

Soil and vegetation carbon turnover times from tropical to boreal forests

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Abstract

1. Terrestrial ecosystems currently function as a net carbon (C) sink for atmospheric CO₂, but whether this C sink can persist with global climate change is still uncertain. Such uncertainty largely comes from C turnover time in an ecosystem, which is a critical parameter for modelling C cycle and evaluating C sink potential. Our current understanding of how long C can be stored in soils and vegetation and what controls spatial variations in C turnover time on a large scale is still very limited.
2. We used data on C stocks and C influx from 2,753 plots in vegetation and 1,087 plots in soils and investigated the spatial patterns as well controlling factors of C turnover times across forest ecosystems in eastern China.
3. Our results showed a clear latitudinal pattern of C turnover times, with the shortest turnover times in the low-latitude zones and the longest turnover times in the high-latitude zones. Mean annual temperature and mean annual precipitation were the most important controlling factors on soil C turnover times, while forest age accounted for the majority of variations in the vegetation C turnover times. Forest origin (planted or natural forest) was also responsible for the variations in vegetation C turnover times, while forest type and soil properties were not the dominant controlling factors.
4. Our study highlights the different dominant controlling factors in soil and vegetation C turnover times and different mechanisms underlying above- and below-ground C turnover. These findings are essential to better understand (and reduce uncertainty) in predictive models of coupled C–climate system.

KEYWORDS

carbon turnover time, climate, forest age, forest origin, forest type, soil property

1 | INTRODUCTION

Carbon (C) turnover time (τ , year), which equals residence time at steady state, refers to the average time elapsed between the input of a C atom through photosynthetic fixation and its loss through respiratory or non-respiratory pathways (Barrett, 2002). It is an important indicator for ecosystem functions and a key parameter in coupled C cycle models (e.g. Earth System Models, ESMs) for predicting global C

storage (Chen et al., 2015). However, substantial uncertainty remains about C turnover time, which prevents us from accurately assessing the size of the terrestrial C sink and predicting future climate–C cycle feedbacks (Anav et al., 2013; Wieder, Cleveland, Smith, & Todd-Brown, 2015). This uncertainty is even larger than that of C input of net primary productivity (Friend et al., 2014). Thus, it is urgently important to have a full understanding of C turnover time and its controlling factors. This understanding, based on empirical observations,

can help to reduce the large degree of uncertainty in predictive models of the Earth's coupled C–climate system (Friedlingstein et al., 2006).

C turnover time at steady state is commonly estimated as the ratio of C stock in a reservoir to input or output flux (Raich & Schlesinger, 1992). Soil is the major C pool in terrestrial ecosystems and has a longer turnover time than vegetation (Schmidt et al., 2011). A central topic in previous studies on soil organic C (SOC) dynamics is SOC turnover time (τ_{soil}) and its determinants (Heckman et al., 2014; Koven et al., 2015; Schimel et al., 1994). It has been documented that at a small spatial scale, soil C turnover is mainly dependent on soil temperature and moisture (Craine, Fierer, & McLauchlan, 2010; Davidson & Janssens, 2006; Thomsen, Schjønning, Jensen, Kirstensen, & Christensen, 1999), soil chemical properties (Schindlbacher et al., 2010; Xu, He, & Yu, 2016; Xu, Shi, et al., 2016), C quality (Chen, Liang, et al., 2016) or soil microbial community (Chen, Li, Lan, Hu, & Bai, 2016; Cleveland, Nemergut, Schmidt, & Townsend, 2007), while at national and global scales, latitude, altitude and associated climatic variables are suggested to be responsible for the variability of τ_{soil} (Chen, Huang, Zou, & Shi, 2013). Moreover, soil C turnover is also affected by natural (e.g. fire and insects) and human disturbances (e.g. fertilizer, clear-cutting and land use) (Reed, Ewers, & Pendall, 2014; Zhou, Zhao, Liu, & Oeding, 2013). Despite the considerable effort made to quantify the variations of SOC turnover among soil types, climatic conditions and under different disturbances (Garten & Hanson, 2006; Six & Jastrow, 2002), large controversy over soil C turnover and its controlling factors remains, due to large spatial heterogeneity (Schmidt et al., 2011) and different experimental methods among case studies, making it difficult to compare τ_{soil} at a large scale and to quantify the key controlling factors. Moreover, the direct and indirect pathways of these abiotic and biotic factors impacting on τ_{soil} are unclear and less quantified in previous studies.

In contrast to τ_{soil} , vegetation C turnover time (τ_{veg}) has been rarely examined although it is a crucial process in regulating stoichiometry and elemental cycle in an ecosystem (Erb et al., 2016), and also an important parameter in the ESMs to predict biomass allocation and productivity of the ecosystem (Bloom, Exbrayat, van der Velde, Feng, & Williams, 2016; Friend et al., 2014). τ_{veg} differs from seconds or months in foliage, years in fine roots, to decades in wood, which can subsequently lead to great variability of τ_{veg} (Malhi, Saatchi, Girardin, & Aragão, 2009; Trumbore, 2000). Previous studies have suggested that τ_{veg} is dependent on the combined effects of vegetation type, climate, soil and land use (Erb et al., 2016). However, our quantitative understanding on the controlling factors of τ_{veg} is still very limited. Moreover, as it is difficult to measure foliage, root and wood C turnover times separately and directly in the field, the ESMs provide an alternative measurement of C turnover times for different vegetation compartments (e.g. Negrón-Juárez, Koven, Riley, Knox, & Chambers, 2015). Models have undoubtedly improved our understanding of τ_{veg} among different compartments, but the challenge for model studies lies in that huge uncertainty which still exists. For example, turnover time of wood in tropical forests has been estimated to be 10–30 years faster in ESMs than the observed value (Negrón-Juárez et al., 2015), and globally ecosystem C turnover times have been underestimated

by 36% in the ESMs (Carvalhais et al., 2014). Most importantly, our understanding of the determinant processes of τ_{veg} is still under debate (Friend et al., 2014). Therefore, more observation-based empirical studies are needed to quantify τ_{veg} and its controlling factors.

