



Linking functional traits with tree growth and forest productivity in *Quercus ilex* forests along a climatic gradient



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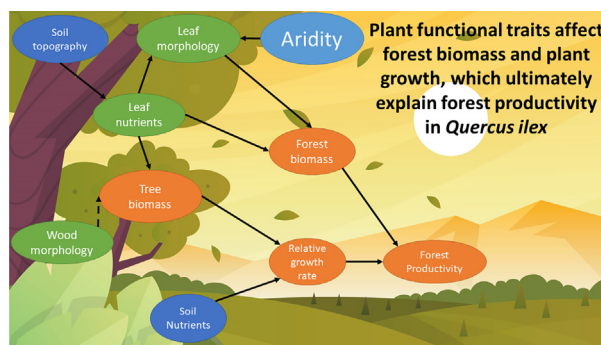
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HIGHLIGHTS

- Aridity is the main environmental factor affecting leaf functional traits.
- Soil nutrients are the main drivers of the relative growth rate in *Quercus ilex*.
- Forest productivity is explained by forest biomass and relative growth rate.
- Trait intraspecific variability has a significant effect on forest biomass.

GRAPHICAL ABSTRACT



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ABSTRACT

Plant functional traits are highly plastic to changes in climatic factors and nutrient availability. However, the intraspecific plant response to abiotic factors and the overall effect on tree growth and productivity is still under debate. We studied forest productivity for 30 *Quercus ilex* subsp. *ballota* forests in Spain along a broad climatic gradient of aridity (mean annual precipitation from 321 to 858 mm). We used linear mixed models to quantify the effect of climatic and edaphic (soil nutrients, topography, and texture) factors on tree functional traits (leaf and branch traits), and subsequently, the effect of such functional traits and abiotic factors on the relative growth rate (RGR) of adult trees. We used piecewise structural equation models (SEMs) to determine the causal effect of intrinsic and extrinsic factors on forest productivity. Our results showed that tree functional traits were mainly explained by climatic and edaphic factors. Functional traits and tree biomass explained forest biomass and RGR, respectively, which ultimately explained forest productivity. In conclusion, intraspecific variability of functional traits has a significant effect on plant biomass and growth, which ultimately may explain forest productivity in *Quercus ilex* forests.

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1. Introduction

Functional traits are biological attributes that directly or indirectly affect plant fitness and generally reflect plant adaptation to local environmental conditions (Lavorel et al., 1997; Violle et al., 2007). Functional trait variability allows plants to minimize their building costs and maximize functional efficiency. Understanding how functional traits vary across environmental gradients is critical to determine plant functioning and their ecological strategies in contrasting environmental conditions (Westoby, 1998), especially relevant under the ongoing climatic change scenario. For instance, drought avoidance creates a trade-off between water conservation and nutrient acquisition. For example, wood density and leaf mass per area (LMA) increase in arid environments to reduce the risk of cavitation and increase defense functions. However, this has the cost of a lower plant biomass and growth (Chave et al., 2009; Vilà-Cabrera et al., 2015).

Empirical studies have shown that functional traits are related to abiotic variables with a direct effect on the relative growth rate (RGR; Chave et al., 2009; Salgado-Luarte and Gianoli, 2017; Violle et al., 2007). At the local scale, the functional traits have an important effect on RGR (Chaturvedi et al., 2011; Dong et al., 2020). Whereas at larger spatial scales, tree size is generally used as the main plant trait and abiotic conditions are summarized through temperature or precipitation to explain plant growth (de la Riva et al., 2016a; Moore et al., 2020). In fact, a weak relationship between LMA and RGR has been found when plant size is taken into account (Gibert et al., 2016; Wright et al., 2010), arguing that LMA is not a clear physiological trait and should be replaced by mechanistic traits (like leaf nutrients or wood density) more associated with plant fitness (Rosas et al., 2019). In any case, the direct and indirect effect of functional traits on RGR is key to understand how plants adapt to environmental changes, and whether or not this has any effect on ecosystem functioning.

Additionally, variation in RGR is associated with intrinsic factors as the tree biomass and abiotic factors such as soil nutrient availability and climate (Antúnez et al., 2001; Cornelissen and Thompson, 1997; Lambers et al., 2008). However, it is still uncertain whether these factors have a direct or indirect effect on plant growth. For instance, Bu et al. (2019) found that changes in abiotic conditions did not directly affect plant growth, but indirectly via changes in plant functional traits. Similarly, it has been shown that RGR negatively correlates with tree biomass during the stand development; however, this relationship disappears when the trees reach the maturity stage (Ruiz-Benito et al., 2015). Therefore, the source of variation in RGR is currently a growing field of research.

Several large-scale studies have analyzed how differences in functional traits between species determine growth responses to plant-plant interactions and forest demography (Kunstler et al., 2016; Ruiz-Benito et al., 2017). It is not well known however the role of intraspecific trait variability in determining forest responses (Wang and Hamzah, 2018), although it has been suggested that functional trait intraspecific variability determines species distribution under a warming climate (Valladares et al., 2015). Furthermore, it has been shown that intraspecific variability can be larger than interspecific variability (Fajardo and Siefert, 2016), and this variation influences the interactions among organisms that ultimately drive the functional community (Bastias et al., 2017; Siefert et al., 2015). Therefore, understanding the source of intraspecific functional trait variations, as well as its contribution to plant growth and ecosystem function is critical to understand forest responses under changing conditions. We focus on the intraspecific variability of *Quercus ilex* (subsp. *ballota*) dominated forests, a key tree species in Mediterranean forests characterized by high plasticity and resistance to drought (Aranda et al., 2004; Quero et al., 2006). Our goal is to assess whether abiotic factors directly affect forest productivity or indirectly influence on it via changes in functional traits and RGR, and how such direct and indirect effects might be disentangled (Fig. 1). We hypothesized that the forest productivity ($\text{kg ha}^{-1} \text{ year}^{-1}$) is related to the forest biomass

(kg ha^{-1}) and RGR ($\text{g kg}^{-1} \text{ year}^{-1}$). The forest biomass can be decomposed in the mean tree biomass and the tree density, whereas RGR can be explained by functional traits and abiotic factors. To study this, we combined data from the Spanish National Forest Inventory (NFI) with field sampling to include functional trait data and soil characteristics. Our specific objectives are: (1) to determine how abiotic factors (climate and soil properties) affect functional traits; (2) to know the effect of abiotic factors, functional traits, and forest structure (tree biomass and density) on relative growth rate; and (3) to model forest productivity as a result of these ecological, physiological and environmental factors.

