The effects of carbon turnover time on terrestrial ecosystem carbon storage

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Abstract. Carbon (C) turnover time is a key factor in determining C storage capacity in various plant and soil pools and the magnitude of terrestrial C sink in a changing climate. However, the effects of C turnover time on C storage have not been well quantified for previous researches. Here, we first compared different definition of mean turnover time (MTT) including ecosystem MTT (MTT_{EC}) and soil MTT (MTT_{soil}) and its variability in MTT to climate changes, and then examined ecosystem C storage over time from changes in C turnover time and/or NPP. Our results showed that total GPP-based ecosystem MTT (MTT_{EC_GPP}:25.0±2.7 years) was shorter than soil MTT (35.5 ±1.2years) and NPP-based ecosystem MTT (MTT_{EC_NPP}:50.8±3 years) ($MTT_{EC\_GPP}=Cpool/GPP$ & $MTT_{soil}=Csoil/NPP$ & $MTT_{EC\_NPP}=Cpool/NPP$, Cpool and Csoil referring as the ecosystem or soil carbon storage, respectively). At the biome scale, temperature is still the predictor for MTT_{EC} ($R^2 = 0.77$, $p<0.001$) and MTT_{soil} ($R^2 = 0.68$, $p<0.001$). There is no clear improvement in the performance of MTT_{EC} predication when incorporating precipitation into the model ($R^2 = 0.76$, $p<0.001$). MTT decreased by approximately 4 years from 1901 to 2011 when temperature just was considered, resulting in a large C release from terrestrial ecosystems. The resultant terrestrial C release driven by MTT decrease only accounted for about 13.5% of than driven by NPP increase (159.3 ± 1.45 vs 1215.4 ± 11.0Pg C) due to the

difference between both of the product factor ($NPP * \Delta MTT$ vs $MTT * \Delta NPP$). Therefore, the larger uncertainties in the spatial variation of MTT than temporal changes would lead in a greater impact on ecosystem C storage from spatial pattern of MTT, which may need to be focused on in the future research.

Key words: ecosystem, mean turnover time, MAT, MAP, biome scale

1 Introduction

Rising atmospheric CO_2 concentrations and the resultant climatic warming can substantially impact the global carbon (C) budget (IPCC, 2007), leading to a positive or negative feedback to global climate change (e.g.,Friedlingstein *et al*., 2006; Heimann and Reichstein, 2008). Projections of earth system models (ESMs) show a substantial decrease in terrestrial C storage as the world warms (Friedlingstein *et al*., 2006), but the decreased magnitude is difficult to quantify due to the complexity of terrestrial ecosystems in response to global change, such as forest dieback (Cox *et al*., 2004), storms (Chambers and Li, 2007), and land use change (Strassmann *et al*., 2008). For example, experimental and modeling studies generally showed that elevated CO_2 would enhance NPP and terrestrial C storage (Nemani *et al*., 2003; Norby *et al*., 2005), but warming may increase soil respiration rates, contributing to reduced C storage, especially in the colder regions (Atkin and Tjoelker, 2003; Karhu *et al*., 2014). Therefore, the response of terrestrial C storage to climate depends on the response of C influx and how C residence time change in various C pools (i.e., plant, litter and soil pools) (Luo *et al*., 2003; Xia *et al*., 2013) as reflected in most of the biogeochemical models (Parton *et al*., 1987; Potter *et al*., 1993). Todd-Brown *et al*. (2013) evaluated soil C simulations from CMIP5 earth system models and found that global soil carbon varied 5.9 fold across models in response to a 2.6-fold variation in NPP and a 3.6-fold variation in global soil carbon turnover times. Thus it is key to quantify the time that carbon resides in terrestrial ecosystems and its relationships with climate, and then the resultant change of terrestrial ecosystem C storage driven by turnover time changes.

In a given environmental condition, the ecosystem C storage capacity refers to the amount of C that a terrestrial ecosystem can store at the steady state, determined by C influx and turnover time (Xia *et al*., 2013). External environmental forces, such as climate change and land use change, would dynamically influence both ecosystem C influx and turnover time, and then change terrestrial C storage capacity. Thus, the changed magnitude of ecosystem C storage sink can be expressed by changes in both NPP and mean C turnover time. The spatial variation of NPP changes and the effects of climate change have been relatively well quantified by manipulative experiments (Rustad *et al*., 2001; Luo *et al*., 2006), satellite data (Zhao and Running, 2010), and data assimilation (Luo *et al*., 2003; Zhou and Luo, 2008; Zhou *et al*., 2012). Todd-Brown *et al*. (2013) also found that differences in NPP contributed significantly to differences in soil carbon across models using a reduced complexity model dependent on NPP and temperature. In contrast, the spatial variation of C turnover time have not well been quantified due to limited data, especially at regional or global scales.

Ecosystem C turnover time is the average time that a C atom stays in an ecosystem from entrance to the exit (Barrett, 2002). Several methods have been used to estimate the C turnover time: C balance method by estimating ratios of C pools and fluxes (Vogt *et al*., 1995), C isotope tracing (Ciais *et al*., 1999; Randerson *et al*., 1999), and measurements of radiocarbon accumulation in the undisturbed soils (Trumbore *et al*., 1996). However, most methods mainly focused on various pools (i.e., leaf, root, soil) and small scale (i.e. C isotope tracing, radiocarbon). The turnover time at region or global scale are often calculated with the ratio of ratios of C storage to flux, such as soil C turnover time (Gill and Jackson, 2000; Chen *et al*., 2013). Although there are many estimates of global C turnover time, those global C turnover time focused on soil C. Spatial distribute of ecosystem C turnover time is relatively difficult to be estimated (Zhou and Luo, 2008), which needs to incorporate individual plant and soil pools and their C turnover time into ecosystem models. The inverse modeling has been used to estimate ecosystem mean C turnover time in USA and Australia (Barrett, 2002; Zhou and Luo, 2008; Zhou *et al*., 2012). Carvalhais et al. (2014) have estimated ecosystem turnover time as the ratio of carbon storage (soil and vegetation C) and influxes and the correlation to climate, which focused on the comparison of global C turnover time calculated by model results from CIMPS with those from observed data as well as their trend over latitude. Thompson and Randerson *et al* (1999) has indicated that there were two types of mean C turnover times for terrestrial ecosystems: the GPP-based or the NPP-based mean turnover time according to the terrestrial C models for some models use NPP as their C input and others use just GPP from atmosphere (i.e., NPP is GPP minus autotrophic respiration). However, there was no clear distinction in most pervious researches. For example, Zhou and Luo (2008) and Zhou *et al*. (2012) estimated mean turnover time as the NPP-based one. In most of previous researches, soil turnover time are usually estimated using field sampling as the global turnover time for model validation. However, the difference between different turnover time definitions was still unclear. Therefore, we considered vegetation and litter C data into soil C to extend the global turnover time and then examined the difference between both. Finally, we focused on the effects of turnover time on ecosystem C storage with the climate changes.

Thus, this study was designed to quantify the global pattern of ecosystem mean turnover time and its effects on ecosystem C storage caused by turnover time changes. Meanwhile, we also quantified the difference between different definitions of turnover time. Ecosystem mean turnover time was estimated using the C balance method, which are ratios of C pools and fluxes. Ecosystem C pools include plant, litter and soil, and C fluxes refer to ecosystem respiration or C influx (GPP/NPP). The current datasets from published or unpublished papers have covered all C pools and fluxes, but they were at different spatial scales, so we estimated ecosystem mean turnover time at the grid ($1^{o}\times1^{o}$) and biome scale for accuracy and data match. Our objectives are: 1) to estimate the different between ecosystem and soil mean turnover time, 2) to explore their relationships with climate, and 3) to quantify the ecosystem C storage changes caused by ecosystem turnover time from 1901 to 2011.

2 Materials and methods

2.1 Data collections

Three datasets were used to calculate ecosystem mean turnover time and its climate effects on C sequestration, including carbon (C) influx (GPP and NPP), C storage in C pools (soil, plant and litter), and climate factors (temperature, precipitation and potential evapotranspiration). GPP and NPP were extracted from MODIS products (MOD17) on an 8-day interval with a nominal 1-km resolution since Feb. 24, 2000. The multi-annual average GPP/NPP from 2000-2009 with the spatial resolution of $0.083^{o}\times0.083^{o}$ were used in this study (Zhao and Running, 2010).

