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Vascular and Cryptogam Richness in the World's Highest Alpine Zone, Tibet

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This study explores the elevational richness patterns of vascular and cryptogam species in the highest alpine zone in the world, the Tibet/Xizang Autonomous Region (78°25′–99°06′E, 26°50′–36°53′N). The data are based on the published flora for vascular plants, bryophytes, and lichens. Elevational ranges have been interpolated for each species recorded in the flora at altitudes between 4500 and 6000 m into 16 elevational bands of 100 m each. A species is assumed to be present at all elevational bands between its lower and upper limits as recorded in the flora. Total richness has been further subcategorized into richness of different functional groups and some dominant angiosperm families. Generalized linear models (GLMs) up to 3 orders are applied to assess the relationship between species richness and elevation and the statistically most appropriate model based on the highest F *value among the significant models is selected. A total of 1585 species, 385 genera, and 111 families are recorded in the flora from this part of the alpine zone. Flowering plants are represented by 1328 species, 261 genera, and 54 families. A significant decreasing quadratic relation with increasing elevation is the most common pattern among most of the functional groups. Bryophytes, lichens, and their functional groups show a linear declining pattern except for a quadratic relation in foliose lichen richness. A significant unimodal relation is found with some angiosperm families. The patterns found are both similar and dissimilar to published results from studies using interpolation or direct observations. Scale, environmental heterogeneities, stress, disturbance, and tolerance by individual species are the likely causes for these patterns.*

Keywords: *Alpine zone; species richness; elevation; declining pattern; interpolation; Tibet; Himalaya.*

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Introduction

Alpine life and its biodiversity are of considerable international interest (Körner 2003; Nagy and Grabherr 2009). How life adapted to alpine environments is a very challenging question, perhaps second only to the fundamental question of why there are so many species in the tropics. Survival in an alpine zone involves adaptation to severe cold and a short growing season. It is a habitat where many new species are yet to be discovered and described, and where a greater rate of speciation may take place due to long-term isolation, which is generally believed to increase with increasing elevation (Kluge et al 2006). Latitudinal and elevational declines in species richness are established patterns of nature first noticed by Alfred Russel Wallace (1878). However, studies of species richness at high elevations and high latitudes are comparatively less common than elsewhere (Körner 2003), partly because these areas are difficult to access and generally have a low number of species.

Present-day rates of global warming and associated melting of alpine glaciers are creating open habitats for colonization by different life forms. These changes are more pronounced in arctic and alpine zones than in other areas. The upward shift of species from lower elevations and the disappearance of alpine species with a narrow niche at lower elevations have already been observed (Klanderud and Birks 2003). Thus, there are now records of a rapid increase in the diversity of alpine zones (Klanderud and Birks 2003; Salick et al 2009). Colonization normally takes place in such open habitats by dynamic or static equilibrium mechanisms (Brown 1981; Huston 1994). One common belief in community ecology is that a certain number of species exists within a particular space and time, but that the number varies according to the scale of measurement (Palmer 2006). Hence a pattern exists (MacArthur 1965) that changes with space, time, and scale of measurement. Commonly, one may expect an elevational decline in species richness when the environment is harsh and difficult to colonize. Species richness will be zero (except for some bacteria) if the environment is too harsh for a particular life form.

The alpine zones cover 5% of the world's land area and support 10,000 flowering plant species, 2000 genera, and 100 families (Chapin et al 1997; Körner 2003). The main characteristic of an alpine zone is its treelessness.

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There are many definitions of what a "tree" is and controversial discussions about the factors determining the upper treeline (Körner 2000, 2003; Miehe and Miehe 2000; Körner and Paulsen 2004; Miehe et al 2007). The Tibet/Xizang Autonomous Region (TAR) has the highest known elevation for treeline in the Northern Hemisphere at about 4850 m for *Juniperus tibetica* (Miehe and Miehe 2000; Miehe et al 2007).

