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Research article

Widespread increasing negative vegetation sensitivity to phenology reshapes GPP dynamics in alpine grassland

Yuanguo Liu [a,1], Xiaoke Zhang [a,b,*,1], Mingze Sun [a], Xindong Du [a], Qihao Zhu [a]

[a] School of Public Administration, Hohai University, Nanjing, China
[b] Center for Environmental and Social Studies, Hohai University, Nanjing, China

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ABSTRACT

Satellite evidence indicates a significant phenological changes in alpine vegetation. However, the effect of phenological changes on vegetation gross primary productivity (GPP) is still poorly understood, which limits understanding of climate changes. Here, we analyze the impact of different phenological factors on alpine grassland GPP based on sensitivity coefficient obtained from explainable machine learning. We found that alpine grassland GPP largely exhibits negative sensitivity to the duration of spring phenology and positive sensitivity to the duration of autumn phenology. Regions with negative sensitivity show an increasing trend in GPP sensitivity to both spring and autumn phenological durations, whereas areas with positive sensitivity indicate a decreasing sensitivity trend. This trend change pattern is related to the warm and humid climate of the Northern Tibetan Plateau. Results indicate a warning sign that phenological changes potentially limit the carbon benefits of alpine grassland derived from ongoing climate changes. This study comprehensively reveals the impact of phenological changes on alpine grassland. Research findings bear significant theoretical implications for the adoption of carbon neutrality strategies in alpine regions.

1. Introduction

Vegetation phenology is a fundamental aspect of vegetation growth, exerting on a strong influence their productivity (Xia et al., 2015; Zhou et al., 2016; Buermann et al., 2018). Vegetation adjusts to climate change by modifying the timing of phenological events. For instance, global warming accelerates the onset of the growing season (Fu et al., 2015; Livensperger et al., 2016; Möhl et al., 2022). In past years, the phenological response to climate change has received abundant attention in the literature and has shown remarkable advancements (Richardson et al., 2013; Li et al., 2016; Piao et al., 2019). However, the impact of phenological event on ecosystem carbon accumulation has received unexpectedly limited attention, although the phenological changes drive seasonal land-atmosphere exchange of carbon, water and energy (Ganjurjav et al., 2020; Wang et al., 2020a; Zhang et al., 2022a). Time available for vegetation growth as a crucial resource, often defined by the duration of the growing season. A growing season's duration can further be divided into different vegetation growth stages (Li et al., 2016; Liu et al., 2016b; Park et al., 2016; Korner et al., 2023), such as greening's duration and browning's duration. The duration of these growing stages has shown significantly impact on ecosystem carbon accumulation (Hu et al., 2010; Meng et al., 2023), yet this impact has not been qualitatively and quantitatively understood. Thus, research regarding the mechanistic relationship between phenological changes and ecosystem carbon accumulation is imperative for enhancing our comprehension of the response of the carbon cycle to ongoing global climate change.

The impact of climate change on vegetation phenology is extensively studied on a global scale. Abundant evidence from remote sensing indicates that climate warming has advanced spring phenology and delayed autumn phenology of vegetation (Liu et al., 2016a; Gonsamo et al., 2018; Wang et al., 2021; Gu et al., 2022). These phenological changes eventually affect carbon accumulation at the end of year (Forkel et al., 2016; Gonsamo et al., 2017). Phenological duration not only directly determines the carbon uptake period of vegetation but may also induce changes in some biophysical and physiological processes (Keenan and Richardson, 2015; Zeng et al., 2017; Li et al., 2023). For example, early springs and prolonged growing seasons may decrease carbon accumulation due to increased transpiration at the onset of the growing season, leaving less water availability in summer and limiting

* Corresponding author. School of Public Administration, Hohai University, Nanjing, China.
E-mail address: xkzhang@hhu.edu.cn (X. Zhang).
[1] These two authors contributed equally to this paper。.

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growth later in the peak growing peak (Wolf et al., 2016; Sippel et al., 2017; Lian et al., 2020). Understanding the influence of these processes on phenological changes is essential for elucidating the response mechanisms between phenology and vegetation productivity. Phenological changes in different period may exert different effects on vegetation carbon accumulation (Wu et al., 2012; Keenan et al., 2014; Peng et al., 2024). However, a more complete picture of phenology impacts on vegetation productivity would require understanding the response of a series of phenological events, such as the duration of greening, browning and peak. Previous studies indicate the intricate relationship between phenology and vegetation productivity, and highlight the limited knowledge in this domain.

Northern Tibetan Plateau is situated on the Qinghai-Tibet Plateau and stands out as one of the most climate change-sensitive regions, predominantly covered by alpine grasslands. The alterations in climate warming and water availability have resulted in notable changes in the phenology and productivity of this area (Li et al., 2016; Zhang et al., 2020a,b; Möhl et al., 2022; Liu et al., 2024). These phenological changes have considerably affected the alpine grasslands GPP (Berdanier and Klein, 2011; Chen et al., 2011; Wang et al., 2020a, 2021); however, the current comprehension of their impact remains limited. Alpine grasslands play a critical role in the sustainable development of animal husbandry and the implementation of carbon neutrality strategies. Hence, it is imperative to elucidate the response of alpine vegetation productivity to phenology.

Here, we used MODIS GPP as a proxy for the alpine grassland productivity, covering the period from 2000 to 2021. We defined five phenological events, namely the start of growing season, the end of growing season, the early-growing season, the mid-growing season, the late-growing season (Methods: Vegetation phenology). Explainable machine learning was used to study the relationship between phenology and alpine grassland GPP, which can isolate the impact of different phenological event on GPP. We first use the Shapley Additive Explanations (SHAP) method in XGBoost model to estimate the sensitivity of GPP to phenology (Methods: Overall sensitivity). We then estimate the temporal change trends in sensitivity based on a 5-year sliding window (Methods: Trends of sensitivity). The main objectives are: (1) to quantify the sensitivity of alpine grassland GPP to different phenological events and (2) to examine the sensitivity trends and the underlying reason induced sensitivity changes.

