

## RESEARCH ARTICLE

# Quantifying carbon storage and sequestration by native and non-native forests under contrasting climate types

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## Abstract

Non-native trees may have significant impacts on the carbon sink capacity of forested lands. However, large-scale patterns of the relative capacity of native and non-native forests to uptake and store carbon remain poorly described in the literature, and this information is urgently needed to support management decisions. In this study, we analyzed 17,065 plots from the Spanish Forest Inventory (covering c. 30 years) to quantify carbon storage and sequestration of natural forests and plantations of native and non-native trees under contrasting climate types, while controlling for the effects of environmental factors (forest structure, climate, soil, topography, and management). We found that forest origin (non-native vs. native) highly influenced carbon storage and sequestration, but such effect was dependent on climate. Carbon storage was greater in non-native than in native forests in both wet and dry climates. Non-native forests also had greater carbon sequestration than native ones in the wet climate, due to higher carbon gains by tree growth. However, in the dry climate, native forests had greater carbon gains by tree ingrowth and lower carbon loss by tree mortality than non-native ones. Furthermore, forest type (classified by the dominant species) and natural forests versus tree plantations were important determinants of carbon storage and sequestration. Native and non-native *Pinus* spp. forests had low carbon storage, whereas non-native *Eucalyptus* spp. forests and native *Quercus* spp., *Fagus sylvatica*, and Eurosiberian mixed forests (especially not planted ones) had high carbon storage. Carbon sequestration was greatest in *Eucalyptus globulus*, *Quercus ilex*, and *Pinus pinaster* forests. Overall, our findings suggest that the relative capacity of native and non-native forests to uptake and store carbon depends on climate, and that the superiority of non-native forests over native ones in terms of carbon sequestration declines as the abiotic filters become stronger (i.e., lower water availability and higher climate seasonality).

## KEYWORDS

carbon sequestration, carbon storage, *Eucalyptus camaldulensis*, *Eucalyptus globulus*, National Forest Inventory, *Pinus radiata*, temporal trends, tree plantation

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## 1 | INTRODUCTION

Forest ecosystems cover large extents of land worldwide (31% of the total land area in 2020) and contain the majority of the Earth's terrestrial carbon stocks, playing a pivotal role in the global carbon cycle (Dixon et al., 1994; FAO, 2020; Harris et al., 2021; Pan et al., 2011). Under the growing worldwide concern about global climate change, large-scale tree plantation programs are being promoted by public entities and other parties (e.g., the European “3 Billion Tree Planting Pledge For 2030” or the international “Bonn Challenge”). These programs may target native tree species, but also fast-growing non-native trees for carbon storage and wood production (Brundu & Richardson, 2016; Castro-Díez et al., 2019). Although the potential of forests to store carbon is often calculated based on the growth rate of dominant species, it also depends on other factors that are often neglected, such as tree longevity, durability of wood products, and resistance and resilience of trees against disturbances or extreme climatic events (Ennos et al., 2019; Nuñez et al., 2021; Suryaningrum et al., 2022). These key variables may widely vary across tree species, and particularly between native and non-native trees.

Tree species inherently differ from each other in their resource-use strategy, which ultimately affects forest carbon storage (i.e., carbon stock per area unit) and carbon sequestration (i.e., carbon accumulated per area and time unit). Resource-use strategies span from acquisitive to conservative, that is, from rapid resource capture and growth to slow growth, long life, and high investment in storage and defense (Díaz et al., 2016; Wright et al., 2004). Many non-native tree species used in forest plantations follow the acquisitive strategy and have been selected to produce timber, despite occasionally growing under suboptimal environmental conditions (Brundu & Richardson, 2016; Castro-Díez et al., 2019; Serrada et al., 2008). A higher dominance of the acquisitive strategy in forests could decrease their long-term carbon sequestration capacity (i.e., non-native trees used in plantations may have high carbon sequestration rates and relatively low carbon durability; Dyderski & Jagodzinski, 2019; Hughes et al., 2014; Montero et al., 2005). Consequently, the promotion of non-native tree plantations may have profound impacts on the carbon cycle and carbon sink capacity of forested lands.

Beyond forest species composition, carbon storage and sequestration are influenced by multiple factors related to forest structure, climate, soil, and human management (Ruiz-Benito, Gómez-Aparicio, et al., 2014; Ruiz-Benito, Madrigal-González, et al., 2014; Ruiz-Peinado et al., 2017; Vayreda et al., 2012). Previous research has shown that forest structural variables, such as tree size and tree density, are major determinants of carbon sequestration (Roces-Díaz et al., 2021; Ruiz-Benito, Gómez-Aparicio, et al., 2014; Ruiz-Benito, Madrigal-González, et al., 2014; Vayreda et al., 2012). Abiotic conditions, including climatic and soil variables, are also important drivers of carbon accumulation due to their direct influence on resource availability (e.g., light, water, and nutrients) (Gurevitch et al., 2002; Vayreda et al., 2012). Disturbances, including human management, may also affect carbon sequestration by altering the forest structure

and demography of target species, such as survival, growth, and recruitment (Hua et al., 2022; Lázaro-Lobo, Ruiz-Benito, Lara-Romero, et al., 2022; Ruiz-Peinado et al., 2017).

Forest plantations represent c. 7% of the land occupied by forest ecosystems (FAO, 2020). The management associated with forest plantation (e.g., soil preparation, removal of understory vegetation) may affect the capacity of forests to store and sequester carbon (Hua et al., 2022; Liao et al., 2010). In Spain, forest plantations represent c. 18% of forested land and were specially promoted between the 1950s and 1970s due to the increasing demand for timber and pulp, and for soil protection (Guiral et al., 2019; Madrigal, 1998; Montero, 1997; Serrada et al., 2008). Plantations involved both native and non-native tree species, the latter are estimated to cover 6.2% of the Spanish woodlands, but to produce 58.8% of the harvested wood (Castro-Díez et al., 2016). Most non-native tree plantations in Spain occur in areas with temperate climate, which is characterized by a relatively high rainfall across the entire year, promoting high tree productivity. However, some tree plantations have been abandoned due to socioeconomic changes and limited productivity (especially in dry Mediterranean areas, where forests have lower potential for carbon uptake in terms of tree biomass) (Ruiz-Benito, Gómez-Aparicio, et al., 2014; Ruiz-Benito, Madrigal-González, et al., 2014; van der plas et al., 2018; Villar-Salvador, 2016). Given that plantations can play a key role in providing ecosystem services, such as climate regulation, this opens a debate regarding their future management. Thus, information of the relative capacity of native forests and non-native tree plantations to uptake and store carbon is urgently needed to support management decisions.

