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Distributions of Dominant Tree Species on the Tibetan Plateau under Current and Future Climate Scenarios

A bioclimatic model was used to simulate distributions of the dominant tree species on the Tibetan Plateau. The model is based on physiological constraints to alpine plant growth. The bioclimatic variables used in this model are: minimum temperature in the coldest month, maximum temperature in the warmest month, accumulated growing-season warmth, and minimum value of soil moisture availability in the growing season. A comparison was made between simulated current distributions of tree species and their actual natural distributions on the Tibetan Plateau. It was shown that there is good agreement between simulated current and actual natural distributions. The simulated current distribution areas of tree species such as Abies spectabilis, Picea likiangensis *var.* linzhiensis, Pinus densata, Larix griffithiana *were a little larger than their actual distributions. For* Quercus aquifolioides *and the relict species* Betula platyphylla, *simulated areas were a little smaller than their actual distributions. Future distributions of dominant tree species were predicted under a climate scenario with a CO_2 concentration of 500 ppmv in the year 2100. The distribution areas of* Abies spectabilis, Picea likiangensis *var.* linzhiensis, Pinus densata, Larix griffithiana *and* Quercus aquifolioides *would shift and extend towards the north and west under the future climate scenario. For* Betula utilis, *the distribution areas would shift towards the north but they would shrink.*

Keywords: *Bioclimatic model; future climate scenario; dominant tree species; tree distribution; Tibetan Plateau; China.*

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Introduction

Global warming is a theory that has been supported by data from climatic monitoring over the past century as well as long-term climate reconstruction covering the past millennium (Hughes 2000). Various climate models have predicted an increase in global temperatures by 1.5–4.5°C by the end of this century (Overpeck et al 1991; Kattenberg et al 1996). It has been shown that a 3°C increase in mean annual temperature will result in a shift in isotherms of approximately 300–400 m in latitude (in the temperate zone) and 500 m in elevation (Hughes 2000). Hence, it has been suggested that the increase in temperature will have profound biological effects, such as shifts in the range of species distribution (Overpeck et al 1991; Shriner and Street 1998). Many studies have indicated that species distribution shifts northwards with increasing temperature (Barry et al 1995; Parmesan 1996). Models have been used to simulate current species distributions and predict shifts in their range caused by climate change. Prentice et al (1991) attempted a more mechanistic representation of tree species' responses to climate. In addition, Sykes et al (1996) made an attempt to predict the ranges of present-day species using a small set of factors representing particular processes that are assumed to control species range limits.

The Tibetan Plateau is one of the important regions in the world with an average altitude over 4000 m. The uplift of the plateau has created and maintained the South Asia monsoon, which affects terrestrial ecosystems in China due to its unique location and high altitude (Zhang 1993). Species on the Tibetan Plateau have a long and continuous evolutionary history. Their development and distribution were impacted significantly by fluctuating climatic conditions during the uplift period (The scientific expedition teams to the Tibetan Plateau, Chinese Academy of Sciences 1980). It has been shown that climate change trends on the Tibetan Plateau are consistent with trends that occurred in other regions in China over the past 40 years (from 1950 to 1990), but at a different rate. The mean annual temperatures have been increasing 0.04°C per 10 years in China, and 0.16°C per 10 years on the Tibetan Plateau in the past 40 years (Tang et al 1998). The variation in precipitation reveals regional discrepancies on the plateau. Trends in annual precipitation show an increase in the northern and southern parts of the plateau, and a decrease in its center (Tang et al 1998). Besides, it has been shown that mean temperatures have increased on the plateau under global climate warming during the past 40 years. In particular, minimum temperatures in the coldest month increased sharply, but the variation of maximum temperatures in the warmest month is not significant (Tang et al 1998).

