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 ecosystem C storage have not been well quantified. Here, we compared mean turnover times (MTTs) of ecosystem and soil, examined their variability to climate, and then quantified the spatial variation in ecosystem C storage over time from changes in C turnover time and/or NPP. Our results showed that mean GPP-based ecosystem MTT ($MTT_{EC\_GPP} = C_{pool}/GPP$, 25.0±2.7 years) was shorter than soil MTT ($MTT_{soil} = C_{soil}/NPP$, 35.5 ±1.2 years) and NPP-based ecosystem MTT ($MTT_{EC\_NPP} = C_{pool}/NPP$, 50.8±3 years, C_{pool} and C_{soil} referred to ecosystem or soil C storage, respectively). At the biome scale, temperature is the best predictor for MTT_{EC} ($R^2 = 0.77$, $p<0.001$) and MTT_{soil} ($R^2 = 0.68$, $p<0.001$), while the inclusion of precipitation in the model did not improve the performance of MTT_{EC} ($R^2 = 0.76$, $p<0.001$). Ecosystem MTT decreased by approximately 4 years from 1901 to 2011 when temperature was just considered, resulting in a large C release from terrestrial ecosystems. The resultant terrestrial C release caused by the decrease in MTT only accounted for about 13.5% of that due to the change in NPP uptake (159.3 ± 1.45 vs 1215.4 ± 11.0Pg C). However, the larger uncertainties in the spatial variation of MTT than temporal changes would lead to a greater impact on ecosystem C

storage, which may deserve to the further study in the future.

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 be quantified due to the complexity of terrestrial ecosystems in response to global change (Chambers and Li, 2007; Strassmann *et al*., 2008). For example, experimental and modeling studies showed that elevated CO_2 would enhance NPP and terrestrial C storage (Nemani *et al*., 2003; Norby *et al*., 2005), but warming could increase ecosystem C release, 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 change depends on the responses of C flux and C turnover time 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 results of soil C simulations from CMIP5 earth system models and found that global soil C varied 5.9 folds across models in response to a 2.6-fold variation in NPP and a 3.6-fold variation in global soil

C turnover times.

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 can be expressed by changes in both NPP and mean C turnover time. The spatial variation of NPP changes over time 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) found that differences in NPP contributed significantly to differences in soil C across models using a reduced complexity model with NPP and temperature. In contrast, the spatial variation of C turnover time in terrestrial ecosystems and its contribution to C storage have not well been quantified, especially at the regional or global scale.

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, such as 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 at small scale (i.e. C isotope tracing, radiocarbon). Spatial pattern of ecosystem C turnover time is relatively difficult to be estimated (Zhou and Luo, 2008), which needs to incorporate individual plant and soil C 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). The ratio of C storage to flux is another common method to estimate ecosystem turnover time at region or global scale (Gill and Jackson, 2000; Chen et al., 2013). For example, Carvalhais et al. (2014) had estimated ecosystem C turnover time as the ratio of C storage (soil and vegetation C) and GPP and examined their correlations to climate, which mainly focused on the comparison of global C turnover time calculated by model results from CIMP5 with those from observed data as well as their trend over latitude. In our study, we extended litter C and vegetation C pools from different datasets into ecosystem C storage to estimate C turnover time and evaluate their uncertainty from datasets. We also examined the changes in ecosystem C storage over time from changes in C turnover time and/or NPP.

In past decades, two types of mean C turnover times has been suggested for terrestrial ecosystems: the GPP-based or the NPP-based mean turnover time according to the terrestrial C models with GPP or NPP as their C inputs, respectively (Thompson and Randerson *et al*., 1999, NPP is GPP minus plant respiration). In addition, soil C turnover time are usually estimated using field sampling as the global turnover time for model validation. However, the difference among different versions of turnover times were still unclear. Therefore, we calculated the GPP-based, NPP-based ecosystem and soil turnover times through the similar method to explore their difference and its variability to climate. Thus, our objectives are: 1) to estimate the difference between GPP- and NPP-based ecosystem and soil mean turnover time, 2) to explore their relationships with climate, and 3) to quantify ecosystem C storage over time from changes in ecosystem C turnover time from 1901 to 2011. Ecosystem C turnover time was estimated using the C balance method with the 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 with different spatial scales. We thus regridded ecosystem mean turnover time at the grid ($1^{o}\times1^{o}$) for the comparison.

2 Materials and methods

2.1 Data collections

Three datasets were used to calculate ecosystem and soil mean turnover times, examine their variability to climate, and investigate effects of C turnover time on ecosystem C storage, including carbon (C) influx (GPP and NPP), C storage in C pools (soil, plant and litter), and climate variables (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 $0.083^{o} \times 0.083^{o}$ 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 provided an estimate of soil C storage at the top 1 m of soil and have largely underestimated total soil C. Jobbagy and Jackson (2000) indicated that global SOC storage in the top 3 m of soil was 56% more than that for the first meter, which could change estimates of the turnover time. We will discuss this caveat in the discussion section. It is well known that HWSD has underestimated soil C in high latitude. We thus estimated turnover time in high latitudes with the Northern Circumpolar Soil Carbon Database (NCSCD), which is an independent survey of soil C 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 C density values based on 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 to the biome types, forming the global pattern of litter C storage using the method of Matthews (1997) in ARCGIS software (ESRI Inc., Redlands, CA).

