

Dependence of ecosystem carbon, nitrogen and phosphorus residence times of mature forests in China on air temperature is segmented

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Abstract

Ecosystem mean residence times of carbon, nitrogen and phosphorus ($\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, respectively) are important ecosystem properties. By analyzing the dependence of the observation-based estimates of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ of 127 mature forests on climate, vegetation, soil and terrain-related variables, we found that climate, particularly mean annual minimum temperature (T_{\min}), had the greatest influence on $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$. Different from previous studies, we found that both $\tau_{e,C}$ and $\tau_{e,P}$ increased with T_{\min} when $T_{\min} > 0$. Despite a decreasing phosphorus input with T_{\min} , vegetation adapted to low phosphorus environment by increasing internal recycling and phosphorus use efficiency, together with the increasing soil clay content with T_{\min} , not the direct response to T_{\min} , explained why both $\tau_{e,C}$ and $\tau_{e,P}$ increased with T_{\min} when $T_{\min} > 0$. Our results highlight the importance of factors beyond climate in regulating residence times, especially in subtropical forests.

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) or 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 response of land C uptake to global change (Luo *et al.* 2017). Friend *et al.* (2014) found that $\tau_{e,C}$ dominated the uncertainty in the modelled land C response to future climate change 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 & Aerts 1987). Longer $\tau_{e,N}$ or $\tau_{e,P}$ contribute to more efficient N or P conservation within the ecosystem to support plant productivity under nutrient-limited conditions (Wang *et al.* 2018b). Understanding drivers of $\tau_{e,N}$ and $\tau_{e,P}$ is helpful in both studying the biogeochemical cycles of N and P, and revealing mechanisms regulating $\tau_{e,C}$.

Variations of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ are complex and depend on multifaceted interplay 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 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). The relationship between $\tau_{e,C}$ (or the MRT of soil C) and MAT was found to be negatively linear or nonlinear, with a change in the slope of the negative relationship towards the high end of MAT (Figure 1 of Koven *et al.* (2017)) or around tropical/subtropical regions (Figure 7 of Fan *et al.* (2020)). 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 $\tau_{e,C}$. But Wang *et al.*(2018a) did not quantify the influences of land use and disturbance history, which were known to significantly influence $\tau_{e,C}$ (Sanderman *et al.* 2017). At regional scales, 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 variation of soil C storage and turnover (Doetterl *et al.* 2015).

There are only limited studies focusing on $\tau_{e,N}$ or $\tau_{e,P}$ especially at regional and global scales. 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 fraction 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; Post *et al.* 1985). 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 & 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 scale. A recent study also 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 lower N:P ratio than the subtropical and tropical soils in China (Zhang *et al.* 2021). So far no studies have been 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. 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 is not at 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 1m depth, and site-specific 30 variables related to climate, vegetation, soil and terrain (see Methods) of 127 mature and undisturbed natural forests in China. 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, cover a wide range of climate and soil conditions and represent all major forest types in China (see Methods). This dataset allow us to thoroughly address the following questions: (1) how climate, vegetation, soil and terrain influence $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$? (2) whether a threshold exists in the response of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ to air temperature? If so, what is the likely mechanism?

METHODS

Site characteristics

As part of the nationwide field campaign (2011-2015) to assess its national terrestrial C storage in China, detailed measurements of vegetation, soil and terrain characteristics were obtained across 7800 forest sites using the same experimental protocol (Fang *et al.* 2012). Details about the measurement protocol can be found in Tang *et al.* (2018) and Liu *et al.* (2019). In this study, we focused on 127 undisturbed mature

forests representing all six major forest types across China: temperate evergreen needle forests (TENF), temperate mixed forests (TMF), subtropical evergreen needle forests (SENF), subtropical mixed forests (SMF), deciduous broadleaved forests (DBF), and evergreen broadleaved forests (EBF) (see Fig. 1). These forests 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} . The dominant soil order is Inceptisols in temperate zones, Ultisols in subtropical regions based on United States Department of Agriculture soil taxonomy (see Figure S1a). Dominant tree genera are Pine (*Pinus*), Spruce (*Picea*), Oak (*Quercus*), Chinkapin (*Castanopsis*), and Gugertree (*Schima*) (see Table S2 and Figure S1b-c).

