



## A modern analogue of the Pleistocene steppe-tundra ecosystem in southern Siberia

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Steppe-tundra is considered to have been a dominant ecosystem across northern Eurasia during the Last Glacial Maximum. As the fossil record is insufficient for understanding the ecology of this vanished ecosystem, modern analogues have been sought, especially in Beringia. However, Beringian ecosystems are probably not the best analogues for more southern variants of the full-glacial steppe-tundra because they lack many plant and animal species of temperate steppes found in the full-glacial fossil record from various areas of Europe and Siberia. We present new data on flora, land snails and mammals and characterize the ecology of a close modern analogue of the full-glacial steppe-tundra ecosystem in the southeastern Russian Altai Mountains, southern Siberia. The Altaian steppe-tundra is a landscape mosaic of different habitat types including steppe, mesic and wet grasslands, shrubby tundra, riparian scrub, and patches of open woodland at moister sites. Habitat distribution, species diversity, primary productivity and nutrient content in plant biomass reflect precipitation patterns across a broader area and the topography-dependent distribution of soil moisture across smaller landscape sections. Plant and snail species considered as glacial relicts occur in most habitats of the Altaian steppe-tundra, but snails avoid the driest types of steppe. A diverse community of mammals, including many species typical of the full-glacial ecosystems, also occurs there. Insights from the Altaian steppe-tundra suggest that the full-glacial steppe-tundra was a heterogeneous mosaic of different habitats depending on landscape-scale moisture gradients. Primary productivity of this habitat mosaic combined with shallow snow cover that facilitated winter grazing was sufficient to sustain rich communities of large herbivores.

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It has long been recognized by mammalian palaeontologists that northern Eurasian ecosystems of cold and dry phases of the Late Pleistocene contained a peculiar mixture of species that do not co-occur at present, being confined to either the Arctic tundra or the temperate steppe (Nehring 1890). This observation was later confirmed also for plants and other groups of animals based on analyses of fossil records (Hibbert 1982; Blinnikov *et al.* 2011). Accumulating evidence led palaeoecologists to introduce the concept of ‘steppe-tundra’ (also called ‘tundra-steppe’ in Russian literature, or ‘mammoth steppe’ by Guthrie 1982, 1990; Zimov *et al.* 2012 and some others) for the vanished, predominantly treeless ecosystem developed under the cold and dry climate of the Late Pleistocene full-glacial landscapes (Yurtsev 1974, 1981; Hopkins *et al.* 1982).

Palaeoecological records suggest that during the Last Glacial Maximum (LGM) steppe-tundra was a dominant ecosystem across vast areas of northern Eurasia and Beringia, spanning from the edges of the continental ice sheet in western Europe to interior Alaska (Hopkins *et al.* 1982; Guthrie 2001). In spite of considerable regional variation in structure and species composition across this large range, different regions shared the general features of this ecosystem (or biome), including predominance of cold- and drought-adapted open-land biota (Bigelow *et al.* 2003; Kienast *et al.* 2005; Sher *et al.* 2005; Bezrukova *et al.* 2010; Müller *et al.* 2010; Blinnikov *et al.* 2011; Tarasov *et al.* 2013; Kuzmina 2015).

While some researchers have emphasized that the full-glacial steppe-tundra was not analogous to any modern

ecosystem (Guthrie 2001), others have made efforts to find at least partial modern analogues that would help us understand the functioning of the demised full-glacial ecosystems. Outstanding work in this direction was done by the Russian botanist Boris Yurtsev, who described vegetation mosaics comprising both tundra vegetation and relict steppes in western Beringia (northeastern Yakutia and Chukotka; Yurtsev 1974, 1981, 1982, 1996, 2001). He emphasized that steppe-tundra is not a single plant community composed of a mixture of species currently confined to either steppe or tundra; instead it is a landscape type including patches of both steppe and tundra, and various transitions between them. North American ecologists have looked for modern analogues of the full-glacial steppe-tundra in eastern Beringia (interior Alaska and the Yukon Territory), although patches of steppe are small and rare there, confined to some south-facing slopes in a landscape dominated by typical tundra ecosystems or woodlands (Edwards & Armbruster 1989; M. D. Walker *et al.* 1991; Roland 1996). D. A. Walker *et al.* (2001) proposed that the best modern match for the vanished steppe-tundra ecosystem in Alaska is the moist non-acidic (calcium-rich) tundra, although it has several properties that are closer to tundra than to steppe, e.g. a distinct accumulation of organic matter on the soil surface and an abundance of mosses.

Although the quest for modern analogues of the Pleistocene steppe-tundra has been focused on Beringia, it has become evident that this region cannot provide good analogues for more southern variants of the full-glacial steppe-tundra, such as those that occurred in central and eastern Europe and southern Siberia. Beringia currently lacks many species that were typical of the European and southern Siberian LGM ecosystems, e.g. equids, saiga antelope (*Saiga tatarica*), yak (*Bos mutus*) and Mongolian gazelle (*Procapra gutturosa*), steppe pikas (*Ochotona pusilla* and *O. dauurica*) and the rodents *Allactaga major*, *A. sibirica*, *Cricetulus migratorius*, *C. barabensis* and *Lagurus lagurus*. Some of these species never occurred there, while others went extinct during the Pleistocene–Holocene transition (Pavelková Řičánková *et al.* 2014, 2018). The Beringian land-snail fauna also lacks many characteristic species of the fossil record from full-glacial sediments of central and eastern Europe (e.g. Ložek 2001; Moine 2014; Hošek *et al.* 2017), which is apparent already in the extant snail fauna of the boreal forest-steppe of central Yakutia (Horsák *et al.* 2013a). There are also differences in relict European and Beringian snail fauna: several relict species of these respective regions are allopatric replacements that share common ancestors (Nekola *et al.* 2015, 2018). Likewise, from the botanical point of view, Beringia lacks many Eurasian temperate steppe species such as those of the genera *Ephedra* and *Stipa* (Meusel *et al.* 1965–1992; Hultén & Fries 1986) that were common during the LGM across large areas

from western Europe to Siberia. It also lacks some boreal trees that were scattered in the European and Siberian LGM landscapes (Feurdean *et al.* 2014) such as *Pinus cembra* s.l. and *P. sylvestris*.

Present-day geographical ranges of many of these European and Siberian LGM species overlap remarkably in the mountain systems at the border between southern Siberia and central Asia, especially in the Altai-Sayan Mountains. Pavelková Řičánková *et al.* (2015, 2018) demonstrated that most species of Late Pleistocene mammals vanished in many Palaearctic regions but persisted in this mountain system. Agadjanian & Serdyuk (2005) demonstrated that there has been a very small change in the composition of mammal fauna in the Altai Mountains between the Late Pleistocene and the present. Currently, this region is inhabited by mammal species with affinities to both the Arctic tundra (e.g. *Gulo gulo*, *Lepus timidus* and *Rangifer tarandus*) and the temperate steppe (e.g. the above-mentioned species absent from Beringia). Many species of plants considered as glacial relicts in Europe (Horsák *et al.* 2015) and the whole set of Euro-Siberian LGM tree species are also common in the Altai-Sayan Mountains (Meusel *et al.* 1965–1992; Hultén & Fries 1986). Palynological studies found a high degree of similarity between the Late Pleistocene pollen spectra from central Europe and surface pollen samples from present-day landscapes of the Altai-Sayan Mountains (Kuneš *et al.* 2008; Magyari *et al.* 2014). Moreover, this and adjacent mountain systems of central Asia are inhabited by extant snails that either represent Beringian allopatric replacements or in some cases the same species known from the European Pleistocene loess record (Meng 2009; Meng & Hoffmann 2009; Horsák *et al.* 2010, 2015; Nekola *et al.* 2018). Many of these became extremely rare or extinct in Europe after the onset of the Holocene or earlier (Horsák *et al.* 2016).

Considerable stability of habitats in the Altai-Sayan Mountains and adjacent areas since the Late Pleistocene is suggested by climate-vegetation models. A dynamic vegetation model based on palaeoclimatic data for the period between 42 000 years BP and the present (Allen *et al.* 2010) suggested that most areas of northern Eurasia experienced remarkable vegetation changes over this period. However, the mountain ranges along the border between Siberia and Kazakhstan on one side and China and Mongolia on the other side, including the Altai-Sayan Mountains, have always been dominated by grassland. Thus the persistence of the LGM biota in this region may be a consequence of long-term stability of suitable habitats (Pavelková Řičánková *et al.* 2018).

All of these independent pieces of evidence suggest that if modern analogues of the Euro-Siberian LGM steppe-tundra ecosystem still exist, they can be most likely found in the dry areas at higher altitudes of the Altai-Sayan or adjacent mountain systems. We conducted a field survey in the Chuya and Kurai intermountain-

tain basins and on the nearby Ukok Plateau in the southeastern Russian Altai because this area was identified as having the highest similarity between Late Pleistocene and recent mammal faunas amongst northern Eurasian regions (Pavelková Řičánková *et al.* 2014). Moreover, local vegetation surveys described direct contacts between steppe and mountain tundra in this area (Kuminova 1960), and we observed an increasing representation of Pleistocene relict plants and snails towards this area in our earlier studies (Horsák *et al.* 2010, 2015). Also, the cold and dry mountain climate of this area closely matches the projections of the Euro-Siberian LGM climate provided by global climate models (Gent *et al.* 2011; Watanabe *et al.* 2011).

The aims of this paper are (i) to describe the habitat mosaic of the largely treeless landscape of the SE Russian Altai Mountains and diversity of its components, (ii) to assess to what extent it can be considered as a modern analogue of the LGM steppe-tundra, and (iii) to characterize primary productivity of this landscape as a food source for large herbivores.

### Study area

The study area is located in the southern part of the Altai Republic (Russian Federation), near the border with Mongolia, China and Kazakhstan (Fig. 1). It encompasses the Kurai Basin and adjacent valleys, the western part of the Chuya Basin with adjacent valleys, the Dzhazator Valley and the Ukok Plateau with adjacent mountain ranges (latitude 49°16'–50°19' N, longitude 87°29'–88°44' E). The bottom of the Kurai Basin is at an altitude of ~1500 m a.s.l., that of the Chuya Basin at ~1750–2000 m a.s.l. and the Ukok Plateau at ~2200–2400 m a.s.l. The sampling sites spanned an altitudinal range of 1463–2924 m a.s.l. Mountain slopes are predominantly formed of acidic, metamorphic, magmatic or sedimentary rocks, while Quaternary sediments occur in depressions (Rudoy *et al.* 2000). Soils are often shallow and stony but can be deeper on soft sediments on the bottom of the basins and in stream flood-plains.

The whole area is rather cold due to high altitude, accumulation of cold air masses in the intermountain basins and night-time heat losses under the frequently clear sky. At the same time, it is dry due to its location in the interior part of the Altai Mountains and in a rain shadow from the adjacent mountain ranges. The mean January temperature is between –30 and –25 °C on the bottom of the Chuya Basin and in the central part of the Ukok Plateau, and about –15 °C on slopes and in the adjacent valleys. The mean July temperature ranges from 8 to 16 °C, with the highest values occurring on the bottom of the Kurai Basin and the lowest values at high altitudes on the mountain ranges above the Ukok Plateau. The total annual precipitation ranges from less than 150 mm at the bottom of the Chuya Basin through ~200 mm in the central part of the Ukok Plateau up to

about 400 mm on the adjacent mountain ranges. A large part of the annual precipitation falls as summer storms (Kharlamova 2004, 2013). The values of annual potential evapotranspiration (PET) vary from 450 to 660 mm ([www.cgiar-csi.org/data/global-aridity-and-pet-database](http://www.cgiar-csi.org/data/global-aridity-and-pet-database)), considerably exceeding annual precipitation and causing aridity. Discontinuous permafrost occurs across the area, being common especially at higher altitudes (Rudoy *et al.* 2000).

The landscape is mostly treeless, with small patches of open woodland dominated by *Larix sibirica* (or less frequently by *Picea obovata* or *Pinus sibirica*) on some north-facing slopes and in narrow belts along streams. The Ukok Plateau is entirely treeless.

### Material and methods

Field sampling was carried out in 2005, 2006 and 2011, always between 20 July and 6 August, which is a period corresponding to the peak of the growing season. We sampled vegetation, snail communities and soils in 182 plots of 10 × 10 m<sup>2</sup> located at different sites of the study area, which were selected purposefully to document all the major habitat types (also called 'habitats' in this paper). The plots were located within physiognomically and ecologically homogeneous habitat patches, avoiding sharp transitional situations. Sites affected by strong recent disturbance by humans, fires or overgrazing were not sampled. Replicated sampling of the same habitat at the same site was avoided.

In each plot, we recorded all species of vascular plants and terricolous bryophytes and lichens, along with their cover-abundances estimated using the nine-degree Braun-Blanquet scale (van der Maarel 1979). Snails were searched for by eye by a single observer for 30–60 min per plot in all the appropriate microhabitats within each plot (for details see Horsák *et al.* 2010, 2015). Small snails (<5 mm in maximum dimension) were recorded by collecting ~3 L of leaf litter, mosses and topsoil. Wetland litter samples were processed via wet sieving (Horsák *et al.* 2015) while dry litter was processed using standard protocols (Nekola & Coles 2010). Taxonomy and nomenclature follow Cherepanov (1995) for vascular plants, Ignatov & Afonina (1992) for bryophytes, Andreev *et al.* (1996) for lichens, and Sysoev & Schileyko (2009) and Nekola *et al.* (2015, 2018) for snails.

Soil samples were collected within each 10 × 10 m<sup>2</sup> plot from a depth of 5–10 cm in four places, mixed and sieved. Soil pH was measured in a suspension of soil and distilled water (ratio 2:5) after 24 h using a PHH-200 pH meter (Omega Engineering, Manchester, UK). Total nitrogen content (N) was determined by the Kjeldahl method, organic carbon by gravimetry and these two measures were then converted to the C:N ratio. Plant-available phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were extracted using the Mehlich III method (strong acid extraction with ion complex)

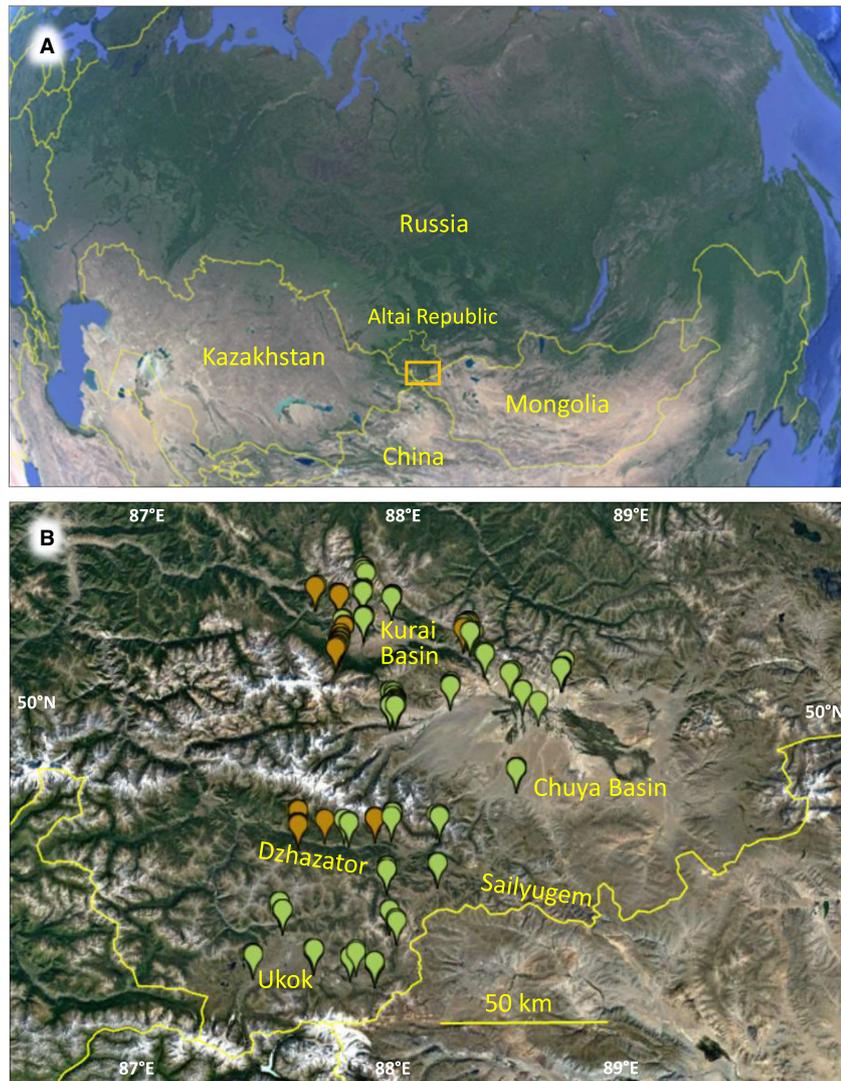


Fig. 1. A. The position of the study area (rectangle) in the Altai Republic, on the border between relatively humid Siberia and the drylands of central Asia. B. Study area in the SE Russian Altai Mountains with locations of sampling sites (green = open vegetation; brown = forest). Background maps taken from Google Earth. [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

and determined by spectrophotometry (P; Spekol 210, Carl Zeiss, Jena, Germany) and atomic absorption spectrophotometry (K, Ca, Mg; AAS 933 Plus, GBC Scientific Equipment, Melbourne, Australia). The analyses were conducted by AgroLab Ltd, Troubsko, Czech Republic, following the analytical protocols described by Zbíral (2005).

