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### **Underestimated ecosystem carbon turnover time and sequestration under the steady state assumption: a perspective from longterm data assimilation**

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1 Underestimated ecosystem carbon turnover time and sequestration under the steady

2 state assumption: a perspective from long-term data assimilation

3 **Running head:** underestimated turnover time at equilibrium

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26 **Abstract**

27 It is critical to accurately estimate carbon (C) turnover time as it dominates the  
28 uncertainty in ecosystem C sinks and their response to future climate change. In the absence  
29 of direct observations of ecosystem C losses, C turnover times are commonly estimated under  
30 the steady-state assumption (SSA), which has been applied across a large range of temporal  
31 and spatial scales including many at which the validity of the assumption is likely to be  
32 violated. However the errors associated with improperly applying SSA to estimate C turnover  
33 time and its covariance with climate as well as ecosystem C sequestrations have yet to be  
34 fully quantified. Here we developed a novel model-data fusion (MDF) framework and  
35 systematically analyzed the SSA-induced biases using time-series data collected from 10  
36 permanent forest plots in the eastern China monsoon region. The results showed that (1) the  
37 SSA significantly underestimated mean turnover times (MTTs) by 29%, thereby leading to a  
38 4.83-fold underestimation of the net ecosystem productivity (NEP) in these forest ecosystems,  
39 a major C sink globally; (2) the SSA-induced bias in MTT and NEP correlates negatively  
40 with forest age, which provides a significant caveat for applying the SSA to young-aged  
41 ecosystems; and (3) the sensitivity of MTT to temperature and precipitation was 22% and 42%  
42 lower, respectively, under the SSA. Thus, under the expected climate change, spatiotemporal  
43 changes in MTT are likely to be underestimated, thereby resulting in large errors in the  
44 variability of predicted global NEP. With the development of observation technology and the  
45 accumulation of spatiotemporal data, we suggest estimating MTTs at the disequilibrium state  
46 via long-term data assimilation, thereby effectively reducing the uncertainty in ecosystem C  
47 sequestration estimations and providing a better understanding of regional or global C cycle  
48 dynamics and C-climate feedback.

## 49 **Introduction**

50 The terrestrial carbon (C) cycle is among the largest uncertainties affecting global C-  
51 climate feedback (Le Quéré *et al.*, 2018). Ecosystem C input (gross primary productivity,  
52 GPP) and C mean turnover time (MTT) are two key factors in determining the C  
53 sequestration capacity of terrestrial ecosystems (Xia *et al.*, 2013; Luo *et al.*, 2017). Terrestrial  
54 GPP has been well studied and exhibits a relatively strong convergence in global modelling  
55 studies (Anav *et al.*, 2013), whereas the C turnover time has become the dominant uncertainty  
56 in terrestrial ecosystem C sequestration and its response to climate change (Carvalho *et al.*,  
57 2014; Friend *et al.*, 2014; He *et al.*, 2016). Therefore, accurately quantifying the ecosystem  
58 MTT and its relationship with climate is crucial for understanding the present and future C  
59 budget dynamics in terrestrial ecosystems.

60 Ecosystem MTT refers to the average time required for atmospheric CO<sub>2</sub> to enter the  
61 ecosystem via plant photosynthesis and return to the atmosphere via C loss pathways, such as  
62 ecosystem respiration (RE) and fire (Barrett, 2002). As the current understanding of these C  
63 cycle processes is mainly based on first-order kinetics (Manzoni and Porporato, 2009), MTT  
64 is commonly defined as the ratio of the C pool to the flux (Bolin and Rodhe, 1973;  
65 Friedlingstein *et al.*, 2006; Koven *et al.*, 2015). Therefore, the flux used for MTT estimation  
66 (i.e., influx or efflux), the state of C pools, as well as the C allocation and turnover rates that  
67 control the C flow in various pools, are all key states and processes that collectively determine  
68 for the overall ecosystem turnover time (Sitch *et al.*, 2003; Trumbore *et al.*, 2006).

69 Currently, MTT estimations are mainly based on two assumptions, the steady-state  
70 assumption (SSA) and the non-steady-state assumption (NSSA), with each corresponding to  
71 specific ecological principles and applicable conditions. Without changes in external driving  
72 forces, such as disturbances and climate change, the internal processes of an ecosystem will  
73 gradually drive the ecosystem C cycle toward equilibrium (Luo and Weng, 2011), at which C

74 influx equals efflux, C pools are stabilized and the long-term net ecosystem C exchange  
75 becomes zero (i.e.,  $\overline{\Delta C} = 0$ ); therefore, the MTT under the SSA can be defined as  
76 “stock/influx” (Rodhe, 1978). When ecosystems are subject to natural (e.g., insect outbreaks  
77 and fire) and anthropogenic (e.g., land-use change) disturbances as well as global changes  
78 (e.g., increasing atmospheric CO<sub>2</sub>, climate warming, and nitrogen deposition), ecosystem C  
79 cycling processes become destabilized (Luo and Weng, 2011; Bellassen *et al.*, 2011).  
80 Therefore, C pools in ecosystems vary dynamically over time (i.e.,  $dC/dt \neq 0$ ), the C influx is  
81 not equal to the C efflux, and the MTT under the NSSA should be defined as “stock/efflux”  
82 (Schwartz, 1979).

83 An exact equilibrium is almost impossible to observe in reality; but when the relative  
84 difference between input and output is negligible, it is justified and valid to apply SSA (Odum,  
85 1969), usually occurring at large or coarse spatial scales where sufficient variation in the  
86 sink/source distribution could balance the gross influx and efflux, or occurring at long-time  
87 scales where the effects of transient changes in climate or atmospheric CO<sub>2</sub> could be ignored.  
88 Specifically, at the global or continental scale near steady state, the more readily obtained  
89 influx can be used to estimate MTT instead of the efflux (Carvalhais *et al.*, 2014; Yan *et al.*,  
90 2014). In addition, key process parameters, such as the allocation and turnover rates, can be  
91 optimized and then incorporated into an analytical expression under the SSA to quantify the  
92 spatial patterns of ecosystem MTT (e.g., Barrett, 2002; Xia *et al.*, 2013). Furthermore, the  
93 state of C pools in global models can be initialized via the spin-up process by iterating from  
94 hundred to thousand years in preindustrial period until equilibrium (Taylor *et al.*, 2012),  
95 which determines the C pool size used in the analysis of MTT (Todd-Brown *et al.*, 2013;  
96 Exbrayat *et al.*, 2014; Koven *et al.*, 2015).

97 In addition to these aforementioned applications, the SSA has also been widely invoked  
98 in MTT research over a considerable range of temporal and spatial scales (e.g., Zhou & Luo,

99 2008; Galbraith *et al.*, 2013; Thurner *et al.*, 2016; Wang *et al.*, 2018), over which non-steady  
100 behaviour may exist. This appears to be an imperative choice in the absence of direct  
101 measurement of C effluxes, such as heterotrophic respiration, or current or past-historical  
102 ecosystem states for constraining the dynamic ecosystem C cycle processes. Specifically, at  
103 the regional scale with considerable C sinks, (1) the MTTs are still obtained based on influx,  
104 which is much higher than efflux, e.g., in the forest ecosystems in eastern China (Wang *et al.*,  
105 2018) and the tropics (Galbraith *et al.*, 2013) that have been shown to be major C sinks  
106 globally (Piao *et al.*, 2009; Pan *et al.*, 2011; Yu *et al.*, 2014); (2) C turnover rates and  
107 allocation coefficients are still retrieved under the SSA but further used in a transient  
108 simulation of the regional MTT and net ecosystem productivity (NEP) (Zhou & Luo., 2008;  
109 Zhou *et al.*, 2010, 2013b); (3) As global C models have been developed to fine spatial scales,  
110 the SSA is also widely used for C pool state initialization at local scales with dynamic C  
111 sources or sinks (e.g., young-aged forests) (Law *et al.*, 2001; Morales *et al.*, 2005; Carvalhais  
112 *et al.*, 2008, 2010; Huang *et al.*, 2011). Previous studies have reported the uncertainty in C  
113 pool states and C cycle parameters induced by the SSA (e.g., Carvalhais *et al.*, 2008, 2010),  
114 which may further affect the validity of MTT estimation via the “stock/flux” approach.  
115 Therefore, a better understanding of the mismatch between the ideal SSA and realistic  
116 disequilibrium state in C turnover time estimation is needed and the effect of such  
117 inconsistencies on C sequestration should be determined.

