“New forests” from the XX century are a relevant contribution for C storage in the Iberian Peninsula

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Abstract

Land-use changes are one of the major drivers of global change. In many developed countries socioeconomic changes have induced forest expansion during the last centuries, with still seldom explored implications for ecosystem services. We assessed the growth rate and the contribution of these “new forests” on C storage under the imprint of land-use history from Mediterranean to temperate forests in two biogeographical regions in the Iberian Peninsula, using data from 6,422 plots of the Spanish National Forest Inventory (1986-2007) and the land-cover map of 1956 to distinguish among pre-existing and new forests (appeared after 1956). Almost a quarter of current forests were new forests and they represented the 22% of the total C pool. New forests maintained similar C stocks than pre-existing ones (~ 45 Mg ha⁻¹), but they are growing at rates 25% higher. Considering the whole Spanish forested territory the new forest growth rate would offset around the 9% of the rate of total C emitted in Spain between 1986 and 2007. The effects of land-use history on forest growth and C stocks varied with environmental conditions (e.g. growth of new forests in areas with less water availability was higher than in pre-existing ones), supporting the idea that agricultural legacies may prevail in the long-term. In a time when European forests exhibit the first signs of carbon sink saturation, our study endows a relevant ecological role to new forests appeared in the second half of the XX century.

Keywords: agricultural abandonment, growth rates, C stocks, land-use history, environmental conditions, forest transitions, new forests, pre-existing forests.
Introduction

Land-use changes are one of the major drivers of global environmental change (Turner II and others 2007) and socioeconomic development is altering forest ecosystems at accelerated rates. Indeed, while deforestation is the main cause of forest lost in the tropics (Laurance 1999), forest transitions have induced a widespread forest expansion in many developed countries over the last centuries (Meyfroidt and Lambin 2011). These shifts have profound ecological implications given the key functions and services forests globally provide, including regulation of nutrient and water cycling, and atmospheric composition and climate (Millennium Ecosystem Assessment 2005). Yet, while there is an extensive literature covering the dramatic negative ecological and socioeconomic consequences of deforestation for ecosystem services (Malhi and others 2008), the effects of forest expansion have been less addressed (but see Kauppi and others 2006).

Forest ecosystems provide essential ecosystem services. For example, they represent around the 45% and 50% of terrestrial C stocks and net primary production, respectively, and also regulate the major terrestrial fluxes of C between the atmosphere and the biosphere (Bonan 2008). Land-use changes are an important driver of forest C dynamics worldwide, and the potential for C accumulation and storage of forests depend on ecosystem history together with ecosystem dynamics and environmental conditions at present (Pan and others 2011). In Europe, forests have been a net sink of C during the last decades as they are mostly recovering from extensive clearing in the past (Ciais and others 2008; Erb and others 2013). Moreover, it has been also estimated that forest cover has increased by ~ 25% across the continent during the second half of the
XX century as a consequence of transitions from croplands and grasslands to woodlands (Fuchs and others 2013). Therefore, contemporary C stocks and dynamics in forests are not merely the outcome of a shift in management practices in forests, but also owing to the recent establishment of new forests over abandoned croplands and pastures (e.g. Kuemmerle and others 2015). Although the relevance for C accumulation of new forests established after land abandonment has been suggested (e.g. Hooker and Compton 2003), their contribution to C storage in comparison to pre-existing forests and the role that environmental conditions may have in this accumulation pattern remain unexplored.

Land-use history can leave important lasting signals in natural ecosystems (Foster and others 2003). Consequently, land-use legacies effects might be expected to occur on the patterns of productivity of new forests expanded in abandoned cropland areas vs. pre-existing forests as a result of the past allocation of croplands to the areas with better site quality (i.e. flat and with deeper soils) while forests remained in sites with poorer conditions (i.e. steep slopes). Moreover, enhancement of soil conditions (e.g. fertilization, amelioration of soil structure) has been a traditional practice carried out in croplands to sustain crop productivity (Cramer and others 2008). Although afforested ecosystems can recover conditions comparable to undisturbed ones in many aspects after crop abandonment (Flinn and Marks 2007), agricultural legacies may last in the long-term, such that can be seen in soil properties and nutrient content, biochemical processes, as well as in the vegetation structure and diversity patterns (Compton and Boone 2000; Dambrine and others 2007; Gerstner and others 2014; Leuschner and others 2014). Differences owing to land-use-legacies could be predicted to increase in
those sites with the less favorable conditions (e.g. lowest rainfall availability or poorest site quality).

The northern rim of the Mediterranean Basin is one of the most evident examples of forest transition in Europe after being managed for millennia (Blondel and Aronson 1995). This forest transition includes two processes: i.e. the recovery of forests from a long-history of human exploitation (Grove and Rackham 2001) and the expansion of new forests to agricultural areas abandoned during the last century (e.g. Basnou and others 2013). Although the northern rim of the Mediterranean Basin has been the latest European region where forests transitions took place (Mather 1990), and global change is increasing their vulnerability (Schröter and others 2005), the contribution of new forests and the imprint of past land-uses on C accumulation and storage at a macroecological scale is largely unknown.

