

Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert

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Abstract

Aim Ants (Hymenoptera/Formicidae) have strong influences on ecosystems especially in arid regions. However, little is known about ants of the vast steppe and desert regions of Central Asia. Here we provide the first comprehensive study of ant communities in Mongolia, conducted along a north-to-south gradient in climate. We examined ants' distribution patterns, assessed the impact of climatic parameters on community structure and species diversity and investigated the influence of the corresponding communities of plants.

Location Mongolia (Central Asia).

Methods We observed 31,956 ants at seed baits at 11 study sites along a transect from steppe to Gobi desert for which we attained meteorological data (mean yearly precipitation: 197 to 84 mm). Extra sampling was conducted at sugar and protein baits and by the inspection of different microhabitats. Vegetation patterns of each plot were recorded. Statistical evaluation comprised ordination and correlation.

Results We observed 15 species of ants at seed baits. Three faunal complexes of ants could be distinguished by detrended correspondence analysis (DCA): (1) in steppe baits were dominated by *Formica*- and *Myrmica*-species, (2) in semi desert we found mostly species of *Tetramorium*, *Myrmica*, *Proformica*, *Plagiolepis*, and *Leptothorax*, and (3) in desert *Cataglyphis aenescens* and *Messor aciculatus* dominated, and *Lasius* was exclusively found there. Another 11 rare ant species were sampled by hand and at sugar baits. Altogether five ant species were new to the Mongolian fauna: *Cardiocondyla koshewnikovi*, *Myrmica koreana*, *Myrmica pisarskii*, *Polyergus nigerrimus*, and *Proformica kaszabi*. Assignment of taxa to functional groups showed that in steppe cold climate specialists dominated, in semi desert we found mainly opportunists, and in desert hot climate specialists. Several functional groups known from arid zones in other parts of the world were missing. In desert certain species were highly dominant. First DCA scores of ant- and plant-communities were highly correlated with each other and with climatic parameters. While plant species diversity was positively correlated with increasing northern latitude, ant diversity and ant species richness were not correlated with latitude and responded neither to precipitation, nor to any other climatic parameter. Semi desert was a transition zone between steppe and desert, with high species richness. Ant genus composition of the ecotone overlapped with both other regions. However, beta diversity between pairs of plots within this zone was low, indicating a small-scale mosaic pattern.

This paper is dedicated to our friend and co-author, the Mongolian botanist Dr Losol Chimedregzen, who tragically died in 1998.

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Main conclusions The ant communities in the Mongolian steppe and desert zones were strongly influenced by low temperatures and differed in many aspects from the ant fauna in other arid ecosystems, especially in terms of species richness, diversity of feeding guilds, and richness of functional groups.

Keywords

Ants, Formicidae, functional groups, species diversity, detrended correspondence analysis, climate, cold desert, semi desert, Central Asia.

INTRODUCTION

Ants of most arid zones of the world have been extensively studied, in America (e.g. Davidson, 1977; Medel & Vásquez, 1994; Whitford *et al.*, 1999; Rojas & Fragoso, 2000; Bestelmeyer & Wiens, 2001; Sanders *et al.*, 2003), Australia (e.g. Andersen, 1995), Africa (e.g. Marsh, 1986; Lindsey & Skinner, 2001), and Europe (e.g. Cerda *et al.*, 1997). In Central Asia, however, where desert and steppe ecosystems are covering large areas, little is known about the ecology of ant communities (e.g. Reznikova, 1980).

Previous ant collections of Mongolia, gathered by famous entomologist Dr Z. Kaszab, were determined by Pisarski (1969a,b; Pisarski & Krzysztofiak, 1981), others by Dlussky (1965; Dlussky & Pisarski, 1970). Although our faunistic and systematic knowledge of ants of the eastern Palearctic region has been greatly improved since that time (e.g. Arnoldi, 1977; Radchenko, 1995; Seifert, 2000; Schultz, 2001; Chang & He, 2002a,b) and interesting details about the behaviour of some of the Central Asian desert ant species have been published from studies in other places (e.g. Onoyama, 1982; Yamaguchi, 1995), a survey of the ant communities of the Mongolian steppe and desert zones was still missing.

Arid regions of Mongolia are characterized by a steep climatic gradient from North to South that shapes the vegetation sequence of steppe, semi desert, and desert. In this paper we examine the structure of the Mongolian ant communities and vegetation patterns along a transect from steppe to Gobi desert. Mongolia's arid zones differ in many aspects from dry regions elsewhere, because of the strong influence of low temperatures on plant and animal life. In hot arid sites, where most previous desert ant studies have been conducted, species richness of ants is often correlated with the rainfall gradient, as productivity in these regions is coupled to precipitation (e.g. Davidson, 1977; Marsh, 1986). The Gobi desert, however, is a typical cold desert, intensively influenced by frost during long winters. As in Mongolia gradients of precipitation and temperature show opposing trends and run contrary from North to South we expected no direct correlation of rainfall and ant diversity patterns.

Besides diversity pattern ant assemblages of different continents may also differ in their guild composition, community structure, and evolutionary history. Form North American desert ant communities a strong influence of

seed-harvester ants has been reported (e.g. Johnson, 2001), particularly because of abundant resources of seeds from annuals (Brown *et al.*, 1979). In Gobi desert spring ephemerals that contribute to seed abundance in other arid places (e.g. in the deserts of western Asia) are missing, because the rainfall pattern is governed by Pacific Monsoon with most precipitation occurring in summer (Breckle *et al.*, 1994). This should have strong influence on guild structure in Gobi's ants, by reducing impact of granivores. Thus we expected less diverse granivorous guilds. Generally, however, the guild concept is unsuitable for detailed studies on ant communities, because interference competition in ants cuts across guild boundaries (Greenslade & Halliday, 1983; Andersen, 1991). An appropriate basis for comparisons of ant communities can be obtained by the use of Andersen's functional group scheme (Andersen, 1995, 1997) that we employ in this study.

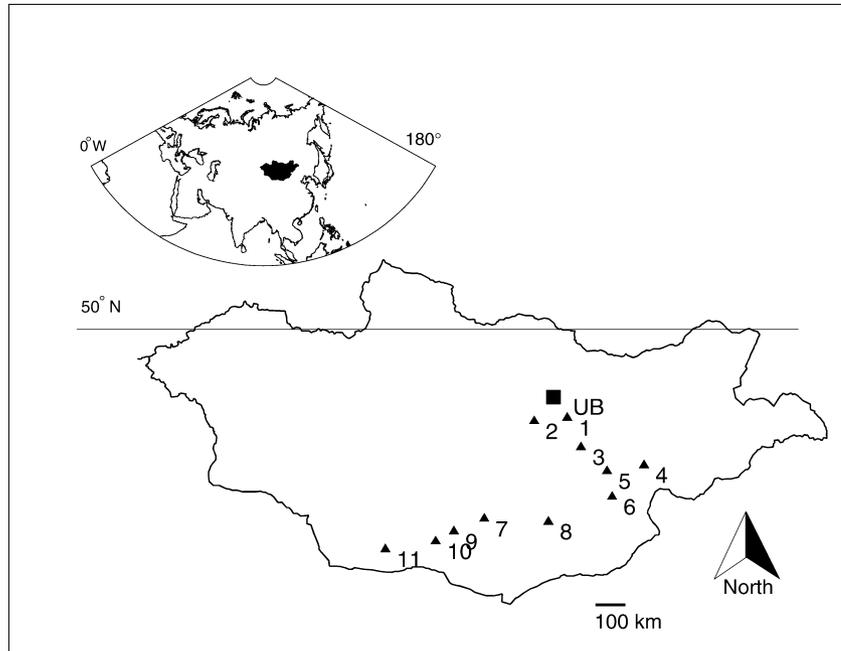
Few studies compared ant community composition across biome transitions and ecotones (e.g. Bestelmeyer & Wiens, 2001). Here we scrutinize a large environmental gradient and ask whether the semi desert represents a transition zone between ant communities of the steppe in the North and Gobi desert in the South of Mongolia.

