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Vegetation types of East Ladakh: species and growth form composition along main environmental gradients

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Abstract

Question: The vegetation of high mountain regions in Himalaya remains poorly assessed despite the expected vulnerability of these ecosystems to global change drivers. What are the main vegetation types in East Ladakh and which environmental factors influence the species composition and growth forms distribution?

Location: The south-westernmost extension of the Tibetan Plateau, an arid mountainous area, in East Ladakh, Jammu & Kashmir State, India.

Methods: Species composition was recorded for 369 plots (each 100 m^2). Plots, sampled from 4180 m a.s.l. (bottom of the Indus Valley) up to 6060 m a.s.l. (close to the snowline), covered a wide range of environmental conditions.

Results: TWINSPAN clusters discriminated eight ecologically interpretable vegetation types, corresponding to the main habitats in the area: animal resting places, salt marshes, semi-deserts and steppes, shrublands, alpine screes and boulder fields, alpine grasslands, water bodies and subnival zone. The most important environmental factors influencing the species composition were altitude, soil moisture and salinity. Screes and alpine grasslands were found to be the most species-rich. The species were ranged into 20 growth forms with regard to life-form and clonality, with growth forms showing different changes in proportion among vegetation types and along the different environmental gradients.

Conclusion: The study summarizes the main vegetation types of East Ladakh in terms of species and growth form compositions. The results can have a heuristic value for designing future monitoring schemes and assess the effects of global change in these diverse, but poorly studied, regions.

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Introduction

On-going climate and land-use changes are increasingly affecting biodiversity in highly constrained environments such as mountain regions (Körner 2003). However, little is still known about the mechanisms by which different levels of diversity (taxonomic and functional) are distributed in space, what the response of these diversity components in the future could be and how to preserve them (Pauli et al. 2007).

In cold areas of Ladakh (Western Himalaya), more than 1180 vascular plant taxa occur according to the latest systematic floristic survey (Klimeš & Dickoré 2006). Although this checklist is preliminary and subspecies as well as cultivated and introduced plants are included, this number is much higher than those reported in previously published floras of the area, e.g. 611 species in Kachroo et al. (1977) and 880 species in Kachroo (1993). These traditional sources of information on species richness of Ladakh are still used by various researchers and in different national and international reports. However, this could result in greatly misleading interpretations of the potential conservation value of plant diversity in the area.

In particular, Northeast India is insufficiently explored in terms of floristic diversity and new vascular plant species are still being described (Al-Shehbaz 2002; Klimeš & Dickoré 2005; Kirschner et al. 2006; Klimeš & German 2008). The main reasons for this are probably the difficult accessibility and logistic problems along with political instability of the region. Description of local vegetation types is not only interesting as a scientific objective but also important for conservation. In the light of the changing climate, whose impacts are predicted to be most prominent in high mountains (Stone 1992) –

along with population increase, which puts a yet higher pressure on natural resources – it is necessary to describe more precisely the different existing vegetation types for future monitoring and conservational purposes.

This study aimed at describing the main vegetation types in the poorly known area of East Ladakh in the Trans-Himalaya, India, in terms of species composition and growth form distribution, and relateing these patterns to the changes in environmental factors. The area occupies an extensive plateau with a close relation to Tibet. Owing to its position in the rain-shadow of the Himalaya Range, the whole area receives very low precipitation ($<100\,mm\,yr^{-1}$), thus forming a high-altitude cold desert (Stewart 1916–1917; Negi 1995). The harsh environment of the area imposes great constraints on plants, which must cope with aridity, extreme diurnal temperature fluctuations, strong winds and abrasion, solifluction at the higher altitudes and salinity at the lower altitudes, nutrient-poor soils and a short growing season. Under such conditions, the productivity is generally very low and the vegetation is most often sparse. Nonetheless, large areas serve as grazing land for yaks, wild sheep and other mammals and host unique flora, with most plants utilized by local people for medicinal purposes (Ballabh & Chaurasia 2007). Owing to the remoteness and the low population, the human impact has remained limited and confined to traditional nomadic herd-keeping. However, in recent decades both human and livestock populations (mostly sheep, goats and yaks) have increased significantly and overgrazing represents a serious problem in many parts of the region (Bhatnagar et al. 2006). Even if the vegetation structure and composition remain natural under the influence of moderate grazing (Shrestha & Wegge 2008; Tambe & Rawat 2009), in the longer term excessive grazing may cause soil degradation, erosion and nutrient-cycle alterations (Holzner & Kriechbaum 2001).

Material and Methods

Study area

The study area is situated in the eastern part of Ladakh, Jammu and Kashmir State, India (32°41.5′-33°59.7′ N, and 77°47.0′-78°33.4′ E) (Fig. 1). It covers a total area of 6912 km^2 delimited by the Eastern Karakorum Range in the north and the Great Himalaya Range in the south, forming the southwesternmost extension of the Tibetan Plateau; it includes several large brackish lake basins without external drainage. The altitude ranges from 4180 m (bottom of the Indus River Valley) to 6670 m (Lungser Kangri Peak) with vascular plants occurring up to 6060 m (near snowline).

Ladakh lies in the rain-shadow of the Himalayas, which poses a barrier to seasonal monsoon precipitations. The climate is therefore generally arid with mean annual precipitations as low as 50–100 mm (Hartmann 1983; Wang 1988). Precipitations are thought to decrease eastward along the Indus Valley from 83 mm at Leh (3514 m, 34°09′ N, 77°34′ E, about 50 km NW of the study area) to 54 mm at Gar in SW Tibet (4232 m, 32°07′ N, 80°04′ E, ca. 160 km SE of the study area) (Miehe 1990). Evaporation exceeds precipitation at lower and middle elevations. The few climatic data available for higher elevations of East Ladakh suggest a mean annual temperature of around 0°C. The mean monthly temperature rises above 0°C from Jun to Aug only and winter temperatures can drop below −30°C (Klimeš & Doležal 2010). The substrate ranges from siliceous rocks (Precambrian granites, Tso Morari gneiss) to calcareous and saline sediments.

Data collection

The field data were collected at nine expeditions lasting 4–7 wk each, from 1998 to 2003, and in 2005, 2008, 2009. The time of sampling always corresponded with the peak of vegetation season, which lasts from late Jul to mid-Aug in the area. Thus, most likely some early growing ephemeral plants were no longer visible during the sampling. The 369 plots (100 m^2 each) were sampled to cover the physiognomically different vegetation types, across multiple environmental gradients over the area, while avoiding places devoid of vascular plants (very unstable slopes, glaciers, lakes and extremely high elevations [over 6100 m]). Elevation above sea level was estimated with an altimeter (Thommen, Switzerland). In each plot, species composition was recorded and species cover was estimated using a Braun-Blanquet scale. Total percentage vegetation cover was estimated for each plot.

Five main environmental variables were assessed in each plot using the following semi-quantitative scales:

(1) *Stability of the substrate*: 1 = unstable (screes, dunes, periglacial soils), 2 = partly stable (grasslands, steppes), 3 = stable (rocky crevices, *Kobresia pygmaea* mats);

