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Above and belowground carbon stock of pine plantations and native oak forests coexisting in central Spain

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Abstract

Promoting nature-based carbon sinks is one of the effective ways to minimise global warming. Different types of forests, resulting from different land-use histories, may coexist under similar macro-environmental conditions, but their efficiency as carbon sinks may differ. In central Spain, many areas are covered by coexisting patches of monospecific plantations of *Pinus halepensis*, established since the 1950's, and native *Quercus* forest coppiced up to the 1960´s. We aimed to compare the carbon stock between both types of forests, considering both above and belowground compartments, in La Alcarria region (central Spain). In each plot, the diameter at breast height and height were measured in every adult tree, along with shrub cover. Three subsamples of litter and soil were collected per plot. The carbon pool of trees and shrubs was calculated using allometric equations, and for roots, litter, and soil, using the carbon content analysed in a laboratory or obtained from the literature. Carbon pools were analysed separately for three independent variables: plot type (*Quercus*/*Pinus*), tree basal area (m^2/ha) and slope (°). Overall, *Quercus* forests stored more carbon than *Pinus* plantations. The carbon allocation pattern across compartments greatly varied between the two forest types, *Pinus* plots storing more than half (55%) of its carbon in the aboveground biomass of trees, while *Quercus* storing more carbon belowground (60%) in roots and soil. We conclude that native *Quercus* forests are more suitable for a long-term carbon storage, as belowground compartments represent an important part of its carbon storage capacity.

Introduction

Climate change induced by the anthropogenic emissions of CO_2 is one of the main challenges humankind will face in the coming decades, as it threatens human security, and water and food supplies (IPCC, 2021). To achieve the ambitious goals of the Paris Agreement to limit global warming by 1.5–2° C above pre-industrial levels, rapid reductions in greenhouse gasses and an improvement of carbon sequestration by natural ecosystems are urgently needed (IPCC 2021). Research has shown that afforestation/reforestation, and a suited management of already existing forests can be effective tools for climate change mitigation (Canadell and Raupach 2008; Doelman et al. 2020; Kimble et al. 2002). In this context, understanding the carbon stock capacity of forests coexisting under similar environmental conditions, but resulting from different land-use histories, is crucial to support forest management policies. Such forests may differ in species composition, but also in forest structure and management practices.

Given that many afforestation's seek productive or soil protection goals, tree species selected are usually early-succession fast-growing ones, which can accumulate quite a lot of aboveground biomass in the short term. This quality have led some stakeholders to defend fast-growing tree plantations as efficient carbon sinks (Silva and Tomé, 2016). Yet, late-successional tree species tend to allocate more biomass to roots compared to early successional tree species (Shukla and Ramakrishnan, 1984; Verdú, 2000). The fact that some late-successional species, particularly in dry regions, are able to root deeper into the ground, suggests that they additionally contribute to storing carbon in deeper layers of the soil, which is

one of the most effective ways of gaining soil organic carbon (SOC) (Jandl et al. 2007). According to Jackson et al. (2017), roots are five times more likely to be stabilized as soil organic matter compared to aboveground litter with the same mass. This belowground storage of soil as SOC is very important to lessen the effects of climate change and reduce carbon in the atmosphere. Terrestrial ecosystems are estimated to store two to three times more carbon in the top meter of soils than in the aboveground part of living vegetation (Houghton, 2007). Despite this fact, there are still many studies that do not take this carbon pool into account, only sampling the aboveground vegetation or, in the best case, the first 10 cm of the soil. This leads to overestimations of the role of early-succession fast-growing trees as carbon sink. Moreover, SOC tends to be more stable than aboveground carbon, as the latter is considerably more prone to be lost by disturbances such as fires, a common natural disturbance in Mediterranean areas. This is because the upper soil acts as an insulator during forest fires, protecting the organic matter stored deeper in the soil (González-Pérez et al. 2004). Certini et al. (2011) found that after a forest fire in Mediterranean pine forests, even though the litter completely burned away, the underlying mineral soil did not show any significant change in its carbon content. Jiménez-González et al. (2016) reported a significant decrease in SOC after a forest fire; however, the carbon level recovered within two years back to original levels.

Several studies have compared carbon sequestration across forest deriving from different land uses, reporting contrasting results. Some found that non-native forests store more carbon than native ones (Arévalo et al. 2013; Bazgir et al. 2020; Meunpong et al. 2010), while others found the opposite (He et al. 2013; Rodríguez-Loinaz et al. 2013; Waller et al. 2020). Some studies found that natural forests store more carbon (Leuschner et al. 2022; Naqash et al. 2021), while others found more carbon stored in tree plantations (Yan et al. 2022). Mechanized forestry work, such as logging or soil preparation for tree plantation, has been found to drastically reduce the amount of soil microbial carbon mass at high soil depth, along with other alterations of soil physical properties (Nazari et al. 2021). Thus, the capacity of forests to store carbon is dependent on many factors, beyond climatic conditions, such as the type of dominant species or the type human management (Castro-Díez et al. 2021; Vayreda et al. 2012).