MATERIAL AND METHODS

Study area

Mongolia occupies an ecological transition zone where the Siberian taiga forest meets the Central Asian Steppe and the Gobi desert. Located in the center of the Asian continent (see Fig. 1), Mongolia has a position leading to an extreme continental climate with very low precipitation. Temperature fluctuations are enormous, both daily and annually. Absolute temperatures vary from $-49\text{ }^{\circ}\text{C}$ in winter to $+40\text{ }^{\circ}\text{C}$ in summer. From North to South mean annual temperatures rise, e.g., from $-1.1\text{ }^{\circ}\text{C}$ in Ulaanbaatar (UB, N $47^{\circ} 56'$, O $106^{\circ} 59'$) to $4.3\text{ }^{\circ}\text{C}$ in Dalanzadgad (DG, N $43^{\circ} 35'$, O $104^{\circ} 25'$). At the same time mean annual precipitation decreases steadily, ranging from, e.g. 257 mm in UB to 125 mm in DG and to < 50 mm in the Transaltai Gobi. Most of the precipitation falls in summer. This gradient of temperature and moisture in combination with different soil conditions and altitudinal changes results in a mosaic of different vegetation types (see Hilbig, 1995, 2000): north of Ulaanbaatar vegetation consists of forest and

Figure 1 A map of Mongolia. Given are the capital Ulaanbaatar and the positions of our study sites. The numbers indicate the following points: (1) Maant, (2) Zorgol, (3) Choir, (4) Delgerekh, (5) Char Airag (6) Saynshand, (7) Bayan-Zag, (8) Manlai, (9) Hongoryn Els, (10) Nemeegt, (11) Ekhin Gol. The world map in the upper right corner shows the geographical position of Mongolia (black) in the centre of Asia.



mountain steppe, south of N 48° latitude a patchy steppe – semidesert (steppe-desert) – desert continuum extends up to the Chinese border (Breckle *et al.*, 1994).

Generally vegetation zones in Mongolia correspond well with the distribution of precipitation. Short bunch grasses are dominant in steppe zone (Lavrenko & Karamysheva, 1993). Semi-deserts are either dominated by *Stipa-Allium* communities (desert steppe) or by shrubs and dwarf shrubs (shrub desert steppe), e.g. *Caragana*, *Artemisia* (Yunatov, 1950). In the desert zone vegetation cover generally reaches values of < 10%, often only 1–2% (Walter *et al.*, 1983). Important components of the desert vegetation are low shrubs and semi-shrubs of the Chenopodiaceae, Tamaricaceae, Zygophyllaceae, Asteraceae, and others (Pyankov *et al.*, 2000). Large herbivores, like Mongolian gazelle (*Procarpa gutturosa*) and Asian wild Ass (*Equus hemionus*) share the pastures with the livestock of nomadic herders (Schaller, 1998). Ants (Formicidae) and darkling beetles (Tenebrionidae) (Medvedev, 1990) are dominant groups of the ground-dwelling insect fauna in these habitats.

Study sites

Ants were collected during two expeditions to the Gobi desert and its adjacent steppe zones from July to September 1997 and in July/August 1999. Study areas, which should represent the typical vegetation zones and follow a gradient of precipitation, were selected on the basis of precipitation records of the Mongolian Ministry of Nature and Environment that we received by the Deutscher Wetterdienst. In the field we chose sampling sites depending on vegetation structure. We tried to compare characteristic, intact, natural plant communities and to

avoid overgrazed regions. This resulted in 11 plots that were situated in mean 85 km (SD = 74.8 km) from the corresponding weather stations.

Study sites' coordinates were determined by GPS (Garmin GPS 12 XL) and are mapped in Fig. 1, geographical and climatic details are given in Table 1. From North to South we investigated following places (named to the geographical place next to them):

1. Maant. A site of the dry steppe zone near to Ulaanbaatar dominated by *Artemisia adamsii* Bess., *Leymus chinensis* Tzvel., and *Carex duriuscula* CA Mey. This plot was partly affected by nests of the common vole *Microtus brandti* Radde.
2. Zorgol. Laying below of Zorgol Khayrkhan Mountain this typical desert steppe plot was dominated by the peashrub *Caragana microphylla* Lam., the Dzungarian Bridlegrass *Cleistogenes squarrosa* (T.), and *Stipa krylovii* Roshev.
3. Choir. Desert steppe dominated by drought-resistant *Cleistogenes squarrosa* and *Carex duriuscula*, and dwarf shrubs *Caragana microphylla* Lam., *C. leucophloea* Pojark., and *C. stenophylla* Pojark.
4. Delgerekh. This site was a meadow near a brook with the highest species richness of our plots and more than 30 plant species, dominated by the Jiji grass *Achnatherum splendens* Trin., Gobi feather grass *Stipa gobica* Roshev., and a *Kochia* species.
5. Char Airag. Desert steppe dominated by the caespitose grasses *Cleistogenes soongorica* (Roshev.) Ohwi and *Stipa glareosa* P. Smirn., and semi-shrub *Caragana pygmaea* (L.) DC.
6. Saynshand. A semi desert plot: the rocky slope of a hill dominated by *Cleistogenes soongorica*, *Allium*

Table 1 Description of our study plots. Given are location, botanical–geographical region, latitude, longitude, annual rainfall, annual mean temperature and mean maxima of daily air temperature, the De Martonne aridity index, and total plant cover

Plot no.	Location	Botanical–geographical region (Grubov, 1982)	North		Precipitation (mm)*year ⁻¹	Mean daily Air Temp (°C)*year ⁻¹	Max. daily Air Temp (°C)*year ⁻¹	Aridity index	Total plant cover (%)
			North	East					
1	Maant	Middle Khalkha	N 47°17'	E 107°38'	196	-2.2	5.7	25.13	40
2	Zorgol	Mongol. Dauria	N 47°10'	E 106°04'	196	-2.2	5.7	25.13	52
3	Choir	Middle Khalkha	N 46°22'	E 108°17'	179	0.2	7	17.55	40
4	Delgerekh	Middle Khalkha	N 45°49'	E 111°15'	197	1.4	8	17.28	43
5	Char Airag	Middle Khalkha	N 45°38'	E 109°30'	149	1.2	8.5	13.30	27
6	Saynshand	East-Gobi	N 44°51'	E 109°45'	112	3.7	10.7	8.18	30
7	Bayan-Zag	East-Gobi	N 44°10'	E 103°42'	125	4.3	11.4	8.74	16
8	Manlai	East-Gobi	N 44°05'	E 106°44'	99	3.6	10.9	7.28	30
9	Hongoryn Els	Gobi-Altai	N 43°47'	E 102°16'	125	4.3	11.4	8.74	56
10	Nemegt	Gobi-Altai	N 43°28'	E 101°24'	84	4.96	11.4	5.61	22
11	Ekhin Gol	Transaltai-Gobi	N 43°14'	E 99°01'	115	9.24	11.4	5.98	14

mongolicum Regel., and gray sage bush *Artemisia xerophytica* Krasch.

- Bayan-Zag. A saks'a'ul (*Haloxylon ammodendron*) forest near Bulgan, co-dominated of *Bassia dasyphylla* (Fisch. & C.A. Mey.) Kuntze and *Setaria viridis* P. Beauv. partly with sandy dunes. The best examined plot of our study.
- Manlai. This place was heavily overgrazed when we visited it the second time in 1999. It was dominated by *Stipa glareosa*, and semi-shrubs of *Artemisia pectinata* Pall. and *Artemisia frigida* Willd.
- Hongoryn Els. This plot was a sandy place near the big dune of Hongoryn Els, about 1 km away from a small river. A mosaic of bare soil and densely covered hillocks, mainly with Nitre *Nitraria sibirica* Paul., *Bassia dasyphylla*, and *H. ammodendron*.
- Nemegt. A true desert plot in the Gobi Altai that laid at the foot of Nemegt mountain. The rich flora of this site was dominated by *H. ammodendron* and the forbs *Artemisia caespitosa* Ledeb. and *Reaumuria soongorica* Pall.
- Ekhin Gol. A stony plot outside the oasis of Ekhin Gol that bore merely two plant species: *H. ammodendron* and *R. soongorica*.