2. Materials and methods

2.1. Study area

Our study focused on alpine grassland in Northern Tibetan Plateau (83–95°E and 29–36°N), located in the central region of the Qinghai-Tibet Plateau and holding significant importance as one of the key areas on the plateau (Fig. 1). Northern Tibetan Plateau is one of the areas with the most severe climate conditions in the Qinghai-Tibet Plateau, representing a typical sub-frigid climate zone. The annual average temperature ranges from −0.9 °C to −3.3 °C, coupled with an annual average rainfall of only between 100 and 200 mm. The sparse population is a salient characteristic. This region was selected for the typical climate and minimal human disruptions, making it an ideal site for investigating vegetation change mechanisms. In this study, a grid with a resolution of 1 km was used as the primary research unit.

2.2. Vegetation growth proxies

Gross Primary Productivity (GPP) is closely correlated to the vegetation photosynthesis and carbon cycle, serving as a critical metric for monitoring vegetation changes (Ryu et al., 2018; Liu et al., 2022; Zhang et al., 2022c). Moderate Resolution Imaging Spectroradiometer (MODIS) GPP is widely utilized in monitoring changes in vegetation activity, vegetation phenology and productivity both regionally and globally as its long time series and high spatial resolution (Zhong et al.; Zeng et al., 2020). Our study utilized MOD17A2H products, which were provided in 8-day composite and 1 km resolution from 2000 to 2021. MOD17A2 GPP product based on the radiation-use efficiency, could be downloaded from the Level-1 and Atmosphere Archive & Distribution System Distributed Active Archive Center (LAADS DAAC; https://ladsweb.modaps.eosdis.nasa.gov/search/).

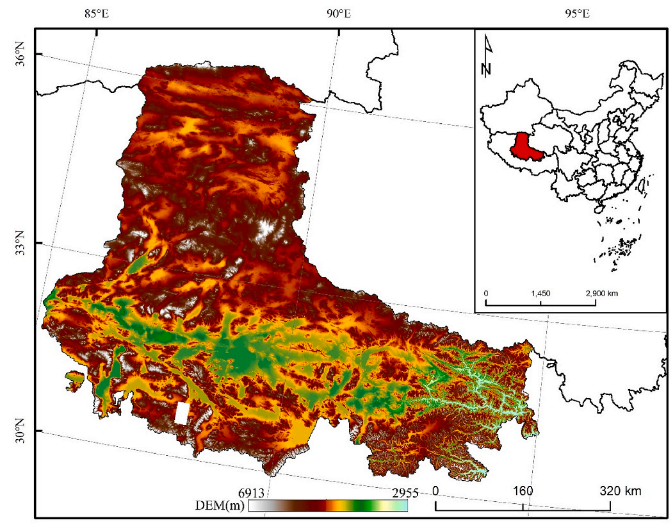

Fig. 1. Location and terrain on the Northern Tibetan Plateau. Note: This map was created based on standard map data downloaded from the National Geo-information Public Service Platform, bearing the map approval number GS (2024) 0650.

2.3. Climate datasets

We used the monthly CRU-TS 4.05 from Climatic Research Unit Time Series (CRU; https://sites.uea.ac.uk/) with a spatial resolution of 0.5° during 2000–2021, including near-surface temperature, precipitation. The de Martonne aridity index, which is widely employed worldwide in assessing the aridity levels in various regions (Tabari et al., 2014; Pellicone et al., 2019), was calculated by monthly temperature and precipitation.

2.4. Vegetation phenology

The HANTS-Maximum method utilizes the harmonic analysis of time series, adapted from the fast Fourier transform algorithm (Jakubauskas et al., 2001; Liu et al., 2016a). Our study employs HANTS-Maximum method to smooth and interpolate GPP with an 8-day interval time series into daily time series. Then, a threshold-based method was used to retrieve the start of growing season (SOS) and the end of growing season (EOS). This method has been extensively utilized and proven effective for capturing vegetation phenology at a regional scale (Cong et al., 2012; Fu et al., 2014; Li et al., 2023). Our analysis specifically targeted areas with a single growing season annually, displaying a nearly normal GPP distribution with a peak in summer. Thus, the areas showing multiple growing seasons within a calendar year or lacking clear phenological cycles was discarded. Then, the dates of SOS and EOS was extracted for each grid cells using a pixel-specific threshold, determined by minimum value plus 30 % of the seasonal amplitude fitting for multiyear averaged smoothed GPP (Zhang et al., 2020a,b).

The growing season was then defined as the period from SOS to EOS for each pixel. The mid-growing season (MGS) was defined as the two consecutive months with the largest GPP but occurring no earlier than April or later than October15 (Lian et al., 2021). The early-growing season (EGS) was defined as the period from the month when SOS occurred to the beginning of the MGS and the late-growing season (LGS) is defined as the period from the end of the MGS to the EOS (Li et al., 2023). Finally, we retrieved the SOS, EOS, EGS, MGS, and LGS for alpine grassland in Northern Tibetan Plateau from 2000 to 2020.

2.5. Overall sensitivity

We utilize explainable machine learning (SHapley Additive exPlanations) to calculate sensitivity of alpine grassland GPP to phenology by disentangling the contribution of each phenological factor to GPP anomalies from the influence of other similar phenological factors. SHapley Additive exPlanations method (SHAP), based on Shaply values in game theory, helps in achieving a balance between global and local explanations and ensuring consistent and reasonable interpretation of the model (Lundberg and Lee, 2017; Besnard et al., 2021). For this purpose, we first train XGBoost models, followed by SHAP to isolate the marginal contributions of each predictor on the target variable. XGBoost, short for eXtreme Gradient Boosting, iteratively trains decision tree models to minimize the loss function and enhance the accuracy and generalization capability of the model (Yuan et al., 2024). This is a supervised learning method that adjusts various parameters through iterative input-output pairs to obtain an optimized model. XGBoost model shows stable training results and high training efficiency, effectively avoiding the occurrence of overfitting (Yang et al., 2021; Yuan et al., 2024).

