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Chronic drought limits new carbon inputs and homogenizes surface soil carbon age and content in Mediterranean forests

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Abstract. Increasing drought frequency and severity are expected to affect carbon cycling and storage in Mediterranean forests substantially. However, the temporal dynamics of carbon within ecosystem pools under long-term drought remain poorly understood. In this study, we present the first comprehensive assessment of the age of all major carbon pools and respired CO₂ in a Mediterranean forest, using ¹⁴C measurements complemented with soil carbon content analyses. Additionally, we fitted compartmental carbon cycle models to empirical data collected through the 25-year rainfall exclusion experiment. We found that carbon in drought plots was generally older than in controls, with consistent trends across most pools, except roots and foliage. Differences were most pronounced in ecosystem respiration and in the 0–5 cm soil layer. Drought homogenized upper soil layers in both carbon content and age, suggesting depletion of older reserves and reduced stabilization of recent inputs. Overall, our results show that long-term drought promotes the microbial use of older carbon substrates in the soil, limits the incorporation of new inputs into slow-cycling reservoirs, and increases the vulnerability of existing soil carbon stocks. These results underscore the need for forest management strategies that maintain sequestered carbon and enhance the stabilization of fresh CO₂ inputs under intensifying aridity.

1 Introduction

Rising atmospheric CO₂ concentrations have markedly altered the global carbon budget (Friedlingstein et al., 2025), affecting climate and ecosystem processes through shifts in carbon, energy, and water dynamics (Schimel, 1995). Although the terrestrial biosphere sequesters large amounts of carbon (Canadell et al., 2007), it remains uncertain whether vegetation and soils can offset anthropogenic CO₂ emissions via enhanced carbon storage under ongoing climate change (Thompson and Randerson, 1999; Sierra et al., 2021b; Muñoz et al., 2023).

Mediterranean ecosystems—where water availability constrains both above- and below-ground processes (Asensio et al., 2007; Sardans et al., 2008)—are highly sensitive to projected increases in drought frequency and intensity, with precipitation declines of up to 30% expected in some regions (Lionello and Scarascia, 2018; IPCC, 2022). Historically, summer drought



reduced respiration rates and, together with forest recovery on abandoned agricultural lands, contributed to the role of these ecosystems as carbon sinks (Rovira et al., 2004; Frei et al., 2024). However, increasing evidence shows that intensified drought
25 reduces carbon uptake, primary productivity, above-ground biomass, and growth; increases mortality; alters recruitment patterns; and modifies physiological and morphological traits of woody species (Ogaya and Peñuelas, 2003; Peñuelas et al., 2008; Barbeta et al., 2013; Peñuelas et al., 2013; Liu et al., 2015; Ogaya and Peñuelas, 2021; Marañón-Jiménez et al., 2022). These shifts disrupt carbon cycling and substantially weaken the carbon sequestration capacity of Mediterranean forests.

Additionally, soils in these ecosystems are nutrient-poor (Yaalon, 1997; Sardans et al., 2020), and drought exacerbates nutri-
30 ent losses and soil degradation, impairing ecosystem water-use efficiency (Peñuelas et al., 2018). This vulnerability increases the risk that forests will transition from net carbon sinks to sources, reinforcing positive climate feedbacks (Giorgi and Lionello, 2008; Liu et al., 2022). Although reductions in photosynthesis and gross primary production (GPP) during drought are well documented (e.g., Barbeta et al., 2013; Peñuelas et al., 2018; Sardans et al., 2020; Yu et al., 2022), little is known about impacts on the transit time—the time that assimilated carbon remains within forest pools before release (Thompson and Randerson,
35 1999). Understanding both the amount and age of stored carbon is crucial to assess the future sink capacity of Mediterranean forests, predict vegetation dynamics under increasing aridity, and design restoration strategies to mitigate these impacts.

Radiocarbon (^{14}C) offers a powerful means to determine how long carbon has been retained in an ecosystem. As a naturally produced radioactive isotope, ^{14}C provides a time-independent signature that can track carbon dynamics (Chiti et al., 2016; Chanca et al., 2022; Muñoz et al., 2023). The excess ^{14}C released during 1950s–1960s nuclear tests—the “bomb ef-
40 fect”—created measurable imbalances in atmospheric and biospheric $^{14}\text{C}/\text{C}$ ratios (Levin et al., 2022), now used to study carbon turnover in terrestrial and marine systems (Beaupré and Druffel, 2009; Shi et al., 2020; Sierra et al., 2021b). Measurements of ^{14}C in CO_2 and carbon pools can also estimate the mean age of ecosystem respiration (Phillips et al., 2015), providing key constraints for terrestrial models and improving predictions of carbon dynamics (Sierra et al., 2017).

Radiocarbon studies in Mediterranean ecosystems are still limited. Existing work includes Chiti et al. (2016), who used
45 ^{14}C to partition heterotrophic respiration; Hättenschwiler et al. (1997), who analyzed ^{14}C in tree rings to evaluate long-term growth responses to elevated CO_2 ; Nadeu et al. (2012), who assessed the impacts of erosion and land use on organic carbon stocks and stability; and Quideau et al. (2000), who examined soil organic matter formation and cycling. Comparable studies in other biomes have characterized forest ^{14}C dynamics in a boreal forest in Sweden (Tangarife-Escobar et al., 2024), a tropical forest in Brazil (Chanca et al., 2025), and a tropical forest in Colombia (Sierra et al. 2026). Only a limited number of studies
50 have explored drought effects on ^{14}C dynamics, including work in a tropical forest in Panama (McFarlane et al., 2024), which also incorporated temperature influences, as well as studies in the Brazilian Amazon (Brando et al., 2008), mixed deciduous forests in the northeastern United States (Borken et al., 2006), and boreal forests in Canada (Czimczik et al., 2006). However, these studies focus exclusively on soil respiration fluxes. To our knowledge, no such studies have yet been conducted in Mediterranean forests.

55 Here, we present a novel approach combining ^{14}C measurements in bulk carbon pools and CO_2 fluxes within a long-term rainfall exclusion experiment in a Mediterranean forest in Spain. By integrating radiocarbon data with 25 years of drought manipulation, we advance understanding of how reduced soil-water availability influences carbon cycling and assess the per-



sistence of carbon in different ecosystem compartments. In addition, ^{14}C measurements are used to validate a carbon-cycling model fitted to carbon stocks and fluxes measured in the different compartments throughout the experiment. Specifically, we address three key questions: (i) does long-term drought alter the age of carbon stored in the bulk compartments of a Mediterranean forest? (ii) does it affect the sources of carbon released through respiration? and (iii) what are the implications of shifts in soil carbon age for soil carbon content? This integrated approach provides new insights into how Mediterranean forests may contribute to climate-change mitigation under future drought conditions.

2 Methodology

2.1 Induced drought experiment

This study was conducted in a Mediterranean holm oak forest located on a 25% south-facing slope in the Prades Mountains, Catalonia, NE Spain (41°21' N, 1°02' E, 950 m a.s.l.), where a long-term drought experiment has been ongoing since 1999. The forest, historically used for charcoal production, has not been coppiced for over 80 years (Sabaté and Gracia, 1994; Liu et al., 2015) and is dominated by *Quercus ilex*, *Phillyrea latifolia*, and *Arbutus unedo*. The soil is classified as a Dystric Cambisol, ranging in depth from 25 to 100 cm. The upper soil layer (horizon A, 0-5 cm) is a sandy loam with a strong to medium granular structure and high organic matter content, while the subsurface layer (horizon B, 5-25 cm) also has a sandy loam texture but with weak subangular blocky structure and moderate organic matter. The area has climate conditions typically Mediterranean with severe summer droughts and rain events concentrated in spring and autumn (López et al., 2001). The forest receives a mean annual rainfall of 539.4 mm and has an average temperature of 12.1°C, according to data collected from 1999 to 2023 by the on-site meteorological station. Trees reach up to 6 meters in height.

The experiment consists of eight plots, each measuring 15×10 m. Four plots are subjected to experimental drought by excluding rainfall, while the other four serve as untreated controls. Rainfall exclusion is implemented using rigid PVC tubes installed about one meter above the ground, and under the canopy, running along the slope and covering 30% of each plot's area. Each plot is also surrounded by a trench approximately 0.8 meters deep to intercept upslope runoff. On average, soil moisture in the drought plots is 15% lower than in the control plots (Ogaya et al., 2020). Further details about the site and experimental setup can be found in Ogaya and Peñuelas (2021).

2.2 Sampling campaign and laboratory analyses

We collected air and solid samples from the different plots in the drought experiment between April 30 and May 3, 2024. This period was chosen based on previous studies at this site, which report higher soil CO_2 fluxes in spring (Asensio et al., 2007), as well as data from the associated ICOS station Las Majadas de Tiétar (Alonso et al., 2024). This station, which has similar vegetation and is the closest eddy covariance tower to the study site, records the largest daily CO_2 variation (up to 140 ppm) during April and May.



For air sampling, we collected 14 samples of forest floor soil respiration (FFSR) from 6 randomly selected sites (3 drought and 3 control), using chambers following the procedure described by Tangarife-Escobar et al. (2024). However, instead of storing air in zeolite cartridges, we stored it in metal canisters. The chambers were installed after removing the litter layer; therefore, the measurements primarily include root respiration and microbial respiration from the underlying soil. Three samples were lost during the CO₂ extraction, and four more were excluded due to unrealistic values (<-400‰), indicative of contamination. This resulted in a final set of seven FFSR samples. We also collected 14 air samples representing a mix of ecosystem respiration and atmospheric background air at heights of about 1 and 4 meters above ground, plus two additional background samples from Tossal de Baltasana, the highest point in the Prades Mountains (41°33' N, 1°00' E, 1202 m a.s.l.). Air was collected in 3-liter glass flasks, pressurized to 1.2–1.4 bar using a portable sampler (Heimann et al., 2022). Sampling times were chosen to capture the full range of CO₂ concentrations, based on patterns observed at Majadas.

A total of 30 sampling points were randomly distributed across the four drought and four control plots, with 3–4 points per plot to capture spatial variability. At each point, we collected foliage (from trees and shrubs), fine litter (leaves and small debris on the ground), coarse litter (fallen branches and wood), and soil cores (0–20 cm depth, divided every 5 cm). Roots were separated from the soil samples. Wood samples were taken from live trees at 11 selected points using a 0.7 mm diameter borer, ensuring minimal damage to the trees. Mixed soil samples (0–5 and 5–10 cm) were incubated, with two replicates per plot, following the procedure described in the Protocols for Ecosystem Radiocarbon Sampling PERSAM for incubations.

All bulk materials were prepared for laboratory analysis following the PERSAM guidelines for solids. We measured total carbon content in soil, roots, and litter, and analyzed all samples for radiocarbon content. Radiocarbon measurements were performed at the Max Planck Institute for Biogeochemistry (Steinhof et al., 2017) using Accelerator Mass Spectrometry (MICADAS). Results are reported as fraction modern (F¹⁴C) and converted to Δ¹⁴C using the formula $\Delta^{14}\text{C} = (F^{14}\text{C}e^{\lambda(1950-t)} - 1) \cdot 1000\text{‰}$, where λ is the revised radiocarbon decay constant (1/8267 y⁻¹) and t is the year of measurement (Stuiver and Polach, 1977).

Weather data were recorded at the on-site meteorological station, and CO₂ concentrations were measured during the campaign using a LI-COR analyzer at intervals of 70 cm, ranging from 0.7 m to 4.9 m above the ground. Fig. A1 presents temperature, precipitation, and CO₂ concentrations during the sampling campaign and three preceding days. Before the sampling campaign, there were precipitation events and low, stable temperatures. During the sampling campaign, there was no rainfall, and the temperature showed greater intradiurnal variability. CO₂ concentrations exhibited daily cycles, with higher values at night, while showing no significant variation between different measurement heights. Some notable peaks likely resulted from the presence of humans and other living organisms.

The atmospheric background in this region is primarily influenced by the North Atlantic Oscillation (NAO), the Western Mediterranean Oscillation, and the Mediterranean Oscillation (Vicente-Serrano et al., 2009). During our fieldwork, radar data from the Weather Channel indicated that prevailing winds originated from the Atlantic Ocean, consistent with the negative phase of the NAO observed at that time (CPC-NOAA). This phase is associated with a more west-to-east orientation of the Atlantic jet stream and storm tracks, resulting in warmer conditions and above-average precipitation in Southern Europe.



2.3 Complementary data

We used carbon stock data collected throughout the entire induced drought experiment, which includes annual measurements of carbon in foliage, wood, coarse litter, and fine litter from 1999 to 2023 (Ogaya and Peñuelas, 2021). Soil carbon stocks for Horizons A and B were also measured in 2005 and 2018 for both drought and control plots (Fig. A5). Additional information on soil CO₂ flux and night-time leaf respiration was obtained from Asensio et al. (2007) and Sperlich et al. (2016), respectively, while the mean and standard deviation of Gross Primary Productivity (GPP) were sourced from Sabaté et al. (2002) (Table A3).

2.4 Data analysis

2.4.1 Determination of radiocarbon signature of ecosystem respiration

The air samples collected at different heights represent a mixture of CO₂ from ecosystem respiration and background atmospheric air. To determine the radiocarbon ($\Delta^{14}\text{C}$) signature specific to ecosystem respiration, it is necessary to separate it from the background air signature. Assuming that the observed CO₂ ($\text{CO}_{2_{obs}}$) is only a combination of background atmospheric ($\text{CO}_{2_{bkg}}$) and CO₂ released by the ecosystem ($\text{CO}_{2_{ER}}$), such that $\text{CO}_{2_{obs}} = \text{CO}_{2_{bkg}} + \text{CO}_{2_{ER}}$, the balance equation for the isotopic signature ($\Delta^{14}\text{C}$) can be written as:

$$\Delta^{14}\text{C}_{obs} \cdot \text{CO}_{2_{obs}} = \Delta^{14}\text{C}_{bkg} \cdot \text{CO}_{2_{bkg}} + \Delta^{14}\text{C}_{ER} \cdot \text{CO}_{2_{ER}} \quad (1)$$

where $\Delta^{14}\text{C}_{obs}$, $\Delta^{14}\text{C}_{bkg}$, and $\Delta^{14}\text{C}_{ER}$ are the isotopic signatures of the observed, background, and ecosystem CO₂, respectively. Similarly, instead of considering the CO₂ concentration mass balance, we can use the CO₂ flux balance within the ecosystem. At night, when photosynthesis is negligible, the ecosystem CO₂ flux (f_{ER}) is a mix of soil (f_s) and vegetation (f_v) respiration fluxes, so $f_{ER} = f_s + f_v$. The corresponding isotopic signature balance is:

$$\Delta^{14}\text{C}_{ER} \cdot f_{ER} = \Delta^{14}\text{C}_s \cdot f_s + \Delta^{14}\text{C}_v \cdot f_v \quad (2)$$

where $\Delta^{14}\text{C}_s$ and $\Delta^{14}\text{C}_v$ are the isotopic signatures of the CO₂ released by soil and vegetation, respectively.