We also compiled key variables related to climate, vegetation, soil and terrain based on the measurements at the sites or global datasets using the geographic locations of the sites. They include eight-climate-related, seven-vegetation-related, ten-soil-related and five-terrain-related variables (see Table S3).

Calculations of C, N and P pools

At each site, the biomass of different plant components (leaves, woody tissues and roots for both overstory trees, and understory trees, shrubs and grasses) were estimated either using the whole-harvest-method or locally developed allometric equations that relates biomass to field measured tree height and diameter at the breast height (see Text S2 of Tang *et al.* (2018)). C, N, and P concentrations (in unit of g C or N or P per g dry matter) of different plant components were measured in laboratory using the biomass samples taken at the sites and used to calculate C, N and P pools in unit of g C or N or P m^{-2} at each site (Equation 1). C, N and P pools of the surface litter were estimated from the measured elemental concentrations and the dry weight of litter (Equation 2). For soil, soil core samples were taken from five different depth intervals (0-10cm, 10-20cm, 20-30cm, 30-50cm, 50-100cm). Bulk density, gravel content, and total C, N, and P concentration were measured at each depth to calculate soil C, N and P pools (Equation 3). That is

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

$$X_L = L \times x_L \quad (2)$$

$$X_S = \sum_{j=1}^5 (1 - g_j) \times \rho_j \times x_j \times d_j \times 10 \quad (3)$$

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 $>2\text{ mm}$ 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} .

Estimating C, N and P input fluxes

NPP were extracted from MOD17A3H product at a spatial resolution of 500 m by 500 m from 2005 to 2014 using the latitude and longitude of each site (S. Running 2015). To account for likely biases in the remote-sensing derived NPP for our forest sites, we selected the grid-cell at which the site was located and its eight surrounding grid-cells, and calculated mean NPP of each of those nine grid-cells from 2005 to 2014. We took the minimum, maximum range and average of the nine mean NPPs across 9 grid-cells as the prior range and initial value of NPP in an optimization framework to estimate the site-specific NPP. The optimization framework was based on the parsimonious framework developed by Wang *et al.* (2018b) that integrated 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. Through this framework, we optimized seven more parameters in addition to NPP (see Table S1), with detailed information in Supplementary Methods.

Direct measurements of N inputs (deposition and biological N fixation (BNF)) and P inputs (deposition and weathering) across these 127 sites were not available. To reasonably estimate these quantities, we extracted

values from available resources that calculate 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 across space.

Mean ecosystem residence time

Our unique datasets from undisturbed mature forests support the rationale to assume these forest ecosystems are at steady states. We then calculated $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ in year through dividing the pool size by the corresponding input fluxes. That is

$$\tau_{e,c} = \frac{\sum_{k=1}^5 C_k}{\text{NPP}} \quad (4)$$

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

where C_k is the amount of C in leaf, wood, root, litter and top 1m depth of soil in g C m^{-2} , NPP is net primary productivity, X_k is the amount of N or P in leaf, wood, root, litter and top 1m 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 $\text{g N or P m}^{-2} \text{ yr}^{-1}$.

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 fit the normal distribution and then logarithmic transformed the non-normal data. Original or transformed data according with normal distribution was test by LSD test (Williams & Abdi 2010), while data inconsistent with normal distribution after transformation was tested by Waerden test (Van der Waerden 1952). We then conducted linear or nonlinear regression between $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ and other variables.

To quantify the contributions of 30 variables related to climate, vegetation, soil and terrain (see Table S3) to the variances of the estimated $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, we used variation partition method in R (“vegan” package, (Jari Oksanen *et al.* 2020)). We analysed contributions from the direct effect by each of the four groups of variables and eleven interactions among the four groups of variables.

