

1   **Implications of the Steady-state Assumption for the Global Vegetation**  
2   **Carbon Turnover**

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17   **Key Points:**

- 18   ● We estimate vegetation carbon turnover times globally in a non-steady state from 1992 to  
19   2016.
- 20   ● Using the assumption of steady-state for vegetation biomass turnover can cause  
21   substantial biases locally.
- 22   ● The validity of steady-state assumption increases with spatial scales.

23

24 **Abstract**

25 Vegetation turnover time ( $\tau$ ) is a central ecosystem property to quantify the global vegetation  
 26 carbon dynamics. However, our understanding of vegetation dynamics is hampered by the lack  
 27 of long-term observations of the changes in vegetation biomass. Here we challenge the steady  
 28 state assumption of  $\tau$  by using annual changes in vegetation biomass that derived from remote-  
 29 sensing observations. We evaluate the changes in magnitude, spatial patterns, and uncertainties  
 30 in vegetation carbon turnover times from 1992 to 2016. We found that the forest ecosystem is  
 31 close to a steady state at global scale, contrasting with the larger differences between  $\tau$  under  
 32 steady state and  $\tau$  under non-steady state at the grid cell level. The observation that terrestrial  
 33 ecosystems are not in a steady state locally is deemed crucial when studying vegetation dynamics  
 34 and the potential response of biomass to disturbance and climatic changes.

35 **Plain Language Summary**

36 Previous studies relied on the assumption that vegetation carbon turnover does not change with  
 37 time. However, this assumption can be substantially violated under the influence of disturbances  
 38 such as climate change and land use. We compared the difference of carbon turnover estimations  
 39 under different assumptions by using a global observations of vegetation biomass.

40

41 **1 Introduction**

42 One of the largest uncertainties in Earth system models is in quantifying how the carbon  
 43 uptake by terrestrial ecosystems will respond to changes in climate (Friedlingstein et al. 2006;  
 44 Friend et al., 2014). As an emergent ecosystem property that partially determines carbon  
 45 sequestration capacity, the vegetation biomass turnover times ( $\tau$ ) have been used as a diagnostic  
 46 metric to quantify the feedback between the carbon cycle and climate (Carvalhais et al., 2014;  
 47 Thurner et al., 2016). However, there is a large uncertainty in the simulations of vegetation  
 48 carbon stock as well as  $\tau$  across earth system models, indicating different representations of the  
 49 response of vegetation to future climate change (Friend et al. 2014). Furthermore, our current  
 50 understanding of  $\tau$  and the dynamic of vegetation is limited due to the lack of long-term  
 51 observations of changes in vegetation. As a result, the estimation of  $\tau$  has relied so far on the  
 52 assumption that the vegetation carbon in an ecosystem will eventually reach a steady state  
 53 (steady state assumption, hereafter SSA) at which the net change of vegetation biomass becomes  
 54 zero ( $\Delta C_{\text{veg}}=0$ ), or so small compared to the total biomass that becomes negligible. The SSA has  
 55 been shown to be a useful assumption at a large spatial scale. However, at local scales, an  
 56 ecosystem is unlikely to maintain a steady state due to the influences from external factors such  
 57 as disturbances and climate variability (Ge et al., 2019). It is still unknown whether the SSA can  
 58 hold at local spatial domains and how much the difference it can make to the  $\tau$  estimation if one  
 59 neglects the temporal changes in vegetation carbon.

60 In this study, we used estimates of annual changes in vegetation carbon derived from a  
 61 multi-decadal dataset and global estimations of gross primary productivity (GPP) that are driven  
 62 by meteorological observations (Besnard et al., 2021; Santoro et al., 2022; Tramontana et al.  
 63 2016; Jung et al. 2020), for estimating and comparing  $\tau$  estimates that are derived from SSA and  
 64 non-steady-state assumption (hereafter NSSA), respectively, at local, biome and global scales.  
 65 The validity of SSA was evaluated in different spatial domains to better quantify the effect of  
 66 spatial scales on the patterns of carbon turnover times.

