



Complex responses of vegetation diversity to Holocene climate change in the eastern Tibetan Plateau

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Abstract

Biodiversity has attracted much attention recently due to its important relationships with ecosystem function under various global warming scenarios. However, an understanding of biodiversity mechanisms requires study over long time scales. Three high-resolution pollen records of Zoige Basin in the eastern Tibetan Plateau are used to reconstruct changes in vegetation diversity during the Holocene, allowing the mechanisms that drove the dynamic to be quantitatively explored. Rarefaction and Hill's indices are used to estimate the diversity richness and evenness based on pollen data. The results show that changes in palynological richness can be divided into five stages: an abnormal change from 10,500 to 9,000 cal BP, an obvious increase from 9,000 to 6,500 cal BP, a decreasing trend from 6,500 to 4,000 cal BP, an increasing trend after 4,000 cal BP until 1,500 cal BP, and a highly fluctuating stage from 1,500 cal BP to the present. Palynological evenness is relatively stable throughout the Holocene except for during a briefly elevated period from ca. 4,000 to 1,500 cal BP. The result of Boosted Regression Tree analysis indicates that climate is the main driving factor and the effect of temperature is stronger than that of precipitation in the study region. However, during ca. 4,000–1,500 cal BP, palynological diversity is primarily affected by vegetation structure, as shown by an increase in palynological evenness, which can in turn be explained by the climate threshold theory. This research provides a long-term, high-resolution reconstruction of palynological diversity which could be used to infer vegetation diversity change in the ecologically sensitive Tibetan Plateau. The results imply that vegetation diversity in the region may increase under global warming if human impacts are not considered.

Keywords Vegetation diversity · Holocene · Quantitative reconstruction · Driving mechanisms · Tibetan Plateau

Introduction

Biodiversity plays a significant role in ecosystem function because of its importance in sustaining ecosystem stability (Cardinale et al. 2012). However, global biodiversity is currently experiencing rapid changes due to habitat destruction and degradation, over-exploitation, species invasions, environmental pollution and climate change (Wake and Vredenburg 2008; Hoffmann et al. 2010; Barnosky et al. 2011). The relationship between current changes and normal fluctuations, as well as identification of ecosystem function degradation can be determined (Swetnam et al. 1999), in order to provide a baseline for the development of a sustainable biodiversity conservation policy (Willis et al. 2005) and a theoretical basis for the restoration of ecosystem function. However, research focusing solely on modern biodiversity change cannot provide a thorough understanding of the driving mechanisms or sufficiently supportive predictions about future trends. Exploring biodiversity history over longer

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time scales, particularly during the Holocene, can provide us useful insights into these topics.

Fossil pollen records can be used to understand changes in prehistoric vegetation dynamics and provide information about how biodiversity responds to environmental changes (Willis et al. 2005; Jaramillo et al. 2006). Positive correlations have been found between vegetation diversity and palynological diversity (Birks 1973; Birks et al. 2016a; Felde et al. 2016) even though pollen representation bias is always affected by various factors, such as identification precision, pollen production, dispersal, and deposition process (e.g. Birks and Line 1992; Weng et al. 2006, 2007; Matthias et al. 2015).

Vegetation diversity can be influenced by internal (e.g. interspecific competition) and external factors. The external factors are generally more influential, which include climate factors, vegetation structure, human activities, and so on (Marquer et al. 2014; de Blasio et al. 2015; Hájek et al. 2016). However, there are conflicting ideas about the main driving forces for the vegetation diversity. Most studies insisted that climate and human activities (especially in the late Holocene) are the main factors affecting the vegetation diversity. However, inconsistent conclusions have been drawn concerning the relative importance of temperature and precipitation, as well as the response pattern of vegetation diversity to climate. Some research indicates that vegetation diversity has a positive correlation with temperature change (Jaramillo et al. 2006; Erwin 2009), while other studies argue that the species richness may increase with decreasing temperature in low-lying regions that could become species shelters in harsh climates (Brown 1999). In order to explore the factors driving the biodiversity dynamic, we must first reconstruct the history of regional biodiversity over an extended time scale and then quantitatively assess the relative influence from a variety of factors.

The Tibetan Plateau is one of the global biodiversity hotspots (Norman et al. 2000). Due to its unique geographical (> 3,000 m in most regions) and climatic conditions, the Tibetan Plateau is one of the regions with the most abundant biodiversity in the world, particularly with respect to alpine biodiversity conservation (Sun et al. 2012). The vegetation dynamics in this area is highly sensitive to climate change. Studies of regional diversity and its driving mechanisms play an important role in ecosystem conservation; however, there are few studies on vegetation diversity in the Tibetan Plateau over long time scales.

This study reconstructs palynological diversity in the eastern part of the Tibetan Plateau during the Holocene using three high-resolution pollen records from the Zoige Basin, which allow us to infer the vegetation diversity changes in this region. Quantitative methods are then used to determine the magnitude of the factors driving the climate's effects on palynological diversity. The objectives of

this study are: (1) to reveal changes in the palynological diversity during the Holocene in the study region and infer the vegetation diversity changes; (2) to discuss and determine the primary factors driving diversity change; and (3) to provide specific changing trend on vegetation diversity in the context of global warming for policy-making.

Study region

The Zoige Basin is located in the eastern part of the Tibetan Plateau (32°10'–34°10'N, 101°45'–103°25'E, 3,350–3,450 m a.s.l.; Fig. 1a) and is covered by a large alpine peatland with an area of approximately 4,500 km² and an average depth of 2–3 m (maximum 9–10 m; Thelaus 1992; Joosten et al. 2008; Zhao et al. 2011).

The climate of the Zoige Basin is determined primarily by the Asian Monsoon (Zhao et al. 2011). According to data from three meteorological stations in the basin, the mean annual precipitation for 1971–2000 was approximately 650 mm, most of which falls in the summer. The mean annual temperature of this region is 1.1 °C, with a mean July temperature of 10.8 °C and a mean January temperature of – 10.2 °C (Sun et al. 2017).

