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3,600 years of human adaptation to drought intensification on the southern Tibetan Plateau

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The development of adaptive survival strategies is crucial for human occupation of the high-altitude areas of the Tibetan Plateau (TP). However, the history of this adaptation and its driving mechanisms are poorly understood. We used records of pollen, coprophilous fungal spores, and charcoal from a well-dated, high-resolution lake sediment core from the Southern Tibetan Plateau (STP) to investigate the history of high-altitude survival strategies, including arable agriculture and pastoralism, spanning the past 3600 years. The results revealed that survival strategies were dominated by arable agriculture, supplemented by pastoralism, from ~3600 to 1800 cal yr BP. However, after 1800 cal yr BP, this strategy shifted to low-level arable agriculture with intensified pastoralism. Comparison of our findings with regional paleoclimatic and archaeological records revealed that this transformation was an adaptive response to drought intensification. This adaptive resilience was a key aspect of human occupation of the high-altitude regions of the TP during the late Holocene.

The Tibetan Plateau (TP), Earth's "Third Pole", has an average elevation of more than 4000 m above sea level (m a.s.l.)[1,2]. It is characterized by cold temperatures, hyper-drought, and capricious weather, resulting in resource scarcity in most of its high-altitude areas, which limit human occupation. Therefore, establishing strategies to obtain adequate living resources in this harsh environment is a major challenge for its inhabitants[3–6]. Remarkably, despite the harsh climate and environmental changes, Tibetans developed a productive arable agricultural and pastoral system on the plateau several thousand years ago[3,6–9]. However, we know very little about how these adaptive survival strategies evolved to form the modern plateau economy, based primarily on pastoralism, supplemented by arable agriculture. In particular, the relationship between this process and climate change remains unclear.

In recent years, great efforts have been made to address the above issues. Previous research has shown that the introduction of cold-tolerant barley and wheat played a critical role in enabling human adaptation to the increasingly harsher plateau climate after ~3600 cal yr BP[7]. This adaptation eventually led to the establishment of permanent human settlements on the northeastern TP[7]. However, the evidence for this process is limited to lower altitude regions (<3500 m a.s.l.) on the northeastern TP, and minimal evidence is available from the higher elevation regions (>3500 m a.s.l.) that comprise ~85% of the land area of the TP[5,10]. Recent archeological investigations in high-altitude regions of the TP have provided compelling evidence of well-adapted agro-pastoral systems during the late Holocene[5,6,8,9,11–13]. Around 3,000 years ago, the Bangga site (3715 m a.s.l.), on the central TP, underwent a transition from a mixed-cropping to a barley-dominated arable system. Although this change was influenced by both climatic and social factors, the evolutionary process behind the development of pastoralism remains unclear[14]. In contrast, previously published zooarchaeological, paleoproteomic, and lipid residue evidence suggests that pastoralism had emerged in higher-elevation regions some ~3500–3000 years ago[5,6,12]. Furthermore, genetic studies indicate that yaks were domesticated on the TP some 7300 years ago[15]. These findings are inconsistent; moreover, it is difficult to obtain continuous and detailed information about successive agricultural and pastoral developments from these scattered archeological records. Hence, our understanding of the historical development of arable agriculture and pastoralism in the high-altitude regions of the TP and their relationship with climate change remains limited.

Fortunately, the microfossil evidence preserved in sediments enables us to obtain a continuous and detailed history of the development of arable agriculture and pastoralism in different regions[16–23]. Records of

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Sporormiella-type fungal spores and crop pollen in the Andes have provided information about the adaptation of agro-pastoral activity to climate change[16,17]. Additionally, a recent record of coprophilous fungal spores and crop pollen in Nile delta sediments indicated an early transition from pastoralism to agriculture some 7000 years ago; this adaptive shift coincided with a change from arid to wet conditions[18]. Besides, a sedimentary record of *Sporormiella*-type spores and the pollen of crop plants from northern China revealed that shifts in animal herding and cultivation practices were influenced by a drying climate[23]. Similarly, *Sporormiella*-type records from northern China indicated the rapid intensification of pastoralism after ~3600 cal yr BP, which may have been related to climate change[19]. Furthermore, a record of coprophilous fungal spores from the northeastern TP indicated a major increase in grazing activity during ~2600–2200 cal yr BP, likely in response to climatic deterioration and/or social factors[20,24]. To conclude, accurately-dated, high-resolution records of pollen, fungal spores, and charcoal from lake sediments can help us to reconstruct the history of arable agriculture and pastoralism and their potential climatic linkage on the southern TP.

In this study we obtained high-resolution records of pollen, coprophilous fungal spores, and charcoal from a precisely-dated lake sediment core from the STP (Fig. 1). Our aims were to determine the history of high-altitude human survival strategies, including both arable agriculture and pastoralism, over the past 3600 years.

Results

Eight environmental indicators were identified in the Angrenjin Co core: two pollen taxa (Poaceae >40 μm and *Stellera*); four fungal spore types (*Sporormiella*-type, *Coniochaeta* sp., *Glomus*-type, *Gelasinospora* sp.); and charcoal particles >100 μm. Among them, Poaceae >40 μm (range of 0–157 grains/g, and mean of 40 grains/g, and the same convention below) and *Sporormiella*-type coprophilous fungal spores (0–346 spores/g, 117 spores /g) are dominant (Fig. 2). Additionally, *Coniochaeta* sp. (0–65 spores/g, 13 spores/g), *Glomus*-type (0–1073 spores/g, 361 spores/g), and charcoal >100 μm (0–132 particles/g, 10 particles/g) are represented. The microfossil diagram is divided into two zones based on CONISS results and the concentrations of Poaceae >40 μm pollen and *Sporormiella*-type spores, and they are described below (Fig. 2).

