

Patterns of plant diversity at high altitudes on the Qinghai-Tibetan Plateau

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Abstract

Aims

To describe the biodiversity patterns of plants along an altitudinal gradient on the Qinghai-Tibetan Plateau and to clarify the bias in plant specimen records at high altitude.

Methods

We conducted a large-scale investigation of vegetation at a wide range of altitudes, focusing on a high-altitudinal range (3 200–5 200 m) at different locations on the Qinghai-Tibetan Plateau. We then compared the altitudinal distribution of plant species obtained from our field investigation with that in plant specimen records from published sources and an online database.

Important Findings

Our data provide evidence that altitude plays a large role in regulating species composition on the Qinghai-Tibetan Plateau. We could not, however, detect a clear relationship between altitude and spe-

cies richness, although a weak monotonically increasing trend of richness was detected with increasing altitude. According to specimen records, most species have been sampled at a wide range of altitudes, and the average range of 145 species is >2 000 m. Despite this wide range, more than half of the species we observed were at higher altitudes than the specimen records indicate. High-altitude areas have probably been so poorly sampled that only a small fraction of the resident species has been recorded. This study clearly shows the regional bias of specimen records in the Qinghai-Tibetan Plateau.

Keywords: altitudinal gradient • alpine plant • species composition • species richness • specimen bias

Received: 12 September 2009 Revised: 8 January 2010 Accepted: 28 January 2010

INTRODUCTION

China is rich in plant biodiversity, ranking third in the world (after Brazil and Colombia) in terms of species number. The estimated number of vascular plant species is nearly 33 000, with 30 000 angiosperms, 250 gymnosperms and 2 600 pteridophytes (Lopez-Pujol *et al.* 2006). China was influenced less by Pleistocene glaciations than the surrounding regions during glacial periods (Shi 2002). The limited ice coverage enabled a lower rate of species extinction during glacial cycles. In addition, China encompasses enormous variations in topographical features, with high mountain ranges and extensive plateaus, resulting primarily from the collision of the Indian

subcontinent with the Asian continent. Such habitat heterogeneity contributes to the maintenance of high biodiversity, presumably by providing various niches and opportunities for speciation.

Altitude is an important factor in habitat diversity because it presents changes in the availability of resources, such as heat and water (Körner 2000). Many researchers have explored altitudinal biodiversity patterns of plants and clarified that altitude has a role in regulating species richness patterns (Grytnes 2003; Kessler 2000; Oommen and Shanker 2005). Altitude plays an even stronger role in maintaining large-scale species richness in China than in other areas (Qian *et al.* 2007), because China encompasses the world's widest range of altitudes.

The Qinghai-Tibetan Plateau is the highest and largest plateau on Earth, occupying >2.5 million km². Average elevation exceeds 4 000 m, and many of the peaks reach >8 000 m. The plateau has unique topographical features and biologically important habitats. More than 12 000 species in 1 500 genera of vascular plants have been identified on the plateau, including 3 500 species that are endemic to the plateau (Lopez-Pujol *et al.* 2006).

Despite its unique habitats, few studies have evaluated the altitudinal patterns of plant diversity on the plateau (Wang *et al.* 2006, 2007). Moreover, most of the detailed studies describing the vegetation have been done at a local scale, and most areas on the plateau have not been studied. Because detailed wide-scale study of this extensive area is difficult even now, large-scale studies have generally analyzed plant diversity along the altitudinal gradient by using database records (Grytnes and Beaman 2006; Wang *et al.* 2007).

The 'Seed Plants of China' database is the product of a national project and describes county-level distributions of 32 308 native and cultivated seed plants. It is derived primarily from plant specimen records, and it is potentially biased by altitudinal differences in sampling (Prendergast *et al.* 1993). However, few studies have addressed the actual altitudinal bias of specimen records by comparing records from the database with detailed vegetation research.

Here, we investigated the vegetation along the altitudinal gradient, focusing on a high-altitudinal range (3 200–5 200 m), at different locations on the Qinghai-Tibetan Plateau. We compared the altitudinal distributions of plant species obtained from our field investigation with those derived from the records of plant specimens from other publications and an online database. Our objectives were to describe the biodiversity patterns of plants along the altitudinal gradient and to clarify the bias in plant specimen records at high altitude.