Vegetation is undisturbed on the Tibetan Plateau, which provides an ideal natural laboratory for research on alpine species distribution and species' responses to climate change. Vegetation distribution on the plateau has been shown to be very sensitive and vulnerable to environmental change due to the high altitude of the plateau, where the growth and distribution of plants depend heavily on local climate conditions (Zhang et al 1996). The distribution of dominant species and vegetation types on the Tibetan Plateau was investigated and surveyed by expedition teams from 1950 to 1970. Climate factors affecting the distribution of dominant species are calculated based on the correlation between the climate and actual species distribution (The scientific expedition teams to the

Species	min α	min T_c	max T_c	max T_a	min GDD
Sub-alpine evergreen conifers					
Abies spectabilis	0.66	–7.0	–1.8	9.8	330
Picea likiangensis* var. *linzhiensis	0.63	–6.0		16.0	650
Pinus densata	0.55	–5.5		17.0	850
Sub-alpine deciduous conifer					
Larix speciosa	0.70	–10.0		10.0	320
Temperate evergreen sclerophyll					
Quercus aquifolioides	0.56	–6.0	5.0		780
Mountainous deciduous broadleaf					
Betula platyphylla	0.75	–10.0			600

TABLE 1 Bioclimatic parameters for major dominant tree species on the Tibetan Plateau. α = Priestley-Taylor coefficient of annual moisture availability; T_c = mean temperature of the coldest month; T_a = mean temperature of the warmest month; GDD = growing degree days on a 5°C basis.

Tibetan Plateau, Chinese Academy of Sciences 1985). However, little is known about the sensitivity and response of species distribution to climate change.

In this study, the distributions of 6 dominant tree species on the Tibetan Plateau were simulated using an adjusted bioclimatic model for potential distributions of northern European tree species (Sykes et al 1996). The responses of tree species to climate change and elevated CO_2 under a GCM (Global Climate Model) scenario at the Hadley Centre (Mitchell et al 1995; Johns et al 1997) were also simulated.

Methods

Bioclimatic model for species distribution

As climate conditions are changing, it is imperative to construct models to understand potential species distribution. As mentioned above, Prentice et al (1991) produced a mechanistic representation of tree species' responses to climate. Sykes et al (1996) improved the model and predicted the current range of species using a small set of factors representing particular processes that were assumed to control species' range limits. The model for the distribution of dominant tree species on the Tibetan Plateau proposed here follows the algorithms and rules of Sykes's bioclimatic model. The climate variables included the minimum temperature in the coldest month, the maximum temperature in the warmest month, accumulative temperatures (or growing degree days) over 5°C (GDD), and the Priestley-Taylor coefficient (ratio of actual transpiration to equilibrium evapotranspiration, α).