Aboveground non-woody biomass of the herbaceous plants and low shrubs was harvested from one to four representative subplots of 0.25 to 1 m<sup>2</sup> within each 10 × 10 m<sup>2</sup> plot. The biomass was oven-dried, weighed and its weight recalculated to 1 m<sup>2</sup>. Annual primary productivity was quantified as the sum of the weights of graminoids, non-graminoid herbs, deciduous leaves and other herbaceous parts of woody plants, and 30% of the weight of evergreen leaves (see Axmanová *et al.* 2013 for reasoning). Biomass was further analysed for the

content of nitrogen using the distillation method applied to biomass mineralized with sulphuric acid and hydrogen peroxide. Other elements (P, K, Ca, Mg) in biomass were analysed from biomass mineralized by microwave heating, using the same methods as used for soil analyses. Crude fibre content was determined by boiling with a mixture of acetic and nitric acids, separating the insoluble residue, and determining the loss of mass on ignition. The biomass analyses were conducted in the same laboratory as the soil analyses. Concentrations of nutrients in biomass were compared with values reported in the literature as optimal for cattle (Whitehead 2000; Suttle 2010; Hejzman *et al.* 2016). This comparison was used as a benchmark for the nutritional value of different habitats for large herbivores, although it is important to note that domesticants have different nutrition requirements than wild animals.

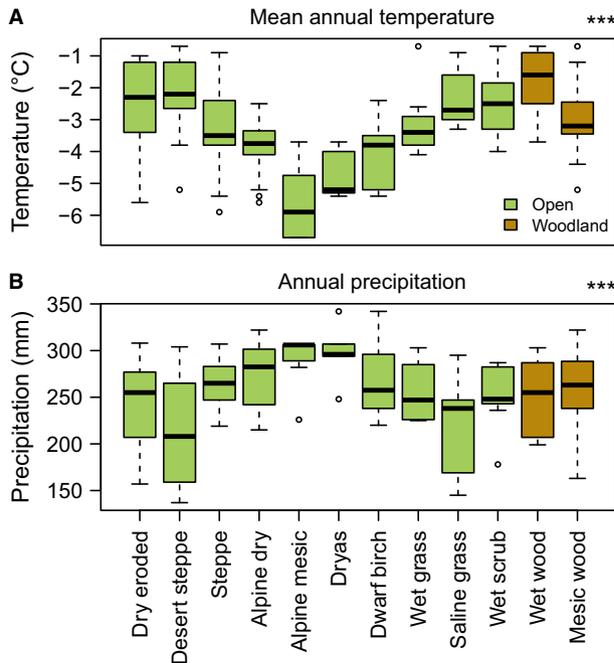


Fig. 2. Mean annual temperature and annual precipitation for different habitats of the Altaian steppe-tundra. Note that the summer and winter temperatures and precipitation are strongly correlated with annual values, resulting in very similar patterns across habitat types (not shown). *p*-values for significant differences amongst groups (Kruskal–Wallis test) are indicated above the top right corner of each graph: \*\*\**p* < 0.001, \*\**p* < 0.01, \**p* < 0.05, n.s. *p* > 0.05. See Table S3 for detailed statistics in numerical format. [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

Values of climatic variables were obtained for each plot based on the overlay of the plot's geographical coordinates with the WorldClim database of interpolated climatic values ([www.worldclim.org](http://www.worldclim.org); Hijmans *et al.* 2005).

For logistical reasons, snails were recorded in a subset of 105 plots, soil pH was measured in 182 plots, soil C, N, P, K and Mg in 104 plots, and biomass was analysed in 100 plots. In all cases, the plots within these subsets representatively covered all the major habitats and most of the study sites. All the data from plots have been made available in the Figshare repository (<https://doi.org/10.6084/m9.figshare.6652319.v2>).

All 182 plots were classified into 12 habitat types based on the overall vegetation physiognomy (e.g. herbaceous vs. scrub vs. woodland), plant species

composition and environment (e.g. dry vs. wet). Differences amongst these habitats in the values of measured variables were compared using Kruskal–Wallis tests calculated with the R program, version 3.2.2 (R Core Team 2015; [www.r-project.org](http://www.r-project.org)). Diagnostic species of each habitat were determined based on the phi coefficient of association between species presence/absence and group membership of plots following Tichý & Chytrý (2006), using the JUICE program (Tichý 2002). The phi coefficient ( $\Phi$ ) was calculated for virtually equalized numbers of plots per group. Species with  $\Phi > 0.4$ , i.e. with a high concentration of occurrence in plots belonging to a particular habitat, were accepted as diagnostic species. In addition, Fisher's exact test for the species–habitat associations was computed and species with associations not significant at *P* < 0.05 were excluded from the lists of diagnostic species proposed on the basis of the phi coefficient.

Plant species from the Altai vegetation plots were assigned to pollen types that frequently appear in the Eurasian Last Glacial pollen spectra (e.g. Tarasov *et al.* 2000; Feurdean *et al.* 2014) based on Beug (2004) and Pelánková & Chytrý (2009). Plant species considered as glacial relicts in Europe were taken from Horsák *et al.* (2015): *Agropyron cristatum* s.l. (*A. cristatum* s.str. in the Altai Mountains), *Allium strictum*, *Artemisia laciniata*, *A. rupestris*, *Astragalus frigidus*, *Baeothryon pumilum*, *Blysmus rufus*, *Carex capillaris*, *C. microglochis*, *C. obtusata*, *Kobresia myosuroides*, *Kochia prostrata*, *Krascheninnikovia ceratoides*, *Ligularia glauca*, *Pentaphragma fruticosum* and *Saxifraga hirculus*. Glacial relict species of snails were taken from Horsák *et al.* (2010, 2015), considering species typical of the full-glacial fossil record from central European loess series (Ložek 2001) but becoming rare, restricted to refugia with suitable climate, or extinct in Europe in the Holocene. They included *Columella columella*, *Pupilla alpicola*, *P. loessica*, *Vallonia tenuilabris*, *Vertigo genesii*, *V. parcedentata* and *V. pseudosubstriata*. A recent phylogenetic study revealed that *Vertigo genesii* is in fact restricted to Europe, whereas Altaian populations represent its cryptic sibling *V. genesioides* (Nekola *et al.* 2018). As habitat preferences of these two species are very similar, we also included *Vertigo genesioides*. Contrary to Horsák *et al.* (2015), we did not include *Pupilla turcmenica*, because its European vicariant *P. sterrii* (Nekola *et al.* 2015) is

Table 1. Median percentage cover of vegetation layers in different habitats of the Altaian steppe-tundra. See Table S3 for more detailed statistics.

	Dry eroded slopes	Desert steppe	Typical steppe	Alpine dry grassland	Alpine mesic grassland	Dryas tundra	Dwarf-birch tundra	Wet grassland	Saline grassland	Wet scrub	Wet woodland	Mesic woodland
Tree layer	0	0	0	0	0	0	0	0	0	0	18	25
Shrub layer	4	0	0	5	0	0	68	12	1	42	24	20
Herb layer	45	38	62	78	66	79	44	69	69	58	57	52
Bryophytes	0	0	2	13	9	13	24	44	12	30	19	40
Lichens	0	2	4	5	30	10	17	1	0	2	1	4

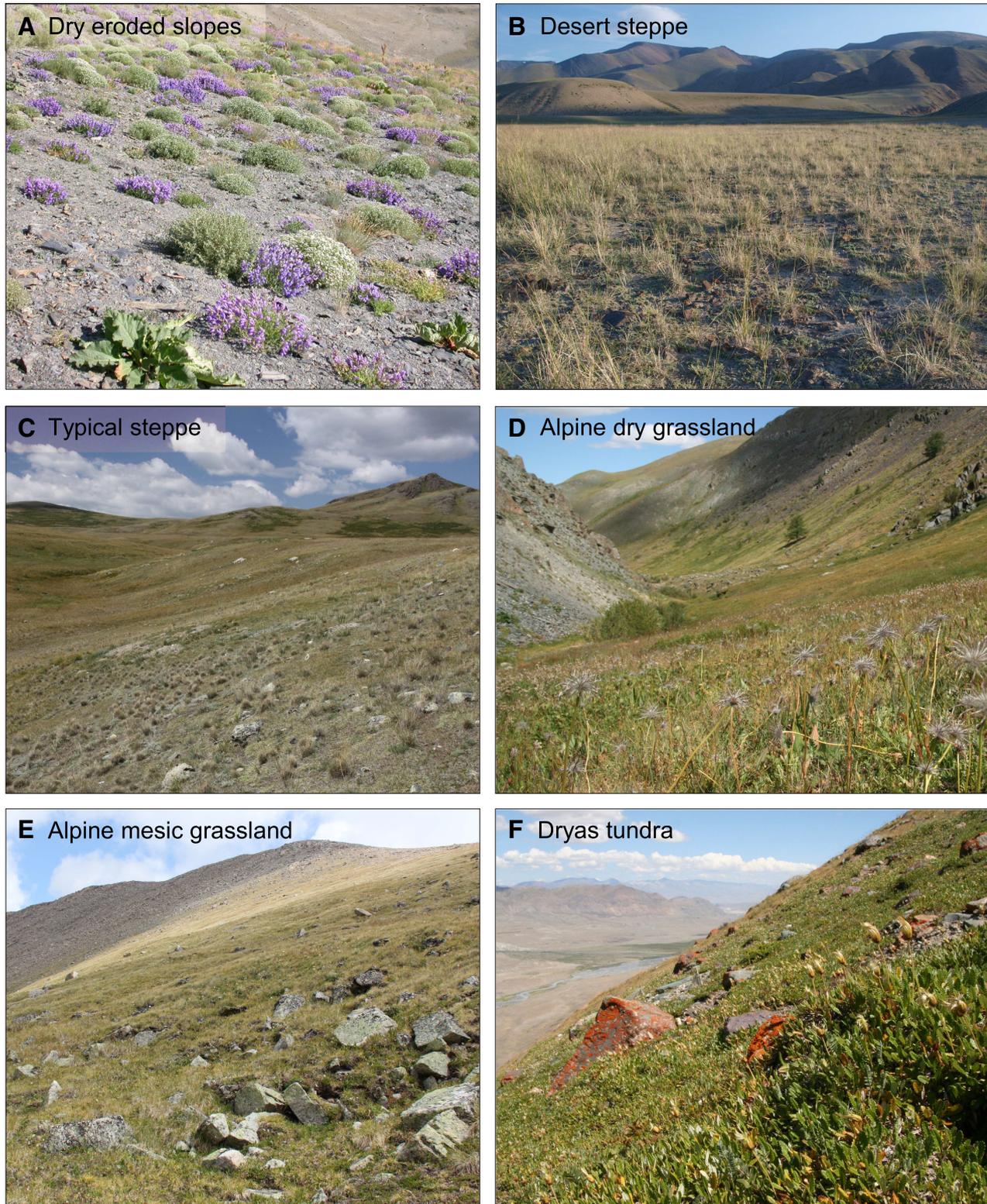
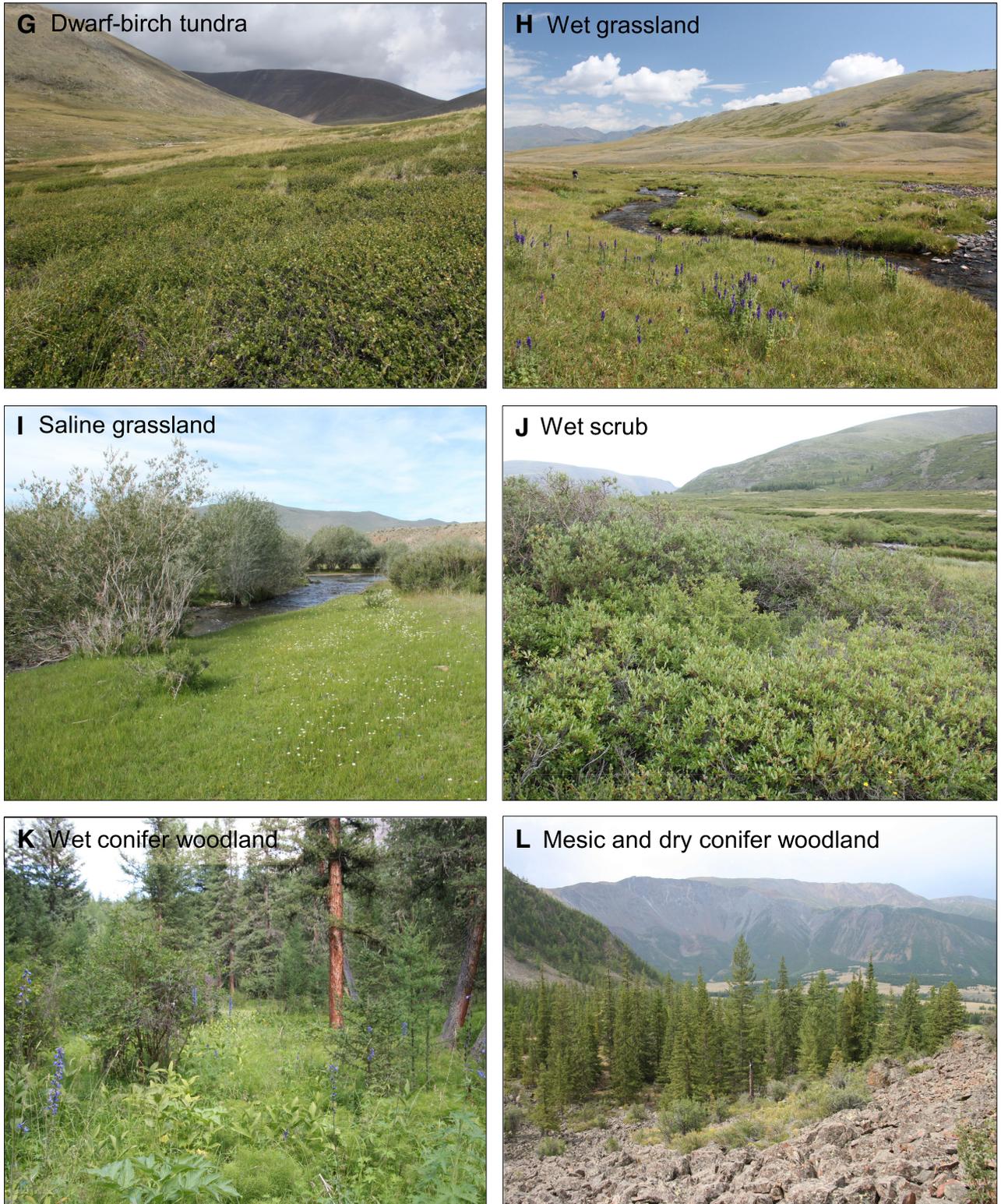


Fig. 3. Habitat types of the Altaian steppe-tundra. Localities: A, D, F = Taldura Valley near Bel'tir (*Dracocephalum peregrinum*, *Rheum compactum* and *Stellaria dichotoma* are visible in A); B = Chuya Basin near Kosh-Agach; C = Dzhazator Valley; E = below Teplyi klyuch Pass; G = Kalguty Valley; H = Ukok Plateau near Lake Zerlyukol; I = Chuya Basin near Tarkhata; J = Zhumaly Valley (*Salix divaricata*); K, L = Kurai Range near Chagan-Uzun (both woodlands with *Larix sibirica* and *Picea obovata*). [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]



*Fig. 3.* Continued.

nowadays common in European areas with non-glacial climate (Horsák *et al.* 2013b).

We compiled lists of Last Glacial and Recent mammal faunas of the Altai-Sayan Mountains and

of the Ukok-Sailyugem area from various literature sources (see Pavelková Řičánková *et al.* 2015: table S3). The Recent faunas also include species extinct since the 16th century AD following the

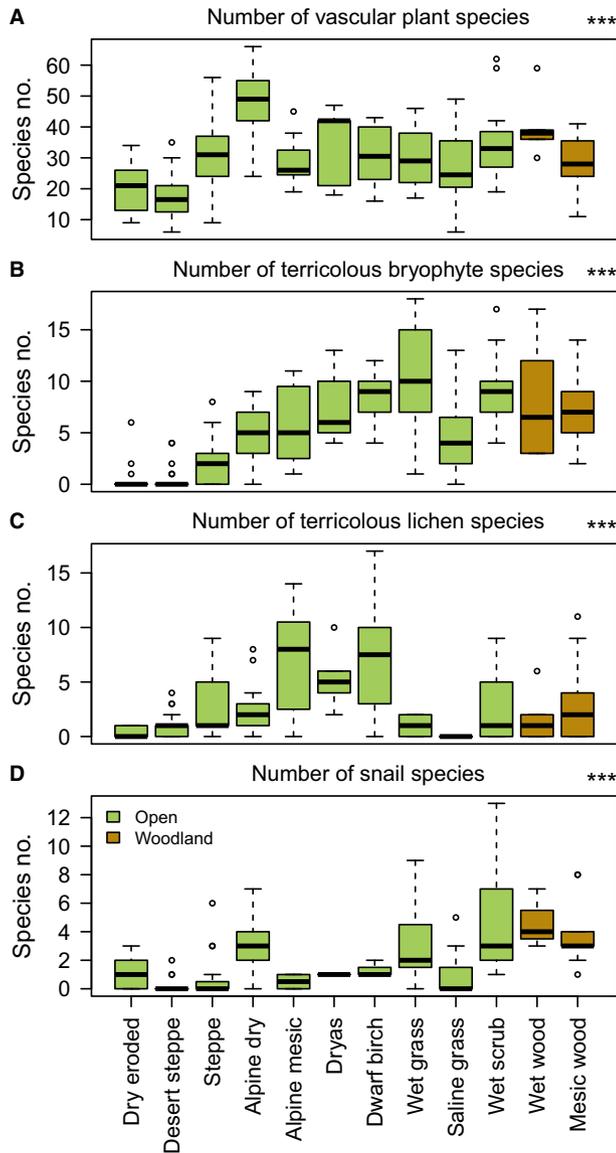


Fig. 4. Species richness measured as the number of species recorded in plots of 100 m<sup>2</sup> in different habitats of the Altaian steppe-tundra. See Fig. 2 for an explanation of significances and Table S3 for detailed statistics in numerical format. [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

IUCN definition of 'recent extinction' ([www.iucnredlist.org](http://www.iucnredlist.org)).

