

# Permafrost Degradation Diminishes Terrestrial Ecosystem Carbon Sequestration Capacity on the Qinghai-Tibetan Plateau

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## Abstract

Effects of permafrost degradation on carbon (C) and nitrogen (N) cycling on the Qinghai-Tibetan Plateau (QTP) have rarely been analyzed. This study used a revised process-based biogeochemical model to quantify the effects in the region during the 21st century. We found that permafrost degradation would expose  $0.98 \pm 0.49$  (mean  $\pm$  SD) and  $2.17 \pm 0.38$  Pg C of soil organic carbon under the representative concentration pathway (RCP) 4.5 and the RCP 8.5, respectively. Among them about 60% will be decomposed, enhancing heterotrophic respiration by  $9.54 \pm 5.20$  (RCP 4.5) and  $38.72 \pm 17.49$  (RCP 8.5) Tg C/yr in 2099. Deep soil N supply due to thawing permafrost is not accessible to plants, providing limited benefits to plant growth and only stimulating net primary production by  $6.95 \pm 5.28$  (RCP 4.5) and  $27.97 \pm 12.82$  (RCP 8.5) Tg C/yr in 2099. As a result, permafrost degradation would weaken the regional C sink (net ecosystem production) by  $303.55 \pm 254.80$  (RCP 4.5) and  $518.43 \pm 234.04$  (RCP 8.5) Tg C cumulatively during 2020–2099. Permafrost degradation has a higher influence on C balance of alpine meadow than alpine steppe ecosystems on the QTP. The shallower active layer, higher soil C and N stocks, and wetter environment in alpine meadow are responsible for its stronger response of C balance to permafrost thaw. This study highlights that permafrost degradation could continue to release large amounts of C to the atmosphere irrespective of potentially more nitrogen available from deep soils.

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## **Key Points:**

- Soil carbon release due to permafrost degradation overwhelms net primary production on the Qinghai-Tibetan Plateau.
- Deep soil nitrogen addition from thawing permafrost has a limited benefit to plant carbon uptake.
- Permafrost degradation has more pronounced influence on carbon cycling of alpine meadow than alpine steppe.

## Abstract

Effects of permafrost degradation on carbon and nitrogen cycling on the Qinghai-Tibetan Plateau (QTP) have rarely been analyzed. This study used a revised process-based biogeochemical model to quantify the effects in the region during the 21st century. We found that permafrost degradation would expose  $0.98 \pm 0.49$  (mean  $\pm$  SD) and  $2.17 \pm 0.38$  Pg C of soil organic carbon under the representative concentration pathway (RCP) 4.5 and the RCP 8.5, respectively. Among them about 60% will be decomposed, enhancing heterotrophic respiration by  $9.54 \pm 5.20$  (RCP 4.5) and  $38.72 \pm 17.49$  (RCP 8.5) Tg C/yr in 2099. Deep soil nitrogen (N) supply due to thawing permafrost is not accessible to plants, providing limited benefits to plant growth and only stimulating net primary production by  $6.95 \pm 5.28$  (RCP 4.5) and  $27.97 \pm 12.82$  (RCP 8.5) Tg C/yr in 2099. As a result, permafrost degradation would weaken the regional carbon sink (net ecosystem production) by  $303.55 \pm 254.80$  (RCP 4.5) and  $518.43 \pm 234.04$  (RCP 8.5) Tg C cumulatively during 2020–2099. Permafrost degradation has a higher influence on C balance of alpine meadow than alpine steppe ecosystems on the QTP. The shallower active layer, higher soil C and N stocks, and wetter environment in alpine meadow are responsible for its stronger response of C balance to permafrost thaw. This study highlights that permafrost degradation could continue to release large amounts of carbon to the atmosphere irrespective of potentially more nitrogen available from deep soils.

## 1 Introduction

Permafrost degradation due to climate warming makes large amounts of frozen soil organic matter (SOM) available for decomposition, leading to a positive feedback to the climate system by releasing greenhouse gases (GHG) (Koven et al., 2011; Koven, Schuur et al., 2015; Schaefer et al., 2014; Schuur et al., 2015). Enhanced decomposition in permafrost regions also increases nutrient availability however (Keuper et al., 2012; Salmon et al., 2016, 2018), stimulating plant production together with the effects of increasing air temperature, expanding growing season, shifting plant community composition, and rising atmospheric CO<sub>2</sub> concentration, resulting in a negative feedback to climate warming (Finger et al., 2016; Liang et al., 2018; Peng, X. et al., 2020; Zhuang et al., 2010). Considerable uncertainty of these positive and negative feedbacks limits our ability to model C balance of the permafrost region (Abbott et al., 2016).

Coupling the impact of permafrost degradation into land surface models has projected that the northern high latitudes would shift from a net C sink (Qian et al., 2010) to a net source to the atmosphere (Burke et al., 2013; Koven et al., 2011; MacDougall et al., 2016; Schaefer et al., 2014; Schaphoff et al., 2013). However, large uncertainties still exist in the magnitude of the estimated changes in soil, vegetation, and ecosystem C stocks (McGuire et al., 2016). Model structural differences, particularly in the soil carbon decomposition processes, have been attributed to be the largest uncertainty in quantifying permafrost carbon-climate feedbacks (Burke et al., 2017).

A critical model structural feature to represent the permafrost carbon-climate feedback is to consider soil C exposure with thaw depth (McGuire et al., 2018). In permafrost regions, part of soil organic carbon (SOC) is protected from decomposition by frozen soil but may become more susceptible to decomposition with warming-induced degradation of permafrost. To better account for the influence of permafrost dynamics on terrestrial carbon balance, soil C exposure due to thawing permafrost should be incorporated into land surface models. Hayes et al. (2014)

assessed the net effect of active layer dynamics on permafrost carbon feedback during 1970–2006 over the circumpolar permafrost region and found that permafrost degradation exposed 11.6 Pg C of thawed SOM to decomposition, resulting in 4.03 Pg C releasing from the decomposition of newly exposed SOM, but only 0.3 Pg C was compensated by net primary production (NPP). Using a carbon-nitrogen model that includes permafrost processes and depth-dependent changes in SOM, Koven et al. (2015a) found similar results and projected that permafrost carbon-climate feedback is sensitive to deep soil carbon decomposability, and the impact of deep soil nitrogen (N) mineralization on C budget is small. However, projections of five biogeochemical models that represent soil C explicitly with depth show that the northern permafrost region would likely act as a net C sink before 2100 due to stronger vegetation C uptake (McGuire et al., 2018). The different result found by McGuire et al. (2018) maybe because they only considered the active layer thickness (ALT) less than three meters. The decomposition of large quantities of deep carbon deposits (Schuur et al., 2015) may reverse this estimation.

The Qinghai-Tibetan Plateau (QTP) is characterized by a deep ALT ( $2.34 \pm 0.70$  m), and about 15% of the QTP permafrost region has ALT greater than 3 m (Wang, T. et al., 2020). SOC storage on the QTP is estimated at 50.43 Pg, of which 35.10 Pg stores below 3 m soils and 37.21 Pg frozen in permafrost currently (Wang, T. et al., 2020). Based on the vertical distribution of SOC and the change of ALT, Wang, T. et al. (2020) estimated that permafrost thaw on the QTP would expose  $1.86 \pm 0.49$  and  $3.80 \pm 0.76$  Pg frozen C to decomposition, which could potentially turn the region from a net C sink to a net source. The lack of the simulation of SOM decomposition, and the use of net biome production (NBP) from CMIP5 models (which did not consider permafrost carbon (Jones et al., 2016) and hence the stimulation of N supply to vegetation production due to permafrost thaw), may bias the estimation of net C budget of Wang, T. et al. (2020). Through repeated soil carbon measurements on the QTP, Ding et al. (2017) suggested that the upper active layer of the QTP permafrost currently represents a substantial regional soil C sink, probably owing to enhanced vegetation growth. However, this study only examined SOC stocks in uppermost 30 cm. Carbon changes associated with deeper and older permafrost remain largely unknown (Mu et al., 2020). Inadequate studies that focus on representing soil C explicitly with depth, particularly representing soil C in deep soils, and simultaneously consider the feedback of vegetation to permafrost thaw impedes our understanding of permafrost carbon-climate feedbacks on the QTP.

Apart from deep ALT, the environment of the permafrost regions on the QTP is also different from the pan-Arctic in water condition. Specifically, annual precipitation decreases from southeastern to northwestern on the QTP. As a result, the eastern QTP receives more precipitation and dominated by alpine meadow ecosystem, while the widespread inner and western parts are controlled by alpine dry climate and dominated by alpine steppe ecosystems. Many studies have found that the alpine steppe and alpine meadow ecosystems respond differently to climate change (Hao et al., 2021; Li, S. et al., 2019; Liu et al., 2020; Peng, F. et al., 2020). For example, warming experiment revealed that warming increased plant productivity in alpine meadow but decreased productivity in alpine steppe (Ganjurjav et al., 2016). Temperature sensitivity of ecosystem respiration ( $Q_{10}$ ) in alpine meadow (3.4) can be twice the number in alpine steppe (1.7) (Wang, L. et al., 2018). The distinct environment and the different responses to climate change of these two ecosystems could result in different permafrost C feedbacks. However, currently the effects of active layer deepening on C balance of these two ecosystems are still not certain.

In this study, a process-based biogeochemical model was revised by coupling thaw depth with soil C exposure to analyze the following issues: (i) the quantity of frozen SOC in deep soils on the QTP that will be exposed to decomposition due to permafrost thaw in the 21st century, and the quantity of C that will be released into the atmosphere; (ii) the stimulation of deep permafrost thaw on vegetation productivity due to extra N supply and the net effect of permafrost thaw on ecosystem C balance (enhanced heterotrophic respiration (RH) versus stimulated net primary production (NPP)); and (iii) the different responses of C balance of the distinct alpine meadow and alpine steppe to permafrost thaw.

## 2 Methods and Data

### 2.1 The Terrestrial Ecosystem Model

The Terrestrial Ecosystem Model (TEM) is a process-based, global scale biogeochemical model, using spatially explicit soil, vegetation, and elevation data and climate forcing of radiation, precipitation, and air temperature data to simulate ecosystem C and N cycling (McGuire et al., 1992; Zhuang et al., 2002). A soil thermal model (STM) has been coupled into TEM to represent vertical soil thermal profile in permafrost- and non-permafrost-dominated ecosystems and gives TEM the ability to describe freeze-thaw cycles in cold regions (Jin et al., 2015; Zhuang et al., 2001, 2010). The effects of freeze-thaw dynamics on gross primary production (GPP) have also been considered in TEM (Zhuang et al., 2011). TEM has been extensively used to evaluate C dynamics in northern high latitudes and Tibet plateau (e.g., Hayes et al., 2014; Jin et al., 2013, 2015; Kicklighter et al., 2019; McGuire et al., 2018).

In previous versions of TEM, soil organic carbon (SOC) in the entire root zone is assumed to be available for decomposition, and thus take part in heterotrophic respiration. However, since active layer thicknesses (ALT) in permafrost regions are often shallower than root depth defined in TEM (Hayes et al., 2011, 2014), part of SOC in root zone is frozen in soil and protected from microbial decomposition. Therefore, SOC considered in heterotrophic respiration quantification is smaller than the entire SOC stock in root zone. TEM6 (Hayes et al., 2011, 2014) has considered the amount of SOC available for decomposition and treated it as a proportion the entire root zone SOC, depending upon the ratio of ALT to rooting depth. By calculating ALT variation over time through the STM module in TEM, this approach has been used to estimate the potential influence of permafrost thaw on the availability of soil organic matter to decomposition (Hayes et al., 2014; Kicklighter et al., 2019). However, this approach did not consider SOC below the rooting zone and assumed that they do not contribute to C flux. When warming continues in the future and ALT deepens below rooting depth, this approach may underestimate the influence of permafrost degradation on the availability of carbon to decomposition (Hayes et al., 2011).

On the QTP, ALT (2.34 m; Wang, T. et al., 2020) is usually much deeper than rooting depth (over 90% of plant roots are distributed within the top 30 cm soil layer; Yang, Y. et al., 2009). Future permafrost degradation would probably happen far below rooting zone. Therefore, we modified the approach by adjusting SOC according to the ratio of ALT of current time step to previous time step, rather than the ratio of ALT to rooting zone depth:

$$SOC_i = SOC_{i-1} * \left( 1 + \frac{prop_i - prop_{i-1}}{prop_{i-1}} \right) \quad (1)$$

$$prop_i = \frac{a * ALT_i}{b + ALT_i} \quad (2)$$

where  $i$  and  $i-1$  denote the current and previous year, respectively;  $ALT_i$  is the maximum ALT of the current year;  $prop_i$  denotes the proportion of SOC in the active layer of current year to the total SOC in the entire soil profile. The hyperbolic function of  $prop_i$  describes the vertical distribution of SOC in soil profile, with high density of SOC in shallow soil layers but decreases towards deep soil, as documented by Hayes et al. (2014).  $a$  and  $b$  are parameters controlling the shape of the curve that how SOC density changes with soil depth. We estimated parameter  $b$  for alpine meadow, alpine steppe, and alpine desert using observation data (Figure S1). For the remaining ecosystems, we set parameters  $b$  according to Kicklighter et al. (2019). Parameter values of  $b$  for various ecosystems are listed in Table S1. Parameter  $a$  will be divided when put eq. (2) into eq. (1).

Using this method, SOC within the soil layers that permafrost degraded was factored into total available SOC pools for soil decomposition. Although we considered the fact that SOC density decreases with soil depth, the vertical variations in SOC turnover time are still missing in this study, which may overestimate SOC decomposition rate to some extent (Shu et al., 2020).