To separate the ecosystem and background signatures, we first used the Miller-Tans method (Miller and Tans, 2003), a two-end-member mixing model. This method manipulates the carbon mass balance in Eq. 1 into a form where the product of $F^{14}\text{C}$ (fraction modern notation) and CO₂ is linearly related to CO₂ (Eq. 3), allowing the estimation of the ecosystem respiration radiocarbon signature as the slope of a regression between CO₂ and $F^{14}\text{C} \cdot \text{CO}_2$. Both type I and type II regressions were applied, and the results were converted back to $\Delta^{14}\text{C}$ notation.

$$F^{14}\text{C} \cdot \text{CO}_2 = F^{14}\text{C}_{ER} \cdot \text{CO}_2 \quad (3)$$

Model II yielded unrealistically high values when compared to values from other carbon pools (Fig. A2a) and previous studies (e.g., Chanca et al., 2025; Tangarife-Escobar et al., 2024). This is likely because the CO₂ concentrations showed limited variability between the sampled heights (1 m and 4 m; ~12 ppm), which weakens the Miller-Tans regressions. This limited variability is probably due to the absence of atmospheric measurement towers at our study site and to the fact that



vegetation height is generally below 5 m, which constrained air sampling to a maximum height of about 4 m. Although the Model I regression provided more plausible values, this method is not entirely appropriate because both $\Delta^{14}\text{C}$ and CO_2 measurements are subject to error. For this reason, these results will not be presented in the Results section (see Annex Fig. A4).

155 To address this limitation, we estimated $\Delta^{14}\text{C}_{ER}$ in two alternative ways: (i) by directly solving Eq. 1 for this variable, and (ii) by simultaneously solving Eqs. 1 and 2. Since CO_{2ER} is not directly known, we performed a sensitivity analysis based on the CO_2 values measured with the LI-COR instrument. When using only the concentration balance equation (Eq. 1), we used the CO_2 value closest in time to the air sample. When solving both equations together (Eq. 1 and 2), we used the mean nocturnal CO_2 concentration from 22:00 to 4:00 on May 3-4, as this night was the most stable. For these calculations, we used

160 $\Delta^{14}\text{C}$ from field-measured soil respiration and the soil and vegetation respiration fluxes listed in Table A3. The sensitivity analysis considered variations in the LI-COR measurements, increasing them from 0% to 50%, and averaged the results for each assumed value of CO_{2ER} .

2.4.2 Statistical analyses

Once $\Delta^{14}\text{C}$ values were determined for all ecosystem pools, we calculated the isotopic disequilibrium (D) for each pool by

165 subtracting the background atmospheric $\Delta^{14}\text{C}$ from the pool's $\Delta^{14}\text{C}$ value. We tested differences between drought and control treatments within each pool using Welch's t-tests when data met normality (Shapiro test) and Mann-Whitney tests otherwise. To assess interactions between radiocarbon (or carbon) and ecosystem pools and depths, we fitted linear models with treatment and pools or depths as fixed effects and plot as a random effect to account for repeated measurements. When the number of plots was insufficient, we fitted models without random effects. All p-values were adjusted for multiple comparisons using the

170 Benjamini–Hochberg procedure.

2.4.3 Relationship between radiocarbon in bulk soil and soil respiration

We examined the relationships between the radiocarbon signatures of bulk soil and soil respiration, considering both FFSR and incubated respiration. These relationships can fall into three categories: I) the age of respired carbon and bulk soil carbon are equal, II) respired carbon is younger than bulk soil carbon, and III) respired carbon is older than bulk soil carbon (Bolin

175 and Rodhe, 1973). A type I relationship lies along the 1:1 line and indicates that the soil system is well mixed, with carbon atoms having a similar probability of being mineralized and released to the atmosphere or as dissolved organic carbon. A type II relationship lies above the 1:1 line and suggests that the system retains carbon for a relatively long time before release. A type III relationship lies below the 1:1 line and implies that most carbon atoms enter and leave the system relatively quickly, while the atoms that remain persist for a long time (Sierra et al., 2018). We also examined the relationship between FFSR

180 and incubated respiration to assess the relative contributions of mixed heterotrophic and autotrophic respiration in FFSR and heterotrophic respiration isolated from roots in incubations.



2.5 Model description

We built three similar compartmental models to simulate carbon transit time distributions in the Prades forest for: i) control conditions, ii) drought conditions with GPP unchanged relative to the control, and iii) drought conditions with a 10% reduction in GPP. All models follow the Porce framework (Sierra et al., 2021b), a data-assimilation approach that combines a compartmental dynamical model with observed carbon stocks and fluxes. Using the dataset described in Section 2.3, we constrain the models by fitting the linear system:

$$\frac{d\mathbf{x}}{dt} = \mathbf{u} + \mathbf{B}\mathbf{x}(t), \quad (4)$$

where the vector $\mathbf{u}$ is the carbon inputs from the atmosphere to the ecosystem, and the matrix $\mathbf{B}$ contains the internal cycling and transfer rates among pools.

Each model has seven pools, x_1 : foliage, x_2 : wood, x_3 : roots, x_4 : fine litter, x_5 : coarse litter, x_6 : soil carbon horizon A, and x_7 : soil carbon horizon B (Fig. 1). GPP enters through the foliage pool ($u_1=\text{GPP}$), and from there, carbon is transferred among pools following the transfer coefficients $\alpha_{i,j}$ that represent the proportional transfers from pool j to pool i . The dynamical models have the form:

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{x}_3 \\ \dot{x}_4 \\ \dot{x}_5 \\ \dot{x}_6 \\ \dot{x}_7 \end{pmatrix} = \begin{pmatrix} \text{GPP} \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} -k_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ \alpha_{2,1}k_1 & -k_2 & 0 & 0 & 0 & 0 & 0 \\ \alpha_{3,1}k_1 & 0 & -k_3 & 0 & 0 & 0 & 0 \\ \alpha_{4,1}k_1 & 0 & \alpha_{4,3}k_3 & -k_4 & 0 & 0 & 0 \\ 0 & \alpha_{5,2}k_2 & \alpha_{5,3}k_3 & 0 & -k_5 & 0 & 0 \\ 0 & 0 & \alpha_{6,3}k_3 & \alpha_{6,4}k_4 & \alpha_{6,5}k_5 & -k_6 & 0 \\ 0 & 0 & \alpha_{7,3}k_3 & 0 & 0 & \alpha_{7,6}k_6 & -k_7 \end{pmatrix} \times \begin{pmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \\ x_6 \\ x_7 \end{pmatrix} \quad (5)$$

where k_i is the cycling rate of each pool.

We generated 1,000 random initial conditions for GPP and carbon stocks at the beginning of the simulations, set 80 years before the field campaign, corresponding to the end of coppicing at the site. Because no data exist for biomass or carbon stocks at that time, these initial conditions were treated as random variables drawn from normal distributions. We then estimated 1,000 parameter sets using the limited-memory BFGS algorithm, which minimizes the mismatch between model predictions and observed carbon stocks.

The radiocarbon version of the model follows Metzler et al. (2020):

$$\frac{d\mathbf{x}^{14}}{dt} = \mathbf{u}^{14} + \mathbf{B}^{14}\mathbf{x}^{14}(t), \quad (6)$$

where $\mathbf{x}^{14}$ is the radiocarbon content in each pool, $\mathbf{B}^{14}$ is the radiocarbon compartmental matrix, defined as $\mathbf{B} + \lambda\mathbf{I}$, with $\lambda = 1/8267 \text{ yr}^{-1}$ the radiocarbon decay constant, and $\mathbf{I}$ the identity matrix. Radiocarbon inputs are constrained by the atmospheric $\Delta^{14}\text{C}$ record of CO_2 , using the datasets of Reimer et al. (2020) and Hua et al. (2022), and extended to 2025 following Sierra et al. (2018). We then solve the model using the same procedure as for carbon stocks. See Sierra et al. (2014) and Sierra et al. (2026) for more details.

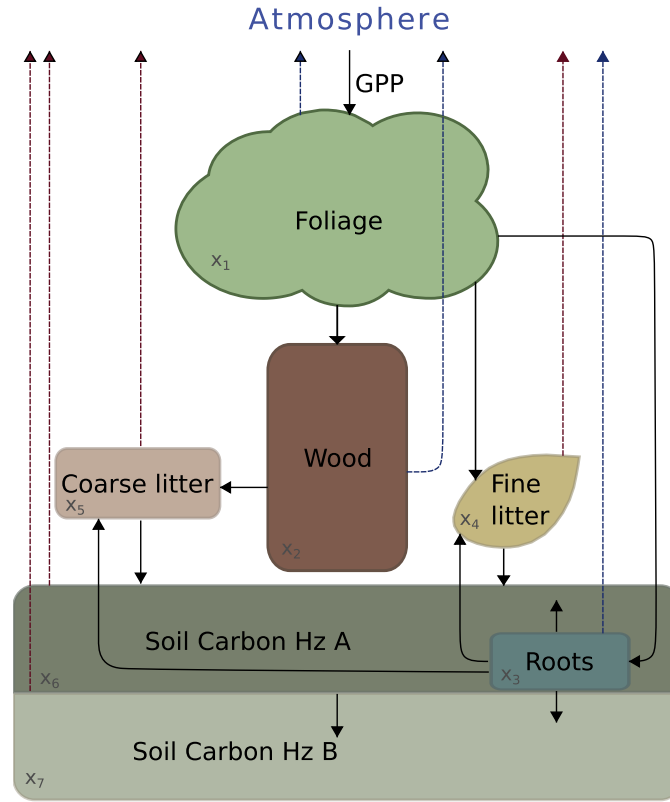


Figure 1. Structure of the compartmental model used to fit the available carbon stocks in Prades. Continuous arrows represent carbon transfer among ecosystem pools, and dashed lines represent respiratory losses to the atmosphere. Autotrophic respiration fluxes are shown in dark blue, while heterotrophic fluxes are in dark red. After Sierra et al. (2021b).

We evaluated all models' performance by predicting the radiocarbon signatures of carbon stocks and ecosystem respiration for 2024, the year of sampling. For each of the 1,000 parameter sets, we simulated radiocarbon from 1900 to 2025 and computed the sum of squared residuals (SSR) between predictions and observations:

$$SSR = \sum_{j=1}^n \epsilon_j^2, \quad (7)$$

where n is the number of variables evaluated, and ϵ_j^2 are squared residuals for each variable j , calculated as:

$$\epsilon_j^2 = \sum_{i=1}^{n_j} \left(\frac{x_{i,j} - \hat{x}_{i,j}}{\bar{x}_{i,j}} \right)^2, \quad (8)$$

where $\hat{x}_{i,j}$ and $x_{i,j}$ correspond to the predictions and the observations, respectively, and $\bar{x}_{i,j}$ to the average of the observed variable. The parameter set with the lowest SSR is retained as the best fit and used to build the final compartmental matrix.



We then computed the equilibrium transit time (τ) distributions for constant inputs, with τ representing the time it takes for carbon entering the ecosystem as GPP to appear in the respiratory flux, as:

$$f_T(\tau) = -\mathbf{1}^\top \mathbf{B} e^{a\mathbf{B}} \frac{\mathbf{x}^*}{\|\mathbf{x}^*\|}. \quad (9)$$

220 At equilibrium, the steady-state carbon stock is $\mathbf{x}^* = -\mathbf{B}^{-1}\mathbf{u}$, and $\|\mathbf{x}^*\|$ corresponds to the total input mass. We also computed the system-age distribution as:

$$f_A(a) = -\mathbf{1}^\top \mathbf{B} e^{a\mathbf{B}} \frac{\mathbf{x}^*}{\|\mathbf{x}^*\|}, \quad (10)$$

where a is the age variable. From these distributions, respiration (R) can be expressed in terms of age and transit time as:

$$R(t) = f_A(a)\|\mathbf{x}_0\| + \int_{t_0}^t f_T(s-t_0)\|\mathbf{u}(s)\|ds, \quad (11)$$

225 assuming $x^* = x_0$ and $a = t - t_0 = \tau$. For more details on the theoretical derivation of Eqs. 10-11, see Metzler and Sierra (2018), Sierra et al. (2021a), Sierra et al. (2021b), and Sierra et al. (2026).

3 Results

Control plots' radiocarbon composition ($\Delta^{14}\text{C}$) ranged from -120 to 466‰ across sample types, while drought plots ranged from -179 to 451‰. Analytical errors for $\Delta^{14}\text{C}$ measurements were as follows: 1.9-3.4‰ (mean=2.4‰) for vegetation pools, 230 1.8-2.7‰ (mean=2.2‰) for soil solid samples, 2.2-4.8‰ (mean=2.8‰) for field soil respiration, 1.8-2.7‰ (mean=2.0‰) for soil incubations, and 1.9-2.6‰ (mean=2.2‰) for sampled air. Radiocarbon results are summarized in Table A1 and Fig. A2, and carbon percentages in Table A2 and Fig. A3.

For clarity, we present the results in four subsections. First, we report the radiocarbon and carbon content of bulk material in control and drought plots. Second, we describe radiocarbon measurements of respiratory fluxes. Finally, we present the results 235 from the fitted models. Throughout, p -values (p) in parentheses indicate comparisons among ecosystem pools and treatments, with higher p signifying a lack of statistically significant differences.