67 **2 Data and Methods**

68 In this section, we first introduce the datasets we used to estimate  $\tau$  including above-  
 69 ground vegetation biomass, below-ground biomass and gross primary productivity. We  
 70 used a forest canopy cover dataset to examine the relationship between the changes in  $\tau$   
 71 and tree canopy cover. Then the calculations of  $\tau$  using three methods are introduced next  
 72 with detailed explanations.

73 **2.1 The multi-decadal estimates of AGB dataset**

74 Annual AGB estimates were derived from C-band satellite radar signals between 1992  
 75 and 2016 with a pixel size of 25 km (Santoro et al., 2022). The very dense time series of  
 76 observations by the European Remote Sensing (ERS) WindScatterometer, the MetOp  
 77 Advanced SCATterometer (ASCAT), and the Envisat Advanced Synthetic Aperture  
 78 Radar (ASAR) were used to maximize the information content of forest structure in the  
 79 signal, allowing for AGB estimates of higher accuracy compared to values obtained from  
 80 a single observation (Santoro et al., 2022). The annual estimation of AGB is obtained by  
 81 synthesizing all daily observations of the radar backscatter at one location in a pixel  
 82 ( $0.25^\circ \times 0.25^\circ$ ), enabling the inference of a continuous time series of AGB estimation. By  
 83 adapting the AGB retrieval method in time and space and computing a weighted average  
 84 of individual AGB estimates, the annual AGB estimates were less impacted by data  
 85 noise, instantaneous moisture conditions, precipitation, and snow cover (Santoro et al.,  
 86 2011).

87 **2.2 Estimation of total vegetation carbon stock**

88 The stock of total vegetation biomass consists of AGB and BGB. Therefore, we  
 89 estimated BGB from the AGB time series by scaling with the root-shoot ratio, Rrs:

90 
$$BGB = AGB \times R_{rs} \quad (1)$$

91 In this study, we used a spatially explicit global dataset of root-shoot ratio, which was  
 92 derived from a machine learning model that is trained on a large number of ground field  
 93 measurements of forest root biomass as a function of shoot biomass, tree height, age,  
 94 species, topography, land management, edaphic and climate covariates (Huang et al.,  
 95 2021).

96 The total vegetation carbon was obtained by summing the carbon in both AGB and BGB  
 97 under the assumption that the carbon stock is 47% of the total dry biomass (IPCC, 2006):

98 
$$C_{veg} = AGB \times (1 + R_{rs}) * 0.47 \quad (2)$$

99 **2.3 GPP dataset**

100 We used estimations of GPP from the FLUXCOM project in which different machine  
 101 learning approaches were applied to upscale global energy and carbon fluxes from eddy  
 102 covariance flux measurements (Tramontana et al., 2016; Jung et al., 2020). In this study,  
 103 GPP annual estimates driven by meteorological observations and remote sensing

104 observations at the spatial resolution of  $0.5^{\circ}$  and the time period from 1992 to 2016 are  
 105 used as carbon influx into the vegetation carbon pool. The dataset was resampled to the  
 106 spatial resolution of  $0.25^{\circ}$  to match the AGB dataset.

107

#### 108 2.4 Forest tree canopy cover change

109 Tree canopy cover (vegetation that is greater than 5 meters in height) was derived from  
 110 the Advanced Very High Resolution Radiometer (AVHRR) remote-sensing  
 111 measurements (Song et al., 2018). The version 4 Long Term Data Record (LTDR) was  
 112 used to generate the data on tree canopy coverage from 1982 to 2016. Daily LTDR  
 113 surface reflectance data were used to compute the normalized difference vegetation index  
 114 (NDVI) at each pixel ( $0.05^{\circ} \times 0.05^{\circ}$ ). Maximum NDVI composition was then used to  
 115 obtain adjusted annual phenological metrics, which were used as input to supervised  
 116 regression tree models to generate the annual product of tree canopy coverage.