National forest inventories are a key tool for monitoring forest structure and dynamics at large spatial and temporal scales (Chirici et al., 2011; Lázaro-Lobo, Ruiz-Benito, & Castro-Díez, 2022). These inventories can be used to assess the amount of carbon stock per unit of forest area (carbon storage;  $\text{Mg C ha}^{-1}$ ) and the changes of carbon stock between consecutive inventories (carbon sequestration;  $\text{Mg C ha}^{-1} \text{ year}^{-1}$ ) (González-Díaz et al., 2019; Ruiz-Benito, Gómez-Aparicio, et al., 2014; Ruiz-Benito, Madrigal-González, et al., 2014). National forest inventories have been previously used to assess carbon dynamics in European forests (Gómez-García, 2020; Mateos et al., 2016; van der Plas et al., 2018; Vayreda et al., 2012). However, a comprehensive study that compares carbon storage and sequestration of multiple native and non-native forests at the national scale is lacking in the literature.

In this study, we quantified carbon storage and sequestration of the most common forest types through available information from the Spanish National Forest Inventory, covering natural forests and plantations of native and non-native trees. We aimed to test whether carbon storage and sequestration (total and its components, i.e., gains by adult tree growth and juvenile-to-adult transition, and losses by mortality) are affected by (1) forest origin (native vs. non-native), climate type (wet vs. dry climate), and their interaction, while controlling for the effects of forest structure, abiotic factors, and tree cutting; (2) forest type (classified by the dominant species); and (3) whether the forests were planted or natural. The

latter was included to separate the effects of forest plantations and the effect of forest origin, given that all non-native forests considered were planted. In this study, we tested two hypotheses. First, we hypothesized that carbon storage and sequestration would differ between native and non-native forests, with climate driving the magnitude of the difference. Given that non-native tree taxa in Spain have been selected for their rapid growth and large size (Serrada et al., 2008), we expected a higher carbon storage and sequestration in non-native forests, as native ones are composed by trees representing a wider range of functional strategies, from pioneer fast-growers to late-successional slow-growers. We also expected that the difference in carbon storage and sequestration between native and non-native forests would be greater in wet environments (i.e., higher water availability and lower climate seasonality) due to a higher resource availability, which allows for faster and higher tree growth. The second hypothesis was that forest type and the planted character would have a significant influence on carbon storage and sequestration. We expected a high variability in carbon storage and sequestration within non-native and native forest types, resulting from inherent characteristics of the dominant species. We also expected that, within the same native forest type and climate type, tree plantations would store less carbon than natural forests, because plantations with native species were generally conducted on poor soils to prevent erosion and at high tree densities without posterior management, which may increase competition for resources, decreasing diameter growth of individual trees (Ruiz-Benito et al., 2012; Vadell et al., 2016; Villar-Salvador, 2016).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

We studied forested areas of peninsular Spain (i.e., forest cover >5%; Villaescusa & Díaz, 1998). There are two major macrobioclimates in Spain: the temperate and the Mediterranean (Rivas-Martínez et al., 2002). The temperate climate occurs in northern Spain and in mountainous areas of central Spain, and it is characterized by moderate/high rainfall spread across the year (Capel Molina, 2000; Loidi, 2017). The Mediterranean climate occurs in the rest of Spain and it is characterized by a period of aridity (evapotranspiration > precipitation) of at least 2 months in summer and most rainfall occurring in spring and autumn (Capel Molina, 2000; Loidi, 2017; Figure 1).

Spanish forests range from productive monospecific plantations to diverse natural communities, and occur across a wide variety of climatic, edaphic, and topographic situations (Blanco-Castro, 1997; Kottek et al., 2006; Lázaro-Lobo, Ruiz-Benito, Lara-Romero, et al., 2022). In areas with temperate climate, non-native tree plantations are mainly formed by *Eucalyptus globulus* (~325,000 ha) and *Pinus radiata* (~280,000 ha) (Serrada et al., 2008). By contrast, in dry Mediterranean areas, the most planted non-native tree is *E. camaldulensis* (~105,000 ha), as its drought tolerance allows it to prosper in

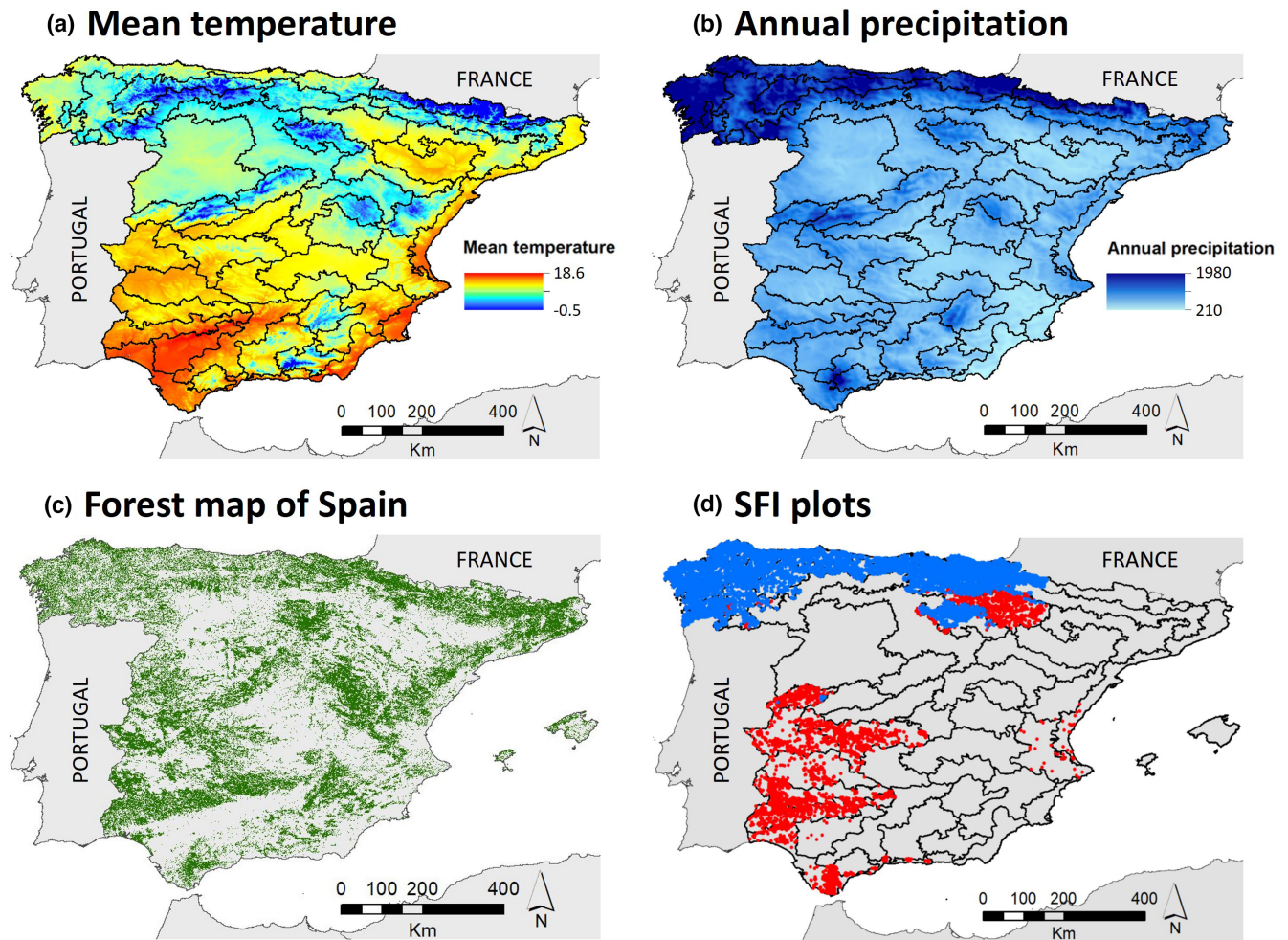
a wide range of rainfall regimes (i.e., from 250 to 1500 mm annual precipitation; Hirsch et al., 2020; Serrada et al., 2008).

