



**Please cite the Published Version**

Titenwi, PN, Sainge, MN , Kargbo, U, Kamara, RAS, Musa, A, Kabba, TM, Buanie, BK, Njouonkou, AL, Aruna, E, Sullivan, MJP , Leite, A and Cuni-Sanchez, A (2025) Carbon recovery in secondary forests: Insights from three West African countries. *Forest Ecology and Management*, 575. 122386 ISSN 0378-1127

**DOI:** <https://doi.org/10.1016/j.foreco.2024.122386>

**Publisher:** Elsevier

**Version:** Accepted Version

**Downloaded from:** <https://e-space.mmu.ac.uk/637541/>

**Usage rights:**  [Creative Commons: Attribution 4.0](https://creativecommons.org/licenses/by/4.0/)

**Additional Information:** This is an author accepted manuscript which first appeared in *Forest Ecology and Management*, published by Elsevier. This version is deposited with a Creative Commons Attribution 4.0 licence [<https://creativecommons.org/licenses/by/4.0/>], in accordance with Man Met's Research Publications Policy. The version of record can be found on the publisher's website.

**Enquiries:**

If you have questions about this document, contact [openresearch@mmu.ac.uk](mailto:openresearch@mmu.ac.uk). Please include the URL of the record in e-space. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from <https://www.mmu.ac.uk/library/using-the-library/policies-and-guidelines>)

1 **Carbon recovery in secondary forests: insights from three West African countries**

2 Paly N. Titenwi<sup>1</sup>, Moses N. Sainge<sup>2,3</sup>, Usif Kargbo<sup>2</sup>, Richard A.S. Kamara<sup>2</sup>, Alex Musa<sup>2</sup>, Timothy M.

3 Kabba<sup>2</sup>, Bockerie K. Buanie<sup>2</sup>, Andre L. Njouonkou<sup>1</sup>, Edward Aruna<sup>2</sup>, Martin J.P. Sullivan<sup>3</sup>, Ana Leite<sup>4</sup>,

4 Aida Cuni-Sanchez<sup>4,5</sup>

5

6 <sup>1</sup>Department of Plant Sciences, Faculty of Sciences, The University of Bamenda, Bamili, Cameroon.

7 <sup>2</sup>Reptile and Amphibian Program Sierra Leone, PMB Freetown, Sierra Leone.

8 <sup>3</sup>Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK.

9 <sup>4</sup>Department of International Environmental and Development Studies (NORAGRIC), Norwegian University of Life  
10 Sciences, Ås, Norway.

11 <sup>5</sup>Department of Environment and Geography, University of York, York, UK.

12

13 **Abstract**

14 Despite the potential of secondary tropical forests to store and sequester substantial amounts of  
15 carbon, little is known about their above-ground carbon (AGC) stocks and the factors affecting them,  
16 especially in West Africa. This information is of key importance if the countries in this region want to  
17 achieve their forest restoration and climate mitigation commitments. To fill in this gap, we  
18 investigated how environmental and local management (e.g. remnant trees) factors influenced AGC  
19 and tree species richness in secondary forests at seven sites across Guinea, Sierra Leone and Liberia.  
20 We established 140 plots (20 x 50m) in fallows <15 years (20 plots per site) and sampled all trees ≥10  
21 cm diameter following standardised protocols. We found that AGC stocks and tree species richness  
22 increased with fallow age, but were highly variable across sites driven by both climatic and local  
23 management practices. While drought stress negatively affected AGC, remnant trees had a positive  
24 effect. AGC recovery rates ranged between 0.72 Mg C ha<sup>-1</sup> y<sup>-1</sup> (second driest site) and 13.76 Mg C ha<sup>-1</sup>  
25 y<sup>-1</sup> (wettest site). Given its low cost, our findings highlight the potential of passive restoration in

26 secondary forests for carbon sequestration, particularly in wetter landscapes and areas with remnant  
27 trees from prior land use.

28 **Keywords**

29 Forest growth, Species composition recovery, Tree diversity, Carbon sequestration, Tropical forests

30 **Research Highlights**

31 Above-ground carbon and tree species diversity increased with fallow age

32 Above-ground carbon recovered slower in drier compared to wetter sites

33 Remnant trees had a positive effect on above-ground carbon and species recovery

34 Previous estimates from Ivory Coast are not applicable to the countries we studied

35

## 36 **1. Introduction**

37 Secondary forests, those growing after the complete clearance of old-growth forests for agricultural  
38 purposes, are expanding across the tropics (Vancutsem et al., 2021). There is an increasing interest  
39 in such forests and their potential for climate change mitigation, biodiversity conservation and water  
40 cycling (Chazdon et al., 2016; Locatelli et al., 2015). For instance, most of the commitments in the  
41 Bonn Challenge, which aims to reforest 350 million hectares globally by 2030 -100 of which in Africa-  
42 (see Bonn Challenge 2020), are likely to be achieved through passive restoration by natural regrowth  
43 (Chazdon et al., 2016). The need to embrace secondary forests as a low-cost, nature-based solution  
44 to meet the United Nations' Sustainable Development Goals and the United Nations' Decade on  
45 Ecosystem Restoration goals (UNEA, 2019), has been highlighted (Poorter, et al., 2021a). Thus, it is of  
46 particular importance to accurately quantify the carbon accumulation rates in these recovering  
47 forests, and understand the factors that influence variation in such rates.

48 Several factors are known to affect forest recovery trajectories at different scales. Climate is an  
49 important factor at larger spatial scales (Chazdon et al., 2016; Poorter et al., 2016). In the Amazon,  
50 for instance, areas with the greatest seasonal moisture limitation and highest incoming shortwave  
51 radiation had slower recovery rates, indicating the role of drought stress in limiting forest recovery  
52 (Heinrich et al., 2021). In the Congo Basin, though, these drought-stress associated variables had  
53 more limited effects (Heinrich et al., 2023). This aligns with previous work on old-growth forests  
54 showing that forests in Central Africa are more resistant to climate extremes than in the Amazon  
55 and Borneo (Bennett et al., 2021), driven in part by more drought-adapted tree species in Central  
56 Africa (Zhou et al., 2014). However, it is unclear whether these limited climate effects also apply to  
57 the Upper Guinean forests of West Africa, as the pantropical study by Heinrich et al., (2023) did not  
58 include data from them. Responses may be different in the Upper Guinean forests as they are  
59 exposed to hotter temperatures on average than those in Central Africa which could exacerbate  
60 seasonal drought stress (Sullivan et al., 2020). Furthermore, this region has a strong south-north

61 climatic gradient, with forests changing from evergreen to semi-deciduous and then to dry forests in  
62 just few hundred kilometres (White, 1983)

63 Connectivity between secondary forests and old-growth forests is also critical, as old-growth forests  
64 serve as seed/propagule reservoirs and often constitute habitats for dispersing animals (Arroyo-  
65 Rodríguez et al., 2017). At local scales, the duration and intensity of cultivation and subsequent  
66 influences on soil fertility and the number of remnant trees (trees from the old-growth forest spared  
67 during land clearing for farming) are known to be key factors for forest recovery trajectories (Amani  
68 et al., 2021; Derroire et al., 2016). With increased duration and intensity (use of pesticides,  
69 ploughing) of cultivation, soils are more depleted of both nutrients and propagules, hampering the  
70 start of secondary succession (Amani et al., 2021). Remnant trees also determine forest recovery as  
71 they modify local microclimate (e.g. shade, moisture) and attract dispersing animals like birds  
72 (Derroire et al., 2016). furthermore, the functional identity of remnant trees is ~~also~~ important, with  
73 nitrogen-fixing species potentially important as they increase the nutrient availability in the soil,  
74 ultimately affecting biomass growth rates in the longer term (Lai et al., 2018).

75 Few studies have focused on forest recovery processes in West Africa (Amani et al., 2021). Recent  
76 work from Ivory Coast has shown that above-ground carbon recovery rates in this country ( $2.1 \text{ Mg C}$   
77  $\text{ha}^{-1} \text{ y}^{-1}$ ) are much lower than in Tropical America (N'Guessan et al., 2019). However, such slow  
78 recovery rates might not be representative for the whole West Africa region, because forested  
79 landscapes in Ivory Coast are known to be so degraded that they support an extremely poor fauna  
80 (Norris et al., 2010), and the lack of dispersal agents (e.g. birds, bats, monkeys) is believed to impede  
81 secondary forest recovery trajectories, even in conditions of good forest connectivity (see Traoré et  
82 al., 2024). Indeed, a rate of  $4.9 \text{ Mg C ha}^{-1} \text{ y}^{-1}$  has been reported for young (<10 year) fallows in  
83 eastern Sierra Leone (Cuni-Sanchez & Lindsell, 2016), while tree diversity increased rapidly in both  
84 eastern Sierra Leone and forest clearings in Ghana (Swaine and Hall 1983). As highlighted by Poorter  
85 et al. (2021b), we need to better understand how and why forest recovery varies across

86 environmental gradients and broad geographic scales, therefore it is necessary to conduct the study  
87 across environmental gradients and broad geographic scales in the West Africa forest region.

88 This study, focused on seven sites in three countries (Guinea, Sierra Leone and Liberia), aims to  
89 provide better understanding of forest recovery trajectories across the West Africa forest region.