Forests contain up to 80% of terrestrial above-ground C and 40% of below-ground C, thus play a critical role in terrestrial C cycle (Dixon et al., 1994). A recent study reveals that forests now serve as a net C sink for atmospheric CO₂ (Pan et al., 2011), but whether this C sink will persist as the climate change remains largely uncertain (Goodale et al., 2002). Thus, studying forest C turnover times will greatly improve our fundamental knowledge of terrestrial C cycle. Previous studies have investigated spatial variations of C turnover times associated with forest type and climate, and found that C turnover times have a latitudinal pattern and also differ among forest types (Chen et al., 2013; Trumbore, 2000; Vesterdal, Elberling, Christiansen, Callesen, & Schmidt, 2012). Unfortunately, these studies have seldom considered the impacts of forest age. In comparing to other terrestrial ecosystems, a forest ecosystem is more complex as it is unevenly aged. Numerous studies have suggested that forest age is a critical factor determining ecosystem C storage and fluxes (Gray, Whittier, & Harmon, 2016; Ryan, Binkley, & Fownes, 1997; Yang, Luo, & Finzi, 2011), thus may affect C turnover times. However, the impact of forest age on C turnover times over large areas is largely unknown.

In this study, we collected data from 2,753 forest plots in vegetation and 1,087 plots in soils from tropical to boreal forests in eastern China, which covers most forest types in the Northern Hemisphere (Fu et al., 2010). The main objectives of this study were to: (1) quantify τ_{veg} and τ_{soil} and their variations with climate zone, forest origin, forest type and forest age; (2) investigate the latitudinal patterns of C turnover times; and (3) reveal the controlling factors on the spatial variations of τ_{veg} and τ_{soil} .

2 | MATERIALS AND METHODS

2.1 | Forest classification

Forest covers a wide latitudinal span from north to south in China. Therefore, the distribution of forest has a wide climatic range extending from boreal to tropical zones (Yu et al., 2006). Based on the principles of Chinese vegetation regionalization (Hou, Sun, Zhang, & He, 1982) and previous studies (He et al., 2017; Peng et al., 2016), we classified China's forests as five forest type groups, including deciduous broadleaf forest (DBF), deciduous needleleaf forest (DNF), evergreen broadleaf forest (EBF), evergreen needleleaf forest (ENF), and needleleaf and broadleaf mixed forest (NBF). The five groups were further divided into 19 forest types associated with climate zones and 39 forest subtypes (Table S1).

2.2 | Data sources and data compilation

Vegetation C stock (C_{veg}) was derived from the 'Strategic Priority Research Program' of the Chinese Academy of Sciences (No. XDA05050000), in which 3,161 plots covering main forest types in

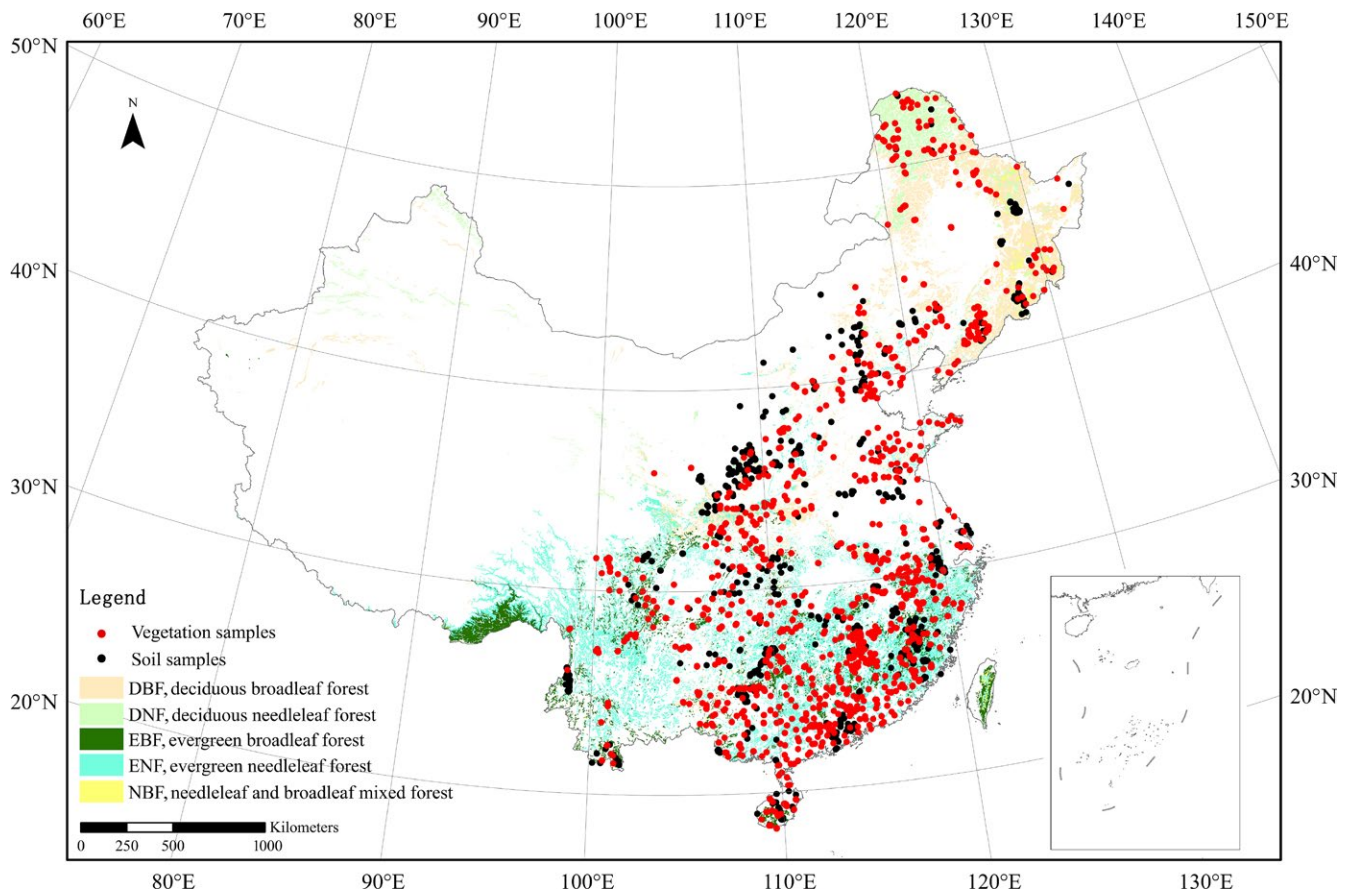


FIGURE 1 Distribution of sampling plots for estimation of C turnover times in vegetation and soils across forest ecosystems in eastern China. Forest type was classified as five groups: DBF, DNF, EBF, ENF and NBF

