



1 **Saturating response of photosynthesis to increasing leaf area index allows selective**  
2 **harvest of trees without affecting forest productivity**

3

4 **Olivier Bouriaud**<sup>1,2\*</sup>, **Ernst-Detlef Schulze**<sup>3</sup>, **Konstantin Gregor**<sup>4</sup>, **Issam Boukhris**<sup>5</sup>, **Peter**  
5 **Högberg**<sup>6</sup>, **Roland Irslinger**<sup>7</sup>, **Phillip Papastefanou**<sup>3</sup>, **Julia Pongratz**<sup>8,9</sup>, **Anja Rammig**<sup>4</sup>,  
6 **Riccardo Valentini**<sup>5</sup>, **Christian Körner**<sup>10</sup>

7

- 8 1. Ștefan cel Mare University of Suceava, Str. Universității 13, 720229 Suceava, Romania.  
9 (obouriaud@usm.ro)  
10 2. ENSG, IGN, Laboratoire d'Inventaire Forestier, 54000 Nancy, France.  
11 3. Max Planck Institute for Biogeochemistry, Jena, Germany. ([dschulze@bgc-jena.mpg.de](mailto:dschulze@bgc-jena.mpg.de),  
12 [papa@bgc-jena.mpg.de](mailto:papa@bgc-jena.mpg.de))  
13 4. Land Surface-Atmosphere Interactions, Technical University of Munich.  
14 ([anja.rammig@tum.de](mailto:anja.rammig@tum.de), [konstantin.gregor@tum.de](mailto:konstantin.gregor@tum.de))  
15 5. University of Tuscia, Dept of Forest Environment and Resources, 01100 Viterbo, Italy.  
16 ([rik@unitus.it](mailto:rik@unitus.it), [issamboukhris@gmail.com](mailto:issamboukhris@gmail.com))  
17 6. Department of Forest Ecology and Management, Swedish University of Agricultural  
18 Sciences, SE-901 83 Umeå, Sweden. ([Peter.Hogberg@slu.se](mailto:Peter.Hogberg@slu.se))  
19 7. Hochschule für Forstwirtschaft Rottenburg, Schadenweilerhof, Rottenburg a.N., Germany  
20 ([irslinger@gmx.de](mailto:irslinger@gmx.de))  
21 8. Ludwig-Maximilians-Universität München (DE) ([julia.pongratz@lmu.de](mailto:julia.pongratz@lmu.de))  
22 9. Max Planck Institute for Meteorology (Hamburg, DE)  
23 10. University of Basel Department of Environmental Sciences Plant Ecology and  
24 Evolution, Schönbeinstrasse 6. CH-4056 Basel. ([ch.koerner@unibas.ch](mailto:ch.koerner@unibas.ch))  
25

26 **Corresponding author:** Olivier Bouriaud, ORCID# 0000-0002-8046-466X,  
27 obouriaud@usm.ro  
28

29

30 **This file includes:**

- 31 Main Text (4904 words)  
32 Figures 1 to 5  
33 Tables 1 to 2  
34 Supplementary 1 to 3  
35

36 **Key Points:**

- 37 • In temperate forests, net CO<sub>2</sub> uptake remains constant after partial harvesting.  
38 • The relation between Gross primary production (GPP) and leaf area index (LAI)  
39 shows saturation above a threshold of 4-5 m<sup>2</sup> m<sup>-2</sup>.  
40 • Harvest-related reduction of leaf area thus has little effects on the uptake if LAI  
41 remains above the threshold.  
42



## 43 **Abstract**

44 Maintaining or increasing forest carbon sinks is considered essential to mitigate the rise of  
45 atmospheric CO<sub>2</sub> concentrations. Harvesting trees is perceived as having negative  
46 consequences on both the standing biomass stocks and the carbon sink strength. However,  
47 harvesting needs to be examined from a forest stand canopy perspective since carbon  
48 assimilation occurs in the canopy. Here we show that a threshold of leaf area exists beyond  
49 which additional leaves do not contribute to CO<sub>2</sub> uptake. The associated biomass can be  
50 harvested without affecting the forest carbon uptake. Based on eddy covariance  
51 measurements we show that CO<sub>2</sub> uptake (GPP) and net ecosystem exchange (NEE) in  
52 temperate forests are of similar magnitude in both unmanaged and sustainably managed  
53 forests, in the order of 1500-1600 gC m<sup>-2</sup> y<sup>-1</sup> for GPP and 542 – 483 gC m<sup>-2</sup> y<sup>-1</sup> for NEE. A  
54 threshold of about 4 m<sup>2</sup> m<sup>-2</sup> LAI (leaf area index) can be used as a threshold of sustainable  
55 harvesting with regard to CO<sub>2</sub> uptake. Simulations based on the LPJ-GUESS model  
56 reproduce the saturation of GPP and NEP and convergence on the LAI threshold range.  
57 Accordingly, in managed forests, trees can be harvested while maintaining a high tree  
58 biomass and carbon sink of the remaining stand. In this case, competition between neighbor  
59 trees in unmanaged forests is replaced by harvest management and provision of wood  
60 products. In unmanaged forests, competition for light, nutrient and water cause self-thinning,  
61 thereby limiting the carbon sink strength.

62  
63

## 64 **Introduction**

65 At times of increasing global change and a demand for wood to replace fossil fuel  
66 products, it becomes of eminent importance to know if forest management and wood  
67 harvest counteracts climate change mitigation. Following the EU definitions on storage and  
68 uptake respectively (EU 2018), two major ways exist by which forests may contribute to the  
69 efforts of climate mitigation: the storage of biomass on site within the forest ecosystem and  
70 the storage of wood in products or their use for substitution of fossil-fuel or carbon-intensive  
71 materials (Gregor et al., 2024). It is assumed that storage and C stocks can be sustained or  
72 increased only by increasing the area of forests, or by stopping wood procurement from  
73 forests (no management). However, halting management will probably have little effects on  
74 the forest carbon sink and long-term stocks at landscape level, considering the environmental  
75 risks associated with climate change that strongly increase the chances of stand collapse  
76 (Roebroek et al., 2023). Furthermore, ageing forests have large biomass stocks, hence a large  
77 C storage, but a very low growth translating into a very low C sink strength once they reach a  
78 natural equilibrium. Forest stocks are thus finite on a given forested land area, with a possible  
79 saturation already reached in European forests (Nabuurs et al. 2013) and this storage capacity  
80 depends on the environmental conditions (Vetter et al., 2005). In contrast, managing forests  
81 for products can be continued nearly endlessly if management is performed in a sustainable  
82 way (Carlowitz, 1713; MCPFE, 1993). According to Pretzsch et al. (2023), self-thinning  
83 losses could be equivalent to wood extraction by management. Luyssaert et al. 2011 also  
84 show that management keeps forest stands close but below self-thinning, albeit at different



85 stand density and volume. Besides ensuring a sustained carbon sink, harvesting wood  
86 products can substitute carbon-intensive materials and the energy use of wood residues and  
87 end-of-life wood products can substitute energy from fossil fuels (Cowie et al., 2021; Schulze  
88 et al., 2022). However, the provision of wood, even from selective cuttings, is considered as a  
89 disturbance for the forest ecosystem, particularly for the carbon sink strength. A reduced  
90 growth may in turn slow down the recuperation of the stocks after harvesting. Thus,  
91 understanding the consequences of selective harvesting on the carbon balance and sink  
92 strength of forests after disturbance is a key element to future projections on the role of  
93 forests to climate change mitigation.

94

95 While harvesting is seen as a disturbance, forest productivity is not necessarily affected by  
96 selective harvesting (including various forms of thinning) across a large range of cutting  
97 intensities (Skovsgaard 2009), suggesting that the assimilation of carbon by forest stands is  
98 not always reduced by harvesting (Amiro et al., 2010; Peters et al., 2013; Bond-Lamberty et  
99 al., 2015; Noormets et al., 2015). The mechanisms involved in explaining the resilience of  
100 productivity to management are based on the enhanced productivity of the remaining trees.  
101 Reasons for this are, for example, improved light conditions, nutrient and water supply and  
102 overall light use (Mund et al., 2010; Saunders et al., 2012; Sohn et al., 2016; del Campo et al.,  
103 2022). Compensatory contribution of subcanopy individuals can locally also be observed  
104 (Vesala et al., 2015). In previous studies several such factors and interaction pathways have  
105 been identified (e.g., Noormets et al., 2015, Fig. 1) but canopy density, as quantified by leaf  
106 area index (LAI, the cumulated area of leaves per ground square meter, expressed in  $\text{m}^2 \text{m}^{-2}$ )  
107 was not taken into consideration despite its key role in  $\text{CO}_2$  uptake.

108

109 Here, we introduce the link between photosynthesis and leaf area as a key element in this  
110 regulation. We hypothesize that LAI is not only the link between the atmosphere and the  
111 plant, but is also central to the response to management. LAI is indeed largely seen as a  
112 driver of both water and carbon fluxes (Reich, 2012; del Campo et al., 2022). Given its high  
113 nutrient demand the production of leaves also affect the nutrient cycle (Ollinger et al., 2008)  
114 and is a potentially crucial driver of forests response to harvesting.