To identify the most dominant variable on the variations of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, we used correlation analysis. Based on the correlation analysis, we identified T_{min} as the most important variable for $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$. To identify possible threshold in the dependence of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ on T_{min} , we applied segmented regression (Muggeo 2003). 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 also done using “segmented” R-package (Muggeo 2021). Linear regression was also used to quantify the dependence of $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ on T_{min} .

RESULTS

ἄριαιτιονς οφ $\tau_{e,C}$, $\tau_{e,N}$ οφ $\tau_{e,P}$ ωιτη λατιτυδε ανδ φορεστ τψπες

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 (see Supplementary Methods) to the framework based on mass balance (see Wang *et al.* (2018b) and Methods). Agreement is 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 ($r^2 = 0.827$) (see Figure S2).

Among different forest types, ecosystem inputs of C (NPP, 669 g C m⁻² yr⁻¹) and N (6.0 g N m⁻² yr⁻¹) of EBF were the greatest, while external input of P (0.13 g P m⁻²yr⁻¹) of DBF was the greatest. Biomass C (9964 g C m⁻²), plant N uptake (12 g N m⁻²yr⁻¹) and biomass N (96 g N m⁻²) in EBF were the greatest. Plant P uptake (0.47 g P m⁻²yr⁻¹) and biomass P pool (5.8 g P m⁻²) of SMF were the smallest. Soil C (17480 g C m⁻²) and N (1949 g N m⁻²) pools were greatest in TENF, while soil P pool (324 g P m⁻²) was greatest in TMF (see Table 1).

Across the latitudes, $\tau_{e,C}$ significantly increased with latitude quadratically (see Fig. 2a), and $\tau_{e,N}$ and $\tau_{e,P}$ significantly increased with latitude linearly (see Fig. 2b-c). Among the different forest types, SMF had the shortest $\tau_{e,C}$, EBF had the shortest $\tau_{e,N}$ and $\tau_{e,P}$, and TMF or TENF had the longest $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ (see Fig. 2, Table 1). Variations of $\tau_{e,C}$ and $\tau_{e,P}$ were greatest in DBF around 35°N, and in TMF around 45°N.

δντριβυτιονς οφ ζλιματε, εγεταιιον, σοιλ ανδ τερραιν το τηε σπατιαλ αριατιονς οφ $\tau_{e,C}$, $\tau_{e,N}$ ανδ $\tau_{e,P}$

To quantify the influences of different factors on $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$, we grouped those factors into four groups: climate, vegetation, soil and terrain (see Table S3), and estimated the contributions by each group to the total variance in the estimated $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ among the 127 forest sites, respectively. Those four groups together explained 57%, 79% and 45% of the variances of the estimated $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ (see Fig. 3a-c). For individual effects, the greatest contributor was climate for $\tau_{e,C}$ (21%) and $\tau_{e,N}$ (14%), but was soil for $\tau_{e,P}$ (16%). Soil was the second largest contributor to the variance of $\tau_{e,C}$ through its individual effect and interaction with climate, and terrain had the smallest influence on the variance of the $\tau_{e,C}$. Vegetation, soil and terrain contributed equally to the variance of $\tau_{e,N}$ through their direct effects and interactions with others. 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 analysed the correlations between $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ and different climate variables (see Fig. 5), and found that correlation coefficients were highest with T_{min} . Correlations were also significant with MAT and MAP for $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ because of the significant correlations between T_{min} and MAT or MAP (see Figure S1).

For ecosystem C, C input increased linearly with T_{min} with no significant difference in its response to T_{min} between $T_{min} < 1.5$ and $T_{min} > 1.5$ (see 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 for $\tau_{e,C}$, 1 for ecosystem C pool), but increased with T_{min} when T_{min} was above their respective breakpoint (see Fig. 4d and 4g), and those changes in the responses below and above the breakpoints were statistically significant. The change in the direction of $\tau_{e,C}$ largely resulted from the change of the sensitivity of ecosystem C pool size rather than NPP, as the breaking point for NPP was insignificant (see Fig. 4a).