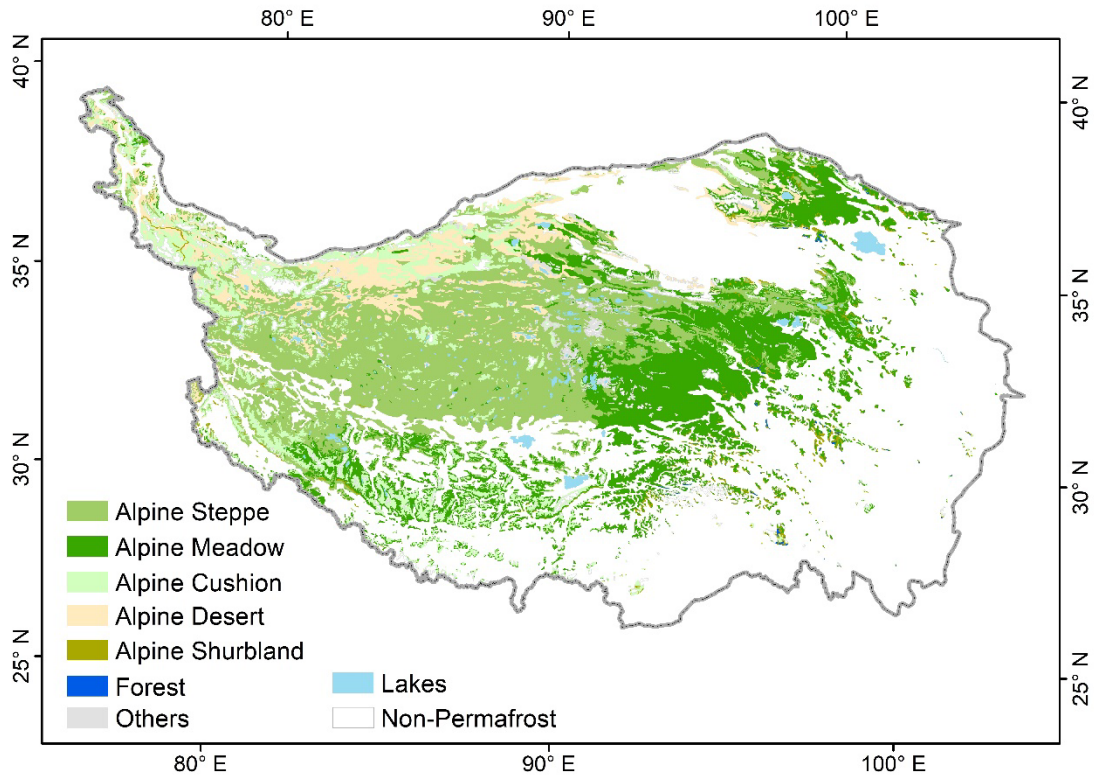
Permafrost degradation influences not only the amount of SOC, but also soil organic N (SON), available inorganic N (AVALN), and soil water content. These variables were also adjusted according to the variation of ALT, in the same method as that for SOC. Although permafrost degradation can increase AVALN pools, if ALT deepens far below rooting depth, we assume that the additional AVALN cannot be accessed by vegetation. Therefore, only AVALN in rooting zone was used for vegetation N uptake (VegNup) calculation when ALT is greater than rooting zone depth.

Two freezing fronts are modeled in TEM, including freezing down due to cold air temperature and freezing up due to permafrost underneath the soils (Zhuang et al., 2001). ALT in permafrost regions is calculated as the total depth of unfrozen soil layers above the two freezing fronts. TEM does not explicitly ‘define’ permafrost occurrence in a grid cell, but infer its depth based on the 0 °C isotherm in the soil thermal profile. The permafrost region of this study was derived from permafrost map of China (Wang, 2019).

## 2.2 Model calibration and validation

TEM has been calibrated for terrestrial ecosystems on the QTP by Zhuang et al. (2010) and Jin et al. (2013, 2015). In this study, some key rate-limiting parameters (such as the maximum rate of photosynthesis, heterotrophic respiration, and plant N uptake and respiration rate) were recalibrated for three major ecosystems (i.e., alpine shrubland, alpine meadow, and alpine steppe), which occupy 82.6% of the permafrost regions on the plateau according to the 1:1000000 vegetation map of China (Figure 1; Chinese Academy of Sciences, 2001). The parameters were optimized by minimizing the differences between observations and simulations through altering parameters and iterating model simulations. The rest of the model parameters were set as previous studies. Site information of these three ecosystems is provided in Table S2. Observations of soil temperature (DST), net ecosystem production (NEP), and soil C and N stocks for each site are derived from references in Table S2 accordingly. The model was validated with 289 observations of soil C and N pools (data derived from Ding et al. (2016), Kou

et al. (2019), and Wang et al. (2020)) on the plateau. These observation sites spread over alpine desert, alpine steppe, alpine meadow, and alpine cushion ecosystems. However, for the analysis of the effects of permafrost degradation, only the dominant ecosystems of alpine steppe and alpine meadow were focused on.



**Figure 1.** Vegetation distribution in the permafrost regions of the QTP. The vegetation distribution was derived from a 1:1,000,000 vegetation map of China (Editorial Committee of Vegetation Map of China, Chinese Academy of Sciences, 2001) provided by the Resources and Environment Science Data Center, Chinese Academy of Sciences. The permafrost map (all the colored patches exclude lakes) was obtained from frozen ground map of China (Wang, T., 2019).

### 2.3 Simulation protocol

To determine the direct effects of ALT deepening on ecosystem C dynamics, we carried out two simulations: the referenced simulation ( $S_R$ ) and the transient simulation ( $S_T$ ). The two simulations share the same model inputs but have differences in model structure. They are identical until 2020. After that, ALT changes with climate in  $S_T$  but remained no change in  $S_R$ . Therefore, C and N pools do not change with ALT in  $S_R$  after 2020 but does influenced by ALT in  $S_T$ . Through comparing the results of these two simulations, the direct effects of ALT changes on ecosystem C dynamics can be estimated.

TEM was spun up for 200 years in both simulations. During the spin-up procedure, climate data from 2006 to 2046 were used to force the model run and repeated continuously until dynamic equilibrium was achieved. The state variables of the dynamic equilibrium were then

used as the initial value for simulations from 2006 to 2009. The spin-up procedures were identical for the  $S_R$  and  $S_T$ .

## 2.4 Data

TEM was driven with spatially referenced information on climate, soils, vegetation, and elevation for spatial extrapolation.

Climate data from 2006 to 2009 include air temperature ( $^{\circ}\text{C}$ ), precipitation (mm), and incident short-wave solar radiation ( $\text{W}/\text{m}^2$ ), deriving from four global circulation models (GCMs: IPSL-CM5A-LR, GFDL-ESM2M, MIROC5, and HadGEM2-ES) in the second simulation round of the Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP 2b). Known issues of previous round of ISIMIP have been solved for the ISIMIP2b through a series of adjustments, and atmospheric data provided by the ISIMIP2b have also been bias-adjusted to a new reference dataset of EWEMBI (Frier et al., 2017). Regional simulation of this century was conducted under two climate scenarios of the Representative Concentration Pathway 4.5 (RCP 4.5) and RCP 8.5, which correspond to radiative forcing levels of 4.5 and 8.5  $\text{W}/\text{m}^2$  by 2100, respectively (Moss et al., 2010).

Soil texture data over the QTP were based on the RegridDED Harmonized World Soil Database v 1.2 (Wieder, 2014). Vegetation and elevation data were derived from the 1:1000000 vegetation map of China (Chinese Academy of Sciences, 2001) and the Shuttle Radar Topography Mission (SRTM; Farr et al., 2007), respectively.

The spatial resolutions of soil texture and elevation data are 0.05 degree and 90 m, respectively. Compared with these land surface datasets, the climate data are much coarser, at the spatial resolution of 0.5 degree. On the QTP, topography, vegetation and soil may change greatly within 0.5-degree spatial resolution. To consider the effects of heterogeneities of these data, we resampled them into a spatial resolution of 0.1 degree. During resampling, we make every 25 grids of the resampled climate data share the same value as the grid of the same location of the original climate data. We did not adjust climate data according to elevation, which may introduce uncertainty. TEM is run on monthly time scale. We averaged the daily climate data to monthly before resampling.

## 3. Results

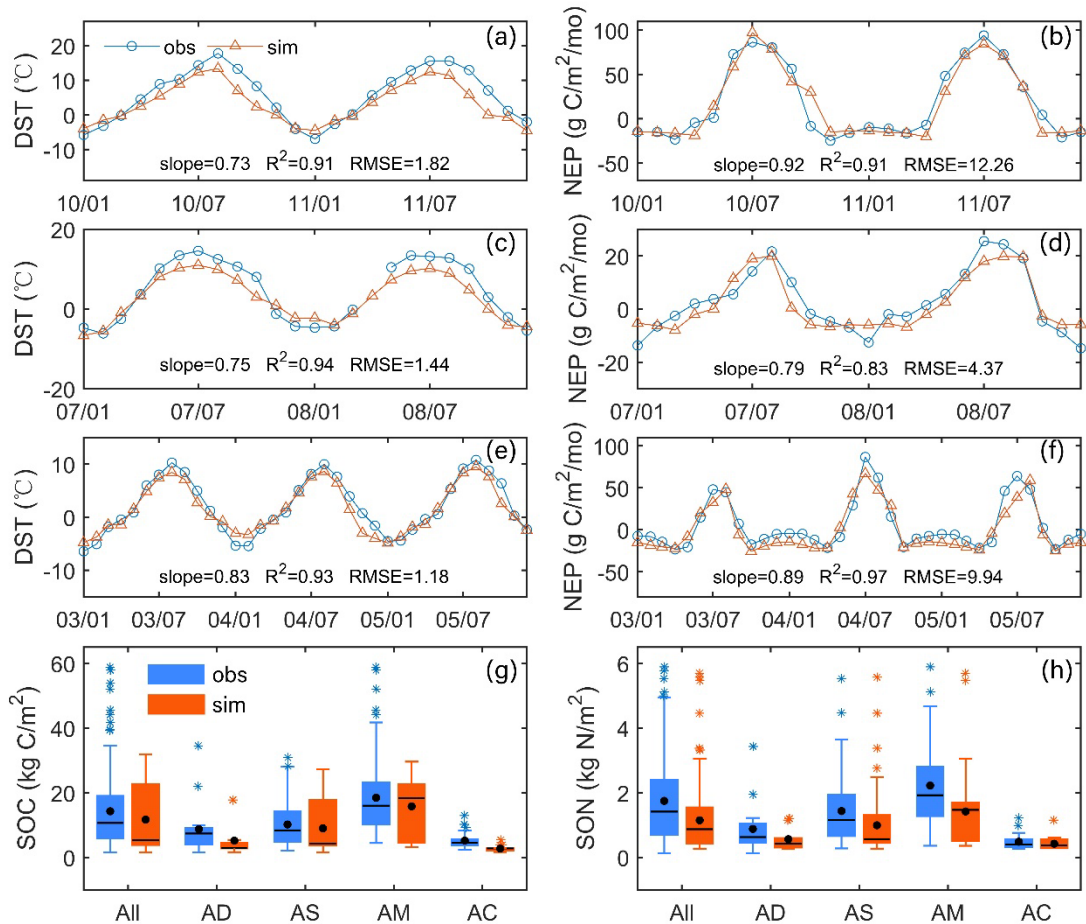
### 3.1 Model validation

We validated TEM with monthly observation data of DST and NEP for three dominant ecosystems on the QTP (Figure 1). TEM well reproduced the seasonal variation of DST and NEP at all the three sites, with  $R^2$  greater than 0.9 and 0.8 for DST and NEP, respectively. Simulated SOC and SON at these three sites are closed to observations (Table S1).

Apart from these three sites, we also compared the simulated SOC and SON with 289 observations on the Plateau (Figure 2 and Figure S2). The discrepancies between modeled and observed data (Figure S2) for SOC and SON may be due to the following reasons. First, the calculated SOC and SON in this study are C and N stocks in active layers, while the observations represent C and N stocks in top two meters (top three meters for 173 sites for SON; Kou et al., 2019) of soil profile. The mean ALT on the QTP is estimated at about 2.3 m during 2006–2015. By comparison, ALT is shallower than 2 m in the northwestern, eastern, and southern QTP (Ni et

al., 2021; Wang, T. et al., 2020). According to Ding et al. (2016), Kou et al. (2019), and Wang et al. (2020), about half of the observation sites are distributed in the regions where ALT is estimated less than 2 m. As a result, the simulated SOC and SON in active layer is smaller than observations (Figure 2). Second, although the heterogeneities in topography, vegetation, and soils were considered by running the model on  $0.1 \times 0.1$  degree of spatial resolution, the great spatial heterogeneities in SOC (Mishra et al., 2021) and SON make it difficult to predict site level observations based on large grid simulations.

In general, the simulated SOC and SON are comparable to observations based on the means across vegetation types (Figure 2). For the entire permafrost regions on the QTP, the estimated SOC stocks in the QTP active layers during 2006–2015 under the RCP 4.5 scenario is  $15.64 \pm 0.78$  Pg C (mean  $\pm$  SD), a little higher than 13.22 Pg C estimated by Wang, T. et al. (2020), but lower than  $19.0 \pm 6.6$  Pg C (in 0–2 m soils) estimated by Mu et al. (2020). The simulated ALT during 2006–2015 ( $2.72 \pm 0.07$  m) is close to but a little higher than  $2.34 \pm 0.70$  m estimated by Wang, T. et al. (2020). The climate forcing data of RCP 4.5 scenario other than meteorological observations might cause this difference. SON stocks in alpine grassland active layers during 2013–2014 are estimated at  $1.47 \pm 0.04$  kg N/m<sup>2</sup>, which is within the range (1.40–1.76 kg N/m<sup>2</sup>) estimated based on observation data within 0–3 m soil depth (Kou et al., 2019). Estimated NPP in the whole QTP is  $240.99 \pm 14.27$  g C /m<sup>2</sup>/yr, which is close to the upper bound of the MODIS normalized difference vegetation index (NDVI) based estimate of 219.8–242.5 g C /m<sup>2</sup>/yr during 2002–2012 (Wang, S. et al., 2017). The use of RCP 4.5 data and the different time spans may be responsible for the higher estimate in this study.