115

116 Harvesting inevitably results in a reduction of the amount of canopy leaves, best quantified  
117 by LAI. It can be assumed that a reduction of LAI would lead to a decrease in productivity.  
118 However, there are indications of a saturation of several canopy processes resulting in a non-  
119 linear relation between leaf area index at stand level (Soimakallio et al., 2021) that make the  
120 response of productivity to disturbances complex and difficult to predict (Glatthorn et al.,  
121 2017; Stuart-Haëntjens et al., 2015). For principal reasons, a rise in LAI must have  
122 diminishing returns in terms of light capture and  $\text{CO}_2$  assimilation, given the exponential light  
123 extinction with canopy depth, as described by Monsi and Saieki 1953 (see Hirose 2005).  
124 Concerning canopy conductance, Schulze et al 1994 concluded to a saturation of around 3.5  
125  $\text{m}^2 \text{m}^{-2}$ . These elements suggest that productivity could have a non-linear response to  
126 reductions of LAI and hence, to management while examined at stand level. Regardless of

127 the mechanisms, however, the effects appear beyond a yet unknown level of biomass  
128 removal. A comparison across temperate forests beyond the site-level analyses is lacking.  
129

130 The impact of harvest on the C cycle is clearly of major importance in the public debate. It is  
131 thus necessary to determine the impact of harvesting on the fluxes of carbon in forests based  
132 on experimental data over a large gradient, and to discuss the limits in the context of leaf area  
133 reduction. In particular, the interactions between management and LAI, and their  
134 consequences for the carbon sink strength need to be determined in order to examine the  
135 consequences of wood harvesting on forests carbon sink strength. Here we intend to show  
136 that sustainable management replaces natural competition by regulating leaf area without  
137 affecting ecosystem fluxes in temperate forests. Based on observational data, literature and  
138 modeling we want to identify mechanistic reasons for this presumption and explore the  
139 possibilities of defining levels of sustainable partial cuttings from the perspective of carbon  
140 fluxes, key to designing forest managements strategies able to maintain high biomass as well  
141 as forest C uptake over multiple cutting cycles.

142

#### 143 **Materials and methods**

144

##### 145 ***Observational flux data based on eddy covariance measurements on the FLUXNET sites.***

146 Overall FLUXNET represents 212 sites worldwide of eddy covariance. In order to measure  
147 the impact of management over the carbon fluxes, we have compiled flux data from the 29  
148 FLUXNET sites (<https://fluxnet.org/data/fluxnet2015-dataset/>) that comprise 19 managed and  
149 10 unmanaged sites (unmanaged is used in the sense of “intact” forests of Roebroek et al.,  
150 2023) with long-term measurements in temperate forests (**Supp. Table S1**). Unfortunately,  
151 there is no site that covers unmanaged conifers. For each site we have compiled the forest  
152 type, stand type, and the fluxes over their monitoring period. We completed these data with  
153 estimations of the LAI during the period 2000-2020 and of the standing biomass.

154 Noticeably, selective harvesting took place on 11 of the managed sites during the period of  
155 flux monitoring, several interventions being quite intensive (Supp. Table S3): for instance,  
156 36% LAI removal in Fontainebleau site (FR), 30% removal in Bily Kriz site (CZ). Other  
157 managed sites have experienced interventions prior to the monitoring but not necessarily  
158 during the monitoring period, given the long periods of time separating interventions.  
159 Furthermore, during the period of flux monitoring, forests experienced repeated events of  
160 storm, drought and heat such as that of 2003, affecting ecosystem fluxes independent of  
161 management.

162 Further, we have compiled LAI estimations for the analyses, for each of the FLUXNET sites.  
163 LAI measurements, however, are not standard across sites, and field measurements are not  
164 always available (5 sites had no field measurements). In this situation remote-sensed  
165 estimations were used instead based on the MCD15A3H version 6.1 MODIS data level 4 (see  
166 **Supplementary Table S1**, with references for each estimation).

167

168 The eddy covariance method does not actually measure the fluxes but instead measures  
169 atmospheric CO<sub>2</sub> concentrations and wind speed which are converted into fluxes, i.e., the net

170 ecosystem exchange (NEE), with different levels of uncertainty. Fluxes data were filtered  
171 based on USTAR threshold levels according to Pastorello et al. (2020) to account for errors of  
172 measurement at low levels of turbulence. Errors have been estimated using bootstrapping 200  
173 times with different friction velocity values.

174 The fluxes of carbon exchanged between the forest ecosystem and the atmosphere are  
175 generally divided into components that are physiologically meaningful: the gross primary  
176 production (GPP) corresponds to the photosynthesis of plants, and the ecosystem respiration  
177 (Reco) releasing CO<sub>2</sub>. Reco consists of plant respiration (so-called autotrophic respiration)  
178 and respiration by heterotrophic organisms (so-called heterotrophic respiration). The NEE  
179 can be estimated by eddy covariance, partitioning into the other elementary fluxes follows  
180 data-driven models (Valentini et al., 2002).

181

182 We compared the mean fluxes during the period of time available of managed and  
183 unmanaged sites. For testing the significance of differences in NEE we used the Wilcoxon  
184 rank test because data were not distributed normally. GPP and Reco have a distribution that  
185 does not differ significantly from a normal distribution. The Mann-Whitney test has been  
186 implemented to compare managed versus unmanaged sites which works with unequal sample  
187 sizes. For GPP and Reco, their distributions being normal, but their variances unequal, the  
188 Welch t-test was used instead. Subsequently, two-way analysis of variance for unbalanced  
189 designs was performed on the data to check if the interaction between the management and  
190 the number of observations by FLUXNET site has a significant effect on GPP, Reco, and  
191 NEE.

192 The relationship between GPP and LAI for the FLUXNET observational site was represented  
193 as a nonlinear asymptotical model. The fitting was based on the nonlinear fit function *nls* (*nls*  
194 standing for nonlinear least square) in R. The pseudo-R<sup>2</sup> represents the proportion of variance  
195 that was explained by the model, in lieu of the R<sup>2</sup> which assumptions cannot be completely  
196 satisfied with nonlinear models (Schabenberger and Pierce 2002). It was computed as  
197  $pseudo-R^2 = 1 - (\text{var}(y_{fit})/\text{var}(y))$ , where  $\text{var}(y_{fit})$  is the variance of the predicted value (GPP  
198 here), while  $\text{var}(y)$  is the variance of the variable (GPP) within the dataset.

199

### 200 ***Harvesting and carbon fluxes***

201 Harvesting takes many forms in forest management and can have different intensities.  
202 Harvesting is defined in a general way as the removal of wood by tree cuttings of any kind,  
203 thus including tending, thinning (targeting either dominant or sub-dominant trees) and  
204 selective cuttings from either status. While short- and medium-term effects of selective  
205 harvesting are being considered, this study will not cover the comparison of forest products  
206 with other bioenergy sources (product and energy substitution). In the following, clear-  
207 cutting, or final felling of a rotation, are treated separately from selective cuttings as they  
208 need an assessment at landscape or management unit-scale. The measurement of carbon  
209 fluxes using the EC method is limited to a plot-scale, with a footprint commonly of about 1  
210 km<sup>2</sup>. Throughout this study, harvesting refers to practices of selective harvesting at low to  
211 moderate intensity as common in temperate forests. For example, removal of harvest



212 residuals is widely seen as negative because of the nutrient and soil carbon depletion it causes  
213 (Achat et al., 2015, Mayer et al., 2020).

214

215

216 ***Modelling analysis of the impact of an increasing LAI gradient on CO<sub>2</sub> fluxes exchanged,***  
217 ***using the process-based model.***

218 To investigate the impact of LAI on GPP, we used the dynamic global vegetation model LPJ-  
219 GUESS v4.1.1 (Smith et al., 2014, Nord, 2021) to simulate the main carbon fluxes (GPP,  
220 Reco and NEP) on all the eddy-covariance sites used in the study. The ability of LPJ-GUESS  
221 to estimate LAI and GPP values worldwide has been proven in numerous studies (e.g., Vella  
222 et al. 2023 and Ito et al. 2017, see also Fig. SF2). Therefore, the model is well suited for the  
223 analyses. LPJ-GUESS simulates detailed vegetation structure (including cohorts of various  
224 ages) based on mechanistic modeling of ecosystem processes including photosynthesis,  
225 establishment, growth, allocation, competition, water and nutrient limitation, and mortality of  
226 plant functional types (PFTs). The latter are represented by parameters defining plant  
227 characteristics such as bioclimatic limits, growth form, or shade-tolerance.

228 In the model, at the end of each year, cumulative net primary productivity is distributed  
229 among the leaf, root, sapwood and heartwood compartments of a plant, based on allometric  
230 equations and allocation routines per year (Smith et al., 2014). LAI is calculated as the  
231 product of the carbon mass of the leaves times the specific leaf area, the specific leaf area  
232 being a PFT parameter. LAI is computed proportionally to the phenology fraction of the  
233 PFTs, that is, the fraction of potential leaf cover. The phenology of a PFT can be raingreen,  
234 summergreen or evergreen. LAI is also influenced by the phenology: depending on the  
235 environmental conditions, the phenology fraction can depend on growing degree days and  
236 drought stress related model states. The amount of light taken up by the canopy, and thus  
237 contributing to carbon allocation, is governed by LAI, based on the Lambert-beer law  
238 (Prentice et al, 1993). The model outputs stand level LAI, taking into account the number of  
239 trees per area and the crown areas of the various cohorts.