Tibet is the highest and the youngest high-altitude plateau in the world with an average elevation of 4500 m (Miehe et al 2007). Körner (2003) defines the alpine area as a life zone between the upper treeline and the snowline. Thus the Tibetan alpine zone is the highest alpine bioclimatic zone in the Northern Hemisphere. The lower and upper elevation limits of the TAR's alpine zones are debated in the literature. The alpine elevation range is defined here as between 4500–6000 m.

The TAR hosts about 5766 flowering plant species, accounting for approximately 19% of the flora of China and 2% of the world's flora (Wu 1983–1987; Barthlott et al 2005; Birks et al 2007). Besides its highest elevational range, the TAR has a pronounced topography with a great influence on the atmospheric circulation that in turn greatly influences global climate. The TAR experiences very high solar insolation and high UV-B radiation and is geologically young because of recent tectonic uplift. The present-day vegetation of the TAR is the result of severe human disturbances in the past (Miehe et al 2009) and/or the result of climate change (Birks et al 2007; Herzschuh et al 2010).

The TAR lies within 2 major biodiversity "hotspots"—the Himalaya (India, Nepal, and Bhutan) to the south and western China (Yunnan and Sichuan) (Birks et al 2007) to the east—and two large "cold spots," the Karakorum Mountains and the Takla Makan Desert (Dickoré and Miehe 2002). No biodiversity studies have been published on the alpine zone of the TAR concerning elevational species richness patterns between 4500–6000 m, namely the mid- to high-alpine zone of the TAR.

Flora provide the best available documentation of diversity. Thus this study is based on previously documented flora to analyze the elevational species richness patterns of different plant and lichen groups. The aim is to evaluate whether total richness and richness for the biological subgroups show a simple monotonically decreasing pattern with increasing elevation.

Material and methods

The TAR is located between 78°25′ to 99°06′E and 26°50′ to 36°53′N. The elevation range of the TAR lies between 700 and 8848 m, the so-called roof of the world. The vegetation ranges from montane forests, high-cold meadows, high-cold steppes, semi-deserts, and high–cold deserts of the subtropical southeast to the areas of the nival northwest (Chang 1981). The mean July temperature is 9°C in the western TAR and 11°C in the eastern TAR (Chang 1981). The boundary between meadow and steppe closely coincides with the 400 mm annual precipitation isohyet in northern Tibet and the 500 mm isohyet in southern Tibet. The transition between steppe and desert is approximately indicated by the 100 mm annual precipitation isohyet (Chang 1981). The climate of southeastern Tibet is mainly controlled by the Asian monsoon, whereas the northwestern area is mainly controlled by the westerlies (Chang 1981).

Flora Xizangica (5 volumes; Wu 1983–1987) for vascular plants, Li (1985) for bryophytes, Wei and Jiang (1986), and Obermayer (1996, 2004) for lichens are the main data sources for this study. I interpolated the elevational range of each species between 4500 and 6000 m above sea level and divided this elevational range into 16 bands of 100 m each. Data matrices for all alpine species between 4500–6000 m were prepared. Each matrix represents a separate taxonomic group. The presence of a species in the data matrix records the known occurrence of that species, usually documented by collections. A species is assumed to be present at all 100 m bands between its upper and lower elevation limits. For example, if a species, such as *Arenaria melandrioides*, is reported as 4200–5020 m in the flora, it is assumed to occur at all elevation bands considered in this study, namely, between the 4500 and 5000 m bands. This method is the same as the one used in interpolation studies from elsewhere in the Himalaya (Grytnes and Vetaas 2002).

Species richness here is an estimate of the total number of species or a particular group of species in an elevation band. It is a macroscale study (gamma diversity, sensu Whittaker 1972) that covers the area between 4500–6000 m of an entire region. Taxonomic ranks below species level were also treated as species as in Grytnes and Vetaas (2002).

There are some limitations to this study. It does not discuss endemism, any other diversity status, or particular geographic distributions, because the information regarding species richness has been taken from published flora written in Chinese, of which the author has limited knowledge.