3.1 Radiocarbon signatures and carbon content in bulk material

3.1.1 Radiocarbon signatures in vegetation and soil pools

Foliage exhibits $\Delta^{14}\text{C}$ values very similar to the atmospheric background in both control and drought plots ($D \approx 0$, $p > 0.5$, 240 Fig. 2a, Table A1), indicating that this pool primarily stores recently fixed carbon and operates as a fast-cycling pool. Fine litter also shows relatively low $\Delta^{14}\text{C}$ values in both control (mean=16‰) and drought (mean=16‰) plots (Fig. 2a, mean=24‰), but these differ significantly from the atmospheric background ($p < 0.01$, Table A1), suggesting that this pool is not composed solely of recent foliage ($p < 0.001$), although it can still be considered as a fast-cycling pool. Coarse litter and wood show



the highest positive D values and substantial variability (Fig. 2a). Their similar radiocarbon signatures ($p=0.45$) suggest that coarse litter largely derives from woody material, while its higher $\Delta^{14}\text{C}$ values relative to wood suggest the presence of older organic matter rather than exclusively recent mortality inputs. These pools can be classified as fast-to-intermediate-cycling carbon pools.

Aboveground pools generally show higher bomb-derived ^{14}C enrichment in drought plots—most notably in foliage and fine litter means and medians, wood medians, and coarse litter means—but these differences are not statistically significant ($p>0.05$, Fig. 2a). Wood also shows much lower variability under drought, with the standard deviation decreasing from 152‰ to 60‰, whereas variability in the other aboveground pools remains similar between treatments. Linear mixed-effects models further show significant differences among aboveground vegetation pools ($p<0.001$) but no effect of drought ($p=0.78$) and no treatment-by-pool interaction, indicating that drought does not alter the radiocarbon age of aboveground vegetation pools.

Roots at all sampled depths show only positive D values (Fig. 2b), indicating enrichment in bomb-derived radiocarbon. No significant differences are detected among depths ($p>0.05$) in any treatment, and although roots in the drought plots contain less bomb-enriched carbon than those in the control plots, this difference is also not significant ($p>0.05$, Fig. 2b). No depth-by-treatment interaction is detected. Overall, the $\Delta^{14}\text{C}$ values, with means ranging from 74–93‰ in control plots and 48–71‰ in drought plots, suggest that roots represent a fast-to-intermediate-cycling carbon pool.

Aboveground and belowground vegetation pools contain only bomb and post-bomb carbon ($D>0$), suggesting no legacy carbon from a previous forest biomass. In contrast, bulk soil shows both positive and negative D values (Fig. 2c). Radiocarbon values exhibited a strong depth gradient ($p<0.01$), decreasing with soil depth: soils above 5 cm have positive values, whereas deeper layers have both positive and negative values, consistent with older, slow-cycling carbon pools. Although the overall effect of drought on soil $\Delta^{14}\text{C}$ is not statistically significant ($p=0.106$), there is a tendency toward lower values under drought. In the 0–10 cm layer of drought plots, mean $\Delta^{14}\text{C}$ values are close to the atmospheric background ($p>0.05$, Fig. 2c), but unlike control plots, these layers include negative D values, which indicate the presence of pre-bomb carbon. At the 0–5 cm depth, both the mean values and their variability differ significantly between the treatments ($p<0.05$). In the 10–15 cm layer, drought plots contain more pre-bomb (older) carbon than controls, whereas the opposite pattern is observed at 15–20 cm; however, these differences are not statistically significant. No significant depth-by-treatment interaction is detected.

3.1.2 Carbon content in vegetation and soil pools

In terms of carbon content, litter is not affected by treatment overall ($p=0.78$) and does not differ between fine and coarse litter under control conditions (~43%, $p=0.78$, Fig. 3a). However, there is a significant treatment-by-litter-type interaction ($p=0.018$): fine litter shows reduced carbon concentration under drought, whereas coarse litter shows a higher mean and greater variability.

Root carbon concentration does not vary significantly with depth ($p>0.37$ for all comparisons, Fig. 3b) or treatment ($p=0.41$), and no depth-by-treatment interaction is detected. By contrast, bulk soil carbon content decreases significantly with depth, falling from 7.7% at 0–5 cm to 2.0% at 15–20 cm ($p<0.001$), and is lower under drought conditions ($p=0.001$,

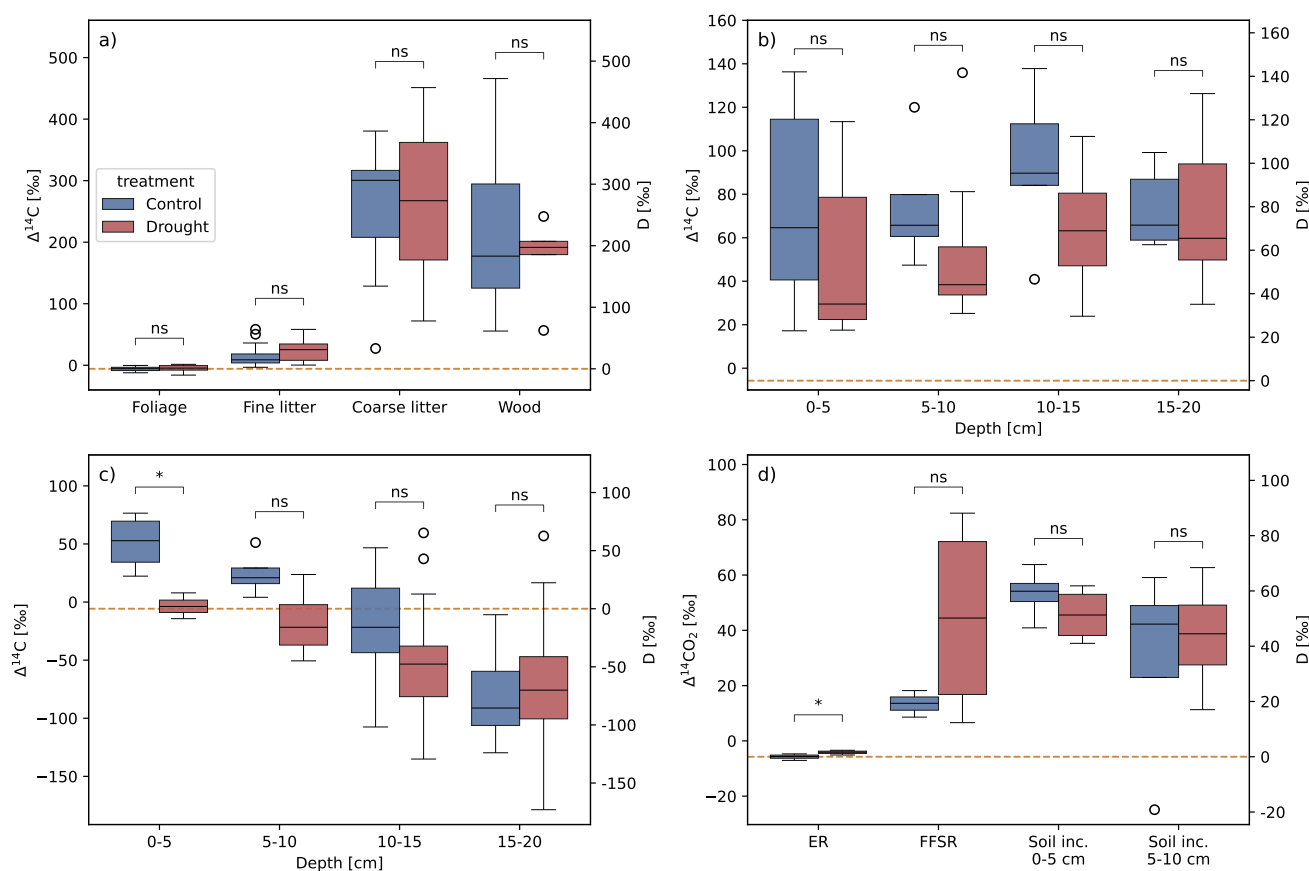


Figure 2. $\Delta^{14}\text{C}$ (left y-axis) and D (right y-axis) values in control and drought plots for bulk material (a-c) and CO_2 fractions (d). Panel a) shows aboveground pools, b) roots at different depths, and c) soil at different depths. The horizontal orange dashed line indicates the atmospheric background ^{14}C - CO_2 value (-6‰). Values above this line reflect the presence of bomb-derived radiocarbon, whereas values below indicate pre-bomb signatures. D=0 marks the transition between positive and negative isotopic disequilibrium. Symbols above the boxplots indicate statistical significance for comparisons between control and drought plots: "ns" denotes no significant difference, and * indicates $p < 0.05$.

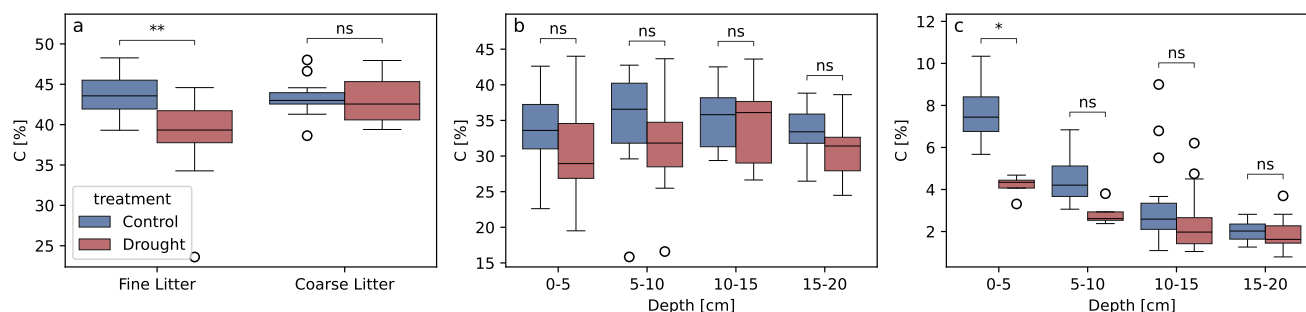


Figure 3. Percentage of carbon values in control and drought plots for a) fine and coarse litter, b) roots at different depths, and c) and soils at different depths. Symbols above the boxplots indicate statistical significance for comparisons between control and drought plots: “ns” denotes no significant difference, and * indicates $p < 0.05$.

Fig. 3c, Table A2). In terms of soil total carbon, this corresponds to a reduction of 25.6 tC ha^{-1} in the 0-5 cm layer (55.6 ± 14.1 in control vs. 30.0 ± 4.3 in drought), and 12.5 tC ha^{-1} in the 5-10 cm layer (33.0 ± 11.7 in control vs. 20.5 ± 4.6 in drought).

A significant depth-by-treatment interaction is observed, with the drought effect being strongest in the topsoil and diminishing with depth, becoming negligible below 10 cm.

3.1.3 Vertical variation in radiocarbon and carbon content

In control plots, both $\Delta^{14}\text{C}$ and %C show a decline with depth, indicating older and less carbon-rich soil in deeper layers. $\Delta^{14}\text{C}$ differs significantly between 0–5 cm and 10–15 cm and 15–20 cm ($p < 0.01$), between 5–10 cm and 15–20 cm ($p < 0.01$), and between the 10–15 cm and 15–20 cm ($p < 0.01$, Fig. 4a). %C shows a similar pattern, differing between 0-5 cm and 10-15 cm and 15-20 cm ($p < 0.01$), and between 5-10 cm and 15-20 cm ($p < 0.001$, Fig. 4c). Under drought, these depth-related patterns disappear for both metrics: $\Delta^{14}\text{C}$ shows no significant differences across depths ($p > 0.05$; Fig. 4b), and %C becomes more homogeneous and reduced, with only the 0–5 cm versus 15–20 cm contrast remaining significant (Fig. 4d).

3.2 Radiocarbon signature in respiratory fluxes

3.2.1 Ecosystem respiration

When Eq. 1 is solved for radiocarbon in ecosystem respiration ($\Delta^{14}\text{C}_{ER}$), using CO_2 values measured by the LI-COR throughout the day and varying them from 0% to 150% as CO_{2ER} , the resulting $\Delta^{14}\text{C}_{ER}$ ranged from -7.1‰ to -4.8‰ in control plots and from -5.2‰ to -3.5‰ in drought plots (Fig. A4c,d). Similarly, when Eq. 1 was solved together with Eq. 2, thereby accounting for the nighttime separation of soil and vegetation fluxes, $\Delta^{14}\text{C}_{ER}$ values remained nearly identical, ranging from -7.1‰ to -4.7‰ in control plots and from -5.1‰ to -3.4‰ in drought plots. Overall, both the daytime and nighttime approaches produced very similar estimates, and in both treatments the values were close to atmospheric equilibrium. However, drought

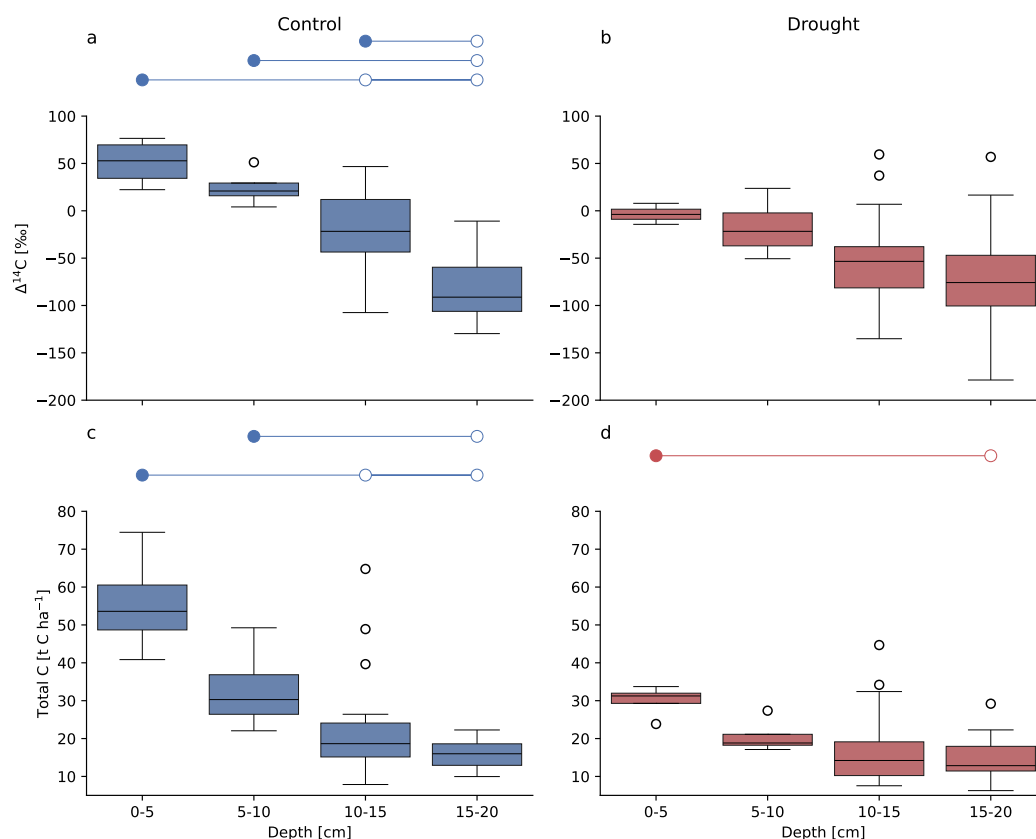


Figure 4. Radiocarbon (a,b) and carbon (c,d) content across soil depths for control (a,c) and drought (b,d) plots. A closed dot connected to one or more open dots denotes a statistically significant difference ($p < 0.05$) between the depth marked by the closed dot and the aligned depths marked by open dots.

plots respired carbon that was significantly more enriched in bomb-derived radiocarbon ($p < 0.05$), consistent with the FFSR results (Fig. 2d).

