



Mixture mitigates the effect of climate change on the provision of relevant ecosystem services in managed *Pinus pinea* L. forests

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ABSTRACT

Forecasted scenarios of climate change are expected to result in a dramatic reduction in the provision of Ecosystem Services (ES) from forests. Increasing tree species diversity has been proposed as a measure for adapting forests and warranting the provision of services, since mixed forests, if compared with monospecific forests, are expected to be more productive, resilient and stable facing disturbances. In the present work we use a modelling approach in order to quantify the provision of different ES under expected climate scenarios, comparing pure forests of *Pinus pinea* L. with mixed forests where the species grows accompanied by different *Quercus* and *Juniperus* species. To this aim we first adapted the existing individual tree level model PINEA2, originally constructed for pure even-aged stands of *P. pinea*, in order to consider the interspecific interactions acting in mixed forests. In a second step we used the so adapted model for forecasting and comparing the provision of different ES – focusing on stocking, growth, yield, CO₂ fixation, economic income and structural diversity – under current climate and expected scenarios RCP 4.5 & 8.5. Our results indicate that although growth and allometry in *P. pinea* trees is enhanced in mixtures, this effect is currently counterbalanced by the expected reduction in growth in the species occupying the understorey, thus under current climate conditions little differences due to composition are observed in the provision of ES. On the other hand, our simulations point to a generalized decrease in the ES supply under more severe climate change scenarios, being this reduction mitigated – at least in part – in mixed *P. pinea* forests, which are more competitive under the most restrictive environmental conditions. As a consequence, the promotion of mixtures by under-planting and/or releasing of pre-existing advanced regeneration of complementary species may be postulated as a management concept for adapting these forests to climate change.

1. Introduction

While forest systems provide a wide range of benefits to human society, defined as ecosystem services (ES, Ojea et al., 2012), it has been recognised that expected climate change may result in a dramatic reduction in the provision of these ES (Lindner et al., 2010). Among the expected impacts on ES provision are severe reductions in the quantity and quality of timber and other non-wood forest products, a decrease in the capacity of forests to act as CO₂ sinks, impacts on water regulation processes, shifts in species composition, local processes of decay and dieback, emerging pests, increased hazard of fire or windthrow and losses in the associated economic value (Hanewinkel et al., 2013, Spathelf et al., 2013). As a consequence, adaptive and an-

ticipatory management of the forests is required to guarantee the ecosystem functions, services and persistence (Seidl et al., 2011).

Among the proposals for adapting forests, different measures aimed at increasing the diversity and composition of forests have been formulated (Kolström et al., 2011). Mixed forests are expected to be more resilient and stable in the face of climate change and other disturbances, thus providing greater opportunity to maintain forest cover and sustain basic ecosystem functions in the long term (Jactel et al., 2017).

Although there is a general consensus on the positive relationship between diversity in forest species and most ecosystem services (Gamfeldt et al., 2013), debate still exists around whether a mixed forest performs better than a monospecific forest or provides a larger number of ES as this often depends on both the type of ES and the species composition (Knoke et al., 2008). As regards productivity, an increment

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in total biomass production – defined as overyielding (Pretzsch and Schutze, 2009) – is expected in mixed stands when compared with the sum of the expected individual yields obtained in pure stands of the different species. However, this effect does not necessarily occur in all the species within the stand, especially if the species show quite different life strategies (Cordonnier et al., 2018), so enhanced growth at individual level is not necessarily reflected at stand-level (Forrester and Pretzsch, 2015). In addition, this increased productivity does not always mean an increase in economic income. In this regard, monocultures with conifers are expected to garner higher revenues in terms of timber productivity and quality (Pretzsch and Rais, 2016), while mixed forest may provide a wider variety of commercial products (Knocke et al., 2008).

The question of how and to what extent an increase in tree species diversity will affect a multitude of ecosystem processes simultaneously is still unclear (Brockerhoff et al., 2017). Some findings suggest a “jack-of-all-trades” effect of species diversity on multifunctionality (van der Plas et al., 2016), especially for ES that are not well correlated. Moreover, while some enhancement associated with increasing tree diversity is observed at tree or patch scale, upscaling to stand and forest scale may result in trade-offs, even incompatibilities between different ES, or in synergies (Van der Plas et al., 2016, Mina et al., 2016, Morán-Ordóñez et al., 2020).

Different approaches have been proposed to quantify the different ES provided by a forest, including expert based knowledge and surveys (Carnol et al., 2014; Ray et al., 2015), meta-analysis or review of existing literature (Brockerhoff et al., 2017), direct static estimation from National Forest Inventories data (Gamfeldt et al., 2013) or the use of forest growth models (Pukkala, 2018). Typical forest growth models acting at stand-level have been directed towards determining the evolution and productivity in terms of timber of a forest stand – commonly a monospecific one – under different management options. However, these types of models can be adapted to determine ES provision if the outputs from the model are used to assess the provision of a wider variety of indicators of ecosystem functioning (Mäkelä et al., 2012). For this purpose, these models must (i) be sensitive to the different underlying environmental and site factors, (ii) implement proposed management alternatives, and (iii) provide outputs at the required spatial and temporal scales, permitting the derivation of the expected ecosystem services.

Current landscape in inner Spain is mainly dominated by pure even-aged pine forests. This is a consequence of the forest management policy applied in the decades of the mid-20th century, where pines were promoted as the main species in both the natural mixtures (e.g. mixtures of *Pinus pinea* L. with *Quercus* and *Juniperus* species) and new afforestations. These monospecific forests have been identified as highly vulnerable ecosystems in the face of climate change and a recent decrease in the provision of ES associated with drought events has been observed (Lindner and Calama, 2013). This fact, together with a recent orientation of towards ‘closer to nature’ ecosystems has led to increasing interest in maintaining and promoting these types of admixtures (Mayoral et al., 2015; de-Dios-García et al., 2015). Within this general framework, the main objective of the present work is to use a model-based approach to study whether increasing the species diversity of the *P. pinea* forests may affect the provision of different ES, and if this effect will remain constant under different forecasted climate scenarios. In order to attain this main aim, our specific objectives were:

(i) To analyse the effect of mixture on tree growth dynamics and allometry of *P. pinea*, *Quercus* and *Juniperus*. This involved adapting the existing climate sensitive individual tree level model PINEA2, originally constructed for pure even-aged stands of *P. pinea*, to the conditions of mixture with *Quercus* and *Juniperus* species.

(ii) To assess and compare the suitability of pure and mixed managed stands in terms of provision of different ecosystem services – focusing on stocking, growth, yield, CO₂ fixation, economic income and structural diversity – over a 90-year timespan (2010–2100) under historical climate conditions and two alternative climate scenarios (RCP 4.5 and 8.5), for a Business as Usual management system.

Our main hypothesis is that individual tree increments are expected to be enhanced in mixed stands with respect to pure stands. This enhanced tree growth, together with better occupancy of the available space, may result in improved provision of ES in terms of stocking, growth, timber and cone production, CO₂ fixation, economic income and structural diversity in mixtures. In addition, we expect a generalized and significant reduction in the ES provision as climate conditions become more limiting, which may be attenuated in mixtures.

2. Material

2.1. Study area

The study area is located on the limestone plains in the east of the province of Valladolid (Spain), within the geographical region of the Spanish Northern Plateau, defined by the basin of the river Duero. Altitude ranges from 800 to 890 m, the average annual precipitation is highly variable (between 220 and 630 mm, with an average value of 400 mm) and the mean annual temperature is 12 °C. The area has a Mediterranean continental climate with a characteristic dry summer period during which the mean monthly precipitation is 21 mm. The main types of soils found in the area are alfisols, entisols and inceptisols, with an average water holding capacity of 248 mm/m (Sánchez-Palomares et al., 2014).

Mixed stands comprising *P. pinea*, *Quercus ilex* subsp. *ballota* (Desf.) Samp., *Quercus faginea* subsp. *faginea* Lam. and *Juniperus thurifera* L. are the most diverse and complex forest systems in the region (Madrigal, 2014). Although these natural forests were transformed in the past (by means of strip clearcutting) into monospecific even-aged stands of *P. pinea* for timber and pine nut production (Gordo, 1999), a tree selection system is currently applied to promote growth and regeneration of individuals of all the species. Biodiversity is currently the main management objective in these forests, together with other ecosystem services such as cone and nut production, timber and biomass, mushrooms and recreational uses.