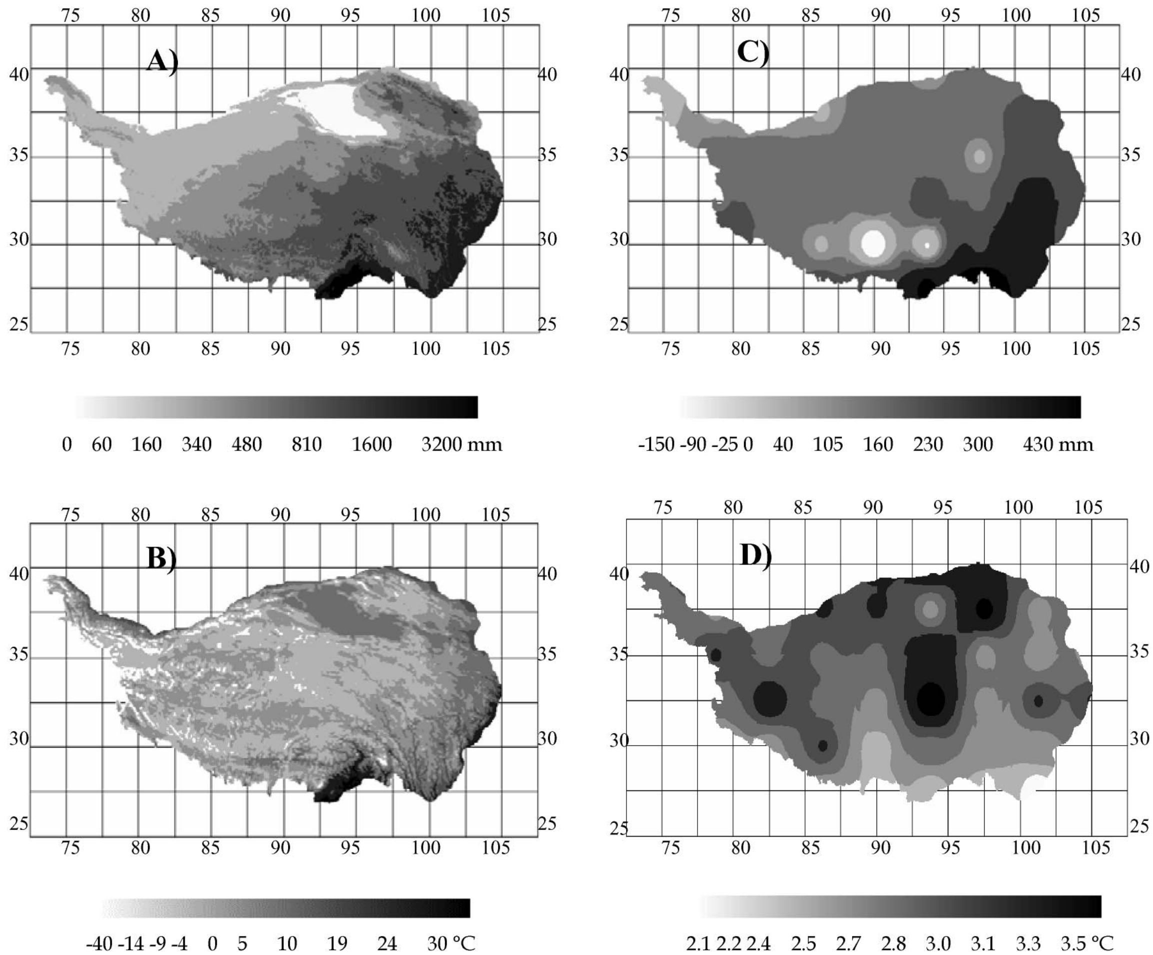
Calculation of bioclimatic variables

The minimum temperature in the coldest month and the maximum temperature in the warmest month were derived from a Chinese 0.05° × 0.05° temperature and precipitation database (1960–1990) and simulated by PRISM (Parameter-elevation Regressions on Independent Slopes Model; Daly et al 2000; Daly et al 2002). The accumulative temperatures over 5°C (GDD) were calculated from the formula: GDD = $(T - T_0)$ dt, where T_0 is 5°C for trees in cold environments, which is the minimum temperature for growth. T was calculated from the quasi-daily mean temperatures interpolated through mean temperatures between mid-months. GDD was derived from summation of $(T - T_0)$ over the days with $T > T_0$ (Prentice et al 1991). The Priestley-Taylor coefficient (α) was considered as an integrated measurement of the annual amount of growth-limiting drought stress on plants (Hare 1980). The algorithm is as follows: potential evapotranspiration and estimated actual evapotranspiration obtained by the WBM (Water Balance Model) (Vörösmarty et al 1989) with the inputs of vegetation types, climate variables (monthly mean temperature, precipitation and cloudiness), soil texture and elevation. Cloud data sets were derived from the 0.5° × 0.5° database of 30-yr mean monthly climatology (New et al 2000), and soil texture from the 1° × 1° database of global soil texture (Webb et al 2000). Forest types on the Tibetan Plateau were from the *Vegetation Map of China* (Hou 1979). Available water capacity in soils was based on vegetation types, soil texture, and root depth. The estimate of plant rooting depth was determined from the data of vegetation types and soil texture (Vörösmarty et al 1989).

Actual species distributions and species parameter values

The distributions of the dominant tree species on the Tibetan Plateau were obtained from *Vegetation of Tibet*

FIGURE 1 Annual precipitation (A) and annual mean temperature (B) on the Tibetan Plateau, and anomalies in annual precipitation (C) and annual mean temperature (D) on the Tibetan Plateau simulated by the Hadley Centre GCM (Mitchell et al 1995; Johns et al 1997).



