Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet

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Abstract We explored patterns of plant species richness and composition along an elevational gradient (4,985–5,685 m a.s.l.) on Buddha Mountain, 100 km northwest of Lhasa, Tibet. We recorded the presence of plants and lichens in 1-m^2 quadrats separated by 25-m elevational intervals (174 quadrats in 29 elevational bands) along a vertical transect with a SE aspect. We recorded 143 total species, including 107 angiosperms, 2 gymnosperms, 27 lichens, and 7 mosses. We measured stone cover in each quadrat, and soil pH, C, N and C/N ratio from two randomly located samples collected from 10-cm depth within each band. C, N and C/N decreased with elevation, stoniness increased and soil pH did not change with altitude. We employed detrended correspondence analysis (DCA), canonical correspondence analysis (CCA) and generalized linear models (GLMs) to assess the relationships of species richness and species composition to the environment. The first two axes of

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the CCA biplot explained 87.7% of total variation in the species-environment relationship, and 27.7% of total variance of species data. The first CCA axis is associated with elevation, while the second axis is related to soil pH and stone cover. We also compared patterns in species richness against expectations from species pools interpolated from the literature. Total species richness was relatively constant between 4,985 and 5,400 m a.s.l. and declined continuously above 5,400 m a.s.l. Similar declining patterns were observed for forbs and graminoids. Cushion plants and lichens abundance exhibited a unimodal relationship with altitude while shrubs declined monotonically. Except for lichens, models derived from our observations and the literature were quite similar in shape. The proportion of the species pool represented in each elevational band increased as a function of elevation for non-vascular plants, but decreased markedly for vascular plants. Thus, vascular plants are more likely to be constrained by dispersal at higher elevations, resulting in more local endemism, while the relatively easily-dispersed high-elevation cryptogams have little local differentiation. Our comparative approach demonstrates that complex scale-dependent differences between life forms may underlie the apparent simplicity of elevational gradients. Furthermore, elevational gradients summarized from distributional notes cannot be assumed to be proxies for elevational gradients on individual mountain slopes.

Plant and lichen nomenclature Wu (1983–1987) for vascular plants; Li (1985) for mosses; Wei and Jiang (1986) for lichens

Introduction

Variation of plant richness with altitude is one of the most prominent biodiversity patterns (Körner 2000; Whittaker et al. 2001; Nogués-Bravo et al. 2008) and has stimulated much interest among naturalists, ecologists, and evolutionary biologists. In a review of 204 published studies, Rahbek (2005) found a unimodal relationship between richness and elevation in almost 50% of the studies, a monotonic pattern in 25% and a mixed pattern in the remaining 25%. However, the mechanisms behind such patterns are a matter of ongoing debate (Rahbek 1995; Odland and Birks 1999; Grytnes and Vetaas 2002; Wang et al. 2007).

Studies that employ niche modelling and interpolation for vascular plants almost invariably reveal unimodal elevational richness patterns (e.g., Colwell and Lees 2000; Grytnes and Vetaas 2002; Rahbek 2005; Wang et al. 2007; Baniya et al. 2010). However, the monotonically declining diversity pattern is particularly marked when conditions supporting life reach their absolute limits at high elevations. A decrease in species richness with altitude is likely caused by an increase in physical and physiological constraints on plant growth associated with frosts and desiccation (Körner 2000).

High mountain biodiversity is sensitive to climate change (Pauli et al. 2007). Observed shifts in elevation range and increasing richness of vascular plants

towards mountain summits have been attributed to climate change (Pauli et al. 2007; Klimeš and Doležal 2010; Dvorský et al. 2011). Climate change has caused sensitive, rare and endangered species to disappear, and invasive species have started to appear in the high alpine zone (Grabherr et al. 1995). Global climate change may greatly impact high mountain ecosystems, especially in poorly studied regions such as the Himalayan range where changes in the precipitation regime, in addition to temperature, may strongly affect alpine species diversity in this region (Jin-Ting 1992).

Our knowledge of high alpine biodiversity in the Himalayas is mainly the result of collection of specimens during expeditions (Grytnes and Vetaas 2002; Wang et al. 2007; Baniya 2010; Baniya et al. 2010). Field based (i.e., quadrat- or transect-based) studies are rare, particularly in high alpine zones. Here, we performed field-based species richness studies in subtropical mountains to substantially higher elevations (>4,900 m a.s.l.). Patterns derived from an interpolation of species ranges (Baniya 2010) were used to represent the species pool and were compared to results of a quadrat-based field study at a similar elevation range.

A number of researchers have contributed to our understanding of elevational determinants of plant distributions in the Himalayas. Du (1992), Jin-Ting (1992), Shu (1992), Weilie et al. (1992) described altitudinal vegetation zonation of Tibet. Wang et al. (2002) investigated vascular plants between 3,255 to 4,340 m a.s.l. Wang et al. (2007) studied the elevation gradient of vascular plants in Gaoligong Mountain between 215 to 5,200 m a.s.l. using secondary data. Knowledge of plant distribution was augmented by several expeditions, culminating with one organized by the Alpine Garden Society (Birks et al. 2007). Miehe (1991) and Birks et al. (2007) reported *Saussurea gnaphalodes* (at 6,400 m a.s.l.) as the highest flowering plant in the Nepalese Himalaya, followed by *Ermania himalayensis* (6,300 m a.s.l.), *Arenaria bryophylla* (6,200 m), and *Stellaria decumbens* (6,100 m). Miehe (1991) further reported an upper limit of continuous vegetation between 4,600 and 5,500 m a.s.l. and patches between 5,700 and 6,000 m a.s.l. in the central Himalaya and East Asia. Dvorský et al. (2011) reported species-rich scree vegetation of Ladakh, West Himalaya.