## Results

### Habitat types within the steppe-tundra landscape

Although predominantly treeless, the steppe-tundra landscape in the SE Russian Altai is a remarkably diverse mosaic of distinct habitats. The following broad habitats with distinctive floristic and land snail composition (Tables S1, S2) were recognized, depending mainly on climatic contrasts in the mountain area and the

topographic distribution of moisture across the landscape (Fig. 2, Table 1):

- Dry eroded slopes (Dry eroded; Fig. 3A) with unstable, usually stony or gravelly substrate affected by erosion, including screes, wadis and alluvial fans. They are covered with open vegetation with frequent occurrences of the suffrutescent wormwood *Artemisia santolinifolia* and the perennial dicot herbs *Dracocephalum peregrinum*, *Stellaria dichotoma*, *Vicia costata* and *Ziziphora clinopodioides*. Graminoids are rare. This habitat occurs on the lower mountain slopes of the Kurai Range, North Chuya Range and South Chuya Ranges adjacent to the Kurai and Chuya basins. The vegetation of rock outcrops with shallow soils corresponds to the phytosociological alliance *Stipion orientalis* of the class *Cleistogenetea squarrosae* (Korolyuk & Makunina 2009), while the vegetation of screes corresponds to the class *Artemisia santolinifoliae-Berberidetea sibiricae* (Ermakov *et al.* 2006). This habitat type is very poor in snails, with *Pupilla loessica*, a characteristic full-glacial species, being the only diagnostic and constant element here.
- Desert steppe (Fig. 3B) is characterized by open vegetation with the low-productive graminoids *Agropyron cristatum*, *Carex duriuscula*, *Koeleria cristata* and *Stipa glareosa*, and perennial wormwoods and chenopods with a woody base, including *Artemisia frigida*, *Kochia prostrata* and *Krascheninnikovia ceratoides*. It is found mainly on dry bottoms of the Kurai and Chuya basins, in their side valleys, and rarely also on the Ukok Plateau. This vegetation belongs to the class *Stipetea glareoso-gobicae* (Ermakov 2012). Snails are very rare in this and the next habitat type.
- Typical steppe (Steppe; Fig. 3C) is denser vegetation than the previous two types. It is usually dominated by the perennial bunch grasses *Festuca valesiaca*, *Helictotrichon altaicum* (*H. desertorum* s.l.) and *Koeleria cristata*, with frequent occurrences of *Ephedra monosperma* and perennial dicot herbs such as *Aster alpinus*, *Potentilla acaulis*, *P. bifurca*, *Pulsatilla patens* s.l. and *Silene repens*. At drier sites, vegetation is more open with a prominence of bunch grasses, whereas at more mesic sites it has a higher total cover with a greater participation of broad-leaved herbs. This habitat occurs throughout the study area except for the dry bottoms of the Kurai and Chuya basins. Its vegetation corresponds to the phytosociological order *Stipetalia krylovii* of the class *Cleistogenetea squarrosae* (Korolyuk & Makunina 2009).
- Alpine dry grassland (Alpine dry; Fig. 3D) is even denser grassland than typical steppe. It occurs in more mesic habitats than steppe and is dominated by a mixture of graminoids and perennial dicot herbs, the former represented especially by *Carex obtusata*, *C. pediformis*, *Festuca kryloviana* and *Helictotrichon hookeri*, the latter by *Aster alpinus*, *Bistorta major*,

*Galium boreale*, *Ligularia altaica*, *Potentilla matsukana* and *Pulsatilla patens* s.l. Its species composition includes species of steppe (e.g. *Carex caryophylla*, *C. pediformis*, *Galium verum*, *Polygala comosa* and *Pulsatilla patens* s.l.), mesic to wet grasslands (e.g. *Bistorta major* and *Galium boreale*) and species of alpine grasslands (e.g. *Festuca kryloviana*, *Helictotrichon hookeri*, *Ligularia altaica* and *Potentilla matsukana*). Low shrubs such as *Pentaphylloides fruticosa* and *Spiraea media* occur in places. Alpine dry grassland occurs in the side valleys of the Kurai and Chuya basins, in the Dzhazator valley and on the Ukok Plateau. It is related to the phytosociological order *Festucetalia lenensis* of the class *Cleistogenetea squarrosae* (Ermakov 2012) and to the formation called cryophytic steppe in Russian literature (Korolyuk & Namzalov 1994). Many glacial relict snails are common in this habitat, including *Pupilla loessica* and *Vallonia tenuilabris*.

- Alpine mesic grassland (Alpine mesic; Fig. 3E) is a closed, mesic to wet grassland consisting of alpine dicot herbs and grasses such as *Gentiana algida*, *Lagotis integrifolia*, *Minuartia biflora*, *Oxytropis altaica*, *Saxifraga melaleuca*, *Schulzia crinita*, *Trisetum mongolicum* and *Viola altaica*. It is rich in bryophytes and lichens. It occurs on higher mountain ranges adjacent to both the basins and to the Ukok Plateau. Most stands of this vegetation correspond to the class *Juncetea trifidi* (Ermakov et al. 2000). This and the next two habitat types provide rather unfavourable conditions for land snails, but the cold-resistant *Pupilla loessica* is not uncommon there.
- Dryas tundra (Dryas; Fig. 3F) is dominated by the creeping dwarf shrub *Dryas oxyodonta*, which is usually accompanied by the tussocky sedge *Kobresia myosuroides* and short alpine dicot herbs such as *Bistorta vivipara* and *Thalictrum alpinum*. Bryophytes and lichens are abundant. This vegetation occurs in the same area as the alpine grasslands but occupies wind-exposed sites with shallower soils. It belongs to the class *Caricirupetris-Kobresietea bellardii* (Ermakov 2012).
- Dwarf-birch tundra (Dwarf birch; Fig. 3G) is dominated by the low shrubby birch *Betula rotundifolia* (a species closely related to *B. nana* and *B. exilis*). The birch stands reach a height of 10–100 cm, depending on snow depth, soil humidity and the degree of wind protection of the site. Dicot herbs such as *Bistorta vivipara* and *Pachypleurum alpinum*, grasses *Festuca altaica* and *Poa sibirica*, and bryophytes and lichens are common in this dwarf scrub. Dwarf-birch tundra is found on the mountain ranges around the Kurai and Chuya basins, in their side valleys, in the upper parts of the Dzhazator valley and on the Ukok Plateau. This vegetation belongs to the alliance *Empetro-Betulion rotundifoliae* of the class *Loiseleurio-Vaccinieta* (Ermakov 2012).

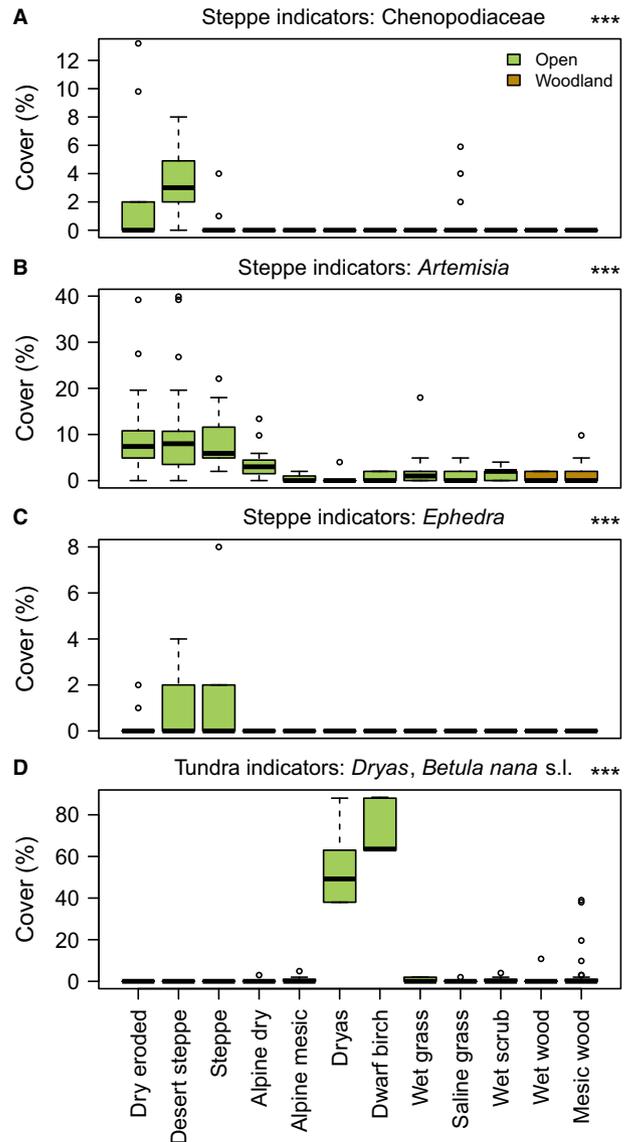


Fig. 5. Cover of species and groups of species that are frequently used as palynological indicators of either steppe or tundra in the Altaian steppe-tundra. See Fig. 2 for an explanation of significances and Table S3 for detailed statistics in numerical format. [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

- Wet grassland (Wet grass; Fig. 3H) occurs in wet or seasonally wet depressions and flood-plains. Locally such sites support the accumulation of a shallow layer of organic sediment (fen) and have a higher cover of bryophytes than the other open habitats of the steppe-tundra. Dominant plants are graminoids such as *Carex altaica*, *C. enervis*, *Festuca rubra* and *Kobresia myosuroides*, which are accompanied by abundant dicot perennial herbs such as *Angelica tenuifolia*, *Bistorta vivipara*, *Gentiana prostrata* and *Saxifraga hirculus*. Patches of moisture-demanding low shrubs, particularly *Pentaphylloides fruticosa* and *Salix coesia*, are common. This vegetation is related to the classes

*Mulgedio-Aconitetea* and *Scheuchzerio-Caricetea fuscae* (Ermakov 2012). This habitat is rich in snails including glacial relict species such as *Pupilla loessica* and *Vertigo parcedentata*.

- **Saline grassland** (Saline grass; Fig. 3I) occurs on terraces and flood-plains of permanent or intermittent streams, especially within the desert-steppe area on the bottoms of the Kurai and Chuya basins and in their side valleys. It is dominated by the short halophilous or halotolerant sedges *Baeothryon pumilum*, *Blysmus rufus*, *Carex delicata*, *C. enervis* and *C. microglochis*, grasses *Calamagrostis macilentata* and *Hordeum brevisubulatum*, and perennial dicot herbs such as *Parnassia palustris*, *Potentilla anserina*, *Triglochin palustre* and *T. maritimum*. This vegetation belongs to the class *Scorzonero-Juncetea gerardii* (Ermakov 2012). Saline habitats are in general unfavourable for snails and only one species, *Oxyloma sarsii*, was recorded frequently.
- Wet scrub (Fig. 3J) is dominated by *Betula fruticosa*, *Lonicera altaica*, *Pentaphylloides fruticosa*, *Salix coesia* and *S. divaricata*. It is often spatially associated with wet grassland, containing many of its typical species in the herb and moss layers. This vegetation partly corresponds to the class *Salicetea purpureae* (Ermakov 2012). This habitat is the richest in snail species, both all species and glacial relicts.
- Wet conifer woodland (Wet wood; Fig. 3K) forms galleries along streams in the valleys around the Kurai Basin and in the Dzhazator valley. The tree layer, which is generally very open, is composed of *Picea obovata* or *Larix sibirica* and characterized by frequent occurrence of the willows *Salix bebbiana* and *S. pyrolifolia*. In the herb and moss layers, it contains species of wet grasslands such as the grass *Deschampsia cespitosa* and the mosses *Aulacomnium palustre* and *Sanionia uncinata*, growing together with mesophilous grasses and perennial dicot herbs such as *Festuca rubra*, *Lupinaster pentaphyllus* and *Vicia cracca*. Most of these woodlands correspond to the alliance *Pino sibiricae-Laricion sibiricae* of the class *Vaccinio-Piceetea* (Ermakov 2012). Sites of this and of the following habitat are rather rich in snails, hosting similar species spectra. While there are several glacial relict species (e.g. *Columella columella* and *Vallonia tenuilabris*), other species have Holarctic or Beringian distributions (*Vertigo beringiana*, *V. microsphaera*, *V. ronneyensis* and *Euconulus fulvus*).
- Mesic and dry conifer woodland (Mesic wood; Fig. 3L) has a sparse tree layer of *Larix sibirica*, in places with an admixture of *Pinus sibirica*. Its herb layer includes the dwarf shrub *Vaccinium myrtillus*, the graminoids *Carex pediformis*, *Festuca altaica* and *Poa sibirica*, the dicot herbs *Dianthus superbus* and *Galium boreale*, the woody vine *Atragene sibirica*, and abundant mesophilous mosses. It occurs on slopes of the side

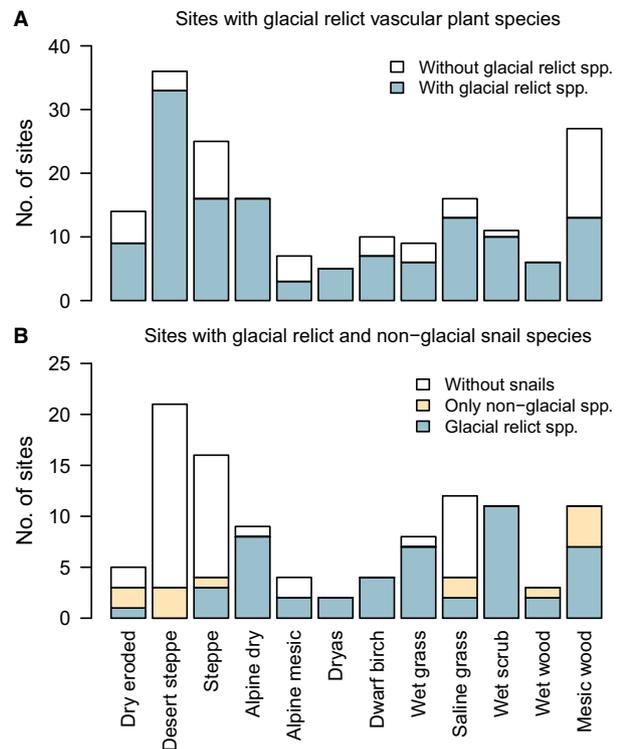


Fig. 6. The numbers of studied plots in different habitats of the Altaian steppe-tundra with the recorded occurrence of glacial relict vascular plant species (A) and glacial relict snail species, only other (non-glacial relict) snail species, and no snail species (B). [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

valleys of the Kurai and Chuya basins and of the Dzhazator valley. This vegetation belongs mainly to the class *Rhytidio rugosi-Laricetea sibiricae* (Ermakov 2012).

#### Species richness of the steppe-tundra landscape

Species richness of vascular plants is highest in the alpine dry grassland, with a median of 49 and a maximum of 66 species in 100 m<sup>2</sup> (Fig. 4; Table S3). It is lowest in the desert steppe, with a median of 16.5 species and a minimum of six species. Terricolous bryophytes are most species-rich in wet grassland, wet scrub and dwarf-birch tundra, and almost absent from dry eroded slopes and desert steppe. Terricolous lichens are most species-rich in alpine grassland, dwarf-birch tundra and dryas tundra, while they are absent from saline grassland. Snails have the highest species diversity in woodlands, wet scrub, and alpine dry and wet grassland, but are absent from most desert-steppe plots.

#### Distribution of palaeoecological indicators in the steppe-tundra landscape

The species producing pollen identified as Chenopodiaceae, *Artemisia* and *Ephedra*, which are commonly

Table 2. Last Glacial and Recent mammals of the Altai-Sayan Mountains and of the steppe-tundra area of Ukok-Sailyugem, based on a compilation from various sources (see Pavelková Řičánková et al. 2014, 2015, 2018; <http://datadryad.org/resource/doi:10.5061/dryad.62p1q/1>). Globally extinct species are marked by daggers. Species occurring currently in the steppe-tundra area of Ukok-Sailyugem in the SE Russian Altai are marked by asterisks.