Zone 1 (3600–1800 cal yr BP) has abundant cereal pollen: Poaceae >40 μm (mean: 54 grains/g), with a high ratio of cereal-type Poaceae to total Poaceae. The representation of grazing indicators is very low; they include *Stellera* (mean: 5 grains/g, and the same convention below), *Sporormiella*-type (37 spores/g), and *Coniochaeta* sp. (3 spores/g). The erosion indicator *Glomus*-type is present (332 spores/g), and the numbers of fire indicators are low, with the sporadic occurrence of *Gelasinospora* sp. and charcoal >100 μm (2 particles/g) (Fig. 2).

Zone 2 (1800 cal yr BP to the present) is characterized by abrupt decreases in cereal pollen, with the mean of Poaceae >40 μm decreasing from 54 grains/g to 32 grains/g, and a low ratio of cereal-type Poaceae to total Poaceae. In contrast, the grazing indicators increase rapidly, including *Stellera* (8 grains/g), *Sporormiella*-type (157 spores/g), and *Coniochaeta* sp. (18 spores/g). The mean of the erosion indicator *Glomus*-type is 376 spores/g. Additionally, the fire indicators increase substantially, with the frequent occurrence of *Gelasinospora* sp. and charcoal >100 μm (14 particles/g) (Fig. 2).

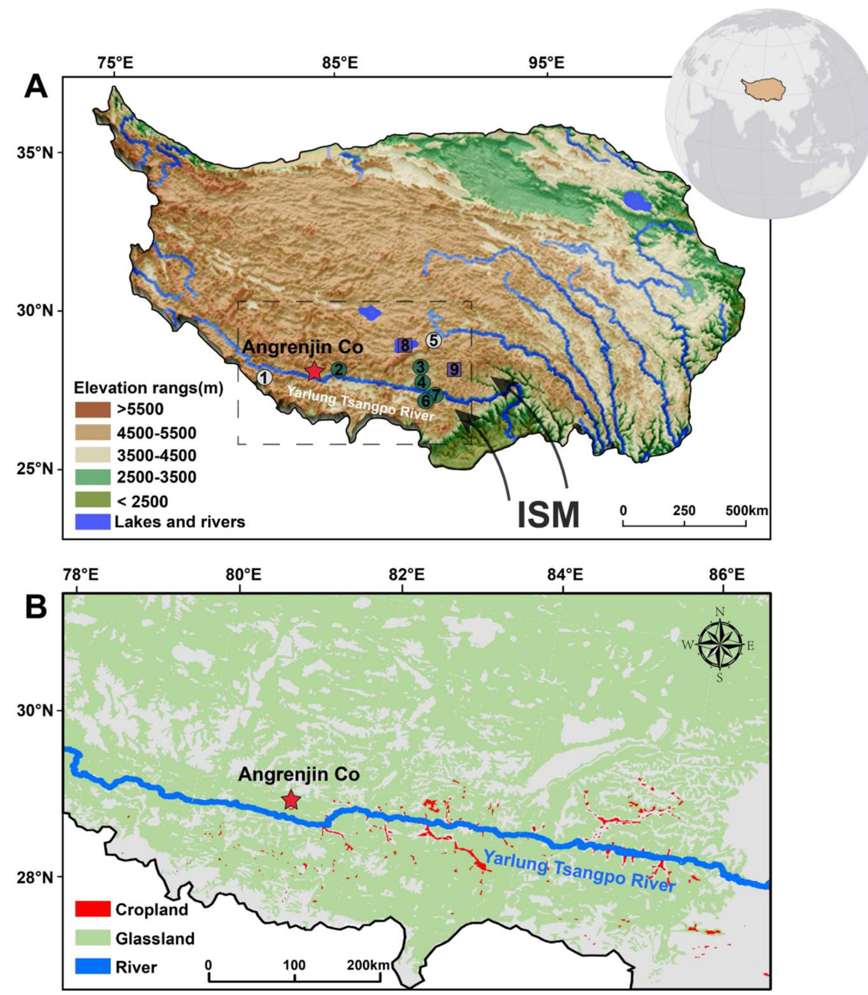

Fig. 1 | Location of Angrenjin Co on the southern Tibetan Plateau (red star) and other sites referenced in the text, and the distribution of modern land use. A Referenced archeological sites: 1. Kyamo (KM, >3600 m a.s.l.)[6]; 2. Khog Gzung (KG, 3920 m a.s.l.)[13]; 3. Qugong (QG, 3700 m a.s.l.)[9,32]; 4. Changguogou (CGG, 3570 m a.s.l.)[11]; 5. Chaxiutang (CXT, 4589 m a.s.l.)[37]; 6. Bangga (BG, 3715 m a.s.l.)[8]; 7. Bangtangbu (BTB, 3620 m a.s.l.)[34]. Sites where barley remains have been found are shown by green circles. Referenced paleoclimatic sites: 8. Nam Co[46]; 9. Paru Co[45] and Angrenjin Co[42–44,47]. The brown shading in the upper right indicates the location of the Tibetan Plateau. The extent of the study area is indicated by the black dashed rectangle, and the solid arrow indicates the modern Indian summer monsoon (ISM) direction. **B** Distribution of modern cultivated land and pastoral land on the STP[90].