The data were first analyzed using total species richness as a response variable and elevation as a predictor variable. Total species richness was further subdivided into richness of vascular, nongraminoid vascular, graminoid, 12 most dominant angiosperm families, total lichen, crustose, foliose, fruticose, bryophyte, pleurocarpous moss, acrocarpous moss, and hepatics. Vascular plants (pteridophytes, gymnosperms, and angiosperms) other than graminoids (Gramineae, Cyperaceae, and Juncaceae) were grouped as nongraminoid vascular richness, and the last 3 were grouped as graminoid richness. Richness patterns in the most dominant families of vascular plants were also analyzed, that is, for Compositae, Brassicaceae,

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Scrophulariaceae, etc, and for 3 groups of bryophytes: pleurocarpous mosses, acrocarpous mosses, and hepatics. Similarly, total lichen richness was subdivided into its 3 life forms. Pteridophytes and gymnosperms were included in the total analysis, but not as separate groups because of their limited distribution at lower elevations.

Generalized linear models (GLMs; McCullagh and Nelder 1989) were used to relate richness to elevation. Because the response variables are counts, dispersion in the data was tested and overdispersion was found. Thus, a quasi-Poisson distribution and a logarithmic link were employed following Crawley (2006). Inspection of diagnostic plots between a logarithmic link and an identity link (assuming a normal distribution of errors) also confirmed that a quasi Poisson with a logarithmic link function was better than a normal distribution and an identity link. Tests were run up to third-order linear models to model 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 the one with the highest *F* value among the significant models). The final graphs were based on the best selected model. An R (version 2.11.0) statistical package (R Development Core Team 2010) was used for all analyses.

Results

A total of 1585 species from 385 genera and 111 families were represented in the flora in the 4500–6000-m elevation range of the TAR's alpine zone. The flowering plants contained 1328 species, 261 genera, and 54 families, which is 27% of the total flowering plants of Tibet.

According to the dataset, the most commonly occurring flowering plant (6000 m) is *Delphinium brunonianum* Royle, and the most commonly occurring lichen is *Lecidea diducens* (Nyl.) Th. Fr. (6100 m). Compositae was the largest angiosperm family with 179 species, followed by 97 species of Gramineae, 83 species of Ranunculaceae, 78 species of Gentianaceae, and 77 species of Primulaceae. *Saussurea simpsoniana* (Field. & Gardn.) Lipsch. (5750 m) and *Saussurea gnaphalodes* Ostenf. (5700 m) were the highest growing Compositae. Interestingly, *S. gnaphalodes* holds the record (6400 m) for the highest vascular plant in the world (Körner 2003), on the north flank of Mount Everest, that is, in Nepal. Similarly, *Kobresia prainii* Kük. (5600 m) and *Littledalea przevalskyi* Tzvelev (5700 m) were the 2 highest recorded graminoids.

Lichens were represented by 71 species, 43 genera, and 28 families. *Sporastatia asiatica* H. Magn. (6000 m) and *Lecidea auriculata* var. *diducens* (6100 m) were the 2 highest recorded crustoses; the rock-dwelling *Lethariella flexuosa* (Nyl.) Wei and Jiang (1986) (5800 m) and the soil-dwelling *Thamnolia vermicularis* f. *qomolangmana* Wei & Jiang (5510–5700 m) were the 2 highest recorded fruticose lichens.

Bryophytes were represented by 160 species, 66 genera, and 20 families. Among them, 124 species were acrocarpous moss, 22 were pleurocarpous, one *Sphagnum*, and 13 hepatics species. *Tortula desertorum* Broth. (5800 m) and *Bryum gossypinum* Gao Chien and Zhang Guang-Chu (5800 m) were the 2 highest recorded acrocarps; *Brachythecium brotheri* Paris (5600 m) and *Haplocladium microphyllum* Brotherus (5550 m) were the 2 highest recorded pleurocarps. *Anastrepta orcadensis* (Hook.) Schiffn. (5100 m) was the highest recorded hepatic.

The highest reported pteridophyte was found at 5500 m. Ferns included 21 species, 11 genera, and 8 families. Gymnosperms are represented by 5 species, 2 genera, and 2 families. Their highest occurrence was recorded at 5300 m.

