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Key Points:

- Tibetan Plateau is one of the most sensitive regions to climatic conditions
- Climatic conditions shape the natural alpine mountain ecosystem shifts
- The major interconnects and drivers to ecosystem imbalance has been explored

Supporting Information:

Supporting Information may be found in the online version of this article.

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Breaking the Ecosystem Balance Over the Tibetan Plateau

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Abstract Ecosystem imbalance is often associated with a feedback mechanism, which a self-amplifying or -dampening process expressed by a pathway of causal processes that come back to its starting point, establishing a cycle. Warming, which is increasing worldwide due to human activities, influences the structure and functioning of ecosystems, has threatened sustainable regional and global development, especially over the mountain regions. This is because, the climatic condition rapidly changes along elevation gradients, which may amplify or mitigate the effects of climate on ecosystems. Based on it, a reference system and standardized techniques are extremely important to understand the ecosystem imbalance. Because of terrestrial oxygen production (TOP), which is the terrestrial biosphere continually absorbs CO_2 and releases O_2 resulting through vegetation photosynthesis, is closely related to the exchange of energy, carbon and other ecosystem factors between the atmosphere and the land. Therefore, whether TOP significantly increases indicate that accelerate in ecosystem imbalance over the Tibetan Plateau (TP) is largely unknown. To do so, integrated with characteristics and drivers of TOP, we investigated how TOP changes respond to ecosystem imbalance over the TP. These changes are influenced by related to climatic conditions, plant productivity, soil fertility, and microbial stability, which can establish a positive feedback loop that standardized direct effect is 0.99, 0.73, 0.75, and 0.75. Our findings suggest that ecosystem imbalance will accelerate with rapid TOP increase over the TP by ∼2,100. This study confirms the importance of the ecosystem imbalance under global warming in the future.

Plain Language Summary Ecosystem is no longer at balance, which refers to a state in natural/semi-natural ecosystems cannot maintain its stability under external stress. Human disturbances have knocked the Earth away from a steady state, which are broken by periods of transience. We consider that the concept of imbalance in ecosystem is useful and should be embraced, owing to human activities are transforming the world so profoundly, such as anthropogenic global climate warming. In the Anthropocene, alpine ecosystems tend to be fragile and sensitive to anthropogenic climate warming, especially over cold-high latitudes regions, such as the Tibetan Plateau (TP) ("third pole" of the world). Conclusions that are derived from researches in non-mountainous regions are not suitable for forecasting the effects of climate changes on alpine mountains, mainly due to the climatic condition rapidly changes with elevation, which may amplify or mitigate the effects of warming. Herein, we evaluated whether increasing terrestrial oxygen production (TOP) responses to ecosystem imbalance are the standard rather than the aberration and if these changes are driven by the existence of one or multiple attributes over the TP. Our results point to that ecosystem imbalance will accelerate with rapid TOP increase over the TP by ∼2,100.

1. Introduction

Regional ecosystems can be affected by global warming and, conversely, can themselves drive the effects of another distant ecosystems, such as the Tibetan Plateau (TP), "third pole" of the world (T. Wang et al., 2021). The TP, where annual average rainfall is <450 mm, cover ∼60% of alpine grassland and is one of the most sensitive to climate change and soil degradation (Jiao et al., 2021). Increasing terrestrial oxygen production (TOP), as a proxy of vegetation growth, driven mainly by net primary productivity (NPP) (Huang, Yu, et al., 2020), is a major indicator of anthropogenic climate warming in drylands (Han et al., 2021; Huang et al., 2016; Huang, Zhang, et al., 2020), and links to the multiple ecosystem attributes (C. Li et al., 2021; Liu et al., 2020; Wei et al., 2021). However, it remains to be elucidated whether these changes in state indicate that the ecosystem imbalance.

The NPP is the net amount of carbon dioxide (CO_2) captured by vegetation through photosynthesis in an ecosystem over a given period (Potter et al., 1999), affecting energy budget, plant productivity, carbon cycle, hydrological cycle, biodiversity, and ecosystem service provision (Crabtree et al., 2009; Haberl et al., 2007; S. L. Piao et al., 2020). Thus, a slight change in NPP could have a major impact on ecosystem balance, especially with respect to the temporal and spatial variations in NPP and its interaction with environmental factors (Dirnböck et al., 2003; Scurlock et al., 2002; Xu et al., 2016). Meanwhile, the vast majority of NPP in the biosphere is derived by the Calvin-cycle (Calvin, 1956) in plants. The Calvin-cycle (carbon reaction) provides *ADP* and *Pi* to the light reaction (oxygenation rates of *Rubisco*) in photosynthesis. Hence, the carbon (carbon fixation-NPP) and light (O_2 continuous production process) reactions of photosynthesis are tightly coupled. These information showed that under the global warming, increasing TOP, as a proxy of vegetation growth, is affected primarily by NPP. The NPP is the driving force, in the context of ecosystem balance, and TOP is the result. Therefore, TOP is closely related to ecosystem balance.

Breaking the ecosystem balance (ecosystem imbalance) is associated with a positive feedback mechanism, which a self-amplifying process expressed by a pathway of causal processes that get back to its starting point, forming a cycle (Rocha et al., 2018). For instance, recent research has shown permafrost degradation induce soil C loss in TP, which is more affected by warming, and potentially reduces the stability of active layer microbial communities (Wu et al., 2021). The soil C loss is not only an essentially nonrenewable phenomenon on human time scales, but also the biggest contributor to variability of terrestrial C dioxide emissions, these processes lead to a positive feedback cycle with the warming reinforcing (Guan et al., 2019; Huang, Li, et al., 2017; Huang, Yu, et al., 2017). Whether increasing TOP responses to ecosystem imbalance are the standard rather than the aberration and if these changes are driven by the existence of one or multiple attributes remain poorly understand.

Ecosystem attributes, which relate to the abiotic and biotic characteristics of an ecosystem (e.g., composition, species, size, and so on), are strongly interactional (Wu & Li, 2019). Variations in a given attribute induced by increases in warming may trigger sequential changes in others (Berdugo et al., 2020), it is likely that largely alters ecosystem functions and processes to mountain ecosystems, owing to the environments rapidly change along elevation gradients (Peters et al., 2019). Ecosystem functions, which refer to the individual components connected with different ecosystem processes such as plant, soil and organisms, are the multiple processes conducted by ecosystems (Boudell, 2016). If these interactional changes are development process, then this could potentially lead to a series of imbalance phases influencing multiple ecosystem attributes in the future. For example, increasing warming may cause a rapid change in vegetation growth such as enhance vegetation photosynthesis, which in turn may trigger shifts in soil-microbial interactions that later result in changes in C cycling (Jansson & Hofmockel, 2020).

Comprehending whether the interacted responses of multiple ecosystem attributes to some accelerate each other away from a stable state, creating a positive feedback to climate warming, or if they are expressed by one or multiple sequential attributes that amplify them is important for improving predictions of ecosystem imbalance responses to climate warming. Therefore, this information is also essential to depict sensitivities and vulnerabilities in TP, which has the largest extent of high-elevation mountain permafrost in global areas that includes 1.06×10^6 km^2 and stores approximately 74% of the soil C (Wu et al., 2021). TP permafrost is experiencing temperature rising at a level that is about double the global mean (He et al., 2021), with active layer thickness and average annual soil temperatures increasing significantly since the mid-1950s, resulting in a decrease in alpine permafrost of ∼23.8% (Wu et al., 2021). TP permafrost warming may induce soil C loss, critical for regional/global C cycling, and be mediated by microbes, and associated with potentially a positive C feedback (Wu et al., 2021).

Here, we evaluated whether multiple ecosystem factors exhibit linear or non-linear responses to increases in TOP along elevational gradients and if these changes are driven by the existence of single or multiple attributes over the TP. To do so, we collected the 44 ecosystem factors, including 14 climatic, 8 plant, 12 soil, and 10 soil microbial indicators, at 30 study sites, along an approximately 2,200 km alpine grasslands that cover all the major natural ecosystems found on an elevational gradient that increases from 3,112 to 4,764 m above sea level over the TP (Tables S1 and S2 in Supporting Information S1). These indicators are highly associated with the ability of TP to provide vital ecosystem services. Ecosystem services are defined as the direct and/or indirect contributions of in natural/semi-natural ecosystems to human well-being (Portman & Elhanan, 2016). Accordingly, the ecosystem biological, chemical, and physical studies and local examples are important for changing in TOP process development in sensitive regions.

The major process in the TOP is manifested in many spheres, such as abiotic and biotic processes, in the Earth's system. TOP, for example, is a biological process that absorbs energy from sunlight to synthesize oxygen and

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carbohydrate molecules from carbon dioxide and water. This process seems simple, but it is closely associated with other essential processes in the thermal cycle (e.g., temperature variations), hydrological cycle (e.g., water storage), and biogeochemical cycle (e.g., carbon fixation) (Huang et al., 2021). Therefore, many studies suggested an origin of TOP was close in time to "Great Oxidation Event" and the rise of atmospheric oxygen was directly driven by the evolution of terrestrial ecosystem (Huang et al., 2021; Soo et al., 2017). Based on this, we also analyzed variables related to climatic-TOP interconnects, plant-TOP interconnects, soil-TOP interconnects, and microbial-TOP interconnects, as well as climatic- plant- soil- and microbial indicator interconnects.

2. Material and Methods

2.1. Plant, Soil, and Microbial Indicators Data Set

We collected 30 sites data set, including 12 meadow sites and 18 steppe sites (Tables S1 and S2 in Supporting Information S1, $n = 30$), along the elevational gradient during the growing seasons between early July and early September in 2013 and 2014 (L. Chen et al., 2019). Field sampling was established five 1×1 m quadrats at the center and the corners of a 10×10 m plot (L. Chen et al., 2019). First, the mean coverage for each species, including grass, forb, and sedge, was estimated at each quadrat; subsequently, the aboveground NPP was obtained by clipping the above-ground plants at ground level; finally, soil samples in a depth of 10 cm from three quadrats, which along a diagonal line in the 10×10 m plot, were mixed as one composite sample for subsequent analyses (L. Chen et al., 2019). These sites were covering a wide range of plant properties (e.g., NPP, 38–488 g m^{-2} yr^{-1}), soil properties (e.g., SOC, 1.1–118 g kg^{-1}), and microbial properties (e.g., TPLFA, 6.83–82.37 nmol g^{-1}) across the plateau. Notably, the principal considerations for selecting the sampling sites were based on climate gradient, owing to climate change induced regional variations in plant properties and soil properties across this study area, thereby further determined the dynamic of soil microbial properties (L. Chen et al., 2019). Except for TC (SOC plus SIC (Yu et al., 2014)), ST10 (from the "climatic indicators data set"), R_s (according to $R_s = \alpha \times e^{\beta \times T}$, where R_s is soil respiration, T is soil temperature at 10 cm depth, along α and β are regression coefficients (B. Chen et al., 2010)), as well as C/N is the TC:TN, residual plant- soil- and microbial data set further details of conditions and measurement set-up are available from previous publication (L. Chen et al., 2019). See Figure 1 for abbreviations.