2. Material and methods

2.1. Study species

The Iberian Peninsula is characterized by evergreen sclerophyllous, semideciduous malacophyllous, and grassland species. Most of the forest landscape is composed of cleared oak forest of *Quercus ilex* or *Q. suber*, constituting the so-called “dehesas” in Spain and Portugal (Gil-pelegrín and Peguero-Pina, 2017). Fluctuating conditions with wet springs and dry summers dominate the Mediterranean climate, which restricts plant growth and forest production (Flexas et al., 2014). We studied *Quercus ilex* subsp. *ballota* (hereafter *Q. ilex*), an evergreen-sclerophyllous and drought-resistant species, which is extensively distributed throughout the Mediterranean basin (Caudullo et al., 2017; Quero et al., 2011; Fig. 2). This species is shade-tolerant characterized by an anisohydric behavior (Sade et al., 2012) and the leaf lifespan ranges from 2 to 3 years (Gratani et al., 2000). It is deep-rooted and has a great capacity to maintain high stomatal conductance during long dry periods (Barbero et al., 1992; Quero et al., 2011).

2.2. Spanish Forest Inventory and experimental design

The Spanish Forest Inventory is a nationwide program that establishes 50 m diameter plots in forested areas of Spain each km^2 . In the NFI plots, adult trees [i.e. those with DBH (diameter at breast height) greater or equal to 7.5 cm and height greater or equal to 1.30 m] were measured using a variable radius sampling protocol. Thus, trees were measured in a 5, 10, and 15 m radius subplots if the DBH was lower than 12.5, 22.5 and 42.5 cm, respectively. Trees in the 25 m radius subplot were only measured if the DBH was higher than 42.5 cm. For each tree measured it is included the DBH, tree height and species identity.

We selected thirty plots dominated by *Q. ilex* from the inventory covering six contrasting climatic regions according to Köppen-Geiger Climate Classification. The plots were selected from the NFI database within certain criteria based on the plot accessibility, location and the *Q. ilex* percentage abundance in the plot. Five plots were randomly chosen within each climatic region (in a nested design), and the distance between plots of each region (13.5 km on average) was considered to avoid pseudoreplication. On average, *Q. ilex* represented 90% of the total forest biomass of the plot, ranging from 60 to 100% (with a total dominance in 18 plots). The mean annual temperature varies between 10.9 and 17.4 °C and the annual precipitation varies from 357 to 858 mm. More details about the selected plots can be found in Table 1.

We used the DBH data from the third National Forest Inventory (1997–2007, NFI3) and we calculated tree biomass (kg tree^{-1}) using the allometric equations from Ruiz-Peinado et al. (2011). For each plot, the forest biomass (Mg ha^{-1}) was calculated as the sum of the individual tree biomass considering the subplot where the tree belongs (i.e. 5, 10, 15 and 25 m radius subplots) (Ruiz-Benito et al., 2014). Similarly, we calculated tree density of each subplot as the sum of tree density (number of trees ha^{-1}) of each radius subplots. In 2018, we re-measured the DBH of all trees in each selected plot to calculate tree biomass increment and forest biomass increment in the last eleven years (2007–2018 period). Moreover, we collected leaf and branch

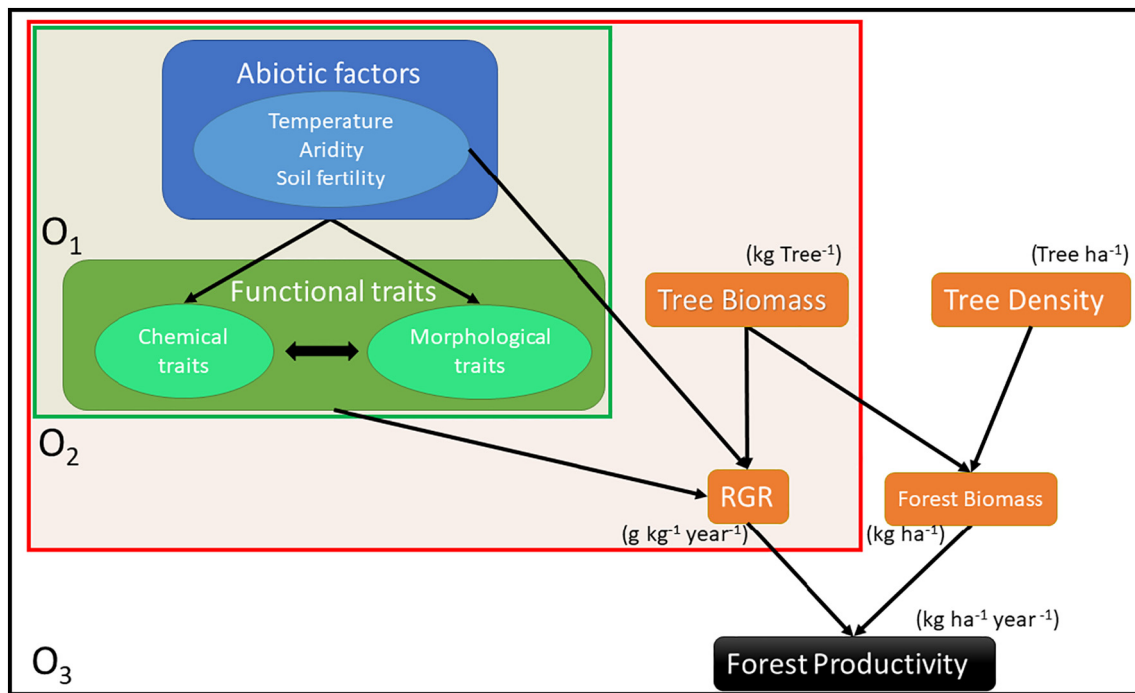


Fig. 1. Theoretical model explaining the hypothesized effects of abiotic factors on functional traits (Objective 1, O₁). The effect of abiotic factors (blue), functional traits (green) and tree factors (orange) as tree biomass (kg tree⁻¹) on relative growth rate (RGR, g kg⁻¹ year⁻¹; Objective 2, O₂), and its effect on forest biomass and all of them on forest productivity (kg ha⁻¹ year⁻¹, black) (Objective 3, O₃).

material from 5 random trees to measure key functional traits related to plant ecological strategy.

Tree relative growth rate (RGR) was calculated as: $RGR = [\ln(B_2) - \ln(B_1)] / [t_2 - t_1]$, where B is tree biomass and t is time, with 2 and 1 referring to our sampling survey data (i.e. 2018) and NFI3 data (i.e. 2007), respectively. RGR is a standardized measure of growth with the benefit of avoiding, as far as possible, the inherent differences in scale among trees of different size, thus their performances can be compared on an equitable basis (Pommerening and Muszta, 2015; Villar et al., 2017). Forest productivity (kg ha⁻¹ year⁻¹) was calculated as the difference of forest biomass between our sampling data and NFI3 for trees alive in both consecutive inventories divided by the time difference between surveys (between 9 and 11 years) with a daily resolution.

