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Temperature dependence of ecosystem carbon, nitrogen and phosphorus residence times differs between subtropical and temperate forests in China

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ABSTRACT

Residence times of ecosystem carbon ($\tau_{e,C}$), nitrogen ($\tau_{e,N}$) and phosphorus ($\tau_{e,P}$) are closely related to efficacies of carbon and nutrients conservation within an ecosystem. However, estimates of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ together are very limited for forest ecosystems, and little is known about the environmental controls. Here we estimated $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ of 127 undisturbed forests based on observed carbon, nitrogen and phosphorus stocks and compiled 30 key variables related to climate, vegetation, soil and terrain for the sites. We then performed a variation partitioning analysis to identify dominant controls on $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, and used segmented regression to identify possible thresholds in the dependence of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ and used segmented regressions with $T_{min} < 0$ °C, $\tau_{e,C}$ and $\tau_{e,P}$ decreased with increasing T_{min} ; and in regions with $T_{min} > 0$ °C, both $\tau_{e,C}$ and $\tau_{e,P}$ increased with increasing T_{min} , as a result of a significant increase in total ecosystem carbon pool and a decrease in external phosphorus input, respectively. Our results challenge the use of a single temperature-dependent function of ecosystem carbon or nutrient turnover rate in global land models, and highlight the importance of other factors, such as soil weathering stage, clay content, in influencing the responses of carbon and nutrients cycles in subtropical forests to global warming.

1. Introduction

Mean residence time (MRT) of an element is the average time taken by an element from entry to exit in a system and can be estimated as the ratio of pool size and input flux at the steady state (Sierra et al., 2017). MRTs of ecosystem carbon (C), nitrogen (N) and phosphorus (P) (hereafter $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, respectively) are key ecosystem properties influencing many ecosystem functions. For example, $\tau_{e,C}$ is critically important for ecosystem C sequestration potential and the responses of land C uptake to global changes (Luo et al., 2017). Friend et al. (2014) found that $\tau_{e,C}$ dominated the uncertainty in the modelled responses of land C to future climate changes and atmospheric CO₂ concentration. $\tau_{e,N}$ and $\tau_{e,P}$ are closely related to nutrient use efficiency, which can be calculated as the product of net primary production (NPP) per unit nutrient and nutrient residence time (Berendse and Aerts, 1987). Longer $\tau_{e,N}$ or $\tau_{e,P}$ contributes to more efficient N or P conservation within an ecosystem to support plant productivity under nutrient-limited conditions (Wang et al., 2018b). Understanding the dominant drivers of $\tau_{e,N}$ and $\tau_{e,P}$ is helpful in improving the representation of biogeochemical cycles of N and P in land ecosystem and earth system models.

Variations of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ are complex and depend on multifaceted interplays among climate, vegetation, soil, terrain, land use and disturbance history. As an integrated outcome of multiple ecological processes (e.g., plant respiration, phenology, plant C allocation, plant mortality, organic matter decomposition and stabilization), $\tau_{e,C}$ can vary from a few decades in the tropical ecosystems to over 1000 years in wetlands at the high latitudes (Fan et al., 2020). Among various regulatory factors, how climate affects $\tau_{e,C}$ has been extensively studied at

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the global scale, partly due to the relative availability of high-resolution climate datasets. Mean annual temperature (MAT) was identified as the most dominant control on the spatial pattern of global $\tau_{e,C}$ (Carvalhais et al., 2014; Fan et al., 2020). It was found that mean residence time of soil C (a dominant component of $\tau_{e,C}$) increased with a decrease in MAT, with a change in the slope of that relationship at MAT near 12 °C (Fig. 1 of Koven et al. (2017)) or between extratropical and tropical regions (Fig. 7 of Fan et al. (2020)). Carvalhais et al. (2014) also found that $\tau_{e,C}$ was negatively correlated with air temperature in most high latitudes, but was positively correlated with air temperature in the tropical region (10–20°N). Therefore, the relationships between carbon and nutrient residence time and air temperature may be segmented.

Using extensive field observations in China, Wang et al. (2018a) identified both MAT and mean annual precipitation (MAP) as the dominant drivers of the spatial variation of $\tau_{e,C}$. At regional scale, vegetation, soil, and terrain were also identified as important drivers of $\tau_{e,C}$ or components of $\tau_{e,C}$. For example, a study along a 4000-km natural transect in South America found that climate and soil geochemical properties co-dominated the spatial variations of soil C storage and turnover (Doetterl et al., 2015).

While quite a few studies were made on the influences of climate on carbon residence time of ecosystems or soils, there have been only limited studies focusing on $\tau_{e,N}$ or $\tau_{e,P}$, especially at regional or global scales because of the scarcity of field measurements (Wang et al., 2018b). In general, $\tau_{e,P} > \tau_{e,N} > \tau_{e,C}$ because of the resorption by plants and immobilization by soil microbes (Wang et al., 2010). Given the greater fractions of total ecosystem C and nutrients in soil than in plants (Fan et al., 2020), the relatively narrow range of C:N ratio of soil organic matter and strong coupling of C and N cycles, spatial variations and key drivers of $\tau_{e,C}$ and $\tau_{e,N}$ were expected to be similar (Post et al., 1982). For $\tau_{e,P}$, the dominant drivers are likely to be different because soil P is also strongly influenced by soil age and geochemical properties (Walker and Syers, 1976). Indeed, a recent study by He et al. (2021) found that soil P concentration down to 1 m soil depth was strongly influenced by parental material, MAT, and soil texture globally, and also by topography at regional scales. A recent study found that the spatial patterns of ecosystem total N and P down to 1 m soil depth were quite different, and that the younger and slighter-weathered temperate soils had a lower N:P

70°E 80°E 90°E 100°E 110°E 120°E 130°E 140°E 50°N 40°N **Bioclimatic region** OTV STF 30°N TÈD TEV Forest type TRF SENF. Tmin>0 SMF, Tmin>0 EBF, Tmin>0 SENF. Tmin<0 20°N SMF. Tmin<0 EBF, Tmin<0 * TENF. Tmin<0 ٥ TMF, Tmin<0 DBF, Tmin<0

ratio than the subtropical and tropical soils in China (Zhang et al., 2021). So far no studies have been conducted on the dominant drivers of the regional or global variations of both $\tau_{e,N}$ and $\tau_{e,P}$.