2.2. Climatic Indicators Data Set

We selected climatic indicators data set consistent with the locations where plant, soil and microbial indicators occurred during 2013–2014, with $n = 30$ study sites. The global land data assimilation system (GLDAS) uses satellite- and ground-based observational data products, which use land surface modeling and data assimilation to generate the fields of land surface states and fluxes (Rodell et al., 2004). All the variables used from the data set of GLDAS 2.1 Land Information System land surface model monthly mean output (available at https://ldas.gsfc.nasa.gov/data). The land surface model was Noah version 3.3.

The input meteorology forcings were from the National Centers for Environmental Prediction, Global Data Assimilation System, National Aeronautics and Space Administration (NASA), Goddard EOS Data Assimilation System (GEOS), the European Centre for Medium Range Weather Forecasting, and the Princeton Global Meteorological Forcing Data Set. The input mean rain rate was determined from disaggregated Climate Prediction Center (CPC) merged analysis of precipitation (CMAP) data, the Global Precipitation Climatology Project, the National Oceanic and Atmospheric Administration/CPC MORPHing technique (CMORPH) for precipitation, NASA/Goddard Space Flight Center (GSFC), Tropical Rainfall Measuring Mission (TRMM) 3B42 (V7) precipitation data, NASA/GSFC TRMM 3B42RT Realtime Huffman precipitation data, Naval Research Laboratory precipitation data and PERSIANN precipitation data. The input shortwave and longwave data were from the Air Force Weather Agency radiation data. In this study, all the GLDAS data were used at a $1.0° \times 1.0°$ resolution. We calculated the annual means of the data and used them as the meteorology and land surface indicators. Figure 1 shows the indicators of 44 ecosystem factors, including 14 climatic, 8 plant, 12 soil, and 10 microbial indicators as well as their acronyms, extended names, and significant changes in elevations.

2.3. Model Simulation

To account for changes in TOP under future warming scenarios, we estimated the terrestrial NPP, NEP, and R_h by the end of the twenty-first century using recent Intergovernmental Panel on Climate Change (IPCC) climate

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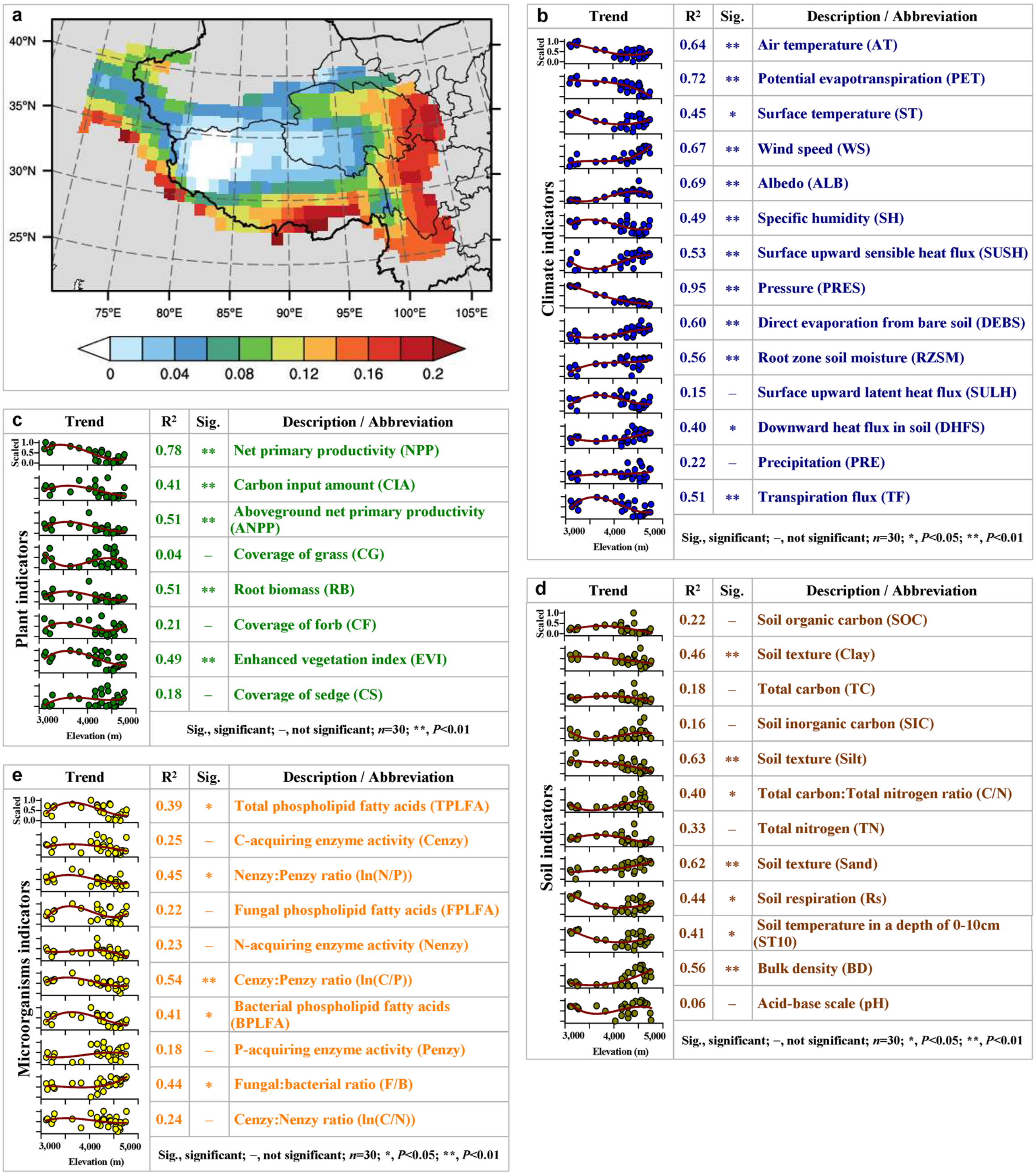

Figure 1. Changes in ecosystem factors with elevation. (a) Spatial pattern of the TOP flux across the Tibetan Plateau over 1990–2005 (historical) on average (kg m^{-2}) based on nine CMIP5 models. Trends in (b) observed-climatic, (c) plant, (d) soil, and (e) microbial indicators along the elevational gradients occurred during 2013–2014. TOP, terrestrial oxygen production; CMIP5, fifth coupled model intercomparison project.

projections (CMIP5). The ensemble means of the CMIP5 models address the uncertainty in inter-model variability and provide better predictions than any individual model. Thus, the nine CMIP5 models (Table S3 in Supporting Information S1) were selected because of the criterion that they provide terrestrial NPP, NEP, and R_h (Huang et al., 2018). Based on the CMIP5 historical simulations end in 2005, we extended them to 2099 by splicing them with the corresponding RCP4.5 and RCP8.5 scenarios (Marvel et al., 2019). As a result, TOP and respiration can be expressed as:

$$6H_2O + 6CO_2 \rightarrow C_6H_{12}O_6 + 6O_2 \quad (1)$$

where $C_6H_{12}O_6$ is the approximate composition of terrestrial organic matter. The net ecosystem productivity refers to the amount of NPP remaining after including the consumption of R_h. Thus, we further calculated the net amount of TOP flux based on the following linear regression:

$$\text{TOP} = ((\text{NPP} - \text{R}_\text{h}) = \text{NEP}) \times 2.667 \tag{2}$$

because the molar mass of oxygen is 32 g per mole and that of carbon is 12 g per mole, the ratio is 2.667. NPP, net primary productivity; NEP, net ecosystem productivity; and R_h, soil heterotrophic respiration. The TOP content (1 Gt = 10^{15} g) was calculated according to the area-weighted sum of oxygen production flux (kg m^{-2}; 1 kg = 10^3 g). Further details of these methods for oxygen analyses have previously been published (Huang et al., 2018).

2.4. Statistical Analysis

Before doing all the statistical analysis, all data was tested for min-max normalized (actual value (y_i) − minimum (y))/(maximum (y) − minimum (y)). Simple regression analysis, Pearson correlation, and Independent-samples t test were used to reveal the relationships between ecosystems factors and elevations, as well as test the effects of elevation gradients and land cover changes on climatic, plant, soil, and microbial properties. Given the strong inter-correlations and connections among the various factors, Pearson correlation matrix, which was performed with R statistical software v.3.6.1 (R Development Core Team, 2016), was first conducted to evaluate the relationships (Peters et al., 2019) between the TOP and the ecosystem factors. Other statistical analyses were performed using SPSS the 17.0 statistical software package for Windows (SPSS, Inc., Chicago, IL, USA) with the significance level at $P = 0.05$.

Before performing the structural equation modeling (SEM), we first standardized each variable using the min-max normalized. Then, established the a priori model based on our prior knowledge of the direct and indirect effects (J. Li et al., 2020) of 14 climatic, 8 plant, 12 soil, and 10 microbial indicators on TOP, respectively. Finally, we selected a final model based on an overall goodness-of-fit (Eldridge et al., 2018), including the Chi-square (χ^2)/degree of freedom (df), root mean square error of approximation, root mean square residual, comparative fit index, goodness of fit index, and normed fit index. The standardized total effect was calculated according to direct plus indirect effects (J. Li et al., 2020). SEM has emerged as a synthesis of factor analysis along with path analysis and widely used in ecological studies as a causal inference tool (J. Li et al., 2020; Z. Li et al., 2022). The SEM analyses were performed using the AMOS 17.0 (IBM., Chicago, IL, USA).

3. Results

3.1. Characteristic Analysis of TOP

3.1.1. Spatial Patterns

Over the TP ecosystem, the regional patterns of TOP in a spatially explicit fashion (Figure 1a). TOP showed an increase from the northwestern to southeastern part, corresponding well to the land cover changes, which from alpine steppe to alpine meadow (Yang et al., 2009), across the plateau. The change in TOP in alpine steppe could be explained by plant attributes (e.g., biomass), much lower than that in alpine meadow (Figure 2b). These differences are primarily driven by the growth-limiting factors (e.g., temperature and humidity as major climatic conditions). Most plant attributes significantly increased with an increase in humidity (e.g., TF, positive correlations) and a decrease in temperature (e.g., ALB, negative correlations) (Figure 2a), due to higher wet conditions can result in a higher plant production and density (Epstein et al., 1997). Additionally, compared with alpine steppe, increased humidity can lead to more accumulated in SOC (as a key determinant of soil fertility) in alpine meadow, shift in bacterial compositions (Jansson & Hofmockel, 2020) and increase in fungal abundance (Figures 2c–2f), ultimately affecting vegetation photosynthesis and TOP capacity.

