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Resilience and sensitivity of ecosystem carbon stocks to fire-regime change in Alaskan tundra

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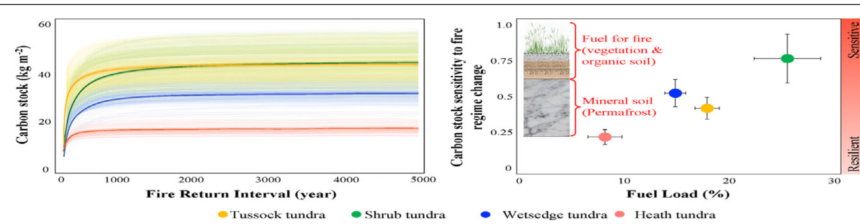
HIGHLIGHTS

- Carbon release from permafrost drives threshold decline of tundra carbon stock.
- Vulnerability to fire regime change is associated with tundra vegetation type.
- Predicted fire regime shifts turn long-standing carbon sink to atmospheric source.

GRAPHICAL ABSTRACT



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ABSTRACT

Fire disturbance has increased in some tundra ecosystems due to anthropogenic climate change, with important ramifications for terrestrial carbon cycling. Assessment of the potential impact of fire-regime change on tundra carbon stocks requires long-term perspectives because tundra fires have been rare historically. Here we integrated the process-based Dynamic Organic Soil version of the Terrestrial Ecosystem Model with paleo-fire records to evaluate the responses of tundra carbon stocks to changes in fire return interval (FRI). Paleorecords reveal that mean FRIs of tundra ecosystems in Alaska ranged from centennial to millennial timescales (200–6000 years) during the late Quaternary, but projected FRIs by 2100 decrease to a few hundred years to several decades (70–660 years). Our simulations indicate threshold effects of changing FRIs on tundra carbon stocks. Shortening FRI from 5000 to 1000 years results in minimal carbon release (<5%) from Alaskan tundra ecosystems. Rapid carbon stock loss occurs when FRI declines below 800 years trigger sustained mobilization of ancient carbon stocks from permafrost soils. However, substantial spatial heterogeneity in the resilience/sensitivity of tundra carbon stocks to FRI change exists, largely attributable to vegetation types. We identified the carbon stocks in shrub tundra as the most vulnerable to decreasing FRI because shrub tundra stores a large share of carbon in combustible biomass and organic soils. Moreover, our results suggest that ecosystems characterized by large carbon stocks and relatively long FRIs (e.g. Brooks Foothills) may transition towards hotspots of permafrost carbon emission as a response to crossing FRI thresholds in the coming decades. These findings combined imply that fire disturbance may play an increasingly important role in future carbon balance of tundra ecosystems, but the net outcome may be strongly modulated by vegetation composition.

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1. Introduction

Wildfire occurrence in high-latitude tundra ecosystems has increased over past decades (French et al., 2015), joining the surge of extreme fire events burning across other types of ecosystems and climatic zones (e.g. boreal Eurasia, Scholten et al., 2021; American west, Radeloff et al., 2018; and tropical savanna, Lindenmayer and Taylor, 2020). The activation of wildfire in the far north attracts special attention because it may bring unprecedented consequences in a region that has rarely burned in the past (Hu et al., 2015). In particular, tundra ecosystems are underlain by permafrost of various ground-ice content that preserves ~50% of global organic soil carbon (Schuur et al., 2015). The dynamics of this enormous carbon pool may have global-scale repercussions, but its responses to the projected shifts in fire regime remain highly uncertain (Genet et al., 2018; McGuire et al., 2018).

Previous studies revealed complex feedbacks between fire disturbance and tundra carbon stocks (Abbott et al., 2016; Mack et al., 2011). On the one hand, the organic-rich soils and flammable tundra vegetation imply potential sensitivity (defined as the degree to which an ecosystem responds to disturbance, Seddon et al., 2016) of tundra carbon stocks to fire disturbance (Higuera et al., 2008, 2011). This is well manifested by the 2007 Anaktuvuk River Fire that scorched across 1039 km^2 of tundra landscape and released a pulse of ~2.1 Tg carbon to the atmosphere (Mack et al., 2011). As climate warming continues, similar events may become more common, raising the possibility of massive carbon stock loss from tundra ecosystems. On the other hand, vigorous regeneration of tundra vegetation, even in severely burned areas (Bret-Harte et al., 2013), implies a degree of resilience (defined as the ability to return to pre-disturbance state following fire, Poorter et al., 2016) of tundra ecosystems to fire disturbance. Specifically, primary productivity of vascular plants equaled that of unburned tundra four years after fire, and total biomass of graminoids returned to preburn levels within five years (Bret-Harte et al., 2013; Jiang et al., 2015). The rapid ecosystem recovery associated with biotic feedbacks starkly contrast with the estimated mean fire return interval (FRI) of ~5000 years over the past 12 millennia in this region (Chipman et al., 2015), illuminating the prospect of carbon restoration via biomass. Therefore, it remains unclear whether predicted fire-regime shifts will convert tundra ecosystems to large atmospheric carbon sources, or only introduce transient carbon stock loss without long-term consequences.

Here we conducted a diagnostic analysis for contemporary tundra ecosystems to gain insights into three fundamental questions regarding carbon stock resilience/sensitivity. First, where are the most resilient and sensitive tundra ecosystems to fire-regime change? Second, what are the attributes underpinning carbon stock resilience in tundra ecosystems? Third, how close are contemporary tundra ecosystems to losing this resilience, and if lost, what are the consequences on tundra carbon stocks? To isolate the impacts of changing fire regime on tundra carbon stocks, we modeled carbon stocks as a function of FRI by constraining all other variables using the process-based Dynamic Organic Soil version of Terrestrial Ecosystem Model (DOS-TEM). We used FRI as proxy for fire-regime, because (1) FRI represents one of the most ecologically significant metrics of fire disturbance (Hoffmann et al., 2012; Kelly et al., 2016), (2) FRI is the most well-characterized metric of tundra fire-regime with reconstructed history dated back to 35,000 years BP (Chipman et al., 2015; Higuera et al., 2011), and (3) fire rotation period (an index closely related to FRI) is projected to shift substantly in the 21st century (Young et al., 2017). This study is built upon paleoecological analyses of natural FRI variations over the late Quaternary, modern FRI observations (1950–2020), and predicted FRI in response to climate change by 2100. Our results illustrate how carbon stock resilience to shifting fire regime may play out across heterogenous tundra landscape. The improved information may facilitate better understanding of future terrestrial-atmospheric feedbacks in one of the most fast-changing biomes on Earth.

