) tashcumiri* Tarbinsky, 1976. Subsequently, these authors studied the subgenera *Austrolasius* and *Dendrolasius* of the genus *Lasius* in Mongolia (Aibek & Yamane 2010), and reported nine species of *Lasius*, two of which, namely *L. (Austrolasius) reginae* Faber, 1967 and *L. (Dendrolasius) fuji* Radchenko, 2005, were new records for the Mongolian fauna. *Lasius obscuratus* Stitz, 1930, which had been excluded from the Mongolian fauna by Pfeiffer *et al.* (2007), who doubted the occurrence of this species in Mongolia, was again listed by Aibek & Yamane (2010). However, the nominal subgenus *Lasius* has not been seriously revised, leaving many problems.

More recently, Yamane & Aibek (2012) studied the distributional patterns of 14 species of the genus *Myrmica* in Mongolia, and provided an identification key for all those species. They omitted *Myrmica commarginata* Ruzsky, 1905 from the species list, but newly added *M. lobicornis* Nylander, 1846.

A significant focus for present-day myrmecologists is the assessment of biodiversity, community composition, biogeography, and other basic investigations of the ecology of a regional ant biota. Such a study would grant researchers a background from which to begin further more detailed studies. The research presented here examines the ant fauna of Mongolia in a biogeographical and ecological context. For the moment we simply attempt to combine what is already known with our unpublished data in order to contribute to a better understanding of the diversity and biogeography of ants in Mongolia. Hopefully, this work will also help to conserve the interesting ant fauna of Mongolia.

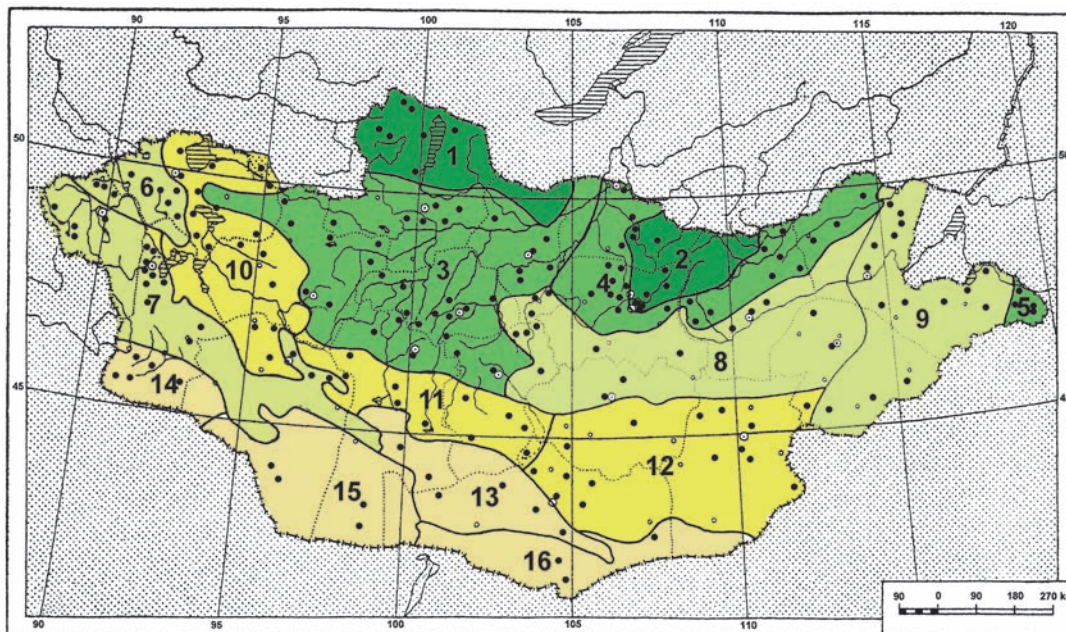


Fig. 1. Phytogeographical regions of Mongolia (modified after Yunatov 1950). Refer to “Study area” subsection for numbering of these regions. White dots represent major cities, black dots the sampling points of our study. Dark green represents mountain taiga forest, light green – forest steppe, yellowish green – steppe, yellow – semi-desert, tawny – desert ecosystems.

MATERIALS AND METHODS

Study area

Mongolia stretches across central and north-east Asia, and occupies several vegetation zones where the Siberian taiga forest meets the Central Asian steppe and desert. The north-south axis measures more than 1,200 km at its maximum, and the widest east-west distance reaches about 2,370 km. Mongolia is an upland country, with an average elevation of 1,580 m (range of elevation: 560 – 4374 m), and about 85% of its area elevated over 1,000 m a.s.l. (Murzaev 1952).

Mongolia has an extreme continental climate, and temperature fluctuates greatly, both daily and annually. As estimated for about 60 years between 1940 and 2000, the lowest temperatures are recorded in January, with monthly averages under -15°C and minimum temperatures as low as -30°C . July is the warmest month, with mean temperature 15°C in the mountains and 25°C in the southern semi-desert and deserts (Natsagdorj

& Dagvadorj 2010). The highest precipitation values do not exceed 600 mm in the northern mountains, whereas southern desert areas receive roughly 50 mm of precipitation. From the north to the south of the country, mean annual precipitation decreases steadily, which is a decisive factor for the distribution of vegetation formations. From north to south it not only gets drier, but warmer as well. From the west to the east some areas show comparatively low precipitation because they are on the lee side of mountain chains. Such a rain shadow effect is most pronounced in the depressions of larger lakes in western Mongolia, but it is recognisable in central and eastern Mongolia (Hilbig 1995). This complex set of parameters, together with the large area of the country, creates a large variety of habitats and has a distinct influence on the biodiversity of the region.

Temperature and vegetation follow a similar pattern of altitudinal zonation, and generally speaking, the north to south distribution of vegetation zones corresponds well with the precipitation pattern. Thus, Mongolia has several

vegetation zones and vertical belts, i.e. from north to south we meet: alpine meadow (alpine vegetation with upper limit of closed turf), mountain taiga-forest, forest-steppe, steppe, desert-steppe (semi-desert), and desert (Yunatov 1950; Murzaev 1952).

Based upon vegetation, floral composition, topographic and climatic characteristics, Mongolia divides into 16 phytogeographical regions (Yunatov 1950; Murzaev 1952; Grubov 1955, 1982; Fig. 1). Two of these regions are mountain taiga forests (1. Khuvsugul, 2. Khentii), three are forest-steppes (3. Khangai, 4. Mongolian Dauria, 5. Great Khyangan), four are steppes (6. Khovd, 7. Mongolian Altai, 8. Middle Khalkh, 9. Eastern Mongolia), four are semi-deserts (10. Depression of Great Lakes, 11. Valley of Lakes, 12. Eastern Gobi, 13. Gobi Altai), and three are desert regions (14. Dzungarian Gobi, 15. Trans-Altai Gobi, 16. Alashan Gobi).