In this study, we aim at assessing the contribution of new forests appeared after 1956 in two biogeographical regions in the Iberian Peninsula on forest growth rate (in terms of C gain and C storage) and the imprint of land-use legacies on current C dynamics of Mediterranean and temperate forests. We hypothesize that: (1) as a result of an intense process of agricultural abandonment during the second half of the XX century, new forests will represent a substantial part of forest ecosystems and C stocks as a whole; (2) because new forests are growing in former agricultural areas and these were traditionally located in higher quality sites new forests will grow at higher rates than pre-existing ones; and (3) this land-use legacies effect will be more apparent under effects of environmental stress. To do so we analyzed 6,422 plots of the Spanish National Forest Inventory to identify the relative contribution of new forests (appeared
after 1956) on growth rates and C stocks, as well as the potential interaction among land-use history and environmental conditions.

Material and methods

Study area

The study area encompasses two large territories in the Iberian Peninsula (Fig. 1): Andalusia (87,268 km²) and Catalonia (32,114 km²), located in the southern and the northeastern Iberian Peninsula, respectively (Fig. 1B-C) where both detailed cartography of land use changes from the second half of the XX century and forest inventories were available. These regions include a substantial altitudinal gradient, from sea level to more than 3,000 m a.s.l., including both coastal and continental land areas. The geographic location of these territories, together with the range of influences and the mountainous orography, determines a very heterogeneous climate. The climatic gradient in both regions ranges from a temperate-alpine climate in Sierra Nevada (Andalusia) and in the Pyrenees (Catalonia) to a Mediterranean climate in most of the territory. There is also a continentality gradient from coastal to inland areas, with increasing thermal amplitudes inland. Mean annual temperature ranges from 18°C (on the southern coast) to 3°C (in mountain areas) in both regions, and annual rainfall varies from 140 mm to more than 2,000 mm in Andalusia and from 400 mm to more than 1,500 mm in Catalonia (Climatic Digital Atlas of the Iberian Peninsula; Ninyerola and others 2005). This climate variability and the geographic location of these territories are the main factors explaining the existence of a rich and varied flora. Vegetation types include Mediterranean, sub-Mediterranean, Eurosiberian and Boreoalpine chorologies. Forest covers approximately 2.9 x 10⁶ ha in Andalusia and 1.6 x 10⁶ ha in Catalonia, representing around the 33% and the 50% of the whole territory respectively (Spanish
In both regions forests are mainly dominated by conifer and broadleaved (deciduous and evergreen) species. Forest types include: Atlantic, sub-Atlantic and sub-Mediterranean deciduous forests; montane, sub-Alpine, and Mediterranean coniferous forests; Mediterranean sclerophyllous, and evergreen scrublands and forests.

**Data sources**

**Forest inventory data**

We used data from the Spanish National Forest Inventory (IFN; Villaescusa and Díaz 1998; Villanueva 2005). The IFN is an extensive database of periodical forest surveys distributed systematically across the forested areas (i.e. those with a tree cover of at least 5%) in Spain repeatedly sampled across time. The IFN is based on a network of permanent plots at a density of 1 plot km\(^{-2}\), which allows forest characterization and includes exhaustive information on the composition of canopy and understory woody species, as well as on forest structure. Within the plots, all adult trees (≥ 7.5 cm in diameter at breast height [dbh]) were labeled, measured for dbh and height, identified to species, and censused for mortality. Sampling followed a nested circular-plot design, i.e. plot size depended on the dbh of the measured trees to guarantee a representative sampling of the tree size distribution. Therefore, all trees with dbh ≥ 7.5 cm were measured within 5 m of the centre of the plots, trees with dbh ≥ 12.5 cm were also measured between 5 and 10 m around the centre of the plots, whereas trees with dbh ≥ 22.5 cm and dbh ≥ 42.5 cm were also considered within 10–15 m and 15–25 m around the centre of the plots, respectively. We used data from the permanent plots surveyed in the second inventory (IFN2; 1986-1996) and revisited again in the third one (IFN3; 1997-2007). We excluded plots with evidence of recent disturbances (mainly fire, but
also storms, and other) detected during the IFN3, and with presence of exotic species (mostly actively planted) in any of the two inventories, in order to assess the patterns of growth and stocks over the same set of plots, and also to avoid potential biases in our analyses.

**Growth rates and C stocks**

Estimates of growth rates and C stocks included in this study were restricted to the aboveground compartment of adult trees (dbh ≥ 7.5 cm) alive between the two inventories (i.e. without including dead trees). To compute carbon content per tree we applied allometric equations obtained in different studies to the data of each IFN2 and IFN3 plot. Aboveground biomass (AGB) of each living tree was computed using specific equations as a function of DBH and height (H) developed in the Ecological Forest Inventory of Catalonia (IEFC, Gracia and others 2004a): $\text{AGB} = a \cdot \text{DBH}^b \cdot H^c$, where $a$, $b$ and $c$ are specific coefficients for the different species. For the least common species we applied the coefficients of generalized equations obtained for the different functional groups (coniferous, deciduous and sclerophyllous species). Total C amount of each living tree was determined by multiplying aboveground biomass by the specific C content of the species obtained in the IEFC from oven-dried samples (Gracia and others 2004b). Growth rate (Mg C ha$^{-1}$ year$^{-1}$) for each plot was estimated in terms of C gain as the sum of C increment due to growth of surviving trees and C of ingrowth of new trees to the canopy (i.e. new trees with dbh ≥ 7.5 cm) between the two surveys, divided by the number of years elapsed between measurements. We used total C amount of living trees per each plot at the IFN3 as an estimate of current C stocks (Mg ha$^{-1}$).
Land-use history

