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# The vegetation of the forest-steppe region of Hustain Nuruu, Mongolia

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## Abstract

The vegetation of a forest-steppe region in Hustain Nuruu, Mongolia, was studied by a phytocoenological approach. Eleven plant communities were recognized, comprising four steppe communities, two meadow communities, a tussock grassland, two shrub communities, a scrub community and a woodland community. The botanical and ecological characteristics of the different communities are discussed, with reference to the existing classification of Mongolian plant communities. Analysis of the present data indicates that a refinement or extension of the classification system is desirable, especially concerning the steppe(-related) communities. Discussion of the relative distribution of steppe and forest reveals that in the relatively dry location of Hustain Nuruu grassland and shrubland dominate the natural vegetation (88% of the area). Forest covers ca. 5% of the area, it is limited to sites where ground water is within rooting depth: north slopes above 1400 m (*Betula platyphylla* woodland) and along erosion gullies (fragmentary *Ulmus pumila* gallery woodland). Under natural conditions forest cover might reach 12%, but it is speculated that wild ungulates could maintain its extension at a lower level. The importance of forest is greater in forest-steppe regions with higher rainfall, but the factors determining the distribution of grassland and forest are expected to be similar.

## Introduction

Steppe vegetation forms the largest fraction of natural grassland in the temperate zone (Coupland 1992, 1993). Its occurrence is largely determined by climatic and edaphic factors which favour grasses and associated herbaceous plants and prevent the dominance of woody plants, i.e. trees and shrubs (Coupland 1979; Walter 1977). The competition by woody plants is reduced or eliminated in steppes by aridity, cold, limited rooting depth, high salinity or a combination of these factors. Natural disturbing agents (*sensu* White & Pickett 1985), such as floods, fires and herbivory, further add to the disadvantageous position of woody plants relative to grasses.

To reveal the outcome of the above-mentioned interacting environmental factors on the dominance of grasses and woody plants, it is necessary to study the border zone between steppe and woodland or forest. In temperate regions few areas still possess a sufficiently low degree of human interference to study these processes. The world's largest remaining area of steppe is situated in Central Asia (Lavrenko *et al.* 1993; Zhu Ting-Chen 1993). To the north it is bordered by the vast coniferous forests of the taiga. The transition zone between steppe and taiga is covered by so-called forest-steppe, which, in Mongolia alone extends over 375,000 km$^2$. The extent of this forest-steppe zone makes it an interesting object for the study of factors that determine the relative distribution of grassland and forest in a temperate environment.

Unfortunately, ecological studies of the vegetation in the area are scarce or have been published in Russian or Chinese journals and are thus hardly accessible to western scientists. Moreover, as noted by Hilbig (1990), the ecological significance of vegetation types from Russian-Mongolian studies using a few dominant plant species as a basis for vegetation classification (e.g. Yunatov *et al.* 1979), often is ambiguous. The available material from German studies provides insight in the geobotany of the Mongolian forest-steppe (Hilbig & Knapp 1983; Hilbig 1987, 1990; Succow &

Kloss 1978; Walter 1974). Yet, these studies have concentrated on the mountainous areas of the Khentei and Khangay ranges and thus fail to cover the steppe vegetation in its full extent. The present paper extends the ecological characterization of the Mongolian forest-steppe by considering the Hustain Nuruu area, which is situated at the drier southern edge of the forest-steppe zone, and therefore contains a higher proportion of typical steppe vegetation.

## Study area

The study took place in the area of Hustain Nuruu (Mongolian for birch mountains, 47° 50′ N 106° 00′ E, Central aimak, somons of Altanbulak, Atar and Nohorlol), situated 100 km west of Ulan Bator, the capital of Mongolia (Fig. 1). The climate is typically continental with a mean annual temperature of +0.2 °C and a yearly precipitation of 270 mm. The vegetation season starts after a spring drought with occasional dust storms and (mainly accidental) fires in April–May and ends in the beginning of September. Over 70% of precipitation falls during summer, which allows for a higher productivity than the temperature regime and total precipitation would lead to expect. The long winter begins in October with temperatures sinking to an average of -23 °C in January. Low winter precipitation in combination with strong winds often leave the soil bare on exposed ridges and mountain slopes.

The study area (500 km$^2$) ranges between 1100 and 1840 m above sea-level, with the following altitudinal distribution of land area: 28% between 1100 and 1300 m, 51% between 1300 and 1500 m and 21% above 1500 m. The landscape is dominated by a central mountain range of granitic rocks, a southwestern spur of the Khentei range, with a SW–NE orientation. To the north, the range slopes down to a rolling plain with agricultural fields (cereals) and to the south it borders the broad valley of the Tuul river. The landforms of the mountains are rounded with abundant rocky outcrops marked by the erosion of wind and frost. The erosion by water from heavy downpours in summer and from the melting of snow in spring have led to the formation of gullies and the accumulation of thick layers of eroded material in the valleys. The gullies carry water only infrequently. Running water originates in springs and mostly fills only the upper range of a gully as it gradually seeps to the subsoil. The springs are fed by rainfall, melting snow and the thawing of the soil layer above the permafrost zone, which reaches up to an approximate depth of one meter on north slopes and seven meters on south slopes.

The area covered during the study has been designated as a nature reserve which serves as a reintroduction site for the Przewalski Horse (*Equus ferus przewalskii*). In November 1993 the reserve status was declared for a somewhat larger area of 567 km$^2$ and conservation measures are actually being implemented. Up till now the area was intensively used by nomad pastoralists for grazing livestock (mainly sheep, goats, cattle and horses) roughly estimated at 15,000 cattle or horse equivalents. Wild ungulates occur mainly above 1500 m, where livestock pressure is low. Three species are present: red deer (*Cervus elaphus*, estimated at 300–350 animals), wild boar (*Sus scrofa*, estimated at 50–100 animals) and roe deer (*Capreolus capreolus*, estimated at less than 50 animals). Argali sheep (*Ovis ammon*) and Mongolian gazelle (*Procapra gutturosa*) have been observed incidentally over the last two decades but may have been more abundant in former times (Foundation Reserves Przewalski Horse 1992; Germeraad *et al.* 1993).

## Methods

The data were collected between late May and early September in 1993. Vegetation relevés were made on homogeneous and representative locations following the Braun-Blanquet method as described in Mueller-Dombois & Ellenberg (1974). Plot size was 5 × 5 m$^2$ in herbaceous vegetation and 10 × 10 m$^2$ in shrubland and woodland. At each location notes were made on the site coordinates, altitude, exposition, topography, vegetation physiognomy, soil texture, soil colour and the horizontal cover of tree, shrub, dwarf shrub and herb layers. The nomenclature of plant species follows Grubov (1982).

A total of 169 relevés were included in the analysis. Ordination of relevés was carried out subjectively in a spreadsheet file. Vegetation types were recognized on the basis of characteristic and differentiating species groups. For each recorded species the presence class and average cover class per vegetation type were indicated. The average cover class was calculated over the cases in which the species was present only, thus reflecting the cover where the species occurred. For this purpose mean cover values were assumed for each class: r = 0.1%, + = 0.5%, 1 = 2%, 2 = 10%, 3 = 35%, 4 = 60%, 5 = 85%.

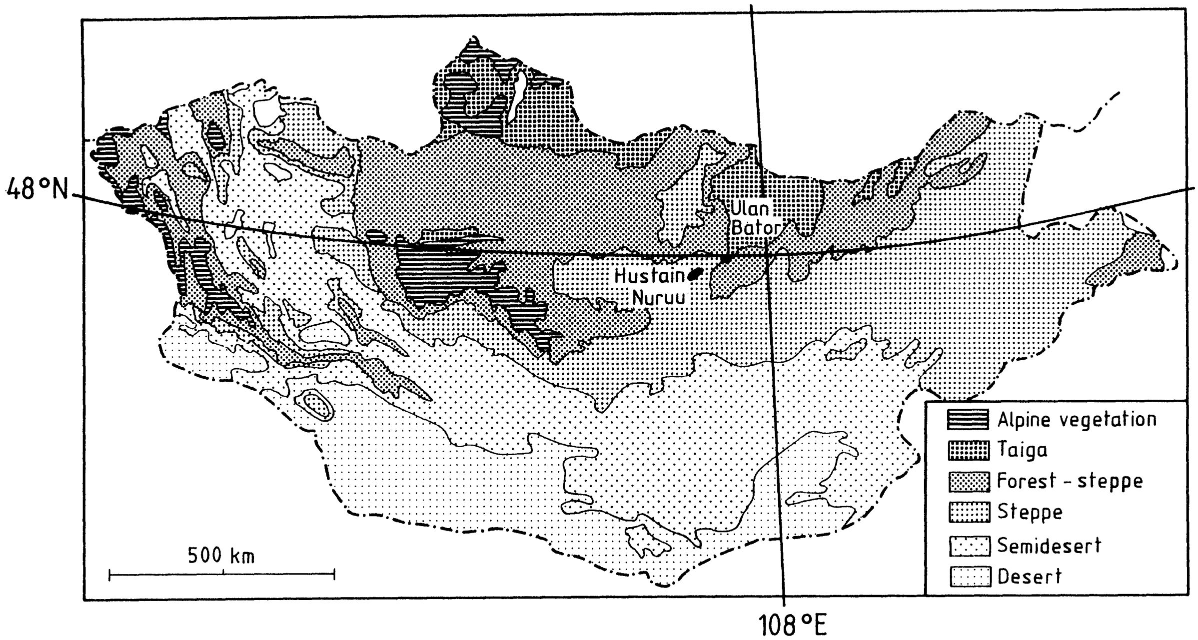


*Fig. 1.* Vegetation zonation in Mongolia (after Yunatov *et al.* 1979) with the location of the study area and the capital.