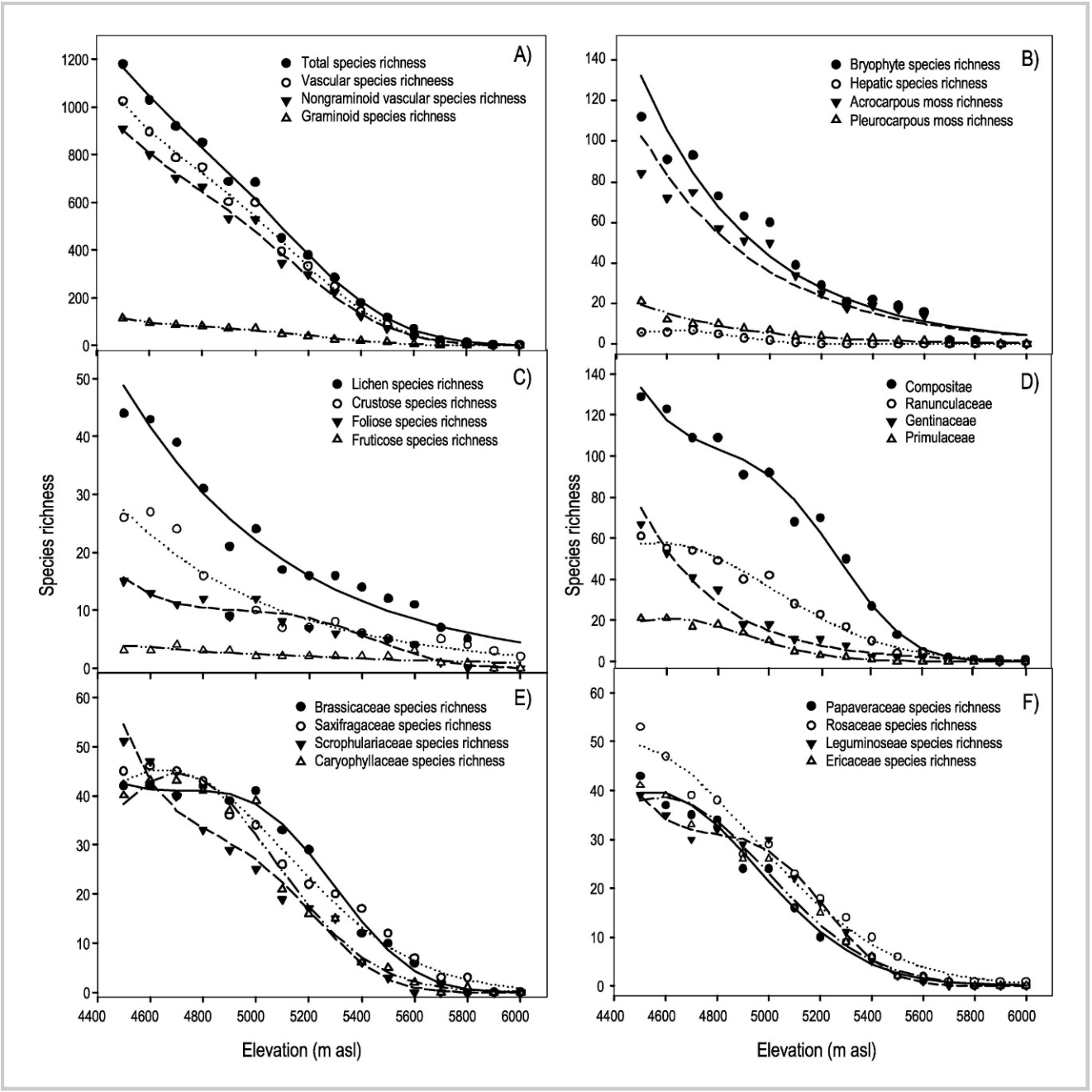
Total species richness ranged from 4 to 1181 species, with an average of 430 species per 100-m elevational band. Likewise, vascular plant species richness ranged from 2 to 1025 species, with an average of 371 species per 100 m elevational band. Nongraminoid vascular and graminoid species showed an average of 329 and 42 species per 100 m elevation band, respectively. All showed a significant declining cubic relationship with elevation (Figure 1A; *Supplemental data*, Appendix S1; http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00057.S1). Bryophytes, pleurocarpous moss, and acrocarpous moss richness (Figure 1B; *Supplemental data*, Appendix S1; http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00057.S1) showed a significant linear declining relationship with elevation. Hepatic richness showed a significant quadratic relation, with the highest richness at 4600 m (Figure 1B; *Supplemental data*, Appendix S1; http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00057.S1). Hepatics and pleurocarpous mosses had far lower richness than acrocarpous mosses. Crustose and fruticose lichens showed a significant linear declining pattern, but a cubic declining relationship was found for foliose lichens (Figure 1C; *Supplemental data*, Appendix S1; http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00057.S1). Among the 12 dominant families, species richness of Compositae, Brassicaceae, Scrophulariaceae, and Leguminosae showed a significant cubic declining relation, Gentianaceae showed a linear declining trend, and the rest showed a quadratic relation with an early hump between 4500 and 4700 m (Figure 1D–F; *Supplemental data*, Appendix S1; http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00057.S1).