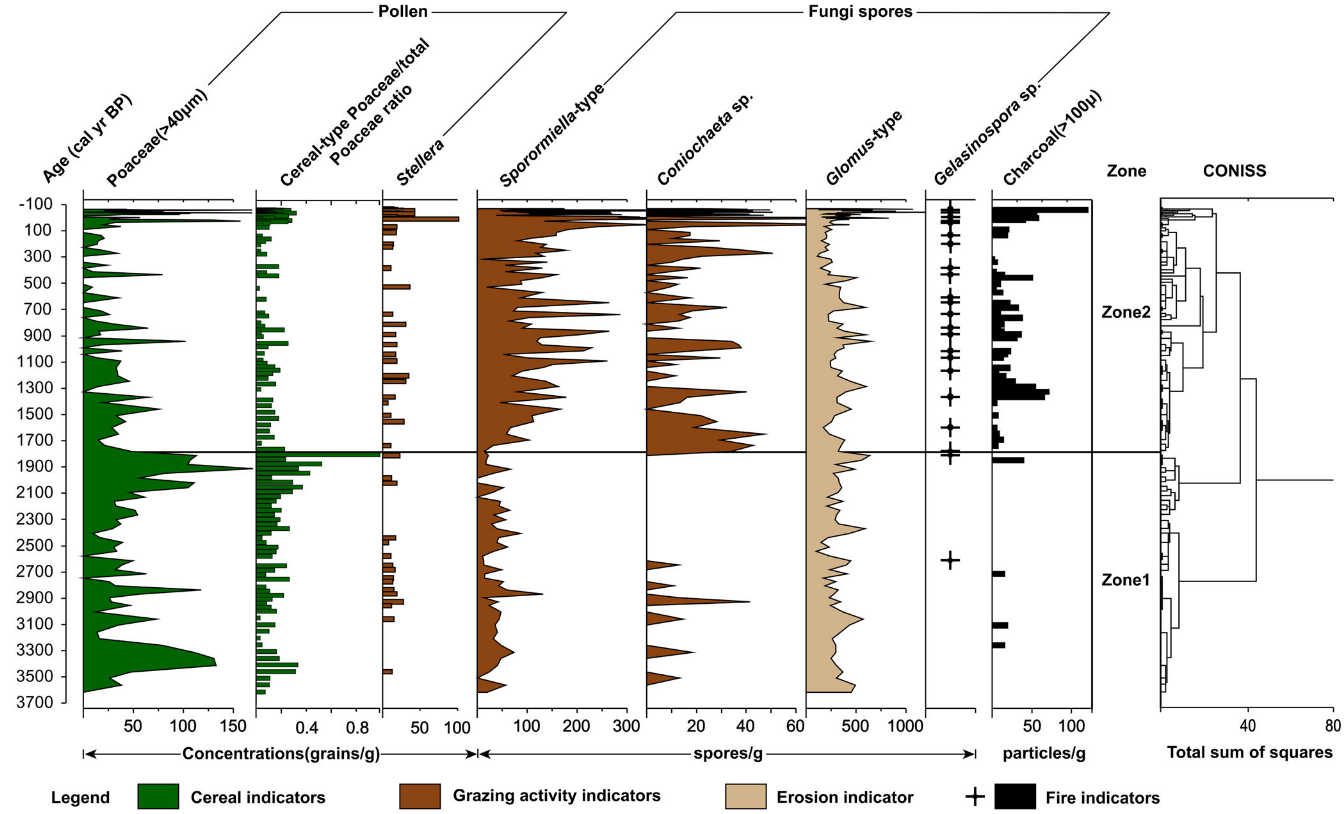

Fig. 2 | Abundance of selected pollen types, fungal spores, and charcoal particles from Angrenjin Co, plotted against time. The records are grouped into four indicator categories: Cereals, Grazing, Erosion, and Fire ("Materials and methods").

Discussion

Evolution of arable agriculture and pastoralism on the STP

The evolution of arable agriculture and pastoralism on the TP is much debated in studies of human development and adaptation to extreme environmental conditions[4,7,10,25,26]. Archeological evidence demonstrates that stable arable agriculture and/or pastoral systems were established on the TP during the late Holocene[7,10,25]. However, the further evolution of arable agriculture and pastoralism after their initial appearance, especially in the high-altitude regions above 3500 m, is less clear. However, our multi-proxy records from Angrenjin Co provide insights into these issues (Figs. 2 and 3).

During the first stage (3600–1800 cal yr BP), the low concentration of pastoral indicators indicates a period of low grazing activity in the Angrenjin Co basin (Fig. 3a, c). Similar indications of low-intensity pastoralism are provided by comparable records from the southern and central TP[21,27,28]. In contrast, the abundance of cereal pollen suggests intensified cultivation around Angrenjin Co and its surroundings (Fig. 3e, f). Additionally, the persistent presence of erosion indicators reveals the continuity of varying levels of human activity in the study area, likely related to arable agriculture or pastoralism (Fig. 3g). However, the low concentrations of fire indicators suggests that local fire events around Angrenjin Co were infrequent (Fig. 3h), possibly due to the limited availability of primary fuel sources in this high-altitude region[24,29–31]. In summary, during 3600–1800 cal yr BP our microfossil and charcoal records suggest that human subsistence around Angrenjin Co was primarily based on arable agriculture, supplemented by pastoralism, while local fire events were at a low level (Fig. 3).

