

# Accelerated terrestrial ecosystem carbon turnover and its drivers

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## Abstract

The terrestrial carbon cycle has been strongly influenced by human-induced CO<sub>2</sub> increase, climate change, and land use change since the industrial revolution. These changes alter the carbon balance of ecosystems through changes in vegetation productivity and ecosystem carbon turnover time ( $\tau_{\text{eco}}$ ). Even though numerous studies have drawn an increasingly clear picture of global vegetation productivity changes, global changes in  $\tau_{\text{eco}}$  are still unknown. In this study, we analyzed the changes of  $\tau_{\text{eco}}$  between the 1860s and the 2000s and their drivers, based on theory of dynamic carbon cycle in non-steady state and process-based ecosystem model. Results indicate that  $\tau_{\text{eco}}$  has been reduced (i.e., carbon turnover has accelerated) by 13.5% from the 1860s (74 years) to the 2000s (64 years), with reductions of 1 year of carbon residence times in vegetation ( $r_{\text{veg}}$ ) and of 9 years in soil ( $r_{\text{soil}}$ ). Additionally, the acceleration of  $\tau_{\text{eco}}$  was examined at biome scale and grid scale. Among different driving processes, land use change and climate change were found to be the major drivers of turnover acceleration. These findings imply that carbon fixed by plant photosynthesis is being lost from ecosystems to the atmosphere more quickly over time, with important implications for the climate-carbon cycle feedbacks.

## KEYWORDS

carbon turnover time, climate change, CO<sub>2</sub> increase, ecosystem, land use change, soil, vegetation

## 1 | INTRODUCTION

Ecosystem carbon turnover time ( $\tau_{\text{eco}}$ ) and net primary production (NPP) are the two dominant factors determining the magnitude and dynamics of ecosystem carbon storage (Koven et al., 2015).  $\tau_{\text{eco}}$  represents the mean time that carbon atoms reside in the ecosystem, from influx via NPP to outflux mainly via heterotrophic respiration and disturbances (e.g., fire; Appendix S1; Figure S1). Ecosystem carbon turnover time is further controlled by other processes, including carbon allocation, plant organ mortality rates, and soil organic carbon decomposition rates (Xia, Luo, Wang, & Hararuk, 2013). Although the carbon turnover processes are complex, researchers

usually estimate the  $\tau_{\text{eco}}$  indirectly as the ratio between the mass of ecosystem carbon storage and NPP (pool/flux) based on the assumption of steady-state conditions (Lu, Wang, Luo, & Jiang, 2018; Zhou et al., 2018). Observation-based steady-state  $\tau_{\text{eco}}$  distributions have been used to assess the environmental drivers of spatial variability in  $\tau_{\text{eco}}$ , and used as a benchmark for ecosystem models (Carvalhais et al., 2014).

Human-induced CO<sub>2</sub> increase, climate change, and land use change have profoundly altered the terrestrial ecosystem carbon dynamics since the 1860s (Fernández-Martínez et al., 2019; Liu et al., 2019; Piao et al., 2018, 2020; Sitch et al., 2015). On the one hand, global vegetation productivity shows an increasing trend

from satellite greenness data and ecosystem models (Kolby Smith et al., 2016; Piao et al., 2020), mainly induced by CO<sub>2</sub> fertilization (Liu et al., 2019; Zhu, Piao, et al., 2016), by extended phenology in response to warming (Peñuelas et al., 2017), and by afforestation and ecosystem conservation (Chen et al., 2019; Zhu, Piao, et al., 2016). On the other hand, these driving factors also affected  $\tau_{\text{eco}}$  (Erb et al., 2016; Koven et al., 2015). For example, global warming could accelerate soil microbial decomposition, which results in shorter carbon residence time in the soil ( $r_{\text{soil}}$ ); forest to cropland conversion accelerates carbon residence time in the vegetation ( $r_{\text{veg}}$ ). Based on theory and experiments, CO<sub>2</sub> fertilization may also alter  $r_{\text{veg}}$  by changing carbon allocation and mortality rates (Brienen et al., 2015; Bugmann & Bigler, 2011; De Kauwe et al., 2014) and changing  $r_{\text{soil}}$  by reducing regional soil water loss through transpiration (Van Groenigen, Osenberg, & Hungate, 2011) due to increased water use efficiency by plants. This implies that  $\tau_{\text{eco}}$  in the real world is dynamic. However, until now, changes of terrestrial  $\tau_{\text{eco}}$  and their specific drivers since industrial evolution have not been quantified yet.

Even though the approximation of pool/flux under steady state can be applied for the static  $\tau_{\text{eco}}$  patterns, implicit error problems may arise if this assumption is used to evaluate the dynamics of non-steady-state carbon cycling systems. For example, such approximation could result in erroneous ecosystem  $\tau_{\text{eco}}$  values because of the "apparent change" phenomenon induced by lagged responses of carbon pools with slower cycling rates under the conditions of changes of carbon inputs caused by external environmental changes (Section 2; Appendix S3; Koven et al., 2015). Based on the dynamic carbon cycling theory (Luo et al., 2017; Rasmussen et al., 2016), dynamic  $\tau_{\text{eco}}$  can be computed by an invertible matrix of cycling and transfer rates (**A**), and a matrix of carbon allocation rates (**B**). For matrix **A**, ecosystem variables related to biomass pools mortality and litterfall rates, soil organic carbon pools decomposition rates, and transfer rates between pools are needed. For matrix **B**, NPP allocation rates in biomass pools (fruit, leaf, root, and wood) are required. In reality, not so many system variables can be observed globally to support the analysis of changes in  $\tau_{\text{eco}}$ . Therefore, an ecosystem process model can give insights about this emergent scientific question for  $\tau_{\text{eco}}$  changes and its driving factors.

In this study, ORganizing Carbon and Hydrology in Dynamic Ecosystems-Meliorated Interactions between Carbon and Temperature (ORCHIDEE-MICT) was applied for studying the changes of ecosystem carbon turnover time. ORCHIDEE-MICT (Guimberteau et al., 2018; Zhu, Peng, et al., 2016) is a recently developed ecosystem model, which has the advantage of discretizing soil carbon vertically and of considering processes influencing permafrost carbon in the high-latitude regions. To quantify temporal changes of ecosystem carbon turnover times and their environmental drivers (CO<sub>2</sub> increase, climate change, and land use change), we performed six experimental simulations (S1–S6) using long-term forcing datasets after simulating an initial steady state spin-up run for carbon pools. Matrices **A** and **B** were established with all the pool and flux variables related with carbon turnover given by ORCHIDEE-MICT, and carbon turnover times were computed for different scenarios and at different spatial scales for two periods (the 1860s decade representing terrestrial

ecosystems in the early stage of the industrial revolution, and the 2000s decade representing terrestrial ecosystems in the present day).