METHODS

Study sites

The vegetation investigation was conducted during late July and early August in 2006 along six hillsides at different locations in the Qinghai-Tibetan Plateau (Table 1, Fig. 1). We selected areas with continuous and gently sloping hills and little variation in aspect. Two to four transects 50–60 m in length were established at different altitudes at each site. The transects were not placed in areas clearly influenced by human activity. All transects were, however, influenced by grazing of domestic animals. Altitude and slope orientation of each transect were recorded. Twenty-five to 30 quadrats (0.25 × 0.25 m) were placed at regular intervals along the transects with the criterion that the quadrats should have a similar aspect

Table 1: a summary of characteristics, including location, altitude, estimated annual mean temperature (Temp.), number of species (No.) and species richness (H') of the 23 study sites

Site	Topography	Vegetation	Longitude (E)	Latitude (N)	Altitude (m)	Temperature (°C)	No.	H'
Damxion 1	South slope	Meadow	91°03'41"	30°28'16"	4 300	1.0	21	2.65
Damxion 2	South slope	Meadow	91°03'13"	30°32'03"	4 950	-2.8	24	2.72
Damxion 3	South slope	Meadow	91°03'08"	30°32'21"	5 200	-4.2	25	2.82
Damxion 4	Flat	Meadow	91°03'44"	30°28'13"	4 282	1.1	17	2.32
Tanggula 1	West slope	Meadow	91°54'54"	32°50'23"	5 149	-6.0	31	3.11
Tanggula 2	West slope	Meadow	91°55'00"	32°50'26"	5 204	-6.3	29	3.02
Tuotuohe 1	North slope	Meadow	92°22'25"	34°06'23"	4 740	-4.8	27	2.99
Tuotuohe 2	North slope	Swamp	92°22'04"	34°05'45"	4 816	-5.2	12	1.99
Tuotuohe 3	North slope	Meadow	92°22'11"	34°05'37"	4 898	-5.7	27	3.08
Tuotuohe 4	Flat	Steppe	92°28'58"	34°15'42"	4 555	-3.9	15	2.15
Xidatan 1	Flat	Shrub	94°20'25"	35°47'07"	3 974	-2.2	15	2.17
Xidatan 2	Flat	Meadow	94°17'54"	35°43'36"	4 182	-3.3	16	2.28
Xidatan 3	North slope	Meadow	94°16'56"	35°42'10"	4 442	-4.7	28	2.91
Xidatan 4	North slope	Meadow	94°17'05"	35°41'49"	4 670	-6.0	30	2.92
Xidatan 5	South slope	Meadow	94°17'15"	35°45'14"	4 441	-4.8	29	3.10
Xidatan 6	South slope	Meadow	94°17'00"	35°45'25"	4 592	-5.6	24	2.89
Dulan 1	Flat	Steppe	98°15'48"	36°27'35"	3 250	0.9	7	1.31
Dulan 2	South-east slope	Steppe	98°13'07"	36°27'41"	3 550	-0.7	21	2.60
Dulan 3	South-east slope	Steppe	98°12'56"	36°27'57"	3 830	-2.4	25	2.83
Xiangpishan 1	Flat	Meadow	99°33'09"	36°42'10"	3 589	-1.3	18	2.67
Xiangpishan 2	North-east slope	Meadow	99°33'02"	36°42'02"	3 614	-1.5	22	2.50
Xiangpishan 3	North-east slope	Meadow	99°32'58"	36°41'55"	3 697	-1.9	22	2.59
Xiangpishan 4	North-east slope	Meadow	99°32'54"	36°41'46"	3 839	-2.7	27	2.94