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 in CRU_TS 3.20 (Harris *et al*., 2013), specifically their means from 2000-2009.

We aggregated all datasets into a biome level for 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 $0.083^{o}\times0.083^{o}$ 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 by ARCGIS 10 to a common projection (WGS 84) and $1^{0}\times1^{0}$ spatial resolution. 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

Terrestrial ecosystem includes many C pools with largely varying turnover times from days to millennia, but it is difficult to collect the observed 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 section. For terrestrial ecosystems, the C pools (C_{pool}) is composed of three parts: plant, litter and soil, and C outfluxes include all C losses (autotrophic [R_a] and heterotrophic respiration [R_h]) as well as by fires and harvest. However, it is difficult to accurately get the observed respiration (R_a and R_h) in terrestrial ecosystem at the global scale. At the steady state, C outflux equals to C influx, which is the C uptake through GPP, so ecosystem C 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:

$$MTT_{EC} = \frac{C_{pool}}{GPP} \quad (1)$$

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 the ecosystem level (Carvalhais *et al*., 2014). We used multi-year GPP 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. To make better comparison, we also estimated the NPP-based ecosystem MTT ($MTT_{EC\_NPP} = C_{pool}/NPP$). The similar method was used to calculate soil MTT ($MTT_{soil} = C_{soil}/NPP$).

2.3 The climate effects on ecosystem mean C turnover time

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

$$AI = \frac{MAP}{PET} \quad (2)$$

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 MTT and mean annual temperature (MAT, ^{o}C), MAP (mm), and AI at the biome level. The regression analyses ($MTT = ae^{-bMATorMAP}$) were performed in STATISTICA 10 (StatSoft Inc., 2011), where *a* and *b* are the coefficients. The coefficient of determination (R^2) was used to measure the phase correlation between MTT 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 $MTT = ae^{-bMATorMAP}$), which is used in most models to simulate C decomposition.

2.4 The effects of turnover time on ecosystem C storage

Ecosystem C storage capacity at the 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:

$$
\begin{aligned}
&\Delta Cpool = NPP_{2011} \times MTT_{2011} - NPP_{1901} \times MTT_{1901} \\
&\Rightarrow \Delta Cpool = NPP_{2011} \times MTT_{2011} - (NPP_{2011} - \Delta NPP) \times (MTT_{2011} - \Delta MRT) \\
&\Rightarrow \Delta Cpool = NPP_{2011} \times \Delta MTT + MTT_{2011} \times \Delta NPP - \Delta NPP \times \Delta MTT
\end{aligned} \quad (3)
$$

where $NPP_{1901(2011)}$ and $MTT_{1901(2011)}$ refer to NPP and MTT at time 1901 or 2011. ΔC_{pool} (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}×ΔMTT) represents the effects of changes in MTT on ecosystem C storage. The second component (ΔNPP×MTT_{2011}) is the effects of changes in NPP on ecosystem C storage, and ΔNPP×ΔMTT is the interactive effects of both changes in NPP and MTT .

To assess ecosystem C storage from the changes in MTT or NPP, ecosystem MTT in 1901 and 2011 was calculated using an exponential equation between ecosystem MTT and temperature ($MTT = ae^{-bMAT}$). Here, we assumed that the spatial correlation between temperature and MTT is identical to the temporal correlation between these variables. 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). Our previous study found that the modeled NPP was near to MODIS-estimated NPP and their difference was mostly less than 0.05 kg C m^{-2} yr^{-1} (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. 1). 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 plant 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

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 was shorter than NPP-based MTT with the value of 35.5 years (with a 95% CI of 34.9-36.7 years). MTT varied among biomes due to the different climate forcing (Table 1 and Fig 2). The long MTT occurred in high latitude while the short one was in tropical zone. Among the 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 had the longest MTT. Therefore, the order of GPP-based 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 to 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 (MTT)

Ecosystem MTT 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 MTT 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 the biome scale. When MAP was incorporated into a multivariate regression function of ecosystem MTT with MAT, the relationships could not be significantly improved. While MAP improved the explanation of variance of soil MTT (R^2

from 0.68 to 0.76), although there was 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. 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). 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 (Fig. 6c). When the regression function between ecosystem MTT and MAT was used to estimate ecosystem MTT in 1901 and 2011 (Fig. 4), the ecosystem MTT decreased by approximately 4 years on average (Fig.6a). The largest change in ecosystem MTT occurred in the cold zones. In tundra, ecosystem MTT decreased by more than 10 years due to the larger increase in temperature (~2°C) than other regions. 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. 6b).