### 2.2 | National Forest Inventory data to calculate carbon storage and sequestration

We extracted forest structure data from the second (1986–1996), third (1997–2007), and fourth (2008–2017) Spanish National Forest Inventory (SFI) datasets (2SFI, 3SFI, and 4SFI, respectively). The SFIs are extensive surveys consisting of circular sample plots distributed on a 1 km<sup>2</sup> grid-cell network across the forested surface of Spain, which are sampled approximately every 10 years (Lázaro-Lobo, Ruiz-Benito, Lara-Romero, et al., 2022; Villaescusa & Díaz, 1998). Each SFI plot consists of four circular concentric subplots of 5, 10, 15, and 25 m radius where each adult tree is measured depending on their diameter at breast height (DBH) (in the concentric subplot of 5-m radius, trees are measured when DBH ≥ 7.5 cm; in the 10-m circle when DBH ≥ 12.5 cm; in the 15-m circle when DBH ≥ 22.5 cm; and in the 25-m circle when DBH ≥ 42.5 cm) (Alberdi et al., 2017). Tree data include DBH, tree height, species identity, and tree status (alive or dead) (Lázaro-Lobo, Ruiz-Benito, Lara-Romero, et al., 2022). We used this information for calculating carbon storage and also sequestration by comparing consecutive surveys in the same plots (see Section 2.3). The estimation of carbon sequestration was limited to 10 of 15 regions where the 4SFI was available and covered the climatic gradient in peninsular Spain.

Based on forest classifications made by Blanco-Castro (1997), the SFI, and the Spanish Forest Map, we classified the SFI plots into 39 forest types according to the dominant species (three dominated by non-native species (*P. radiata*, *E. globulus*, and *E. camaldulensis*) and 36 dominated by native species; Table S1). We considered a plot to be dominated by a species when its basal area represented ≥ 50% of the stand basal area. Plots could also be dominated by several tree species (mixed forests), when none of the dominant species accounted for ≥ 50% of the stand basal area by themselves. To avoid confounding effects between the environment and forest origin (native vs. non-native), we explored plot distribution of each forest type through eco-regions (i.e., ecologically homogeneous environmental units) and discarded eco-regions lacking non-native forest types (< 10 plots of any non-native forest type). We used as eco-regions the “regions of provenance” of tree species in Spain delineated with the divisive method (see <https://www.miteco.gob.es/>; Elena-Rosselló & Castejón-Ayuso, 1996), retaining 19 eco-regions with enough sample size of native and non-native forest types from the Spanish forest inventory.

Within the selected eco-regions and forest types, we subsequently selected SFI plots that met the following eligibility criteria: (1) ≥ 50% of the stand basal area belongs to the dominant species of each selected forest type; (2) plots with ≥ 50% of tree canopy cover; and (3) ≥ 90% of the stand basal area belongs to tree species with available biomass equations (i.e., those that allowed us to calculate carbon from tree DBH and height). We found biomass equations



**FIGURE 1** (a) Mean annual temperature and (b) annual precipitation in the study area (continental Spain) between 1981 and 2010 from CHELSA database (Karger et al., 2017). (c) Forested areas (from Spanish Forest Map, available at <https://www.miteco.gob.es/>). (d) Location of the Spanish Forest Inventory (SFI) plots available in this study. Blue and red dots indicate SFI plots classified as wet and dry climates, respectively (see Section 2.5). The black lines within Spain refer to eco-regions (Spanish regions of provenance delineated with the divisive method; from <https://www.miteco.gob.es/>).

developed in Spain for 40 tree taxa (Table S2), which are the most representative taxa in Spanish forests.

### 2.3 | Quantifying carbon storage and sequestration

For each individual tree within SFI plots, we calculated above- and below-ground biomass by applying species-specific allometric equations obtained from different published studies (Table S2). Then, we calculated above- and below-ground carbon by multiplying biomass values by the specific carbon content of each species (Table S2). We calculated carbon storage per hectare using the plot radius in which each tree was sampled and, then, we calculated carbon storage at plot level by summing carbon of all living trees in each plot ( $\text{MgCha}^{-1}$ ).

Carbon storage was computed for each SFI (2SFI, 3SFI, and 4SFI;  $\text{MgCha}^{-1}$ ), whereas carbon sequestration was calculated among consecutive SFIs (2–3SFI and 3–4SFI;  $\text{MgCha}^{-1}\text{year}^{-1}$ ), by subtracting

the carbon stored in the second survey of the comparison to the carbon stored in the first survey. We also quantified the components of carbon sequestration: (1) tree growth as the carbon gain due to the growth of adult living trees; (2) tree ingrowth as the carbon gain due to the transition from juveniles to adults (i.e., new trees with  $\text{DBH} \geq 7.5$  cm) in the 5-m radius subplot; and (3) tree loss as the carbon loss due to dead trees, which was further divided into carbon loss by natural mortality and carbon loss due to tree harvesting (the percentage of plots with dead trees and signs of tree harvesting between 2–3SFI and 3–4SFI datasets was 44.9% and 51.2%, respectively).

### 2.4 | Environmental data (forest structure, abiotic factors, and management)

We obtained plot-level data regarding forest structure from each SFI, including canopy cover (%), tree density ( $\text{no. trees ha}^{-1}$ ), and stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ). For analyses regarding carbon sequestration,

we used the values from the initial consecutive inventory (2SFI for 2–3SFI and 3SFI for 3–4SFI), and for carbon storage the values of each inventory.