117

#### 118 2.5 Estimation of $\tau$ under steady state

119 Changing  $C_{veg}$  over time is determined by the uptake of carbon and turnover times:

$$120 \frac{dC_{veg}}{dt} = GPP - \frac{C_{veg}}{\tau} \quad (3)$$

121  $C_{veg}$  is the vegetation carbon stock. Assuming that the vegetation carbon pool is in a  
 122 steady state, i.e., the change in  $C_{veg}$  over time ( $dC_{veg}/dt$ ) equals zero, then vegetation  
 123 carbon turnover times can be calculated as the ratio between vegetation carbon stock and  
 124 GPP:

$$125 \tau_{SSA} = \frac{C_{veg}}{GPP} \quad (4)$$

126 Here  $\tau_{SSA}$  is calculated pixel-wise by using annual mean  $C_{veg}$  and GPP over the period  
 127 of 1992-2016.

128

#### 129 2.6 Estimation of $\tau$ under non-steady state

130 Compared with the estimations of  $\tau$  under steady-state assumption, the changes in  $C_{veg}$   
 131 over time are considered ( $dC_{veg}/dt \neq 0$ ) when estimating  $\tau$  under non-steady state ( $\tau_{NSSA}$ ).

132 To derive a robust estimation of  $\tau_{NSSA}$  at each grid cell, we calculated  $\tau_{NSSA}$  using three  
 133 different methods to assess the uncertainty built in the  $\tau$  estimations.

134 Method 1

135 We estimate  $\Delta C_{veg}$  by calculating the annual difference of  $C_{veg}$  between year  $t$  and year  $t$   
 136 – 1. Then, a  $\tau$  estimate can be derived for each year by applying GPP and  $\Delta C_{veg}$  at year  $t$ .  
 137 Finally, we derive the  $\tau$  under a non-steady state by averaging over time:

138 
$$\tau_{NSSA} = \frac{C_{veg,t-1}}{GPP_t - \Delta C_{veg,t}} \quad (5)$$

139 Method 2

140 In the second method, we estimated the mean  $\Delta C_{veg}$  using the trend of  $C_{veg}$  in a certain  
 141 period to avoid the influence of outliers on the results. In this way,  $\tau$  can be inferred as:

142 
$$\tau_{NSSA} = \frac{\overline{C_{veg}}}{\overline{GPP} - \Delta C_{veg,trend}} \quad (6)$$

143 Here the  $\Delta C_{veg,trend}$  is inferred by applying a simple linear regression model (least-  
 144 square robust fitting) between the response variable  $C_{veg}$  and time ( $C_{veg} \sim T$ ). The  
 145 coefficient of  $T$  is, therefore, the average annual  $\Delta C_{veg}$  over the whole period. Thus, the  $\tau$   
 146 under a non-steady state can be estimated with the annual mean values of  $C_{veg}$ , GPP, and  
 147  $\Delta C_{veg}$ .

148

149 Method 3

150 In the third method, we infer  $\tau$  from Eq.3 by applying a linear regression model (least-  
 151 square robust fitting) at each grid cell in which ( $GPP - \Delta C_{veg}$ ) is the target variable while

152  $C_{veg}$  is the predictor, enabling annual turnover time to be inferred from the coefficient of  
 153  $C_{veg}$  ( $1/\tau_{NSSA}$ ):

$$154 GPP - \Delta C_{veg} \sim \frac{1}{\tau_{NSSA}} \cdot C_{veg} \quad (7)$$

155 Here  $\Delta C_{veg}$  is the difference of  $C_{veg}$  between year t and year t - 1. GPP is the carbon input  
 156 in year t and  $C_{veg}$  is the total carbon density in year t - 1, respectively.