Archeological evidence from the high-altitude regions of the STP supports this subsistence model of arable agriculture, supplemented by pastoralism, during 3600–1800 cal yr BP[6,8,9,13,32–34]. The earliest remains of domesticated yak (*Bos grunniens*) were discovered at the Qugong site on the STP, indicating that large herbivores were exploited at least 3600 years ago[32]. Additionally, the remains of domesticated yaks (*Bos grunniens*), sheep (*Ovis aries*) or goats (*Capra hircus*), cattle (*Bos taurus*), and dogs (*Canis familiaris*), as well as of wild animals, have been discovered at contemporary archeological sites on the STP[6,8,13,32] (Supplementary Table 2). Nonetheless, the proportion of domesticated animals was low, indicating that animal herding was relatively limited during this period: for example, the proportion of domesticated animals was only 23% at the Khog Gzung site[6] (Fig. 3b). This low proportion is consistent with the low concentration of grazing indicators at Angrenjin Co (Fig. 3a, b).

However, recent evidence from paleoproteomics and lipid residues indicates that dairy products derived from domesticated animals were used by high-altitude populations on the TP at least 3500–3000 years ago. This utilization has important implications for the successful colonization of high-altitude regions by human communities[5,12]. Nevertheless, it is worth noting that reliable evidence for milk proteins remains scarce in the STP[5], which suggests that the consumption of dairy products may have been less important than arable agriculture during this phase.

Overall, our findings reveal that a low-intensity pastoral economy was established at an early stage in the high-altitude regions of the STP. However, the dominance of an arable agricultural economy is indicated by the abundance of cereal indicators from Angrenjin Co during this period, which is supported by independent archeological evidence (Fig. 3d). For example, abundant crop plant remains (e.g., barley, wheat, millet), and stone knives, sickles, and grinding stones were excavated at contemporary archeological sites on the STP, providing direct evidence of the cultivation and processing of crop plants[8,9,11,13,33,34] (Supplementary Table 2). The cereal indicators from Angrenjin Co suggest that the intensity of arable agriculture peaked at ~2000 cal yr BP and declined rapidly after ~1800 cal yr BP (Fig. 3e, f). This pattern is consistent with archaeobotanical evidence, including the summed probability distribution of radiocarbon dates from the Southeast TP, which indicates that intensive arable agriculture was practiced from ~2000 cal yr BP, but that it declined rapidly after ~1800 cal yr BP[35]. Therefore, based on the available evidence for arable agriculture and pastoralism in the high-altitude regions of the STP, we conclude that subsistence strategies during

