

1 **Increasing soil carbon stocks in eight permanent forest plots in China**

2 **Jianxiao Zhu^{1,2}, Chuankuan Wang³, Zhang Zhou^{2,4}, Guoyi Zhou⁵, Xueyang Hu², Lai**
3 **Jiang², Yide Li⁴, Guohua Liu⁶, Chengjun Ji², Shuqing Zhao², Peng Li², Jiangling Zhu²,**
4 **Zhiyao Tang², Chengyang Zheng², Richard A. Birdsey⁷, Yude Pan⁸, and Jingyun Fang²**

5
6 ¹State Key Laboratory of Grassland Agro-ecosystems, College of Pastoral Agricultural
7 Science and Technology, Lanzhou University, Lanzhou 730020, China

8 ²Department of Ecology, College of Urban and Environmental Science, and Key Laboratory
9 for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871,
10 China

11 ³Center for Ecological Research, Northeast Forestry University, 26 Hexing Road, Harbin
12 150040, China

13 ⁴Research Institute of Tropical Forestry, Chinese Academy of Forestry, No. 682 Guangshanyi
14 Road, Tianhe District, Guangzhou 510520, China

15 ⁵Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South
16 China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

17 ⁶Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing
18 100085, China

19 ⁷Woods Hole Research Center, Falmouth, MA 02540, USA

20 ⁸US Department of Agriculture Forest Service, Durham, NH 03824, USA

21

22 **Correspondence:** Jingyun Fang (jyfang@urban.pku.edu.cn)

23 Tel.: + 86 10 6276 5578; fax: +86 10 6275 6560.

24

25 **Abstract.** Forest soils represent a major stock of organic carbon (C) in the terrestrial biosphere,
26 but the dynamics of soil organic C (SOC) stock are poorly quantified, largely due to lack of
27 direct field measurements. In this study, we investigated the 20-year changes in SOC stocks in
28 eight permanent forest plots, which represent boreal (1998–2014), temperate (1992–2012),
29 subtropical (1987–2008), and tropical forest biomes (1992–2012) across China. SOC contents
30 increased significantly from the 1990s to the 2010s, mostly in the upper 0–20 cm soil depth,
31 and soil bulk densities do not change significantly during the same period. As a result, the
32 averaged SOC stocks increased significantly from $125.2 \pm 85.2 \text{ Mg C ha}^{-1}$ in the 1990s to
33 $133.6 \pm 83.1 \text{ Mg C ha}^{-1}$ in the 2010s across the forest plots, with a mean increase of $127.2 -$
34 $907.5 \text{ kg C ha}^{-1} \text{ yr}^{-1}$. This SOC accumulation resulted primarily from increasing leaf litter and
35 fallen logs, which accounts 3.6–16.3% of above-ground net primary production. Our findings
36 provided direct evidence that China's forest soils have been acting as significant C sinks,
37 although their strength varies in forests with different climates.

38 **Keywords:** soil organic carbon, carbon cycle, forest ecosystems, global change, permanent
39 plot

40 **1 Introduction**

41 Terrestrial ecosystems have absorbed approximately 30% of the carbon dioxide (CO₂) emitted
42 from human activities since the beginning of the industrial era (IPCC, 2013). Forests have
43 contributed more than half of these carbon (C) fluxes of terrestrial ecosystems (Pan et al.,
44 2011). Since soils contain a huge C stock in forest ecosystems, even a slight change in this
45 stock will induce a considerable feedback to atmospheric CO₂ concentrations (Lal, 2004; Luo
46 et al., 2011). Thus, accurate assessment of the changes in soil organic carbon (SOC) is critical
47 to understanding how forest soils will respond to global climate change. However, it is
48 difficult to capture the SOC change with short-term measurements (Smith, 2004) because the
49 soil C pool typically has a longer turnover time and higher spatial variability compared to the
50 vegetation C pool (Schrumpf et al., 2011; Canadell and Schulze, 2014).

51 Previous efforts have estimated the changes in regional SOC stocks with indirect
52 approaches, such as regional assessments (Yang et al., 2014) and model simulations
53 (Todd-Brown et al., 2013). These estimates often involve large uncertainties due to the
54 inherently high spatial variability of soils and lack of direct measurements representing large
55 areas (Sitch et al., 2013). One reliable approach to reducing the uncertainties is to conduct
56 long-term monitoring of forest SOC stocks at sites that represent broader landscapes (Prietzl
57 et al., 2016). Unfortunately, such repeated, accurate field-based measurements of SOC stocks
58 from which to generate change estimates are generally lacking and inadequate worldwide
59 (Zhao et al., 2019).

60 A few soil resampling studies have explored SOC changes in different forests, but the
61 results are often contradictory. For instance, Schrumpf et al. (2014) found that SOC in
62 deciduous broadleaved forests in central Germany increased, with a change rate of 650.0 kg C
63 ha⁻¹ yr⁻¹ from 2004 to 2009. In contrast, Prietzl et al. (2016) indicated that SOC stocks in
64 German forests decreased significantly, with average change rates of 988.2 kg C ha⁻¹ yr⁻¹ in

65 forests in the Alps between 1986 and 2011, and 441.1 kg C ha⁻¹ yr⁻¹ in the Berchtesgaden
66 region between 1976 and 2011. Kiser et al. (2009) found that the hardwood forest soils in
67 central Tennessee, USA, exhibited a slight C source, and that the relative change rate ranged
68 from -0.4% yr⁻¹ to 0.3% yr⁻¹ between 1976 and 2006. Chen et al. (2015) synthesized global
69 SOC changes, and found that the relative rates of change in forest SOC stocks were
70 contradictory among long-term experiments (0.2% yr⁻¹), regional comparisons (0.3% yr⁻¹),
71 and repeated soil samplings (-0.1% yr⁻¹). Such discrepancies can be partly attributed to
72 insufficient observations and inconsistent methodologies. The different effects of changing
73 environmental factors and nitrogen inputs on soil C dynamics may also be involved (Norby
74 and Zak, 2011). In addition, to date these studies have primarily been conducted in the forests
75 of Europe and the USA, but few have been carried out in China's forests.

76 Forests in China cover an area of 156 Mha (Guo et al., 2013), and range from boreal
77 coniferous forests and deciduous broadleaved forests in the northeast to tropical rain forests
78 and evergreen broadleaved forests in the south and southwest. They include almost all major
79 forest biomes of the Northern Hemisphere (Fang et al., 2012). Such variations in climate and
80 forest types have provided ideal opportunities to examine the spatial patterns of SOC in
81 relation to meteorological and biological factors. At the national scale, the mean annual air
82 temperature of China increased by more than 1 °C between 1982 and 2011, which is
83 considerably higher than the global average (Fang et al., 2018). Since the 1980s, the
84 Government of China has implemented several large-scale national forest protection projects.
85 These climatic changes and conservation practices in China have significantly stimulated C
86 uptake into forest ecosystems (Fang et al., 2014, 2018; Feng et al., 2019). Several studies have
87 assessed the temporal dynamics of SOC stock across China's forests, using model simulations
88 (Piao et al., 2009) or regional assessments (Pan et al., 2011; Tang et al., 2018). However, these
89 estimates revealed contrasting trends in SOC dynamics and also lacked direct measurements of

90 SOC change.

91 Therefore, in this study we measured SOC density (C amount per unit area) of eight
92 permanent forest plots from tropical, subtropical, temperate, and boreal forests in China
93 during two periods in the 1990s and 2010s to quantify their SOC changes. We then analyzed
94 the potential biotic and climatic drivers in the SOC dynamics across these forests. Finally, we
95 assessed the changes in SOC stocks in China's forests using the site data obtained from this
96 study.