China were investigated (He et al., 2017). The dimension of each plot was 0.1 ha and each plot was divided into ten 10 m × 10 m quadrats, with tree height and breast-height diameter of each tree, and total number of trees recorded in each quadrat. By using allometric equations based on the tree height and breast-height diameter for different tree species (Ecosystem Carbon Sequestration Project, 2015), we calculated vegetation biomass (kg C m^{-2}) for each plot. Among the 3,161 plots, we used the data of 2,753 plots which located in the eastern China (Figure 1). Of these 2,753 plots, there were 627 DBF plots, 149 DNF plots, 545 EBF plots, 1,176 ENF plots and 256 NBF plots. The forest origin (planted or natural forest) was recorded for each plot. Stand age of planted forests was determined by the time since the afforestation, while the age of natural forests were determined by the mean age of all tree species by measuring tree rings. The C_{veg} (kg C m^{-2}) was converted from the vegetation biomass by a conversion factor of 0.5 (Pregitzer & Euskirchen, 2004).

Soil C stock (C_{soil}) was derived from published studies from 2004 to 2014 in the China National Knowledge Infrastructure (<http://www.cnki.net/>) and in the Web of Science (<http://www.webofknowledge.com>), including field-measured data from 1,087 plots (DBF, 223 plots; DNF, 87 plots; EBF, 359 plots; ENF, 348 plots; NBF, 70 plots) from northern to southern China (Figure 1). The disturbed forest plots (e.g. fire, cutting and fertilizer) were not included in the soil dataset. Data

on reported soil C stock (kg C m^{-2}), SOC or soil organic matter (SOM) content (%), soil bulk density (BD , g cm^{-3}) and soil layer depth (cm) were extracted from the original studies. The SOC content was calculated by the SOM content using the Bemmelen index of 0.58 (Hollis, Hannam, & Bellamy, 2012). For better comparison with different sites, we scaled C_{soil} up to 100 cm in soil depth. When soil depth was more than 100 cm, we directly extracted the data down to 100 cm. When soil depth was less than 100 cm, we used the empirical relationship between SOC content and soil layer depth, proposed by Chai et al. (2015) to fit C_{soil} to the 100 cm soil layer. This empirical relationship between SOC content and depth performed very well in previous studies (e.g. Xu et al., 2015; Xu, He, et al., 2016). Here, we randomly selected 200 sample sites to evaluate the predictive accuracy of the empirical relationship (Figure S1). The results showed that the predicted values of soil C stock were almost identical to measured values for the 0–100 cm soil layer ($R^2 = .95$, $p < .001$) (Figure S1). The reported C_{soil} in the original studies was used directly, if not, the C_{soil} in 0–100 cm soil profiles was calculated using Equation (1):

$$C_{\text{soil}} = \frac{\sum_{i=1}^n \text{SOC}_i \times \text{BD}_i \times D_i \times (1 - C_i)}{10} \quad (1)$$

where SOC_i , BD_i , D_i and C_i represent SOC content, BD, soil depth and volume (%) of >2 mm fraction in soil layer i , respectively; and n is

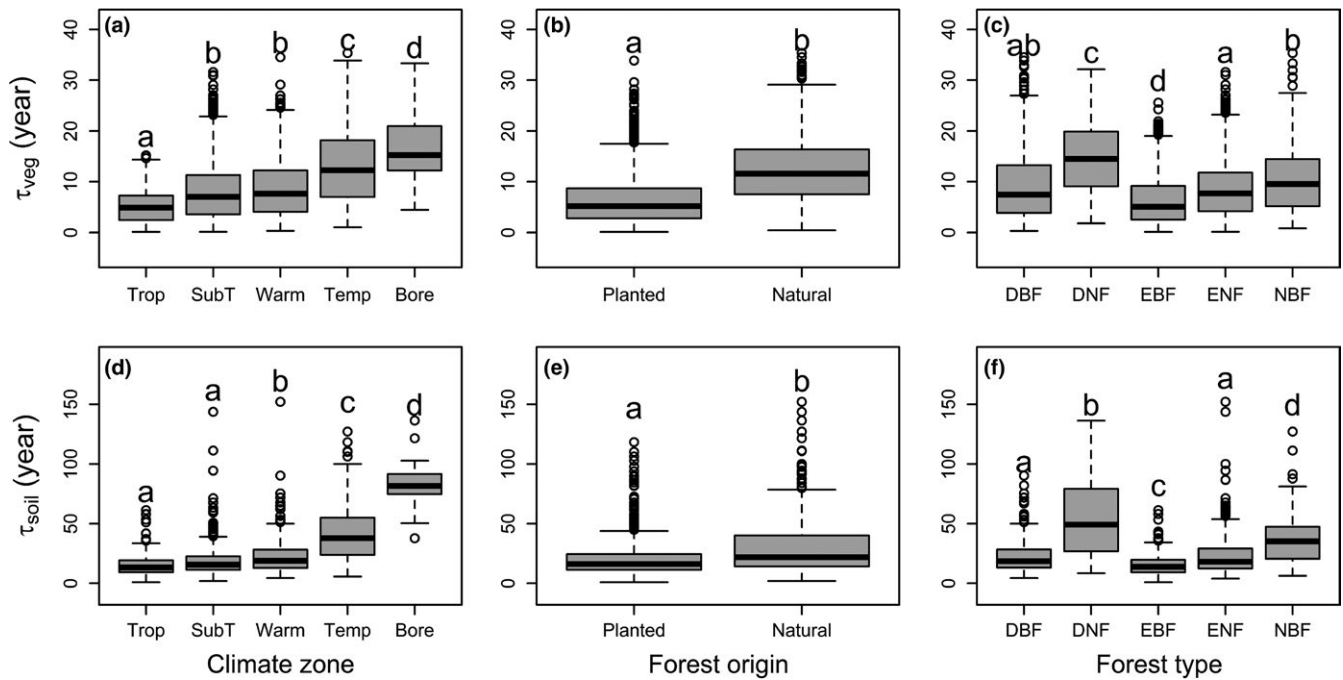


FIGURE 2 C turnover times in vegetation (a–c) and soils (d–f) with different climate zones, forest origin and forest types. Error bars are standard error. Different letters on the top of error bars in each panel indicate significant differences at the $p = .05$ level (Duncan test). Trop, SubT, Warm, Temp and Bore are the abbreviation of tropical, subtropical, warm temperate, temperate and boreal respectively. The abbreviations of forest types are shown in Table S1

the number of soil layers. If soil BD data were not directly reported in the published papers, the values were calculated using the equation proposed by Adams (1973). Furthermore, we also gathered plot information, such as latitude, longitude, mean annual temperature (MAT), mean annual precipitation (MAP), dominant tree species, forest origin and forest age. Any missing geographical coordinates were digitized from Google Maps (<http://maps.google.com>).