### 158 3 Results

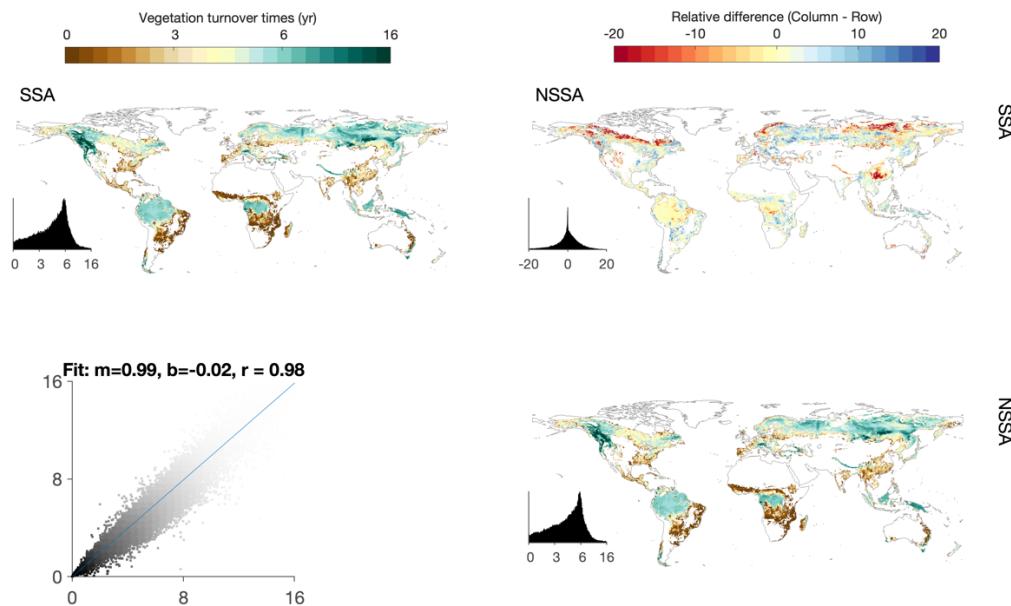
#### 159 3.1 Comparison of $\tau$ under NSSA and SSA at grid cell level and global scale

160 The  $\tau$  values (Figure 1) represent the turnover time of the entire forest living vegetation  
 161 biomass, averaged over the whole period of the observations. The comparison between  
 162 estimates of  $\tau_{NSSA}$  using three different methods and  $\tau_{SSA}$  shows a consistent pattern that  
 163 carbon turnover processes are far from a steady state at the grid cell level (Figure S1).  
 164 Although there is a high correlation in the global spatial patterns ( $R^2 > 0.98$ , bottom off-  
 165 diagonal plots in Figure 1), differences between  $\tau_{NSSA}$  and  $\tau_{SSA}$  are characterized by high  
 166 spatial heterogeneity. Although there are differences in the estimations of  $\tau_{NSSA}$  that derived  
 167 from the three methods, the high global correlation and similar patterns of the difference  
 168 between  $\tau_{NSSA}$  and  $\tau_{SSA}$  shows high consistency in the estimated  $\tau_{NSSA}$ . Our results show a  
 169 high spatial variability of  $\tau$  values ranging from 0 to 15 years. The longest turnover times  
 170 are located in the northern boreal forest ecosystem, where part of the biome has  $\tau$  values  
 171 longer than ten years, whereas carbon in the temperate forest ecosystem turnovers over  
 172 much faster where the  $\tau$  values are mostly under five years. The assumption that vegetation  
 173 biomass is in steady state results in an overall bias of  $\tau$  by 10% (90<sup>th</sup> percentile), compared  
 174 to the  $\tau$  estimates under a non-steady state at the grid cell level (Figure 1). This finding  
 175 indicates that the majority of global forest ecosystems are not in a steady state, although  
 176 the degree of deviation from a steady state differs from one region to another. The  
 177 discrepancies between  $\tau_{SSA}$  and  $\tau_{NSSA}$  are substantially higher in the boreal forest (4.33%)  
 178 ecosystem than in the tropical forest (10.99%) ecosystems indicating that the forests in the  
 179 tropics are closer to a steady state, whereas assuming SSA in the boreal forest may cause  
 180 large bias (Figure S2). Although the difference can be large at the grid cell level, there is a  
 181 high global correlation ( $r > 0.98$ ) between  $\tau_{SSA}$  and  $\tau_{NSSA}$  at the global scale, indicating an  
 182 overall similar spatial pattern with or without considering the changes in annual biomass  
 183 at the global scale. Here we show that the forest biomass at the global scale is roughly in a  
 184 steady state whereas the SSA is largely violated at the grid cell level, especially in the  
 185 northern boreal forest ecosystems where the  $\tau$  values can be substantially underestimated  
 186 or overestimated if assuming SSA.