3.1.2. Elevational Gradients

Changing climatic conditions with elevation shape the natural plant-, soil- and microbial-mediated functions peaked at sub-montane (middle elevations), which affecting changes in TOP (Figures 1–3), are consistent with that observed in ecosystem factor changes on Africa's largest mountain by Peters et al. (2019). In other words, the ecosystem attributes evaluated responded in a non-linear manner to the elevation gradient. Under global anthropogenic warming (outer cycle, external temperature transport), once a warming level was reached over the

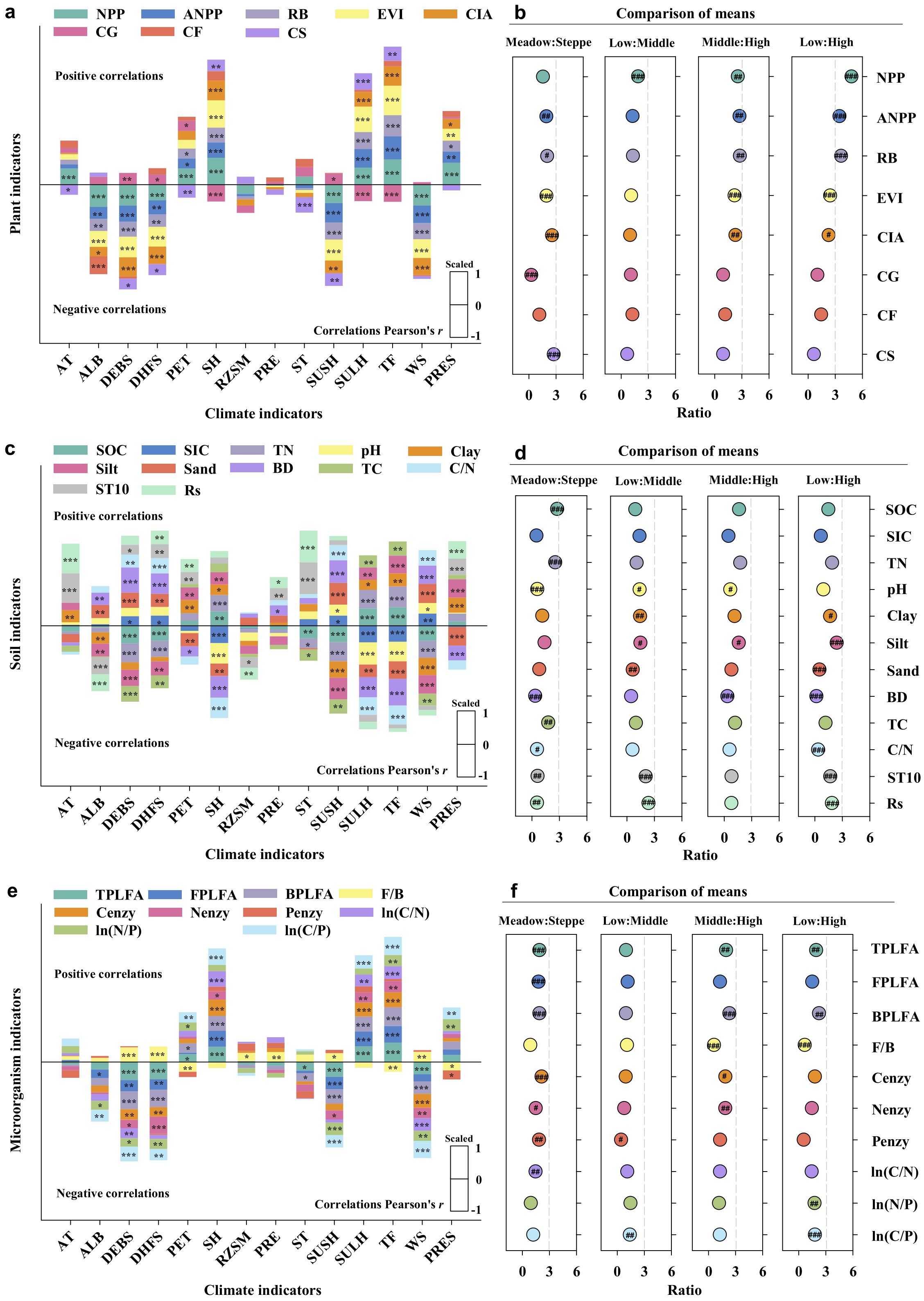
a
NPP ANPP RB EVI CIA CG CF CS
Positive correlations
Negative correlations
Plant indicators
Scaled 1 0 -1
Correlations Pearson's r
AT ALB DEBS DHFS PET SH RZSM PRE ST SUSH SULH TF WS PRES
Climate indicators
b
Comparison of means
Meadow:Steppe Low:Middle Middle:High Low:High
NPP ANPP RB EVI CIA CG CF CS
Ratio
c
SOC SIC TN pH Clay Silt Sand BD TC C/N ST10 Rs
Soil indicators
d
SOC SIC TN pH Clay Silt Sand BD TC C/N ST10 Rs
e
TPLFA FPLFA BPLFA F/B Cenzy Nenzy Penzy ln(C/N) ln(N/P) ln(C/P)
Microorganism indicators
f
TPLFA FPLFA BPLFA F/B Cenzy Nenzy Penzy ln(C/N) ln(N/P) ln(C/P)

Figure 2.

TP, small enhances in warming resulted in drastic variances in the value of the attribute or modified its relationship with warming (Berdugo et al., 2020), consequently accelerate the breaking of TOP stability (an irreversible state). In the TP ecosystem, TOP is projected to increase greatly (Figure 6), this is consistent with the previous results showing the positive effects of climate change, mainly from anthropogenic warmer temperature, driving the vegetation greening in the TP (S. L. Piao et al., 2020; Zhu et al., 2016). TOP plays a crucial indicator role in the ecosystem imbalance, is closely linked to the vegetation greening. Therefore, it is important further to understanding the changes in TOP under future global warming in this fragile ecosystem.

3.1.3. Model Projections

According to the mean of nine CMIP5 models, compared with during the historical period of 1990–2005, the TOP flux was projected to increase by ∼0.01 kg m^{-2} under RCP4.5 and by ∼0.04 kg m^{-2} under RCP8.5 during 2006–2099, respectively (Figures 6a and 6b). Additionally, the TOP content increased significantly ($P < 0.001$) among historical, RCP4.5 and RCP8.5 from an independent samples *t* test (Figure 6c). The highest TOP contents were all found in RCP8.5 scenario per year (Figure 6d), indicating that the high global warming scenario plays a dominant driving role in TOP. Previous results also confirmed that over the global semi-arid areas, the warming of 1.53°C during the boreal cold season from 1901 to 2009 exceeded that for the average annual temperature increase of 1.13°C (Huang et al., 2012; Huang, Li, et al., 2017). Models project that addition warming of over 2°C under RCP4.5 and 4°C under RCP8.5 in drylands by ∼2,100, respectively (Huang, Li, et al., 2017). These changes in temperature may alter the TOP content was higher under RCP8.5 than under RCP4.5 (Han et al., 2021), for example, through enhancing the atmospheric C dioxide concentration and extending the vegetation growing season (S. L. Piao et al., 2020).

3.2. Driving Mechanism of TOP

3.2.1. Climatic-TOP Interconnects

Changing climatic indicators along the natural elevation gradient shape the natural vegetation zones on the TP, affecting terrestrial NPP (Gao et al., 2019) associated TOP variability. Here, we showed that TF had the greatest positive effect, followed by PET, RZSM, and SH, as indicated by the standardized total effects (direct plus indirect effects) in predicting the TOP content. However, ALB had the highest predictive negative power, followed by DHFS, ST, and PRE, in predicting the TOP content over the TP (Figures 3d and 3e).

3.2.2. Plant-TOP Interconnects

Land cover (alpine steppe and alpine meadow) change exerts a considerable but extremely spatially variable affect TOP changes. An SEM was conducted in alpine grassland, indicating that EVI had the strongest total positive effect, followed by CIA, CG, CF, and ANPP, in predicting the TOP (Figures 3a and 3e). This TOP is closely related to a statistically significant increase in annual oxygen releases flux/content at a location resulting, for example, from increases in average vegetation greenness, plant density, species composition, and biomass number per plant because changes in the global anthropogenic warming.

3.2.3. Soil-TOP Interconnects

SOC, which as a major C pools of soils, is driven by vegetation greening due to the rate of plant-C input directly affects the amount of SOC. In turn, SOC can mediate soil physicochemical processes (e.g., soil bulk density and acid-base scale), which determine soil BD and pH levels, thus regulating the vegetation growth and TOP content (Figure 3c). Our results revealed that SOC had the largest total positive effect, followed by SIC, and R_s, in predicting the TOP; in contrast, BD had the largest total negative effect, followed by pH, and C/N (Figure 3e).

3.2.4. Microbial-TOP Interconnects

Soil microbial communities, which govern biogeochemical cycling of elements crucial for the growth of plant, are intimately related to plant biomass, community and type, can regulate the plant photosynthesis through their activity increases (Jansson & Hofmockel, 2020). Of the microbial factors analyzed in this study, Cenzy had the

Figure 2. The response of ecosystem factors to climatic conditions, land cover, and elevation. (a, c, and e) Show that relationships between climatic indicators and plant, soil, and microbial indicators, respectively. *0.05 < P < 0.1, **P < 0.05, and ***P < 0.01. The statistical sample size is $n = 30$ study sites. Correspondingly, in panels (b, d, and f), independent-samples *t* test indicate that comparison of the ratio values between alpine meadow ("meadow," $n = 12$) and alpine steppe ("steppe," $n = 18$), as well as in different elevation zones, including relatively low-montane ("Low," 3112–3650 m a.s.l, $n = 6$), sub-montane ("Middle," 3830–4390 m a.s.l, $n = 10$), and montane ("High," 4417–4764 m a.s.l, $n = 14$). #0.05 < *Sig.* < 0.1, ##*Sig.* < 0.05, and ###*Sig.* < 0.01. See Figure 1 for ecosystem factors abbreviations.