3.2.2 Soil respiration

In laboratory incubations (Fig. 2d), where roots were removed, the 0-5 cm soil layer in control plots released CO_2 with higher $\Delta^{14}\text{C}$ values (53‰) than the deeper 5-10 cm layer (30‰, $p > 0.05$), following the depth-related pattern observed in bulk soil profiles (Fig. 2c). Respiration from the 0-5 cm layer differs from atmospheric background levels ($p < 0.01$), whereas respiration from the 10-15 cm layer does not ($p > 0.05$). Incubation-derived $\Delta^{14}\text{C}$ values do not differ between treatments ($p > 0.05$). When comparing $\Delta^{14}\text{C}$ in bulk soil and incubated soil respiration (5a), most control-plot samples fall close to the 1:1 line, indicating a type I relationship, although some samples show type II or type III behavior. The 5–10 cm layer shows the greatest variability.

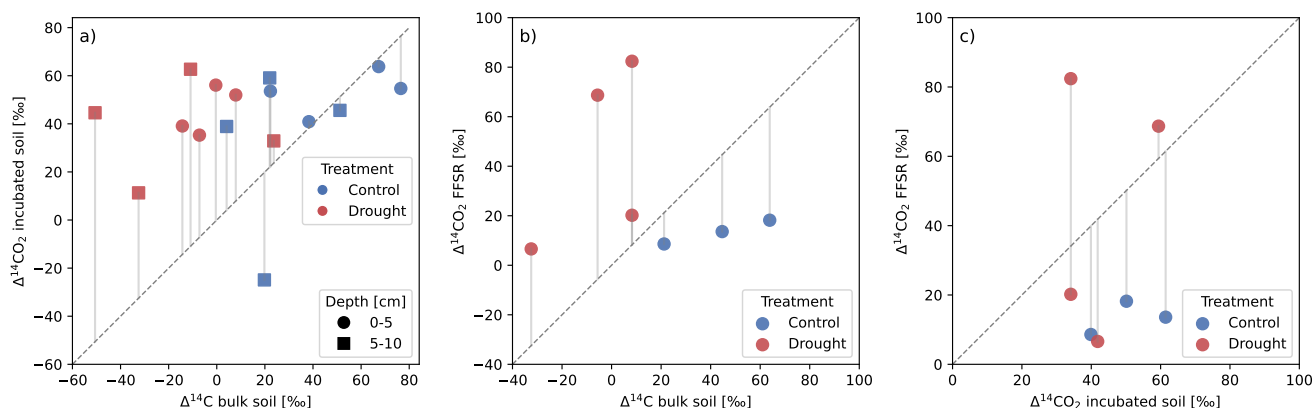


Figure 5. Radiocarbon relationships among a) bulk soil and incubated soil respiration, b) bulk soil and FFSR, and c) incubated soil respiration and FFSR. Dotted lines denote the 1:1 line.

In contrast, all drought-plot samples show a type II relationship, indicating that respired soil carbon is younger than the bulk soil carbon from which it is derived.

FFSR shows $\Delta^{14}\text{C}$ values ranging from +9 to +18‰ (Fig. 2d) in the control plots, indicating significant bomb enrichment compared to current atmospheric CO_2 levels ($p < 0.05$). In the drought plots, FFSR has a higher mean (45‰ vs. 13‰; $p > 0.05$) and greater variability ($p < 0.01$) than in the control plots, suggesting respiration of carbon that is more enriched in bomb-derived ^{14}C , and therefore potentially older, although this difference is not statistically significant. When comparing $\Delta^{14}\text{C}$ in bulk soil and FFSR (5b), the contrast between treatments is clear: control plots show a type III relationship, whereas drought plots show a type II relationship, matching the pattern observed for incubated respiration.

The comparison of $\Delta^{14}\text{C}$ in incubated soil respiration and FFSR (5c) shows that, in the control plots, heterotrophic respiration is older than the combined autotrophic and heterotrophic respiration, whereas drought plots show both Type II and Type III relationships. Furthermore, when comparing soil and ecosystem respiration, ER is less enriched in bomb-derived ^{14}C than FFSR and incubated soil respiration ($p < 0.01$) in the control plots, likely because ER includes a higher contribution from autotrophic respiration. This difference between ER and FFSR is not significant in the drought plots, probably because of the high variability in FFSR under drought conditions.

Overall, the measured respiration fluxes are dominated by carbon fixed on decadal timescales, with little contribution from pre-bomb carbon pools. This indicates that the Prades forest actively cycles recently assimilated carbon, with residence times ranging from days to decades after photosynthetic uptake.



3.3 Model results

The model parameter estimates (mean values and the minimum sum of squared residuals, hereafter 'best-fit model') demonstrate robust representation of both carbon stocks and radiocarbon dynamics across treatments (Fig. 6, Table A4). Model fit performance, evaluated using scaled residual values between predicted and observed radiocarbon, varied across ecosystem compartments (Fig. A7). Under control conditions, residuals were lowest for respired CO₂, foliage, and Soil A, but noticeably higher for fine litter (Fig. A7a). Under drought conditions, the lowest residuals occurred in respired CO₂, wood, and foliage; the fine litter compartment maintained the highest residuals, while SHA shifted to the second highest (Fig. A7b,c).

Comparing parameter fits between treatment conditions revealed that the largest shifts occurred in k_2 , k_3 , and α_{21} . For these three parameters, median and best ¹⁴C-constrained values under drought fell well outside 1.5 times the interquartile range of control values (Fig. 6, Table A4), with all three parameters exhibiting lower values under control conditions than under drought. Moderate increases under drought were observed in k_4 , k_5 , α_{31} , α_{43} , and α_{63} , whereas minor decreases occurred in k_7 , α_{52} , α_{73} , α_{64} , α_{65} , and α_{76} . Minor parameter variations observed when comparing drought with unchanged GPP to drought with reduced GPP—specifically in k_2 (+13%), k_4 (-9%), and k_5 (-18%)—likely reflect model compensation artifacts given that the underlying carbon flow architecture remains identical.

Together, these parameter shifts indicate that drought accelerates carbon loss from woody and root biomass. Although the transfer rate from wood to coarse litter (α_{52}) remained unchanged at the mean and was slightly lower in the best-fit model, wood respiration rose by 40% (from 0.62 to 0.87 Mg C ha⁻¹ yr⁻¹). Concurrently, a larger proportion of root carbon was partitioned toward fine litter and soil A.

These structural shifts substantially alter ecosystem carbon stocks and turnover rates. Total ecosystem carbon dropped from 357 Mg C ha⁻¹ in control plots to 243 Mg C ha⁻¹ under drought with unchanged GPP (a 32% reduction), with reduced GPP driving an additional loss of 34 Mg C ha⁻¹. Soil carbon pools declined substantially under drought: SHA dropped by 30% (from 82 to 58 Mg C ha⁻¹) and SHB by 25% (from 103 to 77 Mg C ha⁻¹). These soil carbon losses were primarily driven by reduced litter input (α_{64} and α_{65}) and a corresponding decline in carbon transfer from SHA to SHB (α_{76}).

Consequently, the best-fit models predict mean carbon transit times (τ) of 7.50, 5.11, and 4.88 years for control, drought, and drought with reduced GPP conditions, respectively (black lines in Fig.7a,d). Autotrophic respiration consistently accounted for 69% of total respiration across all scenarios. The shorter ecosystem transit time under drought is predominantly driven by reduced residence times within slow- and intermediate-cycling pools, including wood (45.7 years in control vs. 40.7 years in drought), coarse litter (30.7 years vs. 27.3 years), and Soil Horizon B (61.6 years vs. 59.7 years). The most pronounced shift occurred in the wood compartment, where accelerated turnover outweighed a minor increase in carbon allocation to wood, ultimately leading to a marked decrease in equilibrium wood carbon stocks (blue lines in Figs.7b,e and A9b,e).

Notably, a key discrepancy emerged between our observational radiocarbon data and compartmental model simulations regarding ecosystem respiration. While field measurements indicated that drought significantly aged respired carbon, the steady-state model predicted older ER under control conditions than under drought. This model-data divergence reveals a fundamental limitation of static, matrix-based transfer models under non-steady-state environmental stress.

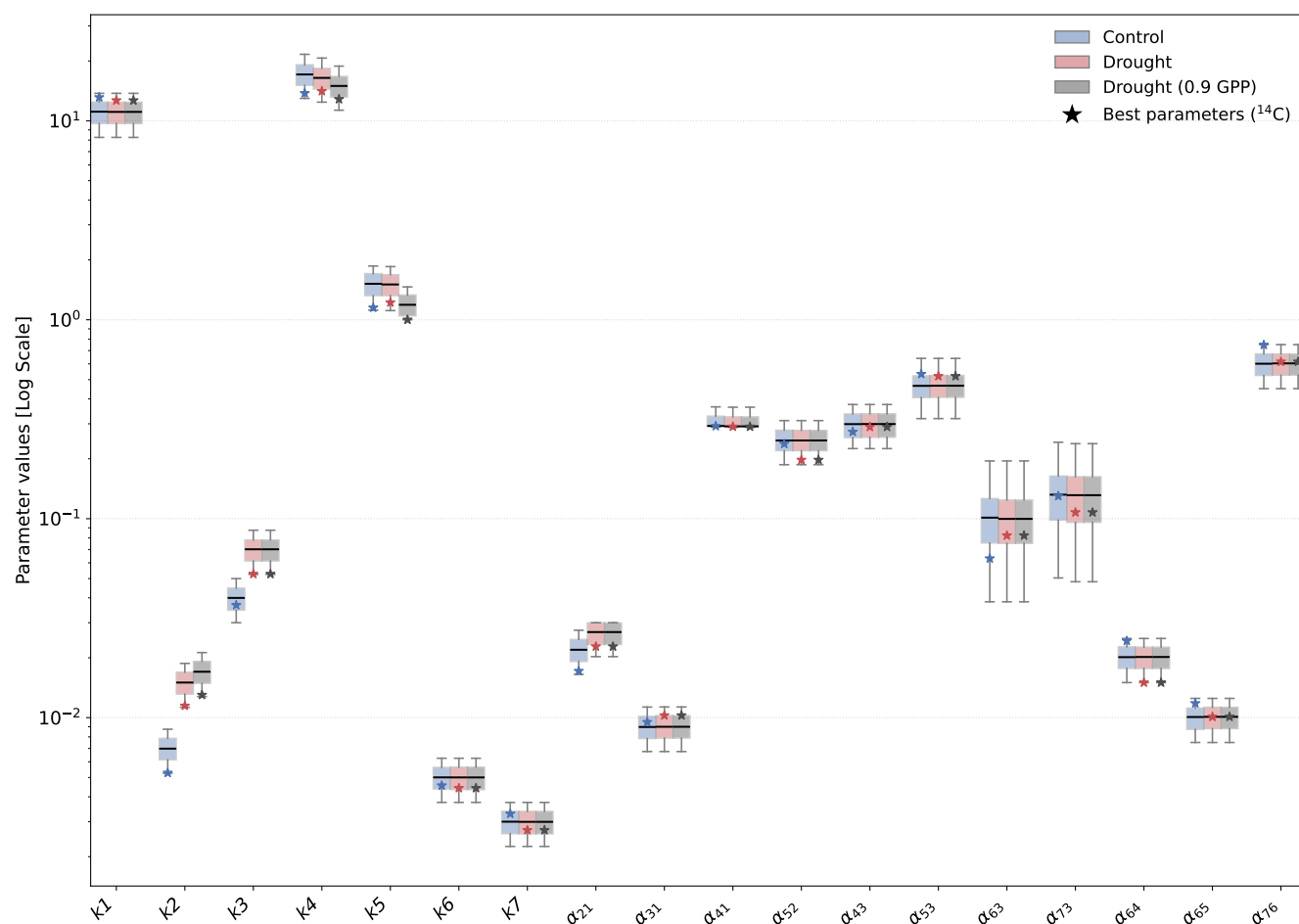


Figure 6. Parameter values obtained from the optimization iterations. Colors indicate the three models, and the star indicates the optimal parameter value constrained by the ^{14}C signatures.