187 In line with a previous study in which the SSA-induced biases are assessed at site level (Ge  
 188 et al., 2019), we show that SSA causes significant underestimations of  $\tau$  up to 40% (99th  
 189 percentile) in China during the period of 2005–2015 (Figure S3). However, our results show  
 190 a high heterogeneity where SSA can also cause overestimation of  $\tau$  up to -12% (1th

percentile). Further analysis shows that the pattern also changes across different periods of time. For instance, there is a contrasting pattern between 2001-2005 and 2009-2013 in which the former is characterized by overestimation of  $\tau$  induced by SSA whereas there is a widespread underestimation of  $\tau$  in the latter.

195



196

197 **Figure 1.** Comparison of  $\tau$  under SSA and NSSA. The upper off-diagonal subplots show  
198 the relative difference between each pair of datasets (column/row). The bottom off-  
199 diagonal subplots show the density plots and major axis regression line between each pair  
200 of datasets ( $m$ : slope,  $b$ : intercept,  $r$ : correlation coefficient). The ranges of both of the  
201 color bars are between the 1st and the 99th percentiles of the data.

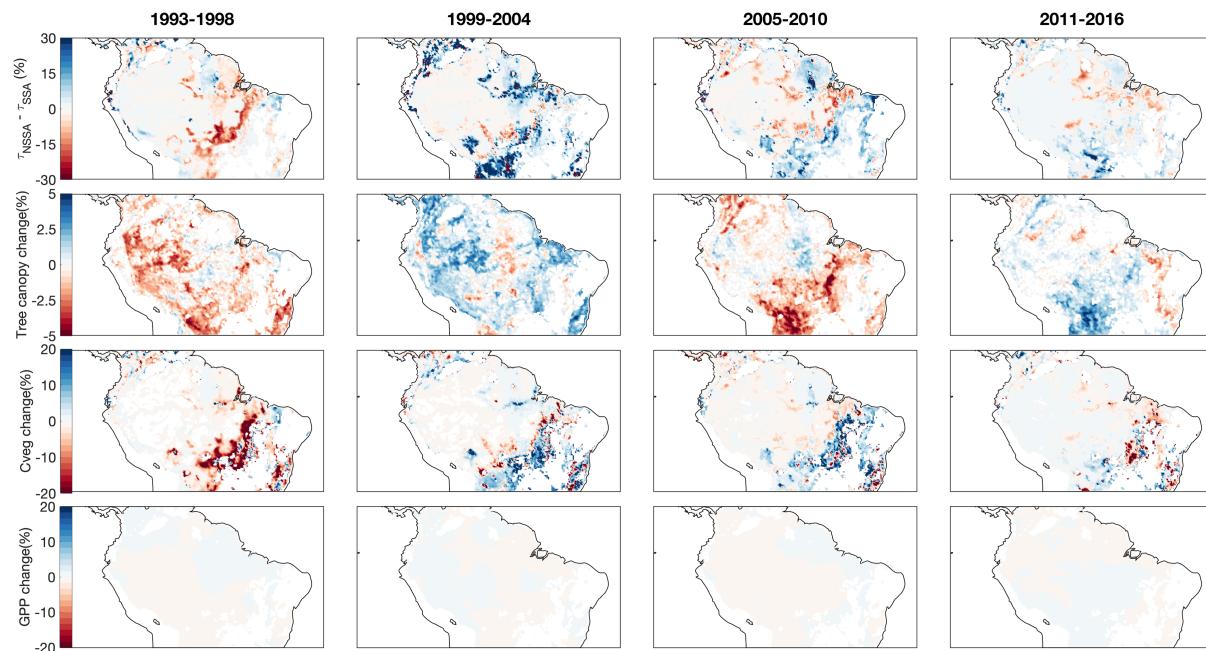
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### 203 3.2 The effect of large-scale disturbances on carbon turnover times