Lack of reliable observations across a wide range of climate-, vegetation-, soil- and terrain- related factors also limits the quantifications of the patterns and dominant drivers of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$. Earlier studies either focused on one category of drivers (Carvalhais et al., 2014) or individual residence time only (Chen et al., 2015; Ge et al., 2019; Wu et al., 2020). Even for the relatively well studied $\tau_{e,C}$, previous studies were subject to large uncertainties with limited observations, such as poor information about disturbance history (Wang et al., 2018b; Chen et al., 2020). Estimate of MRT as the ratio of pool and input or output flux may have large errors if the system significantly deviates from its steady state (Lu et al., 2018), which is true for most recently disturbed ecosystems.

In this study, we compiled the measurements of C, N and P pools of plant biomass, surface litter and soil down to 1 m depth, and 30 sitespecific variables related to climate, vegetation, soil and terrain (Methods) of 127 mature and undisturbed natural forests in China. These 127 forests have been free of disturbance for at least five decades based on the records from local forestry departments, and were considered in this study to be approximately at their steady states. These intact forests are fundamental in understanding ecological processes but have been in sharp decline and are becoming rarer (Potapov et al., 2017), which reflects the importance of this work. These forests span from 22.24°N to 52.42°N, covering a wide range of climate and soil conditions and representing major zonal forest types in China (Methods). This dataset allows us to thoroughly address the following questions: (1) how do climate, vegetation, soil and terrain influence $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$? (2) does a threshold exist in the response of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ to air temperature? If yes, what are the likely mechanisms?

2. Methods

2.1. Site characteristics

As part of the nationwide field campaign (2011–2015) to assess its national terrestrial C storage in China, detailed measurements of

Fig. 1. Locations of the 127 forest sites used in this study. There are 6 different forest types: subtropical evergreen needle forests (SENF, 9 sites), subtropical mixed forests (SMF, 11 sites), evergreen broadleaved forests (EBF, 28 sites), temperate evergreen needle forests (TENF, 22 sites), temperate mixed forests (TMF, 17 sites), and deciduous broadleaved forests (DBF, 40 sites) across temperate and subtropical regions in China based on the classification by Institute of Geographic Sciences and Natural Resources Research, CAS (http://www.resdc.cn/). The bioclimatic regions in China include: subtropical forest region (STF), temperate vegetation region (TEV), and tropical monsoon forestrainforest region (TRF), Qinghai-Tibet alpine vegetation region (OTV), temperate desert region (TED). Red points (39 sites) represent sites distributed in the region where average minimum air temperature of the coldest month $(T_{\min}) > 0$ °C, and green points (88 sites) represent sites distributed in the region where $T_{\rm min} < 0$ °C.

vegetation, soil and terrain characteristics were obtained across 7800 forest sites using the same experimental protocol. Details about the survey protocols and sampling design can be found in Tang et al. (2018a). In this study, we focused on 127 undisturbed mature forests representing six major zonal forest types across China: temperate evergreen needle forest (TENF), temperate mixed forest (TMF), subtropical evergreen needle forest (SENF), subtropical mixed forest (SMF), deciduous broadleaved forest (DBF), and evergreen broadleaved forest (EBF) (Fig. 1). These forests have been free of disturbance for at least five decades based on the records from local forestry departments, span across three bioclimatic zones (79 sites in temperate region, 47 sites in subtropical region and 1 site in tropical region) with the MAT from -1.9 °C to 21.7 °C, MAP from 378 mm yr⁻¹ to 2044 mm yr⁻¹ (Fig. 1 and Table S3), and covered all major forest regions except Daxinganling region in Northern China, which has very limited road access. However, dominant forest type in Daxinganling region, temperate mixed forest, was represented by the samples from the north-east China (see Fig. 1). The dominant soil order is Inceptisols in temperate zone, Ultisols in subtropical region based on the United States Department of Agriculture soil taxonomy (Fig. S1a). Dominant tree genera are Pine (Pinus), Spruce (Picea), Oak (Quercus), Chinkapin (Castanopsis), and Gugertree (Schima) (Table S3).

2.2. Calculations of C, N and P pools

Biomass was estimated for trees, understorey shrubs and grasses separately at each forest site. For trees or forest-like shrubs, the speciesspecific set of allometric relationships between biomass of different components: leaf, woody component (bole, branches and twigs) or belowground root and diameter at breast height and tree height were used. In total, allometric relationships were developed for 158 dominant tree species and 91 forest-like shrubs based on measurements from whole-plant harvest in China. For understorey grass-like shrubs and grasses, whole-harvests of 10 randomised subplots of 10 m by 10 m were used to estimate the aboveground and belowground biomass at each forest site. See Text S2 of Tang et al. (2018a) for further details.

Samples of different biomass components for trees, shrubs and grasses were taken at the site, and brought back to the laboratory for analyzing their C, N and P concentrations (in the unit of g C or N or P per g dry matter). Details about laboratory analyses were provided by Tang et al. (2018b) and Liu et al. (2019). These concentration data were used to calculate the C, N and P pool sizes of leaf, wood and belowground roots of each forest site using Eq. (1). C, N and P pools of the surface litter were estimated from the measured elemental concentrations and the dry weight of litter (Eq. (2)). For soil, soil core samples were taken from five different depth intervals (0–10 cm, 10–20 cm, 20–30 cm, 30–50 cm, 50–100 cm). Bulk density, gravel content, and total C, N, and P pools (Eq. (3)). That is

$$X_B = \sum_{i=1}^{3} B_i \times x_i, \quad i = 1, \ 2, \ 3$$
⁽¹⁾

$$X_L = L \times x_L \tag{2}$$

$$X_{S} = \sum_{j=1}^{5} (1 - g_{i}) \times \rho_{i} \times x_{j} \times d_{j} \times 10$$
(3)

where B_i is the biomass of component *i* (leaf, wood or root) in g (dry matter) m⁻², and x_i is C, N or P concentration in biomass component *i* in g C or N or P g⁻¹ (dry matter). *L* is dry weight of litter in g (dry matter) m⁻², and x_L is C, N or P concentration of litter biomass in g C or N or P g⁻¹ (dry matter). *g_j* represents the volume percentage of gravels with a diameter >2 mm in soil layer *j*, ρ_j is bulk density (g cm⁻³), x_j is total C, N or P content of soil in g C or N or P per kg soil, and d_j is the thickness in cm of the *j*th layer. A factor 10 is for converting from g 10⁻³ cm⁻² to g

 m^{-2} .

