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Potential climatic influence on the  
maximum stand carrying capacity of 15  
Mediterranean conifers and broadleaves

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## RESUMEN

Las proyecciones de cambio climático para la cuenca del Mediterráneo predicen un incremento continuo en episodios de sequía y calor extremos, afectando a la dinámica, estructura y composición de las masas forestales. En este contexto, resulta fundamental comprender cómo el clima influye en la relación tamaño-densidad máxima (recta de autoclareo) de estas masas con el fin de diseñar actuaciones de gestión forestal sostenible adaptadas a este nuevo escenario. Este estudio pretende avanzar en esta línea, analizando los potenciales impactos del clima en el Índice de Máxima Densidad ( $SDI_{max}$ ) de 15 especies forestales pertenecientes a los géneros *Pinus*, *Fagus* y *Quercus*. Para ello se utilizaron las bases de datos del Tercer Inventario Forestal Nacional Español (IFN3) y WorldClim. En primer lugar, se ajustaron rectas de autoclareo básicas mediante regresión cuantílica y se estimaron nuevos valores  $SDI_{max}$  de referencia por especie. En un segundo paso, se seleccionaron 35 variables climáticas anuales y periódicas para ajustar rectas de autoclareo dependientes del clima. El mejor modelo climático-dependiente fue seleccionado para cada especie basándonos en el Índice de Información de Akaike con el fin de analizar las tendencias generales y específicas en la variación de  $SDI_{max}$ . Para todas las especies de estudio, la influencia del clima sobre el  $SDI_{max}$  fue significativa. Los resultados obtenidos mostraron una tendencia común en la variación de  $SDI_{max}$ , con valores más pequeños vinculados a condiciones más secas y cálidas, lo que sugiere reducciones potenciales del stock de estas especies bajo futuros escenarios climáticos. En oposición a esta tendencia, el modelo de *Pinus nigra* sugiere que inviernos más suaves como efecto de incrementos en temperaturas mínimas podrían beneficiar a las especies en zonas de montaña. En general, el estrés hídrico (expresado a través del Índice De Martonne) fue un factor determinante afectando al  $SDI_{max}$  de *Fagus*, mientras que cambios en las temperaturas de primavera y verano explicaron las variaciones  $SDI_{max}$  de las especies del género *Quercus*. Las especies de *Pinus* se vieron indistintamente afectadas por potenciales variaciones de temperatura y humedad. Todos los modelos climático-dependientes seleccionados mejoraron los modelos básicos y los modelos ajustados en estudios similares, como aquellos que utilizan el Índice de Martonne como variable climática independiente. Nuestros hallazgos destacan la necesidad de utilizar variables climáticas periódicas para caracterizar mejor los impactos climáticos en el  $SDI_{max}$ . Los modelos presentados en este estudio permitirán obtener estimaciones más precisas de la máxima densidad admisible por diferentes especies de coníferas y frondosas, proporcionando una herramienta avanzada para la gestión forestal sostenible de masas puras y mixtas mediterráneas bajo diferentes escenarios de cambio climático.