## Results

The results of the vegetation classification have been presented in a synoptic table (Table 1); occasional species are listed in the appendix. Eleven vegetation types have been recognized, comprising four steppe communities, two meadow communities, a tussock grassland, two shrub communities, a scrub community and a woodland community. Aside from their botanical characterization, the different communities can be distinguished according to physiognomy, situation in the landscape, altitude, exposition, soil colour and soil texture (Table 2). These characteristics will be discussed for each vegetation type.

### *Iris lactea-meadow*

This community is found along streams with a permanent water supply at lower elevations. Just outside the study area it also occurs in the Tuul valley. The soil texture shows great variation according to the sedimentation pattern. A microrelief often develops under the influence of cryogenic processes. The availability of moisture allows a comparatively high plant productivity and a high organic matter content in the soil. These conditions attract high numbers of grazing animals, mainly livestock. The abundant occurrence of *Iris lactea* is often seen as a sign for overgrazing (Hilbig 1990).

The vegetation cover of the *Iris lactea*-meadow is high (60–100%) and dominated by a mixture of grasses *(Poa pratensis, Agrostis mongholica, Hordeum brevisubulatum)* and herbs *(Iris lactea, Potentilla anserina, Ranunculus* sp., *Sanguisorba officinalis)* from fresh and saline meadows. The *Iris lactea*-meadow can be considered to belong to the association *Halerpestidi-Hordeetum brevisubulati* which was described more extensively from similar sites by Hilbig (1990). The community is botanically well-defined (Table 1) as most species depend on the occurrence of ground water and are therefore restricted to streamsides. *Glaux maritima* is characteristic for saline soils, which develop by the accumulation of salts from evaporating ground water. Along the Tuul river it was apparent that, in the absence of grazing and natural disturbance (flooding and ice flow), succession can lead to the establishment of *Salix*-bushes.

### *Achnatherum splendens-tussock grassland*

This tussock grassland is encountered on the higher banks of streams and rivers and on terraces in valleys.

*Table 1*. Synoptic table of vegetation types in Hustain Nuruu. The first figure in a cell indicates the presence class, the second gives the mean cover class when the species is present (Abbreviations of vegetation types: Iris = *Iris lactea*, Achn = *Achnatherum splendens*, Art-Stipa = *Artemisia adamsii-Stipa krylovii*, Th-Stipa = *Thermopsis lanceolata-Stipa krylovii*, Amygd = *Caryopteris mongholica-Amygdalus pedunculata*, F. len = *Festuca lenensis*, F. sib = *Festuca sibirica*, Spiraea = *Spiraea aquilegifolia*, Geran = *Geranium pratense*, Betula = *Betula platyphylla*, Brolj = *Betula fusca*)

| Vegetation type | Iris | Achn | Art-Stipa | Th-Stipa | Amygd | F. len | F. sib | Spiraea | Geran | Betula | Borolj |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of relevés | 13 | 6 | 35 | 46 | 14 | 24 | 14 | 4 | 5 | 5 | 3 |
| *Iris lactea* Pall. | 5,2 | 1.r | – | – | – | – | – | – | 1.r | – | – |
| *Potentilla anserina* L. | 5,2 | 1,1 | 1.r | – | – | – | – | – | 1,2 | – | – |
| *Ranunculus* sp. L. | 4,1 | – | – | – | – | – | – | – | – | – | – |
| *Glaux maritima* L. | 2,1 | – | – | – | – | – | – | – | – | – | – |
| *Poa pratensis* L. | 4,2 | 1,1 | 1.r | – | – | – | 1.+ | – | 1.+ | 1.r | – |
| *Agrostis mongholica* Roshev. | 3,3 | 1.1 | – | – | – | – | – | – | – | – | – |
| *Carex enervis* C.A. Mey. | 4,2 | – | 1.+ | – | – | – | – | – | – | – | – |
| *Cirsium esculentum* L. | 2,1 | – | – | – | – | – | – | – | – | – | – |
| *Artemisia mongolica* Fisch. ex Nakia | 2,2 | – | – | – | 1,1 | – | 1,1 | 3,1 | 1,2 | – | – |
| *Medicago lupulina* L. | 2,2 | – | – | – | – | – | – | – | – | – | – |
| *Hordeum brevisubulatum* (Trin.) Link | 3,2 | – | – | – | – | – | – | – | – | – | – |
| *Plantago major* L. | 3,1 | 2.+ | 1.+ | – | – | – | – | – | 1.r | – | – |
| *Potentilla multifida* L. | 2,1 | – | – | – | – | 1.+ | – | – | – | – | – |
| *Taraxacum* sp. Wigg. | 3,2 | 2.+ | 1.+ | 1.r | – | 1.r | 1.r | – | – | – | – |
| *Achnatherum splendens* (Trin.) Nevski | 2,2 | 5.4 | 2,2 | – | – | – | – | – | 1.r | – | – |
| *Stipa krylovii* Roshev. | 1,1 | 5,2 | 5,3 | 5,2 | 3,1 | 2,1 | 1.+ | – | – | – | – |
| *Carex duriuscula* C.A. Mey. | 2,2 | 5,2 | 3,1 | 3,1 | – | 1,2 | 1,2 | – | – | – | – |
| *Elymus chinensis* (Trin.) Keng | 2,2 | 5,2 | 3,1 | 4,2 | 1,2 | 1,1 | 2,2 | 4,1 | 1,1 | – | – |
| *Potentilla bifurca* L. | 1,2 | 5.+ | 2.+ | 1.+ | 1.+ | 1,1 | – | – | 1.r | – | – |
| *Artemisia adamsii* Bess. | 1.+ | 4.+ | 4,2 | 2,1 | – | – | – | – | – | – | – |
| *Heteropappus altaicus* (Willd.) Novopokr. | – | 5.+ | 5,1 | 2,1 | – | 1.r | – | – | – | – | – |
| *Chamaerhodos erecta* (L.) Bge. | – | 1.r | 3.+ | 1.+ | 4.+ | 1.r | – | – | – | – | – |
| *Cleistogenes squarrosa* (Trin.) Keng | – | – | 5.+ | 4,1 | 2.+ | 1,1 | – | – | – | – | – |
| *Cymbaria daurica* L. | – | – | 2.+ | 3.+ | 2.r | 1.+ | 1,1 | – | – | – | – |
| *Sibbaldianthe adpressa* Bge. (Juz.) | – | – | 1.+ | 1.r | 1.r | – | – | – | – | – | – |
| *Dontostemon integrifolius* (L.) C.A. Mey. | – | – | 2.+ | 3.r | 3.+ | 1,1 | 1,1 | – | – | – | – |
| *Caragana pygmaea* (L.) DC. | 1,1 | – | 3.+ | 3.+ | 4,1 | 3.+ | 3.+ | 2.r | – | – | 2.+ |
| *Artemisia frigida* Willd. | 1.+ | 1.+ | 5,2 | 5,2 | 5,1 | 4,1 | 2.+ | – | – | 1.r | – |
| *Agropyron cristatum* (L.) P.B. | 1,2 | – | 4,1 | 3.+ | 4,1 | 3,1 | 2.+ | – | – | – | 2.+ |
| *Caragana microphylla* (Pall.) Lam. | – | – | 2.+ | 2,1 | 3,1 | 2.+ | 1.+ | – | – | – | 2.r |