In the lowlands of central Spain, the most fertile and accessible areas were transformed centuries ago into croplands and pasturelands, while forests were preserved in suboptimal areas. Most of the remaining late-successional *Quercus* spp. forests were submitted to an intensive coppicing for firewood and charcoal. By the beginning of 20th century, Spain was drastically deforested, and the authorities undertook ambitious reforestation plans with the major aim of soil protection (Valbuena-Carabaña et al. 2010; Maestre and Cortina, 2004; Mauri et al. 2016; Vadell Guiral et al. 2019). Most plantations, over 2 million has, were performed during the period 1940–1975, mainly with native pioneer *Pinus* species (Valbuena-Carabaña et el. 2010), under the assumption that late-successional hardwoods would take over in time (Pausas et al. 2004). However, after 50–70 years, this has not happened (Maestre and Cortina, 2004). Simultaneously, coppicing of *Quercus* spp. forests was progressively abandoned due to the expansion of fossil fuels, mostly since the 1960's (Barbero et al. 1990; Ruiz-Peinado et al. 2017). This allowed forests to grow to a particular new structure, characterized by high density, intense competition, reduced vitality, and scarce sexual regeneration (Ruiz-Peinado et al. 2017). Nowadays, both types of

forests (coppice *Quercus* forests and *Pinus* plantations) coexist at local scale, under similar macro environmental conditions, and both may provide relevant regulating ecosystem services, such as water cycle regulation, prevention of soil erosion or carbon sequestration. Understanding the contribution of both forest types to the total forest carbon stock, considering different forest compartments (living trees, the shrub layer, dead mass deposited on the soil and mineral soil) is highly relevant for developing forest management practices focused on enhancing the carbon sequestration (Ruiz-Peinado et al. 2017).

This study aims to assess and compare the carbon stock between native coppice *Quercus* forests, and monospecific *P. halepensis* plantations, coexisting in the centre of the Iberian Peninsula. We assess both above- (tree and shrub canopies) and belowground (roots, litter and soils at two depths) forest compartments. We also compared the carbon allocation pattern between the different compartments of both forest types. Additionally, we also assess the effect of slope on the amount of carbon stored, given the topographic heterogeneity of the study area (from flat plateaus to steep slopes). Although *Pinus* plantations are expected to store more carbon in the aboveground, due to faster growth rate and larger tree height at maturity, *Quercus* forests are expected to store more carbon in the soil, as the soil has been identified as the main carbon storage compartment in coppice *Quercus* forests (Makineci et al. 2015).

Materials and methods

Study site

The sampling was carried out in the northeast of the Community of Madrid and the southeast of the province of Guadalajara, in central Spain (Fig. 1). The altitude of this area ranges between 650 and 920 meter above sea level. The climate is continental Mediterranean, with an annual precipitation between 450 and 500 mm and average temperature between 13.2° C and 14° C (Martínez 2000). The natural late-successional vegetation in this region is dominated by *Quercus ilex* subsp. *ballota* in the dryer areas and *Quercus faginea* in the moister and deeper soils. There are also many pine stands (mostly *Pinus halepensis*) because of intensive plantings on hillsides to prevent erosion in the middle of the 20th century. The area is characterized by carbonate plateaus composed of limestone from the Neogene and valleys with steep hillsides compound by Neogene deposits, consisting out of clay, silt, limestone, marlstone, gypsum and sand layers depending on location (Molina-Navarro et al. 2014).

Twelve representative plots of homogenous vegetation of each forest type (natural *Quercus* forests and planted *Pinus* stands) were selected (Table 1). Plots were initially selected from satellite images of the area, were both forest types can be distinguished. Selection criteria included accessibility and proximity (less than 5 km) to another plot with the other forest type. All plots were sampled between the 17th of March and the 5th of April 2022. Climate and soil type were similar across plots, although slope and orientation varied across them (Table 1). According to IGN (2006) and following Soil Taxonomy (Soil Survey Staff, 2003), Haploxeralfs and Xerorthents are the main soils found in the area (Table 1). The aboveground biomass of *Quercus* and *Pinus* forests are roughly the same age, with *Pinus* stands being planted mainly in the 50's and 60's, and the management of the *Quercus* coppice ceasing in the 60's

(Maestre and Cortina 2004; Mauri et al. 2016; Serrada et al. 2017; Vadell Guiral et al. 2019). In the last decades, both forest types have barely seen any management, except for thinning in some *Pinus* plantations and pruning in one of the *Quercus* plots. *Pinus* plots consist out of monocultures of *P. halepensis* with almost no undercanopy vegetation. The *Quercus* spp. plots varied from each other, from monospecific stands of *Q. ilex* to mixed forest of *Q. ilex, Q. faginea* and *Q. coccifera*, with *Q. ilex* as dominant species, with one exception where *Q. faginea* was dominant (Table 2).

Table 1
Location and site properties of all 24 study plots (P = *P. halepensis* plots, Q = *Q. ilex* plots).

Plot	Dominant species	Coordinates	Slope (°)	Orientation	Altitude (m)	Soil type
Q1	*Q. ilex*	40.52175–3.22893	19	NW	835	Haploxeralf
Q2	*Q. ilex* / *Q. faginea*	40.59223–3.12507	0	n.a.	908	Haploxeralf
Q3	*Q. ilex*	40.44975–3.16550	14.6	SW	823	Haploxeralf
Q4	*Q. ilex*	40.38875–3.14560	20	NE	651	Xerorthent
Q5	*Q. ilex* / *Q. faginea*	40.49826–3.54610	14.3	SW	881	Xerorthent
Q6	*Q. faginea*	40.46853–3.25616	22.2	NW	820	Xerorthent
Q7	*Q. ilex*	40.37896–3.23080	14.7	E	766	Haploxeralf
Q8	*Q. ilex*	40.37959–3.23071	11.2	SE	768	Haploxeralf
Q9	*Q. ilex*	40.54317–3.16855	4.4	NE	920	Haploxeralf
Q10	*Q. ilex*	40.60644–3.11379	0	n.a.	954	Haploxeralf
Q11	*Q. ilex*	40.22384–3.14197	1.6	SE	848	Calcixerept
Q12	*Q. ilex*	40.38071–3.24283	2.9	SE	849	Haploxeralf
P1	*P. halapensis*	40.58683–3.17427	18	N	805	Haploxeralf
P2	*P. halapensis*	40.58459–3.17088	18	NW	912	Haploxeralf
P3	*P. halapensis*	40.42428–3.15521	18.6	NW	723	Xerorthent
P4	*P. halapensis*	40.41945–3.15615	10.9	NW	726	Xerorthent
P5	*P. halapensis*	40.54876–3.17302	4.1	NW	922	Haploxeralf

