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Adapting forests to climate change: an experiment to promote different tree species in mixed Scots pine forests (*Pinus sylvestris* L.)

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Abstract

Key message We have applied various silvicultural treatments to enhance the adaptation of Scots pine (*Pinus sylvestris* L.) mixed forests to climate change in Montesquiu Castle Park (Catalonia, NE Spain). Some treatments have shown positive effects, such as increased growth, reduced defoliation, and greater resistance of Scots pine to drought. However, other treatments may lead to a shift in vegetation from pine-dominated to oak-dominated forests. Future extreme droughts could increase pine mortality, potentially accelerating this shift. These findings are significant for forest management aimed at adapting these species to climate change in their southern distribution range: forest thinning could improve Scots pine's ability to cope with stress, while pine removal may promote the growth of pubescent oak.

Context Forested systems around the globe are being modified and climate change is one of the main drivers. Many regions of Spain, especially in the south and the east, where aridity is predicted to increase, could be some of the most vulnerable places for Scots pine (*Pinus sylvestris* L.) in Western Europe. In some cases, defoliation, mortality, and lack of regeneration of this species have induced a vegetation shift, as has been seen with *Quercus* spp. Adaptive forest management might help adjust the vulnerable forest systems to new climatic conditions.

Aims This study, carried out in north-eastern Spain, applies silvicultural treatments to promote changes in species composition for improving the adaptation to climate change of a Scots pine mixed forest. The main objective is to evaluate how different silvicultural treatments give rise to more adapted stands in terms of survival, growth, and regeneration.

Methods Three experimental treatments (and one control) were applied, two of them to reduce competition for Scots pine and a third pursuing the acceleration of replacement of Scots pine by pubescent oak (*Quercus pubescens* Willd.). The response of the stands to the treatments was monitored during 6 years.

Results Mortality of Scots pine was nil or very low in the different treatments, but defoliation showed significant differences among treatments at the end of the study: 42% in the control treatment (CO), 25% in the understory clearing treatment (C), and 18% in the understory clearing and pine thinning treatment. The increment in the basal area of Scots pine between 2015 and 2021 did not show significant differences among silvicultural treatments ($F = 3.9$, $p > 0.05$), but that of pubescent oak was higher in the pine logging than in the other treatments. Regeneration of Scots pine and pubescent oak did not differ among silvicultural treatments.

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Conclusions These findings have relevant implications for the use of management to adapt forests to climate change: in its southern distribution range, forest thinning could improve the capacity of Scots pine to cope with stress conditions, whereas pine removal may promote pubescent oak.

Keywords Forest management, Forest adaptation, Climate change, Scots pine (*Pinus sylvestris*), Pubescent oak (*Quercus pubescens*), Vegetation shift, Thinning

1 Introduction

Climate change forecasts predict an increase in global surface temperatures—ranging from 1 to 3.7 °C by the end of the twenty-first century—and less water availability (IPCC 2023). This is especially true in the Mediterranean Basin, where the average warming will exceed the global mean value by 20% on an annual basis and 50% in summer, and the annual precipitation will decrease, leading to longer dry periods (MedECC 2020). In general, water-limited forests are expected to suffer a decline in productivity and a decrease in carbon sink capacity (Vayreda et al. 2012). This increased aridity, together with forest expansion due to land-use changes caused by rural abandonment, has widespread impacts on forests, such as forest decline (e.g., Carnicer et al. 2011; Peñuelas et al. 2017) or more recurrent and severe wildfires (e.g., Pausas and Fernández-Muñoz 2012; Ruffault et al. 2020).

Over the last decades, forest management has focused on mitigation of climate change, aiming to reduce and reverse the causes of climate change, and on adaptation, to anticipate changes to help the systems adjust, prepare and accommodate to new climatic conditions (Millar et al. 2008; Ruiz-Peinado et al. 2017; Ramírez-Valiente et al., 2022). The simultaneous consideration of adaptation and mitigation (and their trade-offs; D'Amato et al. 2011; Bradford and D'Amato 2012) is especially important because managers need to consider specific strategies to meet their specific objectives, such as forest growth or forest shift. Adaptive forest management is a key element in promoting forest capacity to deal with increased climate variability and uncertainty (Bolte et al. 2009; Innes et al. 2009; Lucas-Borja et al. 2021). Generally, adaptive management oscillates between two alternatives: trying to maintain the initial forest structure and composition, which includes improving stress resistance or system resilience after a disturbance, or accepting that change is inevitable and then considering a new structure and composition (Millar et al. 2008; Bolte et al. 2009).