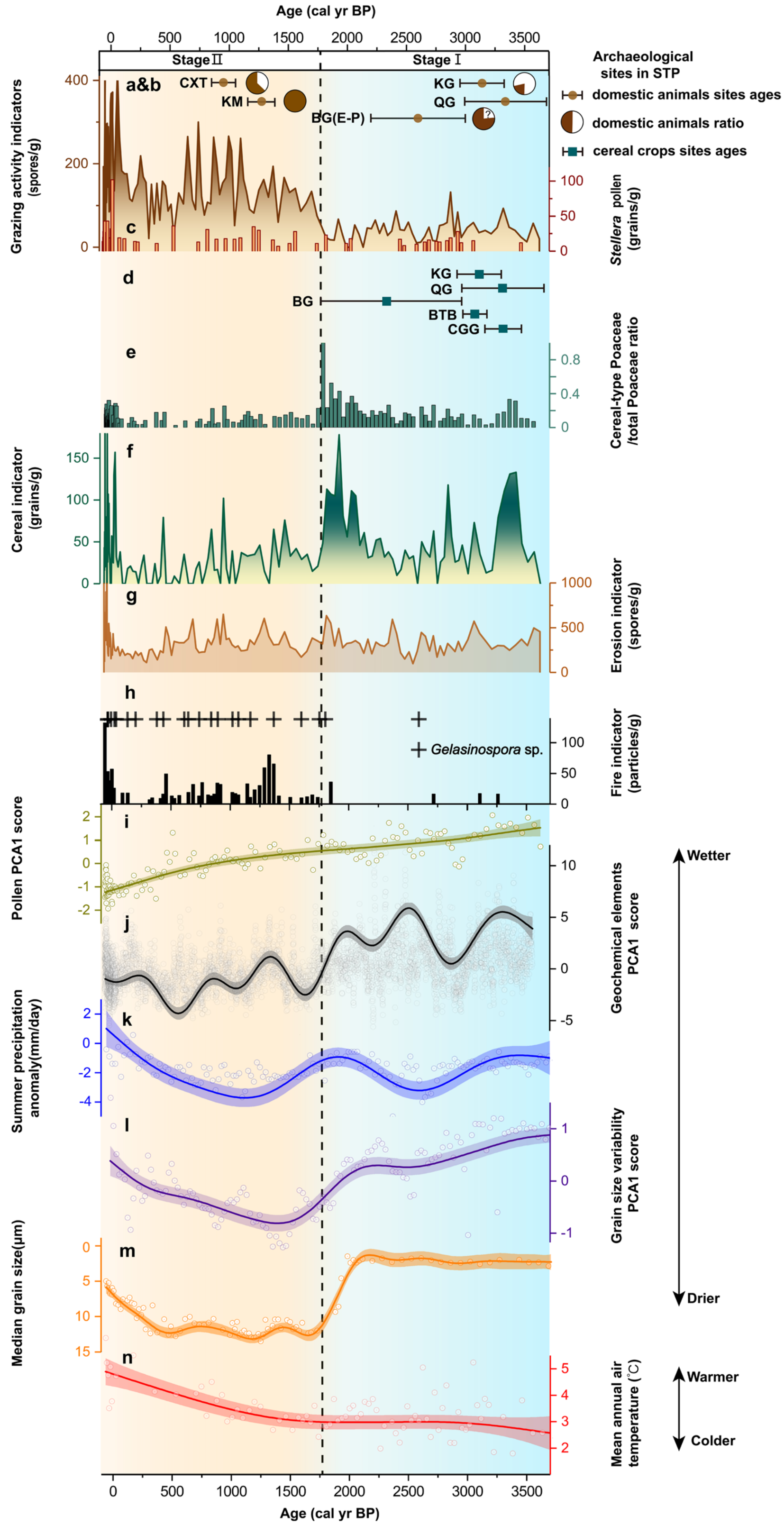

Fig. 3 | Comparison of environmental indicators from Angrenjin Co with other archeological and paleoclimatic records. (**a**) Concentrations of coprophilous fungal spores (grazing indicator) from Angrenjin Co (this study); (**b**) Age distribution of zooarchaeological sites in the high-altitude areas of the STP (the brown pie charts represent the proportion of domesticated animal remains among total animal remains) (Supplementary Table 2), BG (E–P) is the Bangga site (early phase), and the sites correspond to those in Fig. 1A; (**c**) *Stellera* concentrations from Angrenjin Co[42]; (**d**) Age distribution of archeological sites with cereals in the high-altitude areas of the STP (Supplementary Table 2) (site locations are shown in Fig. 1A; (**e**) The ratio of cereal-type Poaceae to total Poaceae, and (**f**) Poaceae >40 μm concentration (cereal indicators) from Angrenjin Co (this study); (**g**) *Glomus*-type concentrations (erosion indicator) from Angrenjin Co (this study); (**h**) *Gelasinospora* sp. distribution and charcoal >100 μm concentration (fire indicators) from Angrenjin Co (this study); (**i**) Pollen PCA1 sample scores from Angrenjin Co[42]; (**j**) Geochemical PCA1 sample scores from Angrenjin Co[43]; (**k**) Reconstructed summer precipitation anomaly (mm/day) from Angrenjin Co[44]; (**l**) Grain size PCA1 sample scores from Paru Co[45]; (**m**) Median grain size (μm) from Nam Co[46]; (**n**) Reconstructed mean annual air temperature (°C)[47]. All climate proxies are fitted with Generalized additive models (GAMs). The shaded bands are 95% confidence intervals.

3600–1800 cal yr BP were dominated by the cultivation of crop plants supplemented by animal herding.

During the second stage (1800 cal yr BP to the present), the increased representation of grazing indicators suggests the significant intensification of pastoralism around Angrenjin Co, compared to the first stage (Fig. 3a). Higher concentrations of *Sporormiella*-type spores, indicating the regional development of pastoralism, were observed on the central and northeastern TP at this time[19,20,24,28,36]. Notably, the reduced pollen representation of Poaceae >40 μm, together with the low ratio of cereal-type Poaceae to total Poaceae during this interval, suggest the decline of arable agriculture in the Angrenjin Co area and its surroundings (Fig. 3e, f). Additionally, the continuous occurrence of erosion indicator at Angrenjin Co indicates the