The vegetation in the Zoige Basin is dominated by sub-alpine meadow, which contains primarily Cyperaceae, Poaceae, *Ranunculus*, and *Artemisia*. The surrounding mountains, especially in the east and south, are covered by scattered forests at up to 4,000 m a.s.l., which are composed mainly of *Picea asperata*, *Abies faxoniana*, *Pinus densata*, *Betula platyphylla*, and *Quercus liaotungensis* (Hou 2001; Shen 2003; Zhou et al. 2010). This area is an ecotone of sub-alpine meadow and alpine coniferous forest (Fig. 1B) and is subject to intense human interference (such as overgrazing and tourism), which has led to ecological fragility and recent declines in biodiversity (Jiao et al. 2007).

Materials and methods

Materials

Three high-resolution pollen records (ZB08-C1, ZB10-C9 and ZB10-C14) from the peat cores in the Zoige Basin are employed to reconstruct the palynological diversity during the Holocene. The original pollen data of ZB08-C1 refer to Zhao et al. (2011), ZB10-C9 refer to Li (2015), and ZB10-C14 refer to Sun et al. (2017) (Table 1).

The chronology at these three sites is based on a large number of AMS ¹⁴C dates from microscopic charcoal particles and sedge seeds (19 dates for ZB08-C1, 20 for ZB10-C9, and 20 for ZB10-C14). Ten more dates for ZB08-C1 were added on the basis of original data (Table 2). We

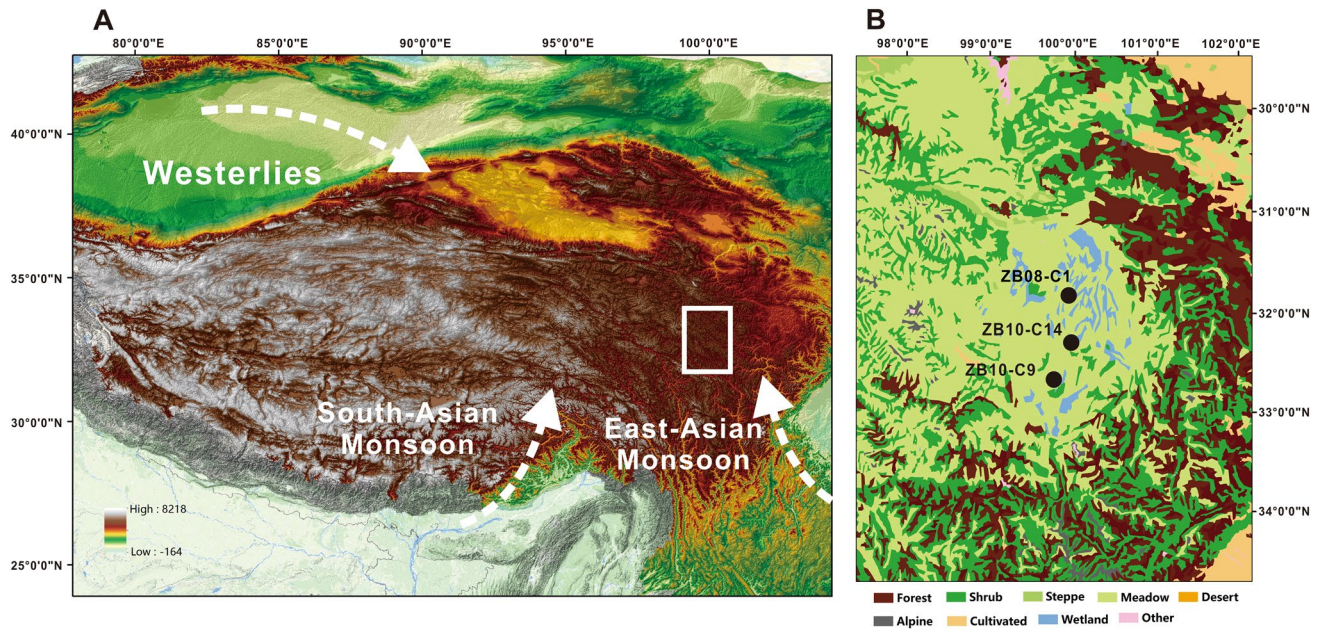


Fig. 1 Location map, climate settings and vegetation status. **a** Elevation map of the Tibetan Plateau and surrounding regions showing the locations of the paleo study sites discussed in the text. **b** The details of vegetation classification in the Zoige Basin and its surrounding areas

Table 1 The basic information of the three pollen records from Zoige Basin on the Eastern Tibetan Plateau

Site	Latitude (°)	Longitude (°)	Altitude (m)	Resolution (yrs)	Number of dating	Time span (cal year BP)	Min. pollen counts	References
ZB08-C1	33.45	102.63	3,467	65	19	10,300–0	200	Zhao et al. (2011)
ZB10-C9	32.78	102.52	3,507	54	20	11,257–0	450	Li (2015)
ZB10-C14	33.09	102.67	3,470	53	20	10,547–0	389	Sun et al. (2017)

Table 2 New AMS radiocarbon dates of ZB08-C1 to re-established the age-depth model

Lab number	Depth (cm)	Material dated	$\delta^{13}\text{C}$ (‰)	^{14}C date (year BP)	Error (\pm year)	Calibrated age, 2σ -range (cal year BP)
UCIAMS-386472	104	Charcoal, sedge leaves	-25.2	670	30	676–559
UCIAMS-386473	176	Charcoal, sedge leaves	-25.4	670	30	676–559
UCIAMS-386474	242	Charcoal, sedge leaves	-26.7	2,000	30	2,032–1,880
UCIAMS-386475	315	Charcoal, sedge leaves	-27.9	3,850	30	4,407–4,155
UCIAMS-386476	390	Charcoal, sedge leaves	-27	5,130	30	5,938–5,753
UCIAMS-386477	460	Charcoal, sedge leaves	-26.7	6,270	30	7,263–7,161
UCIAMS-386478	480	Charcoal, sedge leaves	-26.8	6,530	30	7,506–7,340
UCIAMS-386479	512	Charcoal, sedge leaves	-26.7	7,010	30	7,935–7,763
UCIAMS-386480	555	Charcoal, sedge leaves	-25.4	7,880	30	8,854–8,591
UCIAMS-386481	610	Charcoal, sedge leaves	-25.7	8,490	30	9,533–9,470

applied the ‘Bacon’ model (Blaauw and Christen 2011), i.e. the Bayesian age-depth model, to the ^{14}C dates from the three sites to establish a reliable chronology foundation for in-site comparisons. The Bacon age-depth model performs

better simulation on the actual deposition conditions, in which environmental changes will force responses in the deposition processes, causing accumulation rates to change somewhat from previous rates (Blaauw and Christen 2011).