Lichens, which not only tolerate cold but repeated desiccation, exceed the maximum elevation of phanerogams and mosses (Körner 2003; Feuerer and Hawksworth 2007). The absolute record of lichens is 7,400 m a.s.l. from the Himalayas (Hertel 1977).

Patterns of species composition found in the well-studied temperate zone may differ from those in the subtropics, because weaker seasonality might lead to proportional differences in life forms. Life-form composition may indicate trait-specific patterns along the elevation gradient (Virtanen and Crawley 2010). A qualitative change in species composition and turnover is expected with forbs dominating low elevations followed by cushions and crustose lichens dominating the highest elevations. It is likely that the elevational gradient in richness is differentially expressed in different life forms, both with respect to shape and location of the peak (if any). The purpose of this study is *i*) to assess the elevational gradient in species composition, *ii*) to document the richness-elevation relationship on a high-elevation subtropical mountain, *iii*) compare a quadrat-based richness pattern to models based on interpolated elevational species ranges, and *iv*) to compare and contrast the relationship among life forms.

Materials and Methods

Study Area

Buddha Mountain is situated at 30°11′ N, 90°29′ E, 100 km northwest of Lhasa, central Tibet (Fig. 1). The study area lies between 4,985 to 5,685 m a.s.l. with the permanently snow-covered peak reaching 7,000 m a.s.l.

The Tibetan climate is warm and humid in the southeast and cold and arid in the northwest (Chang 1981; Miehe 1988). Temperature and precipitation decline towards the northwest causing a reduction in plant diversity (Ni 2000). Damxung Climatological Station at 4,200 m a.s.l., and ca. 80 km north of our study area (Fig. 1), is the nearest climatological station. It has an annual mean temperature of 1.5°C, with 14°C summer average and −7°C winter average temperatures, high daily temperature fluctuations from October to March (10°C and −25°C) and a mean annual precipitation of 442 mm (Meteorological Bureau of Lhasa). The rain primarily falls from June to September. Winter precipitation is erratic in Tibet (Harris 2006). Precipitation occurs in the form of snow and hail from October to March and a thin layer of snow often covers the vegetation during winter. Above 5,000 m, aridity, solar radiation, and wind velocity increase as a function of elevation (Ni 2000).

Vegetation on Buddha Mountain consists of alpine steppe and alpine desert with characteristic substrate and dominant plant species (Table S1 in Electronic Supplementary Material, hereafter ESM).
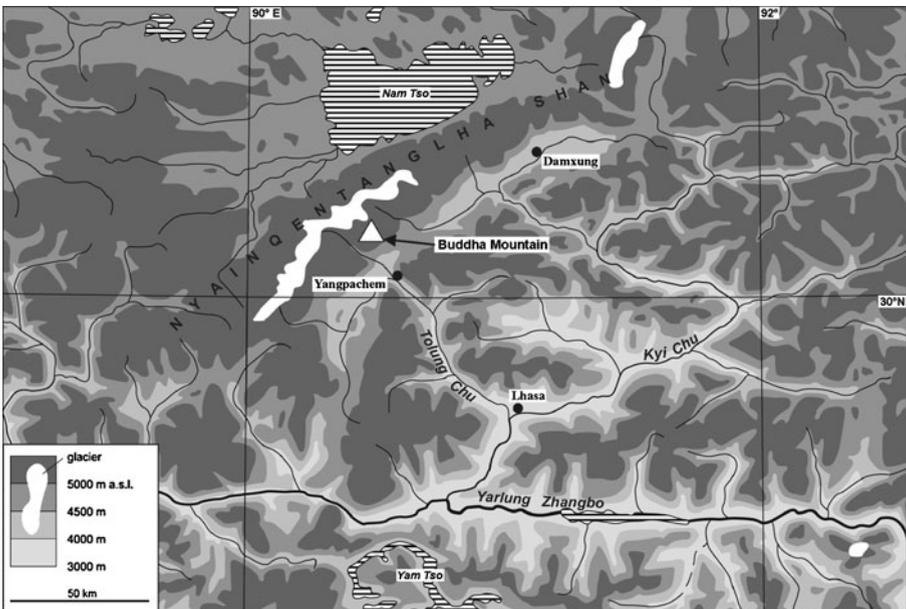

Fig. 1 Map of Central Tibet with location of the study area, the Buddha Mountain. (Modified after Joachim Schmidt, pers. comm.)