Only Last Glacial before 35 000 years BP: *Sorex baikalensis*†, *S. erbaevae*†, *S. palaeosibiricus*†, *Equus hydruntinus*†, *Camelus knoblochi*†

Only Last Glacial (including the period between 35 000 and 12 000 years BP): *Mammuthus primigenius*†, *Homo neanderthalensis*†, *Lepus tanaicus*†, *Panthera leo* s.l., *Crocota spelaea*†, *Ursus rossicus*†, *U. spelaeus*†, *Coelodonta antiquitatis*†, *Megaloceros giganteus*†, *Bison priscus*†, *Ovibos moschatus* s.l., *Spirocerus kiakhtensis*†, *Spermophilus parryi*, *Dicrostonyx torquatus* s.l., *Lemmus amurensis*, *L. sibiricus*, *Microtus middendorffii*

Both Last Glacial and Recent: *Ochotona alpina*\*, *O. hyperborea*, *O. pusilla*, *Lepus capensis* s.l.\*, *L. timidus*\*, *Neomys fodiens*, *Sorex araneus* s.l., *S. daphaenodon*, *S. isodon*, *S. minutissimus*, *S. minutus*\*, *S. roboratus*, *Talpa altaica*, *Eptesicus nilssonii*, *Plecotus auritus* s.l., *Myotis brandtii*, *M. dasycneme*, *M. daubentonii* s.l., *M. ikonnikovi*, *M. myotis* s.l., *Murina hilgendorfi*, *Felis manul*\*, *Lynx lynx*\*, *Uncia uncia*\*, *Canis lupus*\*, *Cuon alpinus*\*, *Vulpes corsac*\*, *V. lagopus*, *V. vulpes*\*, *Ursus arctos*\*, *Gulo gulo*\*, *Martes zibellina*\*, *Meles meles* s.l., *Mustela erminea*\*, *M. eversmanni*\*, *M. nivalis*\*, *Equus ferus* s.l.\*, *E. hemionus*\*, *Alces alces* s.l.\*, *Capreolus pygargus*\*, *Rangifer tarandus*\*, *Cervus elaphus* s.l.\*, *Procapra gutturosa*\*, *Saiga tatarica* s.l.\*, *Bos grunniens* s.l.\*, *B. primigenius*, *Capra sibirica*\*, *Ovis ammon*\*, *O. nivicola*, *Sciurus vulgaris*, *Pteromys volans*, *Marmota baibacina*\*, *Spermophilus erythrogenys*, *S. undulatus*\*, *Tamias sibiricus*\*, *Castor fiber*, *Allactaga major*, *Myospalax myospalax*, *Alticola argentatus*\*, *A. macrotis*\*, *A. strelzovi*\*, *Arvicola amphibius*\*, *Ellobius tancrei*, *Eolagurus luteus*, *Lagurus lagurus*, *Microtus agrestis*, *M. arvalis*\*, *Microtus gregalis*\*, *M. oeconomus*\*, *Myodes glareolus*, *M. rufocanus*\*, *M. rutilus*\*, *Myopus schisticolor*, *Allocricetulus eversmanni*, *Cricetulus barabensis*\*, *Cricetus cricetus*, *Apodemus unguiculatus*\*, *Micromys minutus*

Only Recent: *Ochotona dauurica*\*, *O. pallasi*\*, *O. turuchanensis*, *Hemiechinus auritus*\*, *Crocidura sibirica*, *C. suaveolens* s.l., *Sorex caecutiens*\*, *S. tundrensis* s.l.\*, *Eptesicus bottae*, *E. gobiensis*, *E. serotinus*, *Nyctalus noctula*, *Vespertilio murinus*, *Myotis frater*, *M. mystacinus* s.l., *Felis silvestris* s.l., *Panthera tigris*\*, *Lutra lutra*, *Martes foina*\*, *Mustela altaica*\*, *M. sibirica*\*, *Vormela peregusna*\*, *Sus scrofa*, *Camelus ferus*\*, *Moschus moschiferus*\*, *Marmota sibirica*\*, *Spermophilus pallidicauda*, *Dryomys nitedula*, *Allactaga bullata*, *A. sibirica*\*, *Pygeretmus platyurus*, *P. pumilio*, *Cardiocranius paradoxus*, *Salpingotus crassicauda*, *Dipus sagitta*, *Stylodipus andrewsi*, *S. sungorus*, *S. telum*, *Sicista betulina* s.l.\*, *S. subtilis* s.l., *Alticola barakshin*, *A. semicanus*, *A. tuvinicus*, *Eolagurus przewalskii*, *Lasiopodomys brandtii*, *Microtus levis*, *M. limophilus*, *M. mongolicus*\*, *Allocricetulus curtatus*, *Cricetulus longicaudatus*\*, *C. migratorius*, *Phodopus campbelli*\*, *P. roborovskii*, *P. sungorus*\*, *Meriones meridianus*, *M. tamariscinus*, *Meriones unguiculatus*, *Rhombomys opimus*, *Apodemus agrarius*, *A. uralensis*, *Mus musculus* s.l.\*

considered as steppe indicators in palynology, were concentrated on dry eroded slopes and in steppe habitats of the Altaian steppe-tundra (Fig. 5). The most common producers of Chenopodiaceae pollen are *Kochia prostrata* and *Krascheninnikovia ceratoides*, although a further 17 species of the Amaranthaceae (including the paraphyletic Chenopodiaceae) family of the genera *Atriplex*, *Axyris*, *Ceratocarpus*, *Chenopodium*, *Kochia*, *Salsola*, *Suaeda* and *Teloxys* were found in the studied plots. *Artemisia* pollen is produced by at least 19 species of this genus found in the studied plots, the most common being *A. frigida*, *A. phaeolepis*, *A. santolinifolia*, *A. obtusiloba*, *A. macrantha* and *A. rupestris*. *Ephedra* pollen producers are represented by *E. dahurica* and *E. monosperma*. While Chenopodiaceae and *Ephedra* species are restricted to steppes and dry eroded slopes, *Artemisia* species were found in all habitat types, although being much more prominent in steppes and on dry eroded slopes than elsewhere. Of the tundra indicators, pollen of *Dryas* and *Betula nana* types is produced by *Dryas oxydonta* and *Betula rotundifolia*, the dominant species of the respective habitat types.

Plants considered as glacial relicts in Europe according to Horsák et al. (2015) are most represented in alpine dry grassland, dryas tundra, wet conifer woodland and wet scrub, where they were found in all or nearly all studied plots (Fig. 6A). They are also well represented in steppe habitats, but less represented in mesic and dry conifer woodland. Characteristic snails of European full-glacial loess fauna, considered as glacial relicts (Horsák et al. 2010, 2015), are most represented in the

wet scrub, dwarf-birch tundra, dryas tundra, alpine dry grassland and wet grassland (Fig. 6B). These species are entirely absent from desert steppe and very rare on dry eroded slopes, in typical steppe and saline grassland.

Of 100 species of mammals recorded in various sources for the Last Glacial period of the Altai-Sayan region, 78 species are still living there, and 42 of these were recently recorded in the Ukok-Sailyugem area. Of the 22 species extirpated from the Altai-Sayan region, five disappeared before the LGM (and all of these went extinct globally) and 17 were still living in this region at the end of the Last Glacial period between 35 000 and 12 000 years BP. Of these latter 17 species, 10 went extinct globally (Table 2).

#### *The productivity of the steppe-tundra landscape*

Soil nutrient status differs considerably amongst individual habitats of the steppe-tundra, but in general, all soils are rich in calcium, and most of them have near-neutral reactions (Table 3). Wet and shrubby habitats have a higher content of organic carbon than the others.

The non-woody aboveground biomass measured at the peak of the growing season (a proxy of primary productivity; Fig. 7A) was between 50 and 250 g m<sup>-2</sup>, with a minimum of 14 g m<sup>-2</sup> recorded at one site in the desert steppe and a maximum of 374 g m<sup>-2</sup> recorded at one site in the saline grassland. Overall steppe habitats and woodland herb layers have low productivity, while mesic to wet grasslands are more productive. There is considerable variation in nutrient concentrations in aboveground biomass amongst individual habitats

Table 3. Medians of soil chemistry variables measured in different habitats of the Altaian steppe-tundra. See Table S3 for more detailed statistics.

	Dry eroded slopes	Desert steppe	Typical steppe	Alpine dry grassland	Alpine mesic grassland	Dryas tundra	Dwarf-birch tundra	Wet grassland	Saline grassland	Wet scrub	Wet woodland	Mesic woodland
pH	7.0	7.3	6.8	6.4	6.1	6.6	5.5	6.9	7.3	7.2	7.1	6.5
Organic carbon (%)	7.2	9.2	12.4	17.4	13.3	6.4	14.8	13.4	26.7	30.6	21.2	9.9
C:N ratio	36.1	35.7	31.6	32.7	31.2	39.9	39.2	32.3	29.3	38.5	58.8	51.2
Phosphorus (mg kg <sup>-1</sup> )	9	27	19.5	13	7	7	4	9	4	8	4	21
Potassium (mg kg <sup>-1</sup> )	170.5	218	265.5	220	137	218	162	144	180	180	128	210
Calcium (mg kg <sup>-1</sup> )	11042	3497	2812.5	3093	1003	5891	3032	3914	14713	6363	8228	2669
Magnesium (mg kg <sup>-1</sup> )	358.5	318	371	378	144	275	303	450	882	540	371	317

(Fig. 7B–J). Concentrations of nitrogen and phosphorus are close to the lower limits of the benchmark values recommended for cattle, while concentrations of potassium, calcium and magnesium, as well as ratios considered as important for large herbivore nutrition, are above the recommended values.

## Discussion

### *Is the Altaian steppe-tundra a good analogue of the Pleistocene steppe-tundra?*

Here we describe, for the first time, details of a habitat mosaic of a steppe-tundra ecosystem of the temperate zone (Tuhkanen 1984). This ecosystem contains many species with broad geographical ranges encompassing the temperate zone from central Europe to southern Siberia (Meusel *et al.* 1965–1992; Hultén & Fries 1986; Wilson & Reeder 2005), which makes it a much closer analogue of the LGM ecosystems of Europe and southern Siberia than the previously described steppe-tundra analogues from Beringia (Yurtsev 1981, 2001; Hopkins *et al.* 1982; M.D. Walker *et al.* 1991; D.A. Walker *et al.* 2001; Blinnikov *et al.* 2011). At the same time, however, the Altaian steppe-tundra shares some species with Beringia but not with Europe, e.g. snail species that extend from the Altai Mountains to Alaska (e.g. *Punctum lozeki*: Horsák & Meng 2018; *Vertigo beringiana*, *V. genesioides* and *V. microsphaera*: Nekola *et al.* 2018).

The suitability of the Altaian steppe-tundra as a proxy for the central and eastern European steppe-tundra of the LGM period has been supported by data on flora, land snails and mammals. Magyari *et al.* (2014) compared Late Pleistocene pollen spectra from three cores in Hungary and Romania with modern pollen samples from the Altai-Sayan Mountains. Most of these modern samples were taken from the areas outside the steppe-tundra, but 42 samples were from lower parts of the steppe-tundra area studied here (Kurai Basin and valleys adjacent to the Kurai and Chuya basins; Pelánková & Chytrý 2009). Of these, 16 samples, representing mainly steppe, but also woodland and mesic and wet grassland, could not be statistically distinguished from at least one of the samples from these Late Pleistocene cores. Some other modern samples from this area were similar to the spectra from these cores, although they were not exact analogues with no significant statistical difference from the fossil samples.

Species-level data on the current distribution of plants and snails in a broader area of the Altai Mountains suggest even a more explicit link between the current steppe-tundra landscapes and the European Late Pleistocene ecosystems. The occurrence of species considered as glacial relicts in Europe is notably concentrated in the steppe-tundra of the SE Russian Altai, while they are rare or absent from wetter and warmer areas of the northern Altai (Horsák *et al.* 2015). A similar link exists for mammals. Pavelková Řičánková *et al.* (2014) demonstrated that

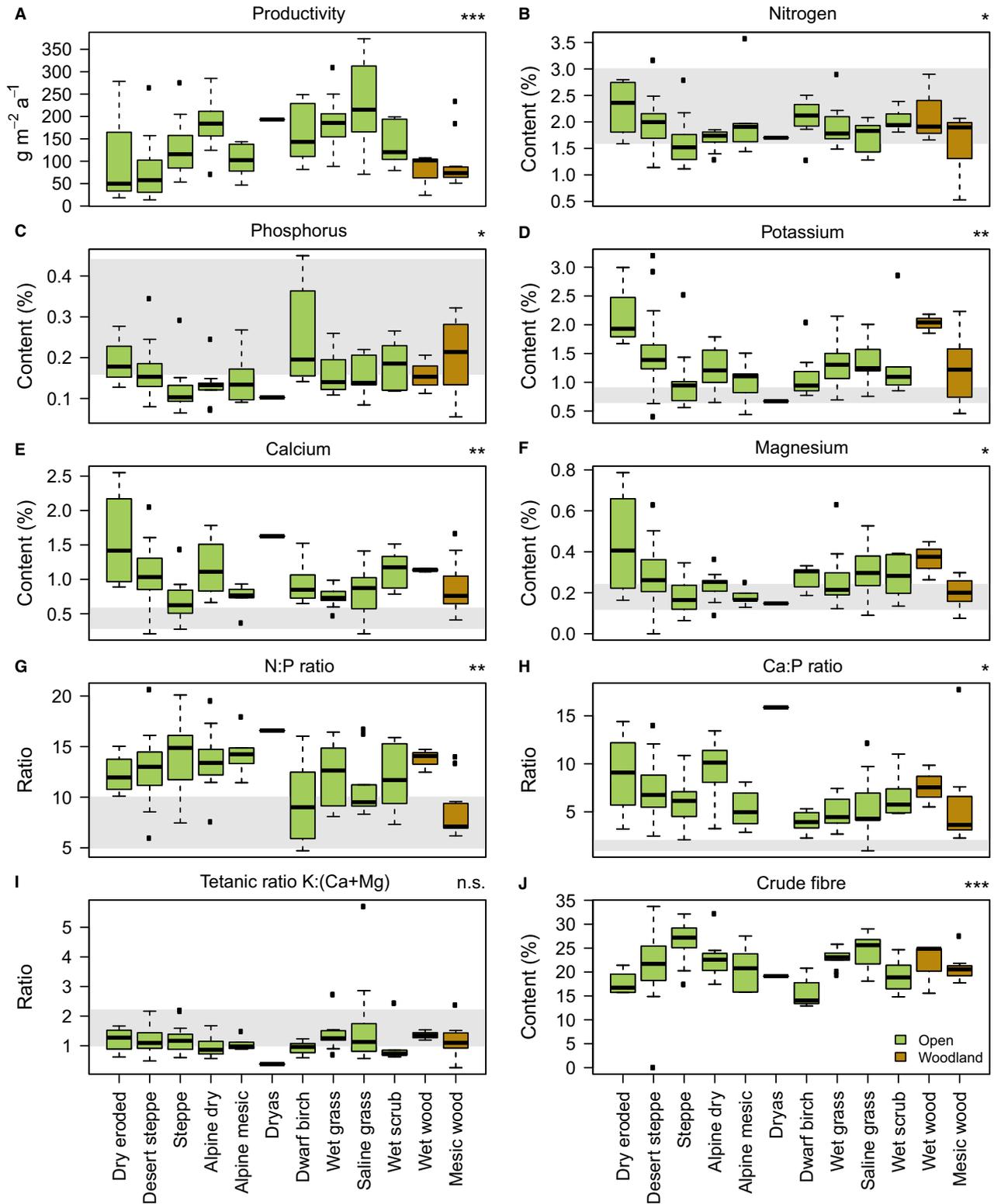


Fig. 7. Aboveground biomass at the peak of the growing season as a measure of primary productivity (A) and characteristics of nutrient content in the aboveground biomass (B–J) of different habitat types in the Altaian steppe-tundra. Grey stripes in the background represent values considered as optimal for cattle, indicating a benchmark of nutrient value for large herbivores. See Fig. 2 for an explanation of significances and Table S3 for detailed statistics in numerical format. [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

the species composition of the modern mammal fauna in the SE Altaian steppe-tundra (Ukok-Sailyugem area) is more similar to the Last Glacial fauna of the Altai-Sayan Mountains than to the modern fauna of any other studied region of northern Eurasia.

All of these independent pieces of evidence based on different taxa support the idea of the steppe-tundra in the SE Russian Altai being one of the closest (or even the closest) modern analogue of the European and southern Siberian ecosystems at the peak of the last glaciation. Still, it is important to keep in mind that even the best modern analogue is far from the true analogue because some features of the current environment are non-analogous to the LGM environments (e.g. the atmospheric CO<sub>2</sub> concentration), and some important species of the Late Pleistocene biota went extinct globally.

#### *Habitat mosaic of the steppe-tundra and diversity patterns*

As species with different present-day habitat affinities co-occur in the full-glacial fossil record, it has been difficult for palaeoecologists to reconstruct the past communities and their distribution across the landscape. Mammalian palaeoecologists hypothesized that the Pleistocene steppe-tundra landscape must have contained a diverse habitat mosaic to sustain large herbivore populations (Guthrie 1990, 2001). Botanical studies by Yurtsev (1981, 1982, 1996, 2001) in the extant Arctic and sub-Arctic steppe-tundra in Yakutia and Chukotka made it clear that the Beringian steppe-tundra landscape consists of patches of steppe vegetation in drier places, tundra vegetation in wetter places, and also of plant communities in which steppe and tundra species co-exist.

In spite of the differences in floristic composition, the habitat mosaic of the Altaian steppe-tundra is very similar to the western Beringian steppe-tundra as described by Yurtsev. It is a mosaic of different habitat types with distinct plant communities, those at drier and warmer sites having stronger affinities to the steppe, while those at wetter and cooler sites, in places with permafrost, having stronger affinities to tundra. Depending on topography, such contrasting habitats often occur next to each other in the landscape. Even small patches of woodland can occur at wetter sites such as flood-plains and north-facing slopes in the marginal areas of the steppe-tundra landscape, forming outposts of the mountain forest-steppe in the generally treeless landscape of the SE Russian Altai (Kuminova 1960; Makunina 2012, 2014).

A remarkable habitat type within the Altaian steppe-tundra landscape is the alpine dry grassland because it contains steppe species together with alpine or arctic-alpine species co-existing in a single plant community. Related vegetation, sometimes called cryophytic steppe, occurs across dry and cold areas of the southern Siberian mountain systems (Korolyuk & Namzalov 1994; Namzalov 1994; Telyatnikov 2013), but it is also known from

the low-altitude steppe landscapes of southern Siberia such as the Minusinskaya Basin (Ermakov *et al.* 2014). This vegetation occurs on wind-exposed elevations where snow is often wind-swept in winter, leading to deep soil freezing. In summer wind causes their rapid drying out. Similar conditions may have been common during the Pleistocene full glacials when precipitation, and consequently also snow cover, was lower than today in most areas of northern Eurasia (Gent *et al.* 2011; Watanabe *et al.* 2011).

