1    **Effects of carbon turnover time on terrestrial ecosystem carbon storage**

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16    **Abstract.** Carbon (C) turnover time is a key factor in determining C storage capacity in

17    various plant and soil pools as well as terrestrial C sink in a changing climate. However, the

18    effects of C turnover time on ecosystem C storage have not been well explored. In this study,

19    we compared mean C turnover times (MTTs) of ecosystem and soil, examined their

20    variability to climate, and then quantified the spatial variation in ecosystem C storage over

21    time from changes in C turnover time and/or net primary production (NPP). Our results

22    showed that mean gross primary production (GPP)-based ecosystem MTT ($MTT_{EC\_GPP}$ =

23    $C_{pool}$/GPP, 25.0±2.7 years) was shorter than soil MTT ($MTT_{soil}$ = $C_{soil}$/NPP, 35.5 ±1.2 years)

24    and NPP-based ecosystem MTT ($MTT_{EC\_NPP}$ = $C_{pool}$/NPP, 50.8±3 years, $C_{pool}$ and $C_{soil}$

25    referred to ecosystem or soil C storage, respectively). At the biome scale, temperature is the

26    best predictor for $MTT_{EC}$ ($R^2$ = 0.77, p<0.001) and $MTT_{soil}$ ($R^2$ = 0.68, p<0.001), while the

27    inclusion of precipitation in the model did not improve the performance of $MTT_{EC}$ ($R^2$ =

28    0.76, p<0.001). Ecosystem MTT decreased by approximately 4 years from 1901 to 2011

29    when only temperature was considered, resulting in a large C release from terrestrial

30    ecosystems. The resultant terrestrial C release caused by the decrease in MTT only accounted

31    for about 13.5% of that due to the change in NPP uptake (159.3 ± 1.45 vs 1215.4 ± 11.0Pg

32    C).  However, the larger uncertainties in the spatial variation of MTT than temporal changes

33    would lead to a greater impact on ecosystem C storage, which deserves further studies in the

34    future.

35    **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 global carbon (C) budget (IPCC, 2007), leading to a positive or negative feedback to global climate change (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 have shown 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 turnover time in various C pools (i.e., plant, litter and soil) (Parton *et al*., 1987; Potter *et al*., 1993; Luo *et al*., 2003; Xia *et al*., 2013). When simulated soil C from CMIP5 earth system models have been evaluated, global soil C changed 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 (Todd-Brown *et al*. 2013).

53    In a given environmental condition, ecosystem C storage capacity refers to the amount of

54    C that a terrestrial ecosystem can store at the steady state, determined by C influx and

55    turnover time (Xia *et al*., 2013). External environmental factors, such as climate change and

56    land use change, would dynamically influence both ecosystem C influx and turnover time and

57    then change terrestrial C storage capacity. Thus, the changed magnitude of ecosystem C

58    storage can be expressed by changes in both NPP and mean C turnover time (Luo *et al*.,

59    2003). The spatial variation of NPP changes over time and the effects of climate change have

60    been relatively well quantified by manipulative experiments (Rustad *et al*., 2001; Luo *et al*.,

61    2006), satellite data (Zhao and Running, 2010), and data assimilation (Luo *et al*., 2003; Zhou

62    and Luo, 2008; Zhou *et al*., 2012). It has been shown that differences in NPP contributed

63    significantly to differences in soil C across models using a reduced complexity model with

64    NPP and temperature (Todd-Brown *et al*. 2013). In contrast, the spatial variation of C

65    turnover time in terrestrial ecosystems and its contribution to C storage have not been well

66    quantified, especially at the regional or global scale.

67    Ecosystem C turnover time is the average time that a C atom resides in an ecosystem from

68    entrance to the exit (Barrett, 2002). Several methods have been used to estimate the C

69    turnover time, such as C balance method by estimating ratios of C pools and fluxes (Vogt *et*

70    *al*., 1995), C isotope tracing (Ciais *et al*., 1999; Randerson *et al*., 1999), and measurements of

71    radiocarbon accumulation in the undisturbed soils (Trumbore *et al*., 1996). However, most

72    methods mainly focused on various C pools (i.e., leaf, root, soil) and at small scale (i.e. C

73    isotope tracing, radiocarbon). Spatial pattern of ecosystem C turnover time is relatively

74    difficult to be estimated (Zhou and Luo, 2008), which needs to incorporate individual plant

75    and soil C pools and their C turnover time into ecosystem models. The inverse modeling has

76    been used to estimate ecosystem mean C turnover time in USA and Australia with high

77    spatially heterogeneous distribution (Barrett, 2002; Zhou and Luo, 2008; Zhou *et al*., 2012).

78    The ratio of C storage to flux is another common method to estimate ecosystem turnover time

79    at region or global scale (Gill and Jackson, 2000; Chen et al., 2013). For example, Carvalhais

80    et al. (2014) had estimated ecosystem C turnover time as the ratio of C storage (soil and

81    vegetation C) and GPP and examined their correlations to climate. However, it mainly

82    focused on the comparison of global C turnover time calculated by modeled results from

83    CIMP5 with those from observed data. In our study, we extended litter C and vegetation C

84    from different datasets into ecosystem C storage to estimate C turnover time and evaluated

85    their uncertainty. We also examined the changes in ecosystem C storage over time from

86    changes in C turnover time and/or NPP.

87  In past decades, two types of mean C turnover times have been suggested for terrestrial

88  ecosystems: the GPP-based or the NPP-based mean turnover time according to the terrestrial

89  C models with GPP or NPP as their C inputs, respectively (Thompson and Randerson *et al*.,

90  1999, NPP is GPP minus plant respiration). In addition, soil C turnover time are usually

91  estimated using field sampling as the global turnover time for model validation. However, the

92  differences in C turnover times among versions C pools remain unclear. Therefore, we

93  calculated the GPP-based, NPP-based ecosystem and soil turnover times through the similar

94  method to explore their difference and its variability to climate. Thus, our objectives were: 1)

95  to estimate the difference between GPP- and NPP-based ecosystem and soil mean C turnover

96  time, 2) to explore their relationships with climatic factors, and 3) to quantify ecosystem C

97  storage over time from changes in ecosystem C turnover time from 1901 to 2011.

98

99  **2    Materials and methods**

100  2.1 Data collections

101  Three datasets were used to calculate ecosystem and soil mean C turnover times, examine

102  their variability to climate, and investigate effects of C turnover time on ecosystem C storage,

103  including C influx (GPP and NPP), C storage in different C pools (soil, plant and litter), and

104    climate variables (temperature, precipitation and potential evapotranspiration). GPP and NPP

105    were extracted from MODIS products (MOD17) on an 8-day interval with a nominal 1-km

106    resolution since Feb. 24, 2000. The multi-annual average GPP/NPP from 2000 to 2009 with

107    the spatial resolution of $0.083^o \times 0.083^o$ were used in this study (Zhao and Running, 2010).

108        The harmonized World Soil Database (HWSD, Hiederer and Köchy, 2012) provided

109    empirical estimates of global soil C storage, a product of the Food and Agriculture

110    Organization of the United Nations and the Land Use Change and Agriculture Program of the

111    International Institute for Applied System Analysis (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012).

112    Global soil organic C (SOC) at the topsoil (0-30cm) and subsoil layers (30-100cm) has been

113    estimated using the amended HWSD with estimates derived from other global datasets for

114    these layers (Hiederer and Köchy 2012). We used the amended HWSD SOC to calculate C

115    turnover time (http://eusoils.jrc.ec.europa.eu). However, HWSD only provides an estimate of

116    soil C storage at the top 1 m of soil and has largely underestimated total soil C. It has been

117    indicated that global SOC storage in the top 3 m of soil was 56% more than that for the first

118    meter, which could change estimates of the turnover time (Jobbagy and Jackson 2000). We

119    discussed this caveat in the discussion section of this study. It is well known that HWSD has

120    underestimated soil C in high latitude (Carvalhais *et al*, 2014). We thus estimated turnover

121   time in high latitudes with the Northern Circumpolar Soil Carbon Database (NCSCD), which

122   is an independent survey of soil C in this region (Tarnocai *et al*., 2009). For biomass, Gibbs

123   (2006) has estimated the spatial distribution of the above- and below-ground C stored in

124   living plant material by updating the classic studies of Olson *et al*. (1983, 1985) with a

125   contemporary map of global vegetation distribution (Global Land Cover database,

126   Bartholomé and Belward, 2005). Each cell in the gridded data set was coded with an estimate

127   of mean and maximum C density values based on its land cover class, so this dataset mainly

128   represents plant biomass C at a biome level (Gibbs, 2006).