Mean annual temperature and mean annual precipitation for each sampling plot in the vegetation dataset and the missing data in the soil dataset were taken from the National Climate Center (<http://ncc.cma.gov.cn/cn/>) using kriging methods. The original meteorological data were derived from long-term observations of 722 meteorological stations in China (Wen & He, 2016). The kriging interpolation analyses were performed using ArcMap 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA). Soil pH and BD were derived from the second National Soil Survey in China (National Soil Survey Office, 1998). The contents of soil SOC, soil nitrogen (N, g/kg), phosphorus (P, ‰), potassium (K, ‰) and clay (%) for each plot were obtained from the China National Science and Technology Platform for Earth System Science Data Sharing (<http://www.geodata.cn/>).

According to the climate zone in which forest distributes across China, we classified the climate zone as five types: boreal ($>50^{\circ}\text{N}$), temperate (40°N – 50°N), warm temperate (33°N – 40°N), subtropical (23°N – 33°N) and tropical ($<23^{\circ}\text{N}$). The forests were divided into five age groups based on the Forestry Standards for “Regulation for age-class and age-group division of main tree-species” of the People’s Republic of China (Table S2). As sample size for some special

age group might be too small to be better analysed, the five age groups were further integrated into three categories: young forests, middle-age forests (mid-aged group plus premature group) and mature forests (mature group plus overmature group).

2.3 | Calculation of carbon turnover times

At steady state, forest C stock is the balance between the productivity and C losses (characterized by turnover times) (Malhi, Doughty, & Galbraith, 2011), thus τ_{veg} and τ_{soil} can be estimated by using Equation (2) (Negrón-Juárez et al., 2015; Todd-Brown et al., 2013):

$$\tau_i = C_i / \text{NPP} \quad (2)$$

where τ is the C turnover time (year), C is the C stock (kg C m^{-2}) and i is vegetation or soils. Annual NPP ($\text{kg C m}^{-2} \text{ year}^{-1}$) on a $0.008^{\circ} \times 0.008^{\circ}$ grid, averaged over the observed years 2004–2014, was extracted from MODIS 17A3 (Smith, Cleveland, Reed, & Running, 2014) (<http://e4ftl01.cr.usgs.gov/MOLT/>).

2.4 | Data analysis

Statistical analyses were performed using R statistical software v3.2.4 (R Development Core Team, 2016). First, one-way ANOVA with Duncan’s multiple-range tests were used to compare the differences of τ_{veg} and τ_{soil} among climate zones, forest origin, forest types and age groups. To explore spatial patterns of τ_{veg} and τ_{soil} , we conducted an ordinary least squares (OLS) regression to evaluate the

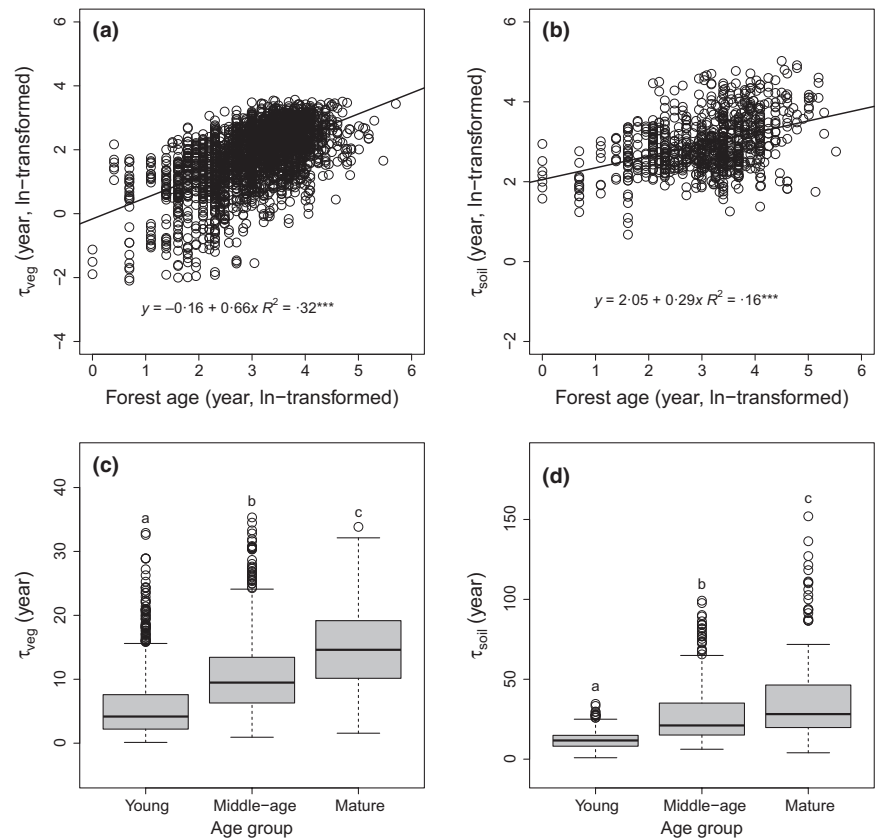


FIGURE 3 C turnover times in vegetation ($n = 2,753$) and soils ($n = 823$) as a function of forest age across all forests (a, b) and in different age groups (c, d). Different letters on the top of error bars (c, d) indicated significant differences at the $p = .05$ level (Duncan test)