There is evidence that flora and snail fauna were poorer during the LGM than today. For plants, this evidence is based on the analysis of ancient DNA from Arctic permafrost (Willerslev *et al.* 2014), and for snails on shell records from European loess sequences (e.g. Ložek 2001; Moine 2014; Hošek *et al.* 2017). Consistently with these observations, both of these taxa are considerably species-poorer in the LGM-like landscape of the SE Altaian steppe-tundra than in the warmer and wetter landscape of the northern Altai, which has Holocene climatic and ecological features (Chytrý *et al.* 2017). Conversely, terricolous bryophytes and lichens were found to be species-richer in the Altaian steppe-tundra than in the northern Altai in the same study. Our current study adds more detail to this broad diversity pattern, revealing considerable variation in richness patterns of all the studied taxa across the habitats of the steppe-tundra mosaic. For all the studied taxa, the driest habitats of dry eroded slopes and desert steppe are poorest, suggesting that much of the diversity in the LGM landscapes was confined to mesic and wet habitats.

#### *Moisture patterns in the full-glacial steppe-tundra*

It is remarkable that species that are often found together in fossil samples from the Late Pleistocene occur in contrasting habitats in the Altaian steppe-tundra. Drought-adapted plant species of *Artemisia*, *Ephedra* and *Chenopodiaceae* (=Amaranthaceae) are distinctly concentrated in the steppe habitats and on dry eroded slopes, and their affinity to these habitats is also reflected in modern pollen spectra (Pelánková & Chytrý 2009). In contrast, most of the glacial relict snails avoid dry habitats, being more common in mesic and wet grasslands, scrub and woodland patches.

This pattern suggests that snails found in the full-glacial loess deposits probably lived in mesic to locally wet habitats. However, such a hypothesis would be contradictory to the classical ideas of central European botanists (e.g. Wendelberger 1954) portraying the full-glacial landscape with loess accumulation as a dry and cold steppe, based on the interpretation of the ecology of some plant species that are considered in central Europe as relicts of the cold Pleistocene steppe (e.g. *Agropyron cristatum* s.l., *Kochia prostrata* and *Krascheninnikovia ceratoides*). Indeed these drought-adapted species are typical of the desert-steppe habitats in the Altaian

steppe-tundra landscape, but this landscape also contains mesic and wet habitats that support further species considered as European glacial relicts (e.g. *Baeothryon pumilum*, *Pentaphylloides fruticosa* and *Saxifraga hirculus*; Horsák *et al.* 2015). These observations suggest that the full-glacial steppe-tundra with loess deposition contained strong moisture gradients, being a mosaic of the desert or typical steppe and more mesic or wetter habitats on north-facing slopes, along streams and in depressions with permafrost.

To make the reconstruction of the full-glacial steppe-tundra more realistic, it has to be considered that the CO<sub>2</sub> concentration in the full-glacial atmosphere was much lower than today (Monin *et al.* 2001). Changes in the atmospheric CO<sub>2</sub> concentration have important direct effects on plants but not on snails. To absorb a certain amount of CO<sub>2</sub> in the full-glacial low-CO<sub>2</sub> atmosphere, plants had to open their stomata for a longer time than in the current high-CO<sub>2</sub> atmosphere, which necessarily led to the higher loss of water through transpiration. Therefore, even the drought-adapted plants such as *Agropyron cristatum* s.l., *Artemisia* spp., *Ephedra* spp. and Chenopodiaceae probably had to grow in more mesic conditions in the full-glacial period than in the contemporary Altaian steppe-tundra. Thus, the niche of steppe plants in the full-glacial steppe-tundra would be shifted to the mesic or wet niche of snails. This perspective would suggest a picture of a generally more mesic full-glacial loess-steppe landscape, with steppe plants and snails having much broader niche overlap than they have in the contemporaneous steppe-tundra of the Altai Mountains.

The hypothesis of a more mesic full-glacial loess-steppe landscape is also supported by sedimentology. Loess deposition depends on dust-trapping topography, vegetation cover, moisture and source sediment supply (Gaylord *et al.* 2003). Both vegetation cover and soil moisture increase dust trapping and loess deposition (Pye 1995; Mason *et al.* 1999; Gaylord *et al.* 2003; Smalley *et al.* 2011; Roberts *et al.* 2013). This would suggest that the places with loess accumulation in the full-glacial period were not necessarily arid and supported productive vegetation. If so, they would be suitable for the drought-avoiding snails that are found in the loess deposits. This would explain the sharp contrast between the high density of land-snail shells in full-glacial loess deposits (Ložek 2001) and their low abundance in modern low-productivity ecosystems (Schamp *et al.* 2010; Horsák *et al.* 2013a).

Regardless of being generally drier or more mesic, the full-glacial loess-steppe landscape had to contain some dry areas with sparse vegetation where the aeolian sediments would have originated from. In the Altaian steppe-tundra landscape, the dry eroded slopes such as scree, wadis and alluvial fans occurring in the desert-steppe landscapes probably serve as a dust source. Thus, it seems that the full-glacial landscape with loess

accumulation comprised the whole moisture gradient from very dry to wet habitats. It was probably not just a matrix of steppe with small areas of wetlands in the stream flood-plains, but instead contained significant areas of mesic habitats.

#### *Is the Altaian steppe-tundra a Pleistocene relict?*

Dynamic vegetation models based on palaeoclimatic data suggest that unlike in other parts of Europe or Asia, large areas of grassland have persisted in the mountain systems of southern Siberia continuously for at least the last 42 000 years (Allen *et al.* 2010). Their continuous persistence was supported by the existence of large unglaciated areas. Although there is some uncertainty about the extent of the LGM glaciation in the Altai Mountains, LGM glaciers probably covered only higher mountain ranges including those in the surroundings of the Kurai and Chuya basins and around the Ukok Plateau, while the basins and the plateau are considered to have been ice-free (Blomdin *et al.* 2016). Consequently, it seems very likely that the steppe-tundra ecosystem survived the LGM directly in the study area or its close surroundings. Co-occurrences of relict plant and snail species support this view (Horsák *et al.* 2015). A model of the LGM vegetation cover of the Russian Altai suggested that the largest part of this area including the present steppe-tundra landscape was covered by desert steppe in association with other steppe types, more mesic grasslands and perhaps also woodland patches (Hais *et al.* 2015). This supports the hypothesis of a relict origin of the steppe-tundra ecosystem in the SE Russian Altai, although it may not have existed continuously in every place where it occurs now, especially not on the bottoms of basins that were flooded by glacial meltwater at the end of the last glaciation (Rudoy 2002), at high altitudes that were glaciated during the LGM, and in the areas where forest expanded during the Holocene climatic optimum (compare Blyakharchuk *et al.* 2004; Mische *et al.* 2007; Tchepakova *et al.* 2009). In contrast, Pleistocene steppe-tundra most probably existed in the lowlands north of the Altai-Sayan Mountains, and some remnants of this demised ecosystem can be recognized in present-day steppe communities with participation of arctic-alpine and alpine plants (e.g. *Dryas oxyodonta*, *Festuca sphagnicola*, *Kobresia filifolia*, *K. myosuroides*, *Minuartia verna*, *Patrinia sibirica*, *Pulsatilla ambigua* and *Saussurea schanginiana*) at low altitudes of the Minusinsk Basin (Ermakov *et al.* 2014).

#### *Can primary productivity of steppe-tundra sustain rich megaherbivore communities?*

There has been a long-standing debate on how the relatively low-productive ecosystem of the Pleistocene steppe-tundra could sustain a species-rich community of herbivores including the abundant populations of

megafauna (Guthrie 1982; Yurtsev 2001). Although most of the full-glacial large herbivores were grazers adapted to open habitats rather than browsers, there was a distinct pattern of diet specialization amongst them (Guthrie 1982). Consequently, the full-glacial herbivore community was most probably dependent on the heterogeneity of habitats within the landscape (Schweger *et al.* 1982). Our study of the present-day Altaian steppe-tundra, as well as previous studies of the Beringian steppe-tundra (Yurtsev 1996, 2001), indicated that although largely treeless, steppe-tundra comprises a range of habitats that provide different qualities of pasture in different parts of the growing season. The pattern of habitat use by large herbivores in the Altaian steppe-tundra is nicely illustrated by tracking the behaviour of domestic livestock and herders. For example, in spring cattle and horses graze on the young grass on steppe slopes while in summer they prefer mesic and wet grasslands along streams (personal communication by local herders). Some herds are also driven to high-altitude pastures in summer.

The habitat heterogeneity of the Altaian steppe-tundra landscape is partly caused by its mountainous topography. However, many Pleistocene large herbivores were species of plains (e.g. mammoth, horse, muskox, saiga and rhino; Guthrie 1982), although our review shows that they also occurred in the Altai-Sayan region. On the northern Eurasian plains, these animals occupied extensive home ranges, in which they were able to use different habitats in spite of the coarser grain of the habitat mosaic than in the mountains. Pollen-based vegetation reconstructions for northern Eurasia (Tarasov *et al.* 2000; Binney *et al.* 2017) indicate that steppe-tundra vegetation mosaics may have been widespread across the plains of northern Eurasia during the LGM. However, fine-scale habitat patterns and ecological features of individual habitats can only be reconstructed hypothetically based on modern analogues like the Altaian steppe-tundra.

Based on the quantity of megaherbivore bones deposited in Pleistocene sediments in northeastern Siberia, Zimov *et al.* (2012) estimated the biomass of large herbivores in the late-Pleistocene steppe-tundra (including the periods before and after the LGM) at  $\sim 10.5 \text{ t km}^{-2}$ , which may correspond to  $\sim 30$  large herbivores per  $\text{km}^2$ , depending on the species. This estimate matches closely the currently observed densities of large herbivores in the East African savanna (Okello *et al.* 2016). Annual productivity measured in grazing exclosures in Serengeti grasslands varied within a range of  $\sim 100\text{--}600 \text{ g m}^{-2}$ , depending on annual rainfall (McNaughton 1985). In the Altaian steppe-tundra, we recorded  $14\text{--}278 \text{ g m}^{-2}$  in steppe grasslands and  $71\text{--}373 \text{ g m}^{-2}$  in mesic and wet grasslands and scrub. It is important to note that our estimates are based on a one-time sampling of aboveground standing biomass without litter in places exposed to grazing. Even though we avoided sampling of strongly disturbed sites,

the Altaian steppe-tundra is grazed by both livestock and wild herbivores, e.g. marmots and pikas. Therefore, our figures are necessarily lower than actual annual productivity. Moreover, grazing stimulates compensatory plant growth, meaning that grassland has considerably greater annual productivity when grazed (McNaughton 1983, 1985). This comparison suggests that the productivity of the Altaian steppe-tundra is close to that of drier areas in African savannas and possibly also to the Pleistocene steppe-tundra, although the comparison with the Pleistocene conditions is not straightforward because of much higher concentrations of  $\text{CO}_2$  in the present-day atmosphere.

Element concentrations in plant biomass are also variable across habitat types of the steppe-tundra mosaic. However, they do not show any visible signs of nutrient deficiency as defined for livestock. Concentration of N and P found there are sufficient for cattle (Whitehead 2000; Suttle 2010; Hejcman *et al.* 2016) and correspond to the requirements for maintenance of body weight in yaks (Long *et al.* 2008) and saiga, although in most habitats they may be low for saiga lactation (Abaturov & Subbotin 2011). N concentrations  $>1.5\%$  of dry biomass measured in most sampled plots indicate fast N cycling resulting in high-quality forage and high carrying capacity of the steppe-tundra ecosystem (Faith 2011).

Vegetation growth at most of the sampled sites is limited by N rather than by P, as indicated by N concentrations  $<2\%$  and N:P ratios  $<10$  (S. Palpurina *et al.*, unpublished data). This is probably because P is released in relatively large amounts in the arid conditions from weathering rocks and blown with dust across the landscape. Interestingly, P concentration is highest in the biomass of the dwarf-birch tundra, which corresponds to a high concentration in leaves of dwarf birch (*Betula nana* s.l.) reported from similar vegetation in Iceland (Hejcman *et al.* 2016; but see D.A. Walker *et al.* 2001 for lower values from Alaska). It is possible that because soils of the dwarf-birch tundra are slightly more acidic than soils of the other habitats in the steppe-tundra, soil P is not so much immobilized in Ca phosphates (Whitehead 2000) as in the high-pH soils of the other steppe-tundra habitats. The dwarf-birch tundra is one of the most nutritious habitats of the steppe-tundra, providing the relatively high amount of leaf biomass with a high amount of not only P, but also N and other minerals, and a low amount of crude fibre. This is consistent with frequent finds of *Betula nana* s.l. in gastrointestinal tracts of fossilized remains of full-glacial herbivores (Ukrainitseva 2013), although production of antiherbivore metabolites was reported in this species (Chapin *et al.* 1986; de Groot *et al.* 1997). Graminoid-dominated typical steppe is at the opposite end of the pasture quality gradient, providing a relatively low amount of biomass, poor in N and P, with a high proportion of crude fibre.

The Ca and Mg concentrations in the sampled plant biomass are within the range of the values recommended for cattle or higher. High values of these elements in biomass result from their high concentrations in near-neutral to basic soils in most habitats of the steppe-tundra (Chytrý *et al.* 2017). The Ca:P ratio in biomass, considered important for animal growth and bone formation, considerably exceeds the optimum values of 1–2, which correspond to the ratio of these two elements in bones. Nevertheless, higher values than 2 usually have no detrimental effect on herbivores (Whitehead 2000). On the contrary, the abundance of Ca and sufficient supply of P suggest that the pastures in the Altaian steppe-tundra are good for bone development, which is in contrast with evidence of osteoporosis and other destructive changes observed in mammoth bones from the end of the Pleistocene, interpreted as a result of soil acidification and associated deficiency of essential nutrients (Leshchinskiy 2015). High concentrations of Ca and Mg also decrease the risk of hypomagnesaemia (grass tetany), as indicated by the values of the tetanic ratio K: (Ca+Mg) being lower than the critical value of 2.2 in nearly all sites of the Altaian steppe-tundra. Still, it has to be noted that our biomass samples were collected in summer, whereas hypomagnesaemia is more likely to occur in spring when herbivores feed on young herbage. These figures show that not only in terms of the amount of herbage but also in terms of nutrient availability, the Altaian steppe-tundra is a suitable habitat for large herbivores, at least in summer. Nevertheless, nutrient availability may have been better in the full-glacial steppe-tundra with loess accumulation due to higher amounts of nutrients being brought in with dust.

A more critical issue for grazers than grassland productivity and nutritional value in the growing season is food availability in winter, which is very long in the steppe-tundra (e.g. the period with mean monthly temperatures below 0 °C lasts from October to April in the Chuya Basin; Kharlamova 2013). Heavy snowstorms are known to cause disastrous livestock mortality in drylands of Mongolia and China (Miller 2005; Tachiiri *et al.* 2008), and snow depth is considered a limiting factor for most of the typical Pleistocene large herbivores if it exceeds 20 cm (Guthrie 1982, 1990, 2001). Indeed, extant ungulate species that are least tolerant of high snow cover, e.g. muskox, yak or saiga, went locally extinct in most of the Eurasian regions between the Last Glacial and the present (Pavelková Řičánková *et al.* 2018). In the dry climate of the Altaian steppe-tundra, snow cover is generally very shallow (7 cm on average throughout January and February in Kosh-Agach; Kharlamova 2013). A thicker snow cover is usually found only in depressions and woodlands, whereas plains and south-facing slopes have a thin or no snow cover. This makes this area suitable for winter grazing, and indeed the bottom of the Chuya Basin is currently

used for free-range winter grazing of cattle and horses (M. Hejcman & V. Pavlů, pers. comm. 2013).

#### *Why did the Pleistocene steppe-tundra survive in the Altai while disappearing elsewhere?*

The Altaian steppe-tundra is a small extant remnant of an ecosystem that once was widespread across northern Eurasia. Its disappearance elsewhere is usually explained by one of two conflicting hypotheses. The climatic hypothesis suggests that the dramatic vegetation change at the Pleistocene–Holocene transition was caused by climate warming and increased precipitation, which triggered the spread of forest at lower latitudes and changes from herbaceous steppe to shrubby and mossy tundra at higher latitudes (Guthrie 1990, 2001; Rabanus-Wallace *et al.* 2017). In contrast, the keystone herbivore hypothesis (Owen-Smith 1987) suggests that the primary cause of this vegetation change was the disappearance of large herbivores, usually attributed to human hunting. There is evidence that grazing by large herbivores can maintain areas of open grassland even under a climate that generally supports forest or tundra (Gill 2014; Bakker *et al.* 2016). In the Arctic and sub-Arctic zones of northern Siberia, Pleistocene forb-rich grassland changed into the current shrub-graminoid tundra (Willerslev *et al.* 2014). Zimov *et al.* (1995) hypothesized that the main cause of this vegetation change was the disappearance of large herbivores at the Pleistocene–Holocene transition. This view is supported by experiments with the introduction of large herbivores to the current tundra landscape, resulting in decline of mosses and dwarf shrubs, increase of herbs and grasses, and enhanced primary productivity, i.e. the reverse of the process that once possibly caused the decline of steppe at high latitudes (Zimov *et al.* 2012).