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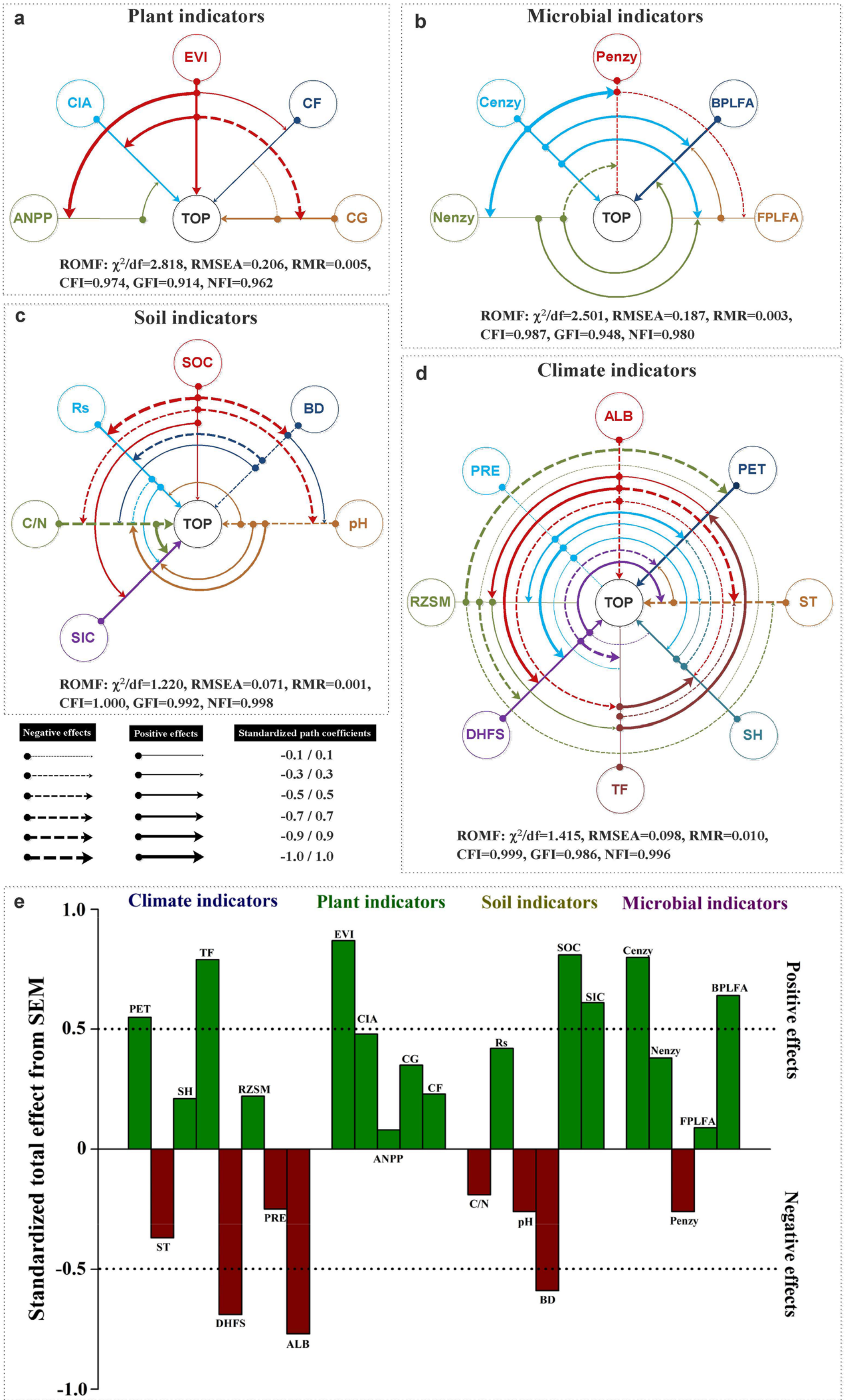

Figure 3.

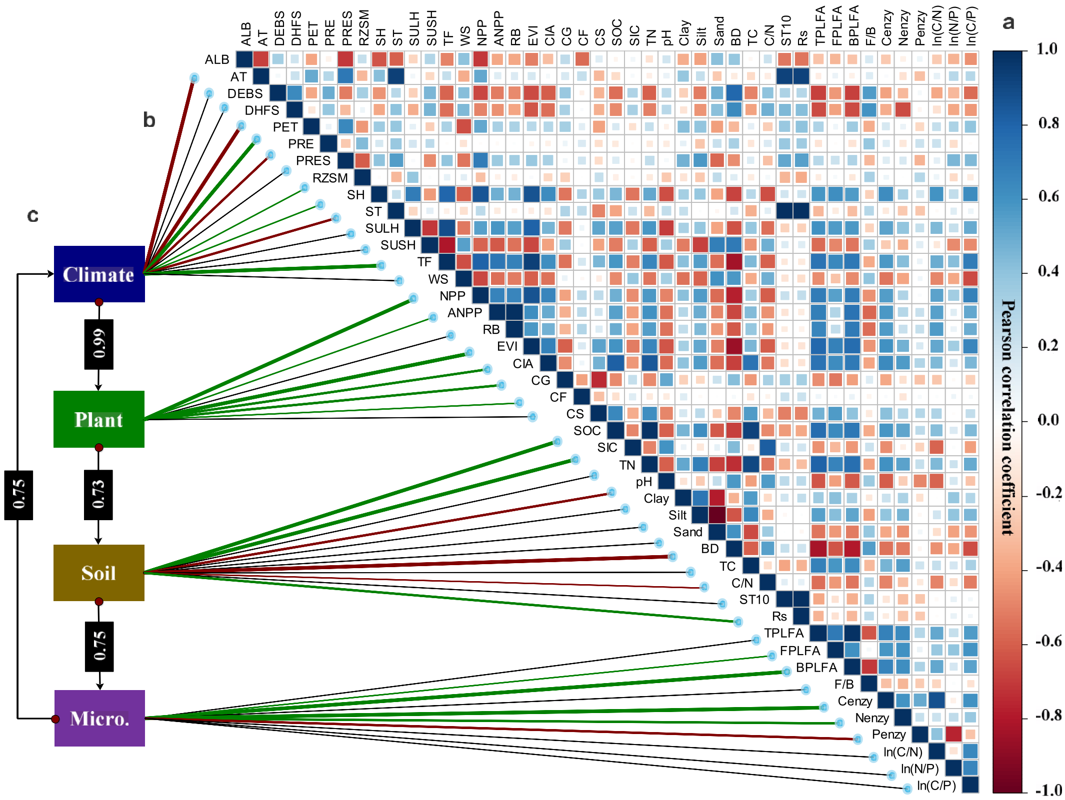

Figure 4. Terrestrial oxygen production (TOP) responses to ecosystem factors. (a) Right, a visualization of a Pearson correlation matrix of 44 ecosystem factors. (b) Middle, structural equation modeling (SEM) analysis of the ecosystem factors-TOP interconnects. Line strength is plotted as a standardized total effect on TOP per ecosystem factor (strong effect = thick lines). The total effect per ecosystem factor is denoted in dark red (negative) or dark green (positive). (c) Left, the SEM describing a positive feedback loop for the four observable variables under the strong effect on TOP. ROMF: χ^2/df = 4.257, RMSEA = 0.275, RMR = 0.002, CFI = 0.982, GFI = 0.922, and NFI = 0.977. Square boxes denote variables included in the model. Values associated with solid arrows represent standardized path coefficients, which reflect the effect size of the relationship. See Figure 1 for ecosystem factors abbreviations.

strongest total positive effect, followed by BPLFA, Nenzy, and FPLFA, in predicting the TOP, whereas Penzy only occurred in the negative effect (Figures 3b and 3e).

Together, these divers evoke a positive feedback loop that aggravate TOP capacity (Figure 4). The *Pearson* correlation matrix of ecosystem factors showed that ecosystem indicators are strongly interconnects (Figure 4a), this result was consistent with the reports of Berdugo et al. (2020) for global ecosystem responses to aridity and that of Jansson and Hofmockel (2020) for soil microbiomes and climate change. Figure 4b indicated that SEMs in different ecosystem factors were conducted for TOP. Aggregately, climatic, plant, soil, and microbial factors are the main driver of TOP, can establish a positive feedback loop, which the standardized direct effect is 0.99, 0.73, 0.75, and 0.75, respectively, in this region (Figure 4c).

4. Discussion

4.1. TOP Changes

We explored the spatial patterns of the multiyear averaged TOP values over the TP during 1990–2005 (Figure 1a), indicating spatially highly heterogeneous TOP changes, because different vegetation sensitivities to climatic

Figure 3. Positive, negative, and total sum of effects on terrestrial oxygen production (TOP) provided by the SEMs. Standardized positive (solid circles associated with solid arrows) and negative (solid circles associated with dashed arrows) of effects of (a) plant, (b) microbial, (c) soil, and (d) climatic on TOP, as derived from the SEM, respectively. The standardized total effects (direct plus indirect) in panel (e). SEM, structural equation modeling; ROMF, results of the optimal model fitting; χ^2/df, chi-square/degree of freedom; RMSEA, root mean square error of approximation; RMR, root mean square residual; CFI, comparative fit index; GFI, goodness of fit index; and NFI, normed fit index. See Figure 1 for ecosystem factors abbreviations.

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conditions and nutrient availability along the elevational gradients (Figures 1b–1e and 2), might play various roles across different regions. For instance, in clod regions, vegetation activity is mostly limited by low temperature (Menzel et al., 2006), and decreased vegetation growth along increasing elevation gradient is therefore probably associated with the cooler temperature at higher elevations (Gao et al., 2019). Meanwhile, many studies refer to homogenized vegetation activities (e.g., autumn leaf senescence and spring leaf unfolding) changes were based on the results of raised warming rate at higher natural elevations (Pepin et al., 2015) and the assumption of the key role of temperature in driving vegetation activities (S. Piao et al., 2007). Thus, vegetation growth link to TOP changes can be more sensitive to climate warming at higher elevations (Tao et al., 2015). In the tropics, elevation-temperature relationship may not be such a main limiting factor for vegetation greening (Gao et al., 2019). Instead, human activities play an important role in driving vegetation greening, such as agricultural intensification (S. L. Piao et al., 2020), affecting soil fertility and TOP capacity (positive feedback to climate warming), especially in developing countries (Han et al., 2021). Therefore, anthropogenic climate changes, for example, have played vital roles in driving the elevational gradients of TOP and their changes (Han et al., 2021).

Additionally, we forecast the temporal trends of the TOP based on ensemble mean of nine CMIP5 models under the high (RCP8.5) and moderate (RCP4.5) emission scenarios for the future period of 2006–2099 (Figure 6). The results showed that TOP for the two scenarios in all TP regions indicate a significant increasing trend at the end of the 21st century, especially under the RCP8.5. We found the temporal patterns of the TOP representing vegetation growth, as well as indicated a clear geographical pattern over the TP regions. Embedded elevational temperature control the elevational changes of TOP suggested that temperature is the key driver shaping the elevation-vegetation relationship, along highlights the significance of understanding TOP and their dominant drivers in the spatial context. Mountainous regions harbor the most diverse terrestrial ecosystems and provide essential ecosystem services (Gao et al., 2019), such as the exchange of energy, carbon, water, and so on between the atmosphere and the land (Viviroli et al., 2007). These exchange factors that determine the elevation-vegetation relationship, as well as their recent changes, are highly heterogeneous across the TP surface. Such heterogeneities possibly support the greatly variable responses of the elevation-vegetation relationship to recent anthropogenic climate changes.