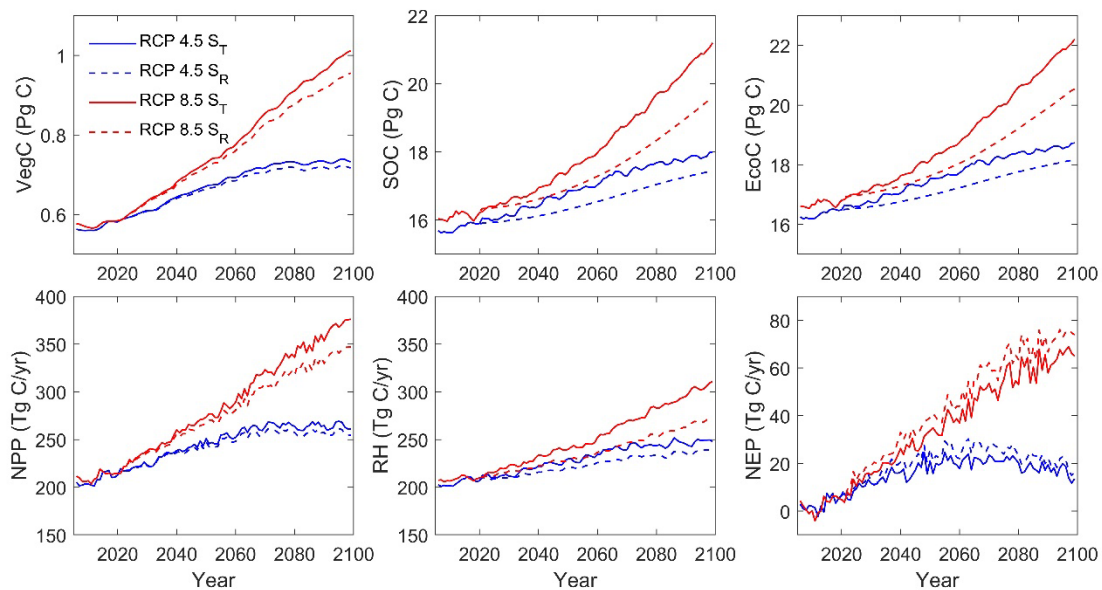


**Figure 2.** Comparison of model simulation (sim) with observations (obs) for soil temperature (DST) and NEP at alpine meadow (a and b), alpine steppe (c and d), and alpine shrub (e and f) sites, respectively. See Table S1 for detailed information of the observation sites. g and h represent the comparison of the simulated SOC and SON with 289 observations on the Plateau. AD, AS, AM, and AC in g and h denote alpine desert, alpine steppe, alpine meadow, and alpine cushion, respectively. The number of observation sites for AD, AS, AM, and AC are 16, 134, 106, and 33, respectively.

### 3.2 Changes in ecosystem C balance and the effects of ALT deepening

Permafrost regions on the QTP are projected to be a stronger C sink during the remaining of this century. VegC and SOC both increase under the RCP 4.5 and RCP 8.5 (Figure 3, S<sub>T</sub>). As a result, by the end of this century, ecosystem C stocks (total VegC and SOC) would increase by  $2.68 \pm 0.22$  Pg C ( $0.17 \pm 0.02$  Pg C gains from VegC and  $2.51 \pm 0.26$  Pg C gains from SOC) and  $5.61 \pm 0.36$  Pg C ( $0.44 \pm 0.08$  Pg C gains from VegC and  $5.18 \pm 0.35$  Pg C gains from SOC), respectively, under the RCP 4.5 and RCP 8.5 scenarios. Under the RCP 4.5, the increases in NPP and RH are close, which are  $53.99 \pm 24.58$  Tg C/yr and  $48.96 \pm 4.19$  Tg C/yr, respectively. However, under the RCP 8.5, the increase in NPP ( $157.93 \pm 21.08$  Tg C/yr) is much higher than RH ( $104.37 \pm 22.30$  Tg C/yr). The permafrost regions on the QTP would sequester more C under the RCP 8.5.

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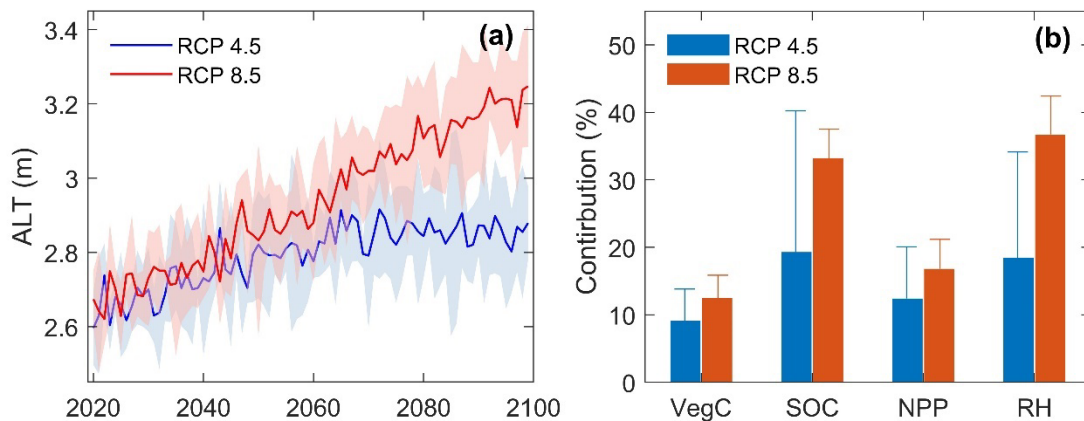
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301 **Figure 3.** Changes in C pools (VegC, SOC, and EcoC) and fluxes (NPP, RH, and NEP) of the  
 302 permafrost regions on the QTP in the 21st century. Differences between the results of the  
 303 transient simulation ( $S_T$ ) and referenced simulation ( $S_R$ ) represent the direct effects of ALT.  
 304 Standard deviation for each simulation did not show for clarity.

305

306 The effects of ALT deepening on C balance are represented by the difference between  $S_T$   
 307 and  $S_R$ . Figure 3 shows that ALT deepening have evident effects on C balance. We calculated the  
 308 contribution of ALT deepening effects to C balance change by dividing the difference in  $S_T$  and  
 309  $S_R$  from the overall C balance changes (Figure 4b). Under the RCP 4.5, ALT deepening can  
 310 contribute 9–18% of the C balance changes, and the contributions increase to 12%–37% under  
 311 the RCP 8.5. The radical change in ALT (Figure 4a) under the RCP 8.5 results in a greater  
 312 contribution. Under both RCPs, the deepening of ALT has more influences on SOC and RH than  
 313 VegC and NPP (Figure 3 and Figure 4b).

314



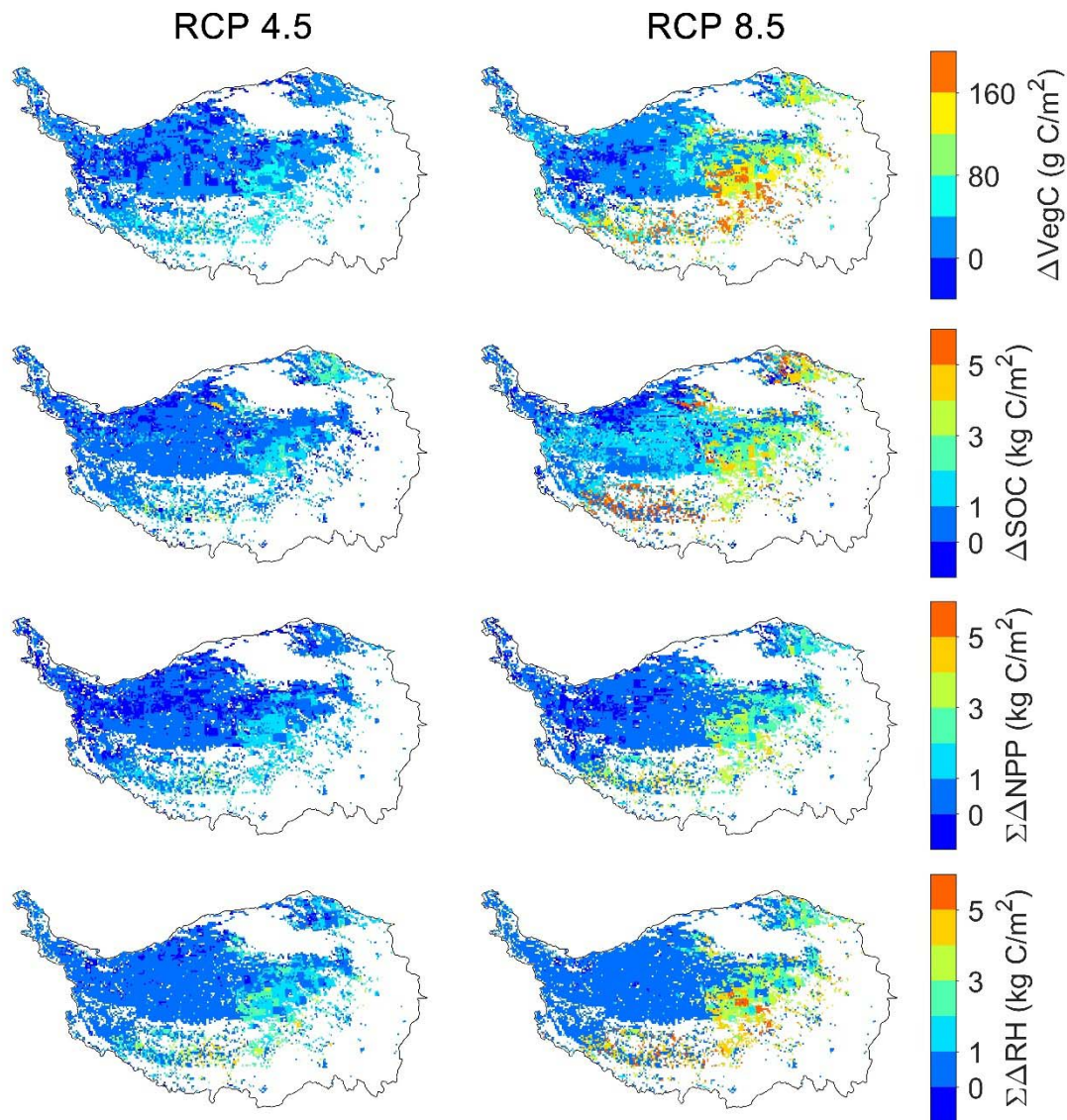
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**Figure 4. (a)** Changes in mean ALT of the QTP under the RCP 4.5 and RCP 8.5 scenarios; **(b)** Contributions of ALT deepening effects to the overall C balance changes caused by climate change in permafrost regions of QTP during the 21st century. The shade in **(a)** and error bars in **(b)** denotes the standard deviation among all GCMs.

The greater values of  $S_T$  than  $S_R$  (Figure 3) under both RCPs suggest that ALT deepening increases ecosystem C storage in the region. However, it should be noted that the increasing in RH ( $9.54 \pm 5.20$  (RCP 4.5) and  $38.72 \pm 17.49$  (RCP 8.5) Tg C/yr) is greater than NPP ( $6.95 \pm 5.28$  (RCP 4.5) and  $27.97 \pm 12.82$  (RCP 8.5) Tg C/yr) due to ALT deepening (Figure 3 and Figure S3), resulting in a smaller NEP in  $S_T$  than  $S_R$ . This result illustrates that, although NPP increases more than RH in the  $S_T$  simulation (Figure 3), resulting in a stronger C sequestration over time, permafrost degradation itself strengthens RH more than NPP and cumulatively decrease NEP by  $303.55 \pm 254.80$  (RCP 4.5) and  $518.43 \pm 234.04$  (RCP 8.5) Tg C during 2020–2099.

### 3.3 Responses of C balance to ALT deepening in different ecosystems

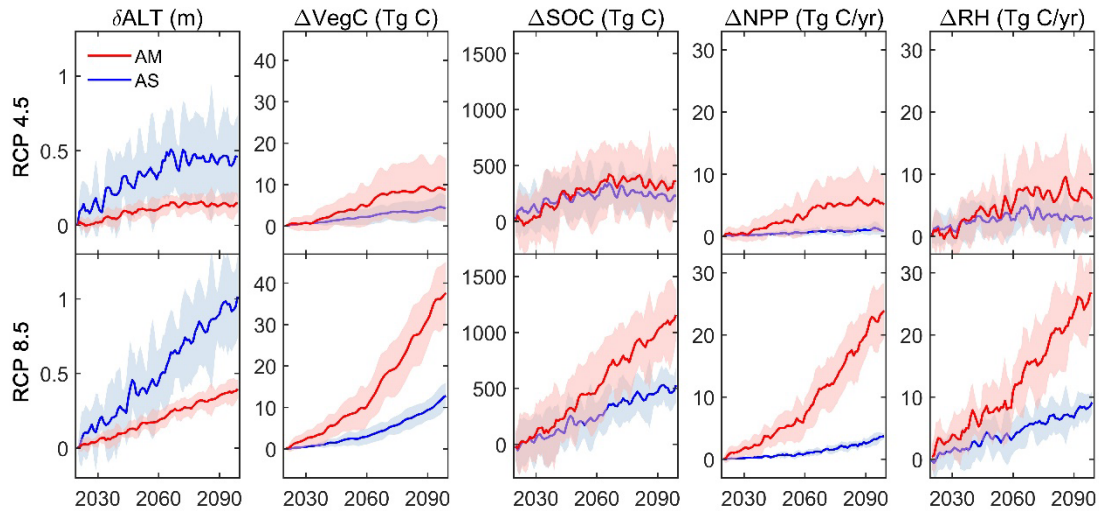
The effects of ALT deepening on C balance of the QTP show an obvious spatial heterogeneity (Figure 5). The east and south parts of the QTP would increase more in both C pools and fluxes than the northwestern part due to ALT deepening, and the spatial heterogeneity is more noticeable under the RCP 8.5 than RCP 4.5. Given that east and south parts of the QTP are dominated by alpine meadow ecosystems and the northwestern part is dominated by alpine steppe ecosystems (Figure 1), these results suggest that ALT deepening has greater influence on C balance of alpine meadow than alpine steppe, particularly under the RCP 8.5. Moreover, changes in regional average ALT of these two ecosystems (Figure 6) show that increase in ALT is smaller in alpine meadow. However, C storage and fluxes of alpine meadow respond more significantly to ALT deepening.



**Figure 5.** Changes in C balance of the QTP due to permafrost degradation under the RCP 4.5 and RCP 8.5.  $\Delta$  before VegC and SOC mean the difference between the results of the transient simulation and referenced simulation ( $S_T - S_R$ ) in 2099, and  $\Sigma$  denotes the accumulation of each C flux from 2020 to 2099.

Under both RCPs and both ecosystems, the increasing in RH is greater than NPP (Figure 6), which is consistent with the results of the whole permafrost region (Figure 3), suggesting again that the direct effects of ALT deepening would weaken C sequestration. When comparing the two types of ecosystems, the C sequestration weakening tends to be stronger in alpine steppe ecosystems. The cumulative difference in NEP between  $S_T$  and  $S_R$  from 2020 to 2099 are  $-122.56 \pm 112.45$  and  $-236.94 \pm 139.55$  Tg C for alpine meadow under the RCP 4.5 and RCP 8.5, respectively, and  $-172.65 \pm 168.75$  and  $-247.32 \pm 97.27$  Tg C for alpine steppe under the RCP 4.5 and RCP 8.5, respectively. Given that the increasing in ALT in alpine steppe is about twice as

much as that in alpine meadow (Figure 6), the C sequestration could reduce more in alpine meadow than alpine steppe with the same degree of ALT deepening.