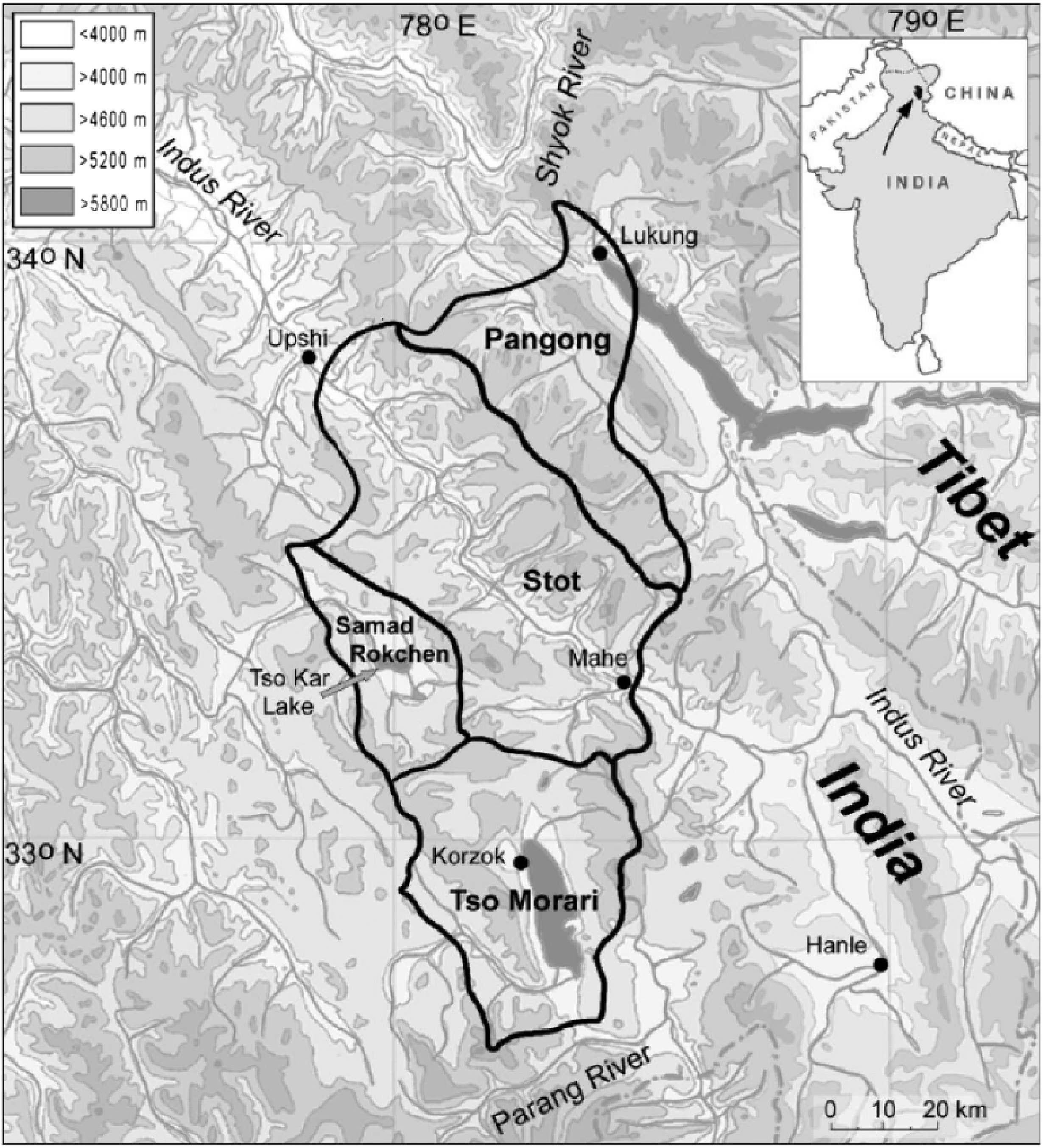

Fig. 1. The study area. The division into four subregions is additional and is not mentioned in the text.

(2) *Light availability*: 1 = shaded (gorges, shaded rocky crevices, walls of stream banks), 2 = partially shaded (dense vegetation cover), 3 = full light (sparse vegetation cover);
(3) *Soil moisture*: 1 = dry (substrate usually without visible traces of water), 2 = mesic, 3 = wet (water level regularly but transiently above soil surface), 4 = permanent surface water;
(4) *Nutrient availability*: 1 = low (semi-deserts, steppes), 2 = medium, 3 = high (stables, animal resting places);
(5) *Soil salinity*: 1 = no salt deposits on soil surface, 2 = salt deposits rare, 3 = salts forming a continuous crust.

The percentage composition of the substrate particles in different size classes was estimated directly in the field by the same experienced person. Seven size classes were distinguished according to the diameter of the particles; the size classes of particles smaller than 2 mm in diameter follow USDA Soil Taxonomy system (clay < 0.002, silt 0.002–0.05, sand 0.05–2, stones 2–10, stones 10–50, 50–200 and stones bigger than 200 mm) (Baldwin et al. 1938).

For plant species identification, a key to the flora of Ladakh was used (Klimeš, unpublished). Problematic species were collected and determined later with the help of a comparative herbary (deposited in the Institute of Botany, Trebon, Czech Republic). The complete list of species is included in the Supporting Information, Appendix SA1. Abbreviations of species used in graphs have eight characters (formed by the first four letters of the genus name and the first four letters of the species name).

Growth forms

Species were ranged systematically into different growth form according to Klimešová et al. (2011). The methodology applied for this classification is based on an identification key using a series of traits and is similar to methodologies already used for Central European vegetation (Klimeš & Klimešová 1999). Twenty growth form categories were delimited by combinations of life-history, clonality and mode of clonal growth (type of root system, presence of various structures of vegetative reproduction, presence and length of rhizomes and their position, etc.) and named after typical representative species (Fig. 2). These growth forms represent an integrated functional classification that enables one to test the response of groups to various environmental variables.

Data analysis

TWINSPAN analysis (Hill & Šmilauer 2005) was used to generate floristic classification of plots. This cluster analysis starts with primary ordination of sites along the first axis of correspondence analysis (CA) and the plots are then divided into two clusters by splitting the first CA axis near its middle (Hill & Šmilauer 2005). Plot classification is refined using a discriminant function that emphasizes species preferential to one or the other half of the dichotomy. After three levels of division, the vegetation of the 369 plots was divided into eight ecologically interpretable groups of vegetation types. The vegetation types were named after their diagnostic species (i.e. species with the highest frequency of occurrence).

For each plot the mean values for the following variables were calculated: species richness (number of vascular plants), total vegetation cover, proportions of clonal and non-clonal species, and proportions of the 20 growth forms. The number of species restricted to only one of the vegetation types (unique species) was calculated for each vegetation type. Growth form proportions were assessed on the basis of species presence/absence data in each plot, and then averaged for the vegetation types. Analysis of variance was used to determine differences in environmental characteristics (altitudinal distribution, soil stability, light availability, soil moisture, nutrient availability, salinity) between TWINSPAN vegetation types. To display significant differences in pairwise comparison between TWINSPAN vegetation types in altitudinal distribution and species richness, boxplots with Tukey notches were used. Boxes in which the notches do not overlap indicate significantly different medians. We also used both linear and quadratic regressions to reveal the relationship between the altitude of the plots and their species richness, and performed this for separate vegetation types as well as for all the plots together.

Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were used to assess the composition variability across plots and to reveal which environmental factors best relate with the main floristic changes; both methods were conducted using CANOCO (ter Braak & Šmilauer 2002). The use of CCA is based on the assumption of unimodal species response (the lengths of the first and second DCA axes were 8.658 and 6.707, respectively, which advocates unimodal methods). Owing to the presence of many rare species with very low cover, the option 'downweighting of rare species' was used (ter Braak & Šmilauer 2002). The constrained and unconstrained methods are complementary: DCA axes correspond to the dominant gradients in species composition, whereas CCA axes correspond to gradients in species composition which best correlate to the measured environmental factors. In CCA, the significant environmental factors obtained by forward selection were used as explanatory variables. We used constrained ordinations to ascribe the explained variability to particular variables using a variance partitioning procedure, in which case the factors not used as predictors were defined as covariables to remove their effects and obtain a net effect of an individual factor (partial CCA, Lepš & Šmilauer 2003). Monte Carlo permutation tests (999 permutations) were used to assess the significance of the relationships found in multivariate analyses.

