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1 **Carbon stock increase during post-agricultural succession in central France: no change**
2 **of the superficial soil stock and high variability within forest stages**

3
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17 **ABSTRACT**

18

19 Forest development following agricultural abandonment concerns extensive areas including
20 the Massif Central region of France where this study was undertaken. This land-use and land-
21 cover (LULC) change is expected to have effects on biodiversity and ecosystem services,
22 including an increase of carbon sequestration – a major concern in the face of climate change.
23 Nevertheless, uncertainties about carbon stock changes during successions are remaining,
24 especially as to the total stock and the contribution of the different carbon pools. Our work
25 contributes to this field by studying carbon stocks in multiple plots of different successional
26 stages. We measured and estimated carbon stocks in aboveground and belowground
27 vegetation, deadwood, litter and superficial soil, and surveyed plant communities and plot
28 conditions (slope, aspect, soil characteristics). The average total carbon stock increased along
29 the succession from 70.60 tC ha⁻¹ at stage 0 to 314.19 tC ha⁻¹ at stage 5. However, the total
30 carbon stocks at the young forest stage (abandoned for 74 years maximum) and the older forest
31 stage (forested for at least 74 years) were not significantly different, and probably reflected
32 strong local heterogeneity in the older forest stage. An increase of the carbon stock was found
33 in all pools, except the soil pool that did not vary significantly between the successional stages.
34 The aboveground carbon stock was found strongly related to the woody species cover,
35 especially the macrophanerophyte cover. This case study supports the view that the succession
36 dynamics of former agricultural plots participates in carbon sequestration, sometimes with
37 great local variations.

38

39

40 **KEYWORDS**

41

42 LULC change, carbon sequestration, agricultural abandonment, forest expansion, carbon
43 pools, aboveground biomass

44

45

Accepted Article

46

47 1. Introduction

48

49 Agricultural abandonment is a major land use and land cover (LULC) change in Europe
50 along with urbanization and agricultural intensification (Gerard et al. 2010; van Vliet et al.
51 2015). Following the cessation of agricultural activity, vegetation succession leads to old fields
52 going through various successional stages (Lepart and Escarré 1983), except under harsh biotic
53 or abiotic constraints. Under temperate climates, succession occurs *via* a transition from open
54 ecosystems dominated by herbaceous plant species to shrubs, and finally forested ecosystems
55 (Cramer and Hobbs 2007). Agricultural abandonment concerns extensive areas worldwide
56 (Chazdon et al. 2020), with an estimated 150 million hectares abandoned between 1700 and
57 1992 (Ramankutty and Foley 1999) and still around 60 million hectares between 2003 and
58 2019 (Potapov et al. 2022). The trend is expected to continue: Perpiña Castillo et al. (2021)
59 predicted that some 5.6 million hectares are likely to be abandoned by 2030 (3.6% of 2015
60 agricultural zones). Abandonment leads to an increase of forest covers (Rudel et al. 2005;
61 Meyfroidt and Lambin 2011) including the Massif Central region of France where this study
62 was led (CEREMAC 2000).

63 Agricultural abandonment clearly impacts biodiversity through changes in vegetation
64 composition and structure, and changes in other related taxa like insects (Dantas de Miranda et
65 al. 2019) and birds (Fonderflick et al. 2010). In their review of the ecological impacts of
66 agricultural changes in Europe, Stoate et al. (2009) report that vegetation development after
67 abandonment altogether tends to have a positive effect on biodiversity associated to shrub and
68 forested ecosystems but negative effects on farmland biodiversity. The changes occurring
69 along secondary successions, i.e. shifts from herb-dominated communities to shrubs and trees
70 (Cramer and Hobbs 2007), come together with changes in ecosystem functioning (Cramer and

71 Hobbs 2007; Romero-Díaz et al. 2017), and effects on ecosystem services (ES) (Lasanta et al.
72 2015; Leal Filho et al. 2017; Ustaoglu and Collier 2018). Ecosystem services are the benefits
73 delivered by ecosystems to humans (Millennium Ecosystem Assessment 2005) stemming from
74 their biological properties and functioning (Villamagna et al. 2013). Abandonment may also
75 lead to ecosystem disservices (EDS), i.e. the harmful and negative inputs from ecosystems
76 (Lyytimaki & Sipila 2009; von Döhren & Haase 2015; Blanco et al. 2020). Various effects of
77 abandonment on ES and EDS have been reported in the literature, such as increased forestry
78 production, increased fire risks, and positive impacts on “water, soil and air protection, and
79 carbon sequestration” (Stoate et al. 2009).

80 The potential impact of abandonment on carbon sequestration represents a crucial issue
81 in the face of climate change, which jeopardizes the living conditions of human beings, e.g.
82 with increased catastrophic climate events (IPCC 2022). Climate change is also an essential
83 issue for biodiversity as it is expected to reduce the habitat ranges of plant and animal species,
84 generates stresses, and increases mortality (Raj et al. 2018; IPCC 2022; Vacek et al. 2023).
85 Defined as the “regulation of chemical composition of atmosphere and oceans” by ecosystems
86 (code 2.2.6.1 of the *Common International Classification of Ecosystem Services* (V5.1)
87 (Haines-Young and Potschin 2018)) carbon sequestration mitigates the effects of climate
88 change by decreasing greenhouse gases in the atmosphere. The expected increase of the carbon
89 stock with vegetation development along succession on former agricultural lands can
90 efficiently participate to carbon sequestration (Ziegler et al. 2012; Bastin et al. 2019). Such an
91 increase of the carbon stock is all the more needed in France, where carbon sequestration
92 objectives are lagging behind (Haut Conseil pour le Climat 2022).

93 Ecological evaluation and quantification of ES is necessary to inform management
94 decisions (de Groot et al. 2002) and to map and accurately model ES (Vigerstol and Aukema
95 2011; Bartholomé et al. 2018; Meraj et al. 2022). From a quantitative point of view,

96 estimations of carbon stock changes after abandonment are still uncertain. Carbon stock
97 changes through spontaneous succession have been studied, e.g. on litter decomposition along
98 successional gradients (Mayer et al. 2008) and on the carbon stocks of aboveground vegetation
99 in Spanish forests since the 1950s (Vilà-Cabrera 2017). Yet, to our knowledge only a few
100 studies have investigated a variety of stages including plots under agricultural use and old
101 forests, while also looking at multiple carbon pools (aboveground, necromass, belowground
102 and superficial soil) (Hooker and Compton 2003; Risch et al. 2008; Aryal et al. 2014;
103 Badalamenti et al. 2019; Facioni et al. 2019; Jones et al. 2019; Finzi et al. 2020; Thibault et al.
104 2022), and none has focused on west-European temperate forests. Such an approach is
105 important because the carbon stock changes during spontaneous vegetation growth are less
106 controlled and straightforward than those that occur in forest plantations: diverse vegetation
107 pathways and local conditions induce variations in carbon accumulation (Benjamin et al. 2005;
108 Foote and Grogan 2010; Kalt et al. 2019; Smith et al. 2020).

109 Following abandonment, the total amount of carbon stored in an ecosystem is expected
110 to increase as a consequence of biomass accumulation in vegetation, litter and soil (Hooker
111 and Compton 2003). Succession stages differ from each other by their carbon pools, in absolute
112 stock (de Jesus Silva et al. 2016; Badalamenti et al. 2019; Facioni et al. 2019; Gogoi et al.
113 2020) as well as in the relative contribution of the different pools (aboveground vegetation,
114 roots, and soil) (Bartholomé et al. 2018). These contrasts are expected because the
115 belowground-to-aboveground biomass ratio is lower in trees than in grasses and shrubs (IPCC
116 2006a, b; Freschet et al. 2017), and aboveground living biomass tends to dominate the carbon
117 stock in late successional stages (Badalamenti et al. 2019). The last stages of old-grown forests
118 are expected to have the highest stock, even if the carbon stores of old-grown forests vary
119 between biomes (Pan et al. 2011; Keith et al. 2014; Badalamenti et al. 2019).

120 In temperate regions, agricultural abandonment is followed by a change in species
121 composition from light-demanding plant species to shade-tolerant ones (Harmer et al. 2001).
122 The shift in dominating life forms from herbaceous (therophyte, geophyte, hemicryptophyte)
123 to woody perennial (chamaephyte, phanerophyte) may be key in explaining changes in the
124 carbon stock. However, the community composition varies within and among stages (Morel et
125 al. 2020; Czurzycki et al. 2021) and can bring additional effects on carbon sequestration
126 patterns, e.g. through dominant tree species in communities (Vallet et al. 2009; Vesterdal et al.
127 2013) and species canopy structure (Hardiman et al. 2013). Carbon stock may also be
128 influenced by plant diversity: more diversified communities tend to enhance niche
129 complementarity and may increase plant aboveground biomass (Loreau and Hector 2001; Li
130 et al. 2017). Along with successional stages and species composition, local factors can affect
131 the carbon stock. Clay-rich soils tend to retain more nutrients (Manrique et al. 1991; Lu et al.
132 2002) and nutrient-richer soils support higher vegetation growth (Moran et al. 2000); slope is
133 also a determining factor: steeper slopes tend to increase water drainage and soil nutrient loss
134 (Robinson et al. 2015).