Sampling

We sampled vegetation in the summer of 2006 and 2007. We followed the approach of Kessler (2000) and Bruun et al. (2006) to study community composition and diversity along elevational transects by subdividing the gradient into 29 elevational bands, each band separated by 25-m vertical elevation. Our transect (4,985–5,685 m a.s.l.) was located on a slope of Buddha Mountain facing southeast, parallel to a small creek. In each band, six 1-m² quadrats were placed horizontally at 10-m intervals. In total, 174 (6×29) quadrats were studied.

We recorded the presence of all vascular plant, bryophyte, and lichen species in each quadrat. No liverworts or pteridophytes were found. The percent stone cover per quadrat was visually estimated. Because we do not have soil data from each quadrat in each band (see below), we pooled data from the six quadrats. Thus, a species is considered present in a band if it is present in at least one of the six quadrats in the band. Preliminary analyses (not shown) based on mean quadrat richness were qualitatively similar to those presented here. We used the average of the stone cover estimates in the six quadrats to represent the stone cover of the band.

Field identification of vascular plants was done using Polunin and Stainton (2001) and Stainton (2001). Unidentified taxa were collected, and final identification and confirmation were done after comparison with identified specimens previously deposited in the Bergen University Herbarium (BG) and by consulting experts. Nomenclature followed Flora Xizangica (Wu 1983–1987) for vascular plants, Li (1985) for mosses and Wei and Jiang (1986) for lichens. All specimens were deposited at Bergen Museum Herbarium (BG). Some taxa remain unresolved due to difficult taxonomy and were listed as *Oxytropis* 1 and 2, *Saussurea* 1, 2 and 3, *Thuidium* sp. and *Funaria* sp. However, we are confident that these undetermined taxa are distinct from each other at the species level, and thus the lack of species epithets will not affect our measures of the elevational richness pattern.

Species Pools Interpolated from Species Ranges in Floras

We subcategorize total richness into vascular richness, graminoid richness and lichen richness as in Baniya (2010). Baniya (2010) published regression models for species richness as a function of elevation, by interpolating elevation ranges of species between 4,900 and 6,000 m a.s.l. from Tibet Autonomous Region based on Flora Xizangica (Wu 1983–1987; Li 1985; Wei and Jiang 1986). In the current paper, we consider these interpolated large-scale species-richness measures to be a measure of the species pool, which we compare to patterns shown by local, quadrat-based, species-richness measures from Buddha Mountain.

Soil Analysis

Two soil samples at a depth of 10 cm were taken randomly from two of six quadrats in each elevation band. Soil pH was measured using a digital pH meter model *131E* in a soil/distilled water suspension (2:5). Soil pH was measured using a digital pH meter (type: 3010, serial no. 3389, Jenway Ltd.) in a soil/distilled water suspension (2:5). Total nitrogen (N) was quantified using the Kjeldahl digestion process and

total carbon (C) with the Walkley-Black method. All these analyses were done in the soil laboratory, Lalitpur, Nepal following Sumner (1999). We averaged the data from the two samples to represent values for the band. Soil C and N were then log transformed.

Data Analyses

We applied ordination to analyze species composition and turnover both with and without environmental variables. Detrended correspondence analysis (DCA) was applied after detrending by segments, non-linear rescaling and down-weighting of rare species to assess gradient length (Lepš and Šmilauer 2003: 50). The length of the first DCA axis was 4.7 SD units, thus justifying use of unimodal methods such as CCA (Lepš and Šmilauer 2003). We used manual forward selection with 499 permutations in CCA to select environmental variables explaining species composition. Ordinations were implemented using CANOCO for Windows 4.5 and CanoDraw 4.0 (ter Braak 2002; ter Braak and Šmilauer 2002).

We analyzed the correlation among environmental variables and total species richness per elevation band, as well as vascular and non-vascular plants (cryptogams) richness separately. The vascular richness was further subdivided into its life forms: forb, shrub, cushion, graminoid (Cyperaceae, Juncaceae, and Poaceae), moss and lichen richness. We employed generalized linear models (GLMs, McCullagh and Nelder 1989) to relate richness to elevation. Because response variables were counts, we tested the dispersion in our data and they showed overdispersion. Thus a quasi-Poisson distribution and a logarithmic link were employed. Inspection of diagnostic plots between a logarithmic link and an identity link (assuming a normal distribution of errors) confirmed that a quasi-Poisson distribution with a logarithmic link function was better than a normal distribution and an identity link. We tested up to third-order linear models to describe the relationship between species richness and elevation. GLMs using linear, quadratic or cubic polynomials were first tested against each other and then with the null model if the previous was statistically significant. An F-test was used to select the best model (the best model is with the highest F-value among the significant models). Similar regression methods were derived for interpolated species range data (Baniya 2010). The best model based on the interpolated data was compared with the best model based on the quadrat data for corresponding life forms. The final graphs were based on the best selected model. We used R 2.8.1 statistical package (R Development Core Team 2008) for all regressions.

Results

We recorded a total of 143 species, including 107 angiosperms in 68 genera, two gymnosperms in two genera, 27 lichens in 23 genera, and seven mosses in seven genera (Table S2 in ESM). The vascular plants are represented by four life forms, among which forbs were the most common with 88 species including succulents (six species) followed by graminoids (eight species), cushions (seven species) and shrubs (six species).