The harmonized World Soil Database (HWSD) (Hiederer and Köchy, 2012) provided empirical estimates of global soil C storage, a product of the Food and Agriculture Organization of the United Nations and the Land Use Change and Agriculture Program of the International Institute for Applied System Analysis (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). Hiederer and Köchy (2012) estimated global soil organic carbon (SOC) at the topsoil (0-30cm) and the subsoil layer (30-100cm) from the amended HWSD with estimates derived from other global datasets for these layers. We used the amended HWSD SOC to calculate C turnover time (http://eusoils.jrc.ec.europa.eu). However, HWSD just only provided an estimate of soil carbon C storage at the top 1 m of soil and may have largely underestimated total soil carbon. Jobbagy and Jackson (2000) indicated that global SOC storage in the top 3m of soil was 56% more than that for the first meter, which could change estimates of the turnover time estimates dramatically. We will discuss this issue in the discussion section. It is well known that HWSD underestimated soil C in high latitude, so we also estimated turnover time in high latitudes with the Northern Circumpolar Soil Carbon Database (NCSCD), which is an independent survey of soil carbon in this region (Tarnocai *et al*., 2009). For biomass, Gibbs (2006) estimated the spatial distribution of the above- and below-ground C stored in living plant material by updating the classic study (Olson *et al*., 1983; Olson *et al*., 1985) with a contemporary map of global vegetation distribution (Global Land Cover database)(Bartholomé and Belward, 2005). Each cell in the gridded data set was coded with an estimate of mean and maximum carbon density values based upon its land cover class, so this dataset mainly represents plant biomass C at a biome level.

The litter dataset was extracted from 650 published and unpublished documents (Holland *et al*., 2005). Each record represents a site, including site description, method, litterfall, litter mass and nutrients. We calculated the mean and median of litter mass for each biome, and then assigned the value for each grid according as the biome types, forming the global pattern of litter C storage using the method of Matthews (1997) in ARCGIS software.

Global climate databases produced by the Climate Research Unit (CRU) at the University of East Anglia were used to analyze the climatic effect on ecosystem mean turnover time. We used mean $0.5^{o}\times0.5^{o}$ gridded air temperature, precipitation and potential evapotranspiration, specifically their means from 2000-2009 in CRU_TS 3.20 (Harris *et al*., 2013).

We aggregated all datasets into a biome level for accuracy and data match, so the biome map was extracted from the GLC 2000 (Bartholomé and Belward, 2005) and regulated by

MODIS. We assigned 22 land cover class among three temperature zones (i.e., tropical, temperate and boreal) by taking the most common land cover from the original underlying $0.083^{o} \times 0.083^{o}$ data. Eight typical biomes were zoned with ARCGIS 10 in corresponding to plant function types (PFTs) in CABLE model that Xia *et al* (2013): evergreen needleleaf forest (ENF), evergreen broadleaf forest (EBF), deciduous needleleaf forest (DNF), deciduous broadleaf forest (DBF), tundra, shrubland, grassland and cropland. All of the data were regridded to a common projection (WGS 84) and $1^{0} \times 1^{0}$ spatial resolution (Todd-Brown *et al*., 2013). The regridding approach for C fluxes and pools (i.e., GPP, NPP, soil C and litter C) assumed conservation of mass that a latitudinal degree was proportional to distance for the close grid cells (Todd-Brown *et al*., 2013). A nearest neighbor approach were used for land cover classes and a bi-linear interpolation were used for climate variables (i.e, temperature, precipitation).

2.2 Estimation of ecosystem mean C turnover time

C turnover time is commonly estimated with the C balance method by calculating the ratio of C total in a C pool and its outflux. Terrestrial ecosystem includes many C pools with largely varying residence times from days to millennia, but it is difficult to collect the observation-based datasets of C pools and flux for each component (e.g. leaf, wood and different soil C fractions) at the global scale. It thus is impossible to estimate individual pools' turnover time. In this study, we estimated the whole-ecosystem C turnover time as the ratio of C pools to flux based on the observed datasets. Certainly, there are some limitations that the ecosystem is taken as a single pool, which will be discussed in the discussion. For terrestrial ecosystems, the C pools (C_{pool}) is composed of three parts: plant, litter and soil, and C outfluxes include all C losses include autotrophic and heterotrophic respiration (R_a, R_h) and losses by fires and harvest. In the steady state, C outfluxes equal to C influx, which is the carbon uptake through gross primary production (GPP), so ecosystem mean turnover time (MTT_{EC}) can be equivalently calculated as the ratio between C storage in vegetation, soils and litters, and the influx into the pools, GPP:

$$MTT_{EC} = \frac{Cpool}{GPP} \qquad (1)$$

The similar method was used to calculate soil MTT (MTT_{soil}):

$$MTT_{soil} = \frac{Csoil}{NPP} \qquad (2)$$

However, the steady-state in nature is rare, so we relax the strict steady-state assumption and computed the ratio of C_{pool} to GPP as apparent whole-ecosystem turnover time and interpret the quantity as an emergent diagnostic at ecosystem level (Carvalhais *et al.*, 2014). In addition, it is difficult to accurately get the observed respiration (R_a and R_h) in terrestrial ecosystem at the global scale. Therefore, we used multi-year GPP or NPP to calculate MTT in order to reduce the effect of the non-steady state, since it is difficult to evaluate how this assumption affects model results.

2.3 The climate effects on ecosystem mean C turnover time

In order to explore the combing effect of precipitation and temperature on ecosystem mean C turnover time, aridity index (AI) was calculated as follows:

$$AI=\frac{MAP}{PET} \qquad (3)$$

where PET is the potential evapotranspiration and MAP is mean annual precipitation (Middleton and Thomas, 1997). AI is a bioclimatic index including both physical phenomena (precipitation and potential evapotranspiration) and biological processes (plant transpiration) related with edaphic factors.

The relationships were examined between ecosystem mean C turnover time and mean annual temperature (MAT, ^oC), mean annual precipitation (MAP, mm) and aridity index (AI) at the biome level. The regression analyses $(MTT = ae^{-bMATorMAP})$were performed in STATISTICA 10, where a and b are the coefficients. The coefficient of determination (R^2) was used to measure the phase correlation between ecosystem mean C turnover time and climate factors. Here, we calculated a Q_{10} value (i.e., Q_{10}, a relative increase in mean turnover time for a 10^{o}C increase in temperature, $Q_{10} = e^{10b}$, b, the coefficients of $MTT = ae^{-bMAT/MAP}$) that is used in most models to simulate C decomposition. The relationship between ecosystem mean turnover time and temperature was used to estimate mean C turnover time in 1901 and 2011. Here, we assumed that the spatial correlation between temperature and MTT is identical to the temporal correlation between these variables.

2.4 The effects of turnover time on ecosystem C storage

Ecosystem C storage capacity at steady state is represented by$NPP \times MTT$ (Lou *et al*., 2003), so the difference of ecosystem C storage from 1901 to 2011 can be calculated as follows:

$$
\begin{aligned}
&\Delta \mathrm{Cpool} = \mathrm{NPP}_{2011} \times \mathrm{MTT}_{2011} - \mathrm{NPP}_{1901} \times \mathrm{MTT}_{1901} \\
&\Rightarrow \Delta \mathrm{Cpool} = \mathrm{NPP}_{2011} \times \mathrm{MTT}_{2011} - (\mathrm{NPP}_{2011} - \Delta \mathrm{NPP}) \times (\mathrm{MTT}_{2011} - \Delta \mathrm{MRT}) \\
&\Rightarrow \Delta \mathrm{Cpool} = \mathrm{NPP}_{2011} \times \Delta \mathrm{MTT} + \mathrm{MTT}_{2011} \times \Delta \mathrm{NPP} - \Delta \mathrm{NPP} \times \Delta \mathrm{MTT}
\end{aligned} \tag{4}
$$

where $NPP_{1901(2011)}$ and $MTT_{1901(2011)}$ refer to NPP and MTT at time 1901 or 2011. ΔCpool (ΔNPP or ΔMTT) is the difference between ecosystem C storage (NPP or MTT) at time 2011 and that at time 1901. The first component ($NPP_{2011}\times\Delta MTT$) represents the effects of MTT changes on ecosystem C storage. The second component ($\Delta NPP\times MTT_{2011}$) is the effects of NPP change on ecosystem C storage, and ΔNPP×ΔMTT is the cross-coupling effects.