Plot	Dominant species	Coordinates	Slope (°)	Orientation	Altitude (m)	Soil type
P6	*P. halapensis*	40.46946–3.25698	22.5	NW	809	Calcixerept
P7	*P. halapensis*	40.43796–3.30831	17.7	N	738	Xerorthent
P8	*P. halapensis*	40.39891–3.27107	11.7	NW	808	Xerorthent
P9	*P. halapensis*	40.54958–3.17096	4.7	N	928	Haploxeralf
P10	*P. halapensis*	40.65755–3.11060	22.2	NW	800	Haploxeralf
P11	*P. halapensis*	40.65738–3.11018	18	NW	815	Haploxeralf
P12	*P. halapensis*	40.39883–3.27077	10.4	NE	846	Xerorthent

Sampling

Aboveground vegetation sampling

Based on the methodology of the Spanish National Forest Inventory (Villaescusa and Díaz, 1998), we sampled circular plots with a radius between five and ten meters, depending on tree density (higher radius with lower tree density). In each plot, tree diameter at breast height (DBH) and total height of all adult trees (i.e., those with a DBH above 7.5 cm) were measured. Every tree with a diameter below 7.5 cm was considered as shrub or sapling and then covered by the sampling of the undercanopy (see below). DBH was measured twice with callipers, angled 90 degrees from each other to account for oval-shaped trunk sections. Height was measured with a 'Vertex 5' (Haglöfs, Sweden) which uses ultrasound to measure distances and a digital inclinometer to measures angles. Tree ramets and stems that split off below 1.3 meter (DBH) were considered as individual trees. DBH was used to calculate the basal area of each tree. The cover of the shrub layer (including tree juveniles < 7.5 cm of DBH) was assessed in every plot in a five-meter radius circle, centred in the same point as the tree plot. We laid out three linear transects centred crossing the plot centre and measured the fraction of the transect intercepting shrub cover. This was done separately for shrubs lower and higher than 1 m. The height of shrubs was measured at 5 to 10 different points on each transect, depending on the cover.

Soil and litter sampling

Soil and litter samples were taken at three subsamples within each forest plot, at a minimum distance of two meters from any tree stems to avoid thick roots. Litter was collected by means of a quadrat of 400 cm^2. All living plants inside the square were removed and litter was kept in a paper bag. After the

sampling of litter, a soil cylinder down to 10 cm depth was extracted by means of a soil auger with a diameter of 7.2 cm (407.2 cm^2). Then a second soil sample was taken from 10 to 30 cm of depth using the same soil auger, thus collecting a soil volume of 814.3 cm^3. This depth is commonly used and is the standard sampling depth recommended by IPCC (Aalde et al. 2006). This is because most organic C can be found relatively high in the soil (Allen et al. 2010). The samples (litter, first 10 cm of soil and 10-30cm of soil) were collected in paper bags and taken to the lab. The three subsamples of each fraction collected in the same plot were bulked in the same container for a composite sample.

Sample processing

Litter was dried at 60°C for 48 hours in a lab oven (J.P. Selecta, Cod 2005161), then kept in desiccators to cool down to room temperature and weighted to obtain the dry weight. After weighing, a representative sub-sample of c.a. 20 g was grounded to < 2mm powder with a 'Culatti mill'. The different soil layers were dried at room temperature, grounded with a rolling pin to break clumps into powder, passed through a 2-mm sieve and mixed to homogenize. After processing, we dried a subsample of every sample at 105°C for 24 hours in the lab oven. Dried soils were weighted, and the bulk soil density calculated. The coarse fragments that were filtered by the sieve were separated in organic fragments (roots) and stones. The stones were separately weighted to assess soil stoniness and discarded, since they do not contain organic carbon. Roots (larger than 2mm) present in the soil core were dried at 60°C for 48 hours in the lab oven, weighted, grounded to a particle size < 2 mm, and bulked in groups of four samples to get enough material for analysis (groups were made with plots close to each other, the same forest type and similar altitude). The grounded root, litter and soil samples were analyzed for organic C with the Walkley-Black method (Walkley and Black, 1934) in an external lab (Nutrilab, Rey Juan Carlos I University).