204 The disturbance from natural causes or anthropogenic activities can make an ecosystem  
205 deviate from a steady state. By estimating carbon turnover times at different periods, we  
206 quantified the degree of deviation if disturbances, e.g., deforestation, happened in a forest  
207 ecosystem. Figure 2 shows that the pervasive deforestation in the 90s primarily affected  
208 the carbon turnover times in the southeast part of the Amazon, which is known as the ‘arc  
209 of deforestation’ (hereafter AOD, Durieux et al., 2003). Our results clearly show  $\tau_{\text{NSSA}}$  is  
210 approximately 20% lower than  $\tau_{\text{SSA}}$  in the AOD region from 1993 to 1998, indicating

anthropogenic activity (mostly deforestation) accelerated the carbon turnover rates to a large extent. Compared with the AOD, forests in the middle of Amazon, where there are less population and disturbances, are closer to a steady state, as shown by the much less difference between  $\tau_{\text{NSSA}}$  and  $\tau_{\text{SSA}}$ . Further analysis shows that tree canopy cover (Figure 2, Row 2) and  $C_{\text{veg}}$  (Figure 2, Row 3) changes decreased mainly during the same period of 1993-1998, whereas the changes in GPP does not follow the trend in the arc of deforestation. These results indicate that the acceleration of turnover times during this period is directly caused by the large decrease in the vegetation biomass, which is intimately associated with a decrease in forest cover in this region. On the other hand, our findings show that the forest ecosystems started to recover during the 1999-2004 period as the vegetation biomass increased by 10% to 20%, in line with the increased tree canopy cover in the AOD region. As a result, the carbon turnover times increased by 10% to 30% during the same period. From 2011 to 2016, the magnitude of changes in  $\tau$ ,  $C_{\text{veg}}$  and tree canopy cover significantly decreased, indicating the forest ecosystems are closer to a steady state due to less disturbances. These findings indicate that turnover times and the steady state of the forest ecosystem can be largely affected by anthropogenic activities.

227



228

229

230 **Figure 2.** Regional changes in the relative difference between  $\tau_{\text{NSSA}}$  and  $\tau_{\text{SSA}}$  ( $(\tau_{\text{NSSA}} - \tau_{\text{SSA}})/\tau_{\text{SSA}} * 100$ ) from 1993 to 2016, row 1, forest cover change (%), row 2, vegetation