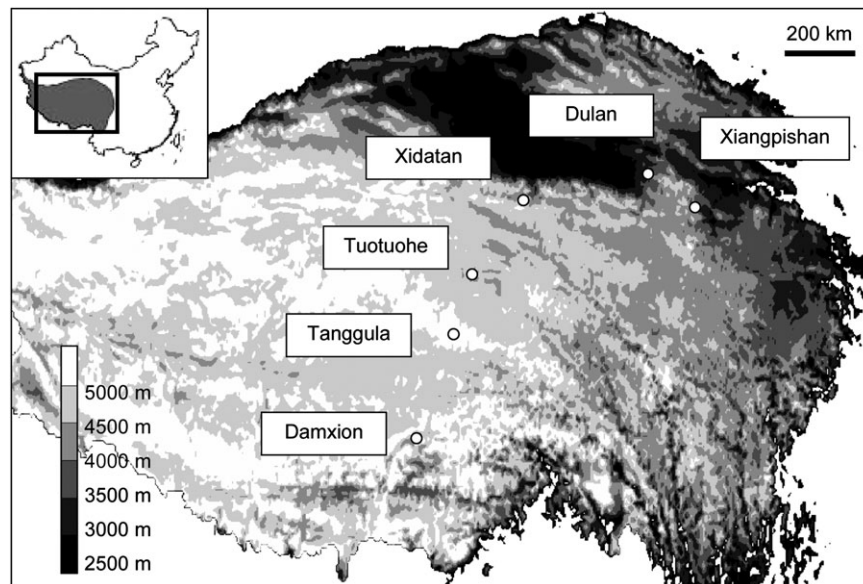


Figure 1: map showing the geographical location of study sites.

throughout the transect. The presence of each species of vascular plant was then recorded within each quadrat.

Temperature can be predicted with a linear model using latitude, longitude and altitude as explanatory variables (He *et al.* 2006), although there are no local meteorological stations for all of the study sites. Using the linear model based on the 30-year average temperature data (1971–2000) at 75 climate stations across the plateau ($R^2 = 0.999$, $P < 0.0001$), we estimated the mean annual temperature at each transect site (Table 1).

Data analysis

The Shannon–Wiener function (H') was calculated using the number of plant species occurring in whole quadrats at each plot to compare species diversity between the study sites.

Although the pattern described for altitudinal richness is the main interest in this study, altitude alone may be insufficient to evaluate the relationship between altitude and species richness. Because climatic conditions (temperature and precipitation) are correlated with latitude, longitude and altitude in the plateau (He *et al.* 2006) and altitude increased from north to south in the plateau, relations of species richness to altitude, latitude, longitude and interaction of altitude and latitude were determined by fitting generalized linear models (Hoffmann 2003) with a Poisson error distribution and logarithmic link function.

To understand the relationship between plant composition and altitude, we analyzed the frequency of species in each transect using detrended correspondence analysis (DCA) with PC-ORD version 4.1 software (McCune and Mefford 1999).

To understand the bias of the specimen records, we compared the altitudinal distribution of each species in our field study with records in four published sources and an online da-

tabase of specimens ‘Chinese Virtual Herbarium’ (<http://www.cvh.org.cn/>). Currently, the Missouri Botanical Garden and the Chinese Academy of Sciences are working together on the *Flora of China* project, an international effort to produce a 25-volume English language revision of *Flora Reipublicae Popularis Sinicae* (FRPS; Wu and Chen 2004). At present, 18 volumes have been published and are available online (<http://flora.huh.harvard.edu/china/>; Wu and Raven 1994–2010). The *Flora of China* is not simply an English translation of the Chinese edition but an extensive revision. When possible, we referred to the *Flora of China* for specimen records. If a species record was not available in published volumes, we referred to FRPS (Wu and Chen 2004), *Flora of Qinghai* (Liu 1996–1999) and *Flora of Xizang* (Wu 1983–1987).

RESULTS

In total, 191 species (including 39 unidentified species) in 72 genera were recorded in 23 plots along the six hillsides. Alpine meadows, with perennial sedges such as *Kobresia pygmaea* (C.B. Clarke) C.B. Clarke (Cyperaceae), are the dominant vegetation types at these study sites. Alpine steppes, with xerophytic and dense tussock grasses such as *Stipa purpurea* Griseb. (Poaceae) or herbs such as *Artemisia* sp. (Asteraceae), occurred at Dulan. The shrubland at Xidatan is dominated by *Potentilla fruticosa* Linn. (Rosaceae). Cushion plants such as *Androsace tapete* Maxim. (Primulaceae), *Arenaria kansuensis* Maxim., *Arenaria lancangensis* L. H. Zhou (Caryophyllaceae) and *Saussurea brunneopilosa* Hand.-Mazz. (Asteraceae) are adapted to the extreme alpine environment and were observed at altitudes of >4 000 m.