240

241 For the LAI analysis, we ran LPJ-GUESS until 2015 using daily climate data from the  
242 FLUXNET2015 sites, i.e., precipitation, temperature, and shortwave radiation. For each site,  
243 we prescribed the forest type as described in Table S2. We used 1000 years for the spinup  
244 period (to bring soil pools close to equilibrium) by detrending and recycling the first 10 years  
245 of each site's climate data. CO<sub>2</sub> concentrations were taken from (Büchner and Reyer, 2022).  
246 We used the default global parametrization of LPJ-GUESS with global PFTs, without any  
247 form of management.

248 Stochastic disturbance intervals were kept at default values while fire was not simulated.

249

## 250 **Results**

251

252 ***Saturated response of fluxes to LAI***



253 Regular management actions were performed in most of the managed sites during the  
254 monitoring period with removals as high as 30% of the stems for some sites during the  
255 monitoring period (**Sup. Table 3**). Managed sites are mostly age-selection (forests stands  
256 composed of trees of similar age, obtained from harvesting trees at a prescribed age) and  
257 plantations. In the whole flux network, there is only one pair of managed and unmanaged  
258 sites: DE-Hai (Hainich, unmanaged) and DE-Lnf (Leinefelde, managed) representing *Fagus*  
259 stands with similar stand densities or basal area.

260

261 The data from the FLUXNET sites show a response of GPP to LAI only for LAI values less  
262 than  $\sim 4 \text{ m}^2 \text{ m}^{-2}$  (**Fig. 1**) but GPP does not increase at higher LAI. It is interesting to note that  
263 most managed forests operate near the range of saturating LAI, despite harvesting. Likewise,  
264 the data shows a saturation of GPP even in managed sites, with values reaching a plateau in  
265 the order of  $1770 \text{ gC m}^{-2} \text{ year}^{-1}$  at LAI values as low as  $4 \text{ m}^2 \text{ m}^{-2}$ . Based on the GPP-LAI  
266 regression, 95% of GPP ( $1680 \text{ gC m}^{-2} \text{ year}^{-1}$ ) is reached at LAI of  $4.5 \text{ m}^2 \text{ m}^{-2}$ . The exact  
267 location of the LAI saturation point can only be approximated given the uncertainty in both  
268 LAI and C flux data. The site at Parco Ticino Forest (Italy) has been fertilized. It indicates the  
269 importance of nutrition in forest ecosystems as a GPP value above  $1800 \text{ gC m}^2 \text{ y}^{-1}$  was  
270 reached at low LAI ( $< 2 \text{ m}^2 \text{ m}^{-2}$ ). However, even with fertilization, the fluxes and LAI values  
271 remain in the range of other sites. Reco had a smaller overall variability than GPP ( $1082 \pm$   
272  $151 \text{ gC m}^2 \text{ y}^{-1}$ ) and showed no response to LAI. Likewise, there was no response to forest  
273 types. The net ecosystem exchange (the balance between photosynthesis and respiration,  $\text{GPP}$   
274  $- \text{Reco} = \text{NEP}$ ) did not show any significant response to LAI, with values largely scattered  
275 around the mean ( $343 \pm 151 \text{ gC m}^{-2} \text{ year}^{-1}$ ).

276 The data represent a mixture of remotely-sensed and field-based LAI for different forest  
277 types. Given the large variability among sites, differences in fluxes for managed and  
278 unmanaged forests in **Figure 1** are not significant (**Table 1**).

279 It is notable that, although not significant, LAI tended to be higher under management ( $4.74 \pm$   
280  $1.33$  for managed sites versus  $4.40 \pm 0.82 \text{ m}^2 \text{ m}^{-2}$  for unmanaged sites, n.s.), despite the  
281 removal of parts of the canopy due to management in the past (**Fig. 2**). LAI was indeed  
282 strongly reduced during the monitoring period by thinnings ranging from 26 to 36% in four  
283 of the managed sites (**Sup Table 3**). For instance, the low ( $3.6 \text{ m}^2 \text{ m}^{-2}$ ) LAI value at site CS-  
284 BK1 (*Picea abies* L.) reflects the 26% removal that occurred at the end of the monitoring  
285 period. The dynamic of LAI on the sites show that the reduction of the LAI by harvesting is  
286 limited to a few years following the harvesting (Sup Fig. 1).

287

### 288 **Responses of fluxes to sustainable harvesting: empirical evidence from eddy covariance**

289 The FLUXNET associated site data showed that past and current management has little  
290 influence on the aboveground biomass and LAI of the sites (**Fig. 2**). Highest biomass was  
291 reached with the old-growth *Eucalyptus regnans* site in Australia (Wallaby Creek site, with  
292  $36.106 \text{ g dry matter m}^{-2}$ ). Unfortunately, there is no managed site of *E. regnans* for  
293 comparison. Otherwise, the range of values is very similar among managed and unmanaged  
294 sites.

295

296 The comparison of the fluxes reveals that the net ecosystem exchange (the balance between  
297 photosynthesis and respiration) was not significantly different in managed and unmanaged  
298 sites ( $-542 \pm 219 \text{ gC m}^{-2} \text{ year}^{-1}$  for managed sites against  $-483 \pm 306 \text{ gC m}^{-2} \text{ year}^{-1}$ , mean  $\pm$   
299 sd for unmanaged sites) over an observation period of more than a decade (**Table 2**).  
300 Management was not a significant effect for GPP or NEP. As shown in **Fig. 3**, Reco and GPP  
301 tended to be higher in managed sites (Reco:  $1213 \pm 121 \text{ gC m}^{-2} \text{ year}^{-1}$  in managed sites  
302 versus  $1079 \pm 98$  in unmanaged sites; GPP:  $1715 \pm 192 \text{ gC m}^{-2} \text{ year}^{-1}$  in managed sites  
303 versus  $1489 \pm 183 \text{ gC m}^{-2} \text{ year}^{-1}$ ). The paired DE-Hai and DE-Lnf unmanaged sites had very  
304 similar values of both GPP ( $1709 \text{ gC m}^{-2} \text{ year}^{-1}$  in the managed site DE-Lnf vs.  $1653 \text{ gC m}^{-2}$   
305  $\text{year}^{-1}$ ) and NEP ( $1189$  vs  $1155 \text{ gC m}^{-2} \text{ year}^{-1}$ ). We investigated whether the forest type had  
306 any influence on the LAI or the fluxes, since conifers tend to have higher LAI values with  
307 few exceptions. A linear model was fitted to the data and showed no significant influence of  
308 management or forest type (**Table 2**). Interactions between forest type and management were  
309 not significant either.

310

#### 311 *Process based model simulations: sensitivity to LAI*

312 We applied the LPJ-GUESS process-based dynamic vegetation-terrestrial ecosystem model to  
313 further investigate the relationship between LAI and GPP, Reco and NEP, on each of the  
314 FLUXNET sites. Within a given site, GPP increased with LAI, near linearly for  $\text{LAI} < 3 \text{ m}^2$   
315  $\text{m}^{-2}$ , showing a clear inflection around this value (**Fig. 4**). Saturation is visible at high LAI  
316 sites at around  $4.5 \text{ m}^2 \text{ m}^{-2}$  and above. Reco followed a very similar pattern, albeit starting at  
317 higher values for very low LAI level and having a smaller increase with LAI than GPP. GPP  
318 and Reco curves cross each other at different LAI values (between 1 and  $3 \text{ m}^2 \text{ m}^{-2}$ ) depending  
319 on the sites, at which point NEP becomes positive but shows a strong saturation after with no  
320 response at all to LAI. Thus, NEP becomes positive (forest acts as a sink) for LAI in excess  
321 of  $3 \text{ m}^2 \text{ m}^{-2}$  but, beyond  $4 \text{ m}^2 \text{ m}^{-2}$ , increases in LAI do not result in increases in NEP.

322

#### 323 **Discussion**

324 With the introduction of the eddy covariance method, long time series of carbon fluxes  
325 became available over a variety of biomes, with most monitoring sites being under regular  
326 forest management (Franz et al., 2018). Based on these time series, our synthesis showed here  
327 that GPP and NEE remain largely unaffected by partial harvesting, as also reported by site-  
328 level analyses for several forest types and species (Granier et al., 2008; Launianen et al.,  
329 2022; Lindroth et al., 2018; Pilegaard et al., 2011; Peichl et al., 2022; Vesala et al., 2005).  
330 Vesala et al., 2005 observed no visible effects of thinnings on the NEE despite the reduction  
331 of LAI from 8 to  $6 \text{ m}^2 \text{ m}^{-2}$  in a Scots pine stand. Granier et al. (2008) reported for Fagus  
332 stands no decrease in either NEE or GPP despite the thinning that decreased LAI from 7.4 to  
333  $4.8 \text{ m}^2 \text{ m}^{-2}$ . These results are in agreement with Herbst et al. (2015) and are confirmed by the  
334 global database of Luyssaert et al. (2007) which shows that managed forests globally  
335 achieved similar, or even larger GPP, than unmanaged forests. A contribution to the lack of  
336 response of eddy covariance fluxes to harvest could be caused by the geographic  
337 displacement of the respiration (typically occurring outside forest when the wood products



338 are burned) and the discrepancy between the location where harvest occurs and the eddy  
339 covariance's footprint (Schulze et al., 2022).