2.2. Experimental design – Data set

Data for this study were collected in two types of managed forests according to species composition: monospecific evenaged *P. pinea* forests and heterogeneous mixed forests where *P. pinea* grows alongside other species. Thirty-two circular plots of variable area (between 120 and 2000 m²) were installed in monospecific even aged stands of *P. pinea* L (Fig. 1). These plots are part of a network of permanent plots for monitoring growth and cone production established by INIA-CIFOR in 1996. At plot installation, each of these plots comprised 20 trees with dbh > 5 cm. The design used to select the plots attempted to include a balanced representation of the age range, density and site index available. At plot installation, tree coordinates, diameter at breast height, stump diameter, total height, height to crown base, and four perpendicular crown radii measured in cardinal directions were recorded for all the trees. Plots were remeasured in 2001, 2008 and 2016. During the study period some trees were felled as part of common thinning practices; the years in which this took place being recorded.

Within the same territory, thirty plots (500 m²) were installed during the summer of 2011 at five experimental sites (3000 m²) where *P. pinea* forms mixtures with *Q. ilex*, *Q. faginea* and *J. thurifera* (Fig. 1).

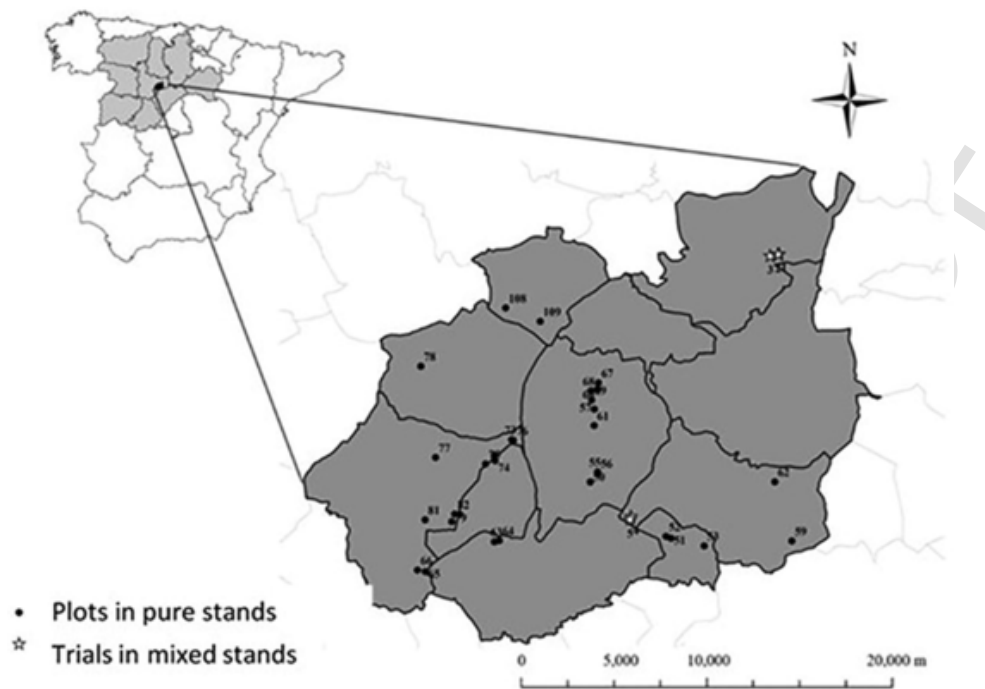


Fig. 1. Location of the study area and experimental plots.

Within each plot, tree coordinates, dbh, stump diameter, total height, height to crown base, and four perpendicular crown radii were recorded for all trees with height > 1.30 m. Position and diameter of all the stumps remaining from earlier cuttings, as well as the date of the last cutting, were also recorded. Attributes of the sampled stands are shown in Table 1.

2.3. Radial increment measurements and BAI reconstruction

In order to study radial growth, a representative sample of trees was selected in both pure and mixed stands, aiming to have a balanced representation of the whole range of species and diameters identified in the study area. In pure stands, the 5 trees closest to the centre of each plot were cored in two perpendicular directions at 1.30 m above ground using a Pressler increment borer in order to obtain the tree ring growth series. In mixed plots, radial increment records at 1.30 m above ground were obtained from 20 to 30 *P. pinea* trees per experimental site (two cores per tree), 8–10 *J. thurifera* trees per experimental site (one core per tree), 10 *Q. faginea* trees per experimental site (one core per tree) and 3–4 *Q. ilex* per experimental site (in this case cross slice sections from felled trees). Cores and slices were obtained in fall season 2011, and processed, measured and cross-dated using standard methods (see supplementary material S1).

From these records of tree radial growth, annual basal area increment (BAI_{ijt} , cm^2) for each cored tree was computed for the period 1997–2011. In addition, we used backdating techniques to reconstruct the state of the plot in each year of the period and computed annual values for the different stand level parameters that act as potential explanatory covariates: basal area, mean squared diameter, dominant height and Reinekés stand density index. See Calama et al. (2019) and supplementary material S1 for further details on the backdating process applied.

2.4. Climate data

Monthly climatic variables, including mean, maximum, and minimum temperatures, as well as total rainfall were collected at a meteorological station located in the proximity of the study area ($41^{\circ}34' = N$, $4^{\circ}20' = W$, 2.5 km from the study site) and which is managed by the local forest service. Missing records (5.9%) were estimated using data from the Valbuena de Duero meteorological station ($41^{\circ}38' = N$, $4^{\circ}17' = W$, 6 km from the study site). The latter data are available from <http://www.inforiego.org>. Given the homogeneity of the orography and climate within the study area these two stations were considered enough representative for the whole territory.

2.5. PINEA2 model

The PINEA2 model is an integrated distance-independent tree-level model developed to predict the growth, dynamics and production of *P. pinea* stands. While originally designed for predictions in pure even-aged stands of the species in 5-year steps, the most recent updates permit its use in uneven-aged structures, include climate sensitive modules for basal area increment and cone production, and allow simulations to be carried out in one-year steps (Calama et al., 2016, 2019; del Río et al., 2017). In the present work our aim was to adapt the PINEA2 model to the conditions of mixture with *Quercus* and *Juniperus* species by fitting new modules for tree basal area increment, height-diameter relationship and crown dimensions for the three species. Outputs from each step of model simulation are presented as a tree-list including breast height diameter, tree height, crown width and cone production for each individual tree. Tree volume, biomass and CO_2 fixation estimates are therefore derived using Calama and Montero (2006), Rodríguez et al. (2008) and Ruiz-Peinado et al. (2011, 2012). More info on PINEA2 is available in Calama et al. (2007).

Table 1

Descriptive statistics for the main variables at plot and tree level recorded in 2011 inventory in pure and mixed plots.

Level	Variable	Statistic	Pure stands		Mixed stands		Total
			<i>P. pinea</i>	<i>P. pinea</i>	<i>Quercus sp</i>	<i>J. thurifera</i>	
Plot level	BA m ² ha ⁻¹	Mean	13.28	11.05	0.50	1.04	12.59
		Min	5.40	2.43	0.00	0.05	4.13
		Max	20.14	22.50	2.10	2.67	23.98
	N stem ha ⁻¹	Mean	207	190	82	101	373
		Min	57	20	0	0	20
		Max	994	680	360	380	1420
	Dg cm	Mean	32.2	31.1	8.9	12.6	23.4
		Min	15.4	18.9	6.2	6.1	14.6
		Max	59.4	42.9	13.7	23.8	36.5
	H m	Mean	7.4	8.4	4.3	5.4	–
		Min	2.5	6.3	3.2	3.9	–
		Max	15.6	10.3	5.2	9.5	–
	SDI	Mean	249	–	–	–	270
		Min	104	–	–	–	87
		Max	459	–	–	–	571
SI_pinea	Mean	14.9	11.7	–	–	–	
	Min	9.0	10.5	–	–	–	
	Max	20.1	12.2	–	–	–	
Tree level	d cm	Mean	31.9	31.4	8.5	12.1	–
		Min	10.9	6.1	3.2	4.5	–
		Max	69.4	53.4	14.9	26.2	–
	h m	Mean	7.4	7.8	4.4	5.3	–
		Min	1.4	3.1	1.9	2.4	–
		Max	19.0	13.7	7.4	9.5	–
	cw m	Mean	4.7	4.5	2.4	2.9	–
		Min	1.25	1.1	1.2	1.2	–
		Max	10.6	11.1	4.9	7.8	–
	BAI cm ⁻² year ⁻¹	Mean	26.6	14.5	2.3	3.7	–
		Min	1.5	0.1	0.1	0.1	–
		Max	170.4	58.2	11.9	19.9	–

Where BA: basal area; N: stand density; Dg: mean squared diameter; H: mean height; SDI: Reineke's stand density index (for the whole stand, not at species level); SI_pinea (site index for *P. pinea*); d: breast height diameter; h: total tree height; cw: crown width; BAI: tree basal area increment.