Although the keystone herbivore hypothesis may be valid for northern Siberia, the climate hypothesis seems to be more plausible for southern Siberia. While in the north annual precipitation exceeds annual potential evapotranspiration, in the south this pattern is reversed ([www.cgiar-csi.org/data/global-aridity-and-pet-database](http://www.cgiar-csi.org/data/global-aridity-and-pet-database)). This creates a more arid climate in southern Siberia, supporting open steppe vegetation even without herbivore impact. Low- and mid-altitude landscapes of the Altai are characterized as the ‘exposure-related forest-steppe’ (Hais *et al.* 2016), a mosaic landscape in which the distribution of forest vs. steppe depends on moisture: forests are consistently confined to north-facing (wetter) slopes while steppe occurs on south-facing (drier) slopes. As the grazing pressure by both wild and domestic herbivores is relatively constant across the landscape, this pattern demonstrates that under warm climate, the forest can spread to sufficiently wet areas even under herbivore impact.

These observations suggest that the steppe-tundra landscape in the SE Russian Altai was preserved mainly

due to a unique combination of climatic factors that resembles the LGM climate, including very low winter temperatures and a short summer (i.e. conditions that are cold enough to maintain some permafrost), annual evapotranspiration considerably greater than precipitation, and shallow snow cover. While the Holocene climatic amelioration at lower altitudes of southern Siberia led to the formation of continuous forest or, in drier areas, of forest steppe, species of full-glacial steppe-tundra were able to move to dry and cold areas at higher altitudes that have preserved the steppe-tundra ecosystem until the present.

## Conclusions

- Independent pieces of evidence based on combining fossil record and recent data on distribution and ecology of vascular plants, land snails and mammals suggest that ecosystems in the cold and dry basins and plateaus of the SE Russian Altai are the closest modern analogue of the full-glacial steppe-tundra ecosystem described so far. This analogue is especially relevant for the southern biogeographical variants of the steppe-tundra that existed in Europe and southern Siberia.
- It is likely that at least in some areas the Altaian steppe-tundra is not only an analogue but also a relict of the full-glacial steppe-tundra, existing there continuously since the Late Pleistocene.
- The Altaian steppe-tundra is a mosaic of dry, mesic and wet habitats depending on the topography-related distribution of moisture in the landscape and climatic contrasts between different parts of this mountain area. These habitats support different types of the steppe, mesic and wet grasslands, dwarf-shrub tundra and restricted patches of woodland. Each vegetation type is characterized by a specific composition and diversity of vascular plants, bryophytes, lichens and snails.
- Plant species considered as glacial relicts in Europe are well represented in all habitat types of the Altaian steppe-tundra. Relict snail species tend to avoid steppe and saline habitats, but they are common in other (mesic, wet, shrubby and wooded) habitats. Several palaeoecological indicators usually co-occurring in fossil record occur in different habitats of the Altaian steppe-tundra. These observations suggest that the full-glacial steppe-tundra also comprised a similar habitat mosaic.
- Primary productivity and nutrient content in plant biomass of the Altaian steppe-tundra are sufficient for maintaining populations of large herbivores. The critical issue for larger grazers is not the forage availability in summer, but survival of the long continental winter. This is enabled by shallow snow

cover and availability of frozen winter forage in this precipitation-poor area.

- Climate change at the Pleistocene–Holocene transition seems to be the primary cause of the steppe-tundra disappearance at low and middle altitudes of southern Siberia. The preservation of this ecosystem on the high-mountain plateaus and in intermontane basins is mainly due to a unique local combination of cold and dry climate that resembles the climate of the Pleistocene cold stages.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at <http://www.boreas.dk>.

*Table S1.* Diagnostic, constant and dominant plant species of the main habitat types in the Altaian steppe-tundra landscape.

*Table S2.* Diagnostic, constant and dominant snail species of the main habitat types in the Altaian steppe-tundra landscape.

*Table S3.* Descriptive statistics for variables measured in 12 habitat types in the Altaian steppe-tundra.

## Supporting Information

**Table S1.** Diagnostic, constant and dominant plant species of the main habitat types in the Altaian steppe-tundra landscape. Diagnostic species are those with the phi coefficient of association  $>0.4$  (species with  $\Phi > 0.6$  are in bold; phi coefficient values multiplied by 100 are shown next to the species names). Constant species are those with a percentage frequency occurrence  $> 40\%$  (species with frequency  $> 60\%$  are in bold; percentage occurrence frequencies are shown next to the species names). Dominant species are those with a cover  $> 25\%$  in more than 10% of plots (species with a cover  $> 25\%$  in more than 20% of plots are in bold; percentage frequencies of occurrence with a cover  $> 25\%$  are shown next to the species names).

### (1) Dry eroded slopes (14 plots)

Diagnostic species: ***Dracocephalum peregrinum* 79.3**, ***Stellaria dichotoma* 74.1**, ***Artemisia santolinifolia* 69.5**, ***Vicia costata* 63.3**, *Ziziphora clinopodioides* 53.0, *Achnatherum sibiricum* 51.4, *Lonicera microphylla* 49.5, *Chenopodium foliosum* 44.7, *Patrinia intermedia* 42.8, *Linaria altaica* 42.8, *Gypsophila patrinii* 42.5, *Artemisia obtusiloba* 42.4, *Orobanche species* 41.6, *Rheum compactum* 40.7

Constant species: ***Artemisia santolinifolia* 86**, ***Stellaria dichotoma* 71**, ***Dracocephalum peregrinum* 71**, *Vicia costata* 50, *Poa transbaicalica* 50, *Artemisia frigida* 50, *Ziziphora clinopodioides* 43, *Artemisia obtusiloba* 43, *Agropyron cristatum* 43

Dominant species: –

### (2) Desert steppe (36 plots)

Diagnostic species: ***Kochia prostrata* 81.4**, ***Goniolimon speciosum* 67.2**, ***Agropyron cristatum* 66.1**, *Stipa glareosa* 53.6, *Krascheninnikovia ceratoides* 53.6, *Artemisia frigida* 53.4, *Allium vodopjanovae* 51.1, *Carex duriuscula* 47.4, *Caragana pygmaea* 45.0, *Convolvulus ammannii* 42.6

Constant species: ***Artemisia frigida* 81**, ***Agropyron cristatum* 81**, ***Kochia prostrata* 72**, ***Goniolimon speciosum* 61**, *Koeleria cristata* 53, *Carex duriuscula* 53, *Potentilla bifurca* 47, *Potentilla acaulis* 44, *Xanthoparmelia camschadalis* 42, *Orostachys spinosa* 42

Dominant species: –

### (3) Typical steppe (25 plots)

Diagnostic species: *Festuca valesiaca* 59.9, *Koeleria cristata* 53.1, *Potentilla pensylvanica* 52.0, *Ephedra monosperma* 49.5, *Potentilla acaulis* 46.0, *Potentilla bifurca* 43.6, *Stellaria petraea* 43.2, *Helictotrichon altaicum* 43.1, *Potentilla sericea* 42.9, *Androsace septentrionalis* 42.9, *Peucedanum vaginatum* 42.1

Constant species: ***Koeleria cristata* 72**, ***Helictotrichon altaicum* 68**, ***Aster alpinus* 68**, ***Festuca valesiaca* 64**, ***Androsace septentrionalis* 64**, *Poa attenuata* 60, *Potentilla bifurca* 56, *Potentilla acaulis* 56, *Galium verum* 56, *Artemisia frigida* 56, *Xanthoparmelia camschadalis* 52, *Silene repens* 52, *Pulsatilla patens* 52, *Carex pediformis* 52, *Orostachys spinosa* 48, *Potentilla sericea* 44, *Potentilla pensylvanica* 44, *Ephedra monosperma* 44

Dominant species: –

### (4) Alpine dry grassland (16 plots)

Diagnostic species: ***Ligularia altaica* 63.5**, *Botrychium lunaria* 56.2, *Polygala comosa* 47.9, *Helictotrichon pubescens* 45.3, *Carex caryophyllea* 45.3, *Pulsatilla patens* 44.6, *Koeleria ledebourii* 44.6, *Campanula altaica* 44.2, *Erigeron eriocalyx* 44.1, *Gentiana uniflora* 42.5, *Draba sibirica* 42.1, *Carex obtusata* 42.0, *Thesium repens* 41.6

Constant species: ***Potentilla matsukana* 81**, ***Galium boreale* 75**, ***Bistorta major* 75**, ***Aster alpinus* 75**, ***Pulsatilla patens* 69**, ***Helictotrichon hookeri* 69**, ***Pentaphylloides fruticosa* 62**, ***Pachypleurum alpinum* 62**, ***Festuca kryloviana* 62**, ***Carex pediformis* 62**, ***Carex obtusata* 62**, *Seseli condensatum* 56, *Rhytidium rugosum* 56, *Poa sibirica* 56, *Lupinaster pentaphyllus* 56, *Artemisia phaeolepis* 56, *Veronica porphyriana* 50, *Thesium repens* 50, *Spiraea media* 50, *Silene repens* 50, *Polygala comosa* 50, *Myosotis imitata* 50, *Ligularia altaica* 50, *Gentiana decumbens* 50, *Galium verum* 50,

*Eritrichium villosum* 50, *Dianthus superbus* 50, *Carex caryophyllea* 50, *Bupleurum multinerve* 50, *Achillea asiatica* 50, *Aconogonon alpinum* 50, *Thalictrum minus* 44, *Gentianella acuta* 44, *Festuca altaica* 44, *Erigeron eriocalyx* 44, *Cladonia pyxidata* 44, *Cerastium arvense* 44, *Artemisia rupestris* 44, *Abietinella abietina* 44

Dominant species: *Iris ruthenica* 12

**(5) Alpine mesic grassland (7 plots)**

Diagnostic species: *Salix nummularia* 67.0, *Taraxacum glabrum* 63.8, *Saxifraga melaleuca* 63.8, *Oxytropis altaica* 63.8, *Gentiana algida* 63.8, *Minuartia biflora* 61.2, *Viola altaica* 58.0, *Schulzia crinita* 55.8, *Trisetum mongolicum* 54.3, *Ranunculus altaicus* 51.8, *Pogonatum urnigerum* 51.8, *Luzula spicata* 51.8, *Luzula confusa* 51.8, *Andreaea rupestris* 51.8, *Lagotis integrifolia* 51.3, *Polytrichum piliferum* 49.2, *Papaver croceum* 48.0, *Thamnia vermicularis* 46.4, *Saxifraga sibirica* 45.0, *Dichodon cerastoides* 43.9, *Hierochloa alpina* 43.3, *Cetraria kamczatica* 43.3, *Carex aterrita* 40.8

Constant species: *Gentiana algida* 86, *Viola altaica* 71, *Trisetum mongolicum* 71, *Schulzia crinita* 71, *Lagotis integrifolia* 71, *Salix nummularia* 57, *Potentilla gelida* 57, *Polytrichum piliferum* 57, *Polytrichum juniperinum* 57, *Pachypleurum alpinum* 57, *Minuartia biflora* 57, *Flavocetraria nivalis* 57, *Flavocetraria cucullata* 57, *Festuca altaica* 57, *Dichodon cerastoides* 57, *Dicranum spadiceum* 57, *Cladonia pyxidata* 57, *Cetraria islandica* 57, *Carex sempervirens* 57, *Bistorta major* 57, *Thamnia vermicularis* 43, *Taraxacum glabrum* 43, *Saxifraga sibirica* 43, *Saxifraga melaleuca* 43, *Rhytidium rugosum* 43, *Rhodiola rosea* 43, *Potentilla matsukana* 43, *Pedicularis amoena* 43, *Oxytropis species* 43, *Oxytropis altaica* 43, *Gentiana grandiflora* 43, *Bistorta vivipara* 43

Dominant species: *Kobresia smirnovii* 14, *Cetraria islandica* 14

**(6) Dryas tundra (5 plots)**

Diagnostic species: *Dryas oxyodonta* 73.6, *Carex ledebouriana* 61.6, *Orthotrichum species* 58.5, *Cladonia pocillum* 57.0, *Pulsatilla campanella* 53.9, *Papaver canescens* 51.8, *Myurella julacea* 48.9, *Myosotis imitata* 48.8, *Pedicularis tristis* 47.8, *Pedicularis lasiostachys* 44.8, *Patrinia sibirica* 44.3, *Salix arctica* 43.3, *Saxifraga oppositifolia* 43.2, *Saxifraga cernua* 43.2, *Rhodobryum roseum* 43.2, *Minuartia species* 43.2, *Gentianella amarella* 43.2, *Entodon schleicheri* 43.2, *Draba fladnizensis* 43.2, *Dicranum species* 43.2, *Desmatodon species* 43.2, *Corydalis species* 43.2, *Carex species* 43.2, *Allium pumilum* 43.2, *Hedysarum neglectum* 43.0, *Minuartia verna* 42.2, *Oxytropis species* 41.8, *Thalictrum alpinum* 41.3

Constant species: *Dryas oxyodonta* 100, *Tortula ruralis* 80, *Thalictrum alpinum* 80, *Rhytidium rugosum* 80, *Oxytropis species* 80, *Myosotis imitata* 80, *Kobresia myosuroides* 80, *Festuca kryloviana* 80, *Bistorta vivipara* 80, *Abietinella abietina* 80, *Potentilla matsukana* 60, *Poa attenuata* 60, *Pedicularis tristis* 60, *Papaver canescens* 60, *Minuartia verna* 60, *Hedysarum neglectum* 60, *Gentiana prostrata* 60, *Flavocetraria cucullata* 60, *Cladonia pocillum* 60, *Bupleurum multinerve* 60

Dominant species: *Dryas oxyodonta* 100, *Kobresia myosuroides* 20

**(7) Dwarf-birch tundra (10 plots)**

Diagnostic species: *Betula rotundifolia* 58.8, *Peltigera malacea* 46.6, *Spiraea alpina* 45.3, *Cladonia cornuta* 44.9, *Cladonia chlorophaea* 42.2, *Stellaria peduncularis* 41.9

Constant species: *Betula rotundifolia* 100, *Festuca altaica* 90, *Pachypleurum alpinum* 80, *Bistorta vivipara* 80, *Sanionia uncinata* 70, *Poa sibirica* 70, *Spiraea alpina* 60, *Saussurea alpina* 60, *Cetraria islandica* 60, *Bistorta major* 60, *Schulzia crinita* 50, *Rhytidium rugosum* 50, *Polytrichum juniperinum* 50, *Lonicera altaica* 50, *Galium verum* 50, *Dicranum spadiceum* 50, *Cladonia pyxidata* 50, *Abietinella abietina* 50

Dominant species: *Betula rotundifolia* 100, *Geranium albiflorum* 10, *Flavocetraria cucullata* 10, *Cladonia stellaris* 10, *Cetraria islandica* 10

**(8) Wet grassland (9 plots)**

Diagnostic species: *Cardamine pratensis* 58.4, *Tomentypnum nitens* 51.4, *Carex enervis* 49.8, *Plagiomnium ellipticum* 46.4, *Saxifraga hirculus* 46.1, *Climacium dendroides* 45.2, *Carex altaica* 44.7, *Gentiana prostrata* 44.5, *Hypnum lindbergii* 44.0, *Stellaria longifolia* 43.2, *Ptilagrostis mongholica* 42.6, *Alopecurus alpinus* 42.3, *Leptobryum pyriforme* 40.9

Constant species: ***Carex enervis* 78, *Bistorta vivipara* 78, *Thalictrum alpinum* 67, *Salix coesia* 67, *Gentiana prostrata* 67, *Festuca rubra* 67, *Tomentypnum nitens* 56, *Saxifraga hirculus* 56, *Poa sibirica* 56, *Kobresia myosuroides* 56, *Comastoma tenellum* 56, *Climacium dendroides* 56, *Carex altaica* 56, *Aulacomnium palustre* 56, *Angelica tenuifolia* 56, *Abietinella abietina* 56, *Seseli condensatum* 44, *Saussurea alpina* 44, *Rhytidium rugosum* 44, *Ptilagrostis mongholica* 44, *Plagiomnium ellipticum* 44, *Pentaphylloides fruticosa* 44, *Leontopodium ochroleucum* 44, *Galium boreale* 44, *Festuca altaica* 44, *Cardamine pratensis* 44**

Dominant species: *Warnstorfia fluitans* 11, *Kobresia smirnovii* 11, *Kobresia myosuroides* 11, *Hypnum lindbergii* 11, *Carex cespitosa* 11, *Carex altaica* 11, *Bryum schleicheri* 11, *Aulacomnium palustre* 11

#### (9) Saline grassland (16 plots)

Diagnostic species: ***Calamagrostis macilenta* 73.6, *Carex delicata* 67.3, *Puccinellia kalininae* 64.5, *Primula nutans* 64.5, *Baeothryon pumilum* 64.5, *Hordeum brevisubulatum* 61.8, *Carex microglochin* 61.6, *Triglochin maritimum* 59.6, *Halerpestes salsuginosa* 59.6, *Glaux maritima* 57.8, *Potentilla anserina* 56.2, *Oxytropis glabra* 54.2, *Gentiana leucomelaena* 54.2, *Eleocharis quinqueflora* 54.2, *Triglochin palustre* 53.9, *Blysmus rufus* 51.9, *Carex enervis* 47.6, *Parnassia palustris* 43.4, *Taraxacum bessarabicum* 41.8, *Pedicularis altaica* 41.8, *Hygroamblystegium tenax* 41.8, *Desmatodon heimii* 41.8, *Dactylorhiza salina* 41.8, *Agrostis stolonifera* 41.8, *Arctopoa tibetica* 41.6**