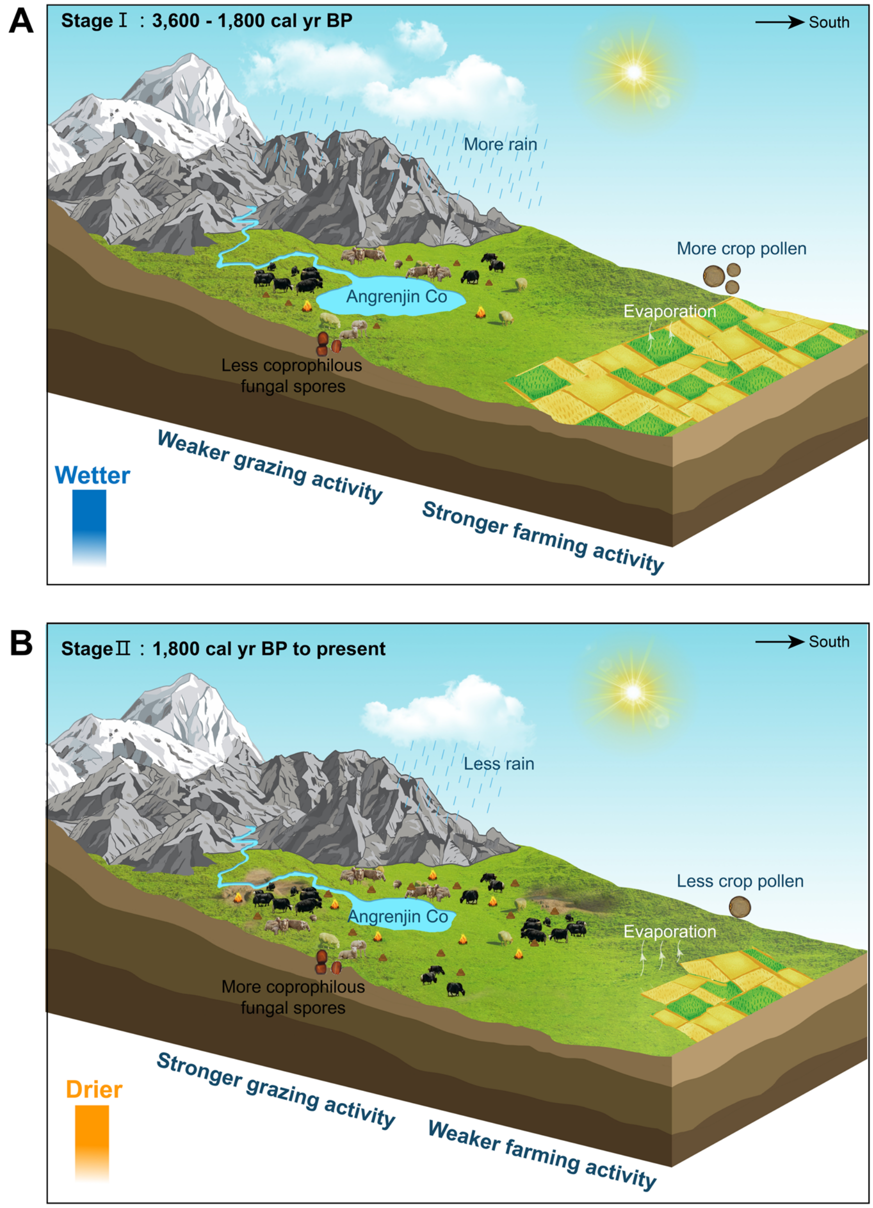

Fig. 4 | Schematic diagram illustrating the adaptive response of subsistence practices (arable agriculture and pastoralism) at Angrenjin Co and the surrounding area in the STP to drought intensification over the past 3600 years. A Weaker grazing activity, stronger farming activity and decreased local fire activity during a relatively wet climatic phase with low evaporation (3600–1800 cal year BP); **B** Stronger grazing activity, weaker arable farming activity and increased local fire occurrence during a drier climatic phase with higher evaporation (after 1800 cal year BP). Credit: livestock and fire icons, Huaban.com.

continuity of human activities around Angrenjin Co (Fig. 3g), while the increasing representation of fire indicators suggests more frequent local fire events, possibly related to the improved fuel availability despite the general fuel scarcity in high-altitude regions (Fig. 3h).

Previous studies have highlighted the use of animal dung as fuel, a strategy adopted by early populations which has persisted among the modern-day inhabitants to cope with the harsh environmental conditions of high-altitude regions[24,29–31]. This strategy is supported by the close association between grazing indicators and fire indicators at Angrenjin Co (Fig. 3a, h). It is reasonable to infer that the use of animal dung as fuel was a common practice in the high-altitude regions of the STP since at least 1800 cal yr BP. Hence, the temporal changes in the concentrations of grazing indicators, cereal cultivation indicators, and fire indicators suggest the significant intensification of animal herding which became dominant, while arable agriculture decreased. The increase in local fire events likely resulted from intensified pastoralism, which in turn produced increased quantities of combustible animal dung during this stage.

This pastoralism-based economy on the southern TP at this time is supported by zooarchaeological evidence from other high-altitude areas of the TP, where domesticated animals comprised a high proportion of the animal remains[6,37]. For instance, at the KM site, domesticated animals comprised 100% of total animal remains[6], while at the CXT site they comprised 73%[37] (Fig. 3b). In contrast, archeological evidence of cultivation is scarce, possibly due to insufficient archeological excavations (Fig. 3d). Alternatively it may reflect an extremely low level of arable agricultural activity during this stage[38].

Based on the above evidence, the subsistence strategies in the high-altitude regions of the STP can be subdivided into two phases. During the first phase (3,600–1,800 cal yr BP), the subsistence strategy was predominantly cultivation, supplemented by animal herding (Fig. 4A). During the second phase (1,800 cal yr BP to the present) there was a shift towards intensive pastoralism, accompanied by low-level cultivation (Fig. 4B).

Adaptation of subsistence strategies on the STP to climate change

In the previous section, we documented two distinct stages of subsistence strategies on the STP (Fig. 3). A transformation of human subsistence patterns in the high-altitude regions of the STP occurred at ~1800 cal yr BP

(Fig. 4), which raises intriguing questions about adaptive responses to environmental change. For example, climate change, including variations in both temperature and precipitation, has emerged as a critical factor influencing the adaptive evolution of human subsistence strategies on the TP during the late Holocene[4,7,14,39–41].