Land-use history of each IFN plot was obtained by overlapping the geographic location of the IFN plots with land-cover maps of 1956-1957, available for the whole territory of Andalusia and for more than 50% of the territory of Catalonia (Figure 1). This land-cover map was digitized by on screen photo-interpretation of historical aerial photographs (Basnou and others 2013) available in the archives of the Spanish army. The definition of forest and scrubland in these maps was essentially the same as the used in the National Forestry Inventories, as stands with at least 5% of tree cover were classified as forests while the rest were considered as scrublands (Villanueva 2005). Combining them with the 1956-1957 land-cover maps, the IFN plots were then classified in three types of land-use history, according to their historical land-use in 1956 and to the corresponding transition: (1) Forest–Forest (hereafter F–F), corresponding to preexisting forests in 1956; (2) Crop–Forest (hereafter C–F), corresponding to current forests growing on existing crops in 1956; and (3) Scrubland/grassland–Forest (hereafter SG–F), corresponding to current forests growing on existing scrublands or grasslands in 1956. The overlapping of these two data sources (i.e. IFN plots and land-cover map of 1956) allowed us to identify the land-use history of each IFN plot, and to distinguish between pre-existing forests (F–F) and new forests (C–F and SG–F). The final sample size resulted in a total of 6,422 plots, 3,753 distributed in Andalusia and 2,669 in Catalonia.

Environmental factors

Climatic gradient. Climatic data for each IFN plot was obtained from the Climatic Digital Atlas of the Iberian Peninsula (Ninyerola and others 2005), a set of digital maps at 200 x 200 m resolution with mean annual and monthly data for precipitation and
maximum, mean and minimum temperatures (reference period 1959-1999). We used an
index of water availability (WAI [%]) to characterize the climatic conditions for each
plot. WAI was calculated as: [(P-PET)/PET] × 100, where P is mean annual
precipitation (in mm) and PET is annual potential evapotranspiration (in mm; calculated
following the Hargreaves-Samani [1982] method). Negative values of WAI correspond
to dry sites and positive to wet sites.

Site conditions. The following variables were used to characterize other environmental
conditions for each IFN plot: (1) Terrain slope as a topographical measure, estimated as
the maximum slope (°) in the center of the plot; (2) Distance to the coast (in m) as a
measure of continentality; and (3) Management, i.e. commercial cutting or thinning
between the IFN2 and IFN3, as a measure of recent human disturbance (managed /
unmanaged).

Biotic conditions. Forest type, structure and development were used to characterize the
biotic conditions of each plot. Forest type was established according to the tree
dominant species within each plot, determined through the highest percentage in basal
area using measured trees (dbh ≥ 7.5 cm). We distinguished four forest types:
deciduous, mediterranean pines, mountain pines and sclerophyllous (see list of
dominant species in Appendix A). To account for the effects of initial forest structure
and forest development on patterns of growth rates we used C stocks (Mg ha⁻¹) of living
trees and stand density of living trees (trees ha⁻¹) at the beginning of the study period
(i.e. at the IFN2). In the case of current C stocks (i.e. at the IFN3) we only used stand
density of living trees (trees ha⁻¹) at the IFN3 as a measure of forest structure and degree
of stand development.

Data analyses
The effects of land-use history and environmental factors on growth rates and C stocks were explored by means of linear models (LMs). The relevance of each source of variation was assessed by comparisons using differences in the AIC (Akaike Information Criterion) among sets of alternative models. A significant effect (at level $\alpha = 0.05$) of a variable included in a model was considered to be important as source of variation when the $\Delta$AIC was at least of 4 units (Burnham and Anderson 2002) under comparison with the same model excluding the targeted variable.

We started by fitting a null intercept-model for each response variable (i.e. growth rates and C stocks). To test overall differences in the averages of growth rates and C stocks among types of land-use history, we added land-use history as explanatory variable. We then assessed the importance of land-use history as source of variation by comparing this model with the null model.

Because the observed differences among types of land-use history may result from environmental heterogeneity and stand structure, we included all these effects as explanatory variables (i.e. forest type, stand density, C stocks at the IFN2, WAI, terrain slope, distance to the coast and management). We constructed a saturated model which included the effects of land-use history and the other factors, as well as the interaction between these factors with land-use history. Region was also included as explanatory variable to take into account overall differences between the two biogeographical areas.

Starting from the saturated model, we created the fully crossed set of models and ranked them from lowest to highest AIC. All best models (lowest AIC) within 4 AIC units were considered to be equivalent in terms of fit (Burnham and Anderson 2002). The relative importance as source of variation of land-use history, forest type, stand structure,
environmental factors, and interactions included in the best adequate model (i.e. lowest AIC) was evaluated by examining their inclusion in the other candidate models, and assessed based on relative ΔAIC when comparing the best adequate model with an alternative model with an identical structure of explanatory variables but ignoring the targeted explanatory variable one at a time. Coefficients of determination were used to assess the contribution (in %) of explanatory variables in explaining variability of growth rates and C stocks.

To satisfy normality assumptions, Box-cox transformations were applied on the two response variables, i.e. growth rates and C stocks, while stand density and C stocks at the IFN2, and distance to the coast were loge and square root transformed, respectively. Correlations between explanatory variables were always < 0.45. The residuals of the models did not show deviation from normality and were not spatially correlated.

Analyses were carried out with R software version 3.1.1 (R Development Core Team, 2014).

Results

Characterizing new forests

Overall, 23% of the 6,422 plots were crops, scrublands or grasslands in 1956, i.e. close to a quarter of forests of these two large regions as a whole are new forests.