## 2 | MATERIALS AND METHODS

### 2.1 | ORCHIDEE-MICT model and simulations

ORCHIDEE-MICT is an improved ecosystem model (Guimberteau et al., 2018; Zhu, Peng, et al., 2016) derived from the ORCHIDEE model (Krinner et al., 2005). The carbon cycle frameworks of the two models are similar, except for the soil pools which have been improved in ORCHIDEE-MICT through discretizing the soil profile into 32 layers with a total soil depth of 38 m. Furthermore, ORCHIDEE-MICT has largely improved the performance of carbon cycle modeling in permafrost regions by incorporating processes such as SOM-dependent soil thermal and hydraulic parameters and optimizing parameters of soil thermal and hydraulic processes. In ORCHIDEE-MICT, there are five vegetation pools (fruit, leaf, reserve, root, and wood), four litter pools (aboveground metabolic and structural litter pools, and belowground metabolic and structural litter pools), and three soil pools (active, slow, and passive) in each soil layer (Figure S2). Similar to the ORCHIDEE model, ORCHIDEE-MICT distinguishes 12 plant function types (PFTs, of which 10 are natural and two agricultural).

In this study, we performed six factorial simulations (S1–S6) using ORCHIDEE-MICT model to analyze the changes of carbon turnover times. Three long-term forcing datasets (changing CO<sub>2</sub>, climate, and land use) from 1860 to 2016 were used to run the model. Global atmospheric CO<sub>2</sub> forcing was constructed by station observations (Mauna Loa Observatory and The South Pole Observatory) provided by NOAA's Earth System Research Laboratory (<http://www.esrl.noaa.gov/gmd/ccgg/trends/>) after 1958 and data inversion with a cubic spline fit to ice core data (Joos & Spahni, 2008) prior to 1958. A 6 hourly, 0.5° × 0.5° CRU-NCEP climatic forcing dataset was used to represent the historical climate dynamics between 1901 and 2016, and years selected from 1901 to 1920 were used to fill the forcing for the period 1860–1900 (Wei et al., 2014). Land use forcing was implemented with latest History of the Global Environment land use/land cover change datasets (Goldewijk, 2001).

First, an initial steady-state spin-up for carbon and water pools was run for preindustrial conditions, applying fixed atmospheric CO<sub>2</sub> concentration, the 1901–1920 CRU-NCEP climate forcing in a loop, and land cover map at the 1860 level. Simulations S1–S5 started from this spin-up state.

In simulation S1, the model was forced by varying CO<sub>2</sub> only, with fixed climate (recycling 1901–1920 climate) and land cover (1860); simulation S2 was prescribed with historical CO<sub>2</sub> and climate, keeping land cover fixed (1860); in simulation S3, the closest to the real world, the model was prescribed with varying CO<sub>2</sub>, climate, and land use change; simulation S4 was prescribed with varying climate only, keeping CO<sub>2</sub> and land cover fixed (1860); in simulation S5, the model was prescribed with varying land use change only, keeping CO<sub>2</sub> and climate fixed (1860 for CO<sub>2</sub> and recycling spin-up climate). Results of S1–S5

were used to identify the relative contribution of main driving factors on changes of carbon turnover times, representing CO<sub>2</sub> effect (S1), CO<sub>2</sub> + climate effects (S2), CO<sub>2</sub> + climate + land use change effects (S3), climate effect (S4), and land use change effect (S5), respectively.

As a major disturbance, fire plays an important role in carbon turnover processes, and may also affect changes in  $\tau_{\text{eco}}$ . We therefore conducted an additional simulation (S6) with ORCHIDEE-MICT with the fire module off (thus no fire-induced mortality and carbon emissions). Before the historical simulation, a new initial steady-state spin-up without fire processes was run, under a similar setup as that used for S1–S5. Starting from the spin-up state, simulation S6 was prescribed with varying CO<sub>2</sub>, climate, and land use change. Therefore, comparison between S6 (fire-off) and S3 (fire-on) can demonstrate the fire effects on  $\tau_{\text{eco}}$ .

In this study, variables were saved annually on a 1° × 1° grid for each carbon pools in the ORCHIDEE-MICT model (five vegetation pools, four litter pools, and three soil pools at each layer), and related influx and outflux for each carbon pools (Figure S2). All variables were used to establish the matrices **A** and **B**, which were used to study the dynamics of terrestrial ecosystem carbon turnover times. Here, we focused on two periods in the 1860s (1860–1869) and 2000s (2000–2009), representing terrestrial ecosystem in the early stage of the industrial revolution and in the present day, to analyze the changes of carbon turnover times and their driving mechanisms.

## 2.2 | Model evaluation

To assess the reliability of our results, we carefully evaluated the overall performance of ORCHIDEE-MICT compared to independent observation-based datasets in four aspects (Appendix S2): (a) ecosystem carbon storage, NPP, and  $\tau_{\text{eco}}$  on the global scale; (b) ecosystem carbon storage, NPP, and  $\tau_{\text{eco}}$  on the grid scale; (c) spatially climatic sensitivities of NPP and  $\tau_{\text{eco}}$ ; and (d) temporal CO<sub>2</sub> exchanges between the atmosphere and the terrestrial biosphere. Results indicated that ORCHIDEE-MICT captured well the static and dynamic patterns of these variables. Therefore, ORCHIDEE-MICT is an appropriate ecosystem model to study the temporal changes of carbon turnover.