Calculating Carbon stock

We calculated the carbon stored in six different forest compartments: 1) aboveground biomass of trees (AG trees), 2) aboveground biomass of shrubs (AG shrubs), 3) roots, 4) litter, 5) topsoil (0–10 cm) and 6) deep soil (10–30 cm). The amount of carbon stored in AG trees and coarse tree roots was calculated with tree height and basal area using species- and region-specific biomass equations and species-specific carbon fraction (Gertrudix et al. 2012; Montero et al. 2005; Ruiz-Peinado et al. 2011). Carbon in AG shrubs was estimated from shrub cover and mean height of both shrub layers. We first calculated aboveground shrub biomass/ha using shrub-type specific equations described in Montero et al. (2020), and then transformed biomass into carbon using the carbon concentration of the corresponding shrub type reported by Montero et al. (2020). The root fraction included the total amount of roots of shrubs and trees (collected with the soil samples) and coarse roots from trees (assessed from biomass equations, see below). Litter included all debris found on the forest floor, mostly shed leaves, but also twigs, acorns, etc. SOC has not a widely agreed upon definition and can contain a wide range of organic carbon components (Kimble et al. 2000). In our study, we considered SOC as all organic carbon stored belowground in the soil fraction smaller than 2 mm (e.g., micro-organisms, fungi and fine-particulate dead organic matter). Roots that pass through a 2 mm sieve were also included in SOC, while any larger roots were assigned to the root pool. The carbon stored in soil roots, litter and soil was estimated with the

results of the carbon fraction analysis. Carbon content of each fraction was estimated per plot and then extrapolated to Mg of C per ha.

Statistical analysis

We compared the amount of carbon stored in forest plots between *Pinus* and *Quercus* forests using linear models (*lm* function in R). The dependent variables were total carbon per ha, and carbon in each compartment (AG trees, AG shrubs, Roots, Litter, 0–10 cm soil and 10–30 cm soil) in Mg of C/ha (one separate model for each variable). Apart of plot type (*Quercus*/*Pinus*), we also included tree basal area of the plot (m^2/ha) as independent variable to control for the effect of tree density and size on carbon storage, and slope (°) as environmental variables that may affect the C stock. We also included the interaction between basal area and plot type to check whether the carbon storage increases with tree density at the same rate in both forest types. We finally excluded orientation of slope from the analysis because most of the plots show a similar value (from Northeast to Southeast) and a preliminary analysis revealed no effect of this factor. Normality of residuals were checked using Shapiro test. All statistical analyses were conducted using R 3.5.1. Software (R Core Team 2019).

Results

Quercus plots have lower mean tree height, higher tree density, thinner stems and lower basal area than *Pinus* plots (Table 2). On average, the total carbon stored by *Quercus* plots (102.16 Mg of C/ha) was higher than that of *Pinus* plots (78.04 Mg of C/ha) (Figs. 2 and 3a), but this trend varied across forest compartments due to the different allocation patterns between plot types (Fig. 2). We found a much higher proportion of carbon in the AG trees compartment of *Pinus* forests (53%) than in *Quercus* plots (34%). However, within *Quercus* plots there was a higher proportion of carbon in soil (31% vs 25%), and roots (25% vs 16%), *Quercus* plots storing almost twice the amount of root carbon (25.2 Mg/ha) compared to *Pinus* plots (12.8 Mg/ha). A slightly higher proportion of carbon stored in the soil appeared in the upper soil (0–10 cm) in *Quercus* forest (19%) than in *Pinus* (17%). The undercanopy of most *Quercus* plots was densely covered by shrubs (Table 2), while the shrub layer in *Pinus* plots was often absent. Consequently, the shrub layer accounted for 6% of the total carbon found in *Quercus* plots, but only 2% in *Pinus* plots. Litter accounted for 4% of total carbon for both *Quercus* and *Pinus* plots (Fig. 2).

Table 2
Variables defining the vegetation structure of all 24 study plots (P = *P. halepensis* plots, Q = *Q. ilex* plots).

Plot	Dominant tree Species	Basal area (m^2/ha)	Tree density	Mean (± SD) tree height (M)	Shrub < 1 M cover (%)	Shrub > 1 M cover (%)
Q1	*Q. ilex*	6.29	707	5.2 ± 0.43	41.8	24.6
Q2	*Q. ilex* / *Q. faginea*	7.11	2034	6.5 ± 1.58	32.4	26.2
Q3	*Q. ilex*	15.71	1415	5.2 ± 0.77	45.2	34.3
Q4	*Q. ilex*	11.96	700	6.1 ± 1.49	45.0	15.6
Q5	*Q. ilex* / *Q. faginea*	5.73	585	4.1 ± 0.50	48.7	37.7
Q6	*Q. faginea*	10.25	1104	4.7 ± 1.14	13.5	31.4
Q7	*Q. ilex*	13.42	828	5.7 ± 1.39	4.8	4.6
Q8	*Q. ilex*	18.05	700	9.0 ± 2.14	20.7	0
Q9	*Q. ilex*	14.54	1429	5.6 ± 0.95	100	0
Q10	*Q. ilex*	24.75	2165	5.8 ± 1.41	79.5	0
Q11	*Q. ilex*	27.86	2829	5.6 ± 1.37	5.7	32.4
Q12	*Q. ilex*	32.85	2292	5.0 ± 0.82	7.3	32.4
P1	*P. halapensis*	29.92	650	10.8 ± 1.76	19.3	0
P2	*P. halapensis*	27.94	1039	11.6 ± 1.21	14.4	0
P3	*P. halapensis*	24.19	844	13.5 ± 2.11	24.0	25.0
P4	*P. halapensis*	18.16	585	10.7 ± 0.93	22.7	4.0
P5	*P. halapensis*	21.24	585	10.0 ± 1.47	20.0	0
P6	*P. halapensis*	31.53	707	13.7 ± 3.39	10.1	0
P7	*P. halapensis*	23.23	715	10.2 ± 2.88	0	0
P8	*P. halapensis*	20.24	585	10.6 ± 0.75	2.8	10.9

Plot	Dominant tree Species	Basal area (m^2/ha)	Tree density	Mean (± SD) tree height (M)	Shrub < 1 M cover (%)	Shrub > 1 M cover (%)
P9	*P. halapensis*	20.90	585	11.4 ± 1.13	6.7	0
P10	*P. halapensis*	20.24	650	9.8 ± 0.91	0	4.5
P11	*P. halapensis*	33.38	973	9.6 ± 1.19	11.1	0
P12	*P. halapensis*	24.28	585	11.0 ± 1.11	29.2	4.1