4.2. Drivers of TOP

Several ecosystem factors are thought to effect on TOP, including climatic conditions, land cover changes, soil fertility, and soil microbial activity (Figure 5). However, non-linear effects and interactions make it challenging to quantify the single contribution of these ecosystem factors to revealed TOP change. We discuss the contribution of several dominant drivers of TOP to quantitatively attribute the studied TOP change in each of these ecosystem factors.

4.2.1. Climatic Conditions

Although changes in TOP depending on many factors, climatic conditions changes, such as temperature and humidity, are the main driver of TOP changes (Figures 2 and 3), which exert significantly impacts on the increasing NPP (Huang et al., 2018). For example, warming increases vegetation photosynthesis by accelerating the rate of carboxylation (S. L. Piao et al., 2020) in the boreal and Arctic regions (Keenan & Riley, 2018) through extending the growing season (S. Piao et al., 2007) and enhancing metabolism (Braswell et al., 1997). Likewise, dynamic global vegetation models' forecasts show that the significantly effects of climate change, mainly from warmer temperature (Lucht et al., 2002), control the greening trend over approximately 55% of the northern high latitudes (S. L. Piao et al., 2020) and in the TP (Zhu et al., 2016). Earlier spring vegetation greening-induced deficit of summer soil moisture, and subsequently aggravate soil disruption (Lian et al., 2020), suggesting a possible unsustainable development of future greening in response to warmer temperature. In water-limited ecosystems, shifts in humidity-reflecting either climate variability or tends from climate warming-were suggested as the vital driving of greening and TOP (Han et al., 2021), such as parts of Australia and African (S. L. Piao et al., 2020).

4.2.2. Land Cover Changes

Land cover change provides a considerable yet highly spatially variable impact on TOP changes over the TP regions (Figures 1a and 6). As the largest source of atmospheric oxygen (e.g., Amazon rain forest), the terrestrial vegetation continually absorbs CO_2 and emits O_2 into the atmosphere through vegetation photosynthesis, thereby maintaining the atmospheric O_2 at a safe level. Previous studies have already showed that vegetation

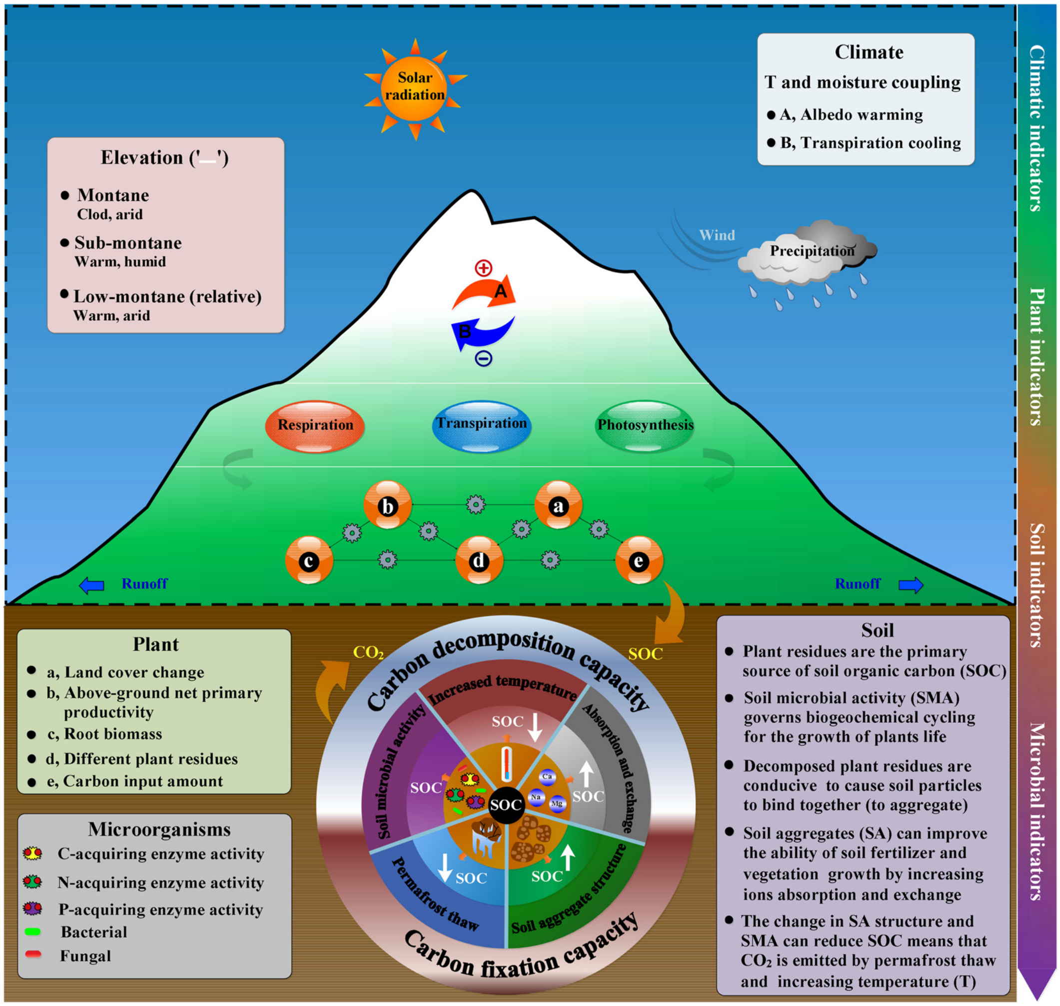

Figure 5. A conceptual framework to explain how the responses of terrestrial oxygen production (TOP) to the ecosystem imbalance over the Tibetan Plateau. Several ecosystem factors are thought to effect on TOP, including climatic conditions, land cover changes, soil fertility, and soil microbial attributes. However, non-linear effects and interactions make it challenging to quantify the single contribution of these ecosystem factors to revealed TOP change. We discuss the contribution of several dominant drivers of TOP to quantitatively attribute the studied TOP change in each of these ecosystem factors. Notably, this conceptual diagram mainly focused on the most important path analysis derived from the structural equation modeling analysis.

activity change ∼19% of the northern temperate vegetation (25–50°N) are mainly driven by land cover change (S. L. Piao et al., 2020; Zhu et al., 2016). This vegetation growth-induced evapotranspiration increase enhances atmospheric water vapor concentration, which, in turn, improves downwind precipitation (S. L. Piao et al., 2020; Teuling et al., 2017). These findings could partially explain nearly the changes of precipitation over the TP, which a northwest (steppe) to southeast (meadow) precipitation gradient ranging from 84 to 593 mm per year (L. Chen et al., 2019). Thus, by controlling the changes in evapotranspiration, land cover change also alters the water distribution between areas and water pools, can either amplify or mitigate runoff regionally through affecting the pattern of precipitation (S. L. Piao et al., 2020). Notably, land cover changes associated with precipitation gradient induced regional variations in soil properties such as SOC (Lugato et al., 2021) and microbial activities such as Cenzy (L. Chen et al., 2019) across the TP, which further controlled the pattern of TOP (Han et al., 2021).

4.2.3. Soil Fertility

Soil fertility is associated with "*provides yield*" (Berdugo et al., 2020). SOC, as the basis of soil fertility and the dominant source of energy for soil microbial activity, plays a key role for vegetation growth and photosynthesis, has been found to change progressively with nutrient availability, is controlled by the balance between C inputs

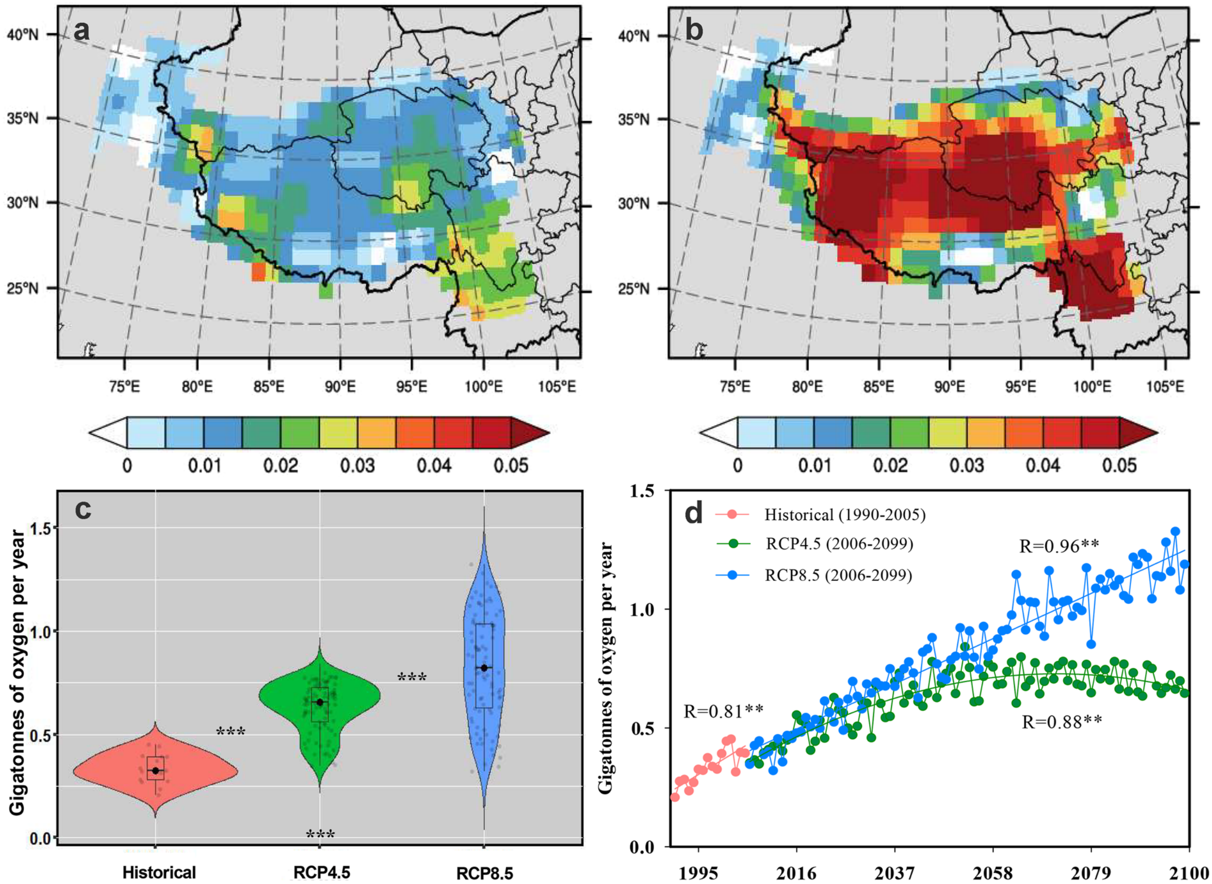

Figure 6. Temporal characteristics of terrestrial oxygen production (TOP) flux based on ensemble mean of nine CMIP5 models. (a, b) show that trend in the TOP flux (kg m^{-2} 15 yr^{-1}) under the RCP4.5 and RCP8.5 scenarios from 2006 to 2099, respectively. In panel (c), the *x*-axis shows historical (1990–2005), RCP4.5 (2006–2099), and RCP8.5 (2006–2099). The *y*-axis shows the comparison among the historical (pink), RCP4.5 (green), and RCP8.5 (blue) TOP content (Gt). ***indicate that the significant difference at $P < 0.001$ from an independent samples *t* test. The violin plot shows the distribution of the data. The top and bottom of each box represent the 75% and 25% quantiles. The point inside and the line outside each box represent the median and 95% confidence interval. (d) Changes in the TOP content as years under different warming scenarios. $^{**}P < 0.01$.