The pollen records from the three sites cover the Holocene with a time resolution of 50–60 years (Table 1). There are 26 pollen types from core ZB08-C1 (18 families + 8 genera, Zhao et al. 2011), 61 pollen types from core ZB10-C9 (31 families + 30 genera, Li 2015), and 63 pollen types from core ZB10-C14 (31 families + 32 genera, Sun et al. 2017). The pollen assemblages are dominated by Cyperaceae (average 60%) in all three cores. Other dominant types include Poaceae, *Picea*, *Pinus*, *Betula*, and *Artemisia*. The Holocene vegetation history at the three sites has been retrieved and discussed qualitatively in terms of pollen percentages (Zhao et al. 2011; Li 2015; Sun et al. 2017). In this paper, we focus on the issue of past vegetation diversity that can be inferred from the fossil pollen records.

Descriptions of diversity indices

We use two different pollen-based indices to measure different aspects of palynological diversity, namely richness and evenness. We apply rarefaction analysis to calculate the palynological richness (PRI), which is used to standardize the pollen count size to a constant number of grains in each sample of each core. In our case, the minimum pollen sum was employed as the constant pollen sum for each site (ZB08-C1, $n=200$; ZB10-C9, $n=450$; ZB10-C14, $n=389$).

We use the probability of interspecific encounter (PIE; Hurlbert 1971) to measure evenness. PIE is the probability that two pieces of pollen drawn randomly from the sample belong to the same species. This index would help us to understand how the total number of taxa in a sample is influenced by a few of dominant species (van der Knaap 2009).

We estimate the evenness-detrended palynological richness (DE-PRI) in order to reduce the influence of evenness. Richness and evenness are not independent from one another (Tuomisto 2012), especially in pollen data (Giesecke et al. 2014). To eliminate this effect, we applied the detrending method by using the relationship between evenness and richness, as estimated by an ordinary least squares (OLS) linear regression equation for each site, with the dependent variable (y) PRI and the independent variable (x) palynological evenness. The PRI residual plus average is used to represent the DE-PRI (Colombaroli and Tinner 2013).

We applied the constrained hierarchical clustering (CONISS) method to divide the richness and evenness synthesis results into different time zones using the Euclidean distance. For all the analysis above, we use the software program R (ver. 3.4.0, R Development Core Team 2008).

Reconstruction of biome and landscape openness

In order to explore the extent to which vegetation structure affects diversity, we used pollen-based Biomization analysis (Prentice et al. 1996) on the fossil pollen assemblages.

The classification schemes of Plant Function Type (PFT) and biome refer to Ni et al. (2010) and Chen et al. (2010). Vegetation changes were expressed with the affinity score variations of each reconstructed biome. We chose the biome types with the highest score during the study period for subsequent comparative analysis. All Biomization calculations were conducted with the PPPBase software (Guiot and Goeury 1996).

The ratio of non-arboreal pollen to arboreal pollen (NAP/AP) was used to measure landscape openness (OPEN; Colombaroli and Tinner 2013). Thus, the results of Biomization, as well as the percentage of arboreal pollen (Tree), were chosen to represent the vegetation structure at the landscape scale. OPEN was also used as an indicator of landscape openness, which could influence the palynological diversity.

Numerical methods

Redundancy Analysis and Boosted Regression Tree were performed in this study to quantify the influence of each environmental factor on palynological diversity and, therefore, infer which variable is the most important driving force.

Redundancy analysis (RDA)

Ordination analysis is applied to visualise the strong correlations among multiple variables. The first axis of the pollen data has a length of 2.1 as determined by the Detrended Correspondence Analysis (DCA). Accordingly, a linear-model ordination, such as RDA, was used for subsequent analysis (Ter Braak and Verdonschot 1995). Two quantitative records of temperature and precipitation obtained from non-pollen indicators from two sites close to Zoige Basin, i.e. an alkenone-based summer temperature reconstruction from Qinghai lake (QH T_{ann} ; Hou et al. 2016) on the eastern Tibetan Plateau, and the summer precipitation variation derived from the oxygen isotope record of Dongge Cave (DG $\delta^{18}O$; Dykowski et al. 2005), are involved in the RDA as environmental variables. Furthermore, the ash-free organic matter bulk density (OMD) records of the three studied cores are used to constrain peat development, i.e. information about the deposition environment, and vegetation growth (Vitt et al. 2000; Zhao et al. 2011). Ultimately, climate variables (QH T_{ann} , DG $\delta^{18}O$), vegetation structure variables (Biomization, Tree), landscape pattern variables (OPEN), and deposition environment variables (OMD) are analysed in the RDA.

The Variance Inflation Factors (VIFs) derived from RDA are used to identify co-linear relationships among variables; we remove those variables containing large amounts of repeat information until the VIF value is small (Ter Braak and Verdonschot 1995). Through this procedure, we select

four variables for the following analysis. The RDA is also performed in the R software.

Boosted regression trees analysis

Boosted regression tree (BRT) analysis is used to indicate the variables which could best explain the changes in palynological diversity. In our case, it is employed between the DE-PRI and each variable selected from the RDA and VIF (Elith and Leathwick 2011). BRT can analyse several variables at the same time and give a comparable explanation percentage, so that it is convenient for us to identify variables with higher contribution. Finally, the model for each pollen record is fitted with a total of more than 5,750 trees. R software is used for BRT analysis.

Results

Chronology and age-depth model

In this study, a Bayesian age-depth model was established based on a large number of age controls, as shown in Fig. 2. When the number of iterations exceeds 1,000, the calculation result of the age is considered reliable. All three records in this study are calculated over more than 6,000 iterations; thus, the age framework established in this study is quite credible. The deposition rate is linear with the gamma distribution, without interruptions or jumps. Its value ranges between 0 and 1, if we consider that the core sedimentation rate remains stable.

Based on the conclusions results above, we can conclude that the established high-resolution chronological framework has high credibility and is sufficient for multi-index

comparisons between different sites (ZB08-C1, ZB10-C9 and ZB10-C14).