Data collection

The material studied has been obtained from our collections as well as from samples provided by other zoologists and students, derived from different regions of Mongolia. Our collections came from 202 sites covering 993 samples, which involved more than 10,500 specimens. Sampled sites covered the main habitats in all phytogeographical regions of Mongolia though the number of samples in each region was different because of their varying area, habitat types and remoteness (see Fig. 1). Ant collections are currently deposited in the Department of Ecology, National University of Mongolia, Ulaanbaatar, Mongolia.

In addition, we collected all previously available information on ant species in Mongolia, including revisions of species groups (Mocsáry & Szépligeti 1901; Ruzsky 1903, 1915; Dlussky 1965; Pisarski 1969b, a; Dlussky & Pisarski 1970; Pisarski & Krzysztofiak 1981; Radchenko 1994a, 1994b, 1995; Seifert 2000, 2002; Pfeiffer *et al.* 2003; Seifert 2004; Radchenko 2005; Aibek *et al.* 2006; Pfeiffer *et al.* 2007; Yamane & Aibek 2007; Aibek & Yamane 2009, 2010; Seifert & Schultz 2009; Yamane & Aibek 2012), as well as species lists from the internet (e.g. <http://www.antbase.org>;

<http://www.antbase.net>; <http://www.antcat.org>; <http://antwiki.org>). In the present paper, the species list by Pfeiffer *et al.* (2007) is updated with some modifications. Generic and species names of ants are listed in alphabetical order.

The relative area of the phytogeographical regions of Mongolia is taken from Ulziikhutag (1989). Plant species richness was estimated based on the number of vascular plant species recorded within each phytogeographical region (Gubanov 1996; Ariuntsetseg & Boldgiv 2009).

Biogeographical analysis of ant species found in Mongolia is based on data in the published literature which provides information on geographical ranges (Seifert 1992, 2000; Bolton 1995; Kupyanskaya 1995; Collingwood 1997; Czechowski *et al.* 2002; Bolton 2003; Imai *et al.* 2003; Radchenko 2005; Aibek & Yamane 2009, 2010; Radchenko & Elmes 2010; Guénard & Dunn 2012). Division of biogeographical regions is based on that applied by Bielawski (1984), Nikolajev & Puntsagdulam (1984), Bayartogtokh (2010) and Bayartogtokh *et al.* (2012).

Data analysis

We assessed the similarity of the ant species in Mongolia and other surrounding regions using Sørensen-Dice's qualitative Index (C_s ; see Jackson *et al.* 1989). If $C_s = 0$, the faunas are completely different from each other, if $C_s = 1$, the faunas are identical. Cluster analysis was performed using Euclidian distance measure and the complete linkage clustering algorithm with the software BioDiversity Professional (McAleece *et al.* 1997).

The occurrences of ants in different altitudes and phytogeographical regions were arranged in presence/absence tables. Multiple regression analysis was used to examine relationships of ant diversity versus plant diversity and area size.

The differences in the number of plant and ant species and in the percentage of cover areas between the various phytogeographical regions, as well as differences in the number of ant species along various elevational gradients, were tested using one-way analysis of variance (ANOVA). We used Pearson's product-moment correlations to examine the relationships of species richness of

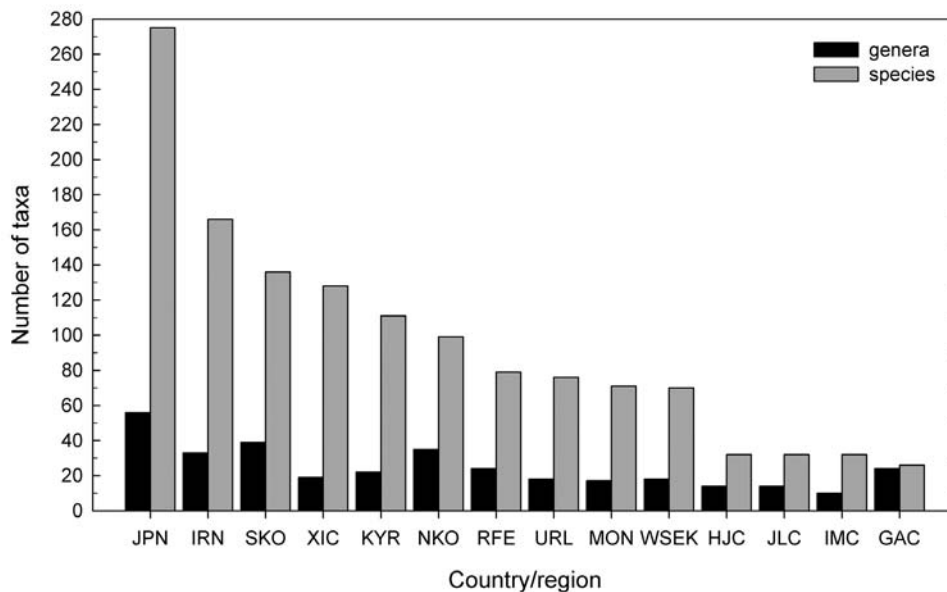


Fig. 2. Relationship of generic and species diversity of ants in Mongolia and its surrounding regions. Abbreviations: JPN – Japan; IRN – Iran; SKO – South Korea; XIC – Xinjiang, China; KYR – Kyrgyzstan; NKO – North Korea; RFE – Russian Far East; URL – Ural region of Russia; MON – Mongolia; WSEK – Western Siberia and eastern Kazakhstan; IMC – Inner Mongolia, China; HJC – Heilongjiang, China; JLC – Jilin, China; GAC – Gansu, China.

ants versus area size, and plant diversity versus ant diversity. All statistical analyses were performed with software Statistica 5.0 for Windows (StatSoft Inc.). For all statistical tests, we considered results significant when $p < 0.05$.

RESULTS

Diversity of ants

Based on our investigations, the ant fauna of Mongolia comprises 71 species belonging to 17 genera in three subfamilies. A list of ant species and their occurrences in various phytogeographical regions of Mongolia is given in Appendix 1. With regard to our species list, the discrepancy with the data from Pfeiffer *et al.* (2007) who listed 68 species for this country arises because six species (*Camponotus aterrimus*, *C. tashcumiri*, *Formica orangea* Seifert & Schultz, 2009, *Lasius reginae*, *L. fuji* and *Myrmica lobicornis*) have recently been added to the fauna of Mongolia (Aibek & Yamane 2009; Seifert & Schultz 2009; Aibek & Yamane 2010; Yamane & Aibek 2012).