Specifically, 5% of forest plots were crops while 18% were scrublands or grasslands in 1956 (Table 1). Similar patterns were observed within each region (Table 1). Across all forest plots, sclerophyllous and Mediterranean pine forests were dominant, although this trend slightly changed within new forests, being sclerophyllous forests comparatively less represented (Table 2A). Mean plot characteristics, i.e. forest structure and
development, climatic and site conditions, as well as management intensity, across all plots and per types of land-use history are shown in Table 2B.

**Overall effects of land-use history on growth rates and C stocks**

On average, new forests showed growth rates 25% higher than pre-existing forests. Mean growth rates were $1.21 \pm 0.01$ Mg C ha$^{-1}$ year$^{-1}$ for F–F, $1.73 \pm 0.06$ Mg C ha$^{-1}$ year$^{-1}$ for C–F, and $1.45 \pm 0.03$ Mg C ha$^{-1}$ year$^{-1}$ for SG–F (Table 2B). These growth rates were significantly higher for new forests in comparison to pre-existing forests when tested in the LM with land-use history as single explanatory variable (Fig. 2A; see Appendix B for parameter estimates). Land-use history explained a small proportion ($R^2 = 3\%$) of variability in growth rates. However, land-use history was relevant as direct source of variation when the model was compared with the null model (Table 3A).

C stocks of new forests represented about the 22% of the total C pool. Current C stocks differed significantly between pre-existing and new forests (Fig. 2B; see Appendix B for parameter estimates), with average values of $45 \pm 0.4$ Mg ha$^{-1}$ for F–F, $49 \pm 1.6$ Mg ha$^{-1}$ for C–F and $42 \pm 0.7$ Mg ha$^{-1}$ for SG–F (Table 2B). Although land-use history was relevant as direct source of variation of current C stocks (Table 3A), the model containing land-use history as single explanatory variable explained less than 1% of total variability (Table 3A).

**Interplay between land-use history and environmental conditions**

The best adequate model for growth rates included the effects of land-use history, stand density, initial C stock, forest type, WAI, terrain slope, management, region as well as the interaction land-use history $\times$ WAI (see Appendix C for parameter estimates).
Explanatory variables explained a substantial proportion of total variability ($R^2 = 65\%$). Land-use history and the interaction land-use history $\times$ WAI emerged as relevant sources of variation in comparison with the models excluding their effects one at a time (Table 3B). There were other 11 candidate models ($\Delta AIC \leq 4$ under comparison with the best adequate model) which always included the effects of land-use history and its interaction with WAI. Therefore, the effect of land-use history on growth rates varied along the gradient of water availability (Fig. 3). Interestingly, new forests showed higher growth rates in drier sites than pre-existing forests, while in wet sites the rates were similar (Fig. 3). For example, at WAI values of $\sim 50\%$ the predicted growth rates for new forests were in average 20\% higher than those for pre-existing forests, while at WAI values of 50\% the predicted rates were comparatively similar. In the two land-history trajectories deciduous and Mediterranean pine forests showed higher growth rates than forests of mountain pines and sclerophyllous species (Appendix D). Additionally, growth rates were higher with increasing stand density and initial C stocks, and also were higher in unmanaged forests and in flatter slopes (Appendix D). Finally, differences between regions were also observed (Appendix D). The relative importance of stand structure, forest type and region effects on growth rates was much greater than any other source of variation (see the high positive $\Delta AIC$ when the effects of structural variables, forest type and region were excluded one at a time from the model; Table 3B). Interestingly, however, the relative importance of land-use history effects was comparatively similar to management effects, and higher than the effects of climate and site conditions (Table 3B). The best adequate model for C stocks included the interactions of forest type, stand density, WAI and distance to the coast with land-use history, as well as the effects of
management, terrain slope and region (see Appendix C for parameter estimates).

Explanatory variables explained a large proportion of total variability ($R^2 = 49\%$). Land-use history emerged as relevant source of variation under comparison with the model excluding its effects (Table 3B). All interactions were significant and also relevant as sources of variation when compared with the same model excluding the targeted interaction one at a time (Table 3B). There were other 2 candidate models ($\Delta AIC \leq 4$ under comparison with the best adequate model) which always included the effects of land-use history and all interactions. Differences in C stocks among types of land-use history were dependent on forest type. C stocks for new forests were predicted to be in average similar to those of pre-existing forests in Mediterranean pines and sclerophyllous, but 41% and 18% lower than pre-existing forests for deciduous and mountain pines, respectively (Fig. 4A). On average, C stocks of new forests were predicted to be lower than pre-existing forests at low stand densities (e.g. 27% lower at ~ 250 trees ha$^{-1}$), but higher at high stand densities (e.g. 9% higher at ~ 4000 trees ha$^{-1}$) (Fig. 4B). C stocks among land-use history types varied along the gradient of water availability (Fig. 4C). Under dry conditions, on average C stocks were similar among land-use history types, but were higher for pre-existing forests under wet conditions (e.g. 36% higher in average at WAI = 50\%). C stocks for pre-existing forests were higher than new forests at large distances to the coast (e.g. 23% higher in average at ~150,000 m), but were higher for C–F at short distances to the coast (e.g. 11% and 23% higher than F–F and SG–F, respectively, at ~10,000 m) (Fig. 4D). Additionally, C stocks were higher in unmanaged forests and in flatter slopes, and differences between regions were also observed (Appendix D). Stand density was the most important factor determining C stocks followed by climate and forest type (Table 3B). The relative
importance of land-use history effect on C stocks was higher to that of site conditions, management and region (Table 3B).