2.3. Functional traits measurements

Leaf and branch material collection was done in late spring and summer, between May and September 2018, when the leaf formation is completed. In each plot, five *Q. ilex* trees were sampled taking two branches per individual. The samples were conserved in a damp paper in a portable refrigerator and transported to the laboratory. Fully mature one-year-old leaves were taken from each branch and processed independently. A subsample of leaves were scanned (excluding petiole) and the leaf area (LA) was measured using Image Pro software (Media Cybernetics, MD, USA). Then, in five leaves we measured the leaf thickness (LT) using a micrometer (Electronic Digital Micrometer Comecta, Barcelona, Spain). After that, the leaves were dried on a stove (60 °C for two days) to calculate leaf dry mass. Leaf mass area (LMA, g m⁻²) was calculated as dry mass (g) / leaf area (m²), leaf density (LD; g cm⁻³) as LMA (g m⁻²) / thickness (μm) and leaf dry matter content (LDMC; g g⁻¹) = dry mass (g) / fresh mass (g). Another leaf subsample was dried on a stove (60 °C for 2 days) and reserved for nutrient analysis.

To analyze leaf nutrients, leaves were dried at 70 °C for 24 h before grinding with a stainless-steel grinder. The leaf N concentration was measured using an elemental analyzer (Eurovector EA3000), and we

also measured the leaf concentrations of macronutrients (P, K, Ca, and Mg) and micronutrients (Na, Fe, Mn, Cu, and Zn). To do so, 0.2 g of leaf sample was digested using 3 ml of nitric acid at 65% during 16 h at room temperature. Then the dissolution was dried up to 80 °C for 1 h before adding 1 ml of perchloric acid at 60%. The sample is later heat up to 180 °C for 4 h until it is almost transparent. Phosphorus concentration was determined according to the molybdate blue method (Murphy and Riley, 1962). Ca and Mg were determined by atomic absorption spectrophotometry, while K and Na were determined by atomic emission spectrophotometry. Lastly, Fe, Mn, Cu, and Zn were determined by atomic absorption spectrophotometry.

Additionally, two branch samples of about 5 cm length and 1 cm diameter were collected from each individual. We weighed them to calculate the branch fresh mass (in g) and we calculated the branch volume using Archimedes' principle (displaced volume of water). Branch samples were dried at 60 °C for 4 days to obtain branch-wood dry mass (BWDM). Branch-wood density (BWD, g cm⁻³) was calculated as BWDM/branch volume, and branch-wood dry matter content (BWDMC) was calculated as branch-wood dry mass/branch-wood fresh mass. All measured functional traits were calculated following the methodology described in Pérez-Harguindeguy et al. (2013).

2.4. Abiotic factors

In each plot, four random points were selected and soil samples were taken at 0–20 cm depth. The soil cores obtained were mixed in two independent samples. Later, the samples were dried at room temperature, ground, sieve (2 mm), and stored in plastic closed bags. Soil texture was determined in 10 g of soil using the Robinson pipette method (Gee et al., 1986). Soil organic carbon was measured by the Walkley and Black (1934) method with potassium dichromate. After a partial extraction of available soil nutrients, we measured soil macronutrients (P, K, Ca, and Mg) and micronutrients (Na, Fe, Mn, Cu, and Zn). To determine P content, we use the NaHCO₃ 0.5 M extraction (Olsen et al., 1982), and for Na, Ca, K and Mg, soil samples were extracted by 1 M NH₄OAc at pH 7. Fe, Zn, Mn, and Cu were determined after extraction