135 To contribute to these challenges, we evaluated carbon sequestration during vegetation
136 successions following abandonment by carrying out field measurements and distinguishing the
137 patterns within various successive vegetation stages. Our aim was also to study the
138 relationships between plant biodiversity, ecosystem functioning and ES (Walker et al. 2010;
139 Prach and Walker 2011). Accordingly, we investigated the relationship between (i) the carbon
140 stock and (ii) successional stages and local environmental conditions. We studied post-
141 agricultural plots belonging to different successional stages and situated in temperate low
142 mountains of central France. We conducted field measurements of the carbon stock to address
143 the three following questions: (i) how much carbon is stored in old fields and forests in total?;
144 (ii) how does the carbon stock change among the different pools during succession?; and (iii)

145 which local biotic and abiotic factors influence the carbon stock in old fields and forests? We
146 tested the following hypotheses: (a) the total carbon store increases with succession, and forest
147 stages store amounts of carbon similar to those measured in other temperate forests, i.e. around
148 346 tC ha⁻¹ (Finzi et al. 2020) to 373 tC.ha⁻¹ (Lecoointe et al. 2006); (b) all above- and below-
149 ground carbon pools increase along the vegetation succession, but their relative contribution to
150 the carbon stock (%) varies between stages; (c) the carbon store varies depending on multiple
151 factors including the species composition of the plant communities, their Raunkiaer life forms
152 (Raunkiaer 1934), richness and diversity, the soil type and its nitrogen content, and the
153 slope aspect and inclination.

155 **2. Materials and methods**

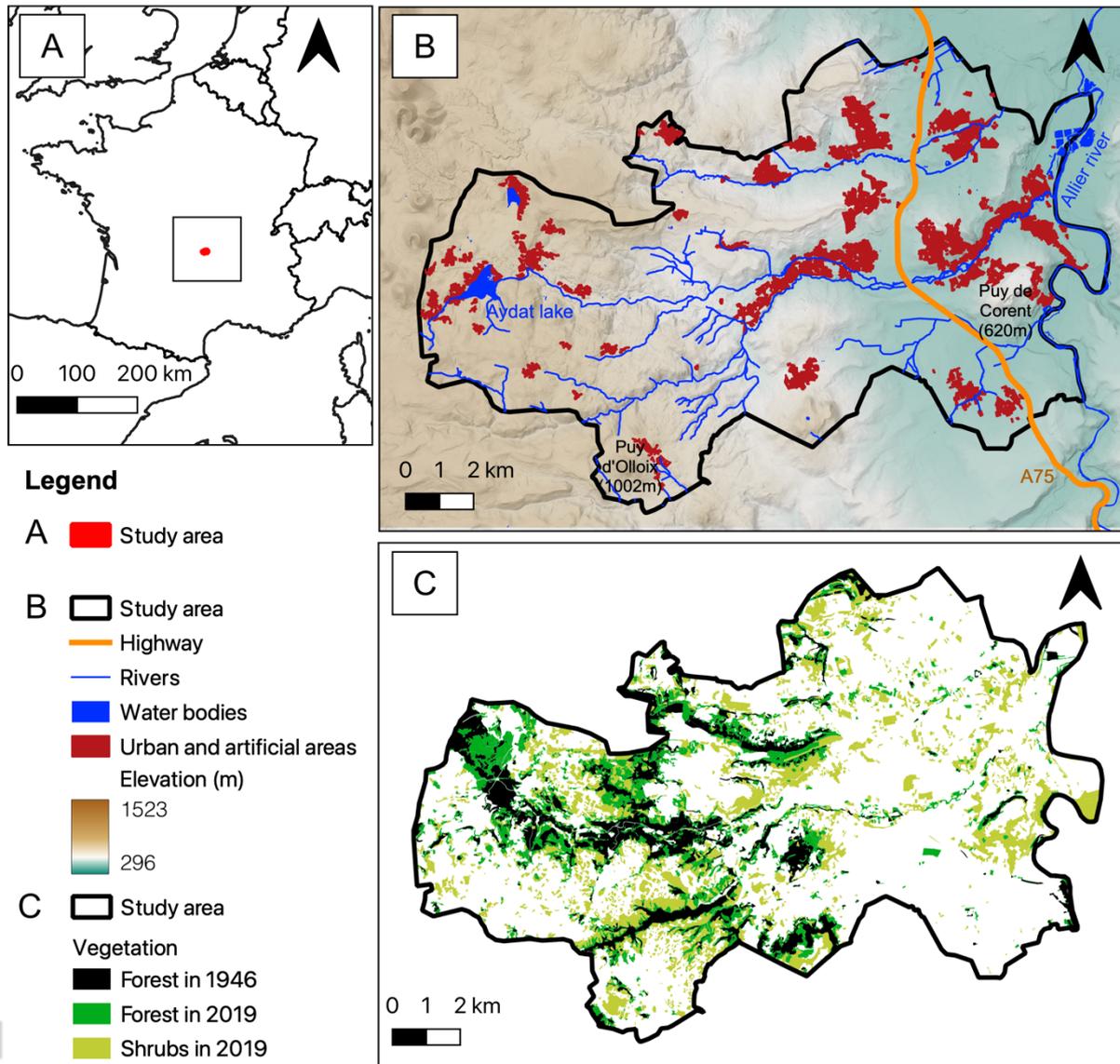
157 **a. Study area**

158
159 The study was conducted in a 166-km² area (45°40'N, 3°06'E) situated in the Massif
160 Central region of France (figure 1a), south of Clermont-Ferrand conurbation, at the junction
161 between mountainous systems of volcanic origin in the west (Chaîne des Puys and Massif des
162 Monts Dore) and a sedimentary basin in the east (Limagne plain, the Allier River alluvial
163 plain). The area comprised granitic and volcanic plateaus and low mountains in the west, a
164 plain in the east made of volcanic and limestone-clay colluvial deposits, and a series of west-
165 to-east valleys in-between (figure 1b). Mean annual temperature varies between 8.7 and 11.6
166 °C, and mean annual precipitation between 578.9 and 796.1 mm (Roux 2017).

167 Agricultural abandonment has been taking place in the area for at least two centuries.
168 We used 13 historical orthophotographs of the study area (1946, 1962, 1974, 1978, 1981, 1984,
169 1986, 1989, 1999-2001, 2004-2009, 2016 and 2019) retrieved from the National Institute of

170 Geographic and Forest Information (IGN) covering a roughly 70-year-long period to determine
171 the historical record of the area and of its agriculture. The analysis of the photographs indicated
172 that 21% of agricultural lands in 1946 had been abandoned and colonized by ligneous
173 vegetation by 2019; shrub, wood, and mature forest covers went from 19% to 34% of the study
174 area during the same period (Weissgerber et al. 2022) (figure 1c). In 1946, the main agricultural
175 activities were arboriculture, viticulture, cattle and sheep farming, and subsistence agriculture,
176 *versus* croplands (cereals, oil seeds) and pastureland in 2019.

177



178

179 **Fig. 1** Characteristics of the study area. (A) Localization of the study area in France. (B)

180 Elevation contrasts, rivers, and urban and artificial areas of the study area at present. (C) Shrub

181 and forest covers in 2019. Black, forests already present in 1946; dark green and light green,

182 forests and shrubs having developed between 1946 and 2019, respectively, indicating

183 agricultural abandonment followed by vegetation succession and forest development.

184

185

186

187 **b. Determination of successional stages in the study area and plot selection**

188
189 Plot selection for carbon stock measurements was based on successional stages (table
190 1). Stages were first identified on aerial photographs, and then plots from five successional
191 stages – plus a first stage (thereafter called ‘0’) corresponding to grazed plots still under
192 agricultural use – were selected after field observations and description (figure 2). Three shrub-
193 rich stages (1, 2, 3) were abandoned but unwooded, with an increasing shrub cover at the
194 expense of herbaceous vegetation from stage 1 to stage 3. Stage 4 corresponded to young
195 forests in plots unforested in 1946 but forested in 2020, when field work was conducted. On
196 the basis of the orthophotographs, the corresponding plots had been forested (visible crowns)
197 at least since 1999-2001. The oldest stage (stage 5) corresponded to plots that showed visible
198 crowns and were already forested on the 1946 orthophotographs. These forests were at least 74
199 years old in 2020. These plots had been under agricultural use at the beginning of the 19th
200 century according to the ‘Napoleon’ land register established between 1808 and 1833 in the
201 region, so we may assume that their abandonment and reforestation happened between 1833
202 and 1946.