## 2.3 | Ecosystem carbon turnover time under dynamic system in non-steady state

Carbon cycle models can be expressed in matrix form based on the mass conservation principle (Anderson, 1983; Bolin, 1981; Luo, Keenan, & Smith, 2015). For a dynamic carbon cycling system in non-steady state with  $d$  carbon pools, the matrix form can usually be described as (Luo et al., 2017):

$$\frac{d\mathbf{X}(t)}{dt} = \dot{\mathbf{X}}(t) = \mathbf{A}(t) \cdot \mathbf{X}(t) + \mathbf{B}(t) \cdot \mathbf{U}(t), \quad (1)$$

where  $\mathbf{X}(t) \in \mathbb{R}^{d \times 1}$  is the carbon storage for year  $t$  and  $\dot{\mathbf{X}}(t) \in \mathbb{R}^{d \times 1}$  represents the balance of carbon pools for year  $t$ .  $\mathbf{A}(t) \in \mathbb{R}^{d \times d}$  describes

the cycling rates for each carbon pool and the transfer rates between carbon pools for year  $t$ . **A** is an invertible matrix and  $\{a_{ij}\}_{i,j \in \{1, \dots, d\}}$  satisfy: (1) for all  $i \in \{1, \dots, d\}$ ,  $a_{ii} < 0$ ; (2) for all  $i \neq j \in \{1, \dots, d\}$ ,  $a_{ij} \geq 0$ ; (3) for all  $j \in \{1, \dots, d\}$ ,  $\sum_{i=1}^d a_{ij} \leq 0$ . The  $i$ th row in **A** represents the carbon dynamics of the  $i$ th pool:  $a_{ij}$  is the transfer rate from pool  $j$  to pool  $i$ ;  $a_{ii}$  is the cycling rate of pool  $i$ , including transfer to other pools and losses from the system.  $\mathbf{B}(t) \in \mathbb{R}^{d \times 1}$  represents the carbon allocation fractions to the  $d$  pools for year  $t$ .  $\mathbf{U}(t) \in \mathbb{R}^{1 \times 1}$  is the total system influx. It should be noted that this is a general linear nonautonomous system representation for dynamic carbon cycle processes, and vectors in the matrix equation are time dependent (Sierra, Ceballos-Núñez, Metzler, & Müller, 2018). Furthermore, the matrix expression can be applied to the ecosystem, or separately for the vegetation or soil systems. In this study, we applied the matrix expression to the ecosystem.

The terrestrial carbon cycle is in non-steady state in response to the human-induced CO<sub>2</sub> increase, climate change, and land use change, and variables in the system show significant trends since the pre-industrial period. To describe the carbon turnover time of a dynamic system in non-steady state, Equation (1) can be transformed into (Luo et al., 2017):

$$\mathbf{X}(t) - \mathbf{A}(t)^{-1} \cdot \dot{\mathbf{X}}(t) = -\mathbf{A}(t)^{-1} \cdot \mathbf{B}(t) \cdot \mathbf{U}(t), \quad (2)$$

where  $\mathbf{X}(t) \in \mathbb{R}^{d \times 1}$  is the carbon storage for year  $t$ ,  $-\mathbf{A}(t)^{-1} \cdot \dot{\mathbf{X}}(t) \in \mathbb{R}^{d \times 1}$  is the storage potential based on system status for year  $t$ , and  $-\mathbf{A}(t)^{-1} \cdot \mathbf{B}(t) \cdot \mathbf{U}(t) \in \mathbb{R}^{d \times 1}$  is the storage capacity based on the system state for year  $t$ . Here, the carbon capacity represents the maximum amount of carbon that an ecosystem can store at given environmental conditions for year  $t$ , which indicate the instantaneous responses of the land carbon cycle to external forcings (e.g., atmospheric CO<sub>2</sub> concentration, climate, and land cover types; Luo et al., 2017). The ecosystem carbon storage potential was defined as the difference between the ecosystem carbon storage capacity and the current carbon storage ( $\mathbf{X}(t) \in \mathbb{R}^{d \times 1}$ ). Therefore, the ecosystems would act as a carbon sink when the carbon storage potential is positive, and a carbon source when carbon storage potential is negative. In addition, we can describe the mean carbon residence times in all carbon pools as (Luo et al., 2017):

$$\mathbf{R}(t) = -\mathbf{A}(t)^{-1} \cdot \mathbf{B}(t) \in \mathbb{R}^{d \times 1}. \quad (3)$$

If we summate both sides of the equation for all pools (2), the formula can be rewritten as:

$$\sum (\mathbf{X}(t) - \mathbf{A}(t)^{-1} \cdot \dot{\mathbf{X}}(t)) = \sum \mathbf{R}(t) \cdot \mathbf{U}(t). \quad (4)$$

Therefore, the system carbon turnover time can be described as:

$$\tau(t) = \sum \frac{(\mathbf{X}(t) - \mathbf{A}(t)^{-1} \cdot \dot{\mathbf{X}}(t))}{\mathbf{U}(t)} = \sum \mathbf{R}(t) = \sum (-\mathbf{A}(t)^{-1} \cdot \mathbf{B}(t)). \quad (5)$$

We conclude that the carbon turnover time ( $\tau(t)$ ), defined as the ratio between the storage capacity and carbon influx ( $\mathbf{U}(t)$ ), equals to

the sum of the carbon residence times ( $R(t)$ ). Furthermore, the system carbon turnover time ( $\tau(t)$ ) is closely related to the variables in matrix  $A(t)$  and  $B(t)$ . Therefore, it is clear that traditional methods for directly calculating the carbon turnover time with  $\sum X(t)/U(t)$  must satisfy the steady-state assumption ( $\dot{X}(t) \approx 0$ ). It is, thus, not reasonable to apply the method of  $\sum X(t)/U(t)$  in a dynamic system in non-steady state. In this work, we treat the ecosystem, including vegetation and soil (including litter pools), as an integrated system. Ecosystem turnover time ( $\tau_{eco}$ ) equals to the sum of the carbon residence time in vegetation ( $r_{veg}$ ) and in soil ( $r_{soil}$ , including litter pools) pools (Appendix S1).