On the other hand, we omitted *Lasius flavus* (Fabricius, 1781) and *Myrmica rubra* as these do not occur in Mongolia (Aibek & Yamane 2010; Wetterer & Radchenko 2011). We also removed *Temnothorax servicus* (Ruzsky, 1902) from the fauna list because its former subspecies, *T. mongolicus* (Pisarski, 1969), exists in Mongolia (Pisarski 1969b), and is now an independent species (the nominal subspecies does not occur in Mongolia). *Camponotus japonicus* Mayr, 1866 was also removed from the list because its former subspecies, *C. aterrimus* is now considered an independent species, while the nominal subspecies *C. japonicus* does not occur in Mongolia (Aibek & Yamane 2009). Kupyanskaya (2012) has listed *Formica japonica* Motschoulsky, 1866 as distributed in Mongolia, but its occurrence in this country has not been confirmed. So, we omitted this species from the list.

Yamane & Aibek (2012) considered the occurrence of *Myrmica ruginodis* Nylander, 1846 in Mongolia improbable as this species was not discovered during the recent extensive explorations throughout the country. However, we include this species in the checklist based

on Radchenko & Elmes (2010), who provided a distribution map in which the geographical range of *M. ruginodis* covered northern Mongolia.

The largest number of Mongolian species belongs to the subfamily Formicinae (39 spp.), followed by Myrmicinae (29 spp.); these two subfamilies comprise more than 95 per cent of the total ant species. A third subfamily, the Dolichoderinae, is poorly represented in Mongolia with only three species (Appendix 1).

The most species rich and commonly encountered genera were *Formica* (19 spp.), *Myrmica* (14 spp.), *Lasius* (7 spp.), *Camponotus* (5 spp.) and *Proformica* (5 spp.). The other genera involved less than five species. *Temnothorax* and *Tetramorium* were both represented by four species, and *Leptothorax*, *Messor* and *Tapinoma* by two species only. Seven genera were represented by a single species, namely: *Cardiocondyla*, *Cataglyphis*, *Crematogaster*, *Dolichoderus*, *Harpagoxenus*, *Plagiolepis* and *Polyergus*. Thus, only a few ant genera were species rich, whereas the majority comprised fewer species, with the mean number per genus 4.2, and the median only 2.0.

We compared the richness of ants in Mongolia with that of the surrounding countries or regions, and found that both genus and species richness of ants in Mongolia were lower than in most neighbouring regions (Fig. 2). Only the

regions of northern China showed much lower richness of ants, but this is most probably due to insufficient investigation of those areas (see Discussion for references and species lists).

The ant fauna of Mongolia shares relatively few species with those of the surrounding regions as a proportion of the total number of species in compared regions or countries; hence the estimated faunal similarity was very low. The Russian Far East and Gansu Province of China showed the closest similarity with the Mongolian ant fauna. Of the countries examined, Japan and Iran had the lowest faunal similarity with Mongolia (Table 1).

Distribution of ants in phytogeographical regions

The number of ant species in the 16 phytogeographical regions ranged from 3 to 39 with a mean of 19. Each of these regions had a peculiar composition of ants, but there were several species dominating in most regions. Thirty-nine species were found in the Khentii mountain-taiga region, 38 species in the Mongolian Dauria forest-steppe region, 30 species in the Khangai forest-steppe region, 28 species in the Middle Khalkh steppe region, 25 species in Mongolian Altai mountain-steppe, 24 species in Depression of Great Lakes desert-steppe regions, and 20 species in the Eastern

Table 1. Faunal similarity of the Mongolian ant fauna with that of the surrounding regions. Total number of species, number of overlapping species, and Sørensen-Dice's Index of similarity (C_s) values.

	KYR	URL	WSEK	IRN	RFE	XIC	IMC	HJC	GAC	JLC	SKO	NKO	JPN
Number species in each country/region	111	76	70	166	79	128	26	32	26	32	136	99	275
Number of common species with Mongolia	26	24	20	11	25	26	12	12	16	11	20	27	9
Similarity with Mongolian ant fauna (C_s)	0.22	0.25	0.22	0.08	0.25	0.21	0.20	0.19	0.25	0.18	0.16	0.24	0.05

Refer to Fig. 2 for abbreviations of the names of the countries/regions. Only native species are considered, exotic species are excluded.

Gobi desert-steppe region. The species richness of ants in other phytogeographical regions varied between 3 and 18 (see Appendix 1).

One species, *Formica candida* Smith, 1878, was common to 12 phytogeographical regions, and another species, *Proformica mongolica* Emery, 1901, inhabited 11 out of 16 regions which provide a variety of habitats. Three species, *Cataglyphis aenescens* (Nylander, 1849), *F. kozlovi* Dlussky, 1965 and *Tetramorium tsushimae* Emery, 1925 were found in ten regions. *Formicalemani* Bondroit, 1917 was recorded from nine regions, and two other species, *F. clarissima* Emery, 1925 and *F. pisarskii* Dlussky, 1964, were distributed in eight regions. The other 63 species were confined to seven regions or fewer. From our data it was apparent that 13 species are rather rare in Mongolia, their distribution being restricted to a single phytogeographical region (see Appendix 1). A large number of species were restricted to only two or three regions (12 and 9 spp., respectively).

Differences between the faunal compositions of ants in various phytogeographical regions are of great interest. Regions were grouped into four main clusters (Fig. 3), and the dissimilarity of the regions reflected their different geographical position and discrepant ecological conditions. Most of these clusters involved the regions that are geographically adjacent to one

another, and reflected the main landscape pattern of Mongolia. For instance, the boreal forest group includes the Khentii, Khangai and Mongolian Dauria regions. The dry steppe group includes Middle Khalkh, Eastern Mongolia and Mongolian Altai regions. The semi-desert group involves Gobi-Altai, Eastern Gobi, Depression of Great Lakes and Khovd regions. The Gobi desert group encompasses Trans-Altai Gobi, Eastern Gobi, Dzungarian Gobi, Valley of Lakes and Alashan Gobi regions. The main surprising pattern here was the relatively low dissimilarity observed between two distant and ecologically different regions, such as Khuvsgul mountain taiga region and Khovd mountain-steppe region. We consider that this was because only a few wide-ranging species (7 spp.) were found in Khuvsgul region. It should be noted here that because of different sampling effort, diversity of ants in some regions, such as Khuvsgul, Great Khyangan, Valley of Lakes, Dzungarian Gobi, Alashan Gobi etc. might be not fully explored yet. Overall, the ant faunas in various regions were relatively distinct, and this fact confirms the well-established classification of the phytogeographical regions in Mongolia.