Environmental Correlations

Elevation had significant correlations with all measured soil- and substrate-related variables except pH (Table 1). Soil N, C, and C/N ratio showed negative correlations with elevation, whereas percent stone cover increased ($r=0.78$, Table 1). Soil pH did not have significant relationships with other measured environmental variables (Table 1).

Species Composition and Distribution

A CCA biplot (Fig. 2) derived from forward selection of explanatory variables revealed that species composition is strongly driven by elevation. The first axis eigenvalue of the CCA is 0.638, which is almost as high as the first axis eigenvalue of correspondence analysis (0.659). This implies that the measured variables successfully explained the strongest gradient. The eigenvalue of the first CCA axis is much stronger than the second (0.213), implying that elevation dominates the species-environment relationship (Jongman et al. 1995), while the second axis is dominated by pH and stone cover.

The soil-related variables C, N and C/N are significantly related with elevation and stone cover (Table 1) but were non-significant during the CCA's manual forward selection. Likewise, soil pH and stone cover are non-significantly correlated with elevation but significant during manual forward selection of CCA. It is likely that elevation acts as a composite surrogate of moisture, temperature and disturbance, and its collinearity with other variables prevented their inclusion during forward selection.

The species towards the left side of the CCA biplot (Fig. 2; Table S2 in ESM) were generally vascular plants (largely forbs) that had higher abundance at lower elevations. Species showing their highest abundance towards higher elevations (right side of the biplot, Fig. 2) were mostly lichens. Forbs such as *Astragalus donianus*, *Potentilla anserina*, *Polygonum campanulatum*, *Stellaria subumbellata* and the dominant graminoid *Kobresia pygmaea* favoured moderate soil pH, moisture and nitrophilic plants at the lower elevation (Fig. 2; Table S2 in ESM). Such plants inhabited stream-bed sediments, with less stone cover than those at high elevation.

Table 1 Spearman's rank correlation coefficient matrix for the environmental variables measured along an elevation gradient of Buddha Mountain. The critical tabulated value for the Spearman's rank correlation coefficient is: $n \leq 29$, $P\alpha(2) \leq 0.05 \geq -0.36$

	Elevation	% stone	pH	N	C
% stone	0.78				
pH	−0.3	−0.01			
N	−0.82	−0.85	0.19		
C	−0.87	−0.9	0.16	0.97	
C/N	−0.67	−0.64	0.16	0.52	0.58

% stone — average percentage of stone cover per band, pH — concentration of H^+ ion of soil, N — % of total nitrogen, C — % soil organic carbon, and C/N ratio — ratio of soil organic carbon and nitrogen.
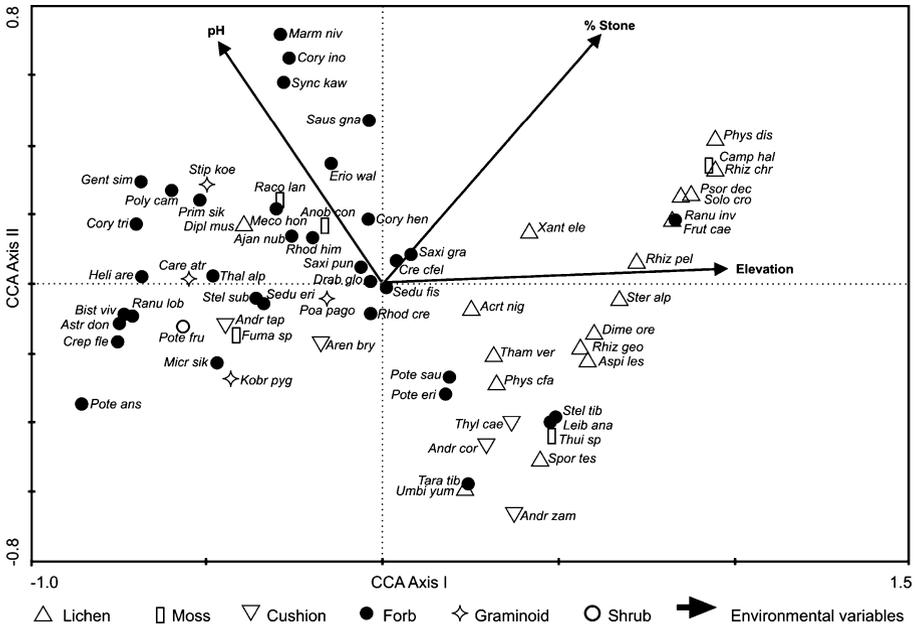
Fig. 2 CCA species-environment biplot for the Buddha Mountain data. The first two axes explained 87.7% of total variation in species-environment relation and 27.7% of total variance in the species data. Scaling is based on the inter-species biplot. The three significant ($P \leq 0.05$) environmental variables were selected after manual forward selection and 499 permutations (Monte Carlo permutations tests). The full name for each species is given in Table S2 in ESM. For clarity, the positions of some species were changed slightly to avoid overlap: only species with abundances greater than 10% of the maximum abundance are displayed

Species occurring between 5,100 and 5,300 m a.s.l. were scree-dwellers. The shrub *Potentilla fruticosa* and stone-created microhabitats may have facilitated the nucleation of herbs such as *Bistorta vivipara*, *Crepis flexuosa*, *Ranunculus lobatus*, graminoid *Carex atrofusca* and the moss *Racomitrium lanuginosum* at these elevations. These species had their optimal abundance towards lower elevations with low stone cover (Fig. 2; Table S2 in ESM), and are characteristic of the alpine steppe or the mid-alpine zone.