340

341 The harvest effect on LAI appears to be short-term in temperate forests (del Campo et al.,  
342 2022) as also suggested by the available LAI time-series of the sites studied here (**Supp. Fig.**  
343 **SF1**). For instance, according to Granier et al. (2008) LAI in *Fagus* stands was restored to its  
344 pre-thinning level within two years. Disturbances, particularly stand-replacing disturbances  
345 such as windthrow, fire or clear-cuts have a different dimension and need to be evaluated at  
346 landscape scale. Our study deals with thinning operations where the main canopy is reduced  
347 but not removed, keeping LAI beyond or near to its saturation threshold. This also justifies  
348 the choice of focusing on temperate forests where the lower species richness and age ranges  
349 may slow the recovery of carbon uptake to catastrophic events, in contrast to tropical forests  
350 (Brando et al., 2019). For boreal forests, the IBFRA-Report (Högberg et al., 2021) shows that  
351 biomass increased significantly over the past decades only in intensively managed  
352 landscapes, but not in less intensively managed forest landscapes (i.e., landscapes with a high  
353 proportion of unmanaged forests). In the latter, large-scale disturbances such as wildfires  
354 caused losses of biomass and prevented a build-up of forest carbon stocks. In comparison, the  
355 biomass gain in non-managed temperate forests is very small (Roerbroek et al., 2023).  
356 Roerbroek et al. (2023) indeed suggests that betting on increasing the forests stocks is not  
357 only risky, given the increases in weather extremes, but loses the societal benefit of wood  
358 products as well as the potential to store a portion of the C over longer term.

359

360 We propose that most of the decoupling between selective harvesting and CO<sub>2</sub> fluxes is  
361 mediated by the intrinsically nonlinear response of the dominant processes to LAI with a  
362 saturation point reached at 4-5 m<sup>2</sup> m<sup>-2</sup>. This nonlinear response, particularly the existence of a  
363 saturation point, is related to the existence of a fraction of the canopy leaf area not necessary  
364 for productivity but serving other functions such as competition, or redundancy in case of  
365 competition. In forest management it is known that about a third of the green foliated tree  
366 crown can be pruned to improve stem quality without affecting growth (Burschel and Huss  
367 2003). Diffuse light can penetrate deeper into the canopy and reach lower levels of leaves,  
368 but the gain in photosynthesis may not counterbalance the cost of producing and maintaining  
369 saturated canopies. The carbon balance of a living branch may be close to the light  
370 compensation point of photosynthesis and respiration (Schulze 1970), with a photosynthesis  
371 activity just at the level needed to keep a shaded branch alive. Similarly, in the simulations of  
372 the model LPJ-GUESS, small trees with low LAI operate at a higher level of light extinction  
373 due to shadowing by bigger trees, which leads to very low GPP as no direct sunlight can  
374 reach any leaves (Fig. 4). Shadowing also leads to a reduction in Reco, however a minimum  
375 maintenance respiration of the leaves is always needed to sustain functioning of the leaves.  
376 While shade tolerance varies among species (Ameztegui et al., 2016), as reflected by  
377 different maximum LAI values (Valladares and Niinemets 2008), the threshold for light  
378 compensation is probably very similar across forest types or species despite variations in the  
379 canopy structure. This suggests that increasing LAI beyond a demand-driven threshold has  
380 other functions, for instance a competitive function with neighboring trees (Pretzsch and  
381 Schütze 2009, Jucker et al., 2014) not only for light but also for nutrients (e.g., in a pre-



382 emption strategy, Craine and Dybzinski 2013), as a buffer against disturbance (e.g.,  
383 herbivory) and a pool of nutrient reserves, ready for rapid re-allocation in case of sudden  
384 demand (Körner 2009). Anten (2005) shows that canopy photosynthesis models predict LAI  
385 values greater than optimal values for photosynthesis and quote theoretical studies that  
386 conclude to a LAI always exceeding the physiologically optimal value for competitive  
387 purposes. Avoiding a neighbor increases the resources of water and nutrients for the  
388 dominant tree. This surplus fraction is temporarily diminished by selective harvesting,  
389 explaining the lack of response of the main C fluxes at canopy level across a wide range of  
390 LAI. Accordingly, a moderated management can be seen as a substitution of self-thinning  
391 when forest stands are kept close but below self-thinning density levels (Luyssaert et al.,  
392 2011).

393

394 These non-linear relations of a variety of processes with LAI caused by a saturation of GPP  
395 and NEE at values around  $4\text{--}5\text{ m}^2\text{ m}^{-2}$  (see ex. Asner et al., 2003; Hirose 2005) have long  
396 been known, although not previously related to the resilience to selective harvesting. This  
397 includes ecosystem respiration: according to Zhao et al. (2021), at high LAI, respiration -  
398 particularly heterotrophic respiration- increases faster than GPP, which results in a reduction  
399 of NPP for values larger than  $5.6\text{ m}^2\text{ m}^{-2}$ . In our analysis, the model did not go so far as to  
400 project a negative impact of LAI on NEP, but the high cost of producing and maintaining  
401 leaves and particularly shade leaves (Niinemets 2010), largely suggests this. A similar result  
402 was obtained using the model CASTANEA which reproduced the nonlinear responses of  
403 fluxes to LAI (Davi et al., 2006). In contrast, field measurements based on leaf collection,  
404 hemispherical photographs or light transmission through plants, frequently report values in  
405 excess of  $5\text{ m}^2\text{ m}^{-2}$  (e.g., **Figure 3**) and even over  $10\text{ m}^2\text{ m}^{-2}$  in shade-tolerant species  
406 (Schulze et al., 1994; Asner et al., 2003; Law et al., 2001; Iio and Ito, 2014). Out of the 29  
407 sites we studied here (Fig. 1), 16 display LAI values in excess of  $4.5\text{ m}^2\text{ m}^{-2}$ .

408 The lack of scaling between forest biomass and plant respiration (Piao et al., 2010) reflects  
409 the fact that the mass of live tissues -that is, of respiring tissues- is much smaller than that of  
410 total biomass, basically scaling to the parenchyma fraction in sapwood volume and small  
411 branches only (Turner et al., 2019). The disturbance-related increase in soil respiration, for  
412 instance promoted by a short-term increase in root mortality (Raich and Nadelhoffer 1989),  
413 could be comparable in magnitude to the reduction in plant respiration due to the amount of  
414 sapwood harvested and the reduced influx of fresh litter (Davidson et al., 2002), and explain  
415 the invariance of Reco. Surveying or modelling respiration has proved to be particularly  
416 difficult (Phillips et al., 2017; Ciaia et al., 2021) and results in uncertainties, which also  
417 impact confidence in GPP estimates that could hide some effects. The lack of response of  
418 Reco to LAI needs further investigations.

419

420 Unfortunately, the Hainich/Leinefelde *Fagus* sites are the only paired sites of managed versus  
421 unmanaged sites within the flux network. The global eddy-flux network was indeed strongly  
422 focused on climate as a main driver of fluxes, rather than management. The management  
423 gradient represented by these sites is thus not complete, for instance the intensity and types of  
424 management actions are not controlled. Although the unmanaged conifer sites are currently



425 not monitored, the NEP values for unmanaged conifer stands reported in synthesis studies  
426 (Luyssaert et al., 2007) do not suggest that unmanaged conifer stands would behave  
427 differently and have higher a NEP than managed ones. We nevertheless highlight the  
428 potential of such paired studies and hope that research on management will be more  
429 integrated in the future to improve our understanding of its short, medium and long-term  
430 impact on the carbon balance of forests. We also underline the lack of common and frequent  
431 reporting on the aboveground biomass and annual LAI on the FLUXNET sites, on harvested  
432 volumes whenever management interventions occur. Annual measurements of LAI and  
433 repeated study after disturbance should be considered. These critical data would strongly help  
434 measure the impact of management on the carbon cycle.

435

#### 436 **Conclusions**

- 437 • Based on observational and modeling evidence, it appears that LAI regularly exceeds
- 438 levels required to sustain carbon assimilation in naturally growing forest ecosystems.
- 439 • Above its saturation value of  $\sim 4 \text{ m}^2 \text{ m}^{-2}$ , additional increases in LAI are not linked to
- 440 increased productivity, but may contribute to other functions selected in evolution,
- 441 such as competition with adjacent trees, resource storage and buffering against
- 442 herbivory.
- 443 • We can explain the lack of impact of harvesting on the  $\text{CO}_2$  uptake by the existence of
- 444 non-linear processes governed that saturate around LAI values of  $4 \text{ m}^2 \text{ m}^{-2}$ .
- 445 • Selective harvesting does not reduce the forest carbon sink strength when LAI is
- 446 maintained beyond its threshold.
- 447 • This threshold can be used to define sustainable metrics for sustainable harvesting, as
- 448 those that do not impact the carbon sink strength of the forest stand.
- 449 • Harmonized and periodic measurements of the forest carbon stock and LAI, and of
- 450 harvesting impacts on these, should be promoted at flux sites.