The range of basal area in *Quercus* plots (5.73–32.85 m^2/ha) was wider than that of *Pinus* plots (18.16–33.38 m^2/ha). Accordingly, the variation range of total carbon in *Quercus* plots was also wider (64.9 to 176.5 Mg of C/ha) compared to the *Pinus* plots (58.0 to 119.9 Mg of C/ha) (Fig. 3a). Total forest carbon increased significantly with basal area for both *Quercus* and *Pinus* forests in all fractions, except for AG shrubs and soil (Table 3, Fig. 3d, f, g and h). Carbon in AG shrubs decreased significantly with tree basal area for both plot types (Table 3, Fig. 3d) and no clear trend was found for soil carbon ($p > 0.10$) (Table 3, Fig. 3f, g and h). In all cases, except soil, the regression line for *Quercus* forests was above that of *Pinus* forests (significant effect of forest type, Table 3), which means that, for the same tree basal area, the amount of C was larger for *Quercus* plots. The regression lines of both forest types were parallel in most cases, but carbon in roots increased with basal area much faster in *Quercus* than that in *Pinus* plots (Fig. 3c, see the significant interaction in Table 3). Slope only affected the carbon pool of roots, which slightly decreased with increasing slope (Table 3).

Table 3
Results of the linear models assessing the effect of basal area, plot type (*Pinus* vs. *Quercus*), and slope on the carbon pool of total and each ecosystem fraction. Coefficients and significances are shown.

Fraction	Basal area		Plot type		Slope		Plot type x Basal area	
Total	3.58	***	60.74	***	-0.80	NS	-0.52	NS
AG tree	2.03	***	9.33	***	0.23	NS	0.21	NS
AG shrubs	-0.07	**	5.06	**	0.07	NS	-0.02	NS
AG total	1.96	***	14.38	***	0.30	NS	0.19	NS
Litter	0.16	*	1.91	**	-0.09	NS	-0.00	NS
Roots	0.58	***	0.81	***	-0.23	***	1.01	**
Total soil	0.89	NS	43.64	NS	-0.79	NS	-1.72	NS
Soil 0–10	0.49	NS	21.17	NS	-0.22	NS	-0.74	NS
Soil 10–30	0.39	NS	22.47	NS	-0.56	NS	-0.98	NS

NS: $P > 0,05$; *: $0,05 \geq P > 0,01$; **: $0,01 \geq P > 0,001$; ***: $P < 0,001$

Discussion

Quercus forests versus Pinus plantations

This study aimed at assessing and comparing the carbon stock between coexisting native coppice *Quercus* forests and *P. halepensis* plantations of similar aboveground age, considering both above and belowground compartments. Overall, we found higher total carbon per ha in *Quercus* forests than in *Pinus* plantations (also after accounting for the effect of forest basal area). When the carbon stock was analysed in separated compartments, the gross C content in AG trees seemed higher in *Pinus* plantations (Fig. 2) due to the larger size (basal area and tree height) attained by pine trees. Indeed, *P. halepensis* grow faster than both *Quercus* species (Cañellas et al. 2008; Montero et al. 2002). However, when this value was relativized to a common basal area, C stock in AG trees was higher in *Quercus* forests, probably due to the higher wood density of *Quercus* trees (888–914 kg/m^3) compared to *Pinus halepensis* (500–630 kg/m^3) (Hevia et al. 2020; Sousa et al. 2021). For most of the remaining fractions, C stock tended to be larger in *Quercus* forests (both gross and per-basal area values) mostly for roots and AG shrubs. The lack of a well-developed shrub layer in most *Pinus* plots may be attributed to the negative effect of *P. halepensis* afforestation on undercanopy radiation, on soil moisture, and to the thick layer of needles, which hampers both the arrival and the germination of shrub seeds (Bellot et al. 2004; Navarro-Cano et al. 2010). We also observed a lack of recruitment of *P. halepensis*, which may be attributed to *P. halepensis* cones being serotinous and mainly opening after a fire (Mauri et al. 2016), and to its litter

showing possible auto allelopathy, preventing the growth and establishment of its own species (Fernandez et al. 2008). By contrast, *Quercus* forests usually have a layer of young trees ready to replace older individuals. This difference in self-regeneration potential adds uncertainty about the potential of *Pinus* plantations as carbon sink in the long term.

We found large differences in the proportion of carbon allocated to roots, which was larger in *Quercus* than in *Pinus* plots. This difference can have large effects on the residence time of the stored carbon. Many re-sprouting species evolved in regions with frequent disturbances, such as grazing or fire, allocate a relatively large amount of their biomass, and so their carbon, to the portion of the plants better protected against disturbances. This is in many cases the roots, where the soil protects plant tissues from disturbances and stored carbon (Langley et al. 2002). Therefore, roots are in many cases a more reliable and stable long-term carbon storage compared to aboveground mass. *Q. ilex* and *Q. faginea* have higher root:shoot ratio than *P. halepensis*, and multi stemmed *Q. ilex* individuals may have root:shoot ratios of more than one 1 (Canadell and Rodà, 1991; Gertrudix et al. 2012; Ruiz-Peinado et al. 2011). Thus, although both *P. halepensis*, *Q. ilex* and *Q. faginea* are well adapted to wildfires and can regenerate quickly after fire (*Quercus* species by re-sprouting and *P. halepensis* by massively seeding and fast germination (Broncano et al. 2005)), *Quercus* forests are a more reliable long-term carbon storage in fire-prone areas.