Discussion

The patterns exhibited by the alpine flora of the TAR are in line with the general patterns expected (Körner 2003), as well as with results from other high-elevation interpolation studies (Grytnes and Vetaas 2002). However, these patterns are not the same for all biological groups, nor is the shape of their declines similar. Total vascular,

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FIGURE 1 Relationships between species richness and elevation, with the fitted polynomial GLM regression model superimposed: (A) Total species richness, vascular richness, nongraminoid vascular richness and graminoid richness; (B) bryophyte richness, hepatic richness, acrocarpous moss richness, and pleurocarpous moss richness; (C) lichen richness, crustose lichens, foliose lichens, and fruticose lichens; (D) Compositae species, Ranunculaceae species, Gentianaceae species, and Primulaceae species; (E) Brassicaceae species, Saxifragaceae species, Scrophulariaceae species, and Caryophyllaceae species richness; (F) Papaveraceae species, Rosaceae species, Leguminosae species, and Ericaceae species richness. Note the major differences in the scale of the ordinate, and the symbols for each response variable in the legend. All analyses are given in *Supplemental data*, Appendix S1 (http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00057.S1).



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nongraminoid vascular, and graminoid species richness showed a similar elevational declining pattern that differed from those of the richness of bryophytes, lichens, and some dominant angiosperm families. The latter diverge from the general pattern and show mixed patterns of either linear, unimodal quadratic, or cubic relationships. The pattern of decline, especially toward higher elevations, is continuously gentle rather than sharp, as has been found in interpolation studies elsewhere (eg Grytnes and Vetaas 2002) or stepwise, as found in an empirical study (Grabherr et al 1995).

One possible reason for these different elevational patterns among biological groups could be the differential adaptational features of individual species in the face of the very harsh and strong environmental filters in the alpine zone (Agakhanyantz and Breckle 1995; Klimes 2003; Körner 2003), which almost certainly apply to alpine species in the TAR. These environmental filters may consist of very high daily temperature ranges (down to freezing temperature at night and relatively high during the day), a short growing season, the different geometry of each landscape, steep environmental gradients, below-freezing soil temperatures, low soil nutrients, low precipitation, periods of lack of humidity, substrate differences, and increased soil disturbances. In addition, artifacts of interpolation such as mid-domain effect, hard-boundary effect (Grytnes and Vetaas 2002), low representation of samples after poor collection from high elevation, and inaccessibility of landscapes may also cause the observed pattern (Colwell and Hurtt 1994; Grytnes and Vetaas 2002).