(The scientific expedition teams to the Tibetan Plateau, Chinese Academy of Sciences 1980), *Forests of Xizang* (The scientific expedition teams to the Tibetan Plateau, Chinese Academy of Sciences 1985) and *Vegetation Atlas of China* (Editorial Board of Vegetation Map of China, Chinese Academy of Sciences 2001).

The climate data sets were transformed into grids with 0.05° latitude by 0.05° longitude (approximately 4–5 km). These were used to generate climate variables for the species and map their distributions. The initial values of species' response parameters were derived from previous research on the distributions of the dominant species on the Tibetan Plateau (The scientific expedition teams to the Tibetan Plateau, Chinese Academy of Sciences 1985; Shi 1999). These parameters were adjusted by iteration and visual comparison between actual and simulated distribution maps (Table 1). The actual distribution of plant species on the Tibetan Plateau was a mosaic affected by soil quality, topography, human disturbance and competition among species. Simulated species distribution was driven by the interpolated continuous climate data, and would be mostly continuous if climate conditions were similar around one place. Therefore, in the case of *Quercus aquifolioides* and *Betula platyphylla*, whose distributions were patchy, the limited climate parameters were adjusted to represent their main distribution.

Climate change scenarios

HadCM3, a coupled atmosphere–ocean GCM (Global Climate Model), was employed to simulate the future distributions of the dominant tree species under a climate scenario (including the effects of greenhouse gases and sulfate aerosols). It was developed at the Hadley Centre and described by Cox et al (1999). In this model, the atmospheric component of HadCM3 has 19 levels, with a horizontal resolution of 2.5° latitude by 3.75° longitude. The scenario for HadCM3/B1A was driven by computing the averages of 1961–1990 and 2081–2100 from the climate model simulation. Mean monthly climate anomalies were interpolated to a fine-scale grid on 0.05° × 0.05° (Figure 1). Future climate data (year 2100) were calculated by adding these interpolated values to the modern climate values (averages of 1961 to 1990) on the fine grid (Figure 1). The emission scenario included an increase in atmospheric CO_2 concentration from 340 to 500 ppmv (Cusack et al 1998). Simulation was performed to produce species distributions under future climate conditions with atmospheric CO_2 concentration of 500 ppmv.

Data comparison

The distributions of 6 dominant tree species on the Tibetan Plateau were simulated. 0.05° × 0.05° grid cells were applied to simulate the distribution areas of these species. Here we assembled these grid cells into continuous distribution areas in 0.1' snap tolerance using a GIS in order to compare the difference between the simulated distribution area and the actual distribution area (snap tolerance is an ARCINFO command. This command was used to connect the grid cells within designated distance). The difference between the 2 maps (ΔV, according to Sykes et al [1996]) was obtained by the ratio of the grid cells in which absent species were simulated as present and present species were simulated as absent, to the total grid cells in both simulated and actual distribution areas. A ΔV value < 0.15 can be interpreted as a sign of excellent agreement between predicted and actual distributions, 0.15–0.30 as very good, 0.30–0.45 as good, 0.45–0.60 as fair, 0.60–0.80 as poor, and > 0.80 as very poor.

TABLE 2 ΔV values for tree species on the Tibetan Plateau. ΔV_p stands for the difference between simulated and actual tree species distributions. Simulation is based on a bioclimatic model under current climate conditions with a CO_2 concentration of 340 ppmv. ΔV_p is the ratio of the grid cells in which absent species were simulated as present and present species were simulated as absent, to the total grid cells in both simulated and actual distribution areas; ΔV_s stands for the difference between future distributions of tree species under a scenario with a CO_2 concentration of 500 ppmv, and their distributions simulated under current climate conditions with a CO_2 concentration of 340 ppmv.