*Table 1.* Continued

| Vegetation type<br>Number of relevés | Iris<br>13 | Achn<br>6 | Art-Stipa<br>35 | Th-Stipa<br>46 | Amygd<br>14 | F. len<br>24 | F. sib<br>14 | Spiraea<br>4 | Geran<br>5 | Betula<br>5 | Borolj<br>3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Poa attenuata* Trin. | – | – | 2,1 | 5,2 | 3,2 | 4,2 | 3,1 | – | – | – | – |
| *Koeleria macrantha* (Ldb.) Schult. | – | – | 1.+ | 4,1 | 4,1 | 3,1 | 3.+ | 2,2 | – | – | 4,1 |
| *Stipa grandis* P. Simm | – | 1.r | – | 2,2 | – | – | – | – | – | – | – |
| *Thermopsis lanceolata* R. Br. | – | – | 1.r | 4,1 | 1,1 | 1,1 | 1,1 | – | – | – | – |
| *Pulsatilla* spp. Mill. | – | – | – | 3,1 | 4,1 | 3,1 | 4,1 | – | – | – | 2.+ |
| *Veronica incana* L. | – | – | – | 3,1 | 1,1 | 1,1 | 3,1 | – | 1.+ | – | 2,1 |
| *Potentilla tanacetifolia* Willd. ex Schlecht. | 1.r | 2.r | 1.r | 4.+ | 4.+ | 1.+ | 2.+ | – | 1.r | – | – |
| *Potentilla accaulis* L. | – | – | 1.+ | 2,1 | 3.+ | 2,1 | 1.r | – | – | – | 2.r |
| *Goniolimon speciosum* (L.) Boiss. | – | – | – | 1.r | 2.r | 1.r | 1.r | – | – | – | – |
| *Erysimum flavum* (Georgi) Bobr. | – | – | 1.+ | 3.+ | 2.r | 1.+ | 1.+ | – | – | – | – |
| *Gentiana decumbens* L. f. | 1.r | – | – | 2.r | 1.+ | 2.+ | 3.+ | 2.r | 1.r | – | – |
| *Bupleurum* sp. L. | 1.r | – | 2.r | 3.+ | 3,1 | 3.r | 4,1 | 2.r | 1.r | – | 2.r |
| *Dianthus versicolor* Fisch. | – | – | 1.r | 1.r | 2.r | 2.+ | 3,1 | 2.r | 1.+ | – | 2.+ |
| *Artemisia commutata* Bess. | – | – | 1.+ | 1.+ | 2.+ | 1.+ | 1.+ | – | – | – | – |
| *Heteropappus biennis* (Ldb.) Tamamsch. | – | – | – | 3,1 | 3.+ | 2.+ | 2,1 | – | – | – | 2.+ |
| *Amygdalus pedunculata* Pall. | – | – | 1.r | 1.+ | 5,2 | 1.+ | 2.+ | – | – | – | 2.r |
| *Stipa sibirica* (L.) Lam. | – | – | 1,1 | 1,1 | 5,2 | – | 3,1 | 3.+ | – | – | – |
| *Caryopteris mongholica* Bge. | – | – | – | – | 4,1 | – | – | – | – | – | – |
| *Rheum undulatum* L. | – | – | – | 1.r | 2.r | – | – | – | – | – | – |
| *Haplophyllum dahuricum* (L.) G. Don | – | – | 1.r | 1.r | 3.+ | 1.r | 1.+ | – | – | – | 2.+ |
| *Silene jenisseensis* Willd. | 1.+ | 1.r | – | 1.+ | 2.r | 1.r | 1.r | 2.r | – | – | – |
| *Artemisia santalinifolia* Turcz. ex Bess. | – | – | – | 1.r | 3,1 | 1.r | 1,1 | – | – | – | – |
| *Thymus* sp. L. | – | – | – | – | 3,1 | 2.+ | 2.+ | – | – | – | – |
| *Festuca lenensis* Drob | – | – | – | 1,1 | 1+ | 5,2 | 3.+ | 2,1 | – | – | 4,1 |
| *Potentilla sericea* L. | – | – | 1.r | 1.r | 2.+ | 3.+ | 2.+ | – | – | – | 4.+ |
| *Chamaerhodos altaica* (Laxm.) Bge. | – | – | – | 1.+ | – | 3,1 | 1,1 | – | – | – | 2.r |
| *Amblynotus rupestris* M. Pop. ex Serg. | – | – | 1.+ | 1.+ | 2.r | 3,1 | 1.+ | – | – | – | – |
| *Androsace incana* Lam. | – | – | 1.r | 1,1 | 1.+ | 4.+ | 2.r | 2.+ | – | – | 2.+ |
| *Arenaria capillaris* Poir. | – | – | 2.+ | 1.+ | 2.+ | 4.+ | 2,1 | – | – | – | 2.r |
| *Orostachys spinosa* (L.) C.A. Mey. | – | – | 1.+ | 1.r | 2.+ | 2,1 | 2.+ | – | – | – | 2.+ |
| *Polygonum angustifolium* Pall. | – | – | 1.r | 1.r | 2.+ | 2.+ | 2.+ | – | – | – | 4.+ |

*Table 1.* Continued

| Vegetation type<br>Number of relevés | Iris<br>13 | Achn<br>6 | Art-Stipa<br>35 | Th-Stipa<br>46 | Amygd<br>14 | F. len<br>24 | F. sib<br>14 | Spiraea<br>4 | Geran<br>5 | Betula<br>5 | Borolj<br>3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Festuca sibirica* Hack. ex Boiss. | – | – | – | 1.r | 2,2 | 2,1 | 5,3 | 5,2 | 1.+ | – | 2,2 |
| *Carex pediformis* C.A. Mey. | – | – | – | – | 2,1 | 2,1 | 4,1 | 5,2 | 1.+ | – | 4,2 |
| *Stellera chmamaejasme* L. | – | – | 1.+ | 1,2 | 1.+ | 2,1 | 3,1 | 3.+ | – | – | 4,1 |
| *Galium verum* L. | – | – | – | 1.+ | 2,2 | 1.r | 3,1 | 3,1 | 1.r | – | 2.r |
| *Leontopodium leontopodiodes* (Willd.) Beauvd. | – | – | 1.r | 1.+ | 1.r | 1.+ | 3.+ | – | – | – | 2.+ |
| *Serratula centauroides* L. | – | – | – | 1.+ | 2.r | 1.+ | 3.+ | 4,r | – | – | 2.r |
| *Scabiosa comosa* Fisch. | – | – | – | 1.r | 1.+ | 1.+ | 3,2 | 2,1 | – | – | 2,1 |
| *Schizonepeta multifida* (L.) Briq. | – | – | – | 1.+ | 2,1 | 1.+ | 3.+ | 4.+ | 2.+ | – | – |
| *Filifolium sibiricum* (L.) Kitam. | – | – | – | – | 1,1 | 1,1 | 2.+ | – | – | – | 4,1 |
| *Spiraea aquilegifolia* Pall. | – | – | – | – | 4.+ | 1.r | 2,1 | 5,2 | 1.+ | – | 2.r |
| *Geranium pseudosibiricum* I. Mayer | – | – | – | – | – | – | – | 3,1 | 1,2 | – | – |
| *Sedum aizoon* L. | – | – | – | – | 2.+ | – | 1.+ | 4,r | – | – | 4,1 |
| *Carex korshinskyi* Kom. | – | – | 1.+ | 1.+ | 3.+ | 1,1 | 2.+ | 3,1 | 2.+ | 1.+ | 2.r |
| *Allium leucocephalum* Turcz. ex Ldb. | – | – | – | – | 2.r | – | 1.+ | 3.r | – | 1.r | – |
| *Adenophora stenanthina* (Ldb.) Kitag. | – | – | – | – | 2.r | – | 1.+ | 4.r | 1.r | – | – |
| *Geranium pratense* L. | – | – | – | 1.+ | – | – | – | 3.+ | 5,3 | 5,1 | – |
| *Sanguisorba officinalis* L. | 2,2 | – | – | 1.+ | 1.r | – | 1.+ | 4,1 | 5,2 | 5.+ | – |
| *Thalictrum simplex* L. | 2.+ | – | – | – | – | – | – | 2,1 | 3.+ | 4.+ | 2.r |
| *Phlomis tuberosa* L. | – | – | – | 1.+ | 1,1 | – | 1,1 | 5,1 | 2.+ | 3.+ | – |
| *Medicago falcata* L. | 1.+ | – | – | 1.+ | – | – | – | 2.+ | 3,2 | – | – |
| *Artemisa laciniata* Willd. | 1.+ | – | – | – | – | – | – | – | 2.r | 3.r | – |
| *Aconitum barbatum* Pers. | – | – | – | – | – | – | – | – | 2.+ | 3.+ | – |
| *Agrimonia pilosa* Ldb. | – | – | – | – | – | – | – | – | 2.+ | 2.+ | – |
| *Elymus dahuricus* Turcz. ex Griseb. | – | – | – | – | – | – | 1,1 | 2,1 | 4.+ | 3.+ | – |
| *Geum aleppicum* Jacq. | – | – | – | – | – | – | – | 2.+ | 2.+ | – | – |
| *Vicia cracca* L. | – | – | – | – | – | – | – | – | 2.+ | 4.+ | – |
| *Campanula glomerata* L. | – | – | – | 1.r | – | – | – | 3.r | 4.+ | 3.r | – |
| *Valeriana officinalis* L. | – | – | – | – | – | – | – | 2.r | 2,1 | 3.+ | – |
| *Vicia amoena* Fisch. | 1.r | – | – | 1.+ | 1.r | – | 1.+ | 3,1 | 3.+ | 1.r | 2.r |
| *Bromus inermis* Leyss. | – | – | – | – | 1.+ | – | 1.+ | 3.+ | 1.+ | 1.+ | – |
| *Cotoneaster melanocarpa* Lodd. | – | – | – | – | 2.+ | – | 2.r | 4,3 | 2,1 | 5,1 | 5,1 |
| *Rosa acicularis* Lindl. | – | – | – | – | – | – | – | 2,r | 3,1 | 4.+ | 2,1 |