3. Methods

3.1. Modelling approach

– Basal Area Increment

Annual basal area increment (BAI_{isjt}, cm²) for tree *i* of the species *s* within plot *j* in year *t* was used as the response variable in the analysis. BAI was log transformed in order to attain normality, reduce heteroscedasticity in the variance, and reflect the non-linear pattern of tree radial increment. We fitted an independent model for log(BAI) for each species, except for *Quercus faginea* and *Quercus ilex*, which were jointly analyzed under the generic name of *Quercus sp.* We made this decision taking into account the small number of radial increment data collected

for *Q. ilex*, the similar ecological role they play as accompanying species in the understory, and the high similarity observed in size and raw increment data. The fitted models for *P. pinea* consider observations from both pure pine plots and multispecies mixed plots.

As the basal area increment dataset includes repeated observations recorded for trees within plots in different years, the observations coming from the same tree, plot and year tend to be more similar to each other than the average. To account for this severe departure from the basic assumption of independence, we utilized a multilevel linear mixed model (MLMM), including random effects acting at tree, plot, year and plot × year levels. The basic structure for the MLMM is:

$$\log(\text{BAI})_{isjt} = X_{isjt}\beta + u_i + v_j + w_t + z_{jt} + e_{isjt} \quad (1)$$

where log(BAI)_{isjt} is the observation for the response variable (log BAI) recorded in the *i*th tree of the *s*th species within the *j*th plot in the *t*th year; X_{isjt} represents a (1 × n) vector containing the observed values for the explanatory covariates in the *isjt*th observation; β is the vector of Best Linear Unbiased Estimators for the fixed parameters; u_i , v_j , w_t and z_{jt} represent the realization of the random effects acting at tree, plot, year and plot × year levels of variability, distributed following a normal distribution with mean zero and variance σ_u^2 , σ_v^2 , σ_w^2 , and σ_z^2 respectively; e_{isjt} represents a residual term, independent realization of a normal distribution with mean zero and variance σ_e^2 .

As a potential set of explanatory covariates X_{isjt} for log(BAI) for the different species involved in the study we first evaluated the attributes acting at different spatiotemporal scales identified in the previous work by Calama et al. (2019), which entered tree diameter and its quadratic form, dominant height, the logarithm of plot basal area, site index (defined as the dominant height for *P. pinea* trees at 100 years), the rainfall occurring during the period between 1st October of the previous year and 30th September of the current growth year, and the average temperature of May and June of the year. In our case total plot basal area was split among three different covariates reflecting the individual basal area of the different species occurring in the plot (*P. pinea*, *J. thurifera* and *Quercus sp.*), while site index and dominant height only refer to *P. pinea*. Once we had fitted these preliminary models – one per species - we evaluated the elimination of nonsignificant covariates and their substitution in the model by other potential covariates acting at tree, plot or temporal level. Among them we tested: number of stems/ha, Reineke's stand density index or mean squared diameter, all computed for each species separately; or different values of monthly, seasonal and annual values of precipitation and mean, maximum and minimum temperatures, starting from the month of September of the year before increment. Logarithmic, root and inverse transformation of these variables were also evaluated as potential predictors. Climate variables were standardized before entering the model by subtracting the mean value and dividing by standard deviation, thus a value of zero represents an average year.

– Height – diameter model

Height – diameter model for *P. pinea* followed the same structure as the interregional nonlinear mixed model for height-diameter relationship proposed for pure even-aged stands of the species (Calama et al., 2007), which has been fitted using data from both pure and mixed stands. The original single parameter *a* was expanded in order to include different mixture effects:

$$h_{ij} = 1.3 + \left[\left(a + c_1 \log(N_{j_ppa}) + c_2 \log(N_{j_oth}) + u_j \right) \left(\frac{1}{d_{ij}} - \frac{1}{D_{oj}} \right) + \left(\frac{1}{H_{oj} - 1.3} \right)^i + e_{ij} \right]$$

For *J. thurifera* and *Quercus* sp. we fitted independent simpler height – diameter log–log mixed models including the similar mixture effects:

$$\log(h_{ij}) = [a + u_j] + c_1 \log(N_{j,ppa}) + c_2 \log(N_{j,oth}) + b \log(d_{ij}) + e_{ij} \quad (3)$$

In Eqs. (2) and (3) h_{ij} and d_{ij} represent the height and breast height diameter of the i^{th} tree within the j^{th} plot; $N_{j,ppa}$ and $N_{j,oth}$ represent respectively the number of stems per ha for *P. pinea* and the other species in the j^{th} plot, u_j is a plot random effect and e_{ij} is the residual error term. The model in Eq. (4) is forced to pass through the point corresponding to the dominant diameter (D_{0j}) – dominant height (H_{0j}) for *P. pinea* of the j^{th} plot.

– Crown diameter model

Crown diameter (cw) of the i^{th} tree within the j^{th} plot was modelled separately for each species through linear mixed models including mixture effects. A linear model was selected in order to maintain the new model similar to the crown model implemented in original PINEA2 (Calama et al., 2007):

$$cw_{ij} = [\alpha + f_1 \text{Mixture} + u_j] + [\beta + f_2 \text{Mixture}] d_{ij} + e_{ij} \quad (4)$$

where *Mixture* is a dummy variable equaling 1 if the tree is located in a pure stand and 0 if it is located in a mixed stand. For *J. thurifera* and *Quercus* sp., as *Mixture* equals 0 (no data on pure stands) we included a proxy of the degree of mixture, given by the log of the number of stems per ha for the dominant species *P. pinea*. The rest of the symbols as previously stated.

All the models were fitted using SAS® procedure MIXED and macro %NLINMIX. BAI, height-diameter and crown-diameter models were validated using an independent data set (see supplementary material section S2).

3.2. Simulation of ES provisions

The models constructed in this way for BAI, height-diameter and crown-diameter, together with the model for cone production by Calama et al. (2016), were jointly used in order to simulate the evolution of two stands (simulation of 1 ha) with similar initial conditions of total basal area ($1.5 \text{ m}^2 \text{ ha}^{-1}$), one being a pure *P. pinea* stand, while in the other, *J. thurifera* accounts for 16% of total basal area, and *Quercus* sp. for another 16%. Initial conditions for both the pure and mixed stands are shown in supplementary material S3. We assumed an even-aged distribution, with an initial age of 30 years, in a stand with site index (defined as the dominant height for *P. pinea* at age 100 years)

of 13 m. The diameter distribution for the plots aims to mimic the frequencies of diameters observed in the younger stratum of the sampled plots.

The simulations were carried out in annual steps over a time span of 90 years, under a current climate scenario (mimicking observed climate between 1980 and 2010) and two alternative climate scenarios derived from the IPCC RCP 4.5 and 8.5 (see Fig. S3.1 in supplementary section S3). These scenarios forecast for the territory reductions in annual precipitation of 15% and 20%, and an increase in temperatures of $+3^\circ\text{C}$ – $+5^\circ\text{C}$ respectively for the studied territory at the end of 21st century. The climate scenario projections – including monthly values of the climate covariates entering the model – were sourced from the EU-CORDEX project at 11 km resolution, using an assemblage of 16 different regional models provided by the Spanish Meteorological Agency (www.adaptecca.es).

Simulated management of the stands mimics typical BAU approach (Table 2), focused on applying in pure stands an initial heavy pre-commercial thinning, and then applying thinnings when total basal area of the stand reaches over $18\text{--}20 \text{ m}^2 \text{ ha}^{-1}$, aiming to reduce the stocking of the stand down to a basal area of $10 \text{ m}^2 \text{ ha}^{-1}$. In the case of mixed stands, the selection of trees to be removed should focus on assuring that 80% of the remaining basal area corresponds to *P. pinea*, while the remaining 20% should be distributed among *Quercus* sp. and *J. thurifera*. Pre-commercial and first thinnings are applied from below, while the rest of the operations are selective. Regeneration cuttings start when the stand reaches 100 years, extending over a period of 20 years, so that by the end of the simulated timespan, all the old-trees will have been removed. Simulations were carried out using a macro programmed in SAS® 9.2. For each climate scenario and composition 10 stochastic simulations were carried out. Based on the outputs from each step of the simulation, we computed different ES, grouped into four different categories (stocking, yield, diversity and economic), as shown in Table 3.