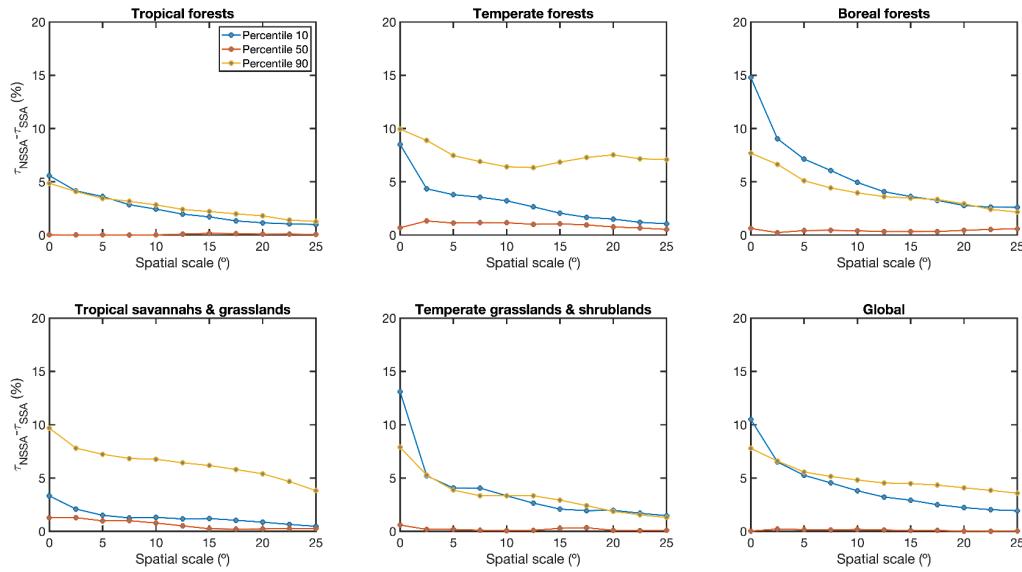
231

232 biomass change (%), row 3, GPP change (%), row 4 at different time periods in Amazon  
233 region.

234

235 **3.3 The effect of spatial scale on the steady-state assumption**

236 We further investigate the effect of spatial scale on the difference between  $\tau_{\text{NSSA}}$  and  $\tau_{\text{SSA}}$   
237 in different biomes by gradually changing the spatial scale from  $0.25^\circ$  (grid cell level) to  
238  $25^\circ$  (continental scale) as shown in Figure 3. Here the difference between  $\tau_{\text{NSSA}}$  and  $\tau_{\text{SSA}}$  at  
239 each spatial scale is quantified by the 10, 50 and 90 percentiles of the relative difference  
240 between  $\tau_{\text{NSSA}}$  and  $\tau_{\text{SSA}}$  ( $Q_{10}$ ,  $Q_{50}$ ,  $Q_{90}$ , Figure 4). We find that the difference between  $\tau_{\text{NSSA}}$   
241 and  $\tau_{\text{SSA}}$  substantially decreases with increasing spatial scales. The  $Q_{10}$  and  $Q_{90}$  tropical  
242 forests decrease by approximately 5%, whereas it decreases by approximately 10% in  
243 temperate and boreal biomes when the spatial scale increases from grid cell to ecosystem  
244 scale. Globally, the difference between  $\tau_{\text{NSSA}}$  and  $\tau_{\text{SSA}}$  is approximately 3% at ecosystem  
245 scale, indicating that steady state assumption will cause less errors in estimating carbon  
246 turnover times at larger spatial scales.



247

248 **Figure 3.** Effects of spatial scale on the difference between  $\tau_{\text{SSA}}$  and  $\tau_{\text{NSSA}}$ . The x-axis  
249 represents the increase of spatial scales from grid cell level ( $0.25^\circ$ ) to continental level  
250 ( $25^\circ$ ). The y-axis represents the 10<sup>th</sup> (absolute value) and 90<sup>th</sup> relative difference between  
251  $\tau_{\text{NSSA}}$  and  $\tau_{\text{SSA}}$ .

252

253 **4 Discussion**

254 Our findings imply that the two different assumptions, i.e., SSA and NSSA, should be  
255 applied based on different ecological principles and spatial scales. The common approach

of defining  $\tau$  as the ratio between carbon stock and carbon influx based on SSA can be justified and properly applied when the changes in net carbon flux are negligible relative to the total carbon stock (Carvalhais et al., 2014). Although disturbances from nature or human beings could cause non-steady-state behavior, neglecting the changes, in some cases, only make a little difference to the quantification of the spatial pattern of  $\tau$ , which does not hamper the understanding of the dynamics of the terrestrial ecosystem carbon cycle. However, at a grid cell level, neglecting the changes in vegetation carbon (assuming vegetation is in a steady state) may result in a large bias. Using three methods, we provide robust estimations of  $\tau$  under a non-steady state. The comparisons between  $\tau_{SSA}$  and  $\tau_{NSSA}$  show high heterogeneity in both space and time. A pioneer study (Ge et al., 2019) showed large SSA-induced biases on  $\tau$  estimation in varied ecosystems of China by using the data at ten FLUXNET sites from 2005 to 2015 which is consistent with our results. However, we further show that the magnitude and the signs of the SSA-induced biases are characterized by high spatial heterogeneity and can change in time. This is mainly caused by the changes in vegetation biomass due to climate change or disturbances (Figure 2).