relationships between C turnover times and latitude, MAT and MAP. The OLS regressions were also used to investigate the relationships between C turnover times and forest age (year). A pairwise correlation analysis was performed to explore correlations of C turnover times with soil variables (pH, BD, clay content, SOC, N, P and K). Second, we performed structural equation modelling (SEM) to analyse direct and indirect pathways determining C turnover times. To facilitate our analysis, we classified all soil variables into two groups, including soil nutrient (SOC, N, P and K) and soil environment (pH, BD and clay content). Mean annual temperature and mean annual precipitation were expressed as climate. Because the variables of climate, soil nutrient and soil environment groups were closely correlated, a principal components analysis (PCA) was performed to create a multivariate index representing each group (e.g. Chen, Li, et al., 2016; Chen, Liang, et al., 2016). Within each group, only variables significantly correlated with C turnover times were included in the PCA. The first principal components (PC1), which explained 65%–95% of the total variance, were subsequently used to the SEM analysis (Table S3). In the SEM analysis, the data were fit to the model using the maximum likelihood estimation method. The χ^2 and associated p value were used to evaluate the fitness of the model (Grace, 2006). The SEM analysis was implemented using Amos 21.0 (Amos Development Corporation, Chicago, IL). Finally, we used general linear models (GLMs) to separate variance explained by climate, forest age, forest origin, forest type, soil nutrient and soil environment on C turnover times. C turnover times were natural logarithm-transformed to meet the parametric assumptions of normality. The explained

variables having significant effects on C turnover times were included in the final model.

3 | RESULTS

3.1 | Carbon turnover times in vegetation and soils

τ_{veg} varied from 0.12 to 35.5 years, with a median value of 7.6 years, while τ_{soil} ranged from 0.9 to 152 years, with a median value of 17.7 years (Figure S2). C turnover times varied significantly ($p < .001$) with forest origin and forest type (Figure 2b,c,e,f). On average τ_{veg} and τ_{soil} in natural forests were larger than those in planted forests ($p < .001$). Mean τ_{veg} for forest types ranged from 6.4 (EBF), 8.6 (ENF), 9.3 (DBF), 10.8 (NBF) to 15.1 years (DNF), while mean τ_{soil} ranged from 15.4 (EBF), 23.5 (DBF), 24.3 (ENF), 37.9 (NBF) to 53.8 years (DNF). Across all forest plots, C turnover times significantly increased with forest age ($p < .001$, Figure 3a,b). There were significant differences among forest age groups ($p < .001$), with mature forests having longer C turnover times than middle-age and young forests (Figure 3c,d).

3.2 | Spatial patterns of carbon turnover times

C turnover times were positively correlated with latitude across all forest plots (Figure 4a,d). There were significant differences among climate zones ($p < .001$), with the longest C turnover times in the boreal zone and the shortest values in the tropical area (Figure 2a,d). C turnover times decreased with increasing MAT and MAP (Figure 4b,c,e,f).

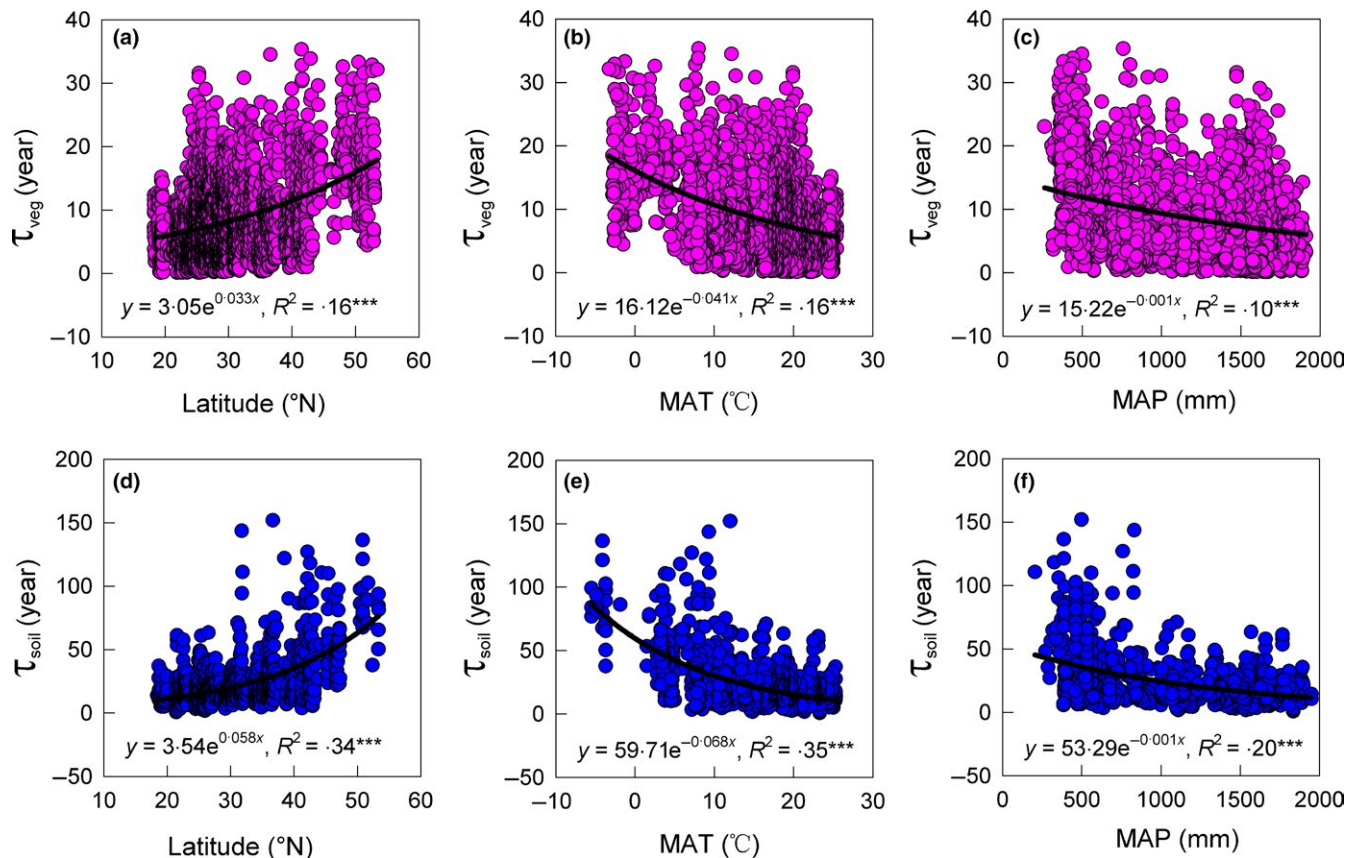


FIGURE 4 Relationships between C turnover times and latitude (a, d), mean annual temperature (MAT; b, e) and mean annual precipitation (MAP; c, f) for vegetation ($n = 2,753$) and soils ($n = 1,087$). Error bars are standard error. $***p < .001$

MAT explained more spatial variations of C turnover times in soils ($R^2 = .35$) than those in vegetation ($R^2 = .16$), while MAP explained 20% variations for τ_{soil} and 10% variations for τ_{veg} .