The Mediterranean Basin represents the southern distribution limit of many tree species in the northern hemisphere, as is the case for Scots pine (*Pinus sylvestris* L.), the most widespread pine species around the globe (Barbéro et al. 1998). With this distribution limit, Spain may be one of the most vulnerable places for Scots pine in terms of mortality (Bogino et al. 2009; Archambeau et al. 2020), as populations appear to be particularly vulnerable to increasing aridity (Hampe and Petit 2005; Herguido et al. 2016). Under water stress conditions, the species has a strict stomatal control of transpiration (isohydric behavior) (Irvine et al. 1998; Martín-Gómez et al. 2017). However, this behavior can affect carbon balance, inducing the consumption of carbon reserves which, in turn, can result in the death of the tree due to C-starvation (McDowell et al. 2008). Defoliation, mortality, and lack of regeneration events are already evident in Scots pine forests (Galiano et al. 2010, 2011; Hereş et al. 2012, 2013; Vilà-Cabrera et al. 2013). In some cases, these events are associated with the enhanced recruitment of other species leading to a vegetation shift, as has been seen with oaks (Carnicer et al. 2014). Consequently, understanding how mortality, growth, and regeneration are affected by climate change may help in the design of management strategies for better-adapted Scots pine forests.

The review by Vilà-Cabrera et al. (2018) classified adaptation strategies in the Mediterranean Basin into five different types (the first two trying to maintain the initial forest structure, and the last three promoting forest change): (a) reduction of stand density, to increase growth, health and value of the remaining trees; (b) management of the understory, to break vertical and horizontal fuel continuity; (c) promotion of mixed forests, to promote diversity; (d) change of species composition, to drive forest composition towards better-adapted provenances or even species; and (e) promotion of spatial heterogeneity at a landscape-scale, to enhance connectivity and prevent the expansion of fires. Research on adaptation in the Mediterranean Basin has mainly focused on strategies aimed at decreasing risk and promoting resistance in the short-term, such as the reduction of stand density or management of the understory (Vilà-Cabrera et al. 2018). There are few experimental approaches promoting long-term adaptation (but see, e.g., Molina et al. 2021), especially those addressing management strategies to promote changes in species composition. To our knowledge, this is the first experimental study in the Mediterranean to apply silvicultural treatments to promote changes in species composition and improve forest adaptation to climate change in a forest currently dominated by Scots pine. In this study we evaluated how different silvicultural treatments that modify the composition of a mixed forest of Scots pine in northeastern Spain give rise to stands that are more adapted in terms of (i) survival (and also defoliation, as a measure of tree health) of the trees that remain, both in the canopy and in the understory; (ii) growth of the different species, in particular in response to drought periods; and (iii) regeneration of species present in the stand. The aim was to verify whether these silvicultural treatments improve the state of the forest and the species present in all or at least some of these basic processes of forest dynamics.

2 Material and methods

2.1 Study site

The study was carried out in the Montesquiu Castle Park in the Pyrenean foothills region (Catalonia, NE Spain), at a latitude of 42° 07′ N and a longitude of 2° 13′ E. The study area was selected for two main reasons. Firstly, the area was inside the perimeter affected by the 2012 drought (Banqué et al. 2013) and pest attacks, such as the beetle *Ips* sp. (J. Jürgens, personal communication, 2014). Secondly, there was great interest among park managers to receive scientific assessments related to the management of the forest. The study site is composed by a mixed forest of Scots pine and, to a lesser extent, pubescent oak. Other accompanying tree species (that is, woody species with individuals with diameter at breast height (DBH) ≥ 7.5 cm) in a much lower proportion in the whole area were field maple (*Acer campestre* L.), Italian maple (*Acer opalus* Mill.), Montpellier maple (*Acer monspessulanum* L.), holm oak (*Quercus ilex* L.), whitebeam (*Sorbus aria* L.), and wild service tree (*Sorbus torminalis* L.). Scots pine regeneration and growth was favored during the twentieth century, until the abandonment of active forest management in the 1970s. Other woody species in the understory (that is, without individuals with maximum diameter at breast height (DBH) ≥ 7.5 cm) were Montpellier maple, whitebeam, common hawthorn (*Crataegus monogyna* Jacq.), common dogwood (*Cornus sanguinea* L.), holly (*Ilex aquifolium* L.), common juniper (*Juniperus communis* L.), and common box (*Buxus sempervirens* L.). The forest studied had a canopy cover of 65% (based on our own measurements).

2.2 Experimental design and implementation

The experimental design consisted of four large pilot areas of approximately 1 ha each, to which different silvicultural treatments were applied in 2014 (Table 1): a control area with no management (CO) and three experimental treatments, two consisting of different intensities of both thinning and understory clearing to reduce competition for Scots pine (understory clearing, UC; and understory clearing and pine thinning, UCPT), and a third pursuing the acceleration of the replacement of Scots pine by oak by eliminating the pines (pine logging, PL). As expected, these treatments resulted in forests with different structures and compositions after their application (Table 2). Ideally, the whole experiment should have been replicated in different locations to provide statistical power and avoid pseudo-replication, but this was not possible due to the significant efforts required and the lack of separate areas that were clearly comparable. The data generated during this experiment are freely available (Retana et al. 2025).

2.3 Data collection

In each area, three permanent plots (10 m radius, 314 m^2 surface) were randomly distributed. The center of the plots was permanently marked with a 1-m iron stick, ensuring their easy location for future monitoring. In each plot, general information was recorded regarding location, orientation, altitude, slope, characterization of soil depth, visual characterization of the position of the slope, and other characteristics that condition the forest or the possible actions to be carried out: percentage of stones in the soil, erosive processes and previous forest management. Each variable regarding forest structure and forest health was monitored over time.