*Table 1.* Continued

| Vegetation type | Iris | Achn | Art-Stipa | Th-Stipa | Amygd | F. len | F. sib | Spiraea | Geran | Betula | Borolj |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of relevés | 13 | 6 | 35 | 46 | 14 | 24 | 14 | 4 | 5 | 5 | 3 |
| *Betula platyphylla* Sukacz. | - | - | - | - | - | - | - | - | 1.+ | 5,3 | 4,2 |
| *Spiraea media* F. Schmidt | - | - | - | - | - | - | - | 2,2 | 2.+ | 4,1 | 4,1 |
| *Populus tremula* L. | - | - | - | - | - | - | - | - | 3,1 | 2.r | |
| *Lathyrus humilis* (Ser.) Spreng. | - | - | - | - | - | - | - | - | - | 3.+ | - |
| *Crataegus sanguinea* Pall. | - | - | - | - | - | - | - | - | - | 2.+ | - |
| *Chamaenerion angustifolium* (L.) Scop. | - | - | - | - | - | - | - | - | 2,2 | 4,2 | - |
| *Rubus saxatilis* L. | - | - | - | - | - | - | - | - | 1,2 | 3,1 | - |
| *Calamagrostis* sp. Adans. | 1,2 | - | - | - | - | - | - | - | 1.+ | 2.+ | - |
| *Poa angustifolia* L. | - | - | - | - | - | - | - | - | - | 3,2 | - |
| *Artemisia changaica* Krasch. | 1.+ | - | - | 1.r | - | - | - | - | 2.+ | 3.+ | - |
| *Betula fusca* Pall. ex Georgi | - | - | - | - | - | - | - | - | - | 1.+ | 5,3 |
| *Saxifraga spinulosa* Adams | - | - | - | - | - | 1.+ | 1,1 | 2.+ | - | - | 5,1 |

The influence of ground water is periodic and no flooding occurs. The vegetation cover is not closed (60–80% cover). The dominant species, the coarse tussock grass *Achnatherum splendens*, is characteristic for these circumstances of fluctuating ground water level. The soils are mostly of alluvial or colluvial origin and have a fine texture with a grey colour. Livestock grazing pressure often is high, although *Achnatherum splendens* itself is only sparsely grazed, mainly by horses.

The *Achnatherum splendens*-community covers the transition between the streamside *Iris lactea*-community and the surrounding steppe vegetation, especially the *Artemisia adamsii-Stipa krylovii*-community. Aside from the name-giving, dominant species itself the community is poorly defined by its species composition. The drier conditions appear to favour the occurrence of steppe species as *Stipa krylovii, Carex duriuscula, Elymus chinensis, Potentilla bifurca, Artemisia adamsii* and *Heteropappus altaicus*. However, its characteristics physiognomy and topographical position appear to warrant the recognition of the *Achnatherum splendens*-community as a separate vegetation type.

Hilbig (1990) has described a similar vegetation as *Glycyrrhizo-Achnatheretum splendentis*. This type is also poorly characterized botanically, and again rather defined by the dominant species and landscape characteristics. The difference between Hilbig's type and the present one is that the former has been described especially from the desert and semi-desert zone. This, and our lack of relevés, may be the reason that its (weak) diagnostic species (*Lactuca tatarica, Glycyrhhiza uralensis, Polygonum sibiricum, Nitraria sibirica* and *Elymus secalinus*; presence class 2–3) have not been observed in the present study.

*Artemisia adamsii-Stipa krylovii-lowland steppe*

The lowland steppe is the most widespread community in the study area. It is found on the dry footslopes of mountainous areas and on rolling plains. The soils are kastanozems with a variable soil texture from loamy to gravel. The vegetation is open (40–80% cover) and dominated by the bunch-grass *Stipa krylovii* and two species of *Artemisia, A. adamsii* and *A. frigida*. Legume dwarf-shrubs *(Caragana pygmaea* and *C. microphylla)* are usually present and may locally reach a cover of 15%. Other typical species are *Heteropappus altaicus, Chamaerhodos erecta, Cleistogenes squarrosa* and *Agropyron cristatum*. The community is grazed intensively by livestock. Overgrazing leads to degradation of the vegetation cover, increased erosion and the spreading of, notably, *Artemisia adamsii* and *Carex duriuscula*.

The *Artemisia adamsii-Stipa krylovii*-community has also been distinguished by Hilbig & Knapp (1983), but Hilbig (1990) has described it as *Cymbario-Stipetum krylovii*. This association includes a number of distinct vegetation types which have been termed subassociations. The community distinguished in this study would belong to the typical subassociation.

*Thermopsis lanceolata-Stipa krylovii-upland steppe*

The upland steppe is generally situated on footslopes and slopes at a higher elevation than the lowland steppe. At lower altitudes it occurs more frequently on the north slopes than higher up. The general conditions regarding topography and soil are similar to the lowland steppe, but the higher elevation appears favourable for the soil moisture regime. The vegetation cover ranges between 45 and 90% and the average cover of 70% is 10% higher than in the lowland steppe. The upland steppe is also grazed heavily by livestock. It is often used as a place for winter camps by nomad pastoralists. Abandoned camp sites can often be recognized by the dominance of *Elymus chinensis*. Areas with a high crop of grasses, especially *Elymus chinensis* and *Stipa grandis*, are often mown at the end of the growing season for the provision of winter fodder. Furthermore, the upland steppe is a main habitat of the bobak marmot *(Marmota bobak)*.

The species composition of the upland steppe shows many similarities to the lowland steppe, but it is well differentiated from it by a species group with *Poa attenuata, Koeleria macrantha, Thermopsis lanceolata, Pulsatilla* spp. *(P. ambigua, P. bungei, P. flavescens, P. turczaninovii), Veronica incana, Potentilla tanacetifolia, Erysimum flavum, Bupleurum* sp. *(B. bicaule* or *B. scorzonerifolia)* and *Heteropappus biennis* (Table 1). *Stipa grandis* is specific to this community but it occurs only locally.

The upland steppe does not fit clearly in the steppe communities described by Hilbig (1990). Its general species composition can be related to the *Stipa grandis*-steppe (which is only mentioned by Hilbig from Russian studies), the *Galium verum*-subassociation of the *Cymbario-Stipetum krylovii* and the *Filifolio sibirici-Stipetum krylovii*, however, *Stipa grandis* is often absent and *Galium verum* and *Filifolium sibiricum* do not or scarcely occur at all in the upland steppe. This does suggest that the *Thermopsis lanceolata-Stipa krylovii*-community is a distinct vegetation type.

*Caryopteris mongholica-Amygdalus pedunculata-shrubland*

The *Amygdalus*-shrubland is widespread on south slopes with stony and rocky soils. It is also developed on the flanks of erosion gullies. The coarse texture of the soil, which develops into shallow kastanozems, enhances the infiltration rate of precipitation. This is probably a decisive advantage for the establishment of shrubs, such as *Amygdalus pedunculata* and *Spiraea aquilegifolia*. Total vegetation cover is often low (30–80%), with a mean cover of 30% for herbs, 25% for shrubs and 15% for dwarf-shrubs *(Caryopteris mongholica, Caragana pygmaea* and *C. microphylla)*. The shrubland is not used frequently by livestock, but red deer visit it regularly (Germeraad *et al.* 1993).

The *Amygdalus*-shrubland is characterized by a separate species group, with *Amygdalus pedunculata, Stipa sibirica* and *Caryopteris mongholica* as the most distinctive species (Table 1). Its southerly exposition explains the occurrence of many lowland and upland steppe species. Yet, at altitudes higher than 1450 m species from the mountain steppe become more abundant, e.g. *Festuca sibirica, Galium verum, Serratula centauroides* and *Schizonepeta multifida*.

Hilbig (1990) has described the *Amygdalus*-shrubland as *Amygdalo pedunculatae-Spriaeetum aquilegifolia*. It is considered to be a degraded form of the *Ulmus pumila*-bush forest *(Spiraeo aquilegifoliae-Ulmetum pumilae)* (Hilbig & Knapp 1983; Hilbig 1987, 1990). In Hustain Nuruu *Ulmus pumila* only occurs along erosion gullies but is absent from the slopes.

*Festuca lenensis-mountain steppe*

This community can be readily recognized in the field by the blue-grey hue it confers to dry mountain ridges and upper slopes. This colour is due to the dominance of the short bunch-grass *Festuca lenensis*, which is accompanied by cushion- and rosette-forming species. Dwarf-shrubs (mainly *Caragana pygmaea*) rarely cover more than 5%. The total vegetation cover averages 60% (range 40–100%). Soils from the *F. lenensis*-mountainsteppe are kastanozems with a top soil consisting mainly of gravel. Signs of erosion usually accompany the occurrence of the community at a lower

*Table 2*. Vegetation type characterization by landscape features in Hustain Nuruu. (Exp. = exposition, F = fine, G = gravel)

| Vegetation types | Formation | Landscape | Altitude (m) | Exp. | Soil colour | Soil texture |
|---|---|---|---|---|---|---|
| 1. *Iris lactea* | Meadow | Streamside | 1100–1400 | – | Black | Mixed |
| 2. *Achnatherum splendens* | Tussock grassland | Valley terrace | 1100–1400 | – | Grey | Fine |
| 3. *Artemisia adamsii-Stipa krylovii* | Lowland steppe | Footslope | 1100–1400 | (S) | Brown | F/G |
| 4. *Thermopsis lanceolata-Stipa krylovii* | Upland steppe | Footslope | 1300–1500 | (S) | Brown | F/G |
| 5. *Caryopteris mongholica-Amygdalus pedunculata* | Shrubland | Rocky slope | 1300–1600 | S | Brown | Stony |
| 6. *Festuca lenensis* | Mountain steppe | Ridge & topslope | >1300 | – | Brown | Gravel |
| 7. *Festuca sibirica* | Mountain steppe | Mountain slope | >1400 | N | Dark | Fine |
| 8. *Spiraea aquilegifolia* | Shrubland | Gully | 1100–1600 | – | Dark | Gravel |
| 9. *Geranium pratense* | Meadow | Combe | >1300 | – | Black | Mixed |
| 10. *Betula platyphylla* | Woodland | Mountain slope | >1400 | N | Black | Fine |
| 11. *Betula fusca* (Borolj) | Scrub | Topslope | >1400 | N | Dark | Gravel |

elevation. Yet, with the exception of horses, it seems to be sparsely visited by livestock.