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

For ecosystem P, the sensitivity of external P input (deposition and weathering) increased with T_{min} when $T_{min} < -2.5$, but decreased with an increase in T_{min} when $T_{min} > -2.5$ (see Fig. 4c), and the sensitivity of ecosystem P pool size varied with T_{min} with two breaking points at $T_{min} = -12.9$ and -2.1 , see Fig. 4f), and both breaking points were statistically significant ($p < 0.05$). $\tau_{e,P}$ decreased with an increase in T_{min} when $T_{min} < 0.2$, and increased with T_{min} when $T_{min} > 0.2$ (see Fig. 4i).

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

Why the sensitivities changed in direction at the breakpoint?

To understand why the sensitivity of $\tau_{e,C}$ and $\tau_{e,P}$ to T_{min} had a breaking point around $T_{min} = 0$, 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 (see Fig. 5).

Correlations between the $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ with T_{\min} or MAT were negative when $T_{\min} < 0$, and became insignificant or positive when $T_{\min} > 0$, which is consistent with the results in Fig. 4. Furthermore, those correlations with several climate-related variables were all negative when $T_{\min} < 0$, suggesting as temperature or precipitation increased, ecosystem residence times became shorter. When $T_{\min} > 0$, correlations with most climate-related variables became positive or insignificant (see Fig. 5), suggesting the direct effect of temperature or precipitation changes on $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ was weakened, as temperature increase is found to shorten ecosystem residence time.

Correlations of $\tau_{e,C}$, $\tau_{e,N}$ or $\tau_{e,P}$ with vegetation-related variables also changed sign between above and below T_{\min} of 0. For example, $\tau_{e,P}$ was negatively correlated with leaf area index (LAI) at $T_{\min} < 0$, but became positively correlated with LAI when $T_{\min} > 0$. Correlation of $\tau_{e,C}$ with the leaf resorption of N or P was not significant at $T_{\min} < 0$, but became significantly negative at $T_{\min} > 0$.

Correlations of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ with soil- or terrain-related variables were generally low. When $T_{\min} < 0$, $\tau_{e,P}$ was negatively correlated with soil clay content, slope gradient, but positively correlated with bulk density and pH. When $T_{\min} > 0$, $\tau_{e,C}$ significantly increased with elevation.

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

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 pattern and its dominant control of the individual MRT in different compartments of the terrestrial ecosystems (Helfenstein *et al.* 2020; Shiet *et al.* 2020). Our study based on extensive field observations across 127 mature 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. Our study 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 (e.g., Carvalhais *et al.* (2014), Chen *et al.* (2021)). Consistent with the previous studies, this study 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 more than half of the climatic influences ($\tau_{e,C}$: 52%; $\tau_{e,N}$: 75%; $\tau_{e,P}$: 57%) resulted from the interactions between climate and soil, vegetation, or terrain. Different from $\tau_{e,C}$ and $\tau_{e,N}$, the influences of soil (23%) and terrain (21%) on $\tau_{e,P}$ were comparable with that of climate (28%). 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 the C input (both quality and quantity) and stabilization (Chen *et al.* 2021), whereas N input is dominated by N fixation in many undisturbed forests, 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 $\tau_{e,N}$ (see 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 were related to soil weathering status, and an increasing fraction of soil P became occluded during pedogenesis (Walker & Syers 1976).