All of main factors (altitude, latitude and longitude) had significant effects on total species richness, but the effects of

latitude and longitude were relatively small (Table 2). There was also a significant interaction of altitude and latitude, reflecting topographic feature increasing in altitude from north to south in the study sites. There were weak monotonically increasing trends of total (Fig. 2a) and average number of species (Fig. 2b) occurring in quadrats in the study plots with increasing altitude. There were monotonically decreasing trends of the total (Fig. 2c) and the average number of species (Fig. 2d) with increasing estimated mean annual temperature. The total and average number of plant species, which were significantly correlated ($R^2 = 0.641$, $P < 0.0001$), showed similar trends in altitudinal or thermal gradients. However, no significant effects on total number of species were detected when data from the lowest site (Dulan 1) were removed, although there

were marginal effects of altitude and interaction of altitude and latitude (Table 2).

The association between species composition and altitude was analyzed by DCA. Eigenvalues for the first and second axes were 0.550 and 0.223, with a total inertia of 2.94; the first and second axes accounted for 18.7 and 7.6%, respectively, of the variance in the species data. The DCA coordinates on the first axis were significantly correlated with altitude ($R^2 = 0.55$, $P < 0.0001$; Fig. 3). This correlation was also detected when the data from Dulan 1 were removed from the analysis ($R^2 = 0.50$, $P < 0.0001$).

We were able to compare the altitudinal ranges of 145 of the 152 identified species with published records; the altitudinal ranges of the 7 other species were not available. Most of the

Table 2: results of a generalized linear model to explain species richness: species of all sites and species of all sites except for Dulan 1

Variable	Total sites			Remove Dulan 1		
	Residual deviance ^a	% Explained ^b	<i>P</i>	Residual deviance ^a	% Explained ^b	<i>P</i>
Altitude	22.6	16.3	0.008	17.3	9.8	0.09
Latitude	20.5	11.5	0.025	16.4	6.6	0.16
Longitude	20.9	12.4	0.019	17.1	9.2	0.10
Altitude × Latitude	23.4	18.1	0.006	21.4	10.8	0.07

^a Residual deviance on removing that factor from a full model.

^b Percentage explained is the increase in residual deviance on removing that factor from a full model, expressed as a percentage of the total deviance.

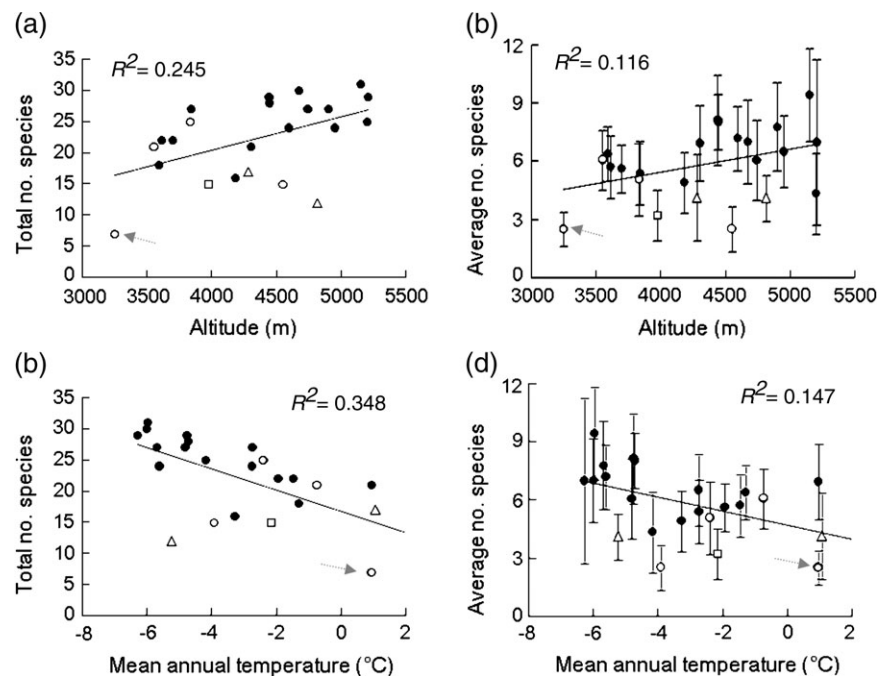


Figure 2: total and average number of plant species occurring in 25–30 quadrats in the study plots by (a, b) altitude and (c, d) estimated mean annual temperature. The mean annual temperatures were estimated based on the linear model using the 30-year average temperature data (1971–2000), latitude and longitude at 75 climate stations across the plateau. Filled circles indicate meadow, open circles indicate steppe, open triangles indicates swamp and open square indicates shrub. Outlier site (Dulan 1) is indicated by arrow.