129       The litter dataset was extracted from 650 published and unpublished documents (Holland

130   *et al*., 2005). Each record represents a site, including site description, method, litterfall, litter

131   mass and nutrients. We calculated the mean and median of litter mass for each biome, and

132   then assigned the value for each grid according to the biome types, forming the global pattern

133   of litter C storage using the method of Matthews (1997) in ARCGIS software (ESRI Inc.,

134   Redlands, CA).

135       Global climate databases produced by the Climate Research Unit (CRU) at the University

136   of East Anglia were used to analyze the climatic effect on ecosystem mean C turnover time.

137   We used mean $0.5^{o} \times 0.5^{o}$ gridded air temperature, precipitation and potential

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

139    to 2009.

140    We aggregated all datasets into a biome level for data match, so the biome map was

141    extracted from the GLC 2000 (Bartholomé and Belward, 2005) and regulated by MODIS. We

142    assigned 22 land cover class among three temperature zones (i.e., tropical, temperate and

143    boreal) by taking the most common land cover from the original underlying $0.083^\circ \times 0.083^\circ$

144    data. Eight typical biomes were zoned with ARCGIS 10 in corresponding to plant function

145    types (PFTs) in CABLE model as described in Xia *et al* (2013): evergreen needleleaf forest

146    (ENF), evergreen broadleaf forest (EBF), deciduous needleleaf forest (DNF), deciduous

147    broadleaf forest (DBF), tundra, shrubland, grassland and cropland. All of the data were re-

148    gridded by ARCGIS 10 to a common projection (WGS 84) and $1^\circ \times 1^\circ$ spatial resolution. The

149    re-gridding approach for C fluxes and pools (i.e., GPP, NPP, soil C and litter C) assumed

150    conservation of mass that a latitudinal degree was proportional to distance for the close grid

151    cells (Todd-Brown *et al*., 2013). A nearest neighbor approach were used for land cover

152    classes and a bi-linear interpolation were used for climate variables (i.e., temperature,

153    precipitation).

154

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 were some limitations when the ecosystem was considered as a single pool, which further 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. 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:

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

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*.,

172    2014). We used multi-year GPP to calculate MTT in order to reduce the effect of the non-

173    steady state, since it was difficult to evaluate how this assumption would affect model results.

174    To make better comparison, we also estimated the NPP-based ecosystem MTT ($MTT_{EC\_NPP}$ =

175    $C_{pool}$/NPP). The similar method was used to calculate soil MTT ($MTT_{soil} = C_{soil}$/NPP).

176

177    2.3 The climate effects on ecosystem mean C turnover time

178    To explore the combining effects of precipitation and temperature on ecosystem and soil C

179    turnover time, aridity index (AI) was calculated as follows:

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

181    where PET is the potential evapotranspiration and MAP is mean annual precipitation

182    (Middleton and Thomas, 1997). AI is a bioclimatic index including both physical phenomena

183    (precipitation and potential evapotranspiration) and biological processes (plant transpiration)

184    related with edaphic factors.

185      The relationships were examined between MTT and mean annual temperature (MAT, $^{o}C$),

186    MAP (mm), and AI at the biome level. The regression analyses $(MTT = ae^{-bMAT or MAP})$

187    were performed in STATISTICA 10 (StatSoft Inc., 2011), where *a* and *b* are the coefficients.

188    The coefficient of determination ($R^2$) was used to measure the phase correlation between

189 MTT and climate factors. Here, we also calculated a $Q_{10}$ value (i.e., $Q_{10}$, a relative increase in

190 mean turnover time for a $10^{\circ}C$ increase in temperature, $Q_{10} = e^{10b}$, b, the coefficients

191 of $MTT = ae^{-bMATorMAP}$), which is used in most models to simulate C decomposition.

192

193 2.4 The effects of turnover time on ecosystem C storage

194 Ecosystem C storage capacity at the steady state is represented by $NPP \times MTT$ (Lou *et al.*,

195 2003), so the difference of ecosystem C storage from 1901 to 2011 could be calculated as

196 follows:

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

197

198 where $NPP_{1901(2011)}$ and $MTT_{1901(2011)}$ refer to NPP and MTT at time 1901 or 2011. $\Delta C_{pool}$

199 ($\Delta NPP$ or $\Delta MTT$) is the difference between ecosystem C storage (NPP or MTT) at time 2011

200 and that at time 1901. The first component ($NPP_{2011} \times \Delta MTT$) represents the effects of

201 changes in MTT on ecosystem C storage. The second component ($\Delta NPP \times MTT_{2011}$) is the

202 effects of changes in NPP on ecosystem C storage, and $\Delta NPP \times \Delta MTT$ is the interactive

203 effects of both changes in NPP and MTT.

204 To assess ecosystem C storage from the changes in MTT or NPP, ecosystem MTT in 1901

13

205    and 2011 was calculated using an exponential equation between ecosystem MTT and

206    temperature ($MTT = ae^{-bMAT}$). Here, we assumed that the spatial correlation between

207    temperature and MTT was identical to the temporal correlation between these variables. NPP

208    in 2011 was derived from products (MOD17) and NPP in 1901 was averaged from the eight

209    models' simulated results (CanESM2, CCSM4, IPSL-CM5A-LR, IPSL-CM5B-LR, MIROC-

210    ESM, MIROC-ESM-CHEM, NorESM1-M and NorESM1-ME). Our previous study found

211    that the modeled NPP was near to MODIS-estimated NPP and their difference was mostly

212    less than 0.05 kg C m$^{-2}$ yr$^{-1}$ (Yan *et al*., 2014).

213

214    2.5 Uncertainty analysis and sensitivity Analysis

215    Limitation of the above datasets is that the uncertainties are poorly quantified. The global

216    mean of C fluxes (GPP and NPP) and pools (soil, litter, and plant) were calculated by 1000

217    simulations, respectively, through Markov chain Monte Carlo (MCMC) sampling from a

218    gamma distribution (CRAN: MCMCpack, Martin, *et al*., 2011). For each variable, the

219    confidence interval (CI) was estimated as the 2.5 and 97.5 percentile of mean values of the

220    1000 simulations. It was also applied to estimate the confidence interval of ecosystem C

221    storage and ecosystem mean C turnover time.

222

## 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 the highest in boreal

evergreen needleaf forest (ENF) and the lowest in deciduous broadleaf forest (DBF). 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 ($34.84 \pm 0.02$ kg C

m$^{-2}$) > deciduous needleleaf forest (DNF, $25.30 \pm 0.03$ kg C m$^{-2}$)> evergreen broadleaf forest

(EBF, $22.70 \pm 0.01$ kg C m$^{-2}$)> shrubland ($18.29 \pm 0.02$ kg C m$^{-2}$) > DBF ($16.51 \pm 0.02$ kg C m$^{-}$

$^{2}$) > tundra ($14.16 \pm 0.02$ kg C m$^{-2}$)/cropland ($14.58 \pm 0.01$kg C m$^{-2}$) > grassland ($10.80 \pm 0.01$

kg C m$^{-2}$).