90 We addressed the following research questions: (a) What are the relative rates of above-ground  
91 carbon and tree diversity recovery in abandoned agricultural fields in West Africa? (b) What is the  
92 relative influence of regional climatic and local variables (e.g. number of remnant trees) on these  
93 recovery rates? (c) What lessons can be drawn for the management of secondary forests in West  
94 Africa? We expect faster recovery rates in wetter sites compared to drier sites, and also faster for  
95 patches with remnant trees compared to those without.

## 96 **2. Materials and Methods**

### 97 **2.1 Study sites**

98 The study was conducted in the secondary forests surrounding seven protected areas in Guinea  
99 (Pinselli-Soyah-Sabouyah National Park and Massif du Ziama Biosphere Reserve), Sierra Leone  
100 (Outamba-Kilimi National Park, Gola Rainforest National Park) and Liberia (Gola Forest National Park,  
101 Wologizi-Wonegizi Nature Reserve, Sapo and Grebo Krahn National Park) (Fig. 1). These sites were  
102 selected to represent an environmental gradient from drier (Pinselli and Outamba) to wetter (Sapo  
103 and Grebo Krahn) sites, while also representing different farming practices at the local level (Table  
104 1). In the drier sites of Pinselli and Outamba, the natural vegetation comprises dry forests and  
105 savannas, while in the other sites the forests are evergreen lowland *terra firme*. Outside the  
106 protected areas secondary forests of different ages and old-growth forests are distributed in patches  
107 within the landscape due to the rotation between slash-and-burn agriculture and the following for  
108 forest regrowth.

### 109 **2.2 Vegetation sampling**

110 In each study area we sampled 20 plots of 20 m x 50 m (total number of plots =140). To capture  
111 spatial variation, we sampled two young (5-7 years) and two old (10-15 years) fallows in five  
112 different villages per study site. Fallow age was determined by local farmers from each village. We  
113 chose these two fallow categories as younger still had open canopy while the older had closed  
114 canopies. Within each plot, we recorded tree diameter at 1.3 m along the stem from the ground (or  
115 above buttresses if present) of each tree  $\geq 10$  cm diameter, following RAINFOR protocols  
116 (<http://www.rainfor.org/>). We choose a 10-diameter threshold as smaller stems contribute little to  
117 plot-level above-ground biomass, as shown for different forest types in nearby Togo (Atsri et al.,  
118 2020). Stems were identified to species where possible by a professional botanist (co-author  
119 M.N.S.), and samples of unidentified trees were collected for identification at either Institut de  
120 Recherche Agronomique de Guinea in Sereidou (Guinea), the Herbaria of Njala University (Sierra  
121 Leone) or Forestry Training institute (Liberia). Families and species names follow the African Plant  
122 Database (<http://africanplantdatabase.ch>). The final dataset consists of 5,247 stems, of which 95.8  
123 % were identified to species, 99.73 % to genus and 99.86 % to family. Data collection took place  
124 between October 2022 and April 2023.

### 125 ***2.3 Aboveground carbon stocks and species composition***

126 For each tree we used Chave et al. (2014) equation to estimate above-ground biomass (AGB), which  
127 includes tree diameter (D), wood mass density ( $\rho$ ) and tree height (H), and is as follows:  $AGB =$   
128  $0.0559(\rho D^2 H)$ . The best taxonomic match wood density of each stem was extracted from a global  
129 database (Chave et al., 2009, Zanne et al. 2009) following (Lewis et al., 2009). For tree height, we  
130 built site-level allometric models to predict height (H) from tree diameter (D) using measurements of  
131 tree height in adjacent old-growth forests at each site (Sullivan et al., 2018). We compared Weibull,  
132 Michalis-Menten and log-log model forms, and selected the Weibull model form [ $H = a(1 - \exp(-bD^c))$ ],  
133 where a, b and c are estimated parameters and D is diameter at breast height] as it was consistently  
134 the best or occasionally second best (lowest root mean square error between predicted and  
135 observed height) at each site, and we wanted to use a consistent model form across sites for

136 consistency of cross-site comparisons. Above-ground biomass was then summed across stems in  
137 each plot, and converted to above-ground carbon (AGC) stocks using a carbon fraction of 0.456  
138 (Martin et al., 2018). For each plot we computed AGC including and excluding remnant trees.  
139 Following Cuni-Sanchez & Lindsell. (2016), stems from non-pioneer species with annual growth >3  
140 cm year<sup>-1</sup> (minimum annual growth rates calculated by dividing tree diameter by fallow age) were  
141 considered remnant trees. For each plot we also calculated AGC recovery rate (slope of the  
142 regression relationship between carbon stocks and fallow age, in Mg C ha<sup>-1</sup> y<sup>-1</sup>), tree species richness  
143 (number of tree species per plot), proportion of N-fixing stems (all stems) and proportion of N-fixing  
144 remnant trees. We assigned species as N-fixing or not according to (Sprent, 2009) and (Diabate et al.,  
145 2005). Overall, 19 species in the dataset were found to be N-fixers (see Table S1). To have an  
146 indication of differences in tree community composition across sites studied, we also quantified the  
147 three most abundant species (in terms of number of stems) in young and old fallows with and  
148 without remnant trees at each study site.

#### 149 **2.4 Climatic and landscape data**

150 We extracted monthly precipitation at each plot location from the Worldclim V2 database (Fick &  
151 Hijmans, 2017), and used this to calculate maximum cumulative water deficit (MCWD). Starting from  
152 the wettest month at each location, we calculated the difference between monthly precipitation and  
153 evapotranspiration, taking a figure of 100mm for the latter following (Malhi et al., 2013). If  
154 precipitation exceeded evapotranspiration, the excess was assumed to have run off so there was a  
155 net balance of zero, while if evapotranspiration exceeded precipitation there would be a negative  
156 water balance. This water balance was used as the starting point for the next month, to which the  
157 monthly precipitation was added, and the monthly evapotranspiration subtracted. This process was  
158 repeated iteratively across the year, and the lowest value was taken as a measure of maximum water  
159 deficit. For ease of interpretation, we then switched the sign, so higher MCWD values indicate  
160 greater water deficits. We also extracted the average maximum annual temperature and average



161 annual shortwave radiation from Worldclim V2 (see Table 1), but these were not further included in  
162 analysis because they were strongly correlated with MCWD (i.e. all sites were on a gradient from hot,  
163 sunny and dry to cooler, wetter and cloudier).

164 To have an indicator of potential forest connectivity in the study areas, we estimated forest cover in a  
165 4-km buffer around the villages sampled, using the Hansen Global Forest Change (v1.11) dataset  
166 (Hansen et al., 2013). We expect that the extent of forest in the local area will provide some  
167 indication of propagule pressure and habitat for forest-associated seed dispersers (Selwyn et al.,  
168 2023), but note that these could also be influenced by the spatial configuration of forest. We  
169 subtracted forest loss (up to 2022) from the tree cover map for the year 2000 (considering canopy  
170 closure greater than 30%). While we cannot determine the age of forests, this method ensures that  
171 only forest that has remained for at least 22 years is included. Only patches greater than 0.5 hectares  
172 (FAO definition of forest) were considered. Google Earth Engine and QGIS 3.34.6 were used to extract  
173 spatial data on forest cover.

## 174 **2.5 Data analysis**

175 We assessed variation in i) AGC stocks (all stems) and ii) AGC stocks (excluding remnant trees)  
176 between sites and with fallow age using linear mixed effects models, with site identity as a random  
177 effect. Age was included as a random intercept, permitting variation in stand age effects between  
178 sites. AGC stocks were log-transformed to meet model assumptions of normality of residuals and  
179 homogeneity of variances across fitted values. P values were obtained using Satterthwaite's  
180 approximation. This analysis was repeated for tree species richness (all stems). For tree species  
181 richness (excluding remnant trees), we used generalised linear mixed effects models with a Poisson  
182 error distribution as the response variable was an integer count.

183 We assessed how site-level variation in AGC stocks and tree species richness related to MCWD using  
184 linear and Poisson generalised linear (respectively) models with fallow age, MCWD and their  
185 interaction as explanatory variables. To further investigate within-site variation in our response  
186 variables, we used the mixed-effects modelling framework described above with age now treated as

187 a continuous variable rather than grouped into age classes, and RT density, % N-fixers (all stems), and  
188 their two-way interactions with fallow age also included as explanatory variables. Alternative models  
189 with remnant trees density replaced with N-fixer remnant tree density were considered but were  
190 less well supported ( $\Delta AIC > 20$ ). The potential for the effect of remnant trees to be non-linear (e.g.  
191 facilitation at low densities switching to inhibition at high densities) was assessed by adding a  
192 polynomial term for remnant trees, but this model was less well supported than the linear-term only  
193 model ( $\Delta AIC = 5.6$ ). Finally, we assessed whether MCWD influenced the effect of remnant trees by  
194 adding a two-way interaction between MCWD and remnant trees' density into the above mixed  
195 effects models. As forest cover was quite similar across the sites studied (see Table 1), we did not  
196 include this as an explanatory variable in the analyses. In highly forested landscapes of DRC,  
197 surrounding forest cover did not influence AGC recovery rates in young secondary forests (Moonen  
198 et al., 2019).