Species-area relations

Regarding the geographical distribution of ant species in various phytogeographical regions of

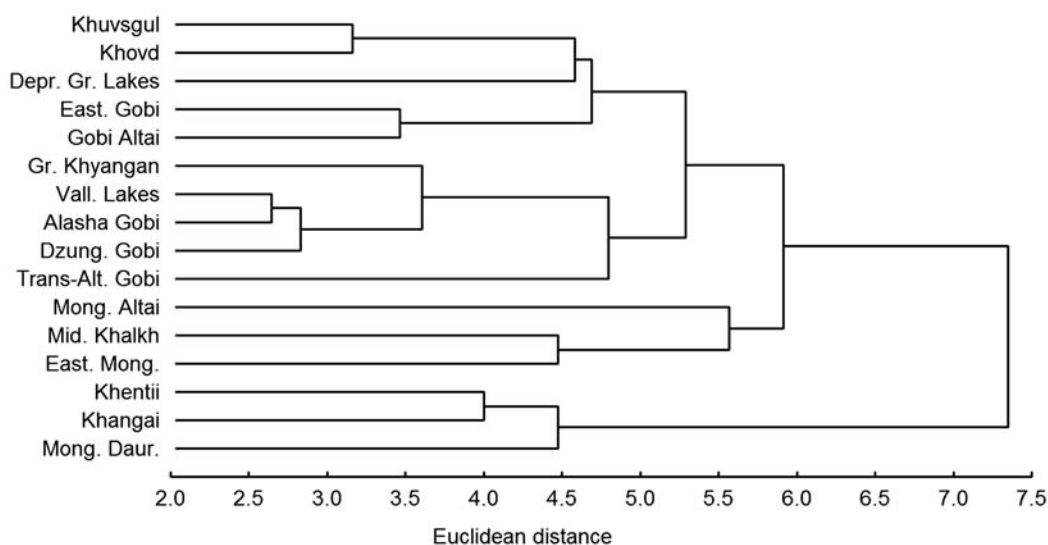


Fig. 3. A dendrogram depicting the faunal dissimilarity of ants among the phytogeographical regions of Mongolia.

Mongolia, we found a mismatch between the regions' extent and the respective number of ant species. The highest number of species (39 of a total 71 spp.) was recorded in Khentii mountain-taiga region, though the total area of this region is only 3.05% of the territory of Mongolia. Thirty-eight species were found from the Mongolian Dauria

forest-steppe region that covers only 6.62% of the country. Thirty species were recorded in Khangai forest-steppe region, which comprises 17.59% of the entire area of the country. Species richness of ants and total land area of regions were not correlated (Pearson's correlation, $n = 16$, $r = 0.44$, $p = 0.08$, n.s., Fig. 4).

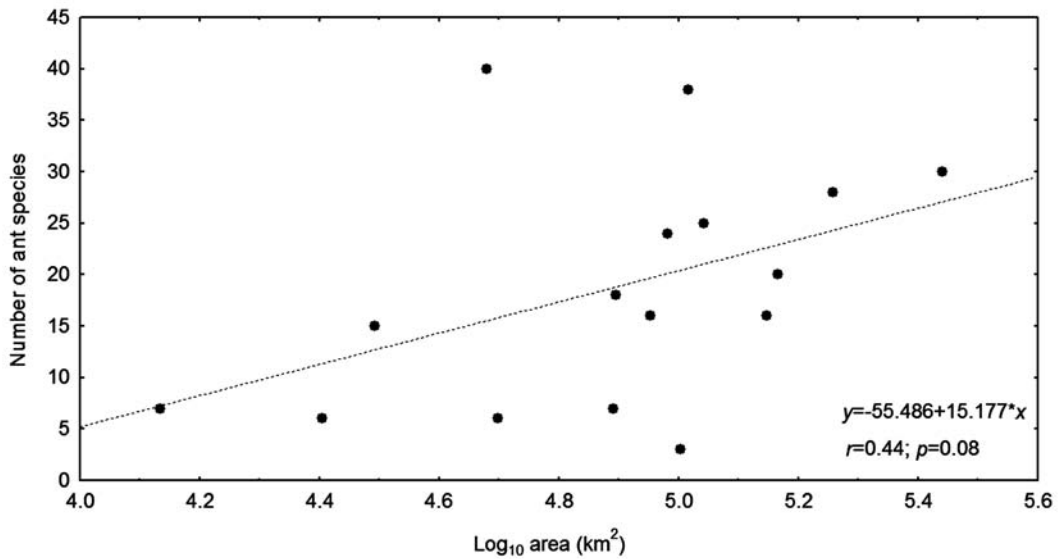


Fig. 4. Non-significant relationship between area size and ant diversity in various biogeographical regions of Mongolia. A regression line was fitted to visualise the hypothesised interdependence.

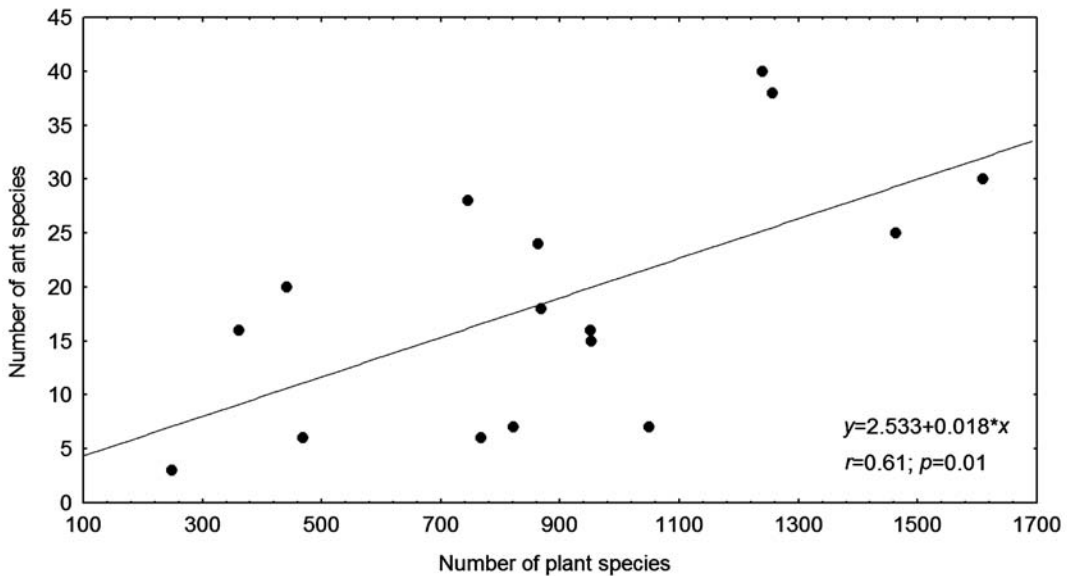


Fig. 5. Relationship between plant and ant diversity in various biogeographical regions of Mongolia. A regression line was fitted to visualise the connection between the two variables.