3.2 Mean C turnover time

239    Ecosystem mean C turnover time (MTT) was 25.0 years (with a 95% CI of 23.3-27.7 years)

240    based on GPP data and 50.8 years (with a 95% CI of 47.8-53.8 years) on NPP data (Table 1),

241    while soil MTT was shorter than NPP-based MTT with the value of 35.5 years (with a 95%

242    CI of 34.9-36.7 years). MTT varied among biomes due to the different climate forcing (Table

243    1 and Fig 2). The longest MTT occurred in high latitude while the shortest one was in tropical

244    zone. Among the forest biomes, DNF had the longest MTT with the lowest mean temperature

245    (-7.9 $^o$C), while the shortest MTT was in EBF with the highest temperature (24.5 $^o$C) and

246    precipitation (2143 mm). Although ecosystem C storage was low in tundra (14.16 kg C m$^{-2}$),

247    it had the longest MTT. Therefore, the order of GPP-based ecosystem MTT among biomes

248    differed for ecosystem C storage, with tundra (99.704±6.14 years) > DNF (45.27±

249    2.43years) or ENF (42.23±2.01 years) > shrubland (27.77±2.25 years) > grassland

250    (26.00±1.41 years) > cropland (14.91±0.40years) or DBF (13.29± 0.68years) > EBF

251    (9.67±0.21 years). Soil MTT had the similar order to ecosystem MTT with the different

252    values (Table 1). In the high latitudes, ecosystem MTT could increase up to 145 years if soil

253    C storage was calculated from NCSCD dataset (500 vs. 290 Pg C from HWSD, Fig. 3) due to

254    higher soil C storage, while the global average of soil MTT could increase up to 40.8 years

255    when NCSCD dataset was considered.

256

257 3.3 Effects of climate on ecosystem mean turnover time (MTT)

258 Ecosystem MTT significantly decreased with mean annual temperature (MAT) and mean

259 annual precipitation (MAP) as described by an exponential equation: $MTT = 57.06e^{-0.07MAT}$

260 ($R^2$=0.77, P<0.001) and $MTT = 103.07e^{-0.001MAP}$ ($R^2$=0.34, P<0.001, Fig 4). There was

261 no correlation between ecosystem MTT and aridity index (AI, Fig. 4c). The similar

262 relationships occurred between soil MTT and MAT/ MAP ($MTT_{soil} = 58.40e^{-0.08MAT}$,

263 $R^2$=0.68, P<0.001) and M$TT_{soil} = 109.98e^{-0.002MAP}$, $R^2$=0.48, P<0.001, Fig. 5). There was

264 the different temperature sensitivity of mean turnover time ($Q_{10}$) for ecosystem MTT

265 ($Q_{10}$=1.95) and soil MTT ($Q_{10}$=2.23) at the biome scale. When MAP was incorporated into a

266 multivariate regression function of ecosystem MTT with MAT, the relationships could not be

267 significantly improved. MAP improved the explanation of variance of soil MTT ($R^2$ from

268 0.68 to 0.76), although there was the significant covariance of MAP and MAT ($R^2$=0.60).

269 However, the relationship between MTT and AI was not clear due to the scale limit. When we

270 separated ecosystem MTT into two categories according to aridity index (i.e., AI >1 and AI<

271 1), the relationships between ecosystem MTT and MAT did not significantly change (Figs.

272 4e, h) compared with that with all data (Fig. 4b). The relationship of ecosystem MTT with

17

273   MAP significantly increased when AI > 1, but decreased when AI <1. However, the same

274   regression function of soil MTT with MAT largely improved the explanation of the variance

275   when AI>1 (Fig. 5e, $MTT = 58.67e^{-0.08MAT}$, $R^2$=0.76, P<0.001). The relationships between

276   soil MTT and MAP were both improved when AI>1 and AI<1 (Fig. 5e, h).

277

278   3.4 Temporal variations of ecosystem mean turnover time and C storage

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

280   the Climate Research Unit (CRU) datasets, ranging from -2.5 to 5.9 °C (Fig. 6c). When the

281   regression function between ecosystem MTT and MAT was used to estimate ecosystem MTT

282   in 1901 and 2011 (Fig. 4), the ecosystem MTT decreased by approximately 4 years on

283   average (Fig.6a). The largest change in ecosystem MTT occurred in the cold zones. In tundra,

284   ecosystem MTT decreased by more than 10 years due to the larger increase in temperature

285   (~2°C) than other regions. The average NPP increased by approximately 0.3±0.003 Kg C m$^{-2}$

286   yr$^{-1}$ over 110 years with most range of 0~0.6 Kg C m$^{-2}$ yr$^{-1}$ (Fig. 6b).

287       The changes in ecosystem MTT and NPP across 110 years would cause decrease or

288   increase in terrestrial C storage. Ecosystem C storage decreased by 159.3 ± 1.45 Pg C from

289   1901 to 2011 (ΔMTT × NPP) from the decrease in MTT, with the largest decrease in tundra

290     and boreal forest (more than 12 g C m$^{-2}$) and little decrease in tropical zones (Fig. 7a & e).

291     The interactive changes of both NPP and MTT caused a decrease of 129.4±1.31 Pg C

292     ($\Delta$MTT × $\Delta$NPP) with the similar spatial pattern (Fig. 7c). However, the increase in NPP

293     directly raised ecosystem C storage up to 1215.4 ± 11.0 Pg C from 1901 to 2011 with a range

294     of 30-150 g C m$^{-2}$ in most areas (MTT × $\Delta$NPP, Fig. 7b). The MTT-induced changes in

295     ecosystem C storage only accounted for about 13.5% of that driven by NPP due to the

296     different weights ($\Delta$MTT × NPP vs. MTT × $\Delta$NPP ). The spatial pattern of the NPP-driven

297     changes mostly represented the spatial pattern of the changes in ecosystem C storage (Fig.

298     7e).

299

300     **4   Discussion**

301     4.1 Global pattern of mean turnover time

302     In this study, we used the ratio of C storage to C flux to calculate the GPP-based, the NPP-

303     based and soil MTT and compared their differences. The global average of ecosystem MTT

304     was 25.0 years for GPP-based estimation and 50.8 years for NPP-based one, and soil MTT

305     was 35.5 years, which were within the global mean turnover times (26-60 years) estimated by

306     various experimental and modeling approaches (Randerson *et al*., 1999; Thompson and

307  Randerson, 1999). In our study, the mean GPP-based MTT was slightly longer than that from

308  23 years, which has been previously reported using the same method (Carvalhais *et al*.,

309  2014). The difference may result from two aspects. Firstly, ecosystem C storage in this study

310  was the sum of soil, vegetation, and litter C pools, whereas Carvalhais *et al*. (2014) only

311  considered soil and vegetation C pools. Secondly, the data source of global vegetation C

312  storage was different with our study from Gibbs (2006), while Carvalhais *et al*. (2014) from a

313  collection of estimates for pan-tropical regions and radar remote-sensing retrievals for

314  northern and temperate forests. The differences between GPP-based and NPP-based MTT

315  were determined by the ratio of GPP and NPP, which was largely influenced by the

316  assumptions of the MODIS NPP algorithm. The ratio of GPP-based and NPP-based MTT

317  (0.49) was smaller than that estimated by Thompson and Randerson (1999, 0.58, 15 year vs.

318  26 year, respectively), largely resulting from different model assumptions for GPP-based

319  (higher normalized storage response function for low turnover time) and NPP-based MTT

320  (for high turnover time) in Thompson and Randerson (1999). Our NPP-based MTTs for the

321  conterminous USA (37.2 years) and Australia (33.4 years) were shorter than the estimates by

322  the inverse models (46 to 78 years) (Barrett, 2002; Zhou and Luo, 2008; Zhou *et al*., 2012).