from plants and C outputs via microbial decomposition (Berdugo et al., 2020; Han et al., 2021). In contrast, soil degradation, owing to soil thermal regime and instability, which particularly over sensitive permafrost regions at high altitudes and latitudes store approximately 50% of the world's SOC (C. C. Mu et al., 2020), will emit more CO_2 into the atmosphere and reduce the SOC storage (C. Mu et al., 2016). SOC decreases as soil BD and pH increases, due to the decrease in soil aggregate stability and soil porosity (Jílková et al., 2021). A weakening soil aggregates combined with the changes in the sources of Ca^{2+}, Mg^{2+}, and Na^{+}, can induce a weakening SOC protection to against biodegradation (L. Chen et al., 2019). Much of the TP regions contain most of the Earth's alpine permafrost, which have a large easily decomposable (labile) fraction of SOC, accounting for ~50% of the total SOC in a depth of 10 cm soil layers (C. C. Mu et al., 2020). Therefore, permafrost regions are much extremely sensitive and vulnerable to enhanced warming than soils of non-permafrost regions (C. C. Mu et al., 2020). The increasing greenness phenomenon may as an indicator of major and persistent changes in the soil degradation; on the other side, affecting the long-term sustainability of TOP in the future. For example, spring-vegetation greening-enhanced evaporation from surfaces and transpiration by plants results in a reduction in soil moisture associated with destroy the soil aggregates, which increases the risk of heatwaves (S. L. Piao et al., 2020).

4.2.4. Soil Microbial Activities

Soil microbial activities are highly responsible for cycling of SOC and other nutrients, have an important role in climate feedback, including consumption or production of greenhouse gases such as CO_2. In turn, climate constrains soil microbial activities to determine the consequences of soil processes that cycle SOC and other nutrients (Jansson & Hofmockel, 2020). Warming can lead to an increase in SOC below ground because increases in plant production, with corresponding shifts in soil microbial community composition and increases in microbial biomass; however, SOC may decompose at a faster rate than it is fixated (Jansson & Hofmockel, 2020). Partly due to N and P availability strongly affects C cycling in soil ecosystems (Luo et al., 2020). These nutrients enhancement can increase C inputs into through increased above- and below-ground biomass, but at the same time can accelerate SOC decomposition (Luo et al., 2020). Nutrient enhancement increased control of fast-growing bacteria, while P enhancement alone intensified the competitive interactions between saprotrophic fungi and arbuscular mycorrhizal (Luo et al., 2020). Above changes resulted in decreases in the microbial C use efficiency of vanillin by 8.5% and of glucose by 1.6%–3.5%, and therefore, reduced SOC in the topsoil (Luo et al., 2020). These changes in soil biogeochemical pathways (e.g., C, N, and P) can have profound effects on vegetation photosynthesis, and lasting impact TOP capacity (Han et al., 2021). Such as some efficient nutrients recycling mitigate nutrients loss from the soil, sustain vegetation growth and maintain soil fertility and TOP capacity.

4.3. The Relationship Between the TOP and Ecosystem Imbalance

4.3.1. Atmospheric Oxygen and TOP

Oxygen budget refers to a state in which atmospheric oxygen fluctuations, associated with the TOP and oxygen consumption. Under the RCP8.5 scenario, the global ∼100 gigatonnes/year of atmosphere oxygen would be removed until 2,100 (from its current level of 20.946%–20.825%), mainly owing to human-induced oxygen consumption, such as fossil fuel combustion, human respiration, livestock respiration, and wildfires (Liu et al., 2020), have caused irreversible atmosphere oxygen decline (Huang et al., 2018). Therefore, TOP is the positive driving force, in the context of atmospheric oxygen fluctuations, and oxygen decline is the result. The unique weather conditions and vegetation types, together with a low intensity of human disturbances (Yang et al., 2008), make the TP an ideal region for exploring spatial-temporal changes and environmental controls of TOP in high-altitude ecosystems. Therefore, under anthropogenic global climate warming, TOP plays a crucial indicator role in the ecosystem imbalance over the TP.

4.3.2. The Mechanism Between Oxygen Variation and Ecosystem Imbalance

Under the RCP8.5 scenario, Han et al. (2021) showed that significant ($P < 0.01$) linear regression positive relationships between oxygen consumption-to-production ratio and air temperature, precipitation, potential evapotranspiration, and dryland areas, respectively. The oxygen variation is related to increase in human disturbances and activities, plays a crucial role in anthropogenic climate warming (Huang et al., 2018). Thus, when oxygen production is unsustainable (e.g., water limitation to vegetation growth) combined with oxygen consumption (e.g., fossil fuel combustion), this scenario will accelerate the ecosystem imbalance (Han et al., 2021). Ecosystem imbalance-induced land degradation, which may lead to soil water constraining vegetation changes (Hoover et al., 2015), affects the photosynthesis rate of vegetation canopy that can absorb CO_2 and emit O_2, alters atmospheric O_2 variation, giving rise to a positive feedback that accelerates global warming.

4.3.3. Oxygen Decline Restricts Ecosystem Growth

A decline in O_2 content is a common phenomenon, accelerating and occurring on a global scale (Wei et al., 2021), owing to rapid population growth, fast economic development, and urbanization (Han et al., 2021). Climate warming has been associated with the quick increase of atmospheric CO_2 but has not been generally considered to the variations of atmospheric O_2 (IPCC, 2013). In fact, the atmospheric percentage of O_2, owing to its contribution to air density and mass, impacts the optical depth of the atmosphere, is suggested as the main factor in climate forcing (Poulsen et al., 2015). Under low partial pressure of O_2 and a reduced-mass atmosphere, shortwave scattering by cloud fractions and air molecules is less frequent, causing a substantial raise in land surface shortwave forcing (Poulsen et al., 2015). Through feedbacks involving the latent heat fluxes to Earth's atmosphere, land surface shortwave forcing drives raises greenhouse forcing, and enhances global land surface temperature (Poulsen et al., 2015). As a result, global land surface temperatures increase with declining O_2 content, which may have amplified greenhouse warming forcing (Poulsen et al., 2015), and ultimately restricting ecosystem growth.

4.4. The Four Phases of Ecosystem Imbalance

TOP is an important indicator of the ecosystem imbalance, especially over the TP associated with a small-intensity of human-induced influences. In the Anthropocene, ecosystem imbalance is often associated with the "external stress." For example, the warming rate on the TP is about three times that of global warming (Qiu, 2008). The so-called "vegetation greening" of the Earth-system, caused by enhanced vegetation growth, largely owing to increasing air temperature, has increased the NPP in recent decades, this process is known as the "extending the growing season" (S. L. Piao et al., 2020). However, increasing atmospheric CO_2 is a major factor driving air temperature increase, and can contribute to a positive feedback loop that aggravates global warming. For instance, warming the soil enhances microbial respiration, and emitting CO_2 back into the atmosphere (Steffen et al., 2018). Thus, in Figure 4s, the Pearson correlation matrix of ecosystem factors linked to SEMs showed that ecosystem indicators are strongly interconnects; climatic, plant, soil, and microbial factors are the main driver of TOP, can establish a positive feedback loop, which the standardized direct effect is 0.99, 0.73, 0.75, and 0.75, respectively, over the TP. According to changes in TOP, our studies suggest that the response of ecosystem imbalance to warming can be organized into four phases characterized by concurring non-linear ecosystem shifts (Figure 5).

First, defined the ecosystem changes with increases in TOP (under different warming scenarios, Figure 6) start with a "climate warming phase" characterized by variations of climatic indicators, associated with positive (e.g., TF) and negative (e.g., ALB) feedbacks to TOP, and have caused the energy imbalance between TF cooling and ALB warming. Vegetation growth reduces ALB and the extra energy available at the surface is efficiently dissipated by TF cooling (inner cycle, within the region), suggesting mitigation of regional warming in the near future. However, under GHGs-induced warming (outer cycle), increased vegetation productivity needs more water, which could lead to terrestrial water storage declines through the depletion of aquifers (J. Wang et al., 2018), may exacerbate the risk of soil degradation, posing a severe threat to ecosystems (Huang, Li, et al., 2017; Huang, Zhang, et al., 2020).

Second, as TOP continues to increase (Figure 6), we identified a "plant rise phase" characterized by an increasing trend in vegetation productivity that is consistent with observed the dominant driver-EVI. Plants increase their above- and below-ground biomass are closely related to SOC fixation during the plant rise phase, but the SOC fixation may need to many years, due to differences the rates of SOC turnover in the different soil biomes (Jansson & Hofmockel, 2020), especially over fragile ecosystems. In addition, plant growth, which combined with changes in ice-snow melting (increased runoff erosion) and permafrost thaw (accelerated C decomposition) may continue over this region under warming (Shen et al., 2015). Therefore, we speculate that the quality and quantity of plant C inputs into the soil may trigger a series of extreme costs needed for extracting nutrients to keep a positive C gain under enhanced warming (Carvajal et al., 2019).

Third, as permafrost warming, we identified a "soil disruption phase" characterized by major variation in SOC (as a vital role in regulating climate). Enhanced TP warming may aggravate the soil degradation, such as permafrost collapse, by causing a higher evaporative demand and vapor pressure deficit (Huang, Li, et al., 2017). Additionally, the decreased soil moisture may lead more energy to sensible heat flux than to latent heat flux (Seneviratne et al., 2010), resulting in an even stronger effect on temperature extremes (Vogel et al., 2017). Changes in temperature-moisture resulting from climate warming are more likely to alter strongly the SOC turnover capacity in high latitude and altitude area, both via vegetation shifts and through direct warming impacts on decomposition and photosynthesis (Huang, Li, et al., 2017; Sjögersten & Wookey, 2016). Furthermore, erosion-induced soil degradation may also result in the emission of SOC (Lal, 2004). Therefore, the soil degradation severely constrains the vegetation growth and effect on the TOP rate of plant that can absorb atmospheric CO_2 and store soil C in the future.