2.3. Estimating C, N and P input fluxes

With the estimated C, N and P pool sizes, and input fluxes of N and P (see next paragraph), we used the optimization approach of Wang et al. (2018b) to estimate NPP and seven model parameters in a set of state equations of C, N and P cycles by assuming steady states (Text S1). For the optimization, we estimated the prior range of NPP based on MOD17A3H NPP product at a spatial resolution of 500 m by 500 m from 2005 to 2014 using the geographical coordinates of each site (Running et al., 2015). To account for the uncertainties in the estimated NPP as a result of spatial mismatch (MODIS NPP at 500 m by 500 m spatial resolution, and our sample plot size is 1000 m², including 10 subplots with 10 m by 10 m resolution) and the potential errors associated with the MODIS NPP product itself for our forest sites, we selected the grid-cell at which the site was located and its eight surrounding grid-cells, and calculated the minimum, mean and maximum of NPP among those nine grid-cells from 2005 to 2014. We took the range from the minimum to the maximum as the prior range of NPP in the optimization. The optimization framework was based on the parsimonious framework developed by Wang et al. (2018b) that integrated the above-mentioned observation-driven datasets, tracked C (N and P) allocations and transfers among different ecosystem compartments from a system viewpoint based on mass balance.

Direct measurements of external N inputs (deposition and biological N fixation (BNF)) and P inputs (deposition and weathering) across these 127 sites were not available. To estimate these quantities reasonably, we extracted values from available resources that calculated these values through combining theoretical understandings (models) with observations. We obtained N and P depositions from Wang et al. (2017) that merged atmospheric transports and field measurements. BNF was derived from Peng et al. (2020) using simulations by the Australian Community Atmosphere-Biosphere-Land Exchange model (CABLE). Weathering P release was estimated through its relationships with runoff, lithology, temperature, and soil properties from Hartmann et al. (2014). Without site-level measurements, we considered those estimates as reasonable first-order approximations for our study sites.

2.4. Mean ecosystem residence time

Our unique datasets from the mature forests undisturbed for at least last five decades support the rationale to assume these forest ecosystems at steady states. We then calculated $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ by dividing the pool size by the corresponding input flux. That is

$$\tau_{e,c} = \frac{\sum_{k=1}^{5} C_k}{NPP} \tag{4}$$

$$\tau_{e,X} = \frac{\sum_{k=1}^{5} X_k + X_{inorg}}{F_X} \tag{5}$$

where C_k is the amount of C in leaf, wood, root, litter and top 1 m depth of soil in g C m⁻², NPP is net primary productivity in g C m⁻² yr⁻¹, X_k is the amount of N or P in leaf, wood, root, litter and top 1 m depth of soil in g N or P m⁻², X_{inorg} is the amount of soil inorganic N or P pool in g N or P m⁻², and F_X is the external input flux of N or P to the ecosystem in g N or P m⁻² yr⁻¹.

2.5. Compiling data on climate, vegetation, soil and terrain

Residence time of C, N or P depends on input flux and pool size, which are influenced by many variables related to climate, vegetation, soil and terrain. However, not all variables are available for all the sites. Based on the available data, we compiled nine climate-related, seven vegetation-related, ten soil-related and five terrain-related variables for each forest site (Table S4). Some variables that may be important for residence times are not readily available, so we used proxies. For example, soil age is known to have significant influence on residence time of soil P (Walker and Syer 1976), and possibly carbon (Doetterl et al. 2015), but is not available for all the sites, we used 12 orders of soil taxonomy, or soil orders based on USDA classification(https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/edu/?cid=nrcs142p2

_053588). Different soil orders are related to soil weathering status and parental material. In the subsequent analysis, we grouped the soils of 127 forest sites into slightly (Inceptisols, Entisols, Cryolls), intermediate (Alfisols), and highly weathered soils (Ultisols), following the method in Zhang et al. (2005),Smeck (1985) and Brady and Weil (2002) (further details in Table S4).

2.6. Statistical analysis

We first tested significance of differences of the pools, fluxes, $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ among different forest types using one-way ANOVA with the software R v.4.0.5 (www.r-project.org/). Before the analysis, we verified whether data fitted the normal distribution, and then logarithmically transformed the non-normal data. Original or transformed data that followed normal distribution were assessed using least significant difference (LSD) test (Williams and Abdi, 2010), while data inconsistent with normal distributions after transformation were tested using Waerden test (Waerden, 1952).

To quantify the contributions of variables related to climate, vegetation, soil and terrain (Table S4) to the variations of the estimated $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, we used variation partitioning analysis (VPA) in R ("varpart" function of "vegan" package, Oksanen et al. (2020)). Site latitude was included as one of the climate variables (Table S4). The method attempts to partition the explanatory strength of different explanatory matrices in relation to the same response matrix (Borcard et al., 1992). We analyzed contributions from the direct effect by each of the four groups of variables and indirect effects through eleven interactions among the four groups of variables.

To identify the most dominant variables on the variations of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, we conducted a random forest analysis (Breiman, 2001). This technique is a machine-learning algorithm that combines regression trees with binary division. The importance of each predictor variable is determined by estimating the decline in prediction accuracy (that is, an increase in the mean square error between observations and out-of-bag predictions) when the data for that predictor is randomly permuted. Random forest analysis alleviates multicollinearity problems in multivariate analyses by building bagged tree ensembles and including a random subset of features for each tree. The analysis was conducted by using the "randomForest" package of R.