323  The NPP-based MTT was shorter than the estimated results from Xia *et al*. (2013) using the

324     CABLE model, although the order of ecosystem MTT across forest biomes was similar. This

325     is because that C turnover time using inverse analysis or CABLE model may be associated

326     with separating ecosystems into several plant and soil C pools with their distinct C turnover

327     time, whereas in our study we assumed an ecosystem as one pool.

328      The spatial patterns of ecosystem and soil MTTs were similar. The magnitude of the

329     difference between NPP-based ecosystem and soil MTTs was determined by the turnover

330     time of vegetation and litter, which was related to plant functional types (PFTs). For instance,

331     the difference between NPP-based and soil MTTs in Australia was smaller (33.4 and 29.8

332     years, respectively) compared with that in other regions, because one of the PFTs accounting

333     for a large areas of Australia was spare grass with short turnover time (3.5 years on average).

334     Additionally, different ecosystems with a specific PFT may have diverse turnover time due to

335     climatic effects. For example, boreal and tropical needleleaf evergreen forest have similar

336     ecosystem C storage (~34 vs. 40 kg C m$^{-2}$) and vegetation C storage (~3.5 kg C m$^{-2}$).

337     However, NPP-based and soil MTTs for boreal neadleaf evergreen forest were about 116

338     years and 98 years, respectively, whereas that for tropical one were about 12 years and 8

339     years. High temperature and humidity in tropical zones, which promote decomposition

340     processes, may largely contribute to the short turnover time compared to those in boreal zone

341    (Sanderman et al., 2003).

342    In our study, we only used soil C in the top 1 m to estimate ecosystem MTT, which would

343    be underestimated for the large amounts of C stored between 1 m and 3 m depth (Jobbagy

344    and Jackson, 2000). According to the SOC estimation of Jobbagy and Jackson (2000), the

345    MTT in the top 3 m could increase to 34.63 years for GPP-based, 70.68 years for NPP-based

346    and 55.38 years for soil. Therefore, the C storage in deep soil layers (>1m) should be

347    considered to estimate ecosystem MTT and the accurate estimate of the deep soil C storage,

348    which deserves to be further explored in the future.

349

350    4.2 The sensitivity of turnover time to climate

351    In our study, the estimated MTT was shortest in tropical zones and increased toward high-

352    latitude zones (Fig. 2), which were often affected by the spatial patterns of temperature and

353    moisture. Our results were consistent with previous studies based on SOC (Schimel *et al*.,

354    1994; Sanderman *et al*., 2003; Frank *et al*., 2012; Chen *et al*., 2013) and root C pools (Gill

355    and Jackson, 2000). Ecosystem MTT had negative exponential relationships with MAT (Fig

356    4), similar to those with soil MTT, due to temperature dependence of respiration rates (Lloyd

357    and Taylor, 1994; Wen *et al*., 2006). Our results showed that the temperature sensitivity of

358     ecosystem MTT was lower than that of soil C pool ($Q_{10}$: 1.95 vs. 2.23, Figs. 4 &5), which has

359     also been previously reported (Sanderman *et al*., 2003), because wood would decompose at

360     much lower rates than SOM (Zhou *et al*., 2012). Ecosystem MTT had no significant

361     differences between very humid zone (AI>1.0) and other zones (AI<1.0, Fig 4). However, the

362     better relationships between MTT and MAP occurred in very humid zone (AI>1.0) than other

363     zones, which was similar to soil pool, but soil MTT have the higher sensitivity to

364     precipitation than ecosystem MTT under AI>1. SOM decomposition often increases with

365     added moisture in aerobic soils (Trumbore, 1997; Bai *et al*., 2017), because the metabolic

366     loss of various C pools increases under warmer and wetter climates (Frank *et al*., 2012),

367     resulting in high sensitivity of MTT to MAP. Thus, the fitting regression combining MAT and

368     MAP clearly improved soil MTT ($R^2$=0.76, p<0.001). In arid or semi-humid regions, the

369     increase in C influx with MAP was more rapid than that in decomposition (Austin and Sala,

370     2002). In addition, water limitation could suppress the effective ecosystem-level response of

371     respiration to temperature (Reichstein et al., 2007). At an annual scale, temperature is still the

372     best predictor of MTT (Chen et al., 2013), which explained up to 77% of variation of MTT

373     (Fig 4). Other ecosystem properties (e.g., ecosystems types, soil nitrogen) could explain the

374     rest of the variation for the MTT estimation.

375

376 4.3 Effects of the changes in mean turnover time on ecosystem C storage

377 Terrestrial ecosystems play an important role in regulating C balance to combat global

378 change. Current studies suggest that the terrestrial biosphere is currently a net C sink (Lund *et*

379 *al*., 2010), but it is difficult to assess the sustainability of ecosystem C storage due to the

380 complexity of terrestrial ecosystem in response to global change (Luo, 2007; Zhou *et al*.,

381 2016). In this study, we quantified the changes in ecosystem C storage from 1901 to 2011 and

382 partitioned it into three parts from the changes in NPP, in ecosystem MTT, and in both NPP

383 and MTT (seeing equation 3). Our results showed that the decrease in MTT increased

384 ecosystem C loss over time due to the increase in C decomposition rates. However, increased

385 NPP enhanced ecosystem C uptake due to the decreased $CO_2$ inputs to atmosphere and

386 increased vegetation C stocks.

387    Current datasets have showed an increase in NPP (e.g., Hicke *et al*., 2002; Potter *et al*.,

388 2012), leading to increased terrestrial C uptake. Our results also showed that the NPP

389 increased by approximately 0.3 kg C $m^{-2}$ $yr^{-1}$ from 1901 to 2011 and the resultant terrestrial C

390 uptake was 1215.4 Pg C (with average year of 11.0 Pg C $yr^{-1}$). The ecosystem C storage in

391 conterminous USA increased 0.4 Pg C $yr^{-1}$, which was larger than that from inverse models

392    (Zhou and Luo, 2008; Zhou *et al*., 2012) and was comparable to C sink from atmospheric

393    inversion (0.30-0.58 Pg C yr$^{-1}$, Pacala *et al*., 2001). The shortened MTT caused C losses from

394    ecosystems from 1901 to 2011 (about 1.45 Pg C yr$^{-1}$), indicating that ecosystem C storage

395    decreased with climate warming (Fig. 7e). However, ecosystem C losses from the decrease in

396    MTT only accounted for 13.5% of that driven by changes in NPP, so terrestrial ecosystem

397    was still a net sink. The largest changes of MTT occurred in high latitude regions (Fig. 6a),

398    resulting in the largest loss of terrestrial C (Fig. 7e), where it is more vulnerable to climate

399    change (Zimov *et al*., 2006). However, the direct release of $CO_2$ in high latitude through

400    thawing would be another large source of decreasing ecosystem C storage under climate

401    warming (Grosse *et al*., 2011), which cannot be assessed by MTT or NPP. Interestingly, our

402    results suggested that the substantial changes in terrestrial C storage occurred in forest and

403    shrubland (50% of total) due to the relatively longer MTT, leading to the larger terrestrial C

404    uptake driven by NPP increase compared with others. In addition, the C uptake in cropland

405    and grassland could be underestimated probably due to the ignorance of the effects of land

406    management.

407

408    4.4 Limitation in estimating mean turnover time and its effects to climate

409     Estimated MTT in this study were based on C influxes (GPP or NPP) and C pools in plants,

410     litter and soil at the grid scale and can be used to quantify global, regional or biome-specific

411     MTT, which was very important to evaluate terrestrial C storage. However, the balance

412     method and data limitation could cause biases to some degree in estimated ecosystem MTT.