## 2.4 | “Apparent change” phenomenon induced by pool/flux approach in non-steady state

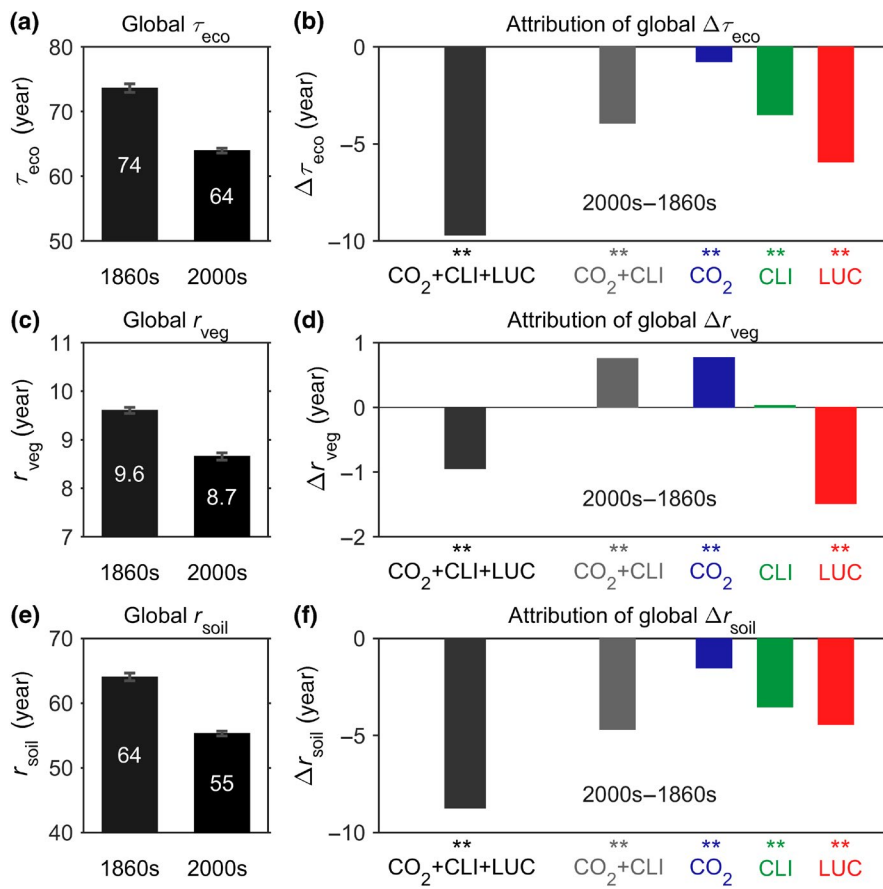
The “apparent change” occurs when we compute the system carbon turnover times using pool/flux approach in non-steady state. We carefully elaborated the mechanisms behind this phenomenon with a case model in Appendix S3. In general, “apparent change” is induced by lagged responses of ecosystem carbon pools with slower cycling rates (e.g., slow pool and passive pool) due to changes in carbon inputs caused by external environmental changes (e.g.,  $CO_2$  increase, global warming, and land use change). The “apparent change” could therefore mislead the estimate of changes of carbon turnover times and their driving mechanisms.

Based on output variables from ORCHIDEE-MICT, we further tested the theory of dynamic carbon cycle in non-steady state (Appendix S4). We computed the carbon turnover times with two methods: (a)  $\sum X(t)/U(t)$  (i.e.,  $C_{eco}/NPP$ ) from the steady-state assumption; and (b)  $\sum (-A(t)^{-1} \cdot B(t))$  based on dynamic theory. The results suggested that the carbon cycle in the 2000s is in non-steady state, and that the calculation of global  $\tau_{eco}$  with  $C_{eco}/NPP$  results in the underestimation of the intrinsic value in non-steady state by 8% for ORCHIDEE-MICT (Figure S10). Therefore, we recommend choosing the matrix inversion method to study the changes of  $\tau_{eco}$  and their drivers to avoid potential issues caused by the “apparent change.”

## 3 | RESULTS

### 3.1 | Changes of ecosystem carbon turnover time

Our simulation showed that the global ecosystem carbon turnover time ( $\tau_{eco}$ ) has been reduced, that is, turnover has accelerated over time, by 13.5% from the 1860s ( $\tau_{eco} = 74$  years) to the 2000s ( $\tau_{eco} = 64$  years; Figure 1). Among the different driving processes evaluated, land use change played the strongest role, leading to a reduction of  $\tau_{eco}$  of 5.9 years, followed by climate change (reduction of 3.5 years). A negative effect on turnover time is also found for  $CO_2$  increase, but the magnitude is smaller compared to the preceding two processes (0.8 year). When separating  $\tau_{eco}$  into carbon residence times in vegetation ( $r_{veg}$ )



**FIGURE 1** Global ecosystem carbon turnover time ( $\tau_{eco}$ ) in the 1860s and the 2000s (a) and attribution of their changes to driving factors (b). Driving factors include  $CO_2$  increase ( $CO_2$ ), climate change (CLI), and land use change (LUC). Furthermore,  $\tau_{eco}$  is divided into carbon residence time in vegetation ( $r_{veg}$ ) and in soil ( $r_{soil}$ , including litter pools). The absolute values in the 1860s and the 2000s as well as their driving factors are shown in (c, d) for  $r_{veg}$  and in (e, f) for  $r_{soil}$ . Asterisks indicate significant differences ( $p < .05$ ) between the 1860s and the 2000s for  $\tau_{veg}$ ,  $r_{veg}$ , or  $r_{soil}$

and in soil ( $r_{\text{soil}}$ ), the effects of driving factors are quite different.  $r_{\text{veg}}$  has been reduced by 9.4% (1 year) from the 1860s and the 2000s, with a trade-off between strong negative effects from land use change and smaller positive effects from increasing  $\text{CO}_2$  (Figure 1d). According to the model, climate change did not have a significant effect on  $r_{\text{veg}}$  at the global scale. By contrast,  $r_{\text{soil}}$  was reduced by 14.1% (9 years), with similar driving factors to those of  $\tau_{\text{eco}}$  (Figure 1e,f).