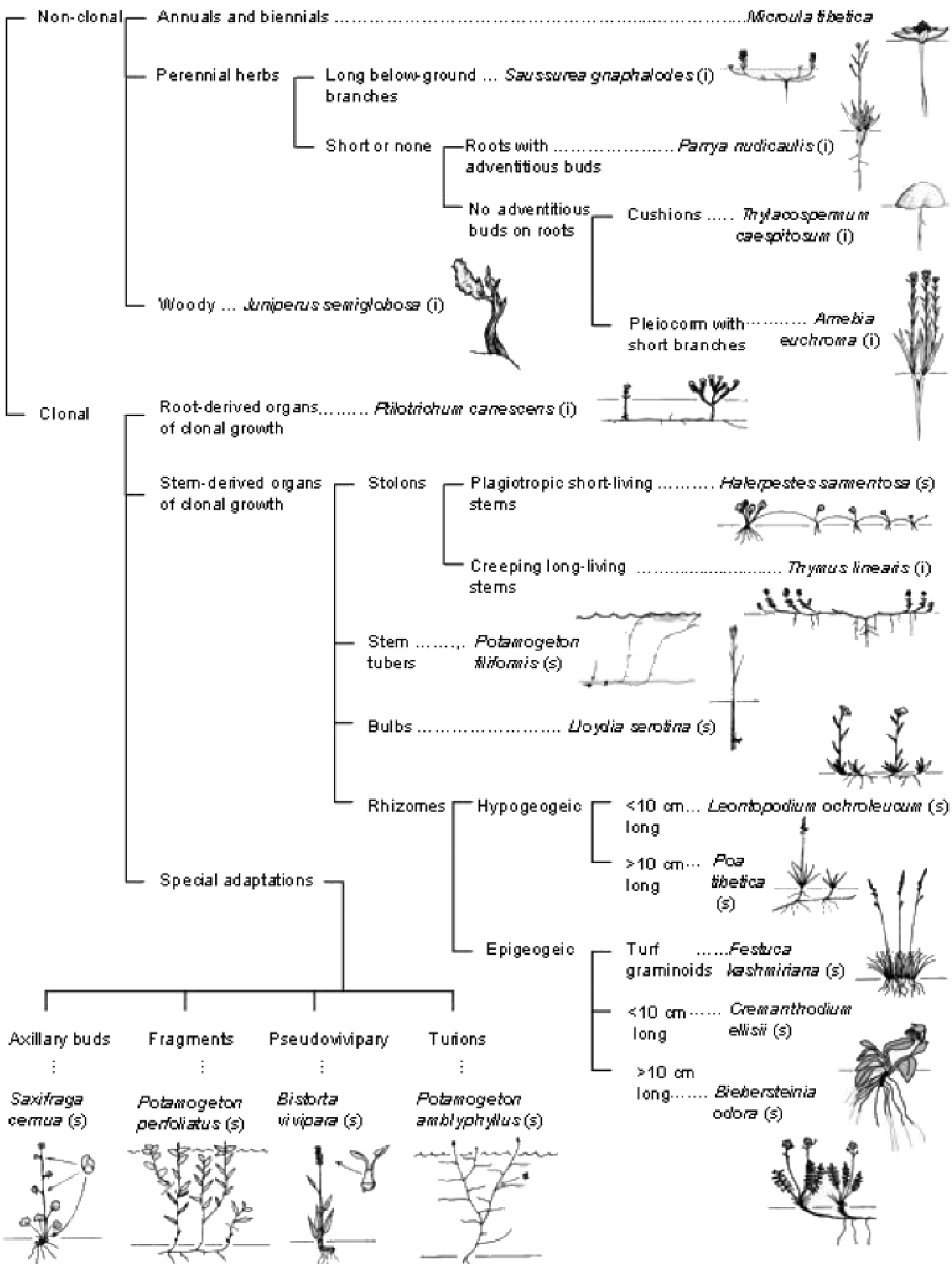

Fig. 2. A key to the 20 clonal-growth categories named according to typical representatives. Integrators (i) and splitters (s) are indicated by the letter in brackets (with permission from Klimešová et al. 2010).

Table 1. TWINSPAN vegetation types and their main characteristics. The Plot section shows numbers of plots belonging to the respective TWINSPAN vegetation types (*n*), their proportions in all plots (%) and mean cover values (MC). The Species section shows number of species found within respective TWINSPAN vegetation types (*n*), proportion of the total of 272 species (%), mean number of species per plot (MS), number of unique species (US; species found within one vegetation type only), proportions of clonal (C) and non-clonal (NC) species. The Altitude section shows mean and maximum values of altitudinal distribution. The Diversity section shows mean values for number of growth forms (GF) and life-forms (LF).

Vegetation type	Plot		MC	Species		MS	US	C	NC	Altitude		Diversity	
	n	%		*n*	%					Mean	Max	GF	LF
Puccinellia himalaica–Polygonum sibiricum Habitat: salt marshes	92	24.9	57	120	44	8	16	70.9	29.1	4592	5140	4.63	2.77
Elymus jacquemontii–Oxytropis tatarica Habitat: shrublands	48	13	20	101	37	10	18	42.3	57.7	4636	5110	4.77	3.33
Potamogeton amblyphyllus–Halerpestes sarmentosa Habitat: water bodies	11	3	65	23	9	4	4	89.8	10.2	4695	5110	3.36	2.27
Oxytropis microphylla–Stipa caucasica Habitat: semi-deserts & steppes	83	22.5	21	79	29	10	14	44.6	55.4	4732	5320	4.55	3.51
Kobresia royleana–Kobresia schoenoides Habitat: alpine grasslands	54	14.6	71	140	52	15	22	71.5	28.5	4775	5510	6.26	3.04
Chenopodium karoi–Leymus secalinus Habitat: animal resting places	9	2.4	56	28	10	6	2	23.6	76.4	4801	5200	3.33	3
Thylacospermum caespitosum–Pleurospermum stellatum Habitat: alpine screes	20	5.4	13	85	31	13	11	30.9	69.1	5057	5620	6.15	3.05
Poa attenuata–Potentilla pamirica Habitat: subnival zone	52	14.1	37	106	39	11	8	42.1	57.9	5243	5750	5.46	3.19

Results

A total of 272 vascular plant species were found over the 369 plots, with an average of 10 per plot. These species belong to 43 families (9 in monocots, 33 in dicots plus family *Ephedraceae*) and 127 genera (24 in monocots, 102 in dicots plus genus *Ephedra*). Eight large families comprised 72.5% of all the species, i.e. *Asteraceae* (12 genera/44 species), *Poaceae* (13/34), *Brassicaceae* (14/23), *Fabaceae* (6/20), *Cyperaceae* (4/18), *Chenopodiaceae* (9/13), *Caryophyllaceae* (5/12) and *Ranunculaceae* (5/10). As many as 20 families were represented by only one species. The ratio of monocots to dicots in the area was 1:3.4 (Appendix SA1).

Description of vegetation types

After applying three-level division in the TWINSPAN cluster analysis, we obtained eight groups of relevés corresponding to the main vegetation types. Here, we use the term 'habitat' for the type of the environment and its abiotic features, while the term 'community' refers to the specific species combination of a vegetation type, which may slightly differ even within one vegetation type over the area of its distribution. The eight distinguished vegetation types differ in terms of altitudinal distribution, species richness and structure (Table 1) as well as in terms of frequent species (Table 2, Appendix SA1).

Puccinellia himalaica–Polygonum sibiricum type (habitat: salt marshes)

This vegetation type includes halophilous communities developed over extensive areas at the bottom of plains, around banks of salty or brackish lakes and near mineral springs. The prevailing substrate was sandy silt with a high salinity level, with salts often forming a continuous crust. Soil fertility level was low. The water level regularly reached the soil surface for a transient period or water covered the surface permanently. The altitudinal optimum was about 4500 m. The vegetation cover was very low (approximately 20%) in places with the highest salinity and highest water level, and increased to 85% in places with more favourable conditions. Species forming this vegetation type were mostly halophilous or salt-tolerant hemicryptophytes. Therophytes were represented by few species, the most abundant of which were *Artemisia macrocephala* and *Suaeda olufsenii*.

Elymus jacquemontii–Oxytropis tatarica type (habitat: shrublands)

The characteristic feature of this vegetation type was the dominance of deep-rooted shrubs. The sub-

Table 2. Synoptic table showing the frequency of the occurrence of the species within the eight vegetation types and the number of plots (of the total of 369 plots) that belong to the respective vegetation types. The vegetation types are sorted from the left to the right according to their average altitudinal distribution. Species are sorted according to their frequency within the respective vegetation types. Species with frequency higher than 30% are shown only. SM, salt marshes; SH, shrublands; WB, water bodies; ST, semi-deserts and steppes; AG, alpine grasslands; RP, resting places of animals; SC, screes; SU, subnival zone.