We compiled a broad representation of geospatially explicit environmental variables related to climate, topography, and soil that may influence carbon storage and sequestration. We obtained seven climatic variables informing about mean and extreme climate, as well as intra-annual variability from the Climatologies at High resolution for the Earth's Land Surface Areas (CHELSA) database, which comprises the average for the years 1981–2010 at 30 arc sec (~1 km) resolution (Karger et al., 2017): mean annual temperature, temperature seasonality (i.e., variation in temperature throughout the year), maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation; precipitation seasonality, and precipitation of driest quarter (June–August). We also calculated an index of water availability, which integrates temperature and rainfall (i.e., annual precipitation minus potential evapotranspiration divided by potential evapotranspiration) (Ruiz-Benito, Gómez-Aparicio, et al., 2014; Ruiz-Benito, Madrigal-González, et al., 2014; Vayreda et al., 2012). Digital elevation data at 90 m spatial resolution was downloaded from the Shuttle Radar Topography Mission (SRTM) database (<https://srtm.csi.cgiar.org/>), which was originally produced by NASA. Slope gradient (slope inclination in degrees) was derived from the elevation grid using ArcGIS 10.8.1 (ESRI). Lastly, we used the SoilGrids database (<https://www.isric.org/explore/soilgrids>) to extract soil properties at 250 m resolution. We selected soil properties related to nutrient and water-holding capacity, including percent of sand, silt and clay, coarse fragments (soil stoniness), cation exchange capacity (CEC), organic carbon, and pH.

We characterized each SFI plot with two variables related to human intervention: (1) occurrence of recent tree cutting; and (2) the identification of the plot as a planted or a natural forest. Tree plantations were identified using SFI data that recorded land uses and signs of mechanical site preparation for planting (i.e., soil excavation). We used the 3SFI and 4SFI datasets to discern between planted and natural SFI plots, because 2SFI followed a different method to identify planted plots. Moreover, we used the “regions of provenance” of forestry species in Spain (<https://www.miteco.gob.es/>) to identify old plantations that may not be registered in the SFI (see Ruiz-Benito et al., 2012). For analyses regarding carbon sequestration, we used the forest classification from the last of the consecutive inventories (3SFI for 2–3SFI and 4SFI for 3–4SFI), and for carbon storage the values of the 3SFI and 4SFI datasets.

## 2.5 | Classification of SFI plots in climate types

To assess whether the factors affecting carbon storage and sequestration varied between dry and wet climates, we grouped the selected SFI plots into two areas with contrasting climate types (Figure 1d), based on a principal component analysis (PCA) using climatic variables (Figure S1). This also allowed us to evaluate carbon storage

and sequestration of the most representative native and non-native forests growing in wet and dry climates, and to avoid confounding effects between climate and forest type (i.e., forest types growing in dry environments may store less carbon than forest types growing in wet environments). The first two PCA axes explained 76.8% of variation. The first axis correlated positively with water availability and negatively with climate seasonality, whereas the second axis correlated positively with variables related to air temperature (Figure S1; Table S3). The PCA analysis allowed us to group SFI plots into two areas with contrasting climate types (Figure 1). The first area roughly corresponded to the temperate climate (wet climate, hereafter) and had higher water availability and lower mean temperature and climate seasonality than the second area, which corresponded to the Mediterranean climate (dry climate, hereafter; Figure S2). We then calculated the number of plots corresponding to each non-native and native forest type within each area (wet vs. dry climate) and retained those forest types with at least 170 plots (Table S4). By doing so, we avoided the inclusion of forest types that are not representative of each climate type, and we ensured having enough replication to conduct statistical analyses.

We used a total of 17,065 permanent plots dominated by native and non-native tree species (13,344 and 3721 plots in wet and dry areas of Spain, respectively; Figure 1).

## 2.6 | Statistical analysis

To evaluate the effect of forest origin (native vs. non-native), climate type (wet vs. dry climate), and their interaction on carbon storage and sequestration (total and due to tree growth, juvenile-to-adult transition–ingrowth, and mortality), while controlling for the effects of environmental predictors (forest structure, abiotic factors, and tree cutting), we used generalized linear mixed models (GLMMs; objective 1). Then, in a separate analysis, we conducted GLMMs for each climate type to compare carbon storage and sequestration across the most representative forest types in each climatic area (wet vs. dry climates), controlling for the effects of environmental predictors (objective 2). Lastly, within a subset of plots with the same climate and forest type, we used GLMMs to evaluate the effect of tree plantation on carbon storage and sequestration in those forest types with a minimum of 50 planted and 50 natural plots (Table S5), controlling for the effects of environmental predictors (objective 3).

For the GLMMs, we tested linearity between each response and explanatory variable. We also tested collinearity among the potential environmental predictors with Pearson's correlations, and we retained those variables that were not highly correlated with each other (Pearson's  $r < .5$ ; sensu Dormann et al., 2013; Table S6). If two variables were correlated, we retained the variable that had the lowest Akaike information criterion (AIC) value to conduct the GLMMs (Akaike, 1974). As environmental predictors, we kept canopy cover, tree density, stand basal area, slope, mean temperature, water availability, sand, coarse fragments, CEC, and tree cutting. We standardized the numerical predictors to make the interpretation

of their effect sizes comparable (i.e., GLMM coefficient estimates; Magnusson et al., 2017; Schielzeth, 2010).

We used the “glmmTMB” R package (Magnusson et al., 2017) to build the GLMMs, following the guidelines for mixed models (Zuur et al., 2009). Carbon storage and sequestration (total and due to tree growth, juvenile-to-adult transition–ingrowth, and mortality) were evaluated with Gamma errors using the log-link function because, due to the skewness of their data distributions, model residuals were not normally distributed, and we obtained lower AIC values when compared to the models with Gaussian error distribution. We used SFI period (2SFI, 3SFI, and 4SFI for analyses regarding carbon storage; 2–3SFI and 3–4SFI for analyses regarding carbon sequestration) as a fixed factor and SFI plot as a random factor to account for observations of our response variables over multiple periods of time. We checked the goodness-of-fit of all the statistical models by plotting observed versus predicted values and model residuals versus predicted values. To analyze the effect of forest origin and forest type within each climate type on carbon storage and sequestration, we conducted post-hoc comparisons of estimated marginal means calculated using the “emmeans” R package (Lenth et al., 2018) with Bonferroni's adjustment, which is appropriate to declare statistical significance ( $p < .05$ ) in multiple-comparison testing analyses (Cabin & Mitchell, 2000; Lázaro-Lobo et al., 2021).

### 3 | RESULTS

#### 3.1 | Effects of forest origin, climate type, and their interaction on carbon storage and sequestration

Forest origin (i.e., native vs. non-native) had a significant effect on carbon storage (Table 1), with non-native forests having higher carbon storage in tree biomass than native forests in both wet and dry climates (Figure 2). However, the effect of forest origin on carbon sequestration differed with climate (wet vs. dry), as denoted by the significant effect of the interaction between forest origin and climate type (Table 1). Non-native forests had greater tree carbon sequestration than native forests in the wet climate, as a result of higher carbon gain by tree growth, and despite higher carbon loss by tree harvest (Figure 2; Figure S3). However, in the dry climate, non-native and native forests had similar carbon sequestration, despite the greater carbon gain by tree ingrowth and lower carbon loss by tree mortality (both natural and due to tree harvesting) in native than non-native forests (Figure 2; Figure S3). Climate type greatly contributed to carbon storage and sequestration, as forests of the wet climate stored and sequestered more carbon than those of the dry climate (Table 1).