The changes in ecosystem MTT and NPP across 110 years would cause decrease or increase in terrestrial C storage. Ecosystem C storage decreased by 159.3 ± 1.45 Pg C from 1901 to 2011 ($\Delta MTT \times NPP$) from the decrease in MTT, with the largest decrease in tundra and boreal forest (more than 12 g C m^{-2}) and little decrease in tropical zones (Fig. 7a & e). The interactive changes of both NPP and MTT caused a decrease of 129.4±1.31 Pg C ($\Delta MTT \times \Delta NPP$) with the similar spatial pattern (Fig. 7c). However, the increase in NPP directly raised ecosystem C storage up to 1215.4 ± 11.0 Pg C from 1901 to 2011 with a range of 30-150 g C m^{-2} in most areas ($MTT \times \Delta NPP$, Fig. 7b). The MTT-induced changes in ecosystem C storage only accounted for about 13.5% of that driven by NPP due to the different weights ($\Delta MTT \times NPP$ vs. $MTT \times \Delta NPP$). The spatial pattern of the NPP-driven changes mostly represented the spatial pattern of the changes in ecosystem C storage (Fig. 7e).

4 Discussion

4.1 Global pattern of mean turnover time

In this study, we used the ratio of C storage to C flux to calculate the GPP-based, the NPP-based and soil MTT and compared their difference. 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 were 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). The mean GPP-based MTT was slightly longer than that from Carvalhais *et al*. (2014, 23 years) with the similar method. The difference may result from two aspects. Firstly, ecosystem C storage in this study was the sum of soil, vegetation and litter C pools, while Carvalhais *et al*. (2014) only considered soil and vegetation C pools. Secondly, the data source of global vegetation C storage was different with our study from Gibbs (2006) and Carvalhais *et al*. (2014) from a collection of estimates for pan-tropical regions and radar remote-sensing retrievals for northern and temperate forests. The difference between GPP-based and NPP-based MTT was determined by the ratio of GPP and NPP, which was largely influenced by the assumptions of the MODIS NPP algorithm. 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), largely resulting from different model assumptions for GPP-based (higher normalized storage response function for low turnover time) and NPP-based MTT (for high turnover time) in Thompson and Randerson (1999). 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, although the order of ecosystem MTT across forest biomes was similar. This is because, in the inverse or CABLE model, ecosystem was often separated into several plant and soil C pools with their distinct C turnover time compared to that with one pool in our study.

The spatial patterns of ecosystem and soil MTTs were similar. The difference between NPP-based ecosystem and soil MTTs was the turnover time of vegetation and litter, which was related to plant functional types (PFTs). For instance, the difference between NPP-based and soil MTTs in Australia was shorter (33.4 and 29.8 years, respectively) compared to that in other regions, because one of the PFTs accounting for a large space of Australia was spare grass with short turnover time (3.5 years on average). In addition, within a specific PFT, different ecosystems may have diverse turnover time due to climate effects. NPP-based and soil MTTs for boreal neadleaf evergreen forest were about 116 years and 98 years, respectively, while both for tropical ones 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}) with the similar vegetation C storage (~3.5 kg C m^{-2}). High temperature and humidity in tropical zone, which promote decomposition processes, may largely contribute to the short turnover time compared to those in boreal zone (Sanderman et al., 2003).

In our study, we only used soil C in the top 1 m to estimate ecosystem MTT, which would be 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. Therefore, the C storage in deep soil layers (>1m) should be considered to estimate ecosystem MTT and the accurate estimate of the deep soil C storage, which deserves to the further study in the future.

4.2 The sensitivity of turnover time to climate

The estimated 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 C pools (Gill and Jackson, 2000). Ecosystem MTT had negative exponential relationships with MAT (Fig 4), similar to those with soil MTT, due to temperature dependence of respiration rates (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 would decompose at much lower rates than SOM due to the longer MTT of wood (Zhou *et al*., 2012). Ecosystem MTT had 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 combining MAT and MAP clearly improved soil MTT (R^2=0.76, p<0.001). 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 could 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) could explain 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 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 changes in ecosystem C storage from 1901 to 2011 and partitioned it into three parts from the changes in NPP, in ecosystem MTT, and in both NPP and MTT (seeing equation 3). Our results showed that the decrease in MTT increased ecosystem C loss over time due to the increase in C decomposition rates, while increased NPP enhanced ecosystem C uptake due to the decrease in CO_2 input to atmospheric and the increase of vegetation C stocks.