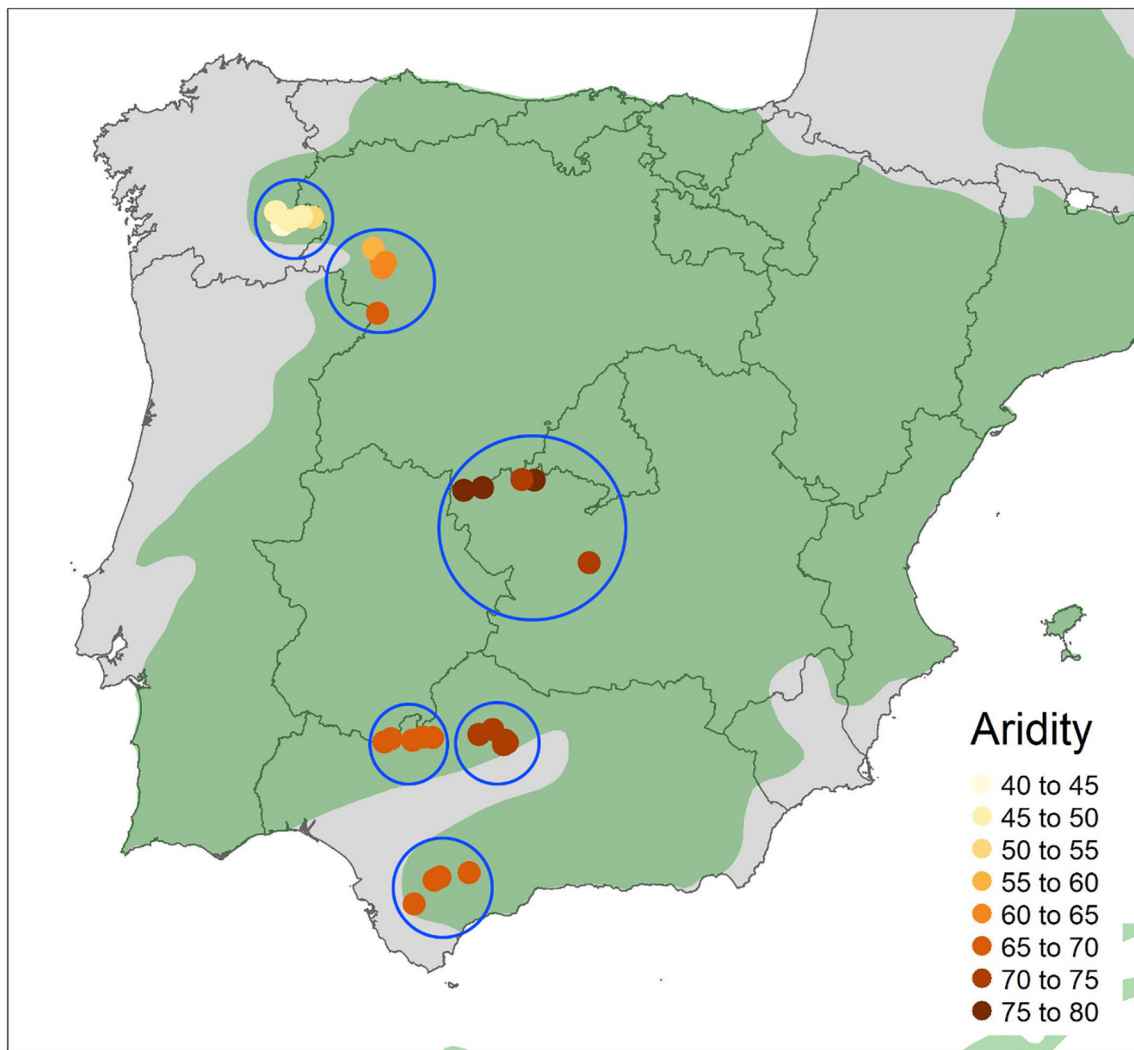


Fig. 2. Spatial distribution of the 30 sampled plots dominated by *Quercus ilex* across an environmental gradient in Spain. Dot colour indicates average aridity index (higher values indicate high aridity). Blue circles indicate the 6 climate regions used as random effect in the models.

Table 1

Descriptive statistics of the functional traits, forest traits, and abiotic factors measured in this study. SD: standard deviation, CV: Coefficient of variation ($100 \times \text{standard deviation}/\text{mean}$).

Abr.	Variable	Mean	SD	Min	Max	CV
LA	Leaf area (cm^{-2})	4.44	1.62	1.66	10.61	36.56
LD	Leaf density (g cm^{-3})	0.53	0.09	0.29	0.82	15.92
LMA	Leaf mass per area (g m^{-2})	216	36	115	321	16
LT	Leaf thickness (μm)	404	57	233	559	14
BWD	Branch-wood density (g cm^{-3})	1.14	0.05	0.88	1.35	4.40
BWDMC	Branch-wood dry matter content (%)	61.5	4.9	51.9	85.7	8.0
TB	Tree biomass (kg tree^{-1})	545	822	15	5754	151
TD	Tree density (number of trees ha^{-1})	263	282	32	1273	107
FB	Forest biomass (Mg ha^{-1})	37.9	16.7	8.7	73.1	44.0
FP	Forest productivity ($\text{Mg ha}^{-1} \text{year}^{-1}$)	2.51	1.65	0.49	6.20	65.70
RGR	Relative growth rate ($\text{g kg}^{-1} \text{year}^{-1}$)	48.3	44.6	0.5	240.9	92.3
	Clay (%)	10.0	9.5	1.0	44.1	95.5
	Aspect ($^{\circ}$)	205	107	2	358	52
	Slope (%)	7.55	5.79	0.21	25.49	76.69
Elev	Elevation (m)	556	170	233	861	31
Hills	Hillshade	0.68	0.08	0.41	0.83	11.39
TPI	Topographic position index	-1.09	2.81	-10.46	4.73	-258.51
TRI	Topographic roughness index	6.83	5.02	0.13	20.64	73.51
MAP	Mean annual precipitation (mm)	622	142	357	858	23
MAT	Mean annual temperature ($^{\circ}\text{C}$)	14.3	1.8	10.9	17.4	12.6
AI	Aridity index	66.0	8.8	45.2	79.4	13.3

with a solution containing 0.1 M triethanolamine (TEA), 0.005 M diethylenetriaminepentaacetic acid (DTPA), and 0.01 M CaCl_2 (Norvell and Lindsay, 1972). Then, soil nutrient analysis was made using the same methodology described before for leaf nutrients.

Soil topography was also considered as an abiotic factor for this study. Digital elevation models (DEM) were downloaded as raster files using the “elevatr” package. The slope, aspect, topographic position index (TPI), terrain ruggedness index (TRI), and hillshade were calculated for all plots. The slope (%) was calculated as the maximum change in elevation between the cell and its eight neighbor cells. The aspect was calculated as the direction of the slope in decimal degrees clockwise from the north (0° North, 180° South). The TPI was calculated as the difference between the maximum and the minimum value of a cell and its eight surrounding cells. Positive TPI values represent cells that are higher than the average of their surroundings cells, while negative values represent cells that are lower than their surroundings cells. The TRI was calculated as the mean of the absolute differences between the value of a cell and the value of its eight neighbor cells. Low TRI values represent even terrain surfaces, while high TRI values (over 250) are considered rugged surfaces. The hillshade calculates the hill shade from the slope and aspect layers as a number from 0 (low sun exposure) to 1 (high sun exposure). Due to the high correlation between TPI, TRI and hillshade, with slope and aspect, we decided to exclude slope and aspect from the models.

Moreover, mean annual temperature (MAT) and precipitation data (MAP) were downloaded from the WorldClim database (Hijmans et al., 2005). Additionally, we downloaded the precipitation in the driest month (DMP) and the temperature in the driest month (DMT) in Celsius degrees to calculate the modified Martonne aridity index (Stephen, 2005) as $AI_m = \{[MAP] / [MAT + 10]\} + \{[12 \times DMP] / [DMT + 10] / 2\}$. Since high AI_m indicates high water availability, we transformed this variable as follows: $AI = 100 - AI_m$. The transformation of AI ($100 - AI_m$) is the inverse of AI_m , and therefore the relationship between these two variables is completely linear and did not affect the results.

2.5. Statistical analyses

To reduce the amount of soil nutrient variables (11 variables), a principal component analysis (PCA) for all soil nutrients (S) was carried out (Fig. S1, Supplementary Material). The main axes (S_1 and S_2) explained 39.6% and 21% of the variance, respectively (Fig. S1A, Supplementary material). The axis S_1 was positively related to Ca and N concentration, while the axis S_2 was positively related to P and Fe concentration (Fig. S1B, Supplementary Material). To explore the overall relationships between abiotic factors (soil and climate variables) and avoid collinearity in the models, a correlation matrix with all potential abiotic variables was performed (Fig. S2A, Supplementary Material). Due to the high correlation between MAT, MAP, and AI ($P > 0.05$), we exclude both MAT and MAP from further analysis.

Similarly, we carried out a PCA for the leaf nutrients (L) to reduce the number of variables (Fig. S3, Supplementary Material). In this case, the amount of variance explained, and the variable scores of the PCA were also used to analyze the leaf nutrient variability and the variables that drive the most variation in each axis. Furthermore, to explore the overall relationships between functional traits and avoid collinearity in the models, a correlation matrix was made (Fig. S2B, Supplementary Material). The LMA, LD, LA, and LT showed a tight correlation between them, while BWDMC was negatively correlated with BWD. Therefore, only LMA and BWD were included as explanatory variables.