Five of these plots (Maant, Zorgol, Manlai, Saynshand and Bayan-Zag) were censused in both years. However, in Manlai, where we had recorded low ant abundance during our first stay, we found no ants at all during our second examination.

Data collection

On each of the sampling sites we placed 75 petri dishes in a 5 × 15 bait grid with approximately 5 m spacing. Petri dishes were dug into the soil so that their edges were flush with the ground to allow easy access by ants. As a bait we used a mixture of barley and millet seeds that were partly ground in a grain mill to produce a variety of particle sizes ranging from whole seeds to flour. This standard procedure

was originally used by Davidson (1977) for the study of harvester ants and has been copied in many studies on granivorous ants (e.g. Medel, 1995; Kaspari, 1996). However, we found that partly ground commercial grain attracts not only harvester ants, but that a wide range of non-granivorous ants also takes seed fragments, just as they take bread crumbs. As ground seeds are much softer than whole seeds they attract species that normally do not forage on naturally occurring seeds and are therefore well suited for an assessment of whole ant communities (A. Radchenko & B. Seifert, Pers. comm.). Sanders & Gordon (2003) who studied the organization of North American desert ant assemblages by pitfall traps, seed baits, and protein baits found that dominance pattern at different baits changed, however, seed baits attracted more species than protein baits, including even honeydew feeders (*Myrmecocystus* spp.).

Baits were monitored every 2 h, when we counted the number of ants during a 60-s observation period. Counting took place at least for a full circle of diurnal and nocturnal surface temperatures. Surface temperature was measured hourly with *Prima long* digital thermometers. Air temperature and humidity were recorded with *Hobo* data loggers (Onset, ONS-H08-032-08).

Ants were counted continuously at the baits. We took several samples of every ant species of each transect. To obtain more data on ants, we offered extra baits outside the plots: sugar water, cheese, and small pieces of meat. Additionally, in each area ants were sampled opportunistically with forceps and aspirator by inspecting different microhabitats for at least 1 h. Samples were preserved in 75% ethanol and returned to laboratory for identification. Vouchers of all specimen will be deposited in the collection of the Department of Ecology of the University of Ulaanbaatar.

Plant diversity within the grids was measured by plant cover estimates of all species. We included all vascular plant species, which were identified according to Gubanov (1996) and Grubov (1982). On each location 10 squares were

mapped. Single square size depended on the scale of the vegetation and was 1 m² in the steppe zone, 10 m² in semi-desert zone, and 20 m² in desert vegetation.

We used a set of environmental parameters (EPs), derived from weather data of the Deutscher Wetterdienst and local weather stations, to compare climatic variation of the plots. We used mean precipitation, mean daily air temperature, mean daily maxima and minima of air temperature, total yearly maxima and minima of air temperature, mean daily air temperature in July, mean wind speed, mean steam pressure, and number of days with frost and with more than 1 mm precipitation, respectively. These data were normalized (mostly by log-transformation) if deviating from normal distribution or only used in non-parametric calculations. For each plot we calculated the De Martonne aridity index $I_a = P/T + 10$, with P is annual precipitation (mm) and T = average annual temperature (°C) (De Martonne, 1927).

Statistical analysis of community structures

Most calculations were based only on the species gathered at the seed baits in our grids, ant species that we collected by hand sampling and sugar baits were only included in the analysis of the beta diversity and functional groups (see below). Data analysis was conducted on species frequency data at our baits. Species richness of ants per site was estimated with the program 'Estimate S' Version 6B1a (Colwell, 2000; for details of the program and estimators, see Colwell & Coddington, 1994; Longino *et al.*, 2002). For rarefaction and diversity analysis we pooled all data gathered at one plot during different sample times. Rarefaction plots were plotted not with the number of samples, but with the number of occurrences on the abscissa (see Gotelli & Colwell, 2001; Longino *et al.*, 2002). Species richness was estimated by Michaelis Menten estimates, calculated from the smoothed species accumulation curves (MMMeans). Rarefaction results for plants are not shown, however, they confirmed sufficient sampling and allowed further calculation of species diversity.

For comparison of plots we calculated species richness (CSR) and a set of alpha-diversity indices using 'Estimate S'. As observed species richness depends strongly upon sample size, direct comparisons among communities that differ in the number of samples are not valid (Magurran, 1988, Lande *et al.*, 2000). Sample sizes differed greatly at our sites. To allow standardization at equivalent number of samples for each plot, we pooled ant data of all censuses and randomized orders of samples 100 times to get random order species accumulation curves. We cut these curves at 33 samples (minimum common sample size after exclusion of Manlai, see Results) and computed 'calculated species richness' and diversity indices on this basis. Plant diversity was also evaluated on the basis of individuals to avoid problems associated with different plot sizes and plant densities (Cannon *et al.*, 1998; Gotelli & Colwell, 2001). CSR and species diversity of plants was calculated on the basis of 237 individuals (= no. of plant individuals found in Ekhin-gol) by use of Ecosim 7.44 (Gotelli & Entsminger, 2001).

To analyse species assemblages at different plots we used detrended correspondence analysis (DCA, with the program PC-ORD 4.0, McCune & Mefford, 1999), an eigenvalue based technique that is particularly suitable for community data gathered at long gradients (Ter Braak, 1995). For analysis we pooled data for each plot and standardized it to equal sample size. Only species with at least three occurrences in all were included in the analysis to avoid accidental records biasing the results. Distances between the 11 plots were calculated with values of the first two DCA axes multiplied with the corresponding eigenvalues, arranged in matrices, and tested for spatial dependence with Mantel tests (see Sokal & Rohlf, 1995).

The DCA extracts theoretical environmental gradients from the species composition data, thus monotonic relations between ordination axes and EPs are to be expected (Ter Braak, 1995). In indirect gradient analysis (Ter Braak, 1989) we correlated the DCA site scores of the first ordination axis with the EPs to evaluate the influence of EPs on community patterns. To overcome the problem of partial correlation of the EPs we (a) eliminated those parameters that were highly correlated to others, and (b) we used principal component analysis (PC-ORD 4.0) to reduce the set of EPs to three PCA axes.

Generally statistics were computed with program STATISTICA 6.0 (StatSoft, 2001). To evaluate the distribution of single ant species along the gradient, we used multiple logistic regression (lost function: Max-Likelihood) and regressed present absence data of the single species with the first three PCA axes of the EPs.

Assignment of taxa to functional groups

In the recent years Andersen (1991, 1995, 1997) has developed a functional group scheme, which allows a comparison of ant communities along our transect. Based on the abundance of ants at our baited grids and the additional records of nests and hand sampled ants, we assigned the Mongolian ant taxa to functional groups. For species that were only hand sampled we took the number of nests that we found at the different sites as an equivalence for the number of baits that were counted in the other species. Only species which occurred at least two times were included in this analysis.

Analysis of beta diversity pattern

We measured ant species overlap at the baited grids with the quantitative Morisita index (MI) (Magurran, 1988) and used Krebs' 'Program for Ecological Methodology' to calculate it (Kennedy & Krebs, 1998). To monitor similarity between ant communities at different sites by present/absence data of all ant species that we found at the sites (see Appendix) we used the formula of the qualitative Sørensen Index:

$$\text{Coefficient of similarity} = \frac{2w}{a+b},$$

where w is the number of species common to both communities and a and b are the numbers of species in each of two communities.