To assess the effects of changes in MTT or NPP on ecosystem C storage, ecosystem MTT in 1901 and 2011 was calculated using an exponential equation between mean turnover time and temperature at a biome level. NPP in 2011 was derived from products (MOD17) and NPP in 1901 was averaged from the eight models' simulated results (CanESM2, CCSM4, IPSL-CM5A-LR, IPSL-CM5B-LR, MIROC-ESM, MIROC-ESM-CHEM, NorESM1-M and NorESM1-ME) for modeled NPP is near to MODIS estimated NPP (Yan *et al*., 2014).

2.5 Uncertainty analysis and sensitivity Analysis

Limitation of the above datasets is that the uncertainties are poorly quantified. The global mean of C fluxes (GPP and NPP) and pools (soil, litter, and plant) were calculated by 1000 simulations, respectively, through Markov chain Monte Carlo (MCMC) sampling from a gamma distribution in R software. For each variable, the confidence interval (CI) was estimated as the 2.5 and 97.5 percentile of mean values of the 1000 simulations. It was also applied to estimate the confidence interval of ecosystem C storage and ecosystem mean C turnover time.

3 Results

3.1 Ecosystem C storage

On average, terrestrial C storage (plant biomass + soil + litter) was 22.0 kg C m^{-2} (with a 95% CI of 21.85- 22.50 kg C m^{-2}) at the global scale, which largely varied with vegetation and soil types (Fig.1d). Among the forest biomes, ecosystem C storage was highest in boreal evergreen needleaf forest (ENF) with high soil C content and lowest in deciduous broadleaf forest (DBF) with the lowest soil C. Soil C was the largest C pool in terrestrial ecosystems, accounting for more than 60% of ecosystem C storage, while C storages in litter and biomass only represented less than 10% and 30%, respectively (Fig. 1b). Among eight typical biomes associated with plant functional types (PFTs) (Table 1), the order of ecosystem C storage followed as: ENF (34.84±0.02 kg C m^{-2}) > deciduous needleleaf forest (DNF, 25.30±0.03 kg C m^{-2})> evergreen broadleaf forest (EBF, 22.70±0.01 kg C m^{-2})> shrubland (18.29±0.02 kg C m^{-2}) > DBF (16.51±0.02 kg C m^{-2}) > tundra (14.16 ±0.02 kg C m^{-2})/cropland (14.58 ±0.01kg C m^{-2})> grassland(10.80±0.01 kg C m^{-2}).

3.2 Mean C turnover time

On average, ecosystem mean C turnover time (MTT) was 25.0 years (with a 95% CI of 23.3-27.7 years) based on GPP data and 50.8 years (with a 95% CI of 47.8-53.8 years) on NPP data (Table 1), while soil MTT is shorter than NPP-based MTT with the value of 35.5 years (with a 95% CI of 34.9-36.7 years). MTT varies among biomes due to the different climate forcing (Table 1 and Fig 2). The long MTT occurred in high latitude while the short ones are in tropical zone. Among forest biomes, DNF had the longest MTT with the lowest mean temperature (-7.9 ^{o}C), while the shortest MTT was in EBF due to highest temperature (24.5 ^{o}C) and precipitation (2143 mm). Although ecosystem C storage was low in tundra (14.16 kg C m^{-2}), it has the longest MTT. Therefore, the order of ecosystem MTT among biomes was different from that of ecosystem C storage, with tundra (99.704±6.14 years) > DNF (45.27±

2.43years) or ENF (42.23±2.01 years) > shrubland (27.77±2.25 years) > grassland (26.00±1.41 years) > cropland (14.91±0.40years) or DBF (13.29± 0.68years) > EBF (9.67±0.21 years). Soil MTT had the similar order with ecosystem MTT with the different values (Table 1). In the high latitude, ecosystem MTT could increase up to 145 years if soil C storage was calculated from NCSCD dataset (Fig. 3) due to higher soil C storage (500 Pg C vs 290 Pg C), compared with the global soil C storage HWSD, while the global average of soil MTT increased to 40.8 years when NCSCD dataset was considered.

3.3 Climate effects on ecosystem mean turnover time

Ecosystem mean C turnover time significantly decreased with mean annual temperature (MAT) and mean annual precipitation (MAP) as described by an exponential equation: $MTT = 57.06e^{-0.07MAT}$ (R^2=0.77, P<0.001) and $MTT = 103.07e^{-0.001MAP}$ (R^2=0.34, P<0.001, Fig 4), but there was no correlation between ecosystem mean turnover time and aridity index (AI, Fig. 4c). The similar relationships occurred between soil MTT and MAT and MAP ($MTT_{soil} = 58.40e^{-0.08MAT}$, R^2=0.68, P<0.001) and $MTT_{soil} = 109.98e^{-0.002MAP}$, R^2=0.48, P<0.001, Fig. 5). There was the different temperature sensitivity of mean turnover time (Q_{10}) for ecosystem MTT (Q_{10}=1.95) and soil MTT

(Q_{10}=2.23) at ecosystem scale, which was estimated as $Q_{10} = e^{10b}$ based on temperature regression function. When MAP was incorporated into a multivariate regression function of ecosystem mean turnover time with MAT, the relationships could not be significantly improved (Fig. 6a). While MAP improved the explanation of variance of soil MTT (R^2 from 0.68 to 0.76, Fig. 6b), although there were the relationships due to the significant covariance of MAP and MAT (R^2=0.60). However, the relationship between MTT and AI is not clear due to the scale limit (biome level). When we separated ecosystem MTT into two categories according to aridity index (i.e., AI >1 and AI< 1), the relationships between ecosystem MTT and MAT did not significantly change (Figs. 4e, h) compared to that with all data together (Fig. 4b), while the relationship of ecosystem MTT with MAP significantly increased when AI > 1, but decreased when AI <1. However, the same regression function of soil MTT with MAT largely improved the explanation of the variance when AI>1 (Fig. 5e, $MTT = 58.67e^{-0.08MAT}$, R^2=0.76, P<0.001). The relationships between soil MTT and MAP were both improved when AI>1 and AI<1 (Fig. 5e, h).

3.4 Temporal variations of ecosystem mean turnover time and C storage

The average increase in global air temperature is around 1°C from 1901 to 2011 based on the

Climate Research Unit (CRU) datasets, ranging from -2.5 to 5.9 °C. When the function between ecosystem MTT and temperature was used to estimate the change in ecosystem mean turnover time (Fig. 4), the average mean turnover time decreased by approximately 4 years (Fig. 7a). The largest change in ecosystem MTT occurred in the cold zones. In tundra, mean C turnover time decreased by more than 10 years due to the larger increase in temperature (~2°C) than other regions. However, the average NPP increased by approximately 0.3±0.003 Kg C m^{-2} yr^{-1} over 110 years with most range of 0~0.6 Kg C m^{-2} yr^{-1} (Fig. 7b).

The changes in ecosystem MTT and NPP across 110 years would cause decrease or increase in terrestrial C storage. Caused by MTT changes, ecosystem C storage decreased by 159.3 ± 1.45 Pg C yr^{-1} from 1901 to 2011 ($\Delta MTT \times NPP$), with the largest decrease in tundra and boreal forest (more than 12 g C m^{-2} yr^{-1}) but little decrease in tropical zones (Fig. 8a). However, the increase in NPP directly raised ecosystem C storage up to 1215.4 ± 11.0 Pg C yr^{-1} from 1901 to 2011 with a range of 30-150 g C m^{-2} yr^{-1} in most areas ($MTT \times \Delta NPP$, Fig. 8b). The MTT-induced changes in ecosystem C storage only accounted for about 13.5% of that driven by NPP due to the difference between both of the product factor, so the spatial pattern of the NPP-driven changes mostly represented the spatial pattern of the changes in ecosystem C storage (Fig. 6d).