The forb *Ranunculus involucratus*, lichens *Frutidella caesioatra*, *Psora decipiens*, *Rhizoplaca chrysoleuca*, *Stereocaulon alpinum*, *Solorina crocea*, and the bryophyte *Campylophyllum halleri* had optima towards the higher elevation, i.e., end of CCA axis I (Fig. 2; Table S2 in ESM). Elevations above 5,300 m a.s.l. had the highest stone cover but sparse vegetation, and were mostly dominated by crustose lichens and a few mosses. These elevations also represent the drier end of the gradient with lower carbon and nitrogen content in soil.

Cushion plants such as *Androsace coronata*, *Androsace tapete*, *Androsace zambalensis*, *Arenaria bryophylla*, and *Thylacospermum caespitosum* occurred towards the middle of CCA axis I (Fig. 2; Table S2 in ESM).

Draba glomerata and *Rhodiola himalensis* (both 5,000–5,500 m a.s.l.), and the saxicolous lichen *Xanthoria elegans* (5,000–5,700 m a.s.l.) were the most dominant species along our elevational gradient and all had a wide elevational range. An

optimal abundance for the crassulacean succulents: *Rhodiola crenulata, Sedum fischeri, Sedum erici-magnusii* and the graminoid *Poa pagophila* occurred towards the center in the CCA biplot (Fig. 2), which may indicate moderately disturbed scree towards undisturbed micro-habitats created by rocks.

Species Richness

Total species richness ranged from 8 to 45 species per band. Vascular plants ranged from 0 to 40 species, and lichens from 0 to 16 species. The average number of species per band was 29 for total species, and 21 for vascular plant species. Forbs and lichens had opposite trends in their contribution to the total richness. The lowermost elevation band had about 80% forbs (Fig. S1 in ESM). Graminoids had the third largest share of species, but did not occur in the six highest elevation bands. Shrubs were limited to the lower half of the measured gradient (Fig. S1 in ESM). Mosses and cushions were minor vegetation components; the highest four bands were devoid of cushions.

Total species richness was relatively constant at about 36 species up to 5,400 m, above which it declined continuously (Fig. 3a; Table S3 in ESM). This pattern also held for vascular plant richness (Fig. 3b), forb richness (Fig. 3d) and graminoid richness (Fig. 3g). However, shrub richness (Fig. 3e) exhibited a monotonic decline within the measured elevational range. Although the fitted curves for vascular plants, forbs, and graminoids seem to indicate unimodality, the data themselves do not (Fig. 3b,d,g; Table S3 in ESM). This disparity between data and models is due to the inability of polynomial functions to describe plateaus. Richness of cushion plants showed a unimodal pattern with a peak between 5,360 and 5,385 m a.s.l. (Fig. 3f).

Similar to the richness of vascular plants, cryptogam species richness also showed marked and differential trends with elevation (Fig. 3c; Table S3 in ESM). Lichen richness (Fig. 3h) behaved like cryptogam richness (Fig. 3c) because most cryptogam species were lichens. Only a few species were mosses (not shown). Richness of lichens increased at elevations where vascular species richness gradually declined (Fig. 3a,c). Both cryptogam and lichen richness had their maximum mean richness at 5,500 m a.s.l. The most frequent lichens at this elevation were *Frutidella caesioatra, Psora decipiens, Rhizoplaca chrysoleuca, Solorina crocea, Stereocaulon alpinum* together with the forb *Ranunculus involucratus*, and the moss *Campylophyllum halleri* (Fig. 2).