We treat the GPP anomaly as the target variable and corresponding phenology anomalies (derived by subtracting their long-term averages) as predictors. The target data and all predictors during 2000–2021 was retrieved for each grid cell to train XGBoost model with a common hyperparameter setting optimized by pixel level tests (numbers of estimators: 100; maximum features: 30 %). We remove grid cells with lower model performance using cross-validation ($R^2 > 0$). Regions with $R^2 < 0$ are possibly associated with very low GPP variability or other factors. Then, we apply SHAP method to independently isolate marginal contributions of each phenological factor on the GPP anomaly. The overall sensitivity is defined as the slope calculated from Theil-sen regression between SHAP values for GPP and each phenology anomalies by assuming that the interaction between GPP and each phenological factor is nearly linear. The overall sensitivity, estimated by linear regression, should not be expected to capture the full response between GPP and phenology. Our analysis combines the advantages of XGBoost model, and feature of the SHAP algorithm, enhancing the robustness of the results compared to traditional statistical methods (Yuan et al., 2024).

2.6. Trends of sensitivity

To address temporal variations of GPP sensitivity to phenological factors, we split the datasets from the entire 2000–2021 analysis period into 17 5-year blocks by a 5-year moving window (2000–2004, 2001–2005, …, 2017–2021). For each 5-year blocks, we infer the sensitivity by SHAP and Theil-sen regression by assuming the interaction between GPP and phenological factors within 5-year blocks is nearly linear. We employed the Theil-Sen regression to quantify trends in GPP sensitivity to phenology and the Mann-Kendall test to assess statistical significance, the latter being a non-parametric method that does not require normally distributed data.We remove grid cells that do not show statistical significance in the Mann-Kendall's test. To confirm the 5-year moving window would not bias results, we additionally detect trends of 3-year and 10-year moving window sensitivity and find no significant differences.

3. Results

3.1. Spatial pattern of GPP sensitivity to phenology

We analyzed the overall sensitivity of GPP to SOS (S_{SOS}), EOS (S_{EOS}), EGS (S_{EGS}), MGS (S_{MGS}), and LGS (S_{LGS}) across all land area in Northern Tibetan Plateau where we disregard non-vegetated regions, as well as grid cells where XGBoost model does not perform well ($R^2 < 0$). S_{SOS} and S_{EOS} shows similar performance, with positive sensitivity regions occupying a marginally larger area fraction than negative sensitivity regions (Fig. 2a–d). Positive sensitivity mainly distributed in the central part, whereas negative sensitivity regions are mainly distributed around study area. The area fraction of negative S_{MGS} also slightly higher than positive S_{MGS} (Fig. 2g). Focusing on S_{EGS} and S_{LGS}, we find them show contrasting patterns. S_{EGS} exhibits widespread negative responsiveness (66 % of the study area), whereas S_{LGS} demonstrates widespread positive reactivity (65 % of the study area) (Fig. 2j–m). Notably, the absolute sensitivity magnitudes of S_{EGS} and S_{LGS} markedly surpassed those of other phenological indices.

We further revealed that the spatial distribution of GPP sensitivity to phenology exhibits pronounced latitudinal and climatic dependencies. Higher GPP sensitivity (including S_{SOS}, S_{EOS}, S_{EGS}, S_{MGS} and S_{LGS}) has been observed in mid and low latitudes, and eastern regions. Although the sensitivity patterns of various phenology indices differ along latitudes and longitudes, they exhibit a significant coupling with the distribution of climate indices (Fig. 2). With rising temperatures, precipitation, and dryness/wetness levels, the sensitivity of GPP to phenology experiences a gradual increase, yet beyond a certain threshold, it begins to decline. Put simply, the more favorable climate (warm and humid), the greater the phenological sensitivity.

Overall, our findings demonstrate the responsiveness of alpine grassland GPP to phenological factors and highlight the significant influence of the EGS and LGS. Notably, we observed a striking antagonistic pattern in GPP responses: negative sensitivity to EGS and positive sensitivity to LGS. Additionally, phenological trend analysis further revealed a significant prolongation of both EGS and LGS durations. These temporal shifts may drive divergent responses: prolonged EGS may suppress GPP, whereas extended LGS could enhance it. The impact of phenology on alpine grassland GPP to appears seasonal difference, which eventually alters the total GPP at the end of the year. This antagonistic effect intensifies under increasingly favorable climatic conditions (e.g., warmer temperatures and higher humidity).

3.2. Phenology control pattern

Research results show that the number of grid cells exhibiting the highest sensitivity to EGS and LGS surpassed the combined total of the other three phenological indicators. Specifically, the fraction of grid cells with negative S_{EGS} outweighed the positive S_{EGS}, whereas the fraction of grid cells with positive S_{LGS} exceeded the negative S_{LGS} (Fig. 3a). This reiteration underscores the pivotal role of both EGS and LGS as crucial determinants of alpine grassland GPP. In view of this, the influence mechanism of phenology on alpine grassland GPP was decomposed into four patterns, $EGS + LGS^-$ (GPP showed positive S_{EGS} and negative S_{LGS}), EGS^-LGS^+ (GPP showed negative S_{EGS} and positive S_{LGS}), $EGS + LGS^+$ (GPP showed positive S_{EGS} and S_{LGS}), EGS^-LGS^- (GPP showed negative S_{EGS} and S_{LGS}), respectively. Notably, the prevalence of area associated with EGS^-LGS^+ was predominant (44 %), significantly surpassing the occurrence in the remaining patterns (Fig. 3b). This observation signifies that EGS^-LGS^+ predominantly shapes the impact of phenology on GPP in alpine grasslands.