Discussion

Even though the steady growth of forest area over recent decades in Europe is a well-known phenomenon (e.g. more than 0.8 million hectares since 1990 according to Forest Europe 2015) their relevance in terms of the provision of ecosystem services, like C sequestration, has been seldom explored. Thus, to the extent our study system may be considered representative of Mediterranean ecosystems and part of Temperate ones in Europe, three main elements are specially relevant: (1) almost a quarter of forests are less than 50 years old with a previous and recent history of non-forest use, now becoming a fundamental piece of current forest ecosystems as a whole, (2) new forests represent the 22% of the total C pool, and are growing at rates 25% higher than pre-existing forests while the amount of C stored is similar in the two forest types, and (3) the imprint of land-use history is apparent on current growth rates and C stocks of forests interacting with environmental variables, such as water availability, forest type and structure or distance to the coast.

The relevance new forests

New forests have spread at accelerated rates on former non-forested land. Certainly, forest transitions have been a fundamental process in our study system. Almost a quarter of current forests were croplands, and scrublands or grasslands half a century ago, suggesting a high forest increase during this time. The most reliable data on forest increase across time in Spain is provided by the SISPARES database (www.sispares.com), made up by 215 landscape samples randomly distributed across
the Spanish territory accounting for land-cover maps of 1956, 1984 and 1999. These data show a net increase in forest cover by 14\% in Spain between 1956 and 1999 (rate ~ 0.33\% year\(^{-1}\)). This observed rate of net increase of forest cover is nearly equal to the assessed in other regions of the northern rim of the Mediterranean Basin such as the Italian Peninsula (rate ~ 0.35\% year\(^{-1}\), 1960 – 2000; Falcucci and others 2007), but it is somewhat lower than the estimated rate for the whole Europe (rate ~ 0.42\% year\(^{-1}\), 1950 – 2010; Fuchs and others 2013). The rapid expansion of forests during the last half of the XX century in our study area might be explained by a fast forest community assembly after land abandonment by a pool of species with a marked pioneer habit that, remaining constricted in scrublands and hedgerows in the past, were able to spontaneously colonize croplands as soon as management ceased (Basnou and others 2016). Notwithstanding this, reforestation programs conducted from the 50s might also have played a key role in forest recovery in many areas of Mediterranean Europe (Barberó 1998; Iriarte-Goñi and others 2013).

This is the first time the relative contribution of new forests in forest growth rates and C storage is empirically assessed at a macroecological scale in Europe (but see e.g. Kuemmerle and others 2015 for a simulation approach). The emergence of these new forests may result into generalized changes in ecosystem function, including C cycling dynamics and storage in forest biomass (Rudel and others 2005). Although there is plenty evidence that Northern hemisphere woodlands have been sequestering C during the last century and decades (e.g. Houghton and others 1999; Ciais and others 2008; Bellassen and others 2011; Vayreda and others 2012), our approach allows identifying the magnitude of recent land-use changes on C dynamics, i.e. new forests represent the 22\% of the total C pool and are growing at a rate 25\% higher than pre-existing ones.
These results provide signs on two fundamental aspects. Firstly, many forests (pre-existing forests here) may be reaching maturity and, as a consequence, have lower potential for C accumulation. Although empirical evidences indicate that old-growth forests may continue to accumulate C (Luyssaert and others 2008), the observed differences in growth between pre-existing and new forests (even after accounting for biotic and abiotic factors) could suggest a decline in productivity with age (Tang and others 2014) and early signs of C sink saturation (Nabuurs and others 2013). Moreover, it should be taken into account that many of these pre-existing forests are oak coppices repeatedly exploited for centuries for charcoal or firewood extraction by means of selective thinning (Terradas and others 1999). This particular forestry practice, based on the vigorous resprouting of these species, involves a reduced genetic replacement and may entail, in the long term, lower growth rates (see Espelta and others 1995).

Secondly, our results show that new forests are already playing an important role in C accumulation. For example, if we extrapolate our results to the whole Spanish forested territory of ca. 18.6 $10^6$ ha (Spanish Ministry of Agriculture, Food and Environment) and we assume the % of new forests and the growth rates observed in our two regional areas, new forests in Spain as a whole might have gained C at $\sim 6.5$ $10^6$ Mg C year$^{-1}$ during the lag of time the forest inventories were carried out (i.e. 1986 – 2007).

Interestingly, this rate would have offset around the 9% of the average rate of total C emitted in Spain during the same period ($\sim 7.4$ $10^7$ Mg C year$^{-1}$; Carbon Dioxide Information Analysis Center, US Department of Energy). Taken together, our results suggest that new forests are already relevant in the mitigation of C emissions and that they will become a substantial C sink in the longer.
Interestingly new forests exhibited higher growth rates and similar C stocks than pre-existing ones in spite they presented, according to the forest inventory surveys, more signs of management (e.g. 44% of C-F and 33% of SG-F plots had been managed in comparison of 31% in the F-F category). Even though we lack information about the intensity of management in the two forest types, we can suggest several hypotheses to explain why new forests are being more exploited and why they still maintain higher rates of C gain. Preferential exploitation of new forests may be due to: 1) they occupy former croplands located in flat and more accessible areas (Basnou and others 2016) where costs of forest exploitation are lower and 2) they are mostly composed by conifers (see Table 2, Basnou and others 2016) with higher commercial value than sclerophyllous pre-existing forests, highly exploited for charcoal production in the past but mostly abandoned during the second half of the XX century (Terradas 1999). Concerning the higher growth rates of new forests in spite of being more exploited, this could be mediated by the dominance of pines in this forest type (see Table 2) with higher growth rates and faster recruitment dynamics (Zavala and others 2000) than the sclerophyllous species (e.g. *Quercus spp*) predominant in pre-existing forests.