Comparison between Local Richness and that of the Species Pool

As expected, richness derived from our measure of the species pool was generally higher than richness of field data. For plants, models from observed and interpolated species ranges demonstrated similar declining patterns (Fig. 4a–d). In contrast, observed lichen richness showed a marked unimodal relationship (Fig. 4d). A unimodal pattern with the maximum lichen richness at 5,500 m a.s.l. (Fig. 4d) is distinguished from its smoothly declining pattern in interpolated species ranges. Minor initial peaks and valleys were also observed in other interpolated curves. The sharper patterns in the quadrat study contrast to the smooth patterns from literature. It is presumably a result of spatial scale used, although we cannot rule out artifacts of interpolation.
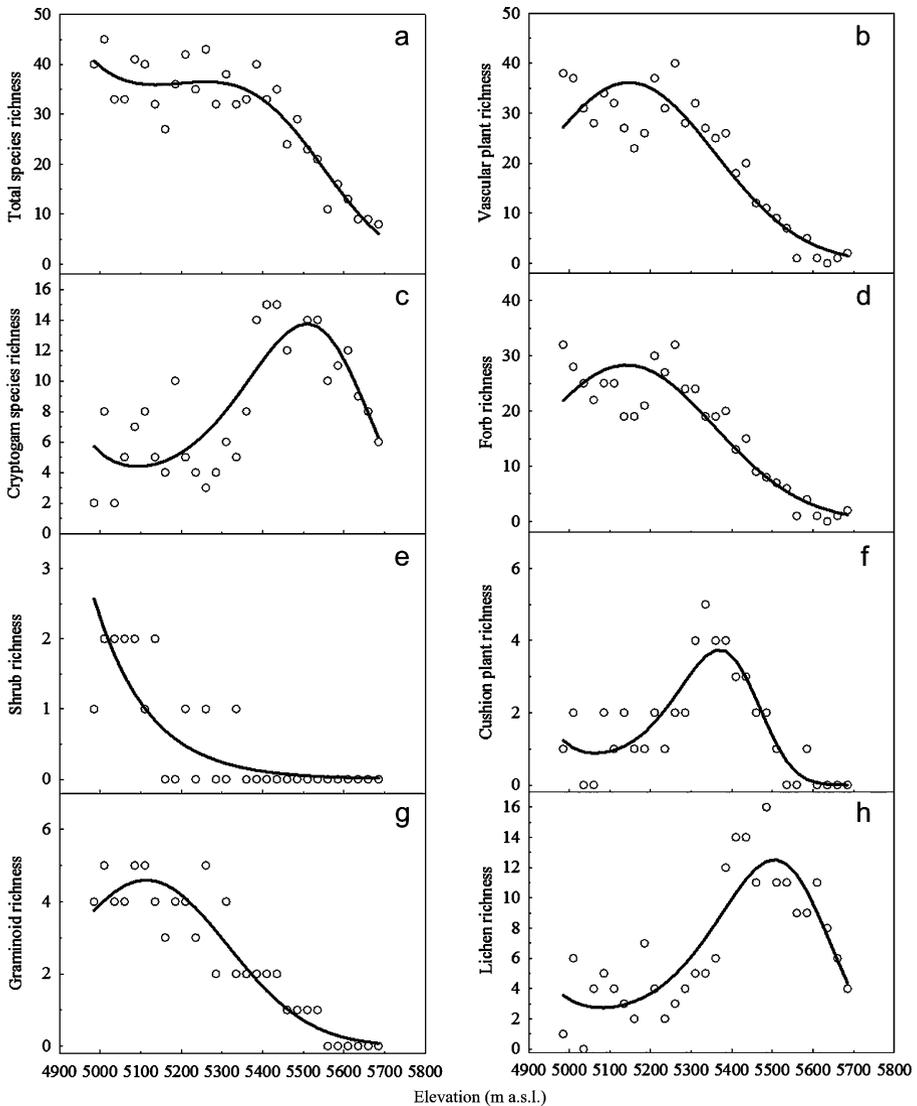
Fig. 3 The relationship between species richness (of six 1 m² quadrats) and elevation, with polynomial regression functions through GLM superimposed: **a** all species; **b** all vascular plants; **c** all cryptogams; **d** forbs; **e** shrubs; **f** vascular cushion plants; **g** graminoids; **h** lichens. Note the differences in the scale of the ordinate

The vascular plant richness in quadrats was, as expected, positively correlated with the species pool (Fig. 5a). In contrast, non-vascular richness exhibited a negative relationship. Thus we found marked differences between the species richness of vascular and non-vascular plants in their relationship with their corresponding species pools (Fig. 5a,b). In particular, vascular plants species richness is a much smaller fraction of the species pool at higher elevations than at lower elevations (Fig. 5b). Non-vascular plant richness is a higher proportion of the species pool at high elevations than at lower elevations.
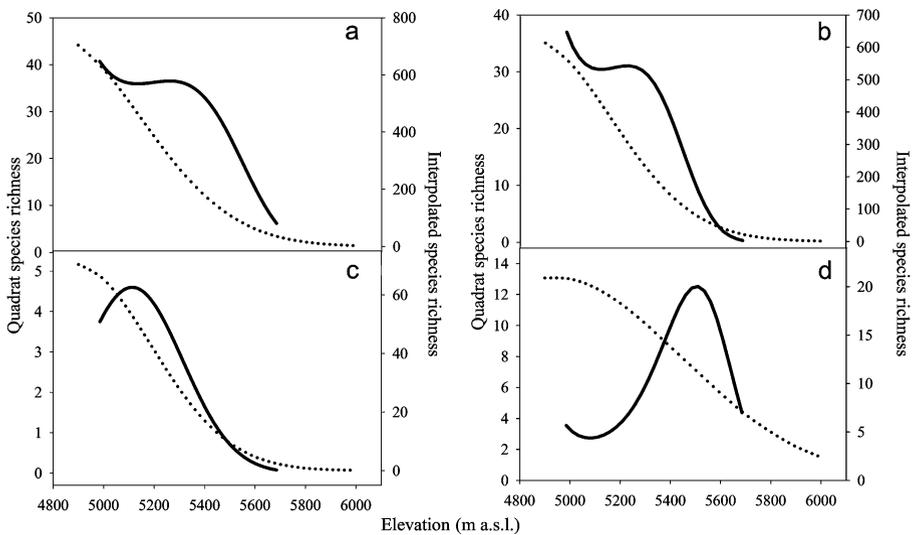
Fig. 4 Polynomial GLM regression models of species richness as a function of area for quadrat richness (*solid lines*; these models are the same as in Fig. 3 and interpolated species ranges (*dotted lines*). Note differences in scale in the ordinates. **a** total richness; **b** total vascular plant richness; **c** graminoid species richness, and **d** lichen species richness