Given that roots are an important source of organic carbon to the soil (Jackson et al. 2017), it was expected that *Quercus* plots, with almost twice the amount of carbon stored in roots, would also have more carbon in soils. Also, the decomposition rate of leaf litter, and thus the rate of carbon release into the soil, was expected to be higher in *Quercus* plots according to the lower C:N ratio reported in both *Q. ilex* and *Q. faginea* litter, as compared to *P. halepensis* (Bueis et al. 2018; Baldantoni et al. 2011; Fioretto et al. 2005). This hypothesis was also supported by a previous study in Spain that concluded that the introduction of *P. halepensis* in native shrubland resulted in the decrease of SOC (Maestre and Cortina, 2004). However, we found that, although the gross carbon stock in soils was slightly higher in *Quercus* plots (see Fig. 2), when it was standardized to a common basal area, there were no significant differences between plot types (Table 3). A potential explanation to this unexpected result may be that the rate of carbon release from roots (particularly fine roots) to the soil might be higher in *Pinus* plots, as fine roots may represent a relevant source of carbon to the soil (Lukac, 2012). Unfortunately, this information is unknown. We cannot rule out some sampling error when calculating soil bulk density due to the use of a soil auger to obtain a known volume of deep soil. This instrument is less precise than a soil cylinder, but the stoniness of soil prevented us to use cylinders for collecting deep soil. Finally, unlike the rest of the fractions, plot basal area was unrelated to soil carbon stock (Table 3). In the case of coppice *Quercus* plots, this indicates that the plots with small basal area may still have a large soil carbon content due to the presence of older roots that remain in the soil since centuries ago. In the case of *Pinus* plot, there is a slight positive trend between soil carbon stock and plot basal area, mainly in the top soil (Fig. 3f).

The different carbon stock and carbon allocation pattern between forest compartments reported here may be partly attributed to the different life strategy between the dominant taxa (pioneer *Pinus* vs. late-

successional *Quercus*), but also to differences in tree age (mainly in the root system) and to the different history of human management. Coppicing may exacerbate the allocation of carbon towards roots as compared to non-coppice *Quercus* forests (Cotillas et al. 2016). In addition, coppice forests may present a poor aboveground growth due to the high density of the stands, which results in a strong intraspecific competition (Vayreda et al. 2012; Ruiz-Peinado et al. 2017). The soil preparation labours during the plantation of pines probably had a profound effect on soil carbon and other properties (Garcia-Franco et al. 2014; Wang et al. 2016), although the legacy effect of such management on soil carbon is not known. Unfortunately, our study system does not allow us to tease apart the effects of tree age, human management (coppicing, soil preparation for plantation) and tree species, as these factors are not independent from each other.

Resilience of carbon stock and recommendations for management

Natural disturbances can lead to large decreases in stored carbon in forests and can even turn forests from carbon sinks to carbon sources (Kurz et al. 2008). Therefore, the forests resilience against these disturbances is very important. Two major threats for forest stability in the Mediterranean area are fire and droughts. *P. halepensis*, *Q. ilex* and *Q. faginea* are all well adapted to wildfires, as explained above. However, fire proneness seems to be much higher in *Pinus* than in *Quercus* forests, and *Q. ilex* was shown to be more resistant to fire than most conifers (Silva et al. 2009). An additional advantage of *Quercus* forests suggested by our results is their larger C pool stored underground, which is more protected against fire than the *Pinus* plantation's C pools. Another common natural disturbance in the Mediterranean area are droughts. Although the study species are well adapted to summer drought, climate change models predict that seasonal droughts will increase in severity (IPCC, 2021). Thanks to its deeper and massive root system, *Q. ilex* is expected to be better adapted than *P. halepensis* for coping with extreme drought (Ferrio et al. 2003; Cotillas et al. 2016). A reduction in growth is expected in both *P. halepensis* and *Q. ilex*, however *P. halepensis* will likely be affected more severely (Didier, 2010). Another natural disturbance with large effects on all forests in Europe are storms (Schelhaas et al. 2010). In general, it is accepted that even aged monoculture plantations, like the *P. halepensis* ones, are very susceptible to storm damage (Pawson et al. 2013). The *Pinus* plantations, with a much higher average height, catch a lot more wind compared to the shorter *Quercus* forests. Finally, the poor regeneration observed in *P. halepensis* stands, also contributes to predict less resilience of these plantations in the study area, given that *P. halepensis* only regenerates by seeds.

Beyond their higher capacity to store carbon in the long term, *Quercus* forests may have other benefits over *Pinus* plantation, such as fire prevention, higher contribution to soil fertility, or higher biodiversity (Silva et al. 2009; Gamfeldt et al. 2013; Castro-Díez et al. 2021). Altogether supports the recommendation of transforming *Pinus* plantations into mixed forests with late successional *Quercus* species, by using the planted pines as nurse plants. This mixed forest may take advantage of the benefits of fast-growing

Pinus (fast aboveground growth) and the resilient *Quercus* (long lifespan, many roots) and results in a more diverse forest (Pausas et al. 2004).

Conclusion

We found that coppice *Q. ilex* forests in La Alcarria region of central Spain stored more carbon compared to *P. halepensis* plantations, mostly in underground compartments, where it is more resilient against many natural disturbances. By contrast, *P. halepensis* plantations store more carbon in the aboveground, thanks to the larger size attained by trees, and despite the lower wood density of this species. The human management history of these two forest stands (coppicing and plantation) may have contributed to exacerbate the difference in the carbon allocation pattern between both forest types. Thus, beyond other benefits, *Q. ilex* forests are also better suited for long-term storage of carbon than *P. halepensis* plantations. Therefore, it can be very beneficial to turn *P. halepensis* plantations into a more diverse forest by planting late successional *Quercus* species under the canopy.