The breakpoint in the relationships between $\tau_{e,P}$ and T_{\min} further reinforces the significant role of P limitation on ecosystem dynamics. The breakpoint around 0 in our study coincided with the direction of changes of external P input with T_{\min} (see Fig. 4c). Our data indicates, in the mature forests located in the subtropical regions with $T_{\min} > 0$ (see Fig. 1), vegetation evolved to make use of increasingly favourable water and temperature conditions (see Figure S1b-c) while P input decreased with T_{\min} , for example, through increasing ecosystem P use efficiency (PUE, defined as the ratio of NPP and P uptake by plants)

(see Fig. 6a, before vs. after breakpoints) and increasing P reportion and uptake (see Fig. 6b-c, before vs. after breakpoints). Previous studies reported different strategies of vegetation to maintain high productivity in mature forest ecosystem from $T_{\min} > 0$ regions under P-limitation (most subtropical and tropical area) (Turner *et al.* 2018; Mo *et al.* 2019). For example, some plant can maintain high productivity in low P environment 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 pattern in $\tau_{e,C}$ and $\tau_{e,N}$, despite the regressions are not statistically significant for $\tau_{e,N}$ ($p > 0.05$).

By analysing 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 Figure 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 $T_{\min} > 0$ (see Fig. 5), therefore increase in precipitation with T_{\min} will unlikely explain the estimated increase in $\tau_{e,C}$ with T_{\min} when $T_{\min} > 0$. This is consistent with the result of Kramer and Chadwick (2018).

Instead, the interplay among climate, vegetation, and soil (geochemical factors) are important in shaping the segmentation 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 ($T_{\min} < 0$) where climate was the primary control. High temperature favours accelerated biological activities, which increased plant turnover, soil organic matter decomposition and nutrient transfers (Leiros *et al.* 1999; Conant *et al.* 2011; Larsen *et al.* 2011; Carvalhais *et al.* 2014; Bloom *et al.* 2016). In the region with $T_{\min} > 0$ where subtropical forests are located, soils generally are highly weathered, and geochemical constraints (parent material and soil status) significantly influenced the ecosystem response to climate (Vitousek *et al.* 2010). We showed that P limitation and vegetation's adaptation to the low P environment were most plausible mechanisms driven the change in the relationship between temperature and $\tau_{e,C}$ and $\tau_{e,P}$ between $T_{\min} < 0$ and $T_{\min} > 0$. In addition to P, we also found a high soil clay content and an increasing trend of soil clay content with T_{\min} when $T_{\min} > 0$ (See Figure S3). Clay content is an important indicator of mineral protection organic matter that favours 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 significantly to the segmented relationship between T_{\min} and $\tau_{e,C}$ and $\tau_{e,P}$. It also is possible that other soil properties, such as metal oxide concentration and clay mineralogy also played a significant role in the positive relationship between $\tau_{e,C}$ and $\tau_{e,P}$ and T_{\min} , whereas T_{\min} didn't directly affect $\tau_{e,C}$ and $\tau_{e,P}$, but their variations were strongly correlated with other physical and geochemical properties in the subtropical and tropical regions (Yu *et al.* 2019; Chen *et al.* 2021).

The segmented relationship suggests that the responses of $\tau_{e,C}$ and $\tau_{e,P}$ to future warming may be significantly different between the subtropical forests and temperate forests in China. As clay content and other geochemical properties that are important to P cycle will not change significantly under warming from decades to century, the direct responses of $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ to future warming in the subtropical regions of China will be quite small, whereas $\tau_{e,C}$, $\tau_{e,N}$ and $\tau_{e,P}$ of temperate forests are very sensitive to warming at a rate of -1 year/ for $\tau_{e,C}$, -23 year/ for $\tau_{e,N}$ and -216 year/ for $\tau_{e,P}$ (see Fig. 4g-i). Global models used for simulating terrestrial biogeochemical cycles under future climate change often applied one temperature-dependence 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 & Chadwick 2018; Basile-Doelsch *et al.* 2020), it is important to include the dependence of C or nutrient stabilization on soil

geochemical in global land models for modelling soil C, N and P cycles (Rasmussen *et al.* 2018; Wang & Goll 2021).

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