97

98 **2 Materials and methods**

99 **2.1 Study sites**

100 We investigated eight permanent forest plots in four forest sites (from north to south: Great
101 Xing'anling, Mt. Dongling, Mt. Dinghu, and Jianfengling) (Fig. 1). The four sites spanned a
102 wide range from 18.7 °N to 52.6 °N in latitude, and belonged to boreal, temperate, subtropical,
103 and tropical climate zones, respectively, with a climatic difference of approximately 26 °C in
104 mean annual temperature and 1,200 mm in mean annual precipitation. The eight plots
105 comprised a boreal larch forest (*Larix gmelinii*), two temperate deciduous broadleaved forests
106 (*Betula platyphylla* and *Quercus wutaishanica*), a temperate pine plantation (*Pinus*
107 *tabuliformis*), a subtropical evergreen broadleaved forest, a subtropical pine plantation (*P.*
108 *massoniana*), a subtropical pine and broadleaved mixed forest, and a tropical mountain
109 rainforest (for details, see Table 1).

110 Stand characteristics of all eight plots are summarized in Table 1. The boreal larch forest
111 was a 100-year-old mature stand at the time of the first sampling (Wang et al., 2001). Three
112 temperate forest plots (birch, oak, and pine forests) were located along an elevation gradient
113 on Mt. Dongling, Beijing. Both birch and oak forest plots were 55-year-old secondary forests
114 at the time of the first sampling, dominated by *B. platyphylla* and *Q. wutaishanica*,

115 respectively. The temperate pine plantation was 30 years old at the time of the first sampling,
116 and was dominated by *P. tabuliformis* (Fang et al., 2007). Three subtropical forest plots were
117 located in Dinghu Biosphere Reserve in Guangdong Province, South China (Zhou et al.,
118 2006). The subtropical evergreen broadleaved forest was an old-growth stand more than 400
119 years old, co-dominated by *Castanopsis chinensis*, *Canarium pimela*, *Schima superba*, and
120 *Engelhardtia roxburghiana*. The subtropical pine (*P. massoniana*) plantation was
121 approximately 40 years old at the time of the first sampling. The mature mixed pine and
122 broadleaved forest was approximately 110 years old at the time of the first sampling, and
123 represented the mid-successional stages of monsoon evergreen broadleaved forest in this
124 region. The tropical mountain rainforest plot was located at the Jianfengling National Natural
125 Reserve, southwestern Hainan (Zhou et al., 2013). It had not been disturbed for more than 300
126 years, and was dominated by species in the families Lauraceae and Fagaceae, such as
127 *Mallotus hookerianus*, *Gironniera subaequalis*, *Cryptocarya chinensis*, *Cyclobalanopsis*
128 *patelliformis* and *Nephelium topengii*. For detailed descriptions on these eight plots, see
129 Supplementary Materials and Methods.

130

131 **2.2 Soil sampling and calculation of SOC content**

132 The first sampling was conducted between 1987 and 1998 in each of the eight forests (Table
133 1). We re-measured the same sample plots in each forest between 2008 and 2014 using
134 identical sampling protocols.

135 In each forest plot, 2–5 pits were dug to collect soil samples for analyzing the physical
136 and chemical properties during the two sampling periods (most in the 1990s during the first
137 sampling period and in the 2010s during the second sampling period). The samples were
138 taken at depth intervals of 10 cm down to the maximum soil depth. In brief, for the boreal
139 forest, three soil pits were established down to the 40-cm soil depth in random locations in the

140 growing season in 1998. In August 2014, three soil pits were again randomly excavated to the
 141 same soil depth to allow sampling for SOC content and bulk density. For the three temperate
 142 forests, two soil profiles (100 cm depth) were dug in each plot to collect soil samples at 10 cm
 143 intervals during the summer of 1992. In the summer of 2012, three soil profiles were dug, and
 144 soils were sampled from the same horizons in each soil profile (Zhu et al., 2015). The first
 145 sampling in the three subtropical forests was conducted in September 1988 in the evergreen
 146 and pine plots, and in 1987 for the mixed plot, both at the end of the rainy season and at the
 147 beginning of the dry season. Five soil pits (60 cm depth) were randomly excavated to collect
 148 samples for the calculation of SOC content and bulk density. In September 2008, the soil
 149 sampling was repeated. For the tropical forest, five soil profiles (100 cm depth) were
 150 established at 10 cm intervals during summer 1992 and again in summer 2012.

151 We used consistent sampling and analysis approaches to determine the bulk density and
 152 SOC content between the two sampling times. Three bulk density samples were obtained for
 153 each layer using a standard container 100 cm³ in volume. The soil moisture was determined
 154 by weighing to the nearest 0.1 g after 48 h oven-drying at 105 °C. The bulk density was
 155 calculated as the ratio of the oven-dried mass to the container volume. Another three paired
 156 samples for C analysis were air-dried, the fine roots removed by hand, and sieved (2 mm
 157 mesh). The SOC content was measured using the wet oxidation method (Nelson and Sommers,
 158 1982) and was calculated according to Eq. (1):

$$159 \quad \text{SOC} = \sum_{i=1}^n CC_i \times Bd_i \times V_i \times HF_i \quad (1)$$

160 where CC_i , Bd_i , and V_i are SOC content (%), bulk density (kg m⁻³), and volume (m³) at the
 161 i -th soil horizon, respectively. HF_i is calculated as $1 - \frac{\text{stone volume} + \text{root volume}}{V_i}$ and is a
 162 dimensionless factor that represents the fine soil fraction within a certain soil volume.

163

164 **2.3 Calculation of above-ground biomass (AGB) and net primary production**

165 Diameter at breast height (DBH, 1.3 m) and height of all living trees with DBH > 5 cm were
166 measured in each plot in the 1990s and 2010s. The AGB of different components (stem, bark,
167 branches, and foliage) was estimated for all tree species using allometric equations (Table S1).
168 A standard factor of 0.5 was used to convert biomass to C (Leith and Whittaker, 1975). The
169 net increment of AGB (ΔStore) was calculated for each plot as the difference between the
170 biomass in the 1990s and the 2010s. The above-ground net primary production (ANPP, kg C
171 $\text{ha}^{-1} \text{yr}^{-1}$) was calculated from Eq. (2):

$$172 \quad \text{ANPP} = \text{Litterfall} + \Delta\text{Store} + \text{Mortality} \quad (2)$$

173 where Litterfall and ΔStore are litter production and above-ground net biomass increment per
174 year, respectively. Mortality (defined as above-ground dead wood production) was estimated
175 as the summed production of fallen logs and standing snags per year.