To quantify the direct effect of abiotic factors (climate variables, topography, soil texture and nutrients) on chemical and morphological leaf traits, we carried out linear mixed-effects (LME) models for each response variable at tree level (Objective 1; Fig. 1). To explore the effect of abiotic factors (climate variables, topography, soil texture and nutrients) and functional traits on the relative growth rate, we carried out

an LME model at the tree level (Objective 2; Fig. 1). All trees in our study were clustered within the plots ($n = 30$), and the plots were clustered within regions ($n = 6$). Therefore, to account for the no independence of our dataset (Lefcheck, 2021), we nested the plot random factor in the region random factor. We used the Gaussian family function to fit the models. Prior to any modeling analysis, data was scale transform using the basic “scale” function in the R software (which subtracts each data by the variable mean and divide it by the standard deviation).

Finally, to explain the causal effect of these variables on forest productivity, and account for both direct and indirect effects, we built two piecewise structural equation models (SEM) using first tree level data to explain the RGR and, second, plot-level data to explain forest productivity (Objective 3). The structure of the hypothesized causal relationships between the selected variables was set based on our expected relationships in Fig. 1. Since forest variables (forest productivity and forest biomass) and abiotic factors (climate variables, soil texture and nutrients, and soil topography) were only calculated at plot level and functional traits (LMA, LT, LD, BWD, BWDMC), tree biomass and RGR were calculated at tree level, we decided to split the analysis into two SEMs to avoid losing intraspecific variability data. First, we used data at the tree level to explain RGR using the results from Objectives 1 and 2. Then, mean values from the tree-level data were calculated to obtain a value of RGR and forest biomass per plot. These variables were then used in a subsequent SEM performed at the forest level to assess their effects on forest productivity. Our theoretical model was changed based on our previous results to exclude non-significant relationships as a function of the highest statistical support according to the significance of the Fisher's C value ($P > 0.05$), indicating that the relationships of the missing paths are neither significant nor related to our model (Shipley, 2009). In both cases, the model was fit by maximizing the restricted log-likelihood.

Data analysis was carried out using the R statistical computing software (R Core Team, 2017). The tidyverse package was used for data manipulation and graphic display (Wickham et al., 2019). Spatial representation of the NFI was done with the package “sp” and “sf” (Pebesma, 2018). Map generation was done with the package “tmap” (Tennekes, 2018). Worldclim data was downloaded and extracted with the package “raster” (Hijmans et al., 2005). The linear mixed effect model analyses were carried out using the “lmer” package (Pinheiro et al., 2017). All the data and the script to generate these results can be accessed from an open repository in github (https://github.com/PabloCSZ/ForChange/tree/forchange_soil).

3. Results

3.1. Variation in functional traits

Functional traits showed high variability, being particularly large for leaf area (Table 1). LMA, LD, and LT had around 14–16% coefficient of variation, and the range between minimum and maximum values was higher than the mean. BWD and BWDMC showed the lowest coefficient of variation among all variables, ranging between 4 and 8% (Table 1).

Leaf nutrients were summarized by the first and second principal component axes (L_1 and L_2) that explained 32.7% and 20.1% of the variance, respectively (Fig. S3A, Supplementary material). The L_1 axis was mainly positively related to Cu, Fe, and Ca concentration, while the L_2 axis was positively related to N, P, and negatively to Na concentration (Fig. S3B, Supplementary Material). The intraspecific variability in leaf functional traits showed strong relationships between them and were orthogonal to those related to branch wood density (see Fig. S2B, Supplementary Material).

The variance of plant morphological traits explained in the models was between 0.52 and 0.9 (see conditional R^2 , Table 2). However, random effects account for a substantial amount of variance, in some cases, higher to the fixed effects (see marginal and conditional R^2 , Table 2). Aridity index was the variable with the strongest effect on

Table 2

Results of the LME models explaining the variation of functional traits with abiotic factors using a restricted maximum likelihood method of fit. Estimates for each independent variable and significant correlations are indicated in bold (* $P < 0.05$ and ** $P < 0.01$) and nearly significant ($0.1 > P > 0.05$) in bold and italic. Marginal R^2 (encompassing variance explained by only the fixed effects) and conditional R^2 (comprising variance explained by both fixed and random effects). See Table 1 for acronyms.

Response variable	Independent variables				Hillshade	TRI	TPI	R^2 M	R^2 C
	AI	S1	S2	Clay %					
LMA	0.42**	-0.21	0.017	0.08	0.26	-0.1	-0.21	0.33	0.52
LD	-0.09	0.23	-0.22	-0.01	-0.10	-0.27	-0.11	0.08	0.43
LT	0.64**	-0.48*	0.27a	0.09	0.44**	0.17	-0.17	0.45	0.62
LA	-0.06	0.22	-0.02	-0.24	-0.07	0.12	0.25	0.1	0.43
BWDMC	0.40	-0.21	0.28a	-0.05	0.22	0.38*	-0.08	0.1	0.43
BWD	-0.02	-0.01	-0.16	0.03	0.02	0.12	-0.28a	0.05	0.43
L1	0.21	0.16	0.09	0.33*	-0.28*	0.05	0.05	0.28	0.79
L2	-0.08	-0.02	-0.05	0.12	0.06	-0.04	0.13	0.03	0.9

LMA and leaf thickness, having a positive effect on both traits (Table 2, Fig. 3A and B). Abiotic factors were not able to significantly explain the intraspecific variability in LD, LA, and BWD in the models. However, hillshade and soil nutrients (S_1 and S_2 axes) showed a significant effect on leaf thickness, whereas terrain ruggedness index (TRI) showed a significant positive effect on BWDMC (Table 2). Leaf nutrients, summarized in the first principal component axes (L_1), were mainly explained by clay percentage (Fig. 3C and D, respectively) and hillshade, yet the models showed a marginal R^2 of 0.28 (Table 2). A high clay percentage was related to a high Ca, Cu, and Fe leaf concentration but low N, P, and Na leaf concentration. Mixed model diagnostics (residual distribution and partial residuals) showed that model assumptions were met for each case (Figs. S4, S5, and S6, Supplementary Material).

3.2. Variation in relative growth rate (RGR)

RGR showed a high coefficient of variance among trees (92.3%), with values ranging between 0.5 to 240.9 $\text{g kg}^{-1} \text{year}^{-1}$ (Table 1). It was explained negatively by the soil PCA second axis and tree biomass (Fig. 4A and B, respectively). Functional traits, soil topography, and climatic factors did not show a significant effect on RGR, and the model showed a marginal R^2 of 0.28 (Table 3).