**The interaction among legacies of land-uses and environmental conditions**

Land-use history remained as relevant source of variation after accounting for environmental variability although, in agreement with other studies, stand structure was the most important factor explaining patterns of growth rates and C storage (e.g. Vayreda and others 2012). However, it is important to stress that the effects of land-use history were similar in magnitude, or even higher, than the effects of climate, site conditions and management. Interestingly, these effects of land-use history on growth rates and C stocks varied along some environmental gradients.
Our results bring support to the idea that the legacies of agriculture in the past might prevail in the long-term. It has been suggested and well documented that water availability is the key limiting factor of forest biomass and C dynamics in Iberian forests (Vilà and others 2007; Vayreda and others 2012; Ruiz-Benito and others 2014).

However, our results suggest that the effects of water availability were mostly relevant in pre-existing forests. As a consequence, the observed patterns under drought conditions, i.e. higher growth rates in new forests as compared to pre-existing forests and similar amounts of C stored among land-use history types, are probably driven by a combination of ecological mechanisms that could partly prevent or buffer new forests from severe drought stress. Past decisions on allocation of land for agriculture in flat areas and deeper soils as well as the continuous amelioration of soil structure by the agricultural practices (e.g. ploughing and manuring) might help to explain why new forests are more able to overcome water shortage in the C dynamics. Moreover, past fertilization can last for more than a century and affect growth dynamics of trees established after crop abandonment (von Oheimb and others 2014). Accordingly, former fertilization might have left nutrient-enriched soils in new forests, enhancing biomass allocation to the aboveground compartment in new forests (Vicca and others 2012) and helping nutrient regulation (Fernández-Martínez and others 2014) which could partly mitigate the detrimental effects of water stress on C acquisition. However, the empirical validation of these hypotheses is an important challenge for the future, given that soil data at the scale of this study is not currently available and because other confounding factors might also be relevant, e.g. growth saturation and the dominance of slow-growing species in pre-existing forests, differences in the time of abandonment among biogeographical regions or differences in structural and species diversity.
In addition to the effects of water availability, C storage varied among land-use history types in interaction with forest types, stand density and distance to the coast. Particularly, it has been argued that changes in species richness and functional composition might affect productivity and C storage in Mediterranean forests (e.g. Vilà and others 2007; Ruíz-Benito and others 2014). However, it is interesting to note that new forests stored similar amounts of C than pre-existing ones in Mediterranean pine and sclerophyllous forests. These results suggest that these two contrasted groups of Mediterranean tree species are able to establish well on abandoned lands through different processes of secondary succession (Sheffer 2012) and reach in few decades structural conditions similar to those of pre-existing forests (see examples in Rodrigo and others 2004). Recent works in part of the study area (Basnou and others 2016) showed that differences in species richness and composition between pre-existing and recent forests are not so dramatic as expected: i.e. community assembly in terms of species richness is fast enough to exhaust most colonization credit in these recent forests. On the other hand, the expected successional differences in species composition between forests types are less clear than expected due to (i) the strong pressure that pre-existing forests have undergone along their history, and (ii) the main role of niche factors in woody species assemblage. Thus, pine species also are common in managed pre-existing forests, especially when these are growing in dry, thin-soil stands. In the present work, there was also evidence that the effect of stand density on C stocks was stronger in new forests, evidencing again their early stage of development still far away from the limit of C storage (Nabuurs and others 2003). Additionally, forests growing on abandoned crops (i.e. C – F) at short distances to the coast showed higher C stocks. Agricultural intensification, socioeconomic development and urbanization in the
Mediterranean basin have been especially intense along the coast (Vallejo and others 2005), so probably reflecting an earlier abandonment of agricultural activities in coastal areas (see also from the effects of distance from the cost on the assembly of new forest communities, Basnou and others 2016). Finally, we cannot discard that other important global change drivers in the Mediterranean basin such as fire regimes and CO\textsubscript{2} fertilization, interacting with the different land-use histories, might have also contributed to the observed differences between new and pre-existing forests.

**Implications for conservation and management**

In a time when the rapid increase in the emission of CO\textsubscript{2} has turned to be one of the main ecological and societal challenge to be addressed by scientists and policymakers, our study endows an important ecological role to new forests. First, new forests represent a noticeable part of forest ecosystems studied and their overall C sink, and are growing at higher rates than pre-existing forests. Moreover, our findings suggest that new forests have been playing a relevant role in counterbalancing the emission of CO\textsubscript{2}, in recent decades and they will continue accumulating C in the mid-term with a great potential to play a non-negligible role in the global terrestrial C sink in the long. To what extent the patterns observed may be similar in other areas in the world, and designing appropriate conservation and management practices in new forests are challenging topics deserving attention. Particularly because the ultimate drivers of returning forests (e.g. socioeconomic, fossil-fuel based energy system) will not last forever so new forests might be bound to play a noticeable role in providing ecosystem services to the human population (Navarro & Pereira 2012), especially in the advent of a new green economy in which increasing pressure on forest products (timber, wood) might substantially affect C stocks. It must be also considered that the widespread
expansion of new forests and the increase of standing biomass in a half of a century might also increase risk and vulnerability to natural disturbances such as fire, storms, droughts and pests. Therefore, at the same time new forests reach maturity and their rates of increase in C accumulation decline there is a high likelihood of C sink saturation, and release of huge amounts of C if management and conservation strategies are not revised and properly implemented (Nabuurs and others 2013). This strongly supports the integration of production together with conservation in new forests management, to sustain the potential for global change mitigation and the multiple ecosystem services they provide (Chazdon 2008).