Among the environmental predictors included in the models (forest structure, abiotic factors, and tree cutting), forest structure (especially stand basal area) had the highest effect on carbon storage and sequestration (Table 1; Tables S7 and S8). Stand basal area was strongly positively related to carbon storage and carbon

gain by tree growth, however, it negatively affected overall carbon sequestration due to the higher carbon loss by mortality and lower carbon gain by tree ingrowth in plots with higher stand basal area. In contrast, tree density had a negative effect on carbon storage and a positive influence on carbon sequestration (due to higher carbon gain by tree ingrowth). Canopy cover positively affected carbon storage, but not overall carbon sequestration, probably because plots with higher canopy cover had higher carbon loss due to tree harvest, thus compensating for the higher carbon gain by tree growth (see  $p$ -value and magnitude of the estimates in Table 1; Tables S7 and S8).

Carbon storage was greater in plots with higher water availability (Table 1). By contrast, carbon sequestration decreased with water availability due to higher carbon loss by tree mortality, and despite the higher carbon gain by tree growth (Table 1; Tables S7 and S8). Mean annual temperature negatively affected carbon storage, but positively affected carbon sequestration, whereas slope had no effect on carbon storage and sequestration (Table 1). Plots with higher sand and coarse fragment content exhibited lower carbon storage and sequestration due to lower carbon gain by tree growth and ingrowth (Table 1; Table S7). Carbon storage and carbon gain by tree growth decreased with soil CEC (Table 1; Table S7). Plots with signs of recent tree cutting exhibited lower carbon storage and sequestration (Table 1).

#### 3.2 | Effects of forest type on carbon storage and sequestration

Forest type was an important determinant of carbon storage and sequestration (Figure 3; Figures S4 and S5). In the wet climate, forests dominated by non-native *E. globulus* had higher carbon storage (c. 100 Mg ha<sup>-1</sup>) and sequestration (c. 40 Mg ha<sup>-1</sup> year<sup>-1</sup>) in tree biomass than most of the other forest types (Figure 3), because of higher carbon gain by tree growth, and despite higher carbon loss by tree mortality (Figures S4 and S5). Native forests dominated by *Quercus robur*, *Q. petraea*, and *Fagus sylvatica*, as well as Eurosiberian mixed forests, also had high values of carbon storage (c. 90–100 Mg ha<sup>-1</sup>) in the wet climate. However, among the native forests of the wet climate, carbon sequestration was higher in forests dominated by *Q. ilex* (c. 35 Mg ha<sup>-1</sup> year<sup>-1</sup>). *P. radiata*, the other widespread non-native species in wet areas of Spain, had low values of carbon storage (c. 50 Mg ha<sup>-1</sup>) and sequestration (c. 10 Mg ha<sup>-1</sup> year<sup>-1</sup>), despite having higher carbon gain by tree growth than native forests (Figure 3; Figure S4).

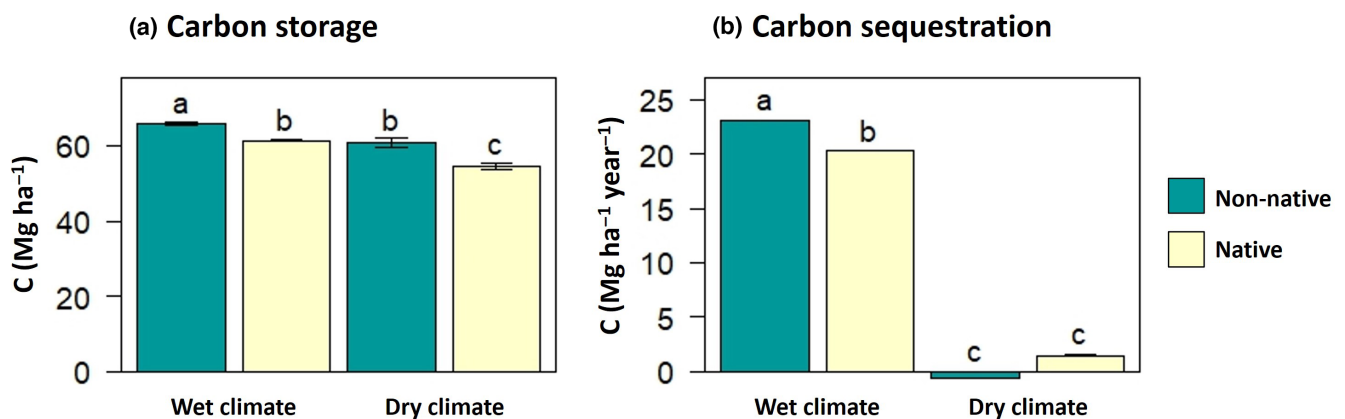
In the dry climate, tree carbon storage was the greatest in native forests dominated by *Q. ilex* (c. 45 Mg ha<sup>-1</sup>), followed by forests dominated by *E. globulus*, *E. camaldulensis*, and *Q. pyrenaica* (c. 40 Mg ha<sup>-1</sup>). However, carbon sequestration was higher in native forests dominated by *P. pinaster* (c. 10 Mg ha<sup>-1</sup> year<sup>-1</sup>). Non-native forests dominated by *E. camaldulensis* had low values of carbon sequestration in the dry climate due to low carbon gain by tree growth and ingrowth, and high carbon loss by mortality (Figure 3; Figures S4 and S5).