RESULTS

Climatic gradients

To analyse climatic gradients along our transect we used PCA to reduce all eleven EP to three PCA axes that were responsible for 93.5% of all variance. After Bonferoni correction (aBc) only the first PCA axis showed significant correlations (all $P < 0.05$) to single EPs, e.g., yearly precipitation ($r = 0.90$), mean daily air temperature ($r = 0.94$), etc., as well as to the aridity index ($r = -0.99$), confirming that variation along PCA1 followed a regime of temperature and precipitation. As PCA1 was highly significant correlated with the degrees of latitude ($r = -0.92$, $P < 0.001$), it thus corroborated that our North–South transect was strongly influenced by climate. Degrees of latitude of plots were negatively correlated with mean daily temperature ($r = -0.91$, $P < 0.001$) and positively with precipitation ($r = 0.90$, $P < 0.001$), thus confirming the steepness of the climatic gradient. As our transect points were not arranged along a straight line but followed the distribution of meteorological stations, we also tested for environmental variation along the West–East gradient, but found no significant correlation (e.g. PCA1 vs. degrees of longitude, $r = -0.04$, ns).

Species richness and abundance

Inside our grids we observed 31,956 individuals of 15 ant species at seed baits, furthermore 11 species of ants were caught at sugar baits or at other occasions during our field work (see species list in the Appendix). Plant communities consisted of a total of 91 species.

Species numbers of ants at the baits in our plots ranged from three to seven species (mean = 4.3, SD = 1.2, $n = 11$)

(Table 2). Rarefaction curves of most sites quickly reached an asymptote confirming that species sampling was representative (Fig. 2). The slope of the rarefaction curves was steeper in plots where we found more than one local unique species (gathered at only one bait, see Table 2). The number of expected and observed species differed on average only by 0.44 species, however, in the Char Airag and Manlai sites by two species. Char Airag was sampled well, therefore missing species seemed to be rare, however, the Manlai plot yielded only nine samples, so missing species might be more important there. Therefore we omitted Manlai from further diversity analyses.

Patterns of species richness and diversity

We used CSR (see Methods) to check for geographical and climatic patterns of diversity using Pearson's correlations coefficient. While ants' CSR was not affected by northern latitude of plot site ($r = -0.18$, ns, see Fig. 3), CSR of plants showed a clear increase towards North ($r = 0.66$, $P < 0.05$).

For ants, we found no significant correlation of any index of diversity with annual precipitation (e.g. Shannon's H, $r = 0.15$, ns), nor with any of the other climatic parameters (including PCA scores). In plant communities alpha diversity patterns were also not significantly correlated with yearly precipitation (plants: $r = 0.49$, ns). Shannon's diversity index for plants was correlated with PCA2 ($r = -0.63$, $P < 0.04$, ns aBc), however, also not significant aBc.

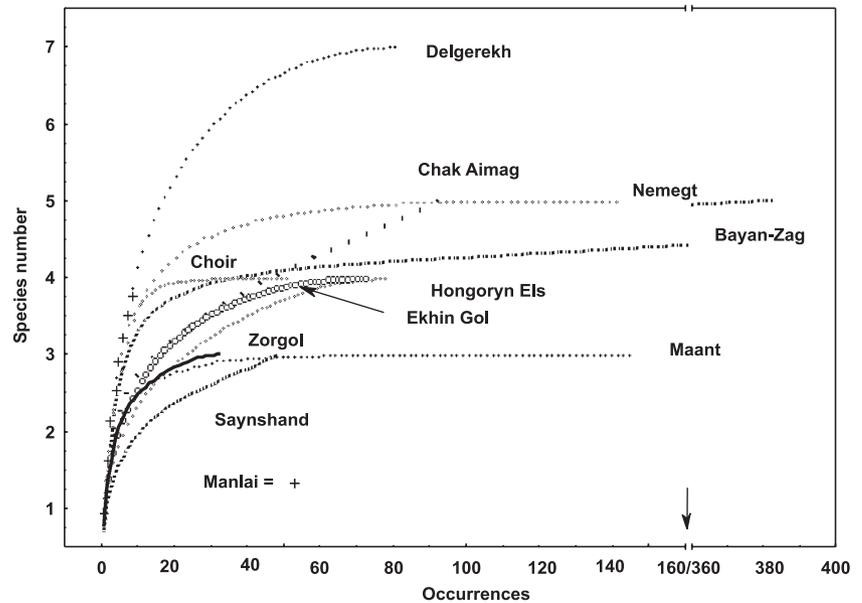
When correlating ant diversity pattern with EPs, we checked whether high ant diversity at Delgerekh, a place with a brook nearby, would alter the results. In that case a local parameter might have changed large-scale trends. However, we found no noteworthy differences with and without this plot, thus we included it in our calculations.

Table 2 Summary statistic for ants at the baits of our plots (sorted from North to South). The table shows the total no. of samples of all investigations, the no. of species occurrences found in these samples, the observed no. of species, the no. of common species, the no. of species found only with one occurrence: the asymptote of the Michaelis–Menten equation (MMMeans) fit to the species accumulation curve, as a species richness estimator, species richness calculated on the basis of 33 samples (CSR), and Shannon's H indices of diversity of ants. For Manlai we did not calculate any diversity index, because the number of samples was too low for comparison

	No. of samples	No. of species 'occurrences'	No. of species at the baits	No. of common* species at the baits	No. of local uniques	MMMeans (max. samples)	Calculated species richness (33 samples)	Shannon (H)Index (33 samples)
Maant	91	146	3	2	0	3	3	0.89
Zorgol	33	34	3	1	0	3	3	0.83
Choir	44	52	4	3	0	4	4	1.31
Delgerekh	55	82	7	3	0	8	7	1.48
Char Airag	62	93	5	2	2	5	4	0.97
Saynshand	48	49	3	2	1	3	3	0.46
Bayan-Zag	186	382	5	4	1	5	4	1.23
Manlai	9	10	4	0	2	6	–	–
Hongoryn Els	58	74	4	2	0	4	4	0.76
Nemegt	74	143	5	4	0	5	5	1.26
Ekhin-gol	63	79	4	2	0	4	5	0.69

*Those species occurring at 10% or more of the baits. CSR, calculated species richness.

Figure 2 Sample based rarefaction curves of the ant fauna found at seed baits in the different plots. The units of the abscissa are number of 'occurrences' (see Methods, Statistical analysis of community structure). Samples of different investigation times are pooled and Maanit, Saynshand, and Zorgol were censused two times, Bayan-Zag was investigated three times, all other plots only once. Note the scale break at 160 occurrences that cut the graph of Bayan-Zag, which had a total of 382 occurrences and five species of ants.



Community patterns and indirect gradient analysis

Community composition was compared among study plots by multivariate analysis with DCA. For ants, total variance (inertia) in the species data was 3.02, eigenvalues¹ of the three axes were 0.89 (first axis), 0.55 (second axis), and 0.16 (third axis), the corresponding lengths of the gradients² were 5.62 SD (first axis), 3.67 SD (second axis), and 2.27 SD (third axis). Three faunal complexes of granivorous ants could be distinguished along the first DCA axis that roughly followed a gradient from South to North along our transect (Fig. 4): (1) the complex of desert ants found in the Gobi plots, (2) the group of semi-desert ants belonging mostly to plots of the Middle Khalkha, and (3) the steppe ants complex of the two northernmost plots. Actually, Manlai is 5' south of Bayan-Zag, but because of species composition DCA arranged it to the Semi desert plots – a result that matched with the plants' community pattern. For plants total variance in the DCA was 5.9, eigenvalues and associated gradient lengths of the axes were 0.98 with 11.98 SD (first), 0.65 with 3.39 SD (second), and 0.35 with 2.70 SD (third axis). In all groups eigenvalues and gradient lengths of the first and second DCA axes showed high values indicating a good separation of species along the first and second axis.

In order to analyse whether changes in ant- and plant-communities were correlated, we compared distance matrices of the DCAs of the concerning groups. Distances

between the 11 different sites in the communities of ants and plants were highly significantly correlated even aBc [Mantel test using Mantel's asymptotic approximation (MAA) for all groups: $P < 0.001$]: for ant vs. plant communities $r_M = 0.90$ ($t = 5.22$).