203 Agricultural activity greatly changed in the area during the last two centuries. Data on
204 the agricultural history of each abandoned plot were limited and mostly derived from the
205 historical aerial photographs, and we had approximately one per 10-year period since 1946.
206 Moreover, succession rates vary depending on multiple causes including soil quality and
207 distance to the seed source (Lepart and Escarré 1983; Acácio et al. 2007; Rühl and Schnittler
208 2011; Ciuzycki et al. 2021), so that abandonment periods can only be determined with low
209 precision. As a result, we adopted semi-quantitative classes based on successional stages (0, 1,
210 2, 3, 4, 5). We selected stage 1, 2, 3, 4 plots formerly managed as grasslands (not as croplands

211 or vineyards or orchards), but the land use of some plots may have changed several times in
212 the decades before their abandonment.

213 Five plots were selected *per* successional stage. All plots were situated on valley sides,
214 at the center of the study area, within a 2.3-km radius (Appendix A). Soils were primarily
215 brown soils (Callot et al. 1966; Hétier 1973) (approximately equivalent to Cambisols in
216 the WRB) that overlaid a bedrock composed of a variety of volcanic rocks and limestone-clay
217 colluvial deposits. Twenty subplots (19 in two cases, see table 1) were delimited in each plot.
218 Two types of subplots were distinguished to capture the heterogeneity of stages 1 and 2: one
219 was dominated by herbaceous vegetation (H), and the other was dominated by woody
220 vegetation (W) (table 1, figure 2). This distinction between 1H and 1W, and 2H and 2W was
221 maintained throughout the study. The subplot size varied to fit the spatial structure of the stages
222 (16 m² for stages 0-1-2-3, 36 m² for stage 4, 100 m² for stage 5).

223

Stage	0	1		2		3	4	5
Vegetation	Herbaceous, under agricultural use	Shrubby grasslands dominated by herbs		Shrubby grasslands dominated by shrubs		Tall shrubland	Forested for less than 74 years	Forested for more than 74 years
Vegetation type		H	W	H	W			
Nb of subplots	20	20	19	20	19	20	20	20

224 **Table 1.** Sampling design: plots and subplots were distributed across one agricultural stage and
225 five successional stages. Two vegetation types were distinguished in the non-homogenous
226 stages, hence 30 plots and 158 subplots. H, herbaceous vegetation type; W, woody vegetation
227 type.

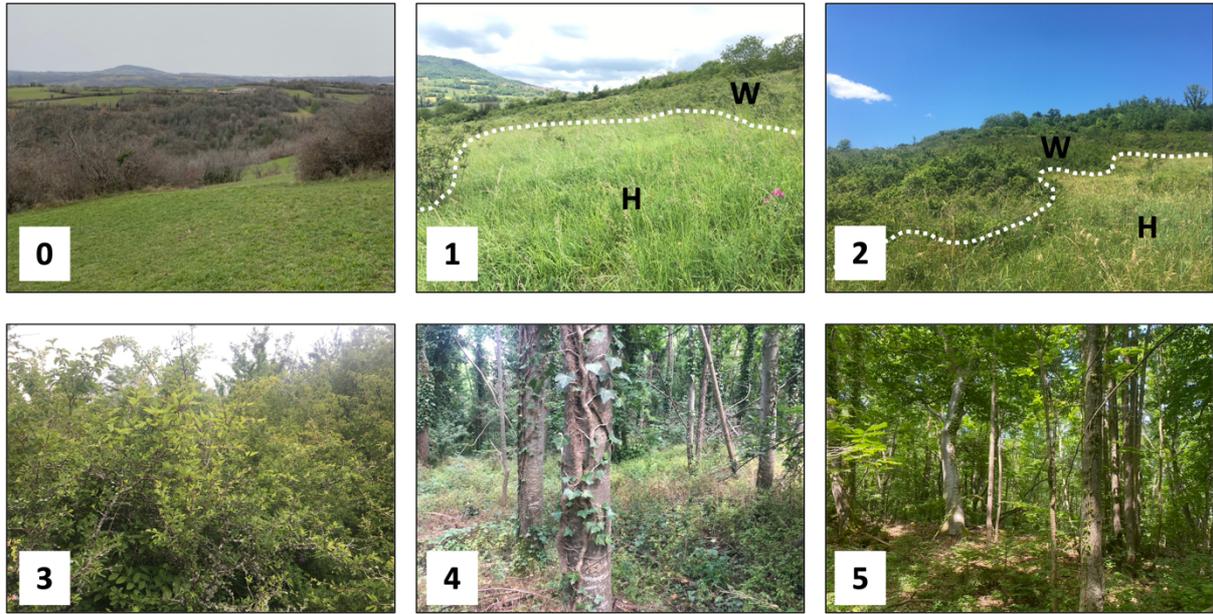


Fig. 2 Pictures showing examples of plots typical of the five studied successional stages. Number in the bottom left corner, successional stage (see text). Plots of stages 1 and 2 include two vegetation types. H, herbaceous vegetation type; W, woody vegetation type (see table 1).

c. Vegetation surveys

The surveys were conducted on the subplots. As stated, their size varied according to the vegetation type (Gillet 1998; Andrade et al. 2019). We pursued observational objectives to characterize plant communities rather than the completeness of their species composition (Andrade et al. 2019). The vascular plant species composition of each subplot was recorded in spring and early summer 2020 (Tison and Foucault 2014). The species cover was determined visually as a percentage of the subplot total area. All vegetation strata (herbs, shrubs, trees) were surveyed, and the total species cover potentially exceeded 100% on the plots harboring several vegetation strata. Vegetation surveys were not conducted on stage 0 plots because regular grazing disturbed plant development.

d. Measurements of the aboveground carbon stock

The aboveground carbon stock in living biomass was measured and estimated according to the vegetation form, i.e. grasses, shrubs, or trees (table 3).

The aboveground biomass of herbaceous plants was measured by determining (i) the relationship between grass height (cm) and grass mass *per* surface unit ($\text{g}\cdot\text{cm}^{-2}$), and (ii) the average grass height of each subplot. The relationship between grass height and grass mass *per* surface unit was established by sampling herbaceous vegetation (400 cm^2 of known height) in each subplot and weighing it after drying at $60\text{ }^\circ\text{C}$ for at least 24 hours; all values were plotted, and the resulting equation was $B = 0.24 \cdot H + 4.98$, where B is the herbaceous aboveground biomass ($\text{g}\cdot\text{cm}^{-2}$) and H is herbaceous vegetation height (cm). The average grass height of each subplot was determined by measuring grass height every 15 cm on the diagonal of the subplot, i.e. 37 points in 16-m^2 subplots.

Shrub biomass was estimated from the volume of vegetation using the equation from Montero et al. (2013):

$$\ln(W) = -2.560 + 1.006 \cdot \ln(H_m) + 0.672 \cdot \ln(FCC_m)$$

where W is the biomass (tons of material *per* hectare), H_m is the average shrub height (dm), and FCC_m is the proportion of the subplot covered by shrubs.

Tree biomass was estimated from the diameter at breast height (DBH) of trees following species-specific equations of the following form:

$$B = a \cdot D^b \text{ or } \exp(B) = a + b \cdot \ln(D)$$

where B is the aboveground biomass (kg) and D the DBH (cm). When species-specific equations were not available, the general equation following Zianis and Mencuccini (2004), and Bartholomée et al. (2018) was used, i.e.:

$$B = 0.1424 \cdot D^{2.3679} .$$

270 The detailed equations are available in appendix B.

271

272 Three types of aboveground dead biomass were considered: standing dead trees, fallen
273 dead trees, and litter lying on the soil. The biomass of standing dead trees was calculated with
274 the general equation following Zianis and Mencuccini (2004), and Bartholomé et al. (2018),
275 i.e.:

$$276 \quad B = 0.1424 \cdot D^{2.3679}$$

277 where B is the aboveground biomass (kg) and D the DBH (cm).

278 The biomass of fallen dead trees was estimated from tree diameter and height. Tree
279 density decreases after death. Consequently, a density of 0.26 g.cm^{-3} was chosen to determine
280 biomass from volume, following Bartholomé et al. (2018). Litter biomass was determined by
281 sampling litter on 400 cm^2 in each subplot and weighing after drying it at $60 \text{ }^\circ\text{C}$ for 24 hours.

282

283 We used ratios to determine carbon contents. For all living vegetation types, the carbon
284 content equated to $0.47 \cdot \text{biomass}$ (IPCC 2006b). We also applied a constant of $0.44 \cdot \text{biomass}$
285 to determine litter carbon, based on Chojnacky et al. (2009) and Bartholomé et al. (2018).
286 However, the litter carbon content is variable, so this caveat should be borne in mind when
287 interpreting the results.

288

289 **e. Estimation of the belowground carbon stock**

290

291 Root biomass was estimated from aboveground biomass using root-to-shoot ratios
292 (table 2) (IPCC 2006a, b; Mokany et al. 2006; Bartholomé et al. 2018).