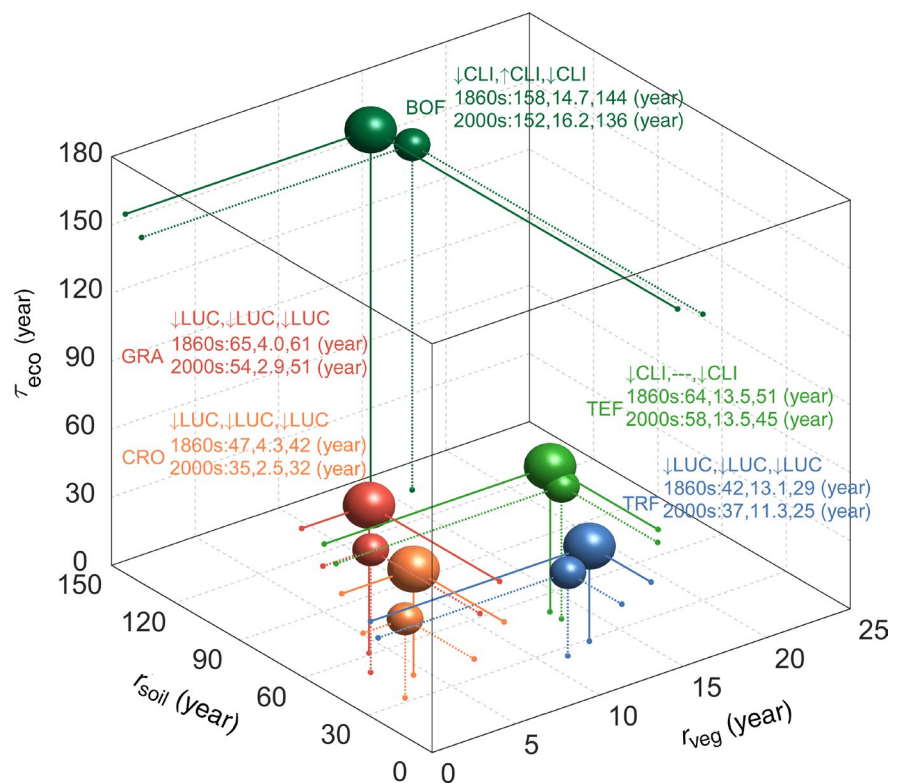
We found different reductions of  $\tau_{\text{eco}}$  across different biomes from the 1860s to the 2000s and different driving processes (Figure 2; Figure S12). Boreal forests have the smallest relative reduction of  $\tau_{\text{eco}}$  (−4%), while cropland experienced the fastest acceleration (−25%) in this period. The land use change is the main factor behind differences between biomes, having very small effects on  $\tau_{\text{eco}}$  in boreal forest, and the largest effects in cropland (−9.3 years). Climate change generally had significant negative effects on  $\tau_{\text{eco}}$ , with the largest influence in grassland and the smallest influence in tropical forest (Figure S12). By contrast, increasing  $\text{CO}_2$  did not significantly affect  $\tau_{\text{eco}}$  across most biomes except for a small positive effect in tropical forests. The effects of each driving factor on  $r_{\text{soil}}$  were similar to those on  $\tau_{\text{eco}}$ , while the response of  $r_{\text{veg}}$  has different sign and magnitude to increasing  $\text{CO}_2$  and climate change. Increasing  $\text{CO}_2$  has positive effects on  $r_{\text{veg}}$  across all biomes. Thus, the overall nonsignificant effect of increasing  $\text{CO}_2$  on  $\tau_{\text{eco}}$  could be explained by the trade-off between a negative effect (acceleration) on  $r_{\text{soil}}$  and a positive effect (slow down) on  $r_{\text{veg}}$ . Climate change had negative effects on  $r_{\text{veg}}$  in grassland and cropland, but positive effects in tropical forests and boreal forests. Nevertheless, the magnitude of climate change effects on  $r_{\text{veg}}$  is small, compared to other driving factors.

Finally, we analyzed the spatial patterns of changes of  $\tau_{\text{eco}}$  at the grid scale (Figure 3; Figures S13 and S14).  $\tau_{\text{eco}}$  has accelerated in most parts of the globe (~83% of vegetated area), with the largest acceleration found in agricultural regions (eastern America, eastern China, India, and sub-Sahara), grassland-dominated regions (southeast South America, southern Africa, and eastern Australia), and tropical forests (Indonesia), and relative smaller acceleration in boreal regions (northern North America and Siberia). The largest acceleration values were mainly associated with regional land use change, consistent with the biome-scale results. The spatial patterns of the acceleration of  $r_{\text{soil}}$  are similar with those of  $\tau_{\text{eco}}$ , while  $r_{\text{veg}}$  has different patterns.  $r_{\text{veg}}$  has increased in most boreal regions, and also in some temperate regions (north-east America, Europe, and China). In most boreal regions, the dominant driving factors are climate change and increasing  $\text{CO}_2$ . By contrast, increasing  $\tau_{\text{veg}}$  in temperate regions was mainly explained by regional land use change. In general,  $\tau_{\text{eco}}$  over 44% of the global vegetated area has been reduced by land use change, over 33% by climate change, and over 6% by increasing  $\text{CO}_2$ .

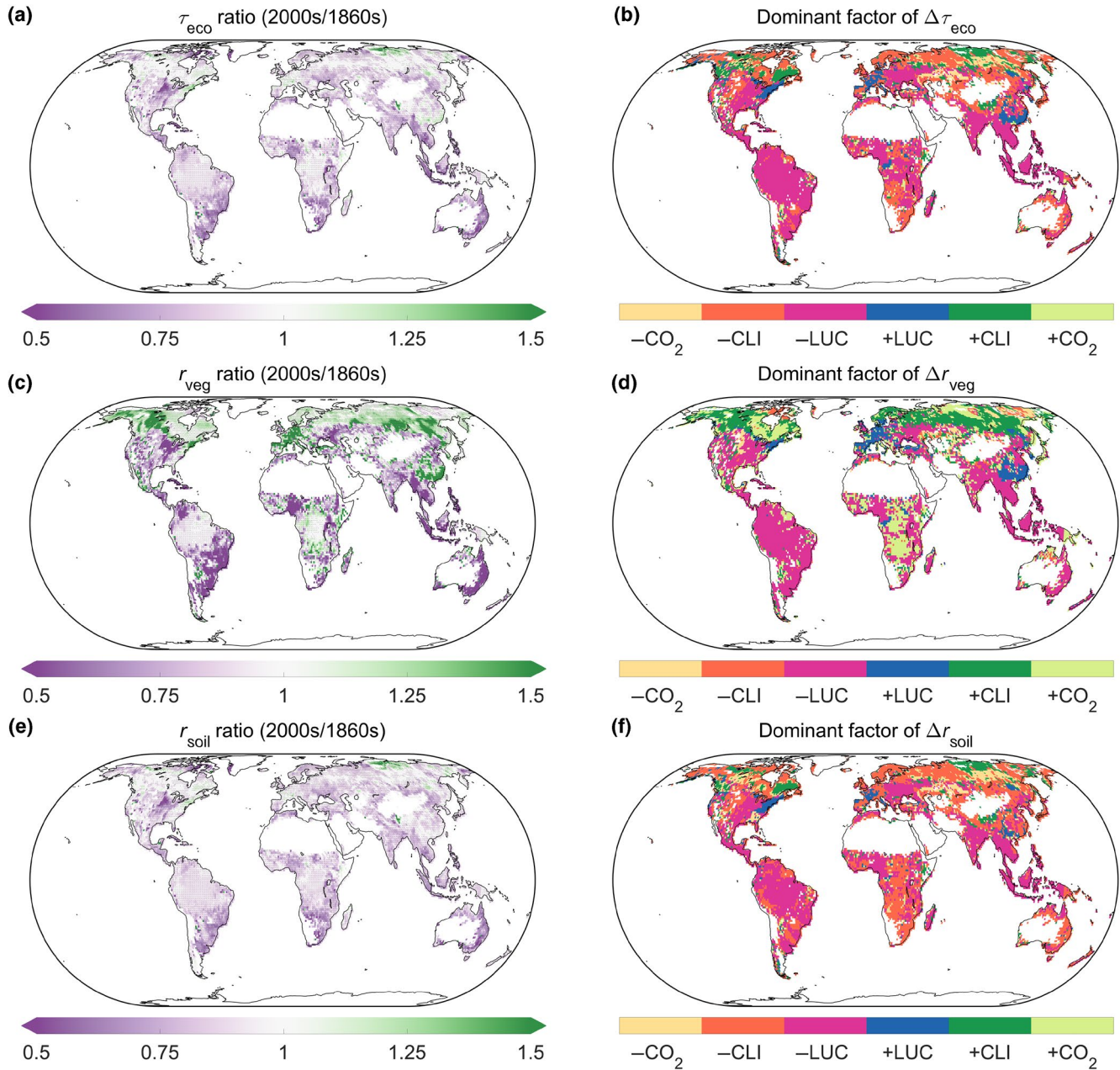
### 3.2 | Fire effects on ecosystem carbon turnover time