The *F. lenensis*-mountain steppe is distinguished not only by *F. lenensis* but also by other low-growing species as *Chamaerhodos altaica, Androsace incana, Arenaria capillaris, Amblynotus rupestris, Potentilla sericea* and *Orostachys spinosa* (Table 1). It usually lacks species from the lower steppe (*Stipa krylovii*- and *Chamaerhodos erecta*-species groups) and only occasionally numbers species from the moister mountain steppe (*Festuca sibirica*-species group).

Hilbig (1990) has classified this community as an *Arctogeron gramineum*-subassociation of the *Cymbario-Stipetum krylovii*, mentioned earlier as the equivalent of the *Artemisia adamsii-Stipa krylovii*-community. The resemblance with Hilbig's single mountain steppe association *Hedysaro inundati-Stipetum krylovii* is only fragmentary. yet, the *F. lenensis*-mountain steppe is clearly recognized in Russian-Mongolian studies (Yunatov *et al.* 1979). This distinction appears justified when considering its specific species composition in Table 1.

### *Festuca sibirica-mountain steppe*

The *Festuca sibirica*-community represents the second type of mountain steppe distinguished in this study. It is found on northern mountain slopes higher than 1400 m. The northerly exposition and the occurrence of permafrost nearer to the ground surface ensure a better water supply. On deeper soils with a finer texture the greater biological activity under these conditions leads to the development of chernozems. The vegetation is rich in herbs and is typically dominated by the tussocks of *F. sibirica. Spiraea aquilegifolia* occurs locally, especially on sites with an improved water infiltration due to a coarser soil texture or to burrowing activities by bobak marmots. Seedlings of *Betula platyphylla* sometimes establish successfully in this mountain steppe. Total vegetation cover ranges mostly between 60–80%. The *Festuca sibirica*-community is one of the main habitats for red deer (Germeraad *et al.* 1993). It appears to be rarely grazed by livestock.

As in the *F. lenensis*-mountain steppe, species from the lower steppe are generally absent from the *F. sibirica*-mountain steppe. The latter community is differentiated form the former by the presence of *F. sibirica, Carex pediformis, Stellera chamaejasme, Galium verum, Leontopodium leontopodioides, Serratula centauroides, Scabiosa comosa, Schizonepeta multifida* and *Filifolium sibiricum.*

The *F. sibirica*-mountain steppe again does not fit the mountain steppes described by Hilbig (1990). When compared to Hilbig's classification, the community would be intermediate between the *F. sibirica*-community from relatively dry rubble slopes and the association *Thalictro petaloidei-Helictotrichetum schelliani* from the relatively moist meadow steppe. Although in some sites with an exceptionally good water supply the species composition from the *F. sibirica*-mountain steppe approaches that of the meadow steppe, it generally occupies drier locations, but rarely occurs on rubble.

*Spiraea aquilegifolia-shrubland*

The vegetation of erosion gullies often consists of a gallery of shrubland, with *Spiraea aquilegifolia* and *Cotoneaster melanocarpa* as dominant shrubs. The gullies are typically steep-sided with a coarse soil texture which rapidly absorbs water. The streambed is therefore generally dry, with the exception of a few permanent streams. Still, the water flow underground guarantees a relatively favourable water supply. Total vegetation cover is high (80–100%), with a shrub cover averaging 60%.

The *Spiraea aquilegifolia*-shrubland is characterized by *Spiraea aquilegifolia, Geranium pseudosisibiricum, Sedum aizoon, Carex korshinskyi, Allium leucocephalum* and *Adenophora stenanthina*. It contains species from both the mountain steppe (*Festuca sibirica*-group) and the mountain meadows (*Geranium pratense*-group) (Table 1). With the exception of *Elymus repens* species from the lower steppe are lacking. This also applies to species from the *Amygdalus pedunculata*-group (except for *Stipa sibirica*). In places the shrubs are accompanied by *Ulmus pumila* trees, which sometimes give the appearance of a narrow gallery forest.

The *Spiraea aquilegifolia*-community shows the closest affinity to Hilbig's (1990) *Spiraeo aquilegifoliae-Ulmetum pumilae*. Relevés with *Ulmus pumila* have not been included in the present analysis, but field observations suggest that stands which include the species do not greatly differ in species composition. In contrast to the association described by Hilbig, the *Spiraea aquilegifolia*-community appears restricted to the vicinity of gullies and does not reach the drier slopes.

*Geranium pratense-meadow*

Meadows of the *Geranium pratense*-community are found in combes, valley bottoms and streamsides above 1300 m. These have a mixed soil texture, as in the *Iris lactea*-meadows from lower ranges. The soils are classified as chernozems. The constant water supply gives a luxurious aspect to the vegetation, which is dominated by tall herbs (70–100% cover). Shrubs like *Cotoneaster melanocarpa* and *Dasiphora fruticosa* sometimes spread into the meadows. Wild boar appear to favour this community for foraging (often uprooting plants) and making wallows. The meadows are sometimes used for hay-making. At lower elevations overgrazing by livestock may transform the vegetation into an *Iris lactea*-meadow.

The *Geranium pratense*-meadow is characterized by one large species group, containing *Geranium pratense, Sanguisorba officinalis, Thalictrum simplex, Medicago falcta, Elymus dahuricus, Campanula glomerata, Vicia amoena* and *Rosa acicularis* as the most steady representatives. Species from the *Geranium pratense*-group also extend into the *Betula*-woodland and the *Spiraea*-shrubland. Steppe species are virtually absent from this community.

The *Geranium pratense*-community can be placed in the *Aconito-Angelicetum decurrentis* association described by Hilbig (1990).

*Betula platyphylla-woodland*

In Hustain Nuruu birch woodlands are concentrated in two locations. They occupy the north slopes from 1400 m upwards in a mosaic together with *Festuca sibirica*-mountain steppes. In the woodland sites, which are often littered with granite blocks, the permafrost layer reaches closest to the soil surface. The summer thawing guarantees a high soil moisture content, leading to the formation of black soils with a high organic matter content (Succow & Kloss 1978). The tree canopy of the birch woodlands is rather open (45–70% cover) and varies between 5–15 m in height. It is dominated by *Betula platyphylla* and *Populus tremula*. The shrub layer (5–50% cover) consists predominantly of *Cotoneaster melancarpa, Spiraea media* and *Rosa acicularis*. The herb layer has a variable cover, averaging 35%. The wild ungulates concentrate in the woodlands to seek shelter, water, wallows and browse (Germeraad *et al.* 1993). Deer browsing pressure is particularly heavy on *Cotoneaster melanocarpa* and saplings of *Populus tremula*. The woodlands of Hustain Nuruu are shrinking due to wood-cutting, although this threat should diminish with the implementation of protection measures.

*Crataegus sanguinea* and *Rubus saxatilis* can be cited as characteristic woody plants for the *Betula platyphylla*-woodland in addition to those mentioned above. Among the herbaceous plants *Lathyrus humilis, Chamaenerion angustifolium, Poa angustifolia* and *Artemisia changaica* are typical to the birch woodland. Furthermore, species from the *Geranium pratense*-group are also frequently present.

Hilbig (1990) has grouped the birch woodlands in the *Betulo platyphyllae-Populetum tremulae* association. They are either considered as an edaphically determined climax or as a degraded larch forest *(Geranio-Laricetum)* under the influence of logging, fires and grazing (Hilbig 1987, 1990). No evidence of a former presence of *Larix sibirica* in Hustain Nuruu was found. Two saplings of a second conifer, *Pinus sylvestris*, were recorded from a gully side and a birch woodland fringe on granite boulders; one dead old tree was found standing at the edge of another woodland.

*Betula fusca-scrub*

The *Betula fusca*-scrub ('borolj' in Mongolian) occurs on topslopes above 1400 m with a north exposition. The scrub is often associated with birch woodland but is also found in isolated patches on dark gravel soils with granite boulders. The dense scrub is a favourite shelter for red deer and wild boar.