293

294

Vegetation type		Aboveground / belowground biomass conversion ratio
Forest	< 75 t/ha	0.46
	75-150 t/ha	0.23
	> 150 t/ha	0.18
Shrubs		1.8
Grasses		2.8

Table 2. Aboveground / belowground biomass conversion ratio (IPCC 2006a, b; Mokany et al. 2006; Bartholomée et al. 2018)

f. Measurements of the soil carbon stock

Two types of soil samples were collected at two soil depths (0-10 cm and 10-20 cm) in each subplot (table 3) (four samples *per* subplot). The first sample type was obtained using a standard stainless-steel 5 cm x 5 cm cylinder and was used to determine soil bulk density ($\text{g}\cdot\text{cm}^{-3}$), following Peco et al. (2017) and Bartholomée et al (2018). Each soil sample was weighed, all roots and stones were carefully removed and weighed, and then all samples were sifted through a 2-mm sieve, dried at 105 °C for 24 h, and weighed. Multiple mass measurements allowed us to ensure that no soil had been lost in the process. For the second sample type, soil from each subplot was placed in a sealable plastic bag. The samples were pooled *per* plot after careful mixing, and sent to the Agronomic Laboratory of Normandie to measure organic carbon ($\text{g}\cdot\text{kg}^{-1}$) (NF ISO 14235), nitrogen ($\text{g}\cdot\text{kg}^{-1}$) (NF ISO 11261) and determine texture (NF X31-107).

The soil organic carbon (SOC) content ($\text{g}\cdot\text{cm}^{-3}$) was determined as the organic carbon content multiplied by the bulk density.

Stage		0	1		2		3	4	5
Vegetation type			H	W	H	W			
Subplots (n =)		20	20	19	20	19	20	20	20
Vegetation survey			x	x	x	x	x	x	x
Carbon stock	Grasses	x	x		x				
	Shrubs		x	x	x	x	x		
	Trees						x	x	x
	Dead trees			x		x	x	x	x
	Litter	x	x	x	x	x	x	x	x
	Superficial soil	x	x	x	x	x	x	x	x

Table 3. Summary of the measurements conducted in each subplot at each stage.

g. Data analysis

A principal component analysis (PCA) on the Hellinger-transformed species-cover matrix (Legendre and Legendre 2012) was performed to compare the vegetation species composition among the different successional stages and vegetation types. Only the plant species with a cumulative cover > 5% in the dataset were taken into account.

The differences in total carbon stock and carbon stored in each pool between the successional stages and the vegetation types were tested using one-way analysis of variance (ANOVA; $P < 0.05$), followed by Student's *post-hoc* test when conditions were met. Otherwise, Kruskal-Wallis test were applied, followed by Dunn's *post-hoc* test with Benjamini-Hochfeld adjustment (Lee and Lee 2018; Jafari and Ansari-Pour 2019).

331 To investigate which environmental variables explained carbon stock variations, we
 332 used generalized linear mixed models (GLMMs, with a gaussian error distribution) with ‘plot’
 333 as a random effect (lme4 package; Bates et al. 2019). Multiple explanatory variables were
 334 considered (table 4). Variables were not scaled to ensure a better interpretability of estimates.
 335 The initial model was as follows: aboveground carbon $tC \cdot ha^{-1} \sim$ species PCA dim1 + species
 336 PCA dim2 + Macrophanerophyte cover + Mesophanerophyte cover + Microphanerophyte
 337 cover + Nanophanerophyte cover + Geophyte cover + Therophyte cover + Hemicryptophyte
 338 cover + Chamaephyte cover + richness + Shannon index + soil nitrogen ($g \cdot kg^{-1}$) + $\cos(\text{aspect})$
 339 + $\sin(\text{aspect})$ + slope inclination + soil clay + soil sand + soil silt + soil depth + (1 | plot).

Biotic factors	Plant species composition	Species PCA (figure 3) coordinates on the first two axes
	Species richness	Total number of species
	Species diversity	Shannon index
	Raunkiaer life forms cover	In the species cover matrix (cumulative cover > 5%), species were associated to their Raunkiaer life forms based on botanical literature (Tison and Foucault 2014) (therophyte, hemicryptophyte, geophyte, chamaephyte, nanophanerophyte (<2 m), microphanerophyte (2-8 m), mesophanerophyte (8-30 m), macrophanerophyte (30-50 m)). The covers were summed to associate each subplot to life form covers.
Abiotic factors	Slope	Derived from Digital Terrain model
	Aspect	Derived from Digital Terrain model. The cos and sin of the original angle value (0° - 360°) were calculated: “North-exposedness”: $\cos(\text{aspect})$ “East-exposedness”: $\sin(\text{aspect})$
	Soil depth	Determined at each plot using a digging bar (max = 75 cm)
	Soil texture	Clay content, silt content, sand content. See section 2f
	Nitrogen content	See section 2f

341 **Table 4.** Biotic and abiotic variables included in the generalized linear mixed models.

342 We produced all candidate models testing all combinations of variables up to a
 343 maximum of 4 variables *per* model to limit the complexity of the models and computation
 344 time. Then, we used a multi-model inference approach to calculate model-averaged parameter

345 estimates (with 95% confidence intervals) for the variables included in the selected models
346 (cumulated weight AICc < 0.95, Akaike information criterion corrected for small sample sizes,
347 Burnham & Anderson, 2002). The dredging and model averaging procedures were performed
348 using the MuMin package (Bartoń, 2016). The effect of an explanatory variable was considered
349 significant when its estimate (the slope of the relation) was different from zero (when its 95%
350 confidence interval excluded zero). The quality of the models was evaluated using the r^2 values
351 calculated for the fixed effects for the global model (marginal r^2 using the “r.squaredGLMM”
352 function in the MuMin package; Bartoń 2016).

353

354 The tests were performed using Excel and Rstudio (R version 4.1.0).

355

356 3. Results

357

358 a. Vegetation composition of the surveyed plots

359

360 The vegetation composition varied between successional stages (figure 3), even if
361 similarities in species composition were found between the herbaceous plant communities of
362 stages 1 and 2 (1H and 2H), and the woody shrub communities of stage 1 (1W). Indeed, the
363 plant communities of stages 1H, 2H and 1W were all dominated by *Bromus erectus* (Huds.)
364 and *Brachypodium pinnatum* (L.). By contrast, stages 2W and 3 were dominated by *Cornus*
365 *sanguinea* (L.). Stage 4 was dominated by *Fraxinus excelsior* (L.) and *Robinia pseudoacacia*
366 (L.), while stage 5 was dominated by *Quercus robur* (L.) and *Abies alba* (Mill.). Some species
367 were present in both last stages, especially *Hedera helix* (L.) but also *Acer campestre* (L.) and
368 *Corylus avanala* (L.). However, the compositions of these two stages globally differed: stage
369 4 still included a high cover of *Prunus avium* (L.), *Crataegus sp.* and *Cornus sanguinea* (L.),

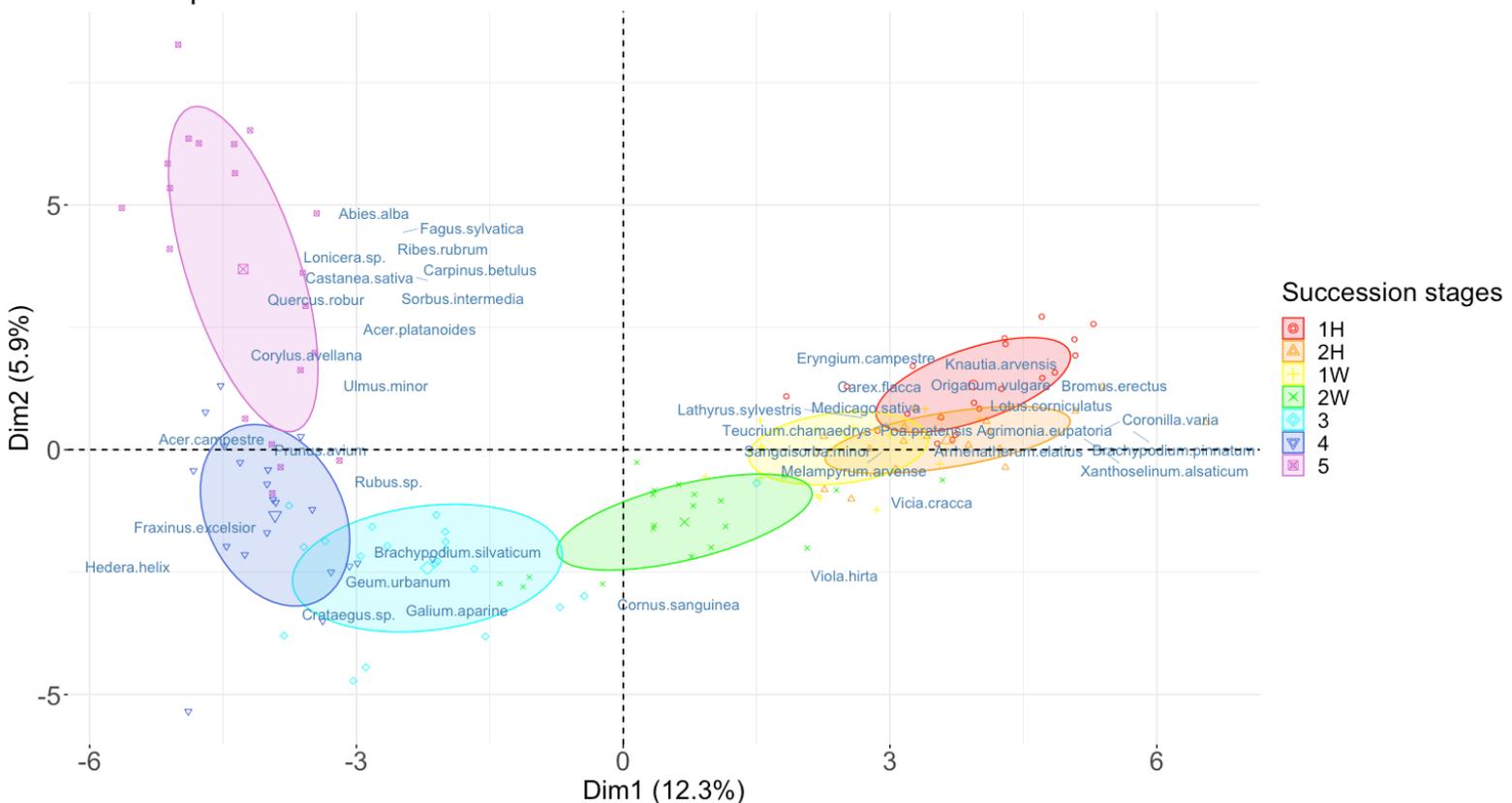
370 while stage 5 included a higher cover of *Fagus sylvatica* (L.) and *Carpinus betulus* (L.).