413     First, we assumed that ecosystem was at the steady state to estimate MTT. It is difficult to

414     define the steady state, especially for soil C dynamics (Luo and Weng, 2011). In reality,

415     maintaining a steady state is rare for a long time and ecosystems could be only close to reach

416     the steady state in the short time. For example, permafrost is thawing both gradually and

417     perhaps catastrophically (Schuur *et al*., 2008). Second, MTT was estimated on the basis of C

418     pool and flux measurements. The quality of the current datasets would determine the

419     accuracy of ecosystem MTT estimates. For example, the amendments of typological data

420     (derived from the global ISRIC-WISE datasets) and soil bulk density had largely improved

421     the estimates of the SOC storage from HWSD (1417 PgC) (Hiederer and Köchy, 2012). Soil

422     C storage calculated from NCSCD dataset would improve the ecosystem MTT in high

423     latitudes (Fig. 3), compared with that from HWSD datasets. The MTT in the top 1 m soil

424     increased to 30.3 years for GPP-based, 66.9 years for NPP-based and 45.7 years for soil when

425     SoilGrids was used compared with HWSD dataset (Hengl et al., 2014). However, it is

426    difficult to quantify the uncertainty in MTT caused by uncertainties of the current datasets

427    due to lack of quantitative uncertainty in these datasets. In addition, disturbance and forest

428    age structure will influence large-scale accumulation biomass, the partitioning of C into pools

429    with different turnover times and thereby the estimates of long-term C storage and turnover

430    time (Zaehle et al., 2006), which cannot be reflected in the current algorithms. Probably, the

431    inverse modeling can be a feasible method to evaluate the effect of the disturbance and forest

432    age on the estimates of C turnover time (Zhou *et al*., 2012).

433    Third, the uncertainties in the relationships of ecosystem MTT with MAT and MAP would

434    influence the estimates of ecosystem MTT, causing additional uncertainty in ecosystem C

435    storage. To simplify the calculation, we aggregated all datasets into a biome level, leading to

436    fixed parameters across biomes. However, the response magnitude in soil respiration to

437    warming varied over time and across sites (Rustad *et al*., 2001; Davidson and Janssens,

438    2006), resulting in multiple temperature response function. Changes in MTT for 1901 and

439    2011 were estimated using the exponential function between MTT and temperature, resulting

440    in underestimation or overestimation of MTT and the resultant changes on ecosystem C

441    storage. For example, when the relationship between soil MTT and temperature was used

442    ($MTT_{soil} = 58.40e^{-0.08MAT}$), the soil C storage due to MTT changes (NPP×ΔMTT) could

443     decrease 161.42 Pg C and that due to NPP changes ($\Delta$NPP$\times$MTT) could increase 1125.6 Pg

444     C, which had the similar spatial pattern to the ecosystem. In addition, we assumed that the

445     current-day spatial correlation between temperature and MTT was identical to temporal

446     correlation between these variables. Such assumptions cannot further reflect some processes

447     like acclimation of microbial respiration to warming or shifts in plant species over time.

448

449     4.5 Implication for land surface models

450     Our results provided insights as to how MTT and ecosystem C storage varied with climate

451     and over time. Our study could thus offer several suggestions for future experimental and

452     modeling research with the goals to improve estimates of ecosystem C storage. First, the

453     substantial changes in terrestrial C storage occurred in forest and shrubland covering large

454     area with the relatively long turnover time, because MTT dominated the uncertainty in the

455     estimates of terrestrial C storage. Therefore, further work should focus on the accurate

456     estimation of C turnover time with numerous observational data at regional or global scale

457     and the evaluation of uncertainty from datasets and the assumption (e.g., the steady-state).

458        Second, there are inconsistent responses of ecosystem C turnover time to climate variables

459     in the current global vegetation models (Friend *et al*., 2013). Our results showed that the

460    temperature sensitivity of ecosystem C turnover time was lower than that of soil C pool ($Q_{10}$:

461    1.95 vs. 2.23), while the relationship between ecosystem C turnover time and precipitation

462    under low aridity conditions (AI>1) was much stronger than those for all or AI<1 conditions.

463    Although global C models have currently considered moisture stress on vegetation, the

464    incorporation of moisture or precipitation stress into soil decomposition should be

465    strengthened, especially in high-latitude zones with greater warming and increased

466    precipitation.

467

468    **Data availability**

469    All of the original data (MOD 17, HWSD, NCSCD, vegetation C production of Gibbs *et al*.

470    (2006), litter dataset from Holland *et al*. (2005), climate variables from the Climate Research

471    Unit (CRU_TS 3.20)) used in this study are open and shared. We provided full citations for

472    data sources in MS and the download links in the supplemental information.

473

29

478

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640 **Table 1**. The density of ecosystem C storage (kg C m$^{-2}$), mean turnover time (MTT, years),

641 mean annual temperature (MAT), and precipitation (MAP) for the eight biomes. Ecosystem

642 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 |

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

644 Broadleaf forest.

645 **Figure Caption List**

646 **Figure 1**. Spatial pattern of soil C (a), biome C (b), litter C (c), and ecosystem C storage (d)

647 at the grid scale ($1°×1°$). Unit: kg C m$^{-2}$. Ecosystem C storage was calculated from plant

648 biomass, soil, and litter C pools.

649 **Figure 2**. Spatial pattern of mean turnover time (MTT, years) based on biome types and GPP

650 (a) or NPP (b) and soil C (c) using the C balance methods.

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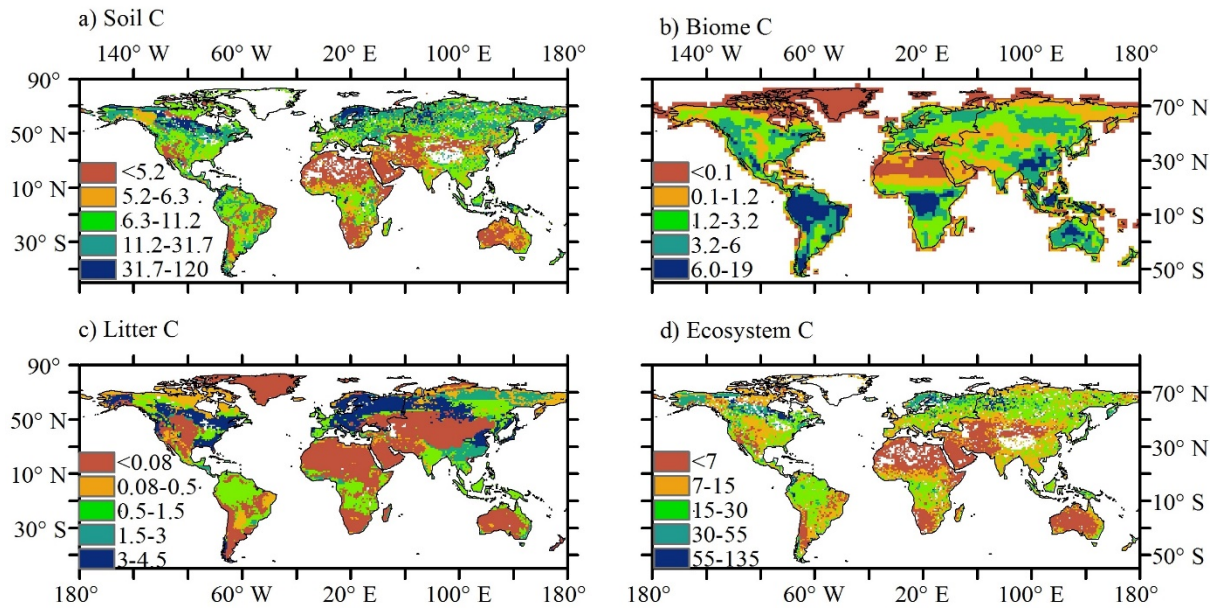
652 storage from HWSD data (a) and NCSCD data (b).