Declarations

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Competing interests

We have no conflicts of interest to disclose.

Availability of data and material

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability

The R code is available from the corresponding author on reasonable request.

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Authors contribution

The study conception was performed by Pilar Castro-Díez and Álvaro Alonso. All authors contributed to the design, and field sampling. Processing of field samples was performed by Bram van den Bor. The first draft of the manuscript was written by Bram van den Bor and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

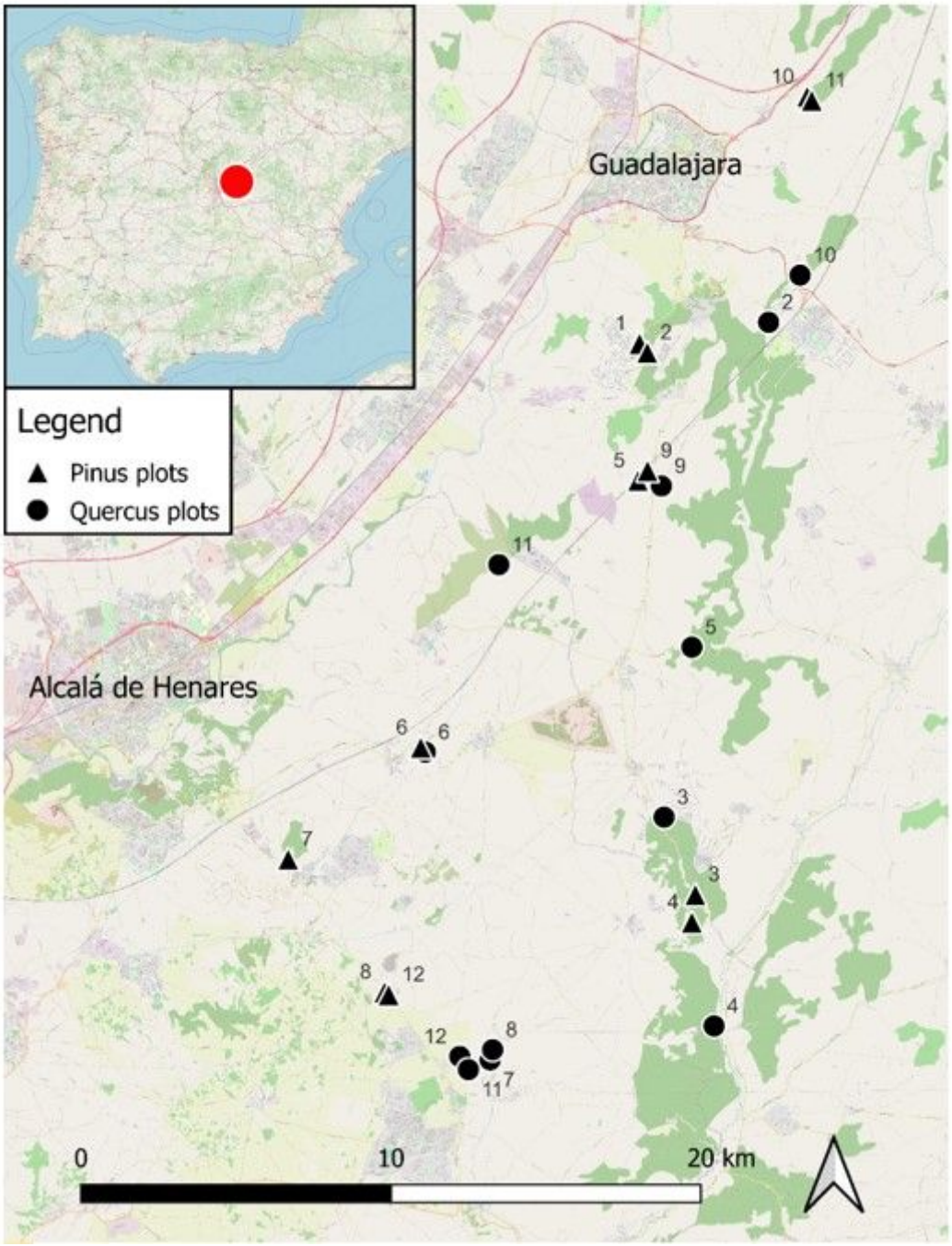


Figure 1

Map of the sampling area with all *Pinus*and *Quercus* plot locations.