Acknowledgements

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Literature cited


Spanish Ministry of Agriculture, Food and Environment (http://www.magrama.gob.es/en/).


Table legends

Table 1. (A) Sample size (total and for each region) according to land-use history types; and (B) Proportion of plots (total and for each region) according to land-use history types. Land-use history types: F–F, Forest–Forest; C–F, Crop–Forest; SG–F, Scrubland/grassland–Forest.

Table 2. (A) Proportion of plots per each forest type across all plots and according to types of land-use history; (B) Mean ± SE of growth rates, C stocks and environmental factors across all plots and according to types of land-use history. Land-use history types: F–F, Forest–Forest; C–F, Crop–Forest; SG–F, Scrubland/grassland–Forest.

Table 3. Outcome of the LMs comparisons testing (A) the direct effects of land-use history on growth rates and C stocks; and (B) the relative contribution of variables included in the best adequate models explaining growth rates and C stocks. In a, a significant effect (at level α = 0.05) of land-use history when included as explanatory variable in the model was considered to be relevant as source of variation when the AIC was at least 4 units lower under comparison with the null model. In b, the relative importance of land-use history, environmental factors and interactions as source of variation was assessed based on the positive ΔAIC when comparing the best adequate model with an alternative model with the same structure of explanatory variables but ignoring the targeted source of variation one at a time. AIC: Akaike information criterion; n.i. not included in the best adequate model; n.t.: not tested
Table 1

<table>
<thead>
<tr>
<th></th>
<th>All plots</th>
<th>F–F</th>
<th>C–F</th>
<th>SG–F</th>
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<tbody>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>6,422</td>
<td>4,954</td>
<td>331</td>
<td>1,137</td>
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<tr>
<td>Andalusia</td>
<td>3,753</td>
<td>2,916</td>
<td>111</td>
<td>726</td>
</tr>
<tr>
<td>Catalunya</td>
<td>2,669</td>
<td>2,038</td>
<td>220</td>
<td>411</td>
</tr>
<tr>
<td><strong>(B) % plots</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>100</td>
<td>77</td>
<td>5</td>
<td>18</td>
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<tr>
<td>Andalusia</td>
<td>58</td>
<td>78</td>
<td>3</td>
<td>19</td>
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<tr>
<td>Catalunya</td>
<td>42</td>
<td>76</td>
<td>8</td>
<td>15</td>
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Table 2

(A) % plots per Forest type

<table>
<thead>
<tr>
<th>Forest type</th>
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<th>Forest</th>
<th>Crop</th>
<th>Shrubland</th>
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<tr>
<td>Deciduous</td>
<td>8</td>
<td>9</td>
<td>10</td>
<td>6</td>
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<tr>
<td>Mediterranean pines</td>
<td>35</td>
<td>30</td>
<td>48</td>
<td>52</td>
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<tr>
<td>Mountain pines</td>
<td>22</td>
<td>20</td>
<td>26</td>
<td>32</td>
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<tr>
<td>Sclerophyllous</td>
<td>35</td>
<td>42</td>
<td>16</td>
<td>10</td>
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</table>

(B) Plot characteristics

<table>
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<th>Crop</th>
<th>Shrubland</th>
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</thead>
<tbody>
<tr>
<td>Growth rate (Mg ha(^{-1}) year(^{-1}))</td>
<td>1.28 ± 0.01</td>
<td>1.21 ± 0.01</td>
<td>1.73 ± 0.06</td>
<td>1.45 ± 0.03</td>
</tr>
<tr>
<td>C stocks IFN3 (Mg ha(^{-1}))</td>
<td>44.7 ± 0.4</td>
<td>45.0 ± 0.4</td>
<td>49.0 ± 1.6</td>
<td>42.0 ± 0.7</td>
</tr>
<tr>
<td>C stocks IFN2 (Mg ha(^{-1}))</td>
<td>34.1 ± 0.3</td>
<td>35.2 ± 0.4</td>
<td>36.0 ± 1.4</td>
<td>28.4 ± 0.6</td>
</tr>
<tr>
<td>Stand density IFN3 (trees ha(^{-1}))</td>
<td>654 ± 7.4</td>
<td>620 ± 8.4</td>
<td>816 ± 31</td>
<td>754 ± 17</td>
</tr>
<tr>
<td>Stand density IFN2 (trees ha(^{-1}))</td>
<td>614 ± 6.7</td>
<td>571 ± 7.5</td>
<td>795 ± 31</td>
<td>747 ± 16</td>
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<tr>
<td>WAI (%)</td>
<td>−31.4 ± 0.3</td>
<td>−30.1 ± 0.3</td>
<td>−33.4 ± 1.1</td>
<td>−36.0 ± 0.7</td>
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<tr>
<td>Terrain slope (°)</td>
<td>20.8 ± 0.1</td>
<td>20.6 ± 0.1</td>
<td>19.1 ± 0.5</td>
<td>21.4 ± 0.3</td>
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<tr>
<td>Distance to the coast (m)</td>
<td>66,806 ± 615</td>
<td>67,746 ± 704</td>
<td>43,877 ± 1901</td>
<td>69,385 ± 1492</td>
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<tr>
<td>Management (% plots)</td>
<td>32</td>
<td>31</td>
<td>44</td>
<td>33</td>
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Table 3