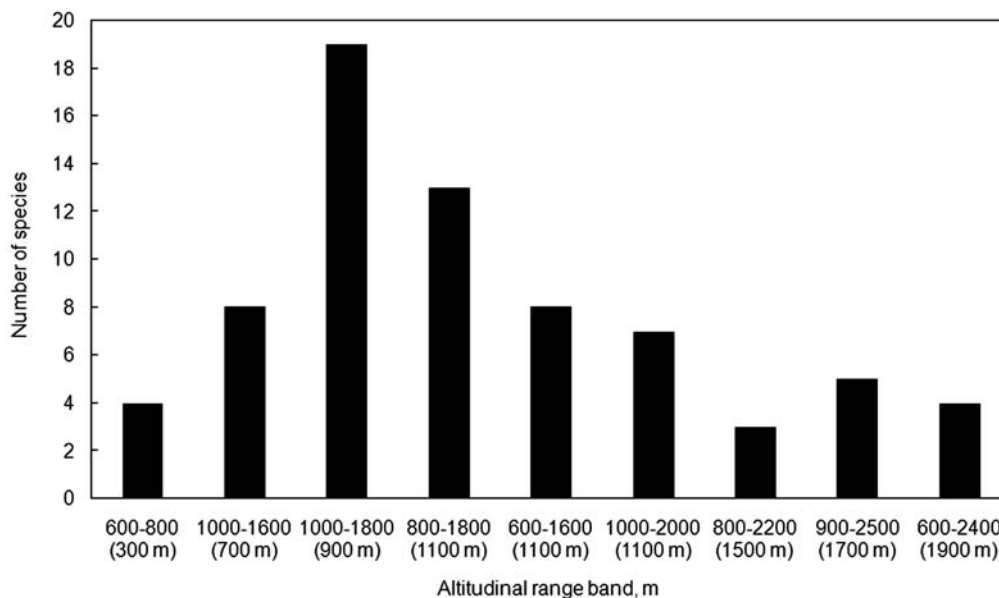


Fig. 6. Altitudinal ranges of ants in Mongolia, showing number of species in each category of altitudinal range, with a minimum range of 300 m and a maximum of 1,900 m (size of altitudinal range is given in parentheses).

Since area size and plant diversity were not correlated for the phytogeographical regions (Pearson's correlation, $n = 16$, $r = 0.31$, $p = 0.24$), we plotted them separately against ant species richness. Within the study region as a whole, plant diversity in different phytogeographical regions varied significantly (ANOVA, $df = 1$, $F = 21.16$, $p = 0.0004$). Diversity of ants and vascular plants within phytogeographical regions showed a significant positive correlation (Pearson's correlation, $n = 16$, $r = 0.61$, $p = 0.01$) (Fig. 5).

Altitudinal pattern of diversity

Our calculation of the altitudinal distribution of ant species was based upon collection data from 307 different elevational points. There was no strong differentiation in ant community composition along an altitudinal gradient, as most of the species were recorded in a wide range of elevations (Fig. 6). The width of altitudinal range was very large for most of the ant species, hence the number of species in various altitudes did not differ significantly (ANOVA: $df = 1$, $F = 1.64$, $p = 0.24$). Only four species, *Myrmica commarginata*, *Proformica coriacea* Kuznetsov-Ugamsky, 1927, *Tapinoma orthocephalum* and *T. sinense* Emery,

1925, were restricted to lower altitudes, between 600 and 800 m a.s.l. Several other species (*Formica exsecta* Nylander, 1846, *Lasius niger* Linnaeus, 1758, *Myrmica lobicornis*, *Polyergus nigerrimus* Marikovsky, 1963, *Proformica kaszabi* Dlussky, 1969, *Tetramorium armatum* Santschi, 1927, *T. concaviceps* Bursakov, 1984 and *T. inerme* Mayr, 1877) were reported at elevations of 600 – 1600 m a.s.l. Twelve species (*Formica candida*, *F. cunicularia* Latreille, 1798, *F. kozlovi*, *F. lemani*, *F. manchu* Wheeler, 1929, *F. pisarskii*, *F. uralensis* Ruzsky, 1895, *Leptothorax acervorum* Fabricius, 1793, *L. muscorum* Nylander, 1846, *Myrmica divergens* Karavaiev, 1931, *M. eidmanni* Menozzi, 1930, *M. kasczenkoi* Ruzsky, 1905) were present at the widest range of elevations, between 600 and 2,400 m a.s.l. Species richness was greatest between 1,000 and 2,000 m a.s.l., as 27 species were recorded in this mid-elevational band, whereas 22 species occurred at 800 – 1,800 m a.s.l. Thus, we found a peak of species richness between 800 and 2,000 m a.s.l.

Geographical distribution of species

The geographical distributions of all known species of ants in Mongolia were compiled, and

the species were divided into groups based upon their range. Table 2 shows the biogeographical composition of the ant fauna of Mongolia. Species with a wide geographical distribution comprise a large proportion of the ant fauna of Mongolia. Three species, *Leptothorax acervorum*, *L. muscorum* and *Tetramorium tsushimae* are widely distributed throughout the Holarctic Region. The quantitatively most important biogeographical elements were Transpalaeartic (24 spp., 33.8%), Central Asian (15 spp., 21.1%), Eastern Palaeartic (13 spp., 18.3%) and East Asian species (10 spp., 14.1%). A few species, *Myrmica arnoldii* Dlussky, 1963, *M. commarginata*, *M. pisarskii* Radchenko, 1994 and *Polyergus nigerrimus*, are restricted to Siberia and Mongolia (4 spp., 5.6%). *Formica pressilabris* Nylander, 1846 is the only representative of European-Siberian species (1 sp., 1.4%). There was only a single species, *Harpagoxenus zaisanicus* Pisarski, 1963, that appears to be endemic to Mongolia. This species

was described by Pisarski (1963) from Mongolia, and has not been found outside the country (Bolton 2010). The absence of Oriental or Afrotropical faunal components in Mongolia is notable.