Too few relevés (3) have been made to give an accurate botanical characteristic of the community. *Betula fusca, Cotoneaster melanocarpa* and *Saxifraga spinulosa* (typical for exposed boulders) were present in all relevés. The species occurring in two of the three relevés are characteristic for woodland *(Betula platyphylla* and *Spiraea media)* and mountain steppe *(Koeleria macrantha, Festuca lenensis, Potentilla sericea, Polygonum angustifolium, Carex pediformis, Stellera chamaejasme, Filifolium sibiricum, Sedum aizoon* and *Poa botryoides).*

The borolj has not been described by Hilbig (1990) and does not seem to fit in this classification. Hilbig does recognize a *Betula fusca*-scrub, but from peaty valley bottoms instead of topslopes. The drier conditions, the presence of mountain steppe species and the absence of meadow (steppe) species also distinguish the community from Hilbig's *Spiraeo mediae-Cotoneasteretum melanocarpae*, which usually occurs as a degraded form of the larch forest. The present community would rather be an equivalent of the subalpine *Betula fruticosa-* and *B. exilis*-scrub mentioned by Hilbig (1990) and Yunatov *et al.* (1979).

## Discussion and conclusions

*Classification of Mongolian plant communities*

Hilbig (1990) has provided the most recent extensive account of Mongolian plant communities. Although 54 of these have been described well enough to accord them the status of associations, a lack of material has not allowed this for many other communities. The vegetation types emerging from the present study contribute to a better understanding of the geobotany of the forest-steppe in Mongolia. Problems with the identification of certain plant species have unfortunately reduced the accuracy of certain relevés. Thus, the status of quite a few species mentioned in the appendix and some species in Table 1 needs clarification; this matter will be addressed in the near future. Further investigations should also shed more light on the identity of some sparsely studied communities. Yet, the present material allows some definite conclusions. Six of the recognized communities confirm the existence of corresponding associations proposed and described by Hilbig (1990), namely the *Halerpestidi-Hordeetum brevisubulati, Cymbario-Stipetum krylovii, Amygdalo pedunculatae-Spiraeetum aquilegifoliae, Spiraeo aquilegifoliae-Ulmetum pumilae, Aconito-Angelicetum decurrentis* and *Betulo platyphyllae-Populetum tremulae* associations. The five other vegetation types indicate that a refinement or extentsion of the classification system is desirable. This mainly concerns the steppe(-related) communities.

The *Achnatherum splendens*-tussock grassland is not truly compatible with the *Glycyrrhizo-Achnatheretum splendentis*. In Hustain Nuruu the community is accompanied by many species from the lowland steppe. It may be that the distinction of a separate steppe subassociation is needed, in analogy to the subdivision followed by Yunatov *et al.* (1979).

The *Thermopsis lanceolata-Stipa krylovii*-upland steppe appears to merit a separate position as an intermediate type between the lowland and the mountain steppe communities. The differentiation with the mountain steppe is sufficiently defined by the different species groups in Table 1. However, the distinction between lowland and upland steppe is less clear, depending only on the *Poa attenuata*-species group. The possibility remains that the difference between the two is not due to a difference in altitude and exposition (viz. moisture regime) but to an impoverishment of the lowland steppe through overgrazing. Present exclosure experiments will perhaps provide an answer to this question.

The *Festuca lenensis-* and *F. sibirica*-mountain steppe communities are readily distinguished in the field by their different environmental location, soil properties and species composition. The difference between the two is therefore not merely a matter of dominant species. As the abundance of *Stipa* species in the two communities is low, we suggest that a reconsideration of their relation to typical *Stipa*-communities is necessary.

Finally, we have tentatively described a new type of *Betula fusca*-scrub or borolj from relatively dry top-slopes. The montane and subalpine birch scrub still awaits a better classification. It is possible that the presented type of *Betula fusca*-scrub is specific to the subalpine zone of lower mountain ranges like Hustain Nuruu. The dominant occurrence of *Betula fusca* in such different environments as peat bogs (as described by Hilbig 1990) and the subalpine zones does appear unlikely. However, it has an equivalent in *Pinus mugo* Turra, which occupies the same position in central Europe (Ellenberg 1982).

*On the distribution of forest and grassland in the forest-steppe zone*

The description of vegetation communities in Hustain Nuruu shows that grassland, shrubland and woodland are distributed in a mosaic over the landscape, in dependence of environmental conditions. There seems to be no doubt that the ecotopes of the *Chamaerhodos-Stipa, Thermopsis-Stipa* and *Achnatherum* communities exclude a succession towards woodland, the soils being too dry and the water infiltration rate too low. The *Festuca lenensis*-community may be the result of degradation through erosion on lower sites, but it is likely to be a climax on exposed slopes and ridges, where both climate and natural erosion are unfavourable to the establishment of trees. Thus, steppe (with a small proportion of tussock grassland) would dominate at least 75% of the Hustain Nuruu landscape under natural conditons. In the area covered by the remaining seven communities trees play a potentially larger role.

In certain areas *Salix* bushes can be found alternating with *Iris lactea*-meadows along the Tuul river. In the Khangay and Khentei mountain ranges these have the potential to develop into riparian *Populus* forests (Hilbig 1987, 1990). The drier conditions and higher soil salinity around Hustain Nuruu may well prevent this development. Flooding, ice flow and heavy grazing pressure present further checks to the establishment of woodland. Although livestock densities nowadays probably exceed those of original wild ungulates, it is likely that herbivory in these comparatively productive sites would also affect the vegetation succession under natural conditions, presumably leading to a park-like distribution of meadow and bushes.

According to Hilbig (1987, 1990) a spreading of *Ulmus pumila* might be expected in the *Caryopteris-Amygdalus* and *Spiraea* shrubland communities (estimated actually at 13% and < 1% of the Hustain Nuruu area respectively) with a reduction of wood-cutting and livestock pressure. In these sites the high water infiltration rate and the availability of ground water around gullies favours the establishment of trees. The formation of *Ulmus*-gallery woodland, with an occassionally dense shrub layer, is presently restricted to a small number of gullies. While we do envisage an extension of the gallery woodland in *Spiraea*-shrubland under a more extensive land-use, we deem it less likely that *U. pumila* will dominate the *Caryopteris-Amygdalus*-shrubland of the southern slopes. Hustain Nuruu is located at the drier edge of the forest-steppe, where it appears that the presence of ground water limits the distribution of trees. Thus, *Ulmus*-woodland would be restricted to less than 1% cover of the Hustain Nuruu territory. In forest-steppe areas with higher rainfall *U. pumila* should potentially have a larger share.

Ground water is usually available in sites covered by *Festuca sibirica*-mountain steppe and *Geranium*-meadow. Establishment of tree seedlings, especially *Betula platyphylla*, has been observed here repeatedly. In the absence of wood-cutting and grazing these communities would therefore probably revert mostly to woodland. As even the actual numbers of wild ungulates, which have been subject to hunting and poaching, do have a clearly visible impact on these vegetation types, it can be expected that natural levels of herbivory and disturbance (uprooting, wallowing) will maintain open areas on preferred locations.

Borolj and *Betula*-woodland actually cover an estimated 5% of the Hustain Nuruu area. A large fraction of borolj is situated on locations which appear suitable for the development of *Betula*-woodland. The natural occurrence of borolj would probably be restricted to high-montane and subalpine sites where climate and soil conditions check a further succession to woodland. It may be wondered whether *Betula*-woodland is the climax community on the north slopes in Hustain Nuruu. Less than 100 km east of Hustain Nuruu, larch forests *(Geranio pseudosibirici-Laricetum)* dominate between 1500–1800 m in the Bogd-uul reserve in conjunction with *Pinus sibirica*- and *Picea obovata*-forests (Hilbig & Knapp 1983). The latter species belong to the boreal dark taiga, but *Larix sibirica* also extends into the forest-steppe. *Betula*-woodlands within the range of *L. sibirica* are mostly degraded larch forests. If *L. sibirica* occurred in Hustain Nuruu, it must have disappeared in former times under growing land-use pressure. A similar case is presented by *Pinus sylvestris*, from which a few individuals remain. Experimental studies could reveal whether these conifers can establish successfully. However, it may well be that conditions in Hustain Nuruu are too marginal for conifers. In that case the *Betula*-woodland would represent a climax community from moist sites in the dry forest-steppe. Nimis *et al.* (1994) have argued that a comparable climax *Betula*-woodland occurs in southwestern Siberia as an extension to the European deciduous forest belt.

Considering all suitable locations, *Betula*-woodland and a minor share of *Ulmus*-gallery woodland could potentially cover ca. 10–12% of the mountain range. It has been argued that the natural vegetation of ca. 88% of Hustain Nuruu consists of steppe, tussock grassland and shrubland. The predominance of natural grassland provides suitable conditions for the build-up of large concentrations of wild ungulates, comparable to those of today's livestock but probably in lower numbers. It can be hypothesized that the 12% of the study area suitable for woodland growth would still be subject to a heavy herbivore impact under natural conditions. Woodland extension would then show a dynamic equilibrium somewhere between the actual 5% and the potential 12%. In forest-steppe areas with higher rainfall, the proportion of woodland tends to be greater, but the factors determining the distribution of grassland and forest should remain the same. This hypothesis may become testable by experimental study in a recreated natural setting.