Discussion

We documented an elevational decline in the total species richness both at the quadrat scale, and by using interpolated species ranges. However, this pattern did not equally apply for all functional and taxonomic subsets of species. In particular, quadrat richness of cryptogams, cushions, and lichens displayed unimodal relationships with elevation. In contrast, the richness derived from elevational range data exhibited smooth declines. The lack of unimodal patterns could be due to a lack of low altitudes considered here. Patterns for vascular plant richness were broadly consistent in both types of data.

The elevational decline of total species richness in quadrats is consistent with other alpine studies both for the Tibetan Plateau and elsewhere (Grabherr et al. 1995; Pavon et al. 2000; Körner 2003; Bruun et al. 2006; Wang et al. 2006; Birks et al. 2007; Baniya 2010; Klimeš and Doležal 2010; Dvorský et al. 2011). However, there are differences in the details of the decline. For example, we observed fairly constant richness up to 5,435 m a.s.l. and then a continuous decline afterwards, in contrast to the stepwise decline as found in the Alps by Grabherr et al. (1995). Habitats such as springs, fens, rock and scree communities, pioneer vegetation on moraines, snow beds, and avalanche paths that are common in our studied sites likely creates azonal communities (Grabherr et al. 1995) instead of stepwise declines. Differences in species-richness patterns between vascular plants and cryptogams have been reported previously (Bruun et al. 2006; Grytnes et al. 2006; Virtanen and Crawley 2010). However, the between-group variation in our study was much stronger and varied than we have found in the literature.

Besides general similarities, there are minor differences in the modelled trends between the quadrat and interpolated species richness, presumably due to the

Fig. 5 The relationship between species pool and local richness based on quadrats. **a** quadrat richness *vs* species pool richness, on a double logarithmic scale. The central diagonal is the line of equality. For both vascular plants and non-vascular plants, the lower-elevation bands are towards the right side (*higher species pool*), and the higher elevation bands are towards the left (*lower species pool*). **b** Species richness in quadrats expressed as a percentage of the species pool, for vascular and non-vascular plants
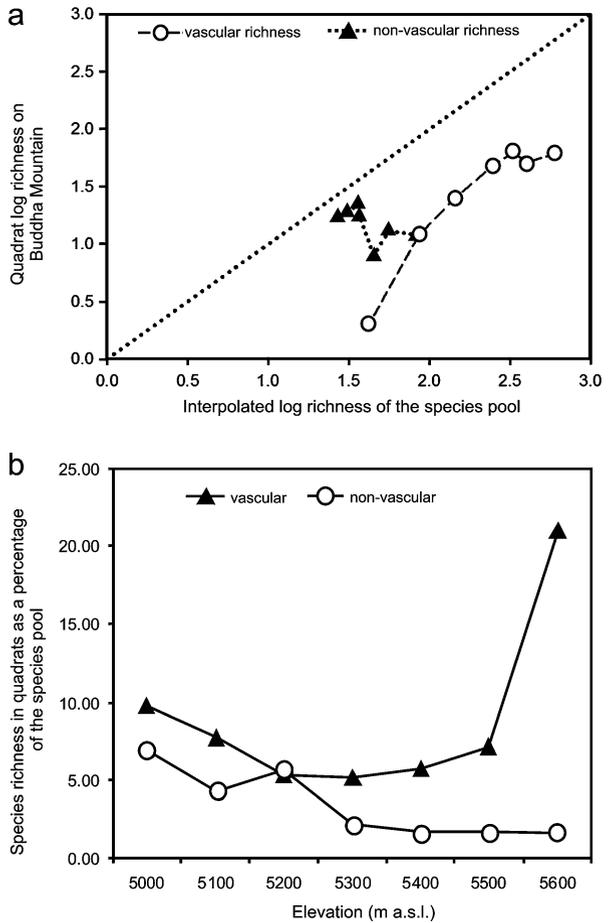
differences in the size of the area studied. Larger areas at lower elevations may inflate species richness simply due to the species-area relationship (Kessler 2000; Jürgen et al. 2006), thus eliminating the plateau we found in our quadrat data. Environmental heterogeneity, largely minimized in our study, may vary as a function of elevation (Palmer and Dixon 1990; Palmer 2006) and thus accentuate differences compared to interpolation-based studies. Fine-scale environmental heterogeneity in factors such as soil pH, N, C, moisture, atmospheric humidity, disturbance, etc. may be effectively 'averaged out' at broader floristic scales. Also, local endemism, which may increase at higher elevations for biogeographic regions (Jürgen et al. 2006; Dvorský et al. 2011), will inflate the high-elevation richness in floras covering many mountains, but not necessarily in quadrat-based studies on a single mountain. Interestingly, the unimodal richness pattern we found for lichens studying quadrats differed from the elevational declining pattern from interpolated species ranges. This implies that the elevational response of lichens, a vastly understudied species-rich taxonomic group, may be strongly influenced by the size of area studied. Micro-environments suitable for cryptogams may be better resolved at a fine scale (quadrat based study) than at larger regional scales.