653 **Figure 4**. Relationships between ecosystem mean turnover time (MTT) and multi-annual

654 temperature (MAT, a) or precipitation (MAP, b) at different aridity indexes (AI, c). Each data

655 point stands for average values of each biome. Biomes were assigned into 62 types according

656 to land cover and three temperature zones.

657 **Figure 5**. Relationships between soil mean turnover time (MTT$_{soil}$) and multi-annual

658 temperature (MAT, a) or precipitation (MAP, b) at different aridity indexes (AI, c). Each data

659 point stands for average values of each biome. Biomes were assigned into 62 types according

660 to land cover and three temperature zones.

661    **Figure 6**. Changes in mean ecosystem mean turnover time (MTT, unit: year) driven by

662    temperature change (a), changes in NPP (unit: kg C m$^{-2}$yr$^{-1}$, b), and changes in temperature

663    ($^{\circ}$C, c) from 1901 to 2011. Changes in MTT from 1901 and 2011 were calculated by the

664    temperature-dependence function showing in Fig. 4. Changes in NPP from 1901 and 2011

665    were derived from models' average and MODIS.

666    **Figure 7**. Altered ecosystem carbon storage due to changes in mean turnover time (MTT,

667    NPP2011×ΔMTT, a), net primary production (NPP, MTT2011×ΔNPP, b), and interaction of

668    NPP and MTT (ΔMTT×ΔNPP, c). Panels d and e are total altered ecosystem C storage

669    changes due to changes in MTT, NPP, and MTT×NPP and their latitudinal gradients from

670    panels a-d, respectively. Unit: g C m$^{-2}$ yr$^{-1}$ ($\Delta C_{pool} = NPP_{2011} \times \Delta MTT + MTT_{2011} \times$

671    $\Delta NPP - \Delta NPP \times \Delta MTT$).

672

a) Soil C
- <5.2
- 5.2-6.3
- 6.3-11.2
- 11.2-31.7
- 31.7-120

b) Biome C
- <0.1
- 0.1-1.2
- 1.2-3.2
- 3.2-6
- 6.0-19

c) Litter C
- <0.08
- 0.08-0.5
- 0.5-1.5
- 1.5-3
- 3-4.5

d) Ecosystem C
- <7
- 7-15
- 15-30
- 30-55
- 55-135
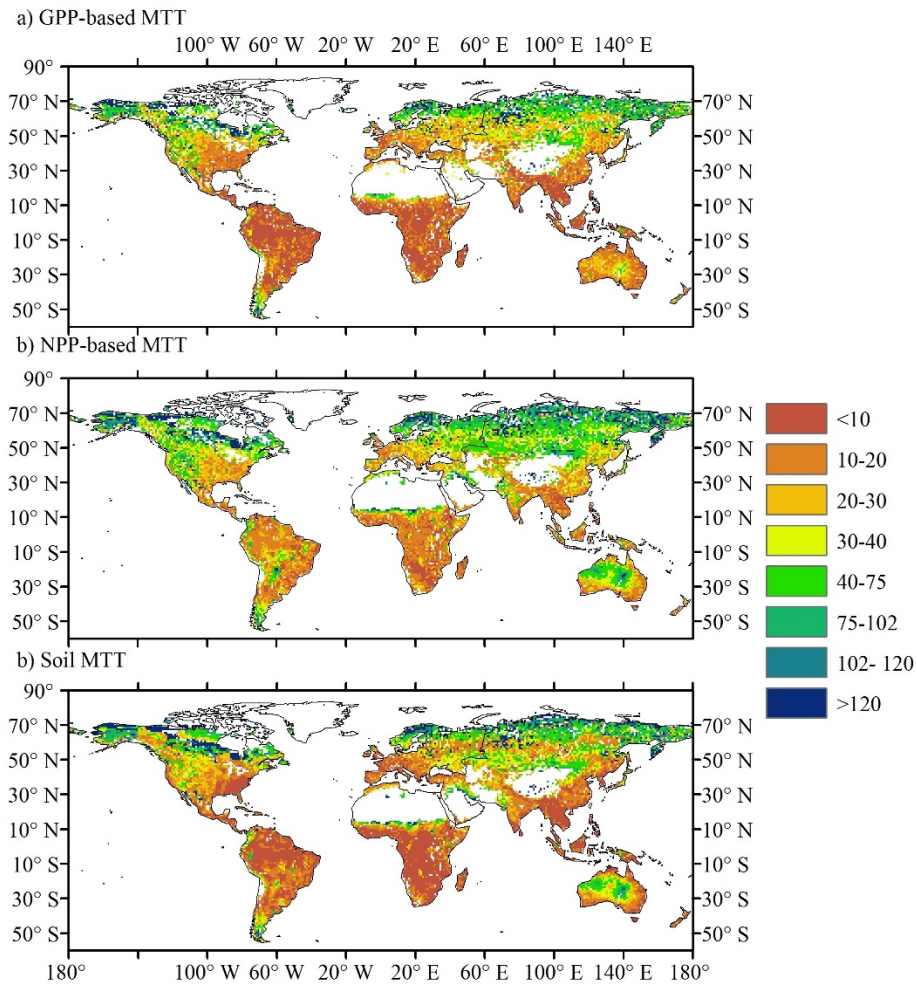
673

**Figure 1**. Spatial pattern of soil C (a), biome C (b), litter C (c), and ecosystem C storage

(d) at the grid scale ($1^\circ \times 1^\circ$). Unit: kg C m$^{-2}$. Ecosystem C storage was calculated from plant

biomass, soil, and litter C pools.

677

a) GPP-based MTT

b) NPP-based MTT

b) Soil MTT

Legend:
- <10
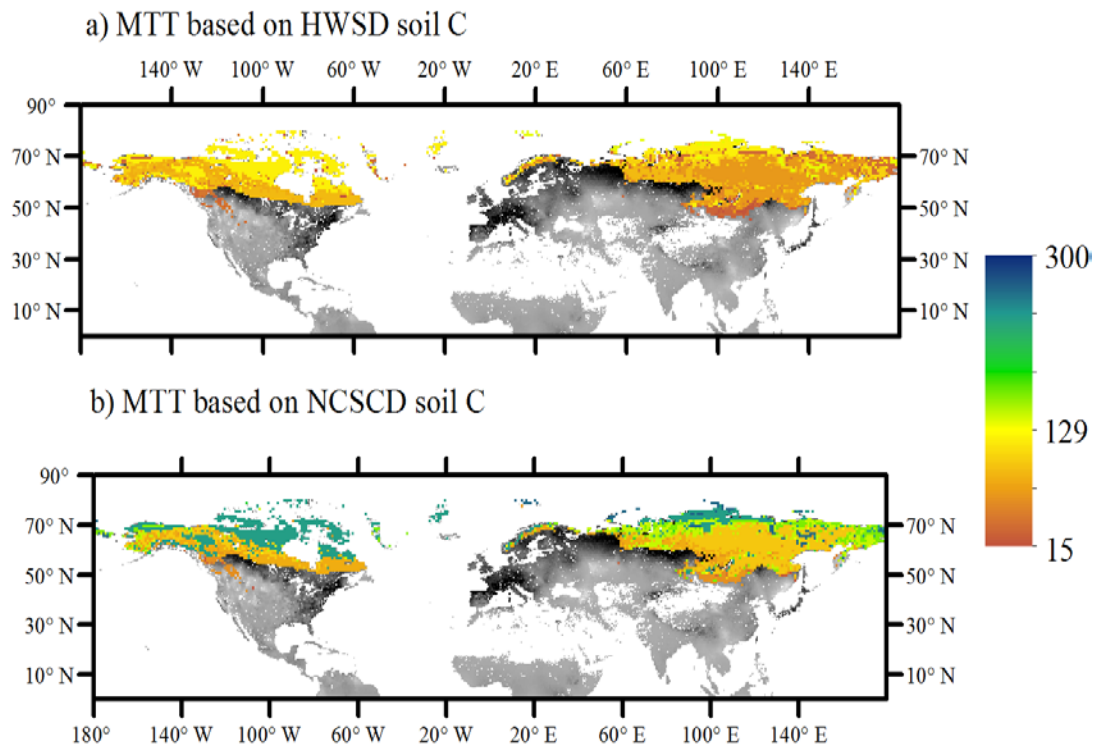- 10-20
- 20-30
- 30-40
- 40-75
- 75-102
- 102- 120
- >120