Current datasets have showed an increase in NPP (e.g., Hicke *et al*., 2002; Potter *et al*., 2012), leading to increasing terrestrial C uptake. Our results showed that the NPP increased by approximately 0.3 kg C m^{-2} yr^{-1} from 1901 to 2011 and the resultant terrestrial C uptake is 1215.4 Pg C (with average year of 11.0 Pg C yr^{-1}). The ecosystem C storage in conterminous USA increased 0.4 Pg C yr^{-1}, which was larger than that from inverse models (Zhou and Luo, 2008; Zhou *et al*., 2012) and was comparable to C sink from atmospheric inversion (0.30-0.58 Pg C yr^{-1}, Pacala *et al*., 2001). The shortened MTT caused C losses from ecosystems from 1901 to 2011 (about 1.45 Pg C yr^{-1}), indicating that ecosystem C storage decreased with climate warming (Fig. 7e). However, ecosystem C losses from the decrease in MTT only accounted for 13.5% of that driven by changes in NPP, so terrestrial ecosystem was still a net sink. The largest changes of MTT occurred in high latitude regions (Fig. 6a), resulting in the largest loss of terrestrial C (Fig. 7e), where it is more vulnerable to climate change (Zimov *et al*., 2006). However, the direct release of CO_2 in high latitude through thawing would be another large source of decreasing 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 shrubland (50% of total) due to the relatively longer MTT, leading to the larger terrestrial C uptake driven by NPP increase compared with others. In addition, the C uptake in cropland and grassland could be 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 could cause biases to some degree in estimated ecosystem MTT. First, we assumed that ecosystem is at the steady state when MTT was estimated. It is difficult to define the steady state, especially for soil C dynamics (Luo and Weng, 2011). Actually, maintaining a steady state is rare for a long time and ecosystems 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. The quality of the current datasets would determine the accuracy of ecosystem MTT estimates. For example, the amendments of typological data (derived from the global ISRIC-WISE datasets) and soil 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. Compared to HWSD dataset, the MTT in the top 1m could increase to 30.3 years for GPP-based, 66.9 years for NPP-based and 45.7 years for soil when SoilGrids was used (Hengl et al., 2014). However, it is difficult to quantify the uncertainty in MTT caused by uncertainties of the current datasets due to lack of quantitative uncertainty 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 the estimates of long-term C storage and turnover time (Zaehle et al., 2006), which cannot be reflected in the current algorithms. Probably, the inverse modeling can be a feasible method to evaluate the effect of the disturbance and forest age on the estimates of turnover time.

Third, the uncertainties in the relationships of ecosystem MTT with MAT and MAP would influence the estimates of ecosystem MTT, causing the propagation of uncertainty in ecosystem C storage. To simplify the calculation, we aggregated all datasets into a biome level, leading to 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. Changes in MTT for

1901and 2011 were estimated using the exponential function between MTT 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 soil C storage from MTT changes could decrease 161.42 Pg C and that driven by NPP uptake could increase 1125.6 Pg C with the similar spatial pattern to the ecosystem. In addition, we assumed that the current-day spatial correlation between temperature and MTT was identical to temporal correlation between these variables, although such assumption cannot reflect some processes like acclimation of microbial respiration to warming or shifts in plant species over time.

4.5 Implication for land surface models

Our results may provide insights as to how MTT and ecosystem C storage varied with climate and over time. Our study could thus offer several suggestions for future experimental and modeling research with the goals to improve estimates of ecosystem C storage. First, the substantial changes in terrestrial C storage occurred in forest and shrubland covering large area with the relatively long turnover time, because MTT dominated the uncertainty in the estimates of terrestrial C storage. Therefore, further work should focus on the accurate estimation of C turnover time with numerous observational data at regional or global scale and the evaluation of uncertainty from datasets and the assumption (e.g., the steady-state).

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 C turnover time was lower than that of soil C pool (Q_{10}: 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 those for all or AI<1 conditions. Although global carbon models have currently considered moisture stress on vegetation, 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, NCSCD, vegetation C production of Gibbs *et al*. (2006), litter dataset from Holland *et al*. (2005), climate variables from the Climate Research Unit (CRU_TS 3.20)) used in this study are open and shared. We provided full citations for data sources in MS and the download links in the supplemental information.

Acknowledgements

This research was financially supported by the National Natural Science Foundation of China (Grant No. 31770559, 31370489), 2012 Shanghai Pujiang Program (12PJ1401400), and "Thousand Young Talents" Program in China (31370489).

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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 on GPP and NPP, respectively.

Biome	Ecosystem C storage (kg C m^{-2})	Ecosystem MTT (years)		Soil MTT(years)	MAT (°C)	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 the grid scale ($1^{o}\times1^{o}$). Unit: kg C m^{-2}. Ecosystem C storage was calculated from plant biomass, soil, and litter C pools.