4 Discussion

4.1 Released CO_2 in the Mediterranean forest is dominated by fast-cycling, very young C

The control plots, although not subjected to experimental drought, have experienced strong natural droughts in years like 2000–2001, 2005–2006, 2011–2012, and 2022–2023 (Liu et al., 2015; EU Drought Observatory), which have likely influenced site carbon cycling. Foliage has radiocarbon values close to atmospheric equilibrium ($D \approx 0$), confirming that canopy leaves in Prades fix modern atmospheric carbon. Compartmental modeling estimates mean foliage carbon ages of only a few months (Fig. A9), markedly lower than the average structural leaf lifespan of 2.3 years reported for *Quercus ilex* (López et al., 2001). This model-data alignment highlights the continuous, high-throughput turnover of non-structural carbohydrate (NSC) pools

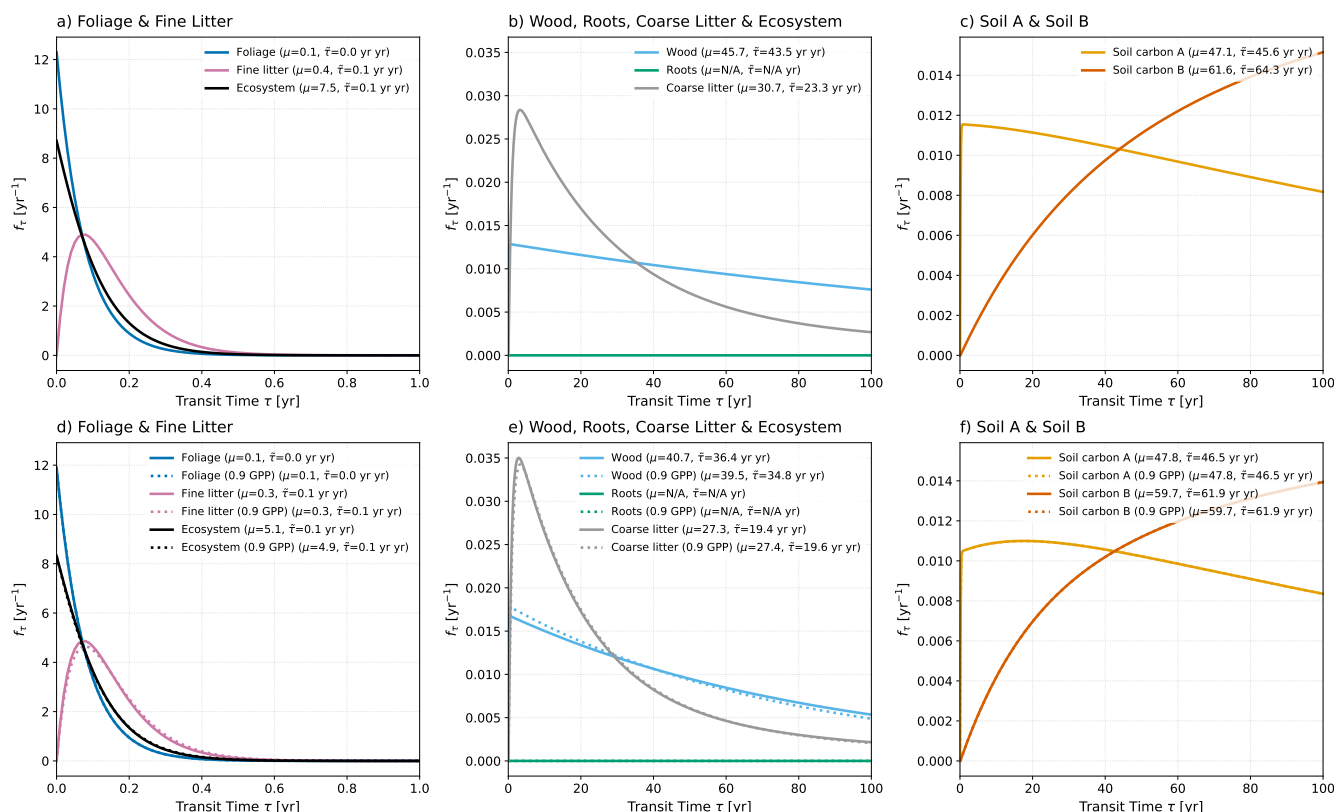


Figure 7. Transit time (τ) density distributions for the ecosystem and individual pools. The upper panels show control plots, and the lower panels show drought plots, each simulated with GPP and 0.9 GPP. Panels (a) and (d) correspond to foliage and fine litter; (b) and (e) to wood, roots, coarse litter, and the total ecosystem; and (c) and (f) to horizon A and horizon B soils. Axis scales differ among panels to improve readability, but corresponding control and drought panels share the same axes. μ denotes the mean and $\tilde{\tau}$ the median. These densities were derived using the parameter set that best fit the ^{14}C measurements.

supporting foliar tissue maintenance, repair, and osmotic regulation rather than long-term cell wall retention. Fine litter displays a similarly rapid turnover time (5 months), though its statistically distinct $\Delta^{14}\text{C}$ signature relative to the atmosphere. This suggests that fine litter consists mainly of foliage, but also includes fine roots and small branches.

Older post-bomb carbon is retained primarily within structural wood, coarse litter, and root networks. High isotopic variability in control wood reflects interspecific differences in longevity and wood density, with *Q. ilex* retaining older heartwood relative to short-lived species like *Arbutus unedo*. Coarse litter exhibits younger mean carbon ages than intact wood, reflecting a dynamic mixture of recent mortality inputs—driven by selective *Q. ilex* crown dieback during historical droughts (Ogaya et al., 2020)—and decaying woody debris. Modeled root radiocarbon ages (33 years in control; Fig.A9) are substantially older than the 125-day fine-root turnover time previously documented at Prades (López et al., 2001). This gap stems from sampling the full root continuum (coarse to fine) and the internal recycling of stored NSC reserves before structural allocation (Gaudinski



et al., 2001). Subsoil roots (15–20 cm) showed slightly younger $\Delta^{14}\text{C}$ signatures, consistent with trees shifting active fine-root production deeper to tap subsoil moisture and avoid surface thermal stress (Canadell and Zedler, 1995; López et al., 2009).

Isotopic signatures across respiration fluxes demonstrate that photosynthetic assimilates return to the atmosphere on transit times of months to a few years, driven by autotrophic metabolism and fresh litter decomposition during peak spring growth (Garbulsky et al., 2013; McFarlane et al., 2024). In contrast, field soil respiration and root-free soil incubations yielded older radiocarbon ages than ER. This isotopic separation directly proves that autotrophic root respiration relies directly on recent photosynthate, whereas heterotrophic microbes process older, partially decomposed soil organic matter (Carbone et al., 2008; Dijkstra et al., 2021; Sierra et al., 2021b; Tangarife-Escobar et al., 2024).

4.2 Drought increases older carbon contributions to released CO_2 and soil profile uniformity

In Mediterranean ecosystems, water availability acts as the primary driver of seasonal photosynthesis (Garbulsky et al., 2013), with carbon transit times inversely correlated to precipitation across the Iberian Peninsula (Carvalhais et al., 2014). This contrasts with tropical systems such as the Amazon, where higher rainfall and soil moisture enrich the $\Delta^{14}\text{C}$ signature of respired CO_2 (Chanca et al., 2025). In contrast, experimental drought systematically altered soil carbon fluxes and reduced ecosystem residence times by restricting fresh photosynthetic inputs and forcing heterotrophic microbes to mineralize older soil organic matter. In Panama, drought increased the age of soil-respired carbon by approximately two years (McFarlane et al., 2024); at Prades, surface respiration (FFSR) and 5–10 cm soil incubations aged by approximately six years. Almost all ecosystem pools exhibited older carbon under drought compared to controls, mirroring the foundational findings of McFarlane et al. (2024). This reduction in ecosystem carbon pools aligns directly with long-term observations at the Prades site, which document drought-induced declines in biomass, increased litterfall, lower fruit production and seedling recruitment, slower stem growth and mushroom production, decreased net primary productivity (NPP), and higher tree mortality (e.g., Ogaya and Peñuelas, 2003; Ogaya and Peñuelas, 2004; Ogaya and Peñuelas, 2005, 2006; Barbeta et al., 2013; Liu et al., 2015, 2018). This structural collapse is driven by four non-mutually exclusive mechanisms operating concurrently across plant and soil reservoirs:

1. **Suppression of fresh carbon inputs and substrate diffusion limits:** Stomatal closure lowers gross primary productivity (GPP) and restricts the downward transfer of recent assimilates, depriving the rhizosphere of labile exudates and causing microbes to rely more on older carbon reserves for energy (Melillo et al., 2017). Concurrently, reduced foliage and plant cover degrade overall soil quality by lowering moisture retention and fertility (Sardans et al., 2020). Drought further restricts soil extracellular enzyme activity by impairing substrate diffusion and physical accessibility within soil micropores (Moyano et al., 2013; Marañón-Jiménez et al., 2022), which lowers substrate affinity and slows hydrolytic reaction rates (Allison et al., 2011; Asensio et al., 2021; Liu et al., 2022). As both plant and microbial metabolic processes decline under moisture stress, total enzyme synthesis decreases even further (Allison et al., 2011; Asensio et al., 2021; Liu et al., 2022). This input restriction is corroborated by optimized compartmental model parameterization (Table A4), which reveals steep reductions in fine litter input coefficients (α_{64}, α_{65}) and Horizon A to B transfer rates (α_{76}). These physical input deficits directly disrupted the soil profile: under control conditions, organic carbon (%C) and $\Delta^{14}\text{C}$



followed steep vertical gradients, whereas experimental drought completely homogenized this structure (Fig. 4). Topsoil carbon stocks collapsed by $25.6 \text{ Mg C ha}^{-1}$ (0–5 cm) and $12.5 \text{ Mg C ha}^{-1}$ (5–10 cm), driven by reduced fine-litter carbon concentrations and suppressed shallow root activity.

2. Reduction in soil CO₂ fluxes and prolonged carbon transit times: Reductions in overall soil CO₂ efflux due to water limitation—typically observed year-round except for brief post-rewetting spikes in August (Asensio et al., 2007)—restrict the convective and diffusive delivery of fresh dissolved organic carbon to decomposer niches, thereby prolonging the residence time of undecomposed organic fractions in surface horizons (McFarlane et al., 2024). Model parameters confirm a 32% collapse in total ecosystem carbon stocks alongside a drop in overall ecosystem transit time, driven by accelerated turnover in intermediate wood and Horizon B soil. Crucially, a key model-data discrepancy provides empirical proof of this mechanism: observed Soil Horizon A under drought exhibited pre-bomb radiocarbon signatures, whereas steady-state model simulations predicted post-bomb values. This discrepancy proves that drought actively blocks the physical incorporation and turnover of recent photosynthates in the surface mineral matrix, leaving legacy carbon unreplenished.

3. Microbial community shifts and metabolic adaptation: Prolonged moisture stress alters plant nutrient balances (Sardans et al., 2008), depresses plant and microbial nutrient uptake (Bista et al., 2018), and degrades microbial resource quality (Asensio et al., 2021). These environmental filters trigger structural shifts in microbial community composition and function (Alster et al., 2013; Schimel, 2018; Preece et al., 2018; Liu et al., 2022), analogous to responses documented in tropical forest soil profiles (Nottingham et al., 2022). Over time, prolonged drought promotes Gram-positive dominance, osmotic acclimation, and the production of resistance structures (Schimel, 2018). To acquire scarce resources, microbes increase metabolic investment in extracellular enzymes, raising their survival carbon demand, lowering microbial carbon use efficiency (CUE) (Schimel, 2018; Peñuelas et al., 2018; Asensio et al., 2021; Marañón-Jiménez et al., 2022), and exhausting younger organic pools (McFarlane et al., 2024). This metabolic shift decreases microbial biomass and compromises soil carbon stabilization and nutrient storage (Peñuelas et al., 2018; Marañón-Jiménez et al., 2022), while increasing the spatial variability of $\Delta^{14}\text{C}$ in soil-respired CO₂ near the surface (McFarlane et al., 2024).

4. Priming effects driven by intermittent pulses and source-sink shifts: Intermittent stress-induced pulses of root exudation or transient rewetting events trigger rhizosphere priming mechanisms, where the rapid metabolism of newly supplied plant carbon provides the activation energy for microbes to mineralize recalcitrant, older carbon pools (Liu et al., 2022). On the plant side, wood autotrophic respiration increased by 40% under drought with no increase in coarse litter transfer (α_{52}), proving that trees metabolize internal non-structural carbohydrate (NSC) reserves during stress. Drought also increased $\Delta^{14}\text{C}$ variability in coarse and fine litter, likely driven by accelerated litterfall from drought-induced xylem cavitation (Ogaya and Penuelas, 2004; Liu et al., 2022). This cavitation triggers rapid branch and leaf senescence, elevated mortality, and leaf area reduction as plants actively limit transpiration to protect hydraulic function (Ogaya and Peñuelas, 2006; Liu et al., 2018). Uniquely, roots exhibited younger carbon ages under drought than in controls (19 vs. 33 years). While contrasting with reports of increased root longevity under moderate stress (López et al., 2001), this



agrees with fine-root growth increases during severe drought (López et al., 2009). Under extreme moisture limitation, trees adjust internal source–sink dynamics, reallocating fresh assimilates directly to root systems to forage for subsoil water (Asensio et al., 2007; Barbeta et al., 2012) and synthesize mucilage, organic acids, and enzymes to facilitate soil penetration and nutrient mobilization (Preece et al., 2018), intermittently fueling rhizosphere priming mechanisms at depth.

The mechanisms driving this site-level collapse also reflect broader functional and species-specific dynamics. While McFarlane et al. (2024) found that reduced dry-season CO₂ emissions in Panama were driven primarily by lower heterotrophic respiration with minimal change in autotrophic root flux, our radiocarbon signatures indicate that autotrophic root respiration at Prades is more severely impacted by drought than heterotrophic fluxes. At the community scale, these physiological impacts vary by species: *Quercus ilex* suffers severe hydraulic failure, reduced stem growth, lower fruit production, and accelerated mortality, whereas co-occurring *Phillyrea latifolia* exhibits greater resilience due to superior radiation dissipation, higher water-use efficiency, and embolism resistance (Martínez-Vilalta et al., 2002; Ogaya and Peñuelas, 2003; Ogaya and Penuelas, 2004; Ogaya and Peñuelas, 2005, 2006; Barbeta et al., 2013; Liu et al., 2015; Ogaya and Peñuelas, 2021). This differential sensitivity suggests that intensifying drought will drive long-term structural transitions from dense oak forests toward sparse shrublands (Sardans et al., 2020). Although the severity of drought impacts may attenuate over time as trees and microbes undergo metabolic acclimation (Barbeta et al., 2013; Liu et al., 2018), the resulting increase in microbial maintenance costs (Schimel, 2018) persistently favors older ecosystem carbon emissions and reduces long-term carbon sequestration. Finally, while relying on a single field campaign limits our ability to capture intra-annual seasonal variations in drought responses (Asensio et al., 2007; McFarlane et al., 2024), the observed reductions in microbial biomass, enzyme activity, and nutrient availability remain consistent across all seasons at Prades (Martin-Benito et al., 2021), providing robust evidence for a persistent, drought-induced degradation of the Mediterranean soil carbon sink.