**TABLE 1** Summary of the generalized linear mixed models for analyses regarding the effect of forest origin (native vs. non-native), climate type (wet vs. dry), their interaction, and the selected environmental predictors (forest structure, abiotic factors, and tree cutting) on carbon storage and sequestration.

| Variable  | Carbon storage (Mg C ha <sup>-1</sup> ) |       |         |         | Carbon sequestration (Mg C ha <sup>-1</sup> year <sup>-1</sup> ) |       |         |         |
|---|---|-------|---------|---------|--|-------|---------|---------|
|   | Estimate                                | SE    | Z-value | p-Value | Estimate   | SE    | Z-value | p-Value |
| Intercept   | <b>3.90</b>                             | 0.013 | 303.4   | <.001   | <b>3.03</b>  | 0.048 | 63.68   | <.001   |
| Forest origin (=non-native)   | <b>0.11</b>                             | 0.019 | 5.71    | <.001   | -0.11  | 0.062 | -1.75   | .080    |
| Climate type (=wet climate)   | <b>0.12</b>                             | 0.015 | 8.09    | <.001   | <b>0.64</b>  | 0.056 | 11.56   | <.001   |
| Forest origin × Climate type  | -0.04                                   | 0.021 | -1.93   | .053    | <b>0.18</b>  | 0.067 | 2.64    | .008    |
| Forest structure  |   |       |         |         |  |       |         |         |
| Canopy cover  | <b>0.05</b>                             | 0.003 | 15.35   | <.001   | 0.00   | 0.010 | 0.31    | .755    |
| Tree density  | -0.01                                   | 0.003 | -3.44   | <.001   | <b>0.17</b>  | 0.011 | 16.14   | <.001   |
| Stand basal area  | <b>0.67</b>                             | 0.004 | 175.18  | <.001   | -0.33  | 0.011 | -31.04  | <.001   |
| Abiotic factors   |   |       |         |         |  |       |         |         |
| Slope   | 0.00                                    | 0.004 | 0.87    | .385    | -0.01  | 0.011 | -0.84   | .398    |
| Mean temperature  | -0.02                                   | 0.005 | -3.47   | <.001   | <b>0.06</b>  | 0.016 | 4       | <.001   |
| Water availability  | <b>0.06</b>                             | 0.004 | 13.33   | <.001   | -0.05  | 0.014 | -3.97   | <.001   |
| Sand  | -0.01                                   | 0.004 | -3.37   | <.001   | -0.07  | 0.012 | 5.47    | <.001   |
| Coarse fragments  | -0.02                                   | 0.004 | -5.35   | <.001   | -0.07  | 0.014 | -5.18   | <.001   |
| CEC   | -0.01                                   | 0.004 | -2.16   | .030    | 0.00   | 0.011 | 0.42    | .672    |
| Tree cutting (=true)  | -0.01                                   | 0.003 | -2.1    | .036    | -0.04  | 0.009 | -4.21   | <.001   |
| Spanish Forest Inventory (SFI2, 3, and 4 for carbon storage; SFI 2-3, 3-4 for carbon sequestration) | <b>0.15</b>                             | 0.007 | 20.7    | <.001   | <b>0.05</b>  | 0.017 | 3.23    | .001    |

Note: Estimate values indicate the magnitude of the influence that predictor variables have on carbon storage and sequestration. Negative effects are indicated with the symbol “-”. Estimates in bold indicate significant relationships ( $p < .05$ ).

Abbreviations: CEC, cation exchange capacity; SE, standard error; SFI, Spanish National Forest Inventory.

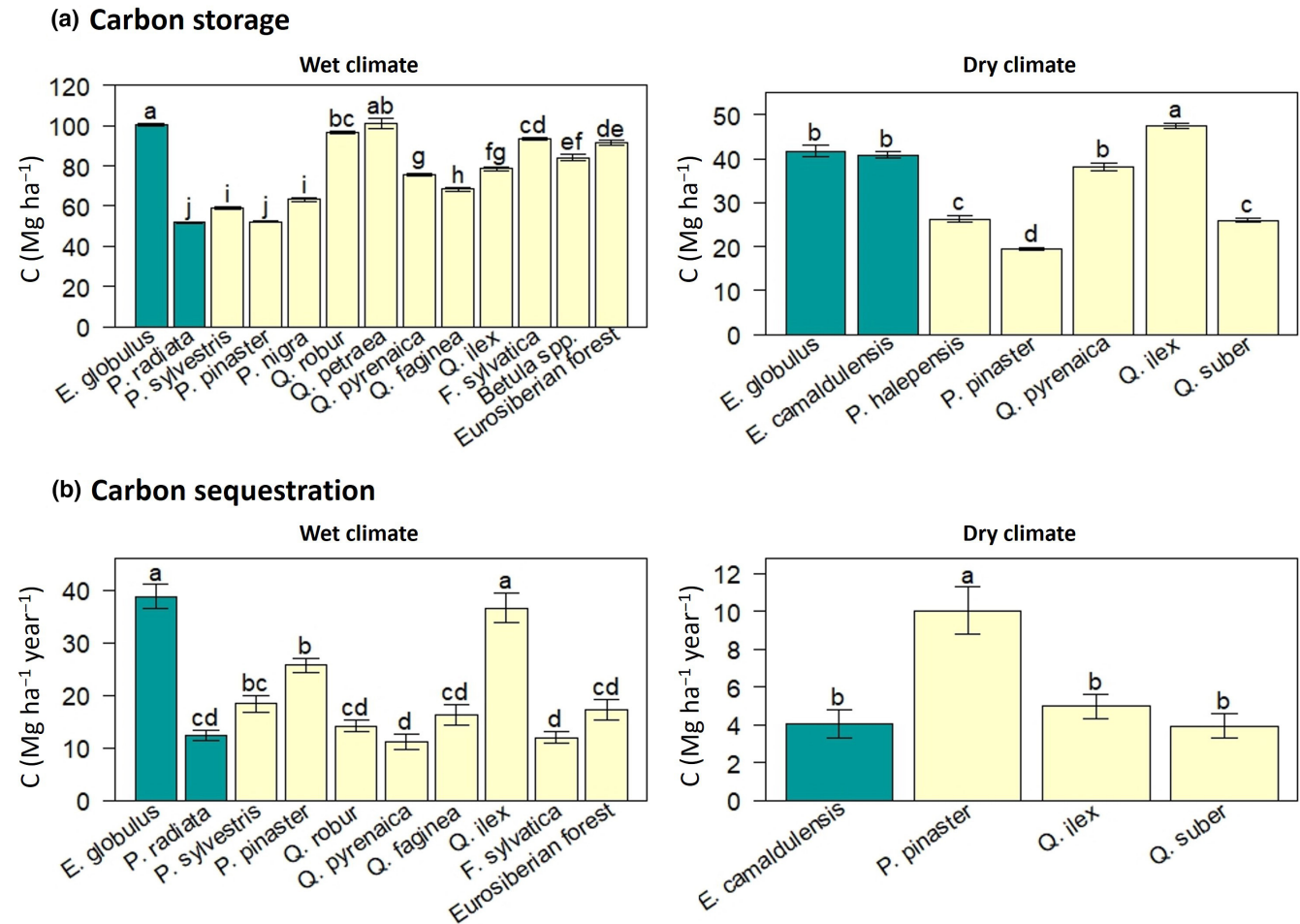


**FIGURE 2** Predicted means of carbon storage and sequestration for non-native and native forests in wet and dry climates. Different letters indicate significant differences between categories after accounting for multiple-comparison Bonferroni correction. Error bars represent standard errors.