We compared our multi-proxy records from Angrenjin Co with regional paleoclimate records processed with GAMs (Fig. 3). Previous records of pollen, geochemical elements, and grain size from Angrenjin Co have revealed a relatively wet climatic interval[42–44], which is supported by GAMs records from Paru Co and Nam Co, spanning the first stage at Angrenjin Co (Fig. 3i–m)[45,46]. Despite local differences between records there was a trend towards drier conditions after 1800 cal yr BP (Fig. 3i–m). For instance, a weaker monsoon and intensified drought during the second stage at Angrenjin Co have been demonstrated at this and other sites[42–46]. Furthermore, an interval of enhanced mean annual air temperature is evident (Fig. 3n)[47]. Interestingly, the period of intensified drought after 1800 cal yr BP is temporally correlative with a subsistence shift observed in high-altitudes regions of the STP (Fig. 3). This relationship suggests that the shift in subsistence strategies was an adaptive response to regional climate change, specifically increased drought. The causes of the drought are linked to two regional climatic factors: the primary factor is the reduction in monsoon rainfall on the STP, causing the seasonal precipitation to fall below the minimum requirement (378 mm) for barley growth in high-altitude areas[48,49]; and the secondary factor is increased evaporation due to rising temperatures[47], which further hindered arable agricultural development in this region.

Previous studies have highlighted the role of aridity as a significant factor driving the expansion of pastoralism due to its greater adaptability compared to arable agriculture. Animal herding may be economically more productive than cultivation during dry intervals[6,18,38,50,51]. Therefore, we propose that relatively high-intensity arable agriculture developed on suitable land during the preceding warm and wet climatic stage, such as in northern China[23,52], while low-intensity pastoralism became the dominant subsistence strategy in the surrounding mountainous areas of the high-altitude STP (Fig. 4A). As drought intensified and the air temperature increased, reduced precipitation and increased regional evaporation led to decreased soil moisture, reducing the potential for cultivation. Reduced crop yields may have failed to sustain the human population during the subsequent drought stage, forcing the local population to expand into the surrounding mountains and develop animal herding strategies[38,40]. Thus, after 1,800 cal yr BP, the subsistence strategies of high-intensity pastoralism and low-level arable agriculture were developed to mitigate the effects of aridification and increased environmental pressures on the human population (Fig. 4B)[38]. Additionally, this shift in subsistence strategy may have facilitated the westward expansion of multiple prehistoric STP populations from the southern plateau from ~1800 cal yr BP[53]. Overall, our findings suggest that the human population of the high-altitude regions of the STP was able to develop resilience in the face of climatic deterioration during the late Holocene. Moreover, this adaptation has persisted in this region up to the present-day.

Conclusion

We have obtained well-dated, high-resolution records of pollen, coprophilous fungal spores, and charcoal from the sediments of Angrenjin Co, in the high-altitude region of the STP. These records enabled us to reconstruct the evolution of regional subsistence strategies over the past 3600 years. Low concentrations of coprophilous fungal spores and the abundant pollen of crop plants during ~3600–1800 cal yr BP suggest that subsistence in the high-altitude STP was dominated by arable agriculture, supplemented by relatively low-level pastoralism. However, increases in coprophilous fungal spores and decreases in cereal-type pollen after 1,800 cal yr BP indicate the intensification of pastoralism and a much lower level of arable agriculture. Regional paleoclimatic records corroborate this shift in subsistence patterns and show that it coincided with a phase of intense drought. This temporal correlation suggests that the shift in subsistence strategies on the high-altitude STP was an adaptive response to the pressures exerted by increasing aridity. Moreover, we suggest that this adaptive transformation provided the basis for the modern economy of the high-altitude regions of the STP.

Materials and methods

Study site

Angrenjin Co (29°17′–29°20′N, 87°9′–87°13′E, 4306 m a.s.l.) is a closed lake on the southern TP, with a watershed area of 194 km^2[54]. This area has a semi-arid alpine climate and it is ecologically sensitive and vulnerable to global climate change. The mean annual precipitation is ~300 mm, more than 90% of which falls between June and September. The recorded mean annual temperature from 1977 to 2015 was ~7.1 °C (Supplementary Fig. 2B). Around 82% of the water vapor entering the region comes from the Bay of Bengal and the Arabian Sea, driven mainly by the Indian summer monsoon (Supplementary Fig. 2A). The vegetation surrounding Angrenjin Co is dominated by alpine steppe and alpine meadow[55]. This area is adjacent to the center of the agro-pastoral zone on the TP, in and around the Yarlung Zangbo River valley, which attracted early human settlement and where agro-pastoralism has a long history[56,57] (Fig. 1B). High-altitude barley (*Hordeum vulgare*), rapeseed (*Brassica rapa*), and wheat (*Triticum aestivum*) are cultivated on well-watered alluvial fans around the lake margins and in the valley areas[56,58]. Additionally, yaks (*Bos grunniens*), sheep (*Ovis aries*), and goats (*Capra hircus*) are the main livestock species in the Angrenjin Co basin[56]. Thus, Angrenjin Co is a potentially important site for documenting the adaptive evolutionary process and possible climatic drivers of arable agriculture and pastoralism on the STP.