**Figure 6.** Anomalies of ALT from 2020 baseline and the effects of ALT deepening on ecosystem C balance of alpine meadow (AM) and alpine steppe (AS) ecosystems under the RCP 4.5 and RCP 8.5 scenarios.  $\delta$  before ALT means the anomalies of ALT from 2020 baseline, and  $\Delta$  before C balance components mean the difference between the results of the transient simulation and referenced simulation ( $S_T - S_R$ ). Red and blue shade denotes the standard deviation among all GCMs for alpine meadow and alpine steppe ecosystems, respectively.

## 4. Discussion

### 4.1 Comparison with other studies

The estimated NPP and RH of the permafrost region on the QTP are 202.5 and 201.1 g C/m<sup>2</sup>/yr during 2006–2011, both within the range of other estimates (120.8–329.6 g C/m<sup>2</sup>/yr for NPP and 149.8–303.5 g C/m<sup>2</sup>/yr for RH; Table 1). However, our NEP estimates are smaller than others. Particularly, our estimates with this version of TEM tends to be in low end of other TEM estimates, which is most likely due to more respiration from deep active layer in this study. In addition, this study focused on the permafrost region on the QTP, while Zhuang et al. (2010) and Jin et al. (2015) studied the entire QTP, and Yan et al. (2015) focused on grasslands on the QTP. Different study areas and ecosystem types considered in these studies may contribute to the discrepancies.

Existing studies show large differences in future carbon dynamics in the region (Table 1). Our estimation of flux density is higher than Jin et al. (2015) but smaller than Bosch et al. (2017). RH estimation of Bosch et al. (2017) depends only on annual precipitation, which may induce large uncertainties in their future projection because important factors like soil temperature and SOC quality and quantity were not considered. Thawing-induced CO<sub>2</sub> emissions are also considered in the study of Bosch et al. (2017). However, the potential C loss from thawing permafrost is estimated from incubation experiments with soil samples from the arctic

region. SOC density on the QTP ( $14.4\text{--}17.5\text{ kg/m}^2$  for alpine meadow and  $6.6\text{--}7.7\text{ kg/m}^2$  for alpine steppe in 0–2 m; Mu et al., 2020) can be substantially lower than that in the arctic ( $55.1\pm 18.9\text{ kg/m}^2$  for lowlands and  $40.6\pm 22.7\text{ kg/m}^2$  for uplands in upper 1 m layer of the North American Arctic; Ping et al., 2008), which may cause an overestimate of RH in Bosch et al. (2017). The projections of Jin et al (2015) are lower for NPP and NEP in the 2090s under the RCP 8.5. TEM used in Jin et al (2015) was mainly calibrated for wetland ecosystems. Under the high warming scenario of the RCP 8.5, warming induced high evapotranspiration may result in water stress and suppress NPP for wetland ecosystems. In this study, TEM has been calibrated with the main ecosystems on the QTP, including alpine meadow, alpine steppe, alpine shrubland, and alpine desert. Different calibrations should partially contribute to the differences in those projections.

**Table 1.** Estimated regional C fluxes on the QTP from different studies. Units for regional total C fluxes are Tg C/yr, and units for regional mean flux density are g C/m<sup>2</sup>/yr.

| Model                 | Area<br>(10 <sup>6</sup> km <sup>2</sup> ) | Period                 | NPP   |         | RH    |         | NEP   |         | Source               |
|-----------------------|--------------------------------------------|------------------------|-------|---------|-------|---------|-------|---------|----------------------|
|                       |                                            |                        | Total | Density | Total | Density | Total | Density |                      |
| CENTURY               | 1.41                                       | 1901–2010              | 344.0 | 244.7   | 336.5 | 239.0   | 7.5   | 5.3     | Lin et al. (2017)    |
| TEM                   | 1.01                                       | 1961–2010              | 193.0 | 193.7   | 182.9 | 183.7   | 10.1  | 10.0    | Yan et al. (2015)    |
| ORCHIDEE              | 1.39                                       | 1961–2009              | 219.8 | 158.1   | 208.2 | 149.8   | 11.6  | 8.3     | Piao et al. (2012)   |
| CASA                  | 1.47                                       | 1982–2009              | 177.2 | 120.8   |       |         |       |         | Zhang et al. (2014)  |
| ORCHIDEE              | 1.39                                       | 1980–2010              | 323.9 | 233.0   |       |         |       |         | Tan et al. (2010)    |
| DOS-TEM               |                                            | 1981–2012              |       | 199.0   |       | 195.0   |       | 4.0     | Yi et al. (2014)     |
| TEM                   | 1.37                                       | 1990s                  | 451.6 | 329.6   | 415.8 | 303.5   | 35.8  | 26.1    | Zhuang et al. (2010) |
| TEM                   | 1.38                                       | 2006–2011              | 235.8 | 170.9   | 221.5 | 160.5   | 14.4  | 10.4    | Jin et al. (2015)    |
|                       |                                            | 2090s <sup>2</sup>     | 319.9 | 231.8   | 247.1 | 198.7   | 45.8  | 33.1    |                      |
|                       |                                            | 2090s <sup>3</sup>     | 348.4 | 252.5   | 321.5 | 233.0   | 27.0  | 19.5    |                      |
| RG <sup>1</sup>       |                                            | 2050 <sup>2</sup>      |       |         |       | 388.6   |       |         | Bosch et al. (2017)  |
|                       |                                            | 2050 <sup>3</sup>      |       |         |       | 391.2   |       |         |                      |
|                       |                                            | 2070 <sup>2</sup>      |       |         |       | 385.9   |       |         |                      |
|                       |                                            | 2070 <sup>3</sup>      |       |         |       | 389.2   |       |         |                      |
| TEM (S <sub>T</sub> ) | 1.19                                       | 2006–2011 <sup>2</sup> | 242.1 | 202.5   | 240.5 | 201.1   | 1.6   | 1.3     | This study           |
|                       |                                            | 2090s <sup>2</sup>     | 315.1 | 263.6   | 296.2 | 247.8   | 18.9  | 15.8    |                      |
|                       |                                            | 2090s <sup>3</sup>     | 441.2 | 369.0   | 363.2 | 303.8   | 78.0  | 65.2    |                      |

Notes: 1. RG denotes regression model; 2 and 3 represent estimations derived from the RCP 4.5 and RCP 8.5, respectively.

## 4.2 Impact of climate change on ecosystem C balance

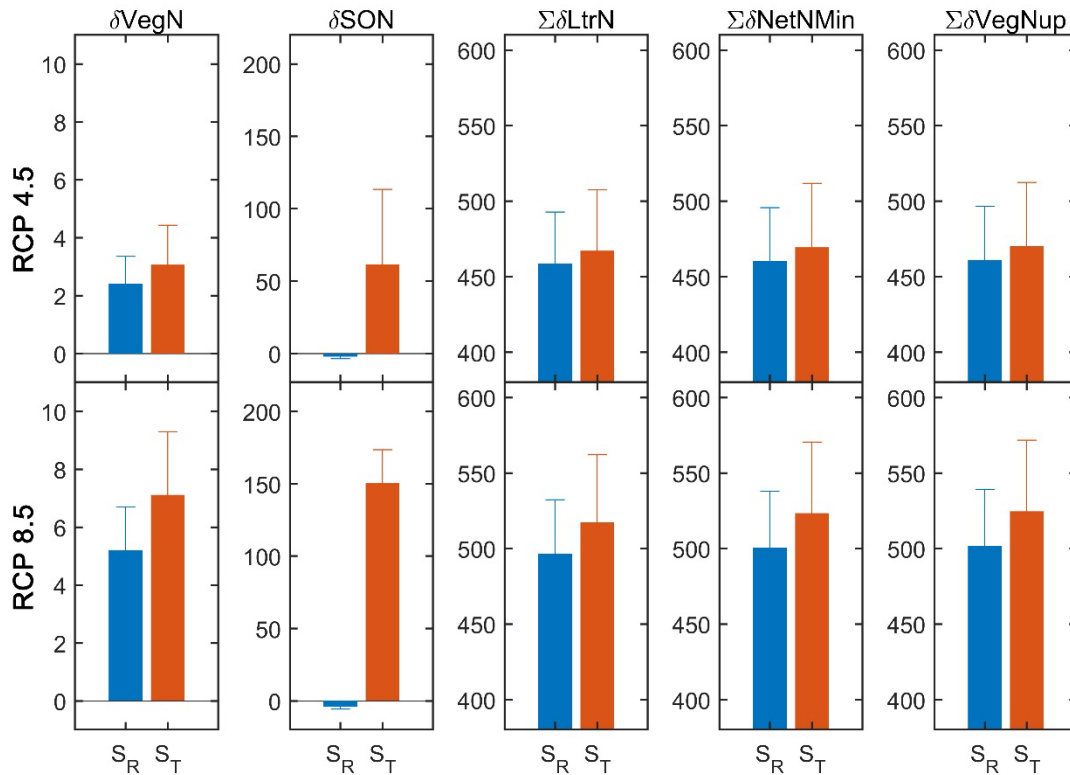
Although permafrost degradation contributes a fraction to the overall changes in C balance (Figure 4), the differences between S<sub>T</sub> and S<sub>R</sub> shows that climate change is still a main factor affecting various ecosystem C processes, controlling the carbon balance (Figure 3). By

2099, ecosystem C storage and NEP of the permafrost region on the QTP would increase by  $1.67 \pm 0.32$  Pg C and  $15.64 \pm 3.52$  Tg C/yr under the RCP 4.5 and  $3.65 \pm 0.49$  Pg C and  $70.56 \pm 9.43$  Tg C/yr under the RCP 8.5, respectively. Six earth system models from phase five of the Coupled Model Inter-comparison Project (CMIP5) that did not consider the effects of permafrost degradation on SOC stocks show that NPP and RH increase from 1850 to 2100, and the carbon sink of the QTP would be higher during 2006–2100 in comparison with 1850–2005 under RCP4.5 scenario (Li et al., 2015). Increasing net nitrogen mineralization rate enhanced N availability, together with warming air temperature and rising CO<sub>2</sub> concentrations, promote the regional C sink on the QTP (Zhuang et al., 2010).

In the northern high latitudes, warming and elevated atmospheric CO<sub>2</sub> concentration have been found as key drivers to NPP and RH dynamics, but precipitation changes are less important (McGuire et al., 2018). In contrast, on the QTP, air temperature, precipitation, and atmospheric CO<sub>2</sub> concentration in permafrost regions would all increase under both the RCPs (Figure S4). Evidence from experimental warming (Ganjurjav et al., 2016; Zhao, J. et al., 2019), model simulation (Zheng et al., 2020), and meta-analysis (Wang, G. et al., 2019) all suggest that C exchange in alpine meadow is mainly regulated by air temperature, but C exchange in dry alpine steppe is dominated by water conditions. Given that the cover of alpine steppe ( $7.5 \times 10^5$  km<sup>2</sup>) is approximately three times higher than alpine meadow ( $2.5 \times 10^5$  km<sup>2</sup>) (Ni, 2000), increment in precipitation should also be associated with C exchanges in the permafrost regions on the QTP as warming and elevated atmospheric CO<sub>2</sub> concentration (Chen, B. et al., 2014; Piao et al., 2012;) do. Carbon dynamics responses on the QTP can be different from the conclusion of McGuire et al. (2018) for northern permafrost regions.

#### 4.3 Nitrogen subsidies from permafrost degradation

Permafrost degradation will not only release old carbon but also supply additional nitrogen that can be utilized to boost plant productivity. The direct effects of permafrost thaw would increase ecosystem C storage and enhance C cycling on the QTP in the remaining of this century (Fig 2 and 4). Our analysis suggests that N subsidies from permafrost degradation should be the main reason for these increases in C storages and fluxes. When considering N addition, soil organic N (SON) experiences a remarkable surge in  $S_T$  ( $73.58 \pm 37.79$  (RCP 4.5) and  $156.92 \pm 21.48$  (RCP 8.5) Tg N) and changes from decrease in  $S_R$  ( $-2.13 \pm 1.63$  (RCP 4.5) and  $-4.12 \pm 1.80$  (RCP 8.5) Tg N) to a large amount of increase in  $S_T$  (Figure 7). The increase of N availability enhances plant N uptake (VegNup;  $S_T - S_R$ :  $12.41 \pm 4.72$  (RCP 4.5) and  $26.56 \pm 13.03$  (RCP 8.5) Tg N/yr) and makes plant gain more N (VegN;  $S_T - S_R$ :  $0.62 \pm 0.46$  (RCP 4.5) and  $1.97 \pm 0.90$  (RCP 8.5) Tg N), which therefore, stimulate plant growth and increase NPP.



**Figure 7.** Changes in ecosystem N balance from 2020 baseline for the referenced simulation ( $S_R$ ) and transient simulation ( $S_T$ ) under the RCP 4.5 and RCP 8.5 scenarios.  $\delta$  means the anomalies of N pools of 2099 from 2020 baseline;  $\Sigma$  denotes the accumulation of each N flux from 2020 to 2099. The error bars represent the standard deviation among all GCMs. Units for N pools (vegetation N (VegN) and soil organic N (SON)) are Tg N, and units for N fluxes (litter N (LtrN), net N mineralization (NetNMin), and vegetation N uptake (VegNup)) are Tg N/yr.

However, although both VegN and SON benefit from permafrost thaw, the increase in VegN is much smaller than in SON (Figure 7). Based on soil C and N balance, this study estimated that  $0.98 \pm 0.49$  and  $2.17 \pm 0.38$  Pg C of SOC, and  $76.14 \pm 39.45$  and  $162.90 \pm 23.44$  Tg N of SON will be added to active layer due to permafrost thaw (Table 2), under the RCP 4.5 and RCP 8.5, respectively. Among them, 57–63% of these additional C would be consumed by microbes and discharged through RH. However, only 10–13% of these addition N would be absorbed by plant.

Figure S5 shows that N subsidies from permafrost thaw only alleviates plant N limit slightly. We find that although there is a large amount of N added to active layer due to permafrost thaw, only a small fraction of the amount can be accessed by plant. The average maximum rooting depth in permafrost regions on the QTP is estimated as 1.2 m, while the average ALT would increase to  $2.9 \pm 0.1$  and  $3.3 \pm 0.1$  m under the RCP 4.5 and RCP 8.5, respectively (Figure 4a), which is much greater than rooting zone depth. Therefore, only a small fraction of N released from thawed permafrost is absorbed by plant. The benefit of permafrost thaw is limited, but the consequence of permafrost thaw to C emission is large. As a result, the net effect of permafrost thaw on the QTP is to weaken C sequestration. Similar results have also

been found over the circumpolar permafrost regions. Permafrost thaw from 1970 to 2006 exposed 11.6 Pg C of SOC to decomposition, resulting in 4.03 Pg C emission but only 0.3 Pg C compensated by the stimulated plant C uptake (Hayes et al., 2014). In the forests of Northern Eurasia, the gain of vegetation C that is benefited from N supply due to permafrost degradation is only 29.8% (RCP4.5) to 49.2% (RCP8.5) of the loss of soil organic C. Permafrost degradation overall diminishes C sequestration in these forests (Kicklighter et al., 2019). Although N released from new thawed permafrost can be used to stimulate plant productivity, plant may not be N limited or may not access to them (Koven, Lawrence et al., 2015). However, new released SOC will be decomposed, although part of them take a longer time. Consequently, the stimulated RH may overwhelm the NPP increase (due to more available N to plant from thawing permafrost), decreasing the regional C sequestration.