We have shown substantial heterogeneity in the degree of validity of the steady-state assumption across space. The comparison between  $\tau_{SSA}$  and  $\tau_{NSSA}$  quantitatively shows that most global forest ecosystems are far from steady-state, especially in the temperate and boreal forests. Even at regions of high biomass density such as Amazon Forest where the changes in vegetation carbon is relatively small, i.e., closer to steady-state, disturbances such as deforestation or fire could drive the forest ecosystem away from steady-state, as our results clearly show that the arc of deforestation in Amazon Forest have large difference between  $\tau_{SSA}$  and  $\tau_{NSSA}$  caused by drastic changes in vegetation biomass (Figure 2). These results indicate that applying SSA at the grid cell level is likely to cause substantial errors, potentially leading to misleading conclusions based on poor estimation of carbon turnover times.

Furthermore, our study quantified the link between spatial scales and the validity of SSA. Our results imply that SSA is approximately valid at large spatial scales ( $>15^\circ$  or 1500km), at which scale the differences are much lower (~5%) than grid cell level. The current understanding of the temporal dynamics of the terrestrial carbon cycle nearly all relies on earth system models in which the carbon turnover rates are retrieved under the SSA, which results in large discrepancies in carbon pools and turnover among different models (Friend et al., 2014; Todd-Brown et al., 2013). The estimation of  $\tau$  under NSSA with observational long-term biomass data provides insights into better understanding and thus modeling turnover rate and its spatial patterns.

## 5 Implications, Limitations and Conclusions

Although we used different streams of data and methods to account for the uncertainties in the estimations of carbon turnover, several factors may limit the results of our study. First, the estimations of AGB by Santoro et al. (2022) is derived at relatively coarse spatial resolution at  $0.25^\circ$  which makes it impossible to compare with measurements of AGB at plot level. To overcome the limitation, Santoro et al. relied on gridded datasets including a

298 vegetation density map, an independent AGB map, a global land cover map and a model  
299 of global elevation to estimate the unknown model parameters that are necessary to infer  
300 vegetation biomass. Second, the estimated total vegetation carbon stock is calculated by  
301 using a spatial explicit root-shoot ratio of biomass that does not change with time.  
302 Therefore, we assume that the relationship between above- and below-ground biomass  
303 does not have a directional change over long-term in this study. Nevertheless, our findings  
304 suggest that the steady state assumption is robust at a global scale yet becomes much less  
305 realistic at the grid cell level as the difference between regional  $\tau_{SSA}$  and  $\tau_{NSSA}$  can be as  
306 large as 20%. The usage of the steady state assumption would result in a substantial bias  
307 of  $\tau$ , especially in the northern boreal forest ecosystems and regions with a high degree of  
308 disturbance, either from anthropogenic sources or natural factors. However, at a larger  
309 spatial scale, the differences in  $\tau$  estimations at SSA and NSSA significantly decrease  
310 because the annual changes in vegetation biomass are small compared with the total  
311 amount of biomass. With the novel long-term observations of vegetation biomass, we  
312 revealed a detailed picture of the spatial distribution of carbon turnover times under  
313 different assumptions and its relationship with spatial scales, which will guide the proper  
314 application of the two assumptions on different conditions.

315

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### 321 **Author Contributions**

322 N.F. and N.C. designed the analysis of this research and wrote the manuscript with contributions  
323 from all authors.

324

### 325 **Data availability**

326 The estimates of vegetation carbon turnover times that supports the findings of this research are  
327 temporarilty available in <https://figshare.com/s/c542bf749f76c8937eaa>. Please note that the data will  
328 be permanently available in figshare.com upon the acceptance of this paper.

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