451

452

453

454 **Author Contributions:** Conceptualization, O.B., E.D.S. and C.K.; methodology, O.B. and  
455 E.D.S.; writing original draft preparation O.B. and E.D.S. All authors contributed to the  
456 writing, and reviewed the manuscript.

457

458 **Competing Interest Statement:** At least one of the (co-)authors is a member of the editorial board of  
459 Biogeosciences.

460

#### 461 **Acknowledgements**

462 This work was supported by a grant of the Ministry of Research, Innovation and Digitization,  
463 CNCS- UEFISCDI, project number PN-III-P4-PCE-2021-1677, within PNCDI III. KG  
464 acknowledges funding by the Bavarian State Ministry of Science and the Arts in the context  
465 of the Bavarian Climate Research Network (bayklif) through its BLIZ project (Grant No.  
466 7831-26625- 2017, \url{[www.bayklif-bliz.de](http://www.bayklif-bliz.de)}). RV and IB are supported by AGRITECH —  
467 PNRR (Italian National Plan of Recovery and Resilience), identification code CN0000022



468 WP 4.3.3. Authors are very grateful to Susan Trumbore for her comments and suggestions on  
469 the manuscript.

470

#### 471 **Open research**

472 The data presented and analyzed in this study are available directly from the supplementary  
473 information files, in tables S1 to S3. These tables also contain references to data sources.

474 Figures were made with R version 4.2 (R Core Team, 2021) (<https://www.R-project.org/>).

475

#### 476 **References**

477 EE Agency, Carbon sink (<https://www.eea.europa.eu/help/glossary/eea-glossary/carbon-sink#:~:text=Forests%20and%20other%20ecosystems%20that,atmosphere%20and%20offsetting%20CO2%20emissions.>). Accessed august 2023.

480 Achat, D. L., Deleuze, C., Landmann, G., Pousse, N., Ranger, J., and Augusto, L.: Quantifying  
481 consequences of removing harvesting residues on forest soils and tree growth—a meta-analysis.  
482 *Forest Ecol. Manag.*, 348, 124–141, 2015.

483 Ameztegui, A., Paquette, A., Shipley, B., Heym, M., Messier, C., and Gravel, D.: Shade  
484 tolerance and the functional trait: Demography relationship in temperate and boreal forests.  
485 *Funct. Ecol.*, 31 (4), 821–830, 2017.

486 Amiro, B. D., Barr, A. G., Barr, J. G., Black, T. A., Bracho, R., Brown, M., Chen, J., Clark, K.  
487 L., Davis, K. J., Desai, A. R., Dore, S., Engel, V., Fuentes, J. D., Goldstein, A. H., Goulden, M.  
488 L., Kolb, T. E., Lavigne, M. B., Law, B. E., Margolis, H. A., Martin, T., McCaughey, J. H.,  
489 Misson, L., Montes-Helu, M., Noormets, A., Randerson, J. T., Starr, G., and Xiao, J.: Ecosystem  
490 carbon dioxide fluxes after disturbance in forests of North America, *J. Geophys. Res.-Biogeo.*,  
491 115, G00K02, <https://doi.org/10.1029/2010JG001390>, 2010.

492 Anten, N. P.: Optimal photosynthetic characteristics of individual plants in vegetation stands  
493 and implications for species coexistence. *Ann. Bot.*, 95(3), 495-506, 2005.

494 Asner, G. P., Scurlock, J. M., and A. Hicke, J.: Global synthesis of leaf area index observations:  
495 implications for ecological and remote sensing studies. *Glob. Ecol. Biogeogr.*, 12 (3), 191–205,  
496 2003.

497 Bond-Lamberty, B., Fisk, J. P., Holm, J. A., Bailey, V., Bohrer, G., and Gough, C. M.:  
498 Moderate forest disturbance as a stringent test for gap and big-leaf models. *Biogeosciences*, 12  
499 (2), 513–526, 2015.

500 Brando, P.M., Silvério, D., Maracahipes-Santos, L., Oliveira-Santos, C., Levick, S.R., Coe,  
501 M.T., Migliavacca, M., Balch, J.K., Macedo, M.N., Nepstad, D.C. and Maracahipes, L. :  
502 Prolonged tropical forest degradation due to compounding disturbances: Implications for CO<sub>2</sub>  
503 and H<sub>2</sub>O fluxes. *Glob. Change Biol.*, 25 (9), 2855–2868, 2019.

504 Burschel, P., and Huss, J.: Grundriss des Waldbaus ein Leitfaden für Stadium und Praxis. 3.  
505 unchanged edition. Eugen Ulmer Verlag, Stuttgart (Hohenheim), 2003.

506 Büchner, M., and Reyer, P.: ISIMIP3b atmospheric composition input data (v1.1). ISIMIP  
507 Repository. <https://doi.org/10.48364/ISIMIP.482153.1>, 2022.

508 Caprez, R., Niklaus, P. A., and Körner, C.: Forest soil respiration reflects plant productivity  
509 across a temperature gradient in the alps. *Oecol.*, 170, 1143–1154, 2012.



- 510 Chen, J. M., Mo, G., Pisek, J., Liu, J., Deng, F., Ishizawa, M., and Chan, D.: Effects of foliage  
511 clumping on the estimation of global terrestrial gross primary productivity. *Glob. Biogeo.*  
512 *Cycles*, 26 (1), 2012.
- 513 Ciais, P., Yao, Y., Gasser, T., Baccini, A., Wang, Y., Lauerwald, R., Peng, S., Bastos, A., Li,  
514 W., Raymond, P.A. and Canadell, J.G.: Empirical estimates of regional carbon budgets imply  
515 reduced global soil heterotrophic respiration. *Natl Sci. Rev.*, 8 (2), nwaal45, 2021.
- 516 Cowie, A. L., Berndes, G., Bentsen, N. S., Brandao, M., Cherubini, F., Egnell, G., Brendan, G.,  
517 Guvstavsson, L., Hanwinkel, M., Harris, Z., Johnsson, F., Junginger, M., Kline, K., Koponen,  
518 K., Koppejan, J., Kraxner, F., Lamers, P., Majer, S., Marland, E., Nabuurs, G.-J., Pelkmans, L.  
519 Sathre, R., Schaub, M., Tattersal Smith, C., Soimakallio, S., Van der Hilst, F., Woods, J. and  
520 Ximenes, F.A.: Applying a science-based systems perspective to dispel misconceptions about  
521 climate effects of forest bioenergy. *Glob. Change Biol. Bioenergy*, 13 (8), 1210–1231, 2021.
- 522 Craine, J. M., and Dybzinski, R.: Mechanisms of plant competition for nutrients, water and  
523 light. *Funct. Ecol.*, 27(4), 833-840, 2013.
- 524 Davi, H., Bouriaud, O., Dufrêne, E., Soudani, K., Pontailier, J.Y., Le Maire, G., François, C.,  
525 Bréda, N., Granier, A. and Le Dantec, V.: Effect of aggregating spatial parameters on modelling  
526 forest carbon and water fluxes. *Agric. For. Meteorol.*, 139 (3-4), 269–287, 2006.
- 527 Davidson, E.A., Savage, K., Bolstad, P., Clark, D.A., Curtis, P.S., Ellsworth, D.S., Hanson, P.J.,  
528 Law, B.E., Luo, Y., Pregitzer, K.S. and Randolph, J.C.: Belowground carbon allocation in  
529 forests estimated from litterfall and IRGA-based soil respiration measurements. *Agric. For.*  
530 *Meteorol.*, 113 (1-4), 39–51, 2002.
- 531 del Campo, A. D., Otsuki, K., Serengil, Y., Blanco, J. A., Yousefpour, R., and Wei, X.:  
532 A global synthesis on the effects of thinning on hydrological processes:  
533 Implications for forest management. *Forest Ecol. Manag.*, 519, 120324, 2022.
- 534 Franz, D., Acosta, M., Altimir, N., Arriga, N., Arrouays, D., Aubinet, M., Aurela, M., Ayres, E.,  
535 López-Ballesteros, A., Barbaste, M. and Berveiller, D.: Towards long-term standardised carbon  
536 and greenhouse gas observations for monitoring Europe’s terrestrial ecosystems: a review. *Intl.*  
537 *Agrophys.*, 32(4), 439-455, 2018.
- 538 Glatthorn, J., Pichler, V., Hauck, M., and Leuschner, C.: Effects of forest management on stand  
539 leaf area: Comparing beech production and primeval forests in Slovakia. *Forest Ecol. Manag.*,  
540 389, 76–85, 2017.
- 541 Granier, A., Bréda, N., Longdoz, B., Gross, P., and Ngao, J.: Ten years of fluxes and stand  
542 growth in a young beech forest at Hesse, North-Eastern France. *Ann. For. Sci.*, 65 (7), 1, 2008.
- 543 Gregor, K., Krause, A., Reyer, C. P., Knoke, T., Meyer, B. F., Suvanto, S., and Rammig, A.:  
544 Quantifying the impact of key factors on the carbon mitigation potential of managed temperate  
545 forests. *Carbon Balance Manage.*, 19(1), 10, 2024.
- 546 Herbst, M., Mund, M., Tamrakar, R., and Knohl, A.: Differences in carbon uptake and water use  
547 between a managed and an unmanaged beech forest in central Germany. *Forest Ecol. Manag.*,  
548 355, 101–108, 2015.
- 549 Hirose, T.: Development of the Monsi–Saeki theory on canopy structure and function. *Ann.*  
550 *Bot.*, 95 (3), 483–494, 2005.
- 551 Högborg, P., Ceder, L.A., Astrup, R., Binkley, D., Dalsgaard, L., Egnell, G., Filipchuk, A.,  
552 Genet, H., Ilintsev, A., Kurz, W.A. and Laganière, J.: Sustainable boreal forest management  
553 challenges and opportunities for climate change mitigation. Swedish Forest Agency Report No.  
554 11. ISBN 978-91-986297-3-6, 2011.