We used Mantel statistics (with MAA) to further evaluate the relations of distances between single DCA-scores of ant and plant communities with spatial distances: distances calculated between communities of all organisms were highly significantly correlated with distances measured in minutes of longitude between plots (plants: $r_M = 0.86$, ants: $r_M = 0.83$, for all groups $P < 0.001$ aBc), showing that changes within the communities were correlated with distances between plots.

In indirect gradient analysis DCA1 (= first axis) scores obtained for ants ($r = 0.90$) and plants ($r = 0.89$) were highly correlated with the PCA1 (= first axis) of the EPs ($P < 0.01$ aBc) confirming that changes along our transect followed a climatic gradient. In a second approach we looked for correlations of single EPs to the DCA scores: DCA1s of all groups were significantly correlated ($P < 0.01$ aBc for all variables) with mean daily temperature, daily maxima of temperature, number of days below 0 °C, and yearly precipitation, DCA2 for ants was correlated with wind speed ($P < 0.01$ aBc) (correlation coefficients in Table 3). High wind speeds are characteristic for spring and summer in the Mongolian desert-steppe regions (Lavrenko & Karamysheva, 1993).

Ant genera composition and species distribution

Ant genera composition of the three geographical zones differed significantly (Chi square test: $\chi^2 = 241.6$, $P < 0.01$, Fig. 5). Eight ant genera were found at the baits in the semi desert zone, while the desert zone was

¹In DCA eigenvalues measure the importance of each of the axes (values between 0 and 1), but cannot be interpreted directly as proportions of variance explained; values over 0.5 often denote a good separation of species along the axis (Ter Braak, 1995).

²The length of the gradient is expressed in standard deviation units of species turnover (SD).

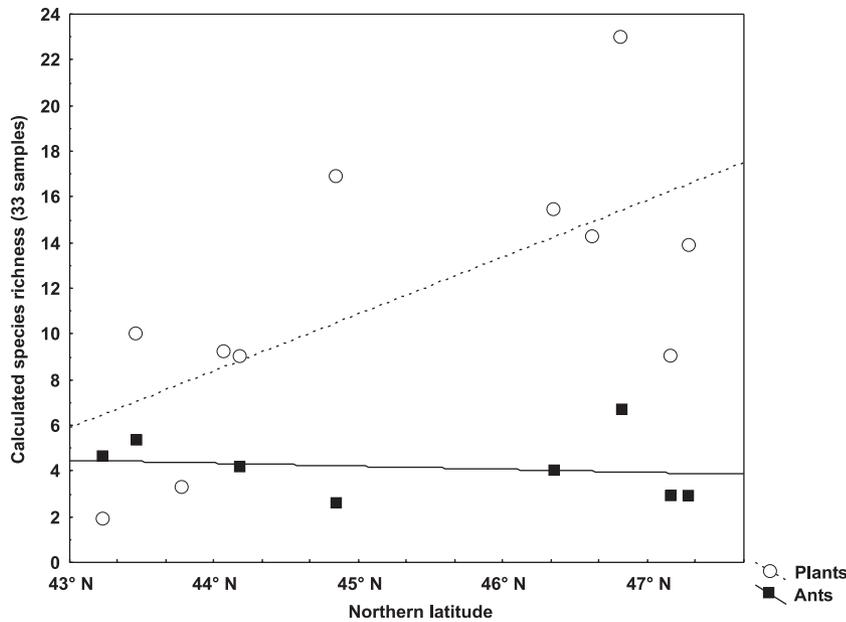


Figure 3 Calculated species richness of granivorous ants and plants plotted against northern latitude. For easy interpretation we show the regression lines of these correlations between diversity and latitude: simple line = ants, dotted line = plants.

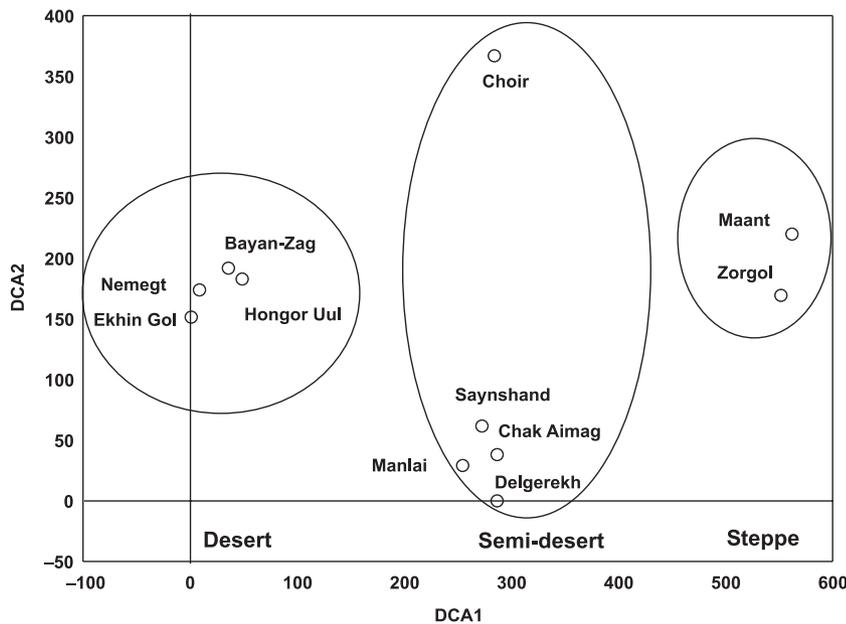


Figure 4 Detrended correspondence analysis (DCA) of the ant assemblages at different sites of our transect. Plots are arranged from South to North along the first DCA axis, starting with Ekhin Gol as the southernmost site. Ant communities were organized in three groups that are marked by circles (from left to right): desert ants, semi-desert ants (divided in two groups by DCA2), and steppe ants.

inhabited by seven, and the steppe zone by only three genera. Baits in steppe zone were dominated by *Formica*- and *Myrmica*-species. *Formica* disappeared from the baits to a large extent in semi-desert zone. *Proformica*, *Tetramorium*, *Myrmica*, and *Plagiolepis* showed their main distribution within semi-desert and *Leptothorax* was found only there, but semi-desert also harbored ant genera that had their main abundance in the two other zones (*Cataglyphis*, *Messor*, *Formica*). In desert zone *Messor* was more abundant, however, most baits were dominated by a single *Cataglyphis* species (*C. aenescens*). Abundance of *Profor-*

mica-, *Formica*-, and *Tetramorium* species was reduced in desert as compared with semi desert zone. Extra sampling yield two more ant genera in the steppe (*Camponotus*, *Polyergus*) and three in the desert (*Camponotus*, *Cardiocondyla*, *Plagiolepis*).

Multiple logistic regression of individual species with the three PCI axes showed that nine of 19 ant species depended significantly in their distribution on environmental factors (see Appendix). This included the two dominant species of the desert *C. aenescens* and *M. aciculatus*, as well as species of *Proformica*, *Tetramorium*, and others.