Palynological diversity reconstruction

There is good agreement between PRI and DE-PRI, both of which possess relatively consistent trends over all three core records (Fig. 3). The estimated richness of ZB08-C1 is in the range of 7–14, while the ZB10-C9 richness varies more widely between 10 and 22; the richness of ZB10-C14, which ranges from a minimum of 10 to a maximum of 20, is similar to that of ZB10-C9. Palynological diversity changes in the Zoige Basin during the Holocene can be divided into five zones according to CONISS.

Zone I (10,500–9,000 cal BP): The palynological richness of ZB10-C9 shows a slight increasing trend, while those of ZB10-C14 and ZB08-C1 show decreasing trends. The evenness during this period is relatively high with some fluctuations.

Zone II (9,000–6,500 cal BP): The general richness and evenness trends are consistent among the three cores during this period. An obvious increase in richness is observed from 9,000 to 6,500 cal BP, with a marked peak at 6,500 cal BP; the rate of richness increase is higher during this period than during any other period in the Holocene. Evenness declines slowly in comparison to the previous period.

Zone III (6,500–4,000 cal BP): Palynological richness rapidly decreases, reaching a Holocene minimum at 4,000 cal BP. Evenness declines at the beginning of this period of time; after reaching a minimum, it begins to increase significantly.

Zone IV (4,000–1,500 cal BP): After 4,000 cal BP, the richness increases again. Some differences exist between the DE-PRI and PRI results due to the influence of evenness, but the general trends are similar. Evenness remained relatively

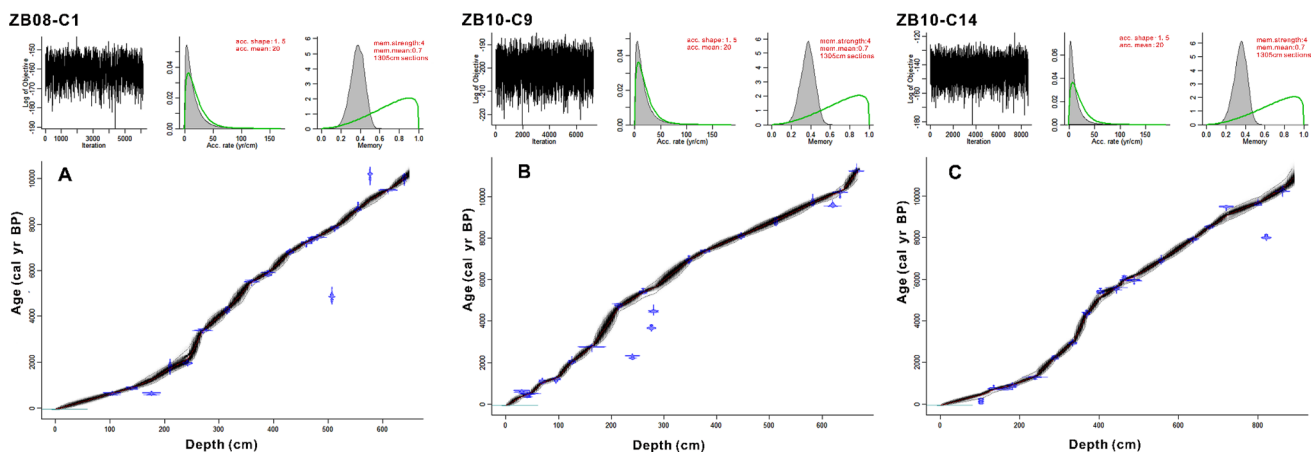


Fig. 2 Age-depth models for three peat cores established with the Bacon software of Blaauw and Christen (2011) and based on the ^{14}C dates (reference presented in Tables 1, 2). **a** ZB08-C1; **b** ZB10-C9; **c**

ZB10-C14. From left to right, the upper panel of each part shows the number of iterations, the deposition rate and the autocorrelation coefficient of the sedimentation rate

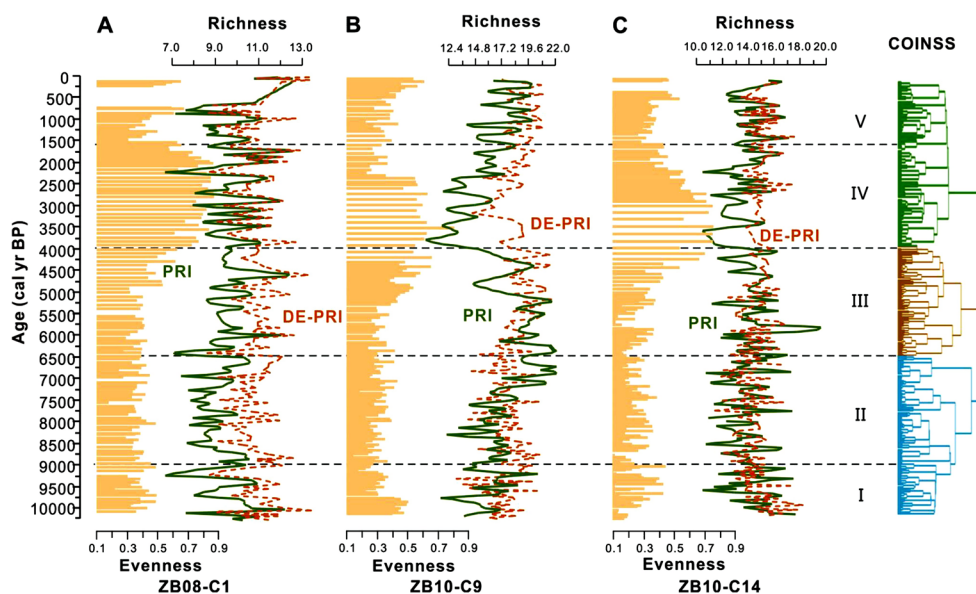


Fig. 3 Results of the diversity reconstruction of three cores in Zoige Basin. Palynological evenness (yellow histogram, calculated by the probability of interspecific encounter, PIE); palynological richness (green line, PRI, expressed as the expected number of pollen types)

and detrended palynological richness (red line, DE-PRI, expressed as the palynological richness without the influence of evenness). **a** ZB08-C1; **b** ZB10-C9; **c** ZB10-C14. The right panel shows the result of constrained hierarchical clustering (CONISS)

high throughout this whole period, which is the highest in the Holocene.

Zone V (1,500–0 cal BP): During this period, palynological richness remains high, but fluctuates considerably. The evenness value remains low.