3.3. Forest productivity model

The two piecewise SEM built based on our initial hypothesized model to explain RGR and forest productivity showed a high goodness of fit (Fisher's $C = 28.9$, P value = 0.15, and Fisher's $C = 8.1$, P -value

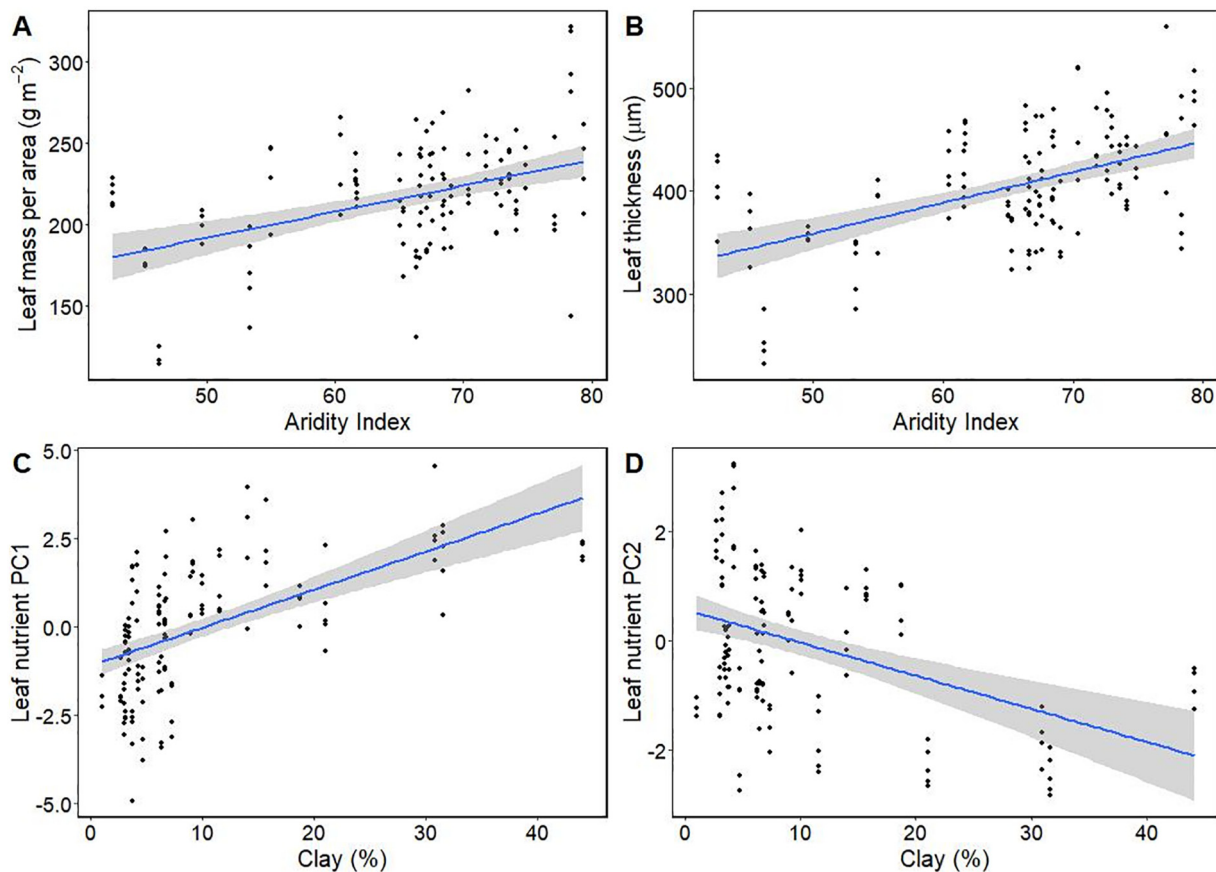


Fig. 3. Relationships of LMA and LT with Aridity (A and B, respectively), and relationships of leaf nutrient first (L_1) and second (L_2) PC axes with clay percentage (C and D, respectively) at tree level. Grey area indicates 95% confidence interval.

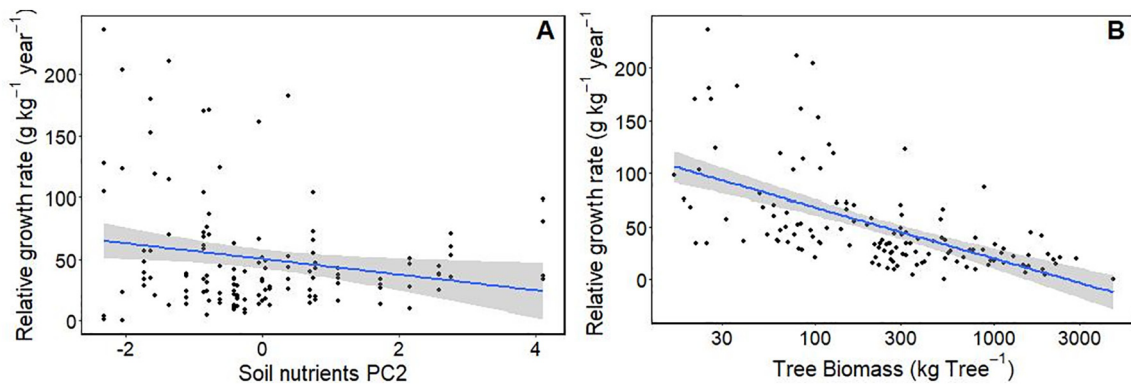


Fig. 4. Relationships of the relative growth rate with soil nutrients PC2 and tree biomass (axis log transformed) (A and B, respectively) at tree level. Grey area indicates 95% confidence interval.

= 0.74, respectively) and account for both direct and indirect effects of functional traits and abiotic factors. At the tree level, the soil texture and topography explained the leaf nutrients (L_1) (Fig. 5). L_1 and branchwood density explained the tree biomass and together with the soil nutrients (S_1 and S_2) explained the RGR of each tree. At the plot level, aridity and L_1 explained the mean LMA of the plot, which alongside L_1 explained the forest biomass. Ultimately, the mean RGR of the plot, and the forest biomass, explained the forest productivity (Fig. 5).

4. Discussion

Our results showed that forest productivity was mainly explained by RGR, which, in turn, was affected by tree biomass and soil nutrients, with an indirect effect of functional traits and climate factors. We found a positive effect of LMA and leaf nutrients on forest biomass that directly affected forest productivity. This suggests that the variability of functional traits in response to climate factors might directly affect forest carbon storage in the long run.

5. Effects of abiotic factors on functional traits

LMA constitutes the most measured and commonly used trait to describe plant ecological strategies. Our results indicated that LMA was positively related to aridity and sun exposure time due to the hill shade effect. Similarly, LMA has also been found to decrease with precipitation (Ogaya and Peñuelas, 2007) and temperature (Poorter et al., 2009; Vilà-Cabrera et al., 2015). Leaf thickness was also explained by aridity and hillshade and showed a high correlation with LMA. This suggests that the increase in LMA under drought conditions and high light exposure is linked with an increase in leaf thickness, associated with a larger volume of mesophyll area in the leaf tissue (Poorter et al., 2009; Villar et al., 2013). In theory, this morphological change has a direct impact on the gas exchange (Maire et al., 2015) and water transport (Rosas et al., 2019), and it may reduce the impact of abiotic stress on plant growth.