Table 1 Description of the silvicultural treatments applied in each treatment and the objective sought

Treatment	Description
Control (CO)	No intervention. No actions were carried out in the forest, leaving Scots pine and the understory species at their initial density levels
Understory clearing (UC)	Application of understory clearing to reduce tree competition. The clearing implied a 50% reduction of the basal area of oak and other associated understory species. Pine trees were not removed. Plant residues were left in the forest
Understory clearing and pine thinning (UCPT)	Application of low thinning of pines and complete understory clearing to reduce tree competition. This treatment involved the total elimination of oak and other associated species and the reduction of the Scots pine basal area by 30%. Branches were cut up and spread within the plots while logs were removed
Pine logging (PL)	Elimination of Scots pines to accelerate the replacement of pines by oaks and evaluate the oaks' future development. This treatment involved the total elimination of all Scots pines to enhance oak dominance. Branches were cut up and spread within the plots while logs were removed

Table 2 Mean ± SE values of the plots before and after the different silvicultural treatments. Abbreviations: control (CO), understorey clearing (UC), understorey clearing and pine thinning (UCPT), pine logging (PL)

Plot	Species	Density (individuals/ha)		Basal area (m^2/ha)	
		Before	After	Before	After
CO	*P. sylvestris*	589 ± 16	589 ± 16	22.7 ± 1.7	22.7 ± 1.7
	Q. pubescens	239 ± 79	239 ± 79	5.0 ± 2.6	5.0 ± 2.6
	Other species	48 ± 48	48 ± 48	0.3 ± 0.3	0.3 ± 0.3
UC	*P. sylvestris*	499 ± 65	488 ± 74	22.6 ± 1.5	22.2 ± 1.8
	Q. pubescens	117 ± 117	64 ± 53	1.2 ± 1.2	1.1 ± 1.0
	Other species	244 ± 153	127 ± 55	3.6 ± 2.3	2.4 ± 1.4
UCPT	*P. sylvestris*	573 ± 217	406 ± 98	26.4 ± 7.96	18.2 ± 4.0
	Q. pubescens	202 ± 70	0	2.8 ± 1.0	0
	Other species	212 ± 70	0	18.4 ± 17.5	0
PL	*P. sylvestris*	586 ± 10	0	17.3 ± 0.6	0
	Q. pubescens	585 ± 22	530 ± 56	9.8 ± 2.1	9.1 ± 1.3
	Other species	137 ± 56	127 ± 55	6.2 ± 5.0	0.9 ± 0.4

Within each plot, all trees (defined as individuals with a diameter at breast height (DBH) ≥ 7.5 cm) were surveyed, identified, measured, and censused for mortality. The trees were measured in 2014 (before the treatment), 2015 (after the treatment), and 2021. The diameter at breast height was measured in all trees inside the plot with diametric tape. In the case of Scots pine, 10 trees per plot of the different diameter classes were chosen randomly. The trees were marked and labeled with a number plate to follow changes throughout the project. These 10 trees per plot were monitored to visually estimate the percentage of defoliation (proportion of non-present leaves in relation to leaves present on a healthy tree) using a field visual identification method based on the DEBOSCAT project (Banqué et al. 2013) and the Spanish ICP Forest Monitoring Network (Level II www.magrama.gob.es). Scots pine defoliation was measured in spring and autumn 2015, 2016, and 2017; and in autumn 2019 and 2020. Scots pine mortality, measured as the percentage of dead trees per plot, and defoliation, estimated as the mean percentage of crown defoliation of living individuals, was used to assess the species decline at plot level. Scots pine mortality was measured in 2014 (before the treatment), 2015 (after the treatment), and 2021. Density (number of trees per ha) and basal area per plot of Scots pine, pubescent oak, and other accompanying tree species were determined (see list of accompanying tree species in Sect. 2.1).

The abundance of seedlings and saplings in each plot was used as a measure of potential regeneration. Saplings (defined as individuals with 2.5 < DBH < 7.5 cm) were identified to species and counted across the plot. Seedlings (defined as individuals with DBH < 2.5 cm) were recorded in a 2 × 4 m^2 quadrat in each plot. Regeneration was measured before the treatments in 2014. To evaluate the effect of the treatments, the number of saplings and seedlings was counted again in 2021.

Finally, using a hand increment borer, we sampled one stem core at 1.30 m above the ground for four to five Scots pine individuals in each plot. The pines were randomly selected within the plot and did not show differences of mean diameter at breast height among treatments (ANOVA, $F = 0.3$, $p = 0.74$; mean values of 28.1, 27.7, and 26.0 cm for the pines of the UCPT, UC, and CO treatments, respectively). One core was extracted per tree parallel to the slope. Cores were air-dried and smoothed using sandpaper until their tree rings could be easily recognized. Ring widths were measured to a precision of 0.01 mm, using CooRecorder computer software (version 8.1, Cybis Elektronik & Data AB). CDendro computer software (version 8.1, Cybis Elektronik & Data AB) was used to help analyze ring series and calculate ring width. Four cores did not cross-date well and were excluded from further analyses.