The effect of the composition (pure vs. mixed) and climate scenario (Historical, RCP 4.5 and 8.5) on the provision of the different services and categories was tested by means of ANOVAs and visually assessed using amoeba diagrams. For the purposes of graphical comparisons each ecosystem service was standardized by dividing the observed value for each combination of climate scenario*composition*realization by the maximum value observed for the service over the whole set of simulations. In addition, the occurrence of trade-offs and synergies in the provision of Ecosystem Services was assessed by means of Pearson's correlation coefficients between pairs of ES computed for each climate scenario and type of stand (Morán-Ordóñez et al., 2020).

Table 2
Proposed BAU schedule for pure and mixed stands, indicating remaining number of pines (n_pp), quercus (n_qu) and juniperus (n_jt) after treatment.

Pure stands			Mixed stands				
Age	Treatment	n_pp	Age	Treatment	n_pp	n_qu	n_jt
Initial		780	Initial		520	300	430
30	Precommercial thinning	500	30	Precommercial thinning	250	200	250
45	Low thinning	250	50	Low thinning	150	200	125
60	Selective thinning	150	60	Selective thinning	100	100	125
85	Selective thinning	110	75	Selective thinning	75	75	75
100	Seedling cutting	75	100	Seedling cutting	50	25	25
110	Shelterwood cutting 1	40	110	Shelterwood cutting	25	25	25
115	Shelterwood cutting	20					
120	Final cutting		120	Final cutting			

Table 3
Ecosystem services indicators derived from the outputs of the model.

Type	Indicator	Abbreviation & units	Computation	
Stocking	Stocking Volume	V_stock (m ³ ha ⁻¹)	Average of the annual standing stocking values	
	Stocking Basal Area	BA_stock (m ² ha ⁻¹)		
	Stocking Biomass	Wt_stock (t D.M. ha ⁻¹)		
	Crown Coverture	Crown_cov (%)		
	Carbon stock	CO2fix_stock (t ha ⁻¹)		
	Diversity	Horizontal structure	CV_D	Variance coefficient for the diameter of the trees in the stand (mean value)
		Vertical structure	CV_H	Variance coefficient for the height of the trees in the stand (mean value)
Yield	Shannon index	Shannon	Shannon index referred to basal area per species (mean value)	
	Annual cone production	Cone (kg ha ⁻¹ year ⁻¹)	Average value for annual cone production	
	Mean annual timber increment	MAI (m ³ ha ⁻¹ year ⁻¹)	Considering standing stock + trees released in thinning and regeneration cuttings	
	Mean annual biomass increment	MBTI (t D.M. ha ⁻¹ year ⁻¹)		
	Mean annual CO2 fixation	CO2fix_tot (t ha ⁻¹ year ⁻¹)		
	Saw timber	Saw (m ³ ha ⁻¹)	Volume of saw-wood (diameter > 35 cm) released over the whole cycle	
	Economic	Annual income from cones	Inc cone (€ ha ⁻¹ yr ⁻¹)	Stumpage price: 0.20 €/kg
		Annual income from timber	Inc timber (€ ha ⁻¹ yr ⁻¹)	Stumpage price: 35 € m ⁻³ for <i>P. pinea</i> saw-wood, 15 € m ⁻³ for <i>P. pinea</i> and <i>J. thurifera</i> pulpwood
		Annual income from fuelwood	Inc fuel (€ ha ⁻¹ yr ⁻¹)	Stumpage price: 10 € t ⁻¹ (thick branches of all species, and the whole stem of <i>Quercus</i> sp.)
		Total annual income	Inc_tot (€ ha ⁻¹ yr ⁻¹)	Sum of the annual incomes from timber, fuelwood and cones
Net present value		NPV (€ ha ⁻¹)	Assuming a discount rate of 3%	

4. Results

4.1. Calibrating the PINEA2 model for mixed stands

– Basal area increment modelling

The best set of explanatory covariates finally included in the specific tree basal area increment model for each species, as well as their associated parameter estimates and level of significance, are shown in Table 4. In addition, variance components, information criteria and goodness-of-fit statistics for the marginal prediction (i.e. not including EBLUPS for random effects) in anti-logarithmic real scale for the new model are presented. Validation of the model on an independent data set is shown in section S2.

The results showed that basal area increment in *P. pinea* was favoured by the presence of an understorey of *J. thurifera*, whereas it was constrained by the competition from its own conspecifics. In the case of *J. thurifera*, the competition exerted by the dominant layer of *P. pinea* reduces its growth, although this effect was diminished by the presence of *Quercus* sp. In addition, *Quercus*' radial increment was limited by increasing competition from its own conspecifics as well as from *P. pinea*. Increment in all three species was favoured by rainfall; annual in the case of *P. pinea* and *Quercus* or spring rainfall for *Juniperus*, while high spring temperatures constrain the increment in *Pinus* and *Quercus*. Finally, site index exerted a negative influence on the growth of *J. thurifera* but it had a positive effect on *P. pinea*.

The remaining variability, not explained by the included covariates, in the case of *P. pinea* is mainly related to unobserved factors acting at plot (36.5% of non-explained variability) and tree level (27.4%), while in *Juniperus* it is mainly associated with tree level factors (70.9%) and in *Quercus* with tree (37.6%) and residual (tree × year, 26.2%) factors.

– Height-diameter and crown diameter modelling

Parameter estimates, associated level of significance and goodness-of-fit statistics for height-diameter and crown-diameter models are shown in Table 5. The height-diameter model for *P. pinea* shows a significant effect of stand density on the relationship, resulting in high slenderness (larger ratio height/diameter) in denser stands. However, this effect is mitigated if the percentage of other species in the stand is increased. In addition, in the case of *P. pinea*, the effect of mixture resulted in larger crowns – for a tree of the same diameter. For the other species we found no significant effect of mixture either on height-diameter or on crown-diameter relationships, hence, this term was removed in the final models. All the developed models resulted in unbiased marginal predictions, except for the *J. thurifera* height-diameter model. Validation of the models on an independent data set is shown in section S3.

4.2. Ecosystem services provision

The ANOVAs revealed a significant effect of the climate scenario, composition as well as the interaction climate × composition for all the evaluated ES, with a p-value < 0.0001 for all the services and factors, except for MAI, where differences in composition are significant at a p-value of 0.0169. However, the relevance of each factor is not consistent (see supplementary material S4), with the climate scenario accounting for more than 80% of variability for all the ES, except for the ES associated with structural diversity and crown coverture, where the main part of the variability was explained by composition. Interaction, though significant, did not explain more than 3% for any of the ES.

The results from our simulations (Table 6) forecasted a significant and generalized decrease in the provision of all the ES for both pure and mixed stands as climate moves from historical conditions to scenarios RCP 4.5 & 8.5 (Fig. 2). The only exception is found in the structural diversity indices, which remain constant or even increase (as observed for the Shannon diversity index in mixed stands). Our results indicated that under the RCP 4.5 and 8.5 scenarios, and for similar management options, forests in the region will show significantly smaller volume and biomass (CO₂) stocks and increments, a significant decrease in mean timber and biomass annual increments, smaller cone yields, and a subsequent significant reduction in the expected income derived from the forest. In this regard, expected reduction reaches relative values of 30%-40% in stocking services, 30%-50% in yield services associated with timber, biomass and CO₂ fixation, and 50–70% in eco-

Table 4
Parameter estimates for fixed effects, variance components and goodness of fit statistics in BAI model (Eq. (1)).