Table 3

Results of the relative growth rate (RGR) model explained by tree biomass (TB), functional traits (LMA, BWDMC), leaf nutrients main PC axes (L_1 and L_2), soil nutrients main PC axes (S_1 and S_2), soil texture and topography (Clay, TPI, TRI, and Hills), and aridity using a restricted maximum likelihood method of fit. Significant correlations are indicated (* $P < 0.05$ and ** $P < 0.01$). Marginal and conditional R^2 are included. The table is displayed in two rows. See Table 1 for acronyms.

Independent variable	TB	LMA	BWDMC	L_1	L_2	S_1	S_2
	-0.58**	0.05	0.07	0.01	0.14	0.34*	-0.39**
Independent	Clay	TPI	TRI	Hills	AI	R^2 M	R^2 C
	-0.19	0.02	0.03	0.04	-0.04	0.28	0.41

The leaf chemical traits were mainly explained by the clay percentage and sun exposure due to the hill shade effect, rather than aridity or soil nutrients. A high clay percentage in the soil is generally associated with low water drainage and high nutrient storage (Anderson et al., 2006). Overall, this leads to a high soil nutrients availability (Table S1, Supplementary material), and ultimately, a high leaf nutrient concentration. However, for some nutrients, a high clay percentage associated with a high concentration of iron oxide can also lead to a more negative soil matric potential in summer and autumn and reduce soil nutrient transport, a situation referred to as the inverse texture effect (Fernandez-Illescas et al., 2001). This might be our case based on the negative correlation between clay percentage and the L_2 axis (mainly explained by the leaf N and P concentration), and the negative effect of clay percentage on soil P concentration (data not shown). Furthermore, an increase in leaf P concentration seems to be paired up with high leaf Mn concentration (Fig. S1, Supplementary material). The accumulation of Mn in the leaf is relatively common when P mobility in the soil is limited (Lambers et al., 2015). It seems that root exudates can locally modify the soil pH, which makes P more available alongside Mn (White et al., 2013). Therefore, it is possible that the clay percentage in the soil can increase soil nutrients concentration, but reducing its mobility in highly demanded nutrients, like P. The increase in sun exposure due to the hillshade effect can lead to oxidative stress and damage the parenchymal tissue despite the increase in leaf thickness (Demmig-Adams and Adams, 2006). This would reduce photosynthetic rate and leaf nutrients mimicking water stress in arid conditions. Thus, our results highlight the importance of soil texture and topography to shape the leaf chemical composition. However, the random effects associated to the location of the plots explain a large portion of the variation in functional traits. Therefore, it is possible that other biotic or abiotic factors play a key role in plant functioning at a regional scale.

5.1. Effect of abiotic factors, functional traits, and forest structure on RGR

The individual tree biomass was the main intrinsic factor explaining the RGR of the trees. This negative relationship suggests that larger trees tend to grow more slowly, which could be explained by a lower proportion of leaves (Villar et al., 2017). Thus, as the tree biomass and the number of resources required for growing increase, nutrient assimilation and transport proportionally decrease, reducing RGR. Competitive interactions for light and nutrients between surrounding trees reduce plant growth, at least in the early years (Binkley, 2004). Thus, the magnitude of the biomass-growth relationship depends also on the competitive environment (Ruiz-Benito et al., 2015). Furthermore, hydraulic and nutrient limitations appear in older trees due to mechanical constraints in vessel size, which reduces both water and nutrient transport (Mencuccini et al., 2005). An increase in soil nutrient concentration should yield high plant biomass, however, this only seems to be true for small trees (Li et al., 2018). The increase in soil

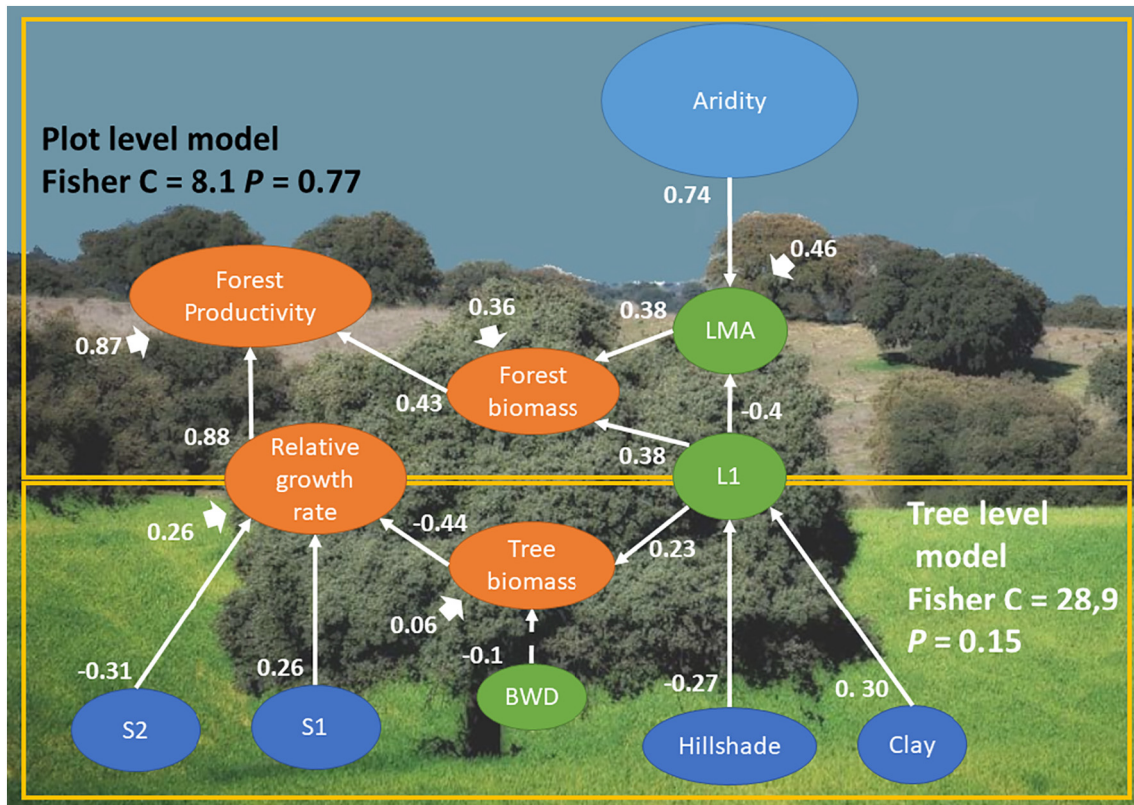


Fig. 5. (Top) Piecewise structural equation modeling explaining forest productivity with forest biomass and RGR based on our initial hypothesis (see Fig. 1) using data from 30 plots. (Bottom) Piecewise structural equation modeling explaining the RGR of each tree in our study ($n = 135$). Dashed lines (from BWD to tree biomass) indicate non-significant relationships. Boxes colour indicate the type of variable (blue: abiotic factor, green: functional trait, and orange: tree factor). Short arrows indicate the correlation coefficient for each response variable ($n = 135$). S_1 and S_2 (first and second axes of soil PCA), LMA (leaf mass per area), L_1 and L_2 (first and second axes of leaf PCA), BWD (branch-wood density).