**Table 2.** Changes in soil C and N balance due to permafrost thaw.

| C       | $\Delta$ SOC | $\sum\Delta$ LtrC | $\sum\Delta$ RH      | SOC <sub>PF</sub> | $\sum\Delta$ RH/ SOC <sub>PF</sub>     |
|---------|--------------|-------------------|----------------------|-------------------|----------------------------------------|
| RCP 4.5 | 0.65±0.26    | 0.33±0.27         | 0.66±0.53            | 0.98±0.49         | 0.57±0.41                              |
| RCP 8.5 | 1.59±0.21    | 0.84±0.49         | 1.42±0.74            | 2.17±0.38         | 0.63±0.24                              |
| N       | $\Delta$ SON | $\sum\Delta$ LtrN | $\sum\Delta$ NetNMin | SON <sub>PF</sub> | $\sum\Delta$ VegNup/ SON <sub>PF</sub> |
| RCP 4.5 | 75.57±39.08  | 8.46±7.18         | 9.04±7.69            | 76.14±39.45       | 0.10±0.09                              |
| RCP 8.5 | 160.93±22.55 | 20.84±12.12       | 22.81±13.05          | 162.90±23.44      | 0.13±0.06                              |

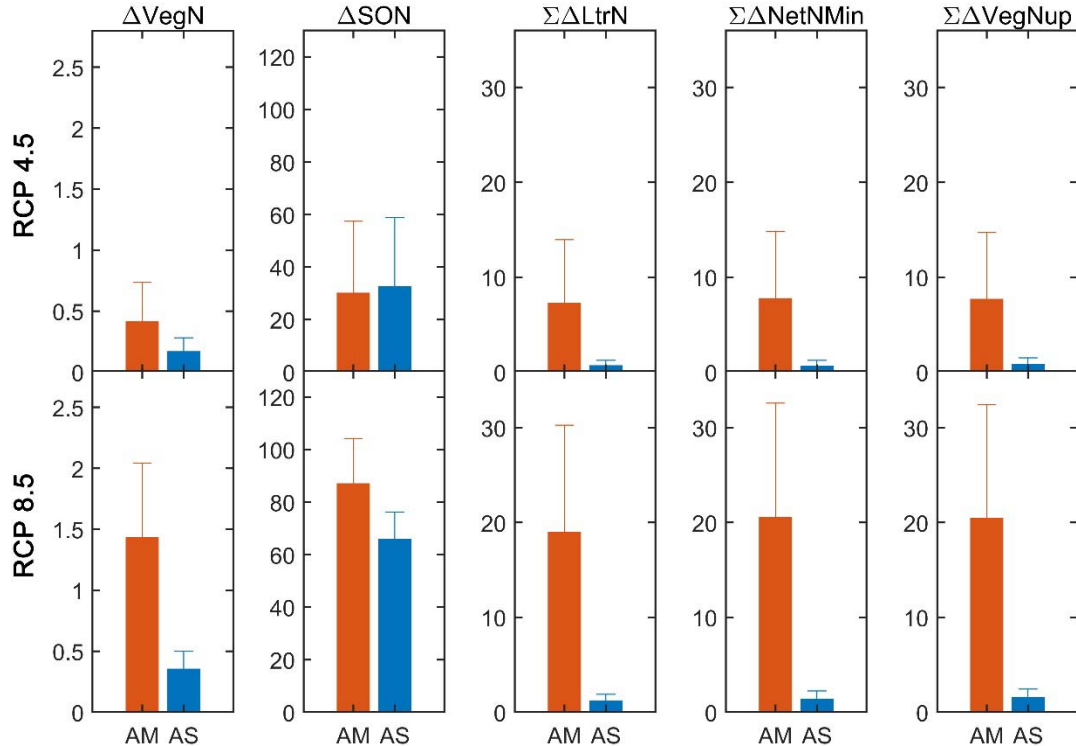
*Notes:*  $\Delta$  means the differences between the transient simulation and referenced simulation ( $S_T - S_R$ );  $\sum\Delta$  means the cumulative of  $S_T - S_R$  from 2020 to 2099; SOC<sub>PF</sub> and SON<sub>PF</sub> mean SOC, and SON added to active layers from permafrost thaw, respectively. LtrC, LtrN, NetNMin, and VegNup denote litter C, litter N, net N mineralization, and vegetation N uptake, respectively. Units for C and N variables are Pg C and Tg N, respectively.

There are several reasons in the limited plant access to N released from permafrost degradation on the QTP. First, ALT (greater than 2 m; Ni et al., 2021; Wang, T. et al., 2020; Wu, X.B. et al., 2018) on the QTP is already much deeper than rooting depth (generally smaller than 30 cm; Yang et al., 2009) currently. N released from further deep permafrost in the future, therefore, could be far beyond plant accessibility if there are no substantial changes in plant species. Second, N mineralization in permafrost soils on the QTP has been found largely regulated by microbial traits (Mao et al., 2020; Zhang et al., 2020). Microbial biomass in permafrost on the QTP is 91.3% lower than that in active layer soils (Mao et al., 2020). The low abundance of microbes can become a key restriction on N mineralization after permafrost thaw, because of the direct role that microbes play in N transformation (Schimel and Bennett, 2004) and the positive effects of the extracellular enzymes (Ali et al., 2021; Luo et al., 2017) and microbial biomass (Li, Z. et al., 2019; Wu, H. et al., 2021) on soil N mineralization. Apart from microbial biomass, the higher abundance of bacteria than fungi in QTP permafrost may also has negative impacts on net N mineralization processes (Mao et al., 2020), because of the significantly higher metabolic N-demand and immobilization in bacteria than fungi (Kooijman et al., 2016). Further, the phase lag of heat transfer into deep soils can shift the deep soil organic matter mineralization later into fall and winter, producing a seasonal offset from the peak period of N demand during spring and summer (Koven, Lawrence et al., 2015), and reducing the access

of plant to the additional N released from deep permafrost thaw. The remaining large fraction of N that cannot be used by plant could leach into aquatic ecosystems, causing far-reaching consequences on their functions and structure (Guo et al., 2019; Wickland et al., 2018), or could be lost via gaseous form of  $N_2O$  through nitrification and denitrification processes (Elberling et al., 2010; Voigt et al., 2017, 2020; Wilkerson et al., 2019), intensifying non-carbon feedback to climate warming (IPCC, 2013; Xu et al., 2012; Yang, G. et al., 2018). Considering the serious consequences and the large amount of these additional N, sufficient attention should be paid to their fate on the QTP.

#### 4.4 Nitrogen subsidy regimes from ALT deepening in different ecosystems

The more pronounced influences of ALT deepening on C balance in alpine meadow than alpine steppe on the QTP can be due to different C and N subsidies from permafrost thaw. Although the increase in ALT is smaller in alpine meadow comparing to alpine steppe, alpine meadow gains more C and N (Figure 6 and Figure 8). The maximum rooting depth of alpine meadow and alpine steppe ranges from 0.5 to 1.9 m, but the average ALT in alpine meadow ( $2.05 \pm 0.01$  m) is shallower than alpine steppe ( $2.96 \pm 0.03$  m) currently. Although ALT increases more in alpine steppe, it mainly occurs in deep soils far from rooting zone, therefore, only very limited N released from thawed permafrost can be accessed by alpine steppe. On the contrary, owing to the shallower ALT in alpine meadow, more N released from thawed permafrost is within its rooting zone, thus can be used. The addition of SOC and SON released from permafrost degradation in these two ecosystems (Table 3) support such explanations.



**Figure 8.** Differences in N balance between alpine meadow (AM) and alpine steppe (AS) ecosystems due to ALT deepening.  $\Delta$  means the simulation differences between the transient

simulation and referenced simulation ( $S_T-S_R$ ) in 2099;  $\Sigma$  denotes the accumulative differences in N fluxes from 2020 to 2099. The error bars represent standard deviations among all GCMs. Units for N pools (vegetation N (VegN) and soil organic N (SON)) are Tg N, and units for N fluxes (litter N (LtrN), net N mineralization (NetNMin), and vegetation N uptake (VegNup)) are Tg N/yr.

In addition, SOC and total nitrogen stocks in alpine meadow is about twice of that in alpine steppe on the QTP (Ding et al., 2016; Zhao, L. et al., 2018), which may result in the significant increasing in ecosystem C and N pools in alpine meadow ecosystem even with less increases in ALT. The higher density of SOC underneath alpine meadow can provide more substrates for microbe than that underneath alpine steppe, triggering a stronger RH response (Crowther et al., 2016). More SOC can also stimulate microbial activities and increase microbial biomass in alpine ecosystems (Li, Y. et al., 2019), strengthening RH. Apart from quantity, incubation experiments found that SOM under alpine meadow is highly decomposable (Chen, L. et al., 2016), while SOM under steppe is largely composed of stable organic compounds (Wu, X. et al., 2014). These differences may also contribute to a more sensitive RH in alpine meadow ecosystems (Eberwein et al., 2015). The consumption of SOC that released from permafrost thaw (Table 3) also shows that most of the additional SOC (79–85%) in alpine meadow would be consumed by microbe through RH, while only nearly a half (44–51%) of them would be consumed in alpine steppe.

The stronger response of  $\Delta NPP$  to ALT in alpine meadow can partly be explained by the significantly higher usage of N supplied by permafrost thaw (Table 3). More than 25% of additional N is utilized in alpine meadow, while only less than 3% is absorbed by alpine steppe, therefore, contributing to distinct vegetation responses in  $\Delta NPP$ . Alpine meadow ecosystem is mainly distributed in the eastern QTP. Relatively adequate precipitation, but also cold climate makes alpine meadow has higher soil water content than alpine steppe, which is distributed in arid climate. High soil water content in alpine meadow can facilitate N utilize by plant as water availability influences the diffusion of soil N to plant (Humbert et al., 2016; Simkin et al., 2016). Conversely, water limiting in alpine steppe constrains its nutrient availability and make it respond differently to climate warming and nitrogen addition from alpine meadow (Ganjurjav et al., 2016; Li, S. et al., 2019; Zheng et al., 2020). Different water conditions in these two ecosystems may result in distinct differences in N usage (Table 3) and fluxes (Figure 8).

**Table 3.** Changes in SOC and SON in alpine meadow and alpine steppe ecosystems due to permafrost thaw.

| C       | Alpine meadow     |                                  | Alpine steppe     |                                  |
|---------|-------------------|----------------------------------|-------------------|----------------------------------|
|         | SOC <sub>PF</sub> | $\Sigma\Delta RH / SOC_{PF}$     | SOC <sub>PF</sub> | $\Sigma\Delta RH / SOC_{PF}$     |
| RCP 4.5 | 0.57±0.31         | 0.85±0.22                        | 0.42±0.25         | 0.51±0.29                        |
| RCP 8.5 | 1.40±0.37         | 0.79±0.30                        | 0.79±0.14         | 0.44±0.13                        |
| N       | SON <sub>PF</sub> |                                  | SON <sub>PF</sub> |                                  |
|         | SON <sub>PF</sub> | $\Sigma\Delta VegNup / SON_{PF}$ | SON <sub>PF</sub> | $\Sigma\Delta VegNup / SON_{PF}$ |
| RCP 4.5 | 30.70±29.23       | 0.31±0.13                        | 32.60±27.48       | 0.02±0.00                        |

|         |             |           |            |           |
|---------|-------------|-----------|------------|-----------|
| RCP 8.5 | 88.73±18.62 | 0.25±0.09 | 66.15±7.41 | 0.03±0.01 |
|---------|-------------|-----------|------------|-----------|

Notes:  $\sum\Delta$  means the cumulative difference between the transient simulation and referenced simulation ( $S_T - S_R$ ) from 2020 to 2099;  $SOC_{PF}$  and  $SON_{PF}$  mean SOC, and SON added to active layers from permafrost thaw, respectively. Units for soil C and N are Pg C and Tg N, respectively.

## 5. Conclusions

We modified a process-based biogeochemistry model by considering the effects of extra carbon and nitrogen from thawing permafrost to quantify ecosystem C balance on the Qinghai-Tibetan plateau in the 21st century. Permafrost regions on the plateau would sequester more C and become a stronger C sink by the end of this century under both RCP 4.5 and RCP 8.5 scenarios. However, permafrost degradation on the QTP is projected to diminish the ecosystem C sequestration capacity, because the increase of NPP stimulated by N supply from thawing permafrost is smaller than the enhanced soil carbon respiration. Due to the deep active layer on the QTP, N released from thawing permafrost is mainly distributed in deep soils, which is not accessible by plant, thus having a limited benefit to plant carbon uptake. As a result, the C sink would decrease by  $303.55 \pm 254.80$  (RCP 4.5) and  $518.43 \pm 234.04$  (RCP 8.5) Tg C during 2020–2099.

Permafrost degradation on the QTP has different effects on C balance of the distinct ecosystems of alpine meadow and alpine steppe. C storages and fluxes respond more significant to ALT deepening in alpine meadow than alpine steppe, which could be due to the shallower ALT, the higher C and N stocks, and the wetter environment in alpine meadow.

Although more than half of the C released from thawing permafrost would be decomposed and emitted into the atmosphere, only 10% of the released N is utilized by plant. The remaining large amount of N could have significant impacts on aquatic ecosystems and may intensify climate warming through another potent greenhouse gas  $N_2O$  release. Therefore, the study on this gas release shall draw sufficient attention on the plateau.

This study highlights the important effects of permafrost thaw on C and N cycling in permafrost dominated ecosystems and underscore the critical role of factoring deep permafrost carbon into land surface modeling in order to make more reliable projections of future permafrost carbon-climate feedbacks.