Further research findings reveal that as the climate gradually becomes more favorable, there is an increase in the prevalence of the four patterns (Fig. 3c–e). Particularly, the dominance of EGS^-LGS^+ relative to the others is projected to further enhance, while the number difference among the remaining patterns remains non-significant changes. Furthermore, the temperature range which EGS^-LGS^+ exhibits a notable upsurge is noticeably narrower than the corresponding precipitation range, and the curve of the number of EGS^-LGS^+ as temperature change is steeper compared to precipitation. The aforementioned findings suggest that temperature serves as the primary factor constraining the

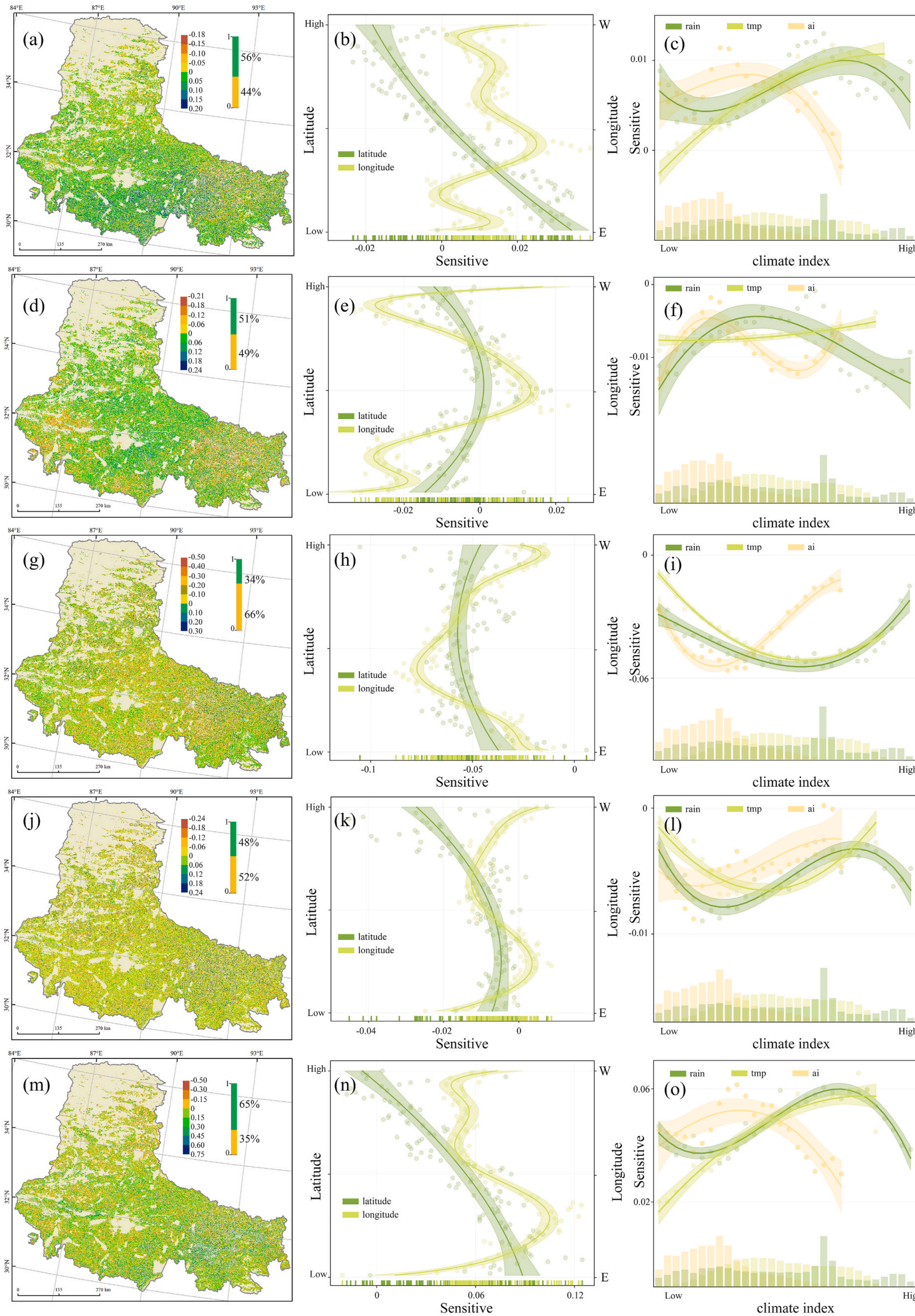

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Fig. 2. Spatial patterns of GPP sensitivity to phenology in Northern Tibetan Plateau in the period 2000–2021. **a**, The spatial pattern of sensitivity to start of growing season (SOS) in Northern Tibetan Plateau. The inset in **a** show the area fraction of both positive and negative sensitivity. **b**, The response of the sensitivity to SOS along latitude and longitude. From top to bottom in **b**, the left y axis shows a gradual decrease in latitude and the right y axis shows the direction oriented from west to east. **c**, The response function along each climate variable, including growing season mean precipitation/rain (rain), growing season mean temperature (tmp), and growing season mean aridity (ai). Probability distributions of climate indexes are shown at the bottom of **c**. Points of different colors in **b-c** indicate mean values of the sensitivity to SOS in each observational ensemble, solid lines of different colors indicate the results from polynomial regression for different climate indexes, and shades of different colors indicate the 95 % confidence interval. The second row shows spatial patterns of sensitivity to end of growing season (EOS)(**d-f**), third row to early-growing season (EGS) (**g-i**), forth row to mid-growing season (MGS) (**j-l**), fifth row to late-growing season (LGS) (**m–o**).