nutrients concentration does not mitigate the morphological changes associated with nutrient transport when the tree gets older and the biomass increases (Drake et al., 2010). In our case, RGR was explained by the soil nutrients summarized in the soil PCA axes (S_1 and S_2). However, opposite results have also been found (Paoli and Curran, 2007; Zemunik et al., 2018), and further studies are still required to understand the effect of soil nutrients on plant growth under field conditions.

Climate factors had a low effect on RGR, in agreement with previous results for several *Quercus* species suggesting a lower explanatory power of climate in comparison to local factors as nutrient availability, soil texture, and tree density (Villar et al., 2017). Furthermore, functional traits did not show a significant effect on RGR either, which contradicts several studies that suggested functional trait variability has a physiological impact at the whole-plant level (Poorter et al., 2009; Violle et al., 2007). However, most of those studies have been performed in young seedlings rather than adult trees (Bastias et al., 2018). When this distinction has been made, results have shown that LMA does not correlate with RGR for adult trees (Laughlin et al., 2017; Wright et al., 2010). The lack of relationship has been justified by the absence of a clear physiological basis in the so-called "soft traits", like LMA and leaf thickness, and tree height (Rosas et al., 2019). However, this kind of terminology has been questioned because it focuses on methodological aspects (how easy or difficult it is to measure a certain trait) and underestimates the functional meaning of leaf morphology (Violle et al., 2007). In *Q. ilex* evergreen leaves, high LMA is the result of high sclerenchymatic tissues (de la Riva et al., 2016b) that confer leaf resistance to water diffusion from the vein to the mesophyll during climatic stress. Most likely, the leaf functional trait plasticity is reducing the negative effect of environmental stress, thus, limiting the reduction of RGR

(Gratani, 2014). According to this, morphological changes in the leaf are made to keep plant growth steady regardless of climate conditions.

5.2. Modeling forest productivity depending on ecological, physiological, and environmental factors

Our models confirm our initial hypothesis, which suggests that forest productivity depends on both RGR and forest biomass. Key functional traits like LMA and BWD affect forest productivity, but not directly as we initially hypothesized. For instance, the effect of LMA and climatic factors (i.e. aridity) over RGR did not occur directly, instead, increases of LMA directly affect tree biomass (Antúnez et al., 2001; Lambers and Poorter, 2004). However, this relationship does not hold itself when the tree size increases because respiratory losses for maintenance increases in large trees (Mencuccini et al., 2005). Thus, even though LMA is a highly sensitive trait to environmental factors, its variation does not always represent an adaptive advantage to increase the RGR. Instead, we found a positive effect of LMA on forest biomass. This suggests that a thick and dense leaf increases forest biomass in the long term. Similar results have been found when limited conditions are present (van der Sande et al., 2018), and in temperate forests (Yuan et al., 2019). Similarly, other abiotic factors, such as soil topography and texture, showed an indirect effect on tree biomass by affecting leaf nutrient concentration. Therefore, leaf chemical and morpho-physiological changes might be a strategy to maintain water transport, leaf nutrition, and C uptake under abiotic stress, therefore increasing the forest biomass.

The positive effect of intraspecific trait variability on tree biomass and tree growth could be potentially occurring in other *Q. ilex* forests, which are well distributed across the South of Europe and around the Mediterranean basin (Urbietta et al., 2011) or even for other tree species.

The specific effect of abiotic factors on functional traits and plant growth should be further explored in other Mediterranean ecosystems in South America, Southwest Australia or South Africa where summer aridity can have a detrimental effect on species distribution and functional diversity (Christie et al., 2011; Gil-Pelegrín and Peguero-Pina, 2017). The intraspecific variability of leaf traits, such as LMA, are related to their adaptation to xeric conditions (Gil-pelegrín and Peguero-Pina, 2017), and should influence forest demographic characteristics across the globe. Here, we focused our analysis on tree growth and forest productivity but other key demographic processes as tree mortality and regeneration are critical determining long-term forest dynamics (e.g. Astigarraga et al., 2020; Lines et al., 2020). Furthermore, differential demographic responses can alter population density and the diversity in functional traits affecting to plant-plant competition and forest productivity (Beckage and Clark, 2003; Gillner et al., 2013). Ultimately, our study showed that forest productivity is mainly explained by RGR, which is affected by tree biomass and soil nutrients. This result suggests that protecting established forests increases forest biomass, and utterly, forest productivity (Morán-Ordóñez et al., 2020). Scheduling pruning and wood harvesting allow for a reduction in stand density, increase light availability in dense patches, and eliminate competitive interactions between trees (Reyes et al., 2008). Similarly, protecting species diversity and regulating animal foraging increase soil fertility in the long term (Ammer, 2019; James et al., 2009). Thus, the implementation of regional forest policies may be as important as national environmental regulations to protect *Q. ilex* forest productivity (Mokany et al., 2008).

6. Conclusion

Our findings highlight that the large intraspecific variation in key functional traits (i.e. LMA) was associated with a climatic gradient and shows that plant changes to abiotic stress do not always have direct effects on plant growth or forest productivity, but indirect effects can be important. Instead, soil fertility and tree biomass have a fundamental effect on the relative growth rate, suggesting forest management may have a bigger role than we originally thought to maintain forest ecosystem services.

CRedit authorship contribution statement

Pablo Salazar Zarzosa: Formal analysis, Software, Writing – original draft. **Aurelio Diaz Herraiz:** Writing – review & editing, Data curation, Investigation. **Manuel Olmo:** Conceptualization, Data curation, Investigation. **Paloma Ruiz-Benito:** Conceptualization, Methodology, Writing – review & editing, Validation. **Vidal Barrón:** Methodology, Supervision. **Cristina C. Bastias:** Writing – review & editing, Methodology. **Enrique G. de la Riva:** Conceptualization, Writing – review & editing. **Rafael Villar:** Conceptualization, Writing – review & editing, Funding acquisition, Methodology.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.147468>.

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