678

**Figure 2**. Spatial pattern of mean turnover time (MTT, years) based on biome types and

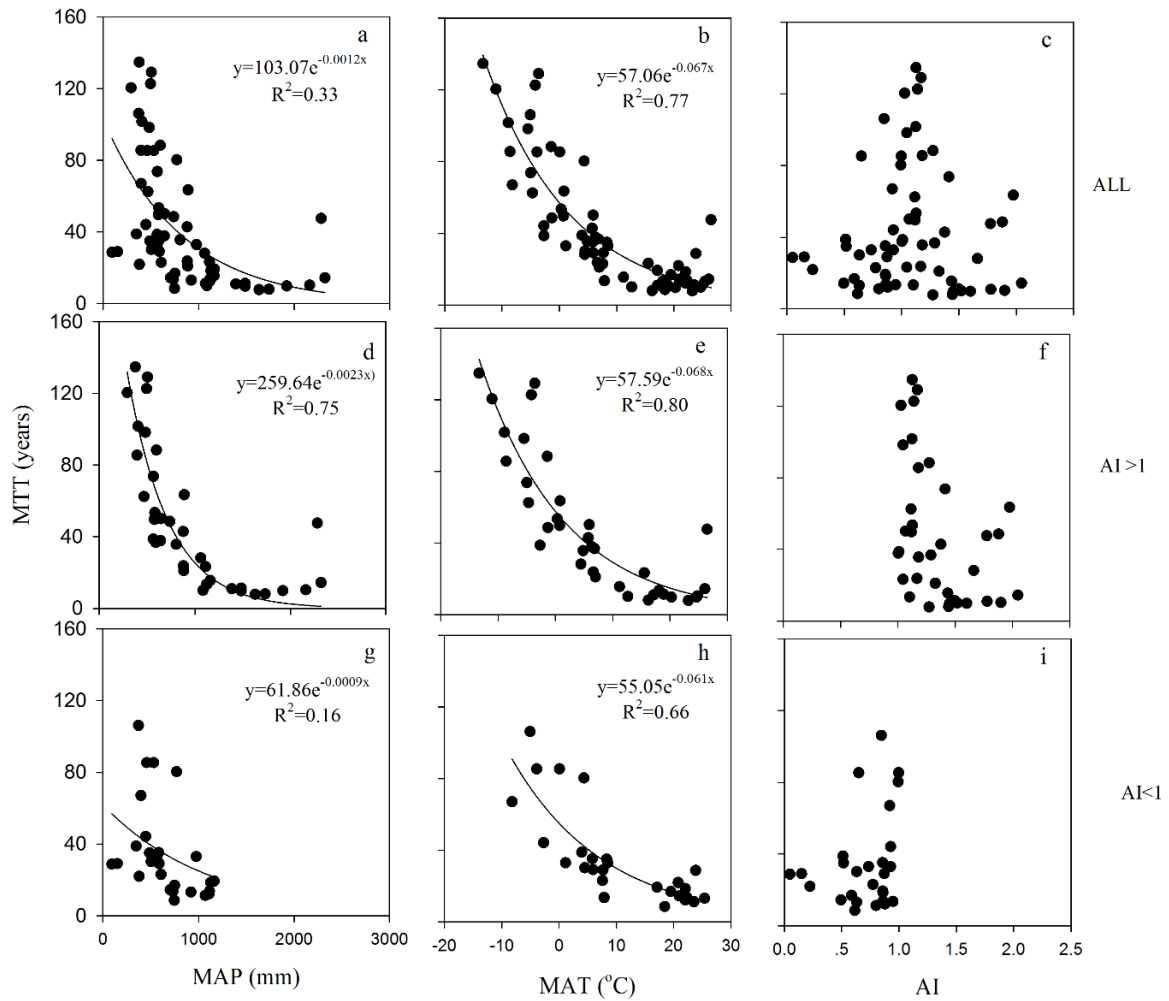GPP (a) or NPP (b) and soil C (c) using the C balance methods.

681

682

683



a) MTT based on HWSD soil C

b) MTT based on NCSCD soil C

684    **Figure 3**. Spatial pattern of mean turnover time (years) in high latitude based on soil C

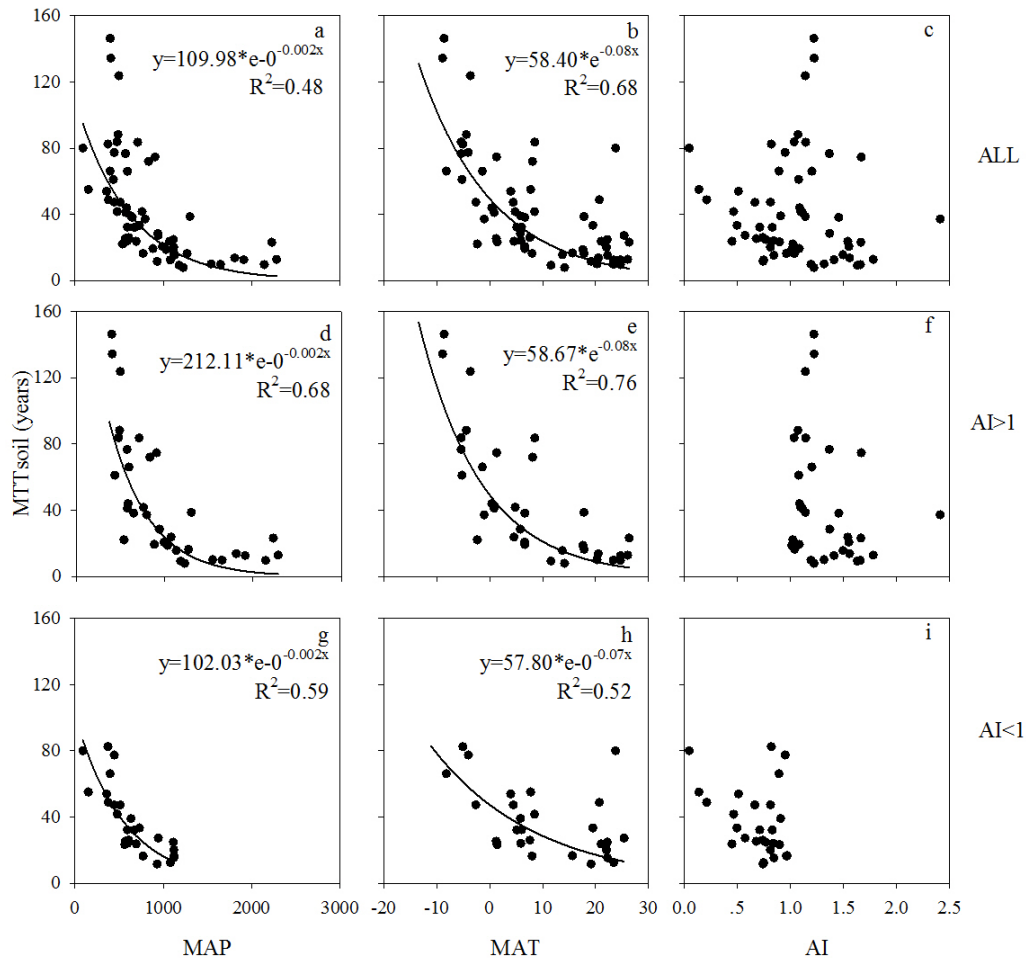685    storage from HWSD data (a) and NCSCD data (b).