2. Materials and methods

2.1. Study area

Our study area encompasses four Alaskan tundra ecoregions that differ in fire history, vegetation type and climate regime (Fig. 1): Brooks Foothills, Noatak River Watershed (Noatak), Brooks Range Transition (Brooks Transition) and Yukon-Kuskokwim Delta (YK Delta). The Brooks Foothills is characterized by a paucity of fire disturbance (Fig. 1a), with an estimated mean FRI of 5300 years during the late Quaternary (Fig. 1c). The region is dominated by shrub and tussock tundra (Fig. 1b) with mean summer (June–September) temperature (MST) of 10.1 °C, and total summer precipitation (TSP) of 123.7 mm (Fig. 1d). The Noatak is situated in northwestern Alaska, characterized by relatively warm and humid climate (MST of 11.6 °C and TSP of 191.3 mm, Fig. 1d). The Noatak has a relatively active fire-regime in the flammable tundra lowlands, where reconstructed fire history based on lake sediment cores revealed a mean FRI of ~200 years over the past 6000 years (Fig. 1c), a regime comparable to those of modern boreal forests (Higuera et al., 2011; Kelly et al., 2013). Vegetation in the Noatak is predominately shrub tundra and tussock tundra (Fig. 1b). The Brooks Transition is an ecotone between Arctic tundra and boreal forests of central Alaska (Fig. 1a). The regional MST and TSP is 11.3 °C and 185.5 mm, respectively (Fig. 1d). Vegetated area in the Brooks Transition is characterized by a mixture of shrub, tussock and heath tundra (Fig. 1b), and regional mean FRI is estimated to be ~1600 years during the late Quaternary (Fig. 1c). The YK Delta is the warmest and wettest tundra ecosystem among the four ecoregions, with MST of 12.2 °C and TSP of 202.8 mm (Fig. 1d). The estimated mean FRI of YK Delta is ~6000 years during the late Quaternary (Fig. 1c, Chipman et al., 2015), and the landscape is largely characterized by wetsedge tundra and shrub tundra (Fig. 1b).

2.2. Model description

We used the DOS-TEM to simulate the relationship between FRI and ecosystem carbon stocks across Alaskan tundra ecosystems (Fig. 2). The DOS-TEM is a process-based, spatially-explicit ecosystem model that has been extensively validated in tundra and boreal forests (Genet et al., 2018; Yi et al., 2013). The DOS-TEM has been widely implemented in the studies of carbon and nitrogen cycling between soil, vegetation, and the atmosphere, and it is capable of realistically reproducing the temporal patterns of postfire carbon recovery and hydrothermal dynamics in permafrost soils (Euskirchen et al., 2016; Genet et al., 2018). Specifically, the model has been well calibrated for a diversity of tundra ecosystems to represent the vertical complexity of structured soil horizons in the unique permafrost environment (Genet et al., 2013, 2018).

The DOS-TEM has four interacting modules (Fig. 2). The environmental module (EnvM) takes inputs of climate (e.g. monthly temperature and precipitation) and topography (e.g. slope and elevation) coupled with the outputs from the ecological module (EcoM) and dynamic organic soil module (DOSM) to compute biophysical processes in soil and the atmosphere. In particular, the EnvM adapts the two-directional Stefan Algorithm to simulate soil temperature and soil moisture conditions within each soil horizon ranging from the surface moss layer through the organic soil to the deep mineral soil horizons. It has been used to satisfactorily reproduce the dynamic movement of the freeze-thaw front and the active-layer thickness in variable Arctic and sub-Arctic ecosystems (Yi et al., 2013; Yuan et al., 2012).

The EcoM explicitly simulates the dynamics of carbon and nitrogen production, decomposition and transportation between vegetation, soil and the atmosphere driven by input data on climate, vegetation and atmospheric CO_2 concentration. The model computes carbon and nitrogen stocks in each soil horizon and in the above- and belowground vegetation. Specifically, the vegetation inputs carbon and nitrogen to the soils via litterfall. The aboveground litterfall is only