176

177 **2.4 Litter and fallen log production**

178 Annual litterfall was collected from June 2010 to June 2013 in the tropical sites; from June
179 1990 to June 2008 in the subtropical sites; from April to November 2011–2014 in the
180 temperate sites; and from May to October 2010–2014 in the boreal sites. Litter (leaves,
181 flowers, fruits, and woody material < 2 cm diameter) was collected monthly from 10–15 litter
182 traps ($1 \times 1 \text{ m}^2$, 1 m above ground) in each plot to calculate annual litter production. After
183 collection, the samples were taken to the laboratory, oven-dried at 65 °C to a constant mass
184 and weighed. The 10–15 replicates from each plot were averaged as the monthly mean value.
185 Annual litter production ($\text{kg C ha}^{-1} \text{yr}^{-1}$) was estimated as the sum of the monthly production
186 in the year of collection.

187 Log production represents the mortality (that is, death of entire trees) per year. Annual
188 log production was determined from 2010 to 2013 in tropical sites; from 1989 to 1996 in
189 subtropical sites; from 2011 to 2014 in temperate sites; and from 2010 to 2014 in boreal sites.

190 Stocks of fallen logs were harvested and weighed during each investigated year.

191

192 **2.5 Forest area and fossil fuel emission data**

193 To calculate the amount of C sequestration in China's forest soils, we estimated the changes
194 in the national forest SOC stocks. We used the mean SOC accumulation rates obtained from
195 this study and the data of forest area for each forest type documented in the national forest
196 inventory in 1989–1993, which approximates the first sampling period in the present study
197 (Guo et al., 2013). The changes in national forest SOC stock were calculated as the product of
198 SOC density, SOC density change rate, and forest area for major forest types during the
199 period 1989–1993. In addition, to evaluate the relative importance of forest soil C
200 sequestration in the national C budget, we obtained the data of fossil fuel emissions during
201 1991–2010 from the Carbon Dioxide Information Analysis Center (Zheng et al., 2016).

202

203 **3 Results**

204 **3.1 Changes in SOC**

205 SOC stocks were investigated in eight permanent forest plots in four forest sites from northern
206 to southern China, in two periods: the 1990s and 2010s. The changes in SOC contents, bulk
207 density, and SOC stocks in the top 20 cm soil layer between the 1990s and the 2010s are
208 shown in Fig. 2, Fig. S1 and Fig. S2. The paired *t*-test analysis indicated that SOC contents in
209 the 0–20 cm depth was significantly higher in the 2010s than in the 1990s ($3.2\pm 0.7\%$ vs.
210 $2.9\pm 0.6\%$; $t = -5.65$, $P < 0.001$) (Table 2). The average rate of increase in SOC content was
211 $0.02\% \text{ yr}^{-1}$ in the top 20 cm depth, ranging from $0.01\% \text{ yr}^{-1}$ to $0.04\% \text{ yr}^{-1}$ across the study
212 sites. These rates of increase in SOC content in the 0–10 cm horizon ($0.03\pm 0.02\% \text{ yr}^{-1}$) were
213 three times larger than those in the 10–20 cm horizon ($0.01\pm 0.01\% \text{ yr}^{-1}$) (Table S2). At the
214 same time, the bulk density of the top 20 cm soil layer decreased in most sites (6 of 8 sites),

215 with an average rate of decrease of $2.7 \pm 3.7 \text{ mg cm}^{-3} \text{ yr}^{-1}$ (Table S3). As a result, the SOC
216 stock in the top 20 cm soil layer was found to have increased significantly in the past two
217 decades ($t = -5.85$, $P < 0.001$, Table 2), with an average accumulation rate of $332.4 \pm 200.2 \text{ kg}$
218 $\text{C ha}^{-1} \text{ yr}^{-1}$ ($0.7 \pm 0.4\% \text{ yr}^{-1}$; Fig. 2; also see Table S3). The temperate pine plantation
219 experienced the largest increase in SOC stock in the top 20 cm depth ($630.8 \pm 111.2 \text{ kg C ha}^{-1}$
220 yr^{-1}). In contrast, the smallest rate of increase was observed in the subtropical mixed forest
221 ($117.3 \pm 25.2 \text{ kg C ha}^{-1} \text{ yr}^{-1}$). It should be noted that SOC stock in the top 20 cm depth in the
222 subtropical evergreen old-growth forest increased from $35.6 \pm 6.0 \text{ Mg C ha}^{-1}$ in 1988 to
223 $45.6 \pm 6.9 \text{ Mg C ha}^{-1}$ in 2008 (increased by $498.3 \pm 78.8 \text{ kg C ha}^{-1} \text{ yr}^{-1}$), which led to the highest
224 relative accumulation rate ($1.4 \pm 0.2\% \text{ yr}^{-1}$) among the study sites.

225 We further compared SOC stocks of the whole soil profile between 1990s and 2010s at a
226 depth of 0–40 cm in the boreal site, 0–60 cm in the subtropical site, and 0–100 cm in the
227 temperate and tropical sites (Fig. 3). The SOC stocks of all sampling sites in the 2010s were
228 higher than those in the 1990s. The paired t -test analysis revealed a significant increase in
229 SOC stocks for the whole soil profile during the sampling period ($t = -4.15$, $P < 0.01$; Table 2).
230 The mean SOC stocks of the whole soil profile in the eight forests increased from 125.2 ± 85.2
231 Mg C ha^{-1} in the 1990s to $133.6 \pm 83.1 \text{ Mg C ha}^{-1}$ in the 2010s, with an accumulation rate of
232 $421.2 \pm 274.4 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ and a relative increase rate of $0.6 \pm 0.5\%$ (Fig. 2). The SOC
233 accumulation rates displayed large variability among different climate zones and forest types.
234 For different climate zones, the SOC accumulation rates in the subtropical and tropical sites
235 were relatively higher than those in the boreal and temperate sites (Fig. 3). The greatest
236 increase in SOC stock occurred in the subtropical evergreen old-growth forest ($907.5 \pm 60.1 \text{ kg}$
237 $\text{C ha}^{-1} \text{ yr}^{-1}$), and the least in the temperate deciduous oak forest ($127.2 \pm 25.3 \text{ kg C ha}^{-1} \text{ yr}^{-1}$;
238 Table S3). The relative rates of increase in the subtropical evergreen old-growth forest
239 ($1.3 \pm 0.1\% \text{ yr}^{-1}$) and the subtropical mixed forest ($1.5 \pm 0.2\% \text{ yr}^{-1}$) were higher than those in the

240 temperate forests ($0.1 \pm 0.0\% \text{ yr}^{-1}$ in the oak forest, $0.1 \pm 0.0\% \text{ yr}^{-1}$ in the pine forest, and
241 $0.2 \pm 0.0\% \text{ yr}^{-1}$ in the birch forest; Table S3).