Type	<i>Pinus pinea</i>			<i>Quercus sp.</i>			<i>Juniperus thurifera</i>		
	Covariate	Estimate	p-value	Covariate	Estimate	p-value	Covariate	Estimate	p-value
Tree	Intercept	1.9501	<0.0001	Intercept	-0.9444	0.1662	Intercept	5.6226	0.0369
	d	0.0778	<0.0001	d	0.3914	<0.0001	d	0.3138	<0.0001
	d ²	-0.0007	<0.0001	d ²	-0.0131	<0.0001	d ²	-0.0093	<0.0001
Competition	BA_Pp	-0.0319	<0.0001	BA_Pp	-0.0286	0.0275	BA_Pp	-0.1006	<0.0001
	BA_Jt	0.0816	0.0229	BA_Jt			BA_Jt		
	BA_Qu			BA_Qu	-0.2239	0.0649	BA_Qu	0.2536	0.0603
Maturity & site	Hdom_Pp	-0.1370	<0.0001				SI_Pp	-0.4832	0.0075
	SI_Pp	0.0808	0.0001						
Climate	Rain_year	0.1972	<0.0001	Rain_year	0.2135	<0.0001	Rain_spr	0.1747	0.0001
	Tmed_56	-0.1450	0.0003	Tmed_56	-0.0774	0.0198			
Variance component	Plot	0.08892	0.0002	Plot	0.0740	0.1422	Plot	0	-
	Tree	0.06686	<0.0001	Tree	0.1078	0.0010	Tree	0.3781	0.0001
	Year	0.01232	0.0101	Year	0	-	Year	0.03188	0.0183
	Plot × year	0.04595	<0.0001	Plot × year	0.0297	0.0005	Plot × year	0.01359	0.0176
	Residual	0.02968	<0.0001	Residual	0.0753	<0.0001	Residual	0.1098	<0.0001
Information criteria & goodness of fit	AIC	-410.9		AIC	279.5		AIC	626.5	
	-2LL	-438.9		-2LL	257.5		-2LL	604.5	
	E	1.213		E	-0.489		E	-0.060	
	p-value	0.1076		p-value	0.089		p-value	0.9003	
	MEF	0.423		MEF	0.368		MEF	0.177	
	RMSE	47.187		RMSE	5.618		RMSE	11.598	

Where d: diameter at breast height (cm), BA: basal area (m² ha⁻¹) of *Pinus pinea* (Pp), *Juniperus thurifera* (Jt) and *Quercus sp.* (Qu), Hdom_Pp: dominant height (m) for *Pinus pinea*, SI_Pp: site index (m) for *Pinus pinea*, Rain_year: annual rainfall from 1st October – 30th September, Rain_spr: cumulative rainfall (mm), between 1st April – 30th June; tmed_56: mean daily temperature for may and june. Climate covariates enter the model standardized. AIC: Akaike's information criteria, -2LL: -2 log likelihood, E: mean error, p-value: level of significance for E, MEF: modelling efficiency; RMSE: root mean square error. E, MEF and RMSE referred to the marginal prediction on real scale.

Table 5
Parameter estimates for fixed effects, variance components and goodness of fit statistics in height-diameter and crown diameter models (Eqs. (2)–(4)).

Height-diameter models (Eqs. (2) and (3))							
Type	Covariate	<i>Pinus pinea</i>		<i>Quercus sp.</i>		<i>Juniperus thurifera</i>	
		Estimate	p-value	Estimate	p-value	Estimate	p-value
Tree	Intercept	6.3302	<0.0001	0.5596	<0.0001	0.5852	<0.0001
	log (d)			0.4304	<0.0001	0.4485	<0.0001
	Competition	N_ppa	-0.5720	0.0040			
Variance component		N_other	-0.1055	0.0497			
	Plot	0.6541	0.0024	0.0032	0.1081	0.0046	0.0901
	Residual	1.4412	<0.0001	0.0372	<0.0001	0.0334	<0.0001
Goodness of fit	E	-0.0361		0.0164		0.1295	
	p-value	0.1745		0.5263		<0.0001	
	MEF	0.910		0.780		0.863	
	RMSE	0.802		0.565		0.616	
	Crown diameter models (Eq. (4))						
Type	Covariate	<i>Pinus pinea</i>		<i>Quercus sp.</i>		<i>Juniperus thurifera</i>	
		Estimate	p-value	Estimate	p-value	Estimate	p-value
Tree	Intercept	0.9660	<0.0001	0.9164	0.0004	1.1236	<0.0001
	d	0.1591	<0.0001	0.2096	<0.0001	0.1865	<0.0001
Composition	Mixture	-0.3950	0.0155				
	Variance component	Plot	0.1016	0.0002	0.0272	0.1039	0.0159
Goodness of fit	Residual	0.4191	<0.0001	0.2187	<0.0001	0.2657	<0.0001
	E	-0.0373		0.0161		-0.0167	
	p-value	0.1237		0.4708		0.4621	
	MEF	0.857		0.557		0.711	
	RMSE	0.728		0.486		0.523	

Where d: diameter at breast height (cm), N_ppa & N_other: number of stems for ha of P. pinea or other species, respectively. Mixture: a dummy variable equalling 1 in pure stands, 0 in mixed stands, E: mean error, p-value: level of significance for E, MEF: modelling efficiency, RMSE: root mean square error. E, MEF and RMSE referred to the marginal prediction on real scale.

Table 6

Expected provision of ES for the three climate scenarios evaluated in pure and mixed stands. Pairs in bold indicates highly-significant differences (p-value < 0.001) between pure and mixed stands for that scenario. Pairs in italics and blue indicate slight-significant (0.05 > p-value > 0.001) differences between type of stand for that scenario. In the rest of cases, differences are non-significant (p-value > 0.05). Rate of change refers to the expected relative change between historical and RCP 8.5 scenarios.

Type	Indicator	Historical Climate		RCP 4.5		RCP 8.5		Rate of change (Hist – RCP 8.5)	
		PURE	MIXED	PURE	MIXED	PURE	MIXED	PURE	MIXED
Stock	V_stock (m ³ ha ⁻¹)	45.3	44.2	31.6	34.1	27.6	30.5	-39%	-31%
	BA_stock (m ² ha ⁻¹)	14.3	13.9	9.9	10.6	8.8	9.5	-38%	-32%
	Wt_stock (t D.M. ha ⁻¹)	85.2	85.6	56.9	63.0	49.5	55.6	-42%	-35%
	Crown_cov (%)	44.2	57.2	31.9	47.3	28.6	44.0	-35%	-23%
	CO2fix_stock (t ha ⁻¹)	151.5	152.2	101.1	112.1	88.0	98.8	-42%	-35%
Diversity	CV_D	0.21	0.65	0.21	0.59	0.21	0.56	0%	-14%
	CV_H	0.11	0.30	0.12	0.30	0.13	0.30	18%	0%
	Shannon	0.00	-0.83	0.00	-0.98	0.00	-1.04	-	25%
Yield	Cone (kg ha ⁻¹ year ⁻¹)	229	209	81	74	37	35	-84%	-83%
	MAI (m ³ ha ⁻¹ year ⁻¹)	1.542	1.463	1.070	1.113	0.929	0.997	-40%	-32%
	MBTI (t D.M. ha ⁻¹ year ⁻¹)	2.592	2.551	1.687	1.835	1.437	1.596	-45%	-37%
	CO2fix_tot (t ha ⁻¹ year ⁻¹)	4.609	4.536	3.000	3.264	2.555	2.839	-45%	-37%
	Saw (m ³ ha ⁻¹)	94.3	85.2	53.7	53.6	41.9	43.5	-56%	-49%
Economic	Inc_cone (€ ha ⁻¹ yr ⁻¹)	46.25	42.17	16.41	15.04	7.41	7.13	-84%	-83%
	Inc_timber (€ ha ⁻¹ yr ⁻¹)	44.30	39.72	28.18	27.63	23.45	23.75	-47%	-40%
	Inc_fuel (€ ha ⁻¹ yr ⁻¹)	6.13	7.19	3.57	4.83	2.92	4.07	-52%	-43%
	Inc_tot (€ ha ⁻¹ yr ⁻¹)	96.68	89.07	48.15	47.50	33.78	34.94	-65%	-61%
	NPV (€ ha ⁻¹)	1799	1660	933	885	529	535	-71%	-68%

conomic services, in all cases compared to the historical climate scenario. The most affected services will be those related to cone production and income, which present reductions of over 80% (Table 6).