118         With the development of observational technology and the accumulation of multiple and  
119 time-series C cycle datasets over the past decade, our understanding of terrestrial C dynamics  
120 has improved; accordingly, C effluxes can be better constrained to return to the definition of  
121 MTT at the realistic disequilibrium state (e.g., Bloom *et al.*, 2016). On this basis, researchers  
122 have attempted to develop the model-data fusion (MDF) method to estimate ecosystem MTT  
123 under the NSSA, which integrates the process-based model and observational data to estimate

124 these C cycle dynamics in better agreement with the actual disequilibrium state (Luo *et al.*,  
125 2003; Xu *et al.*, 2006; Zhang *et al.*, 2010; Zhou *et al.*, 2013b; Bloom *et al.*, 2016). Moreover,  
126 the uncertainty in allocation and turnover parameters as well as C pool states have largely  
127 been reduced based on the time-series observations under the NSSA, thereby significantly  
128 enhancing the model's ability to predict MTT and NEP (Safta *et al.*, 2015; Smallman *et al.*,  
129 2017).

130       Regardless, a detailed comparative analysis of ecosystem MTT estimations under the  
131 NSSA and SSA has not been conducted based on multi-source and long-term continuous  
132 observational data. In this study, we systematically examined differences in ecosystem C  
133 cycle states and processes estimated under the two assumptions as well as the underlying  
134 mechanisms within a robust analytical framework, using large amounts of long-term  
135 continuous observational soil, biology, and climate data for 10 typical forest ecosystems from  
136 the Chinese Ecosystem Research Network (CERN) that represent the East Asian monsoon  
137 region, a large C sink accounting for 8% of the global forest NEP (Yu *et al.*, 2014). Our  
138 analysis mainly focuses on the mismatch between the two assumptions with regard to (1) the  
139 magnitude and spatial pattern of the ecosystem MTT, (2) the relationship between the  
140 ecosystem MTT and climate, and (3) the ecosystem C sink in these forest ecosystems. These  
141 quantitative comparisons using the proposed framework could provide a reference for future  
142 MTT research in terms of SSA/NSSA method selection and facilitate an awareness of the  
143 corresponding uncertainty.

## 144 **Materials and Methods**

### 145 **2.1 Site description**

146       The eastern China monsoon region covers tropical, subtropical, warm temperate, and  
147 temperate climate zones from south to north, and subhumid and humid areas from north-west

148 to south-east. The large precipitation and temperature gradients support diverse forest  
149 ecosystems ranging from evergreen broad-leaved and coniferous forests to deciduous  
150 coniferous and broad-leaved forests. Here we selected 10 permanent plots with long-term  
151 observational data from CERN to cover the typical forest types with various ages in this  
152 region (Fig. 1; Table S1). All 10 sites are well protected and subject to minimal disturbance.

153

## 154 **2.2 Data**

155 The collected data are divided into four meteorological driving data, five stock-related  
156 constraint datasets of soil, foliage, root, wood, and leaf area index (LAI), and three flux-  
157 related constraint datasets of litterfall, net ecosystem exchange (NEE) and soil respiration (Rs).  
158 The time-series observations at most of the sites cover the period from 2005 to 2015, but  
159 those of SNF, which was incorporated into CERN later, are from 2010 to 2015 (Table S2).

### 160 2.2.1 Biometric data

161 At each site, the biomass of leaves, branches, stems, and roots were estimated from the  
162 measured diameters at breast height (DBHs) and tree heights using the allometric method.  
163 The biomass inventory was performed at least once every five years. To split fine and coarse  
164 root biomass, the ratio of the fine root biomass to the entire root biomass in typical Chinese  
165 forests was obtained from Zhang *et al.* (2001), and the coarse root biomass was then  
166 combined with the branch and stem biomasses to constitute the woody biomass. Estimates of  
167 leaf, fine root, and woody biomass were used to constrain the corresponding C pools in the  
168 inverse analysis.

169 The aboveground litterfall biomass was measured by 10 replicates of 100 cm × 100 cm  
170 baskets monthly during the growing season or once during the non-growing season. All  
171 collected litter was dried at 70 °C for 24 h and weighed. We used annual litterfall biomass



172 data for the inverse analysis to avoid the effect of wind on the measurement of litterfall  
173 biomass within an individual month.

174 The LAI at each site was measured optically with a LAI-2000 plant canopy analyser (LI-  
175 COR, Lincoln, NE, USA) at least quarterly every year and corrected by the foliage clumping  
176 index, which was set for plant functional type (PFT)-specific empirical values as reported in  
177 Zhu *et al.* (2012). The seasonal variation in the LAI combined with the leaf C mass per leaf  
178 area (LCMA) parameter constrained the dynamic trajectory of the leaf C pool in the MDF  
179 analysis.

### 180 2.2.2 Soil data

181 Soil C content was calculated from soil organic matter (SOM) measured by the  
182 potassium dichromate oxidation titrimetric method and soil bulk density measured by the  
183 cutting ring method in each field campaign at 10 forest sites. At least three samples were  
184 collected from each of five soil layers (0–10, 10–20, 20–40, 40–60, and 60–100 cm) once  
185 every five years. We calculated the soil organic C (SOC) as follows (Post *et al.*, 1985; Eqn. 1).

$$186 \quad SOC = \sum_{i=1}^n 0.58 \times H_i \times B_i \times O_i \times 100 \quad (1)$$

187 where *SOC* is soil organic C density (g C/m<sup>2</sup>) of all *n* layers, *H<sub>i</sub>* is soil thickness (cm), *B<sub>i</sub>* is  
188 soil bulk density (g/cm<sup>3</sup>), and *O<sub>i</sub>* is SOM content of the *i*<sub>th</sub> layer (%).

### 189 2.2.3 Flux data

190 NEE data were obtained from ChinaFLUX, covering CBF, QYF, ALF, and BNF. The  
191 data were aggregated to the daily time step from half-hourly CO<sub>2</sub> flux data measured by the  
192 eddy covariance technique and processed by quality control and gap filling (Li *et al.*, 2008).  
193 To reduce the impact of gap-filled data on parameter estimations, we only aggregated NEE

194 data for the days with at least 50% observed half-hourly fluxes, which were relatively evenly  
195 distributed in the daytime and nighttime.

196 Rs data were measured using static chamber-gas chromatography techniques at CBF,  
197 QYF, DHF, HSF, and BNF (Zheng, 2010). A total of 4–6 replicates were measured 2–3 times  
198 per month with sampling times between 9:00 am and 11:00 am. In this study, the monthly  
199 averaged heterotrophic respiration (Rh) was obtained according to the ratio of root respiration  
200 to Rs in the typical Chinese forest ecosystem to constrain the seasonal variation of C efflux  
201 from litter and soil in the inverse analysis (Chen *et al.*, 2008).

#### 202 2.2.4 Meteorological data

203 In situ observations of daily air temperature (T), photosynthetically active radiation  
204 (PAR), relative humidity (RH), and saturated vapour pressure difference (VPD) at the 10 sites  
205 from 2005 to 2015 were obtained from the CERN scientific and technological resources  
206 service system (<http://www.cern.org.cn/>) and processed by standardized quality control and  
207 gap filling (Li *et al.*, 2008; Liu *et al.*, 2017a).