Results from random forest analysis identified T_{\min} as one of the most important variables for $\tau_{e,C}\text{, }\tau_{e,N}\text{ and }\tau_{e,P}\text{.}$ To identify possible thresholds in the dependence of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ on T_{min} , we applied segmented regression (Muggeo, 2021). We tested the significance of the change in the regression slope at the breakpoints ("Different-in-slope") using Davies test (Davies, 1987). The analysis was done using "segmented" R-package (Muggeo, 2021). Linear and quadratic nonlinear regressions were also used to quantify the dependence of $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ on T_{min} . To assess the robustness of the estimated breakpoints, we also conducted bent linear regression (Zhang and Li, 2017) and bent cable regression (Chiu, 2002) to identify the breakpoints in the relationships between residence times and T_{min}. Bent linear regression combines piecewise linear regression and rank-based regression to minimize the residuals so that the contribution of large residuals to the sum of the residual square is reduced through ranks in the score function. The fitting procedures were implemented using R-packages "Rbent" and "Rfit". Bent cable regression model comprises two linear segments, joins smoothly by a quadratic bend, the model can identify both the breakpoint and the transition region. Bent cable regression was conducted using R-package "Sizer".

3. Results

3.1. Model fit after optimization and sensitivity analysis

By assuming steady state, we calculated $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ as the ratio of total pool size and input flux for C, N or P. NPP and seven model parameters for each site were estimated by applying optimization (Text S1) to the framework based on mass balance (Wang et al. (2018b) and Methods). Agreement was good between the simulated pool sizes by the optimized models and the observed values for biomass pools ($r^2 = 0.926-0.981$), litter C pool ($r^2 = 0.932$), and soil N ($r^2 = 0.822$) and P pools ($r^2 = 0.827$) (Fig. S2).

We tested the steady state sensitivity of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ to the external inputs by calculating the relative changes of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ when the external inputs varied by $\pm 10\%$ and $\pm 20\%$. Sensitivity analysis (Fig. S3) showed that sensitivities of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ to their respective external input flux were similar. Residence times decreased by 9% and 17% when the inputs increased by 10% and 20%, respectively, while increased by 11% and 25% when the inputs decreased by 10% and 20%, respectively.

3.2. Variations of $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ with latitude and forest types

Among different forest types, external inputs of C (NPP, 669 g C m⁻² yr⁻¹) and N (6.0 g N m⁻² yr⁻¹) of evergreen broadleaf forest were the greatest, while external input of P (0.13 g P m⁻² yr⁻¹) of deciduous broadleaf forest was the greatest. Biomass C (9964 g C m⁻²), plant N uptake (12 g N m⁻² yr⁻¹) and biomass N (96 g N m⁻²) in evergreen broadleaf forest were the greatest. Plant P uptake (0.47 g P m⁻² yr⁻¹) and biomass P pool (5.8 g P m⁻²) of subtropical mixed forest were the smallest. Soil C (17,480 g C m⁻²) and N (1949 g N m⁻²) pools were greatest in temperate evergreen needle forest, while soil P pool (324 g P m⁻²) was greatest in temperate mixed forest (Table 1).

 $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ were positively correlated with latitude (Fig. 2). Among the different forest types, subtropical mixed forests had the shortest $\tau_{e,C}$, evergreen broadleaf forests had the shortest $\tau_{e,N}$ and $\tau_{e,P}$, and temperate mixed forests and temperate evergreen needle forests had the longest $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ (Fig. 2 and Table 1). Variations of $\tau_{e,C}$ and $\tau_{e,P}$ were greatest in deciduous broadleaf forests around 35°N, and in temperate mixed forests around 45°N.

3.3. Contributions of climate, vegetation, soil and terrain to the spatial variations of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$

Results of variance partitioning analysis indicated that four factor groups (climate, vegetation, soil and terrain) together explained 56%, 76% and 43% of the variances of the estimated $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, respectively (Fig. 3a–c). For individual effects, the greatest contributor was climate for $\tau_{e,C}$ (37%), $\tau_{e,N}$ (24%) and $\tau_{e,P}$ (17%). Soil was the second largest contributor to the variance of $\tau_{e,C}$ and $\tau_{e,N}$ through its individual effect and interaction with climate, and terrain had the smallest influence on the variance of $\tau_{e,C}$. For $\tau_{e,P}$, vegetation was the smallest contributor, and soil and terrain had similar influences, and interactive effect of climate and terrain was strongest.

Given the importance of climate to all three mean ecosystem residence times, we further identified four most important controls on $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ using random forest analysis (Fig. 3d–f), and found that average minimum temperature of the coldest month (T_{\min}) was important for $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$. Mean annual temperature (MAT) and frost period per year (FF) were also important for $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ because of the significant correlations between T_{\min} and MAT or FF (Fig. S5).

For ecosystem C, external C input increased linearly with T_{\min} with no significant difference in its response to T_{\min} between $T_{\min} < 1.5$ °C and $T_{\min} > 1.5$ °C (Fig. 4a), whereas responses of both ecosystem C pool size and $\tau_{e,C}$ to T_{\min} decreased linearly with an increase in T_{\min} when T_{\min} was below their respective breakpoint (-0.9 °C for $\tau_{e,C}$, 1 °C for

Table 1

Means and one-standard errors (mean \pm one se) of different pool sizes and fluxes of C, N and P of different forest types in China. Different letters represent significant differences at p < 0.05 among different forest types. Mean residence time ($\tau_{e,C}$, $\tau_{e,N}$, $\tau_{e,P}$) is calculated as the mean of the residence times of all the forests in each forest type. Abbreviations of headers for forest types are: TENF, temperate evergreen needle forests; TMF, temperate mixed forests; DBF, deciduous broadleaved forests; SENF, subtropical evergreen needle forests; SMF, subtropical mixed forests; EBF, evergreen broadleaved forests. NPP represents net primary production, external N input includes N deposition and N fixation and external P input includes weathering and deposition.