DISCUSSION

Species richness

Mongolia has representatives of about 7.4% of the known world ant genera and 0.52% of the currently described species (Bolton 2010), altogether 71 species from 17 genera – a relatively impoverished fauna compared to most of the surrounding regions. Thus, Tarbinsky (1989) found 103 species belonging to 23 genera from Tien-Shan and Alai mountains in Central Asia (Kyrgyzstan); Schultz *et al.* (2006) and Borowiec *et al.* (2009) recorded 111 species (22 genera) from Kyrgyzstan; Gridina (2003) recorded 76

Table 2. Biogeographical composition of ants in Mongolia.

Species name	Species number	Geographical range
<i>Leptothorax acervorum</i> , <i>L. muscorum</i> , <i>Tetramorium tsushimae</i>	3	Holarctic
<i>Cataglyphis aenescens</i> , <i>Crematogaster subdentata</i> , <i>Formica aquilonia</i> , <i>F. candida</i> , <i>F. clara</i> , <i>F. cunicularia</i> , <i>F. exsecta</i> , <i>F. forsslundi</i> , <i>F. lemani</i> , <i>F. lugubris</i> , <i>F. pisarskii</i> , <i>F. pratensis</i> , <i>F. sanguinea</i> , <i>F. truncorum</i> , <i>F. uralensis</i> , <i>Lasius distinguendus</i> , <i>L. gebaueri</i> , <i>L. niger</i> , <i>L. reginae</i> , <i>Myrmica divergens</i> , <i>M. lobicornis</i> , <i>M. ruginodis</i> , <i>M. sulcinodis</i> , <i>Temnothorax nassonovi</i>	24	Transpalaeartic
<i>Camponotus aterrimus</i> , <i>Formica kozlovi</i> , <i>F. manchu</i> , <i>F. obscuratus</i> , <i>Myrmica angulinodis</i> , <i>M. eidmanni</i> , <i>M. koreana</i> , <i>M. transsibirica</i> , <i>Plagiolepis manczshurica</i> , <i>Proformica buddhaensis</i> , <i>P. jacoti</i> , <i>Temnothorax kaszabi</i> , <i>T. mongolicus</i>	13	Eastern Palaeartic
<i>Camponotus tashcumiri</i> , <i>C. turkestanus</i> , <i>Cardiocondyla koshewnikovi</i> , <i>Formica clarissima</i> , <i>F. orangea</i> , <i>F. subpilosa</i> , <i>Lasius przewalskii</i> , <i>Messor excursionis</i> , <i>Proformica coriacea</i> , <i>P. kaszabi</i> , <i>Tapinoma orthocephalum</i> , <i>Temnothorax melleus</i> , <i>Tetramorium armatum</i> , <i>T. concaviceps</i> , <i>T. inerme</i>	15	Central Asian and Iran-Turanian
<i>Formica pressilabris</i>	1	Europe-Siberian
<i>Myrmica arnoldii</i> , <i>M. commarginata</i> , <i>M. pisarskii</i> , <i>Polyergus nigerrimus</i>	4	Siberia-Mongolian
<i>Camponotus sachalinensis</i> , <i>C. saxatilis</i> , <i>Dolichoderus sibiricus</i> , <i>Lasius fuji</i> , <i>Messor aciculatus</i> , <i>Myrmica forcipata</i> , <i>M. kamtschatica</i> , <i>M. kasczenkoi</i> , <i>Proformica mongolica</i> , <i>Tapinoma sinense</i>	10	East Asian
<i>Harpagoxenus zaisanicus</i>	1	Mongolian endemic

species from 18 genera in the Ural region of Russia; Reznikova (2003) revealed 70 species (18 genera) along a transect from taiga-forest to desert in western Siberia and eastern Kazakhstan. Another Asian country, Iran, which has a similar land area to Mongolia, supports a much higher diversity of ants, according to Paknia *et al.* (2008, 2010), Radchenko & Paknia (2010), Firouzi *et al.* (2011), Ghahari & Collingwood (2011), Mohammadi *et al.* (2012), and Nezhad *et al.* (2012), who altogether listed 166 species (33 genera) from this country. Kupyanskaya (1995) reported 79 species (24 genera) in the Russian Far East. Concerning northern China, Guénard & Dunn (2012) reported 128 species (19 genera) from Xinjiang, 26 species (10 genera) from Inner Mongolia, 26 species (24 genera) from Gansu, 32 species (10 genera) from Heilongjiang, and 32 species (14 genera) from Jilin provinces. Three other East Asian countries, more distantly located from Mongolia, also have a much higher diversity of ants: Kim & Park (2003) reported 136 species (39 genera) from South Korea; Radchenko (2005) found 99 species (35 genera) in North Korea, and Imai *et al.* (2003) listed 275 species (56 genera) from Japan.

This might reflect the intensity of the investigations carried out in different countries or regions. It should be noted that, with the exception of Japan, the ant faunas of most of the nearby regions (especially in northern China) have not been fully explored, and the number of species known from those regions may increase significantly when remote or unexplored areas have been surveyed and all available material has been examined (see Guénard & Dunn 2012). Nevertheless, current information is considered to be adequate to gain an understanding of the major faunal patterns in these regions (see Kim & Park 2003; Radchenko 2005; Paknia *et al.* 2008; Guénard & Dunn 2012).

On the other hand, the extremely harsh and fluctuating climates, as well as arid or very dry conditions in most areas of Mongolia, make the country unfavourable for the habitation of species that require humid, sub-continental mild climates. This pattern of climatic and environmental conditions in Mongolia might be considered the main basis for the relatively poor composition of the ant fauna as compared with

the surrounding regions or countries, regardless of land area. In general, ant species diversity declines with latitude and altitude elsewhere (Kusnezov 1957; Cushman *et al.* 1993; Dunn *et al.* 2009a, b; Guénard & Dunn 2012), and this effect may, to some extent, explain the relatively low diversity of ants in Mongolia as the country lies at northern latitudes and relatively high altitudes possessing a cold climate.

Concerning the faunal composition of ants in Mongolia, two major subfamilies, Formicinae and Myrmicinae, comprise more than 95% of the total recorded species, while another subfamily, Dolichoderinae, is represented by only three species. The Formicinae and Myrmicinae are the largest ant subfamilies in the world and the dominant groups in most terrestrial habitats. The prevalence of these subfamilies has been reported to increase with increasing aridity (Marsh 1986; Lindsey & Skinner 2001). In contrast, Australian and North American semi-arid areas are characterised by a more even spread of species across subfamilies such as the Dolichoderinae and Ponerinae (Briese & Macauley 1977; Whitford *et al.* 1978; Andersen 1986). This may reflect the different evolutionary histories of the ant faunas of the arid areas in these places.