### 208 **2.3 Model**

209 Data Assimilation Linked Ecosystem Carbon (DALEC) has been applied extensively in  
210 the MDF framework (Richardson *et al.*, 2010; Bloom *et al.*, 2016). It is a box model of C  
211 pools connected via fluxes running at a daily time step, and its main structure (i.e., C cycle, C  
212 allocation, and turnover process) is generally consistent with the state-of-the-art process-based  
213 models (Fig. 2). Here, we used two versions of DALEC, an evergreen forest-specific version  
214 (DALEC-E; Williams *et al.* 2005) with five pools (i.e., foliage, fine root, woody (including  
215 branch, stem, and coarse root), litter and SOM) and a deciduous forest-specific version  
216 (DALEC-D; Fox *et al.*, 2009) with an additional labile pool of stored C that supports leaf  
217 flushing.

218 The detailed C cycle of forest ecosystems can be characterized by several properties (Xia  
 219 *et al.*, 2013): (1) the C cycle is usually initiated with the canopy C influx GPP. Specifically,  
 220 GPP is estimated herein using a canopy photosynthesis model (Ji, 1995; Appendix S1), which  
 221 is a function of LAI, PAR, T, and RH. Note that the daily LAI is estimated as the ratio of the  
 222 simulated foliar C pool and optimized LCMA parameter. (2) GPP is consumed in a certain  
 223 fraction ( $f_{auto}$ ) as autotrophic respiration (Ra) and partitioned into various plant pools (i.e.,  
 224 foliar, labile, wood, and fine roots); then, the degraded C from biomass pools goes to two  
 225 dead organic matter pools with temperature-dependent losses (Rh). (3) C transfers are  
 226 dominated by the donor pools (e.g., the litter decomposing into soil). (4) C exiting from C  
 227 reservoirs is based on the first order differential equation. These properties of the forest C  
 228 cycle in DALEC can be mathematically described by a matrix model as Eqn. 2 and  
 229 determined as a function of key C cycle parameters (Table S3). All these parameters will be  
 230 optimized based on the stock- and flux-related observations.

$$231 \quad \frac{dC}{dt} = BI(t) - A\xi kC(t) \quad (2)$$

232 where  $C(t)$  is a vector of C pool sizes at time  $t$ ;  $B = (f_{fol} \ f_{roo} \ f_{woo} \ 0 \ 0)^T$  represents the  
 233 partitioning fractions from photosynthetically fixed C input to the foliage ( $f_{fol}$ ), root ( $f_{roo}$ ),  
 234 woody ( $f_{woo}$ ), litter, and soil pools;  $I(t)$  is the input flux of fixed C via plant photosynthesis;  
 235  $k = diag(\theta_{fol}, \ \theta_{roo}, \ \theta_{woo}, \ \theta_{min} + \theta_{lit}, \ \theta_{som})$ , a diagonal matrix of exit rates to quantify the  
 236 fraction of C left from the foliage ( $\theta_{fol}$ ), root ( $\theta_{roo}$ ), woody ( $\theta_{woo}$ ), soil ( $\theta_{som}$ ), litter ( $\theta_{lit}$ ) pool,  
 237 and the litter mineralization rate into soil ( $\theta_{min}$ ); and  $\xi = diag(1, \ 1, \ 1, \ f(T), \ f(T))$ , a  
 238 diagonal matrix of temperature scalar  $f(T)$  to quantify response of C decay rate to changes in  
 239 temperature. The response to soil moisture was not considered in DALEC given the overall  
 240 good moisture condition in these forest ecosystems (MAP=1160.18±413.79 mm).  $A$  is a  
 241 square matrix of transfer coefficients to quantify C movement among pools as follows:

242

$$A = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ -1 & -1 & 0 & 1 & 0 \\ 0 & 0 & -1 & -\frac{\theta_{min}}{\theta_{min} + \theta_{lit}} & 1 \end{pmatrix}$$

## 243 2.4 Estimation of ecosystem MTT and NEP based on the MDF framework

244 The analytical framework developed here systematically considered the C pool initial  
 245 state, cost function, observational and forcing data involved in the inverse analysis, and  
 246 formula for estimating MTT to diagnose the SSA-induced bias in contrast to the NSSA,  
 247 which affected parameter retrieval and the estimation of MTT and NEP (Fig. 3). Note that  
 248 models were the same in the NSSA and SSA setups. The temporal domains for model  
 249 simulation were from 2005 to 2015.

### 250 2.4.1 Parameter estimation under the SSA and NSSA

251 Under the NSSA, C pools are time-variant, i.e., C influx is not equal to the C efflux, thus  
 252 not restricted to  $NEP \sim 0$ ; the dynamic long-term observations of C stocks and fluxes were  
 253 used to constrain the DALEC model. As an important factor that may affect the estimated  
 254 MTT and NEP, the initial state of the C pools was determined by the initial observation of C  
 255 stocks or optimized (i.e., the labile pool, which cannot be directly observed) to avoid the  
 256 uncertainty arising from the spin-up process. Then, the turnover and allocation parameters  
 257 were inverted under the disequilibrium state (Eqn. 3) with dynamic environmental forcing.

$$258 \begin{cases} \frac{dC}{dt} \neq 0 \\ C_i(t+1) = C_i(t) + I_i(t) - k_i C_i(t), i = 1, 2 \dots n \\ C_i(t=0) = C_{i0} \end{cases} \quad (3)$$

259 where  $C_i$ ,  $I_i$ ,  $k_i$  represent the size, input and turnover rate of the  $i_{th}$  C reservoir, respectively;  
 260  $C_{i0}$  represent the initial state of the  $i_{th}$  C reservoir; and  $t$  represent the daily step. According to

261 the Bayesian theory, the posterior distributions of parameters are calculated by maximizing  
 262 the likelihood function (Eqn. 4).

$$263 \quad L_{NSSA} = \prod_{j=1}^m \prod_{i=1}^{n_j} \frac{1}{\sqrt{2\pi}\sigma_j} e^{-\left(x_{j,i} - \mu_{j,i}(P_{NSSA})\right)^2 / 2\sigma_j^2}, \quad m = 1, 2, \dots, 8 \quad (4)$$

264 where  $L_{NSSA}$  is the integrated likelihood function under the NSSA;  $m$  is the number of  
 265 multiple data types;  $n$  is the number of data points in the  $j$ th data type;  $x_{j,i}$  is the measured  
 266 value composed of eight dynamic C stock and flux observations;  $\mu_{j,i}(P_{NSSA})$  represents the  
 267 modeled fluxes and stocks based on parameters under the NSSA ( $P_{NSSA}$ ); and  $\sigma_j$  is the standard  
 268 deviation of each data point in the  $j$ th data type.

269 Under the SSA, C pools are stabilized such that an additional constraint of long-term  
 270 NEP  $\sim 0$  was used to constrain the initial state of C pools at steady state, in addition to the  
 271 observed C stock and flux constraints. As the meteorological forcing spans 2005 to 2015, we  
 272 averaged total ecosystem C pools ( $C_{TOT}$ ) over each 10-year segment to obtain  $\overline{C_{TOT}}$ , and  
 273 determined steady-state criterion by which changes in  $\overline{C_{TOT}}$  (Eqn. 6) between two  
 274 neighbouring segments are within a threshold of  $0.5 \text{ g C m}^{-2} \text{ yr}^{-1}$  (as one criterion in Thornton  
 275 and Rosenbloom, 2005 and Xia *et al.*, 2012).

$$276 \quad \Delta \overline{C_{TOT}} = \left| \overline{C_{TOT}(t+1)} - \overline{C_{TOT}(t)} \right| \leq 0.5 \quad (5)$$

277 where  $t$  represents the period for parameter optimization during 2005 to 2015.