Fluxes/ pools/ residence times	TENF	TMF	DBF	SENF	SMF	EBF
NPP (g C m ⁻² yr ⁻¹)	$\begin{array}{c} 502 \pm \\ 39 \\ ^{b} \end{array}$	$\begin{array}{c} 483 \pm \\ 12 \\ ^{b} \end{array}$	$\begin{array}{c} 501 \pm \\ 25 \\ ^{b} \end{array}$	$\begin{array}{c} 503 \ \pm \\ 17 \ ^{b} \end{array}$	$\begin{array}{c} 551 \pm \\ 42^{\ b} \end{array}$	$\begin{array}{c} 669 \pm \\ 29 \end{array}^a$
Biomass C (g C m ⁻²)	$\begin{array}{l} 8067 \pm \\ 1186^{ab} \end{array}$	${8814} \pm 736 \ ^{a}$	$7101 \pm \\ 664 \ ^{b}$	$\begin{array}{l} 8075 \pm \\ 457^{ab} \end{array}$	$\begin{array}{l} 7801 \pm \\ 1218^{ab} \end{array}$	9964 \pm 706 ^a
Soil C (g C m ⁻²)	$\begin{array}{c} 17,\!480 \\ \pm 1338^a \end{array}$	14,823 ± 1163 ^{abc}	11,505 ± 1179 d	11,412 ± 680 ^{bcd}	12,042 ± 2684 ^{cd}	15,335 ± 1079 ^{ab}
$ au_{e,C}$ (yr) External input (g N m ⁻² yr ⁻¹)	$\begin{array}{l} 56\pm5 \\ 3.0\pm\\ 0.2 \\ ^{c}\end{array}$	$\begin{array}{l} 50 \pm 3 \\ 3.1 \pm \\ 0.2 \\ ^{bc} \end{array}$	$\begin{array}{c} 39\pm2^{\ b} \\ 3.5\pm \\ 0.1^{\ \ b} \end{array}$	$\begin{array}{l} 40 \pm 2 {}^{b} \\ 4.4 \pm \\ 0.2^{b} \end{array}$	$\begin{array}{c} 36\pm5 \\ 5.7\pm\\ 0.4 \\ ^{a} \end{array}$	$\begin{array}{c} 39\pm2^{\ b} \\ 6.0\pm \\ 0.2^{\ a} \end{array}$
N uptake (g N m ⁻² yr ⁻¹)	$\begin{array}{c} \textbf{7.1} \pm \\ \textbf{0.7}^{\text{ c}} \end{array}$	$\begin{array}{l} \textbf{7.9} \pm \\ \textbf{0.3}^{\text{ bc}} \end{array}$	$\begin{array}{c} 8.9 \pm \\ 0.6 \end{array} \\ ^{b}$	$\begin{array}{c} 6.5 \pm \\ 0.3 \end{array}^{c}$	$\begin{array}{l} 9.1 \pm \\ 1.0 \\ ^{b} \end{array}$	$\begin{array}{c} 12 \pm \\ 0.7 \\ ^{a} \end{array}$
Biomass N (g N m ⁻²)	$\begin{array}{c} 76 \pm 10 \\ _{ab} \end{array}$	$79\pm5~^a$	64 ± 7 ^b	$\begin{array}{c} 75 \pm 4 \\ _{ab} \end{array}$	$\begin{array}{c} 87 \pm 25 \\ _{ab} \end{array}$	96 ± 8 ^a
Soil N (g N m ⁻²)	1949 ± 268^{a}	1535 ± 118^{ab}	$1032 \pm 101^{\circ}$	$1005 \pm 41^{\circ}$	1286 ± 392 ^{bc}	1235 ± 113 ^{bc} 226 \pm
^{<i>i</i>} e,N (y1)	710 ⊥ 85 ^a	87 ^a	30 ^b	18 ^{bc}	121 ^c	220 ⊥ 19 °
External input (g P m ⁻² yr ⁻¹)	0.10 ± 0.01 ^{ab}	0.09 ± 0.01 ^b	0.13 ± 0.01 ^a	0.11 ± 0.01^{ab}	0.11 ± 0.01 ^a	0.11 ± 0.01 ^a
P uptake (g P m^{-2} vr^{-1})	$0.68 \pm 0.08 \ ^{a}$	0.74 ± 0.03^{a}	$0.75 \pm 0.04 \ ^{a}$	0.69 ± 0.05^{a}	0.47 ± 0.06 ^b	0.72 ± 0.05^{a}
Biomass P (g P m ⁻²)	$\begin{array}{l} 8.6 \pm \\ 0.9 \end{array} \\ ^{ab}$	$\begin{array}{c} 12 \pm \\ 0.9 \\ ^{a} \end{array}$	$\begin{array}{l} \textbf{7.8} \pm \\ \textbf{1.2}^{\text{ bc}} \end{array}$	$\begin{array}{c} 12 \pm \\ 1.4 \\ ^{a} \end{array}$	$\begin{array}{c} \textbf{5.8} \pm \\ \textbf{1.3}^{\ c} \end{array}$	$\begin{array}{l} 8.3 \pm \\ 0.7 \end{array} \\ ^{ab}$
Soil P (g P m ⁻²) τ _{e,P} (yr)	$\begin{array}{l} 456 \ \pm \\ 75 \ ^{ab} \\ 5619 \ \pm \\ 1160 \ ^{a} \end{array}$	$\begin{array}{l} 324 \pm \\ 30 \\ ^{b} \\ 4528 \pm \\ 482 \\ ^{a} \end{array}$	$\begin{array}{l} 504 \pm \\ 44 \\ 5291 \pm \\ 770 \\ a \end{array}$	$\begin{array}{l} 406 \ \pm \\ 28 \ ^{ab} \\ 5148 \ \pm \\ 745 \ ^{ab} \end{array}$	$\begin{array}{l} 412 \pm \\ 112 \\ ^{b} \\ 4047 \pm \\ 1270 \\ ^{a} \end{array}$	$\begin{array}{r} 383 \pm \\ 38 \\ ^{b} \\ 3724 \pm \\ 333 \\ ^{a} \end{array}$

ecosystem C pool), but increased with $T_{\rm min}$ when $T_{\rm min}$ was above their respective breakpoint (Fig. 4d and g). Those changes in the responses below and above the breakpoints were statistically significant (Davies test, p < 0.05). The change in the direction of $\tau_{\rm e,C}$ largely resulted from the change of the sensitivity of ecosystem C pool size rather than NPP, as the breaking point for NPP was insignificant (Fig. 4a).