Species	Abbreviation	Vegetation type							
		SM	SH	WB	ST	AG	RP	SC	SU
	No. of plots	92	48	11	83	54	9	20	52
Puccinellia himalaica	*PuccHima*	71	6	18	2	30	11	5	4
Polygonum sibiricum	*PolySibi*	41	17	0	4	17	33	0	2
Carex moorcroftii	*CareMoor*	39	0	0	23	9	11	5	29
Elymus jacquemontii	*ElymJacq*	8	69	0	33	13	11	65	29
Oxytropis tatarica	*OxytTata*	3	65	0	49	4	11	60	38
Caragana versicolor	*CaraVers*	1	52	0	10	9	0	10	0
Ephedra gerardiana	*EpheGera*	0	40	0	6	0	0	0	0
Elymus schrenkianus	*ElymSchr*	9	33	0	12	19	22	10	12
Dracocephalum heterophyllum	*DracHete*	1	31	0	27	0	0	15	13
Potamogeton amblyphyllus	*PotaAmbl*	2	0	64	0	2	0	0	0
Halerpestes sarmentosa	*HaleSarm*	46	0	64	0	28	0	0	0
Catabrosa aquatica	*CataAqua*	1	0	45	0	0	0	0	2
Oxytropis microphylla	*OxytMicr*	5	23	0	76	0	0	0	6
Stipa caucasica	*StipCauc*	0	10	0	72	0	0	0	0
Ptilotrichum canescens	*PtilCane*	0	2	0	70	0	11	0	0
Krascheninnikovia pungens	*KrasPung*	2	46	0	58	0	11	0	2
Stipa subsessiliflora	*StipaSubs*	2	23	0	51	0	0	5	15
Chamaerhodos sabulosa	*ChamSabu*	1	0	0	34	2	0	0	4
Kobresia royleana	*KobrRoyl*	18	4	0	0	67	0	20	8
Kobresia schoenoides	*KobrScho*	20	0	0	0	54	0	5	15
Calamagrostis holciformis	*CalaHolc*	32	8	0	1	44	0	15	0
Potentilla multifida	*PoteMult*	20	25	0	0	43	0	5	19
Astragalus strictus	*AstrStri*	11	10	0	2	39	0	5	23
Thalictrum alpinum	*ThalAlpi*	2	0	0	0	37	0	0	0
Lomatogonium carinthiacum	*LomaCari*	18	0	9	1	31	0	0	0
Chenopodium karoi	*ChenKaro*	4	4	0	27	0	56	0	2
Leymus secalinus	*LeymSeca*	23	13	0	25	2	56	0	6
Artemisia macrocephala	*ArteMacr*	22	15	0	8	4	44	0	10
Axyris prostrata	*AxyrPros*	3	4	0	8	0	44	0	2
Microgynoecium tibeticum	*MicrTibe*	2	0	0	0	2	44	0	4
Physochlaina praealta	*PhysPrae*	2	0	0	7	0	33	0	0
Thylacospermum caespitosum	*ThylCaes*	0	0	0	0	7	0	60	48
Pleurospermum stellatum	*PleuStel*	0	4	0	0	9	0	50	2
Rhodiola tibetica	*RhodTibe*	2	4	9	0	24	0	50	8
Marmoritis rotundifolia	*MarmRotu*	0	2	0	0	0	0	45	0
Saussurea bracteata	*SausBrac*	0	4	0	0	11	0	45	15
Poa attenuata	*PoaAtte*	3	33	0	11	31	11	70	83
Potentilla pamirica	*PotePami*	3	10	0	5	33	0	50	63
Saussurea gnaphalodes	*SausGnap*	0	4	0	0	6	0	40	48
Draba altaica	*DrabAlta*	0	0	9	0	9	0	25	44
Arenaria bryophylla	*ArenBryo*	0	4	0	6	4	0	15	38
Carex sagaensis	*CareSaga*	30	2	27	1	22	0	10	35
Stellaria depressa	*StelDepr*	11	2	9	1	22	0	20	31

strate was a mixture of sand and silt with a high proportion of gravel. The nutrient and salinity levels were generally low while water content was moderate to high. The altitudinal distribution varied from 4200 to 5000 m. Vegetation cover was low in most plots, usually not exceeding 30%. The most common and dominant species was the thorny shrub *Caragana versicolor*, being up to 60 cm in height, accompanied by less common shrubs such as *Ephedra gerardiana* and *Krascheninnikovia pungens* (indicating drier substrate) or *Hippophaë tibetana* and *Myricaria germanica* (indicating water surplus). Herbs were represented mostly by perennials and a few annual species, such as *A. macrocephala* and *Polygonum molliaeforme*.

***Potamogeton amblyphyllus–Halerpestes sarmentosa* type (habitat: water bodies)**

This vegetation type included habitats with permanent fresh-water bodies or places with excessive water supply during most of the year. This vegetation was not common in the study area. The substrate consisted of sand mixed with silt and clay and the nutrient level was low to moderate. The vegetation cover was generally high, and in most plots more than 60%. The species of this vegetation type included hydrophytes and hydrophilous species, both annuals and perennials (e.g. *Catabrosa aquatica* and *H. sarmentosa*).

***Oxytropis microphylla–Stipa caucasica* type (habitat: semi-deserts and steppes)**

This vegetation type occurred over large areas. Semi-deserts and steppes were the most common, together with salt marshes. The substrate was mostly dry with low nutrient and salinity levels and consisted of sand mixed with bigger stones. The altitudinal optimum range was 4500-4900 m. Insufficient water supply resulted in very low vegetation cover values. Most common species were stress-tolerant hemicryptophytes. Steppe genera such as *Artemisia*, *Oxytropis* and *Stipa* were highly represented. Annuals such as *A. macrocephala, Chenopodium karoi, Lepidium apetalum* or *Salsola jacquemontii* occurred sporadically and tended to occupy places with better nutrient and/or water availability. *Caragana versicolor* shrubs dominated in some plots although they were not very common as a whole.

***Kobresia royleana–Kobresia schoenoides* type (habitat: alpine grasslands)**

Alpine grasslands occurred mainly along streams and had the greatest species richness in the study area. The substrate consisted of sandy silt and was typically well supplied with water. Nutrient and salinity levels were moderate to low. The altitudinal optimum was between 4600 m and 4900 m. The vegetation cover was very high. Large proportion of alpine grasslands was represented by sturdy *K. pygmaea* mats. This vegetation type was dominated by clonal hemicryptophytes; annuals were absent or rare.

***Chenopodium karoi–Leymus secalinus* type (habitat: animal resting places)**

This vegetation type of rather limited extent in the studies area included gathering places of animals and stables and was typically species poor. The substrate was mesic to dry with a high nutrient content owing to deposition of faeces. The altitudinal optimum was 4600-5000 m. The vegetation cover was low, never exceeding 60% of a plot area. Prevalence of annual species was characteristic (e.g. *Axyris prostrata* and *Microgynoecium tibeticum*).

***Thylacospermum caespitosum–Pleurospermum stellatum* type (habitat: alpine screes and boulder fields)**

This vegetation covered steep slopes with an unstable substrate at high altitudes (4750-5620). The substrate consisted of weathered rocks with a high proportion of stones bigger than 20 cm in diameter. Soil moisture was moderate to high, particularly in deeper horizons. The nutrient level was low. Vegetation cover was poorly developed and in most plots varied from 5% to 15%. Dominant species were hemicryptophytes (e.g. *Rhodiola tibetica*). Annuals were absent or rare.

***Poa attenuata–Potentilla pamirica* type (habitat: subnival zone)**

This vegetation type occupied the highest elevations up to the snow-line and included the highest-growing plant communities in the whole Ladakh. Surface stability was moderate, although severely affected by solifluction. Soils were poorly developed and consisted mainly of sand and bigger stones. Water availability was good due to a rather high amount of precipitation, but the nutrient level was low. This vegetation type occurred at altitudes from 4600 to 5700 m, but at extreme altitudes near the snow line only individual plants were discovered. The vegetation cover varied greatly among plots, mostly between 20% and 60%. The majority of species were low-growing hemicryptophytes (e.g. *Draba altaica, Saussurea gnaphalodes* or *Saxifraga nanella*).