278 The C turnover and allocation parameters were retrieved under the repeated 10 year  
 279 (2005–2015) cycle of meteorological forcing until the initial state of C pools were stationary  
 280 at the annual time scales (i.e., long term NEP  $\sim 0$ , Eqn. 5), and the likelihood function was  
 281 maximized compared to the observations (Eqn. 6).

$$282 \quad L_{SSA} = \prod_{j=1}^m \prod_{i=1}^{n_j} \frac{1}{\sqrt{2\pi}\sigma_j} e^{-\left(x_{j,i} - \mu_{j,i}(P_{SSA})\right)^2 / 2\sigma_j^2}, \quad m = 1, 2, \dots, 8 \quad (6)$$

283 where  $\mu_{j,i}(P_{SSA})$  represents the modelled values based on parameters under the SSA ( $P_{SSA}$ ),  
 284 and  $L_{SSA}$  is the integrated likelihood under the SSA and consists of five stock-related  
 285 observations, two efflux observations (litterfall and Rs), and the tolerance of long-term NEE  
 286 described in Eqn. 5.

287 Specifically, we applied the Metropolis simulated annealing algorithm, a variation of the  
 288 Markov Chain Monte Carlo (MCMC) technique, for parameter estimation (Zobitz *et al.*,  
 289 2011). Besides, ecological and dynamic constraints were imposed on the DALEC parameters  
 290 and pool dynamics (Appendix S2) which can significantly reduce uncertainty in model  
 291 parameters and simulations (Bloom and Williams, 2015).

#### 292 2.4.2 Estimation of ecosystem MTT under the SSA and NSSA

293 Here, we use the MTT\_(MDF scheme, i.e., SSA/NSSA)\_ (flux term used, i.e., Input (I)  
 294 /Output (O) ) to consistently define the C turnover times in different analyses. Under the SSA,  
 295 long-term NEP = 0; i.e., the C influx equalizes the efflux, such that the ecosystem MTT can  
 296 be defined as the ratio of retrieved total ecosystem C stocks to the ecosystem influx  
 297 (Sanderman *et al.*, 2003, Eqn. 7):

$$298 \quad MTT\_SSA\_I = \frac{\overline{C_{pool\_SSA}}}{I_{SSA} - \Delta C_{pool}} = \frac{\overline{C_{pool\_SSA}}}{I_{SSA}} \quad (7)$$

299 where  $MTT\_SSA\_I$  is the ecosystem MTT under the SSA as estimated from C influx,  $\overline{C_{pool\_SSA}}$   
 300 is the mean annual ecosystem C pool,  $\overline{I_{SSA}}$  is the mean annual ecosystem C input (GPP), and  
 301  $\overline{\Delta C_{pool}}$  is the change in the ecosystem C pool.

302 We have further derived an analytical expression for MTT\_<sub>SSA</sub>\_I (Eqn. 8):

$$303 \quad MTT\_SSA\_I = \frac{\sum_i^n \overline{C_{pool\_i\_SSA}}}{I_{SSA}} = \frac{\overline{I_{SSA}}}{I_{SSA}} \times \frac{\sum_i^n \overline{C_{pool\_i\_SSA}}}{\overline{I_{SSA}}} \quad (8)$$

$$= \left( \frac{f_{fol}}{\theta_{fol}} + \frac{f_{roo}}{\theta_{roo}} + \frac{f_{woo}}{\theta_{woo}} + \frac{f_{fol}+f_{roo}}{(\theta_{min}+\theta_{lit})\times\xi} + \frac{f_{woo}+(f_{fol}+f_{roo})\times\frac{\theta_{min}}{\theta_{min}+\theta_{lit}}}{\theta_{som}\times\xi} \right) \times (1 - f_{auto})$$

$$= (1 \ 1 \ \dots \ 1)(A\xi k)^{-1}B(1 - f_{auto})$$

where  $\overline{C_{pool_i_{SSA}}}$  and  $\overline{I_{i_{SSA}}}$  represent the mean annual size and influx of the  $i_{th}$  C pool, respectively, which are simulated based on the site-specific SSA-optimized parameters at each site.

This form is compatible with the inverse matrix composed of the optimized allocation, turnover, and transit parameters (Xia *et al.*, 2013; Luo *et al.*, 2017), which consider the ecosystem MTT to be aggregated from the sum of turnover times for pools in series and the influx-weighted turnover time of pools in parallel (Barrett, 2002). The inherent consistency is theoretically supported by Sierra *et al.* (2017), because both forms are based on the hypothesis that the size of the C pool is equivalent to the product of C input flux and C turnover time in the equilibrium state (Bolin and Rodhe, 1973).

Under the NSSA, each C pool is an instantaneous state variable; thus, the efflux-weighted turnover time of pools is also time-variable and cannot be parameterized. Therefore, constructing an inverse matrix explicitly composed of the turnover and allocation parameters to represent the MTT is difficult. In this case, the ratio of the total ecosystem C stock to the efflux simulated based on these optimized parameters under NSSA is used to estimate ecosystem MTT (Schwartz, 1979; Bloom *et al.*, 2016; Eqn. 9).

$$MTT_{NSSA\_O} = \frac{\overline{C_{pool_{NSSA}}}}{I_{NSSA} - \Delta C_{pool}} = \frac{\overline{C_{pool_{NSSA}}}}{O_{NSSA}} \quad (9)$$

$$= \frac{\sum_i^n \overline{C_{pool_i_{NSSA}}}}{O_{NSSA}} = \frac{\overline{O_{i_{NSSA}}}}{O_{NSSA}} \times \frac{\sum_i^n \overline{C_{pool_i_{NSSA}}}}{\overline{O_{i_{NSSA}}}}$$

$$= (1 \ 1 \ \dots \ 1)(\xi k)^{-1}w$$

325 where  $w = \left( \frac{\overline{O_{fol\_NSSA}}}{\overline{O_{NSSA}}}, \frac{\overline{O_{woo\_NSSA}}}{\overline{O_{NSSA}}}, \frac{\overline{O_{roo\_NSSA}}}{\overline{O_{NSSA}}}, \frac{\overline{O_{lit\_NSSA}}}{\overline{O_{NSSA}}}, \frac{\overline{O_{som\_NSSA}}}{\overline{O_{NSSA}}} \right)$ ;

326  $MTT\_NSSA\_O$  is the ecosystem MTT under the NSSA based on C output;  $\overline{C_{pool\_NSSA}}$  is the  
327 mean annual ecosystem C pool;  $\overline{I_{NSSA}}$  is the mean annual ecosystem C input (GPP);  $\overline{O_{NSSA}}$  is  
328 the mean annual ecosystem C output (RE);  $\overline{C_{pool\_i\_NSSA}}$  and  $\overline{O_{i\_NSSA}}$  represent the mean annual  
329 size and output of the  $i$ th C pool, respectively;  $w$  represents the output-dependent weight of C  
330 pools; and  $\overline{O_{fol\_NSSA}}$ ,  $\overline{O_{woo\_NSSA}}$ ,  $\overline{O_{roo\_NSSA}}$ ,  $\overline{O_{lit\_NSSA}}$ , and  $\overline{O_{som\_NSSA}}$  represent the mean annual  
331 output of the foliage, wood, root, litter and soil pools, respectively. All C stocks and fluxes  
332 were simulated based on the site-specific NSSA-optimized parameters at each site. Because  
333 the C reservoirs, fluxes, and turnover times are instantaneous values, we used the average of  
334 the fluxes and reservoirs for multiple years to reflect the average turnover time during a  
335 specific period (i.e., 2005-2015). Note that with few natural and anthropogenic disturbances at  
336 these well-protected CERN sites (Zhou *et al.*, 2006; Zhang *et al.*, 2010), the total ecosystem  
337 output was approximately equivalent to the RE.