However, this expected reduction in the provision of ES was not consistent between pure and mixed stands, the reduction being less severe in the case of the mixed stands. Under the climate scenario mimicking the historical climate, pure stands (under BAU management) provided significantly better results in terms of cone production, mean annual increment for timber, saw-wood production, as well as all the economic indicators (except income derived from fuelwood). In the case of mixed stands, the same scenario provided significantly better results for structural diversity indices, crown cover and fuelwood, while for the rest of indicators (stock indices, and annual rates of increment in biomass and CO₂ fixation) non-significant (p-value > 0.05) or only slightly significant (p-value > 0.005) differences were found. When moving from the historical scenario to the most severe RCP 8.5 scenario, we observed a general shift in this behaviour (Fig. 3), with mixed stands providing significantly higher values for most of the evaluated indicators, while pure stands were no longer significantly better for any of the indicators. Only for cone and saw-wood production, cone and timber income, and NPV did we observe non-significant or only slightly significant differences (Table 6, Figs. 2 & 3) between pure and mixed stands. In contrast, larger shifts are expected in mean annual increment for timber and mean total biomass increments, as well as in the capacity of mixed forests to fix atmospheric CO₂. However, larger differences between pure and mixed stands were maintained for those indicators focusing on structural diversity (horizontal and vertical) as well as on crown cover. When the annual evolution is observed it is possible to identify how the decrease in the provision due to different climate scenarios starts as early as the 2030 s, while the mitigation effect due to mixture becomes more evident from 2040 onwards (see examples in Fig. 4 for total cumulative biomass and standing volume).

The analysis of correlation among ES (Fig. 5) showed that in pure stands synergies (positive correlations) tend to dominate, especially between the main part of the services related with stocking, yield and economic revenue. The only exception was the case of structural diver-

sity indices, which showed that the more irregular the stand, the lower provision of the rest of services. In the case of mixed stands synergies are mainly observed between the ES related with timber, while we detected trade-offs between timber related services and cone production, biomass stock and crown cover. In general the strength of the correlations in pure stands is stronger than in mixed ones, and synergies tend to be more significant than trade-offs. This differential pattern in ES correlation observed in pure and mixed stands was exacerbated under most severe climate scenarios (figura S5.1).

5. Discussion

5.1. Modelling approach

Empirical forest-growth models aimed at predicting the state, evolution and yield of a forest system at different scales and scenarios can be useful tools for forest management planning if the indicators of sustainability and provision of ES can be derived directly from the state of the stand (Brang et al., 2001). In this study we present a proposal for adapting the integrated single-tree-level empirical model PINEA2, originally constructed for pure even-aged stands of *P. pinea*, to the conditions of mixture with *J. thurifera* and different species of *Quercus*. The basis of our adaptation consists of incorporating mixing-effects into the climate-sensitive tree annual basal area increment module (Calama et al., 2019) by adding species-specific competition indices (Pretzsch et al., 2015), in our case, the basal area of each species (Mina et al., 2018). In addition, we have fitted new height-diameter and crown width-diameter models to account for differences in the allometry of trees growing in mixtures when compared to trees grown in pure stands (Forrester et al., 2017), and therefore also for structural changes at stand level.

The new version of the model permits simulations to be performed at one-year steps in pure and mixed stands. It includes climate-sensitive modules for basal area increment and cone production and allows the provision of different ES to be derived or estimated at stand-level, including stand stocking; biomass and CO₂ fixation; timber, fuelwood and cone yield; structural diversity and economic revenue.

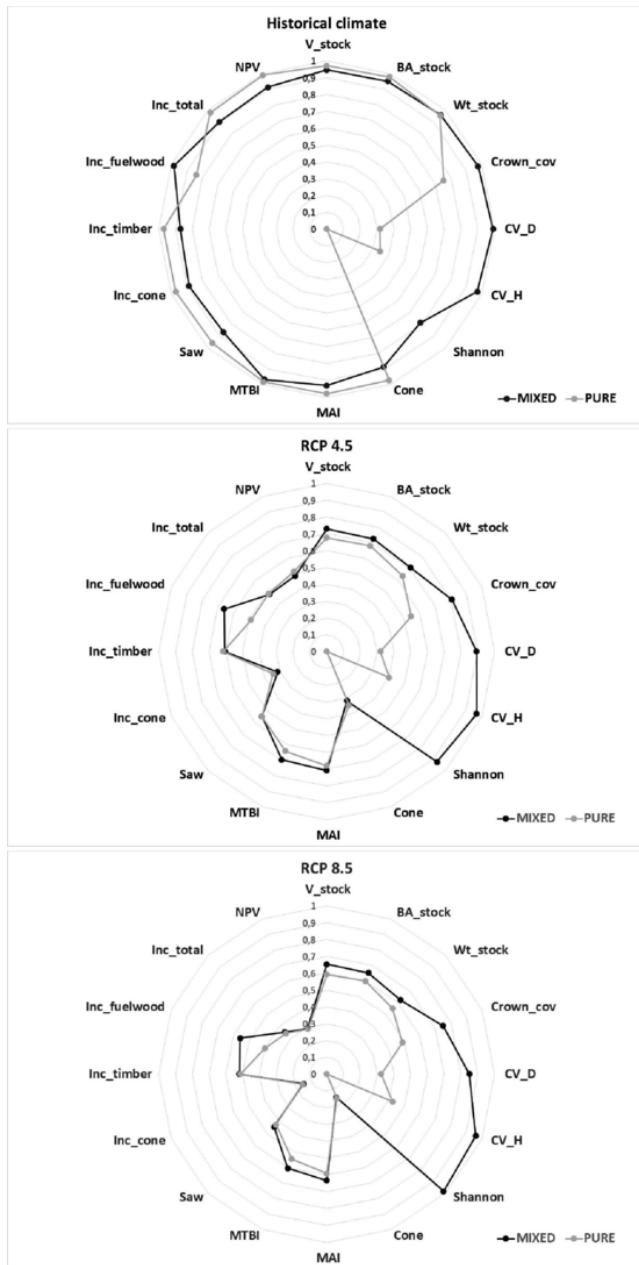


Fig. 2. Amoebe diagrams for the different indicators. The value 1 represents the maximum value observed for the indicator in the different simulations.

5.2. Factors influencing specific growth response and allometry

Our results indicate that at individual tree-level the BAI of *P. pinea* is favoured in mixtures, since competition from *Quercus* sp. does not significantly affect it and the presence of *J. thurifera* leads to an enhanced BAI in *Pinus*. These results for *P. pinea* are consistent with the hypothesis of niche complementarity (Loreau et al., 2001). In contrast, our modelling approach indicates that as competition from *P. pinea* increases, the growth of both *J. thurifera* and *Q. ilex* decreases, this negative effect being more pronounced for *Juniperus* trees. These results agree with previous results for *P. pinea* growing in the same or similar *Quercus* – *Juniperus* mixtures (de-Dios-García et al., 2015; Mayoral et al., 2015) or when mixed with *Pinus pinaster* (Vergarechea, 2020) and indicate that the benefits to growth associated with mixture

are neither general for all the mixtures nor of similar intensity for all the species in the mixture (Pretzsch and Forrester, 2017).

In our case we observed that the growth of the species occupying the dominant layer of the forest (*P. pinea*) is enhanced by the presence of a dominated storey of other species, while these accompanying species show a decline in their growth associated with an increase in the stocking of the dominant species (Amoroso and Turnblom, 2006). The attenuated competition or even facilitation of growth due to interspecific interactions observed in *P. pinea* was previously explained (de-Dios-García et al., 2015) by differential root stratification of the species. This fact, together with the temporal differences in phenology (de-Dios-García et al., 2018) and physiological responses (Pardos et al., 2019) observed between the species may result in a spatio-temporal complementarity in the use of the below-ground resources. In contrast, the growth decline observed in *Quercus* and *Juniperus* may be explained by the asymmetric competition exerted by the overstorey crowns of *P. pinea*, which reduces the amount of light reaching the understorey species. In this regard, while the presence of a shaded environment has been identified as necessary for the initial establishment of *Quercus* and *Juniperus* seedlings (Pardos et al., 2019), Mayoral et al. (2015) reported that the best physiological performance of saplings of *Q. ilex* and *Juniperus oxycedrus* was attained in medium-shaded areas to large gaps.

Apart from inter- and intraspecific effects of competition, both rainfall and spring maximum temperature mediate the growth of the different species. In the case of rainfall, *Pinus* and *Quercus* are sensitive to total annual rainfall, while *Juniperus* is largely affected by spring rainfall. A negative effect of increasing spring temperatures was detected for *Pinus* and *Quercus* (more evident for *P. pinea*) while *Juniperus* seems to be less sensitive to this factor, probably due to its delayed phenology. The isohidric character of *P. pinea* in comparison to the other two species may explain this reduction in growth in the warmest springs (Mayoral et al., 2015).