Tree species	ΔV_p	ΔV_s
Sub-alpine evergreen conifers		
Abies spectabilis	0.10	0.45
Picea likiangensis var. *linzhiensis*	0.29	0.43
Pinus densata	0.21	0.51
Sub-alpine deciduous conifer		
Larix speciosa	0.40	0.35
Temperate evergreen sclerophyll		
Quercus aquifolioides	0.24	0.30
Mountainous deciduous broadleaf		
Betula platyphylla	0.27	0.37

Results

Current distributions

A good agreement was shown between simulated current distributions and the actual natural distributions of the 6 species, but there are differences between these relations (Figure 2 and Table 2). The simulated distribution areas were larger than the actual distribution areas for *Abies spectabilis, Picea likiangensis* var. *linzhiensis, Pinus densata* and *Larix speciosa,* and smaller for *Quercus aquifolioides* and *Betula platyphylla*. For *Picea likiangensis* var. *linzhiensis* and *Betula platyphylla*, the simulated distribution areas were continuous, but their actual distributions were patchy. The simulated distribution area for *Betula platyphylla* is a little smaller than its patchy distribution (Figure 2).

Scenario analysis

Future distribution maps of the 6 species showed that tree species responded to climate change in different ways (Figure 3). The comparisons between the maps show significant differences in species distribution under current climate conditions and future climate scenarios (Table 2). The distribution areas of *Abies spectabilis, Picea likiangensis* var. *linzhiensis* and *Pinus densata* would shift and extend towards the north and west under the future climate scenarios (Figure 3), while the distribution areas of *Larix griffithiana* and *Quercus aquifolioides* would extend towards the west and shift towards the north (Figure 3). *Betula utilis* showed shrinking distribution under the future climate scenario (Figure 3), the only one among the 6 species to show potential shrinking.

Discussion

The Tibetan Plateau is a unique natural landscape, with broad areas and intricate physiognomic types. Results show a clear horizontal and vertical transformation of vegetation patterns caused by temperature and humidity trends, and a vertical transformation due to the combined effects of topography and atmospheric circulation (The scientific expedition teams to the Tibetan Plateau, Chinese Academy of Sciences 1980). The well-regulated vegetation patterns along the climate gradients indicate that climate factors control the distributions of vegetation species. The simulated current distributions of 6 tree species are consistent with their actual distributions. This implies that the climate variables used in bioclimatic models are crucial factors in determining the range limits of alpine tree species. In general, species distributions towards the northern and