4.3 Implications for carbon sequestration

Ecosystem carbon sequestration depends not only on how much carbon ecosystems store, but also on how long it persists in vegetation and soil compartments before returning to the atmosphere (Sierra et al., 2021a; Muñoz et al., 2024; Sierra, 2025). In Mediterranean forests, climate change is already altering carbon cycling through more frequent and intense droughts that reduce growth, increase mortality, and shift species composition (Ogaya and Peñuelas, 2006; Barbeta et al., 2013; Sardans et al., 2020; Asensio et al., 2021; Ogaya and Peñuelas, 2021; Ali et al., 2022). These changes limit allocation to stem biomass and are projected to worsen even under moderate emission scenarios (Liu et al., 2018; Ali et al., 2022).

Our experimental drought results show that drying alters both the age of carbon in ecosystem compartments and the carbon emitted. Older carbon in drought plots suggests reduced inputs of fresh carbon alongside increased losses of previously stabilized carbon through enhanced decomposition (McFarlane et al., 2024). The homogenization of the top 20 cm of soil—marked by lower carbon content and older carbon typically found at depth—is especially concerning in arid soils where inputs already



limit SOC (von Fromm et al., 2024). Meanwhile, newer carbon in roots and leaves indicates a shift toward shorter-lived pools
475 rather than slower-cycling wood or soil, reducing overall sequestration capacity.

Rising temperatures compound these effects. Unlike northern forests, Mediterranean systems are unlikely to benefit from
warming since temperature is not limiting (Rovira et al., 2004). Instead, higher temperatures increase respiration—an effect
that elevated CO₂ alone cannot offset without increased rainfall (Sabaté et al., 2002). As in tropical forests, warming is likely
to increase the $\Delta^{14}\text{C}$ of respired CO₂, reflecting greater losses of older soil carbon (Vogel et al., 2014; McFarlane et al.,
480 2024). Together, drought and warming heighten soil carbon vulnerability by reducing the incorporation of fresh carbon and
accelerating the loss of older carbon.

These pressures are expected to drive vegetation shifts, particularly forest-to-shrubland transitions (Liu et al., 2015; Peñuelas
et al., 2018; Sardans et al., 2020). Since shrublands have lower carbon inputs, such shifts could turn forest soils into carbon
sources (Rovira et al., 2004). In the Prades experiment, *Q. ilex* showed lower biomass increment under drought than the more
485 tolerant *P. latifolia*, suggesting structural and functional changes in holm oak forests (Ogaya and Peñuelas, 2006; Ogaya and
Peñuelas, 2021; Sardans et al., 2020).

Drought also increases wildfire risk, creating unstable conditions when fire frequency and intensity exceed recovery capacity
(Rovira et al., 2004). Both fire and drought reduce soil fertility through nutrient losses, particularly nitrogen, while increased
root growth may intensify depletion and lead to nutrient limitation (Rovira et al., 2004). Such limitations feed back on carbon
490 balances (Peñuelas et al., 2013; Sardans et al., 2020) and their timescales.

In short, climate change—especially drought—triggers interconnected processes that heighten carbon vulnerability through
positive feedbacks, driving long-term declines in sequestration.

Management must therefore prioritize not only carbon uptake (Sabaté et al., 2002; Rovira et al., 2004) but also storage
persistence (Muñoz et al., 2024; Sierra, 2025). Effective strategies should stabilize new CO₂ inputs into slow-cycling reservoirs
495 (Tangarife-Escobar et al., 2024), integrating radiocarbon and content measurements with age and transit-time metrics (Sierra
et al., 2021b; Muñoz et al., 2023, 2024).

5 Conclusions

Although increasing drought frequency and severity are known to strongly disrupt carbon cycling in Mediterranean forests,
the temporal dynamics and retention times of carbon across specific ecosystem pools under moisture stress have remained
500 poorly understood. This study provides the first comprehensive characterization of carbon ages across all major ecosystem
pools and respired CO₂ fractions in a Mediterranean forest. By integrating $\Delta^{14}\text{C}$ signatures of vegetation bulk pools, soil
radiocarbon profiles and ecosystem and soil respiration, with soil organic carbon stocks under experimental drought, our key
findings demonstrate that:

- Carbon is generally older in drought plots compared to controls, with the trend consistent across most ecosystem pools
505 except roots. Significant differences were particularly evident in the shallow soil layer.



- Drought tends to homogenize the upper soil layers (at least up to 20 cm) in both carbon content and radiocarbon age. This structural loss reflects a double impact: the depletion of legacy carbon reserves alongside a severe reduction in the physical incorporation and stabilization of fresh photosynthetic inputs.
- Comparing field soil respiration with root-free laboratory incubations revealed a distinct divergence in radiocarbon signatures under control conditions that disappeared under drought. This lack of divergence indicates that roots either shifted toward respiring older reserve carbon or substantially reduced their overall autotrophic contribution to soil surface flux.
- End-member mixing analysis proved less effective in Mediterranean oak forests than in dense tropical systems like the Amazon (Chanca et al., 2025), primarily due to smaller concentration gradients and strong diurnal variations. Alternative methodological approaches are therefore needed.
- While field measurements showed older ecosystem respiration under drought, steady-state compartmental modeling predicted the opposite trend. This mismatch highlights that future modeling efforts must explicitly incorporate non-steady-state, drought-induced carbon allocation shifts and variable microbial substrate preferences to accurately match empirical radiocarbon signatures.

Together, these findings show that prolonged drought increases the vulnerability of existing soil carbon stocks by forcing microbial reliance on older substrates while suppressing the stabilization of new assimilates. Moving forward, Mediterranean forest management must prioritize maintaining existing soil carbon stocks and enhancing the long-term stabilization of fresh CO₂ inputs into slow-cycling reservoirs.

Our conclusions are constrained by single-campaign sampling, which cannot capture intra-annual or inter-annual variations in $\Delta^{14}\text{C}$ signatures and flux sources (Sardans et al., 2020). Fully resolving the mechanisms governing carbon storage duration will require continuous, multi-year radiocarbon sampling of ecosystem respiration, along with dynamic modeling to capture transit-time distributions across individual pools. Moreover, the absence of tower-restricted CO₂ variability measurements and background atmospheric characterization underscores the need for long-term $\Delta^{14}\text{C}$ in CO₂ time series in the Mediterranean region.



Appendix A: Supplementary Information

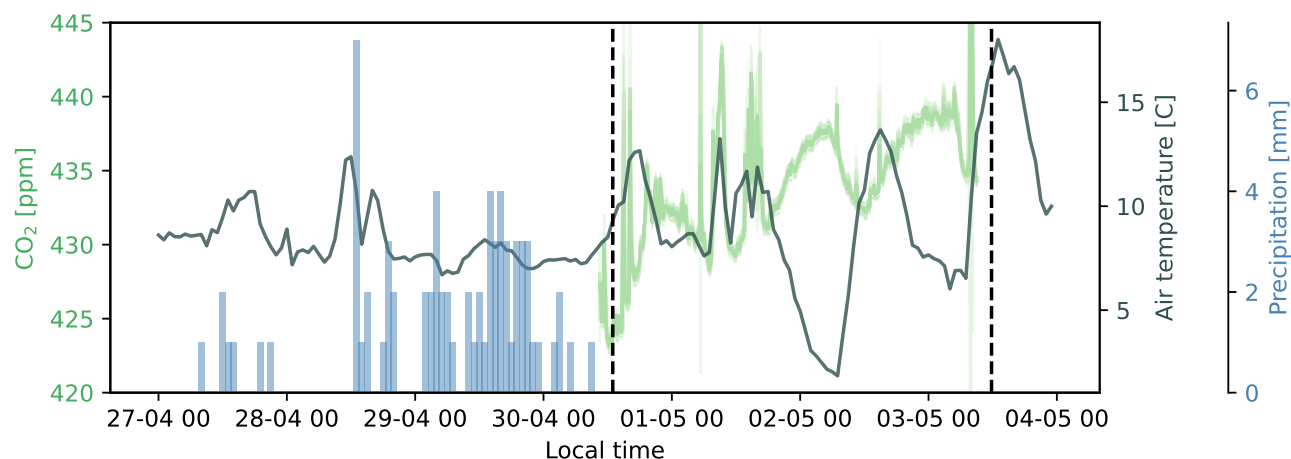


Figure A1. Time series of carbon dioxide concentration (green lines), air temperature (dark blue lines), and precipitation (light blue bars) recorded during the field campaign and the preceding three days. Vertical dashed lines mark the beginning and end of the campaign period. CO₂ concentrations were measured at heights between 0.7 and 4.9 meters, with a 0.7 m interval, due to their similarity; all heights are displayed in the same color.



Table A1. $\Delta^{14}\text{C}$ statistics for pools in control and drought plots in the Prades forest. Reported values include the mean, standard deviation (σ), minimum (min.), and maximum (max.), all expressed in ‰. The sample size (n) indicates the number of samples analyzed. The p -value reflects the statistical significance of differences between the $\Delta^{14}\text{C}$ values of each pool and the atmospheric background (atmosphere).

Control							Drought					
Pool	n	mean	σ	min.	max.	p -value	n	mean	σ	min.	max.	p -value
Atmosphere	2	-1.7	5.7	-5.7	2.3		-	-	-	-	-	-
ER	14	-7.2	7.1	-20.4	4.9	0.470	14	-5.2	5.9	-18.8	4.9	0.723
FFSR	3	13.5	4.8	8.6	18.2	0.020	4	44.5	36.7	6.6	82.4	0.072
Soil inc. 0-5	4	53.3	9.4	40.9	63.8	<0.01	4	45.6	10.0	35.3	56.1	<0.01
Soil inc. 5-10	4	29.7	37.3	-24.9	59.1	0.154	4	37.9	21.5	11.3	62.7	0.027
Wood	6	219.7	151.9	55.6	465.9	0.015	5	174.2	69.8	56.6	241.8	<0.01
Foliage	12	-6.0	3.6	-12.2	-0.3	0.785	15	-5.2	5.1	-16.0	1.5	0.699
Fine litter	12	16.5	20.2	-3.3	58.4	<0.01	12	23.9	17.8	0.3	58.3	<0.01
Coarse litter	12	261.3	103.4	27.3	380.6	<0.01	12	269.9	120.1	72.0	451.2	<0.01
Roots 0-5	5	74.6	49.9	17.2	136.3	0.023	9	48.0	34.7	17.5	113.4	<0.01
Roots 5-10	4	74.7	31.4	47.4	120.0	0.014	9	54.4	35.3	25.2	135.9	<0.01
Roots 10-15	5	93.0	36.0	40.9	137.8	<0.01	9	65.1	25.3	23.9	106.6	<0.01
Roots 15-20	5	73.5	18.7	56.8	99.2	<0.01	8	70.8	32.1	29.4	126.3	<0.01
Soil 0-5	4	51.1	25.2	22.3	76.5	0.020	4	-3.5	9.5	-14.3	7.9	0.669
Soil 5-10	4	24.3	19.6	4.1	51.2	0.055	4	-17.6	31.9	-50.6	23.7	0.512
Soil 10-15	15	-19.7	45.4	-107.5	46.7	0.254	15	-52.1	55.2	-135.1	59.5	<0.01
Soil 15-20	11	-82.2	39.0	-129.7	-10.9	<0.01	13	-71.7	61.1	-178.7	56.9	<0.01

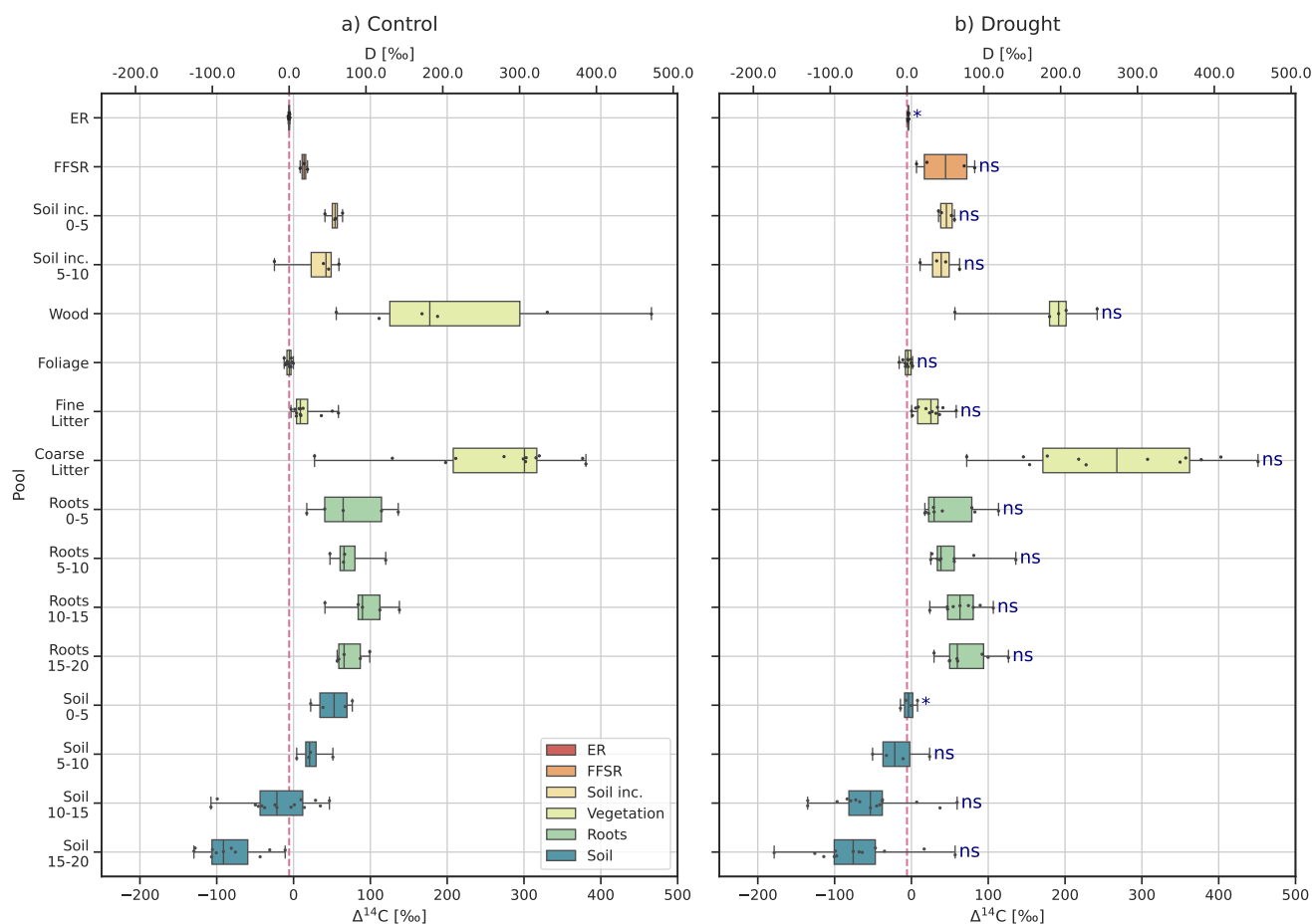


Figure A2. $\Delta^{14}\text{C}$ values from ecosystem pools in bulk material and CO₂ fractions for a) control plots and b) drought plots. The vertical red dashed line indicates the atmospheric background ^{14}C -CO₂ value (-5.7‰). Data points to the right of this line reflect the presence of bomb-derived radiocarbon, while negative values to the left indicate pre-bomb radiocarbon signatures. D at 0 marks the transition between positive and negative isotopic disequilibrium. Symbols above the boxplots in panel b indicate statistical significance when comparing each pool between control and drought plots: "ns" denotes no significant difference, and * indicates $p < 0.05$.