199 All data analysis was conducted in R version 4.2.2 (R Core Team 2022), with the raster package  
200 (Hijmans, 2023) used to process spatial environmental variables, the BIOMASS package (Rejou-  
201 Mechain et al., 2017) used to estimate above-ground carbon stocks, the lme4 package (Bates et al.,  
202 2015) used to fit mixed effects models, and the lmerTest package (Kuznetsova et al., 2017) used to  
203 obtain P values from mixed effects models.

### 204 **3.Results**

#### 205 **3.1 AGC stocks**

206 Across sites older fallows contained significantly more AGC (mixed effects model:  $t = 3.5$ ,  $df = 6.0$ ,  $P =$   
207  $0.013$  for all stems,  $t = 19.8$ ,  $df=50.2$ ,  $P<0.001$  excluding RT), but this difference was less pronounced  
208 in drier sites (Fig. 2, a-b). Mean AGC estimates (all stems) for old fallows ranged between  $21.1 \text{ Mg C}$   
209  $\text{ha}^{-1}$  (Pinselli, driest) and  $125.9 \text{ Mg C ha}^{-1}$  (Sapo, wettest) while AGC recovery rates were  $0.72 \text{ Mg C ha}^{-1}$   
210  $\text{y}^{-1}$  (Outamba, second driest) and  $13.76 \text{ Mg C ha}^{-1} \text{y}^{-1}$  (Sapo, wettest). Mean AGC estimates (all  
211 stems) for young fallows ranged from  $13.6 \text{ Mg C ha}^{-1}$  (Wonegizi, third wettest) to  $35.1 \text{ Mg C ha}^{-1}$   
212 (Gola-L, second wettest).

213 AGC stocks (all stems) showed a significantly negative relationship with MCWD ( $t = 3.3$ ,  $df = 10$ ,  $P =$   
214  $0.009$ ), which was more pronounced in older fallows than younger fallows (Fig. 3a). The MCWD-age  
215 interaction was not statistically significant for AGC stocks excluding remnant trees ( $t = 1.0$ ,  $df=10$ ,  $P =$   
216  $0.323$ ), but absolute differences were modelled to be greater in wetter sites because of back  
217 transforming long-scale predictions (Fig. 3b). Within-site variation in AGC stocks increased with  
218 fallow age and with number of remnant trees (Fig. 4, Table S2). When remnant trees were excluded  
219 from AGC calculations, there was a significant interaction between age and number of remnant  
220 trees, meaning that older fallows with more remnant trees had higher AGC stocks in non-remnant  
221 trees than fallows with fewer remnant trees (Fig. 4b, Table S2).

### 222 **3.2 Tree diversity and composition**

223 Across sites older fallows contained significantly more tree species (Poisson mixed effects models,  $z =$   
224  $5.2$  and  $6.8$  for all stems or excluding remnant trees respectively,  $df= 135$ ,  $P<0.001$ ), but this  
225 difference was again less pronounced in drier sites (Fig. 2, c-d). Tree species richness (all stems)  
226 showed a significantly negative relationship with MCWD ( $t=2.6$ ,  $df = 10$ ,  $P = 0.026$ ), which was more  
227 pronounced in older fallows than younger fallows (Fig. 3c). Tree species richness (excluding remnant  
228 trees) also showed a significantly negative relationship with MCWD ( $t = 2.3$ ,  $df = 10$ ,  $P = 0.048$ ) (Fig.  
229 3d). As for AGC, within-site variation in tree species richness increased with fallow age and with  
230 number of remnant trees (Fig. 4c-d, Table S2). In terms of tree composition, most abundant species  
231 varied across sites, especially between the two driest sites (Pinselli and Outamba) and the others  
232 (Table 2). Except in these two driest sites, rapidly-growing pioneer species (such as *Musanga*  
233 *cecropioides* and *Macaranga* spp.) were more abundant in plots without remnant trees while long-  
234 lived pioneer species (*Funtumia* and *Albizia* spp.) were more abundant in plots with remnant trees  
235 (see Table 2).

236 At site level there was positive relationship between tree diversity (mean tree species richness) and  
237 AGC change (slope =  $1.43$ ,  $SE = 0.43$ ,  $t = 3.37$ ,  $df = 5$ ,  $P = 0.020$ ), but this is probably because both  
238 were related to a moisture gradient. AGC stocks also increased with tree diversity (slope with log

239 carbon = 0.106, SE = 0.010,  $t = 11.0$ ,  $df = 138$ ,  $P < 0.001$ ). When all stems were considered, there was  
240 a marginally non-significant interaction between fallow age and the proportion of N-fixers ( $P = 0.056$ ,  
241 Table S2), with an initially negative effect of N-fixer dominance in young fallows reversing to be  
242 positive in old fallows. N-fixer dominance (with regard to % of stems) varied considerably across  
243 sites, from 2.4% to 35% (Pinselli and Ziama respectively, see Table 2).

## 244 **4. Discussion**

### 245 **4.1 AGC stocks**

246 We found that AGC stocks of 10-15-year fallows ranged from 21 to 126 Mg C ha<sup>-1</sup> across the  
247 landscapes studied (including remnant trees, see Fig. 2), with rates of recovery influenced by both  
248 regional climatic factors and by local scale factors. Our results add to the evidence that water  
249 availability is a key constraint on AGC recovery of tropical forests (Fig. 3). This pattern has been well  
250 documented in tropical American forests (Chazdon et al., 2016; Heinrich et al., 2021), but was found  
251 to be weaker in Central African forests, potentially due to the inherent drought resistance of African  
252 tropical forest tree communities (Heinrich et al., 2023). By sampling of the hotter and drier Upper  
253 Guinean forests, our results show that West African tropical forests do show a pronounced biomass  
254 recovery response to water availability. Our results also showed that the effect of water availability  
255 was not limited to AGC recovery, as tree species richness of secondary forests was also lower when  
256 water availability was most limited. The support our study provides for the role of water availability  
257 limiting forest recovery in West Africa has implications for biome-wide predictions of forest recovery,  
258 as water availability, together with other climate variables, could be used to predict secondary forest  
259 recovery. The sensitivity of secondary forests to water availability also has implications for the  
260 temporal sustainability of forest restoration in climates that have the potential to become drier in the  
261 future.

262 Our results also provide support for the role of remnant trees in determining AGC recovery and  
263 species richness of non-remnant trees (see Fig. 4). This is consistent with previous research in West  
264 Africa (e.g. Amani et al., 2022; Cuni-Sanchez & Lindsell, 2016), but extends this research by showing

265 that effects persist over a broad climate gradient, and provides further support for their effect on  
266 tree species richness (Sandor & Chazdon, 2014). The positive relationship between the number of  
267 remnant trees and the AGC and tree species richness of newly established trees is consistent with  
268 remnant trees facilitating the establishment of other trees (i.e. facilitated succession sensu Connell &  
269 Slatyer, 1977, e.g. by modifying the local microclimate through shading), or could also arise through  
270 remnant trees attracting seed dispersers (Guevara et al., 1986).

271 Within a West African context, we found some differences between our results and patterns of forest  
272 recovery from previous work. Our AGC estimates are greater than those reported for Ivory Coast: e.g.  
273 below 20 Mg C ha<sup>-1</sup> were recorded for 10-year fallows in several sites across that country (Amani et  
274 al., 2022) while 22.1 Mg C ha<sup>-1</sup> were recorded for 20-year fallows in the south-east (N'Guessan et al.,  
275 2019). This would be consistent with the higher forest degradation and lack of dispersing agents in  
276 Ivory Coast limiting forest recovery there relative to our study areas. Our AGC estimates are within  
277 those reported for similar-aged fallows elsewhere in the Congo Basin (see Table 3), although our  
278 estimates from our wettest site are slightly greater, probably because of larger number of trees left  
279 when land clearing in Sapo.

280 In terms of recovery rates, estimated rates ranged between 0.7 and 13.7 Mg C ha<sup>-1</sup> y<sup>-1</sup> across the  
281 landscapes studied, also being greater in wetter sites. Our findings differ from those from Ivory  
282 Coast, where AGC recovered faster in the drier northern region (compared to central or southern  
283 regions) and authors linked it lower competition between understory annual herbaceous plants and  
284 tree seedlings in that region (compared to central/southern regions with perennial herbaceous  
285 plants) (Amani et al., 2022). In all our study sites, given high canopy cover, perennial herbaceous  
286 plants were rare in the understory (M.S. Pers. Obs. 2024), which is very different from the situation  
287 reported in Ivory Coast. Another possible explanation of differences in AGC recovery rates between  
288 Ivory Coast and our study is crop(s) cultivated and farming practices. N'Guessan et al. (2019) showed  
289 lower AGC recovery rates for abandoned rice fields compared to yam, cassava or maize abandoned

290 fields, which were all grown in mostly monocropping systems. In our study sites, though,  
291 polycropping is the norm (as shown in Table 1).  
292 AGC recovery estimates in our wetter sites are much greater than estimates from elsewhere in  
293 tropical Africa, probably because of larger number of trees left when land clearing. For instance, 1.98  
294 Mg C ha<sup>-1</sup> year<sup>-1</sup> have been reported for the Congo Basin (Heinrich et al., 2023), while 3.2 Mg C ha<sup>-1</sup>  
295 year<sup>-1</sup> has been reported for Kenya (Ojoatre et al., 2024). Previous work from Cameroon also  
296 reported relatively high rates which range from 3.9 Mg C/ha<sup>-1</sup>year<sup>-1</sup> (see Njomgang et al., 2011) to 9.4  
297 Mg C ha<sup>-1</sup> year<sup>-1</sup> (see Kotto-Same et al., 1997) . Most likely greater number and sizes of remnant  
298 trees left when land clearing in our wetter sites explain these differences, although local soil  
299 properties – which we did not investigate in this study- might also be of importance.