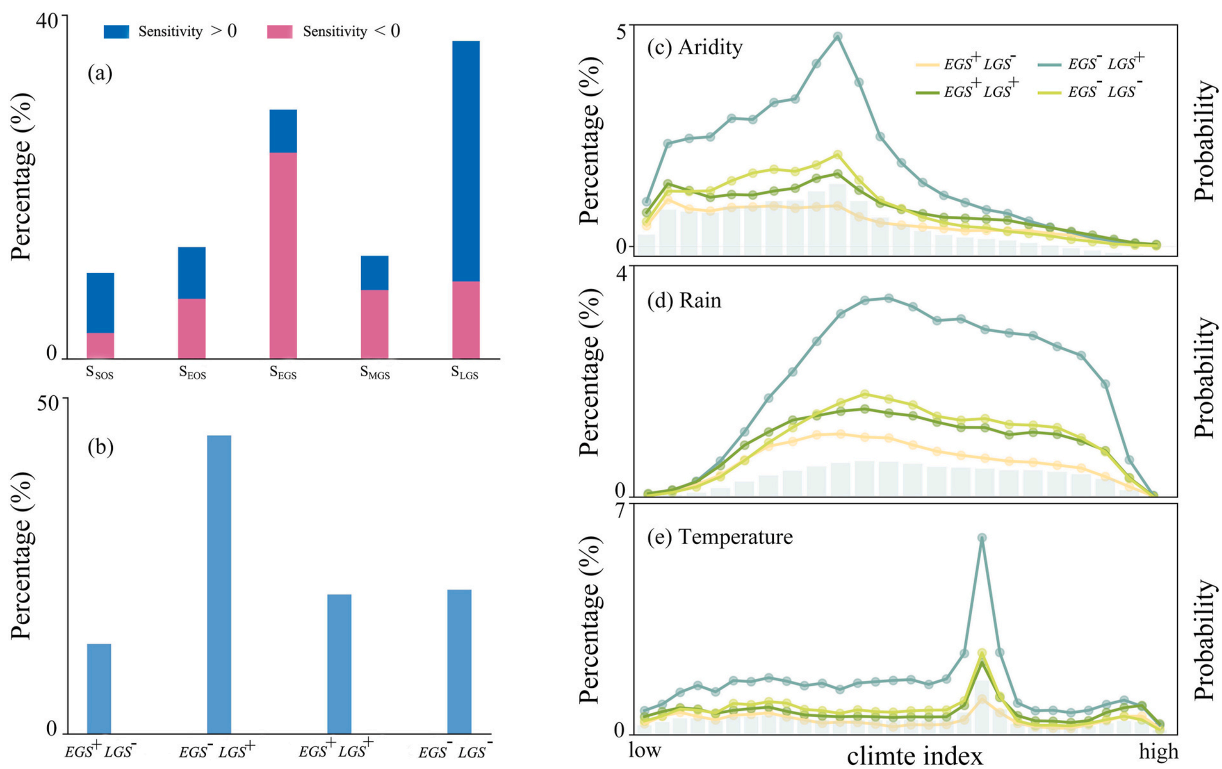

Fig. 3. Comparison of sensitivity of alpine grassland GPP to different phenological factors and main phenological control patterns. **a**, The area fraction of grid cells showing largest GPP sensitivity to start of growing season (SOS), end of growing season (EOS), early-growing season(EGS), mid-growing season(MGS), and late-growing season (LGS). **b**, The area fraction of the $EGS^{+}LGS^{-}$ (grid cells showing positive sensitivity to EGS but negative sensitivity to LGS), $EGS^{-}LGS^{+}$ (grid cells showing negative sensitivity to EGS but positive sensitivity to LGS), $EGS^{+}LGS^{+}$ (grid cells showing positive sensitivity to both EGS and LGS), $EGS^{-}LGS^{-}$ (grid cells showing negative sensitivity to both EGS and LGS). **c-e**, The response of the $EGS^{+}LGS^{-}$, $EGS^{-}LGS^{+}$, $EGS^{+}LGS^{+}$, and $EGS^{-}LGS^{-}$ along each climate variable, including growing season mean precipitation/rain (Rain), growing season mean temperature (Temperature), and growing season mean aridity (Aridity).

influence of $EGS^{-}LGS^{+}$ on the alpine grassland GPP. The interaction between temperature and precipitation can be elucidated in terms of aridity index. Results indicate that a warm and humid climate is conducive to the increase of $EGS^{-}LGS^{+}$. Collectively, these discoveries imply that the warm and humid climate will amplify the impact of $EGS^{-}LGS^{+}$ on the alpine grasslands in Northern Tibetan Plateau.

3.3. *Temporal variability of GPP sensitivity to phenology*

Moving beyond overall sensitivity of alpine grassland GPP to phenology in Northern Tibetan Plateau, we now analyze sensitivity trends in the 5-year sliding window to study their temporal variability from 2000 to 2021. For this purpose, we focus solely on regions showing significance in the MK trend test. We partition the study area into segments exhibiting positive and negative sensitivity determined by overall sensitivity, to independently analyze the temporal changes in positive sensitivity and negative sensitivity.

The research findings indicate that the positive S_{SOS} and S_{EOS} was on the rise, whereas the negative sensitivity was declining. Importantly, the positive S_{EGS} shows a slight increasing trend but S_{MGS} and S_{LGS} shows a decreasing trend (Fig. 4a). This finding implies that in the region of positive sensitivity, the GPP response to EGS is strengthening; however, the response to subsequent phenology weakens gradually as growth proceeds. Contrarily, the negative S_{EGS}, S_{MGS}, and S_{LGS} all show increasing trend, suggesting that in areas of negative sensitivity, the prolonged EGS, MGS, and LGS might further hinder GPP. In general, both positive and negative S_{EGS} were strengthening and the increase in negative sensitivity outweigh that of positive sensitivity (Fig. 4b). The positive S_{LGS} was decreasing, while the negative sensitivity was strengthening. These evidences indicate that the negative impact of phenological changes on alpine grassland GPP was strengthening.