371 Therefore, the plant species composition at stage 4 – corresponding to agricultural plots

372 abandoned for approximately 65-75 years –, was different from that of older forests.

373

PCA - Biplot



374 **Fig. 3** PCA of the plant species compositions of the 138 subplots sampled in 5 successional
375 stages and distinguishing two vegetation types for stages 1 and 2 (H, herbaceous vegetation
376 type; W, woody vegetation type).

377

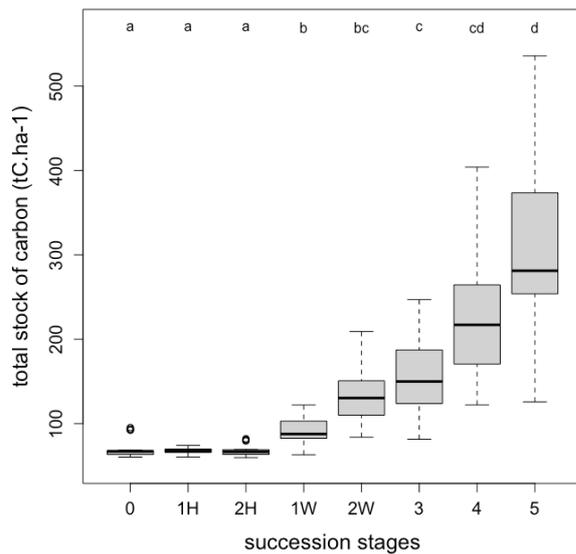
378 **b. Total carbon stock: an increase with succession but heterogeneity at the** 379 **last stage**

380

381 The total carbon stock increased from stage 0 to stage 5, and was multiplied by 4.5 on
382 average (figure 4). The total carbon stocks of the woody vegetation types of stages 1 and 2 (1W
383 and 2W) were not significantly different, but they differed from the stocks of the herbaceous

384 communities (1H and 2H). The average total carbon stocks were 216.80 tC ha⁻¹ in stage 4, and
385 314.19 tC ha⁻¹ in stage 5, with high variation between subplots (min. 125.71 tC ha⁻¹; max.
386 535.82 tC ha⁻¹).

387



388 **Fig. 4** Total carbon stock of each successional stage, and vegetation types at stages 1 & 2.
389 Different letters indicate significant differences (Kruskal test, $P < 0.0001$).

390

391 **c. Carbon pools: aboveground biomass drives the increase of the total carbon**
392 **stock, but no variation of the soil stock**

393

394 The carbon stored in aboveground vegetation varied between 1.1 tC ha⁻¹ minimum at
395 stage 0 (2.68 tC ha⁻¹ on average) and 326.6 tC ha⁻¹ maximum at stage 5 (175 tC.ha⁻² on average)
396 (table 5). Estimations of the belowground (root) carbon stock ranged from 3.0 tC ha⁻¹ at stage
397 0 to 117.14 tC ha⁻¹ at stage 3. The amount of carbon stored in the belowground vegetation of
398 stage 3 was not significantly different from the stock in the woody vegetation of stages 1 (1W)
399 and 2 (2W) or from the overall amounts of stages 4 and 5. The carbon stored in litter and

400 deadwood increased with the successional stages, and the greatest stock was found at stage 5.

401 No significant difference in superficial SOC emerged between the different stages.

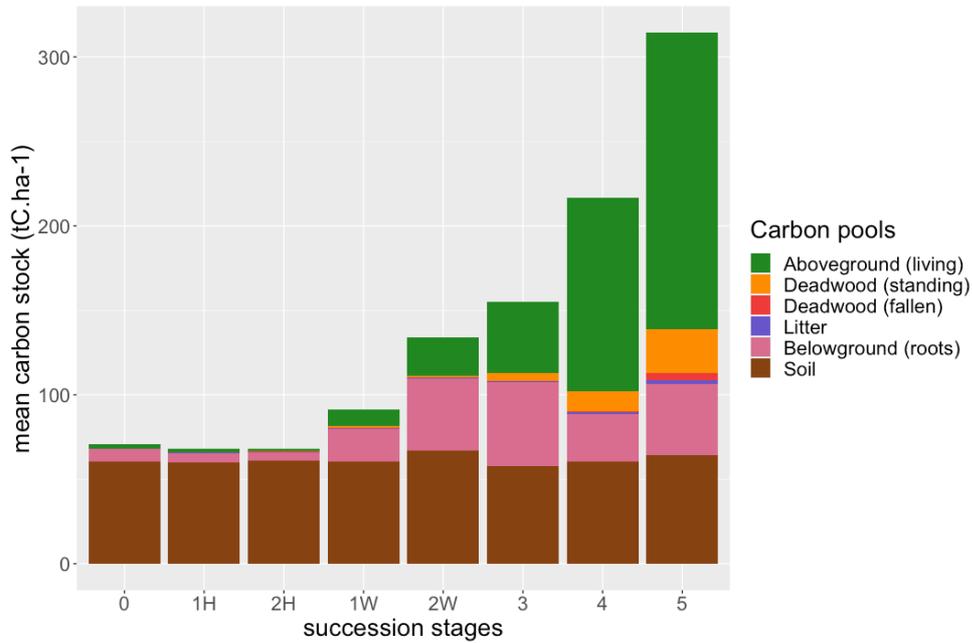
402 Clear differences appeared between the herbaceous and woody vegetation types within
403 stages 1 and 2: although the soil pool stored the most carbon in both stages, the development
404 of shrubs brought about an important increase of the aboveground and belowground carbon
405 stocks. In the last stages of the succession (stages 4 and 5), aboveground vegetation was the
406 largest carbon pool (table 5, figure 5).

	0			1H			2H			1W		
Pools	mean	SD	%	mean	SD	%	mean	SD	%	mean	SD	%
Aboveground	2.68 a	0.86	3.80	2.13 a	1.02	3.14	1.85 a	0.29	2.71	9.87 b	4.93	10.81
Belowground	7.52 a	2.40	10.65	5.49 a	2.06	8.09	4.96 a	0.54	7.27	19.57 b	8.90	21.43
Litter	0.03 a	0.07	0.04	0.33 b	0.27	0.49	0.17 b	0.08	0.25	0.36 b	0.35	0.39
Deadwood (standing)	0.00 a	0.00	0.00	0.05 a	0.11	0.07	0.21 a	0.52	0.31	1.22 b	1.69	1.34
Deadwood (fallen)	0.00 a	0.00	0.00	0.00 a	0.00	0.00	0.02 a	0.05	0.03	0.04 ab	0.07	0.04
Superficial soil (SOC)	60.37 a	11.42	85.51	59.90 a	5.18	88.22	61.00 a	7.10	89.43	60.26 a	8.28	65.99
Total	70.60 a	12.09		67.90 a	3.64		68.21 a	7.21		91.32 b	15.45	

407

	2W			3			4			5		
Pools	mean	SD	%	mean	SD	%	mean	SD	%	mean	SD	%
Aboveground	22.72 bc	12.22	16.94	42.34 c	16.24	27.30	114.91 c	63.05	53.00	175.36 d	82.94	55.81
Belowground	42.49 cd	21.64	31.67	49.87 bed	38.28	32.16	27.99 bc	14.54	12.91	42.01 d	20.03	13.37
Litter	0.30 b	0.59	0.22	0.41 b	0.48	0.26	1.07 c	1.01	0.49	2.26 c	1.19	0.72
Deadwood (standing)	1.35 bc	2.39	1.01	4.46 cd	5.62	2.88	11.49 d	11.24	5.30	26.00 d	25.81	8.28
Deadwood (fallen)	0.07 ab	0.24	0.05	0.16 b	0.19	0.10	0.90 c	1.30	0.42	4.27 c	2.60	1.36
Superficial soil (SOC)	67.21 a	11.02	50.10	57.84 a	7.64	37.30	60.44 a	16.40	27.88	64.29 a	11.98	20.46
Total	134.15 bc	34.37		155.08 c	43.01		216.80 cd	69.80		314.19 d	104.38	

408 **Table 5.** Carbon stocks in the different pools at each successional stage (from 0 to 5).