242 In addition, the rates of SOC increase ($127.2\text{--}907.5 \text{ kg C ha}^{-1} \text{ yr}^{-1}$) was equivalent to 3.6–
243 16.3% of ANPP ($3340.1\text{--}6944.7 \text{ kg C ha}^{-1} \text{ yr}^{-1}$), with the highest rate in the subtropical
244 evergreen forest ($16.3 \pm 4.2\%$) and the lowest in the temperate oak forest ($3.6 \pm 3.4\%$) (Tables 3
245 and S4).

246

247 **3.2 Relationships between SOC change rates and biotic and climatic variables**

248 To understand the possible mechanisms for the rates of SOC increase as described above, we
249 analyzed the driving forces for this significantly increased SOC stock using measurements of
250 AGB growth rate, above-ground litter and fallen log production, and ANPP (Table 3). The
251 linear regression analysis showed that there was no significant correlation between SOC
252 change rates and AGB growth rate ($P > 0.05$; Fig. 4a). The SOC accumulation rates were
253 positively and significantly associated with annual litter ($R^2 = 0.66$, $P = 0.01$; Fig. 4b) and
254 fallen log production ($R^2 = 0.69$, $P = 0.01$; Fig. 4c). The SOC accumulation rates across these
255 forests were closely associated with the observed ANPP ($R^2 = 0.55$, $P = 0.03$; Fig. 4d), and
256 also showed an increasing trend with increasing mean annual temperature and precipitation,
257 despite insignificant (both $P > 0.1$; Figs. 4e and 4f). The multiple regression analysis indicated
258 the relative effects of biotic factors (AGB growth rate, litter and fallen log production) and
259 climatic factors (mean annual temperature and precipitation) on the rates of SOC increase (Fig.
260 4g). When the effects of climatic factors were under control, the biotic factors independently
261 explained 56.4% of the variations. By comparison, when the effects of biotic factors were
262 under control, only 7.5% of the variations were explained by the climatic factors.

263

264 **4 Discussion**

265 **4.1 SOC accumulation**

266 Previous evidence of forest SOC changes comes mainly from individual experiments (Prietzl
267 et al., 2006; Kiser et al., 2009; Häkkinen et al., 2011) or regional comparisons (Letten
268 2005; Pan et al., 2011; Ortiz et al., 2013) in European and American forests. In this study, we
269 performed a broad-scale forest soil resampling to evaluate changes in SOC stock across eight
270 permanent forest plots in China. Our measurements suggest that SOC stocks exhibited a
271 significant accumulation in these forests from the 1990s to the 2010s, at the accumulation rate
272 of 127.2–907.5 kg C ha⁻¹ yr⁻¹. These accumulation rates are comparable to those of other
273 studies that were primarily conducted in boreal and temperate forests in other regions (-11.0–
274 812.0 kg C ha⁻¹ yr⁻¹, Fig. 5). In detail, the rate of SOC accumulation of the boreal forest in the
275 present study was estimated as 243.4 kg C ha⁻¹ yr⁻¹, which was within the range of boreal
276 forests in European and American forests (115.6–740.0 kg C ha⁻¹ yr⁻¹) (Prietzl et al., 2006;
277 Häkkinen et al., 2011; Rantakari et al., 2012; Chapman et al., 2013; Schrumpf et al., 2014).
278 The rates of SOC accumulation in the three temperate forests ranged from 127.2 to 390.8 kg
279 C ha⁻¹ yr⁻¹, comparable to the regional comparison data of 200.0 kg C ha⁻¹ yr⁻¹ in the
280 temperate forests of China (Yang et al., 2014). Evidence from soil inventory-based studies of
281 SOC dynamics also demonstrated that soil of boreal and temperate forests in European
282 countries is likely to accumulate C (Berg et al., 2009; Nielsen et al., 2012; Grüneberg et al.,
283 2014). The mean rate of SOC accumulation in the humus layers of boreal forests in Sweden
284 was estimated to be 251.0 kg C ha⁻¹ yr⁻¹ during the period 1961–2002 (Berg et al., 2009).
285 Nielsen et al. (2012) assessed the rates of SOC change in Denmark’s broadleaved deciduous
286 and coniferous forests by two soil inventories conducted during 1990 and 2005. The estimated
287 rates of SOC change in the broadleaved and coniferous forests were 90.0 and 310.0 kg C ha⁻¹
288 yr⁻¹, respectively. Two soil inventories provided data for analysis of the mineral soils of
289 forests in Germany, which were found to have sequestered 410.0 kg C ha⁻¹ yr⁻¹ during the

290 period of 1987–2008 (Grüneberg et al., 2014). Therefore, evidence from long-term
291 observations, and from the repeated soil sampling in individual studies and in national soil
292 inventory reports, suggests that soils of boreal and temperate forests in the northern
293 hemisphere have functioned as C sinks during past decades.

294 In other subtropical and tropical forest ecosystems, direct evidence of SOC dynamics is
295 relatively scarce. However, based on the estimates from regional comparisons, Pan et al.
296 (2011) showed that global tropical forests were a source of $1.4 \text{ Pg C ha}^{-1} \text{ yr}^{-1}$ from 1990 to
297 2007. At the global scale, tropical land-use changes have caused a sharp drop in forest area,
298 which also led to a large release of C from tropical forest soils. Without land-use change and
299 deforestation, soils in subtropical and tropical forests have been functioning as a considerable
300 C sink during the past two decades in this study (627.6 ± 370.1 and $397.9 \pm 84.2 \text{ kg C ha}^{-1} \text{ yr}^{-1}$,
301 respectively, Table 3). Limited forest management (e.g., litter and dead wood harvest), as well
302 as catastrophic land-use changes, can result in the loss of C from forest soil. Prietzel et al.
303 (2016) reported a large loss of SOC in forests in the German Alps, where half of the woody
304 biomass and dead wood had been harvested over recent decades. On the one hand, harvesting
305 the forest floor can decrease litter and dead wood inputs into soils and subsequently lead to
306 the loss of soil C (Davidson and Janssens, 2006). On the other hand, a decrease in the amount
307 of the forest floor may lead to an increase in soil erosion, especially in mountain forests
308 (Evans et al., 2013). Additionally, high-elevation ecosystems are expected to be more
309 sensitive to warming than other regions, with associated changes in soil freezing and thawing
310 events and in snow cover, which may be another reason for the SOC losses in forests in the
311 German Alps.

312

313 **4.2 Links between biotic and climatic factors and in SOC accumulation**

314 The forest biomass of China has functioned as a significant C sink over recent decades (Pan et

315 al., 2011; Fang et al., 2014, 2018). The increase in C accumulation by vegetation supplied
316 more C inputs into soils, including inputs of litter, woody debris, and root exudates, and
317 resulted in SOC accumulation (Zhu et al., 2017). However, the rate of SOC change did not
318 increase with the rate of biomass change in this study (Table S4). We found that soil in the
319 subtropical old-growth forest increased at the highest sink rate of $907.5 \pm 60.1 \text{ kg C ha}^{-1} \text{ yr}^{-1}$,
320 but that vegetation functioned as a significant C source ($-1000.3 \pm 78.2 \text{ kg C ha}^{-1} \text{ yr}^{-1}$). This
321 was because the relatively higher annual litterfall and fallen log production occurred in the
322 old-growth forest, which subsequently resulted in soil C accumulation (Fig. 4). The positive
323 (but not significant) trend between climatic factors and SOC dynamics may largely be
324 induced by the internal correlations between climatic and biotic factors (Fig. 4).