#### 300 **4.2 Tree diversity and composition**

301 Tree diversity and composition were also highly variable across the landscapes studied, modulated  
302 by climate (MWCD) and remnant trees (Fig. 3-4), with higher diversity in wetter sites and in plots  
303 with remnant trees. Our results support previous work from southern Sierra Leone (Cuni-Sanchez &  
304 Lindsell, 2016) showing that rapidly growing pioneer species such as *Musanga cecropioides*, or  
305 *Macaranga* spp. are more abundant in plots without remnant trees while long-lived pioneer species  
306 are more abundant in plots with remnant trees, indicating that remnant tree presence shortened  
307 fallow tree species' composition recovery. In a certain way, remnant trees facilitated the  
308 establishment of the 'second stage' of the succession with abundant longer-lived pioneers like *Albizia*  
309 or *Funtumia* spp., skipping the 'first stage' of the short-lived *Musanga cecropioides* . Results from  
310 secondary forests in Ivory Coast have highlighted that tree diversity recovers faster than composition  
311 or AGC (Amani et al., 2022), with no details on species recorded, so we were unable to compare our  
312 results with theirs. In Yangambi in DRC, *Musanga cecropioides* and *Albizia adianthifolia* were also  
313 amongst the three most abundant tree species in 5–10-year fallows (Mangaza et al., 2022), indicating  
314 what would be a mix of the first and second stage of the succession as we describe here in West  
315 Africa.

316 When considering tree diversity effects on AGC, we found a weak positive relationship between tree  
317 diversity and AGC recovery, but this is likely to be driven by moisture effects rather than niche  
318 complementarity as both AGC and tree species richness increased along the gradient of moisture  
319 availability. Other studies on secondary forests have found that tree species diversity alone was not a  
320 good predictor of AGC change over time. For example, in secondary forests in Mexico, forest age-  
321 mediated effects on stand structural changes and species composition were better predictors of AGC  
322 than the changes in tree diversity during succession (Aryal et al., 2024). In South Africa, niche  
323 complementarity between canopy, sub-canopy, and emergent tree species explained the  
324 relationships between stand diversity and biomass storage (Mensah et al., 2018).

325 With regard to N-fixer effects on AGC recovery, we found limited effects. N-fixation tends to be  
326 common in early stages of the forest recovery succession – as there is abundant light and trees can  
327 easily provide carbohydrates to their nitrogen-fixing symbionts (Batterman et al., 2013). But it  
328 declines over time as light availability in the stand drops (Matsuo et al., 2021), and nitrogen fixation  
329 becomes too costly (Battmerman et al., 2013). In DRC, a decrease in abundance of pioneer species  
330 and an increase in N-fixing species early in succession of secondary was observed after repeated  
331 clearing (Bauters et al., 2021). It is possible differences in clearing cycles or local soil properties, such  
332 as Phosphorous or other Cations being more limiting than N in some sites, explain some of the  
333 differences observed across the seven sites we studied, factors which should be considered in future  
334 research. Future research focusing on tree diversity or composition should also consider using a  
335 smaller tree diameter threshold, as trees <10cm diameter might not be major contributors to plot-  
336 level AGC, but can be important components of forest composition and diversity (e.g. (Atsri et al.,  
337 2020).

### 338 ***4.3 Implications of the findings***

339 What specific lessons can be drawn for the management of secondary forests in West Africa? First,  
340 our findings show that previous work on trajectories of secondary forest recovery in Ivory Coast (a  
341 country characterised by high forest degradation, see Traoré et al. 2024) is not applicable to

342 secondary forests found in Guinea, Sierra Leone or Liberia. Second, our findings also show that AGC  
343 recovery is highly variable in these countries, driven by both regional climate (e.g. MWCD) and local  
344 farming practices (e.g. remnant trees). Therefore, insights into local contexts should be gathered  
345 before making any decision on their management. We recommend the consideration of MCWD  
346 instead of other climatic variables such as annual rainfall or precipitation seasonality (used by e.g.  
347 Amani et al. 2022; Traoré et al. 2024), as this variable has been shown to be more meaningful in  
348 tropical forest contexts (Sullivan et al., 2020), including in the study of secondary forests (Heinrich et  
349 al., 2021, 2023).

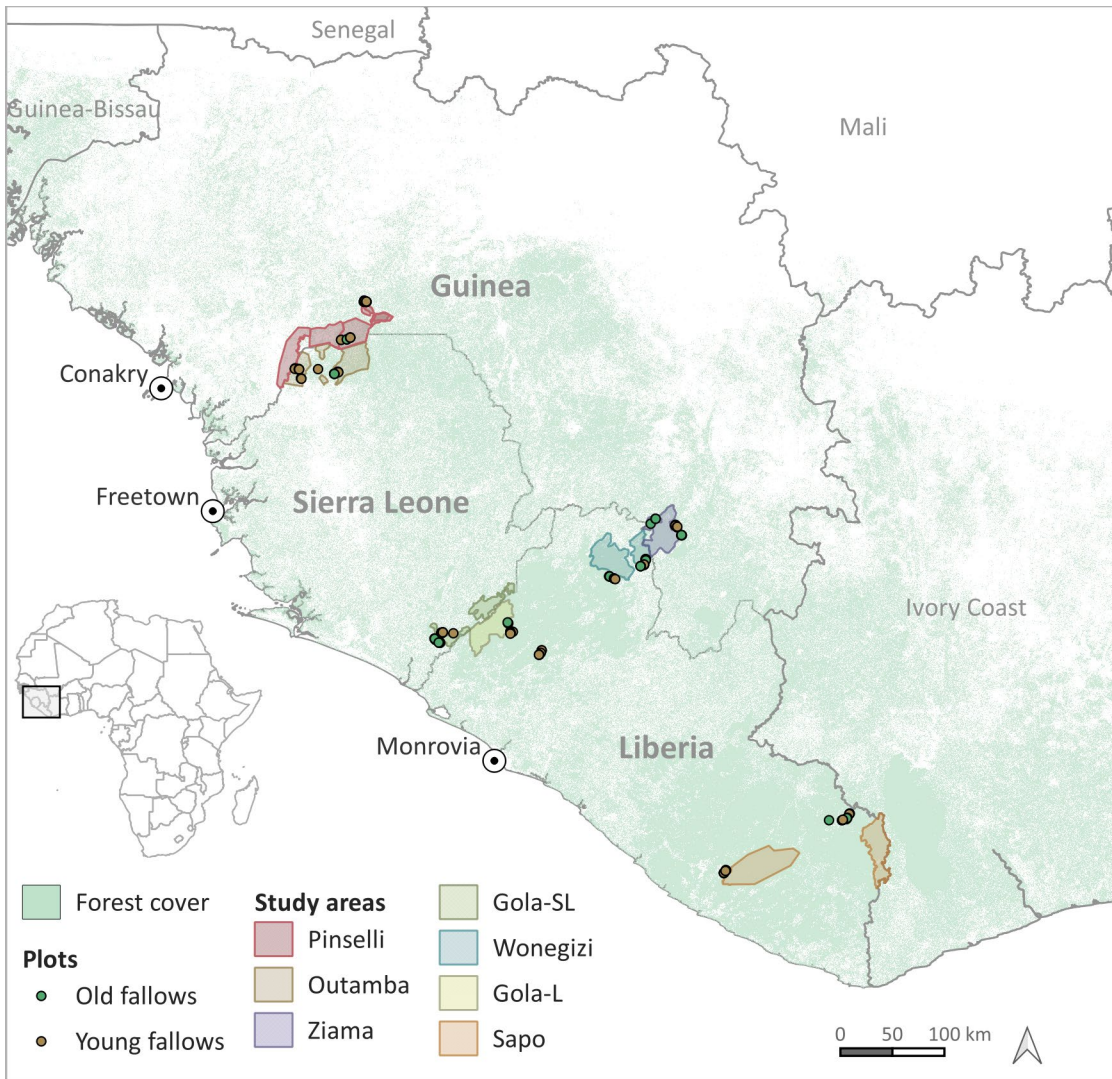
350 Overall, our findings also highlight the potential role of passive restoration of secondary forests for  
351 carbon sequestration in most of the West African landscapes we studied, except in driest sites, where  
352 active restoration might be needed. Apart from helping contribute to these countries' restoration  
353 commitments in the Bonn Challenge (see Bonn Challenge 2020), secondary forests are likely to gain  
354 importance to local communities, as old-growth forests continue to disappear. In fact, a complete  
355 loss of old-growth forest before 2100 has been predicted for Guinea and Sierra Leone under a  
356 business-as-usual scenario, including inside protected areas (see, Vieilledent et al., 2022). Notably,  
357 for secondary forests to be left to continue recovering and sequestering carbon, local farmers would  
358 need to change their farming practices from slash-and-burn to permanent farming, in which case  
359 both external support and training would be needed. As secondary forests remain a source of  
360 important ecosystem services to local communities, such as wild edible fruits and medicinal  
361 plants(Cuni-Sanchez et al. in press), continued access to these important ecosystem services should  
362 be ensured, even if carbon sequestration is a management priority at regional or national level.  
363