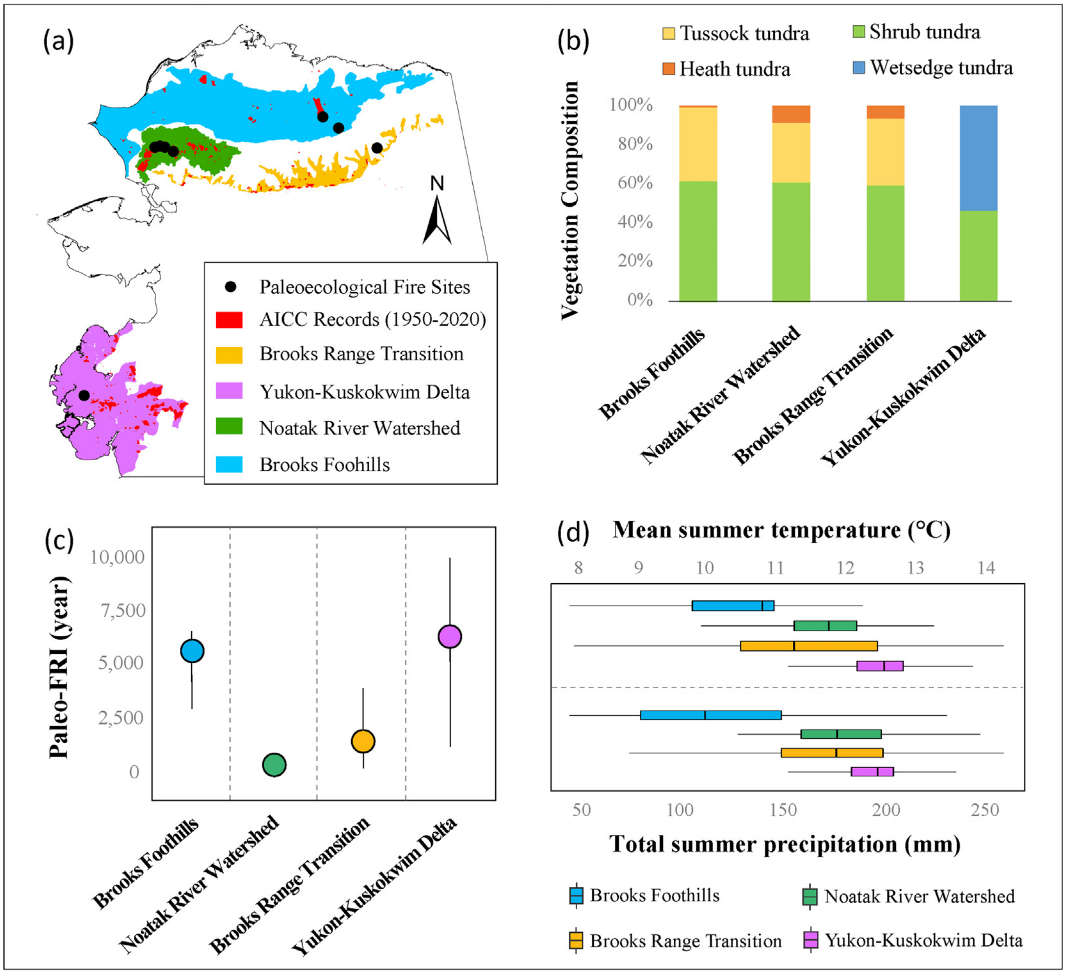

Fig. 1. Study area. (a) Map of the four Alaskan tundra ecoregions. The fire perimeters shown in red refer to the Alaska Interagency Coordination Center (AICC, http://fire.ak.blm.gov/) observational data archive. (b) Composition of vegetation types in each ecoregion. (c) Paleoecological analyses (Chipman et al., 2015; Higuera et al., 2011) of long-term fire return intervals (means ± ranges). (d) Boxplot of summer temperature and precipitation by ecoregion.

incorporated into the surface organic soil, whereas belowground litterfall (i.e. dead roots, assumed to be proportional to aboveground litterfall based upon the aboveground to belowground net primary productivity ratio) is assigned to different soil horizons depending on the distribution of fine roots with soil depth (Yi et al., 2013). The simulation of carbon and nitrogen is informed by outputs from the other three modules regarding soil environments (by EnvM), soil structures (by DOSM) and fire occurrence (by the disturbance module, DSBM). In turn, the EcoM outputs information on litterfall and leaf area index to the DOSM and the EnvM, respectively.

The DOSM is at the center of DOS-TEM. It defines soil structure and divides soil column from top to bottom into distinct horizons (Fig. 2): the fibrous organic soil horizon (slightly decomposed fibric organic matter), the amorphous organic soil horizon (moderately to heavily decomposed organic matter), and the mineral soil horizon (i.e. permafrost soil). The DOSM updates the thickness and the carbon stocks of each organic horizon on annual basis after they are modified by ecological processes (e.g. litterfall and decomposition, from EcoM) or by fire disturbance (e.g. vegetation and organic layer consumption, from DSBM) (Yi et al., 2010, 2013). In the DOSM, the carbon stocks move downwards along the soil column with the accumulation of organic matter, and are eventually incorporated into the mineral horizons (Fig. 2). Fire disturbance removes part of the organic soils, and converts the remaining fibrous layers to amorphous layer. Meanwhile, a thin fibrous layer (2 cm) is immediately added on top of the amorphous layer for organic matter to re-accumulate after fire (Yi et al., 2010).

The DSBM uses information on topography, fire disturbance, soil environments (output from the EnvM), and soil structures (output from the DOSM) to calculate the dynamics of carbon and nitrogen associated with fire disturbance (Fig. 2). The dynamics of nitrogen is computed based upon the carbon to nitrogen ratio in vegetation and soils (Yi et al., 2010). The nitrogen lost to the atmosphere by fire consumption is reintroduced to the system annually via productivity. The simulated carbon emission as well as the fate of unburned carbon in the ecosystem is influenced by fire severity. Due to the scarcity of fire severity data in tundra ecosystems, our study assumes that fire severity is uniform across tundra ecosystems with a median 32% of plant biomass and soil organic carbon loss in each fire (Mack et al., 2011).

2.3. Model application

We ran the DOS-TEM at a 10 km × 10 km resolution ($n = 2288$ pixels) across all vegetated area of the four tundra ecoregions to encompass sufficient spatial heterogeneity while maintaining computational feasibility. The model was forced with long-term mean climate data (1980–2010) based on downscaled CRU TS v.4.05 dataset accessible at the Scenarios Network for Alaska and Arctic Planning (Yuan et al., 2012). There are four climatic inputs, monthly air temperature, precipitation, vapor pressure, and incoming shortwave radiation (Table S1 in supplementary materials). The soil texture and vegetation type inputs were derived from the Global Gridded Soil dataset (Hengl et al., 2017) and the NLCD Land Cover dataset (Homer et al., 2015), respectively