Table 3 Pearson correlation coefficients for all significant correlations ($P < 0.01$ aBc) of single environmental parameters with the detrended correspondence analysis (DCA) scores of ants and plants

	Daily mean temp.	Mean daily max. temp	No. of days below 0 °C	Precipitation	Wind speed
DCA1 ants	-0.90	-0.90	0.94	0.74	-
DCA2 ants	-	-	-	-	-0.85
DCA1 plants	0.86	0.95	-0.87	-0.84	-

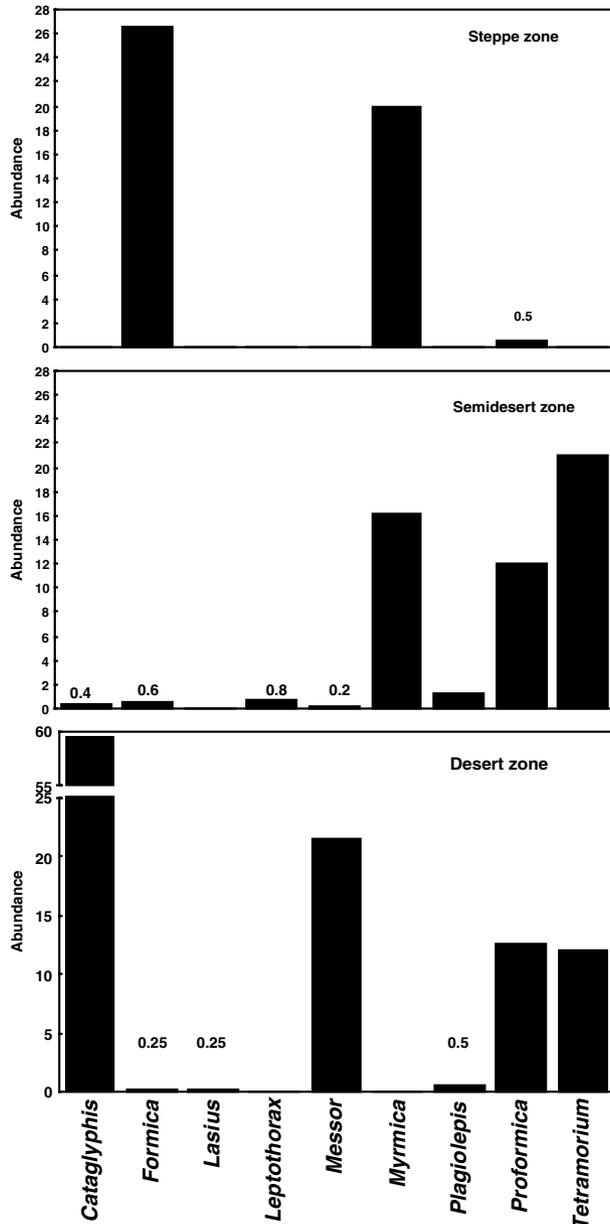


Figure 5 The mean abundance of ant genera per plot of the different climatic zones. Abundance numbers below one are given in digits. Mind different scaling and scale break of the Y-axes in the lowermost figure. The abundance of ants in plots of different zones did not differ significantly (ANOVA $F(2,8) = 3.1$; $P = 0.1$, ns).

Biogeographical patterns of functional groups composition

For a comparison of ant community composition along the environmental gradient we used Andersen's (1997) functional group scheme and assigned most species to functional groups. Only some very rare species, e.g. *Cardiocondyla koshewnikovi*, were not included in the analysis, because our knowledge about them was not sufficient for that. Following groups were separated (see also Appendix):

Cold climate specialists

The Mongolian taxa belonging here have distributions centred in the steppe region. They include the dominant holarctic *F. transcaucasica* and the temporary social parasite and slave-maker *F. sanguinea* that occurred frequently in the same nests (see Kutter, 1969). Ants of the *Formica exsecta* group that we found in some steppe localities, but not in our transects (M. Pfeiffer, Unpubl. observations) may also contribute to this group. We assigned *Myrmica pisarskii* as a cold climate specialist, too, because this mostly night-active ant was found only in the northern plots of our transect.

Hot climate specialists

The most dominant hot climate specialist was *Cataglyphis aenescens* that occurred all over the desert region and was observed to forage at surface temperatures up to 55 °C. *Messor aciculatus* was also a dominant species, merely found in the South and we counted it to this group, although the species was mainly night active.

Subordinate Camponotini

We only found one species *Camponotus turkestanus* that occurred at the desert sites. Existing mostly on phloem sap (M. Pfeiffer, Pers. observation) this night active species never fed at the seed baits.

Cryptic species

The only cryptic species in our plots was *Plagiolepis mancshurica*.

Opportunists

These taxa are defined by their wide geographical ranges, broad habitat distribution, unspecialized diets, and poor competitive ability. Here we put *Tetramorium*, *Proformica*, *Leptothorax*, and *Myrmica* (others than *M. pisarskii*), as well as some rare *Formica* species.

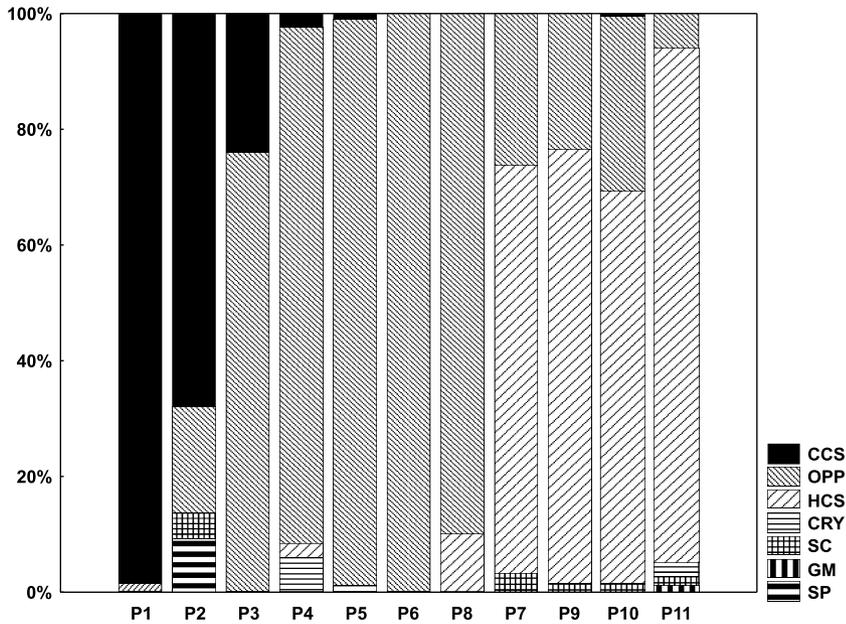


Figure 6 Functional group composition along the north-south transect. The functional groups are: CSS, Cold Climate Specialists; OPP, Opportunists; HCS, Hot Climate Specialists; CRY, Cryptic species; SC, Subordinate Camponotini; SP, Specialist Predators; GM, Generalized Myrmicinae; P1–P2, steppe; P3–P6, P8, semi desert; P7, P9–P11, desert.

Table 4 Beta-diversity between our plots (excluded Manlai) as measured by the Morisita Index calculated for ants at the baits inside the grids (above diagonal) and Sørensen qualitative Index calculated for all ant species found at the sites (below diagonal). Morisita indices of ant communities in pairs of plots along the transect are shown in bold numbers

	Maant	Zorgol	Choir	Delgerekh	Char Airag	Saynshand	Bayan-Zag	Hongoryn Els	Nemegt	Ekhin Gol
Maant		0.98	0.30	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Zorgol	0.55		0.20	0.09	0.13	0.00	0.00	0.00	0.00	0.00
Choir	0.40	0.31		0.00	0.02	0.03	0.24	0.16	0.10	0.00
Delgerekh	0.31	0.50	0.27		0.95	0.77	0.15	0.07	0.07	0.05
Char Airag	0.20	0.15	0.17	0.53		0.71	0.08	0.01	0.00	0.00
Saynshand	0.00	0.20	0.22	0.50	0.44		0.10	0.01	0.05	0.00
Bayan-Zag	0.00	0.14	0.15	0.25	0.15	0.20		0.74	0.85	0.77
Hongoryn Els	0.00	0.31	0.33	0.27	0.17	0.44	0.62		0.74	0.96
Nemegt	0.17	0.27	0.29	0.24	0.14	0.18	0.53	0.71		0.76
Ekhin Gol	0.00	0.12	0.00	0.21	0.13	0.00	0.35	0.38	0.56	

Generalized Myrmicinae

According to Andersen, taxa belonging to here are dominant ants that are abundant in warmer regions. However, in Mongolia we found only one ant species that fits to this pattern, *Crematogaster subdentata*, occurring in the most southern plot of Ekhin-gol.

Specialist predators

The only specialist predator in our records was *Polyergus nigerrimus*, an obligate slave-maker with highly specialized mandibles that forages exclusively for the brood of other ants.