364

## Figures and Tables

365

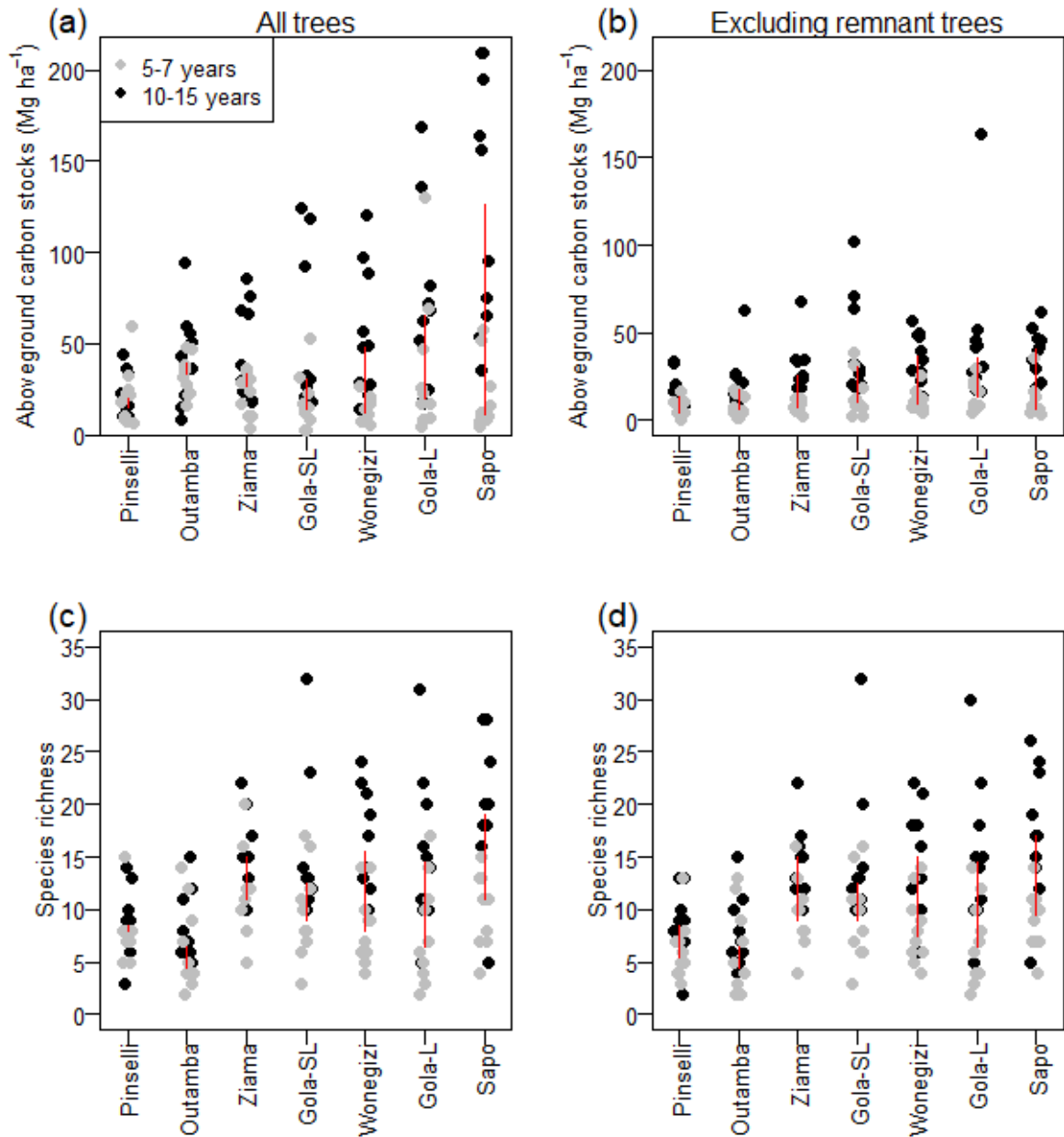


366

367 **Fig. 1.** Selected study sites. For details see Table 1.