3.3 | Controlling factors of carbon turnover times

The results of pairwise correlation analysis indicated that soil nutrient and soil environment variables were significantly correlated with C turnover times for both vegetation and soils ($p < .01$, Table S4). Overall, C turnover times exhibited a significant increase with increasing SOC, N and P contents. Conversely, C turnover times were negatively correlated with clay content.

The SEM analysis showed that the model explained 27% of the variance in τ_{veg} (Figure 5a). Climate had direct negative effects on τ_{veg} and presented indirect effects on τ_{veg} by negatively affecting soil nutrient, which consequently led to shorter τ_{veg} . Soil nutrient showed direct positive effects on τ_{veg} , while soil environment had no significant effects on τ_{veg} . Forest age exerted a positive effect on τ_{veg} through its direct effect on τ_{veg} and the indirect effect via its positive correlation with soil nutrient. Latitude had an indirect effect on τ_{veg} by changing climate. Taken together, forest age and latitude were the most important direct and indirect controlling factors of τ_{veg} variation respectively (Figure S3a, c).

The model explained 44% of the variance for τ_{soil} (Figure 5b). Climate, forest age, soil nutrient and soil environment were the direct predictors

of τ_{soil} . Among the direct predictors, climate was the most important control on τ_{soil} . Compared with the standardized path coefficients for τ_{veg} , the direct effects of climate increased from -0.27 to -0.55 , while the direct impact of forest age decreased from 0.30 to 0.28 in τ_{soil} (Figure S3b). Latitude also exerted a strong indirect effect on τ_{soil} with standardized path coefficient increased from 0.30 in τ_{veg} to 0.48 in τ_{soil} (Figure S3d).

The GLMs analysis presented that climate, forest age, forest origin, forest type and soil nutrient exhibited a combined control on C turnover times for both vegetation and soils (Table 1). Specifically, climatic variables accounted for 9.4% and 28.8% of the variance for τ_{veg} and τ_{soil} , respectively, whereas forest age explained 12.4% and 8.6% of the corresponding variance. Forest origin accounted for 7.5% of the variance for τ_{veg} , while the corresponding variance could be only explained by 0.9% for τ_{soil} . Furthermore, forest type explained an additional 0.7% and 1.2% of the variance for τ_{veg} and τ_{soil} , respectively, while soil nutrient accounted for 0.5% and 1.5% of the corresponding variance in the final model (Table 1).

4 | DISCUSSION

4.1 | Influences of abiotic factors on carbon turnover times

Our results demonstrate a latitudinal pattern of C turnover times and climate controls (MAT, MAP) on the spatial patterns of C turnover