Our modelling approach also allowed us to identify different responses to inter and intraspecific interactions in tree allometric relationships (Pretzsch, 2014). While trees growing in higher densities tend to show both greater slenderness (height/diameter ratio) and narrower crown widths, this effect can be mitigated in *P. pinea* by increasing the percentage of mixing with *Juniperus* and *Quercus*, an effect previously observed in other pine-oak mixtures (del Río et al 2019). In our case, in dense monospecific stands of *P. pinea* it is common to observe that the lateral expansion of individual crowns is confined, with the individual crowns of adjacent trees overlapping to form a single umbrella shaped crown (Calama et al., 2019); while mixing with species that form a lower layer permits an increase in the lateral expansion of the crown (Dieler and Pretzsch, 2013). In addition, pine exhibited increased height for a given diameter when growing in a pure stand compared to trees growing in mixtures, pointing to an effect of species interaction on vertical structuring (Pretzsch and Forrester, 2017) and a greater allocation of carbon to stemwood in more intolerant species growing in mixed stands (Wang et al., 2000). In contrast, no effect of mixture proportions was found in the allometries of *Juniperus* or *Quercus*, although this may be due to the lack of pure stands of the species in the territory.

5.3. Effect of climate and composition on current and future provision of ES

There is growing evidence that mixed-species forests can supply many ecological, economical and socio-cultural forest goods and services in a similar or even better way than far-from-nature monocultures (Gamfeldt et al., 2013), although this improvement is not observed for all the services, environmental conditions and mixture typologies (van der Plas et al., 2016). In our case study we identified that, under current climate conditions, very little or no differences between

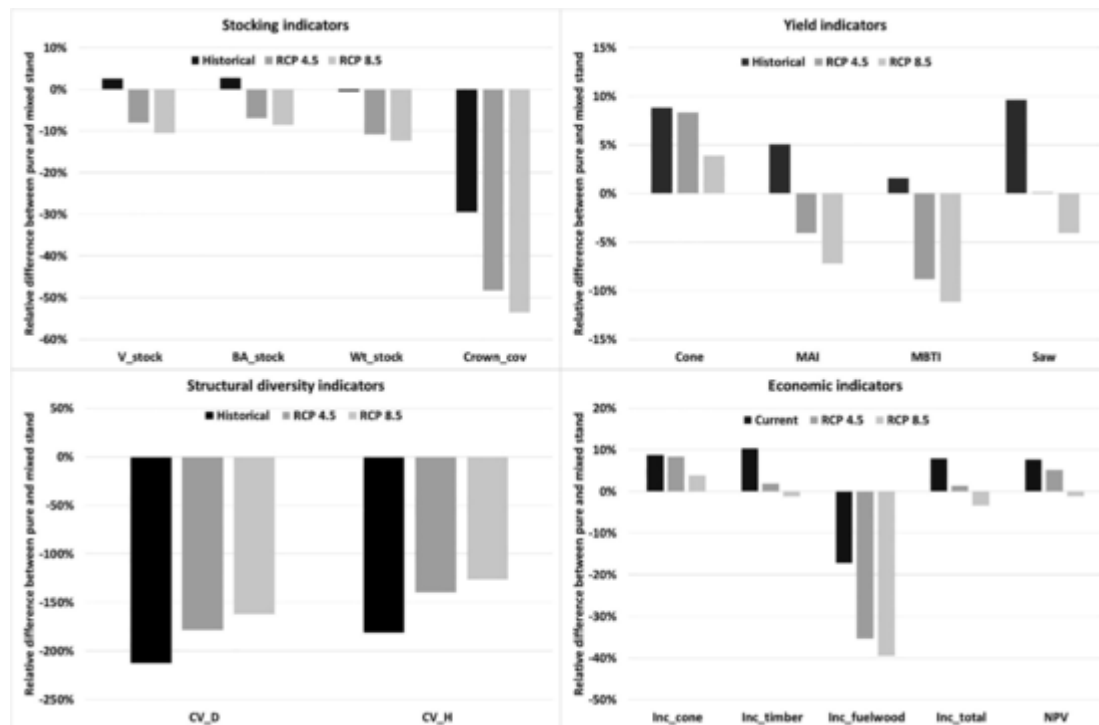


Fig. 3. Relative difference among the value observed for the indicator in pure and mixed stands ($[\text{value observed in pure} - \text{value observed in mixed}] / \text{value observed in pure}$), as a function of expected climate scenario.

pure and mixed stands are observed in the supply of ES associated with stand stocking volume, basal area, total biomass and CO₂ fixation, or in terms of annual increments in biomass and CO₂ fixation. The tree-level response to interspecific competition observed in *P. pinea* in terms of enhanced growth or modified allometry is not necessarily found when up-scaling to stand level, since it is counterbalanced by the expected reduction in growth in the species occupying the understorey. Consequently, we did not observe the typical overyielding effect of mixture (Pretzsch and Schütze, 2009). Overyielding in stratified mixtures has been associated with clear differences in shade tolerance among the species, leading to an optimized light-interception (Kelty, 1992). In this regard, both *Juniperus* and *Quercus* may show greater tolerance to shade than *Pinus* in the initial phases of development, although in later phases both species (especially *Quercus* sp) are highly light-demanding, hence photosynthetic activity is not maximized in the understorey.

Because of the non-observed overyielding, ES associated with timber, saw timber and cone production are maximized in pure stands, since the accompanying species in mixtures (*Juniperus* and *Quercus*) contribute very little or nothing at all to these specific services (Ray et al., 2015; Pukkala, 2018). Moreover, the analysis of trade-offs and synergies showed that under current climate all productive services in pure stands are highly positively correlated. As these services, especially cones, are the most profitable in economic terms, all the services associated with income revenues are also maximized in pure stands, a pattern not observed in other types of mixtures where all the species contribute equally to the economic revenue (Knoke et al., 2008). However, we found that mixed stands showed greater vertical and horizontal complexity due to the canopy stratification, changes in allometry and the interspecific differences in size and lifeforms (Varga et al., 2005). This increased structural diversity may provide other benefits not analysed here, such as a broader range of optimal niches for wildlife and enhanced aesthetic values (Amoroso and Turnblom, 2006) as well as increased provision of services such as water quality or air purification (Carnol et al., 2014). On the other hand, maximizing vertical and structural diversity on pure stands (by means of irregu-

larization) may result in losses in timber and biomass production, as previously stated by del Río et al. (2017). We also detected a significant increase in crown cover in mixed stands, confirming the proposed hypotheses of over-packing along with much denser and vertically layered canopies (Pretzsch, 2014). However, this observed increment in crown cover in mixtures, due to occupation by other species, also results in slight trade-offs with timber and biomass production.

Our simulations indicated that ES supply is threatened under climate change scenarios (Lindner et al., 2010; Hanewinkel et al., 2013; Mina et al., 2016). Irrespective of the composition, we forecasted a highly significant decrease in all the stocking, yield and income services, with the most severe decrease being that of cone production, presenting decreases of up to 80%. This long-term high sensitivity of cone production to climate scenarios and the expected decrease in yield in *P. pinea* agrees with previous simulation studies using process-based models (Pardos et al., 2015) and the recently observed decline in production associated with dry years (Lindner and Calama, 2013). In addition, under these climate change scenarios, *P. pinea* forests will supply less timber, stock less biomass, and be less efficient in fixing atmospheric CO₂, which reflects the expected common trend for Southern Europe (Hanewinkel et al., 2013). An important finding is that these reductions in ES are forecasted to occur not only by the end of the simulated period, but also in the short term (Pardos et al., 2016).