2.4 Climatic characterization

Meteorological data, including daily maximum temperatures, minimum temperatures, mean temperatures, and rainfall, were obtained from the meteorological station of Montesquiu, which belongs to the Catalan Meteostation Network (public meteodata server https://www.meteo.cat) and is located in the same Natural Park, 600 m apart from the experimental area. The period was limited from January 1987 to January 2021. The Standardized Precipitation-Evapotranspiration Index (SPEI), calculated as the difference between cumulative precipitation and potential evapotranspiration for a given period at monthly intervals, was computed to identify drought severity in the study area (Vicente-Serrano et al. 2010) using the SPEI R package (package cran).

The climate of the area is sub-Mediterranean, with an average temperature of 12.7 °C and an average annual precipitation of 764 mm (for the period 1987–2021), mainly concentrated in the summer period. Maximum summer temperatures can exceed 37 °C, while minimum winter temperatures can drop below −7 °C. SPEI showed the alternation of dry and wet periods, with a similar distribution in the frequency, intensity, and continuity of the dry/wet periods (Fig. 1).

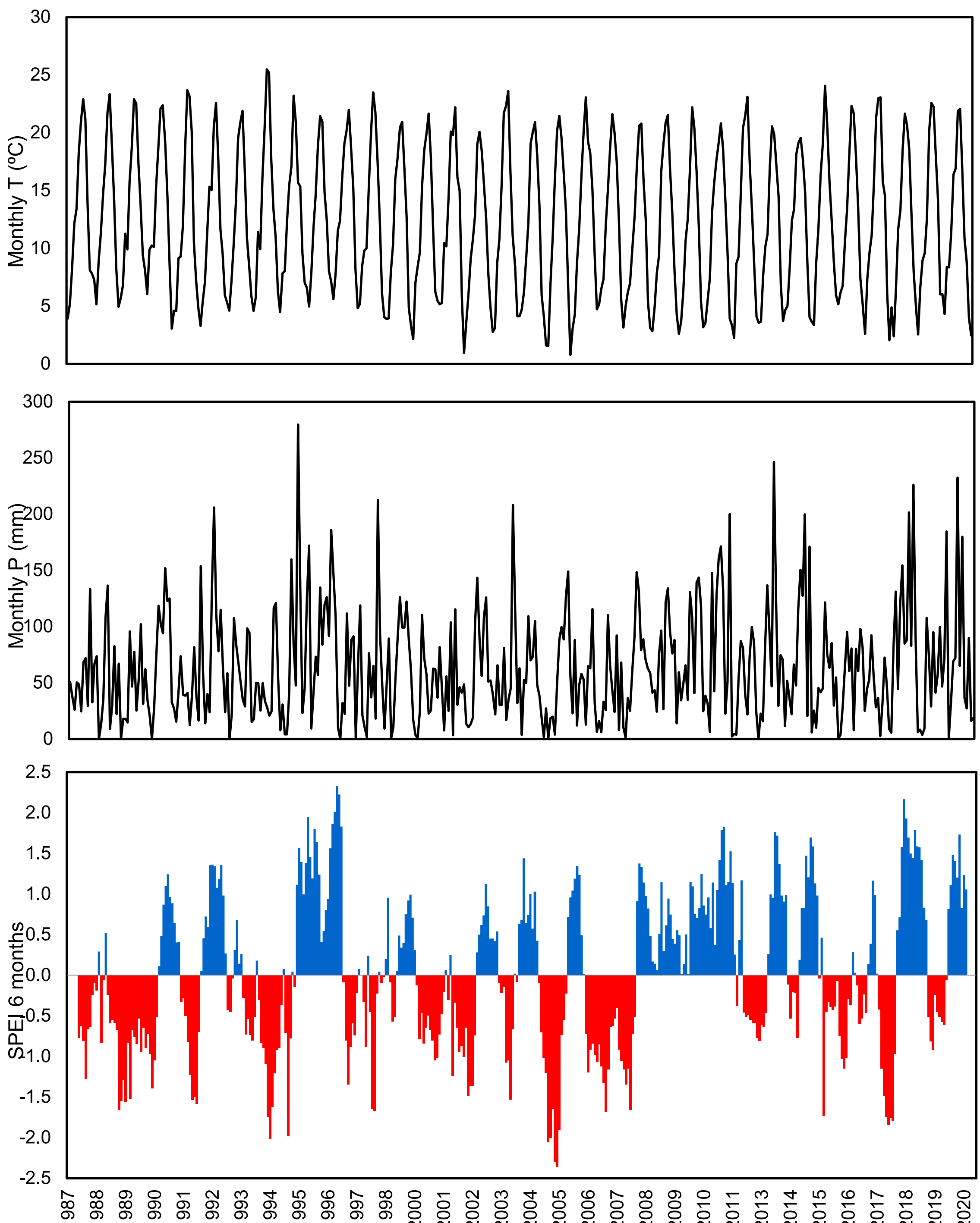

Fig. 1 Monthly temperature, monthly precipitation, and standardized precipitation-evapotranspiration index (SPEI) at the timescale of 6 months in Montesquiu from 1987 to 2020