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## References

- Abbott, B. W., Jones, J. B., Schuur, E. A. G., Chapin Iii, F. S., Bowden, W. B., Bret-Harte, M. S., et al. (2016), Biomass offsets little or none of permafrost carbon release from soils, streams, and wildfire: An expert assessment. *Environmental Research Letters*, 11(3), 034014. doi: 10.1088/1748-9326/11/3/034014
- Ali, S., Dongchu, L., Jing, H., Ahmed, W., Abbas, M., Qaswar, M., et al. (2021), Soil microbial biomass and extracellular enzymes regulate nitrogen mineralization in a wheat-maize cropping system after three decades of fertilization in a chinese ferrosol. *Journal of Soils and Sediments*, 21(1), 281-294. doi: 10.1007/s11368-020-02770-5
- Bosch, A., Schmidt, K., He, J.-S., Doerfer, C., & Scholten, T. (2017), Potential co2 emissions from defrosting permafrost soils of the Qinghai-Tibet plateau under different scenarios of climate change in 2050 and 2070. *CATENA*, 149, 221-231. doi: <https://doi.org/10.1016/j.catena.2016.08.035>
- Burke, E. J., Ekici, A., Huang, Y., Chadburn, S. E., Huntingford, C., Ciais, P., et al. (2017), Quantifying uncertainties of permafrost carbon-climate feedbacks. *Biogeosciences*, 14(12), 3051-3066. doi: 10.5194/bg-14-3051-2017
- Burke, E. J., Jones, C. D., & Koven, C. D. (2013), Estimating the permafrost-carbon climate response in the cmip5 climate models using a simplified approach. *Journal of Climate*, 26(14), 4897-4909. doi: 10.1175/JCLI-D-12-00550.1
- Chen, B., Zhang, X., Tao, J., Wu, J., Wang, J., Shi, P., et al. (2014), The impact of climate change and anthropogenic activities on alpine grassland over the Qinghai-Tibet plateau. *Agricultural and Forest Meteorology*, 189-190, 11-18. doi: <https://doi.org/10.1016/j.agrformet.2014.01.002>
- Chen, L., Liang, J., Qin, S., Liu, L., Fang, K., Xu, Y., et al. (2016), Determinants of carbon release from the active layer and permafrost deposits on the Tibetan plateau. *Nature Communications*, 7(1), 13046. doi: 10.1038/ncomms13046
- Chinese Academy of Sciences. (2001). *Vegetation Atlas of China*. Science Press, Beijing.
- Crowther, T. W., Todd-Brown, K. E. O., Rowe, C. W., Wieder, W. R., Carey, J. C., Machmuller, M. B., et al. (2016), Quantifying global soil carbon losses in response to warming. *Nature*, 540(7631), 104-108. doi: 10.1038/nature20150
- Ding, J., Chen, L., Ji, C., Hugelius, G., Li, Y., Liu, L., et al. (2017), Decadal soil carbon accumulation across Tibetan permafrost regions. *Nature Geoscience*, 10(6), 420-424. doi: 10.1038/ngeo2945
- Ding, J., Li, F., Yang, G., Chen, L., Zhang, B., Liu, L., et al. (2016), The permafrost carbon inventory on the Tibetan plateau: A new evaluation using deep sediment cores. *Global Change Biology*, 22(8), 2688-2701. doi:10.1111/gcb.13257
- Eberwein, J. R., Oikawa, P. Y., Allsman, L. A., & Jenerette, G. D. (2015), Carbon availability regulates soil respiration response to nitrogen and temperature. *Soil Biology and Biochemistry*, 88, 158-164. doi: <https://doi.org/10.1016/j.soilbio.2015.05.014>
- Editorial Committee of Vegetation Map of China, Chinese Academy of Sciences. (2001). *Vegetation Atlas of China*. Science Press, Beijing.

- Elberling, B., Christiansen, H. H., & Hansen, B. U. (2010), High nitrous oxide production from thawing permafrost. *Nature Geoscience*, 3(5), 332-335. doi: 10.1038/ngeo803
- Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., et al. (2007), The shuttle radar topography mission. *Reviews of Geophysics*, 45(2). doi: <https://doi.org/10.1029/2005RG000183>
- Finger, R. A., Turetsky, M. R., Kielland, K., Ruess, R. W., Mack, M. C., & Euskirchen, E. S. (2016), Effects of permafrost thaw on nitrogen availability and plant-soil interactions in a boreal Alaskan lowland. *Journal of Ecology*, 104(6), 1542-1554. doi: 10.1111/1365-2745.12639
- Frieler, K., Lange, S., Piontek, F., Reyer, C. P. O., Schewe, J., Warszawski, L., et al. (2017), Assessing the impacts of 1.5 degrees c global warming - simulation protocol of the inter-sectoral impact model intercomparison project (isimip2b). *Geoscientific Model Development*, 10(12), 4321-4345. doi: 10.5194/gmd-10-4321-2017
- Fu, Y., Liu, C., Lin, F., Hu, X., Zheng, X., Zhang, W., & Cao, G. (2018), Quantification of year-round methane and nitrous oxide fluxes in a typical alpine shrub meadow on the Qinghai-Tibetan plateau. *Agriculture, Ecosystems & Environment*, 255, 27-36. doi: <https://doi.org/10.1016/j.agee.2017.12.003>
- Ganjurjav, H., Gao, Q. Z., Gornish, E. S., Schwartz, M. W., Liang, Y., Cao, X. J., et al. (2016), Differential response of alpine steppe and alpine meadow to climate warming in the central Qinghai-Tibetan plateau. *Agricultural and Forest Meteorology*, 223, 233-240. doi: 10.1016/j.agrformet.2016.03.017
- Guo, Y. D., Song, C. C., Tan, W. W., Wang, X. W., & Lu, Y. Z. (2019), Export of dissolved nitrogen in catchments underlain by permafrost in northeast china. *Science of the Total Environment*, 660, 1210-1218. doi: 10.1016/j.scitotenv.2018.12.464
- Hao, A., Xue, X., Wang, X., Zhao, G., You, Q., Peng, F., et al. (2021), Different response of alpine meadow and alpine steppe to climatic and anthropogenic disturbance on the Tibetan plateau. *Global Ecology and Conservation*, 27, e01512. doi: <https://doi.org/10.1016/j.gecco.2021.e01512>
- Hayes, D. J., Kicklighter, D. W., McGuire, A. D., Chen, M., Zhuang, Q., Yuan, F., et al. (2014), The impacts of recent permafrost thaw on land-atmosphere greenhouse gas exchange. *Environmental Research Letters*, 9(4), 045005. doi: 10.1088/1748-9326/9/4/045005
- Hayes, D. J., McGuire, A. D., Kicklighter, D. W., Gurney, K. R., Burnside, T. J., & Melillo, J. M. (2011), Is the northern high-latitude land-based co2 sink weakening? *Global Biogeochemical Cycles*, 25(3). doi: <https://doi.org/10.1029/2010GB003813>
- Humbert, J. Y., Dwyer, J. M., Andrey, A., & Arlettaz, R. (2016), Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: A systematic review. *Global Change Biology*, 22(1), 110-120. doi: 10.1111/gcb.12986
- Huo, L., Chen, Z., Zou, Y., Lu, X., Guo, J., & Tang, X. (2013), Effect of zoige alpine wetland degradation on the density and fractions of soil organic carbon. *Ecological Engineering*, 51, 287-295. doi: <https://doi.org/10.1016/j.ecoleng.2012.12.020>
- IPCC, 2013: *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker,

- 681 T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and  
 682 P.M. Midgley (eds.)). Cambridge University Press, Cambridge, United Kingdom and New York,  
 683 NY, USA, 1535 pp.
- 684 Jin, Z., Zhuang, Q., He, J.-S., Luo, T., & Shi, Y. (2013), Phenology shift from 1989 to 2008 on  
 685 the Tibetan plateau: An analysis with a process-based soil physical model and remote sensing  
 686 data. *Climatic Change*, 119(2), 435-449. doi: 10.1007/s10584-013-0722-7
- 687 Jin, Z., Zhuang, Q., He, J.-S., Zhu, X., & Song, W. (2015), Net exchanges of methane and  
 688 carbon dioxide on the Qinghai-Tibetan plateau from 1979 to 2100. *Environmental Research*  
 689 *Letters*, 10(8), 085007. doi: 10.1088/1748-9326/10/8/085007
- 690 Jones, C. D., Arora, V., Friedlingstein, P., Bopp, L., Brovkin, V., Dunne, J., et al. (2016), C4MIP  
 691 – the coupled climate–carbon cycle model intercomparison project: Experimental protocol for  
 692 cmip6. *Geoscientific Model Development*, 9(8), 2853-2880. doi: 10.5194/gmd-9-2853-2016
- 693 Keuper, F., van Bodegom, P. M., Dorrepaal, E., Weedon, J. T., van Hal, J., van Logtestijn, R. S.  
 694 P., & Aerts, R. (2012), A frozen feast: Thawing permafrost increases plant-available nitrogen in  
 695 subarctic peatlands. *Global Change Biology*, 18(6), 1998-2007. doi: 10.1111/j.1365-  
 696 2486.2012.02663.x
- 697 Kicklighter, D. W., Melillo, J. M., Monier, E., Sokolov, A. P., & Zhuang, Q. (2019), Future  
 698 nitrogen availability and its effect on carbon sequestration in northern eurasia. *Nat Commun*,  
 699 10(1), 3024. doi: 10.1038/s41467-019-10944-0
- 700 Kooijman, A. M., Bloem, J., van Dalen, B. R., & Kalbitz, K. (2016), Differences in activity and  
 701 n demand between bacteria and fungi in a microcosm incubation experiment with selective  
 702 inhibition. *Applied Soil Ecology*, 99, 37-47. doi: 10.1016/j.apsoil.2015.11.011
- 703 Kou, D., Ding, J., Li, F., Wei, N., Fang, K., Yang, G., et al. (2019), Spatially-explicit estimate of  
 704 soil nitrogen stock and its implication for land model across Tibetan alpine permafrost region.  
 705 *Science of the Total Environment*, 650, 1795-1804. doi:  
 706 <https://doi.org/10.1016/j.scitotenv.2018.09.252>
- 707 Koven, C. D., Lawrence, D. M., & Riley, W. J. (2015a), Permafrost carbon-climate feedback is  
 708 sensitive to deep soil carbon decomposability but not deep soil nitrogen dynamics. *Proceedings*  
 709 *of the National Academy of Sciences of the United States of America*, 112(12), 3752-3757. doi:  
 710 10.1073/pnas.1415123112
- 711 Koven, C. D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., et al.  
 712 (2011), Permafrost carbon-climate feedbacks accelerate global warming. *Proceedings of the*  
 713 *National Academy of Sciences*, 108(36), 14769-14774. doi: 10.1073/pnas.1103910108
- 714 Koven, C. D., Schuur, E. A. G., Schadel, C., Bohn, T. J., Burke, E. J., Chen, G., et al. (2015b), A  
 715 simplified, data-constrained approach to estimate the permafrost carbon-climate feedback.  
 716 *Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering*  
 717 *Sciences*, 373(2054), 23. doi: 10.1098/rsta.2014.0423
- 718 Li, S., Dong, S., Shen, H., Han, Y., Zhang, J., Xu, Y., et al. (2019), Different responses of  
 719 multifaceted plant diversities of alpine meadow and alpine steppe to nitrogen addition gradients  
 720 on Qinghai-Tibetan plateau. *Science of the Total Environment*, 688, 1405-1412. doi:  
 721 <https://doi.org/10.1016/j.scitotenv.2019.06.211>

- Li, Y., Lv, W., Jiang, L., Zhang, L., Wang, S., Wang, Q., et al. (2019), Microbial community responses reduce soil carbon loss in Tibetan alpine grasslands under short-term warming. *Global Change Biology*, 25(10), 3438-3449. doi: <https://doi.org/10.1111/gcb.14734>
- Li, Z. L., Tian, D. S., Wang, B. X., Wang, J. S., Wang, S., Chen, H. Y. H., et al. (2019), Microbes drive global soil nitrogen mineralization and availability. *Global Change Biology*, 25(3), 1078-1088. doi: 10.1111/gcb.14557
- Liang, J., Xia, J., Shi, Z., Jiang, L., Ma, S., Lu, X., et al. (2018), Biotic responses buffer warming-induced soil organic carbon loss in arctic tundra. *Global Change Biology*, 24(10), 4946-4959. doi: <https://doi.org/10.1111/gcb.14325>
- Lin, X., Han, P., Zhang, W., & Wang, G. (2017), Sensitivity of alpine grassland carbon balance to interannual variability in climate and atmospheric co<sub>2</sub> on the Tibetan plateau during the last century. *Global and Planetary Change*, 154, 23-32. doi: <https://doi.org/10.1016/j.gloplacha.2017.05.008>
- Liu, Y., Geng, X., Tenzintarchen, Wei, D., Dai, D., & Xu, R. (2020), Divergence in ecosystem carbon fluxes and soil nitrogen characteristics across alpine steppe, alpine meadow and alpine swamp ecosystems in a biome transition zone. *Science of the Total Environment*, 748, 142453. doi: <https://doi.org/10.1016/j.scitotenv.2020.142453>
- Luo, L., Meng, H., & Gu, J. D. (2017), Microbial extracellular enzymes in biogeochemical cycling of ecosystems. *Journal of Environmental Management*, 197, 539-549. doi: 10.1016/j.jenvman.2017.04.023
- MacDougall, A. H., & Knutti, R. (2016), Projecting the release of carbon from permafrost soils using a perturbed parameter ensemble modelling approach. *Biogeosciences*, 13(7), 2123-2136. doi: 10.5194/bg-13-2123-2016
- Mao, C., Kou, D., Chen, L., Qin, S., Zhang, D., Peng, Y., & Yang, Y. (2020), Permafrost nitrogen status and its determinants on the Tibetan plateau. *Global Change Biology*, 26(9), 5290-5302. doi: 10.1111/gcb.15205
- McGuire, A. D., Koven, C., Lawrence, D. M., Klein, J. S., Xia, J. Y., Beer, C., et al. (2016), Variability in the sensitivity among model simulations of permafrost and carbon dynamics in the permafrost region between 1960 and 2009. *Global Biogeochemical Cycles*, 30(7), 1015-1037. doi: 10.1002/2016gb005405
- McGuire, A. D., Lawrence, D. M., Koven, C., Klein, J. S., Burke, E., Chen, G. S., et al. (2018), Dependence of the evolution of carbon dynamics in the northern permafrost region on the trajectory of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 115(15), 3882-3887. doi: 10.1073/pnas.1719903115
- McGuire, A. D., Melillo, J. M., Joyce, L. A., Kicklighter, D. W., Grace, A. L., Moore, B., & Vorosmarty, C. J. (1992), Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in north america. *Global Biogeochemical Cycles*, 6(2), 101-124. doi: 10.1029/92gb00219
- Mishra, U., Hugelius, G., Shelef, E., Yang, Y., Strauss, J., Lupachev, A., et al. (2021), Spatial heterogeneity and environmental predictors of permafrost region soil organic carbon stocks. *Science Advances*, 7(9), eaaz5236. doi: 10.1126/sciadv.aaz5236

- Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., van Vuuren, D. P., et al. (2010), The next generation of scenarios for climate change research and assessment. *Nature*, 463(7282), 747-756. doi: 10.1038/nature08823
- Mu, C., Abbott, B. W., Norris, A. J., Mu, M., Fan, C., Chen, X., et al. (2020), The status and stability of permafrost carbon on the Tibetan plateau. *Earth-Science Reviews*, 211, 103433. doi: <https://doi.org/10.1016/j.earscirev.2020.103433>
- Ni, J. (2000), A simulation of biomes on the Tibetan plateau and their responses to global climate change. *Mountain Research and Development*, 20(1), 80-89. doi: 10.1659/0276-4741(2000)020[0080:Asobot]2.0.Co;2
- Ni, J., Wu, T., Zhu, X., Hu, G., Zou, D., Wu, X., et al. (2021), Simulation of the present and future projection of permafrost on the Qinghai-Tibet plateau with statistical and machine learning models. *Journal of Geophysical Research: Atmospheres*, 126(2), e2020JD033402. doi: <https://doi.org/10.1029/2020JD033402>
- Nieberding, F., Wille, C., Fratini, G., Asmussen, M. O., Wang, Y., Ma, Y., & Sachs, T. (2020), A long-term (2005–2019) eddy covariance data set of co<sub>2</sub> and h<sub>2</sub>o fluxes from the Tibetan alpine steppe. *Earth Syst. Sci. Data*, 12(4), 2705-2724. doi: 10.5194/essd-12-2705-2020
- Peng, F., Xue, X., Li, C., Lai, C., Sun, J., Tsubo, M., et al. (2020), Plant community of alpine steppe shows stronger association with soil properties than alpine meadow alongside degradation. *Science of the Total Environment*, 733, 139048. doi: <https://doi.org/10.1016/j.scitotenv.2020.139048>
- Peng, X., Zhang, T., Frauenfeld, O. W., Wang, S., Qiao, L., Du, R., & Mu, C. (2020), Northern hemisphere greening in association with warming permafrost. *Journal of Geophysical Research: Biogeosciences*, 125(1), e2019JG005086. doi: 10.1029/2019jg005086
- Piao, S., Tan, K., Nan, H., Ciais, P., Fang, J., Wang, T., et al. (2012), Impacts of climate and co<sub>2</sub> changes on the vegetation growth and carbon balance of Qinghai–Tibetan grasslands over the past five decades. *Global and Planetary Change*, 98-99, 73-80. doi: <https://doi.org/10.1016/j.gloplacha.2012.08.009>
- Ping, C.-L., Michaelson, G. J., Jorgenson, M. T., Kimble, J. M., Epstein, H., Romanovsky, V. E., & Walker, D. A. (2008), High stocks of soil organic carbon in the north American arctic region. *Nature Geoscience*, 1(9), 615-619. doi: 10.1038/ngeo284
- Qian, H. F., Joseph, R., & Zeng, N. (2010), Enhanced terrestrial carbon uptake in the northern high latitudes in the 21st century from the coupled carbon cycle climate model intercomparison project model projections. *Global Change Biology*, 16(2), 641-656. doi: 10.1111/j.1365-2486.2009.01989.x
- Salmon, V. G., Schadel, C., Bracho, R., Pegoraro, E., Celis, G., Mauritz, M., et al. (2018), Adding depth to our understanding of nitrogen dynamics in permafrost soils. *Journal of Geophysical Research-Biogeosciences*, 123(8), 2497-2512. doi: 10.1029/2018jg004518
- Salmon, V. G., Soucy, P., Mauritz, M., Celis, G., Natali, S. M., Mack, M. C., & Schuur, E. A. G. (2016), Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw. *Global Change Biology*, 22(5), 1927-1941. doi: 10.1111/gcb.13204

- Schaefer, K., Lantuit, H., Romanovsky, V. E., Schuur, E. A. G., & Witt, R. (2014), The impact of the permafrost carbon feedback on global climate. *Environmental Research Letters*, 9(8), 085003. doi: 10.1088/1748-9326/9/8/085003
- Schaphoff, S., Heyder, U., Ostberg, S., Gerten, D., Heinke, J., & Lucht, W. (2013), Contribution of permafrost soils to the global carbon budget. *Environmental Research Letters*, 8(1), 014026. doi: 10.1088/1748-9326/8/1/014026
- Schimel, J. P., & Bennett, J. (2004), Nitrogen mineralization: Challenges of a changing paradigm. *Ecology*, 85(3), 591-602. doi: 10.1890/03-8002
- Schuur, E. A. G., McGuire, A. D., Schadel, C., Grosse, G., Harden, J. W., Hayes, D. J., et al. (2015), Climate change and the permafrost carbon feedback. *Nature*, 520(7546), 171-179. doi: 10.1038/nature14338
- Shang, W., Wu, X. D., Zhao, L., Yue, G. Y., Zhao, Y. H., Qiao, Y. P., & Li, Y. Q. (2016), Seasonal variations in labile soil organic matter fractions in permafrost soils with different vegetation types in the central Qinghai-Tibet plateau. *Catena*, 137, 670-678. doi: 10.1016/j.catena.2015.07.012
- Shu, S., Jain, A. K., Koven, C. D., & Mishra, U. (2020), Estimation of permafrost soc stock and turnover time using a land surface model with vertical heterogeneity of permafrost soils. *Global Biogeochemical Cycles*, 34(11), e2020GB006585. doi: <https://doi.org/10.1029/2020GB006585>
- Simkin, S. M., Allen, E. B., Bowman, W. D., Clark, C. M., Belnap, J., Brooks, M. L., et al. (2016), Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the united states. *Proceedings of the National Academy of Sciences of the United States of America*, 113(15), 4086-4091. doi: 10.1073/pnas.1515241113
- Tan, K., Ciais, P., Piao, S., Wu, X., Tang, Y., Vuichard, N., et al. (2010), Application of the ORCHIDEE global vegetation model to evaluate biomass and soil carbon stocks of Qinghai-Tibetan grasslands. *Global Biogeochemical Cycles*, 24(1). doi: <https://doi.org/10.1029/2009GB003530>
- Tao, Z., Shen, C., Gao, Q., Sun, Y., Yi, W., & Li, Y. (2007), Soil organic carbon storage and soil co2 flux in the alpine meadow ecosystem. *Science in China Series D: Earth Sciences*, 50(7), 1103-1114. doi: 10.1007/s11430-007-0055-3
- Voigt, C., Marushchak, M. E., Abbott, B. W., Biasi, C., Elberling, B., Siciliano, S. D., et al. (2020), Nitrous oxide emissions from permafrost-affected soils. *Nature Reviews Earth & Environment*, 1(8), 420-434. doi: 10.1038/s43017-020-0063-9
- Voigt, C., Marushchak, M. E., Lamprecht, R. E., Jackowicz-Korczynski, M., Lindgren, A., Mastepanov, M., et al. (2017), Increased nitrous oxide emissions from arctic peatlands after permafrost thaw. *Proceedings of the National Academy of Sciences of the United States of America*, 114(24), 6238-6243. doi: 10.1073/pnas.1702902114
- Wang, G., Li, F., Peng, Y., Yu, J., Zhang, D., Yang, G., et al. (2019), Responses of soil respiration to experimental warming in an alpine steppe on the Tibetan plateau. *Environmental Research Letters*, 14(9), 094015. doi: 10.1088/1748-9326/ab3bbc

- Wang, L., Liu, H., Shao, Y., Liu, Y., & Sun, J. (2018), Water and co<sub>2</sub> fluxes over semiarid alpine steppe and humid alpine meadow ecosystems on the Tibetan plateau. *Theoretical and Applied Climatology*, 131(1), 547-556. doi: 10.1007/s00704-016-1997-1
- Wang, S. Y., Zhang, B., Yang, Q. C., Chen, G. S., Yang, B. J., Lu, L. L., et al. (2017), Responses of net primary productivity to phenological dynamics in the Tibetan plateau, china. *Agricultural and Forest Meteorology*, 232, 235-246. doi: 10.1016/j.agrformet.2016.08.020
- Wang T. (2019). *Frozen ground map of China based on a Map of the Glaciers, Frozen Ground and Deserts in China*. National Cryosphere Desert Data Center (<http://www.ncdc.ac.cn>).
- Wang, T., Yang, D., Yang, Y., Piao, S., Li, X., Cheng, G., & Fu, B. (2020), Permafrost thawing puts the frozen carbon at risk over the Tibetan plateau. *Science Advances*, 6(19), eaaz3513. doi: 10.1126/sciadv.aaz3513
- Wickland, K. P., Waldrop, M. P., Aiken, G. R., Koch, J. C., Jorgenson, M. T., & Striegl, R. G. (2018), Dissolved organic carbon and nitrogen release from boreal Holocene permafrost and seasonally frozen soils of Alaska. *Environmental Research Letters*, 13(6), 065011. doi: 10.1088/1748-9326/aac4ad
- Wieder, W. (2014), RegridDED harmonized world soil database v1.2, edited, ORNL Distributed Active Archive Center.
- Wilkerson, J., Dobosy, R., Sayres, D. S., Healy, C., Dumas, E., Baker, B., & Anderson, J. G. (2019), Permafrost nitrous oxide emissions observed on a landscape scale using the airborne eddy-covariance method. *Atmospheric Chemistry and Physics*, 19(7), 4257-4268. doi: 10.5194/acp-19-4257-2019
- Wu, H., Cai, A., Xing, T., Huai, S., Zhu, P., Xu, M., & Lu, C. (2021), Fertilization enhances mineralization of soil carbon and nitrogen pools by regulating the bacterial community and biomass. *Journal of Soils and Sediments*, 1-11. doi: 10.1007/s11368-020-02865-z
- Wu, X., Fang, H., Zhao, L., Wu, T., Li, R., Ren, Z., et al. (2014), Mineralisation and changes in the fractions of soil organic matter in soils of the permafrost region, Qinghai-Tibet plateau, china. *Permafrost and Periglacial Processes*, 25(1), 35-44. doi: <https://doi.org/10.1002/ppp.1796>
- Wu, X. B., Nan, Z. T., Zhao, S. P., Zhao, L., & Cheng, G. D. (2018), Spatial modeling of permafrost distribution and properties on the Qinghai-Tibet plateau. *Permafrost and Periglacial Processes*, 29(2), 86-99. doi: 10.1002/ppp.1971
- Xu, R., Prentice, I. C., Spahni, R., & Niu, H. S. (2012), Modelling terrestrial nitrous oxide emissions and implications for climate feedback. *New Phytologist*, 196(2), 472-488. doi: 10.1111/j.1469-8137.2012.04269.x
- Yan, L., Zhou, G. S., Wang, Y. H., Hu, T. Y., & Sui, X. H. (2015), The spatial and temporal dynamics of carbon budget in the alpine grasslands on the Qinghai-Tibetan plateau using the terrestrial ecosystem model. *Journal of Cleaner Production*, 107, 195-201. doi: <https://doi.org/10.1016/j.jclepro.2015.04.140>
- Yang, G. B., Peng, Y. F., Marushchak, M. E., Chen, Y. L., Wang, G. Q., Li, F., et al. (2018), Magnitude and pathways of increased nitrous oxide emissions from uplands following

- 882 permafrost thaw. *Environmental Science & Technology*, 52(16), 9162-9169. doi:  
883 10.1021/acs.est.8b02271
- 884 Yang, Y., Fang, J., Ji, C., & Han, W. (2009), Above- and belowground biomass allocation in  
885 Tibetan grasslands. *Journal of Vegetation Science*, 20(1), 177-184. doi:  
886 <https://doi.org/10.1111/j.1654-1103.2009.05566.x>
- 887 Yi, S., Wang, X., Qin, Y., Xiang, B., & Ding, Y. (2014), Responses of alpine grassland on  
888 Qinghai–Tibetan plateau to climate warming and permafrost degradation: A modeling  
889 perspective. *Environmental Research Letters*, 9(7), 074014. doi: 10.1088/1748-9326/9/7/074014
- 890 Zhang, Y., Qi, W., Zhou, C., Ding, M., Liu, L., Gao, J., et al. (2014), Spatial and temporal  
891 variability in the net primary production of alpine grassland on the Tibetan plateau since 1982.  
892 *Journal of Geographical Sciences*, 24(2), 269-287. doi: 10.1007/s11442-014-1087-1
- 893 Zhang, Y., Zhang, N., Yin, J., Zhao, Y., Yang, F., Jiang, Z., et al. (2020), Simulated warming  
894 enhances the responses of microbial n transformations to reactive n input in a Tibetan alpine  
895 meadow. *Environment International*, 141, 105795. doi:  
896 <https://doi.org/10.1016/j.envint.2020.105795>
- 897 Zhao, J., Luo, T., Wei, H., Deng, Z., Li, X., Li, R., & Tang, Y. (2019), Increased precipitation  
898 offsets the negative effect of warming on plant biomass and ecosystem respiration in a Tibetan  
899 alpine steppe. *Agricultural and Forest Meteorology*, 279, 107761. doi:  
900 <https://doi.org/10.1016/j.agrformet.2019.107761>
- 901 Zhao, L., Wu, X. D., Wang, Z. W., Sheng, Y., Fang, H. B., Zhao, Y. H., et al. (2018), Soil  
902 organic carbon and total nitrogen pools in permafrost zones of the Qinghai-Tibetan plateau.  
903 *Scientific Reports*, 8, 1-9. doi: 10.1038/s41598-018-22024-2
- 904 Zheng, Z. T., Zhu, W. Q., & Zhang, Y. J. (2020), Seasonally and spatially varied controls of  
905 climatic factors on net primary productivity in alpine grasslands on the Tibetan plateau. *Global*  
906 *Ecology and Conservation*, 21, e00814. doi: 10.1016/j.gecco.2019.e00814
- 907 Zhuang, Q., He, J., Lu, Y., Ji, L., Xiao, J., & Luo, T. (2010), Carbon dynamics of terrestrial  
908 ecosystems on the Tibetan plateau during the 20th century: An analysis with a process-based  
909 biogeochemical model. *Global Ecology and Biogeography*, 19(5), 649-662. doi: 10.1111/j.1466-  
910 8238.2010.00559.x
- 911 Zhuang, Q., McGuire, A. D., Melillo, J. M., Clein, J. S., Dargaville, R. J., Kicklighter, D. W., et  
912 al. (2011), Carbon cycling in extratropical terrestrial ecosystems of the northern hemisphere  
913 during the 20th century: A modeling analysis of the influences of soil thermal dynamics. *Tellus*  
914 *B: Chemical and Physical Meteorology*, 55(3), 751-776. doi: 10.3402/tellusb.v55i3.16368
- 915 Zhuang, Q., McGuire, A. D., O'Neill, K. P., Harden, J. W., Romanovsky, V. E., & Yarie, J.  
916 (2002), Modeling soil thermal and carbon dynamics of a fire chrono sequence in interior Alaska.  
917 *Journal of Geophysical Research: Atmospheres*, 107(D1), FFR 3-1-FFR 3-26. doi:  
918 <https://doi.org/10.1029/2001JD001244>
- 919 Zhuang, Q., Romanovsky, V. E., & McGuire, A. D. (2001), Incorporation of a permafrost model  
920 into a large-scale ecosystem model: Evaluation of temporal and spatial scaling issues in  
921 simulating soil thermal dynamics. *Journal of Geophysical Research: Atmospheres*, 106(D24),  
922 33649-33670. doi: 10.1029/2001jd900151