Species-environment relationships

Detrended correspondence analysis provided the basic outline of the compositional gradients in the data, coherently with the TWINSPAN ordination (Fig. 3). The first two ordination axes explain 9.4% of the variability in species data. A high value of species-environment correlations on the first two axes ($r = 0.98$ and 0.95) show that the selected environmental factors were determinants of species variation in the data set. They explain up to 22% of the total variability when projected into already determined ordination space (Fig. 3). The second axis is well correlated with environmental data, indicating that there is no single dominant gradient. The projection of environmental variables (Fig. 3) reveals that the first axis is positively correlated with moisture (0.95) and soil fertility (0.92), and with

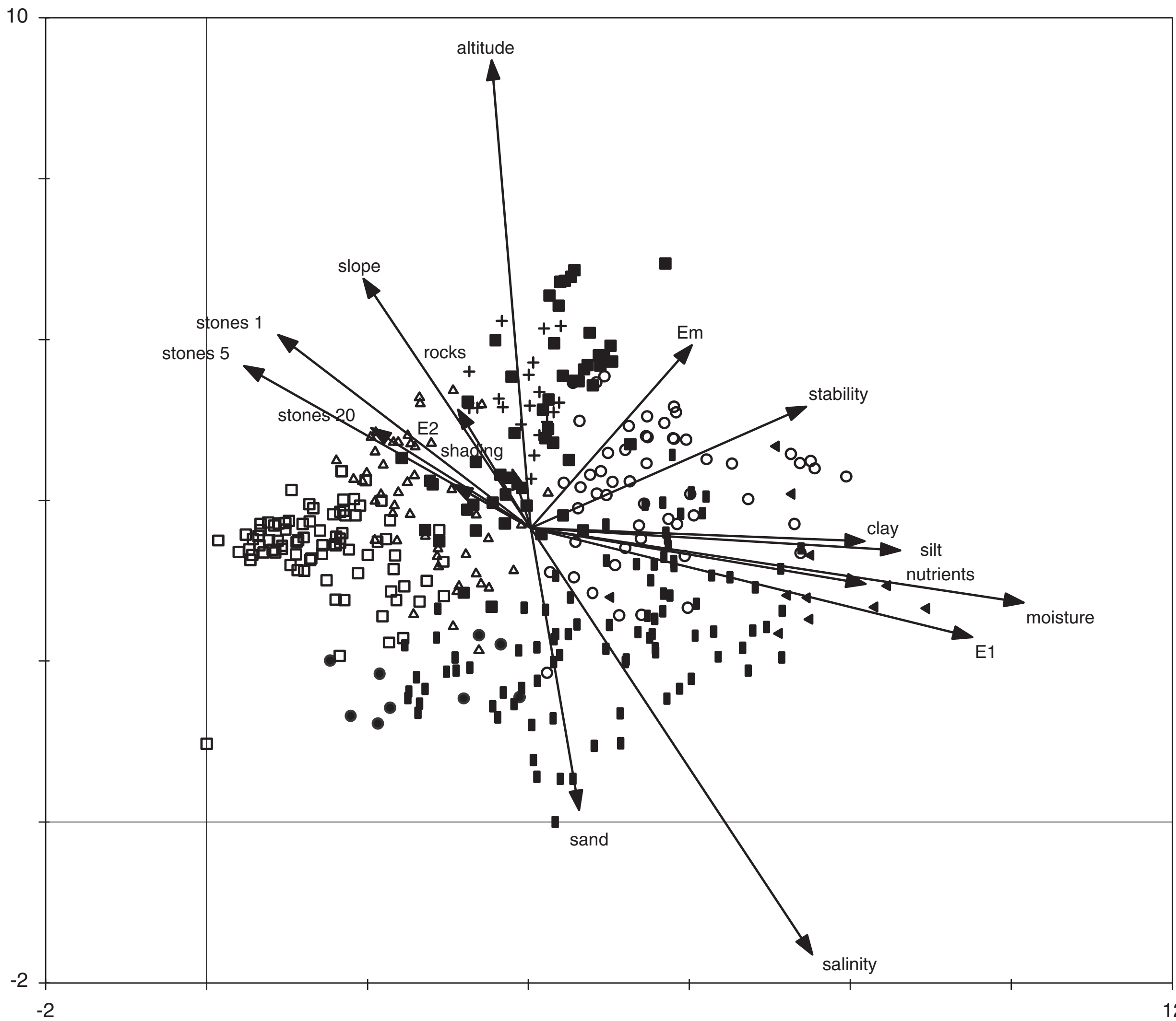

Fig. 3. Detrended correspondence analysis (DCA) correlation diagram showing distribution of plots and environmental factors. The first two axes correspond to the most important gradients in the floristic composition of the plots, moisture and altitude in this case. Symbols depict plots belonging to individual vegetation types (+, screes; ■, subnival zone; ○, wet grasslands; ▶, water bodies; , salt marshes; ●, animal resting places; □, semi-deserts and steppes; Δ, shrublands). Abbreviations: E2, shrub layer cover; E1, herb layer cover; Em, moss and lichen cover; Rocks, percentage cover of stones bigger than 20 cm in diameter; Stones 20, percentage cover of stones in the size class 5–20 cm diameter; Stones 5, percentage cover of stones 1–5 cm in diameter; Stones 1, percentage cover of stones up to 1 cm in diameter.

surface stability (0.81) and herb cover (0.69), and negatively correlated with the proportion of bigger stones (>20 cm, − 0.23) and gravel (grain size ~1-5 cm, − 0.44) (Table 3). The second axis is positively correlated with altitude (0.67), and negatively with salinity (− 0.72) and percentage of sand (− 0.39).

The position of individual species and vegetation types supports this interpretation (Fig. 4). The first floristic gradient describes compositional changes from dry semi-deserts and steppes (with species like *Tanacetum fruticulosum*, *S. caucasica*, *Ptilotrichum canescens*, *Artemisia salsoloides*, *Crepis flexuosa*, *Stipa subsessiliflora*, *Chamaerhodos sabulosa*, etc.) to alpine grasslands and water bodies (with typical species such as *H. sarmentosa*, *C. aquatica*, *Eleocharis quinqueflora*, *Juncus thomsonii*, *P. amblyphyllus*, etc.; Fig. 4). The positions of individual clonal-growth and life-form categories (Fig. 5) reveal that the first floristic gradient is positively correlated with the abundance of clonal plants, in particular splitters, plants with long (>10 cm) below-ground hypogeogeic rhizomes (*Poa tibetica* category) prevailing in salt marshes, plants with above-ground

Table 3. Correlations of environmental factors with the first two detrended correspondence analysis (DCA) axes, and explained variability and significance levels from the canonical correspondence analysis (CCA) for both marginal effects (variability explained by a given factor without considering other factors) and net effects (variability explained by a given factor after accounting for the effects of other factors (covariables). Significance levels: ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$. Abbreviations: E2, shrub layer cover; E1, herb layer cover; Em, moss and lichen cover; Rocks, percentage cover of stones bigger than 20 cm in diameter; Stones 20, percentage cover of stones in the size class 5–20 cm in diameter; Stones 5, percentage cover of stones 1–5 cm in diameter; Stones 1, percentage cover of stones up to 1 cm in diameter.

Factor	DCA	DCA	CCA	CCA
	Correlation with 1st axis	Correlation with 2nd axis	Marginal effect (% explained)	Net effect (% explained)
Stability	0.81	0.16	4.5***	2.0***
Moisture	0.96	− 0.1	5.3***	3.0***
Salinity	0.7	− 0.64	4.6***	2.1***
Fertility	0.92	− 0.04	5.0***	1.8***
Shading	− 0.14	0.21	1.6***	1.1***
Altitude	− 0.03	0.68	3.1***	1.9***
Slope	− 0.25	0.34	1.3***	0.5***
E2	− 0.1	0.02	1.7***	1.4***
E1	0.7	− 0.17	3.4***	0.6***
Em	0.27	0.24	1.0***	0.5***
Rocks	− 0.1	0.17	0.7**	0.5***
Stones 20	− 0.24	0.14	1.4***	0.6***
Stones 5	− 0.45	0.23	2.1***	0.4*
Stones 1	− 0.37	0.25	2.4***	0.5***
Sand	0.07	− 0.39	1.1***	0.3
Silt	0.59	− 0.04	2.4***	0.4*
Clay	0.54	− 0.02	2.1***	0.4*

stolons (*H. sarmentosa* category) prevailing in water bodies, and plants with short epigeogeic (*Cremantodium ellisii* category) and hypogeogeic (*Leontopodium ochroleucum* category) rhizomes being more abundant in alpine grasslands. Plants negatively correlated with the first DCA axis are non-clonal plants, chamaephytes, root-sprouters (*P. canescens* category) and perennials with a pleiocorm having short branches (*Arnebia euchroma* category) prevailing in semi-deserts and steppes (Fig. 5).