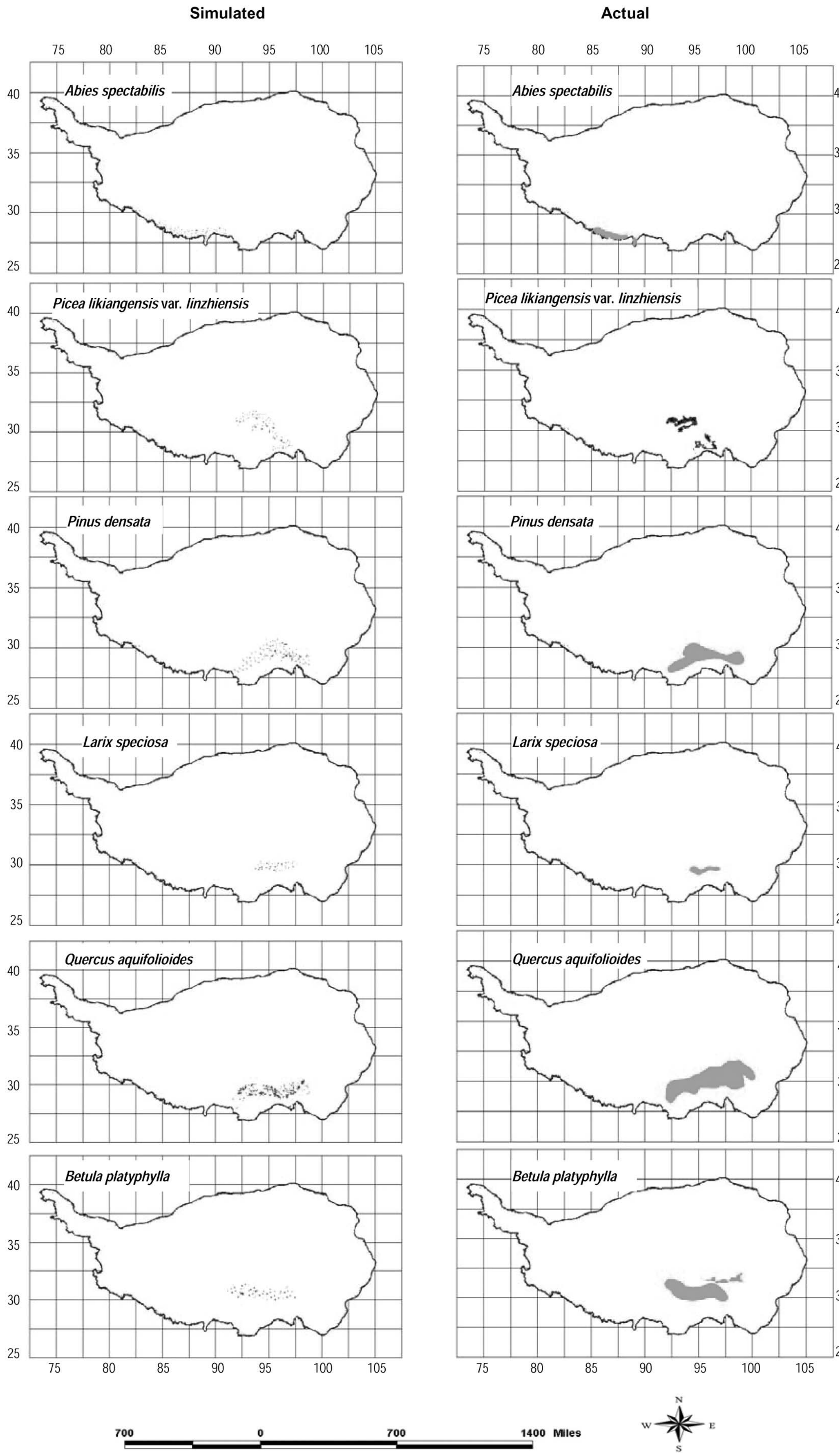
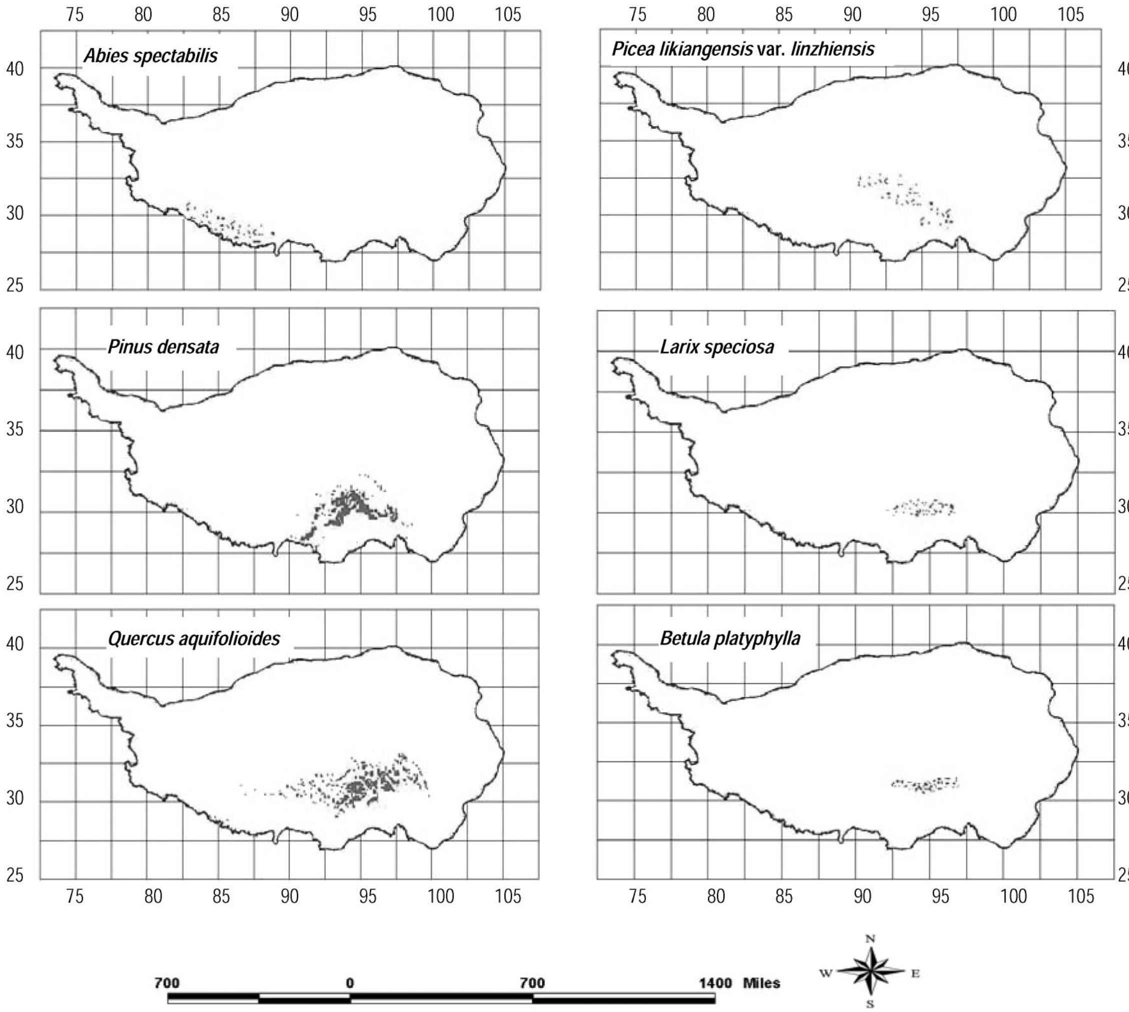