4 Discussion

In Carvalhais et al. (2014), global C turnover times and its covariation with climate were mainly examined. They also compared global C turnover time calculated by the model results from CIMP5 with those from observed data as well as their trend over latitude. Based on their work, we focused on the uncertainty from different observed data (HWSD vs. NCSCD), especially in high latitude. Litter data was updated compared to the study of Carvalhais et al. (2014). More importantly, we examined ecosystem C storage over time from changes in C turnover time and/or NPP. In addition, we estimated the GPP-based the NPP-based and soil MTT to explore the difference among them. Therefore, our study advance the understanding of the uncertainty of global C turnover time (especially in high latitude) and ecosystem C storage from C turnover time with updated data.

4.1 Global pattern of mean turnover time

In this study, we estimated spatial patterns of mean turnover time (MTT) with ecosystem C influxes (GPP and NPP) and C pools in plants, litter and soil using the C balance method.

Here, we assumed that the nature was the steady state and took the whole ecosystem as a single pool similar in Sanderman *et al* (2003), which have some caveats in the estimation of mean turnover time. Terrestrial ecosystems comprise of compartments varying greatly in their individual turnover times (for example leaves, wood, different soil organic carbon fractions), but we cannot estimate turnover time for each pools using observation datasets. In addition, it is difficult to accurately get the observed respiration (R_a and R_h) in terrestrial ecosystem at the global scale, or carbon allocation between outflux and influx. It is thus difficult to evaluate how this assumption affects model results. Maybe, inverse models would be a valid method to estimate turnover time for the both (e.g., Zhou *et al*., 2012).

The global average of ecosystem MTT was 25.0 years for GPP-based estimation and 50.8 years for NPP-based one and soil MTT was 35.5 years, which was within the global mean turnover times (26-60 years) estimated by various experimental and modeling approaches with NPP-based estimation (Randerson *et al*., 1999; Thompson and Randerson, 1999) mostly focused on soils, but not ecosystem MTT. The spatial pattern of ecosystem MTT was similar to soil MTT for soil C storage accounted for a large amount of ecosystem C storage. The difference between NPP-based ecosystem and soil MTT depended on the residence time of vegetation and litter, a trait related to plant functional types (PFTs). For instance, NPP-based and soil MTT in Australia was 33.4 and 29.8 years, respectively. Here, one of the PFTs was spare grass with the short residence time (average value: 3.5 years), accounting for a large space of Australia. Within a specific vegetation, different biomes have different residence times due to climate effects. NPP-based and soil MTT for boreal needleaf evergreen were about116 years and 98 years, respectively, while both for tropical needleaf evergreen were about 12 years and 8 years, although ecosystem C in boreal and tropic zone was in the same order of magnitude (~34 vs 40 kg C m^{-2} yr^{-1}) with the similar vegetation C storage (~3.5 kg C m^{-2} yr^{-1}). Highest temperature and precipitation in tropical zone is the crucial factor for C decomposition.

We used the same method (the ratio of total C storage to GPP) as Carvalhais et al (2014) to calculate the GPP-based MTT, but two main factors resulted in the difference between both. Firstly, ecosystem C storage in this study was the sum of the soil, vegetation and litter C storage, while Carvalhais et al (2014) just considered the soil and vegetation C. Secondly, vegetation C came from the result of Gibbs (2006) while Carvalhais et al (2014) used remote sensing based carbon stock estimates for tropical and Northern Hemisphere vegetation. The ratio of GPP-based and NPP-based MTT (0.49) was smaller than that estimated by Thompson and Randerson (1999) (0.58, 15 year vs. 26 year, respectively). Our NPP-based MTTs for the conterminous USA (37.2 years) and Australia (33.4 years) were shorter than the estimates by the inverse models (46 to 78 years) (Barrett, 2002; Zhou and Luo, 2008; Zhou *et al*., 2012). The NPP-based MTT was shorter than the estimated results from Xia *et al*. (2013) using the CABLE model, though the order of MTT across forest biomes is similar. The difference between GPP-based and NPP-based NPP was determined by the ratio of the ratio of GPP and NPP which entirely determined by the assumptions of the MODIS NPP algorithm. In addition, we only used soil C in the top 1 m to estimate ecosystem MTT, which would be largely underestimated for the important amounts of C stored between 1 and 3m depth (Jobbagy and Jackson, 2000). According to the SOC estimation of Jobbagy and Jackson (2000), the MTT in the top 3 m could increase to 34.63 years for GPP-based, 70.68 years for NPP-based and 55.38 years for soil. If SoilGrids (Hengl et al., 2014) was used to estimate C MTT, the MTT in the top 1 m could increase to 30.3 years for GPP-based, 66.9 years for NPP-based and 45.7 years for soil. Therefore, the accurate estimates of total soil C are important to estimate ecosystem MTT.

4.2 The sensitivity of turnover time to climate

The estimated mean turnover time (MTT) was shortest in tropical zones and increased toward high-latitude zones (Fig. 2), which were often affected by the spatial patterns of temperature and moisture. The results was similar to those the previous studies based on SOC data set (Schimel *et al*., 1994; Sanderman *et al*., 2003; Frank *et al*., 2012; Chen *et al*., 2013) and root pools (Gill and Jackson, 2000). Ecosystem MTT had negative exponential relationship with MAT (Fig 4), similar to those with soil MTT, probably due to the temperature dependence of respiration (Lloyd and Taylor, 1994; Wen *et al*., 2006). Our results showed that the temperature sensitivity of ecosystem MTT was lower than that of soil C pool (Q_{10}: 1.95 vs. 2.23, Figs. 4 &5), which was similar to the previous research (Sanderman *et al*., 2003), because wood may decompose at much lower rates than SOM due to the longer MTT of wood (Zhou *et al*., 2012). Ecosystem MTT was no significant differences between very humid zone (AI>1.0) and other zones (AI<1.0, Fig 4). However, the better relationships between MTT and MAP occurred in very humid zone (AI>1.0) than other zones, which was similar to soil pool, but soil MTT have the higher sensitivity to precipitation than ecosystem MTT under AI>1. SOM decomposition often increased with added moisture in aerobic soils (Trumbore, 1997), because the metabolic loss of various C pools increased under warmer and wetter climates (Frank *et al*., 2012), resulting in high sensitivity of MTT to MAP. Thus, the fitting regression combined MAT and MAP clearly improved soil MTT (R^2=0.76, $p<0.001$, Fig 6b). In arid or semi-humid regions, the increase in C influx with MAP was more rapid than that in decomposition (Austin and Sala, 2002). In addition, water limitation may suppress the effective ecosystem-level response of respiration to temperature (Reichstein et al., 2007). At an annual scale, temperature is still the best predictor of MTT (Chen et al., 2013), which explained up to 77% of variation of MTT (Fig 4). Other ecosystem properties (e.g. ecosystems types, soil nitrogen) may cause the rest of the variation in the estimates of MTT.

4.3 Effects of the changes in mean turnover time on ecosystem C storage

Terrestrial ecosystems play an important role in regulating C cycling balance to combat global change. Current studies suggest that the terrestrial biosphere is currently a net C sink (Lund *et al*., 2010), but it is difficult to assess the sustainability of ecosystem C storage due to the complexity of terrestrial ecosystem in response to global change (Luo, 2007). In this study, we quantified the ecosystem C storage changes from 1901 to 2011 and separated it into three parts: caused by the changes in NPP, the changes in ecosystem MTT and the co-changes of both NPP and MTT (seeing equation 4). Our results indicated that the decrease in MTT increased ecosystem C loss over time while increased NPP enhanced ecosystem C uptake.