325 The heterotrophic respiration of global forest soil has increased significantly over past
326 decades (Bond-Lamberty et al., 2018), suggesting that the increment in the rate of soil C input
327 outweighs that of the rate of soil C output. The increasing heterotrophic respiration of forest
328 soil is mainly due to ongoing climate change, and especially to increasing temperature. The
329 increment in forest growth rate is due to increasing temperature, together with increasing CO_2
330 and nitrogen fertilization (Norby et al., 2010; Feng et al., 2019). Thus, the sensitivity of forest
331 net primary production to ongoing climate change should outweigh that of respiration. We
332 also found that SOC stock increased from $68.4 \text{ Mg C ha}^{-1}$ to $86.6 \text{ Mg C ha}^{-1}$, albeit the
333 biomass C stock decreased significantly from 1988 to 2008 in the subtropical old-growth plot.
334 The greatest amount of litter and dead wood production and standing crop occurred in the
335 old-growth plot, which resulted in relatively higher soil C sequestration in the old-growth plot
336 compared to other plots (Fig. 4, Table S4). Biotic factors explained the variation in SOC
337 dynamics better than climatic factors. In this study, we did not, however, measure
338 root-derived C inputs to SOC, although below-ground production also makes a significant
339 contribution to SOC accumulation (Nadelhoffer and Raich, 1992; Majdi, 2001; Pausch and

340 Kuzyakov, 2018). Above-ground inputs are mineralized from litter and dead wood, and
341 below-ground inputs may benefit from interactions with soils (Rasse et al., 2005). Even if the
342 effect of climatic factors were controlled and below-ground biotic factors were not included in
343 the analysis, the above-ground biotic factors would explain 56.4% of the variation in the rate
344 of SOC accumulation.

345

346 **4.3 Regional carbon budget**

347 The rate of SOC accumulation ($421.2 \pm 274.4 \text{ kg C ha}^{-1} \text{ yr}^{-1}$, Fig. 2 and Table S3) is more than
348 one-half of the vegetation C uptake rate in China's forests ($702.0 \text{ kg C ha}^{-1} \text{ yr}^{-1}$) (Guo et al.,
349 2013; Fang et al., 2018). This result suggests that China's forest soils have contributed to a
350 negative feedback to climate warming during the past two decades, rather than the positive
351 feedback predicted by coupled C-climate models (Cox et al., 2000; He et al., 2016; Wang et
352 al., 2018).

353 If we roughly use the inventory-based forest area of 138.8 Mha in China (Guo et al., 2013)
354 and extend the current SOC sink rates obtained in this study to all the forests in the country,
355 China's forest soils have sequestered approximately $1.1 \pm 0.5 \text{ Pg C}$ during the past two decades
356 ($57.1 \pm 26.5 \text{ Tg C yr}^{-1}$). This C accumulation would be equivalent to 2.4–6.8% of the country's
357 fossil CO₂ emissions during the contemporary period (1991–2010) (Zheng et al., 2016). By
358 comparing forest SOC data obtained from published literature during the 2000s and a national
359 soil inventory during the 1980s, Yang et al. (2014) estimated significant C accumulation in the
360 forest soils of China. Although they did not estimate the national C budget of these forest soils,
361 we can calculate the national C sequestration rate of forest soil as $67.2 \text{ Tg C yr}^{-1}$, based on the
362 C sequestration rates and forest areas of the different forest types in their study. Our results
363 further confirm the assessment, based on repeated measurements at eight permanent forest
364 plots, that soils in China's forests have functioned as a C sink for atmospheric CO₂ during the

365 past two decades.

366 According to previous estimates, the C sinks of three C sectors: forest vegetation biomass
367 (Fang et al., 2014), dead wood, and litter (Zhu et al., 2017) during the past two decades were
368 70.9, 3.9, and 2.8 Tg C yr⁻¹, respectively (Table S5). If these previous estimates are
369 incorporated into the soil C accumulation rate of 57.1±26.5 Tg C yr⁻¹ in the current study, then
370 China's forests may have sequestered a total of 134.7 Tg C per year between the 1990s and
371 the 2010s. This is equivalent to 14.5% of the contemporary fossil CO₂ emissions in the
372 country (Zheng et al., 2016). According to the estimate of Pan et al. (2011), the C sink rate of
373 forests in the temperate regions of the northern hemisphere was 647.1 Tg C yr⁻¹. The C
374 sequestration of China's forests represents 20.8% of the total temperate regions. The
375 sequestration rate of China's forests is slightly higher than the mean value of the total
376 temperate regions, relative to the forest area of China (i.e., 18.9% of the forest areas in the
377 temperate regions). This result indicates that the role of forest soils in the regional C cycle
378 cannot be ignored, although a large uncertainty about the national C budget of forest soils
379 remains in our estimates.

380

381 **4.4 Uncertainty analysis**

382 We investigated the SOC stocks in eight permanent plots across four forest biomes in China.
383 These plots spanned a long-term timescale (approximately 20 years) and a broad spatial scale
384 (approximately 34 ° of latitude). We also measured several C fluxes (i.e., biomass change rate,
385 production of litterfall and dead wood) that were relevant to the rate of SOC change. Even so,
386 the following three factors may introduce uncertainties related to the estimation of SOC
387 dynamics.

388 First, the sampling times and intervals between SOC investigations were different across
389 the sites. The first sampling was performed from 1987 to 1998 and the second was carried out

390 from 2008 to 2014. As a result, the sampling interval ranged from 16 years in the boreal forest
391 plot to 21 years in the subtropical mixed forest plot (Table 1). Non-uniform sampling times
392 and intervals may lead to uncertainties in relation to SOC stocks across the forest plots.

393 Second, the depth of soil varied substantially, ranging from 40 cm in the boreal site to 100
394 cm in the temperate and tropical sites. In addition, different numbers (2–5) of soil profiles were
395 dug in different plots during the first sampling period. To ensure consistency between the two
396 sampling times, the same number of soil profiles were dug, and in similar locations, to perform
397 SOC stock investigations during the second sampling period. We performed continuous
398 observation of litterfall and dead wood production, but the observation times and durations
399 varied across the plots. Variability in these items may reduce the comparability of SOC
400 dynamics among plots.

401 Finally, the rates of SOC change in our study and in inventory-based forest areas and
402 forest types were used to estimate the C budget of forest soil in China. However, only eight
403 permanent forest plots were observed in this study, and this will inevitably lead to uncertainty
404 with respect to national estimations.