Biomization reconstruction results

The score of two major biomes, cool evergreen needle-leaved forest (COEG) and temperate grassland (TEGR), are higher than the other biome types, and Holocene vegetation in the Zoige Basin is mainly characterized by these two vegetation types (Fig. 6). The biome changes in the three records are quite similar. COEG scores show a gradual increase starting in the early Holocene, with a maximum at 6,500 cal BP. After that, a slight decrease in COEG is accompanied by increasing TEGR scores. Beginning at 4,000 cal BP, the biome is characterized by a sharp decrease in COEG scores and a synchronous increase in TEGR scores.

Numerical analysis results

The RDA axis1 and axis2 explain more than 64% of the variations in richness (64.7% for ZB08-C1, 64% for ZB10-C9, and 67.9% for ZB10-C14). Pair-plots of the 7 variables (Fig. 4) indicate that Tree is highly correlated with COEG. TEGR and OMD are perpendicular to the trend of sample change trend, indicating that these two variables explain little of the variability.

As shown in Table 3, the VIF analysis results for 7 variables from the three cores are integrated (see Run1). Tree is removed because of its high VIF value (Run2). Both COEG and TEGR represent vegetation structure, only COEG variables are preserved, because of the trend of COEG and palynological diversity are more relevant (Fig. 3). As the overall trend of OMD (arrow) and palynological diversity changes is almost perpendicular, it cannot explain the variability of diversity and is therefore excluded in the follow-up analysis. Furthermore, the OPEN variable is retained to represent the landscape pattern. Similarly, QH T_{ann} and DG $\delta^{18}O$ are used to represent the temperature and precipitation information respectively. After simplification, the VIF value is < 1.6 (Table 3, Run3), which indicates that the amount of overlapping information is sufficiently small. Consequently, four variables are selected for subsequent BRT: QH T_{ann} , DG $\delta^{18}O$, OPEN, and COEG.

The BRT results are almost the same among the three cores (Fig. 5) and show that temperature contributes more than any other variables (39.3% for ZB08-C1, 34.4% for ZB10-C9, and 29.7% for ZB10-C14) in the developed model. We can thus conclude that it is the most significant variable. The precipitation contributes more than 23% (25.6% for ZB08-C1, 23.3% for ZB10-C9, and 25.6% for ZB10-C14), and COEG reaches approximately 20%, while the OPEN index is the lowest (with a minimum of 16%).

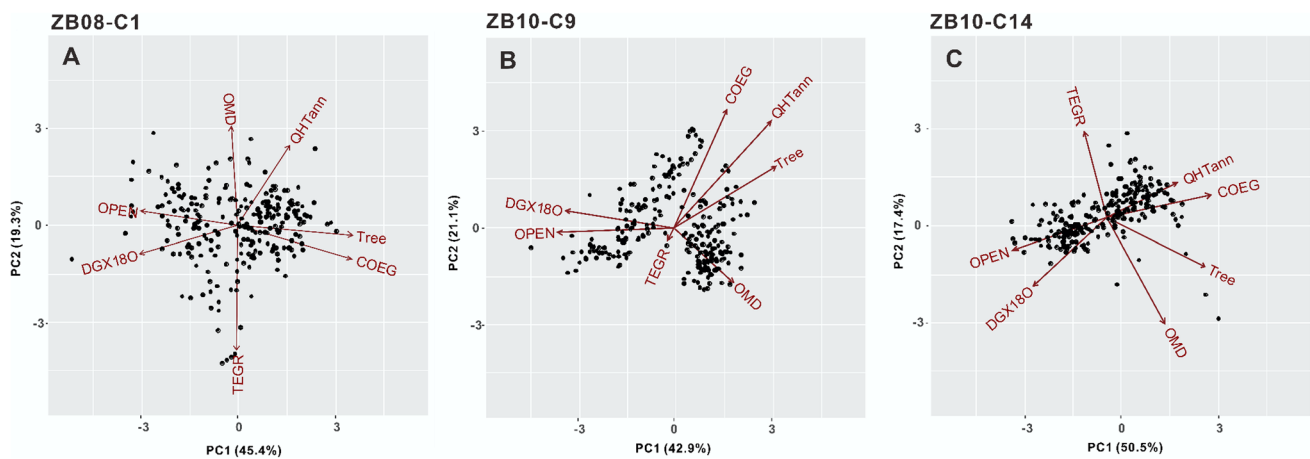


Fig. 4 Plot of the first two axes of the canonical redundancy analysis (RDA) from three cores (**a** ZB08-C1; **b** ZB10-C9; **c** ZB10-C14) in Zoige Basin, showing the relationships between the pollen samples (points) and 7 climatic variables (arrows). Tree: percentage of arboreal pollen; OPEN: the ratio of non-arboreal pollen to arboreal pollen; QH T_{ann} : alkenone-based summer temperature records from Qinghai

lake; DG $\delta^{18}O$: the summer precipitation variation derived from the oxygen isotope record of Dongge Cave; TEGR: the score of temperate grassland in biome reconstruction; COEG: the score of cool evergreen needle-leaved forest in biome reconstruction; OMD: the ash-free organic matter bulk density

Table 3 Summary statistics for variance inflation factors (VIF) with 7 variables of ZB08-C1, ZB10-C9 and ZB10-C14

	ZB08-C1			ZB10-C9			ZB10-C14		
	Run1	Run2	Run3	Run1	Run2	Run3	Run1	Run2	Run3
Tree	3.44	–	–	19.17	–	–	23.03	–	–
OPEN	1.97	1.92	1.09	4.68	4.47	1.32	3.30	3.25	1.03
QH T_{ann}	1.61	1.57	1.17	2.09	1.95	1.19	1.55	1.50	1.17
DG $\delta^{18}O$	2.77	2.41	1.19	3.64	3.03	1.58	2.85	1.91	1.12
TEGR	2.38	2.06	–	1.55	1.51	–	4.29	4.03	–
COEG	3.71	3.14	1.03	2.25	2.25	1.39	1.94	1.84	1.07
OMD	1.11	1.09	–	1.47	1.41	–	3.23	2.72	–

Run1–3 illustrates the process of variable simplification. Run 1: with all variables; Run 2: without the variable of Tree; Run 3: remove the variables Tree, TEGR and OMD (see the text for more explanations)

