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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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23 **Keywords:** steady state, non-steady state, turnover time, climate sensitivity, carbon
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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 (Carvalhais *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 CO₂ 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 CO₂, 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 CO₂ 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/m²) of all *n* layers, *H_i* is soil thickness (cm), *B_i* is
188 soil bulk density (g/cm³), and *O_i* is SOM content of the *i*_{th} 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 CO₂ 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 (θ_{fol}), root (θ_{roo}), woody (θ_{woo}), soil (θ_{som}), litter (θ_{lit}) pool,
 237 and the litter mineralization rate into soil (θ_{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 σ_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 ~ 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 $\overline{\Delta C_{TOT}}$ (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).

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

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 ~ 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__{SSA}_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⁻² yr⁻¹), 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 (θ_{woo} and θ_{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 (θ_{woo} and θ_{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⁻² d⁻¹, 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 (Δ MTT) deserved further analysis. Both the θ_{woo} and θ_{som} were

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

400 The ecosystem Δ 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 Δ MTT with a significantly
405 negative correlation (Fig. 7a, $p < 0.005$). Further analysis revealed that rather than the
406 overestimation of θ_{som} , the overestimation of θ_{woo} under the SSA ($\Delta\theta_{woo}$), which exhibited a
407 significant power function relationship with forest age, dominated the age-dependent Δ 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⁻²
427 yr⁻¹ at CBF, respectively, and 465.9 and 469.3 g C m⁻² yr⁻¹ at QYF. Overall, the mean annual
428 NEP for 10 typical forest ecosystems in eastern China monsoon region reached 325.2 g C m⁻²
429 yr⁻¹ based on NSSA-inverted parameters, which was 4.83 times that estimated with SSA-
430 inverted parameters (67.3 g C m⁻² yr⁻¹). 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_{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_{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). θ_{wood} and θ_{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., θ_{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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645

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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 (Δ 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