Constant species: ***Carex enervis* 75, *Carex delicata* 69, *Potentilla anserina* 62, *Hordeum brevisubulatum* 62, *Triglochin palustre* 56, *Calamagrostis macilenta* 56, *Bistorta vivipara* 56, *Potentilla multifida* 50, *Parnassia palustris* 50, *Carex microglochin* 50, *Bryum species* 50, *Blysmus rufus* 50, *Puccinellia kalininae* 44, *Primula nutans* 44, *Glaux maritima* 44, *Gentianopsis barbata* 44, *Baeothryon pumilum* 44**

Dominant species: *Kobresia myosuroides* 12

#### (10) Wet scrub (11 plots)

Diagnostic species: *Ribes glabellum* 50.6, *Salix coesia* 50.0, *Veronica longifolia* 47.7, *Betula fruticosa* 42.1, *Rhinanthus vernalis* 41.1, *Galium pseudorivale* 41.1

Constant species: ***Salix coesia* 82, *Saussurea alpina* 73, *Poa sibirica* 73, *Pentaphylloides fruticosa* 73, *Festuca rubra* 73, *Bistorta vivipara* 73, *Abietinella abietina* 64, *Veronica longifolia* 55, *Tortula ruralis* 55, *Seseli condensatum* 55, *Galium boreale* 55, *Deschampsia cespitosa* 55, *Betula fruticosa* 55, *Thalictrum alpinum* 45, *Sanionia uncinata* 45, *Rhytidium rugosum* 45, *Lonicera altaica* 45, *Bryum species* 45, *Bryum pseudotriquetrum* 45, *Aulacomnium palustre* 45**

Dominant species: *Salix divaricata* 18, *Salix coesia* 18, *Rhytidium rugosum* 18, *Aulacomnium palustre* 18

#### (11) Wet conifer woodland (6 plots)

Diagnostic species: ***Salix bebbiana* shrub 78.0, *Picea obovata* tree 75.7, *Salix bebbiana* tree 72.3, *Picea obovata* 71.2, *Larix sibirica* tree 67.8, *Salix pyrolifolia* shrub 57.7, *Salix bebbiana* tree 56.1, *Vicia cracca* 54.8, *Saussurea stubendorffii* 52.7, *Equisetum pratense* 52.7, *Lupinaster pentaphyllus* 51.9, *Salix pyrolifolia* 50.7, *Elymus transbaicalensis* 50.7, *Pyrola rotundifolia* 49.2, *Salix rosmarinifolia* 48.7, *Ribes nigrum* 48.7, *Carex capillaris* 48.7, *Carex redowskiana* 47.3, *Erigeron lonchophyllus* 46.4, *Larix sibirica* 46.3, *Aster sibiricus* 46.2, *Deschampsia cespitosa* 45.3, *Carex nigra* 42.9, *Carex orbicularis* 41.1, *Calamagrostis obtusata* 40.4, *Erigeron acris* 40.2**

Constant species: ***Larix sibirica* tree 100, *Picea obovata* tree 83, *Picea obovata* 83, *Lupinaster pentaphyllus* 83, *Vicia cracca* 67, *Salix bebbiana* shrub 67, *Salix bebbiana* 67, *Larix sibirica* 67, *Festuca rubra* 67, *Deschampsia cespitosa* 67, *Bistorta vivipara* 67, *Taraxacum species* 50, *Sanionia uncinata* 50, *Salix pyrolifolia* shrub 50, *Pyrola rotundifolia* 50, *Pentaphylloides fruticosa* 50, *Aulacomnium palustre* 50, *Angelica tenuifolia* 50**

Dominant species: *Equisetum pratense* 17

**(12) Mesic and dry conifer woodland** (27 plots)

Diagnostic species: *Larix sibirica* tree 58.8, *Pinus sibirica* tree 56.1, *Hylocomium splendens* 53.2, *Larix sibirica* 49.5, *Atragene sibirica* 47.0, *Carex rhizina* 45.6, *Lonicera altaica* 45.4, *Moehringia lateriflora* 42.3, *Ptilidium ciliare* 41.5

Constant species: ***Larix sibirica* tree 89, *Lonicera altaica* 74, *Rhytidium rugosum* 70, *Larix sibirica* 70, *Sanionia uncinata* 63, *Hylocomium splendens* 63, *Poa sibirica* 56, *Dianthus superbus* 48, *Carex pediformis* 48, *Lupinaster pentaphyllus* 44, *Galium boreale* 44, *Chamaenerion angustifolium* 41, *Festuca altaica* 41, *Ceratodon purpureus* 41, *Atragene sibirica* 41**

Dominant species: ***Larix sibirica* tree 26, *Rhytidium rugosum* 22, *Hylocomium splendens* 22, *Vaccinium vitis-idaea* 19**

**Table S2.** Diagnostic, constant and dominant snail species of the main habitat types in the Altaian steppe-tundra landscape. Diagnostic species are those with the phi coefficient of association  $>0.2$  (species with  $\Phi > 0.4$  are in bold; phi coefficient values multiplied by 100 are shown next to the species names). Constant species are those with a percentage frequency occurrence  $> 20\%$  (species with a frequency  $> 40\%$  are in bold; percentage occurrence frequencies are shown next to the species names). Surveyed plots in which no snails were found were included in the calculations.

**(1) Dry eroded slopes** (5 plots)

Diagnostic species: ***Pupilla turcmunica 41***

Constant species: ***Pupilla turcmunica 60***

**(2) Desert steppe** (21 plots)

No diagnostic or constant species.

**(3) Typical steppe** (16 plots)

No diagnostic or constant species.

**(4) Alpine dry grassland** (9 plots)

Diagnostic species: *Vallonia tenuilabris 27*

Constant species: ***Pupilla loessica 67***, ***Vallonia tenuilabris 56***, *Euconulus fulvus 33*, *Pupilla turcmunica 33*, *Columella columella 22*

**(5) Alpine mesic grassland** (4 plots)

Diagnostic species: –

Constant species: ***Pupilla loessica 50***

**(6) Dryas tundra** (2 plots)

Diagnostic species: –

Constant species: ***Pupilla loessica 100***

**(7) Dwarf-birch tundra** (4 plots)

Diagnostic species: –

Constant species: ***Pupilla loessica 75***, *Euconulus fulvus 25*, *Vertigo genesioides 25*

**(8) Wet grassland** (8 plots)

Diagnostic species: *Vertigo parcedentata 38*, *Vertigo genesioides 37*

Constant species: ***Vertigo genesioides 62***, ***Pupilla loessica 50***, ***Vertigo parcedentata 50***, *Columella columella 38*, *Oxyloma sarsii 25*, *Pupilla alpicola 25*

**(9) Saline grassland** (11 plots)

Diagnostic species: *Oxyloma sarsii 26*

Constant species: *Oxyloma sarsii 36*

**(10) Wet scrub** (11 plots)

Diagnostic species: ***Cochlicopa lubrica 41***, *Novisuccinea altaica 36*, *Vertigo parcedentata 34*, *Deroceras altaicum 33*, *Vertigo genesioides 30*, *Euconulus praticola 27*, *Vallonia tenuilabris 26*, *Columella columella 22*, *Pupilla alpicola 22*

Constant species: ***Pupilla loessica 64***, ***Vallonia tenuilabris 55***, ***Vertigo genesioides 55***, ***Columella columella 45***, ***Vertigo parcedentata 45***, *Deroceras altaicum 27*, *Euconulus praticola 27*, *Novisuccinea altaica 27*, *Oxyloma sarsii 27*, *Pupilla alpicola 27*

**(11) Wet conifer woodland** (3 plots)

Diagnostic species: ***Vertigo microsphaera 56***

Constant species: *Columella columella* 67, *Euconulus fulvus* 67, *Vallonia tenuilabris* 67, *Euconulus praticola* 33, *Nesovitrea hammonis* 33, *Oxyloma sarsii* 33, *Pupilla alpicola* 33, *Pupilla loessica* 33, *Vertigo genesioides* 33, *Vertigo microsphaera* 33, *Vertigo parcedentata* 33

**(12) Mesic and dry conifer woodland (11 plots)**

Diagnostic species: *Vertigo beringiana* 51, *Vertigo ronnebyensis* 46, *Euconulus fulvus* 45, *Vallonia ladacensis* 37

Constant species: *Euconulus fulvus* 73, *Pupilla loessica* 55, *Pupilla turcmenica* 36, *Vallonia ladacensis* 36, *Vertigo ronnebyensis* 36, *Columella columella* 27, *Vallonia tenuilabris* 27, *Vertigo beringiana* 27

**Table S3.** Descriptive statistics for variables measured in 12 habitat types in the Altaian steppe-tundra.

Habitat type no.	1	2	3	4	5	6	7	8	9	10	11	12
Habitat type name	Dry eroded slopes	Desert steppe	Typical steppe	Alpine dry grass-land	Alpine mesic grass-land	Dryas tundra	Dwarf-birch tundra	Wet grass-land	Saline grass-land	Wet scrub	Wet wood-land	Mesic wood-land
<b>Numbers of sites in different habitat types with individual types of analyses</b> (total numbers of analyzed sites are in brackets)												
Snail analyses (105)	5	21	16	9	4	2	4	8	11	11	3	11
Soil analyses (104)	4	19	16	9	5	1	7	9	9	11	3	11
Biomass analyses (100)	4	20	16	9	5	1	7	9	9	6	3	11
All other analyses (182)	14	36	25	16	7	5	10	9	16	11	6	27
<b>Cover tree layer (%)</b> , n = 182, P < 0.001 (Kruskal-Wallis test)												
- minimum	0	0	0	0	0	0	0	0	0	0	4	5
- lower quartile	0	0	0	0	0	0	0	0	0	0	8	20
- median	0	0	0	0	0	0	0	0	0	0	18	25
- upper quartile	0	0	0	0	0	0	0	0	0	5	24	32
- maximum	0	0	0	0	0	0	0	0	0	50	40	50
- mean	0	0	0	0	0	0	0	0	0	7	18	26
- standard deviation	0	0	0	0	0	0	0	0	0	16	13	11
<b>Cover shrub layer (%)</b> , n = 182, P < 0.001 (Kruskal-Wallis test)												
- minimum	0	0	0	0	0	0	64	0	0	4	3	7
- lower quartile	0	0	0	2	0	0	65	2	0	18	14	12
- median	4	0	0	5	0	0	68	12	1	42	24	20
- upper quartile	18	3	6	15	1	2	88	18	8	57	33	42
- maximum	53	39	26	26	8	25	90	40	20	90	38	51
- mean	12	3	4	9	1	5	75	12	5	40	23	25
- standard deviation	17	7	7	9	3	11	12	13	8	28	13	15
<b>Cover herb layer (%)</b> , n = 182, P < 0.001 (Kruskal-Wallis test)												
- minimum	23	15	35	64	45	76	22	47	50	33	43	33
- lower quartile	35	31	54	74	57	79	34	64	59	46	47	46
- median	45	38	62	78	66	79	44	69	69	58	57	52
- upper quartile	54	54	71	81	68	83	52	77	74	74	65	58
- maximum	64	73	82	84	75	92	78	80	84	80	76	81
- mean	44	42	62	77	62	82	45	69	67	58	57	52
- standard deviation	12	15	12	5	10	6	16	11	10	16	13	11
<b>Cover bryophytes (%)</b> , n = 182, P < 0.001 (Kruskal-Wallis test)												
- minimum	0	0	0	0	2	10	8	2	0	7	6	5
- lower quartile	0	0	0	7	6	10	17	30	6	20	6	20
- median	0	0	2	13	9	13	24	44	12	30	19	40
- upper quartile	0	0	7	15	23	56	34	50	28	67	37	54
- maximum	10	7	19	29	34	57	54	66	78	75	51	68
- mean	1	1	4	12	15	29	27	38	21	40	23	38
- standard deviation	3	2	5	8	12	25	15	20	22	26	19	20
<b>Cover lichens (%)</b> , n = 182, P < 0.001 (Kruskal-Wallis test)												
- minimum	0	0	0	0	0	5	0	0	0	0	0	0
- lower quartile	0	0	0	2	8	8	7	0	0	0	0	0
- median	0	2	4	5	30	10	17	1	0	2	1	4

- upper quartile	2	3	11	6	39	11	24	3	0	10	4	8
- maximum	2	38	35	48	63	22	74	4	0	24	12	29
- mean	1	3	9	7	27	11	22	2	0	7	3	6
- standard deviation	1	6	11	12	23	6	23	2	0	8	5	8

**Mean annual temperature (°C), n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	-5.6	-5.2	-5.9	-5.6	-6.7	-5.4	-5.4	-4.1	-3.3	-4.0	-3.7	-5.2
- lower quartile	-3.3	-2.6	-3.8	-3.9	-6.7	-5.3	-4.9	-3.8	-2.9	-3.3	-2.3	-3.5
- median	-2.3	-2.2	-3.5	-3.8	-5.9	-5.2	-3.8	-3.4	-2.7	-2.5	-1.6	-3.2
- upper quartile	-1.2	-1.2	-2.4	-3.4	-4.8	-4.0	-3.5	-2.9	-1.6	-1.8	-1.0	-2.5
- maximum	-1.0	-0.7	-0.9	-2.5	-3.7	-3.7	-2.4	-0.7	-0.9	-0.7	-0.7	-0.7
- mean	-2.6	-2.1	-3.2	-3.9	-5.6	-4.7	-4.0	-3.2	-2.4	-2.6	-1.8	-2.9
- standard deviation	1.6	1.0	1.2	0.9	1.3	0.8	1.0	1.1	0.8	1.0	1.1	1.1

**Annual precipitation (mm), n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	157	137	219	215	226	248	220	225	145	178	199	163
- lower quartile	211	159	247	243	289	294	240	226	174	243	217	238
- median	255	208	265	282	306	296	258	247	238	248	255	263
- upper quartile	277	265	283	299	306	307	290	285	246	282	281	288
- maximum	308	304	307	322	307	342	342	303	295	287	303	322
- mean	243	218	265	273	290	297	267	257	213	256	251	262
- standard deviation	476	53	25	35	30	34	39	31	47	33	42	36

**Number of vascular plant species, n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	9	6	9	24	19	18	16	17	6	19	30	11
- lower quartile	14.2	12.8	24	43	24.5	21	23.5	22	20.8	27	36.5	24
- median	21	16.5	31	49	26	42	30.5	29	24.5	33	38	28
- upper quartile	25.2	20.5	37	54.5	32.5	42	39	38	34.8	38.5	38.8	35.5
- maximum	34	35	56	66	45	47	43	46	49	62	59	41
- mean	20.6	17	31	47.5	29.1	34	30.4	30.6	26.6	35.5	40	29
- standard deviation	7.8	6.8	10.9	10.6	9	13.4	9.3	11.1	10.9	13.7	9.9	7.9

**Number of terricolous bryophyte species, n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	0	0	0	0	1	4	4	1	0	4	3	2
- lower quartile	0	0	0	3.5	2.5	5	7.2	7	2	7	3	5
- median	0	0	2	5	5	6	9	10	4	9	6.5	7
- upper quartile	0	0	3	7	9.5	10	10	15	6.2	10	11.5	9
- maximum	6	4	8	9	11	13	12	18	13	17	17	14
- mean	0.6	0.3	2.2	4.7	5.9	7.6	8.7	10.6	4.6	9.3	8	7.1
- standard deviation	1.6	1	2.2	2.6	4.2	3.8	2.5	5.4	3.7	3.6	5.9	3

**Number of terricolous macrolichen species, n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	0	0	0	0	0	2	0	0	0	0	0	0
- lower quartile	0	0	1	1	2.5	4	3.2	0	0	0	0	0
- median	0	1	1	2	8	5	7.5	1	0	1	1	2
- upper quartile	1	1	5	3	10.5	6	9.5	2	0	5	2	4
- maximum	1	4	9	8	14	10	17	2	0	9	6	11
- mean	0.4	0.8	2.7	2.5	6.9	5.4	7	0.9	0	2.8	1.7	2.8
- standard deviation	0.5	1	2.7	2.3	5.4	3	5.2	0.9	0	3.3	2.3	3.1

**Number of snail species, n = 105, P < 0.001 (Kruskal-Wallis test)**

- minimum	0	0	0	0	0	1	1	0	0	1	3	1
- lower quartile	0	0	0	2	0	1	1	1.8	0	2	3.5	3
- median	1	0	0	3	0.5	1	1	2	0	3	4	3
- upper quartile	2	0	0.2	4	1	1	1.2	3.8	1.5	7	5.5	4
- maximum	3	2	6	7	1	1	2	9	5	13	7	8
- mean	1.2	0.2	0.8	3	0.5	1	1.2	3.1	1	4.8	4.7	3.9
- standard deviation	1.3	0.5	1.7	2.1	0.6	0	0.5	2.9	1.7	4.2	2.1	2.2

**Cover of various species of *Chenopodiaceae* (%), n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	0	0	0	0	0	0	0	0	0	0	0	0
- lower quartile	0	2	0	0	0	0	0	0	0	0	0	0
- median	0	3	0	0	0	0	0	0	0	0	0	0
- upper quartile	2	4.9	0	0	0	0	0	0	0	0	0	0
- maximum	13.2	63.7	4	0	0	0	0	0	5.9	0	0	0
- mean	2.2	5	0.2	0	0	0	0	0	0.7	0	0	0
- standard deviation	4.1	10.3	0.8	0	0	0	0	0	1.8	0	0	0