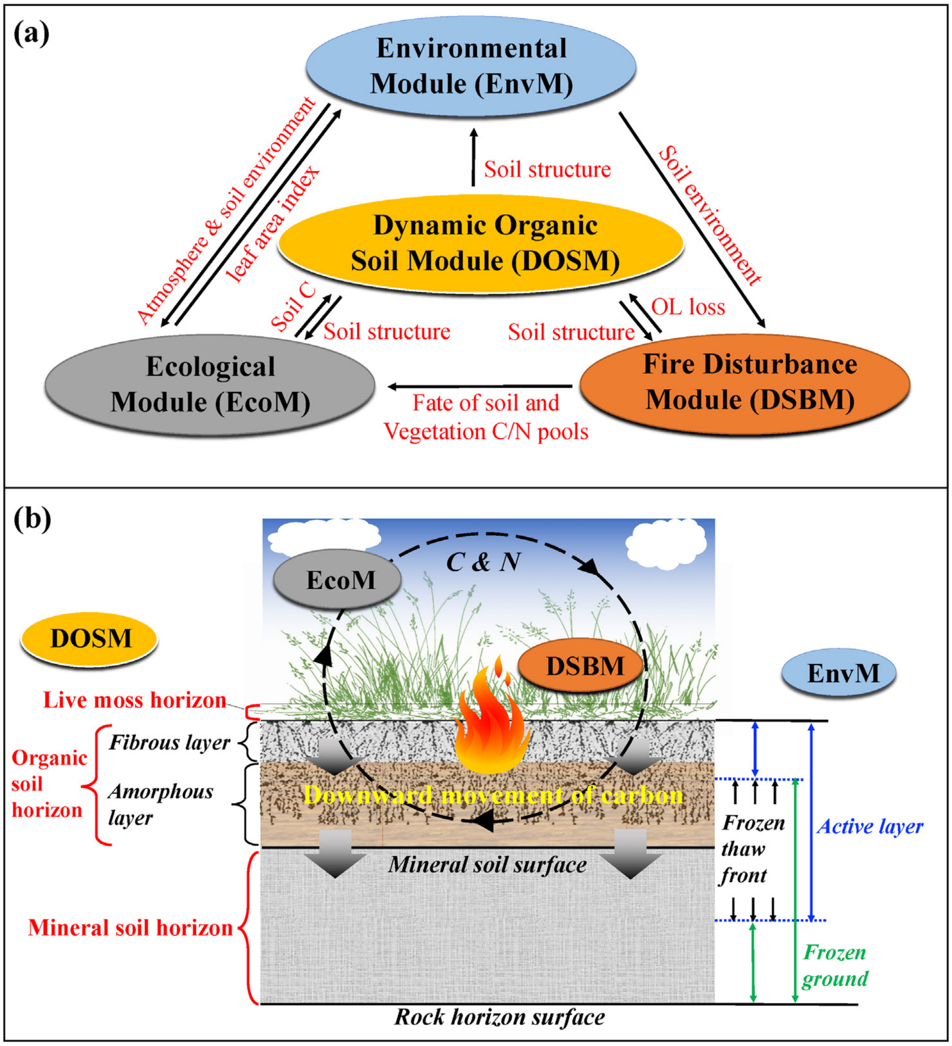

Fig. 2. Model structure. (a) Schematic representation of data exchange among modules (Yuan et al., 2012) in the Dynamic Organic Soil version of the Terrestrial Ecosystem Model (DOS-TEM). (b) Key carbon (C) and nutrient (N) pools/processes represented in DOS-TEM. The DOSM, EcoM, EnvM and DSBM respectively correspond to the dynamic organic soil module, ecological module, environmental module and disturbance module.

(Table S1 in supplementary materials). The DOS-TEM does not incorporate dynamic vegetation change, and vegetation type is treated as constant in the model. Each pixel was assigned to one vegetation type, determined by aggregating the NLCD dataset to 10 km by 10 km using “majority”. The topography inputs (e.g. elevation, aspect, and topographic slope) were accessed from the ArcticDEM Database (Table S1 in supplementary materials). The simulated ecosystem carbon stocks in the DOS-TEM are distributed among four carbon pools: vegetation pool, fibrous organic soil pool, amorphous organic soil pool, and mineral soil pool (Fig. 2).

To estimate the baseline carbon stocks (the fire-free scenario), we ran the model with the DSBM turned off. By comparing simulations forced with different fire scenarios to the baselines, we were able to assess the impacts of fire disturbance on tundra carbon stocks (Fig. S1 in supplementary materials). We computed fuel load of each ecosystem using results of the baseline simulations. Fuel load (%) is defined as the ratio of fuel (sum of combustible carbon pools: vegetation and organic soils) to overall ecosystem carbon pool (sum of combustible and noncombustible mineral soil carbon pools). Fuel load reflects the stratified structure of carbon stocks within an ecosystem, and thus influences landscape flammability. Under the same amount of total carbon stocks, ecosystems of high fuel load tend to lose more carbon to fire consumption than those of low fuel load.

We then turned on the DSBM and ran the model for a range of FRIs. The input FRIs were informed by paleoecological FRI records (Chipman et al., 2015), modern FRI estimates (Rocha et al., 2012), and predicted FRI by 2100 (Young et al., 2017). We simulated ecosystem carbon stocks at each FRI, ranging from 10 to 5000 years at 50 years increment (i.e. 101 simulations per pixel) (Figs. S1–S2 in supplementary materials). For each FRI, we ran the model by repeatedly burning the tundra until reaching equilibrium (i.e. constant soil and vegetation carbon stocks). All simulations were initiated as unburned and ran for 45,000 model years (Fig. S1 in supplementary materials). The carbon stocks averaged across the span of FRI at equilibrium was then used as the stocks associated with the specific fire (FRI) regime (Fig. S2 in supplementary materials). We then assembled the simulations of each FRI scenario, and plotted the simulated carbon stocks against the range of FRIs to evaluate how ecosystem carbon stocks change as a function of FRI.

2.4. Model validation

We extracted the spatially-explicit FRI predictions of modern Alaskan tundra (1950–2010) by Young et al. (2017) corresponding to the four tundra ecoregions (Fig. 1). The resulting dataset was resampled to 10 km by 10 km resolution using bilinear interpolation. We ran the DOS-TEM for each pixel forced with the predicted FRI to model present-day soil carbon stocks. The simulated carbon stocks from the fibrous, amorphous, and mineral soils were summed as total soil carbon, and the results were compared to the Northern Circumpolar Soil Carbon Database (NCSCD v2) for model validation (Hugelius et al., 2014).

2.5. Data analysis

Piecewise regression was conducted on the simulated carbon stock of each pixel to identify the break point (i.e., threshold FRI) where the change of carbon stock begins to accelerate with decreasing FRI. The threshold FRI was used as an indicator of carbon stock resilience/sensitivity to fire-regime change. To be specific, ecosystems with relatively small (short) threshold FRIs imply that abrupt carbon stock loss from the system is unlikely unless future FRI decreases substantially from the present FRI, whereas ecosystems exhibiting relatively large (long) threshold FRIs suggest that rapid carbon stock loss may initiate with a small shift of FRI from present. After the threshold FRIs of all pixels were identified, we normalized the results to the range of 0 to 1 (the S-score, a unitless measure of carbon stock resilience), with 1 representing the greatest sensitivity and 0 the greatest resilience of tundra carbon stocks to shortening FRI.