**Palabras clave:** Autoclareo, Reineke, cambio climático, modelización, ciencia de datos

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## ABSTRACT

Climate change projections for the Mediterranean basin predict a continuous increment in extreme drought and heat episodes, affecting forest dynamics, structure and composition. Understanding how climate influences the maximum size-density relationship (MSDR) is therefore critical to design adaptative silvicultural guidelines based on the potential stand carrying capacity of tree species. With this aim, data from the Third Spanish National Forest Inventory (3NFI) and WorldClim databases were used to analyze climate related variations of the maximum stand carrying capacity for 15 species from the *Pinus*, *Fagus* and *Quercus* genus. First, basic MSDR were fitted using linear quantile regression and observed size-density data from monospecific 3NFI plots. Reference values of maximum stocking, expressed as  $SDI_{max}$ , were estimated by species. In a second step, climate-dependent MSDR models including 35 different annual and seasonal climatic variables were fitted. The best climate-dependent MSDR model was selected by species according to the Akaike Information Criteria in order to analyze general and species-specific trends in the  $SDI_{max}$  variation. Results showed a common trend across species in  $SDI_{genus}$  variation with smaller  $SDI_{max}$  values linked to drier and warmer conditions, suggesting potential reductions of the maximum stocking for this species based on projected climatic scenarios. Opposed to this trend, results for *Pinus nigra* suggest that milder winters as effect of increments in minimum temperatures could beneficiate mountainous species. Humidity (expressed as the De Martonne Index) was found as key driver affecting  $SDI_{max}$  of *Fagus* species, since changes in spring and summer temperatures explained  $SDI_{max}$  variations of *Quercus* species. *Pinus* species were indistinctively affected by temperature and water stress. All the selected climate-dependent models improved the goodness of fit over the basic and the business-as-usual models including the De Martonne Index as independent climatic variable. Our findings highlight the importance of using specific climatic variables to better characterize climatic impacts on the MSDR. Models presented in this study will allow to obtain more precise estimations of the maximum stocking for different coniferous and broadleaved species, providing an advanced tool for managing Mediterranean pure and mixed forests under different scenarios of climate change.

**Keywords:** Self-thinning, climate change, National Forest Inventory, data programming, Reineke, natural mortality

## 1.- INTRODUCTION

The maximum stand carrying capacity is a key variable commonly used in forest management to sustainably utilize site resources maintaining a healthy and optimal stand growth. Reineke (1933) was the first who addressed this concept when proposing the Maximum Stand Density Index ( $SDI_{max}$ ), which is an attribute defining full site occupancy (Zeide, 2005). He discovered that for any given tree size (i.e. 25 cm), a species' physiological attributes constrain the maximum number of trees that a fully stocked stand can support before natural mortality takes place. This relationship is widely recognized as the Maximum Size-Density Relationship (MSDR) in forest science (Reineke, 1933; Drew and Flewelling, 1977) as in ecology (Yoda et al., 1963; Fowler, 1981). Also known as the self-thinning line, its applications encompass studies related to habitat distribution (Moore and Deiter, 1992), assessment of risks due to abiotic and biotic factors (Fettig et al., 2007; Ducey et al., 2017) or the capacity of forests as carbon sinks (Woodall et al., 2011; Brunet-Navarro et al., 2016). Its use also extends to the development of forest management tools such as forest growth models (Makela et al., 2000; Yang and Titus, 2002), density management diagrams (Long and Shaw, 2005; Valbuena et al., 2008) and the development of management plans (Jack and Long, 1996; Churchill et al., 2013). Initially, Reineke (1933) and Yoda et al (1963) claimed that the MSDR, and therefore the maximum stand carrying capacity, might not be influenced by environmental conditions or site quality. However, recent studies show that this relationship vary with site quality (Bi, 2001; Comeau et al., 2010), stand origin (Weiskittel et al., 2009), nutrient availability (Morris, 2003; Reyes-Hernandez et al., 2013) and stand age (Zeide, 2005). In particular, climate deserves special attention in regard to its influence on the MSDR since it is widely accepted that climate is currently changing, and forest stands are already experiencing variations in its composition, structure and dynamics (IPCC, 2018). Climate projections suggest that climate change will lead to different site conditions modifying the stand carrying capacity, species distribution and niche suitability. In this context of climate change, recent studies have shown that the size-density relationship is affected by climate, finding an important decline in the maximum stand carrying capacity related to potential drought conditions in different areas of the Mediterranean basin (Condés et al., 2017; Aguirre et al., 2018). These studies frequently use annual climatic variables, such as the De Martonne Index (1926) in order to study the climatic influence on MSDR. However, further studies need to consider more precise (monthly or seasonal) climatic variables in order to better understand this relationship. An example is found at Kweon and Comeau (2017), who used periodic climatic variables such as degree-days above 5 °C, degree-days below 0°C or summer heat moisture index, defined as the ratio between mean warmest month temperature and mean summer precipitation, in order to better characterize environmental conditions. They found that higher temperatures and longer free frost period could affect negatively the maximum stand carrying capacity. The effect of climate on the MSDR has been also widely studied in mixed stands (Condés et al., 2013; del Río et al., 2014; Pretzsch and Biber, 2016; Andrews et al., 2018). Recent research has focused on the estimation of size-density relationship for coniferous species (Brunet-Navarro et al., 2016; Aguirre et al., 2018), but less has been done related to broadleaved species. Future works should focus on broadleaved species in order to discover potential changes on the structure, composition and dynamics of pure and