686

**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.

The figure contains the following panel equations:

Panel a: $y = 109.98 * e^{-0.002x}$, $R^2 = 0.48$ (ALL)

Panel b: $y = 58.40 * e^{-0.08x}$, $R^2 = 0.68$ (ALL)

Panel d: $y = 212.11 * e^{-0.002x}$, $R^2 = 0.68$ (AI>1)

Panel e: $y = 58.67 * e^{-0.08x}$, $R^2 = 0.76$ (AI>1)

Panel g: $y = 102.03 * e^{-0.002x}$, $R^2 = 0.59$ (AI<1)

Panel h: $y = 57.80 * e^{-0.07x}$, $R^2 = 0.52$ (AI<1)

Y-axis: MTT$_{soil}$ (years); X-axes: MAP, MAT, AI

692

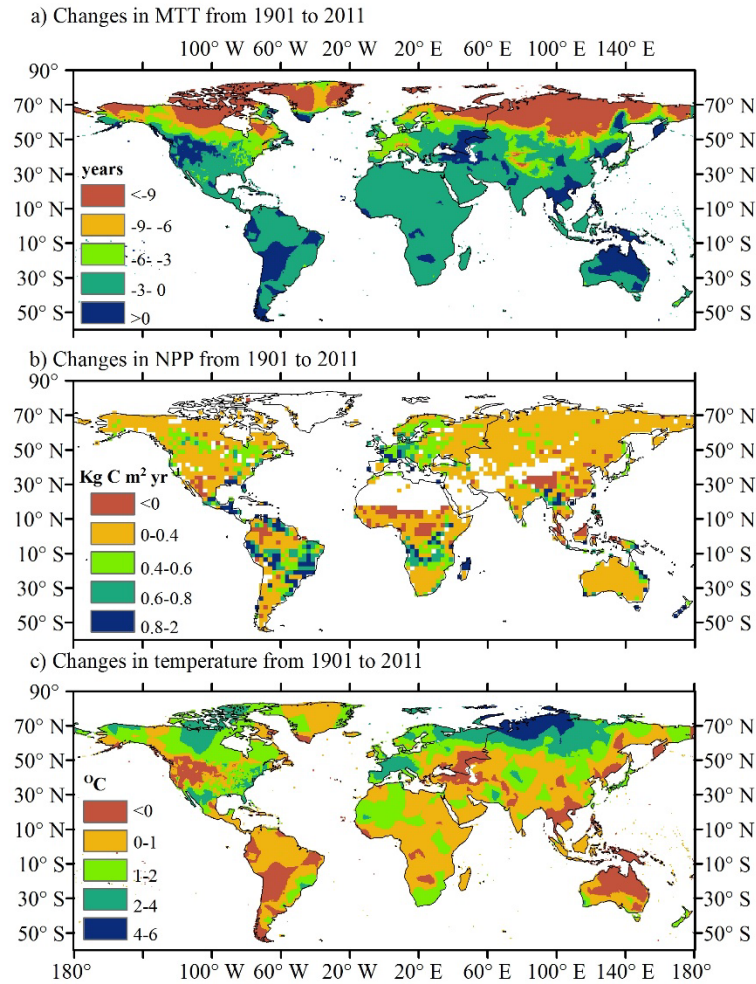**Figure 5**. Relationships between soil mean turnover time (MTT$_{soil}$) and multi-annual temperature (MAT, a) or precipitation (MAP, b) at different aridity indexes (AI, c). Each data point stands for average values of each biome. Biomes were assigned into 62 types according to land cover and three temperature zones.
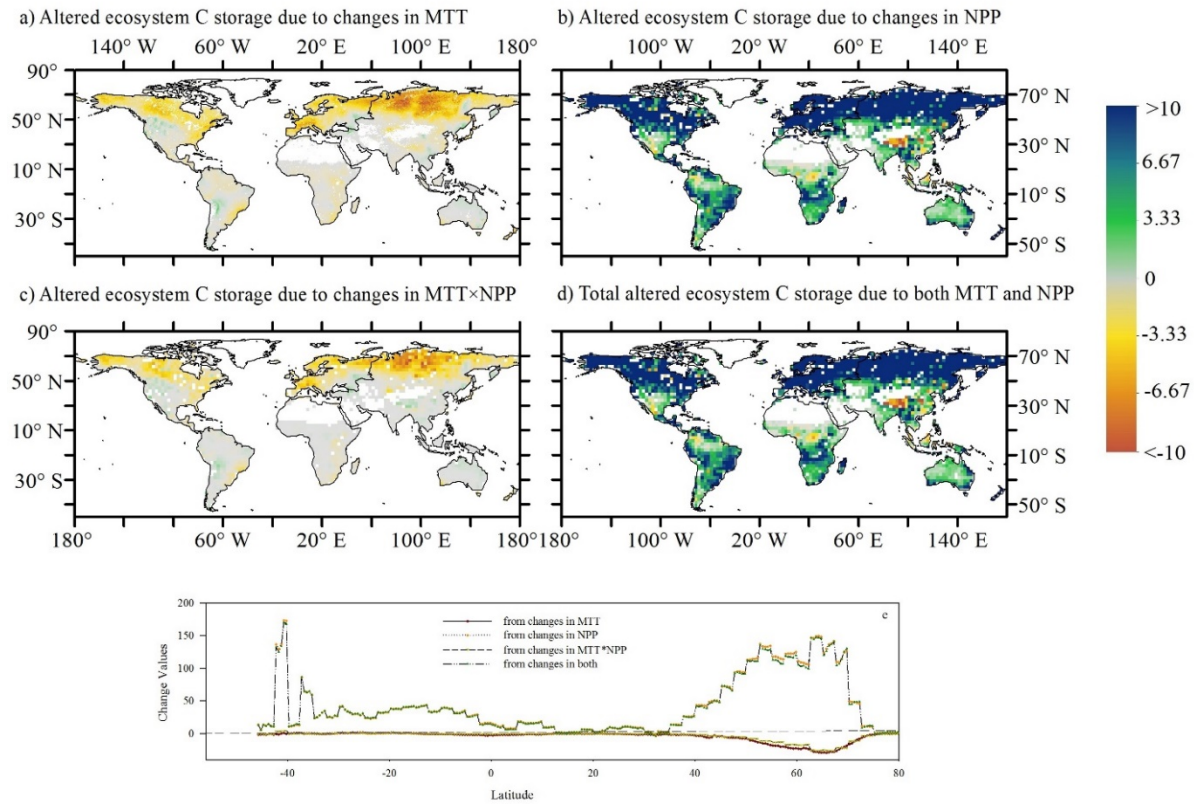
a) Changes in MTT from 1901 to 2011

b) Changes in NPP from 1901 to 2011

c) Changes in temperature from 1901 to 2011

697

**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

48

701  temperature-dependence function showing in Fig. 4. Changes in NPP in 1901 and 2011 were

702  derived from models' average and MODIS.

**Figure 7.** Altered ecosystem carbon storage due to changes in mean turnover time (MTT, $NPP2011 \times \Delta MTT$, a), net primary production (NPP, $MTT2011 \times \Delta NPP$, b), and interaction of NPP and MTT ($\Delta MTT \times \Delta NPP$, 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$^{-1}$ ($\Delta C_{pool} = NPP_{2011} \times \Delta MTT + MTT_{2011} \times \Delta NPP - \Delta NPP \times \Delta MTT$).