### 338 2.4.3 Estimation of ecosystem NEP based on the SSA- and NSSA-inverted parameters

339 The optimized parameter values under the NSSA and SSA along with the initial  
340 observations of corresponding C pool sizes were used in forward modeling driven by the  
341 dynamic environmental variables from 2005 to 2015 (Zhou *et al.*, 2008). NEP was further  
342 derived from the difference between the ecosystem C influx and RE to examine the effects of  
343 retrieved parameters on C sequestration under different hypotheses.

## 344 2.5 Estimation of ecosystem MTT based on observation

345 To test the robustness of  $MTT\_SSA\_I$  based on SSA-inversion at the 10 sites, the MTT  
346 under the SSA based on observed influx ( $MTT\_OBS\_I$ ) was calculated from the ratio of mean  
347 annual total ecosystem stock measurements in CERN and the mean annual GPP observed



348 from moderate resolution imaging spectroradiometer (MODIS) (Carvalhais *et al.*, 2014).  
349 MODIS products of GPP (MOD17A2H, 500m) at each site were downloaded from the  
350 University of Oklahoma Data Center (<http://www.comf.ou.edu/visualization/manual/>) and  
351 then accumulated to the annual time step from the 8-day observational data. Because the  
352 annual MODIS GPP values are consistent with the tower-based GPP at the flux sites (Fig. S1,  
353  $R^2 = 0.90$ ,  $p < 0.01$ , mean absolute error (MAE) = 37.39 g C m<sup>-2</sup> yr<sup>-1</sup>), it is reasonable to use  
354 this high-resolution product as a reliable observation at the site scale.

## 355 **Results**

### 356 **3.1 Key parameters retrieved under the SSA and NSSA**

357 Under the NSSA, the ratio of Ra to GPP ( $f_{auto}$ ) varied from 0.3 to 0.7, with a mean  
358 value of 0.53, showing a trend of first decreasing and then increasing with decreasing  
359 latitude (Figs. 4a and S2). The proportion of NPP allocated to wood ( $f_{woo}$ ) ranged from 0.5  
360 to 0.9, with a mean value of 0.67, showing an increasing trend with decreasing latitude (Figs.  
361 4d and S2). The MTTs (i.e., the inverse of the turnover rate) of wood, soil, foliage, fine root,  
362 and litter at the 10 sites were 48.54, 86.55, 3.12, 2.40, and 1.13 years, respectively.  
363 Specifically, the turnover rate of wood and soil ( $\theta_{woo}$  and  $\theta_{som}$ ), the two largest C pools in  
364 living vegetation and dead organic matter, respectively, showed obvious increasing trends  
365 with decreasing latitude (Figs. 4g, 4i, and S2). The temperature sensitivity of soil  
366 decomposition ( $Rh_{temp}$ ) exhibited a spatial pattern of tropical forest > temperate forest >  
367 subtropical forest (Figs. 4k, and S2). However, compared to the key C-cycle parameters  
368 under the NSSA, the allocation to faster-turnover C pools under the SSA was mostly  
369 overestimated ( $f_{auto}, f_{fol}$ ), but to slow-turnover pools ( $f_{woo}$ ) was underestimated; turnover  
370 rate of major pools ( $\theta_{woo}$  and  $\theta_{som}$ ) were overestimated; furthermore, the sensitivity to

371 climate ( $Rh_{temp}$ ) was underestimated; and these parameters lacked obvious spatial patterns  
372 (Figs. 4a, 4c, 4d, 4g, 4i, and 4k).

373 We compared the modelled and observed datasets to validate the inverted parameters  
374 based on multi-source data. Under the NSSA, the simulated and observed vegetation and soil  
375 C stocks and C fluxes agreed well, with the scatter points falling along the 1:1 line (Fig. 5).  
376 Specifically, the determination coefficients ( $R^2$ ) for C stocks varied between 0.94 and 0.99,  
377 and the root-mean-square errors (RMSEs) were small relative to their magnitudes (Fig. 5a-e).  
378 In contrast,  $R^2$  for C fluxes (NEE and  $R_s$ ) were slightly lower (0.45–0.50), but the RMSEs  
379 were only 1.37 and 0.67 g C m<sup>-2</sup> d<sup>-1</sup>, respectively (Fig. 5 g, h). Under the SSA, the model  
380 performance regarding the C stocks was comparable with that under the NSSA (Fig. 5a-e),  
381 but due to the overestimation of C turnover rates (Fig. 4e-j), simulated C effluxes, such as  
382 litterfall and  $R_s$ , were markedly overestimated, which in turn overestimated NEE (Fig. 5f-h).

### 383 **3.2 Magnitude of MTT and its relationship with forest age under the SSA and NSSA**

384 At the 10 sites, the MDF-based ecosystem MTT under NSSA (MTT\_NSSA\_O) and SSA  
385 (MTT\_SSA\_I) and the observation-based ecosystem MTT under SSA (MTT\_OBS\_I) ranged  
386 from 9.64 to 38.23, 7.29 to 33.59, and 8.73 to 36.31 years, with averages of 24.44, 17.27, and  
387 17.20 years, respectively. As MTT\_SSA\_I and MTT\_OBS\_I were nearly identical (Fig. 6b,  
388 MAE = 0.25,  $R^2 = 0.86$ ,  $p < 0.001$ ), MTT\_SSA\_I was selected to represent the estimated MTT  
389 under SSA in the ensuing analyses.

390 The ecosystem MTT\_SSA\_I was significantly lower (with an average of 29%) than the  
391 MTT\_NSSA\_O (Fig. 6a,  $p < 0.05$ ). Because wood and soil are the two largest C pools in  
392 forest ecosystems, the differences in their turnover rates estimated under the SSA and NSSA  
393 and the relative contributions to the difference between the whole-ecosystem MTT\_SSA\_I and  
394 MTT\_NSSA\_O ( $\Delta$ MTT) deserved further analysis. Both the  $\theta_{woo}$  and  $\theta_{som}$  were

395 significantly overestimated under the SSA (Figs. 4g, 4i) with the magnitude of the  
396 overestimation for  $\theta_{wo0}$  being greater than that for  $\theta_{som}$  (1.24E-04 vs 5.02E-05), which  
397 largely accounted for the ecosystem  $\Delta$ MTT. Meanwhile, less C was allocated to slow-  
398 turnover structural C pools under the SSA (Fig. 4d,  $f_{wo0\_SSA} = 0.46$  vs  $f_{wo0\_NSSA} = 0.68$ ), thus  
399 leading to underestimations of the vegetation MTT and ecosystem MTT.

400 The ecosystem  $\Delta$ MTT varied among different ecosystems (Fig. 6a), and these  
401 differences should be closely associated with how far the ecosystems deviate from the  
402 equilibrium state, as most likely reflected by the age-related growth. Thus, forest age was  
403 used as a proxy of the gap between the actual and equilibrium state. We found that the forest  
404 age accounted for more than 50% of the variation in ecosystem  $\Delta$ MTT with a significantly  
405 negative correlation (Fig. 7a,  $p < 0.005$ ). Further analysis revealed that rather than the  
406 overestimation of  $\theta_{som}$ , the overestimation of  $\theta_{wo0}$  under the SSA ( $\Delta\theta_{wo0}$ ), which exhibited a  
407 significant power function relationship with forest age, dominated the age-dependent  $\Delta$ MTT  
408 in the entire ecosystem (Figs. 7b, S3).