conifer-broadleaved mixed stands. Species composition and functional traits have also proven to be key drivers affecting the maximum stand carrying capacity (Ducey et al., 2017; Kimsey et al., 2019). All of these works highlight the importance to consider a gradient of different environmental conditions in order to better understand regional landscape patterns in the estimation of maximum stocking. To achieve that, National Forest Inventory (NFI) data has been proved to be a suitable database to study the climatic influence on MSDRs, since it cover a wide variety of forest types, stand structures and species distributed along a gradient of environmental conditions (Condés et al., 2017; Andrews et al., 2018; Toigo et al., 2018). Previous studies have used these sources of information in the fitting basic and climate-dependent MSDR models by different statistical methods (Zhang et al., 2005; Hann, 2014). Principal component analysis (Hutchings and Budd, 1981; Weller, 1987; Bégin et al., 2001), stochastic frontier analysis (Bi et al., 2000; Bi, 2004; Charru et al., 2012) and linear quantile regression (Zhang et al., 2013; Vospernik and Sterba, 2015) have been the most used methods used to fit the self-thinning line. In this study, linear quantile regression was chosen since this method is capable of providing statistical analysis and estimation for linear model fit to any part of the response distribution, including near upper bounds, without stringent assumptions on the error distribution (Koenker and Bassett, 1978). Exploring the relationship between climate and the maximum carrying capacity of a forest stand is therefore key to understand its dynamics, as well as to manage and use sustainably the products and services it provides.

## 2.- OBJECTIVES

The aim of this study was to analyze the influence of climate on the maximum stand carrying capacity (expressed as  $SDI_{max}$ ) of 15 coniferous and broadleaved species in Spain.

Our specific objectives were:

1. To fit basic and climate-dependent MSDR models, discovering the key climatic drivers influencing the MSDR by species.
2. To estimate maximum stand carrying capacity for these species with and without climate influence
3. To analyze and quantify general and species-specific trends in  $SDI_{max}$  variation for the studied species.



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### 3.- MATERIAL AND METHODS

#### 3.1. Data

Spanish Third National Forest Inventory (3NFI) plots were used. 3NFI plots consisted on four concentric circles with radii of 5,10,15 and 25 meters where different tree level variables of all trees over 7,5; 12,5; 22,5 and 42,5 cm diameter at breast height (1,3 m), respectively, were recorded between 1997 to 2007 (Herrero and Bravo, 2012; Alberdi et al., 2016). Expansion factors were used to estimate stand variables from individual tree variables, such as density (N), quadratic mean diameter (Dg), basal area (G) and dominant height ( $H_{dom}$ ). 3NFI plots located in monospecific stands of different coniferous and broadleaved species (Table 1) were selected. Plots were considered as monospecific when the main species accounted for more than 90% of the total basal area. Low-density plots from open-forest areas were discarded (Riofrio et al., 2016). Plots with quadratic mean diameter outside the range 10-60 cm were dismissed in order to avoid including under-represented stands (Condés et al., 2017). Climatic data were obtained from Worldclim 2 (Fick and Hijmans, 2017). Worldclim 2 is a high-resolution global geodatabase (30 arc seconds or ~ 1km at equator) of monthly average data based on a high number of climate observations and SRTM topographical data. Climatic variables over a 30-year climate normal period (1970-2000) were considered including annual, seasonal and monthly temperature and precipitation records. Variables related to temperature were expressed in Kelvin degrees (K) since logarithmic models fitted in this study does not accept negative values of the independent variables. In addition, the De Martonne Index (De Martonne, 1926) and the Temperature Annual Range were calculated to represent water supply and annual heat. Potential evapotranspiration data from the Global Potential Evapotranspiration Geospatial Database (Trabucco and Zomer, 2009) were also considered in this study. 35 climatic variables were used in this study to characterize climate annual and seasonally (Table 2). All climatic variables were derived to selected monospecific plots using a GIS software and the plot-specific latitude and longitude. A complete statistic summary of the climatic variables used in this study is shown in Supplementary Tables 1 and 2.