The second floristic gradient is associated with altitudinal changes from salt marshes, forming azonal vegetation on valley bottoms, towards *Caragana* shrublands and alpine screes at higher elevations, and finally to subnival vegetation at the highest positions. The positions of growth and life form categories show that the second floristic gradient is positively correlated with non-clonal plants with a pleiocorm having long branches (*S. gnaphalodes* category), being significantly more abundant in alpine screes, and with compact cushion plants (*T. caespitosum* category) prevailing in the subnival zone (Fig. 5). Annuals and biennials prevailing in animal resting places (higher soil nitrogen and intensity of disturbances) are negatively correlated with the second DCA axis and are also more abundant in salt marshes.

The species richness was also affected by altitude. A regression model for all the plots together showed an unimodal, rather weak, response of the species richness, culminating between 4500 m a.s.l and 5000 m a.s.l. (quadratic regression, $R^2 = 0.03$, $P = 0.004$; Fig. 6). The regression for plots of separate vegetation types was significant only for semi-deserts and steppes (unimodal response, $R^2 = 0.09$, $P = 0.018$), shrublands (unimodal response, $R^2 = 0.09$, $P = 0.049$) and the subnival zone vegetation (linear response, $R^2 = 0.15$, $P = 0.004$). The altitudinal distribution of the vegetation types and the differences in the species richness are shown in Fig. 7.

Canonical correspondence analysis on relative species cover with habitat variables is summarized in Table 3. In the analysis of all plots, CCA showed that 22.05% of the compositional variability was explained by 16 significant factors selected by forward selection out of 17 explanatory variables tested ($P = 0.001$). The variance partitioning procedure (Table 3) revealed that the soil moisture index is the most important factor influencing species composition, followed by salinity, surface stability and soil fertility indices. Several habitat variables investigated are closely correlated (e.g. percentage of sand and silt). Consequently, after silt was selected, the net effect of sand decreased dramatically. The net effects of all variables investigated were significant with the Monte Carlo permutation test ($P<0.05$), except for sand ($P = 0.082$).

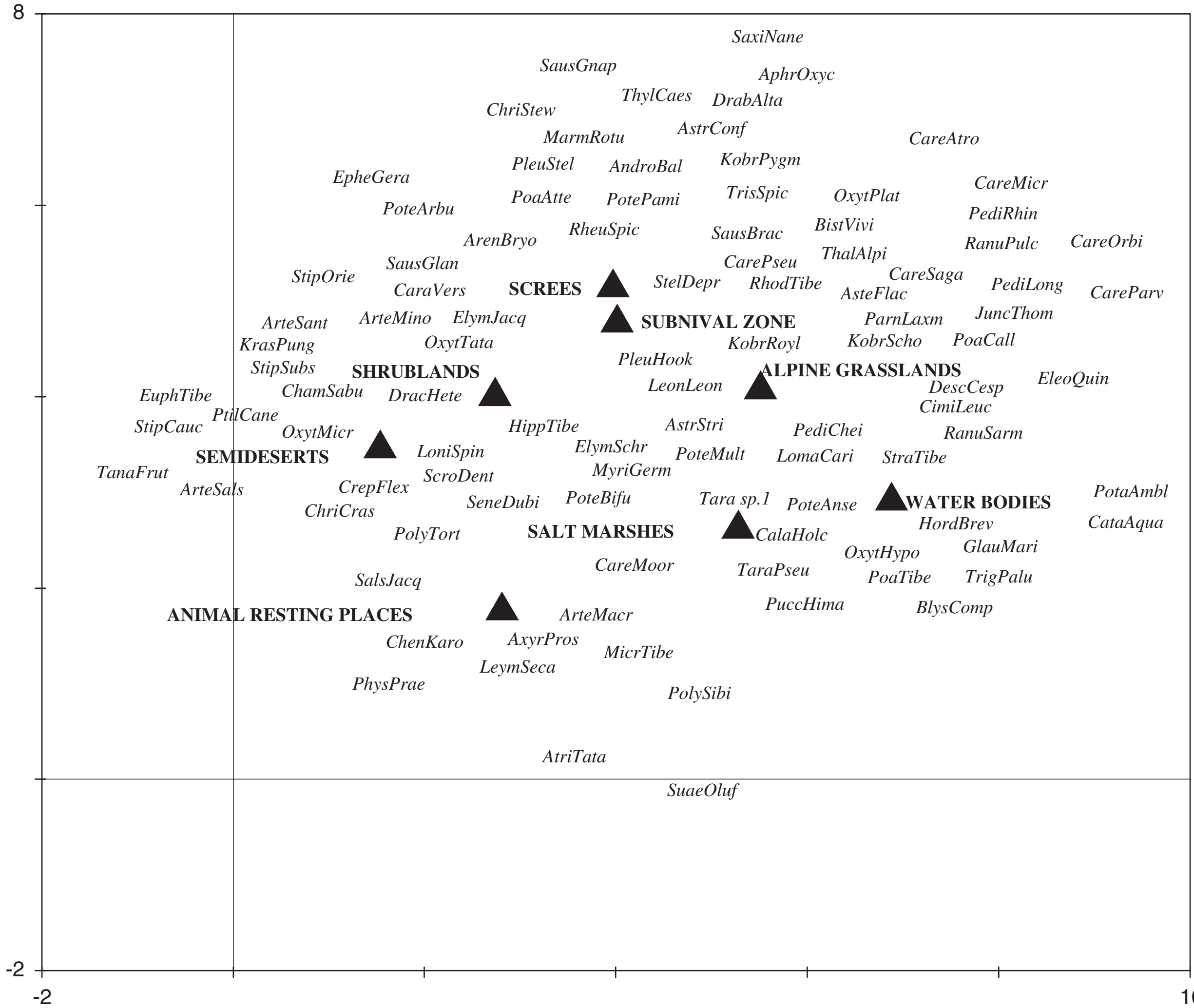

Fig. 4. Indirect detrended correspondence analysis (DCA) analysis showing plant species optimum performances with regard to the main vegetation types in E Ladakh. The first two axes are well correlated with moisture and elevational gradient, respectively. A total of 102 most abundant species are shown. Closed triangles (▲) depict the centroids of the vegetation types. For abbreviations of species names see Table 2 and Appendix SA1.

Discussion

As human population and its impact on the environment is on increase even in hardly accessible areas, the knowledge of plant diversity patterns within different vegetation types provides a first sound basis for the potential assessment of conservation priorities and monitoring schemes (Dhar et al. 2000). There are relatively few recent studies dealing directly with the vegetation of the Trans-Himalaya (Kala & Mathur 2002; Rawat & Adhikari 2002, 2005a, b; Klimeš 2003). The most valuable work on the vegetation of Ladakh was provided by Hartmann (1983, 1984, 1987, 1990, 1995, 1997, 1999) who based his geobotanical description of the area on about 280 vegetation records. Kala & Mathur (2002) analysed the floristic composition of Ladakh within preselected landscape types; their results, however, suffer from many taxonomic misinterpretations as the sources of plant identification (Kachroo et al. 1977; Polunin & Stainton 1984) are incomplete (Klimeš & Dickoré 2006). At a smaller spatial scale, Rawat & Adhikari (2005a) focused on the vegetation of the Tso Kar basin, a part of our study area, and observed patterns similar to those seen in our study: vegetation types largely follow moisture and altitudinal gradients with plant cover and species richness influenced mostly by microhaitat conditions. To the best of our knowledge, our study is the first comprehensive work that