Current datasets have showed an increase in NPP (e.g., Hicke *et al*., 2002; Potter *et al*., 2012), leading to increasing terrestrial C uptake. Driven by NPP changes from 1901 to 2011, our results showed that global C storage would increase by 11.0 Pg C yr^{-1} and 0.4 Pg C yr^{-1} at the global scale and conterminous USA, respectively. Our estimated ecosystem C storage in USA was larger than the one from inverse models (Zhou and Luo, 2008; Zhou *et al*., 2012) but comparable to C sink from atmospheric inversion (0.30-0.58 Pg C yr^{-1}) (Pacala *et al*., 2001). However, the shortened MTT caused C losses from ecosystems from 1901 to 2011 (about 1.45 Pg C yr^{-1}), indicating that the magnitude of ecosystem C uptake is likely to decrease under warming due to decreased MTT. Ecosystem C release caused by MTT decrease only accounted for 13.5% of that driven by NPP increase, still causing a net sink in terrestrial ecosystem. The largest changes in terrestrial C storage occurred in high latitude, where it is more vulnerable to loss with climate change (Zimov *et al*., 2006). However, the direct release of CO_2 in high latitude through thawing would be another large source in the decrease of ecosystem C storage under climate warming (Grosse *et al*., 2011), which cannot be assessed by MTT or NPP. Interestingly, our results suggested that the substantial changes in terrestrial C storage occurred in forest and shrub (50% of total) due to the relatively longer MTT, which caused the larger terrestrial C uptake driven by NPP increase compared with others. Moreover, the largest absolute and relative changes of MTT occurred in high latitude regions (Fig. 7a), which would largely decrease the terrestrial C uptake driven by NPP under global warming. Furthermore, the C uptake in cropland and grassland has been underestimated probably due to the ignorance of the effects of land management.

4.4 Limitation in estimating mean turnover time and its effects to climate

Estimated MTT in this study were based on C influxes (GPP or NPP) and C pools in plants, litter and soil at the grid scale and can be used to quantify global, regional or biome-specific MTT, which was very important to evaluate terrestrial C storage. However, the balance method and data limitation may cause biases to some degree in estimated ecosystem MTT in a few sources. First, we assumed that ecosystem C cycle is at the steady state, when MTT was estimated. It is difficult to define the steady state, especially soil C dynamics (Luo and Weng, 2011). Actually, maintaining a steady state without change is rare for a long time and any ecosystem process could be only close to reach the steady state in the short time. For example, permafrost will be thawing both gradually and catastrophically (Schuur *et al*., 2008). The assumption of the steady state would cause the overestimation or underestimation of ecosystem MTT (Zhou *et al*., 2010). Second, MTT was estimated on the basis of C pool and flux measurements, whose uncertainties in the current datasets of C pools and fluxes would limit the estimated MTT. For example, the amendments of typological data and bulk density had largely improved the estimates of the SOC storage from HWSD (1417 PgC) (Hiederer and Köchy, 2012). Soil C storage calculated from NCSCD dataset would improve the ecosystem MTT in high latitudes (Fig. 3), compared with that from HWSD datasets. However, it is difficult to quantify the uncertainty in MTT caused by uncertainties of the pool and flux datasets due to lack of quantitative uncertainty estimates in these datasets. In addition, disturbance and forest age structure will influence large-scale accumulation biomass, the partitioning of C into pools with different turnover times, and thereby long-term C sequestration and turnover time estimates (Sönke et al., 2006), which cannot be reflected in the current algorithms. Combining the current disturbance and forest age structure into models should improve the estimate of turnover time. The calculation of MTT by the ratio of the pool to flux would reduce these uncertainties associated with the pool and flux data sets in some degree.

Third, the uncertainties in ecosystem MTT would cause the uncertainties in the relationship between MAT, MAP and ecosystem MTT. To simplify the calculation, we aggregated all datasets into a biome level, leading in a fixed parameters across biomes. However, the response magnitude in soil respiration to warming varied over time and across sites (Rustad *et al*., 2001; Davidson and Janssens, 2006), resulting in multiple temperature response function. MTT for 1901and 2011 were estimated using the exponential function between mean turnover time and temperature, resulting in underestimation or overestimation of MTT and the resultant changes on ecosystem C storage. For example, when the relationship between soil MTT and temperature was used ($MTT_{soil} = 58.40e^{-0.08MAT}$), the changes on ecosystem C storage caused by MTT could decrease to 161.42 Pg C and that driven by NPP could be 1125.6 Pg C, with the similar spatial pattern as the ecosystem. In addition, we assumed the current-day spatial correlation between temperature and MTT is identical to the temporal correlation between these variables. However, such assumption cannot reflect the processes like acclimation of microbial respiration to warming or shifts in plant species over time.

4.5 Implication for land surface models

First, this study demonstrated that spatial variability of ecosystem mean C turnover time had higher uncertainties compared to temporal variability, which was mainly caused by the estimation of soil C storage. Further work should focus on the accurate estimation of soil C storage with numerous observational data in estimating the spatial patterns of mean C turnover time at regional or global scale.

Second, there were the inconsistent responses of ecosystem C turnover time to climate variables in the current global vegetation models (Friend *et al*., 2013). Our results showed that the temperature sensitivity of ecosystem turnover time was lower than that of soil C pool (Q10: 1.95 vs. 2.23), while the relationship between ecosystem C turnover time and precipitation under low aridity conditions (AI>1) was much stronger than for all or AI<1 conditions. Now all global carbon cycle models have considered moisture stress on vegetation, but the incorporation of moisture or precipitation stress into soil decomposition should be strengthened, especially in high-latitude zones with greater warming and increased precipitation.

Data availability

All of the original data (MOD 17, HWSD, vegetation C production of Gibbs et al (2006) and litter dataset from Holland et al., 2005) used in this study are referenced in Fig 1 of the manuscript and full citations for data sources are provided.

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Table 1. The density of ecosystem C storage (Kg C m-2), mean turnover time (MTT, years), mean annual temperature (MAT) and precipitation (MAP) for the eight biomes. Ecosystem MTT were calculated based GPP and NPP, respectively.

Biome	Ecosystem C storage (kg C m^{-2})	Ecosystem MTT (years)		Soil MTT(years)	MAT (^oC)	MAP (mm)
		MTT_{GPP}	MTT_{NPP}			
ENF	34.8±0.02	42.23±2.01	58.54±2.16	39.62±1.22	3.5	760.5
EBF	22.7±0.01	9.67±0.21	18.43±0.43	8.96±0.21	24.5	2143.5
DNF	25.3±0.03	45.27±2.43	75.80±2.71	53.50±1.71	-7.9	401.4
DBF	16.5±0.02	13.29±0.68	22.02±1.00	12.08±0.69	16.1	988.4
tundra	14.2±0.02	99.74±6.14	132.86±4.40	122.88±5.54	-11.1	291.1
Shrubland	18.3±0.02	27.77±2.25	43.41±2.37	36.22±2.01	9.3	643.6
Grassland	10.8±0.01	26.00±1.41	39.51±2.11	34.37±2.20	9.4	605.5
Cropland	14.6±0.01	14.91±0.40	23.06±0.84	17.72±0.58	15.4	885.7

*ENF: Evergreen Needleleaf forest; EBF: Evergreen Broadleaf forest; DNF: Deciduous Needleleaf forest; DBF: Deciduous Broadleaf forest.

Figure Caption List

Figure 1. Spatial pattern of soil C (a), biome C (b), litter C (c) and ecosystem C storage (d) at grid scale ($1^{o}\times1^{o}$). Unite: Kg C m^{-2}. Ecosystem C storage was calculated from biomass, soil and litter C pools.

Figure 2. Spatial pattern of mean turnover time (MTT, years), calculated based on biome types and GPP (a) or NPP (b) and soil (c) using the C balance methods.