To identify potential drivers and their relative contribution to carbon stock resilience, we analyzed the S-scores with a set of candidate predictors using multiple linear regression. We selected a total of 12 predictors (Table S1 in supplementary materials) based upon previous studies on carbon cycling and fire emissions in high latitudes (Abbott et al., 2021; Higuera et al., 2008, 2011; Hu et al., 2010; Jiang et al., 2017; Kelly et al., 2016; Klupar et al., 2021; Mcguire et al., 2009; Parker et al., 2015; Rocha et al., 2012; Rocha and Shaver, 2011; Rocha and Shaver, 2011; Walker et al., 2019, 2020; Young et al., 2017). These variables can be broadly categorized into two groups: (1) meteorological variables, including summer air temperature, summer precipitation, length of growing season, solar radiation, vapor pressure deficit (Harris et al., 2014), and surface soil temperature (Luo et al., 2014); and (2) biophysical variables, such as vegetation type, permafrost probability (Pastick et al., 2015), topographic position, elevation, slope, and aspect (Table S1 in supplementary materials). All variables were resampled to the same spatial resolution (10 × 10 km) using bilinear or nearest-neighbor interpolation for continuous and categorical data, respectively. Our approach was to initially fit the model with all candidate variables, and remove insignificant variables in a stepwise fashion following the principle of maximum parsimony and avoiding cross-dependent or cross-correlative variables (*Pearson* correlation test, $|\rho| > 0.7$). Eventually, we achieved a single reduced model that retains only significant variables at the level of $\alpha < 0.05$. All statistical analyses were performed in R (v 4.1.1) with the packages of *gbm* (Ridgeway, 2019), *raster* (Hijmans et al., 2021) and *segmented* (Muggeo, 2008).

3. Results

The simulated soil carbon stocks generally matched the amount and the spatial pattern of NCSCD carbon estimates for the four tundra ecoregions ($R^2 = 0.77$, $P < 0.001$; Fig. S3 in supplementary materials), showing the highest stocks in the Brooks Foothills and the lowest stocks in the Brooks Transition (Fig. S4 in supplementary materials). However, our simulation overestimated soil carbon stocks for shrub tundra (9.7 kg m^{-2}) and tussock tundra (11.4 kg m^{-2}) in YK Delta and Noatak due to the fact that the DOS-TEM is primarily calibrated in the relatively carbon-rich Brooks Foothills ecosystems (Table S2 in supplementary materials).

Our control simulations (i.e. fire-free scenario) suggest vast spatial heterogeneity in baseline tundra carbon stocks, reflecting spatially-variable climate, vegetation and topographical conditions in the study domain. The greatest proportion of tundra carbon stocks resides in mineral soil horizons (i.e. permafrost soils), accounting for ~80% of total carbon stocks. Compared at the maximum FRI of 5000 years (an analogy to the fire-free scenario), we found that the Brooks Foothills has the largest tundra carbon stocks (43.7 kg m^{-2}) among all, followed by YK Delta (40.2 kg m^{-2}), Noatak (30.1 kg m^{-2}), and Brooks Transition (27.2 kg m^{-2}) (Fig. 3).

As fire regime shifts towards shorter FRIs, tundra carbon stocks exhibit non-linear behavior with changing fire regime (Figs. 3). The estimated mean threshold FRI of all tundra ecosystems is 824 ± 112 years ($n = 2288$). When compared between ecoregions, the threshold FRI of Brooks Transition is the longest (956 ± 132 years), followed by Brooks Foothills (880 ± 91 years), YK Delta (793 ± 76 years) and Noatak (724 ± 78 years) (Fig. 3). Except for Noatak, the estimated threshold FRIs are much shorter than the FRIs inferred from paleofire records (6000 years for YK Delta, 5300 years for Brooks Foothills, and 1600 years for Brooks Transition) or modern observations (2000 years for YK Delta, 4400 years for Brooks Foothills, and 1200 years for Brooks Transition).

Tundra carbon stocks remain relatively stable before FRIs decrease below the thresholds (Fig. 3-4). Shortening FRI from 5000 years to 1000 years causes slight carbon stock losses, mostly from the combustible organic soils, and the mineral carbon stock is comparatively intact (Fig. 4, and Fig. S1 in supplementary materials). Nonetheless, changes in FRI modify soil hydrothermal regimes. As compared to FRI at 5000 years, organic layer thickness at FRI of 1000 years decreases by 12.8% and active layer depth increases by 4.1% (Fig. 4). As FRIs shift further towards the threshold, carbon stock loss begins to accelerate. Once the threshold is crossed, rapid thinning of the insulating organic layers coupled with abrupt deepening of active layers incurs massive carbon release from deep mineral soil horizons (Fig. 4).

Our analysis with multiple regression model ($R^2_{adj} = 0.67$, $P < 0.0001$) revealed that the variation of threshold FRI (i.e. S-score, a unitless measure of carbon stock resilience) is largely determined by vegetation type (38%) and to a lesser degree by temperature (14%) and precipitation (8%). In particular, we found that fuel load (defined as the proportion of combustible carbon stock to overall carbon stock), a metric closely related with vegetation type, is a good indicator ($r = 0.71$) of carbon stock resilience. Particularly, shrub tundra has the highest fuel load (~25%) and demonstrates the greatest sensitivity (S-score ~ 0.7) to a shrinkage of FRI (Fig. 5). Rapid carbon stock loss begins

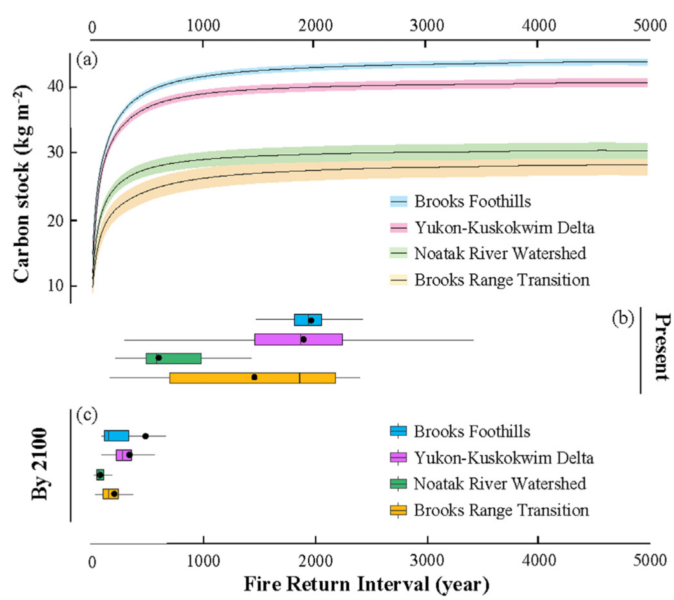

Fig. 3. Tipping-point behavior of tundra carbon stocks in response to fire-regime shifts. (a) Ecosystem carbon stocks change as a function of FRI. The shaded envelops represent 95% confidence interval. (b) Reconstructed FRIs of modern (1950–2010 CE) tundra ecosystems. (c) Predicted FRIs by 2100 CE in the four tundra ecoregions (Young et al., 2017).