species have been sampled from wide altitudinal ranges (Fig. 4); e.g., *Triglochin maritimum* Linn. (Juncaginaceae) from 0 to 4 300 m, *P. fruticosa* from 400 to 5 000 m and *Neotorularia humilis* (C. A. Meyer) Hedge & J. Léonard (Brassicaceae) from 1 000 to 5 300 m. According to specimen records, the average range of the 145 species is >2 000 m. Despite these wide ranges, we observed more than half (77) of the species at altitudes higher than those given in the specimen records.

DISCUSSIONS

Our data provide further evidence that altitude plays a large role in regulating species composition (Fig. 3). We could not, however, detect a clear relationship between altitude and species richness, although a weak monotonically increasing trend of richness was detected with increasing altitude (Fig. 2). This trend could be affected by the outlier, because there were no significant trends when the Dulan 1 was

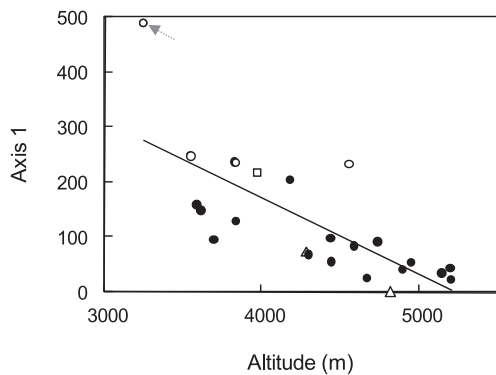


Figure 3: relationship between the first axis of DCA and altitude. Filled circles indicate meadow, open circles indicate steppe, open triangles indicates swamp and open square indicates shrub. Outlier site (Dulan 1) is indicated by arrow.

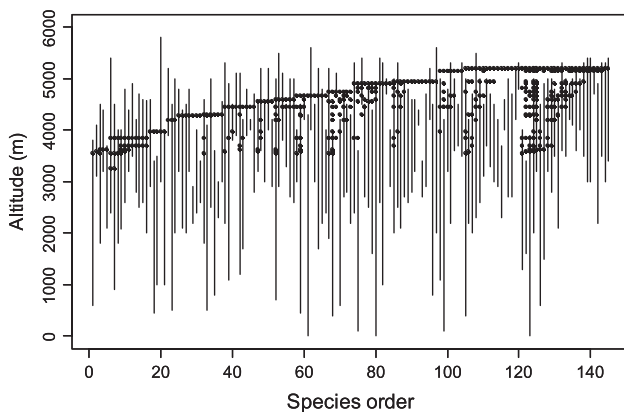


Figure 4: distribution of 145 species by altitude. Vertical bars indicate the range from specimen records. Filled circles indicate the altitude at which the plant was recorded in this study. Species are ordered on the basis of maximum altitude records from the field data.

removed from the analysis. Our data are notable, however, because most previous studies have reported monotonically decreasing trends in species richness with increasing altitude in high-altitude areas.

In recent years, many researchers have examined altitudinal biodiversity patterns, and different patterns have been observed in different organisms and in different regions. The two most common forms of diversity patterns are a monotonically decreasing curve with increasing altitude and a hump-shaped curve with high diversity at intermediate altitudes (Rahbek 1995, 2005). Almost 50% of studies showed a hump-shaped curve, whereas ~25% showed a monotonically decreasing pattern and ~25% followed other distributions. The relationship between species richness and altitude varies greatly with scale (Nogues-Bravo *et al.* 2008). When the entire altitudinal gradient is surveyed, the pattern is hump shaped, but as the scale of the study diminishes, the pattern changes progressively to a monotonically decreasing pattern. This trend is particularly apparent when the lower limit of the gradient is excluded from the analyses.