Table A2. Carbon percentage statistics for pools in control and drought plots in the Prades forest. Reported values include the mean, standard deviation (σ), minimum (min.) and maximum (max.), all expressed in %. The sample size (n) indicates the number of samples analyzed.

Control						Drought				
Pool	n	mean	σ	min.	max.	n	mean	σ	min.	max.
Fine litter	12	43.8	2.6	39.3	48.3	12	38.5	5.4	23.6	44.6
Coarse litter	12	43.4	2.4	38.6	48.0	12	42.9	2.8	39.4	47.9
Roots 0-5	9	33.0	6.1	22.6	42.6	11	30.7	7.0	19.5	44.0
Roots 5-10	9	34.2	8.1	15.8	42.8	10	31.2	7.1	16.6	43.7
Roots 10-15	12	35.4	4.2	29.4	42.5	9	35.0	5.9	26.6	43.6
Roots 15-20	7	33.4	4.2	26.5	38.8	8	30.9	4.4	24.5	38.6
Soil 0-5	4	7.7	2.0	5.7	10.3	4	4.2	0.6	3.3	4.7
Soil 5-10	4	4.6	1.6	3.1	6.8	4	2.9	0.6	2.4	3.8
Soil 10-15	15	3.3	2.1	1.1	9.0	15	2.5	1.5	1.0	6.2
Soil 15-20	11	2.0	0.5	1.3	2.8	13	1.9	0.8	0.8	3.7

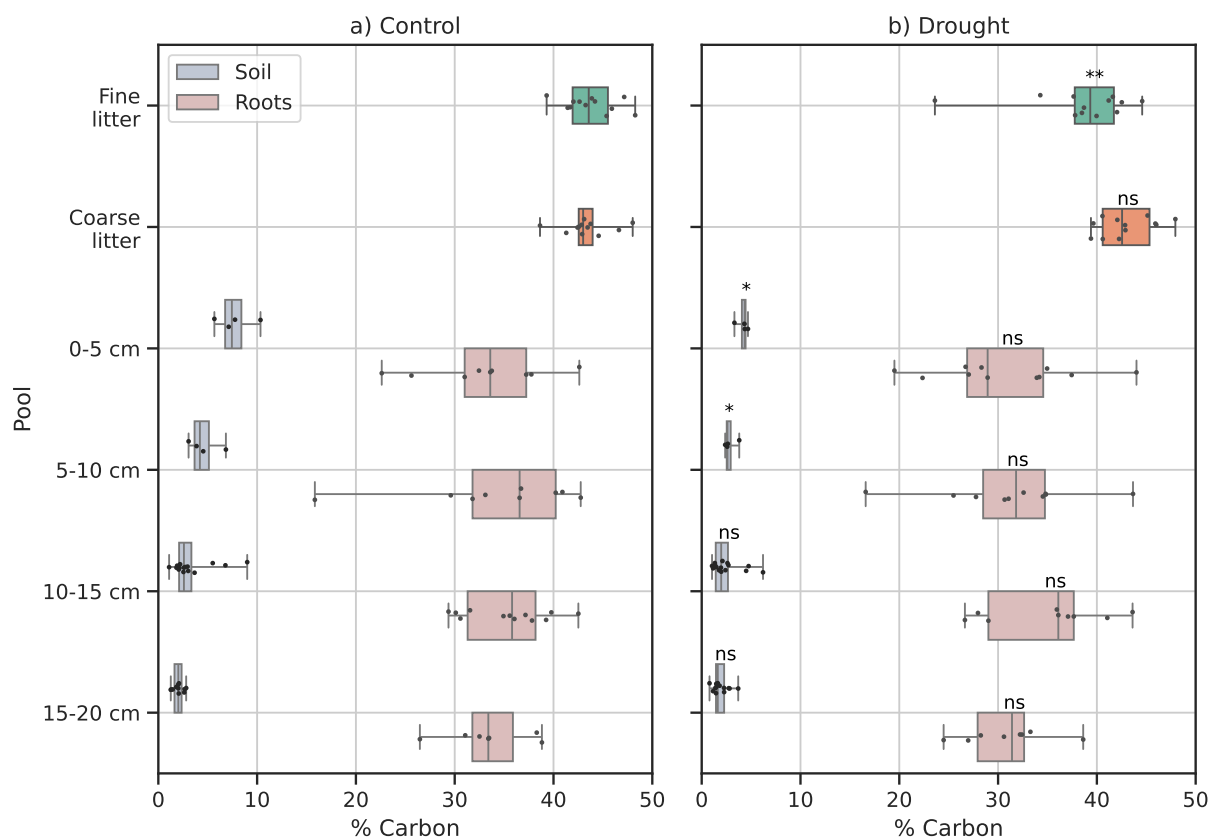


Figure A3. Percentage of carbon in ecosystem pools for a) control and b) drought plots. Symbols above the boxplots in panel b indicate statistical significance when comparing each pool between control and drought plots: "ns" denotes no significant difference, * indicates $p < 0.05$, and ** indicates $p < 0.01$.

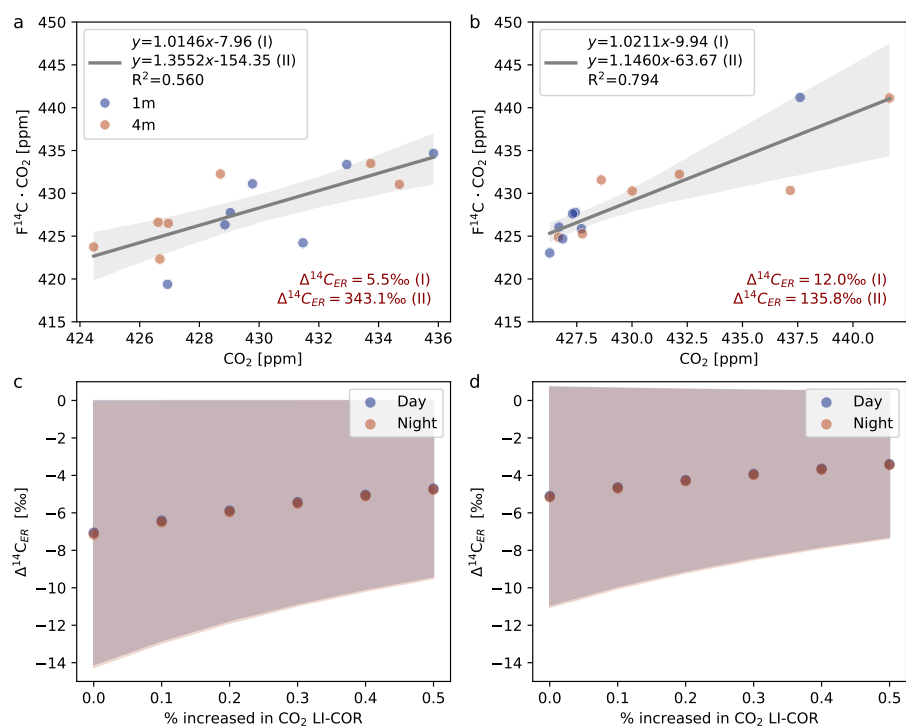


Figure A4. Ecosystem respiration estimated using the Miller-Tans approach with both Type I and Type II regressions (a,b), and by solving the carbon balance in Eq. 1 for $\Delta^{14}C_{ER}$ (c,d) in control (a,c) and drought (b,d) plots. In panels a and b, colored dots represent the measurement heights. In panels c and d, blue dots show solutions from Eq. 1 using LI-COR measurements throughout the day, while red dots indicate results from combining Eq. 1-2 for nighttime fluxes. Shaded areas in all panels represent uncertainty.

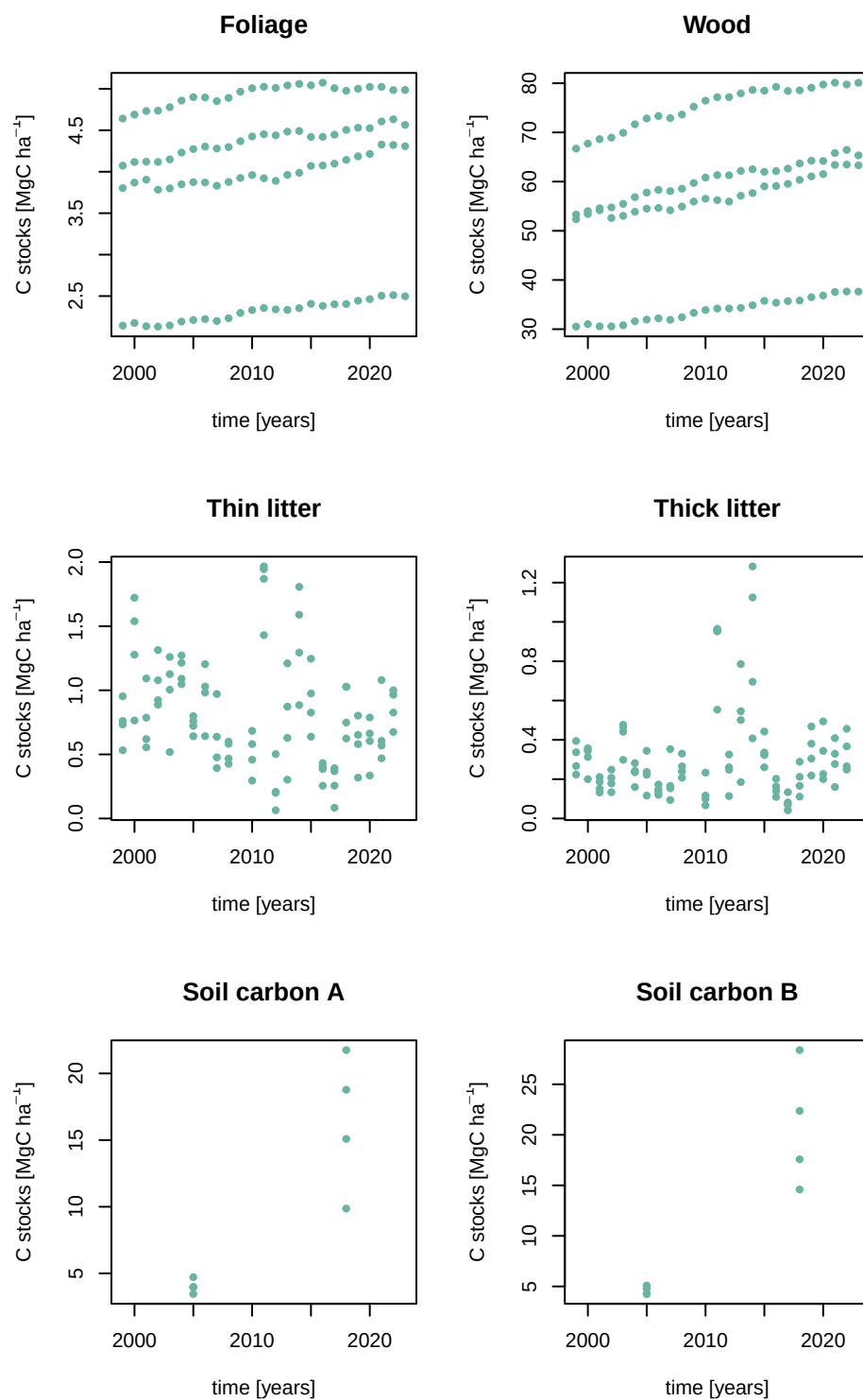


Figure A5. Carbon stocks data collected throughout the entire induced drought experiment in Prades (Ogaya and Peñuelas, 2021).



Table A3. Carbon fluxes from soil and leaves in the Prades forest. Mean and standard deviation (σ) are expressed in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, except for GPP that is expressed in $\text{MgC ha}^{-1} \text{ yr}^{-1}$.

Variable	Description	mean	σ	Treatment	Source
f_s	Soil CO_2 flux	3.49	0.85	Control	Asensio et al. (2007)
f_s	Soil CO_2 flux	2	0.3	Drought	Asensio et al. (2007)
f_v	Leaf respiration	1.53	0.28	Control	Sperlich et al. (2016)
f_v	Leaf respiration	1.79	0.13	Drought	Sperlich et al. (2016)
GPP	Gross primary production	47.63	6.91	Control	Sabaté et al. (2002)

Table A4. Mean and standard deviation (SD) of parameter estimates derived from the 1,000 optimization iterations, along with the optimal parameter values inferred from the ^{14}C signatures for each model.