405

406 **5 Conclusions**

407 The SOC stocks within the top 20 cm increased by 2.4–12.6 Mg C ha⁻¹ across the forests
408 during the past two decades, with an annual accumulation rate of 332.4±200.2 kg C ha⁻¹. If all
409 soil horizon profiles were included, the soils may have been found to have sequestered 3.6–
410 16.3% of the annual net primary production across the investigated sites, and the averaged
411 accumulated rate (421.2 kg C ha⁻¹ yr⁻¹) may have been more than one-half of the vegetation C
412 uptake rate (702.0 kg C ha⁻¹ yr⁻¹) in China's forests. These results demonstrate that these
413 forest soils have functioned as an important C sink over recent decades, although the
414 phenomenon may not occur uniformly in forests worldwide. Forest soils store large amounts

415 of C, and accumulate it steadily and often slowly, but will release it rapidly to the atmosphere
416 once they are disturbed.

417

418 **Data availability.** All relevant data are available from the corresponding author upon
419 request.

420

421 **Author contributions.** JF designed the research; JZ and JF designed the data analysis. JZ, JF,
422 ZZ, LJ, XH, HY, GL, CW and GZ performed SOC measurements. JF, YL, CJ and GL
423 designed sampling and analytical programmes and performed data quality control. JZ, JF, CW,
424 SZ, PL, JZ, ZT, CZ, RB and YP contributed to the writing of the manuscript.

425

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427

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431

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622

623 **Table 1.** Location, forest type, mean annual temperature (MAT), and mean annual precipitation (MAP) at eight forest plots in four climate zones,
 624 together with forest origin and study periods.

Site	Forest	Origin	Latitude (°)	Longitude (°)	Elevation (m)	Area (m ²)	MAT (°C)	MAP (mm)	Study period
Great Xing'anling (Boreal)	Larch	Mature	52°38'42.06"N	123°46'7.80"E	466	20×30, 25×40	-4.3	477	1998–2014
	Birch	Secondary	39°57'05.82"N	115°25'38.93"E	1,350	30×35	4.7	519	1992–2012
Mt. Dongling (Temperate)	Oak	Secondary	39°57'26.66"N	115°25'29.14"E	1,150	30×40	4.6	519	1992–2012
	Pine	Plantation	39°57'33.94"N	115°25'39.40"E	1,050	20×30	5.5	506	1992–2012
	Evergreen	Old growth	23°10'11.21"N	112°32'21.97"E	275	50×50	20.9	1698	1988–2008
Mt. Dinghu (Subtropical)	Mixed	Mature	23°9'58.51"N	112°32'23.32"E	265	30×40	21.6	1680	1987–2008
	Pine	Plantation	23°10'02.75"N	112°32'30.59"E	250	30×40	21.9	1677	1988–2008
Jianfengling (Tropical)	Evergreen	Old growth	18°43'47.01"N	108°53'23.79"E	870	100×100	20.6	1628	1992–2012

625

626 **Table 2.** Results of the paired-samples *t* tests for soil organic carbon (SOC) content, bulk
 627 density, and SOC stock at different soil depths in the eight forest plots between the 1990s and
 628 the 2010s.

Soil horizon	SOC content			Bulk density			SOC stock		
	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>
0 – 10 cm	-4.22	7	<0.01	2.19	7	0.06	-6.50	7	<0.001
10 – 20 cm	-4.09	7	<0.01	3.30	7	<0.05	-3.26	7	<0.05
Top 20 cm	-5.65	7	<0.001	1.01	7	0.35	-5.85	7	<0.001
Whole soil profile	-	-	-	-	-	-	-4.15	7	<0.01

629

630 **Table 3.** Measured C stocks and fluxes of the four forest sites in China during the 1990s and
 631 the 2010s.

Parameter	Boreal	Temperate	Subtropical	Tropical
Carbon pool (Mg C ha⁻¹)*				
AGB	91.1±25.0	89.6±17.4	107.0±41.7	213.6±41.4
Litter	4.4±0.0	3.9±1.3	2.1±0.7	1.8±0.2
Dead wood	1.3±0.5	4.5±1.2	7.3±6.7	5.7±0.8
Soil	69.4±6.2	231.6±14.6	67.2±19.5	102.6±19.9
Ecosystem total	166.2±31.7	329.6±34.5	183.7±68.5	323.7±62.3
Carbon flux (kg C ha⁻¹ yr⁻¹)				
AGB growth	899.4±411.0	1809.5±521.2	798.7±1572.4	684.1±145.0
litterfall	2424.2±283.1	1946.7±361.2	3385.4±1444.6	3970.0±279.8
Fallen log	13.0±3.7	106.1±74.5	986.7±967.3	1034.2±71.6
Standing snag	3.5±1.8	276.7±111.1	220.0±135.7	803.4±62.4
ANPP	3340.1±698.8	4139.0±607.7	5390.8±1655.3	6491.6±559.2
Soil accumulation	243.4±31.1	283.6±138.5	627.6±370.1	397.9±84.2
Ratio of soil accumulation to ANPP (%)	7.3±7.8	6.7±2.8 (3.6~9.2)	11.0±5.3 (5.7~16.3)	6.1±3.3

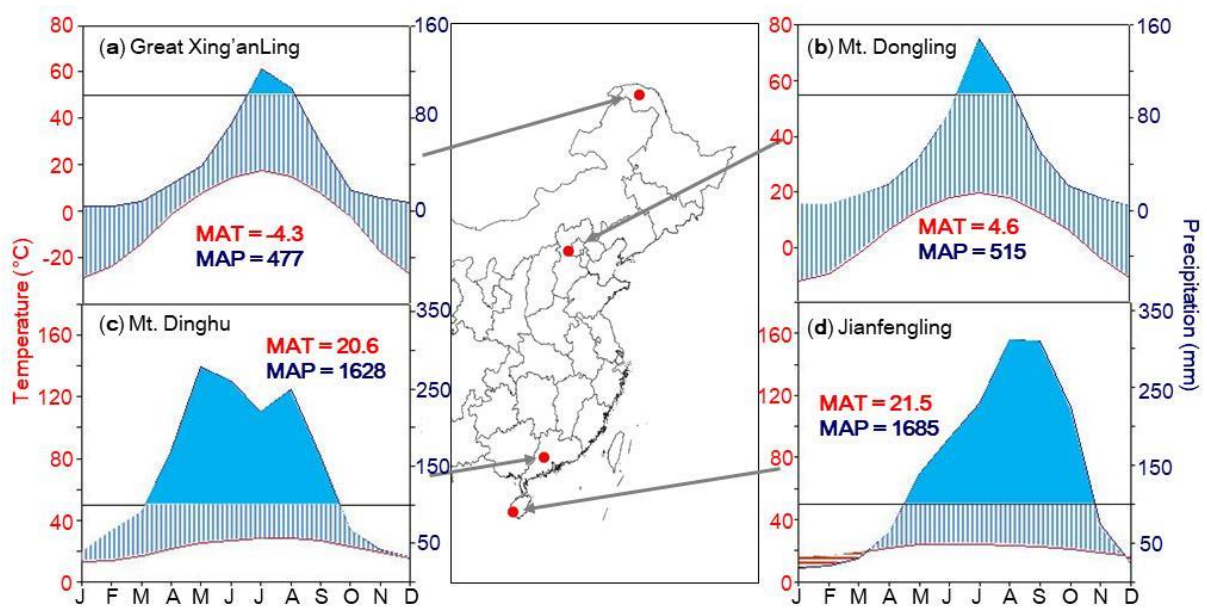
632 Note: Carbon pool of each ecosystem component at the time of the second sampling (2010s).