We calculated the effects of fire in  $\tau_{\text{eco}}$  based on fire-on and fire-off simulations. Results suggest that fire mainly affects  $\tau_{\text{eco}}$  in boreal forests and in African grasslands (Figure S15), consistent with the higher fire occurrence in these regions (Giglio, Randerson, & Werf, 2013). For example, fire shortens the  $\tau_{\text{eco}}$  by more than 20%

**FIGURE 2** Ecosystem carbon turnover time ( $\tau_{\text{eco}}$ ) in the 1860s and the 2000s per biome. Biomes include boreal forest (BOF), temperate forest (TEF), tropical forest (TRF), grassland (GRA), and cropland (CRO). Furthermore,  $\tau_{\text{eco}}$  is divided into carbon residence time in vegetation ( $r_{\text{veg}}$ ) and in soil ( $r_{\text{soil}}$ ), including litter pools). For each biome, absolute values of  $\tau_{\text{eco}}$ ,  $r_{\text{veg}}$ , and  $r_{\text{soil}}$  in the 1860s and the 2000s are showed from left to right. Up arrows (or down arrows) represent significant ( $p < .05$ ) increase (or decrease) between the 1860s and the 2000s for  $\tau_{\text{eco}}$ ,  $r_{\text{veg}}$ , or  $r_{\text{soil}}$ , accompanied with its dominant driving factor ( $\text{CO}_2$  increase [ $\text{CO}_2$ ], climate change [ $\text{CLI}$ ], or land use change [ $\text{LUC}$ ])







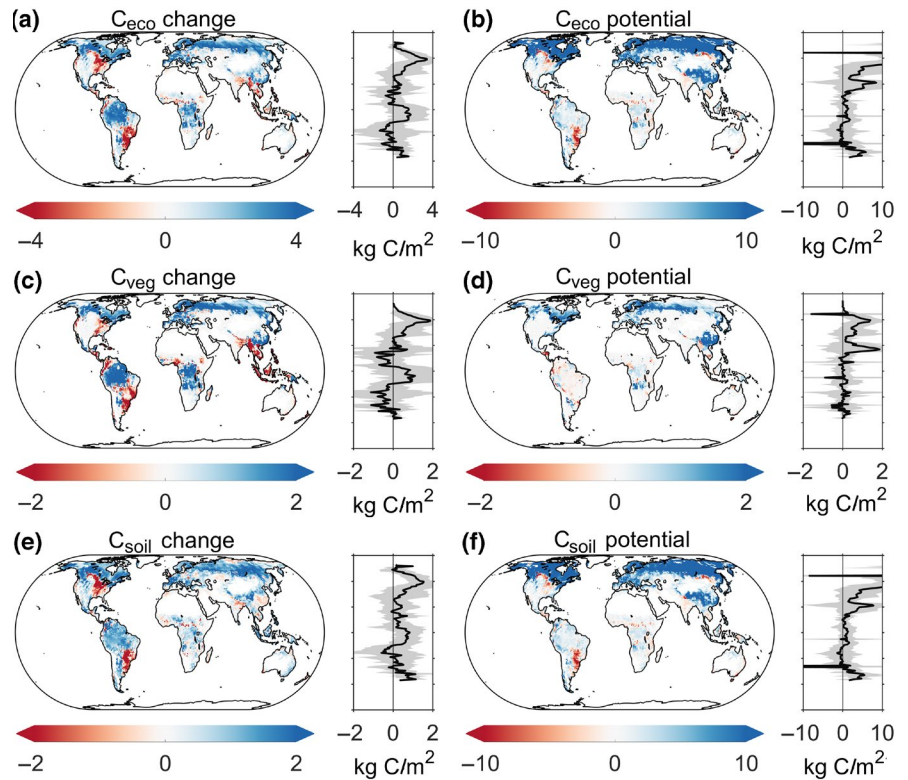
**FIGURE 3** Ratio of ecosystem carbon turnover time ( $\tau_{eco}$ ) between the 2000s and the 1860s (a), and the corresponding dominant driving factor (b). Furthermore,  $\tau_{eco}$  is divided into carbon residence time in vegetation ( $r_{veg}$ ) and in soil ( $r_{soil}$ , including litter pools). Their ratio values between the 2000s and 1860s and dominant driving factor are shown in (c, d) for  $r_{veg}$  and in (e, f) for  $r_{soil}$ . In (a), (c), and (e), stippling indicates pixels with significant difference ( $p < .05$ ) between the 2000s and the 1860s for  $\tau_{eco}$ ,  $r_{veg}$ , or  $r_{soil}$ . In (b), (d), and (f), driving factors include  $CO_2$  increase ( $CO_2$ ), climate change ( $CLI$ ), and land use change ( $LUC$ ). A prefix “+” of the driving factors indicates a positive effect (slow down) on  $\tau_{eco}$ ,  $r_{veg}$ , or  $r_{soil}$ , whereas “-” indicates a negative effect (acceleration)

in the sub-Saharan regions. Then, we calculated the changes of  $\tau_{eco}$  between 1860s and 2000s based on fire-on and fire-off simulations. We found no significant differences of the relative changes of  $\tau_{eco}$  either on the global scale (Figure S16) or on the grid scale (Figure S17) possibly because the simulations do not account for human-driven historical fire changes (Knorr, Arneth, & Jiang, 2016; Mouillot & Field, 2005). Therefore, although fire plays significant effect on the patterns of  $\tau_{eco}$ , fire effect on the trend of  $\tau_{eco}$  is weak in our simulations.