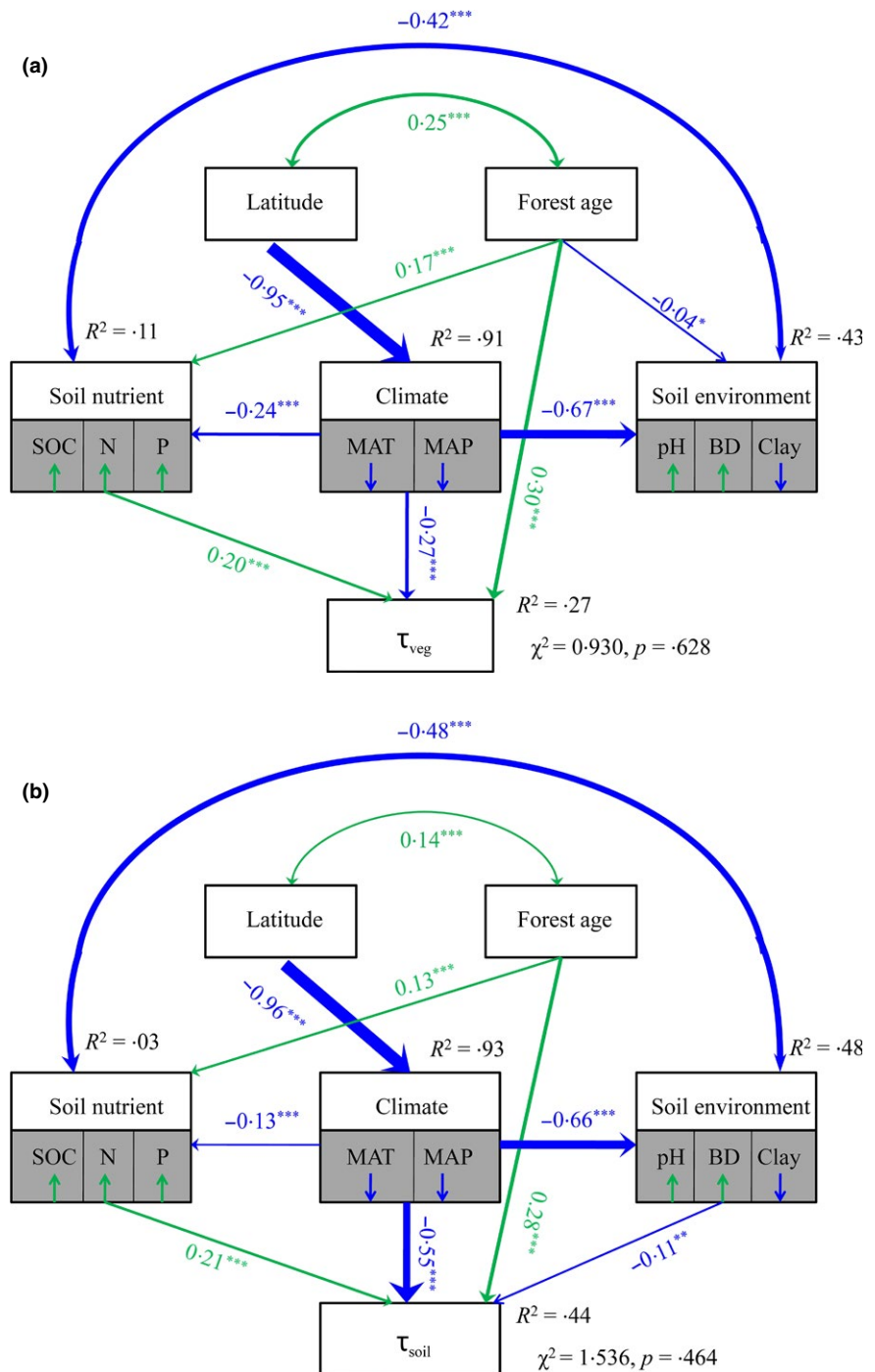


FIGURE 5 Structure equation modelling examining the direct and indirect effects on C turnover times in vegetation (a) ($n = 2,753$) and soils (b) ($n = 823$). Double-headed arrows represent covariance between related variables. Single-headed arrows indicate the hypothesized direction of causation. Dark green and blue arrows indicate positive and negative relationships respectively. Arrow width is proportional to the strength of the relationship. Double-layer rectangles represent the first component from the PCA conducted for soil nutrient, climate and soil environment. The dark green “↑” and blue symbol “↓” indicate a positive or negative relationship, respectively between the variables and C turnover times. The numbers adjacent to arrows are standardized path coefficients. The proportion of variance explained (R^2) appears alongside each response variables in the model. Goodness-of-fit statistics for the model are shown alongside each model. * $p < .05$, ** $p < .01$, *** $p < .001$

times across all forests (Figure 4). The results agree with previous studies that reported the shortest turnover times in the low-latitude zones and the longest turnover times in the high-latitude zones (Bird, Chivas, & Head, 1996; Bloom et al., 2016; Carvalhais et al., 2014; Chen et al., 2013). τ_{soil} was negatively related with MAT for all forests in this study (Figure 4), which is not consistent with Giardina and Ryan (2000) who reported that there were no significant trends of τ_{soil} with temperature in global forests. Negative correlations between temperature and τ_{soil} are widely observed in soil incubations (Knorr, Prentice, House, & Holland, 2005), field measurements (Sanderman, Amundson, & Baldocchi, 2003; Trumbore, 2000), isotope

trace (Trumbore, Chadwick, & Amundson, 1996) or modelling studies (Schimel et al., 1994; Townsend, Vitousek, & Trumbore, 1995; Xu, He, et al., 2016; Xu, Shi, et al., 2016). This negative relationship could be explained by the fact that increasing MAT or soil temperature enhances soil C mineralization by stimulating soil microbes and enzymes activities (Conant et al., 2011; Leirós, Trasar-Cepeda, Seoane, & Gil-Sotres, 1999), and subsequently accelerates τ_{soil} . Mean annual precipitation also determines the variations of τ_{soil} . Previous field or model studies both indicated that increase in precipitation or increasing soil water content accelerates soil C decomposition (Davidson, Verchot, Cattânio, Ackerman, & Carvalho, 2000; Knapp et al., 2008; Reichstein

TABLE 1 Summary of general linear models for vegetation and soil C turnover times

Factor	τ_{veg} (ln-transformed)			τ_{soil} (ln-transformed)		
	Main-effect model		Final model	Main-effect model		Final model
	MS	F		MS	F	
Climate	212.58	356.42***	9.36	107.28	394.97***	28.80
Forest age	281.17	471.42***	12.38	32.17	118.45***	8.63
Forest type	16.33	27.38***	0.72	4.34	15.98***	1.16
Forest origin	169.86	284.79***	7.48	3.18	11.71***	0.85
Soil nutrient	10.57	17.72***	0.47	5.74	21.14***	1.54
Soil environment	3.31	5.55		0.11	0.42	

***F values in bold indicate $p < .001$. Climate, first components from a PCA conducted with MAT, MAP; Soil nutrient, first components from a PCA conducted with soil SOC, N and P; Soil environment, first components from a PCA conducted with soil pH, BD and clay content; MS, mean square; SS%, percentage of sum square explained.

et al., 2003), and thereby results in faster SOC turnover. Multiple mechanisms have been suggested underlying the positive effect of increasing precipitation on the SOC turnover, including stimulating microbial activities, enhancing nitrogen availability and increasing above- and below-ground C inputs (Posada & Schuur, 2011; Schimel et al., 1994). A global synthesis of precipitation manipulation experiments indicated that the normalized increased precipitation of 28% of the MAP increased soil respiration on average by 16% and decreased precipitation reduced soil respiration by 17% (Liu, Wang, et al., 2016). However, it is noticeable that MAP may not be an accurate predictor of soil water content because the MAP hides its temporal distribution (Sanderman et al., 2003). This is the reason why MAP is not as important as the MAT in controlling τ_{soil} , especially at large scales (Figures S4 and S5).

Climate controls on the variations of τ_{veg} are not as dominant as that for soils (Table 1, Figures 4 and 5). In fact, at the plot scale, the determinant of climate on τ_{veg} is likely to be confounded by forest age, tree density and other factors. At larger scales, e.g. within 2° latitude interval (Figure S4) or 5° latitude interval (Figure S5), the impact of climate on τ_{veg} becomes more evident. The negative correlations between τ_{veg} and climate may also be related to biomass allocations. Luo, Wang, Zhang, Booth, and Lu (2012) and Reich et al. (2014) both indicated that more biomass is allocated into roots at the expense of foliage in cold and relative dry climates, as roots, especially coarse roots, have slower turnover rates than foliage and are more likely to contribute to the latitudinal variations of τ_{veg} .

Compared with previous studies, this study advances our understanding on the controlling mechanisms of C turnover times by revealing the direct and indirect pathways of abiotic factors (Figure 5). On the one hand, the direct impacts of climate factors explained more variations of τ_{soil} and τ_{veg} than those of soil environment and nutrients. On the other hand, climate factors indirectly impacted τ_{soil} and τ_{veg} by substantially changing soil environment and nutrients. These findings emphasize the need to incorporate climate impacts into biogeochemical model development and evaluation.