633 AGB, above-ground biomass; ANPP, above-ground net primary production. For details, see

634 Table S1 in the supplementary information.

635 **Figures**

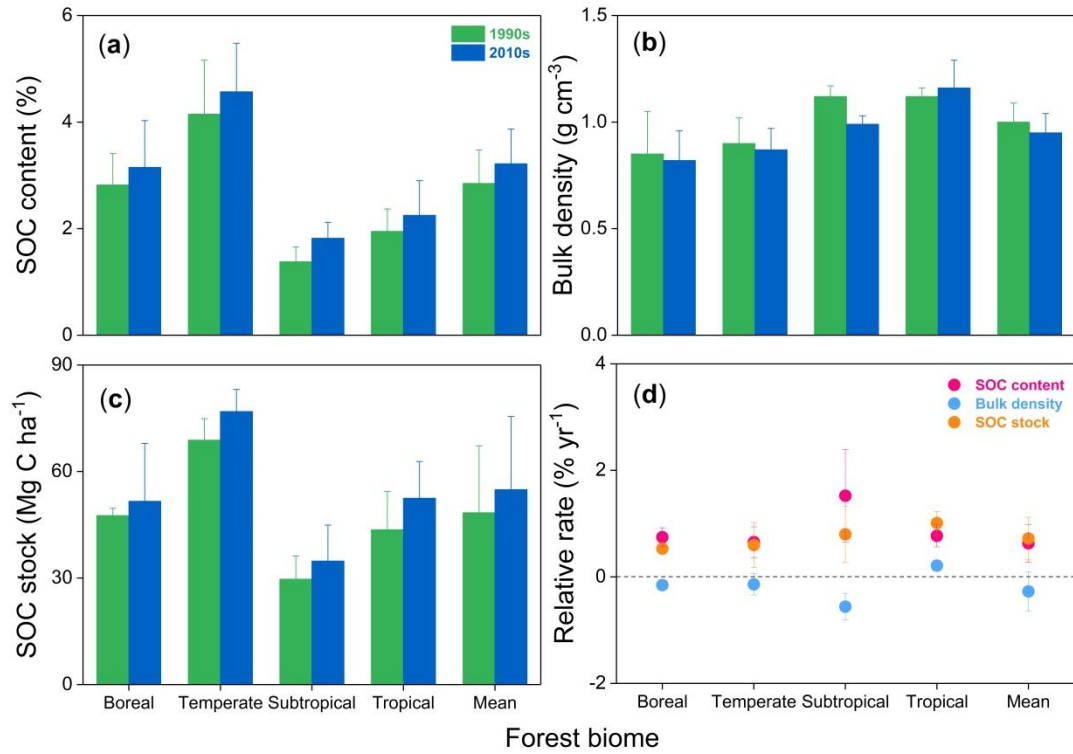
636 **Figure 1.** Locations and climatic conditions of the sites. (a) Great Xing'anling, the boreal site,
637 (b) Mt. Dongling, the temperate site, (c) Mt. Dinghu, the subtropical site, and (d) Jianfengling,
638 the tropical site. The blue and red lines in climatic diagrams are the monthly mean values of
639 precipitation and temperature, respectively. The blue areas indicate the period in the year
640 when the precipitation exceeded 100 mm per month. MAT, mean annual temperature; and
641 MAP, mean annual precipitation.



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644 **Figure 2.** Mean soil organic carbon (SOC) content (a), bulk density (b), SOC stock (c) and
 645 their relative change rates (d) within 0–20 cm soil depth in the 1990s and the 2010s for the
 646 four forest sites in China. For more details, see Table S2 in the supplementary information.



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650 **Figure 3.** Comparison of soil organic carbon (SOC) stocks in eight forest plots in China

651 between the 1990s and the 2010s. The SOC stocks in all forests during the two periods are

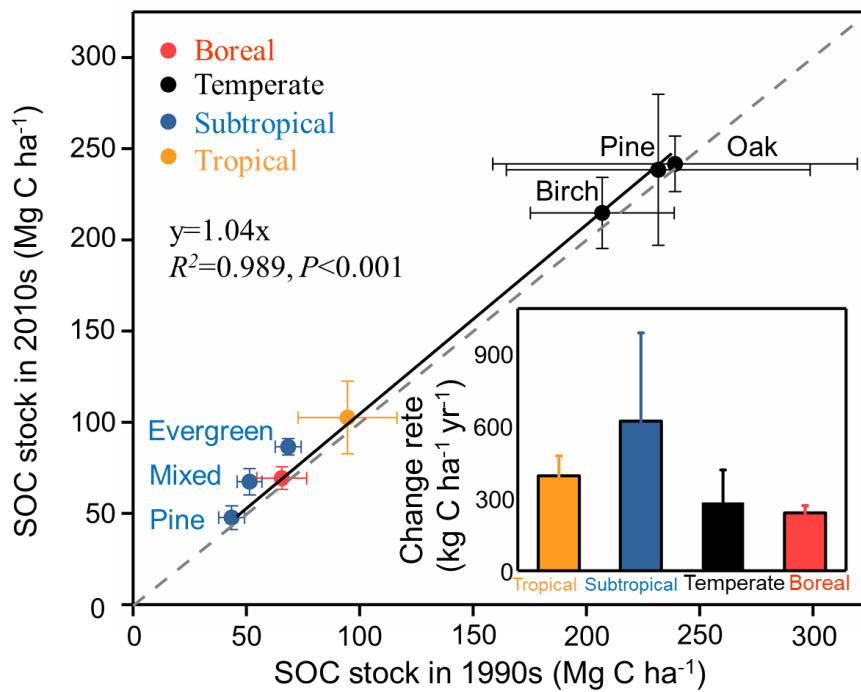
652 above the 1:1 line, suggesting that all these forests have increased their SOC stock during the

653 study period. The inset graph shows the SOC sink rates by forest biome (i.e., boreal,

654 temperate, subtropical, and tropical forests), which are categorized from the eight forest plots.