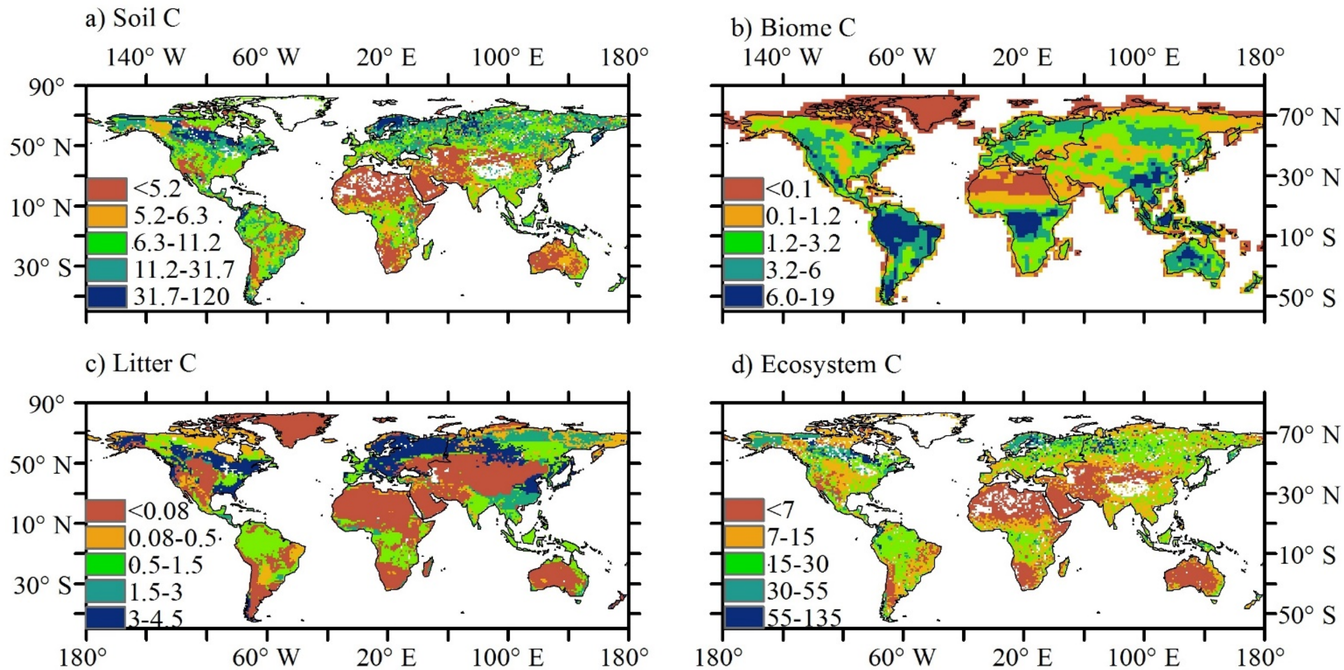
Figure 3. Spatial pattern of mean turnover time (years) in high latitude. (a) Based on soil C storage from HWSD data, (b) based on soil C storage from NCSCD data.

Figure 4. Relationships between ecosystem mean turnover time (MTT) and multi-annual temperature (MAT, a), precipitation (MAP, b) at different aridity indexes (AI, c). Each data point stands for average values of each biome. Biomes were assigned into 62 types according to land cover and three temperature zones.

Figure 5. Relationships between soil mean turnover time (MTTsoil) and multi-annual temperature (MAT, a), precipitation (MAP, b) at different aridity indexes (AI, c). Each data point stands for average values of each biome. Biomes were assigned into 62 types according to land cover and three temperature zones.

Figure 6. Change values of ecosystem mean ecosystem mean turnover time (MTT, unit: year a) driven by temperature change and NPP (unit: Kg C m-2yr-1) and temperature (OC) from 1901 to 2011. MTT for 1901 and 2011 was calculated by the temperature-dependence function showing in Fig. 4. NPP in 1901 and 2011 was derived from models' average and MODIS.

Figure 7. Change values of ecosystem carbon storage caused by mean turnover time change ($NPP_{2011}\times\Delta MTT$, a), by NPP change ($MTT_{2011}\times\Delta NPP$, b) and by NPP change and MRT change ($\Delta MTT\times\Delta NPP$, c) and total ecosystem C storage changes (d). Unit: g C m^{-2} yr^{-1} ($\Delta C_{pool} = NPP_{2011} \times \Delta MTT + MTT_{2011} \times \Delta NPP - \Delta NPP \times \Delta MTT$).



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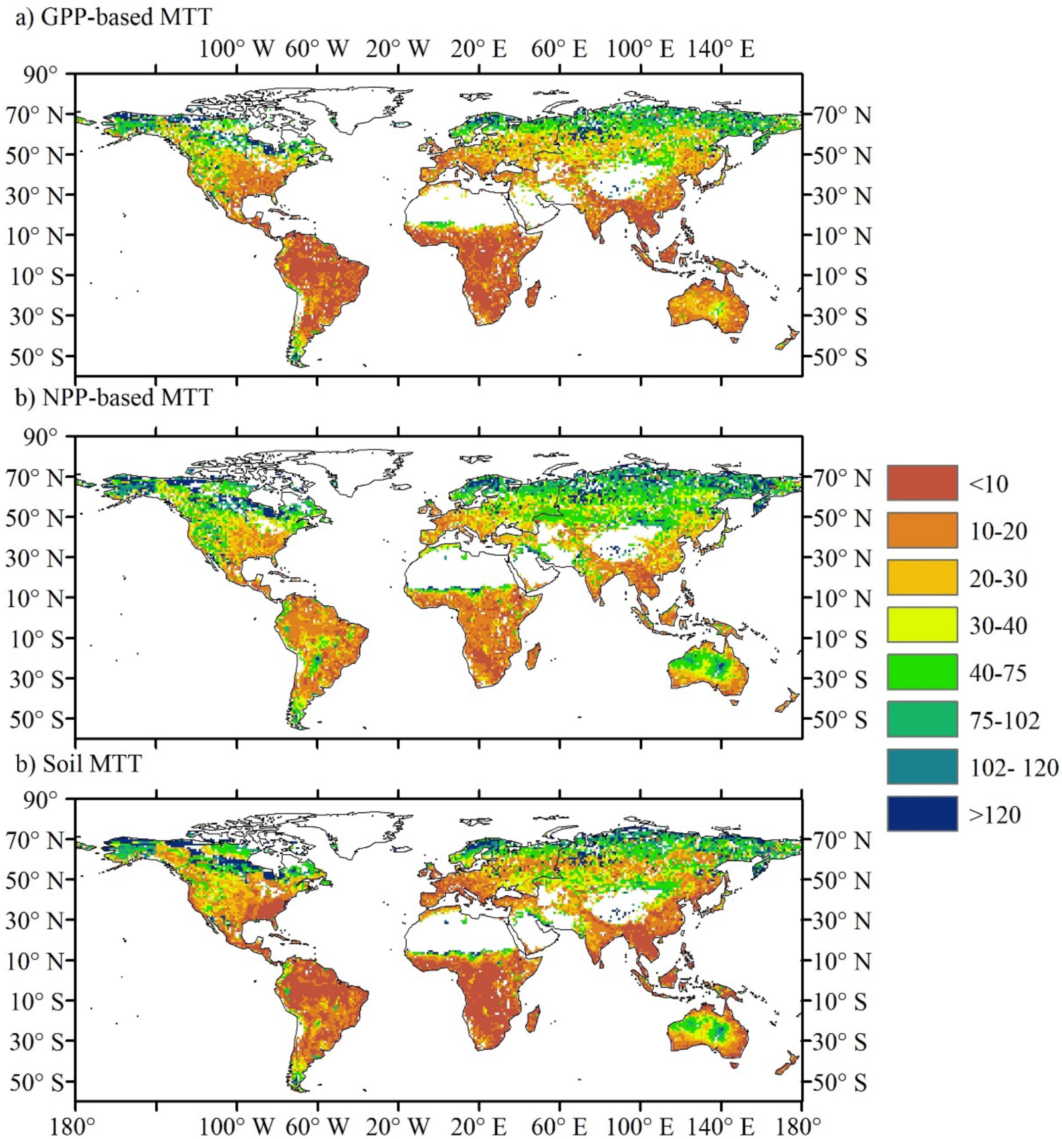

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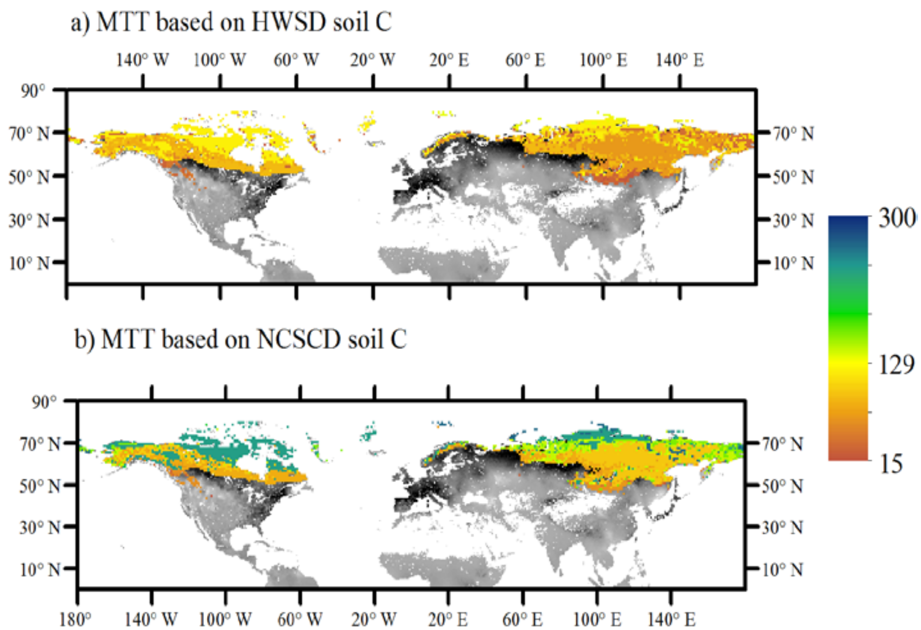