### 3.3 | Effects of native tree plantations on carbon storage and sequestration

Tree planting had differential effects on carbon storage. In some native forest types (*Q. robur*, *P. sylvestris*, and Eurosiberian mixed

forests), planted forests stored less carbon than natural forests (Table 2). Other forest types had similar carbon storage in planted and natural plots (*Betula* spp., *Pinus pinaster*, and *P. halepensis*), and one forest type (*Q. pyrenaica*) had higher carbon storage in planted plots. Tree planting had no effect on overall carbon sequestration



**FIGURE 3** Predicted means of (a) carbon storage and (b) sequestration for each forest type in wet and dry climates. Different letters indicate significant differences between forest types after accounting for multiple-comparison (Bonferroni) correction. Error bars represent standard errors. Non-native and native forest types are indicated with blue and yellow colors, respectively. Note variation in Y-axes among bar plots. See [Table S1](#) for forest type nomenclature.

**TABLE 2** Summary of the generalized linear mixed models for analyses regarding the effect of tree plantation on carbon storage and sequestration.

| Forest type               | Carbon storage (Mg Cha <sup>-1</sup> ) |       |         |         | Carbon sequestration (Mg Cha <sup>-1</sup> year <sup>-1</sup> ) |       |         |         |
|---------------------------|--|-------|---------|---------|---|-------|---------|---------|
|                           | Estimate                               | SE    | Z-value | p-Value | Estimate  | SE    | Z-value | p-Value |
| <i>Betula</i> spp.        | -0.02                                  | 0.025 | -1.09   | .277    | -   | -     | -       | -       |
| <i>Quercus pyrenaica</i>  | <b>0.03</b>                            | 0.016 | 2       | .048    | 0.04  | 0.095 | 0.47    | .636    |
| <i>Quercus robur</i>      | -0.04                                  | 0.012 | -3.4    | <.001   | 0.09  | 0.051 | 1.86    | .062    |
| <i>Pinus pinaster</i>     | 0.01                                   | 0.020 | 0.8     | .442    | 0.05  | 0.077 | 0.67    | .502    |
| <i>Pinus sylvestris</i>   | -0.03                                  | 0.009 | -3.7    | <.001   | -0.07   | 0.068 | -0.98   | .325    |
| Eurosiberian mixed forest | -0.03                                  | 0.012 | -2.3    | .023    | 0.16  | 0.133 | 1.2     | .228    |
| <i>Pinus halepensis</i>   | 0.04                                   | 0.027 | 1.45    | .148    | -   | -     | -       | -       |

Note: All forest types occurred in wet climate, except for *Pinus halepensis*, which occurred in dry climate. We show the results regarding tree plantation, but we included as covariates other environmental variables related to forest structure (canopy cover, tree density, stand basal area), abiotic factors (slope, mean temperature, water availability, sand, coarse fragments, cation exchange capacity) and management (tree cutting) in the models. Negative effects of tree plantations on C storage and sequestration are indicated with the symbol “-”. Estimates in bold indicate significant relationships ( $p < .05$ ).

Abbreviation: SE, standard error.



for the evaluated native forest types. However, planted plots of *P. pinaster* had higher carbon gain by tree growth and ingrowth, and higher carbon loss by tree mortality than natural plots of the same species (Tables S9 and S10). Planted plots of *P. sylvestris* also had higher carbon gain by tree growth.

## 4 | DISCUSSION

Forest origin (non-native vs. native) highly influenced tree carbon storage and sequestration of Spanish forests, but there were strong differences for carbon sequestration in wet and dry climates. As we initially hypothesized, carbon storage, on average, was greater in non-native forests than in native forests in both wet and dry climates. The high carbon storage in non-native forests may be linked to the large size of *Eucalyptus* spp. trees (45–55 m of maximum height; Castroviejo, 1986), which can store in the aboveground biomass larger amounts of carbon than most native trees (e.g., the maximum height of *Quercus pyrenaica*, *Q. ilex*, *Q. robur*, *F. sylvatica*, *P. pinaster*, and *P. sylvestris* is 25, 27, 30, 40, 40, and 40 m, respectively as stated in Castroviejo, 1986), and also to the high densities in which non-native productive forests are usually planted (Vadell et al., 2016).

Carbon sequestration was greater in non-native forests than in native forests, but only in the wet climate. This result is in line with the selection of fast-growing non-native tree species to satisfy increasing demands for timber or other wood-derived products (Castro-Diez et al., 2019; MacDicken et al., 2016). However, we found a different pattern in the dry climate, where native forests had higher carbon gain due to greater tree ingrowth and lower carbon loss by tree mortality than non-native forests. This suggests that native forests are better adapted to the arid conditions of the dry climate than the non-native species selected for forestry in this area. This finding agrees with previous research conducted in harsh Mediterranean environments, where native species generally have a higher performance than non-natives due to their higher stress resistance and resilience (Bochet, García-Fayos, et al., 2010; Bochet, Tormo, et al., 2010; Martínez-Ruiz et al., 2007; Matesanz & Valladares, 2007). Abandonment of agricultural and traditional forest uses in rural areas in Mediterranean Spain is leading to forest encroachment and colonization of native tree species (Vilà-Cabrera et al., 2017). The relatively young trees in those recently colonized areas grow fast and can also contribute to explain higher ingrowth and lower mortality in native forests growing in the dry climate (Astigarraga et al., 2020; Vilà-Cabrera et al., 2017). Overall, our result suggests that the superiority of non-native forests over native ones in terms of carbon sequestration declines as the abiotic filters become stronger (i.e., lower water availability and higher climate seasonality).

We found a high variability in tree carbon storage and sequestration within non-native and native forest types. In the wet climate, non-native *E. globulus* stands stored and sequestered more carbon than most forest types, due to a high positive balance between ingrowth, growth, and mortality. However, non-native *P. radiata* stands stored low amounts of carbon, which could be

due to the extensive negative impacts of plagues on this pine species, including defoliation by pine processionary caterpillars (*Thaumetopoea pityocampa*), the red band needle blight (caused by fungal pathogens *Dothistroma septosporum* and *D. pini*) and the brown spot needle blight (caused by *Lecanosticta acicola*), which can significantly decrease tree performance (Barnes et al., 2004; Cobos-Suarez & Ruiz-Urrestarazu, 1990; Coops et al., 2003). Among native forest types, we found that stands dominated by *F. sylvatica*, *Q. robur*, *Q. petraea*, as well as Eurosiberian mixed forests, stored large amounts of carbon in the wet climate, nearly comparable to *E. globulus*. The tree species that dominate such native forest types are generally long-lived, late-successional species, with high investment in storage and defense; this may allow them to store large carbon amounts in the long term. However, stands dominated by *Pinus* spp. had the lowest carbon storage in the wet climate, despite their rapid growth rates (Cornelissen et al., 1996; Serrada et al., 2008), which can be due to their lower long-term carbon stock durability (i.e., acquisitive strategy). We also found that *Q. ilex* forests had high carbon sequestration rates, probably due to their spread onto recently abandoned agricultural lands, forming young forests that grow fast (Astigarraga et al., 2020; Vilà-Cabrera et al., 2017).