Finally, we detected a "microbial response phase" characterized by soil microbial responses to environmental stress in different ways, depending on their physiological states. Across terrestrial biomes, soil microbial communities-driven greenhouse gas emissions such as C dioxide are elevating and positively feeding back on climate warming (Cavicchioli et al., 2019), forming a cycle. Ignorance of the role of, impacts on and feedback response of soil microbial communities to climate warming can result in our own peril (Cavicchioli et al., 2019). Our results indicated that climate and other drivers are the dominant causal mechanism of TOP, can lead to a positive feedback loop that aggravates ecosystem imbalance over TP regions (Figure 4c). We also note that these concerns are generally consistent with the recent "warning to humanity" (Cavicchioli et al., 2019) that acts as a wake-up call to the significance of soil microbiomes in creating ecosystem stability in the near future as climate changes (Jansson & Hofmockel, 2020).

5. Conclusions

We emphasize that this work goes beyond current knowledge by identifying and first proposing four phases of ecosystem imbalance characterized by consecutively increasing TOP. The four phases, which "climate warming phase," "plant rise phase," "soil disruption phase," and "microbial responses phase" of changes in ecosystem play an important role in understanding the development of ecosystem imbalance over the TP. According to this driving mechanism, alpine meadow showed stronger resistance and less resilience to ecosystem imbalance than that of alpine steppe, due to differences among ecosystem functions in turnover time (e.g., SOC) and ecosystem imbalance adaptive strategies (e.g., microbial communities). Thus, it is essential for improve us know of the grassland's management and its ecosystem attributes. In summary, our study provides a well-defined framework for ecosystem imbalance to explore TOP responses to climatic, plant, soil, and microbial factors. The framework introduced can be used to identify the environmental factors affecting TOP to indicate the consequences of ecosystem change, especially in sensitive and fragile areas. In addition, our findings also set up future works to explore potential catastrophic shifts, such as soil quality assessment, to maintain essential ecosystem services that need regional sustainable development.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Plant, soil and microbial indicators data set are available at L. Chen et al. (2019). Coupled Model Intercomparison Project Phase Five (CMIP5) model outputs are available at https://esgf-node.llnl.gov/projects/cmip5/. The Global Land Data Assimilation System (GLDAS) and associated climatic data are available at https://ldas.gsfc.nasa.gov/data.

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References

Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J., et al. (2020). Global ecosystem thresholds driven by aridity. *Science*, *367*(6479), 787–790. https://doi.org/10.1126/science.aay5958

Boudell, J. A. (2016). Ecosystem function. In C. M. Finlayson, M. Everard, K. Irvine, R. J. McInnes, B. A. Middleton, A. A. van Dam & N. C. Davidson (Eds.), *The wetland book*. Springer. https://doi.org/10.1007/978-94-007-6172-8_93-1

Braswell, B. H., Schimel, D. S., Linder, E., & Moore, B. (1997). The response of global terrestrial ecosystems to interannual temperature variability. *Science*, *278*(5339), 870–873. https://doi.org/10.1126/science.278.5339.870

Calvin, M. (1956). The photosynthetic carbon cycle. *Journal of the Chemical Society*, 1895–1915. https://doi.org/10.1039/JR9560001895

Carvajal, D. E., Loayza, A. P., Rios, R. S., Delpiano, C. A., & Squeo, F. A. (2019). A hyper-arid environment shapes an inverse pattern of the fast-slow plant economics spectrum for above-but not below-ground resource acquisition strategies. *Journal of Ecology*, *107*(3), 1079–1092. https://doi.org/10.1111/1365-2745.13092

Cavicchioli, R., Ripple, W. J., Timmis, K. N., Azam, F., Bakken, L. R., Baylis, M., et al. (2019). Scientists' warning to humanity: Microorganisms and climate change. *Nature Reviews Microbiology*, *17*(9), 569–586. https://doi.org/10.1038/s41579-019-0222-5

Chen, B., Liu, S., Ge, J., & Chu, J. (2010). Annual and seasonal variations of Q_{10} soil respiration in the sub-alpine forests of the Eastern Qinghai-Tibet Plateau, China. *Soil Biology and Biochemistry*, *42*(10), 1735–1742. https://doi.org/10.1016/j.soilbio.2010.06.010

Chen, L., Liu, L., Qin, S., Yang, G., Fang, K., Zhu, B., et al. (2019). Regulation of priming effect by soil organic matter stability over a broad geographic scale. *Nature Communications*, *10*(1), 5112. https://doi.org/10.1038/s41467-019-13119-z

Crabtree, R., Potter, C., Mullen, R., Sheldon, J., Huang, S., Harmsen, J., et al. (2009). A modeling and spatio-temporal analysis framework for monitoring environmental change using NPP as an ecosystem indicator. *Remote Sensing of Environment*, *113*(7), 1486–1496. https://doi.org/10.1016/j.rse.2008.12.014

Dirnböck, T., Dullinger, S., & Grabherr, G. (2003). A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, *30*(3), 401–417. https://doi.org/10.1046/j.1365-2699.2003.00839.x

Eldridge, D. J., Maestre, F. T., Koen, T. B., & Delgado-Baquerizo, M. (2018). Australian dryland soils are acidic and nutrient-depleted, and have unique microbial communities compared with other drylands. *Journal of Biogeography*, *45*(12), 2803–2814. https://doi.org/10.1111/jbi.13456

Epstein, H., Lauenroth, W., & Burke, I. (1997). Effects of temperature and soil texture on ANPP in the U.S. Great Plains. *Ecology*, *78*(8), 2628–2631. https://doi.org/10.2307/2265921

Gao, M. D., Piao, S. L., Chen, A. P., Yang, H., Liu, Q., Fu, Y. S. D., & Janssens, I. A. (2019). Divergent changes in the elevational gradient of vegetation activities over the last 30 years. *Nature Communications*, *10*(1), 2970. https://doi.org/10.1038/s41467-019-11035-w

Guan, X., Ma, J., Huang, J., Huang, R., Zhang, L., & Ma, Z. (2019). Impact of oceans on climate change in drylands. *Science China Earth Sciences*, *62*(6), 891–908. https://doi.org/10.1007/s11430-018-9317-8

Haberl, H., Erb, K. H., Krausmann, F., Gaube, V., Bondeau, A., Plutzar, C., et al. (2007). Quantifying and mapping the human appropriation of net primary production in Earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(31), 12942–12945. https://doi.org/10.1073/pnas.0704243104

Han, D. L., Huang, J. P., Ding, L., Liu, X. Y., Li, C. Y., & Yang, F. (2021). Oxygen footprint: An indicator of the anthropogenic ecosystem changes. *Catena*, *206*, 105501. https://doi.org/10.1016/j.catena.2021.105501

He, Y., Tian, W., Huang, J., Wang, G., Ren, Y., Yan, H., et al. (2021). The mechanism of increasing summer water vapor over the Tibetan Plateau. *Journal of Geophysical Research: Atmospheres*, *126*(10), e2020JD034166. https://doi.org/10.1029/2020JD034166

Hoover, D. L., Duniway, M. C., & Belnap, J. (2015). Pulse-drought atop press-drought: Unexpected plant responses and implications for dryland ecosystems. *Oecologia*, *174*(4), 1211–1221. https://doi.org/10.1007/s00442-015-3414-3

Huang, J., Guan, X., & Ji, F. (2012). Enhanced cold-season warming in semi-arid regions. *Atmospheric Chemistry and Physics*, *12*, 5391–5398. https://doi.org/10.5194/acp-12-5391-2012

Huang, J., Huang, J., Liu, X., Li, C., Ding, L., & Yu, H. (2018). The global oxygen budget and its future projection. *Science Bulletin*, *63*(18), 1180–1186. https://doi.org/10.1016/j.scib.2018.07.023

Huang, J., Li, Y., Fu, C., Chen, F., Fu, Q., Dai, A., et al. (2017). Dryland climate change: Recent progress and challenges. *Reviews of Geophysics*, *55*(3), 587–854. https://doi.org/10.1002/2016RG000550

Huang, J., Liu, X., He, Y., Shen, S., Hou, Z., Li, S., et al. (2021). The oxygen cycle and a habitable Earth. *Science China Earth Sciences*, *64*(4), 511–528. https://doi.org/10.1007/s11430-020-9747-1

Huang, J., Yu, H., Dai, A., Wei, Y., & Kang, L. (2017). Drylands face potential threat under 2°C global warming target. *Nature Climate Change*, *7*(6), 417–422. https://doi.org/10.1038/nclimate3275

Huang, J., Yu, H., Guan, X., Wang, G., & Guo, R. (2016). Accelerated dryland expansion under climate change. *Nature Climate Change*, *6*(2), 166–172. https://doi.org/10.1038/nclimate2837

Huang, J., Yu, H., Han, D., Zhang, G., Wei, Y., Huang, J., et al. (2020). Declines in global ecological security under climate change. *Ecological Indicators*, *117*, 106651. https://doi.org/10.1016/j.ecolind.2020.106651

Huang, J., Zhang, G., Zhang, Y., Guan, X., Wei, Y., & Guo, R. (2020). Global desertification vulnerability to climate change and human activities. *Land Degradation & Development*, *31*(11), 1380–1391. https://doi.org/10.1002/ldr.3556

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*. Cambridge University Press.