Almost half of the recorded species in the Mongolian ant fauna belong to the genera *Formica* and *Myrmica*. Five other genera contain four or more species in Mongolia: *Camponotus* (5 spp.), *Lasius* (7 spp.), *Proformica* (5 spp.), *Temnothorax* (4 spp.) and *Tetramorium* (4 spp.). Together, the seven most diverse genera constitute nearly 81% of the ant species known from Mongolia, while other genera, such as *Cardiocondyla*, *Cataglyphis*, *Crematogaster*, *Dolichoderus*, *Harpagoxenus*, *Leptothorax*, *Messor*, *Plagiolepis*, *Polyergus* and *Tapinoma*, comprise a much smaller proportion of the fauna. Similar faunistic patterns are found in other arid Asian regions, e.g. eastern Kazakhstan and western Siberia (Reznikova 2003), the Ural region of Russia (Gridina 2003), Kyrgyzstan (Tarbinsky 1989; Schultz *et al.* 2006) and northern China (Guénard & Dunn 2012).

We suppose that the main faunal composition of ants of Mongolia is already revealed, but some cryptic species likely remain undiscovered because previous collecting has

been mostly limited to nest collections, pitfall traps and rarely baited traps. Extraction of ants from sifted leaf litter using Winkler traps has proved to be very productive when conducting systematic inventories of ants (Fisher 1999; Longino *et al.* 2002), but – to our knowledge – still has not been conducted in higher altitudes.

Distribution in phytogeographical regions

Based on the similarity analysis of the ant faunas of various phytogeographical regions, three main groups can be distinguished. The “forest-steppe” group encompasses the Khentii, Mongolian Dauria, Khangai, Middle Khalkh, Eastern Mongolia and Great Khyangan regions. The “steppe-semidesert” group includes the Khovd, Depression of Great Lakes, Mongolian Altai, Valley of Lakes, Eastern Gobi, Gobi Altai and Trans-Altai Gobi regions. The “desert” group consists of the Alashan Gobi and Dzungarian Gobi regions. Surprisingly, the Khuvs gul taiga forest region fell within “steppe-semidesert” group, but we consider this is because of the very low ant diversity discovered in Khuvs gul region, as only seven species were recorded there. As we noted above, due to lower sampling intensity and completeness in various phytogeographical regions of Mongolia, the actual diversity of ants may increase, when remote or unexplored areas have been surveyed.

It is notable that the most common species (e.g. *Cataglyphis aenescens*, *Formica aquilonia*, *F. candida*, *F. kozlovi*, *F. lemani*, *F. pisarskii*, *Proformica mongolica*) tended to be widely distributed across various phytogeographical regions, but in contrast, the rare species (*Dolichoderus sibiricus*, *F. pressilabris*, *Lasius reginae*, *L. obscuratus*, *Messor excursionis*, *Myrmica commarginata*, *M. jessensis*, *M. kamtschatica*, *M. ruginodis*, *M. transsibirica*, *Tapinoma orthocephalum*, *T. sinense*, *T. melleus*, *Tetramorium concaviceps*) were highly restricted in their distribution, generally occurring only in one region. However, this might also be a sampling artefact as rare species are hard to find and detect.

Pfeiffer *et al.* (2003) noted the considerable change of ant communities along the environmental gradient from steppe to desert,

and found that the steppe was dominated by cold-resistant species; semi-desert supported mainly opportunistic species, whereas desert involved mostly hot climate specialists. However, these authors, and also Morton & Davidson (1988) and Medel (1995), found no correlation between precipitation and diversity of ants.

Generally, the species richness of local ant communities is primarily influenced by climatic conditions (e.g. temperature regimes, precipitation), landform, nest sites, microhabitat patterns (e.g. vegetation cover, soil type, moisture, texture), and food resource availability (Koen 1988; Andersen 1993, 2000; Bestelmeyer & Wiens 2001; Fergnani *et al.* 2008). In Mongolia, however, due to the high habitat heterogeneity, species diversity of ants in various phytogeographical regions may differ as a consequence of small microclimatic factors that can determine whether a species is present or absent within a location (Pfeiffer *et al.* 2003); thus small-scale patterns of habitat distribution are important for ant life in Mongolia, especially in arid regions. Li *et al.* (2011) revealed that in arid ecosystems of Central Asia, the species richness and abundance (nest density) of ants are closely associated with silt content, soil organic matter, nitrogen and soil moisture, as well as topsoil temperature. Similarly, in humid subtropical and dry tropical areas, habitat strongly influences the composition and community structure of ants (Lindsey & Skinner 2001; Calcatera *et al.* 2010).

Relation between plant and ant richness

Positive correlation between plant diversity and diversity of ants is frequently reported (Andersen 1997; Paknia & Pfeiffer 2012), and this was in accordance with our results on the relationship between the diversity of ants and that of vascular plants in the various phytogeographical regions of Mongolia. Other investigations showed that habitats with more complex vegetation structure and higher primary productivity support more diverse and dense ant assemblages (Andersen 1997; Kaspari *et al.* 2000; Sarty *et al.* 2006; Paknia & Pfeiffer 2012). Moreover, in arid habitats of central and southern Mongolia, Pfeiffer *et al.* (2003) revealed that structures of ant and plant communities were highly correlated.

These authors also indicated that the ant diversity pattern could be a result of the productivity of resources that is a consequence of soil texture, small-scale topography and other mosaic-like local environmental variations.

Elevational distribution

We suggest that the unclear differentiation of elevational distribution for the majority of ant species is due to local mosaic-like topographic relief, as the vast majority of the country contains mountainous landscapes (about 85% of its area is over 1,000 m a.s.l.), the exception being the plain grasslands in eastern Mongolia. Nevertheless, the observed patterns conform to the mid-elevational rise in species richness recorded in temperate (Sanders *et al.* 2003; Glaser 2006), subtropical (Bharti *et al.* 2013) and tropical regions (Fisher 2004). At similar altitudes, the northern Palaearctic, Europe-Siberian and Boreo-montane species show a mid-elevational peak between 900 and 1,800 m a.s.l. in the Eastern Alps (Glaser 2006).

The mid-elevational peak in ant diversity is sometimes attributed to the more open and dry litter habitat conditions and prey resource availability at mid-elevations. Based on their research in tropical montane forests, Brühl *et al.* (1999) and Sabu *et al.* (2008) observed that ground ant abundance is higher in more open and drier conditions, as moist and humid habitat conditions limit ants' foraging ability and reduce the time availability for foraging on the litter floor.