2.5 Data analyses

2.5.1 Growth responses to drought

We investigated tree-ring responses to two drought events that occurred in 1994 and 2017, before and after the application of the treatments. These 2 years were the driest between 1987 and 2020 for the summer aridity index (AI; i.e., the average ratio of potential evapotranspiration to precipitation, UNEP 1992; AI < 0.20). To evaluate the effect of drought on tree growth dynamics, we calculated three indexes following Lloret et al. (2011):

- Resistance (Rt), indicating the ability to tolerate stress conditions without lowering ecological performance and calculated as $Rt = RWI_0/RWI_{pre}$
- Recovery (Rc), indicating the capacity to recover from damage suffered during the disturbance and calculated as $Rc = RWI_{post}/RWI_0$
- Resilience (Rs), indicating the capacity to recover from disturbances and reach pre-disturbance levels and calculated as $Rs = RWI_{post}/RWI_{pre}$,

where RWI_0 is the tree-ring width corresponding to the year of drought, and RWI_{pre} and RWI_{post} are the tree-ring width corresponding to the years before and after the drought event, respectively.

2.5.2 Statistical analyses

A one-way analysis of variance (ANOVA), with silvicultural treatment as the fixed factor, was performed to test for significant differences among the different treatments for the following variables: mortality, basal area increment, ring width, drought indexes (resistance, recovery, and resilience), seedling and sapling regeneration (to reach normality, these values were log-transformed). Post hoc testing was done using Tukey's HSD. All variables were checked for normality. To test defoliation tendency over time and throughout the treatments, a general linear mixed model (GLMM) was performed, with defoliation as the response variable, management as the fixed factor, time as a repeated measures variable with their interaction as explanatory variables, and individual trees as a random factor.

Statistical analyses were carried out using R software (R Development Core Team 2009) (packages: ggplot2, SPEI, tidyverse, ggpubr, broom, dplyr). Tree-ring data were analyzed using the dplR package, tree responses to drought using rstatix, and the GLMM using nmle. Significance for all statistical tests was accepted at $p = 0.05$.

3 Results

3.1 Survival and defoliation

After 6 years from the start of the experiment, the mortality of Scots pine was nil in UCPT and very low in the other two treatments (mean ± SE; CO: 2.6 ± 2.6%, UC: 3.5 ± 1.8%). The mortality of pubescent oak was nil in UC and low in the other treatments (CO: 5.0 ± 5.0%; PL: 6.6 ± 4.1%). The tests showed no significant differences for Scots pine (ANOVA: $F = 1.4$, $p > 0.05$) or pubescent oak (Kruskal–Wallis: $H = 4.5$, $p > 0.05$).

Defoliation patterns for Scots pine in the different silvicultural treatments are represented in Fig. 2. In 2015, after the silvicultural treatments were applied, the percentage of defoliation showed small differences. However, these increased over time. Differences among treatments were evident in autumn 2020 when defoliation reached 42% in the control treatment, 25% in the UC treatment, and 18% in the UCPT treatment.

The GLMM results indicated significant effects of date, management, and the interaction date × management on mean crown defoliation (Tables 3 and 4). Thus, defoliation increased over time in the CO and, to a lesser extent, the UC treatment, while it decreased in the UCPT treatment.

3.2 Growth

Basal area increment (BAI) of Scots pine between 2015 and 2021 did not show significant differences among silvicultural treatments (Table 5). There were, however, significant differences in the BAI of pubescent oak from 2015 to 2021 among silvicultural treatments (Table 5):

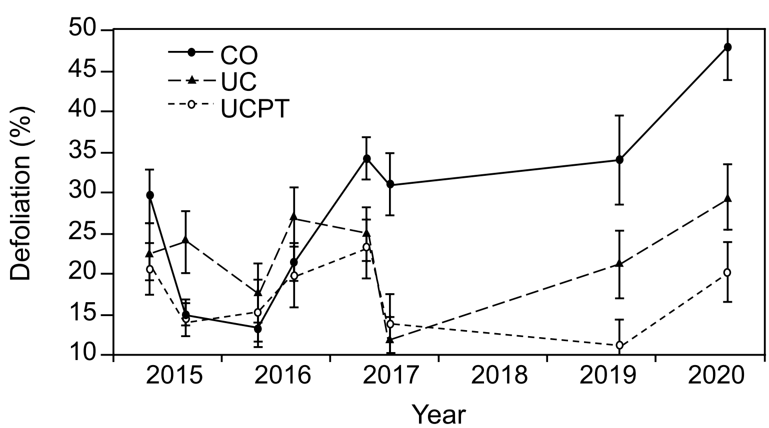

Fig. 2 Variation of Scots pine crown defoliation (mean ± se) from 2015 to 2021 in the different treatments. CO, control; UC, understory clearing; UCPT, understory clearing and pine thinning