### 409 **3.3 Latitudinal pattern of MTT and its covariance with climate under the SSA and** 410 **NSSA**

411 The ecosystem MTT\_NSSA\_O and MTT\_SSA\_I exhibited similar latitudinal patterns,  
412 both of which decreased with decreasing latitude (Fig. 8a), showing a pattern of temperate  
413 MTT > subtropical MTT > tropical MTT (Fig. 6a). ALF appears to be an outlier, mainly due  
414 to its high elevation (2488 m) and special vertical zonality. We further analysed the  
415 relationship between MTT and climate, which is recognized as an important factor regulating  
416 the latitudinal MTT gradient (Carvalho *et al.*, 2014). Both the ecosystem MTT\_SSA\_I and  
417 MTT\_NSSA\_O were negatively correlated with temperature and precipitation (Figs. 8b, 8c),  
418 but the sensitivity of the MTT\_SSA\_I to these two climatic variables was significantly lower

419 than that of the MTT\_NSSA\_O, which decreased from 1.02 yr/°C to 0.80 yr/°C (by 22%) for  
420 temperature and from 1.34 yr/100 mm to 0.78 yr/100 mm (by 42%) for precipitation.

### 421 **3.4 Ecosystem C sequestration based on the SSA- and NSSA-inverted parameters**

422 Under the dynamic environmental conditions, all 10 forests were net C sinks based on  
423 both the SSA- and NSSA-inverted parameters (Fig. 9). However, with respect to actual eddy  
424 covariance observations, the NEP was obviously underestimated with the SSA-inverted  
425 parameters, whereas the NEP based on NSSA parameters was highly consistent (Fig. 5g); for  
426 example, the mean annual NSSA-estimated and observed NEP were 347.4 and 306.6 g C m<sup>-2</sup>  
427 yr<sup>-1</sup> at CBF, respectively, and 465.9 and 469.3 g C m<sup>-2</sup> yr<sup>-1</sup> at QYF. Overall, the mean annual  
428 NEP for 10 typical forest ecosystems in eastern China monsoon region reached 325.2 g C m<sup>-2</sup>  
429 yr<sup>-1</sup> based on NSSA-inverted parameters, which was 4.83 times that estimated with SSA-  
430 inverted parameters (67.3 g C m<sup>-2</sup> yr<sup>-1</sup>). Furthermore, the SSA-induced bias in NEP was  
431 significantly greater ( $p < 0.05$ ) in young and middle-aged forests (7.3-fold) than that in mature  
432 forests (3.8-fold). The underestimation of NEP in SSA analysis was largely due to the  
433 overestimation of RE, which is closely associated with the overestimation of C turnover rates  
434 and allocations to fast-turnover pools (Fig. 4); whereas GPP was comparable to that under the  
435 NSSA (Fig. S4).

## 436 **Discussion**

### 437 **4.1 Robustness of MTT estimations under SSA and NSSA**

438 The robustness of MTT\_SSA\_I estimations in the 10 ecosystems has been assessed with  
439 respect to MTT\_OBS\_I, which is generally recognized as a benchmark in current research  
440 (e.g., Thurner *et al.*, 2017). Although eddy covariance measurements for MTT\_OBS\_I  
441 estimation are lacking for some of the sites, the MOD17A2H product performed as a suitable  
442 alternative for GPP observations because its spatial resolution is finer than the footprint of the

443 flux towers (Mi *et al.*, 2006; Zhao *et al.*, 2005). Furthermore, we found the magnitude and  
444 spatial pattern of ecosystem MTT\_SSA\_I in eastern China monsoon forests were consistent  
445 with various MTT\_SSA estimations by observation or inversion approach in regional or global  
446 forest ecosystems (Table S4). A negative correlation of MTT\_SSA\_I with both temperature  
447 and precipitation was observed in this study, which was supported by research on  
448 MTT\_SSA\_I based on forest inventory and remote sensing observations (Gill and Jackson,  
449 2000; Sanderman *et al.*, 2003; Carvalhais *et al.*, 2014). The high consistency and robustness  
450 of MTT\_SSA calculated by various methods indicated that the deviation in MTT\_SSA  
451 identified in this study has broad implications for various SSA applications in C cycle  
452 research.

453 Due to the complexity of ecosystem C emission processes and the scarcity of ecosystem  
454 efflux data, it remains challenging to validate the inverted MTT\_NSSA\_O of whole-  
455 ecosystem with respect to observation-based estimates at disequilibrium state. However, the  
456 magnitude of the key process parameters regulating the ecosystem MTT under the NSSA as  
457 inferred in this study was broadly consistent with a number of empirical studies on C  
458 allocations, vegetation turnover rates and mortality, and soil decomposition rates (Table S5).  
459 The turnover times of fine roots measured from  $\delta^{13}\text{C}$  signals tend to be systematically  
460 overestimated due to sampling biases, with the finest and most ephemeral roots being missed  
461 (Strand *et al.*, 2008). Regarding the pattern of these key processes,  $f_{\text{auto}}$  first decreased and  
462 then increased as temperature increased at the turning point of approximately 11°C, which  
463 was highly congruent with the synthetic analysis based on the global forest database and  
464 could be ascribed to the asymmetric response of RE and GPP to rising temperature (Piao *et al.*,  
465 2010). The decrease in  $f_{\text{woo}}$  with increasing latitude and decreasing temperature was supported  
466 by the inventory-based synthesis in Chinese forests (Li *et al.*, 2009), and this pattern may be  
467 explained by the adaptive strategies of forest trees to temperature (Reich *et al.*, 2014) as well

468 as the age-structure-related strategy (Zhou *et al.*, 2013b), which tends to allocate less C to the  
469 structural pool in old forests mainly distributed in cold, high-latitude regions in China (Zhang  
470 *et al.*, 2014).  $\theta_{woo}$  and  $\theta_{som}$  both increased with rising temperature, which agrees well with  
471 the variation in the plant mortality rate based on forest inventory (Mantgem *et al.*, 2009; Zhou  
472 *et al.*, 2013a) and the variation in soil C decomposition based on Rs observations from the  
473 chamber or isotope method (Karhu *et al.*, 2010; Frank *et al.*, 2012; Chen *et al.*, 2013). In  
474 addition,  $Rh_{temp}$  was higher in tropical and temperate forests than subtropical forests, which is  
475 consistent with the regional variation in temperature sensitivity in Chinese forests based on  
476 field sampling and incubation experiments (Liu *et al.*, 2017b; Zhou *et al.*, 2009).

477 Overall, the robustness of estimations under the NSSA compared to the empirical  
478 research indicates that the C cycle dynamics estimated by NSSA method match the realistic  
479 observations well. Thus, the SSA-induced bias in MTT estimation and the underlying  
480 mechanism can be reliably quantified in contrast to our estimations under NSSA.

#### 481 **4.2 Identification of the uncertainty in MTT under SSA**

482 Under the background of global environmental changes, extensively distributed  
483 disturbances drive the ecosystems far from a steady state at local scales (Luo and Weng,  
484 2011), which makes the spatially-specific research a great challenge. Although the spatial  
485 aggregation of regional/global may approximately estimate the MTT under the SSA (Odum,  
486 1969), identifying the explanatory mechanism is difficult because the aggregation also merges  
487 some spatially heterogeneous influencing factors, such as temperature and terrain, that  
488 nonlinearly impact the MTT. In addition, previous studies have challenged the inherent  
489 concept behind SSA for the ecosystem C cycle (Lugo & Brown, 1986; Cannell & Thornley,  
490 2003), e.g., whether SSA-applicable old-growth forests are quasi-neutral or large C sinks  
491 (Zhou *et al.*, 2006; Luysaert *et al.*, 2008). Moreover, some uncertainties from the SSA have  
492 been revealed in C cycle studies; e.g., model initialization until equilibrium systematically

493 overestimated the C pools (Pietsch & Hasenauer, 2006), exhibiting a 6-fold range among  
494 various global C models (Exbrayat *et al.*, 2014). This further led to compensatory biases in  
495 NEP simulation, whereas relaxing the SSA in initialization made a 92% decrease in NEP  
496 errors (Carvalhais *et al.*, 2008, 2010). Besides, key turnover parameters determined under the  
497 SSA were overestimated, e.g., the decay rate of recalcitrant pools (Wutzler & Reichstein,  
498 2007); this further resulted in underestimation of NEP in transient simulation, which may be  
499 up to 30% even when C sinks only account for 10% of the C input in disequilibrium  
500 ecosystems (Zhou *et al.*, 2013b). It is noteworthy that these biases in pool initialization and  
501 parameter inversion will propagate into the MTT estimation via the “pool/flux” method and  
502 need to be determined.