As we found no ants belonging to the subfamily Dolichoderinae the functional group 'Dominant Dolichoderinae', which is most dominant in Australia (Andersen, 1997), could not be assigned.

Functional group composition varied systematically along our N-S transect (see Fig. 6): In steppe (P1–P2) cold climate specialists dominated, while in semi desert (P3–P6, P8) we found mostly opportunists. Desert sites (P7, P9–P11) were clearly distinguished by high abundances of hot climate specialists. Most other functional groups were rare.

Ant species turnover

We checked for similarity of ant communities in our plots with the MI (Magurran, 1988) by using quantitative data (see Table 4). Morisita indices were significantly negatively correlated with distance between compared plots, measured either in km ($r = -0.57$, $P < 0.001$ aBc) or in degrees of longitude ($r = -0.55$, $P < 0.001$ aBc). Similarity of plots within one of the three geographical regions detected by

DCA was significantly higher (MI = 0.64, SD = 0.36, $n = 13$) than in comparisons between plots of different groups [MI = 0.06, SD = 0.07, $n = 32$, Mantel test: Monte Carlo method (MCM), 1000 runs, $r = 0.92$, obs. $Z = 290$, $P < 0.001$].

Morisita indices of pairs of plots succeeding from North to South along our transect were subjected to sudden changes (Table 4). We identified three breaks in species composition within the N-S sequence of locations: site-pairs Zorgol–Choir, Choir–Delgerekh, and Saynshand–Bayan–Zag had significantly less similarity (0.1, SD = 0.1, $n = 3$) than the rest of the pairs [0.81, SD = 0.12, $n = 6$, Mantel test (MCM), 1000 runs, $r = 0.81$, obs. $Z = 290$, $P < 0.001$], thus splitting up the transect in four groups and corroborating the results of the DCA analysis, where Choir site was separated from the other semi-desert plots by the DCA2 axis.

Ant beta-diversity was further assessed by qualitative Sørensen Index (QSI) calculated for all species that we found using different methods of ant collection: steppe and semi-desert had a QSI of 0.50 [for ant species only found at the baits (asb) QSI = 0.55], semi-desert and desert had a QSI of 0.48 (asb: QSI = 0.61), and similarity of steppe and desert was lowest with only 0.24 (asb: QSI = 0.27). Again, semi desert appeared as an intermediate zone with the highest species overlap. However, species richness of ants was highest in desert with 17 species (asb = 10), whereas in semidesert we found 16 species (asb = 13), and in steppe only eight (asb = 5).

We used the QSI further to evaluate similarity of ant communities between single sites within geographical regions (Table 4). Mean within- β -diversity in semi desert and desert plots differed significantly [semi desert QSI = 0.36, $n = 6$; SD = 0.16; desert QSI = 0.52, $n = 6$; SD = 0.14, Mantel test of dissimilarity matrices (MCM), 1000 runs, $r = 0.84$, obs. $Z = 99$, $P < 0.05$], the low QSI values confirming the patchiness of the semi desert. QSI for the two steppe plots was 0.55, mean QSI for all plots ($n = 45$) was 0.27 (SD = 0.18).

DISCUSSION

Mongolia's ant communities changed considerably along the environmental gradient from steppe to Gobi desert as proven by correspondence analysis. While the steppe was dominated by cold resistant species of *Formica* and *Myrmica* (cold climate specialists), semi desert supported mainly opportunistic genera (e.g. *Tetramorium*, *Proformica*), and desert assemblages consisted mostly of hot climate specialists, especially *C. aenescens* and *M. aciculatus*.

As we had expected, we found no direct correlation of precipitation and diversity pattern in the Mongolian ant assemblages. This may be largely a result of the gradient in temperature which runs contrarily to the rainfall gradient. Although ant diversity may be coupled to rainfall as an indirect measure of productivity in arid regions (Davidson, 1977), ants are a thermophilic taxon (Hölldobler & Wilson, 1990; Andersen, 1991), which reacts negatively to low mean

annual temperatures. On the contrary, diversity pattern could be a result of the productivity of resources that are a consequence of soil texture, small-scale topography, and other mosaic-like local environmental variation. These parameters are especially important in a landscape where productivity is at its minimum. Small microclimatic benefits may decide whether a species is present or absent within a location. As a possible result of these influences ant diversity was not correlated with precipitation in Australia (Morton & Davidson, 1988), nor in South America (Medel, 1995). During our study we looked for habitats with the highest productivity within the respective zone and preferred patches with intact vegetation to the bare soil beneath them. The striking differences that we experienced – especially in the more arid regions – taught us that small scale patterns are also most important for ant life in Mongolia.

However, large scale environmental pattern may have stronger influences, because abiotic variables can restrict access to a habitat's resources, which is especially true for ectotherm species (Kaspari & Valone, 2002). The ample seed resources of the Mongolian steppe, e.g., are probably mostly used by homoiotherm rodents that are better suited to forage for mature seeds in the cold autumn than ants. The distribution of the granivorous ant genera *Messor* and *Tetramorium* towards North seemed to be hindered by climatic effects³. A parallel pattern was found by Nash *et al.* (2001) in North America who compared ant communities of a sagebrush-steppe in Idaho with those of a salt-desert shrub in Utah, both habitats similar to our sites: *Formica* and generalists inhabited the steppe region, while *Messor* and most other harvester ants were merely found in the southern desert region (actually its peak abundance in North America is in the warm deserts, particularly the Mojave). Similar in Europe harvester ants are abundant only in the Mediterranean region but not in the North.

The cold climate seems to be also a major factor working against the diversification of certain ant genera. Within the huge region of central Asia (region east from Tien-Shan – Himalaya Mts) there is only one *Messor* species – *M. aciculatus*, distributed from Kirgizia-Uzbekistan till Japan (A. Radchenko, Pers. comm.), the same is true for *Cataglyphis aenescens*, while other *Cataglyphis* species are reported only far more in the South (Chang & He, 2002b). The extremely harsh and fluctuating climatic conditions within this region might reduce the number of competing species and/or allow larger ranges for those species adapted to it. The extensive distribution of *M. aciculatus* and *C. aenescens* in Gobi desert coincides with an impoverished fauna and may be an example of the dominance-impoverishment rule (Hölldobler & Wilson, 1990).

Productivity of resources is also linked to functional types (life forms) of plants. Grasses have limited access to water resources, compared with forbs and shrubs. Mongolia's desert vegetation is dominated by woody plants with deep reaching roots, e.g., the saksa'ul (*Haloxylon ammodendron*)

³A. Radchenko (Pers. comm.) also looked in vain for nests of *Messor* in steppe zone, but found some *Messor* ants in the stomach of resident birds.

that has a high productivity (Slemnev *et al.*, 1999). Due to the missing rain in springtime desert annuals are scarce and most of the ant's resources originate from shrubs and dwarf shrubs. These plants contribute not only seeds but also nectar and phloem fluids to the ants, a factor with strong influence on Mongolian ant communities that were dominated by omnivores, not by granivores.

Although we had no time for a detailed analysis of feeding strategies, our observations (M. Pfeiffer, Unpubl. results) show that most Mongolian ant species were opportunists, feeding on different matters, including phloem sap from plant wounds, insect corpses, fruits and seeds, etc. Although most species were attracted to our seed baits, specialist granivores were rare, only the genera of *Messor* and *Tetramorium* include well known harvester ant species, with a substantial reliance on seeds (Marsh, 1987; Hölldobler & Wilson, 1990). This resembles ant communities in deserts of South America, where generalist ants comprised seven of 11 genera at baits of crushed seeds (Medel & Vásquez, 1994; Medel, 1995), or in Namib desert, where all ant species are highly opportunistic (Marsh, 1985). In North American deserts Sanders & Gordon (2003) found a rich assemblage of ants at seed baits, including also omnivores, insectivores, and nectarivores species, but generally seed baits were dominated by a large guild of ant granivores (see also Davidson, 1977), for which we found no equivalent in Gobi desert.