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*Appendix*. Occassional species not included in the synoptic table. The first figure in a cell indicates the presence class, the second gives the mean cover class when the species is present (Abbreviations of vegetation types in Table 1)

| Vegetation type | Iris | Achn | Art-Stipa | Th-Stipa | Amygd | F. len | F. slib | Spiraea | Geran | Betula | Boroij |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Achillea asiatica* Serg. | – | – | – | – | – | – | – | – | 1.+ | – | – |
| *Achillea millefolium* L. | – | – | – | – | – | – | – | – | 3.+ | – | – |
| *Agrostis trinii* Turcz. | – | – | – | – | – | – | 2.+ | – | – | – | – |
| *Allium anisopodium* Ldb. | – | – | 1.r | 1.+ | 2.r | 1.+ | 1.+ | – | – | – | – |
| *Allium bidentatum* Fisch. ex Prokh. | – | – | 1.r | 1.+ | – | 1.r | – | – | – | – | 2.r |
| *Allium eduardii* Stern | – | – | – | 1.+ | 1.r | – | – | – | – | – | – |
| *Allium odorum* L. | – | – | – | 1.r | 1.+ | – | – | – | – | – | – |
| *Allium prostratum* Trev. | – | – | 1.+ | – | – | – | – | – | – | – | – |
| *Allium senescens* L. | – | 1.+ | 1.+ | – | 2.r | – | – | – | 1.r | – | – |
| *Allium* sp. L. | – | – | 1.r | 1.+ | 1.r | 1.+ | 2,1 | – | – | – | – |
| *Alyssum lenense* Adams | – | – | – | – | 1.+ | 1.+ | 1.+ | – | – | – | – |
| *Alyssum obovatum* (C.A. Mey.) Turcz. | – | – | 1.r | – | – | 1,1 | 1.r | – | – | – | – |
| *Androsace septentrionalis* L. | – | – | – | 1.r | – | – | 1.+ | – | – | – | 2.r |
| *Androsace* sp. L. | – | – | – | 1.r | 1.+ | 1.r | – | – | – | – | 2.r |
| *Arctogeron gramineum* (L.) DC. | – | – | – | – | 1.r | 1.r | – | – | – | – | – |
| *Artemisia dracunculus* L. | 1.+ | – | – | 2,1 | – | – | – | 2,1 | – | – | – |
| *Artemisia glauca* Pall. | – | – | – | 1,1 | – | 1.+ | 1,1 | – | – | – | – |
| *Artemisia leucophylla* (Turcz. ex Bess.) Turcz. | – | 1.+ | 1.r | – | 1.+ | – | – | – | – | – | – |
| *Artemisia macrocephala* Jacquem. | 1,1 | – | 1.+ | – | 1.+ | – | – | – | – | – | – |
| *Artemisia monostachya* Bge. ex Maxim. | – | – | 1.r | – | 1.r | – | 2,1 | – | – | – | 2.+ |
| *Artemisia* cf. *palustris* L. | – | 1.+ | – | 1.+ | 1.r | – | – | – | – | – | – |
| *Artemisia pectinata* Pall. | – | 2.+ | 1.+ | – | – | – | – | – | – | – | – |
| *Artemisia rutifolia* Steph. ex Spreng | – | – | – | – | 1.r | 1.+ | – | – | – | – | – |
| *Artemisia scoparia* Waldst. et Kit. | – | 1.+ | – | 1.+ | 1,2 | – | – | – | – | – | – |
| *Artemisia* sp. L. | – | – | – | – | 1.+ | – | – | – | – | – | – |
| *Artemisia tanacetifolia* L. | – | – | – | – | 1.r | 2,1 | 2.+ | – | 1.+ | – | – |
| *Artemisia xantochroa* Krasch. | – | – | – | – | 1.+ | – | – | – | – | – | – |
| *Asparagus* sp. L. | – | – | – | – | 1.r | – | 1,1 | – | – | – | – |
| *Aster alpinus* L. | – | – | – | 1,1 | 1.+ | 2,1 | 2,1 | 1.r | 2.+ | – | 2.+ |
| *Astragalus adsurgens* Pall. | – | – | 1,1 | – | – | – | – | – | – | – | – |
| *Astragalus melilotoides* Pall. | – | – | – | – | – | 1,1 | – | – | – | – | – |
| *Astragalus* sp. L. | – | – | 1.r | 1,1 | 2,1 | 3.+ | 2,1 | 1.r | – | – | – |
| *Betula hippolytii* Sukacz. | – | – | – | – | – | – | – | – | – | – | 2.+ |
| *Blysmus* sp. Panz. ex Schult. | 1.+ | – | – | – | – | – | – | – | – | – | – |
| *Bromus* sp. L. | – | – | – | – | 1,1 | – | – | – | – | – | – |

*Appendix.* Continued

| Vegetation type | Iris | Achn | Art-Stipa | Th-Stipa | Amygd | F. len | F. slib | Spiraea | Geran | Betula | Boroij |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Caragana stenophylla* Pojark. | – | 1.r | 1.+ | – | – | – | – | – | – | – | – |
| *Carex delicata* Clarke | 1.+ | – | – | – | – | – | – | – | – | – | – |
| *Carex schmidtii* Meinsh. | 1,2 | – | – | – | – | – | – | – | – | – | – |
| *Carum carvi* L. | 1.r | – | – | – | – | – | – | 1.r | – | – | – |
| *Chenopodium album* L. | – | 1.r | – | – | – | – | – | – | – | – | – |
| *Chenopodium aristatum* L. | – | – | 1.r | 1.r | – | – | – | – | – | – | – |
| *Chrysanthemum zawadskii* Herb. | – | – | – | – | – | 1.+ | 2,1 | 1.r | – | – | 2.r |
| *Convolvulus ammanii* Desr. | – | 1.r | 1.r | 1.+ | 1.r | – | – | – | – | – | – |
| *Dasiphora fruticosa* (L.) Rydb. | – | – | – | – | – | – | 1.+ | – | – | – | 2.+ |
| *Delphinium grandiflorum* L. | – | – | – | – | 1.r | – | 1.+ | 1.r | – | – | 2.r |
| *Draba nemorosa* L. | – | – | – | 1,1 | – | – | – | – | – | – | – |
| *Dracocephalum foetidum* Bge. | – | – | 1.+ | – | – | – | 1.r | 2.+ | – | – | – |
| *Elymus gmelinii* (Ldb.) Tzvel. | – | – | – | – | 1.r | – | – | 2,1 | – | 2.+ | – |
| *Elymus secalinus* (Georgi) Bobr. | 1,1 | – | – | – | – | – | – | – | – | – | – |
| *Elymus sibiricus* L. | – | – | – | – | – | – | – | – | 2,1 | 1.r | – |
| *Elymus* sp. L. | 1.+ | 1.r | 1,2 | – | – | – | – | – | – | – | – |
| *Ephedra monosperma* G.G. Gmel. ex C.A. Mey. | – | – | 1.r | – | 1.+ | 1.+ | – | – | – | – | – |
| *Equisetum arvense* L. | 2,2 | – | – | – | – | – | – | – | – | – | – |
| *Erigeron* sp. L. | – | – | – | – | – | – | – | 1.r | – | – | – |
| *Euphorbia* sp. L. | – | – | – | 1.+ | – | – | 1.+ | – | – | – | – |
| *Euphrasia tatarica* Fisch. ex Spreng. | 2.+ | – | – | – | – | – | 1.r | 1.r | – | – | – |
| *Fagopyrum* sp. Gaertn. | – | – | – | 1.r | – | – | – | – | – | – | – |
| *Festuca rubra* L. | – | – | – | – | – | – | – | – | – | – | 2,2 |
| *Festuca* sp. L. | – | – | – | 1,1 | 1,1 | – | – | – | 1,1 | – | 2.r |
| *Galum boreale* L. | – | – | – | – | – | – | – | – | – | 1,1 | 2,1 |
| *Gentiana barbata* Froel. | 1.+ | – | – | – | – | 1.+ | 1.+ | 1.+ | 2.+ | – | 2.r |
| *Gentiana macrophylla* Pall. | – | – | – | – | – | – | – | 1.r | – | 1.r | 2.r |
| *Gentiana squarrosa* Ldb. | 1.r | – | – | 1.r | 1.+ | 1.+ | 1,1 | – | – | – | 2.r |
| *Glycyrrhiza uralensis* Fisch. | – | – | – | – | – | – | – | – | – | – | 2.+ |
| *Helictotrichon schellianum* Kitag. | – | – | – | – | – | – | 1,2 | – | 1.+ | 1,1 | 2.+ |
| *Heteropappus hispidus* (Thunbg.) Less. | – | – | – | 1.+ | – | – | – | – | – | – | – |
| *Hieracium* sp. L. | – | – | – | – | – | – | – | – | – | 1.+ | – |
| *Inula britannica* L. | 1.+ | – | – | – | – | – | – | – | 2.+ | – | – |
| *Iris ruthenica* Ker. Gawl. | – | – | – | 1.r | 1.r | – | 1,2 | – | – | – | – |
| *Iris tenuifolia* Pall. | – | – | – | – | 1.r | – | – | – | – | – | – |
| *Iris tigrida* Bge. | – | – | – | 1.+ | 1.+ | 1.+ | – | – | – | – | – |
| *Juncus bufonius* L. | 1.+ | – | – | – | – | – | – | – | – | – | – |