Wang *et al.* (2006) investigated vegetation in eastern Tibet and found a monotonically decreasing pattern between 3 200 and 4 500 m. That study included forested areas, which usually have higher levels of diversity than alpine areas, and may be one of the reasons why our study showed a different trend in plant diversity. This study was conducted in the range between 3 200 and 5 200 m of alpine area and it would be expected that the trend of richness along altitudinal gradient is more obscure than that of an area containing the different ecotone.

There are other several possible reasons why we found no significant trends in species richness with altitude. First, the plateau encompasses an enormous range of altitude and latitude, both of which contribute to maintaining a wide range of species distribution. The plateau lies approximately between latitudes 28° and 38°N. Assuming a standard temperature decline of -0.5°C for every 1-degree increase in latitude, there is a temperature difference of $\sim 5^{\circ}\text{C}$ at equal altitudes between areas in the south and north. The estimated mean annual temperature is likely to be more reliable in evaluating the relationship between altitude and species richness because it includes both information of altitude and latitude.

Second, in recent years, the pressures to increase animal production have led to degradation of plant diversity in the plateau (Liu and Diamond 2005). Many natural grasslands have been destroyed or deteriorated by overgrazing (Wang *et al.* 2009). Areas at higher altitudes are more likely to be a refuge for large numbers of species, because human impact decreases almost monotonically with increased altitude (Nogues-Bravo *et al.* 2008). Ohtsuka *et al.* (2008) studied vegetation properties along an altitudinal gradient (4 400–5 300 m) on the Tibetan Plateau and found that the vegetation cover decreased on lower parts of the slope, most likely because grazing intensity is greater at lower altitudes. Zhang and Mi (2007) reported monotonically increasing trends in species richness

with increasing altitude between 2 100 and 3 050 m in northern China. They suggested that this trend may have been the result of differences in grazing intensity.

Third, regional differences in levels of investigation also bias the results (Prendergast *et al.* 1993). For example, some areas have been sampled sufficiently to record most of the resident species, whereas others have been so poorly sampled that only a small fraction of the resident species have been recorded. The latter bias is much more likely to occur at higher altitudes (Grytnes and Beaman 2006), and our results clearly showed the altitudinal bias of specimen records in the Qinghai-Tibetan Plateau (Fig. 4).

Generally, large-scale studies that have analyzed plant diversity along the altitudinal gradient using database records (Grytnes and Beaman 2006; Wang *et al.* 2007) have applied corrections for specimen bias. For example, to compensate for the potential bias introduced by regional differences in levels of investigation, Tang *et al.* (2006) used genus richness instead of species richness to explore patterns of biodiversity within China. However, the diversity in high-altitude areas is potentially underestimated, because about half of the species in our study were observed at higher altitudes than the specimen records indicate. This proportion will most likely increase as more intensive field investigations are conducted.

An understanding of species distribution patterns and the resulting spatial patterns of biodiversity is fundamental to the study of not only evolutionary biology but also of conservation biology. There is growing concern over the large number of development projects on the Qinghai-Tibetan Plateau, such as the 1 142-km-long Glomud-Lhasa railway. In addition, climate change will become increasingly pronounced over the next 100 years (IPCC 2001), and alpine flora are regarded as highly sensitive to the impacts of climate change (Dirnbock *et al.* 2003; Theurillat and Guisan 2001). Climate-induced vegetation change has already been documented in various mountainous regions (DeChaine and Martin 2004; Henry and Molau 1997). We therefore should accelerate our efforts to assess species diversity on the Qinghai-Tibetan Plateau.

FUNDING

The study was funded by the Global Environment Research Coordination System, Ministry of the Environment, Government of Japan to the project "Early detection and prediction of climate warming based on long-term monitoring on the Tibetan Plateau", and by KAKENHI (Grant-in-Aid for Young Scientists (B) 19770020).

ACKNOWLEDGEMENTS

This study was part of a joint research project between the National Institute for Environmental Studies, Japan, and the Northwest Institute of Plateau of Biology, China. We are grateful to the members of the

Northwest Plateau Institute of Biology for their cooperation during our field survey. We also thank Dr Takenaka, National Institute for Environmental Studies, for his helpful comments and encouragement.

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