Table 3 Analysis of deviance table for the GLMM analysis carried out with Scots pine crown defoliation percentage as a response variable from 2015 to 2021 and among the different silvicultural treatments

	Df	Chi-square	*P*
Intercept	1	4.0	0.045
Date	1	13.7	< 0.001
Treatment	2	36.8	< 0.001
Date × treatment	2	41.4	< 0.001

Table 4 Summary and correlation of the general mixed model with defoliation (%) as a response, and time-treatment interaction as the explanatory variable

	Estimate	Std. error	*t*-value		*p*-value
(Intercept)	– 24.5	12.2	– 2.0		0.045
Date	0.002	0.001	3.7		0.000
UC	– 111.9	18.6	– 6.0		0.000
UCPT	44.4	16.6	2.7		0.009
Date × UC	0.007	0.001	6.4		0.000
Date × UCPT	– 0.007	0.001	– 2.7		0.007
AIC	5022.2				
BIC	5057.7				
logLik	– 2503.1				
	(Intr)	Date	UC	UCPT	Date x UC
Date	– 1.0				
UC	0.2	– 0.2			
UCPT	– 0.1	0.1	– 0.6		
Date × UC	– 0.2	0.2	– 1.0	0.6	
Date × UCPT	0.1	–0.1	0.6	– 1.0	– 0.6

BAI was higher in PL than in the other treatments. In contrast, BAI of other species did not show significant differences among silvicultural treatments (Table 5). Concerning the Scots pine tree-ring width, the more intense the silvicultural treatment applied, the higher the annual growth of Scots pine (Table 5). Thus, the annual ring width in UCPT was significantly higher than in the other two, UC and CO.

In relation to the effect of drought on tree growth dynamics, no significant differences were found among management treatments in the three indices computed after the 1994 drought event, when the forest was still not managed: resistance, recovery, and resilience index (Table 6). In the analyses of the response of Scots pine to the 2017 drought, there were significant differences among treatments for the resistance index and the resilience index, but not for the recovery index (Table 6). Both the resistance and the resilience indices showed higher values in UCPT than in UC and CO treatments (Table 6), especially the resilience index, which was twice as important after the drought than before.

3.3 Regeneration

In 2014, before the treatments, there was no difference among treatments for saplings or seedlings (Table 7). In 2021, the ANOVA tests for living saplings for Scots pine and pubescent oak indicated that there was no difference among silvicultural treatments (Table 7). Saplings of other species differed among treatments (Table 7). Concerning the abundance of seedlings in the different silvicultural treatments, no seedlings of Scots pine were registered in 2021 (Table 7), while there were high numbers and large variability of pubescent oak and seedlings from other species in all treatments, without significant difference among them (Table 7).

4 Discussion

4.1 Scots pine development under different silvicultural treatments

The impact of competition and water availability on the mortality of Scots pine has been reported previously in the Mediterranean (Vilà-Cabrera et al. 2013) and in central Europe (Bigler et al. 2006; Rigling et al. 2013). Moreover, some studies have revealed a delayed effect of drought that may result in a high mortality of the species (Martínez-Vilalta and Piñol, 2002; Galiano et al. 2010; Vilà-Cabrera et al. 2014). In our study, the mortality of Scots pine was very low or nil in the different treatments. However, crown defoliation of Scots

Table 5 Basal area increment (BAI) of Scots pine, pubescens oak and other species, and tree ring width of Scots pine between 2015 and 2021. *F* and *p* of each ANOVA test are given. Abbreviations: control (CO), understory clearing (UC), understory clearing and pine thinning (UCPT), pine logging (PL)

	F	*p*	CO	UC	UCPT	PL
BAI Scots pine	3.9	> 0.05	4.35 ± 1.17^a	4.24 ± 0.85^a	4.57 ± 1.78^a	-
BAI pubescent oak	31.8	< 0.001	0.67 ± 0.06^b	0.50 ± 0.25^b	0.08 ± 0.08^b	3.10 ± 0.36^a
BAI other species	1.3	> 0.05	0.20 ± 0.20^a	1.16 ± 0.47^a	0.57 ± 0.46^a	1.51 ± 0.61^a
Tree ring width pines	13.2	< 0.001	0.95 ± 0.03^b	1.08 ± 0.03^b	1.24 ± 0.05^a	-

Table 6 Resistance, recovery, and resilience indices, calculated for a 3-year period for each silvicultural treatment in a dry year (either 1994 or 2017), before and after the treatment. Abbreviations: control (CO), understory clearing (UC), and understory clearing and pine thinning (UCPT). *F* and *p* of each ANOVA test are given. Different letters correspond to significant differences according to the post hoc Turkey test among treatments for each year (1994 and 2017), not across the different indexes