- 555 Iio, A., and Ito, A.: A global database of field-observed leaf area index in woody plant species,  
556 1932-2011, <https://doi.org/10.3334/ORNLDAAC/1231>, 2014.
- 557 Ito, A., Nishina, K., Reyer, C.P., François, L., Henrot, A.J., Munhoven, G., Jacquemin, I., Tian,  
558 H., Yang, J., Pan, S. and Morfopoulos, C.: Photosynthetic productivity and its efficiencies in  
559 ISIMIP2a biome models: benchmarking for impact assessment studies. *Environ. Res. Lett.*,  
560 12(8), 085001, 2017.
- 561 Jucker, T., Bouriaud, O., Avacaritei, D., Danila, I., Duduman, G., Valladares, F., and Coomes,  
562 D. A. : Competition for light and water play contrasting roles in driving diversity–productivity  
563 relationships in Iberian forests. *J. Ecol.*, 102 (5), 1202–1213, 2014.
- 564 Körner, C.: Responses of humid tropical trees to rising CO<sub>2</sub>. *Annu. Rev. Ecol. Evol. Syst.*, 40,  
565 61–79, 2009.
- 566 Launiainen, S., Katul, G.G., Leppä, K., Kolari, P., Aslan, T., Grönholm, T., Korhonen, L.,  
567 Mammarella, I. and Vesala, T.: Does growing atmospheric CO<sub>2</sub> explain increasing carbon sink  
568 in a boreal coniferous forest? *Glob. Change Biol.*, 28 (9), 2910–2929, 2022.
- 569 Law, B. E., Cescatti, A., and Baldocchi, D. D.: Leaf area distribution and radiative transfer in  
570 open-canopy forests: implications for mass and energy exchange. *Tree Physiol.*, 21 (12-13),  
571 777–787, 2001.
- 572 Lindroth, A., Holst, J., Heliasz, M., Vestin, P., Lagergren, F., Biermann, T., Cai, Z. and Mölder,  
573 M.: Effects of low thinning on carbon dioxide fluxes in a mixed hemiboreal forest. *Agric. For.*  
574 *Meteorol.*, 262, 59–70, 2018.
- 575 LU Vienna, Improved pan-European indicators for sustainable forest management in Fourth  
576 ministerial conference on the protection of forests in Europe. Ministerial Conference on the  
577 Protection of Forests in Europe, Vienna, Austria. [online] URL: <http://timberold.unece.org/fileadmin/DAM/publications/improved-indicators-sfm.pdf>, 2003.
- 579 Luysaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichstein, M., Papale, D., Piao, S.L.,  
580 Schulze, E.D., Wingate, L., Matteucci, G. and Aragao, L.E.: CO<sub>2</sub> balance of boreal, temperate,  
581 and tropical forests derived from a global database. *Glob. Change Biol.*, 13 (12), 2509–2537,  
582 2007.
- 583 Mayer, M., Prescott, C., Abaker, W., Augusto, L., Cécillon, L., Ferreira, G., and Vesterdal, L.:  
584 Influence of forest management activities on soil organic carbon stocks: a knowledge synthesis.  
585 *Forest Ecol. Manag.*, 466: 118127, 2020.
- 586 Mund, M., Kutsch, W. L., Wirth, C., Kahl, T., Knohl, A., Skomarkova, M. V., and Schulze, E.-  
587 D.: The influence of climate and fructification on the inter-annual variability of stem growth and  
588 net primary productivity in an old-growth, mixed beech forest. *Tree Physiol.*, 30 (6), 689–704,  
589 2010.
- 590 Nabuurs, G.J., Thürig, E., Heidema, N., Armolaitis, K., Biber, P., Cienciala, E., Kaufmann, E.,  
591 Mäkipää, R., Nilsen, P., Petritsch, R. and Pristova, T.: Hotspots of the European forests carbon  
592 cycle. *Forest Ecol. Manag.*, 256(3), 194-200, 2008.
- 593 Niinemets, Ü.: A review of light interception in plant stands from leaf to canopy in different plant  
594 functional types and in species with varying shade tolerance. *Ecol. Res.*, 25, 693–714, 2010.
- 595 Noormets, A., Epron, D., Domec, J.-C., McNulty, S., Fox, T., Sun, G., and King, J.: Effects of  
596 forest management on productivity and carbon sequestration: A review and hypothesis. *Forest*  
597 *Ecol. Manag.*, 355, 124–140, 2015.



- 598 Nord, J., Anthoni, P., Gregor, K., Gustafson, A., Hantson, S., Lindeskog, M., Meyer, B., Miller,  
599 P., Nieradzick, L., Olin, S. and Papastefanou, P.: (2021). LPJ-GUESS Release v4. 1.1 model code,  
600 Zenodo [code], 2021.
- 601 Ollinger, S. V., Richardson, A. D., Martin, M. E., Hollinger, D. Y., Frohling, S. E., Reich, P. B.,  
602 Plourde, L.C., Katul, G.G., Munger, J.W., Oren, R. and Smith, M.L.: Canopy nitrogen, carbon  
603 assimilation, and albedo in temperate and boreal forests: Functional relations and potential  
604 climate feedbacks. *Proc. Natl Acad. Sci.*, 105 (49), 19336–19341, 2008.
- 605 Pan, N., Wang, S., Wei, F., Shen, M., and Fu, B.: Inconsistent changes in NPP and LAI  
606 determined from the parabolic LAI versus NPP relationship. *Ecol. Indic.*, 131, 108134, 2021.
- 607 Pastorello, G., Trotta, C., Canfora, E., Chu, H., Christianson, D., Cheah, Y. W., Poindexter, C.,  
608 Chen, J., Elbashandy, A., Humphrey, M. and Isaac, P.: The FLUXNET2015 dataset and the  
609 ONEFlux processing pipeline for eddy covariance data. *Sci. Data*, 7(1), 225, 2020.
- 610 Peichl, M., Martínez-García, E., Fransson, J. E., Wallerman, J., Laudon, H., Lundmark, T., and  
611 Nilsson, M. B.: Landscape-variability of the carbon balance across managed boreal forests. *Glob.*  
612 *Change Biol.*, 2022.
- 613 Peters, E. B., Wythers, K. R., Bradford, J. B., and Reich, P. B.: Influence of disturbance on  
614 temperate forest productivity. *Ecosystems*, 16, 95–110, 2013.
- 615 Phillips, C.L., Bond-Lamberty, B., Desai, A.R., Lavoie, M., Risk, D., Tang, J., Todd-Brown, K.  
616 and Vargas, R.: The value of soil respiration measurements for interpreting and modeling  
617 terrestrial carbon cycling. *Plant Soil*, 413 (1), 1–25, 2017.
- 618 Piao, S., Luysaert, S., Ciais, P., Janssens, I. A., Chen, A., Cao, C., Fang, J., Friedlingstein, P.,  
619 Luo, Y. and Wang, S.: Forest annual carbon cost: A global-scale analysis of autotrophic  
620 respiration. *Ecology*, 91 (3), 652–661, 2010.
- 621 Pilegaard, K., Ibrom, A., Courtney, M. S., Hummelshøj, P., and Jensen, N. O.: Increasing net CO<sub>2</sub>  
622 uptake by a Danish beech forest during the period from 1996 to 2009. *Agric. For. Meteorol.*, 151  
623 (7), 934–946, 2011.
- 624 Prentice, I. C., Sykes, M. T., and Cramer, W.: A simulation model for the transient effects of  
625 climate change on forest landscapes. *Ecol. Mod.*, 65(1-2), 51-70, 1993.
- 626 Pretzsch, H., del Río, M., Arcangeli, C., Bielak, K., Dudzinska, M., Forrester, D. I., Ledermann,  
627 T., Matthews, R., Nagel, R., Ningre, F.: Competition-based mortality and tree losses. An essential  
628 component of net primary productivity. *Forest Ecol. Manag.*, 544, 121204, 2023.
- 629 Pretzsch, H., and Schütze, G.: Transgressive overyielding in mixed compared with pure stands of  
630 Norway spruce and European beech in Central Europe: evidence on stand level and explanation  
631 on individual tree level. *Eur. J. For. Res.*, 128, 183–204, 2009.
- 632 Raich, J. W., and Nadelhoffer, K. J.: Belowground carbon allocation in forest ecosystems: global  
633 trends. *Ecology*, 70 (5), 1346–1354, 1989.
- 634 Reich, P. B.: Key canopy traits drive forest productivity. *Proceedings of the Royal Society B:*  
635 *Biol. Sci.*, 279 (1736), 2128–2134, 2012.
- 636 Roebroek, C. T., Duveiller, G., Seneviratne, S. I., Davin, E. L., and Cescatti, A.: Releasing global  
637 forests from human management: How much more carbon could be stored? *Science*, 380 (6646),  
638 749–753, 2023.
- 639 Saunders, M., Tobin, B., Black, K., Gioria, M., Nieuwenhuis, M., and Osborne, B.: Thinning  
640 effects on the net ecosystem carbon exchange of a Sitka spruce forest are temperature-dependent.  
641 *Agric. For. Meteorol.*, 157, 1–10, 2012.