However, the finding of similar declining patterns for total, vascular, nongraminoid vascular, graminoid, and other groups, families, and their functional groups is unlikely to be the result of a poor representation of collections or artifacts from interpolation. But cubic declining richness patterns shown by foliose lichens and a quadratic declining pattern for hepatics deviate from the linear declining patterns of other lichens and linear relations for other bryophytes. In addition, a significant linear declining pattern for Gentianaceae species contradicts quadratic and cubic declining richness patterns of the 12 dominant families, probably for many reasons. Biologically, some lichens proved their capacity to survive under both simulated (de Vera et al 2004) and real (Sancho et al 2007) outer space conditions. Nonbiological stress factors such as periods of lack of humidity, strong UV-B and solar radiation, and below freezing air and soil temperature strongly impact the distribution of vascular plant life but may not necessarily be destructive to lichens. Similarly, there were 13 species of liverworts collected up to 5100 m. Liverworts are extremely rare at high elevations above 4800 m in the Tibetan Himalaya (Birks HJB, unpublished observation), but the other taxa show a fairly good representation at both lower and higher elevations. This signifies a sharp decline in soil moisture, soil humidity, or snow cover with increasing elevation. Findings by Proctor et al (2009) also support the hypothesis that alpine hepatics distribution depends on soil humidity or snow cover rather than temperature. Higher richness of acrocarpous mossses (124 species) versus pleurocarpous mosses (22 species) is a further indication of dry habitats.

The declining richness patterns for the TAR can be explained in term of an energy-related hypothesis (Brown 1981; Wright 1983). This hypothesis is mainly proposed for woody plant richness in the tropics and subtropics, where there are generally more stable environments. Both temperature and precipitation decreased with elevation, but not uniformly, because of heterogeneous topography. Other hypotheses related to disturbance (Huston 1994), stress, and stability (Begon et al 1990) are more plausible for further explanations of this decline in richness than the energy hypothesis. The TAR alpine zone receives strong solar radiation that warms the landscape and evaporates great amounts of water. Plants occupy microhabitats in the high alpine zone, which may have relatively flat slope, more soil, or shelter among rocks. Some high-alpine plants have special structures such as silky hairs all over the plant, as with Compositae (*Saussurea* spp.), to avoid overheating and decrease transpiration (Gauslaa 1984), or to repel water and reflect short peaks of high radiation (Yang et al 2008). Other adaptational features such as succulent leaves for crassulacean acid metabolism photosynthesis, as in Crassulaceae (*Sedum* and *Rhodiola* spp.), are common in desert plants (Körner 2003), as are cushion growth forms in Caryophyllaceae (e.g. *Androsace*, and *Thylacospermum* spp.). Low-latitude mountain regions may receive high doses of UV-B radiation (Willis et al 2009), which lichens can screen by having a high concentration of melanin and/or parietin in the outermost body cells (Gauslaa and Ustvedt 2003). Cloud formation, strong wind, and high moisture content in the air are common toward mountain summits where air pressure may be low. Lack of multilayers in the vertical stratification in alpine vegetation also creates a high amount of convective long-wave radiation during the night, which cools air far below freezing temperature (Körner 2003).

Thus strong selection will take place among species, and species not adapted to this high harsh environment will be eliminated, thereby causing a decline in species richness with increased elevation. Different richness patterns shown by particular groups (foliose lichens, hepatics, and angiosperm families such as Compositae, Ranunculaceae, Primulaceae, Brassicaceae, Saxifragaceae, etc) may indicate their selective microhabitat preference in the single-layered high alpine ecological zone. Mesic ground with scattered *Kobresia prainii* would be suitable habitats for low-growing hepatics and pleurocarpous mosses, whereas stone outcrops surrounded by humid air will be appropriate habitats for acrocarpous mosses and lichens. Lichens show a higher resistance to extreme environments than other species, and thus they have a higher richness at higher elevations than other species.

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Fast drying and wetting cycles at this altitude may also favor their high degree of richness.