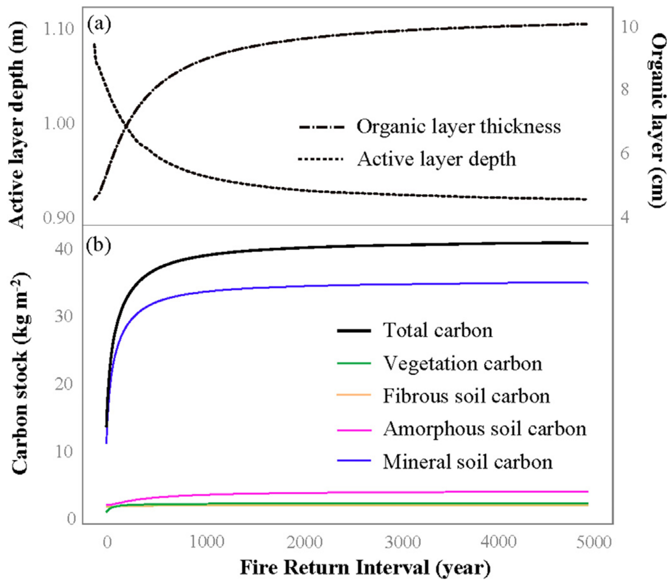

Fig. 4. Carbon stock loss from permafrost soils drives critical decline of ecosystem carbon stocks. (a) Active-layer depth and organic-layer thickness change with FRI. (b) Dynamics of different ecosystem carbon pools with FRI. Data shown here were the average of the four tundra ecoregions. Total carbon stock is the sum of individual ecosystem carbon pools: vegetation carbon pool, fibrous soil carbon pool, amorphous soil carbon pool, and mineral soil carbon pool.

in shrub tundra when FRI decreases towards ~1000 years (Fig. 5). In contrast, heath tundra has the lowest fuel load (~10%) and manifests the greatest resilience (S-score ~ 0.2) to shortening FRI. In these ecosystems, threshold stock loss does not occur until FRIs decrease considerably to ~200 years (Fig. 5). Tussock tundra and wetsedge tundra have intermediate fuel loads (14–18%) and moderate degree of carbon stock resilience (S-score between 0.3 and 0.6). Correspondingly, the estimated threshold FRIs of these ecosystems span a medium range between 400 and 850 years.

4. Discussion

The simulated tundra carbon stocks remain relatively stationary in response to FRIs changing from 5000 years to 1000 years – a range representative of fire regimes in most paleo and modern tundra ecosystems (Chipman et al., 2015; Higuera et al., 2011; Rocha et al., 2012). The resilience of tundra carbon stock to fire regime change is achieved by vegetation feedbacks, as supported by a number of field and remote-sensing observations (Bret-Harte et al., 2013; French et al., 2016; Jiang et al., 2015). Specifically, our simulation elucidates that fire disturbance introduces temporary attenuation of organic layers that extends thawing depth into perennially frozen horizons and mobilizes permafrost carbon pool (Fig. 4, and Fig. S1 in supplementary materials). Nonetheless, rapid returning of tundra vegetation gradually builds up organic layers that reestablishes soil thermal regime and refills the permafrost carbon pools (Fig. S1 in supplementary materials). This negative feedback gives rise to the simulated ecosystem carbon stock in dynamic equilibrium in spite of five-fold fire frequency change. However, it also entails that a net transfer of carbon stocks to the atmosphere may ensue once this internal vegetation feedback is overwhelmed by sufficient fire-regime shift.

Evidence is accumulating that anthropogenic climate change has induced a departure of contemporary fire regime from long-term norms in many ecosystems (Demenocal et al., 2000; Kelly et al., 2013). Altered fire regime can disrupt information and material legacies associated with ecosystem resilience, triggering directional, and sometimes abrupt changes in ecosystem functions (Johnstone et al., 2016; Scheffer and Carpenter, 2003). In this study, we identified a threshold FRI around 800 years, below which tundra ecosystems succumb to rapid stock loss and head towards atmospheric carbon sources. This non-linear, tipping-point behavior mirrors those detected in many other ecosystems in response to a variety of press and pulse disturbances. Studies in the savanna-forest ecosystems illustrate that surpassing certain FRI thresholds provokes sudden conversion of savanna to forests with potentially large consequences on regional carbon stocks (Hoffmann et al., 2012). More recently, in some boreal forests, increased wildfires triggered threshold changes in vegetation composition and converted historical carbon sinks to atmospheric sources (Barrett et al., 2011; Kelly et al., 2013, 2016; McLauchlan et al., 2014; Stralberg et al., 2018). Identifying tipping-elements is increasingly recognized as a key research priority as restoring ecosystem function is much more expensive than maintaining when critical thresholds exist (Arani et al., 2021).

Although our results suggest tipping-point behavior of all tundra ecosystems, the position of the tipping-point (i.e. S-score) varies considerably between ecosystems. As pointed out by Tepley et al. (2018), carbon stock resilience is ultimately determined by the counteraction between fire-induced stock change and the subsequent recovery. Following this paradigm, factors that amplify stock change elevate ecosystem sensitivity, pushing the system towards a net loss of carbon stocks. On the contrary, factors facilitating ecosystem recovery enhance