503 Our study provides a new MDF framework to trace the uncertainty in turnover time  
504 induced by traditional SSA through direct comparison with the realistic disequilibrium state  
505 rather than conducting sensitivity experiments as reported in Carvalhais *et al.* (2008) or Zhou  
506 *et al.* (2014). Additionally, we collectively consider the factors resulting in the mismatch  
507 between MTT\_SSA\_I and MTT\_NSSA\_O, i.e., the pool initialization, the turnover and  
508 allocation parameter inversions as well as the formulas for estimating MTT used under two  
509 assumptions (Fig. 3). Via this framework, a significant underestimation in MTT\_SSA\_I was  
510 observed in these sites, which may be partly explained by the overestimated turnover rates and  
511 underestimated allocation to structural pools under SSA (Fig. 4). Moreover, in ecosystems  
512 with substantial sinks where GPP is much higher than RE, the input-based MTT\_SSA\_I  
513 should be smaller than the output-based MTT\_NSSA\_O, which might be more evident in  
514 younger forests due to the intrinsic relationship between age and forest growth (Zaehle *et al.*,  
515 2006; Goulden *et al.*, 2011).

516 To further distinguish the SSA-induced biases arising from the parameterization or the  
517 MTT estimation, we contrasted MTT\_NSSA\_O vs MTT\_SSA\_O ( $R^2 = 0.76$ , RMSE = 9.01 yr)

518 and MTT\_NSSA\_I vs MTT\_SSA\_I ( $R^2 = 0.74$ , RMSE = 4.41 yr) to obtain the biases that only  
519 stem from the improper use of SSA in parameterization. We found that these biases were  
520 much higher than those induced by only using SSA in MTT estimation, i.e., MTT\_NSSA\_I vs  
521 MTT\_NSSA\_O, or MTT\_SSA\_I vs MTT\_SSA\_O (Table S6). This indicated that the effect  
522 of the improper SSA on parameterization was deeper than that on MTT estimation, which  
523 provides a significant caveat for SSA applied especially in model optimization (e.g., Barret *et*  
524 *al.*, 2002; Zhou & Luo, 2008; Zhou *et al.*, 2010, 2013b). In the future, with the accumulation  
525 of spatiotemporal observations (Le Toan *et al.*, 2011), we suggest evaluating the dynamic  
526 disequilibrium state of C cycle (e.g., Bloom *et al.*, 2016), and further quantifying and  
527 reducing the SSA-induced uncertainty at large scales, especially with non-steady-state  
528 behavior, using this proposed framework.

#### 529 **4.3 Implications of SSA-induced uncertainty in MTT for C cycle research**

530 As a key factor determining the ecosystem C sequestration capacity, the uncertainty of  
531 MTT tends to dominate the uncertainty in terrestrial ecosystem C sequestration (Friend *et al.*,  
532 2014; He *et al.*, 2016). Thus, identifying the relative contribution of this highly uncertain  
533 ecosystem trait to C sequestration has become a hot topic in C cycle research (Todd-Brown *et*  
534 *al.*, 2013; Carvalhais *et al.*, 2014; Yan *et al.*, 2017). We employed a systematic framework  
535 and quantified that the deviation in MTT when improperly invoking SSA directly results in a  
536 pronounced underestimation of ecosystem NEP (4.83-fold) in this large C uptake region. The  
537 substantial underestimation of NEP found is supported by Yu *et al.* (2014), who revealed that  
538 state-of-the-art process-based models under the SSA tended to underestimate NEP by five- to  
539 seven-fold relative to eddy covariance observations in eastern Asia monsoon subtropical  
540 forests. Moreover, process-based models significantly underestimated NEP compared to other  
541 approaches, e.g., biomass and soil inventory, and atmospheric inversion (Piao *et al.*, 2009).  
542 This is mainly because the models consistently assume that the ecosystem has approached an



543 equilibrium state, which obviously neglects age-structure-related effects and underestimates  
544 the turnover times at regional and global scales (Carvalhais *et al.*, 2014; Yan *et al.*, 2014;  
545 Thurner *et al.*, 2017).

546 Here, we firstly reveal that the deviation in ecosystem MTT induced by SSA has a  
547 clearly decreasing relationship with increasing forest age. Furthermore, the biases in  
548 vegetation allocation and turnover, rather than those in soil turnover, dominate the magnitude  
549 of the deviation in MTT and its dependency on forest age. This finding is most likely due to  
550 the significantly stronger relationship between vegetation C turnover and stand age, whereas  
551 soil C turnover is mostly affected by climatic factors (Wang *et al.*, 2018). In addition, the  
552 vegetation C partition scheme varies with stand age (Zhou *et al.*, 2013b). The decisive role of  
553 whole-vegetation turnover time in determining the uncertainty in ecosystem C storage  
554 capacity has been supported by recent modelling and experimental research (Friend *et al.*,  
555 2014; Medlyn *et al.*, 2015; Xue *et al.*, 2017). Therefore, our results further highlight the need  
556 to focus on the deviation in vegetation C turnover time under the SSA to avoid considerable  
557 bias in ecosystem MTT and thus the C sequestration estimation.

558 The East Asian monsoon forest ecosystems represent one of the highest C uptake regions  
559 worldwide, including mid- and high-latitude European and North American forests.  
560 Particularly, the young age structure of forest stands in this region has been identified as a  
561 major driver of the large NEP (Yu *et al.*, 2014). Therefore, our result offers a significant  
562 caveat for applying SSA in regions with a large portion of young ecosystems. We expect that  
563 improved representations of forest age-driven growth and mortality into calibrated process-  
564 based models will help reduce the aforementioned biases for the C balance of ecosystems  
565 regionally and globally. Additionally, our finding on the age-dependent deviation of MTT  
566 could also offer an opportunity to correct the MTT\_OBS\_I at regional or global scales (e.g.,

567 Thurner *et al.*, 2016) with spatially-explicit forest age information, thereby providing a better  
568 benchmark to inform or parameterize C cycle models.