368

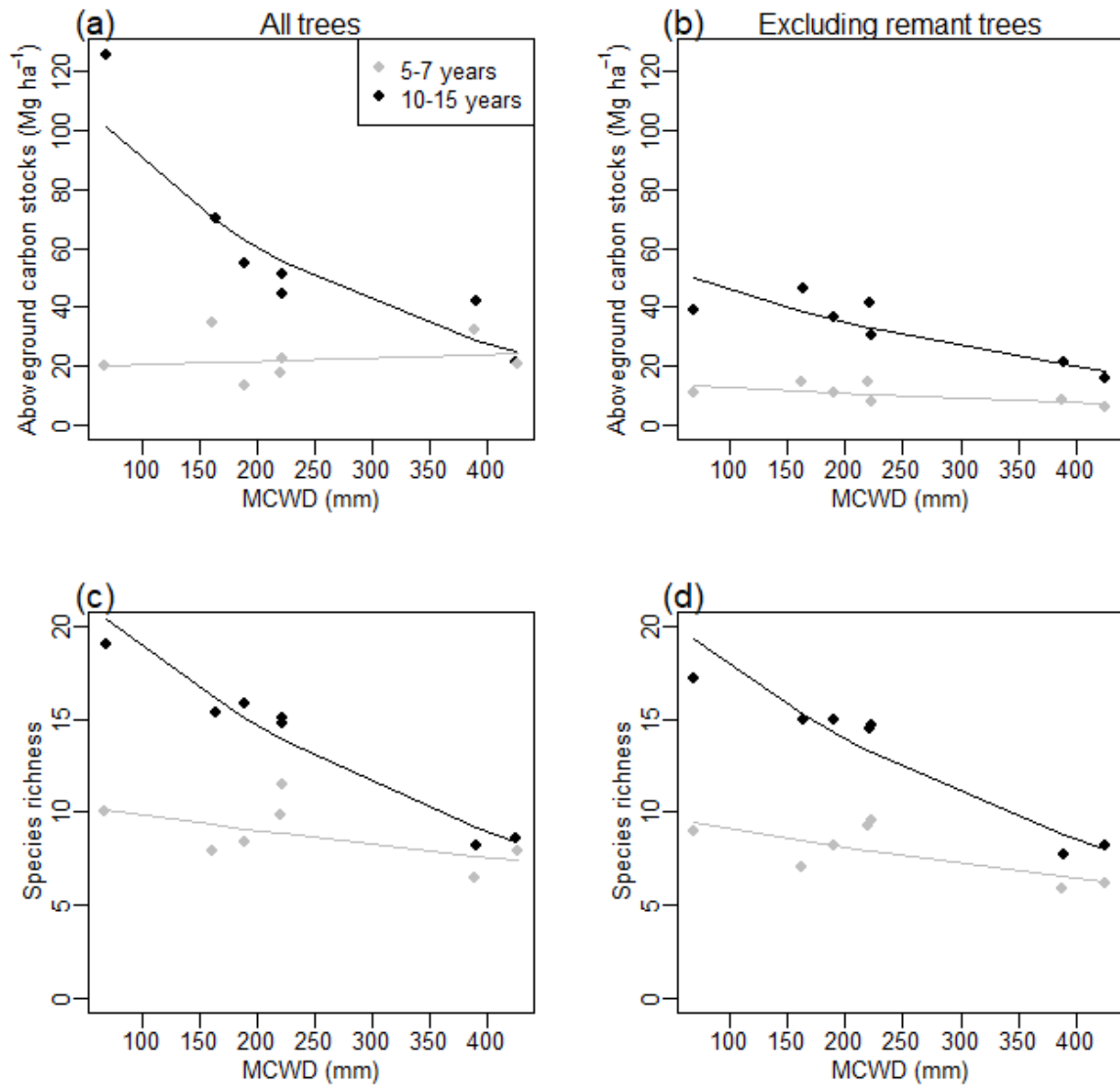
369



370

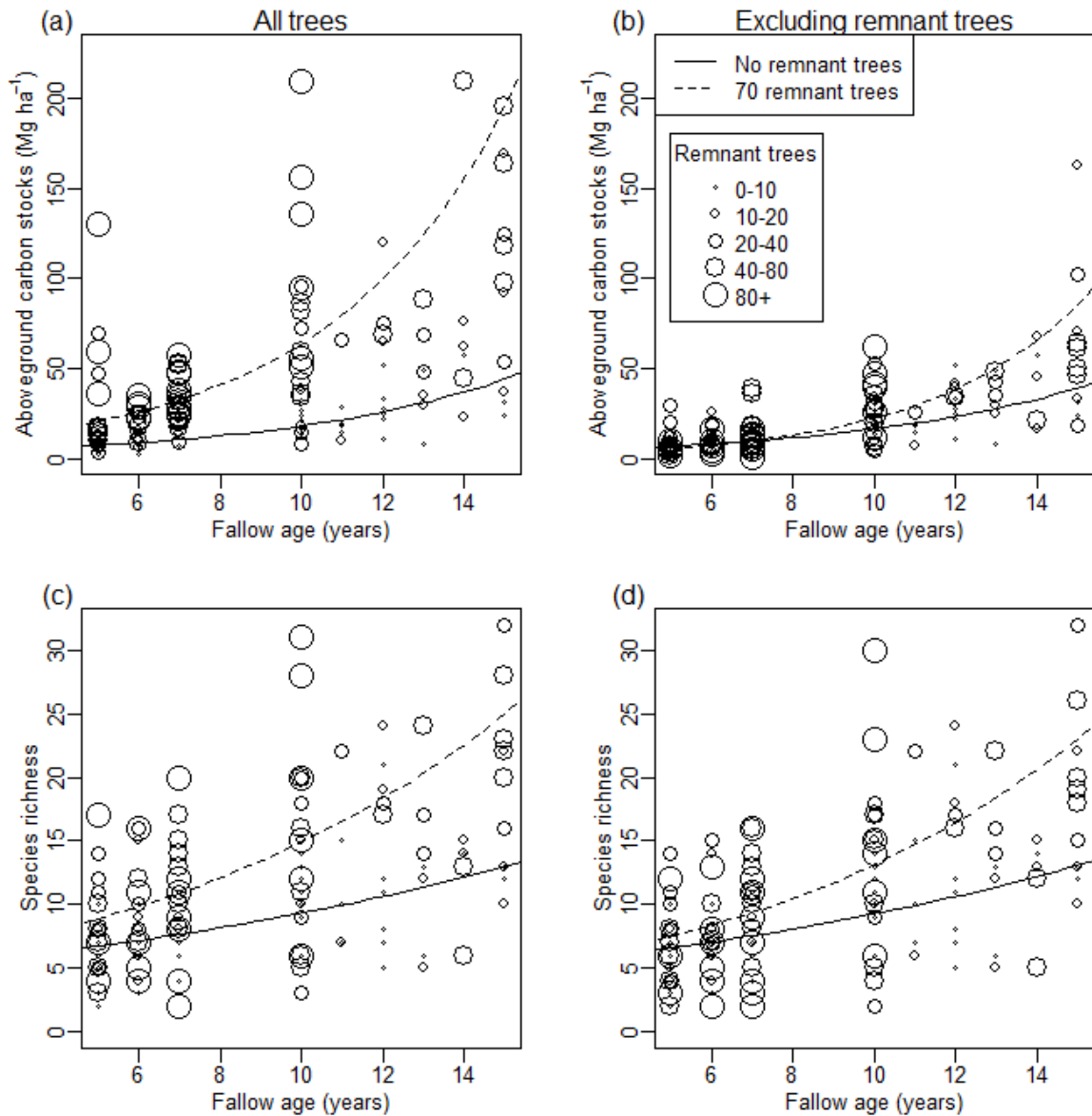
371 **Fig. 2.** Variation in above-ground carbon (AGC) stocks (a-b) and tree species richness (c-d) within and  
 372 between sites. Sites have been ordered from driest (left) to wettest (right) based on the maximum  
 373 cumulative water deficit. Grey points: young fallows (5-7 years old); black points: old fallows (10-15  
 374 years old). The red lines show the difference between the mean AGC stocks (or tree species richness)  
 375 in young/old fallows in each site.

376



377

378 **Fig. 3.** Relationship between the maximum cumulative water deficit (MCWD) and above-ground  
 379 carbon stocks (a-b) and tree species richness (c-d). High MCWD values indicate greater moisture  
 380 limitation. Black and grey points indicate mean values per site considering old (10-15 years) and  
 381 young (5-7 years) fallows, respectively. Lines indicate modelled relationships from linear models with  
 382 MCWD, age category and their interaction as explanatory variables.



383

384

**Fig. 4.** Effect of fallow age and number of remnant trees on above-ground carbon stocks (a-b) and

385

tree species richness (c-d). Symbol sizes indicate the number of remnant trees. Lines show model

386

predictions with no remnant trees (solid line) and 70 remnant trees (dashed line, representing one

387

standard deviation above the mean). Model coefficients are presented in Table S1.

388

**Table 1.** Overview of selected study sites, ordered by maximum cumulative water deficit (MCWD).

Code	Full name	Annual rainfall (mm)	Maximum temperature-warmest month (°C)	Mean annual temperature (°C)	MWCD (mm)	Dry season length (months)*	Shortwave radiation (kJ m <sup>-2</sup> day <sup>-1</sup> )	Main crops**	Forest cover (%)
<b>Pinselli</b>	Pinselli-Soyah-Sabouyah National Park (Guinea)	1959	34.1	26.1	426	6	18350	peanuts, rice, millet	65
<b>Outamba</b>	Outamba-Kilimi National Park (Sierra leone)	2445	35.4	27.6	389	5	18055	peanuts, rice, millet, sesame	56
<b>Ziama</b>	Massif du Ziama Biosphere Reserve (Guinea)	2270	32.7	24	222	4	16635	rice, cassava, banana	76
<b>Gola-SL</b>	Gola Rainforest National Park, Sierra Leone	2933	32.5	26.2	221	4	16216	rice, cassava, sweet potatoes	66
<b>Wonegizi</b>	Wonegizi Nature Reserve (Wologizi is proposed only) (Liberia)	2331	33.4	24.6	190	3	16289	rice, cassava, banana	55
<b>Gola-L</b>	Gola Forest National Park, Liberia	2684	32.5	25.5	163	3	16006	rice, cassava, sweet potatoes	91
<b>Sapo</b>	Sapo and Grebo Krahn National Parks (Liberia)	2542	31.8	25.5	69	2	16174	rice, cassava	82

\*Dry season length defined as months with &lt;100mm precipitation, \*\*order of main crops does not reflect importance.

**Table 2.** Comparison between the top three most abundant tree species in old fallows at each study site, considering plots with or without remnant trees. (n) refers to number of plots. \* indicates N-fixing species

	No remnant tree	With remnant tree
	Pinselli (n=6)	Pinselli (n=4)
1	<i>Piliostigma thonningii</i> 37	<i>Spondias mombin</i> 28
2	<i>Terminalia schimperiana</i> 22	<i>Ficus sur</i> 15
3	<i>Margaritaria discoidea</i> 21	<i>Anthothena crassifolia</i> 14
% stems	47.4	44.2
% N fixers	2.4	6.5
No. of Spp. recorded	26	20
	Outamba (n=5)	Outamba (n=5)
1	<i>Pterocarpus erinaceus</i> * 36	<i>Gmelina arborea</i> 30
2	<i>Combretum glutinosum</i> 30	<i>Spondias mombin</i> 20
3	<i>Crossopteryx febrifuga</i> 27	<i>Sterculia setigera</i> 11
% stems	51.7	37.4
% N fixers	25.9	14.4
No. of Spp. recorded	19	35
	Ziama (n=6)	Ziama (n=4)
1	<i>Albizia zygia</i> * 36	<i>Albizia zygia</i> * 18
2	<i>Cathormion altissimum</i> 21	<i>Funtumia africana</i> 18
3	<i>Margaritaria discoidea</i> 21	<i>Funtumia elastica</i> 10
% stems	34.8	26.9
% N fixers	35.3	27.6
No. of Spp. recorded	47	48
	Gola-SL (n=7)	Gola-SL (n=3)
1	<i>Macaranga barteri</i> (95)	<i>Smeathmannia pubescens</i> (16)
2	<i>Margaritaria discoidea</i> (44)	<i>Funtumia africana</i> (15)

3	<i>Musanga cecropioides</i> (27)	<i>Baphia nitida</i> * (15)
% stems	47.03	25.7
% N fixers	13.2	16.3
No. of Spp. recorded	37	45
<hr/>		
	Wonegizi (n=7)	Wonegizi (n=3)
1	<i>Albizia zygia</i> * 47	<i>Funtumia africana</i> 19
2	<i>Albizia adianthifolia</i> * 39	<i>Albizia zygia</i> * 12
3	<i>Macaranga barteri</i> 39	<i>Myrianthus libericus</i> 12
% stems	39.6	26.7
% N fixers	33.8	20.6
No. of Spp. recorded	64	46
<hr/>		
	Gola-L (n=4)	Gola-L (n=6)
1	<i>Musanga cecropioides</i> (66)	<i>Macaranga barteri</i> 66
2	<i>Harungana madagascariensis</i> 33	<i>Ficus mucuso</i> 31
3	<i>Margaritaria discoidea</i> 20	<i>Funtumia africana</i> 26
% stems	63.6	30.9
% N fixers	7.3	13.0
No. of Spp. recorded	21	66
<hr/>		
	Sapo (n=1)	Sapo (n=9)
1	<i>Albizia zygia</i> * 9	<i>Funtumia africana</i> 105
2	<i>Macaranga barteri</i> 8	<i>Macaranga barteri</i> 50
3	<i>Funtumia africana</i> 7	<i>Macaranga hurifolia</i> 28
% stems	88.9	37.6
% N fixers	37.0	9.7
No. of Spp. recorded	5	85
<hr/>		

**Table 3.** Literature-derived estimates of above-ground carbon (AGC Mg C ha<sup>-1</sup>), AGC change (in Mg C ha<sup>-1</sup>y<sup>-1</sup>), number of plots sampled, minimum tree diameter sampled (Diam, in cm), equation used to estimate AGC and references.