	Resistance index		Recovery index		Resilience index	
	1994	2017	1994	2017	1994	2017
CO	0.71 ± 0.04 [a]	0.73 ± 0.04[b]	1.61 ± 0.18 a	1.60 ± 0.08[a]	1.11 ± 0.10[a]	1.16 ± 0.06[b]
UC	0.79 ± 0.06[a]	0.99 ± 0.07[b]	1.66 ± 0.10 a	1.38 ± 0.11[a]	1.26 ± 0.08[a]	1.31 ± 0.11[b]
UCPT	0.82 ± 0.04[a]	1.43 ± 0.12[a]	1.69 ± 0.12 a	1.52 ± 0.13[a]	1.38 ± 0.11[a]	2.16 ± 0.23[a]
F	1.2	0.1	1.9	1.0	13.1	17.5
p	> 0.05	> 0.05	> 0.05	> 0.05	< 0.001	< .0001

Table 7 Mean ± SE density (individuals per hectare) of (a) seedlings and (b) saplings of Scots pine, pubescent oak, and other species in each management treatment before (2014) and 7 years after the treatments (2021). *F* and *p* of each ANOVA test are indicated below the means. Abbreviations: control (CO), understory clearing (UC), understory clearing and pine thinning (UCPT), pine logging (PL). Different letters correspond to significant differences among treatments according to the post hoc Turkey test

	P. sylvestris		*Q. pubescens*		Other species	
	2014	2021	2014	2021	2014	2021
(a) Seedlings						
CO	0	0	17,900 ± 9,058	10,600 ± 625	26,700 ± 6245	11,200 ± 2500
UC	0	0	2500 ± 2041	1670 ± 833	13,300 ± 5148	24,600 ± 6138
UCPT	0	0	58303 ± 4262	5000 ± 3819	11,700 ± 7,128	14,100 ± 2732
PL	0	0	9166 ± 6980	13,750 ± 6960	38,300 ± 10.040	29,600 ± 2083
F	-	-	1.0	2.3	1.9	4.4
p	-	-	0.442	0.150	0.205	0.052
(b) Saplings						
CO	286 ± 120	143 ± 48	276 ± 118	111 ± 15	414 ± 73	2,101 ± 350 [a]
UC	127 ± 63	105 ± 56	117 ± 21	53 ± 28	467 ± 101	254 ± 143 [c]
UCPT	32 ± 32	21 ± 21	85 ± 56	170 ± 56	541 ± 80	318 ± 37 [c]
PL	138 ± 59	0	541 ± 306	202 ± 106	743 ± 228	1030 ± 258 [b]
F	1.9	2.8	1.8	1.4	0.6	15.4
p	0.201	0.115	0.215	0.322	0.615	0.002

pine trees varied among the silvicultural treatments. As defoliated trees are more vulnerable, loss of photosynthetic tissue can lead to further decline of the trees (Salmon et al. 2015). Our study reports that mean tree crown defoliation was positively correlated with higher stand competition and, consequently, lower water availability during summer, as also seen in other studies (Galiano et al. 2010; Rigling et al. 2013). Defoliation patterns did not show the same patterns in the different treatments (Fig. 2): defoliation tended to increase in the control treatment (CO) and it showed a slight increase in the understory clearing treatment (UC), whereas in the most severe silvicultural treatment, the one with understory clearing and pine thinning (UCPT), it slightly decreased over time, suggesting that forest management could reverse defoliation patterns.

Our results also revealed that silvicultural treatments had a positive effect on Scots pine growth. Even though the basal area increment was not significantly different, individual tree-ring width varied among treatments. The most severe silvicultural treatment, UCPT, showed a higher tree-ring width compared to the other two treatments, CO and UC. Higher growth rates have frequently been observed after thinning for Scots pine (Sohn et al. 2016; Aldea et al. 2017). According to previous studies, this effect is related to more water availability in soils because of reduced competition, especially during extreme drought events (Bogino and Bravo 2013; Sohn et al. 2016).

Additionally, in our case, we were able to evaluate the effect of two dry years, 1994 and 2017, in terms of resistance, resilience, and recovery. As expected, the impact of the silvicultural treatments on Scots pine response to drought was well recorded in tree-ring widths (Table 6). No differences were seen after the 1994 drought event, when the forest was still not managed. But after the 2017 drought, the capacity to both cope with stress conditions (resistance) and reach pre-disturbance levels (resilience) was higher in UCPT (i.e., the treatment with understory clearing and pine thinning) than in the other two treatments. However, the recovery index, that is, the capacity of Scots pine to recover from the drought, did not differ among treatments. This is probably related to water availability before and after this drought period. Thus, the years before the drought event were also dry (see SPEI in Fig. 1), involving higher competition for water in denser plots and consequently affecting growth. In contrast, the following years were more humid and probably did not involve competition for water, which may explain the lack of differences in recovery among treatments.