However, for comparisons of ant communities across regions and continents the use of Andersen's functional group scheme provides an appropriate basis that is better suited than a discussion on the basis of feeding guilds. Along our transect we found a clear North–South sequence of cold climate specialists, opportunists, and hot climate specialists, while all other groups had minor influence. Compared with North America and Australia (Andersen, 1997) several functional groups were absent, or sparsely casted, however, this paper deals only with ants along a limited transect, not with whole continent assemblages. Nevertheless, if we restrict comparison with the functional groups which we can expect in a steppe-desert continuum, we see that Dolichoderinae that are dominating in Australia and also some of the hot habitats of North America are absent in Mongolia at all and that 'Generalized Myrmicinae' a functional group containing species of *Pheidole*, *Crematogaster*, and *Monomorium*, is hardly represented, with the exception of a single record of *Crematogaster subdentata* in the most southern plot. Although our records may not be complete, we exclude a strong influence of these groups on the Mongolian fauna on the basis of older species lists (Dlussky, 1965; Pisarski, 1969a,b; Dlussky & Pisarski, 1970; Pisarski & Krzysztowiak, 1981). Chang & He (2002a), who sampled the ant fauna in Northwest China (34°N–41°N) found Dolichoderinae (*Tapinoma*, *Limetopum*) occurring mostly in humid forest sites in China, with the exception of *Tapinoma rectinotum*, the only species reported from grasslands in the Qinghai-Xizang region. But 'Generalized Myrmicinae' seem to be missing also far more South. So it

seems that the organization of ant communities in Central Asia differs considerably from those in North America and Australia. Yet it has to be stated that this paper is only a first access to this problem and that a more intensive study, including other Mongolian regions, as well as other sampling methods (e.g. pitfall traps), has to be conducted before conclusions can be finalized.

Along our transect we distinguished three different ant assemblages in steppe, semi desert, and desert. If we compare β -diversity and species richness of the three geographical zones, it becomes clear that the semi desert as a whole is a transition zone where species of both other regions overlap in their ranges. But overlap on regional scale does not certainly imply local co-occurrence of species. On a local scale species inventories of single plots differed largely from each other. On this sampling level the semi desert appeared to be an especially patchy, mosaic-like region with low species overlap between the sites. The large regional species pool led to low local β -diversity, probably because competition for resources prohibited coexistence of all species. Beta diversity varied along the spatial North–South sequence of our whole transect as well, as shown by Morisita indices.

Bestelmeyer & Wiens (2001) studied a biome transition between shortgrass steppe and Chihuahuan desert vegetation on a local scale and found no intermediate ant species community composition within the phytogeographical transition zone, while diversity occurring within the biome transition (in matched habitats types) was lower than outside. Like those authors, we found small values of ant species overlap on a local scale and along our transect. However, on a regional scale ant species composition in semi desert was intermediate, and changes of ant and plant communities were well correlated within the whole transect (as proven by distant values of DCA1 scores). These results illustrate a reliance of species turnover on survey extent and 'grain size', that was also found in other studies (Williams, 1996).

Taken together, our results show that Mongolian ant communities differ in many aspects from ant communities in the deserts of America and Australia, especially in terms of species richness, diversity of feeding guilds, and richness of functional groups. Cold deserts seems to be governed by other factors than hot deserts and local selection pressures on the structures of ant assemblages differ widely. More research is urgently needed for a better understanding of the crucial differences between cold and hot desert ecosystems.

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Appendix Ant species composition at the different study sites (site numbers as in Table 1). Species that were new to the Mongolian fauna (not listed in the cited literature) are marked with *. Ant species gathered at our baits are given with bold letters and with standardized abundance numbers. Additional species that we collected at sugar baits and by hand sampling and that were not included in quantitative calculations are indicated with x. Generally, these species were rare, only the nocturnal *Camponotus turkestanus* was frequently found at the desert sites. Most additional species were collected in Ekhin Gol (site11), where desert plus oasis were hand sampled. For species that distributions were found to be significantly correlated with environmental parameters the χ^2 values of a logistic regression are given (for details see Material & Methods). Mind that site 8 (Manlai) is shifted to the semi desert sites

Ant species	Subfamily	Functional group												Chi ² value of significant logistic regressions
			Steppe			Semi-desert				Desert				
			1	2	3	4	5	6	8	7	9	10	11	
<i>Camponotus turkestanus</i> Andre	For.	SC	-	x	-	-	-	-	-	x	x	x	x	
<i>Cardiocondyla kosheunikovi</i> Ruzsky*	Myr.	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Cataglyphis aeneszens</i> Nylander	For.	HCS	-	-	-	2	-	-	-	49	55	74	59	9.92
<i>Crematogaster subdentata</i> Mayr	Myr.	GM	-	-	-	-	-	-	-	-	-	-	x	
<i>Formica clara</i> Forel	For.	OPP	-	-	-	-	-	-	-	-	-	x	x	
<i>Formica clarissima</i> Emery	For.	OPP	-	-	-	-	-	-	-	x	-	-	-	
<i>Formica sanguinea</i> L.	For.	CCS	5	-	-	-	1	-	-	-	-	-	-	
<i>Formica transcaucasica</i> Sensu Seifert	For.	CCS	35	10	-	2	-	-	-	-	-	x	-	15.27
<i>Formica uralensis</i> Ruzsky	For.	CCS	-	-	x	-	-	-	-	-	-	-	-	
<i>Lasius obscuratus</i> Seifert	For.	-	-	-	-	-	-	-	-	1	-	-	-	
<i>Leptothorax mongolicus</i> Pisarski	Myr.	-	-	-	-	x	-	-	-	-	-	-	-	
<i>Leptothorax nassonovi</i> Ruzsky	Myr.	OPP	-	-	-	4	-	-	-	-	-	-	-	10.65
<i>Messor aciculatus</i> F. Smith	Myr.	HCS	-	-	-	-	-	-	1	45	2	25	14	16.30
<i>Myrmica bergi</i> Ruzsky	Myr.	OPP	-	-	16	-	-	-	-	-	-	-	-	
<i>Myrmica koreana</i> Elmes, Radchenko & Kim (2001)*	Myr.	OPP	-	2	-	12	41	-	-	-	-	-	-	
<i>Myrmica pisarskii</i> Radchenko*	Myr.	CCS	33	5	12	-	-	-	-	-	-	-	-	16.30
<i>Plagiolepis manczshurica</i> Ruzsky	For.	CRY	-	-	-	5	1	-	-	-	-	-	2	
<i>Polyergus nigerrimus</i> Marikovskiy*	For.	SP	-	x	-	-	-	-	-	-	-	-	-	
<i>Proformica buddhaensis</i> Dlussky	For.	OPP	x	x	x	x	-	-	-	-	-	-	-	
<i>Proformica kaszabi</i> Dlussky*	For.	OPP	-	-	18	-	-	-	-	26	13	11	-	15.28
<i>Proformica mongolia</i> Emery	For.	OPP	-	x	-	35	-	1	6	-	x	-	-	12.97
<i>Tetramorium annectens</i> Wheeler†	Myr.	OPP	-	-	6	x	6	3	1	-	4	4	-	
<i>Tetramorium armatum</i> Santschi	Myr.	OPP	-	-	-	-	-	-	-	-	-	28	2	10.81
<i>Tetramorium concaviceps</i> Bursakov	Myr.	OPP	-	-	-	-	-	-	-	-	-	-	x	
<i>Tetramorium inerme</i> Mayr	Myr.	OPP	-	-	-	-	-	-	-	-	-	-	x	
<i>Tetramorium jacoti</i> Wheeler	Myr.	OPP	-	-	-	22	44	21	2	8	-	-	-	13.34
Total no. of species			4	7	6	9	6	3	4	7	6	8	10	

†In Radchenko (1992) *T. annectens* was a junior synonym of *T. jacoti*, however, after examination of additional type material this author has revised his opinion, so *T. annectens* can now be considered a true species (A. Radchenko, Pers. comm.).