Location	AGC	AGC change	No plots	Plot age	Diam	AGB equation	Publication
Seven sites across Guinea, Sierra Leone and Liberia	21-125	0.7 -13.7	70	10-15 yrs	10	Chave et al., 2014	this study
Gola-SL, Sierra Leone	80	4.9	33	7-10 yrs	5	Chave et al., 2014	Cuni-Sanchez & Lindsell, 2016
Agbo I State Forest, south-east Ivory Coast	22.16*	2.1	26	<11 yrs	2.5	Chave et al., 2014	N'guesssan et al., 2019
Eight sites across Ivory Coast	<10.94*		32	<11 yrs	2.5	Chave et al., 2014	Amani et al., 2022
Maringa- Lopori- Wamba landscape, Tshopo Province, DRC	65.7		3	<25 yrs	10	Chave et al., 2014	Bauters et al., 2019
3 villages, Tshopo Province, DRC	34.66*		6	10 yrs	5	Chave et al., 2014	Moonen et al., 2019
Yangambi Forest, Tshopo Province, DRC	13.68*		4	5-10yrs	10	Chave et al., 2014	Mangaza et al., 2022
Yoko Forest, Tshopo Province, DRC	25		3	5yrs	10	Chave et al., 2014	Makelele et al., 2021
Mean Congo Basin (remote sensing analysis)	50	1.98	na	20 yrs	na	na	Heinrich et al., 2023
Five permanent forest estates, Ghana	47.25*		17	48 yrs	10	Chave et al., 2014	Brown et al., 2020

\*values reported in publication refer to AGB, converted to AGC using 0.456 ratio.



## **Acknowledgments**

We are deeply grateful to the communities whose secondary forests we studied, for allowing us to conduct this research. We thank our field assistants in these villages for making this research possible.

## **Funding**

This research was supported by USAID (grant number: WABiLED-G-003). P.N.T was supported by the 2022 ATBC seed grant for travels and IDEAL WILD equipment grant same year.

M.N.S. was supported by a Biodiversity Informatics Training Curriculum program (BITC2) grant from the JRS Biodiversity Foundation.

**Conflicts of Interest:** No conflict of interest.

## **Author contributions**

M.N.S. and A.C.-S. conceived the study. P.N.T and M.N.S. led the field campaigns, assisted by U.K., R.A.S.K, A.M, T.M.K, and B.K.B, with help from E.A., A.L. P.N.T, M.J.P.S. and A.C.-S. analysed the plot data and wrote the manuscript. All co-authors read and approved the manuscript.

## **References**

Amani, B. H. K., N'Guessan, A. E., Derroire, G., N'dja, J. K., Elogne, A. G. M., Traoré, K., Zo-Bi, I. C., & Hérault, B. (2021). The potential of secondary forests to restore biodiversity of the lost forests in semi-deciduous West Africa. *Biological Conservation*, 259.  
<https://doi.org/10.1016/j.biocon.2021.109154>

- Amani, B. H. K., N'Guessan, A. E., Van der Meersch, V., Derroire, G., Pioniot, C., Elogne, A. G. M., Traoré, K., N'Dja, J. K., & Hérault, B. (2022). Lessons from a regional analysis of forest recovery trajectories in West Africa. *Environmental Research Letters*, *17*(11). <https://doi.org/10.1088/1748-9326/ac9b4f>
- Arroyo-Rodríguez, V., Melo, F. P. L., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., Norden, N., Santos, B. A., Leal, I. R., & Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, *92*(1), 326–340. <https://doi.org/10.1111/brv.12231>
- Aryal, D. R., De Jong, B. H. J., Sánchez-Silva, S., Haas-Ek, A., Esparza-Olguin, L., Ochoa-Gaona, S., Ghimire, R., & Morales-Ruiz, D. E. (2024). Biomass recovery along a tropical forest succession: Trends on tree diversity, wood traits and stand structure. *Forest Ecology and Management*, *555*(January). <https://doi.org/10.1016/j.foreco.2024.121709>
- Atsri, H. K., Kokou, K., Abotsi, K. E., Kokutse, A. D., & Cuni-Sanchez, A. (2020). *Above-ground biomass and vegetation attributes in the forest- savannah mosaic of Togo , West Africa. April*, 1–13. <https://doi.org/10.1111/aje.12758>
- Bates, D. M., Walker, S., & Zurich, M. M. E. (2015). Package 'lme4 .' In *Statistical Software* (Issue January).
- Batterman, S. A., Hedin, L. O., Van Breugel, M., Ransijn, J., Craven, D. J., & Hall, J. S. (2013). Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature*, *502*(7470), 224–227. <https://doi.org/10.1038/nature12525>
- Bauters, M., Moonen, P., Summerauer, L., Doetterl, S., Wasner, D., Griepentrog, M., Mumbanza, F. M.,

Kearsley, E., Ewango, C., Boyemba, F., Six, J., Muys, B., Verbist, B., Boeckx, P., & Verheyen, K. (2021). Soil Nutrient Depletion and Tree Functional Composition Shift Following Repeated Clearing in Secondary Forests of the Congo Basin. *Ecosystems*, *24*(6), 1422–1435.

<https://doi.org/10.1007/s10021-020-00593-6>

Bennett, J., Rachunok, B., Flage, R., & Nateghi, R. (2021). Mapping climate discourse to climate opinion: An approach for augmenting surveys with social media to enhance understandings of climate opinion in the United States. *PLoS ONE*, *16*(1 January), 1–16.

<https://doi.org/10.1371/journal.pone.0245319>

Bonn challenge. (2020). Impact and potential of forest landscape restoration. In *Restore Our Future*.

Brown, H. C. A., Berninger, F. A., Larjavaara, M., & Appiah, M. (2020). Above-ground carbon stocks and timber value of old timber plantations, secondary and primary forests in southern Ghana. *Forest Ecology and Management*, *472*(May). <https://doi.org/10.1016/j.foreco.2020.118236>

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366.

<https://doi.org/10.1111/j.1461-0248.2009.01285.x>

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*(10), 3177–3190. <https://doi.org/10.1111/gcb.12629>

Chazdon, R. L., Broadbent, E. N., Rozendaal, D. M. A., Bongers, F., Zambrano, A. M. A., Aide, T. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Craven, D., Almeida-Cortez, J. S.,

- Cabral, G. A. L., De Jong, B., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ... Poorter, L. (2016). Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances*, 2(5). <https://doi.org/10.1126/sciadv.1501639>
- Connell, J. H. ., & Slatyer, R. O. . (1977). Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *The American Naturalist*, 111(982), 1119–1144. <http://www.jstor.org/stable/2460259>
- Cuni-Sanchez, A., & Lindsell, J. A. (2016). The role of remnant trees in carbon sequestration, vegetation structure and tree diversity of early succession regrowing fallows in eastern Sierra Leone. *African Journal of Ecology*, 55(2), 188–197. <https://doi.org/10.1111/aje.12340>
- Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D. K., Lebrija-Trejos, E., Leiva, J. A., Odén, P. C., Powers, J. S., Rico-Gray, V., Tigabu, M., & Healey, J. R. (2016). Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos*, 125(10), 1386–1397. <https://doi.org/10.1111/oik.03229>
- Diabate, M., Munive, A., Faria, S. M. de, Ba, A., Dreyfus, B., & Galiana, A. (2005). Occurrence of nodulation in unexplored leguminous trees native to the West African tropical rainforest and inoculation response of native species useful in reforestation. *New Phytologist*, 166, 231–239.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2 : new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, march. <https://doi.org/10.1002/joc.5086>
- Guevara, S., Purata, S. E., & Van der Maarel, E. (1986). The role of remnant forest trees in tropical secondary succession. *Vegetatio*, 66(2), 77–84. <https://doi.org/10.1007/BF00045497>
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., &

- Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853. <https://doi.org/10.1126/science.1244693>
- Heinrich, V. H. A., Dalagnol, R., Cassol, H. L. G., Rosan, T. M., de Almeida, C. T., Silva Junior, C. H. L., Campanharo, W. A., House, J. I., Sitch, S., Hales, T. C., Adami, M., Anderson, L. O., & Aragão, L. E. O. C. (2021). Large carbon sink potential of secondary forests in the Brazilian Amazon to mitigate climate change. *Nature Communications*, 12(1), 1–11. <https://doi.org/10.1038/s41467-021-22050-1>
- Heinrich, V. H. A., Vancutsem, C., Dalagnol, R., Rosan, T. M., Fawcett, D., Silva-Junior, C. H. L., Cassol, H. L. G., Achard, F., Jucker, T., Silva, C. A., House, J., Sitch, S., Hales, T. C., & Aragão, L. E. O. C. (2023). The carbon sink of secondary and degraded humid tropical forests. *Nature*, 615(7952), 436–442. <https://doi.org/10.1038/s41586-022-05679-w>
- Hijmans, R. J. (2023). *Package 'raster' R topics documented :Golicher, Duncan Gray, Josh Greenbe.*
- Kotto-Same, J., Woomer, P. L., Appolinaire, M., & Louis, Z. (1997). Carbon dynamics in slash-and-burn agriculture and land use alternatives of the humid forest zone in Cameroon. *Agriculture, Ecosystems and Environment*, 65(3), 245–256. [https://doi.org/10.1016/S0167-8809\(97\)00060-1](https://doi.org/10.1016/S0167-8809(97)00060-1)
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82(13), 1–26. <https://doi.org/10.18637/JSS.V082.I13>
- Lai, C., Li, J., Wang, Z., Wu, X., Zeng, Z., Chen, X., Lian, Y., Yu, H., Wang, P., & Bai, X. (2018). Drought-induced reduction in net primary productivity across mainland China from 1982 to 2015. *Remote Sensing*, 10(9). <https://doi.org/10.3390/rs10091433>
- Lewis, S. L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T. R., Ojo, L. O., Phillips, O. L., Reitsma, J. M., White, L., Comiskey, J. A., Djuikouo K, M. N., Ewango, C. E. N., Feldpausch, T. R.,

Hamilton, A. C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J. C., ... Wöll, H. (2009). Increasing carbon storage in intact African tropical forests. *Nature*, *457*(7232), 1003–1006.