In the dry climate, native forests of *Q. ilex* stored the largest amount of carbon (Montero et al., 2005). *Q. pyrenaica* also stored large amounts of carbon in the dry climate, comparable to forests dominated by *E. globulus* and *E. camaldulensis*. Forests dominated by *Q. suber* stored less carbon per area unit than other *Quercus* forests, probably because they are highly managed forest for cork and firewood production. Like in the wet climate, *Pinus* forests were the ones storing less carbon, despite having the largest carbon sequestration, probably due to their shorter longevity, as corresponds to pioneer trees.

The effect of tree plantation on carbon storage and sequestration varied across forest types. Most significant effects on carbon storage were negative, which agrees with previous research (Hua et al., 2022; Liao et al., 2010). This result could be explained by two plausible processes. First, the high tree densities used in tree plantations and the lack of silviculture practices that regulate stand composition and structure (Vadell et al., 2016; Villar-Salvador, 2016) can increase competition for resources, decreasing diameter growth of individual trees and, thus, carbon storage. Alternatively, the occurrence of tree plantations with native species on poorer soils than natural forests (on average; Ruiz-Benito et al., 2012), resulting from reforestation of areas with high erosion and low productivity, can result in lower tree growth and thus carbon storage.

Beyond forest origin and forest type, variables related to forest structure played an important role in carbon storage and sequestration, as found by previous research (Roces-Díaz et al., 2021; Ruiz-Benito, Gómez-Aparicio, et al., 2014; Ruiz-Benito, Madrigal-González, et al., 2014; Vayreda et al., 2012). Forests formed by larger trees with wide, spreading canopies had higher carbon storage, but lower carbon sequestration, as their higher carbon gain by tree growth is overcompensated by their higher carbon loss by tree mortality (natural and due to tree harvesting) and by a lower tree

ingrowth. Thus, mature stands, made up of large trees, are relevant natural reservoirs of carbon, but their carbon sequestration capacity is lower than in younger forests with higher tree density and smaller basal areas, which allow for higher productivity (Gundersen et al., 2021; Vayreda et al., 2012).

Our results show that the carbon storage and sequestration of Spanish forests is highly dependent on the general abiotic environmental conditions. Forests in environments with higher water availability and lower climate seasonality (wet climate) stored and sequestered more carbon than forests in areas with opposed characteristics (dry climate). This result may be due to the key role that climate plays on tree growth, recruitment, and mortality (Benito-Garzón et al., 2013; Coll et al., 2013; Lázaro-Lobo, Ruiz-Benito, Lara-Romero, et al., 2022; Ruiz-Benito, Gómez-Aparicio, et al., 2014; Ruiz-Benito, Madrigal-González, et al., 2014). The Mediterranean climate is characterized by having at least two consecutive months of aridity in the summer (Loidi, 2017), which can lead to slower growth and higher mortality, ultimately affecting carbon storage and sequestration (Gazol et al., 2021). Our results also show that a high content of large soil particles (sand and coarse fragments) reduces carbon storage and sequestration. Sandy soils have a lower ability to retain mineral nutrients and water than clayed soils, which are necessary for plant functioning and growth (Gurevitch et al., 2002). Thus, nutrient and moisture deficiency could reduce tree performance in forested areas (Lázaro-Lobo, Ruiz-Benito, Lara-Romero, et al., 2022; Merino et al., 2003), which affects carbon storage and sequestration.

Our results suggest that tree cutting can reduce carbon storage and sequestration in forests. However, the reduction of tree density after thinning, which temporarily reduces carbon storage, could trigger an immediate growth in neighboring trees due to competition release, which are able to store higher carbon amounts in the long term (Ruiz-Benito, Gómez-Aparicio, et al., 2014; Ruiz-Benito, Madrigal-González, et al., 2014; Vayreda et al., 2012).

In environments with high water availability and low climate seasonality (wet climate), conservation and restoration actions could consider native forests dominated by *F. sylvatica*, *Q. robur*, *Q. petraea*, as well as Eurosiberian mixed forests, when improving ecosystem service provisioning due to their high carbon storage. However, in dry environments (dry climate), long-term programs that aim to increase carbon storage should conserve and promote native *Q. ilex* and *Q. pyrenaica* forests. *Eucalyptus* spp. stands stored more carbon than most native forests in the wet climate. However, societies demand multiple ecosystem services from forests and non-native *Eucalyptus* spp. stands may cause severe negative effects on biodiversity and other ecosystem services, such as depletion of soil water and nutrients, changes in biological communities, and alteration of soil properties (Deus et al., 2018; Lázaro-Lobo, Ruiz-Benito, Lara-Romero, et al., 2022; Soumare et al., 2016).

Although we conducted a large-scale study considering carbon storage and sequestration in tree biomass (trunks, branches, and roots), we did not include understory and soil carbon storage and sequestration, which can be important carbon sinks in Mediterranean

climates (Ruiz-Peinado et al., 2017; Whitehead, 2011). Future research should consider other factors beyond those that were obtained from the SFI datasets (e.g., shrub biomass, soil organic matter, litter mass, microbial biomass, etc.). Another limitation of our study is the low availability of non-native tree species information. Even though there are several non-native tree species present in Spain (e.g., *Ailanthus altissima*, *Q. rubra*, *Pseudotsuga menziesii*, *Robinia pseudoacacia*, *Populus × canadensis*, *E. nitens*, etc.), only *E. globulus*, *E. camaldulensis*, and *P. radiata* dominated stands are well-represented in the SFI. Those fast-growing species were introduced to produce timber and pulp (Serrada et al., 2008). Our results could differ if we considered trees introduced for other purposes or unintentionally. Thus, future studies could be extended to larger areas covering a wider variety of non-native trees and climate types to study whether the effect of native versus non-native forests on carbon storage and sequestration under contrasting climate types depends on the characteristics of the introduced species.

## 5 | CONCLUSIONS

Our results provide broad insight into the effect of forest origin (native vs. non-native) and forest type on carbon storage and sequestration of Spanish forests under contrasting climate types. Our results indicate that fast-growing non-native trees may have higher carbon storage and sequestration, but also be less adapted to the arid environments where they are introduced, than native forests. However, we found a high variability in tree carbon storage and sequestration within non-native and native forest types. The results of this study also demonstrate that forest structure (especially stand basal area), climate, soil capacity to retain nutrients and water, and human management have a great impact on carbon storage and sequestration of forests through their effects on tree growth, ingrowth, and mortality. Lastly, we recommend the expansion of these comparisons to larger regions with a wider variety of non-native forest types and climatic conditions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Mendeley Data at <http://doi.org/10.17632/v2vfnnwrgf1>.

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## SUPPORTING INFORMATION

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