This decrease in ES may be mitigated – at least in part – in mixed *P. pinea* forests, which would be more competitive in terms of ES supply under the most severe climate change scenarios, in agreement with previous findings for different forest types (Seidl et al., 2011; Ray et al., 2015; Pardos et al., 2016). The enhanced growth and tree allometry observed for *P. pinea* in mixtures, together with the lower sensitivity of *Quercus* and *Juniperus* to the forecasted increasing temperatures and reduction in rainfall, explain this superior behaviour of mixed stands in terms of ES supply, including timber, biomass and cone production, stocking, CO₂ fixation, structural diversity and economic rev-

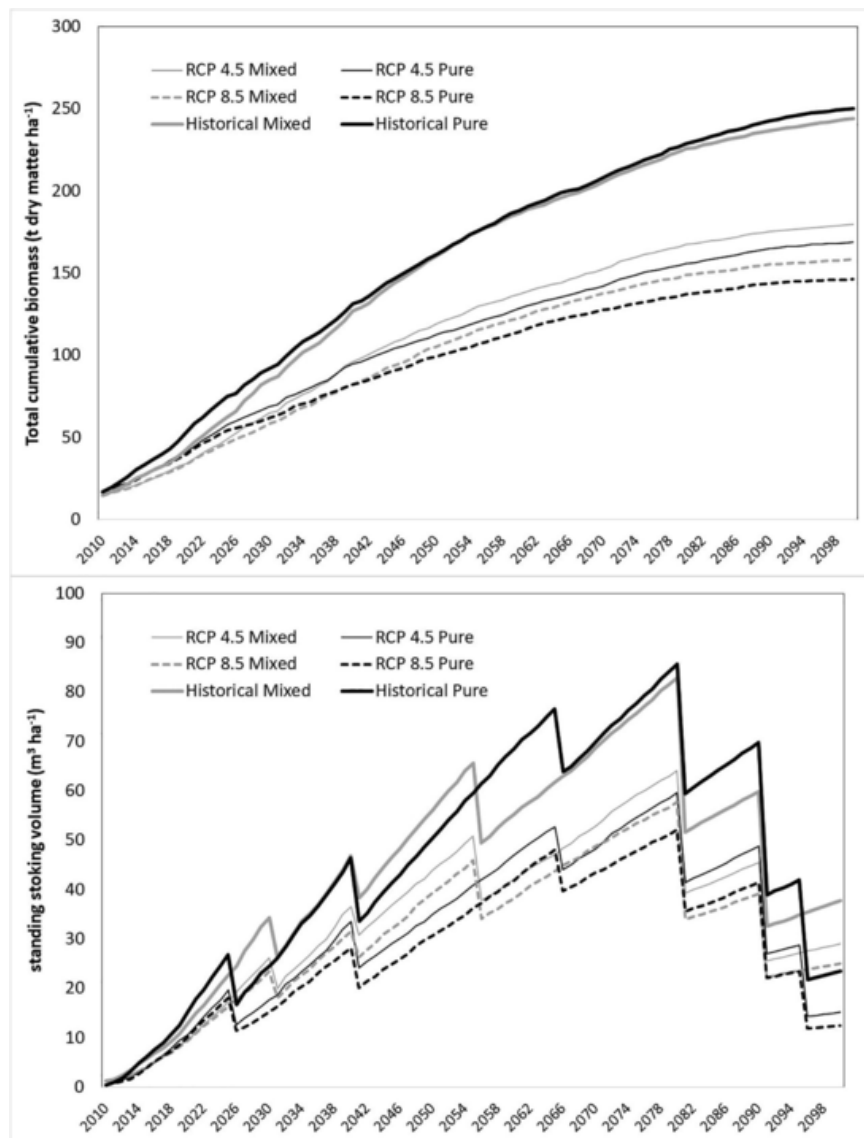


Fig. 4. Evolution of total cumulative biomass (stocking + extracted in thinnings and regeneration cuttings, above) and standing volume (below) in pure (black) and mixed (grey), for historical (thick solid lines), RCP 4.5 (thin solid lines) and RCP 8.5 (dashed lines) climate scenarios.

enue, but is also related with more complex synergies and trade-offs among services (Mina et al., 2016).

5.4. Final remarks

Our results evidence that mixed managed stands of *P. pinea*, when compared to pure forests, will be less vulnerable in terms of ES supply under more restrictive climate scenarios. As a consequence, the promotion of mixtures by under-planting and/or releasing of pre-existing advanced regeneration of complementary species may be postulated as a management concept for adapting to climate change in these forests. However, it should be emphasized that despite shifting from pure to mixed stands, the provision of ES will be substantially threatened. In accordance with this expectation, it will be necessary to prioritize between different ecosystem services, to consider potential synergies and trade-offs among them, and to define and compare different management alternatives apart from BAU for both pure and mixed stands, these being aspects not considered in the present study. In this regard, future research should focus on defining the optimal management of these forests by means of multicriteria analyses and goal programming

(Ezquerro et al., 2019). Finally, as some ES cannot be directly derived from our modelling approach, new models focusing on indicators such as deadwood; suitability for wildlife; water availability; vulnerability to pests or hazards (fire, windthrows); and aesthetic values, should be developed and integrated into the analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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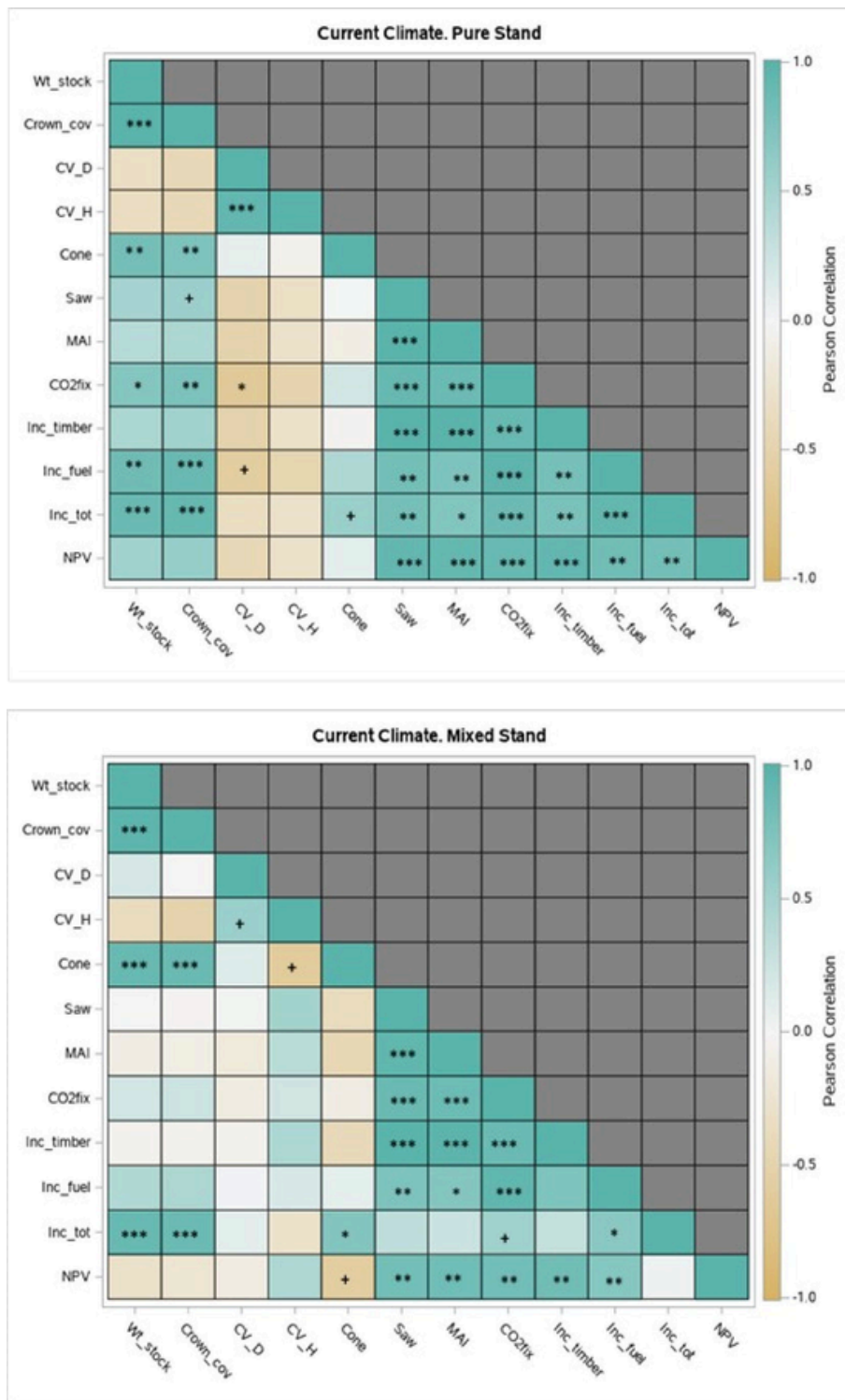


Fig. 5. Synergies and trade-offs for the provision of the main Ecosystem Services analysed under current climate in pure and mixed stands. ***, **, * and + indicates p-values of < 0.001, < 0.01, < 0.05 and < 0.10 respectively. Abbreviations as shown in Table 3. Correlations for volume stock, basal area stock, CO₂ stock are not shown, given its high correlation with biomass stock. Correlation for annual income from cones and mean biomass increments are not shown, since are similar to those for annual cone production and annual CO₂ fixation.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118782>.

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