There is a long tradition of pastoralism in Tibet, and grazing pressure from wild and domestic animals (yak, sheep, horse, goat) in the Tibetan highlands (Miehe et al 2009) may easily take place. In general, species richness may increase after moderate foraging (Smith and Foggin 1999), and depending on the intensity of grazing, environmental conditions, herbivore types, and elevation. At high elevations, a small amount of grazing may have a high impact due to the harsh conditions but would not be such a problem for plants growing in lower, more congenial environments. Herbivores shape plant communities through their selective foraging behavior (Evju et al 2009). Alpine rangeland dominated by grasslands and steppes may indicate strong selection. Also, the harvesting of large amounts of high-altitude medicinal plants from high elevations in Tibet is important (Salick et al 2009). However, all these factors are relevant for local to landscape scales of disturbances, which may play little or no role in macroscale species richness patterns.

Climate-related large-scale variables such as glaciation history and/or present climate change may define the present pattern, which is consistent with the generalization made by Whittaker et al (2001) and palaeoecological findings of past climate change within the TAR (Herzschuh et al 2010).

The alpine zone of the TAR has much higher angiosperm richness (1328 species and 54 families) than the corresponding zones in the European Alps (200–280 species and 40 families) (Körner 2003). Results for the Hokkaido alpine zone of Japan (225 species and 45 families) (Tatewaki 1968) and Ladakh, northwest Himalaya (404 alpine vascular species) (Klimes 2003) are also far less in number than in the TAR. The alpine flora of the TAR represent an accumulated flora (large area) from different regions, each of which may differ at the species level and may be somewhat similar at their family level, which could account for the high number of species. Another likely explanation for this high diversity is the species pool, because the TAR has geographical proximity and environmental similarity to the alpine zones of 2 large biodiversity "hotspots": the Himalaya, and the Yunnan and Sichuan provinces (Barthlott et al 2001, 2005; Birks et al 2007).

The rate of reduction in total richness per 100 m elevation is 100 species; for higher plants it is 80 species per 100 m. Both figures are higher than the mean value (40 spp. per 100 m) for individual alpine regions (Körner 2003). This higher reduction rate may be a feature of this unique region with its steep elevational gradient of environmental harshness, which results in greater instability but also provides more opportunities for colonization. To a great extent, it is also a matter of scale.

The increasing plant diversity found in the alpine zone of the Scandes (Klanderud and Birks 2003) and within eastern Tibet (Salick et al 2009) were derived from a multitemporal comparison, whereas the declining species richness in the TAR alpine zone is only the species number difference between 100 m elevational bands.

These smooth declining richness patterns may also be connected to species–area relationships. Higher areas at lower elevation may inflate species richness simply because of the species–area relationship (Kluge et al 2006). Environmental heterogeneity may vary as a function of elevation (Palmer 2006), and local endemism may increase at higher elevations, especially at the landscape scale (Birks et al 2007), ultimately leading to species richness decline. This is most likely true for all higher group, although to different degrees among individual groups of species and their families, such as foliose lichen, hepatics, Ranunculaceae, Saxifragaceae, Scrophulariaceae, Papaveraceae, Rosaceae, and Ericaceae at intermediate elevation (4700 m), with an almost similar decline toward higher elevations.

Conclusion

This study concludes that there are more similarities than dissimilarities in the high-alpine species richness pattern of vascular and cryptogam species in the TAR. A continuous cubic decline with total, vascular, nongraminoid, and graminoid vascular richness was as predicted. The richness patterns found differed from earlier interpolation studies by having gentler and continuous declines with increasing elevation and also differed from observed species richness studies done elsewhere. Apart from the spatial scale of study, longer periods in glaciation history and environmental heterogeneities such as stress, disturbance, and tolerance by individual species are possible causes of these patterns. The TAR is rich in biodiversity, and there is much scope for further research in this high elevation range. This study can provide a basis for future climate change research, such as how climate change can impact the flora in the highest alpine zone in the world.

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Supplemental data

Appendix S1 Results of regression analysis on vascular and cryptogam richness patterns in the world's highest alpine zone, Tibet, modeled after different species, with their functional group as response variables and alpine elevation range as predictor variable. The quasi-Poisson family of error fitted in the GLM model after F test statistics ($P \leq 0.05$). Each response variable was modeled up to the third polynomial order. The bold entries indicate the significant selected model, which is represented graphically in the text. Resid. Df = residual degree of freedom, Resid. Dev = residual deviance.

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