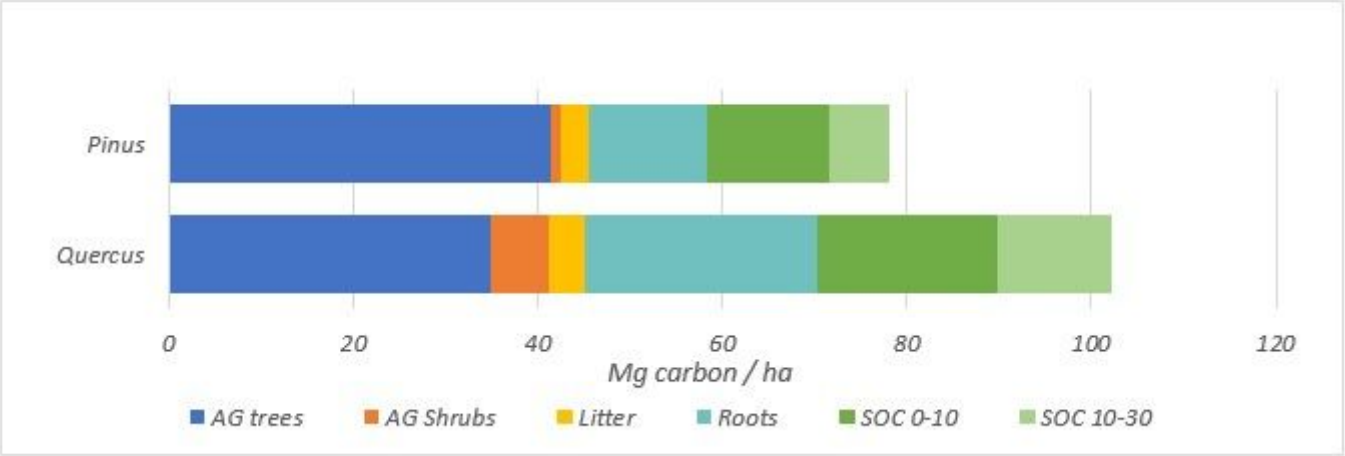


Figure 2

Average carbon allocation of *Quercus* and *Pinus* plots between the different forest compartments in Mg/ha. AG- aboveground, SOC- soil organic carbon.

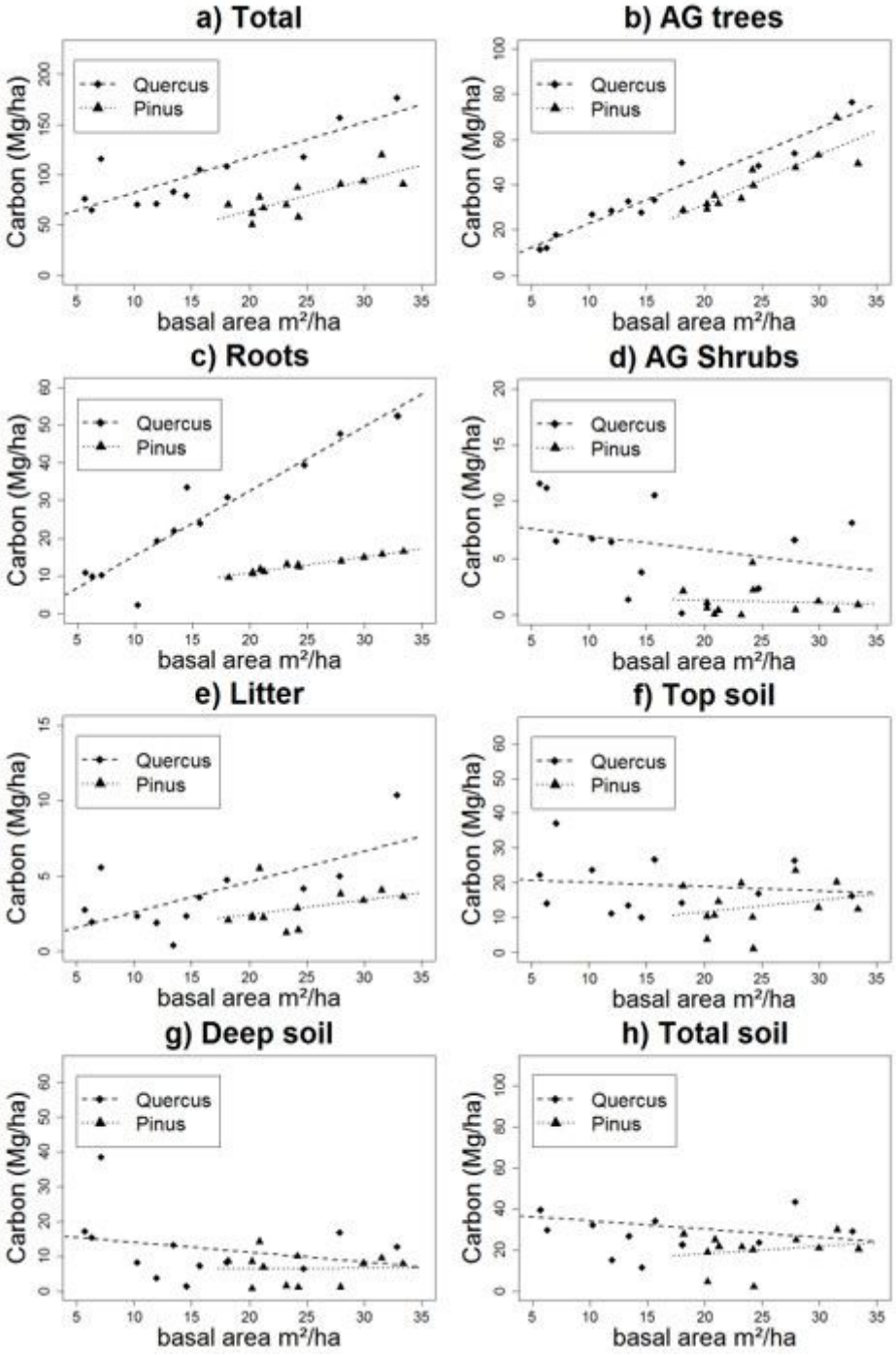


Figure 3

Total forest carbon pool (panel a) and carbon in each forest compartment (panel's b-h) plotted against tree basal area of the plot. The dashed line and diamonds correspond to *Quercus* forests, while the dotted lines and triangles correspond to *Pinus*stands.