Jansson, J. K., & Hofmockel, K. S. (2020). Soil microbiomes and climate change. *Nature Reviews Microbiology*, *18*(1), 35–46. https://doi.org/10.1038/s41579-019-0265-7

Jiao, K. W., Gao, J. B., & Liu, Z. H. (2021). Precipitation drives the NDVI distribution on the Tibetan Plateau while high warming rates may intensify its ecological droughts. *Remote Sensing*, *13*(7), 1305. https://doi.org/10.3390/rs13071305

Jílková, V., Devetter, M., Bryndová, M., Hájek, T., Kotas, P., Luláková, P., et al. (2021). Carbon sequestration related to soil physical and chemical properties in the high Arctic. *Global Biogeochemical Cycles*, *35*(9), e2020GB006877. https://doi.org/10.1029/2020GB006877

Keenan, T. F., & Riley, W. J. (2018). Greening of the land surface in the world's cold regions consistent with recent warming. *Nature Climate Change*, *8*(9), 825–828. https://doi.org/10.1038/s41558-018-0258-y

Lal, A. (2004). Carbon sequestration in dryland ecosystems. *Environmental Management*, *33*(4), 528–544. https://doi.org/10.1007/s00267-003-9110-9

Li, C., Huang, J., Ding, L., Liu, X., Yu, H., & Huang, J. (2021). Increasing escape of oxygen from oceans under climate change. *Geophysical Research Letters*, *47*(11), e2019GL086345. https://doi.org/10.1029/2019GL086345

Li, J., Pei, J., Pendall, E., Fang, C., & Nie, M. (2020). Spatial heterogeneity of temperature sensitivity of soil respiration: A global analysis of field observations. *Soil Biology and Biochemistry*, *141*, 107675. https://doi.org/10.1016/j.soilbio.2019.107675

Li, Z., Tang, Z., Song, Z., Chen, W., Tian, D., Tang, S., et al. (2022). Variations and controlling factors of soil denitrification rate. *Global Change Biology*, *28*(6), 2133–2145. https://doi.org/10.1111/gcb.16066

Lian, X., Piao, S., Li, L. Z. X., Li, Y., Huntingford, C., Ciais, P., et al. (2020). Summer soil drying exacerbated by earlier spring greening of northern vegetation. *Science Advances*, *6*(1), eaax0255. https://doi.org/10.1126/sciadv.aax0255

Liu, X., Huang, J., Huang, J., Li, C., Ding, L., & Meng, W. (2020). Estimation of gridded atmospheric oxygen consumption from 1975 to 2018. *Journal of Meteorological Research*, *34*(3), 646–658. https://doi.org/10.1007/s13351-020-9133-7

Lucht, W., Prentice, I. C., Myneni, R. B., Sitch, S., Friedlingstein, P., Cramer, W., et al. (2002). Climatic control of the high-latitude vegetation greening trend and Pinatubo effect. *Science*, *296*(5573), 1687–1689. https://doi.org/10.1126/science.1071828

Lugato, E., Lavallee, J. M., Haddix, M. L., Panagos, P., & Cotrufo, M. F. (2021). Different climate sensitivity of particulate and mineral-associated soil organic matter. *Nature Geoscience*, *14*(5), 295–300. https://doi.org/10.1038/s41561-021-00744-x

Luo, R., Kuzyakov, Y., Liu, D., Fan, J., Luo, J., Lindsey, S., et al. (2020). Nutrient addition reduces carbon sequestration in a Tibetan grassland soil: Disentangling microbial and physical controls. *Soil Biology and Biochemistry*, *144*, 107764. https://doi.org/10.1016/j.soilbio.2020.107764

Marvel, K., Cook, B. I., Bonfils, C. J. W., Durack, P. J., Smerdon, J. E., & Williams, A. P. (2019). Twentieth-century hydroclimate changes consistent with human influence. *Nature*, *569*(7754), 59–65. https://doi.org/10.1038/s41586-019-1149-8

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., et al. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*(10), 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Mu, C., Zhang, T., Zhang, X., Li, L., Guo, H., Zhao, Q., et al. (2016). Carbon loss and chemical changes from permafrost collapse in the northern Tibetan Plateau. *Journal of Geophysical Research: Biogeosciences*, *121*(7), 1781–1791. https://doi.org/10.1002/2015JG003235

Mu, C. C., Abbott, B. W., Norris, A. J., Mu, M., Fan, C. Y., Chen, X., et al. (2020). The status and stability of permafrost carbon on the Tibetan Plateau. *Earth-Science Reviews*, *211*, 103433. https://doi.org/10.1016/j.earcirev.2020.103433

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., & Forsythe, N. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5*, 424–430. https://doi.org/10.1038/nclimate2563

Peters, M. K., Hemp, A., Appelhans, T., Becker, J. N., Behler, C., Classen, A., et al. (2019). Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature*, *568*(7750), 88–92. https://doi.org/10.1038/s41586-019-1048-z

Piao, S., Friedlingstein, P., Ciais, P., Viovy, N., & Demarty, J. (2007). Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Global Biogeochemical Cycles*, *21*(3), GB3018. https://doi.org/10.1029/2006GB002888

Piao, S. L., Wang, X. H., Park, T., Chen, C., Lian, X., He, Y., et al. (2020). Characteristics, drivers and feedbacks of global greening. *Nature Reviews Earth & Environment*, *1*, 14–27. https://doi.org/10.1038/s43017-019-0001-x

Portman, M. E., & Elhanan, Y. (2016). Ecosystem services assessment from the mountain to the sea: In search of a method for land- and seascape planning. In J. Gatrell, R. Jensen, M. Patterson, & N. Hoalst-Pullen (Eds.), *Urban sustainability: Policy and Praxis* (Vol. 14). Springer. https://doi.org/10.1007/978-3-319-26218-5_3

Potter, C. S., Klooster, S., & Brooks, V. (1999). Interannual variability in terrestrial net primary production: Exploration of trends and controls on regional to global scales. *Ecosystems*, *2*(1), 36–48. https://doi.org/10.1007/s100219900056

Poulsen, C. J., Tabor, C., & White, J. D. (2015). Long-term climate forcing by atmospheric oxygen concentrations. *Science*, *348*(6240), 1238–1241. https://doi.org/10.1126/science.1260670

Qiu, J. (2008). The third Pole. *Nature*, *454*(7203), 393–396. https://doi.org/10.1038/454393a

10.1029/2022EF002890

Rocha, J. C., Peterson, G., Bodin, O., & Levin, S. (2018). Cascading regime shifts within and across scales. *Science*, *362*(6421), 1379–1383. https://doi.org/10.1126/science.aat7850

Rodell, M., Houser, P. R., Jambor, U., Gottschalck, J., Mitchell, K., Meng, C.-J., et al. (2004). The global land data assimilation system. *Bulletin of the American Meteorological Society*, *85*(3), 381–394. https://doi.org/10.1007/978-94-010-0029-1_30

Scurlock, J., Johnson, K., & Olson, R. J. (2002). Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology*, *8*, 736–753. https://doi.org/10.1046/j.1365-2486.2002.00512.x

Seneviratne, S. I., Corti, T., Davin, E. L., Hirschi, M., Jaeger, E. B., Lehner, I., et al. (2010). Investigating soil moisture-climate interactions in a changing climate: A review. *Earth-Science Reviews*, *99*(3–4), 125–161. https://doi.org/10.1016/j.earscirev.2010.02.004

Shen, M., Piao, S., Jeong, S. J., Zhou, L., Zeng, Z., Ciais, P., et al. (2015). Evaporative cooling over the Tibetan Plateau induced by vegetation growth. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(30), 9299–9304. https://doi.org/10.1073/pnas.1504418112

Sjögersten, S., & Wookey, P. A. (2016). The impact of climate change on ecosystem carbon dynamics at the Scandinavian mountain birch forest-tundra heath ecotone. *Ambio*, *38*(1), 2–10. https://doi.org/10.1579/0044-7447-38.1.2

Soo, R. M., Hemp, J., Parks, D. H., Fischer, W. W., & Hugenholtz, P. (2017). On the origins of oxygenic photosynthesis and aerobic respiration in Cyanobacteria. *Science*, *355*(6332), 1436–1440. https://doi.org/10.1126/science.aal3794

Steffen, W., Rockström, J., Richardson, K., Lenton, T. M., Folke, C., Liverman, D., et al. (2018). Trajectories of the Earth system in the Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(33), 8252–8259. https://doi.org/10.1073/pnas.1810141115

Tao, J., Zhang, Y. J., Dong, J. W., Fu, Y., Zhu, J. T., Zhang, G. L., et al. (2015). Elevation-dependent relationships between climate change and grassland vegetation variation across the Qinghai-Xizang Plateau. *International Journal of Climatology*, *35*(7), 1638–1647. https://doi.org/10.1002/joc.4082

Teuling, A. J., Taylor, C. M., Meirink, J. F., Melsen, L. A., Miralles, D. G., van Herrwaarden, C. C., et al. (2017). Observational evidence for cloud cover enhancement over Western European forests. *Nature Communications*, *8*(1), 14065. https://doi.org/10.1038/ncomms14065

Viviroli, D., Durr, H. H., Messerli, B., Meybeck, M., & Weingartner, R. (2007). Mountains of the world, water towers for humanity: Typology, mapping, and global significance. *Water Resources Research*, *43*(7), W07447. https://doi.org/10.1029/2006WR005653

Vogel, M. M., Orth, R., Cheruy, F., Hagemann, S., Lorenz, R., van den Hurk, B. J. J. M., & Seneviratne, S. I. (2017). Regional amplification of projected changes in extreme temperatures strongly controlled by soil moisture-temperature feedbacks. *Geophysical Research Letters*, *44*(3), 1511–1519. https://doi.org/10.1002/2016GL071235

Wang, J., Song, C., Reager, J. T., Yao, F., Famiglietti, J. S., Sheng, Y., et al. (2018). Recent global decline in endorheic basin water storages. *Nature Geoscience*, *11*(12), 926–932. https://doi.org/10.1038/s41561-018-0265-7

Wang, T., Tang, T., Sun, M., Liu, X., Huang, Y., Huang, J., et al. (2021). Identifying a transport mechanism of dust aerosols over south Asia to the Tibetan plateau: A case study. *Science of the Total Environment*, *758*, 143714. https://doi.org/10.1016/j.scitotenv.2020.143714

Wei, Y., Wu, J., Huang, J., Liu, X., Han, D., An, L., et al. (2021). Declining oxygen level as an emerging concern to global cities. *Environmental Science & Technology*, *55*(12), 7808–7817. https://doi.org/10.1021/acs.est.1c00553

Wu, M. H., Chen, S. Y., Chen, J. M., Xue, K., Chen, S. L., Wang, X. M., et al. (2021). Reduced microbial stability in the active layer is associated with carbon loss under alpine permafrost degradation. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(25), e2025321118. https://doi.org/10.1073/pnas.2025321118

Wu, S., & Li, S. (2019). Ecosystem service relationships: Formation and recommended approaches from a systematic review. *Ecological Indicators*, *99*, 1–11. https://doi.org/10.1016/j.ecolind.2018.11.068

Xu, H., Wang, X., & Zhang, X. (2016). Alpine grasslands response to climatic factors and anthropogenic activities on the Tibetan Plateau from 2000 to 2012. *Ecological Engineering*, *92*, 251–259. https://doi.org/10.1016/j.ecoleng.2016.04.005

Yang, Y., Fang, J., Pan, Y., & Ji, C. (2009). Aboveground biomass in Tibetan grasslands. *Journal of Arid Environments*, *73*(1), 91–95. https://doi.org/10.1016/j.jaridenv.2008.09.027

Yang, Y., Fang, J., Tang, Y., Ji, C., Zheng, C., He, J., & Zhu, B. (2008). Storage, patterns and controls of soil organic carbon in the Tibetan grasslands. *Global Change Biology*, *14*(7), 1592–1599. https://doi.org/10.1111/j.1365-2486.2008.01591.x

Yu, P., Li, Q., Jia, H., Li, G., Zheng, W., Shen, X., et al. (2014). Effect of cultivation on dynamics of organic and inorganic carbon stocks in Songnen Plain. *Agronomy Journal*, *106*(5), 1574–1582. https://doi.org/10.2134/agronj14.0113

Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., et al. (2016). Greening of the Earth and its drivers. *Nature Climate Change*, *6*(8), 791–795. https://doi.org/10.1038/nclimate3004