**Cover of various species of *Artemisia* (%), n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	0	0	2	0	0	0	0	0	0	0	0	0
- lower quartile	5.4	3.8	4.9	1.8	0	0	0	0	0	0	0	0
- median	7.4	8	5.9	3	0	0	0	1	0	2	0	0
- upper quartile	10.6	10.2	11.6	4.2	1	0	1.8	2	2	2	1.5	2
- maximum	39.2	39.9	22.1	13.4	2	4	2	18	4.9	4	2	9.8
- mean	11.1	9.6	8	3.6	0.6	0.8	0.7	3.1	1.1	1.3	0.7	1.2
- standard deviation	10.7	9.2	5	3.6	1	1.8	0.9	5.8	1.8	1.3	1	2.2

**Cover of *Ephedra dahurica* and *E. monosperma* (%), n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	0	0	0	0	0	0	0	0	0	0	0	0
- lower quartile	0	0	0	0	0	0	0	0	0	0	0	0
- median	0	0	0	0	0	0	0	0	0	0	0	0
- upper quartile	0	2	2	0	0	0	0	0	0	0	0	0
- maximum	2	4	8	0	0	0	0	0	0	0	0	0
- mean	0.2	0.8	1.1	0	0	0	0	0	0	0	0	0
- standard deviation	0.6	1.1	1.7	0	0	0	0	0	0	0	0	0

**Cover of *Dryas oxyodonta* and *Betula rotundifolia* (*B. nana* s.l.) (%), n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	0	0	0	0	0	38	63	0	0	0	0	0
- lower quartile	0	0	0	0	0	38	63	0	0	0	0	0
- median	0	0	0	0	0	49.2	63.5	0	0	0	0	0
- upper quartile	0	0	0	0	1	63	88	2	0	1	0	1
- maximum	0	0	0	3	4.9	88	88.4	2	2	4	10.8	39
- mean	0	0	0	0.2	1	55.2	73.2	0.7	0.1	0.7	1.8	4.2
- standard deviation	0	0	0	0.8	1.9	21	12.9	1.0	0.5	1.3	4.4	10.7

**Soil pH, n = 182, P < 0.001 (Kruskal-Wallis test)**

- minimum	6.4	5.9	5.8	5.4	4.7	6.4	4.2	5.6	6.8	6.0	6.8	5.2
- lower quartile	6.8	7.1	6.2	6.2	5.0	6.5	5.2	6.5	6.9	6.9	6.8	5.8
- median	7.0	7.3	6.8	6.4	6.1	6.6	5.5	6.9	7.3	7.2	7.1	6.5
- upper quartile	7.4	7.6	7.0	6.5	6.3	7.0	6.4	7.1	7.6	7.3	7.4	6.9
- maximum	8.0	8.2	8.0	7.5	6.4	7.8	7.2	7.4	8.6	7.8	7.8	7.5
- mean	7.1	7.3	6.7	6.4	5.7	6.9	5.7	6.7	7.4	7.1	7.2	6.4
- standard deviation	0.4	0.4	0.6	0.4	0.7	0.6	0.9	0.6	0.6	0.5	0.4	0.7

**Soil organic carbon content (%), n = 104, P = 0.002 (Kruskal-Wallis test)**

- minimum	2.6	3.4	4.2	9.1	8.7	6.4	10.3	7.1	5.3	6.3	4.3	4.3
- lower quartile	3.2	5.9	8.0	14.6	10.8	6.4	11.4	8.0	17.0	12.7	12.7	9.1
- median	7.2	9.2	12.4	17.4	13.3	6.4	14.8	13.4	26.7	30.6	21.2	9.9
- upper quartile	10.9	11.7	15.5	25.2	19.2	6.4	28.5	34.8	41.8	46.5	24.6	21.3
- maximum	11.0	32.1	28.5	30.4	24.1	6.4	37.5	54.8	76.1	67.5	27.9	42.9
- mean	7.0	9.8	13.2	19.3	15.2	6.4	20.3	22.6	32.1	30.6	17.8	16.2
- standard deviation	4.6	6.3	7.0	7.0	6.3	NA	11.1	17.3	22.4	21.2	12.2	11.5

**Soil C:N ratio, n = 104, P = 0.055 (Kruskal-Wallis test)**

- minimum	17.2	27.8	23.5	30.0	26.9	39.9	30.2	3.3	17.7	28.0	38.9	3.9
- lower quartile	26.0	30.4	30.2	31.1	27.4	39.9	35.3	24.5	27.3	32.5	48.8	38.2

- median	36.1	35.7	31.6	32.7	31.2	39.9	39.2	32.3	29.3	38.5	58.8	51.2
- upper quartile	46.1	47.8	32.5	34.0	34.2	39.9	44.5	34.8	32.8	44.8	61.1	67.0
- maximum	54.4	160.6	72.1	91.2	70.8	39.9	59.1	42.4	65.6	63.4	63.5	200.9
- mean	35.9	49.5	33.1	40.0	38.1	39.9	41.2	27.5	34.0	39.6	53.7	62.6
- standard deviation	16.3	34.6	11.0	19.7	18.5	NA	9.9	13.4	14.1	10.1	13.1	53.5

**Soil phosphorus content (g.kg<sup>-1</sup>), n = 104, P < 0.001 (Kruskal-Wallis test)**

- minimum	5	10	7	5	3	7	2	5	1	1	4	6
- lower quartile	7.2	21	10	8	3	7	3.5	7	2	4	4	10.5
- median	9	27	19.5	13	7	7	4	9	4	8	4	21
- upper quartile	11	32.5	23.8	15	9	7	11.5	10	10	10	5.5	46
- maximum	14	62	31	64	12	7	66	29	799	38	7	186
- mean	9.2	28.3	17.8	17	6.8	7	14.6	11	155.7	10.2	5	39.2
- standard deviation	3.8	11.7	8.3	18.4	3.9	NA	23.2	7.5	305.9	10.6	1.7	52.2

**Soil potassium content (g.kg<sup>-1</sup>), n = 104, P = 0.004 (Kruskal-Wallis test)**

- minimum	130	143	169	92	91	218	130	90	115	103	104	124
- lower quartile	153.2	191	195.2	164	125	218	153.5	120	136	146	116	160.5
- median	170.5	218	265.5	220	137	218	162	144	180	180	128	210
- upper quartile	198	288.5	370.2	277	138	218	176.5	198	223	196.5	186.5	223
- maximum	252	457	475	343	162	218	207	340	6352	464	245	283
- mean	180.8	245.8	283.9	223.1	130.6	218	165.6	170.1	896.7	192.6	159	197.1
- standard deviation	51.8	88.2	102.5	90.8	25.9	NA	25.7	75.3	2050.2	97.5	75.4	47.3

**Soil calcium content (g.kg<sup>-1</sup>), n = 104, P = 0.001 (Kruskal-Wallis test)**

- minimum	2318	1291	1510	1500	510	5891	930	2269	1522	1600	1623	1233
- lower quartile	3024.5	3002	2218.8	2637	662	5891	1517	3525	7725	4976.5	4925.5	2011.5
- median	11041.5	3497	2812.5	3093	1003	5891	3032	3914	14713	6363	8228	2669
- upper quartile	19365.5	8880	3761	5251	1376	5891	5672	4919	23026	7531	10410	5026.5
- maximum	20993	28086	16246	7068	1997	5891	7643	6134	30900	9965	12592	11409
- mean	11348.5	7894.4	3665.2	3865.2	1109.6	5891	3711.9	4104.7	15662	6264.4	7481	4161.5
- standard deviation	9930.7	8869	3469.3	1895	597.8	NA	2640.1	1239.3	10464.4	2499.2	5522.5	3317.1

**Soil magnesium content (g.kg<sup>-1</sup>), n = 104, P < 0.001 (Kruskal-Wallis test)**

- minimum	290	174	216	175	87	275	158	234	396	182	218	206
- lower quartile	323.8	240.5	311.5	324	115	275	259	286	680	293.5	294.5	276.5
- median	358.5	318	371	378	144	275	303	450	882	540	371	317
- upper quartile	390.8	467	413.2	476	169	275	399	465	899	616.5	608	386
- maximum	417	2957	534	610	254	275	577	2316	2438	814	845	879
- mean	356	495.5	370.2	395	153.8	275	336.3	609.1	1082.7	488.3	478	375.4
- standard deviation	55.4	619.1	84.8	134.7	63.9	NA	138.4	651.2	747.1	221	326.9	193.8

**Productivity (aboveground biomass without litter at the peak of the growing season, g.m<sup>-2</sup>), n = 100, P < 0.001 (Kruskal-Wallis test)**

- minimum	18	14	53	71	47	193	82	88	71	79	24	51
- lower quartile	41	32	90	156	78	193	111	154	166	105	63	64
- median	50	58	116	184	102	193	143	186	215	120	102	74
- upper quartile	108	97	156	212	138	193	229	206	313	179	105	87
- maximum	278	264	275	285	144	193	249	309	374	199	108	234
- mean	99	74	128	186	102	193	165	185	228	136	78	95
- standard deviation	120	61	60	69	41	NA	70	66	97	50	47	59

**Nitrogen content in the aboveground biomass (%), n = 100, P = 0.040 (Kruskal-Wallis test)**

- minimum	1.6	1.1	1.1	1.3	1.4	1.7	1.3	1.5	1.3	1.8	1.7	0.5
- lower quartile	1.9	1.7	1.3	1.6	1.6	1.7	1.9	1.7	1.4	1.9	1.8	1.3
- median	2.4	2.0	1.5	1.7	1.9	1.7	2.1	1.8	1.8	1.9	1.9	1.9
- upper quartile	2.7	2.1	1.7	1.8	2.0	1.7	2.3	2.1	1.9	2.1	2.4	2.0
- maximum	2.8	3.2	2.8	1.9	3.6	1.7	2.5	2.9	2.1	2.4	2.9	2.1

- mean	2.3	1.9	1.6	1.7	2.1	1.7	2.1	1.9	1.7	2.0	2.2	1.6
- standard deviation	0.6	0.4	0.4	0.2	0.8	NA	0.4	0.4	0.3	0.2	0.7	0.5

**Phosphorus content in the aboveground biomass (%), n = 100, P = 0.018 (Kruskal-Wallis test)**

- minimum	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
- lower quartile	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1
- median	0.2	0.2	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.2	0.2
- upper quartile	0.2	0.2	0.1	0.1	0.2	0.1	0.4	0.2	0.2	0.2	0.2	0.3
- maximum	0.3	0.3	0.3	0.2	0.3	0.1	0.4	0.3	0.2	0.3	0.2	0.3
- mean	0.2	0.2	0.1	0.1	0.2	0.1	0.3	0.2	0.2	0.2	0.2	0.2
- standard deviation	0.1	0.1	0.1	0.1	0.1	NA	0.1	0.1	0.0	0.1	0.0	0.1

**Potassium content in the aboveground biomass (%), n = 100, P = 0.004 (Kruskal-Wallis test)**

- minimum	1.7	0.4	0.6	0.7	0.4	0.7	0.8	0.7	0.8	0.9	1.9	0.5
- lower quartile	1.9	1.2	0.7	1.0	0.8	0.7	0.9	1.1	1.2	1.0	1.9	0.7
- median	1.9	1.4	0.9	1.2	1.1	0.7	0.9	1.3	1.2	1.1	2.0	1.2
- upper quartile	2.2	1.6	1.0	1.6	1.1	0.7	1.2	1.5	1.6	1.3	2.1	1.6
- maximum	3.0	3.2	2.5	1.8	1.5	0.7	2.0	2.1	2.0	2.9	2.2	2.2
- mean	2.1	1.5	1.0	1.2	1.0	0.7	1.1	1.3	1.3	1.4	2.0	1.2
- standard deviation	0.6	0.7	0.5	0.4	0.4	NA	0.4	0.4	0.4	0.8	0.2	0.6

**Calcium content in the aboveground biomass (%), n = 100, P = 0.002 (Kruskal-Wallis test)**

- minimum	0.9	0.2	0.3	0.7	0.4	1.6	0.6	0.5	0.2	0.8	1.1	0.4
- lower quartile	1.0	0.9	0.5	0.8	0.7	1.6	0.7	0.7	0.6	0.9	1.1	0.6
- median	1.4	1.0	0.6	1.1	0.8	1.6	0.8	0.7	0.9	1.2	1.1	0.8
- upper quartile	2.0	1.3	0.8	1.5	0.9	1.6	1.1	0.8	1.0	1.3	1.1	1.0
- maximum	2.6	2.0	1.4	1.8	0.9	1.6	1.5	1.0	1.4	1.5	1.2	1.7
- mean	1.6	1.1	0.7	1.2	0.7	1.6	0.9	0.7	0.8	1.1	1.1	0.9
- standard deviation	0.8	0.4	0.3	0.4	0.2	NA	0.3	0.2	0.4	0.3	0.0	0.4

**Magnesium content in the aboveground biomass (%), n = 100, P = 0.018 (Kruskal-Wallis test)**

- minimum	0.2	0.0	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.3	0.1
- lower quartile	0.3	0.2	0.1	0.2	0.2	0.1	0.2	0.2	0.2	0.2	0.3	0.2
- median	0.4	0.3	0.2	0.3	0.2	0.1	0.3	0.2	0.3	0.3	0.4	0.2
- upper quartile	0.6	0.4	0.2	0.3	0.2	0.1	0.3	0.3	0.4	0.4	0.4	0.3
- maximum	0.8	0.6	0.3	0.4	0.2	0.1	0.3	0.6	0.5	0.4	0.4	0.3
- mean	0.4	0.3	0.2	0.2	0.2	0.1	0.3	0.3	0.3	0.3	0.4	0.2
- standard deviation	0.3	0.1	0.1	0.1	0.0	NA	0.1	0.2	0.1	0.1	0.1	0.1

**N:P ratio in the aboveground biomass, n = 100, P = 0.009 (Kruskal-Wallis test)**

- minimum	10.1	6.0	7.5	7.6	11.4	16.6	4.7	8.1	8.3	7.3	12.5	6.2
- lower quartile	11.1	11.2	12.0	12.2	13.3	16.6	5.9	9.1	9.1	9.9	13.3	7.0
- median	12.0	13.0	14.9	13.4	14.2	16.6	9.0	12.6	9.5	11.7	14.1	7.1
- upper quartile	13.1	14.4	16.0	14.7	14.9	16.6	12.5	14.8	11.2	14.4	14.4	9.4
- maximum	15.0	20.6	20.1	19.5	17.9	16.6	16.0	16.4	16.7	15.9	14.7	14.0
- mean	12.3	12.8	14.2	13.7	14.4	16.6	9.5	12.4	11.1	11.9	13.7	8.6
- standard deviation	2.1	3.2	3.4	3.4	2.4	NA	4.6	3.1	3.2	3.3	1.2	2.7

**Ca:P ratio in the aboveground biomass, n = 100, P = 0.015 (Kruskal-Wallis test)**

- minimum	3.2	2.5	2.1	3.3	2.9	15.9	2.3	2.7	1.0	4.8	5.5	2.3
- lower quartile	7.0	5.5	4.6	8.1	3.8	15.9	3.3	3.8	4.2	5.1	6.5	3.1
- median	9.1	6.8	6.1	10.1	5.0	15.9	3.9	4.5	4.3	5.8	7.5	3.6
- upper quartile	11.1	8.6	7.0	11.4	7.0	15.9	4.9	6.3	7.0	7.0	8.7	6.6
- maximum	14.4	14.0	10.9	13.4	8.1	15.9	5.3	7.4	12.1	11.0	9.8	17.7
- mean	8.9	7.1	6.0	9.4	5.3	15.9	4.0	4.9	5.6	6.6	7.6	5.6
- standard deviation	4.6	3.2	2.2	3.1	2.2	NA	1.1	1.7	3.7	2.3	2.2	4.4

**Tetanic ratio (K:(Ca+Mg)) in aboveground biomass, n = 100, P = 0.176 (Kruskal-Wallis test)**

- minimum	0.6	0.5	0.6	0.6	0.9	0.4	0.6	0.7	0.6	0.6	1.2	0.3
- lower quartile	1.0	0.9	0.9	0.7	0.9	0.4	0.8	1.2	0.8	0.7	1.3	0.9
- median	1.3	1.1	1.2	0.9	1.0	0.4	1.0	1.3	1.1	0.7	1.3	1.1
- upper quartile	1.5	1.4	1.4	1.1	1.1	0.4	1.1	1.5	1.7	0.8	1.4	1.4
- maximum	1.7	2.2	2.2	1.7	1.5	0.4	1.2	2.7	5.7	2.4	1.5	2.4
- mean	1.2	1.2	1.2	1.0	1.1	0.4	0.9	1.4	1.8	1.0	1.4	1.2
- standard deviation	0.4	0.4	0.5	0.4	0.2	NA	0.2	0.6	1.6	0.7	0.2	0.5

**Crude fibre content in aboveground biomass (%), n = 100, P < 0.001 (Kruskal-Wallis test)**

- minimum	15.7	0.0	17.4	17.5	15.8	19.1	12.9	19.3	18.1	14.8	15.6	17.7
- lower quartile	15.7	18.3	25.3	20.3	15.8	19.1	13.4	22.5	21.7	17.0	20.2	19.3
- median	16.7	21.7	27.2	22.6	20.8	19.1	14.0	23.1	25.6	18.9	24.9	20.6
- upper quartile	18.6	25.3	29.1	23.9	23.8	19.1	17.8	24.0	26.8	20.9	24.9	21.3
- maximum	21.4	33.7	32.2	32.2	27.5	19.1	20.8	25.8	29.0	24.7	24.9	27.5
- mean	17.6	21.2	26.3	22.7	20.7	19.1	15.7	22.9	24.3	19.2	21.8	20.7
- standard deviation	2.7	6.9	3.9	4.2	5.1	NA	3.1	2.0	3.7	3.5	5.4	2.6