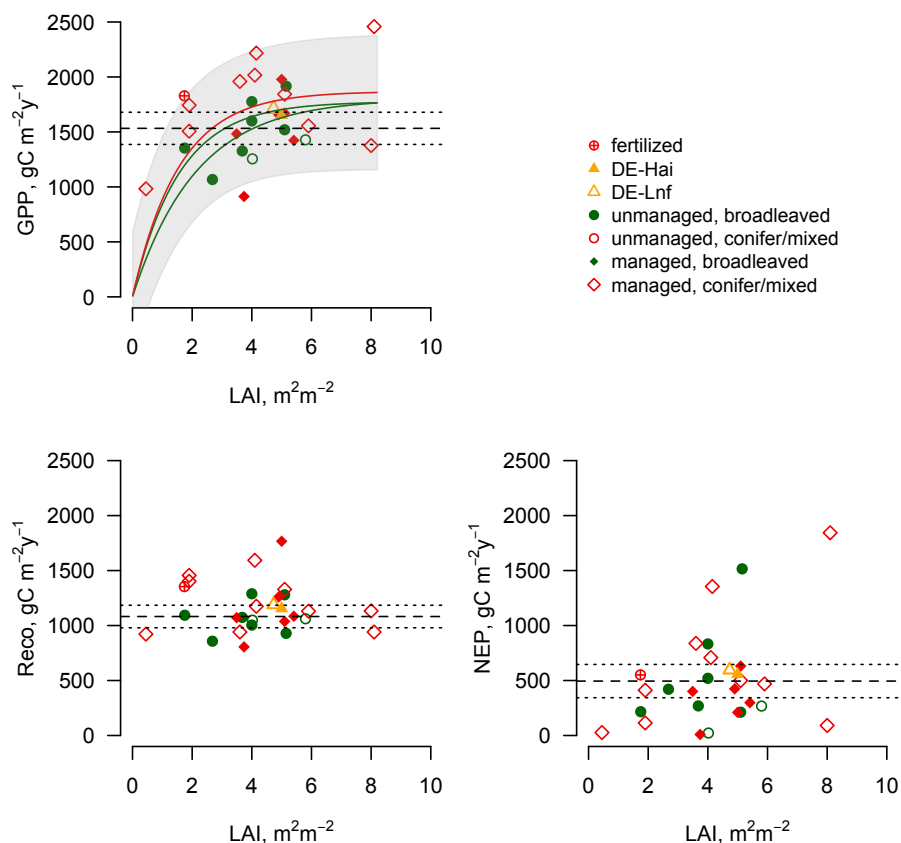
- 642 Schabenberger, O., Pierce, F.J.: Contemporary statistical models for the plant and soil  
643 sciences. Taylor and Francis, CRC Press, Books, 2002.
- 644 Schulze, E.-D.: Der CO<sub>2</sub>-gaswechsel der Buche (*Fagus sylvatica* L.) in abhängigkeit von den  
645 Llimafaktoren im Freiland. Flora, 159 (1-2), 177–232, 1970.
- 646 Schulze, E. D., Bouriaud, O., Irslinger, R., and Valentini, R.: The role of wood harvest from  
647 sustainably managed forests in the carbon cycle. Ann. For. Sci., 79 (1), 1–13, 2022.
- 648 Schulze, E.-D., Kelliher, F. M., Körner, C., Lloyd, J., and Leuning, R.: Relationships among  
649 maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and  
650 plant nitrogen nutrition: a global ecology scaling exercise. Ann. Rev. Ecol. Syst., 25 (1), 629–  
651 662, 1994.
- 652 Skovsgaard, J. P.: Analysing effects of thinning on stand volume growth in relation to site  
653 conditions: a case study for even-aged sitka spruce (*Picea sitchensis* (bong.) carr.). Forestry, 82  
654 (1), 87–104, 2009.
- 655 Smith, B., Wärlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., and Zaehle, S.:  
656 Implications of incorporating n cycling and n limitations on primary production in an individual-  
657 based dynamic vegetation model. Biogeosciences, 11 (7), 2027–2054, 2014.
- 658 Sohn, J. A., Saha, S., and Bauhus, J.: Potential of forest thinning to mitigate drought stress: A  
659 meta-analysis. Forest Ecol. Manag., 380, 261–273, 2016.
- 660 Soimakallio, S., Kalliokoski, T., Lehtonen, A., and Salminen, O.: On the trade-offs and synergies  
661 between forest carbon sequestration and substitution. Mitigation and Adaptation Strategies for  
662 Global Change, 26 (1), 1–17, 2021.
- 663 Stuart-Haëntjens, E. J., Curtis, P. S., Fahey, R. T., Vogel, C. S., and Gough, C. M.: Net primary  
664 production of a temperate deciduous forest exhibits a threshold response to increasing disturbance  
665 severity. Ecology, 96 (9), 2478–2487, 2015.
- 666 Thurner, M., Beer, C., Crowther, T., Falster, D., Manzoni, S., Prokushkin, A., and Schulze, E.-D.:  
667 Sapwood biomass carbon in northern boreal and temperate forests. Glob. Ecol. Biogeogr., 28 (5),  
668 640–660, 2019.
- 669 Valentini, R., Matteucchi, G., Dolman, H., Schulze, E.-D., Rebmann, C., Moors, E. J., Granier,  
670 A., Gross, P., Jensen, N. O., Pilgaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T.,  
671 Aubinet, M., Ceulemans, R., Kowalski, A. S., Vesala, T., Rannik, Ü., Berbigier, P., Lousteau, D.,  
672 Gudmundsson, J., Thorgairsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J.,  
673 Montagnani, L., Minerbi, S., and Jarvis, P. G.: Respiration as the main determinant of carbon  
674 balance in European forests, Nature, 404, 861–865, 2000.
- 675 Valladares, F., and Niinemets, Ü.: Shade tolerance, a key plant feature of complex nature and  
676 consequences. Ann. Rev. Ecol. Syst., 39, 237–257, 2008.
- 677 Vella, R., Forrest, M., Lelieveld, J., and Tost, H.: Isoprene and monoterpene simulations  
678 using the chemistry–climate model EMAC (v2. 55) with interactive vegetation from LPJ-  
679 GUESS (v4. 0). Geoscientific Model Development, 16(3), 885-906, 2023.
- 680 Vesala, T., Suni, T., Rannik, U., Keronen, P., Markkanen, T., Seivanto, S., Gronholm, T.,  
681 Smolander, S., Kulmala, M., Ilvesniemi, H., Ojansuu, R., Uotila, A., Levula, J., Makela, A.,  
682 Pumpanen, J., Kolari, P., Kulmala, L., Altimir, N., Berninger, F., Nikinmaa, E., and Hari, P.:  
683 Effect of thinning on surface fluxes in a boreal forest, Global Biogeochem. Cy., 19, GB2001,  
684 doi:10.1029/2004gb002316, 2005.





- 685 Vetter, M., Wirth, C., Böttcher, H., Churkina, G., Schulze, E.-D., Wutzler, T., and Weber, G.:  
686 Partitioning direct and indirect human-induced effects on carbon sequestration of managed  
687 coniferous forests using model simulations and forest inventories. *Glob. Change Biol.*, 11 (5),  
688 810–827, 2005.
- 689 Vienna, L. U.: Improved pan-European indicators for sustainable forest management. In Fourth  
690 ministerial conference on the protection of forests in Europe. ministerial conference on the  
691 protection of forests in Europe, Vienna, Austria.[online] url:  
692 <http://timberold.unece.org/fileadmin/dam/publications/improved-indicators-sfm.pdf>, 2003.
- 693 Viovy, N.: CRUNCEP version 7 — atmospheric forcing data for the community land model.  
694 Research Data Archive at the National Center for Atmospheric Research, Computational and  
695 Information Systems Laboratory. Accessed February 17, 2019.
- 696 Von Carlowitz, H. C.: *Sylvicultura oeconomica*. Braun, 1732.
- 697 Zhao, W., Tan, W., and Li, S.: High leaf area index inhibits net primary production in global  
698 temperate forest ecosystems. *Environ. Sci. Pollut. Res. Int.*, 28 (18), 22602–22611, 2021.
- 699 Zheng, G., and Moskal, L. M.: Retrieving leaf area index (LAI) using remote sensing: theories,  
700 methods and sensors. *Sensors*, 9 (4), 2719–2745, 2009.