The elevation of maximum richness of lichens (5,500 m a.s.l.) was the highest among all biological groups in this elevational gradient. In general, lichens reach higher maximum elevations than phanerogams and mosses (Hertel 1977; Körner 2003; Feuerer and Hawksworth 2007). Frost action, below-freezing temperature, strong wind, snow, poor soil, lack of humidity, strong solar radiation and short growing season may strongly impact the distribution of vascular plants at high elevation. However, such conditions are not necessarily destructive to lichens that have the capacity to survive simulated (de Vera et al. 2004) and real (Sancho et al. 2007) conditions in interplanetary space. A linearly increasing elevational richness pattern for lichens has also been reported (Körner 2003; Grytnes et al. 2006). European Alps have a higher richness of moss than lichens (Theurillat et al. 2003; Virtanen et al. 2003), but as the Alps have lower alpine zones than the Himalayas, they do not capture the descending part of the unimodal richness curve.

In this study, the observed patterns for the total species richness and richness within life-form groups are consistent with general hypotheses of diversity concerning available energy, disturbance, and environmental stress and stability (Whittaker et al. 2001). Temperature and precipitation decrease with increasing elevation, and limit the distribution of most species. Normally, we expect high species richness at lower elevations with high energy than at higher elevations with low energy, as predicted by the energy hypothesis (Brown 1981; Wright 1983). This hypothesis was proposed for woody species richness in the tropics and subtropics at a macro scale (Brown 1981; Wright 1983; O'Brien 1993) but may also apply to non-woody species. Other general hypotheses related to disturbance (Huston 1994) and stress and stability (Callaway 2002) are plausible explanations for local-scale patterns; although we have no data to address such hypotheses here.

Numerous studies (e.g., Cornell 1993) describe strong positive relationships between the size of the species pool, as inferred from species ranges, and the number of species in a local community. Indeed, we found such a pattern for vascular plants. In contrast, we found a surprising negative relationship (which we believe to be unprecedented in the literature) for non-vascular plants. At the higher elevations, non-vascular plant richness represented a higher proportion of the species pool than at lower elevations. It may be harder for vascular plants to reach suitable habitat at high elevations, while the diaspores of non-vascular plants may easily reach suitable habitats. It is also possible that local extinction rates of vascular plants are higher at the higher elevations. Our observation may also imply that there is local geographic segregation of vascular species at lower elevations, and non-vascular plants at higher elevations.

Our ordination analysis clearly indicated a transition from alpine steppe to desert steppe vegetation. We found a dominant elevational gradient in the species composition that was only slightly modified by other environmental factors. The Tibetan Plateau is unique because of its very high elevation and strong solar radiation. Elevation is confounded with gradients in temperature, moisture, precipitation, disturbance (not measured). In addition, low precipitation is likely to be a limiting factor (Chang 1981; Birks et al. 2007; Klimeš and Doležal 2010). Other studies on vegetation of the region indicate the importance of moisture and temperature affecting zonation (Du 1992; Jin-Ting 1992; Shu 1992; Weilie et al. 1992). In a palaeoecological study of pollen sediments in 112 lakes in the Tibetan

Plateau, Herzschuh et al. (2010) demonstrate that regional vegetation has been sensitive to changes in temperature and moisture over the past 50 millennia.

Grazing is another factor that may influence elevational distributions of plants, as the highlands of Tibet represent one of the largest extensively grazing rangeland systems in the world. Tibetan pastoralism has a history of more than a millennium (Spicer et al. 2003; Miehe et al. 2006; Klein et al. 2007). While we have no data supporting this view, it is worth noting that *Stellera chamaejasme*, which is resistant to tramping and grazing (Miehe et al. 2006), occurred towards the lower elevation in our study. This supports the possibility that the elevational gradient in vegetation is, in part, a gradient of decreasing grazing intensity. Klein et al. (2007) suggests, the quality of Tibetan rangeland has been changed after global warming through invasion of the non-palatable *Stellera chamaejasme.* Although high elevation vegetation in Tibet has been sensitive to climate, and perhaps grazing, there is no palaeo evidence that conditions were favorable for forests or woodlands in the elevational range studied (Miehe et al. 2006; Baniya 2010; Herzschuh et al. 2010).

We conclude that while there are broad consistencies between richness models derived from species ranges, and those derived from field data, they differ in important aspects. Some of the differences are subtle, such as differences in the shapes of curves while others are prominent, such as the opposing patterns of non-vascular *vs* vascular plant richness as a proportion of the species pool. Important questions regarding the differences between growth forms and taxonomic groups remain unanswered. As these questions involve the roles of spatial scale, environmental heterogeneity, and biogeographic processes, we believe that comparisons of range-derived and field-derived richness measures are a fruitful avenue of biogeographic research.

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