Parameter	Control			Drought			Drought (0.9 GPP)		
	Mean	SD	Best	Mean	SD	Best	Mean	SD	Best
k_1	11.041	1.581	13.121	11.041	1.571	12.663	11.041	1.571	12.663
k_2	0.007	0.001	0.005	0.015	0.002	0.011	0.017	0.002	0.013
k_3	0.040	0.006	0.037	0.070	0.010	0.053	0.070	0.010	0.053
k_4	17.136	2.404	13.767	16.440	2.322	14.099	14.979	2.115	12.846
k_5	1.509	0.218	1.150	1.499	0.214	1.221	1.196	0.152	1.000
k_6	0.005	0.001	0.005	0.005	0.001	0.004	0.005	0.001	0.004
k_7	0.003	0.000	0.003	0.003	0.000	0.003	0.003	0.000	0.003
α_{21}	0.022	0.003	0.017	0.026	0.003	0.023	0.026	0.003	0.023
α_{31}	0.009	0.001	0.009	0.009	0.001	0.010	0.009	0.001	0.010
α_{41}	0.309	0.024	0.292	0.307	0.023	0.290	0.307	0.023	0.290
α_{52}	0.248	0.035	0.238	0.248	0.035	0.198	0.248	0.035	0.198
α_{43}	0.298	0.045	0.273	0.298	0.045	0.289	0.298	0.045	0.289
α_{53}	0.467	0.073	0.534	0.469	0.074	0.521	0.469	0.074	0.521
α_{63}	0.102	0.034	0.063	0.101	0.034	0.082	0.101	0.034	0.082
α_{73}	0.133	0.042	0.130	0.132	0.042	0.108	0.132	0.042	0.108
α_{64}	0.020	0.003	0.024	0.020	0.003	0.015	0.020	0.003	0.015
α_{65}	0.010	0.001	0.012	0.010	0.001	0.010	0.010	0.001	0.010
α_{76}	0.601	0.087	0.748	0.602	0.085	0.616	0.602	0.085	0.616

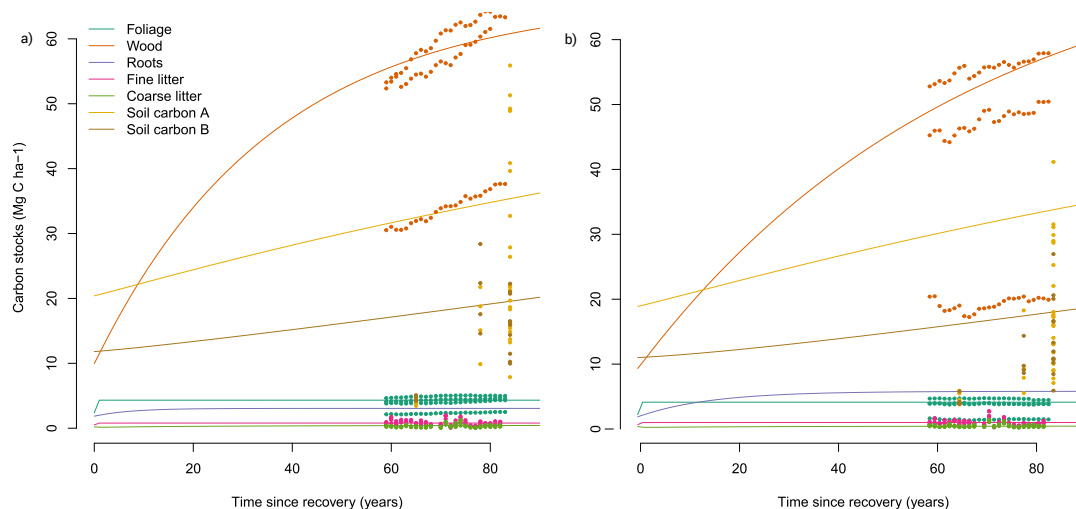


Figure A6. Observations of carbon stocks (points) along a successional sequence and mean model predictions for a) control and b) drought. Each color represents a different ecosystem pool.

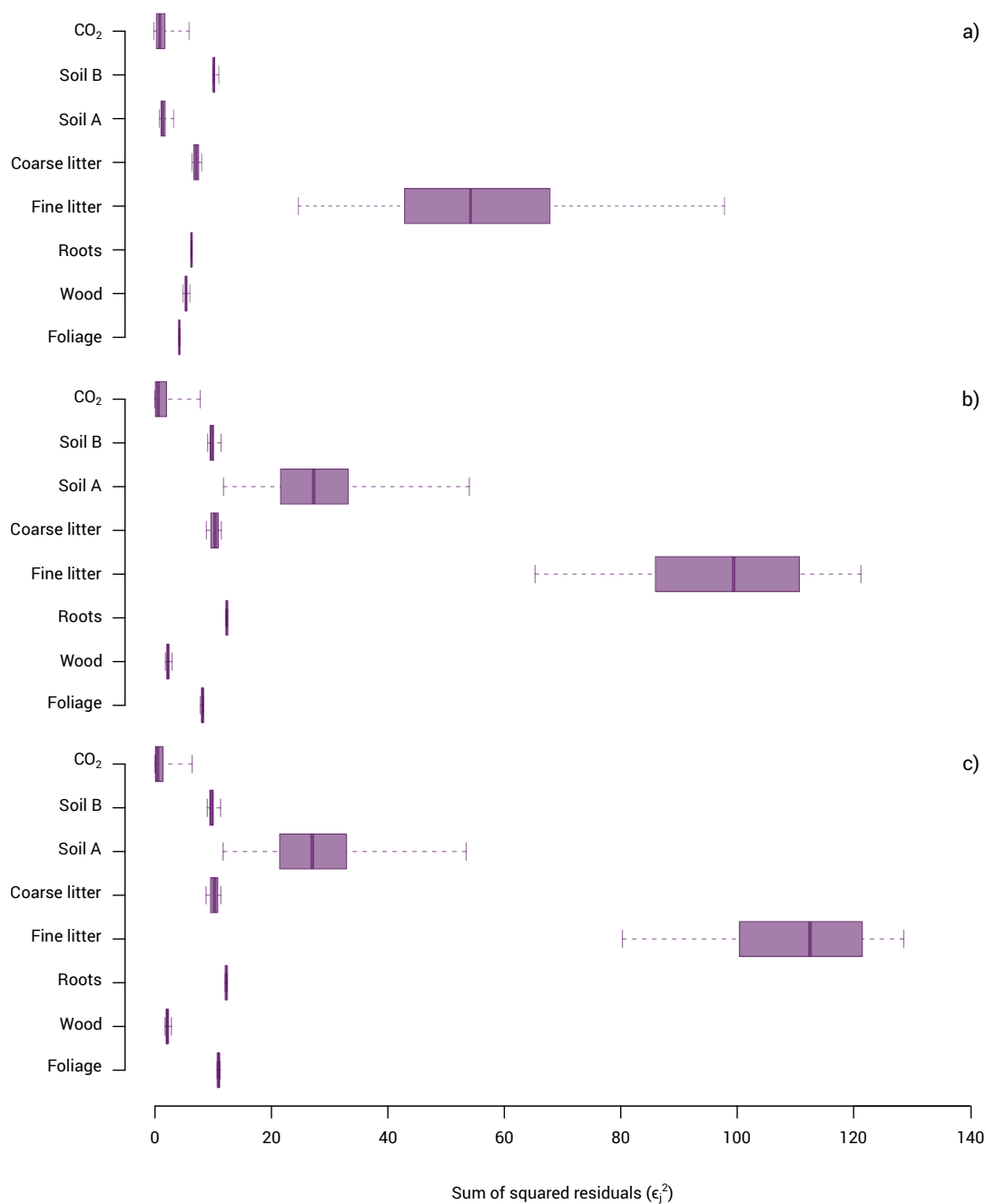


Figure A7. Boxplots of the sum of squared residuals scaled by their mean value (8), for a) control, b) drought with GPP, and c) drought with 0.9 GPP. Values of ϵ_j^2 are unitless and reflect the difference between predictions and observations and the number of available measurements.

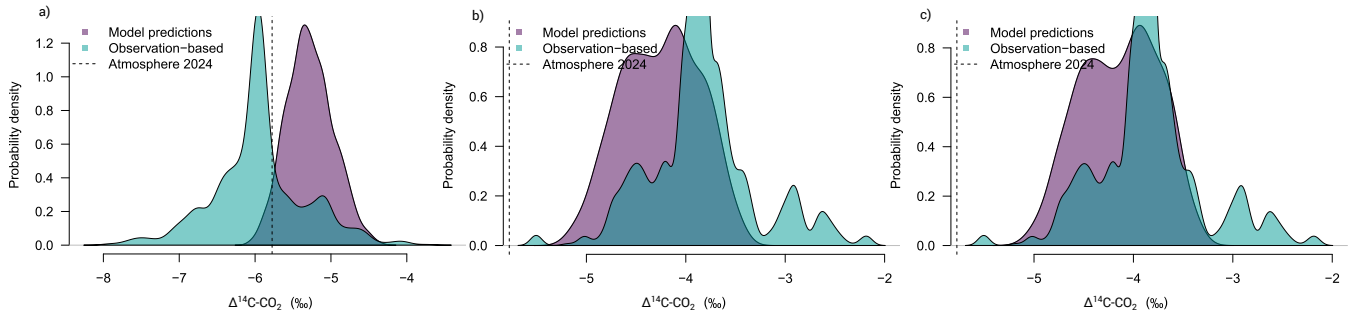


Figure A8. Probability density distributions of $\Delta^{14}\text{C-CO}_2$ in ecosystem respiration obtained from direct atmospheric measurements of below-canopy air, and from predictions of the ecosystem carbon model for a) control plots, b) drought with GPP, and c) Drought with 0.9 GPP.

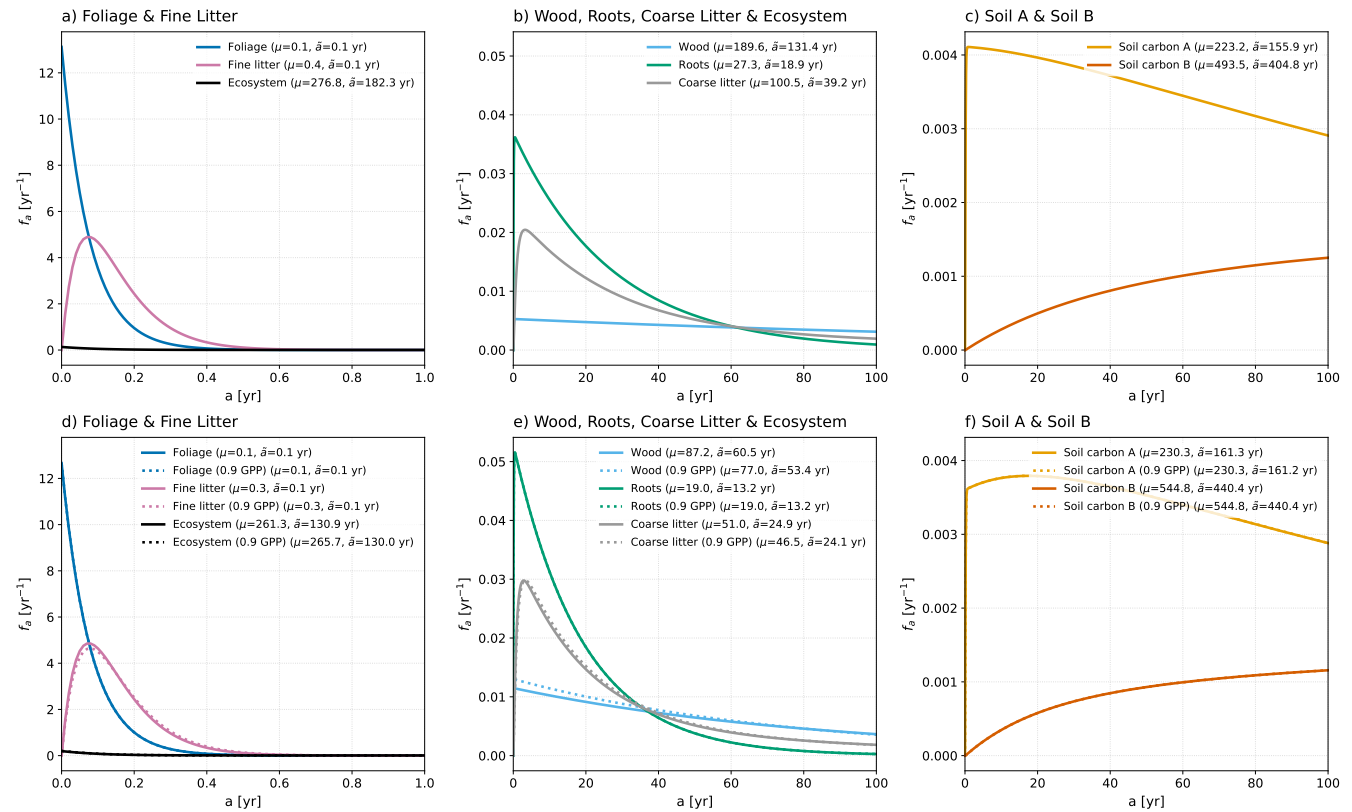


Figure A9. Age (a) density distributions for the ecosystem and individual pools. The upper panels show control plots, and the lower panels show drought plots, each simulated with GPP and 0.9 GPP. Panels (a) and (d) correspond to foliage and fine litter; (b) and (e) to wood, roots, coarse litter, and the total ecosystem; and (c) and (f) to horizon A and horizon B soils. Axis scales differ among panels to improve readability, but corresponding control and drought panels share the same axes. μ denotes the mean and $\tilde{a}$ the median. These densities were derived using the parameter set that best fit the ^{14}C measurements.



530 *Author contributions.* Fieldwork: EM, RO, JC, GM, XS, CAS; Lab: EM, XS; Data analysis: EM, KM, CAS.

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