409
 410 **Fig. 5** Average amounts of carbon stored in the different pools depending on the successional
 411 stage and the vegetation type.

412
 413 **d. Variations of the aboveground carbon stock: determining factors**

414
 415 The relationship between carbon stocks and biotic and abiotic variables was tested
 416 considering the aboveground living biomass pool. The stocks of the other pools were
 417 considered to show the same pattern because their carbon stores were correlated (appendix C).
 418 Modeling indicated that the aboveground carbon stock was positively related to the
 419 macrophanerophyte, mesophanerophyte and chamaephyte covers, and negatively related to the
 420 plant species composition as approached by the first axis of the PCA (table 6 and figure 3).
 421 The PCA first axis captured changes in the herbaceous species cover (more positive scores)
 422 and tree species (more negative scores). This shows that the plant community composition has
 423 a major effect on carbon stocks, beyond the effect of the successional stage. In particular, the
 424 presence of bigger, late-successional tree species was related to higher carbon stocks.

Explained variable	Biotic and abiotic variables	Estimate (mean and 95% CI)		R ² _m	R ² _c	P
Aboveground carbon stock				0.6	0.82	
	Life form: macrophanerophyte cover	118.585	[75.51 - 161.66]			<0,0001
	Life form: mesophanerophyte cover	39.216	[1.09 - 77.34]			0.04
	Life form: chamaephyte cover	73.910	[9.08 - 138.74]			0.03
	Vegetation composition (PCA axis 1)	-5.636	[-10.31 - 0.97]			0.02

Table 6. Results of the best model of the aboveground living biomass carbon stock. Only significant variables from the model selections are provided (mean and 95% CI of each estimate).

4. Discussion

a. Vegetation succession and total carbon stocks in the plots

We measured the carbon stocks of many plots representing five successional stages, plus one stage still under agricultural use (grazing) in an area concerned by agricultural abandonment in central France.

As expected, carbon stocks increased along the succession. Furthermore, vegetation surveys showed that the species composition varied along the successional stages following succession models (Lepart and Escarré 1983; Cramer and Hobbs 2007). Early stages were characterized by herbaceous species and dominated by poaceae. Then, shrub species colonized the plots, followed by pioneer trees (*Fraxinus excelsior*, *Robinia pseudoacacia*). After approximately 65-75 years of development, young forests had not reached the composition of

443 older forests dominated by oak and fir. Holmes et al. (2018) showed similar tendencies for
444 forest herb communities that differed from those of old forest communities 80 years after
445 abandonment.

446 As hypothesized, the total amounts of carbon stored in abandoned plots increased along
447 with the successional stages. However, the differences between stages were not all significant,
448 and in particular the carbon stocks of forest stages 4 and 5 were not significantly different. This
449 is in line with Yue et al. (2018) who studied forests of various ages in northwestern China, but
450 contradicts Badalamenti et al. (2019) who found a higher carbon stock in old Mediterranean
451 forests compared to young forests. Literature shows that the timespan for forest biomass to
452 recover after abandonment is variable (Aryal et al. 2014). Stages 4 (<74 years) and 5 (>74
453 years) had globally similar total carbon stocks but different vegetation compositions. Our
454 results are not in agreement with Bauters et al. (2019) who studied tropical forest of the central
455 Congo Basin and found a quick recovery of species diversity and functional composition but a
456 lag in carbon storage during secondary succession.

457 Regarding the amount of carbon stored in the forest stages, we hypothesized that the
458 forests of the study area would store carbon in similar amounts to other forests in Europe and
459 temperate regions. As expected, young forests (stage 4) stored between 122.09 tC ha⁻¹ and
460 403.9 tC ha⁻¹ (216.8 tC ha⁻¹ on average), and older forests (stage 5) between 125.71 tC ha⁻¹ and
461 535.82 tC ha⁻¹ (314.19 tC ha⁻¹ on average). When looking at the total carbon stock of forests
462 following spontaneous post-abandonment succession, Finzi et al. (2020) found 345.73 ± 53.82
463 tC ha⁻¹ in an 80-120 year-old forest (oak, maple, hemlock) in central Massachusetts (USA),
464 while Badalamenti et al. (2019) found nearly 150 tC ha⁻¹ in a young forest (Mediterranean
465 forest-maquis) and about 198 tC ha⁻¹ in an old-growth forest, in the same range as the stocks
466 estimated in the present study. In France, many studies concern planted forests, but our mean
467 values remain close to those stocks. For instance, Lecoite et al. (2006) found 230.5 ± 14.6 tC

468 ha⁻¹ in 15-60 year-old stands of broad-leaved forests, that increased up to 373.0 ± 36.9 tC ha⁻¹
469 in > 90-year-old stands. In central Italy, Facioni et al. (2019) found a higher stock: nearly 600
470 tC ha⁻¹ in new woods and nearly 700 tC ha⁻¹ on average in old woods, but it should be noted
471 that those woods were managed coppice, which may explain the higher stock. As for a larger-
472 scale approach, the French General Committee for Sustainable Development (Commissariat
473 général au développement durable 2019) estimated that the French continental forest stored
474 730 tC ha⁻¹, while Pan et al (2011) found a stock of 155 tC ha⁻¹ in temperate forests based on
475 forest inventory data and long-term ecosystem carbon studies. Such a large variation in
476 estimations suggest heterogeneity in temperate forests carbon stock, while probably also
477 related to methodological differences.

478 The carbon stocks of successional stages 4 and 5 were quite heterogenous, which may
479 explain why these stages were not significantly different. Some of the mentioned studies do
480 find a high heterogeneity as well (Facioni et al. 2019) while others only consider one site per
481 stage (Badalamenti et al. 2019). This heterogeneity in the forested stages we studied could be
482 attributable to climate contrasts among plots (e.g. rainfall variability) (Facioni et al. 2019;
483 Velázquez et al. 2022) or slope aspect (Sharma et al. 2011). Further work in our study area
484 should be solely focused on forests to examine the factors of carbon stock variation within
485 these stages.

486 487 **b. Contribution of the different carbon pools to the total carbon stock**

488

489 The relative contributions of the carbon pools (aboveground, belowground, soil) to the
490 total carbon stock (%) were expected to vary between the successional stages. They varied
491 accordingly and to a large extent throughout the succession, following plant community
492 changes. From stage 0 to stage 3, the highest proportion of carbon was in the soil, while carbon

493 was predominantly stored in aboveground vegetation at stages 4 and 5 (table 5, figure 5).
494 Dominance of aboveground vegetation in the carbon stock has been reported: vegetation-stored
495 carbon has been found higher than soil-stored carbon only in the last stage of the succession
496 (oak dominated old-growth forest more than 105 years old (Badalamenti et al. 2019) and dry
497 semi-deciduous mature secondary forest (Robinson et al. 2015)); in the Swiss Alps, Risch et
498 al. (2008) measured a higher carbon stock in the belowground pool (soil and roots) than in the
499 aboveground pool ($125 \pm 16 \text{ tC ha}^{-1}$ vs. $90 \pm 6 \text{ tC ha}^{-1}$, respectively) in a young mountain pine
500 forest, but the opposite in an older mixed conifer forest ($107 \pm 7 \text{ tC ha}^{-1}$ vs. $166 \pm 24 \text{ tC ha}^{-1}$,
501 respectively). Badalamenti et al. (2019) also found that aboveground vegetation stored 53.1%
502 of carbon in the older forest stage, in line with our results (55.81%). Moreover, we observed
503 that nearly 10% of the carbon was stored in deadwood in stage 5 while litter carbon stock varies
504 only slightly during succession, but such result should be considered carefully as we did not
505 measure litter carbon content directly.