#### 3.2. Data modeling

Basic MSDR (without climatic influence) and climate-dependent MSDR models were fitted by species in order to analyze the influence of climate on the MSDR and the maximum stand carrying capacity.

**Table 1:** Means and ranges (minimum-maximum) of the main stand characteristics of the 3NFI plots selected to fit the basic and climate-dependent MSDR models

Functional group	Species	n	Elev	N	Dg	G	H <sub>dom</sub>
Conifers	<i>Pinus canariensis</i>	1000	1341 (347-2343)	352 (44-1945)	28,55 (15-50)	18,19 (4,49-54,52)	14,68 (4,93-30,70)
	<i>Pinus halepensis</i>	5887	668 (0-1549)	443 (33-2769)	19,64 (10,01-39,91)	11,14 (2,10-46,13)	8,69 (2,69-23,43)
	<i>Pinus nigra</i>	2297	1118 (292-2141)	737 (49-3945)	19,90 (10,14-39,99)	18,73 (3,51-62,45)	10,44 (1,39-33,20)
	<i>Pinus pinaster</i>	4563	793 (5-1842)	514 (45-2886)	26,48 (15-44,97)	23,18 (4,42-87,01)	12,52 (4,54-29,48)
	<i>Pinus pinea</i>	1051	528 (3-1063)	318 (29-3360)	27,38 (10,07-49,66)	13,66 (2,99-64,48)	9,06 (2,56-19,31)
	<i>Pinus radiata</i>	822	394 (8-1443)	422 (46-2637)	34,62 (20,01-59,49)	33,31 (6,99-89,91)	24,30 (7,55-45,10)
	<i>Pinus sylvestris</i>	3653	1334 (301-2341)	717 (50-3491)	23,70 (15-49,58)	27,25 (4,87-84,42)	12,77 (3,38-30,48)
	<i>Pinus uncinata</i>	362	1904 (1337-2496)	775 (114-2851)	23,35 (15,17-38,63)	28,94 (8,48-65,34)	11,29 (1,82-20,70)
Broadleaves	<i>Fagus sylvatica</i>	1348	1009 (143-1943)	556 (35-2544)	29,40 (15,07-59,97)	27,80 (4,03-64,84)	19,09 (5,05-36,35)
	<i>Quercus faginea</i>	498	884 (261-1552)	854 (99-3088)	15,03 (10,01-29,76)	13,02 (3,87-39,71)	7,81 (3,25-18,29)
	<i>Quercus ilex</i>	3911	647 (57-1980)	262 (31-2005)	24,85 (10-49,98)	6,68 (2,39-22,78)	6,27 (3,95-20,14)
	<i>Quercus petraea</i>	229	974 (72-1909)	799 (44-3519)	22,13 (10-49,17)	23,07 (5,09-59,49)	12,71 (5,33-28,82)
	<i>Quercus pyrenaica</i>	1442	1028 (289-1840)	857 (48-3947)	17,42 (10,01-39,96)	15,43 (3,95-55,14)	9,95(3,55-22,52)
	<i>Quercus robur</i>	591	495 (31-1598)	396 (29-1791)	29,40 (15,07-54,92)	20,20 (3,75-61,49)	13,96 (3,85-28,98)
	<i>Quercus suber</i>	732	398 (18-1065)	230 (20-1287)	33,09 (15,06-59,69)	13,67 (3,16-41,87)	8,20 (2,38-15,55)