*Appendix*. Continued

| Vegetation type | Iris | Achn | Art-Stipa | Th-Stipa | Amygd | F. len | F. slib | Spiraea | Geran | Betula | Boroij |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Juncus* sp. L. | 2.+ | – | – | – | – | – | – | – | – | – | – |
| *Kochia prostrata* (L.) Schrad. | – | – | 1.r | 1.r | 1.+ | – | – | – | – | – | – |
| *Koeleria altaica* (Domin) Kryl. | – | – | – | – | – | – | 1.+ | – | – | – | – |
| *Lactuca* cf. *sibirica* Benth. ex Maxim. | – | – | – | – | – | – | – | – | 2,2 | – | – |
| *Lactuca* sp. L. | – | – | – | – | 1.r | – | 1.+ | – | – | – | 2.+ |
| *Lappula myosotis* Moench | – | – | – | 1.+ | – | – | – | – | – | – | – |
| *Lepidum ruderale* L. | 1,1 | – | – | – | – | – | – | – | – | – | – |
| *Lespedeza dahurica* (Laxm.) Schindl. | – | – | – | – | 2.+ | – | – | – | – | – | – |
| *Lilium pumilum* DC. | – | – | – | – | 2.+ | – | 1.r | – | – | – | – |
| *Limonium flexuosum* (L.) Ktze. | – | – | – | – | – | 1.+ | – | – | – | – | – |
| *Linaria acutiloba* Fisch. ex Reichb. | – | – | – | – | – | – | – | 2.+ | – | – | – |
| *Linaria* sp. Mill. | – | – | – | – | 2.+ | – | – | – | – | – | 2.+ |
| *Linum sibiricum* DC. | – | – | – | 1.+ | – | 1,1 | – | – | – | – | – |
| *Lomatogonium carinthiacum* (Wulf.) A. Br. | 1.+ | – | – | – | – | – | 1.+ | – | – | – | – |
| *Medicago ruthenica* (L.) Ldb. | – | 2.r | 1.r | 1.r | – | 1,2 | – | – | – | – | – |
| *Myosotis* sp. L. | – | – | – | 1,1 | – | 1.+ | 1,1 | 1,1 | – | – | – |
| *Odontites rubra* (Baumg.) Pers. | 1,1 | – | – | – | – | – | – | – | – | – | – |
| *Orchis salina* Turcz. | 1.+ | – | – | – | – | – | – | – | – | – | – |
| *Orostachys fimbriata* (Turcz.) Berger | – | – | 1.r | 1.+ | – | – | – | – | – | – | – |
| *Orostachys malacophylla* (Pall.) Fisch. | – | – | – | 1.r | 1.+ | 1.+ | 1.+ | – | – | – | – |
| *Oxytropis filliformis* DC. | – | – | – | 1.+ | – | 1,1 | – | – | – | – | – |
| *Oxytropis salina* Voss. | 2.r | – | – | – | – | – | – | – | – | – | – |
| *Oxytropis* sp. DC. | 1.+ | – | 1.+ | 2.+ | 1.+ | 1.r | 2.+ | – | – | 1.r | 2.+ |
| *Papaver rubro-aurantiacum* (DC.) Fisch. ex Steud. | – | – | – | – | – | 1,1 | 1,1 | – | – | – | – |
| *Parnassia palustris* L. | 1.+ | – | – | – | – | – | 1.r | – | – | – | – |
| *Patrinia rupestris* (Pall.) Dufr. | – | – | – | – | 1.r | – | – | – | – | – | – |
| *Pedicularis flava* Pall. | – | – | – | 1.r | – | 1.+ | 1,1 | – | – | – | 2.+ |
| *Pediularis myriophylla* Pall. | – | – | – | – | – | 1,1 | 1,1 | – | – | – | – |
| *Pedicularis* sp. 1 L. | – | – | – | 1.+ | 1.+ | 2.+ | 2,1 | – | – | 1.r | – |
| *Pedicularis* sp. 2 L. | – | – | 1,1 | 1.r | 1.+ | – | 1,1 | 1.+ | – | 1.r | – |
| *Pedicularis striata* Pall. | – | – | – | 1.r | – | – | – | – | – | – | 2.r |
| *Peucedanum hystrix* Bge. | – | – | – | – | – | 1,1 | 1.+ | – | – | – | – |
| *Plantago* cf. *depressa* Willd. | 1,2 | – | 1.r | 1.+ | – | – | – | – | – | – | – |
| *Poa botryoides* Trin. | – | – | – | 1,2 | 1,2 | 1,1 | – | – | – | – | 4.+ |
| *Poa sibirica* Roshev. | – | – | – | – | – | – | – | – | – | – | 2,2 |
| *Poa subfastigiata* Trin. | 2,1 | – | – | – | – | – | – | – | – | – | – |
| *Polygala hybrida* DC. | – | – | – | 1.+ | 1,1 | – | – | – | – | – | 2.r |

*Appendix.* Continued

| Vegetation type | Iris | Achn | Art-Stipa | Th-Stipa | Amygd | F. len | F. slib | Spiraea | Geran | Betula | Boroij |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Polygonatum odoratum* (Mill.) Druce | – | – | – | – | – | – | – | – | – | 1.r | – |
| *Polygonum aviculare* L. | – | 2.r | – | – | – | – | – | – | – | – | – |
| *Polygonum sericeum* Pall. ex Georgi | – | – | 1.+ | – | – | – | – | – | – | – | – |
| *Polygonum* sp. L. | – | – | 1.+ | 1.+ | – | 1,1 | – | – | – | – | – |
| *Potentilla conferta* Bge. | – | – | 1.r | 1,1 | 1.r | 1.+ | 2.+ | – | – | – | – |
| *Potentilla* sp. L. | – | – | 1.r | – | – | 1.r | – | – | – | – | – |
| *Potentilla viscosa* G. Don | – | – | – | – | – | 1.+ | 1.+ | – | – | – | – |
| *Primula farinosa* L. | 1.+ | – | – | – | – | – | – | – | – | – | – |
| *Ptilagrostis* sp. Griseb. | – | – | – | – | – | – | 1.+ | – | – | – | – |
| *Ptilotrichum canescens* C.A. Mey. | – | – | – | 1.+ | 1.r | – | – | – | – | – | – |
| *Puccinellia tenuiflora* (Griseb.) Scribn. | 1.+ | – | – | – | – | – | – | – | – | – | – |
| *Rhodiola* sp. L. | – | – | – | – | 1.+ | – | – | – | – | – | – |
| *Ribes diacantha* Pall. | – | – | – | – | 1.r | – | – | – | – | – | – |
| *Ribes pulchellum* Turcz. | – | – | – | – | 1.+ | – | – | 1.r | – | 1.r | 2.r |
| *Rumex* sp. L. | 1.r | – | – | – | – | – | 1.r | – | 1.+ | – | – |
| *Salix* sp. L. | – | – | – | – | – | – | – | – | – | 1.r | – |
| *Salsola collina* Pall. | – | – | – | 1.r | – | – | – | – | – | – | – |
| *Saposhnikovia divaricata* (Turcz.) Schischk. | – | – | – | – | 1.+ | – | – | – | – | – | – |
| *Saussurea salicifolia* (L.) DC. | – | – | 1.r | 1.r | 2.+ | 1.r | – | – | – | – | – |
| *Scorzonera austriaca* Willd. | 1.r | – | – | – | – | – | 1,2 | – | – | – | – |
| *Scorzonera* sp. L. | – | – | 1.r | – | 1.r | – | – | – | – | – | – |
| *Scutellaria scordifolia* Fisch. ex Schrank | – | – | – | 1.+ | 1,1 | – | – | 1.r | – | – | – |
| *Senecio* sp. L. | – | – | – | – | – | – | 1.r | – | – | – | – |
| *Silene repens* Pstr. | – | – | – | – | – | – | – | 1.r | – | – | – |
| *Stellaria dichotoma* L. | – | – | – | 1.+ | 1.r | – | – | – | – | – | – |
| *Stellaria media* (L.) Cyr. | 1.r | – | – | – | – | – | – | – | – | – | – |
| *Thalictrum minus* L. | – | – | – | – | – | – | 1,1 | – | – | 1.+ | – |
| *Thalictrum squarrosum* Steph. ex Willd. | – | – | – | 1.r | 2.r | – | – | 1,1 | – | – | – |
| *Trifolium lupinaster* L. | – | 1.r | – | – | – | – | – | – | – | – | 4.+ |
| *Urtica cannabina* L. | 1.r | – | – | 1,1 | – | – | – | 1,1 | 2,1 | – | – |
| *Veronica longifolia* L. | – | – | – | – | – | – | – | – | 1.+ | 1.r | – |
| *Veronica* sp. L. | – | – | – | – | 1.r | – | – | – | – | – | – |
| *Youngia tenuifolia* (Willd.) Babc. et Stebbins | – | – | – | 1.r | – | – | 1.r | – | – | – | – |