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

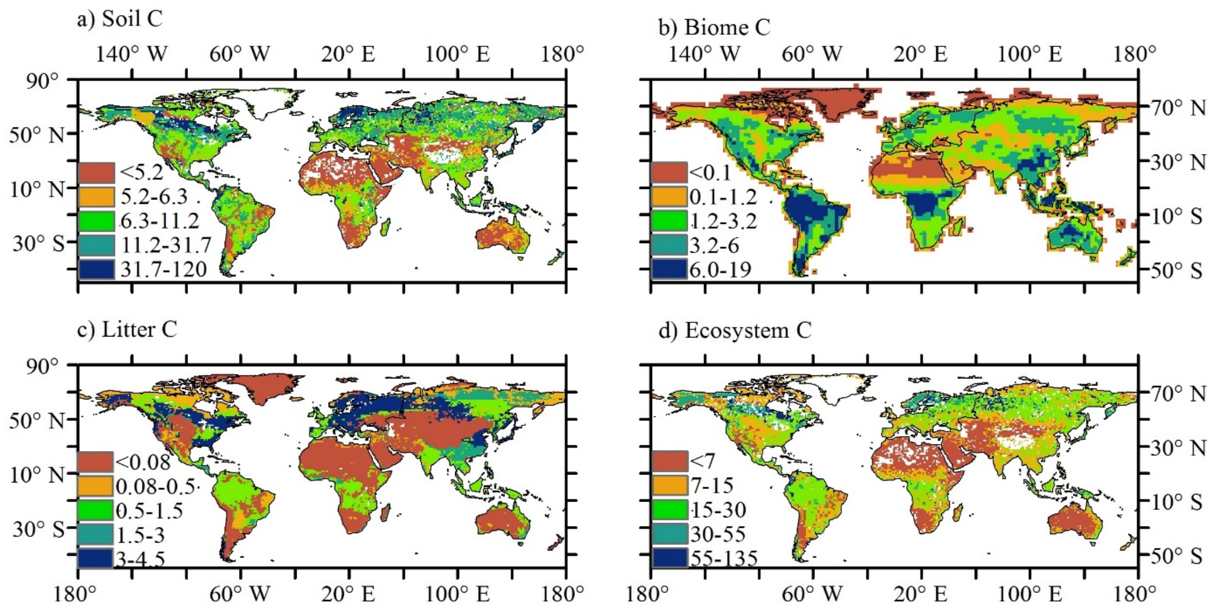
Figure 3. Spatial pattern of mean turnover time (years) in high latitude based on soil C storage from HWSD data (a) and NCSCD data (b).

Figure 4. Relationships between ecosystem mean turnover time (MTT) and multi-annual temperature (MAT, a) or 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) or 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. Changes in mean ecosystem mean turnover time (MTT, unit: year) driven by temperature change (a), changes in NPP (unit: kg C $m^{-2}yr^{-1}$, b), and changes in temperature (^{o}C, c) from 1901 to 2011. Changes in MTT from 1901 and 2011 were calculated by the temperature-dependence function showing in Fig. 4. Changes in NPP from 1901 and 2011 were derived from models' average and MODIS.

Figure 7. Altered ecosystem carbon storage due to changes in mean turnover time (MTT, NPP2011×ΔMTT, a), net primary production (NPP, MTT2011×ΔNPP, b), and interaction of NPP and MTT (ΔMTT×ΔNPP, c). Panels d and e are total altered ecosystem C storage changes due to changes in MTT, NPP, and MTT×NPP and their latitudinal gradients from panels a-d, respectively. 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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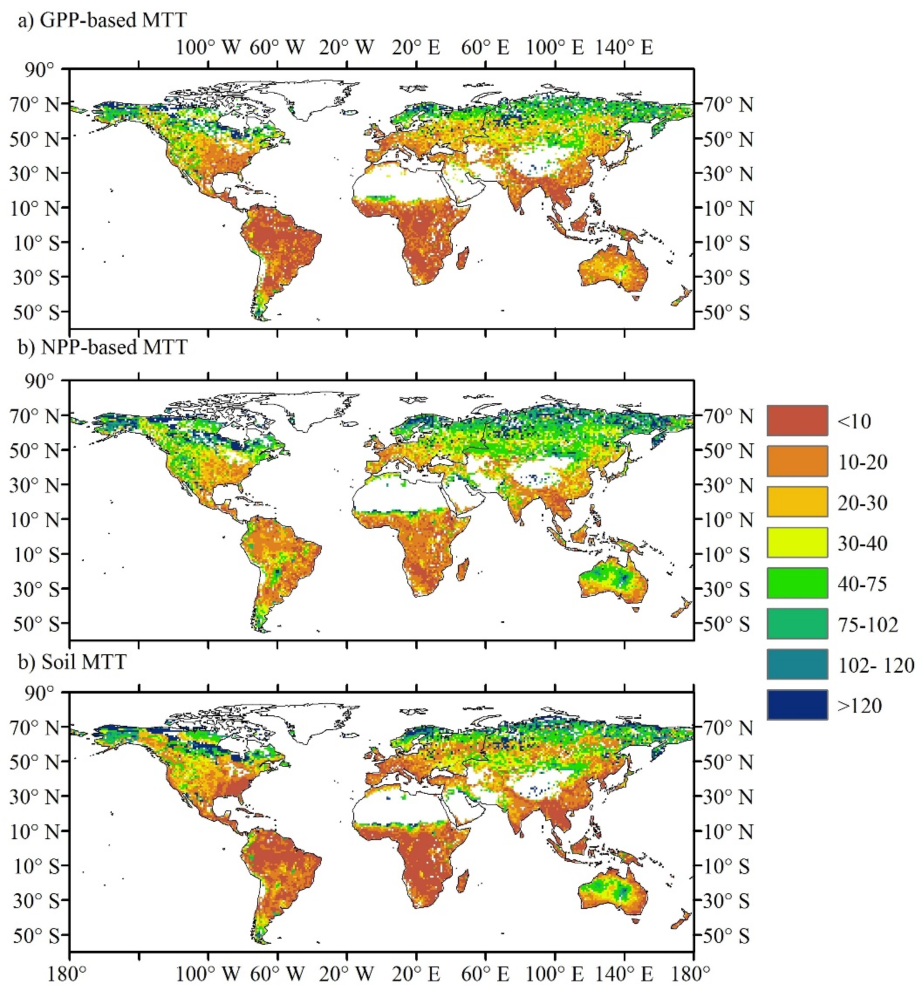