FIGURE 2 Simulated and actual distributions of major dominant tree species on the Tibetan Plateau. (Actual distribution maps reproduced from *Vegetation of Tibet* [The scientific expedition teams to the Tibetan Plateau, Chinese Academy of Sciences 1980] and *Vegetation Atlas of China* [Editorial Board of Vegetation Map of China, Chinese Academy of Sciences 2001].)

FIGURE 3 Simulated distributions of major dominant tree species on the Tibetan Plateau using a climate scenario with a CO_2 concentration of 500 ppmv.



northwestern boundaries are limited by minimum GDD values and minimum coldest month temperature; and towards the west by the minimum values for annual growth-limiting drought stress on plants.

Spruce and fir tree species are the major components of sub-alpine coniferous forests on the Tibetan Plateau. Spruce prefers to grow in moist habitats, but if conditions are too moist this becomes a limiting factor for their development and distribution. This is why they are absent in the eastern Himalayas. With regard to horizontal distribution, spruce is usually the dominant tree species near the treeline. The vertical distribution of fir species usually reaches higher than for spruce species. But fir forests are stunted and shrub-like when they grow higher than 4000 m, due to thermal constraints. The development and evolution of spruce and fir was affected by the alternation of cold and warm climate conditions during the uplift of the Tibetan Plateau. Palynology has shown that the oldest spruce and fir sporopollens come from the Eocene and Oligocene in the north of the Tibetan Plateau (Wang et al 1975). In the Pleiocene stratum, spruce and fir sporopollens were found in the north, center and south of the Tibetan Plateau (Song and Liu 1982). This indicates that spruce and fir species extended under a trend with a colder and moister climate at the beginning of the Quaternary period, but disappeared in the north and center of the Tibetan Plateau due to the barrier of the northwest monsoon caused by the uplift of the Tibetan Plateau in the late Pleistocene (The scientific expedition teams to the Tibetan Plateau, Chinese Academy of Sciences 1985). Minimum temperature and soil moisture are the primary limiting climatic factors for species distribution. Our results predict that *Abies spectabilis* and *Picea likiangensis* var. *linzhiensis*, the major dominant tree species in evergreen coniferous forests, would shift towards the north and west under a climate scenario with a CO_2 concentration of 500 ppmv (Figure 3).