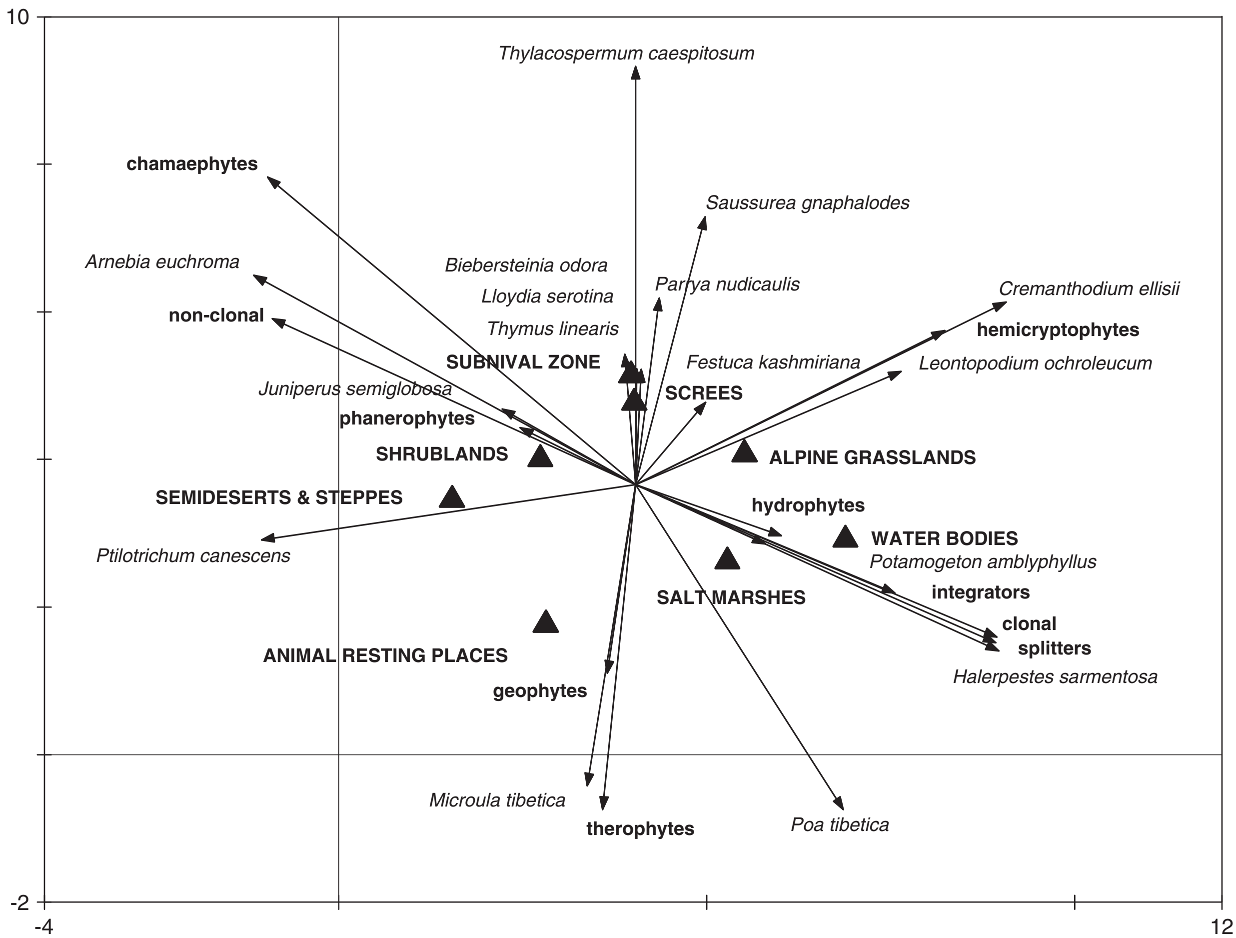

Fig. 5. Ordination diagram showing correlation of distribution of clonal-growth forms, life-form categories and clonal types with respect to the main vegetation types in E Ladakh. Closed triangles (▲) depict the centroids of the vegetation types. Names in italic depict the growth forms. Four of the 20 categories are not shown because they were represented by none or one species in the dataset only.

presents extensively the main vegetation types of East Ladakh in the Trans-Himalaya, the underlying environmental gradients that shape them and the sensitivity of growth forms to these environmental factors.

On the basis of differences in floristic composition, eight main vegetation types were delimited. These vegetation types are relatively broad units, which enable the classification of basically every vegetation type occurring across the vast area of East Ladakh into one of eight units. This could be very useful, especially in areas with scarce or incomplete information on vegetation, where such a broad classification could give a first indication of the diversity of the system and the main environmental factors that influence vegetation. Although this classification does not reflect minor differences in ecological conditions among microhabitats, this approach seems appropriate to perform a basic vegetation mapping of rather uniform vegetation of Ladakh.

Salt marshes, semi-deserts and steppes prevail among the vegetation types, providing a first indication of the importance of these communities in the landscape of Ladakh. The desert–steppe communities show similar species composition to neighbouring parts of Karakorum Range (Eberhardt et al. 2007) as well as to other regions of Ladakh. In his works, Hartmann (1995, 1997, 1999) concentrated on this dominant vegetation type (referred to as ''Wüstensteppe'') and provided a closer sub-classification of different steppe types according to the altitude and composition. Peer et al. (2007) provided a detailed study on *Artemisia* steppes in Hindu Kush in Northern Pakistan; a comparison between our data and that study shows similarities in the structure, but Tibetan floristic elements are represented more in East Ladakh.

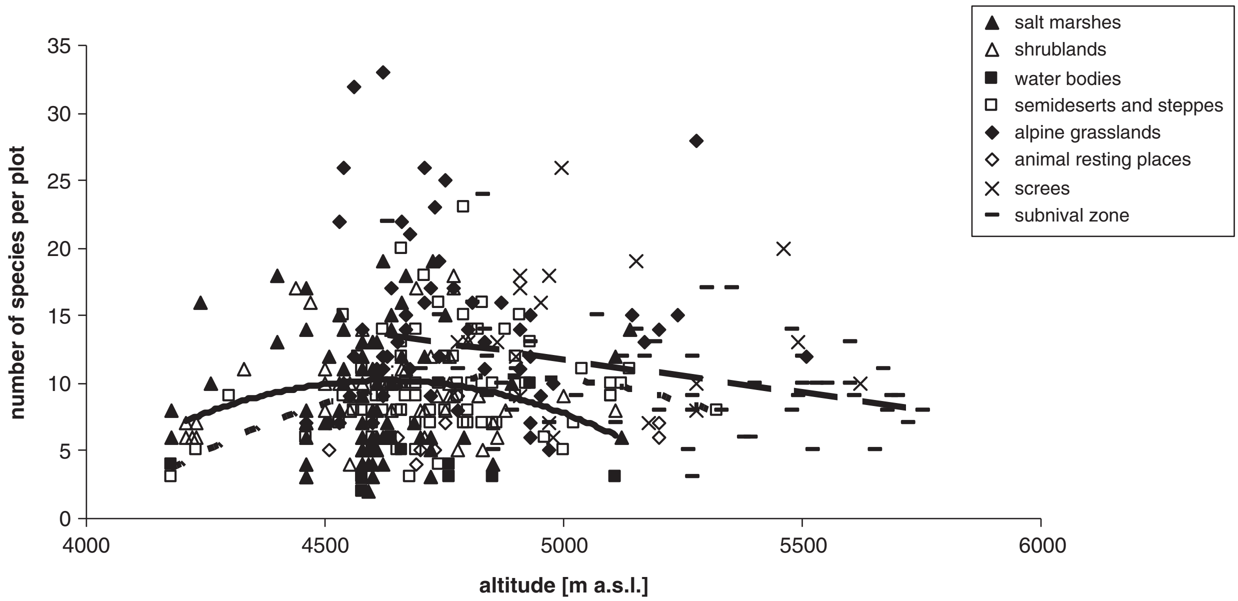

Fig. 6. Species richness and the altitudinal distribution of the plots. Response curves are shown for separate vegetation types in case of a significant trend; shrublands (solid line), semi-deserts and steppes (dotted line), subnival zone (dashed line). A regression model for all the plots together showed an unimodal response of the species richness ($R^2 = 0.03$, $P = 0.004$; curve not shown).