*n* - Number of pure plots, *Elev* - Plot altitude (m), *N* - Stand density (trees ha<sup>-1</sup>), *Dg* - Quadratic mean diameter (cm), *G* - Basal area (m<sup>2</sup> ha<sup>-1</sup>), *H<sub>dom</sub>* - Dominant height (m)

**Table 2:** List of climatic variables used in this study.

Variable	Definition
T	Annual Mean Temperature (Kelvin degrees)
T <sub>i</sub>	Mean Temperature (Kelvin) of the i season (i = 1,2,3,4)
MNT	Annual mean Minimum Temperature (Kelvin degrees)
MNT <sub>i</sub>	Minimum Temperature (Kelvin degrees) of the i season (i = 1,2,3,4)
MXT	Annual Mean Maximum Temperature (Kelvin degrees)
MXT <sub>i</sub>	Maximum Temperature (Kelvin degrees) of the i season (i = 1,2,3,4)
MXTWM	Maximum Temperature of Warmest Month (Kelvin degrees)
MNTCM	Minimum Temperature of Coldest Month (Kelvin degrees)
TAR	Temperature Annual Range (Kelvin degrees) (MXTWM - MNTCM)
P	Total Annual Precipitation (mm)
P <sub>i</sub>	Total precipitation (mm) of the i season (i = 1,2,3,4)
PWM	Precipitation of Wettest Month (mm)
PDM	Precipitation of Driest Month (mm)
M	Annual De Martonne Index (mm °C <sup>-1</sup> )
M <sub>i</sub>	De Martonne Index (mm °C <sup>-1</sup> ) of the i season (i = 1,2,3,4)
PET	Annual Potential Evapotranspiration (mm)
PET <sub>i</sub>	Potential Evapotranspiration (mm) of the i season (i = 1,2,3,4)

i: 1=Autumn (October, November, December), 2=Winter (January, February, March), 3=Spring (April, May, June), 4=Summer (July, August, September)

Firstly, basic MSDR models were fitted using the Reineke's (1933) equation (Eq.1) after logarithmic transformation (Eq.2):

$$N_{\max} = \alpha_0 \cdot Dg^{\beta_0} \quad (\text{Eq.1})$$

$$\ln(N_{\max}) = \alpha_0 + \beta_0 \cdot \ln(Dg) \quad (\text{Eq.2})$$

where:  $\alpha_0$  and  $\beta_0$  were the species-specific intercept and slope parameters, respectively for the MSDR model

Basic MSDR coefficients were estimated by linear quantile regression for each species using the `quantreg` R package (Koenker, 2015) available at R software (R Core Team, 2018). Models were fitted for the upper quantiles (95<sup>th</sup>, 97<sup>th</sup> and 99<sup>th</sup>) since the MSDR is a limiting boundary (Ducey and Knapp, 2010).

Secondly, climate-dependent MSDR models were fitted by expanding coefficients in Eq.(2) as a function of climate:

$$\ln(N_{\max}) = \alpha_0 + \alpha_1 \cdot \ln(\text{Clim}_n) + (\beta_0 + \beta_1 \cdot \text{Clim}_n) \cdot \ln(Dg) \quad (\text{Eq.3})$$

Where:  $\text{Clim}_n$  was a climatic variable from Table 2 and  $\alpha_0$ ,  $\alpha_1$ ,  $\beta_0$  and  $\beta_1$  were the MSDR model coefficients

Coefficients of the climate-dependent MSDRs were obtained by fitting linear quantile regression for the same quantiles as basic MSDRs. From a total of 525 climate-dependent MSDR models fitted, those with all the coefficients significant ( $p < 0.05$ ) were selected for each species. Among them, the best climate-dependent model by species was selected based on the Akaike Information Criterion (AIC). Goodness of fit of the selected model was compared to the basic MSDR in terms of pseudo- $R^2$  for quantile regression (Koenker and Machado, 1999). The efficiency of the selected models was also compared to the climate-dependent MSDRs fitted with dependent variable equal to the De Martonne Index (when significant) since this Index has been widely used in similar studies (Brunet-Navarro et al., 2016; Condés et al., 2017; Aguirre et al., 2018).