The increasing trend of positive S_{EGS} and decreasing trend of positive S_{LGS} also is observed in regions with $EGS + LGS^{-}$, $EGS^{-}LGS^{+}$, and $EGS + LGS^{+}$, respectively (Fig. 4c–b). The positive S_{EGS} shows a weak increasing trend but an evident decreasing trend observed in positive S_{LGS} across these three patterns. On the other hand, the negative S_{EGS} and S_{LGS} also consistently exhibit increasing trend in $EGS + LGS^{-}$, $EGS^{-}LGS^{+}$ and $EGS^{-}LGS^{-}$, respectively. Notably, these trend magnitudes exhibit a clear consistency across various patterns. These findings indicate that the impact of EGS^{+} LGS^{+} on alpine grassland GPP was diminishing, whereas the impact of $EGS^{-}LGS^{-}$ was strengthening. Additionally, it was noticed that there is no direct connection between the

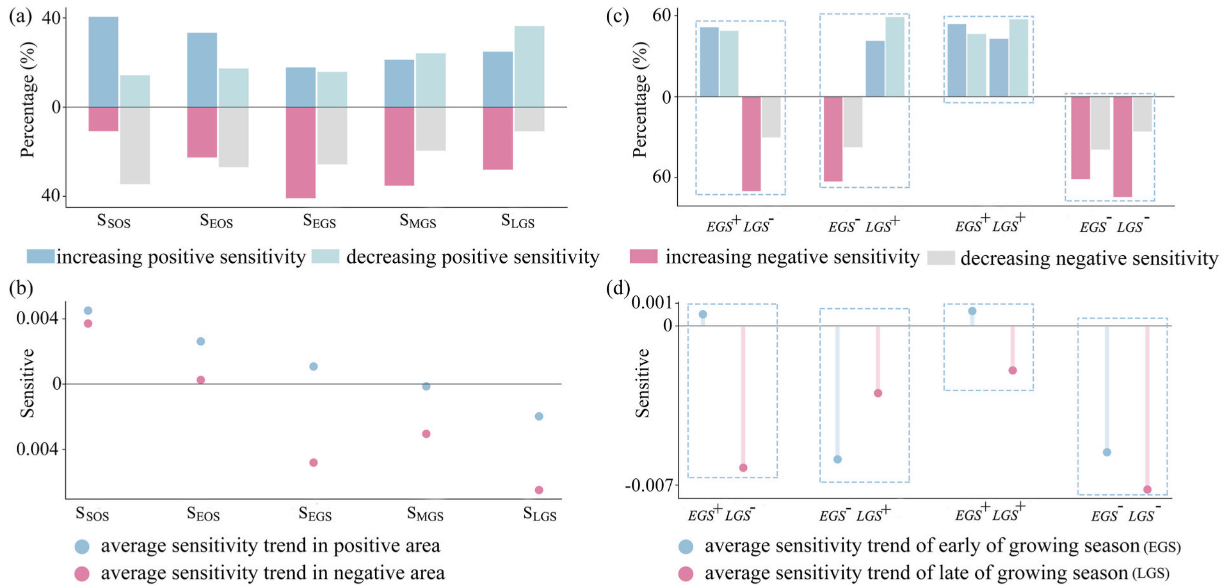

Fig. 4. Trends of GPP sensitivity to different phenological factors. **a**, The area fraction of grid cells with different sensitivity trend to start of growing season (SOS), end of growing season (EOS), early-growing season (EGS), mid-growing season (MGS), and late-growing season (LGS) in different region. **b**, The blue points represent the mean trend of the positive sensitivity region, and the red points represent the mean trend of the negative sensitivity region. **c**, The area fraction of grid cells with different sensitivity trend for EGS and LGS in different phenological pattern. Above the 0 line in **a** and **c**, the area fraction of grid cells with increasing trends and decreasing trends in the positive sensitivity region is indicated, while the opposite indicates the area fraction of grid cells with increasing trends and decreasing trends in the negative sensitivity region. **d**, the mean sensitivity trend of EGS and LGS in different phenological pattern.