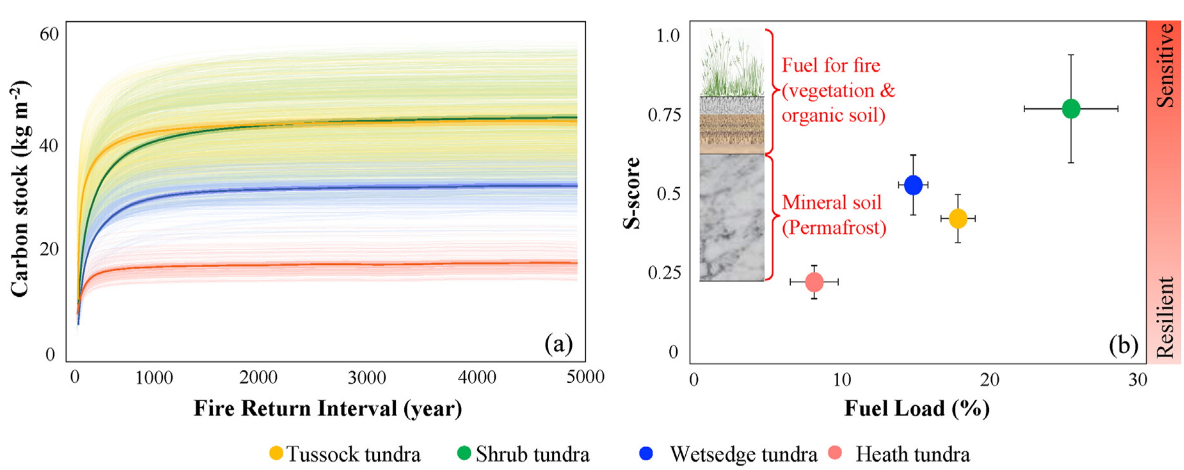

Fig. 5. The resilience/sensitivity of tundra carbon stocks to fire-regime change vary by tundra vegetation type. (a) Simulations of individual pixels (transparent lines), differentiated by tundra types. Solid lines and shaded areas respectively correspond to mean and 95% confidence interval of different tundra types. (b) The S-score (an unitless measure of carbon stock resilience to fire-regime change) is plotted against fuel load, defined as the percentage of combustible vegetation and organic soils in overall ecosystem carbon pool. The data is shown as mean ± one standard error.

resilience, tipping the balance in favor of carbon stock persistence. By analyzing the threshold FRIs with a range of environmental drivers, we identified vegetation type as the most influential factor responsible for the spatial variations of carbon stock resilience.

Tundra vegetation strongly dictates fuel abundance and ecosystem productivity (Martin et al., 2017; Hu et al., 2015), which closely regulate the magnitude of fire consumption (Mack et al., 2011) and the rate of postfire carbon recovery (Bret-Harte et al., 2013). In particular, we found that shrub tundra is the most vulnerable tundra type to shifting fire regime as it allocates a larger proportion of carbon stocks to the combustible biomass and organic soils (Sistla et al., 2013; Mekonnen et al., 2021) that elevates ecosystem flammability. Although large variability in fuel load and productivity exists within the same vegetation type due to spatially variable climate and topography, on average, shrub tundra loses 2–15 times more carbon stocks than other tundra types each fire. Consequently, it takes 0.5–3 times longer for shrub tundra to regain the stock than other tundra types in spite of the comparatively high productivity of shrub tundra. Therefore, as fire regime shifts, slowly recovering ecosystems represented by shrub tundra will allow subsequent fires to burn deeper and deeper into insulating soils that eventually mobilizes the enormous ancient carbon pool (Walker et al., 2019; Veraverbeke et al., 2021). In contrast, under similar magnitude of fire-regime shifts, relatively resilient ecosystems like tussock tundra may rapidly replenish organic soils (Bret-Harte et al., 2013) that allows re-stabilization of permafrost horizons shortly after fire. Thus, returning fires will only consume newly accumulated organics without long-term consequences on ancient carbon stocks (Mack et al., 2011).

With predicted shrub cover to increase by ~50% by 2050s in Arctic tundra (Pearson et al., 2013), this result may have profound implications for future carbon balance in high latitudes. Some studies suggest that the replacement of native tundra vegetation by more productive shrubs will enhance tundra carbon stocks (Loranty and Goetz, 2012; Sistla et al., 2013). Nevertheless, our results imply that restructuring of tundra carbon profile associated with shrubification (Sistla et al., 2013) may prime tundra landscape for wildfires, discounting or even reversing the benefits of biomass.

Tundra ecosystem has long been characterized by small, infrequent wildfires that contributes to the formation of substantive carbon reservoirs over geologic times (Hu et al., 2015). Although fire disturbance is anticipated to increase pervasively across tundra biome in coming decades, the predicted magnitude of fire-regime change is spatially heterogeneous (Moritz, 2012; Young et al., 2017). Particularly, the greatest fire-regime change is projected in areas where fire disturbance has been historically rare due to extreme climates (Chipman et al., 2015; Rocha et al., 2012). In the Brooks Foothills where low temperatures have strongly suppressed wildfires to burn every several millennia, regional carbon stocks have been allowed to accumulate into enormous size (Hugelius et al., 2014). Assuming FRIs of the Brooks Foothills will decrease to 300–400 years by 2100 as predicted, the estimated fire threshold will be crossed (Fig. 3). According to our simulations, such a degree of fire-regime change may translate into 13.7 kg C m^{-2} loss from the ecosystem. As a contrast, in ecosystems where fire disturbance has been historically active such as the Noatak – one of the warmest and most fire-prone tundra ecosystems on earth (Higuera et al., 2011; Hu et al., 2015), shifting fire-regime to the similar frequency of every ~300 years may cause a much smaller amount of carbon stock loss (6.9 kg m^{-2}). Although these estimates are speculative given uncertainties inherent in fire projections and our simulations, it underscores that tundra carbon stocks of the 21st century may be intimately linked to fire disturbance, with potentially heightened threat towards large, long-standing carbon sinks.

Process-based models offer a useful tool for analyzing ecosystem resilience (Johnstone et al., 2016; Scheffer et al., 2009). However, due to the inherent stochasticity of mechanisms involved and the numerous processes driving carbon stock variations, our ability to assess carbon stock resilience remains limited. Several factors exist that may cause a deviation from our expected fire thresholds, including (1) concurrent changes in other fire metrics, (2) interactions between fire and other disturbances or processes, (3) shifts in external drivers, and (4) uncertainty intrinsic to models as simplified representation of real ecosystems.

First, changes in other fire metrics, such as fire intensity, severity, and duration, may accelerate carbon stock loss from tundra ecosystems. In our simulation, these metrics were assumed to be spatially and temporally uniform, limited by the fact that they are poorly characterized in tundra landscape (Hu et al., 2015). As Arctic warming continues, changes in these metrics may greatly augment fire emissions, as already happening in some boreal forests (Kelly et al., 2013; Yuan et al., 2012). For instance, a study from interior Alaska detected that it is becoming more common for fires to burn overwinter that increase organic soil consumption (Scholten et al., 2021). These emerging fire behaviors may push high-latitude carbon pools towards early onset of threshold decline.