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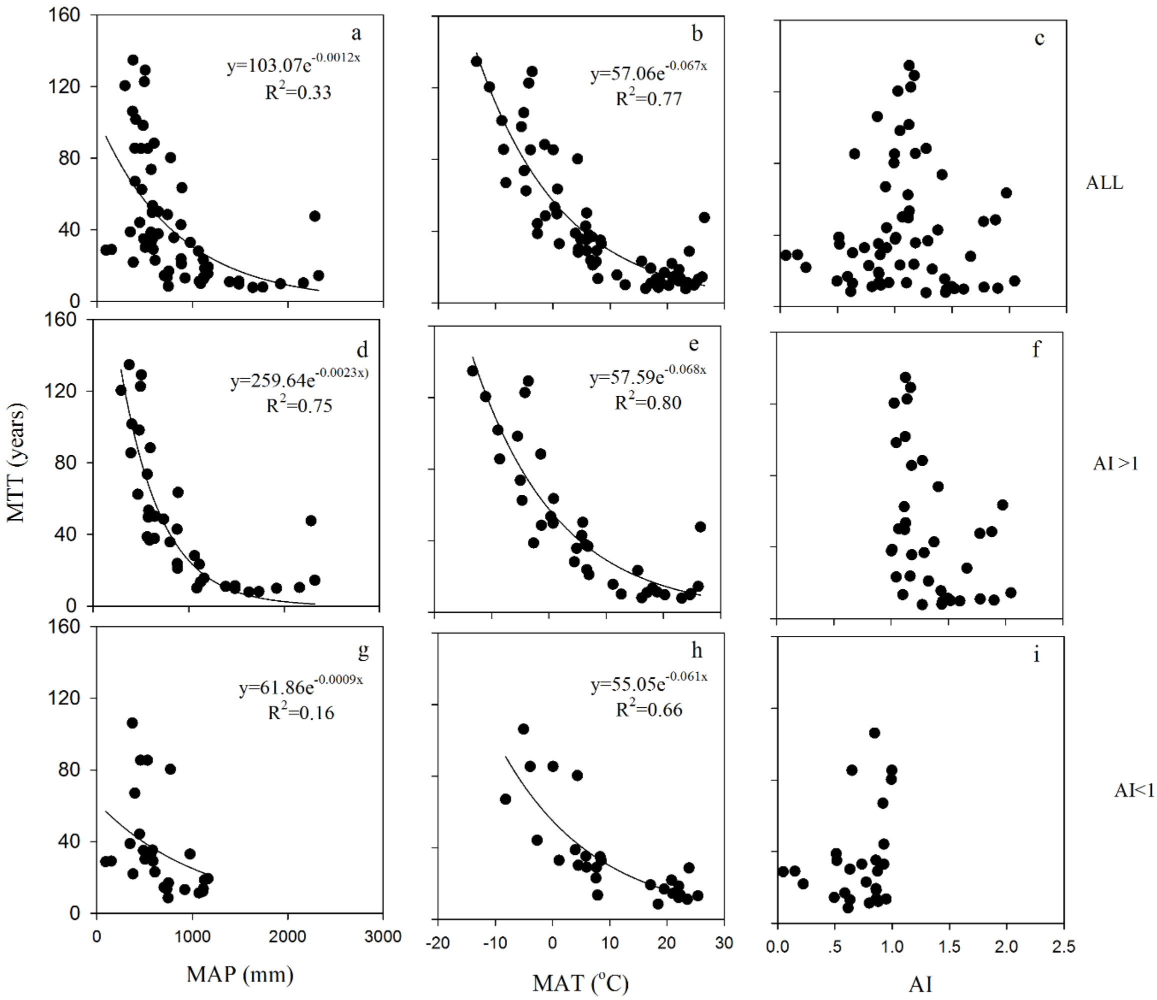

Figure 4. Relationships between ecosystem mean turnover time (MTT) and multi-annual temperature (MAT, a), precipitation (MAP, b) at different aridity indexes (AI, c). Each data point stands for average values of each biome. Biomes were assigned into 62 types according to land cover and three temperature zones.

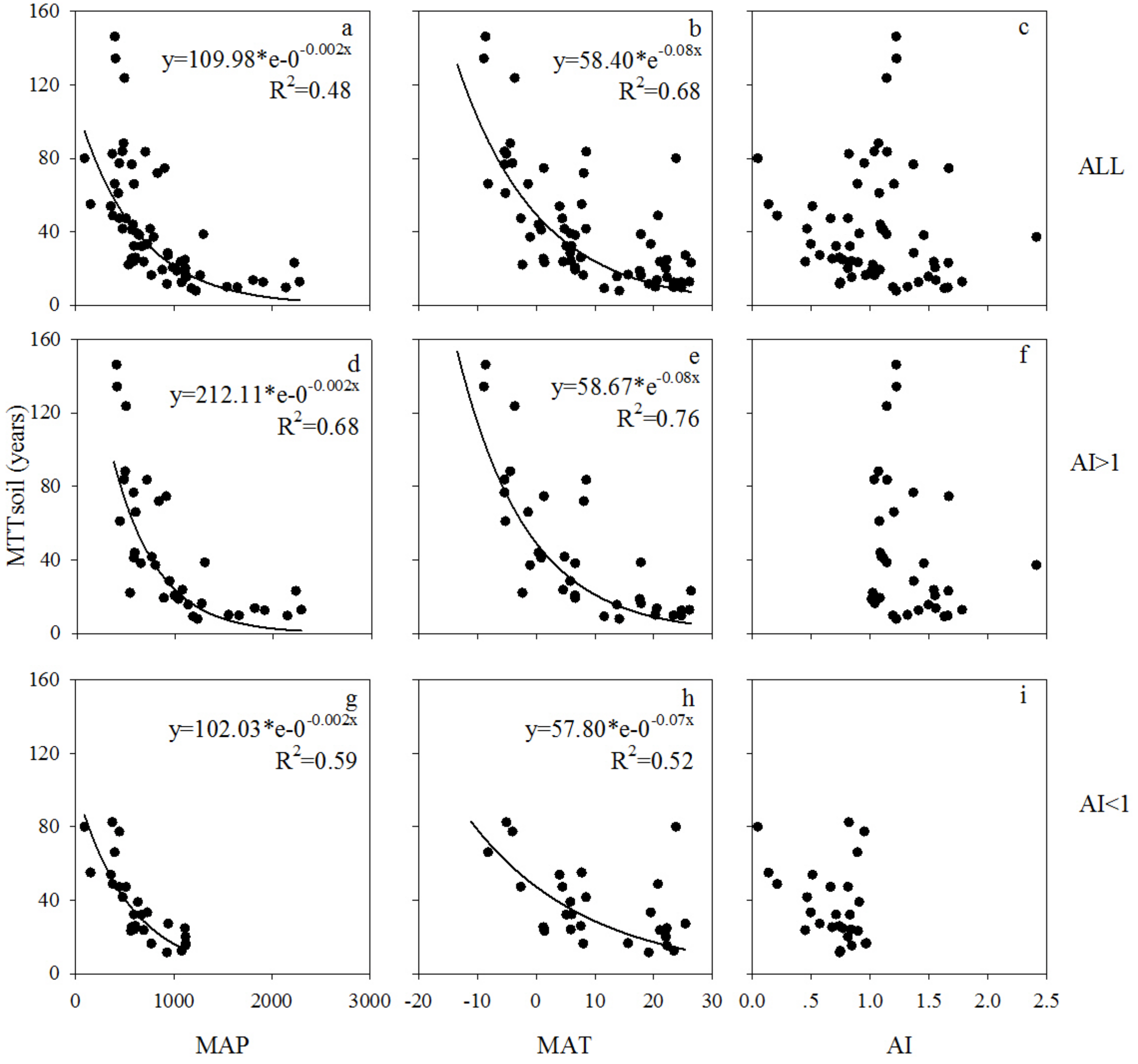

Figure 5. Relationships between soil mean turnover time (MTT_{soil}) and multi-annual temperature (MAT, a), precipitation (MAP, b) at different aridity indexes (AI, c). Each data point stands for average values of each biome. Biomes were assigned into 62 types according to land cover and three temperature zones.