### 3.3 | Ecosystem carbon storage change and potential

Accelerated  $\tau_{eco}$  implied that carbon atoms fixed by plant photosynthesis stay shorter time in terrestrial ecosystems in the 2000s, compared to early stage of the industrial revolution. In parallel, global ecosystem productivity has increased during this period ( $41 \pm 1$  Pg C/year in 1860s vs.  $53 \pm 1$  Pg C/year in 2000s). These combined processes resulted in an ecosystem carbon sink from the 1860s to

**FIGURE 4** Spatial patterns of ecosystem carbon storage ( $C_{eco}$ ) change between the 1860s and the 2000s (a), and ecosystem carbon storage potential-based ecosystem state in the 2000s (b). Furthermore, ecosystem carbon storage is divided into vegetation carbon storage ( $C_{veg}$ ) and soil carbon storage ( $C_{soil}$ , including litter carbon). Their corresponding carbon storage change between the 1860s and the 2000s and the carbon storage potential-based ecosystem status in the 2000s are showed in (c, d) for  $C_{veg}$  and in (e, f) for  $C_{soil}$ . The right panel for each subgraph represents carbon storage changes or carbon storage potential averaged by latitude



the 2000s in most regions, especially in the tropics and high latitudes (Figure 4a; Figure S18), which played a significant role in mitigating the human-induced carbon emissions into atmosphere (Ciais et al., 2014). According to ORCHIDEE-MICT, both vegetation and soils have contributed to the carbon sink (Figure 4c,e; Figure S18), which is supported by observation-based studies (Pan et al., 2011).

Beyond the historical change, we are interested in whether the present-day terrestrial ecosystems in non-steady state have extra potential for carbon sequestration. Here, the ecosystem carbon storage potential was defined as the difference between the ecosystem carbon storage capacity and the present-day carbon storage (Section 2). Results from the analysis of the ecosystem carbon storage potential indicated as carbon sink in high northern latitudes and in some temperate forests (northeast America, Europe, and China), but a saturation of the carbon sink or even a carbon source elsewhere (Figure 4; Figure S18). It should, however, be noted that in the model, the carbon sink function in tropical forest biomass tends to saturation. To sum up, terrestrial ecosystems could store carbon up to 763 Pg based on the current system state, with 41 Pg C in vegetation and 722 Pg C in soil. Noticeably, China accounted for 25% global vegetation carbon potential, mainly in the afforested regions.

## 4 | DISCUSSION

### 4.1 | Impacts from land use change

It is remarkable that human-induced land use change has such a strong effect on  $\tau_{eco}$ ; however, our results indicate both positive

(slow down) and negative (acceleration) impacts. The negative effects of land use change on  $\tau_{eco}$  occurred in most parts of world, mainly because of cropland expansion at the expense of the natural forests and grasslands (Figures S19 and S20; Foley et al., 2005; Ramankutty & Foley, 1999). In contrast, positive effects of land use change on  $\tau_{eco}$  are found in some temperate regions with increasing forest cover, and conversion from agricultural to natural vegetation. The enhanced forest fraction can be attributed to afforestation in China (Chen et al., 2019) and forest conservation in Europe (Luyssaert et al., 2010; McGrath et al., 2015). A related study also concluded that land use change greatly reduced biomass turnover times globally (Erb et al., 2016). Nevertheless, it should be noted that the change of biomass turnover times in previous study compared the present-day ecosystem state under the assumption on steady-state and a hypothetical condition in the absence of land use but under current climate (Erb et al., 2016). By contrast, our study makes a step forward to decomposing the effects of  $CO_2$  increasing, climate change, and land use change based on a dynamic system rather than a steady-state one.

Furthermore, only net land cover transitions were accounted for the land use change processes simulated by ORCHIDEE-MICT, and that the simultaneous, bidirectional transitions between two vegetation types within the same grid cell were not considered (Arneth et al., 2017; Yue et al., 2018). Even though the conclusions of this study would not be affected by these processes, considering the bidirectional transitions in the model could provide a clearer picture for the effects of land use change on  $\tau_{eco}$  changes, especially on shorter timescales (e.g., decades). The effects from bidirectional transitions should be specially explored in future work.

## 4.2 | Changes of vegetation carbon residence time

The mechanisms behind changes in  $\tau_{eco}$  for vegetation and soil components can be explained by the specific processes in each pool.  $r_{veg}$  is mainly dominated by the residence time in woody pools which can be estimated as the ratio between the wood allocation proportion ( $all_w$ ) and the wood turnover rates ( $k_w$ ) including senescence, mortality, and external disturbances (e.g., fire; Thurner et al., 2016). This robust relationship is well simulated by ORCHIDEE-MICT (Figure S21). Thus, we can further explain the changes of  $r_{veg}$  via examining the response patterns of  $all_w$  and  $k_w$  to the environmental drivers (Figure S22). At the global scale, increasing  $CO_2$  increased  $all_w$  (+5%) and decreased  $k_w$  (−3%), resulting in positive effects of  $CO_2$  on  $r_{veg}$ . In contrast, land use change has significantly decreased  $all_w$  (−2%) and increased  $k_w$  (+18%), which led to shorter  $r_{veg}$ . Lengthened  $r_{veg}$  due to increasing  $all_w$  (2%) by climate change has been partly offset by increasing  $k_w$  (1%). Because effects of land use change are stronger than those of increasing  $CO_2$ ,  $r_{veg}$  ultimately accelerated. The sign and magnitude of  $all_w$  and  $k_w$  in responses to the different drivers are biome dependent, especially for land use change. It should be noted that effects of land use change on  $r_{veg}$  are mainly through changing  $k_w$ , with the largest value in croplands (+87%) and the smallest in boreal forests (−2%).