Sediment sampling and chronology

A 142 cm–long gravity core (AR-02) was obtained at a water depth of ~14 m from near the center of Angrenjin Co in October 2011. The sediments are composed of gray silt (142–80 cm), interbedded black and gray silt layers (80–50 cm), and black silt (50–0 cm) (Supplementary Fig. 1). Owing to the absence of macroscopic plant remains in the sediments, eight radiocarbon dates were obtained from the bulk organic fraction, conducted by Beta Analytic (Florida, USA). These dates were calibrated using the IntCal20 calibration curve[59] with Oxcal 4.4.1[60]. Additionally, to refine the age model, we obtained ^{210}Pb and ^{137}Cs profiles from the uppermost 40 cm of the core, measured at 1-cm intervals, with the ^{210}Pb ages calculated using the CRS model[61]. Additionally, the paleomagnetic secular variation (PSV) record from Angrenjin Co was compared with a well-dated PSV record from East Asia (EA PSV)[62], and with the results from a global geomagnetic field model (Pfm9k.1a)[63] (Supplementary Fig. 2). The eight ^{14}C-dates, validated by independent ^{210}Pb-^{137}Cs and PSV dating, combined with Bacon age–modeling[64], indicate that the core spans the past ~3,600 years (Supplementary Fig. 2). The detailed age-depth model is presented in our previous study[65].

Pollen, fungal spores, and charcoal analysis

A total of 142 samples from core AR-02 (0–142 cm) were used for analyses of pollen[42] and fungal spores and charcoal (this study). All samples were prepared using the standard acid-alkali treatment[66]. *Lycopodium* spores (27,560 spores per tablet) were added to each sample to calculate the concentrations of microfossils and charcoal particles. The sample residues were passed through a 7-μm mesh with ultrasonic agitation to concentrate the pollen, fungal spores, and charcoal particles. Fungal spores were identified with reference to published fungal spore plates and descriptions[20,67–72]. Pollen, fungal spores, and charcoal particles were counted using a Leica DM 750 microscope at ×400 magnification. The pollen, fungal spores, and charcoal records were analyzed using stratigraphically constrained cluster analysis CONISS (Fig. 2). Tilia 3.01[73] was used to process and plot the data. Specifically, we counted the numbers of Poaceae pollen grains with diameters > 40 μm, fungal spores, and charcoal particles >100 μm. *Stellera* pollen grains were identified as described in a previous investigation[42].

To facilitate interpretation and discussion, pollen, fungal spores, and charcoal records (Fig. 2) are classified into four groups based on their specific ecological implications, following recent studies:

(1) Cereal indicators: Poaceae >40 μm is a reliable indicator of the development of arable agriculture[74–77]. Poaceae (>40 μm) is well represented in modern agricultural land in the arid areas of northwest China, and changes in its abundance in sedimentary records reflect changes in the intensity of prehistoric cultivation[77]. Additionally, given the influence of the pollen productivities of the other pollen taxa, we chose the ratio of cereal-type Poaceae to total Poaceae as another indicator of arable agriculture. Thus, we adopted the comprehensive approach of quantifying the abundances of Poaceae >40 μm and the ratio of cereal-type Poaceae to total Poaceae to capture detailed information about changes in arable activity (Supplementary Fig. 4 and Fig. 2).

(2) Grazing indicators: Ecological studies on the TP have indicated that the abundance of *Stellera* in pollen records is an indicator of the intensity of animal grazing[21,27,78]. Additionally, the abundance of coprophilous fungal spores in sedimentary records has been shown to be a reliable proxy of changes in the population of large herbivores[79,80] and grazing intensity[19,20,23,24,36,51,67,72]. Hence, in this study we determined the abundance of coprophilous fungal spores, including *Sporormiella*-type and *Coniochaeta* sp.[70,71] (Supplementary Fig. 4).

(3) Erosion indicator: These include *Glomus*-type fungal bodies and cells. *Glomus* is the largest genus of arbuscular mycorrhizal fungi, commonly associated with certain host plants, and their presence is an indirect indicator of soil erosion[67,70,81] (Supplementary Fig. 4).

(4) Fire indicators: *Gelasinospora* sp. thrives predominantly on burnt substrates, with fire acting as a stimulus for spore germination or heat inducing the fungus to produce fruiting bodies[68,82]. Hence, *Gelasinospora* sp. is a useful indicator of local fires in paleoecological studies[83,84]. Additionally, the abundance of larger charcoal particles (>100 μm) is an indicator of the intensity of local fire activity[20,85,86].

Generalized additive models

Generalized additive models (GAMs) are used to estimate significant changes in trend in regional climate time-series. GAMs can model nonlinear relationships between time and a response variable, and it can accommodate the irregularities in sample spacing and resolution typical in paleoecological time-series[87]. We used the restricted maximum likelihood (REML) method to fit the smoothed GAMs, which has been used to identify trends within climate time-series[87]. GAMs were performed using the mgcv package in R[88,89].

Data availability

The abundance of selected pollen types, fungal spores, and charcoal particles from Angrenjin Co on the southern Tibetan Plateau in this study are freely available online (https://doi.org/10.6084/m9.figshare.26962855).

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Author contributions

Deke Xu, Houyuan Lu and Naiqin Wu conceived and designed the study; Hao Li wrote the first draft; Deke Xu and Houyuan Lu revised the manuscript; Hao Li identified and analyzed the microfossil and charcoal data and performed the data analysis; Deke Xu constructed the age-depth model; Chang Li, Anning Cui, Xinxin Zuo, Yajie Dong and Can Wang conducted the fieldwork and collected the samples; and Deke Xu, Hao Li and Anning Cui prepared the samples. All authors discussed the results and provided input to the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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