Regarding regeneration, Scots pine is a shade-intolerant species that requires high irradiance but also an adequate supply of soil moisture and air humidity to germinate and establish (Castro et al. 2004). Although Scots pine dominates the overstorey, seedlings were absent in all the silvicultural treatments, including in the UCPT, where we would expect new recruits due to the existence of open gaps (Huth et al. 2022). The lack of germination could be a consequence of the small size of the gaps, or the inability to germinate under dry conditions (Galiano et al. 2010; Vilà-Cabrera et al. 2013). Apart from the seedlings, the density of saplings plays an important role in determining the future composition of the forest. In Montesquiu, the number of Scots pine saplings was not significantly different among silvicultural treatments, but density was remarkably low, below 200 individuals·ha^{-1} in all the cases. Therefore, regeneration of Scots pine was not guaranteed by any of the treatments.

4.2 Response of pubescent oak in the current scenario

The lack of regeneration, together with increasing defoliation, could have a severe impact on the long-term persistence of Scots pine in the studied communities. In contrast, pubescent oak, which may be a potentially dominant species, showed a different pattern. Although the silvicultural treatments did not show differences in mortality, in the PL treatment, where pines were completely removed, the growth of pubescent oak was larger than in the other three treatments. This fact confirms, as expected, that this species responds positively to the removal of the dominant species in the area. Furthermore, although the response of pubescent oak to the 2017 drought year was not evaluated in this study, Steckel et al. (2020) reported that *Quercus* species had a greater capacity to withstand water stress and return to previous growth rates, and consequently, higher resistance and resilience indices than Scots pine. The same study revealed that the combination of Scots pine and *Quercus pyrenaica* showed a complementary behavior of the species through niche partitioning and facilitation, but this relationship could be reversed under water-limited conditions, leading to competition.

Furthermore, pubescent oak had a higher abundance of seedlings and saplings in two of the treatments (Table 7). This may be because of its competitive advantage under drought stress conditions (Marañón et al. 2004; Galiano et al. 2010) but, especially, because saplings and seedlings of *Quercus* spp. are shade-tolerant, owning the capacity to persist in the understory until new canopy gaps are created, providing them with the opportunity to grow. Regeneration of pubescent oak was not significantly different among the four treatments, but the pool of seedlings and saplings in each treatment could determine the future composition of the forest. Further research is needed to detect the mid- and long-term impacts of this regeneration.

4.3 Potential vegetation shift and forest management implications

In the case of Montesquiu, pubescent oak grew and regenerated well, with healthy individuals, whereas Scots pine trees survived and kept growing, but they generally showed a weak condition and very low regeneration, although it is true that the treatments applied were not selected to regenerate Scots pine. The future drier conditions expected in the area (Field et al., 2014; Calbó et al. 2016) will probably not improve the situation of Scots pine. According to the Third Report on Climate Change in Catalonia (Calbó et al. 2016), precipitation in the region is predicted to decrease by 5.3% by the end of 2050, with summer and autumn being the periods with the most pronounced declines; meanwhile, temperatures will increase by around 1.6 °C by 2050, with a higher increase in summer and autumn. Both conditions will lead to even more severe drought episodes and water scarcity. In this future scenario, we would expect an expansion of *Quercus* spp. and the loss (i.e., higher mortality) of Scots pine in the area, a situation that has already been reported in other studies (Galiano, et al. 2010; Rigling et al. 2013; Vilà-Cabrera et al. 2013; Batllori et al. 2020). This might result in a vegetation shift from a pine-dominated to an oak-dominated forest.

Our study also reveals the significance of the application of silvicultural treatments for forest adaptation to climate change. Different adaptation strategies were applied to achieve different goals. Firstly, understory clearing had no effect on the dynamics of any of the species. Understory clearing, together with the removal of the associated species and the reduction of Scots pine density, leads to short-term efficacy in Scots pine individuals (i.e., higher growth, decreasing defoliation, and higher resistance and resilience to droughts), but more research is needed to detect long-term impacts. We expect that some of these tendencies will intensify with time, and the delayed mortality of Scots pine will be evident in a few years. Finally, Scots pine removal implied a higher growth of pubescent oak. Accelerating the substitution of the dominant species towards species better adapted to droughts could also benefit the long-term resilience of ecosystems (Elkin et al. 2015).

These findings have relevant implications for the use of management to adapt forests to climate change and can be of help to forest managers in the decision-making process. Our results support the idea that forest thinning could improve the capacity of Scots pine to cope with stress conditions, whereas pine removal in its southern distribution range may promote pubescent oak. This study suggests that there are management options to maintain particularly important Scots pine habitats, which may be combined with stronger management actions to accelerate the successional change undermore adverse scenarios. Ultimately, proactive forest management strategies will be essential in fostering resilience and ensuring the sustainability of these ecosystems in the face of ongoing climate change.

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Authors' contributions
DP, EP, and JR have made substantial contributions to the conception and design of the work; SB, DP, EP, and JR have participated in the acquisition, analysis, and interpretation of data; SB, DP, EP, and JR have written the work and substantially revised it. All authors have read and approved the final manuscript.

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Data availability
The data generated during this experiment are freely available following this link: Retana, Javier; Buscà, Sara; Pascual, Diana; Pla, Eduard. 2025, "Montesquiu forest inventory data", https://doi.org/10.34810/data2056, CORA. Repositori de Dades de Recerca.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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