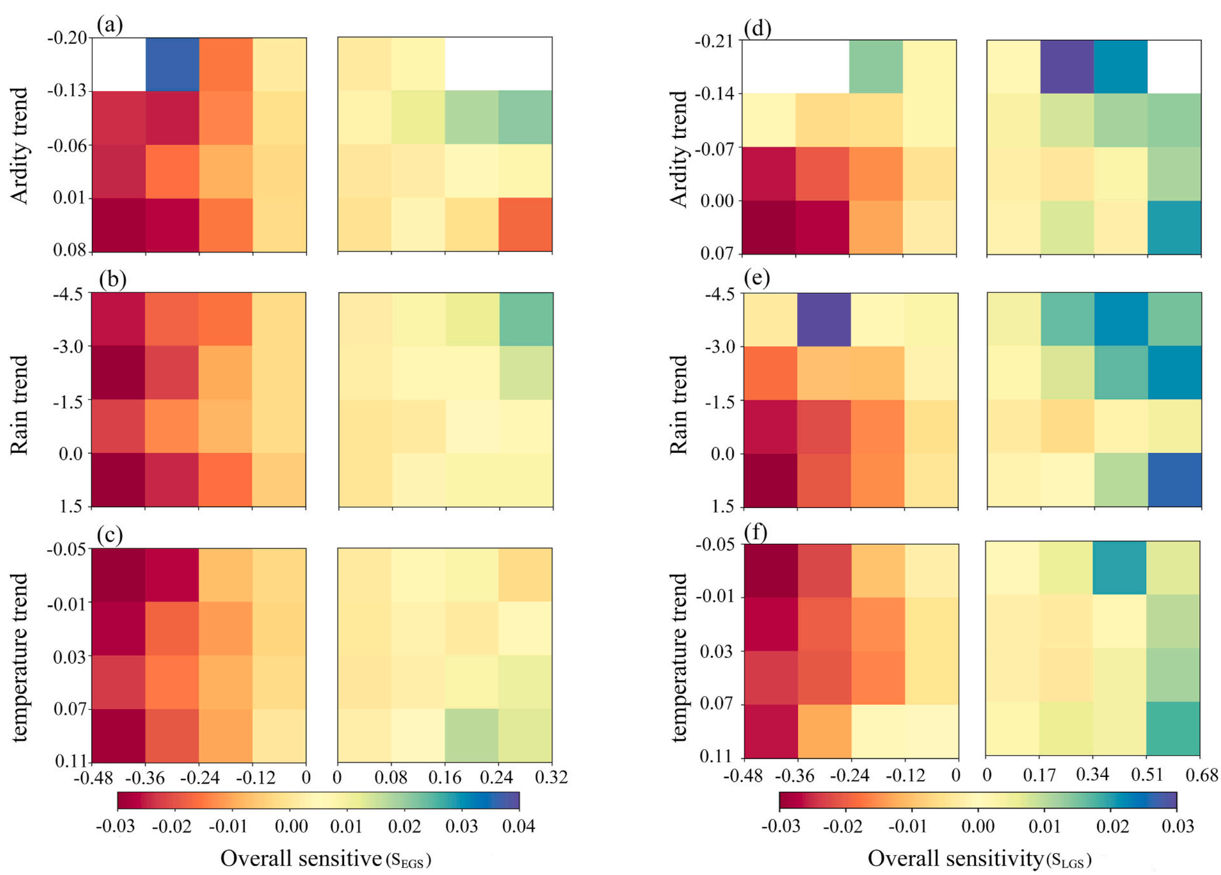

Fig. 5. Trends of GPP sensitivity to early-growing season and late-growing season grouped by climate trend and overall sensitivity. **a-c**, Colors indicate mean values of trends in GPP sensitivity to early-growing season (EGS) in each observational ensemble grouped by aridity trend, rain trend as well as temperature trend, and overall sensitivity. **d-f** Similar as in **a-c** but for trends in GPP sensitivity to late-growing season (LGS).

changes in S_{EGS} and S_{LGS}. Directly, the variations between S_{EGS} and S_{LGS} are independent of each other. Despite S_{EGS} changes occurring in the initial phase of the growing season, they do not impact the subsequent sensitivity to phenology. We also analyze the sensitivity trends using a 3-year and 10-year moving window, and the results did not show significant differences. Notably, the trend of increasing negative sensitivity becomes more pronounced at a large timescale (10-year).

3.4. Attribution of trends of GPP sensitivity to phenology

We perform an attribution analysis to understand sensitivity changes of alpine grassland GPP to phenology by coupling sensitivity and climate change trends. The chosen climate factors included annual average precipitation, temperature, and aridity, given their comprehensive assessment of the climatic conditions. We exclusively focus on the EGS and LGS in this context as the alpine grassland GPP is more strongly influenced by them compared to other phenological factors, and the observed coupling between sensitivity trends and climate change trend is captured relatively well.

The coupling between sensitivity trends and climate changes shows an evident pattern (Fig. 5). As overall sensitivity and precipitation trends substantially decrease, the increasing trend of positive S_{EGS} and S_{LGS} is strongly decreasing, while the decreasing trend of negative S_{EGS} and S_{LGS} is strongly increasing. On the other hand, we found that the significant increasing trend of positive S_{EGS} and S_{LGS} is accompanied by a substantial increase in overall sensitivity and temperature trends, while negative sensitivity trends decrease significantly in regions with higher overall sensitivity and substantial decreases in temperature trends. Sensitivity trends were influenced by precipitation and temperature, and aridity index offers insight into their collective impacts. The results show that the significant decrease in sensitivity trends for positive S_{EGS} and S_{LGS} is accompanied by a substantial increase in overall sensitivity and aridity trends, while negative sensitivity increases significantly.

The findings of our study clearly reveal the fact that in alpine grasslands of Northern Tibetan Plateau, warm and humid climate decreased the positive GPP sensitivity to phenology, whereas amplifying the negative sensitivity to phenology. This fact is particularly notable in regions with the higher overall sensitivity. Significantly, precipitation changes play a determinant role in changes in phenological sensitivity. Against the backdrop of climate warming, the more precipitation, the more substantial the increasing trend of the negative phenological sensitivity, whereas the less precipitation, the more substantial the decreasing trend of the positive phenological sensitivity. Overall, our evidence unequivocally demonstrates that climate change in the northern Tibetan Plateau is restructuring the phenology-GPP response dynamics in the region.

4. Discussion

4.1. Different GPP sensitivity to spring and autumn phenology

The effects of phenology on GPP included biophysical feedbacks, physiological changes and other seasonal processes (Piao et al., 2019; Lian et al., 2020, 2021). Our results show the seasonal difference in the impact of vegetation phenology on GPP. Firstly, we observed a negative sensitivity of alpine grassland GPP to the duration of EGS in most regions, with being particularly pronounced in areas characterized by highly favorable climates. An experimental study also reveals that an earlier start and end of the rapid growth period for vegetation can be advantageous for enhancing GPP (Wang et al., 2020a). The changes in the duration of EGS may lead to changes in water cycles in alpine ecosystems, thus resulting in negative feedback. A prolonged EGS means heightened water demand. As vegetation biomass and temperature rise, the transpiration and water consumption also increase, intensifying vegetation water stress (Wolf et al., 2016; Buermann et al., 2018; Lian et al., 2020; Wang et al., 2023). Our findings support this potential mechanism that the sensitivity response curve to aridity index and temperature exhibits a steeper incline than that to precipitation, indicating a greater negative sensitivity to decreased water availability. Previous studies have also revealed the pivotal role of precipitation in influencing carbon sequestration in grassland ecosystems (Wang et al., 2023; Zhang et al., 2023). Additionally, the decrease in soil fertility and the increase in water competition leaded by a prolonged EGS also negatively impact GPP (Wang et al., 2021).

In contrast to the EGS, the prolonged LGS positively impacts GPP in alpine grasslands. This beneficial effect may be due to physiological changes by climate change. Prolonged LGS are often accompanied by higher temperatures and precipitations (Li et al., 2016; Liu et al., 2016b), which decelerate the chlorophyll degradation process to slow down the senescence in plants (Lang et al., 2019; Ren and Peichl, 2021). The physiological activity of vegetation largely depends on temperature and strengthens with temperature and water availability increase (Yang et al., 2015; Cong et al., 2016; Ren and Peichl, 2021). Prolonged LGS provides a longer the carbon uptake period and ensure the enough carbon accumulation (Shen et al., 2022; Wang et al., 2023). These two key underlying processes jointly determine GPP dynamics. Our findings corroborate this perspective by indicating a notably higher sensitivity of GPP to LGS in regions with higher temperatures and precipitation compared to other periods. Another potential explanation is that the temperature rise diminishes the likelihood of frost damage in autumn (Liu et al., 2018). Although a prolonged LGS may lead to increased water stress, its beneficial impacts outweigh the potential drawbacks.