701 **Figures and Tables**

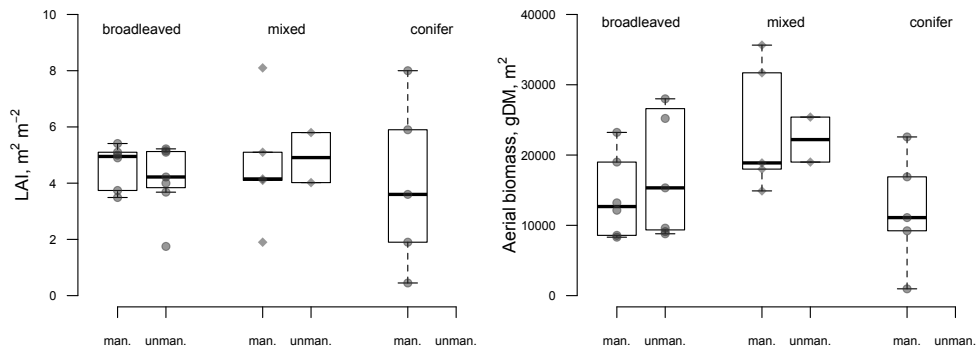


702

703 **Figure 1.** Relation between the GPP, the Reco, the NEP (= -NEE) and the LAI on the eddy  
704 covariance sites (FLUXNET sites, see Supp. Table S1,2) of both managed and unmanaged  
705 temperate forests per stand types.

706 The dashed lines represent mean and confidence interval of the GPP and NEP across all sites.  
707 Curves show the fits for broadleaves (green), conifers and mixed forests (red), and all sites  
708 together (black). The gray band represents the confidence interval of the regression on all  
709 sites. The fertilized site is identified (Parco Ticino), along with the couple DE-Hai  
710 (unmanaged) and DE-Lnf (managed). The exponential models illustrate the tendencies (Tab.  
711 1),  $\pm 10\%$  confidence intervals are displayed in gray.

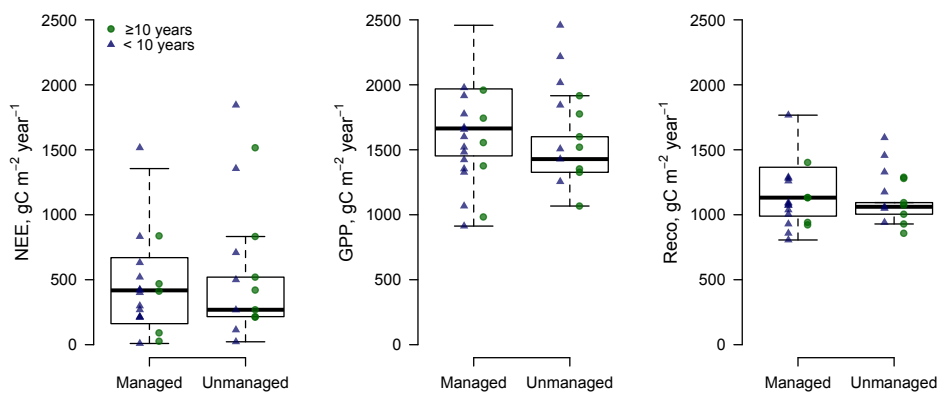
712



713

714 **Figure 2.** Comparison of the LAI and aboveground biomass values for the managed and  
715 unmanaged sites, depending on the forest type. The site AU-Wac (Australia, natural  
716 *Eucalyptus regnans*) is an extreme value due to low decomposition (Supp. Fig. 2) and was  
717 not included in the biomass comparison.

718



719

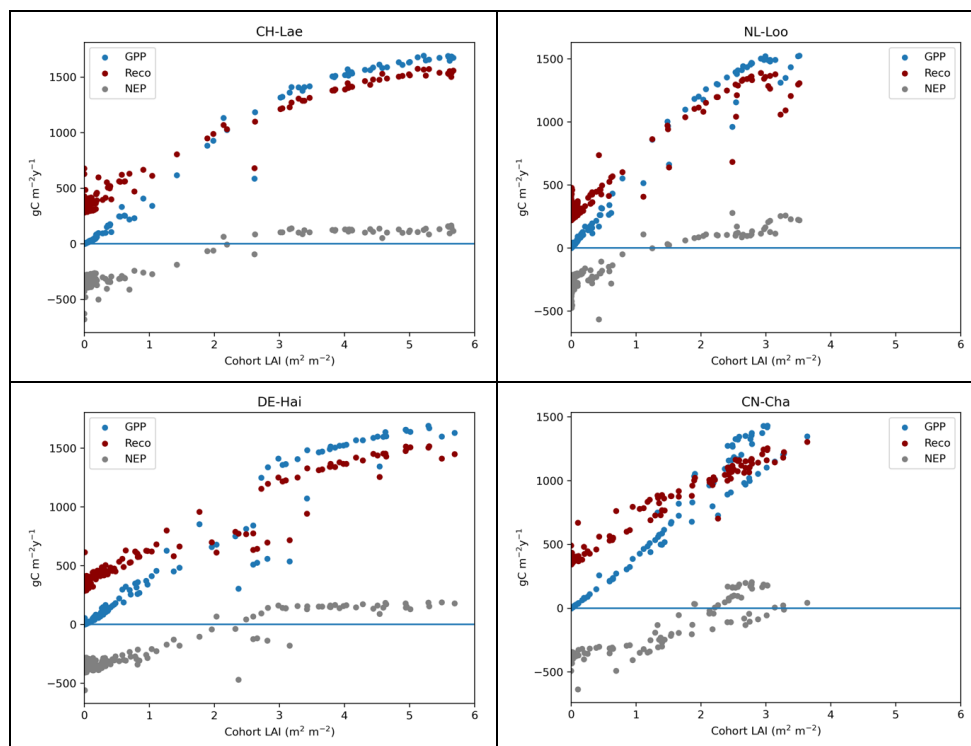
720

721

722

**Figure 3.** Comparison of the flux data from managed and unmanaged FLUXNET sites.

Dots represent the site-level mean values over the monitoring period.



723

724 **Figure 4.** Variations of GPP, NEP and Reco along a gradient of LAI as modelled using LPJ-  
725 GUESS shown for 4 sites with contrasted maximum LAI and forest types: CH-Lae for mixed  
726 forest type with high LAI, NL-Loo for conifers with low LAI, DE-Hai broadleaved with high  
727 LAI and CN-Cha with low LAI broadleaved. Each dot represents the fluxes of a particular  
728 tree cohort simulated at a given site.

729 The model runs reveal that LAI in excess of  $\sim 4 \text{ m}^2 \text{ m}^{-2}$  does not promote GPP or NEP. NEP  
730 becomes positive (forest acts as a sink) for LAI in excess of  $3 \text{ m}^2 \text{ m}^{-2}$  but, beyond  $4 \text{ m}^2 \text{ m}^{-2}$ ,  
731 increases in LAI do not result in increases in NEP.

732



733 **Table 1.** Effect of management type over the fluxes monitored on eddy correlation sites of  
 734 temperate northern-hemisphere (N = 29 FLUXNET sites, of which 18 managed and 10  
 735 unmanaged, after the exclusion of the Parco Ticino site (IT) of fertilized Populus), and fit  
 736 statistics of the nonlinear asymptotical models. Management is tested as a two-levels fixed  
 737 factor (managed/unmanaged) taken as Wilcoxon rank test for NEE, Welch t-test for GPP,  
 738 Reco and LAI. Pseudo-R<sup>2</sup> values were estimated from modeled and observed values (see  
 739 Methods section).

740

<i>Flux</i>	Welch / t-test	<i>p-value</i>
NEE	W = 83	0.7595
GPP	t = 1.745	0.0929
Reco	t = 1.711	0.0991
<i>GPP ~ a*(1 - exp(c*LAI)), pseudo-R<sup>2</sup> = 0.517</i>		
<i>Estimate (std error)</i>	<i>t value</i>	<i>Pr(&gt; t )</i>
a = 996.798 (116.443)	15.242	5.99e-16
c = -0.184 (0.161)	-4.011	0.000354
<i>NEE ~ a*(b - exp(c*LAI)), pseudo-R<sup>2</sup> = 0.935</i>		
<i>Estimate (std error)</i>	<i>t value</i>	<i>Pr(&gt; t )</i>
a = 648.998 (15180.454)	0.043	0.966
b = 1.199 (4.684)	0.043	0.966
c = -1.091 (51.191)	-0.79	0.938

741

742



743 **Table 2.** Estimation of the effect of management and forest type on the LAI or on the fluxes.  
744 Interactions (management x type) were tested and not found significant, and are therefore not  
745 presented here.

	Estimate	std. error	t value	Pr(> t )
LAI_mix ~ Management + type, F(3, 25) = 0.3592, p = 0.7829				
Intercept	4.233	0.789	5.358	1.48e-05***
Management	0.064	1.029	0.062	0.951
Conifer	1.209	1.258	0.961	0.346
Mixed	0.488	1.109	0.440	0.664

746