### 3.3. Climatic influence on the maximum stand carrying capacity

Maximum stand carrying capacity was expressed as the Maximum Stand Density Index ( $\text{SDI}_{\max}$ ) derived from Reineke's (1933) equation. Reference values of  $\text{SDI}_{\max}$  ( $\text{SDI}_{\max, \text{REF}}$ ) were calculated by species using estimated coefficients from basic MSDR models (Eq.2).

$$\text{SDI}_{\max, \text{REF}i} = e^{[\alpha_0 + \beta_0 \cdot \ln(25)]} \quad (\text{Eq.4})$$

In a similar way, estimated coefficients from the selected climate-dependent models were used to calculate the climate-dependent  $\text{SDI}_{\max}$  ( $\text{SDI}_{\max, \text{CLIM}}$ ) [Eq.5]:

$$\text{SDI}_{\max, \text{CLIM}_i, j} = e^{[(\alpha_0 + \alpha_1 \cdot \ln(\text{Clim}_n)) + (\beta_0 + \beta_1 \cdot \text{Clim}_n) \cdot \ln(25)]} \quad (\text{Eq.5})$$

Where:  $\text{SDI}_{\max, \text{CLIM}_i, j}$  is the maximum stand carrying capacity of species  $i$ , using the climatic variable  $j$ .  $\text{Clim}_n$  is the mean value of each climatic variable.

$\text{SDI}_{\max, \text{CLIM}}$  values were estimated and plotted along the range of values for each selected climatic variable. Then, potential climatic impacts were quantified by means of unitary difference using the estimated  $\text{SDI}_{\max, \text{CLIM}}$  and the climatic values at the extremes (percentiles 1 and 99) of each climatic variable distribution (Supplementary Tables 2,3) as shown in Eq. 6:

$$\Delta SDI_{\max CLIM_{i,j}} = \frac{SDI_{\max CLIM_{i,j,p99}} - SDI_{\max CLIM_{i,j,p1}}}{Clim_{i,j,p99} - Clim_{i,j,p1}} \quad (\text{Eq.6})$$

Where:  $\Delta SDI_{\max CLIM_{i,j}}$  is the unitary difference in the maximum stand carrying capacity based on the climatic variable  $j$  for the species  $i$ .  $SDI_{\max CLIM_{i,j,p99}}$  and  $SDI_{\max CLIM_{i,j,p1}}$  are the estimated values of  $SDI_{\max CLIM}$  at the 1<sup>st</sup> and 99<sup>th</sup> percentiles of the climatic variable  $j$  for the species  $i$ .  $Clim_{i,j,p99}$  and  $Clim_{i,j,p1}$  are the 1<sup>st</sup> and the 99<sup>th</sup> percentile of the climatic variable  $j$  for the species  $i$ .