4.2 | Influences of biotic factors on carbon turnover times

We discovered that forest age is a dominant biotic factor that modulates C turnover times, especially for vegetation (Table 1, Figures 3 and 5). On the one hand, C stock in the vegetation increases with stand development, (Cheng et al., 2015; Fonseca, Benayas, & Alice, 2011). For instance, in a natural vegetation succession, C storage in biomass increased from 1.70 (grasslands), 4.15 (shrublands), 22.3 (shrub forests), 70.3 (secondary forests) to 142.2 Mg C ha⁻¹ (primary forest) in karst regions (Liu, Liu, et al., 2016). On the other hand, with forest growth, stand NPP declines as trees age (Gray et al., 2016), which may result from nutrient limitation, stomatal constraint, declines in photosynthesis during stand development (Gower, McMurtrie, & Murty, 1996; McDowell, Phillips, Lunch, Bond, & Ryan, 2002; Tang, Luyssaert, Richardson, Kutsch, & Janssens, 2014). Moreover, it has been demonstrated that increases in heterotropical respiration (R_h) in early succession following disturbances are commonly evident (McKinley et al. 2011). In global temperate forests, R_h has been reported decline from 9.7 Mg C ha⁻¹ year⁻¹ in young forests (0–10 years) to 2.8 Mg C ha⁻¹ year⁻¹ in old forests (121–200 years) (Pregitzer & Euskirchen, 2004). The combination of increasing vegetation C pool size and decreasing NPP or R_h results in the increment of τ_{veg} with stand development. Therefore, forest age is a main determinant of τ_{veg} across all forests (Figures 3 and 5). For τ_{soil} , forest age plays a less important role than climate factors in determining the variations of τ_{soil} . This is likely because soils consist of both newly fixed and old C, with C age ranging from months to decades, and even over several hundred years (Parton, Schimel, Cole, & Ojima, 1987).

Our findings also show that forest origin, to some extent, shapes τ_{veg} (Table 1). This could be due to planted forests having higher relative growth rates and photosynthetic rates than natural forests, resulting in a relative higher NPP. The reason might also be that planted forests and natural forests have different biomass allocation patterns. Plants usually allocate more biomass to roots than to foliage with plant growth (Shipley & Meziane, 2002). Planted forests are usually

young forests with fast-growing species, so allocate more biomass to foliage to compete for light. Natural forests are generally old forests that allocate more biomass to roots and stem to support their standing (Peichl & Arain, 2007). The slower turnover rates in roots and stem than foliage (Negrón-Juárez et al., 2015) leads to a relative longer τ_{veg} in natural forests. Such differences in biomass allocation between planted forests and natural forests also highlight the importance of the impact of forest age. Our results about C turnover times in different forest types were similar to the model study in Zhou, Shi, Jia, Li, and Luo (2010), where there were shorter C residence times in broadleaved forests than in needleleaf forests, and shorter residence times in evergreen forest than in deciduous forests. However, forest type was not a key factor determining C turnover times in the final model in this study (Table 1). This may be because climate, forest age and forest origin in combination offsets the impact of forest type on C turnover times.

In summary, biotic factors (forest age, forest origin and forest type) accounted for 21% of the variations in the τ_{veg} , thus acted as the dominant determinants of vegetation C turnover, while for τ_{soil} , biotic factors accounted for 11% of the variations, thus played a relative weaker role than climate factors (Table 1). The various dominant controlling factors for τ_{veg} and τ_{soil} imply different mechanisms underlying above- and below-ground C turnover, which needs further investigation to improve our fundamental knowledge of C cycling in forest ecosystems.

4.3 | Implications and sources of uncertainties

By using C stock/NPP method, the τ_{soil} in this study was 24.3 years on average (Figure S2). This estimate is in agreement with the reported value of 24 years for the globally mean τ_{soil} estimated by the same method (Todd-Brown et al., 2013). Carvalhais et al. (2014) reported a mean ecosystem C turnover time of 22.5 years for different biomes of the world using C stock/influx method. The present result of τ_{soil} is also comparable to the reported range of 21.0–23.2 years (Chen et al., 2013), and 32 years (Raich & Schlesinger, 1992) in the studies using the ratio of C stock over C efflux (R_h).

Besides the experimental methods mentioned above, modelling approaches have been also performed to estimate C turnover times. For instance, Negrón-Juárez et al. (2015) conducted the work on τ_{veg} in tropical forests based on 22 ESMs, which demonstrated various C turnover times for different compartments (e.g. τ_{leaf} , 0.30–3.3 years; τ_{wood} , 11–54 years; τ_{root} , 3–23 years). Although modelling is an important tool in studying C turnover times, the performance of models is always unsatisfactory. A recent analysis of 11 ESMs showed that large uncertainties still existed among different models (Todd-Brown et al., 2013), which subsequently constrains their ability to predict C storage capacity in terrestrial ecosystems (Chen et al., 2015). Thus, the empirical results in this study could provide a useful benchmark for model parameterization.

We also acknowledge that our estimates of C turnover times in the present work may have the following uncertainties. The first uncertainty is that we estimated C turnover times based on the steady-state

assumption that rarely happens in reality. In fact, C turnover times are constantly affected by environmental conditions and C input fluxes for the C cycling. Thus, C turnover times are always time-dependent, except at longer time-scales where the effects of environmental conditions and C input fluxes can be ignored, considering the ecosystem is at or near steady state (Sierra, Müller, Metzler, Manzoni, & Trumbore, 2017). Moreover, C turnover times and other metrics of C cycling rates are always model-dependent, and it is difficult to obtain them from observations alone without steady-state assumption (Sierra et al., 2017). Nevertheless, C turnover times at steady state could be useful to inform and parameterize the C cycle models. As discussed here, τ means the apparent turnover times, like that in the study of Carvalhais et al. (2014). In addition, we also assumed that soils are a homogeneous pool, which disregards the reality that soils consist of C that turns over with different rates ranging from single years to centuries (Davidson et al., 2000). So far, it has been a big challenge to separate soils into different pools and quantify each pool's turnover time in empirical study. With those inevitable uncertainties, however, this study provides empirical evidences and dataset on the variations of τ_{veg} and τ_{soil} at a large scale (Figure 1), which is invaluable for model evaluation and benchmark analysis. Furthermore, the controlling factors for turnover times revealed in this study will provide insight into the sensitivity and potential response of forest C cycling to future climate change.

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AUTHORS' CONTRIBUTIONS

J.W. and S.N. conceived the ideas and designed methodology; J.W., J.S., J.X., N.H. and M.L. contributed the data; J.W. analysed the data; J.W. and S.N. drafted the manuscript and all authors contributed critically to the writing and gave final approval for publication.

DATA ACCESSIBILITY

All data used in this manuscript are present in the manuscript and its supporting information.

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