4.2. Roles of climate changes

Under the warm and humid climate in the Northern Tibetan Plateau, we observed that, in regions with higher sensitivity, the positive sensitivity of GPP to the EGS and LGS exhibit a notable decreasing trend, while the negative sensitivity of GPP exhibit a notable increasing trend. These sensitivity changes are primarily driven by climate changes, and are further influenced by the combined effects of vegetation on phenology and responses to climate changes. Increasing temperatures and precipitation directly contribute to increased photosynthesis, leading to alterations in vegetation biomass (Lehnert et al., 2016; Wang et al., 2020b), particularly in water-limited regions areas (Li et al., 2022; Wang et al., 2023). Previous research indicates that alpine grasslands benefit significantly from the enhanced photosynthesis induced by water, resulting in a substantial increase in vegetation biomass (Wang et al., 2021, 2023; Liu et al., 2024). However, the substantial increase in biomass can consequently elevate water demand (Jiao et al., 2021), along with heightened evapotranspiration (Yuan et al., 2019; Fu et al., 2022) and reduced runoff (Ukkola et al., 2016), causing water stress. The prolonged EGS may escalate the overall water demand of vegetation, thereby indirectly exacerbating water stress by climate change. Likewise, the prolonged LGS intensifies vegetation water stress, exerting a more pronounced influence on carbon accumulation due to reduced autumn moisture (Zhang et al., 2020a,b). In positive sensitivity regions, the heightened water stress from EGS and LGS may attenuate their positive feedback on carbon accumulation, leading to a decline in the sensitivity trends of GPP to EGS and LGS. Conversely, in regions with negative sensitivity, increased water stress intensifies negative feedback, resulting in an upward sensitivity trend.

In conclusion, the sensitivity trend changes are indirectly triggered by water stress caused by climate change. As a result, the warm and humid climate of the Northern Tibetan Plateau may modify the effect of phenological changes on vegetation GPP through the biophysical processes. The increasing temperature and precipitation significantly promote vegetation growth, but also increases water demand, which exacerbating water stress (Lian et al., 2020; Wang et al., 2023). Prolonged EGS and LGS lead to higher water consumption, further intensifying vegetation water stress. These processes suggest that the carbon benefits of alpine grassland derived from phenological changes will decrease.

4.3. Implications and limitations

In the current era of climate change, our results indicate a warning sign that phenological changes potentially limit the carbon benefits of alpine grassland derived from ongoing climate changes. Our study revealed the influence mechanism of phenological changes to carbon accumulation in alpine grasslands and discussed how this mechanism is influenced by climate change. Considering the pivotal role of alpine grasslands in terrestrial carbon cycling, our finding holds significant importance for the realization of China's and global carbon neutrality objectives. This sensitivity model is most applicable to high-altitude alpine grasslands undergoing warm and humid climate transitions. Other arid regions with analogous climatic and hydrological feedbacks may also exhibit similar patterns. Adapting this model requires meeting critical criteria: firstly, warming trends coupled with limited water retention (e.g., shallow soils and high evapotranspiration rates); secondly, vegetation adapted to cold conditions with shallow roots, rendering it vulnerable to seasonal water scarcity; and finally, comparable phenological dynamics (e.g., pronounced growing season extensions under warming). In essence, the model offers a robust lens for high-altitude systems but demands tailored adaptations elsewhere.

There are several limitations that should be considered when generalizing the findings of this study. First, while the study explains the sensitivity trend of alpine grassland GPP from a hydrological perspective in the context of climate change, other factors may also impact this sensitivity trend. For example, changes in stomata conductance driven by the increasing global CO_2 concentration (Zhang et al., 2022b), and underground microbial processes related to permafrost melting due to climate warming (Wu et al., 2021). Further studies focusing on these aspects could provide valuable insights to complement this framework. Second, different satellite proxies may introduce uncertainties. For example, the datasets used here employed GPP as a proxy for photosynthesis, which may introduce different results compared to greenness indices such as NDVI and EVI (Zeng et al., 2020). In addition, the abundance of different vegetation types with different phenological patterns has an influence on the signal of remote sensing (Meng et al., 2017, 2024), which also challenges the remotely sensed findings. Hence, there is an urgent need for diverse satellite datasets and precise ground-level data to supplement our research findings. Future researches should investigate the phenomena and potential mechanisms highlighted in our study at a finer scale to enhance our comprehension of the dynamics of alpine vegetation.

5. Conclusion

Environmental changes directly or indirectly impact the annual total GPP by influencing vegetation phenology. However, few studies have examined how phenological changes affects vegetation GPP. Our study conducted the sensitivity analysis to assess the impact of five phenological factors (SOS, EOS, EGS, MGS, LGS) on vegetation GPP using explainable machine learning. We determined that the negative impact of EGS and the positive impact of LGS on alpine grassland are predominant. However, in the positive sensitivity area, the warm and humid climate diminish the sensitivity of GPP to EGS and LGS, while increasing this sensitivity in negatively-sensitive areas. The study highlights the warm and humid climate amplify the negative effect of phenology on alpine ecosystems, which potentially limiting the carbon benefits derived from ongoing climate changes. The research results clarified the impact of phenological changes on the alpine grassland GPP and could provide valuable insights into the influence of climate change on the grassland carbon cycle.

CRediT authorship contribution statement

Yuanguo Liu: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Xiaoke Zhang:** Writing – review & editing, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mingze Sun:** Writing – review & editing. **Xindong Du:** Writing – review & editing, Visualization. **Qihao Zhu:** Writing – review & editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126680.

Data availability

Data will be made available on request.

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