Alpine *quercus* species are dominant in evergreen sclerophyllous forest on the Tibetan Plateau. They cover sub-tropical regions with more winter precipitation. Alpine *quercus* spp. are characterized by small, thick, coarse leaves and a good ability to adapt to cold and dry habitats (Schimper 1898). They are abundant in the middle of the Himalayas, but they become stunted in the higher regions and resemble brushwood at the treeline. The oldest *quercus* fossil has been found in the Tertiary Pliocene stratum (Li and Guo 1976). In the early Miocene era, evergreen sclerophyllous forest dominated by *quercus* spp. replaced the sclerophyllous forest dominated by eucalypts due to the combined impact of Mediterranean climate and monsoon from the Indian Ocean (Tao 1992). With the uplift of the Tibetan Plateau, the climate changed towards cold and drought, and evergreen sclerophyllous forest dominated by *quercus* spp. was confined to the south of the Gangdisi and Nianqingtanggula mountains. At present, *quercus* spp. are distributed mainly in the middle of the Himalayan range. With an increase in both temperature and precipitation, they would extend to the west, and shift towards the north.

Mountainous deciduous broad-leaved forest is characterized by fragmented distribution. For example, *Betula utilis* occurs mainly in the northern Himalayas, with patchy distribution near the Jinsha River. *Betula platyphylla* is a relict after destruction and shrinkage of forests. The oldest sporopollen of *Betula platyphylla* has been found in the Tertiary stratum (The scientific expedition teams to the Tibetan Plateau, Chinese Academy of Sciences 1980). The scenario analysis showed that *Betula utilis* would shift towards the north, but the areas of distribution would shrink.

On the Tibetan Plateau, the distributions of current species were influenced by the severe plateau uplift and climate oscillations. It has been shown that the development of vegetation and environment went through several abrupt transitions (Tang et al 1998). It is important to research vegetation succession from a spatio-temporal perspective. This will throw light on the formation and distribution of the present species, and their sensitivity and responses to climate change. The precipitation pattern on the Tibetan Plateau would change from an increase in the northeast to a decrease in the southwest (Tang et al 1998). The response of life zones on the Tibetan Plateau to climate change shows that they would shift northwards and westwards (Zhang et al 1996; Zheng 1996), and natural vegetation such as tropical and sub-tropical forests, coniferous forests, and alpine meadows would increase, but decrease on alpine steppe, alpine desert, and polar desert (Ni 2000). The climate scenario analysis shows that most of the dominant tree species would shift northwards and westwards as the climate gets warmer.

Bioclimatic variables (minimum temperature in the coldest month, maximum temperature in the warmest month, accumulated growing-season warmth, and minimum value of relative moisture availability in the growing season) are responsible for the physiological mechanism of plants' responses to climate change. But the predictive model can be improved by including a full Priestley-Taylor analysis. In this study, we considered only soil water balance, but ignored individual plant species characteristics owing to a lack of data on LAI and stomatal conductance. Neilson's model (1995) contains a plant transpiration module. It is feasible to incorporate plant transpiration in soil water balance analysis. In addition, elevated CO_2 could dramatically affect the plant water use efficiency of species, hence their drought sensitivity, and their distribution. If these factors could be incorporated into Priestley-Taylor calculations, it would be a major improvement of the Priestley-Taylor model, as well as a significant advance in statistical methods.

We concentrated on simulating alpine tree species distributions based on relatively few factors. What mechanisms lie behind the restrictive impacts of continental climate on the distribution of alpine species? What mechanisms lie behind the responses of species to climate change during their evolution? Such questions require further research.

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