## 4.3 | Changes of soil carbon residence time

Changes in decomposition and transfer rates among the soil carbon pools mainly explained the reduction of  $r_{soil}$ . Changes in climate mainly affected soil carbon decomposition rates (Bond-Lamberty, Bailey, Chen, Gough, & Vargas, 2018), and higher soil temperature and moisture are expected to accelerate soil organic carbon decomposition (Davidson & Janssens, 2006). At the global scale, we find that  $CO_2$  increase indirectly increased soil moisture, and had nonsignificant effects on soil temperature in the model simulation (Figure S22). These combined effects increased the decomposition rates of soil organic carbon, that is, accelerated  $r_{soil}$ . This conclusion is line with experimental findings (Van Groenigen, Qi, Osenberg, Luo, & Hungate, 2014). In addition, climate change and land use change both increased global soil temperature and soil moisture (Figure S22). The significant changes in the transfer rate between soil pools by the environmental changes may also contribute to the accelerated  $r_{soil}$ . For different biomes, the decomposition and transfer rates varied in magnitude in responses to environmental forcing (Figure S22). Furthermore, land use change had the largest effect on the decomposition and transfer rates in cropland regions (Figure S22), which is consistent with previous conclusions from fieldwork using radiocarbon observations (Sanderman, Creamer, Baisden, Farrell, & Fallon, 2017).

## 4.4 | Ecosystem carbon storage potential

Based on the model simulations of ecosystem states in the 2000s, our results indicate that tropical forests, especially in Amazon basin,

will not provide such a strong carbon sink in the future, as they did in historical period. In addition, there is still a large carbon sink potential in terrestrial ecosystems, mostly in high northern latitudes, especially in the soil system. However, because of relatively slower soil decomposition and transformation rates in these cold regions (He et al., 2016), it requires thousands of years to accomplish this goal. It should be noted that, in reality, the ecosystem carbon potential is also changing based on given ecosystem states under external forcing (e.g., atmospheric  $CO_2$  concentration, climate, and land cover types). Therefore, the ecosystem carbon potential evaluated in this way provides meaningfully theoretical estimates for the policy makers in a long-term perspective, and shows that the ecosystem carbon storage potential could be increased via sustainable means. For example, forest conservation and afforestation could improve the ecosystem carbon storage potential, by lengthening  $\tau_{eco}$  and increasing ecosystem productivity.

## 4.5 | Limitations of model

In this study, the ORCHIDEE-MICT ecosystem model provided reasonable patterns of  $\tau_{eco}$  changes and their corresponding drivers, consistent with observation-based studies. Even so, the model still showed some major limitations which might obscure our understanding of the role of certain processes. First, in the experimental simulations, the dynamic global vegetation model (DGVM) module was not activated. Thus, the forest mortality rates were fixed for each plant functional type. This simplification may underestimate the magnitude of  $r_{veg}$  changes because forest mortality rates have been increasing universally in response to ongoing climate change (Allen et al., 2010; Brienen et al., 2015). The mechanisms of forest mortality include a series of physiological processes (e.g., carbon starvation and hydraulic failure) and external forces (e.g., windthrow, insect outbreaks, drought, competition, and burning) associated with rising temperature and vapor pressure deficit (Choat et al., 2018; McDowell et al., 2018; Raffa et al., 2008; Stephenson et al., 2011). These effects are not fully incorporated in any DGVM. Introducing these complex processes in a DGVM model is challenging because we lack enough understanding of the operating rules of the vegetation turnover especially at the global scale. Due to the imperative of more comprehensive mortality schemes in DGVM models rather than fixed mortality rates, future DGVM modelers could probably sort out the major influential turnover-related drivers in corresponding regions rather than considering the all-side turnover-related processes in each region. For example, frost damage effects should be considered in boreal forests, and insect outbreaks should be considered in temperate forests (Thurner et al., 2016). Second, ORCHIDEE-MICT ecosystem model includes a structural improvement of soil carbon cycle processes by discretizing the integral soil profile into multilayers including burial in permafrost (cryoturbation) and bioturbation. In a previous model evaluation (Guimbertau et al., 2018), it was showed that ORCHIDEE-MICT could capture the mean value and average vertical profile of soil organic carbon density in high-latitude regions. Another study by Huang et al.



using a matrix-based representation of ORCHIDEE-MICT soil organic carbon also evaluated systematically the sensitive parameters among 34 parameters that control soil organic carbon profiles and found critical sensitivities to the active layer thickness and the cryoturbation rate (Huang et al., 2018). Here, to further improve the robustness of soil carbon turnover processes, we recommend that future versions should consider the radiocarbon data, which provide an independent constrain for the total soil carbon turnover (He et al., 2016; Lawrence et al., 2019; Mathieu, Hatté, Balesdent, & Parent, 2015; Trumbore, Sierra, & Hicks Pries, 2016). Third, nitrogen cycle plays an important role in regulating  $\tau_{\text{eco}}$ . For example, nitrogen availability could affect  $r_{\text{veg}}$  via changing carbon allocation (Friedlingstein, Joel, Field, & Fung, 1999; Li et al., 2020). In addition, nitrogen availability usually plays an impact on  $r_{\text{soil}}$  by altering the microbial activities and soil decomposition rates (Greaver et al., 2016; Janssens et al., 2010). The increase in nitrogen deposition (Galloway et al., 2004) could, therefore, affect changes in  $\tau_{\text{eco}}$ . Unfortunately, these effects cannot be evaluated in our study because ORCHIDEE-MICT did not include a coupled nitrogen cycle module.

We concluded that  $\tau_{\text{eco}}$  has generally accelerated between 1860s and 2000s. The mechanisms behind this acceleration vary across biomes and spatial scales, and the partitioning between  $r_{\text{veg}}$  and  $r_{\text{soil}}$  indicated different driving processes. Our study attributed the accelerating  $\tau_{\text{eco}}$  in a large degree to human-induced global change, with land use change playing a dominant role in most parts of the globe. Our analysis of the ecosystem carbon sink potential also shows potential benefits of human actions by slowing  $\tau_{\text{eco}}$  by sustainable pathways, for example, through land management, supporting their key role in keeping carbon for longer times in ecosystems.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

All data used in this study are available from the corresponding author upon request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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