569 In addition to the uncertainty in the magnitude of C storage capacity, previous studies  
570 have revealed that the major uncertainty in the response of ecosystem C storage to climate  
571 arises from the uncertainty in the response of MTT to climate, which is 30% higher than that  
572 caused by NPP (Friend *et al.*, 2014). However, to our knowledge, this is the first attempt to  
573 quantify the relationship between climate and ecosystem MTT in the disequilibrium state and  
574 to discuss the differences with that at the equilibrium state. Theoretically, an ecosystem at  
575 equilibrium is stable for a long time under the local climate (Luo and Weng, 2011); thus, a  
576 relatively strong correlation can be expected between the ecosystem MTT and climate.  
577 However, it is inappropriate to invoke the ideal SSA in ecosystems at dynamic disequilibrium,  
578 with the MTTs underestimated to a greater extent in young and middle-aged forests (by more  
579 than 50%) than mature forests (less than 20%). This age-induced inconsistency in MTT  
580 underestimations disturbs the actual spatial pattern of MTT and its covariance with climate,  
581 thereby leading to a decreased sensitivity of MTT to climate under the SSA. In contrast, the  
582 MTT\_NSSA estimation based on long-term observational data in this study implicitly  
583 incorporated the age-structure-related effect on C cycle dynamics, thus providing a proper  
584 perspective on the actual correlation between MTT and climate. Currently, the contributions  
585 of climate-driven changes in C turnover times to C storage are usually underestimated in  
586 modelling studies (Hararuk *et al.*, 2015; Koven *et al.*, 2015, 2017). Therefore, the substantial  
587 underestimation we revealed in sensitivities of MTT to temperature and precipitation induced  
588 by the SSA calls for more attention in future C-climate feedback research. Under global  
589 warming and changes in precipitation regimes (IPCC, 2013), the underestimated response of  
590 MTT to climate will apparently underestimate the spatial and temporal changes in MTT,  
591 thereby underestimating the change in predicted global NEP. Here the exchange of space for

592 time to interpret the sensitivity of MTT to climate could cause some degree of bias, as such  
593 inference cannot include certain processes like acclimation of microbial respiration to  
594 warming or shifts in plant species over time (e.g., Koven *et al.*, 2017; Yan *et al.*, 2017).  
595 Nonetheless, the present-day spatial correlation between climate and MTT approximated the  
596 temporal correlation between these variables (Fig. S5) and well supported this inference.

#### 597 **4.4 Advantages and challenges of C cycle MDF based on long-term data**

598 Carbon turnover times and C cycle dynamics are always model-dependent because of the  
599 difficulty obtaining them from observations alone under the NSSA (Sierra *et al.*, 2017).  
600 However, even the state-of-the-art models fail to accurately capture the observed C  
601 allocations and turnover processes, resulting in high uncertainties in C dynamic simulations  
602 (De Kauwe *et al.*, 2014; Negrón-Juárez *et al.*, 2015). Therefore, applying MDF technology to  
603 constrain these C states and processes becomes important for accurately estimating MTT and  
604 C sequestration in the disequilibrium state (Bloom *et al.*, 2016).

605 The uncertainties in the current ecosystem MTT and C sequestration estimates mainly  
606 result from the lack of initial state of the C pools and inaccurate model parameters (Bellassen  
607 *et al.*, 2011; Wang *et al.*, 2011), because C cycle modelling typically relies on pre-arranged  
608 parameters retrieved from literature, prescribed PFT or spin-up processes (Exbrayat *et al.*,  
609 2014; Zhou *et al.*, 2013b). In this study, the long-term and multi-source observations  
610 combined with a series of experimental constraints directly provided the initial values of the  
611 corresponding C pools and better constrained the NSSA parameters and dynamic C pool  
612 trajectories (Smallman *et al.*, 2017; Bloom and Williams, 2015), thus substantially reducing  
613 the uncertainties arising from the SSA and limited data. Furthermore, insights into the  
614 underlying mechanisms that regulate the ecosystem C cycle can be provided based on the key  
615 process parameters, which are difficult to obtain from observations without SSA. For example,

616 we might explore how the C allocation and turnover in live and dead C respond to climate,  
617 thereby regulating the response of the whole-ecosystem MTT to climate (Fig. S6).

618 The uncertainty from the model structure and observational data also induce errors in the  
619 estimations of ecosystem MTT and C sequestration (Ahlström *et al.*, 2012). However, as this  
620 study aimed to compare the differences in MTTs estimated under different hypotheses with  
621 the same model and data, these two factors would not undermine the main conclusions. When  
622 applied at the regional scale, some external disturbances such as fire and land-use change (Erb,  
623 2016); vegetation mortality dynamics affected by drought, insect pests, and frost (Thurner *et*  
624 *al.*, 2016); as well as the dynamic scheme of C allocation limited by resources availability  
625 (Xia *et al.* 2015) should be added to the model. Although the model without moisture effect  
626 did not significantly affect the results in these forests (Table S7), the explicit representation of  
627 moisture effect may improve the model simulation when applied at large scales. Besides,  
628 more underground process observations should be added in future research to better constrain  
629 the corresponding parameters, e.g.,  $\theta_{min}$ , reflecting the decomposition of litter into soil.

630 In this study, we provided insights into the large biases associated with the improper  
631 application of the SSA, causing considerable underestimation in the magnitudes of MTT and  
632 its sensitivities to climate, and spatiotemporal variations in ecosystem C sequestration. Our  
633 findings on the age-dependent uncertainty in MTT provide significant implications for the  
634 implementation of mitigation policies for regional to global ecosystems with substantial  
635 young plantations. Moreover, the MDF framework we developed has the potential to facilitate  
636 future model intercomparisons, benchmarking and optimization at large scales, as well as to  
637 effectively quantify and then reduce the uncertainty in ecosystem C sequestration by  
638 estimating MTT in the disequilibrium state with long-term and multi-source observations.

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## 890 **Figure captions**

- 891 Figure 1. Map showing the distribution of 10 forest ecosystems in the Chinese Ecosystem Research  
892 Network (CERN). BNF: Xishuangbanna tropical seasonal rainforest, HSF: Heshan subtropical  
893 evergreen broad-leaved forest, DHF: Dinghu Mountain subtropical evergreen coniferous and  
894 broad-leaved mixed forest, ALF: Ailao subtropical evergreen broad-leaved forest, QYF:  
895 Qianyanzhou subtropical evergreen artificial coniferous mixed forest, HTF: Huitong subtropical  
896 evergreen broad-leaved forest, SNF: Shennongjia subtropical evergreen deciduous broad-leaved  
897 mixed forest, MXF: Maoxian warm temperate deciduous coniferous mixed forest, BJF: Beijing  
898 warm temperate deciduous broad-leaved mixed forest, CBF: Changbai Mountain temperate  
899 deciduous coniferous and broad-leaved mixed forest.
- 900 Figure 2. Structures of the Data Assimilation Linked Ecosystem Carbon (DALEC)-evergreen model  
901 (grey) and the DALEC-deciduous model (grey and black). Dotted arrows show the inputs into the  
902 photosynthesis model.
- 903 Figure 3. Flow chart of the model data fusion framework under the steady state assumption (SSA) and  
904 non-steady state assumption (NSSA).
- 905 Figure 4. Optimized key parameters involved in the allocation and turnover processes under the non-  
906 steady state assumption (NSSA) and steady state assumption (SSA) at 10 sites along a decreasing  
907 latitudinal gradient. The black and grey boxes denote NSSA and SSA, respectively.

908 Figure 5. Comparisons between the observed and modelled values at all sites under the non-steady  
909 state (NSSA: black dots) and steady state (SSA: red dots) assumptions

910 Figure 6. Magnitude of ecosystem C turnover times under the equilibrium and disequilibrium  
911 hypotheses. The black, light-grey, and dark grey boxes denote the inversion-based MTT under  
912 non-steady state (MTT\_NSSA\_O), inversion-based MTT under steady state (MTT\_SSA\_I), and  
913 observation-based MTT under steady state (MTT\_OBS\_I), respectively.

914 Figure 7. Relationships between forest age and differences of the entire-ecosystem MTT ( $\Delta$ MTT) as  
915 well as wood turnover rates ( $\Delta\theta_{\text{wood}}$ ) estimated under the steady state assumption (SSA) and non-  
916 steady state assumption (NSSA) hypotheses.

917 Figure 8. Associations of mean carbon turnover times with temperature and precipitation under the  
918 steady state assumption (SSA, grey triangles) and non-steady state assumption (NSSA, black  
919 dots).

920 Figure 9. Comparison of net ecosystem productivity (NEP) estimated with the parameters inverted  
921 under the steady state assumption (SSA) and non-steady state assumption (NSSA) in 10 forest  
922 ecosystems of different ages