Second, synergy between fire and other disturbances/processes may generate unexpected outcomes. For example, retrogressive thaw slumps frequently follow after wildfires in ice-rich tundra that strongly modifies soil hydrology and surface energy balance (Chen et al., 2020; Jones et al., 2017; O'Donnell et al., 2012; Olefeldt et al., 2016; Quinton et al., 2011). Similarly, in situ and remote-sensing observations reveal complex interplay between tundra vegetation and wildfires that may dynamically modify carbon stock resilience (Abbott et al., 2021; Klupar et al., 2021; Parker et al., 2015). A study in the Brooks Foothills revealed that wildfire changed soil nutrient availability, leading to tussock tundra replaced by shrub dominance (Klupar et al., 2021). Such a shift in vegetation type may reorganize the landscape towards elevated fire risks. In contrast, a study in lowland Noatak indicated that fire disturbance destabilized soil moisture optima that initiated a transition from shrub tundra to wetsedge tundra, feeding negatively back to future fires (Chen et al., 2021). The diverse interactions between fire, permafrost and vegetation underscore the complexity of high-latitude ecosystems, and enormous knowledge gap needs to be filled before carbon stock resilience can be confidently quantified in the remote landscape.

Third, concurrent shifts in external forces, especially climate change and CO_2 fertilization, may exert countervailing effects on carbon stock resilience. For example, while warming may intensify wildfires to magnify carbon emission, a positive relationship is also found between temperature and productivity that can accelerate post-fire carbon accumulation (Chen et al., 2021; Jiang et al., 2017). Similarly, elevated CO_2 concentration may enhance plant productivity to boost post-fire carbon recovery (Higgins and Scheiter, 2012), but it may also raise fuel abundance and connectivity to escalate fire emissions. Therefore, comprehensive assessment of carbon stock resilience requires an integrated framework taking into consideration of all climate-driven processes at the same time, which may take decades to centuries to fully unveil.

Finally, model uncertainties in formulation and parameterization may have large influence on the results. This is especially true for sub-Arctic ecosystems like YK Delta, where long-term, broad-scale data is currently lacking for comprehensive model testing (Euskirchen et al., 2016; Genet et al., 2018). Although our model validation suggests that the DOS-TEM is generally capable of simulating carbon stocks of tundra soils without much overall bias (Fig. S3 and S4 in supplementary materials), substantial uncertainty remains regarding the representation of important ecosystem processes in response to wildfires, especially post-fire nitrogen dynamics, soil hydrology, and the transport of dissolved organic carbon (Genet et al., 2018; McGuire et al., 2018), all of which strongly influence soil carbon accumulation and therefore tundra carbon resilience to fire disturbance (Klupar et al., 2021; Parker et al., 2015).

Previous study in the extreme Anaktuvuk River Fire found that this unique event consumed ~50 years of carbon accumulation but emitted ~400 years of nitrogen accumulation (Mack et al., 2011). The excessive nitrogen loss may severely limit plant productivity and thus constrain long-term carbon uptake. However, depletion of soil nitrogen is not represented in the DOS-TEM due to the scarcity of data regarding tundra wildfires. In the model, the loss of nitrogen is assumed to be proportional to that of carbon based on the carbon to nitrogen ratio measured in tundra vegetation and soil. Thus, our simulation likely underestimates the time taken for carbon restoration after fire. Another source of uncertainty is associated with abrupt and often drastic changes of soil hydrology as exemplified by localized ponding or wholesale draining of hillslope tundra (Chen et al., 2020, 2021; Jorgenson et al., 2015). These disruptive processes exert cascading impacts on a myriad of ecosystem functions such as nutrient availability, vegetation composition and soil thermal regimes (Chen et al., 2020; Nauta et al., 2015). In spite of its significance, disruptive hydrological process is currently missing from the modeling framework due to enormous uncertainties surrounding permafrost thawing (McGuire et al., 2018; Schuur et al., 2015). Unlike gradual thawing conceptualized in the model, abrupt changes in soil hydrology often disrupt the entire soil profile that may aggravate carbon stock loss from deep horizons (Abbott and Jones, 2015; Jones et al., 2015; Turetsky et al., 2019). Moreover, postfire expansion and extension of drainage networks intensify lateral movement of dissolved organic carbon – a mechanism that may propel carbon export from the ecosystem (Frost et al., 2018; Jones et al., 2015). However, the spatial heterogeneity and unpredictability of these processes pose substantial obstacles for model parameterization. These factors combined may greatly lengthen the time taken for postfire carbon restoration or even prevent the ecosystem from returning carbon stocks to pre-fire states. Thus, our simulation may overestimate the resilience of contemporary tundra to fire regime change. However, with data accumulating from the integrated networks of palaeoecological records, field-based manipulative experiments, and broad-scale remote-sensing monitoring, we are optimistic that an improved understanding of the fire-carbon linkage will be endowed for more sophisticated model parameterization in future efforts.

5. Conclusion

In spite of large uncertainties, our study offers a risk analysis with clear management implications for tundra ecosystems. By isolating fire disturbance from other environmental drivers, we were able to diagnose when, where, and how tundra carbon stock may be modified in a shifting fire regime. The result may serve as a benchmark against which more complicated hypotheses can be tested. These findings, in combination with the projected fire activation across tundra landscape, highlight that future carbon balance in high latitudes will be increasingly hinged on fire disturbance with potentially large consequences on the feedbacks of the Arctic ecosystem to the atmosphere.

CRediT authorship contribution statement

Yaping Chen: Conceptualization, Methodology, Software, Writing - Original draft preparation, Data curation, Visualization, Investigation.

Ryan Kelly: Conceptualization, Data curation, Writing- Original draft preparation.

Mark Jason Lara: Validation, Writing - Reviewing and Editing.

Hélène Genet: Validation, Writing - Reviewing and Editing.

Melissa Lynn Chipman: Writing - Reviewing and Editing.

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Feng Sheng Hu: Conceptualization, Supervision, Writing - Reviewing and Editing.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.151482.

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