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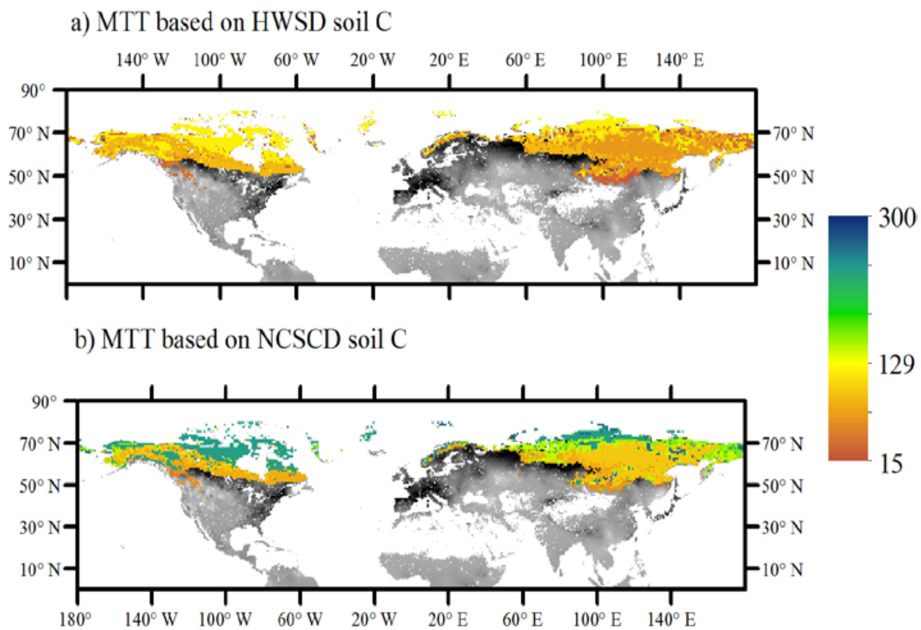