506 The greatest accumulation of biomass during the succession was in aboveground living
507 vegetation (min. 1.3 tC ha^{-1} ; max. 327 tC ha^{-1}), in accordance with results obtained in the
508 Mediterranean area (Badalamenti et al. 2019) and in the east of Brazil (Matos et al. 2020). In
509 our study area, stage 5 was characterized by a significantly higher carbon stock in aboveground
510 vegetation compared to stage 4, and this fits with a difference observed between a 35 year-old
511 secondary forest and an old forest (Aryal et al. 2014).

512 Although we expected all carbon pools to increase along the vegetation succession, the
513 superficial soil pool did not. The absence of a SOC pattern along the succession contrasts with
514 the majority of other studies, which show either an increasing SOC with succession related to
515 an increased biomass input (Zornoza et al. 2009; Foote and Grogan 2010; Piché and Kelting
516 2015; Chang et al. 2017; Nunes 2019; Lasanta et al. 2020) or a higher SOC content in
517 undisturbed older forests compared to young forests due to land-use legacy (Yesilonis et al.

518 2016). However, SOC does not always increase during forest regrowth after abandonment
519 (Alberti et al. 2008; Gosheva et al. 2017); Alberti et al. (2008) attributed variations in SOC
520 across sites to precipitation, vegetation type, previous land uses, and a time-lag for litter
521 changes to impact the soil carbon content, while Gosheva et al. (2017) attributed these
522 variations to climate, soil chemistry and tree species. In tree plantations on agricultural lands,
523 a worldwide meta-analysis showed that SOC changes depend on the previous land use, and
524 that increases are detected when cropland – not grasslands – are afforested (Shi et al. 2013);
525 moreover, an analysis of 619 sites in China showed that the overall mean change in SOC
526 density was not significant, but SOC density increased when the initial SOC density was low,
527 and *vice versa* (Hong et al. 2020). These trends could explain why we did not observe any
528 significant SOC variation. The absence of a superficial SOC increase with succession may also
529 have been due to a rapid turnover of organic matter that limited its accumulation, as found by
530 Yan et al. (2006). This result on the soil carbon stock calls for an extended analysis of the soil
531 nutrient content (e.g. nitrogen) and plot temperature and moisture because they are important
532 factors of the carbon dynamic (Post and Kwon 2000; Marín-Spiotta and Sharma 2013; Sierra
533 et al. 2015; Palmer et al. 2019).

534 The absence of significant SOC changes along stages may also be explained by our
535 sampling strategy. We only considered superficial soil (0-20cm) because it tends to contain the
536 greatest proportion of SOC (Batjes 1996; Jobbagy and Jackson 2000). But this may have led
537 us to underestimate the soil carbon stock, as deeper soil horizons also participate to the carbon
538 stock (Rumpel and Kögel-Knabner 2011; Shi et al. 2013; Jackson et al. 2017). Moreover, we
539 did not use the equivalent soil mass procedure for SOC quantification (Wendt and Hauser
540 2013). This may have influenced our results (Guidi et al. 2014), possibly overestimating SOC
541 (Wendt and Hauser 2013).

542

543 c. Drivers of the aboveground carbon stock

544
545 The vegetation composition played a main role in the carbon stock increase along the
546 succession through the positive effect on aboveground carbon stock of woody species. The
547 presence of large trees greatly influenced the aboveground carbon stock, as already reported
548 by Lecointe (2006) in western France, Måren & Sharma (2021) in Nepal and Dimobe et al.
549 (2019) in eastern Burkina Faso, who showed that big trees ($DBH \geq 25$ cm) stored 70% of the
550 total aboveground carbon.

551 Contrary to the expectations of Robinson et al. (2015), we found no relationship
552 between the carbon stock and the slope, possibly due to the absence of very steep slopes in the
553 plots (ranging from 2° to 19°). Our results neither showed relationship between the
554 aboveground carbon stock and soil nutrients (the nitrogen concentration), in accordance with
555 Holl and Zahawi (2014) and contrary to Moran (2000). This may indicate that the soil nutrient
556 content is not a limiting factor for forest regrowth in the study area.

557 Our results altogether show a limited relationship between local conditions and the
558 aboveground carbon stock in a large range of successional stages, but major effects related to
559 the vegetation composition and the late successional species.

560 561 5. Conclusion

562
563 We measured carbon stored in an ecosystem after agricultural abandonment. Multiple
564 successional stages were considered, from grazed plots (stage 0) to a forest at least 74 years
565 old (stage 5). Several carbon pools were measured: aboveground living and dead biomass,
566 belowground biomass (roots), and superficial soil.

567 As hypothesized, the amount of carbon stored in old fields increased with the
568 successional stages: the last forest stage reached 314.19 tC ha⁻¹ on average. Younger and older
569 forest stages stored amounts of carbon similar to those stored by other forests in temperate
570 Europe, but quite remarkably our results show great variability within stages. The relative
571 contribution of each pool to the carbon stock varies between successional stages, and
572 aboveground living biomass drives the carbon stock increase in the last stages. In contrast, the
573 carbon stored in the soil did not increase with the succession. Stored carbon was related to
574 successional stages and large trees, but carbon stock changes throughout the succession was
575 not significantly related to slope or to the soil clay and nitrogen contents.

576 Further research in our study area should concentrate on detailing the soil dynamic and
577 investigating the drivers of the carbon stock in the forest stages.

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586

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588

589 MW conducted the surveys and reviews of existing research. MW and AB worked on
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591 prepared figures. AB and LC supervised the project and reviewed the manuscript.

592

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597

598 **DATA ACCESSIBILITY STATEMENT**

599

600 The data that support the findings of this study are openly available in Zenodo at
601 <http://doi.org/10.5281/zenodo.10966030>

602

603 **STATEMENTS AND DECLARATIONS**

604

605 The authors have no conflicts of interest to declare. All co-authors have seen and agree
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608

609

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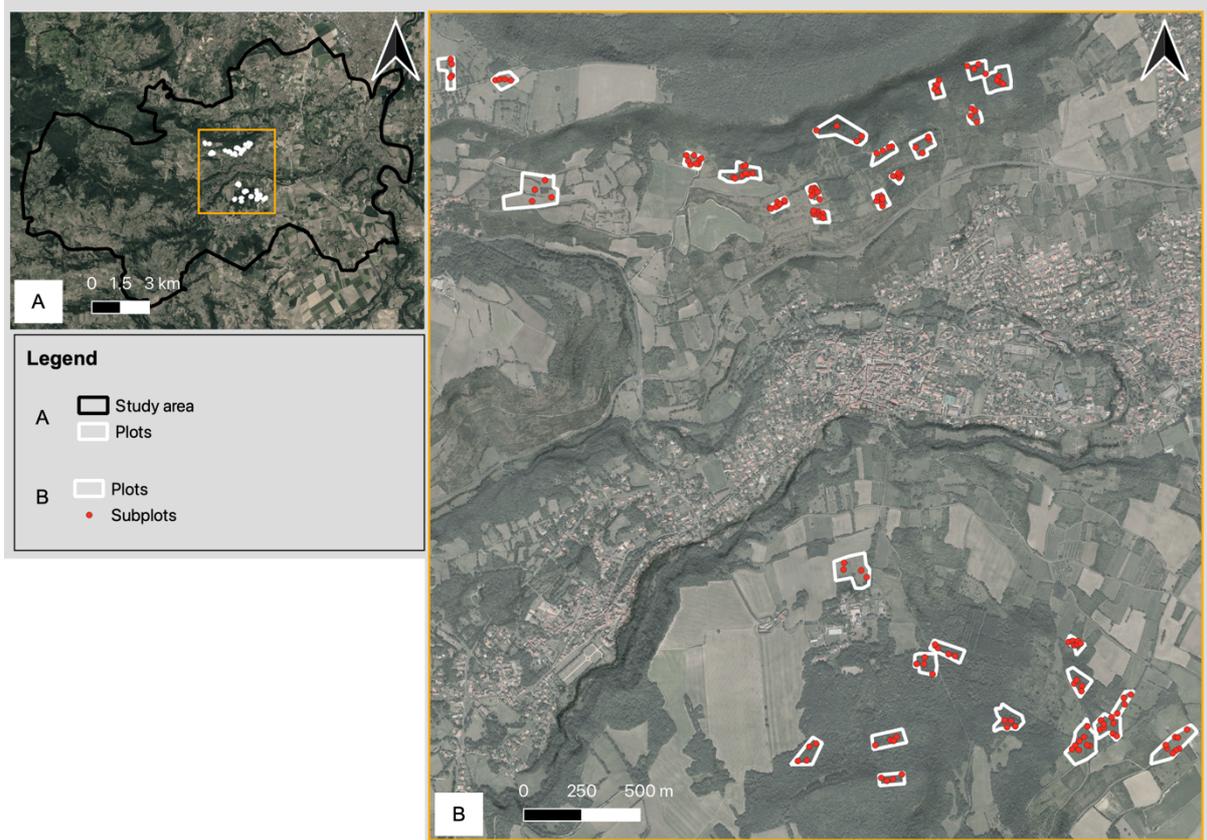
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945