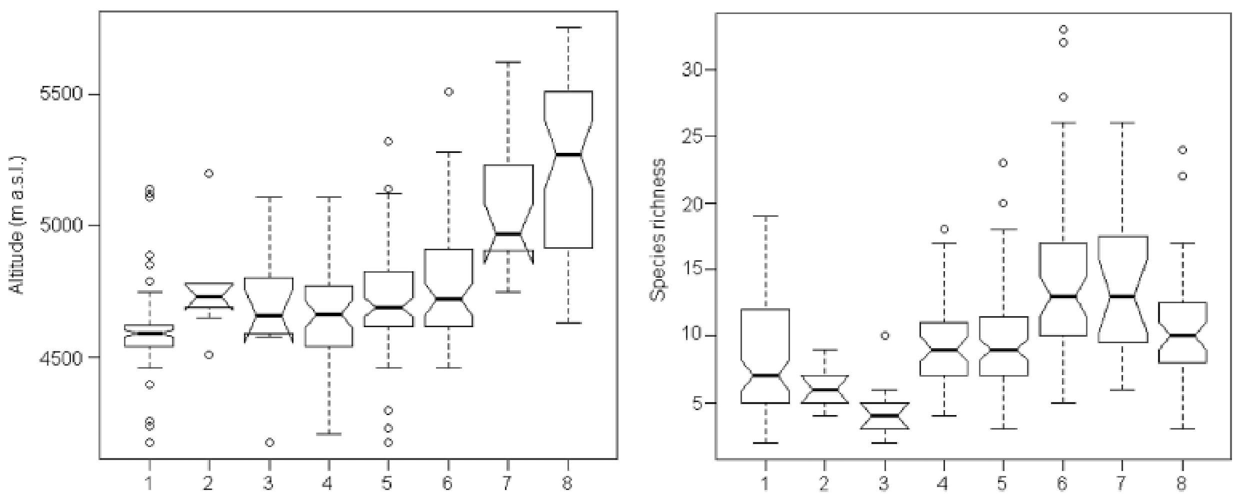

Fig. 7. Boxplots with Tukey notches for pairwise comparisons, showing significant differences between TWINSPAN vegetation types in altitudinal distribution and species richness. (1, salt marshes; 2, animal resting places; 3, fresh-water bodies; 4, shrublands; 5, semi-deserts and steppes; 6, alpine grasslands; 7, alpine screes; 8, subnival zone).

Alpine grasslands and the subnival vegetation are common vegetation features of the landscape at the highest elevations. As proposed by Miehe et al. (2008), these specific alpine communities might originate with human pasture activities. *Kobresia pygmaea* is usually the dominant species here, and *Kobresia* mats are generally considered the most characteristic vegetation type over the Tibetan Plateau (Dickoré 1995). Shrublands are less common in the study area; as local people use the shrubs for firewood, this could lead to the reduction of shrubland (Samant et al. 2000). The least common vegetation type is that of fresh-water bodies, which are naturally rare in the study area, while the vegetation of animal resting places is expected to increase with the rising number of domestic animals.

Although strongly overlapping, there are significant differences in the mean values of the altitudinal ranges of the vegetation types. The lowest elevations are occupied by salt marshes, fresh-water bodies, shrublands, semi-deserts and steppes, all of them occurring on valley bottoms and around salty lakes (Tso Morari, Tso Kar, Pangong). Both fresh-water bodies and salt marshes are limited to specific sites, but salt marshes are much more common and occur up to 5140 m a.s.l. Semi-deserts and steppes as zonal formations are the most common vegetation types in the whole area, dominating vast plains and gentle slopes of high-altitude plateaus continually up to 5320 m a.s.l. The vegetation type of animal resting places is scattered along the elevation gradient quite haphazardly because its distribution is partly of human origin. Alpine grasslands often follow streams along their entire length in a wide altitudinal range from 4460 to 5510 m a.s.l. The distribution centre of screes and of subnival vegetation is mostly above 5000 m a.s.l. with exceptions at lower sites, such as narrow gorges of subalpine streams (screes) and northern or exposed windward slopes (subnival vegetation). At about 6000 m a.s.l., only individual plants are observed, scattered at microsites that provide at least a minimal shelter against severe conditions (e.g. bigger stones). The highest growing vascular plant (*Saussurea hypsipeta*) was found at 6060 m a.s.l., which is the highest occurrence of a vascular plant known from the area.

Regarding plant diversity, alpine grasslands in East Ladakh can be characterized as the most species-rich vegetation type, moreover harbouring the highest number of unique species. This fact was also documented by Rawat & Adhikari (2005a), who described moist meadows to have the greatest species richness in the area. Hartmann (1968) in his study from Biafo Glacier area in the neighbouring Karakorum Range described a similar vegetation type of alpine grasslands ("alpine Wiesen") with dominant *Carex* and *Kobresia* species and also considered it to be the most species-rich community. Alpine grasslands very likely experience the greatest grazing pressure in the whole area, so the dominance of a few clonal species of graminoids is in accord with their grazing history (Bock et al. 1995). However, the processes connected with grazing (nutrient deposition, trampling creating new microsites for seedling establishment and reducing the biomass of dominants provided by animals) create suitable conditions for species coexistence (Bakker 1989; Olff & Ritchie 1998). In comparison, alpine screes harbour a much lower number of species, but this vegetation type has a comparable mean number of species per plot and the greatest diversity of growth forms. An explanation for the greater species richness of screes might be the fact that this habitat is apparently not as hostile as it seems; an accumulation of fine substrates among big stones and a specific microclimate (higher humidity, less extreme temperature fluctuations, etc.) likely favour pedogenetic processes in deeper layers so that species with a long taproot can profit from this habitat (Körner 2003). Animal resting places and fresh-water bodies were poorest in species (see also Kala & Mathur 2002; Rawat & Adhikari 2005a), which partly results from the limited extent of these habitats in the study area and the fact that high disturbance regime is likely to reduce diversity by increasing plant mortality (Bakker 1989; Olff & Ritchie 1998).

Across all vegetation types, the greatest species richness was observed between 4500 and 5000 m a.s.l., with a gradual decline towards both lower and higher altitudes. A similar trend with the unimodal distribution of the species richness was shown for the vegetation of semi-deserts and steppes, indicating that this zonal vegetation has its optimum around 4800–5000 m a.s.l. in the area. According to our preliminary results, this can be ascribed to water limitation at lower elevations and temperature limitation at higher elevations, respectively. Subnival vegetation is the only type showing significant linear decline of species richness, suggesting that the subnival zone is enriched by other species at lower altitudes, whereas higher up it consists of fewer subnival specialists.

Life-forms and clonality in East Ladakh were already partially studied by Klimeš (2003; see also Hartmann 1995) but, here, we expand this description and combine it with a more comprehensive classification scheme and vegetation description. The above-mentioned authors concluded that the life-form spectrum is closer to desert-steppes and steppes (e.g. a high proportion of hemicryptophytes, a high number of turf grasses and a low proportion of therophytes) rather than to deserts or cold deserts, as the vegetation of Ladakh is often referred to by local authors (Negi 1995). Clonal species prevailed in habitat types with good water availability and average nutrient status: in salt marshes an of average 70.9% of the species present were clonal, in water bodies 89.8%, and alpine grasslands 71.5%. Of the clonal species, splitters prevailed in water bodies only (67.9% of all species), while integrators were dominant in alpine grasslands (68.4%) and salt marshes (60.4%). Accordingly, Rawat & Adhikari (2005a) found the communities of wet meadows to have the highest density of stems because of the dominance of clonal species forming tillers and dense tussocks. Non-clonal species were prevalent in the rest of the vegetation types with the highest representation in animal resting places (76.4%) and screes (69.1%). The proportion of non-clonal species increases with altitude, as was already reported by Klimeš (2003). The large number of non-clonal species in animal resting places results from a large number of annual species, attaining on average 55.5% of all species present. On screes, in addition to the majority of species being non-clonal, practically all the clonal species belonged to the integrator type (94.2% of clonal species). This suggests the advantage of a compact growth in conditions with frequent disturbances. The advantage is also apparent for plants with a main taproot, which is located in suitable deeper layers of scree and which enables regeneration of branches lost in a disturbance in upper layers. Both solifluction with its daily thaw-freeze cycles at high altitudes and movements of stones and boulders in screes damage the connections between ramets (Klimeš 2003). Thus, nutrients and energy invested into ramet production and connection maintenance are lost, and this leads to a selection against such clonal types (Körner 2003). Finally, it is rather difficult for rhizomes to penetrate hard substrates, which frequently occur in East Ladakh, so that compact growth forms are favoured here (Klimešová et al. 2011).

In conclusion, we proposed a classification system of the main vegetation types in East Ladakh, and we related the distributional patterns of these types to the main environmental factors. Such a classification system could be useful for a large-scale vegetation mapping of the region as well as a prerequisite for designing conservational practices.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix SA1: Checklist of species recorded in the plots and their frequencies within the eight vegetation types. The species abbreviations used in graphs are formed from the first four letters both from genus and species name. SM = salt marshes, SH = shrublands, WB = water bodies, ST = semi-deserts and steppes, AG = alpine grasslands, RP = resting places of animals, SC = screes, SU = subnival zone.

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