For ecosystem N, only the sensitivity of external N input (deposition and biological N fixation) to T_{\min} had a breaking point at T_{\min} of $-6.9 \,^{\circ}$ C (Davies test, p < 0.05, Fig. 4b), the sensitivities of both ecosystem N pool and $\tau_{e,N}$ decreased with an increase in T_{\min} without a significant breaking point (Fig. 4e and h).

For ecosystem P, the sensitivity of external P input (deposition and weathering) increased with $T_{\rm min}$ when $T_{\rm min} < -2.5$ °C, but decreased with an increase in $T_{\rm min}$ when $T_{\rm min} > -2.5$ °C (Fig. 4c), and the sensitivity of ecosystem P pool size varied with $T_{\rm min}$ with a breaking point at $T_{\rm min} = -12.7$ °C (Fig. 4f). $\tau_{\rm e,P}$ decreased with an increase in $T_{\rm min}$ when $T_{\rm min} < 0.2$ °C, and increased with $T_{\rm min}$ when $T_{\rm min} > 0.2$ °C (Fig. 4i). Breakpoints in the relationships between these P-related variables and $T_{\rm min}$ were statistically significant (Davies test, p < 0.05).

We also found dependences of $\tau_{\rm e,N}$ on MAT and $\tau_{\rm e,P}$ on FF were segmented and the breaking points were significant (Davies test, p < 0.05, Fig. S4c and f). Because of the strong correlation of $T_{\rm min}$ with MAT ($r^2 = 0.904$, Fig. S5a) and FF ($r^2 = 0.864$, Fig. S5b), we would obtain overall similar results if MAT and FF were used as the explanatory variable.

To ensure the robustness of the estimated breakpoints for $\tau_{e,C}$ and $\tau_{e,P}$ around $T_{min} = 0$ °C, we used bent linear regression and bent cable regression to identify breakpoints between residence times and T_{min} (Table 2). Results of the other two methods were similar to the results of segmented linear regression. We also compared the segmented regression with two other functions (a linear regression and a quadratic nonlinear regression) fitted the data, and found that segmented regression models had the lowest Akaike information criteria (AIC) and highest r^2 among the models (Table S5).

In summary, both $\tau_{e,C}$ and $\tau_{e,P}$ had a breaking point around $T_{min} = 0$ °C, which largely resulted from changes in the directions of the sensitivity of ecosystem C pool size and external P input, respectively.

3.4. Why the sensitivities changed in direction at the breakpoint?

To understand why the sensitivity of $\tau_{e,C}$ or $\tau_{e,P}$ to T_{\min} had a breaking point at T_{\min} around 0 °C, we divided the data from 127 forest sites into two groups using the T_{\min} values for those sites, and estimated the correlations between $\tau_{e,C}$ and $\tau_{e,P}$ with 30 variables (Fig. S6).

Correlations between temperature (T_{min} , MAT and frost-free days) with $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ were significantly negative when $T_{min} < 0$ °C (t-test, p < 0.05), and the correlations became insignificant for $\tau_{e,C}$ and



Fig. 2. Variations of ecosystem residence time for C ($\tau_{e,C}$), N ($\tau_{e,N}$) and P ($\tau_{e,P}$) with latitude. Lines represent the best fitted linear regression. Different colors of symbols represent different forest types. EBF, MF, DBF and ENF represent evergreen broadleaf forest, mixed forest, deciduous broadleaf forest and evergreen needle leaf forest, respectively. MF and ENF are distributed across temperate and subtropical areas, and are classfied as temperate mixed/needle forest (TMF/TENF) and subtropical mixed/needle forest (SMF/SENF), respectively.



Fig. 3. Contributions of climate (Clim), vegetation (Veg), soil, and terrain (Ter) related variables to the variance of the estimated ecosystem residence times for C ($\tau_{e,C}$) (a, d), N ($\tau_{e,N}$) (b, e) and P($\tau_{e,P}$) (c, f) across 127 mature forests. Panels a–c represent results of variance partitioning analysis. The black pillars above the *x*-axis and the numbers above the pillars represent individual effect (the left four pillars and the corresponding black dots below the *x*-axis) and interactive effects (the right four pillars, and the corresponding vertical lines joining black dots below the *x*-axis) of climate, vegetation, soil and terrain. The number of dots on the vertical lines below the *x*-axis represents the number of interactive factors. Total contributions (individual and interactive effects) of climate, vegetation, soil or terrain are shown by the horizontal colored bars beside each variable group. The amount of unexplained variance is also shown in each panel. Panels d to f show the top four important variables identified using random forest analysis. An increase in the percentage of mean square error (MSE) was shown using the horizontal bar, and definitions of abbreviated variables in (d, e and f) can be found in Table S4.

significantly positive (*t*-test, *p* < 0.05) for $\tau_{e,N}$ and $\tau_{e,P}$ when $T_{min} > 0$ °C, which was consistent with the results in Fig. 4. Furthermore, those correlations with several climate-related variables (MAP and relative humidity) were all significantly negative when $T_{min} < 0$ °C (*t*-test, *p* < 0.05), suggesting as temperature or precipitation increased, ecosystem residence times became shorter. When $T_{min} > 0$ °C, correlations with most climate-related variables became significantly positive (*t*-test, *p* < 0.05) or insignificant (Fig. S6), suggesting that factors other than temperature or precipitation changes had a significantly impact on $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, as ecosystem residence times should decrease with temperature increase.

Correlations of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ with soil- or terrain-related variables were generally insignificant. We analyzed the correlations of soil weathering stage and parent material with $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ using Spearman correlation analysis (Fig. S6) and random forest model. Results indicated that correlations between parent materials (or soil weathering stages) and residence times were insignificant.