655 SOC stocks and change rates are presented as means \pm 1 SD. For details, see Fig. 1, Table 1,

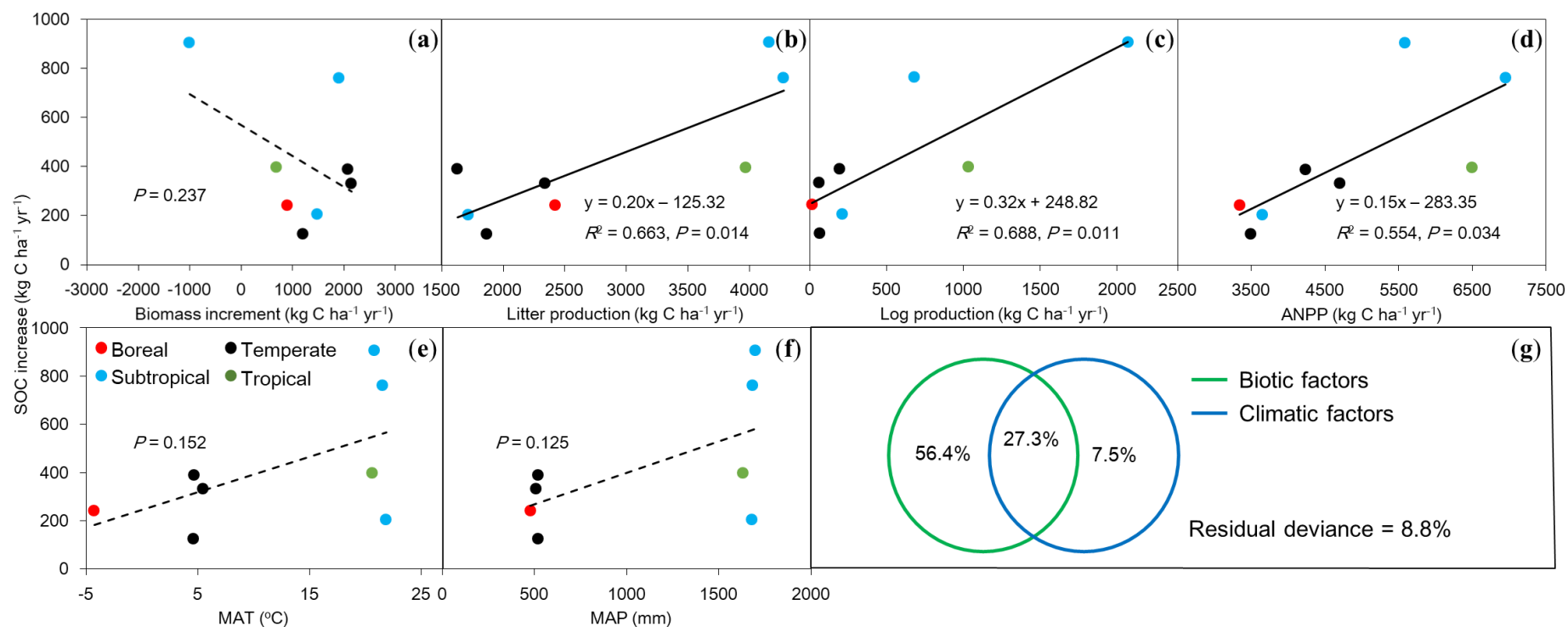
656 and Table S1.



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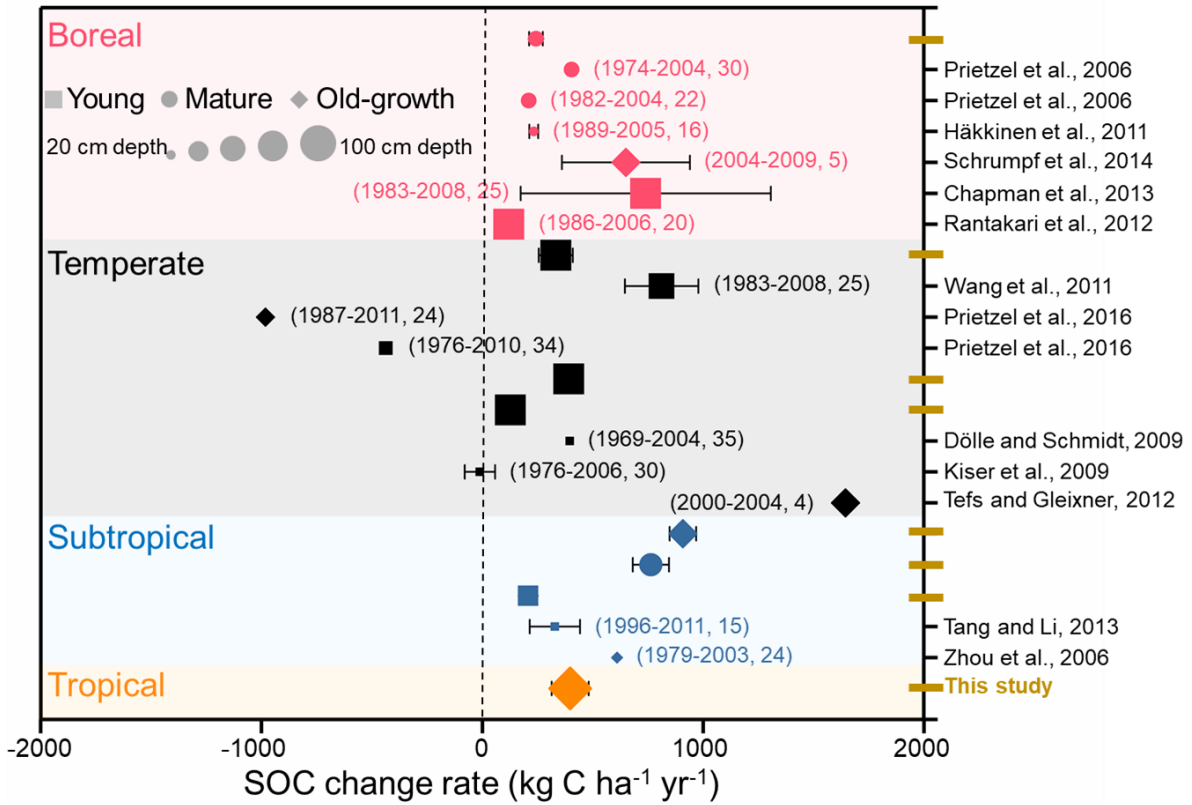
659 **Figure 4.** Relationships between rates of increase in soil organic carbon (SOC) against biotic and climatic factors in eight forests in China. (a)
 660 Biomass increment, (b) litter production, (c) log production, (d) above-ground net primary production (ANPP), (e) mean annual temperature
 661 (MAT), (f) mean annual precipitation (MAP), and (g) the relative effects of biotic (a, b and c) and climatic (e and f) factors on SOC increase
 662 rates ($\text{kg C ha}^{-1} \text{ yr}^{-1}$) using partial regression analyses. Solid lines indicate significant relationships ($P < 0.05$) and dashed lines represent
 663 insignificant trends ($P > 0.05$) between SOC increase rates and biotic and climatic factors.



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666 **Figure 5.** Comparison of the changes in forest soil organic carbon (SOC) stocks according to
 667 repeated soil samplings and/or long-term observation. Different colors, shapes, and sizes
 668 represent different forest biomes, ages, and soil depths, respectively. The numbers in
 669 parentheses indicate the sampling times and intervals between the two soil samplings.



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