**Permafrost Degradation Diminishes Terrestrial Ecosystem Carbon Sequestration  
Capacity on the Qinghai-Tibetan Plateau**

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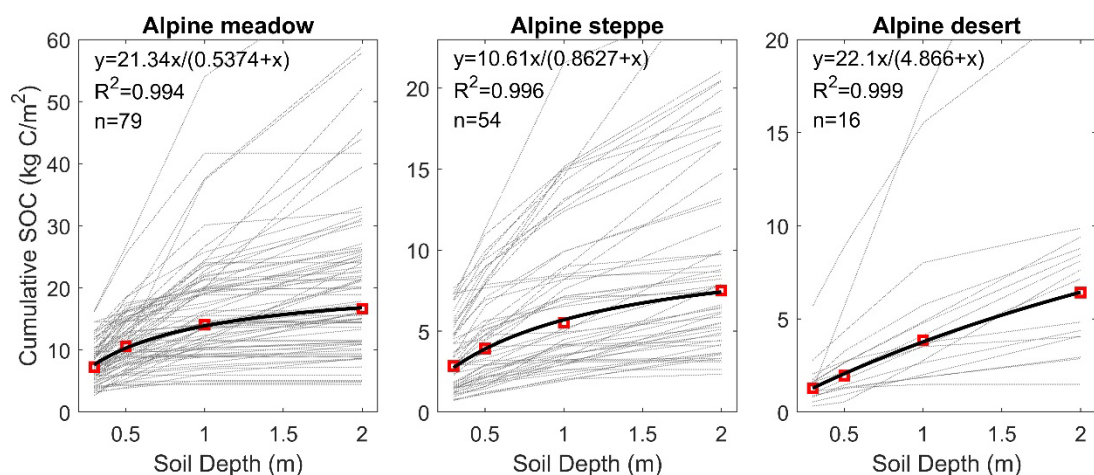
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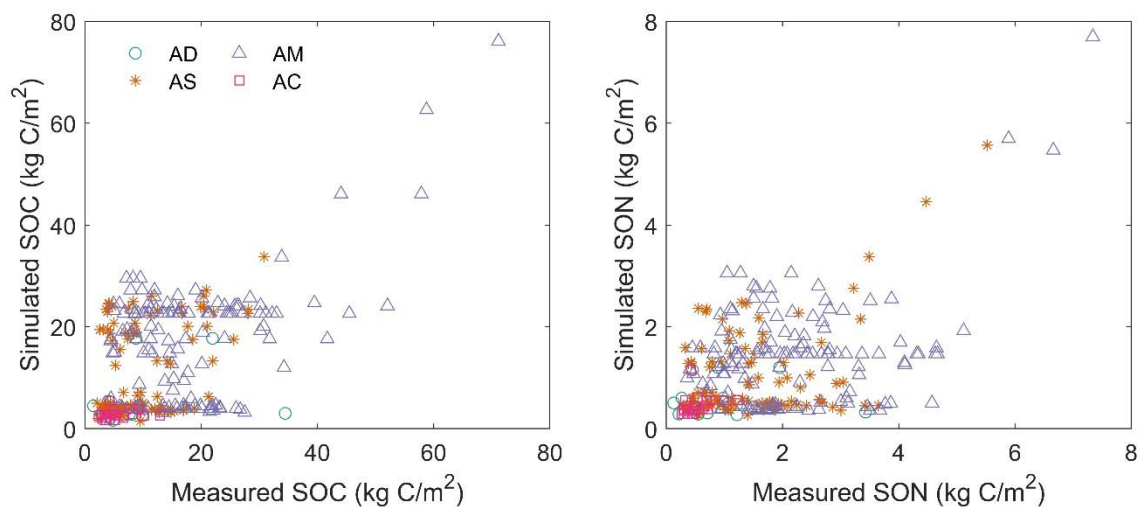
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Figures S1 to S5

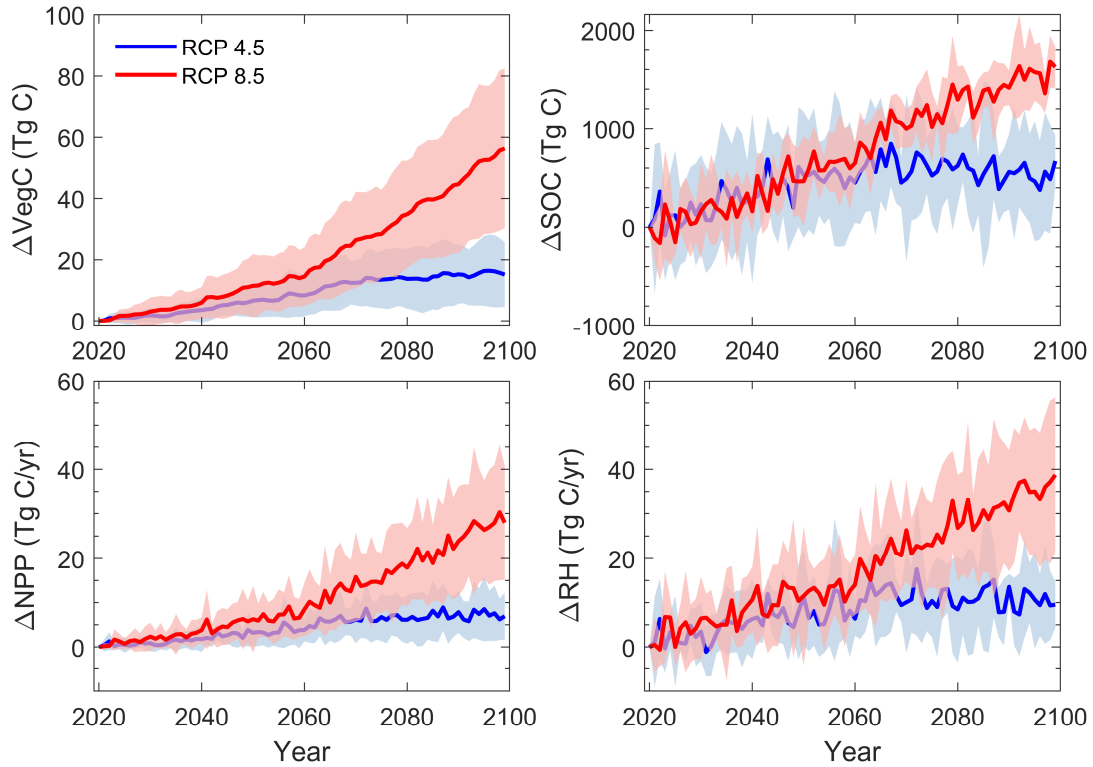
Tables S1 to S2



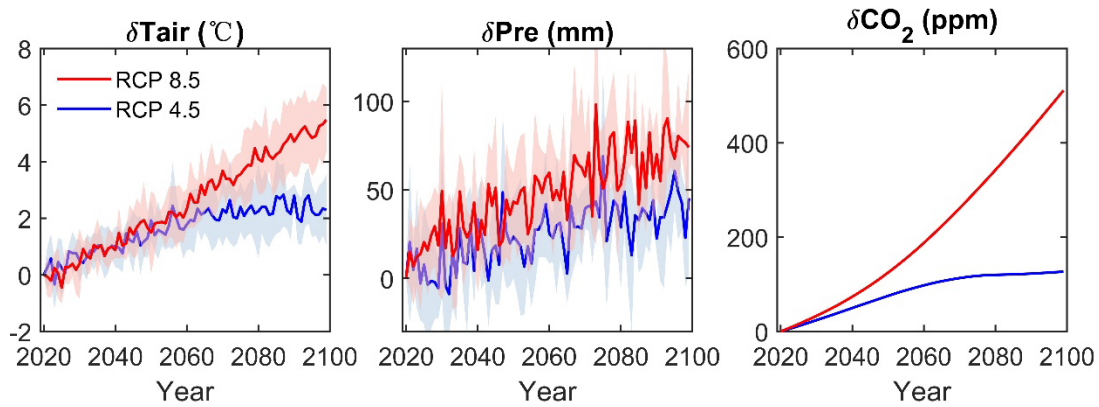
**Figure S1.** Changes of cumulative SOC with soil depth in alpine meadow, alpine steppe and alpine desert ecosystems in the permafrost region of the QTP. The dotted gray lines denote observation results; the red rectangles represent the median value of every soil depths; and the thick black lines are regression curves. 'n' in each panel is the number of observation sites. Observation data derived from Zhao et al. (2018).



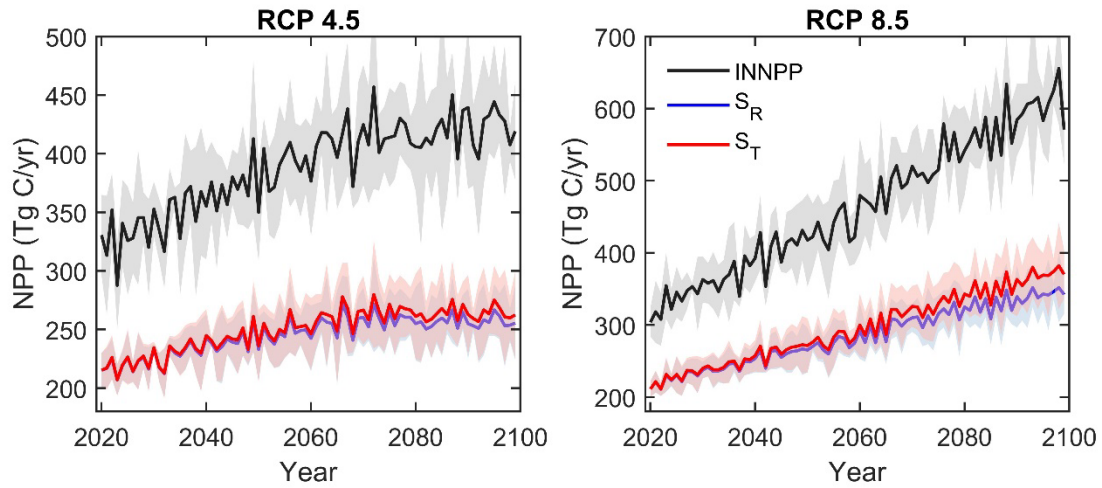
**Figure S2.** Validation of simulated SOC and SON vs. 289 observations on the QTP. AD, AS, AM, and AC represent alpine desert, alpine steppe, alpine meadow, and alpine cushion, respectively.



**Figure S3.** Effects of ALT deepening on ecosystem C balance of permafrost regions on the QTP under the RCP 4.5 and RCP 8.5 scenarios.  $\Delta$  means the difference between the results of ST and SR (ST-SR).



**Figure S4.** Changes in air temperature ( $T_{\text{air}}$ ), precipitation ( $\text{Pre}$ ), and atmospheric  $\text{CO}_2$  concentration of the permafrost region on the QTP based on 2020.



**Figure S5.** Changes in NPP in ST and SR simulations and changes in INNPP during 2020-2100 under the RCP 4.5 and RCP 8.5. INNPP is the NPP estimated by TEM that is not constrained by N supply but only regulated by climate.

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| Steppe              | Meadow              | Sparse               | Desert             | Shrubland            | Forest               | Others               |
|---------------------|---------------------|----------------------|--------------------|----------------------|----------------------|----------------------|
| 0.8627 <sup>*</sup> | 0.5374 <sup>*</sup> | 0.5937 <sup>**</sup> | 4.866 <sup>*</sup> | 1.2553 <sup>**</sup> | 0.4746 <sup>**</sup> | 0.6920 <sup>**</sup> |

62 **Table S1.** The value of parameter b in eq. (2) for each ecosystem in the permafrost region of  
63 QTP.

64 *Notes:* \* denotes the data calculated from observation data (Fig. S1); \*\* denotes data derived  
65 from Kicklighter et al. (2019).

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| Ecosystem             |                  | Alpine meadow                           | Alpine steppe                                                      | Alpine shrubland                                                 |
|-----------------------|------------------|-----------------------------------------|--------------------------------------------------------------------|------------------------------------------------------------------|
| Site                  |                  | Zoige                                   | NamCo                                                              | Haibei                                                           |
| Latitude              |                  | 33°53' N                                | 30°46' N                                                           | 37°37' N                                                         |
| Longitude             |                  | 102°8' E                                | 90°57' E                                                           | 101°19' E                                                        |
| Elevation (m)         |                  | 3423                                    | 4730                                                               | 3190                                                             |
| SOC                   | obs <sup>*</sup> | 30895.51                                | 4698.55                                                            | 23440.00                                                         |
| (g C/m <sup>2</sup> ) | sim <sup>*</sup> | 30329.27±37.4                           | 4723.02±5.57                                                       | 22581.90±14.97                                                   |
| SON                   | obs <sup>*</sup> | 1984.78                                 | 399.04                                                             | 2616.20                                                          |
| (g N/m <sup>2</sup> ) | sim <sup>*</sup> | 2032.76±1.83                            | 398.78±0.25                                                        | 2793.79±0.40                                                     |
| Reference             |                  | Huo et al., 2013;<br>Shang et al., 2016 | Ding et al., 2016;<br>Kou et al., 2019;<br>Nieberding et al., 2020 | Tao et al., 2007;<br>Fu et al., 2018;<br>ChinaFLUX <sup>**</sup> |

73 **Table S2.** Information of observation sites for model validation.

74 *Notes:* \*: obs and sim denote observation and simulation, respectively; \*\*: <http://www.chinaflux.org/gczd/index.aspx?nodeid=1003>

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