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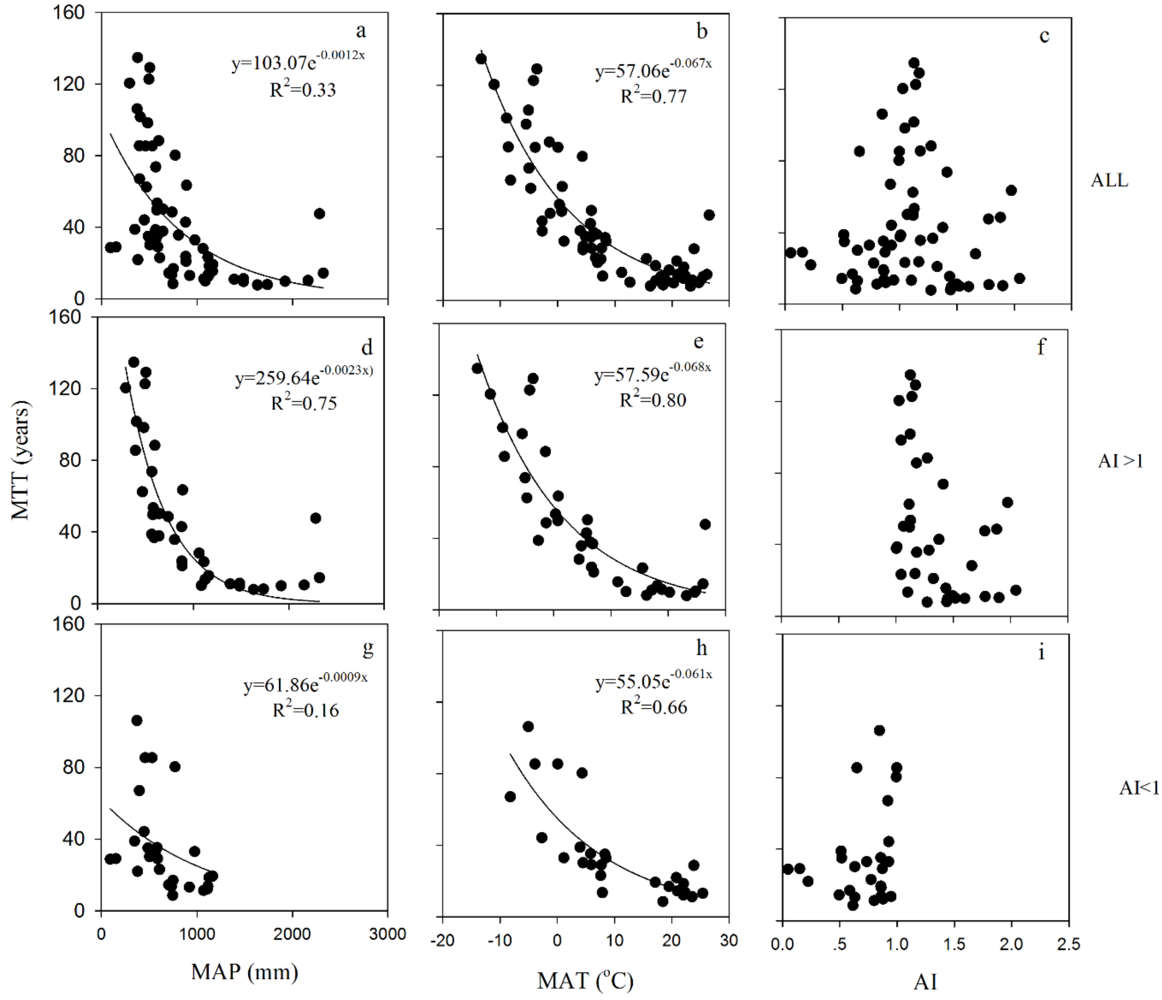
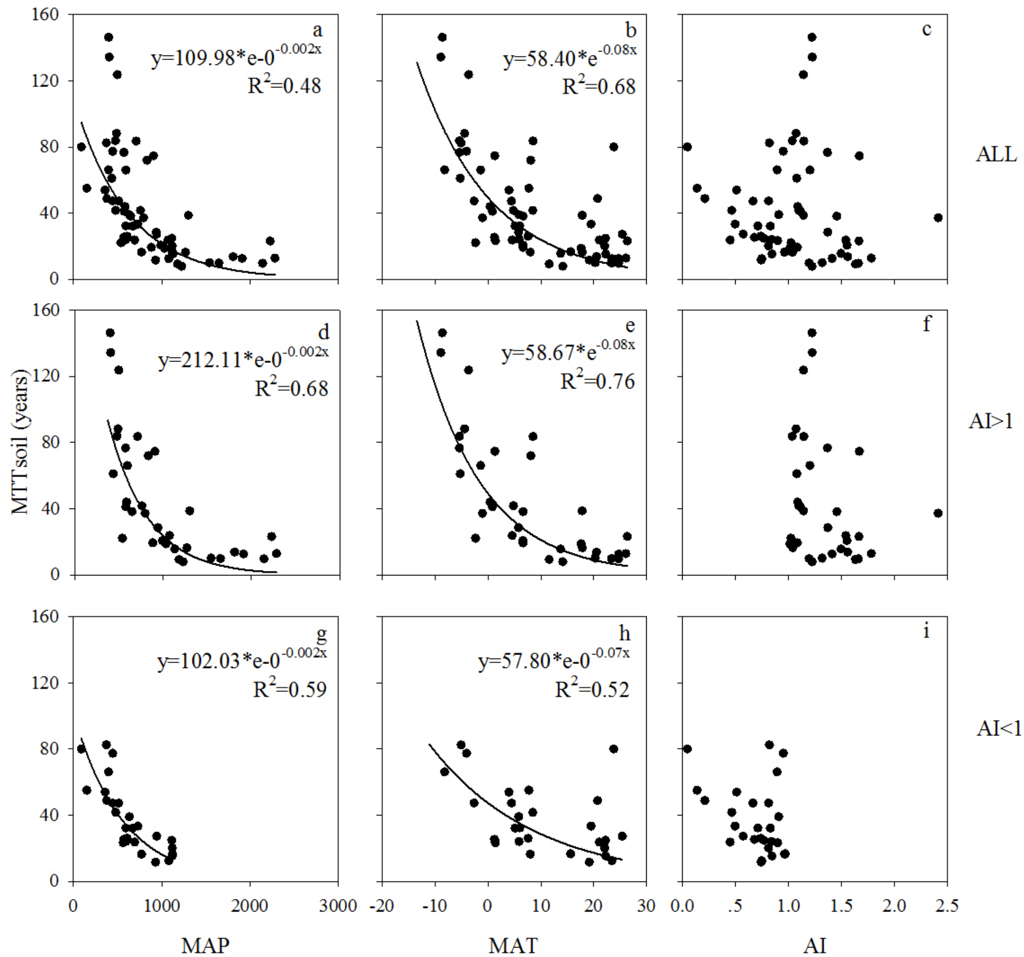


684

685 **Figure 4**. Relationships between ecosystem mean turnover time (MTT) and multi-annual temperature (MAT, a) or 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.