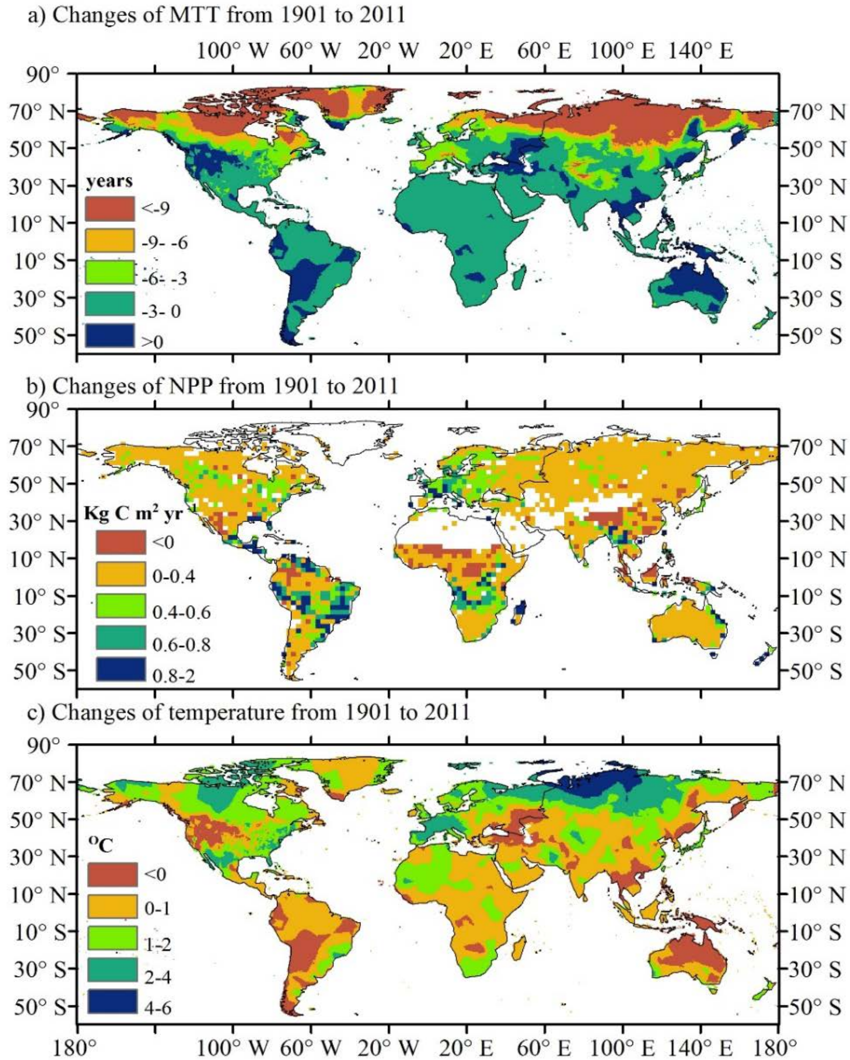

Figure 6. Change values of ecosystem mean ecosystem mean turnover time (MTT, unit: year a) driven by temperature change and NPP (unit: Kg C m^{-2}yr^{-1}) and temperature (^{O}C) from 1901 to 2011. MTT for 1901 and 2011 was calculated by the temperature-dependence function showing in Fig. 4. NPP in 1901 and 2011 was derived from models' average and MODIS.

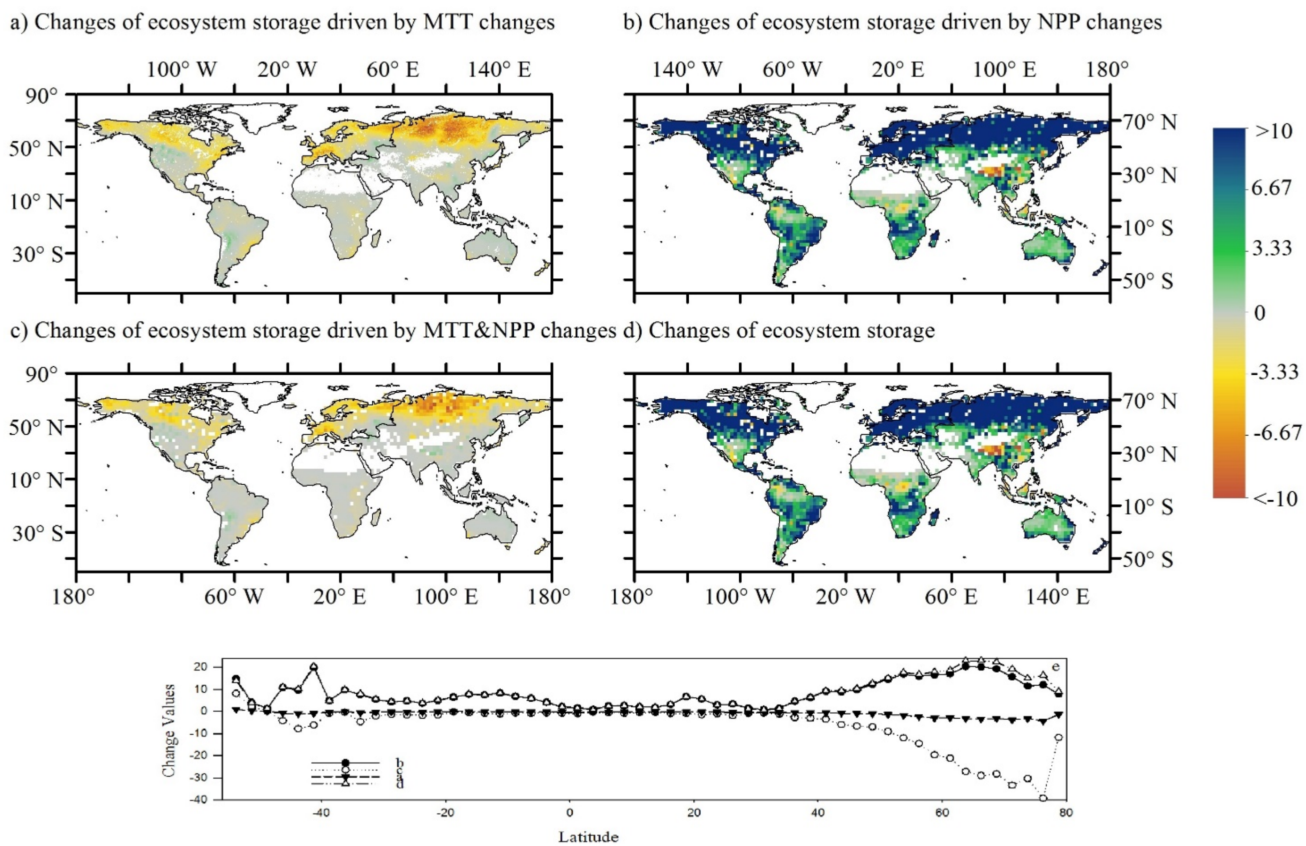

Figure 7. Change values of ecosystem carbon storage caused by mean turnover time change (NPP2011×ΔMTT, a), by NPP change (MTT2011×ΔNPP, b) and by NPP change and MRT change (ΔMTT×ΔNPP, c) and total ecosystem C storage changes (d), and latitudinal gradients of whole ecosystem carbon storage change values for a, b, c and d (e). Unit: g C m^{-2} yr^{-1} ($\Delta C_{pool} = NPP_{2011} \times \Delta MTT + MTT_{2011} \times \Delta NPP - \Delta NPP \times \Delta MTT$).