Tree: percentage of arboreal pollen; OPEN: the ratio of non-arboreal pollen to arboreal pollen; QH T_{ann} : an alkenone-based summer temperature records from Qinghai Lake; DG $\delta^{18}O$: the summer precipitation variation derived from the oxygen isotope record of Dongge Cave; TEGR: the score of temperate grassland in biome reconstruction; COEG: the score of cool evergreen needle-leaved forest in biome reconstruction; OMD: the ash-free organic matter bulk density

Discussion

Reliability and uncertainty in pollen-based richness reconstructions

The Zoige Basin is primarily covered by alpine meadows, and the surrounding mountains, especially to the east and south, are covered by forests mainly composed of *Picea* and *Abies* (Shen 2003). Comparing the results of Biomization, which indicates that the Holocene was mainly characterized of cool evergreen needle-leaved forest (COEG) and temperate grassland (TEGR), it can be seen that COEG can be used to denote the change in the surrounding forest

land while TEGR can indicate the change in the alpine meadows. In addition, the major pollen taxa identified in the samples are consistent with the major vegetation taxa according to the “Vegetation Atlas of China” (Scale: 1:1,000,000) (Hou 2001). It is therefore reasonable to assume that the diversity information contained in the pollen assemblages properly represents the vegetation diversity, as has been found in numerous studies showing that pollen and floristic diversity have a statistically significant positive correlation (Birks and West 1972; Flenley 2005; Meltsov et al. 2011; Birks et al. 2016a; Felde et al. 2016).

However, uncertainties may exist due to identification level, pollen production and deposition process. Evenness is usually affected by pollen production between different plant

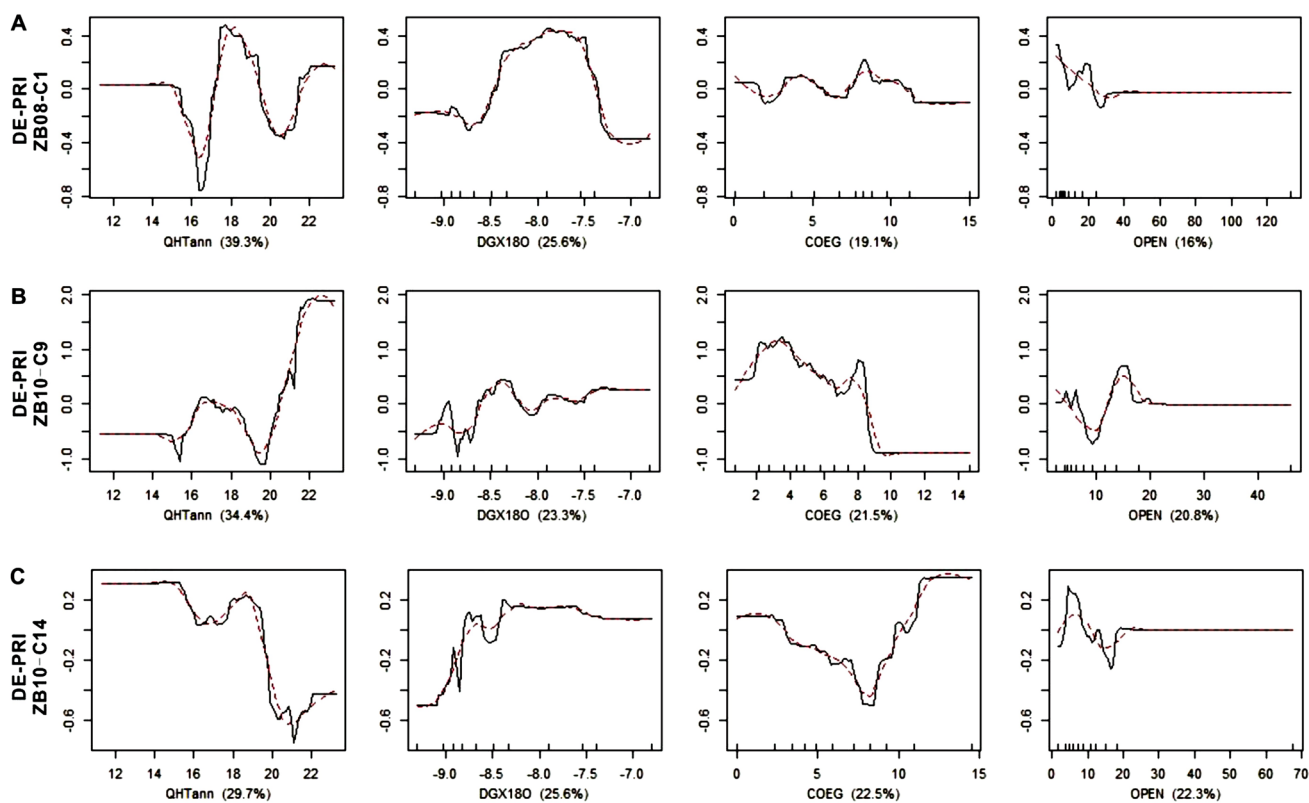


Fig. 5 Partial dependence plots for the four most influential variables of vegetation diversity change according to the result of BRT. **a** ZB08-C1; **b** ZB10-C9; **c** ZB10-C14. The carpet map at the top of the plot shows the distribution of the variable in the decimal place