946 **Appendix A. Map of the plots and subplots studied.**

947 A zone in the middle of the study area was chosen to localize the plots. Ground for this choice is the
948 presence of multiple succession stages in a limited radius (2.3km) limiting sources of heterogeneity.
949



950 **Appendix B. Table of allometric equations**

951 Following Bartholomée et al. (2018) allometric equations were found in literature directly or using the
 952 *GlobAllomeTree* international web platform. When no equation for the surveyed species was found,
 953 either an equation from another phylogenetically close species was used or the general equation from
 954 Zianis and Mencuccini (2004). When multiple equations existed, selection was based on a list of
 955 criteria: larger range of DBH, greater number trees surveyed, consistent latitude and closer climatic
 956 conditions, appropriate tree parts considered and appropriate equation form.
 957

Species surveyed	Species the equation is from	Biomass unit	DBH unit	Equation form	Parameter values	Number of trees in reference study	DBH range in reference study	Reference
Abies alba	<i>Abies balsamea</i>	Kg	cm	$AGB = \exp(a + b \cdot \ln(DBH))$	a = -1.8337 b = 2.1283 CF = 1.03	50	2.0 - 32	Ker 1980
Acer campestre	<i>Acer pensylvanicum</i>	g	in	$AGB = \exp(a + b \cdot \ln(DBH))$	a = 7.227 b = 1.6479	12	0.1 - 1	Young 1980
Acer platanoides	<i>Acer pensylvanicum</i>	g	in	$AGB = \exp(a + b \cdot \ln(DBH))$	a = 7.227 b = 1.6479	12	0.1 - 1	Young 1980
Acer pseudoplatanus	<i>Acer rubrum</i>	Kg	cm	$AGB = \exp(a + b \cdot \ln(DBH))$	a = -1.721 b = 2.334 CF = 1.0007	150	10 - 52	Crow 1983
Acer sp	Zianis & Mencuccini 2004	Kg	Cm	$AGB = a \cdot DBH^b$	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Carpinus betulus	<i>Carpinus betulus</i>	Kg	cm	$AGB = a \cdot DBH^b$	a = 4.046 b = 1.599	30	25-75	Shahrokhzadeh et al., 2015
Castanea sativa	Zianis & Mencuccini 2004	Kg	Cm	$AGB = a \cdot DBH^b$	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Cornus sanguinea	<i>Cornus florida</i>	Lb	In ²	$AGB = a \cdot (DBH^2)^b$	a = 3.08355 b = 1.14915	48	1.0 - 24	(Phillips, 1981)
Corylus avellana	<i>Carpinus betulus</i>	Kg	Cm	$AGB = a \cdot DBH^b$	a = 4.046 b = 1.599	30	25-75	Shahrokhzadeh et al., 2015
Crataegus sp	Zianis & Mencuccini 2004	Kg	Cm	$AGB = a \cdot DBH^b$	a = 0.1424 b = 2.3679			(Zianis and Mencuccini, 2004)
Daphne laureola	Zianis & Mencuccini 2004	Kg	Cm	$AGB = a \cdot DBH^b$	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Euonymus europaeus	<i>Wimmeria concolor</i>	Kg	Cm	$AGB = a \cdot DBH^b$	a = 0.346847 b = 1.99059	24	/	(Rodríguez-Laguna et al., 2010)
Fagus sylvatica	<i>Fagus sylvatica</i>	Kg	Cm	$AGB = a \cdot DBH^b$	a = 0.453 b = 2.139	20	6.0 - 62	(Cienciala et al., 2005)
Fraxinus excelsior	<i>Fraxinus excelsior</i>	Kg	Cm	$AGB = a \cdot DBH^b$	a = 0.17 b = 2.46	40	5.0 - 25	(Alberti et al., 2005)
Juglans regia	<i>Juglans regia</i>	Kg	Cm	$AGB = \exp(a + b \cdot \ln(C130))$	a = 2.1933 b = 0.9136	1	/	Adhikari 1995
Laburnum anagyroides	Zianis & Mencuccini 2004	Kg	Cm	$AGB = a \cdot DBH^b$	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)

Lonicera etrusca	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Lonicera sp	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Pinus nigra	Pinus nigra	Kg	Cm	AGB= exp(a+b.ln(DBH))	a = - 1.481858 b = 1.908228	75	4-88	Miller 1981
Pinus sp	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Pinus sylvestris	Pinus sylvestris	Kg	Cm	AGB=exp(a+b.ln(DBH))	a = -2.202 b = 2.112	110	/	Oleksyn, 1999
Prunus avium	Prunus pensylvanica	Lb	In	AGB=exp(a+b.ln(DBH))	a = 0.9758 b = 2.1948	30	1 - 9	(Young et al. 1980)
Prunus sp	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Prunus spinosa	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Pseudotsuga menziesii	Pseudotsuga menziesii	Kg	Cm	AGB=exp(a+b.ln(DBH))	a = -1.957 b = 2.2996	69	9-27	Menguzzato, G. 1988
Quercus petraea	Quercus petraea	g	m	AGB=exp(a+b.ln(C130))	a = -1.854 b = 2.536	20	0-0.7	Bouchon et al. 1985
Quercus robur	Quercus spp.	Kg	Cm	AGB=exp(a+b.ln(DBH))	a = -0.883 b = 2.14	33	/	(Hochbichler, 2002)
Quercus sp	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Ribes rubrum	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Robinia pseudoacacia	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Rosa canina	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Rosa rubiginosa	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Rubus sp	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Sambucus nigra	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Sorbus aria	Sorbus aucuparia	G	mm	AGB=exp(a+b.ln(C130))	a = -4.415 b = 2.373	14	/	(Ranger et al., 1981)
Sorbus intermedia	Sorbus aucuparia	G	mm	AGB=exp(a+b.ln(C130))	a = -4.415 b = 2.373	14	/	(Ranger et al., 1981)
Sorbus sp	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)
Sorbus terminalis	Sorbus aucuparia	G	mm	AGB=exp(a+b.ln(C130))	a = -4.415 b = 2.373	14	/	(Ranger et al., 1981)
Taxus baccata	Zianis & Mencuccini 2004	Kg	Cm	AGB=a.DBH ^a b	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)

Tilia cordata	Tilia amurensis Rupr.	G	Cm	$\text{Log}_{10}(\text{AGB}) = a + b \cdot \text{log}_{10}(\text{DBH})$	a = 1.606 b = 2.668 CF = 1.027	10	1.3-43.5	(Wang, 2006)
Ulmus minor	Ulmus spp.	Lb	In ²	$\text{AGB} = a \cdot (\text{DBH}^2)^b$	a = 1.61626 b = 1.2764	15	1-117	Clarck 1986
Ulmus sp	Ulmus spp.	Lb	In ²	$\text{AGB} = a \cdot (\text{DBH}^2)^b$	a = 1.61626 b = 1.2764	15	1-117	Clarck 1986
Viburnum lantana	Zianis & Mencuccini 2004	Kg	Cm	$\text{AGB} = a \cdot \text{DBH}^b$	a = 0.1424 b = 2.3679	/	/	(Zianis and Mencuccini, 2004)

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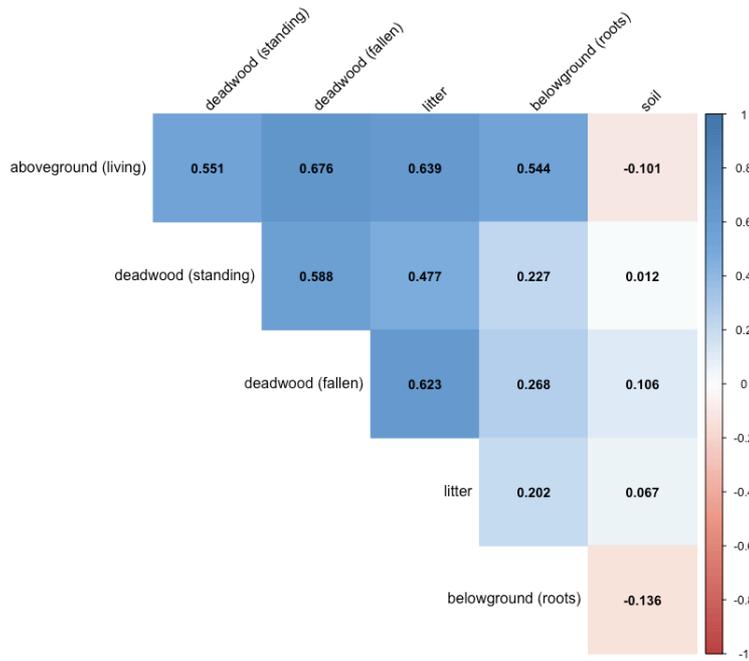
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998 **Appendix C. Correlation between the different carbon pools (all stages combined)**

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