(A) Growth rate

<table>
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<tr>
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<th>df&lt;sub&gt;model&lt;/sub&gt;</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>df&lt;sub&gt;model&lt;/sub&gt;</th>
<th>AIC</th>
<th>ΔAIC</th>
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<tr>
<td>Null model</td>
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<td>16,212</td>
<td></td>
<td>2</td>
<td>21,238</td>
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<tr>
<td>Land-use history</td>
<td>4</td>
<td>16,022</td>
<td>190</td>
<td>4</td>
<td>21,223</td>
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(B) Growth rate

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<tr>
<th>Model</th>
<th>df&lt;sub&gt;model&lt;/sub&gt;</th>
<th>AIC</th>
<th>ΔAIC</th>
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<th>ΔAIC</th>
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<tr>
<td>Best adequate model</td>
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<td>9,559</td>
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<td>25</td>
<td>16,965</td>
<td></td>
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<tr>
<td>No Land-use-history</td>
<td>11</td>
<td>9,644</td>
<td>85</td>
<td>11</td>
<td>17,146</td>
<td>181</td>
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<tr>
<td>No Stand density</td>
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<td>11,732</td>
<td>2,173</td>
<td>22</td>
<td>19,619</td>
<td>2,654</td>
</tr>
<tr>
<td>No C stocks at the IFN2</td>
<td>14</td>
<td>10,385</td>
<td>826</td>
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<tr>
<td>No Forest Type</td>
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<td>188</td>
<td>16</td>
<td>17,251</td>
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<td>9,598</td>
<td>39</td>
<td>22</td>
<td>17,645</td>
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<tr>
<td>No Terrain slope</td>
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<tr>
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<td></td>
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<td>17,003</td>
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<td>No Management</td>
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<td>9,649</td>
<td>91</td>
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<td>16,980</td>
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<td>No Region</td>
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<td>9,788</td>
<td>229</td>
<td>24</td>
<td>16,983</td>
<td>18</td>
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<tr>
<td>No Land-use history × WAI</td>
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<td>9,567</td>
<td>8</td>
<td>23</td>
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<tr>
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<td></td>
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<td>17,021</td>
<td>56</td>
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<tr>
<td>No Land-use history × Forest Type</td>
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<td></td>
<td>19</td>
<td>16,998</td>
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<tr>
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<td></td>
<td></td>
<td>23</td>
<td>16,974</td>
<td>9</td>
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<tr>
<td>No Land-use history × C stocks at the IFN2</td>
<td>n.i</td>
<td></td>
<td></td>
<td>n.t</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No Land-use history × Terrain slope</td>
<td>n.i</td>
<td></td>
<td></td>
<td>n.i</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No Land-use history × Management</td>
<td>n.i</td>
<td></td>
<td></td>
<td>n.i</td>
<td></td>
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</tr>
</tbody>
</table>
**Figure legends**

**Figure 1.** (A) Location of Andalusia and Catalonia in the Iberian Peninsula, and distribution of the sampling plots of the National Forest Inventory of Spain (IFN); (B) Distribution of the sampling plots of the IFN in Catalonia; and (C) Distribution of the sampling plots of the IFN in Andalusia. Land-use history types: F–F, Forest–Forest; C–F, Crop–Forest; SG–F, Scrubland/grassland–Forest (see Material and methods section for a detailed description).

**Figure 2.** Boxplots of (A) growth rates and (B) C stocks as a function of types of land-use history. The limits of boxes indicate the first and third quartiles, and the horizontal line within boxes corresponds to the median. The upper whisker extends from the third quartile to the highest value within 1.5 x IQR (inter-quartile range) of the third quartile. The lower whisker extends from the first quartile to the lowest value within 1.5 x IQR of the first quartile. Different letters between land-use history types represent significant differences according to the LMs testing the overall effect of land-use history on the response variables (see Table 3 and Appendix B). Grey crosses are outliers. Land-use history types: F–F, Forest–Forest; C–F, Crop–Forest; SG–F, Scrubland/grassland–Forest.

**Figure 3.** Predicted effects (mean and 95% confidence intervals) of land-use history on growth rates along the gradient of WAI. Predicted values were based on the WAI effects of the best adequate model (see Appendix C) and were averaged across the levels of categorical variables (forest type, management and region). The effects of the other covariates were fixed at the observed mean. Approximate confidence intervals of the prediction were calculated from de variance-covariance matrix of the explanatory variables (±2 × SE of prediction). Land-use history types: F–F, Forest–Forest; C–F, Crop–Forest; SG–F, Scrubland/grassland–Forest.
Figure 4. Predicted effects (mean and 95% confidence intervals) of land-history on C stocks along the gradients of (A) forest type; (B) stand density; (C) WAI; and (D) distance to the coast. Predicted values were based on the effects of explanatory variables of the best adequate model (see Appendix C) and were averaged across the levels of categorical variables (forest type, management and/or region). The effects of the other covariates were fixed at the observed mean. Approximate confidence intervals of the prediction were calculated from the variance-covariance matrix of the explanatory variables (± 2 × SE of prediction). In A different letters correspond to significant differences among forest types according to Tukey's post hoc tests. Land-use history types: F–F, Forest–Forest; C–F, Crop–Forest; SG–F, Scrubland/grassland–Forest.
Figure 1
Figure 2
Figure 3

Land-use history

- F-F
- C-F
- SG-F

Growth rate (Mg C ha\(^{-1}\) year\(^{-1}\))

Water availability (%)
Figure 4