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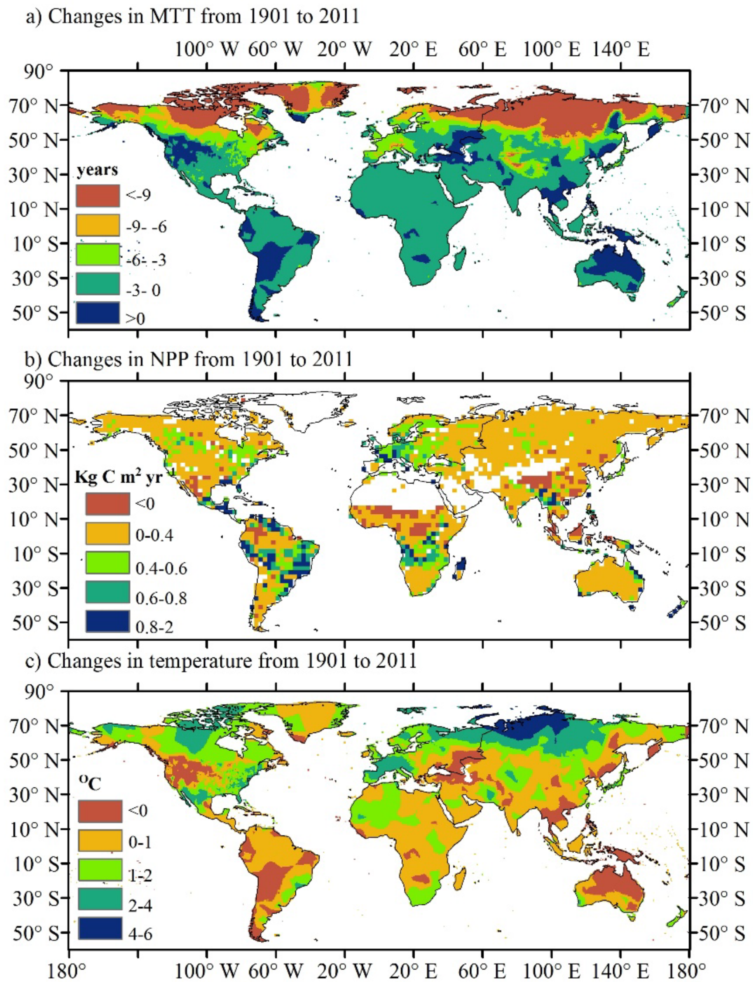

Figure 6. Altered mean ecosystem mean turnover time (MTT, unit: year) driven by temperature change (a), changes in NPP (unit: Kg C $m^{-2}yr^{-1}$, b), and changes in temperature (^{o}C, c) from 1901 to 2011. Changes in MTT for 1901 and 2011 were calculated by the

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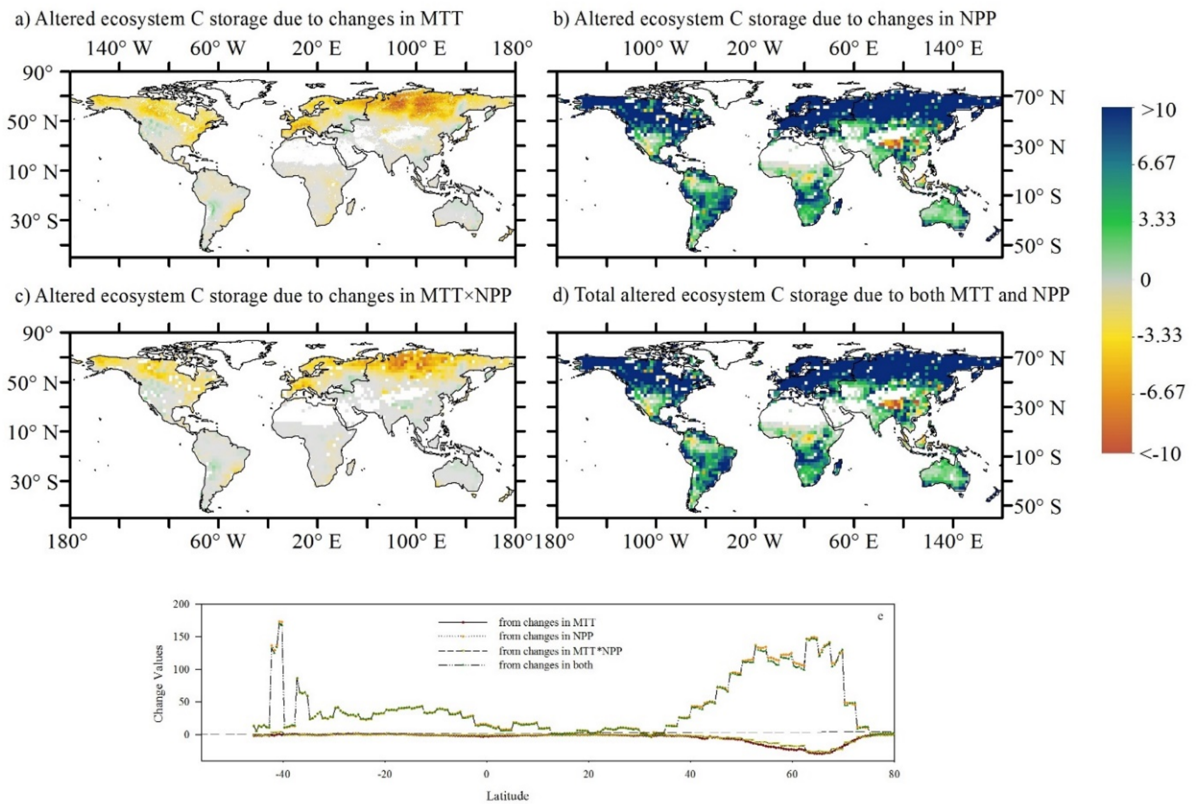

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