The absence of ant species at elevations above 2,500 m a.s.l. might be due to low temperature and strong winds, both of which would preclude their distribution at high altitudes in Mongolia. As ants are thermophiles (Hölldobler & Wilson 1990), which react negatively to low mean annual temperatures, the cold climate seems to be a major factor working against the diversification of certain ant genera in Mongolia (Pfeiffer *et al.* 2003). Sanders *et al.* (2003) revealed that, generally, species of the subfamilies Dolichoderinae and Myrmicinae are more common at lower elevations than at higher elevations, while species of Formicinae are more common at high elevations. However, we did not observe such a pattern in altitudinal ant distributions in Mongolia.

It is worth noting that this is the first report on the elevational distribution of ants in Mongolia, and the indistinct pattern of ant distribution in various elevation steps might also be caused by varying investigation intensities in different regions of the country. This emphasises the importance of intensive biogeographic research to get more realistic elevational distribution maps.

Biogeography

The biogeographic composition of ants in Mongolia confirms it as one of the representative parts of the Palaearctic ant fauna, as there are neither Oriental nor Afrotropical species. Such a pattern was predicted by Fellowes (2006) at the generic level. The majority of ant species in Mongolia seem to be widespread in the whole Palaearctic region, with the addition of a few Holarctic elements. Thus, species which are widely distributed in these areas comprise more than half of the total species (56%).

The other specific character of the Mongolian ant fauna is the presence of strong western, northern and eastern components. Nearly one fifth (21%) of Mongolian species are distributed in various regions or countries in the Eastern Palaearctic region, such as Siberia, Russian Far East, north-eastern China, Korean Peninsula and Japan. The remaining species (22%) seem to be distributed in the arid regions of Central Asia. Although the number of species shared with surrounding regions was relatively small, the whole ant fauna of Mongolia does not differ significantly from that of the neighbouring regions, and the majority of species occurring in Mongolia probably originated in neighbouring areas to the west, north and east.

Only a single species, *Harpagoxenus zaisanicus*, is still known only from Mongolia since its discovery, and thus is considered endemic. This species has a very cryptic life style as a nest parasite (see Pisarki 1963), and is known from the dry steppe habitats in central, western and north-western Mongolia. There is a possibility of finding this species in areas neighbouring Mongolia, especially in Siberia, eastern Kazakhstan or northern China, and its endemic status cannot be confirmed until more detailed studies are performed in these areas.

There are several species occurring in the surrounding regions which might possibly be found in Mongolia in the future. These are *Myrmica schencki* Viereck, 1903, currently known from Kyrgyzstan, Xinjiang of China and the Russian Far East; *Lasius umbratus* (Nylander, 1846), currently recorded from Heilongjiang and Xinjiang provinces of China, southern Siberia, the European part and Far East of Russia, North Korea, South Korea, Japan and Taiwan; *Proformica epinotalis* Kuznetsov-Ugamsky, 1927, currently found in Heilongjiang and Xinjiang provinces of China, Kyrgyzstan, Chita region, Tuva and Buryat republics, Far East and European part of Russia; and *Camponotus itoi* Forel, 1912, distributed in Xinjiang province of China, Taiwan, North Korea, South Korea and Japan.

It should be mentioned here that we excluded the exotic species, *Monomorium pharaonis* (Linnaeus, 1758) from the species list of Mongolian ants. This species is distributed nearly all over the world, without any biogeographical significance. In Mongolia it has been found only in a human settlement, and not in natural habitats (Aibek 2011).

Finally, it should be noted that seven ant species found in Mongolia are listed as threatened species in the Red List of the International Union for Conservation of Nature. Thus, *Harpagoxenus zaisanicus*, *Lasius reginae* and *Polyergus nigerrimus* are categorised as Vulnerable species, whereas *Formica aquilonia*, *F. lugubris*, *F. pratensis* and *F. uralensis* are treated as Near-threatened species (IUCN 2012). In order to conserve Mongolia's biodiversity, the development of conservation strategies for maintaining threatened ant species and the assessment of their endangerment are required for the future.

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38	<i>L. muscorum</i> (Nylander, 1846)	0	1	1	1	0	0	1	1	0	1	0	0	0	0	0	
39	<i>Messor aciculatus</i> (Smith, 1874)	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
40	<i>M. excursions</i> Ruzsky, 1905	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
41	<i>Myrmica angulinodis</i> Ruzsky, 1905	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
42	<i>M. arnoldii</i> Dlussky, 1963	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
43	<i>M. commarginata</i> Ruzsky, 1905	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
44	<i>M. divergens</i> Karavaiev, 1931	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0
45	<i>M. eidmanni</i> Menozzi, 1930	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
46	<i>M. forcipata</i> Karavaiev, 1931	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
47	<i>M. kamschatica</i> Kupyanskaya, 1986	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	<i>M. kaszabii</i> Ruzsky, 1905	0	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0
49	<i>M. koreana</i> Elmes, Radchenko et Kim, 2001	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0
50	<i>M. lobicornis</i> Nylander, 1846	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
51	<i>M. pisarskii</i> Radchenko, 1994	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
52	<i>M. ruginodis</i> Nylander, 1846	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	<i>M. sulcinodis</i> Nylander, 1846	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
54	<i>M. transsibirica</i> Radchenko, 1994	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	<i>Plagiopsis manczhurica</i> Ruzsky, 1905	0	0	0	1	0	0	0	1	0	0	0	1	1	0	1	0
56	<i>Polyergus nigerrimus</i> Marikovskiy, 1963	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
57	<i>Proformica buddhaensis</i> Ruzsky, 1915	0	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0
58	<i>P. coriacea</i> Kuznetsov-Ugamsky, 1927	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
59	<i>P. jacoti</i> (Wheeler, 1923)	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0
60	<i>P. kaszabii</i> Dlussky, 1969	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0
61	<i>P. mongolica</i> Emery, 1901	0	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0
62	<i>Tapinoma orthocephalum</i> Stitz, 1934	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
63	<i>T. sinense</i> Emery, 1925	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
64	<i>Temnothorax kaszabi</i> (Pisarski, 1969)	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0
65	<i>T. melleus</i> (Forel, 1904)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
66	<i>T. mongolicus</i> (Pisarski, 1969)	0	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0
67	<i>T. nassonovi</i> (Ruzsky, 1895)	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
68	<i>Tetramorium armatum</i> Santschi, 1927	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
69	<i>T. concaviceps</i> Bursakov, 1984	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
70	<i>T. inerme</i> Mayr, 1877	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
71	<i>T. tsushimae</i> Emery, 1925	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1

Refer to “Study area” subsection for abbreviations of the names of phytogeographical regions.