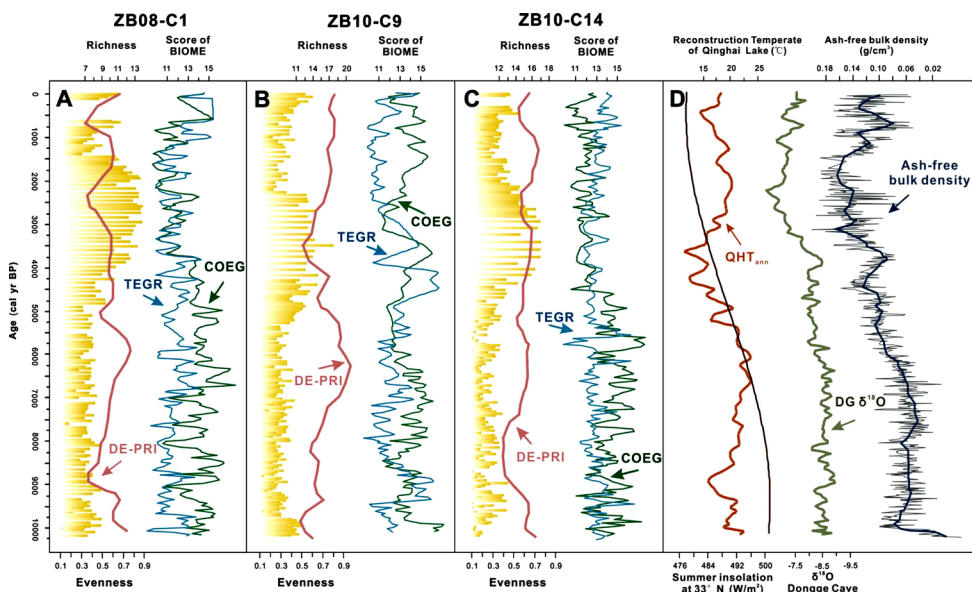


Fig. 6 Comparisons between palynological diversity, vegetation structure and climate variables. **a** ZB08-C1; **b** ZB10-C9; **c** ZB10-C14. Each panel includes: palynological evenness (yellow histogram, PIE), five-points moving average of detrended palynological richness (pink line), BIOME score of cool evergreen needle-leaved forest (green line) and temperate grassland (blue line). **d** Regional climate

variables. Alkenone-based summer temperature curve reconstructed from Qinghai Lake, northeastern Tibetan Plateau (orange line, Hou et al. 2016); summer insolation at 33°N (dark red line); Oxygen isotopes of Dongge Cave (light green line, Dykoski et al. 2005); mean ash-free bulk density of these three cores (gray line, and 5-point smoothing data in dark blue line)

taxa, while richness is less influenced by pollen production (Smith and Wilson 1996; Giesecke et al. 2014). We use the DE-PRI to eliminate the effect of evenness on richness and reduce the inherent representation bias caused by production in pollen assemblages. The error due to deposition is consistent between the samples in each core during the Holocene (Xiao et al. 2008). Therefore, the reconstruction trends remain comparable even though these errors may affect the absolute value.

Pollen identification in terms of taxonomic levels may also cause uncertainty in the reconstruction of palynological diversity. We argue that the reconstruction is still comparable due to the identification does not affect the trend. The content of ZB08-C1 is, essentially, identified at the family level (18 families + 8 genera), while the other two cores are identified predominantly at the genus level (ZB10-C9: 31 families + 30 genera; ZB10-C14: 31 families + 32 genera). Even so, the three records still have the similar trend, despite the absolute value in the richness of ZB08-C1 not being as significant as in the others. Due to limited data information, many biodiversity assessments today are based on genus or higher taxa that perform well (Williams and Gaston 1994; Andersen 1995; Pearman and Weber 2007). In this case, vegetation “types” can be thought of as “higher” (or broader) taxonomic divisions (Birks et al. 2016a). In addition, the palynological diversity is comparable within a given core over an extended time series (Xiao et al. 2008; Birks et al. 2016b), so the bias effect from pollen identification should be consistent.

The openness of the site may lead to the inconsistency of palynological diversity and that of flora by affecting pollen dispersal. However, in this study, we find that this effect is smaller compared with the climatic factors, which is not enough to affect the trend of palynological diversity change. During 9,500–6,000 cal BP, forest expansion led to a decline in openness, which could hinder pollen dispersal. However, palynological richness still showed an increasing trend, which indicated that this uncertainty will not affect the impact of climate factors on the general trend. This conclusion is also confirmed in the BRT analysis. The interpretation ratio of OPEN is far less than that of climatic factors.

Each of the peat deposition records we used can represent local vegetation information. Considering these three cores are located along the North–South transect of the region across 80 km, the trends of palynological diversity of them should be able to represent the regional vegetation diversity.

Climate controls on vegetation diversity

In order to demonstrate the change trend more clearly, we conducted a five-point moving average of the DE-PRI reconstruction of all three cores (Fig. 6), which generally shows similar trends to those found in the summer temperature

change inferred from alkenone at Qinghai Lake and the precipitation changes deduced from stalagmite oxygen isotopes in Dongge Cave. In the early Holocene, the Qinghai Lake reconstructed temperature increases beginning in 9,000 cal BP; the palynological richness increases at the same time. Temperature and richness both reach their maximum at 6,500 cal BP, and then decrease synchronously. Richness begins to increase abruptly after 4,000 cal BP, while the temperature continues to decrease gradually until 3,750 cal BP. Apart from this short time, the temperature and richness showed the same trend until 1,500 cal BP. Richness fluctuates at a relatively high value beginning in 1,500 cal BP, while the climate change does not.

The BRT results indicate that climatic factors (i.e. temperature plus precipitation) explain about 60% of the variation in richness, while vegetation structure and openness explain < 40% (Fig. 5). Climate factors clearly constitute the major controls on diversity changes. This result is consistent with the species-energy hypothesis, which posits that vegetation diversity is highly dependent on the evolution of climate variables (Lomolino 2001; Stanisci et al. 2005).

According to the species-energy hypothesis (Currie and Paquin 1987; Currie 1991), the increase in insolation will lead to an increase in temperature and precipitation, which will cause an increase in the amount of energy and resources that the ecosystem obtains. This kind of change will allow more individuals for survival, leading to an increase in ecosystem richness. The maximum pollen influxes during 9,000–6,500 cal BP suggest that the climate was suitable for vegetation success (Sun et al. 2017), which may have caused higher richness. Additionally, climatic factors may reach the survival boundary conditions of some species, resulting in the emergence or disappearance of some species, i.e. changes in vegetation diversity. Changes of vegetation diversity along with the climate will be reflected in palynological diversity.

The palynological richness and temperature curves are the most similar among the various possible factor pairings (Fig. 6), suggesting that temperature has a greater effect on palynological diversity than does precipitation in our study region. This conclusion is quantitatively confirmed by the BRT results (Fig. 5). The percentages of variance due to temperature, at greater than 30% (39.3% for ZB08-C1, 34.4% for ZB10-C9, and 29.7% for ZB10-C14), outweighs the variance explained by other factors. Precipitation accounts for ~ 23% of the variance (25.6% for ZB08-C1, 23.3% for ZB10-C9, and 25.6% for ZB10-C14).

There is a monotonic relationship between richness and temperature; however, its relationship with precipitation shows obvious regional differences. In a study involving thousands of quadrats worldwide, Francis and Currie (2003) found that species richness was linearly related to air temperature under sufficient precipitation. Kreft et al.