Correlations of residence times with soil properties also varied between $T_{min} > 0$ °C and $T_{min} < 0$ °C. For example, when $T_{min} < 0$ °C, $\tau_{e,P}$ was negatively correlated with soil clay content and slope gradient (*t*test, p < 0.05), but positively correlated with bulk density and pH (*t*-test, p < 0.05). When $T_{min} > 0$ °C, $\tau_{e,C}$ significantly increased with elevation (*t*-test, p < 0.05).

In summary, $\tau_{e,C}$ and $\tau_{e,P}$ decreased with an increase in T_{min} when $T_{min} < 0$ °C, which is consistent with most previous studies, but increased with T_{min} when $T_{min} > 0$ °C, which differs from most previous studies on the effect of temperature change on ecosystem residence time.

4. Discussions

 $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ are important ecosystem properties, and are subject of extensive theoretical (Sierra et al., 2017; Lu et al., 2018) and observation-based studies (Carvalhais et al., 2014; He et al., 2016). Previous studies identified the spatial patterns and its dominant controls of the individual MRT in different compartments of the terrestrial ecosystems (Helfenstein et al., 2020; Shi et al., 2020). Our study based on extensive field observations across 127 mature and undisturbed forests in China assessed how climate, vegetation, soil and terrain affected $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ through their direct effects and interactions. We identified not only some patterns similar to previous studies but also some new patterns that are seemingly inconsistent with the existing theory of terrestrial biogeochemistry.

Climate is generally considered to exert a dominant control on terrestrial C dynamics (Carvalhais et al., 2014; Chen et al., 2021). Consistent with the previous studies, we found that climate variables together not only explained the largest portion of variance in the estimated $\tau_{e,C},$ but also for $\tau_{e,N}$ and $\tau_{e,P}.$ In addition, we found that approximate half of the climatic influences ($\tau_{e,N}$: 64%; $\tau_{e,P}$: 43%) resulted from the interactions with soil, vegetation, or terrain. Different from $\tau_{e,C}$ and $\tau_{e,N}$, the influences of soil (21%) on $\tau_{e,P}$ were comparable with that of climate (30%). This pattern is consistent with our understanding of the biogeochemical cycles of C, N and P. In undisturbed natural ecosystems, MRT of soil C is jointly controlled by C input (both quality and quantity) and stabilization (Chen et al., 2021), whereas N input is dominated by N fixation, and rate of N fixation is strongly controlled by available C (Wang et al., 2007), therefore vegetation plays an important role in $\tau_{e,C}$ and $\tau_{e,N}$ (Fig. 3). Unlike $\tau_{e,C}$ and $\tau_{e,N}$, soil and terrain had much greater influences on $\tau_{e,P}$ than vegetation, as these two factors are related to soil weathering status, and an increasing fraction of soil P becomes occluded during pedogenesis (Walker and Syers, 1976).

The breakpoint in the relationship between $\tau_{e,P}$ and T_{min} further reinforces the significant role of P limitation on ecosystem dynamics. The breakpoint around 0 °C in our study coincided with the direction of changes of external P input with T_{min} (Fig. 4c), and significantly higher P limitation in $T_{min} > 0$ °C region than $T_{min} < 0$ °C region (Fig. S7a-b). Ecological theory suggests that plants increase nutrient use efficiency by increasing resorption or nutrient residence time under increasing nutrient limitations (Aerts and Chapin, 1999). Our data showed that both leaf C:P ratio and P use efficiency in $T_{min} > 0$ °C were significantly greater than those in $T_{min} < 0$ °C (Fig. S7). Therefore, in the mature forests located in the subtropical region with $T_{min} > 0$ °C (Fig. 1), vegetation may have evolved to make use of increasingly favorable



Fig. 4. Segmented regression analysis of the dependence of input fluxes (panels a to c), ecosystem pool sizes (panels d to f), and $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ (panel g to i) on T_{min} (in °C). Green lines are fitted lines by segmented regression, gray lines are fitted lines by ordinary linear regression. Solid and dashed lines of the regressions represent statistically significant (p < 0.05) and insignificant (p > 0.05) relationships, respectively. In the legend for each panel, "s1" and "s2" represent the slopes of segmented regression before and after the breakpoint, respectively. "slm" represents the slope of linear regression. "BP" represents T_{min} breakpoint. Colored points represent different forest types, and the abbreviations for different forest types are the same as in Fig. 2.

Table 2

Estimates of the breakpoint and 95% confidence or transition region for segmented linear regression, bent linear regression and bent cable regression. $\tau_{e,}$ _C, $\tau_{e,N}$ and $\tau_{e,P}$ represent ecosystem residence times for C, N and P, respectively.

Varia- bles	Model	Breakpoint (°C)	se/smooth bend (transition region)	95%CI (1.96*SE)	p value
$ au_{ m e,C}$ (yr)	segmented linear	-0.9	2.5	(-5.7, 4.0)	0.03*
	bent linear regression	-0.6	2.2	(–4.8, 3.7)	0.02 *
	bent cable regression	-0.9	0.1		
$ au_{ m e,N}$ (yr)	segmented linear regression	1.1	2.1	(-3.0, 5.3)	0.1
	bent linear regression	-0.4	3.0	(-6.2, 5.4)	0.1
	bent cable regression	1.1	0.2		
$\tau_{e,P}$ (yr)	segmented linear	0.2	1.4	(-2.7, 3.0)	0.003 *
	bent linear regression	-0.5	1.7	(-3.8, 2.8)	0.06
	bent cable regression	-0.1	0.2		

Note: Bent cable regression has a smooth band instead sharp break in a snapped stick. "*" represents the breakpoints were statistically significant (p < 0.05).

water and temperature conditions (Fig. S1b-c) while P input decreased with an increase in T_{\min} , for example, through increasing plant P uptake (Fig. 5a-c, before vs. after breakpoints). Previous studies reported different strategies of vegetation to maintain high productivity in mature forest ecosystems from T_{min} > 0 °C region under P-limitation (most subtropical and tropical areas) (Turner et al., 2018; Mo et al., 2019). For example, some plants can maintain high productivity in low P environments through reducing P demand for metabolism (Mo et al., 2019), replacing phospholipids with non-phospholipids during leaf development (Lambers et al., 2012), and absorbing soil organic P compounds (Turner, 2008). Under P-limited conditions, through long-term natural selection and adaptation, vegetation evolved to minimize P losses as indicated by increasing $\tau_{e,P}$ with decreasing external P inputs (Vitousek et al., 2010). As a considerable portion of plant usable P in soil is bonded in organic matter, the conservation of P in ecosystems also means the retention of C and N because of the narrow range of variation of C:N:P ratio of soil organic matter (Tipping et al., 2016). Our study revealed the similar breakpoint patterns in $\tau_{e,C}$ and $\tau_{e,C}$ $_{\rm N}$, although the regressions were not statistically significant for $\tau_{\rm e,N}$.