<https://doi.org/10.1038/nature07771>

Locatelli, B., Catterall, C. P., Imbach, P., Kumar, C., Lasco, R., Marín-Spiotta, E., Mercer, B., Powers, J. S., Schwartz, N., & Uriarte, M. (2015). Tropical reforestation and climate change: Beyond carbon. *Restoration Ecology*, *23*(4), 337–343. <https://doi.org/10.1111/rec.12209>

Makelele, I. A., Verheyen, K., Boeckx, P., Cizungu Ntaboba, L., Mujinya Bazirake, B., Ewango, C., & Bauters, M. (2021). Afrotropical secondary forests exhibit fast diversity and functional recovery, but slow compositional and carbon recovery after shifting cultivation. *Journal of Vegetation Science*, *32*(5), 1–13. <https://doi.org/10.1111/jvs.13071>

Malhi, Y., Adu-Bredu, S., Asare, R. A., Lewis, S. L., & Mayaux, P. (2013). African rainforests: Past, present and future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1625). <https://doi.org/10.1098/rstb.2012.0312>

Mangaza, L., Makana, J.-R., Hubau, W., Sonwa, D. J., Batsi, G., & Fayolle, A. (2022). Impacts du changement d'utilisation des terres sur la biomasse et la diversité dans le paysage forestier de la réserve de biosphère de Yangambi en République démocratique du Congo. *Bois & Forêts Des Tropiques*, *353*, 61–73. <https://doi.org/10.19182/bft2022.353.a36836>

Martin, A. R., Doraisami, M., & Thomas, S. C. (2018). Global patterns in wood carbon concentration across the world's trees and forests. *Nature Geoscience*, *11*(12), 915–920. <https://doi.org/10.1038/s41561-018-0246-x>

Matsuo, T., Martínez-Ramos, M., Bongers, F., van der Sande, M. T., & Poorter, L. (2021). Forest structure drives changes in light heterogeneity during tropical secondary forest succession. *Journal of*

*Ecology*, 109(8), 2871–2884. <https://doi.org/10.1111/1365-2745.13680>

Mensah, S., du Toit, B., & Seifert, T. (2018). Diversity–biomass relationship across forest layers: implications for niche complementarity and selection effects. *Oecologia*, 187(3), 783–795. <https://doi.org/10.1007/s00442-018-4144-0>

Moonen, P. C. J., Verbist, B., Boyemba Bosela, F., Norgrove, L., Dondeyne, S., Van Meerbeek, K., Kearsley, E., Verbeeck, H., Vermeir, P., Boeckx, P., & Muys, B. (2019). Disentangling how management affects biomass stock and productivity of tropical secondary forests fallows. *Science of the Total Environment*, 659, 101–114. <https://doi.org/10.1016/j.scitotenv.2018.12.138>

N'Guessan, A. E., N'dja, J. K., Yao, O. N., Amani, B. H. K., Gouli, R. G. Z., Pioniot, C., Zo-Bi, I. C., & Hérault, B. (2019). Drivers of biomass recovery in a secondary forested landscape of West Africa. *Forest Ecology and Management*, 433(September 2018), 325–331. <https://doi.org/10.1016/j.foreco.2018.11.021>

Njomgang, R., Yemefack, M., Nounamo, L., & Moukam, A. (2011). Dynamics of shifting agricultural systems and organic carbon sequestration in Southern Cameroon. *Tropicultura*, 29(2), 176–182.

Norris, K., Asase, A., Collen, B., Gockowski, J., Mason, J., Phalan, B., & Wade, A. (2010). Biodiversity in a forest-agriculture mosaic - The changing face of West African rainforests. *Biological Conservation*, 143(10), 2341–2350. <https://doi.org/10.1016/j.biocon.2009.12.032>

Ojoatre, S., Barlow, J., Jacobs, S. R., & Rufino, M. C. (2024). Recovery of aboveground biomass, soil carbon stocks and species diversity in tropical montane secondary forests of East Africa. *Forest Ecology and Management*, 552(November 2023), 121569. <https://doi.org/10.1016/j.foreco.2023.121569>

Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., Boukili, V.,

- Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Craven, D., De Almeida-Cortez, J. S., Cabral, G. A. L., De Jong, B. H. J., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ... Rozendaal, D. M. A. (2016). Biomass resilience of Neotropical secondary forests. *Nature*, *530*(7589), 211–214. <https://doi.org/10.1038/nature16512>
- Poorter, L., Craven, D., Jakovac, C. C., Sande, M. T. Van Der, Amissah, L., Bongers, F., Chazdon, R. L., Farrior, C. E., Kambach, S., & Meave, J. A. (2021). *Multidimensional tropical forest recovery*. December, 1–7.
- Poorter, L., Rozendaal, D. M. A., Bongers, F., de Jarcilene, S. A., Álvarez, F. S., Luís Andrade, J., Arreola Villa, L. F., Becknell, J. M., Bhaskar, R., Boukili, V., Brancalion, P. H. S., Cèsar, R. G., Chave, J., Chazdon, R. L., Colletta, G. D., Craven, D., de Jong, B. H. J., Denslow, J. S., Dent, D. H., ... Westoby, M. (2021). Functional recovery of secondary tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(49), 12. <https://doi.org/10.1073/pnas.2003405118>
- Rejou-Mechain, M., Tanguy, A., Piponiot, C., Chave, J., & Hérault, B. (2017). BIOMASS : an R package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution*, *8*, 1163–1167. <https://doi.org/10.1111/2041-210X.12753>
- Sandor, M. E., & Chazdon, R. L. (2014). Remnant trees affect species composition but not structure of tropical second-growth forest. *PLoS ONE*, *9*(1). <https://doi.org/10.1371/journal.pone.0083284>
- Sprent, J. I. (2009). Nodulation in a Taxonomic Context. In *Legume Nodulation* (Issue 1995, pp. 1–33). <https://doi.org/10.1002/9781444316384.ch1>
- Sullivan, M. J. P., Lewis, S. L., Affum-Baffoe, K., Castilho, C., Costa, F., Sanchez, A. C., Ewango, C. E. N., Hubau, W., Marimon, B., Monteagudo-Mendoza, A., Qie, L., Sonké, B., Martinez, R. V., Baker, T. R., Brienen, R. J. W., Feldpausch, T. R., Galbraith, D., Gloor, M., Malhi, Y., ... Phillips, O. L. (2020). Long-



term thermal sensitivity of earth's tropical forests. *Science*, 368(6493), 869–874.

<https://doi.org/10.1126/science.aaw7578>

Sullivan, M. J. P., Lewis, S. L., Hubau, W., Qie, L., Baker, T. R., Banin, L. F., Chave, J., Cuni-Sanchez, A., Feldpausch, T. R., Lopez-Gonzalez, G., Arets, E., Ashton, P., Bastin, J. F., Berry, N. J., Bogaert, J., Boot, R., Brearley, F. Q., Brienen, R., Burslem, D. F. R. P., ... Phillips, O. L. (2018). Field methods for sampling tree height for tropical forest biomass estimation. *Methods in Ecology and Evolution*, 9(5), 1179–1189. <https://doi.org/10.1111/2041-210X.12962>

Traoré, S., Zo-Bi, I. C., Pioniot, C., Aussenac, R., & Hérault, B. (2024). Fragmentation is the main driver of residual forest aboveground biomass in West African low forest-high deforestation landscapes. *Trees, Forests and People*, 15(December 2023). <https://doi.org/10.1016/j.tfp.2023.100477>

Vancutsem, C., Achard, F., Pekel, J. F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Aragão, L. E. O. C., & Nasi, R. (2021). Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Science Advances*, 7(10), 1–22. <https://doi.org/10.1126/sciadv.abe1603>

Vieilledent \*, G., Vancutsem, C., Bourgoin, C., Ploton, P., Verley, P., & Achard, F. (2022). Spatial scenario of tropical deforestation and carbon emissions for the 21st century. *BioRxiv*, 7, 1–9. <https://doi.org/10.1101/2022.03.22.485306>

White, F. (1983). The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa (3 Plates, Northwestern Africa, Northeastern Africa, and Southern Africa, 1: 5,000,000). In *United Nations Educational, Scientific and Cultural Organization, Paris, France*.

Zhou, L., Tian, Y., Myneni, R. B., Ciais, P., Saatchi, S., Liu, Y. Y., Piao, S., Chen, H., Vermote, E. F., Song, C., & Hwang, T. (2014). Widespread decline of Congo rainforest greenness in the past decade. *Nature*,

508(7498), 86–90. <https://doi.org/10.1038/nature13265>