(2008) studied 1,032 geographic units worldwide, finding that the effect of precipitation was significantly reduced and the relationship between richness and air temperature was stronger when the mean annual precipitation was higher than 505 mm. The ash-free bulk density of the three cores in Zoige, which can indicate the moisture conditions of peatland, has the same trend comparing with the isotope of Dongge cave (Fig. 6d). With reference to the wetness and precipitation change, modern precipitation of Zoige basin (600 mm) was relatively low when compared to other periods of the Holocene. Thus, we may infer that precipitation was relatively abundant during the Holocene, which may explain the important role of temperature in vegetation diversity in the study region.

Impacts of peatland initiation and vegetation composition on vegetation diversity

The changes in palynological diversity during the Holocene are consistent considering the possible uncertainties caused by the age constraint estimates. An exception can be noted at 10,500–9,000 cal BP, during which the palynological richness in ZB08-C1 and ZB10-C14 decreases slightly, while that in ZB10-C9 displays an increasing trend; this difference clearly cannot be explained by climate change, as well as the abnormal fluctuations in palynological diversity since 1,500 cal BP.

Differences among the three cores in the timing of initial peat development, i.e. the changes in the lithology, could account for inconsistencies in the palynological diversity in the early Holocene that cannot be explained by climate. Loss-on-ignition data indicate that the Zoige Basin experienced a change from shallow water sediments to initial peat development (Zhao et al. 2011; Sun et al. 2017). There are significant differences between peat deposition and lake sediments in the size of the pollen source area (Sugita 2007), so the palynological diversity changes in the conversion period are abnormal. For ZB10-C9, peat began to develop much earlier, at 11,000 cal BP. Thus, during the time period covered by our study (i.e. the last 10,500 years), peat formation continuously dominated the depositional environment, resulting in similar trends between Zone I and Zone II. However, for ZB10-C14 and ZB08-C1, 10,500–9,000 cal BP is a transitional period with a different trend in Zone I (Zhao et al. 2011; Li 2015; Sun et al. 2017).

The impact of climate change on palynological diversity is primarily achieved through changing vegetation structure and survival status. Under normal circumstances, climate and palynological diversity change simultaneously. At 9,000–6,500 cal BP, richness shows a substantial increase. Because the temperature at this stage is high and the precipitation is sufficient, the percentage of tree pollen rises and peaks at 6,500 cal BP, while herbaceous pollen decreases

with a few shrub developments. This trend agrees with that of the Biomization model reconstruction (Fig. 6). The vegetation type at this stage indicates a transition from meadow to coniferous forest. The results of Sun et al. (2017) also show that this period contains several forest expansion events. Due to the rapid development of forest, the original vegetation structure, which was dominated by Cyperaceae and Poaceae, changes. The development of trees, shrubs, and selected low-abundance herbs may have led to a rapid increase in vegetation richness, which could lead to an increase in palynological richness.

The temperature decreases after 6,500 cal BP, but does not reach the threshold at which it might change the vegetation structure. The vegetation composition is stable and similar to that in the previous stage; however, it is accompanied by a sharp decline in the pollen influx, which reveals poor vegetation survival (Sun et al. 2017). Thus, the richness decreases significantly, reaching a minimum at 4,000 cal BP.

When the temperature is reduced to the threshold, the vegetation structure may collapse, resulting in non-synchronous changes in vegetation diversity and temperature. This is also shown in our reconstruction results. During ca. 4,000–1,500 cal BP, the trends in palynological richness and temperature are quite different. An ecosystem can maintain its stability within a range of external environmental stresses, but it will respond more strongly when the external environment approaches critical thresholds (Scheffer et al. 2001). Palynological richness increases after 4,000 cal BP, but the temperature continues to decline until 3,750 cal BP. The evenness reaches a maximum, indicating a breakdown of the original community structure. Around 4,000 cal BP, Cyperaceae increases rapidly, indicating that the forest retreat, accompanied by the meadow development, was caused by the temperature continuously declining to the critical threshold. The COEG and TEGR reconstructed by the Biomization model show staggered manifestations during this period (Fig. 6), which indicates that species in the two ecosystems coexisted, generating a rapid increase in vegetation richness, thus palynological richness increases sharply, and a highest value of evenness. Zhao et al. (2017) argues that a vegetation regime shift occurred in the Zoige Basin region during 6,000–4,000 cal BP, which is in agreement with the timing of the shift found in this study.

With the increased temperature, the single ecosystem, and the dominant species therein, are gradually restored to a steady state. Consequently, the development of the meadow led to the restoration of the dominant species, and ultimately the evenness decreased.

After 1,500 cal BP, meadow becomes the main vegetation type in this region and forms a stable vegetation structure dominated by Cyperaceae plants. Thus, the change in palynological diversity should be smooth; however, it shows variability. Neither climate nor vegetation composition can

explain these fluctuations. However, human activities, such as excessive deforestation and grazing, have probably led to substantial fluctuations in diversity (Li 2015). The population in north-western Sichuan Province has increased exponentially since the late Holocene (Zhao 2012). The charcoal records from ZB08-C1 shows an increasing trend in fire intensity, which can be closely linked with human activity (Zhao et al. 2017). The fluctuations in vegetation diversity since 1,500 cal BP are therefore likely to be caused by human disturbance.

Conclusions

This study presents a long-term and high-resolution reconstruction of the palynological diversity in a climate-sensitive area of the Tibetan Plateau. The reconstruction shows almost entirely consistent trends in palynological diversity of the three peat cores. Changes in palynological diversity during the Holocene can be divided into five stages: an abnormal change from 10,500 to 9,000 cal BP, an obvious increase in richness from 9,000 to 6,500 cal BP, a decrease in richness from 6,500 to 4,000 cal BP, and finally, a recovery in richness after 4,000 cal BP. From 1,500 cal BP to present, the richness fluctuated within relatively high amplitude. Palynological evenness is relatively stable throughout the Holocene, with an exception of a brief maximum at ca. 4,000–1,500 cal BP. Temperature condition is testified to be the most important factor affecting palynological diversity in this region. The results provide insights into the changes in the vegetation diversity inferred from the palynological diversity under different climate conditions during the Holocene. Our results imply that vegetation diversity will likely increase with the global warming in the north-eastern Tibetan Plateau.

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