By analyzing the direct and indirect (through interactions) effects of different climate variables that may contribute to the segmentation patterns, we confirmed that interactions among climate variables were not the primary drivers. Precipitation was identified as another important factor influencing $\tau_{e,C}$ by Carvalhais et al. (2014). As shown in Fig. S1b, precipitation increased linearly with T_{min} among the 127 forest sites, and correlations between precipitation and $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ were not significant when $T_{min} > 0$ °C (Fig. S6), therefore increase in precipitation with T_{min} will unlikely explain the estimated increase in $\tau_{e,C}$



Fig. 5. Variation of annual plant P uptake (a, P_{uptake}), ecosystem residence time for C ($\tau_{e,C}$) (b), or P ($\tau_{e,P}$) (c) with avergage minimum temperature of the coldest month in a year (T_{min}). gray points are for the forest sites with $T_{min} < 0$ °C. and green points are for the forest sites with $T_{min} > 0$ °C. Solid and dash lines represent statistically significant (p < 0.05) or insignificant (p > 0.05) regression, respectively. Regression coefficient (r^2) and p value of significant relationships were also shown.

with T_{\min} when $T_{\min} > 0$ °C. This is consistent with the result of Kramer and Chadwick (2018).

Instead, the interplays among climate, vegetation, and soil (geochemical factors) are important in shaping the segmented patterns identified in this study. Consistent with previous studies, we found faster turnover rates of C, N or P under higher temperature in cold regions ($T_{min} < 0$ °C) where climate was the primary control. High temperature favors accelerated biological activities, which increases plant turnover, soil organic matter decomposition and nutrient transfers (Carvalhais et al., 2014; Bloom et al., 2016). In the region with $T_{min} > 0$ °C where subtropical forests are located, soils generally are highly weathered, and geochemical constraints (parent material and soil status) significantly influence the ecosystem responses to climate (Vitousek et al., 2010). We showed that P limitation and vegetation's adaptation to the high P limitation were the most plausible mechanisms driving the change in the relationships between temperature and $\tau_{e,C}$ and $\tau_{e,P}$ between $T_{min} < 0$ °C and $T_{min} > 0$ °C regions.

In addition to P, we also found a high soil clay content and an increasing trend of soil clay content with T_{\min} when $T_{\min} > 0$ °C, despite the trend was not statistically significant (Fig. S8). Clay content is an important indicator of mineral protection organic matter that favors soil C retention (Kindler et al., 2011; Hemingway et al., 2019; Chen et al., 2021), especially in forest soil (Six et al., 2002). This high clay content, associated with the strong weathering of soils, likely contributed to the segmented relationships between T_{\min} and $\tau_{e,C}$ and $\tau_{e,P}$. It is possible that other soil properties, such as metal oxide concentration and clay mineralogy also played a significant role in the positive relationships between $\tau_{e,C}$ and $\tau_{e,P}$ and T_{min} , whereas T_{min} did not directly affect $\tau_{e,C}$ and $\tau_{e,P}$, but their variations were linked with other physical and geochemical properties in the subtropical and tropical regions (Yu et al., 2019; Chen et al., 2021). That being said, we conducted the segmented regression analysis for the relationships between each of the 30 explanatory variables (Table S6) and T_{min} . We did not detect any statistically significant breakpoints around 0 °C (with the clay – $T_{\rm min}$ relationship having a significant breakpoint at -10 °C), indicating the covariations with other environmental variables were unlikely to play an important role.

Global models used for simulating terrestrial biogeochemical cycles under future climate changes often applied one temperaturedependence function of soil organic C decomposition globally (Exbrayat et al., 2013), these models may significantly overestimate the temperature sensitivity and underestimate the soil C accumulation under future warming in the subtropical and tropical forests in China. With increasing evidence to support the significant role of soil geochemical properties on soil C stabilization (Kramer and Chadwick, 2018; Basile-Doelsch et al., 2020), it is important to include the dependence of C or nutrients stabilization on soil geochemical properties in global land models for modeling soil C, N and P cycles (Rasmussen et al., 2018; Wang and Goll, 2021).

5. Conclusion

We estimated $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ based on field measurements and compilation of 30 related variables for 127 undisturbed forests across China. We also quantified the influences of vegetation, climate, soil physical and chemical properties and terrain on $\tau_{e,C}\text{, }\tau_{e,N}$ and $\tau_{e,P}\text{. }$ Our results indicated that climate was the dominant control on $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ at the continental scale. Regionally, $\tau_{e,C}$ and $\tau_{e,P}$ decreased with an increase in T_{\min} in the temperate region, but increased with T_{\min} in the subtropical region. As clay content and other geochemical properties that are important to P cycle in the subtropical region will not change significantly under warming from decades to century, the direct responses of $\tau_{e,C}$ and $\tau_{e,P}$ to future warming in the subtropical region of China would be quite small, whereas $\tau_{e,C}$ and $\tau_{e,P}$ of temperate forests are very sensitive to $T_{\rm min}$ increase at a rate of -1 year/°C for $\tau_{\rm e,C}$ and -216year/°C for $\tau_{e,P}$ (Fig. 4g, i). Our study highlights the importance of P limitation in projecting responses of ecosystem carbon and nutrients in a warmer environment, especially in subtropical forests.

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.

Data Availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in

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