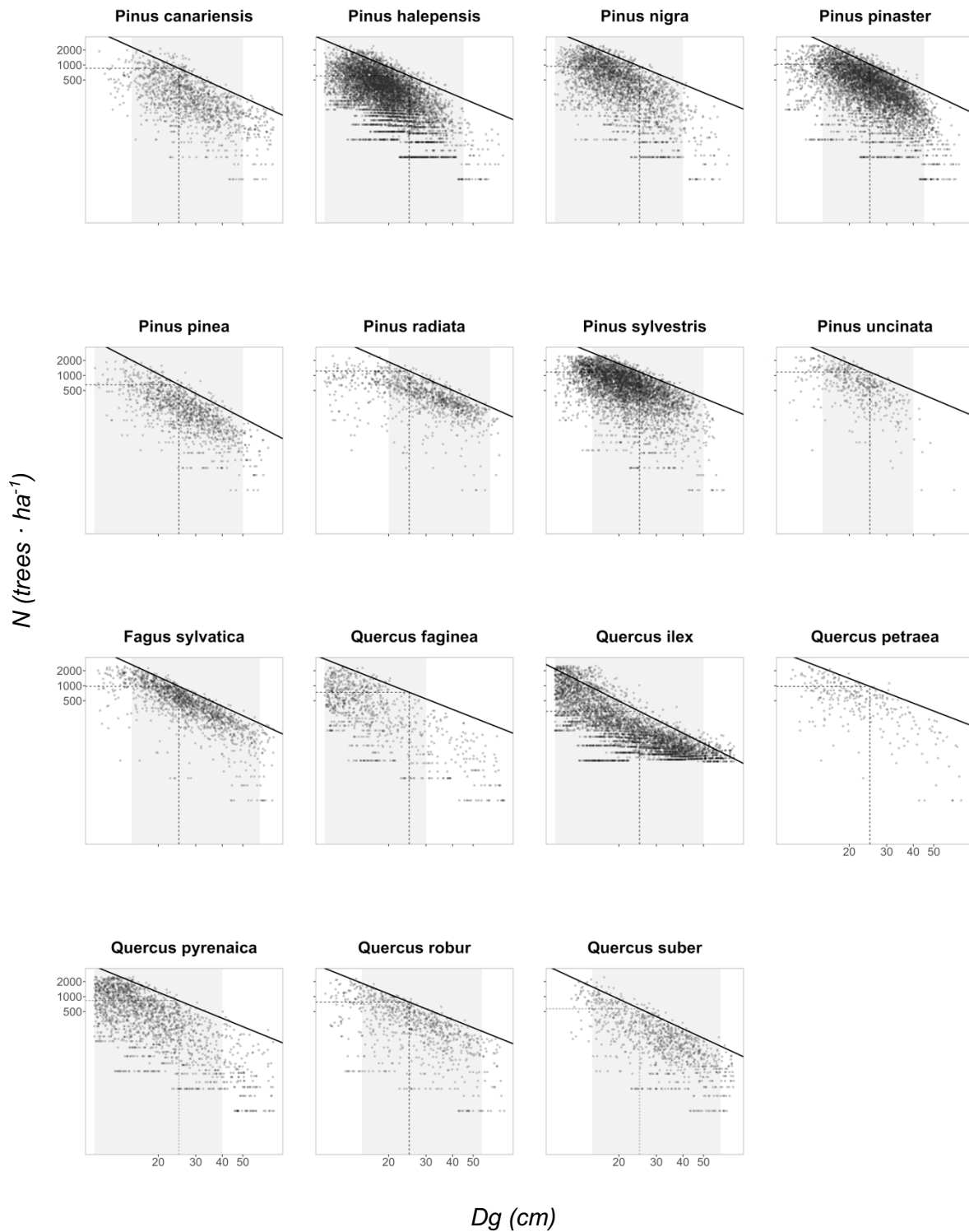
## 4.- RESULTS

### 4.1. Basic MSDR models

The intercept ( $\alpha_0$ ) and slope ( $\beta_0$ ) of the basic MSDRs were highly significant ( $p < 0.001$ ) for all the coniferous (Table 3) and broadleaved (Table 4) species. The 97<sup>th</sup> quantile was selected for each model as the reference in order to allow the comparison of results among all the studied species, since  $SDI_{maxREF}$  estimations resulted very low for the 95<sup>th</sup> and very high for the 99<sup>th</sup> quantiles in comparison with similar studies. The results of the basic MSDR models fitted at these quantiles ( $\tau = 0,95$  and  $0,99$ ) are available in the Supplementary Table 3. For the coniferous species, predicted slopes of the basic MSDRs ranged from  $-2,20$  for *Pinus pinea* and  $-1,73$  for *Pinus sylvestris*. The estimated  $SDI_{maxREF}$  values for these species were 652 and 1169 trees per hectare (Table 3), respectively. In general, broadleaved species presented smaller maximum stand carrying capacities than coniferous species, ranging from 307 to 972 trees per hectare. Higher intercepts and shallower slopes were found in a gradual way for *Quercus ilex* ( $-2,13$ ), *Quercus suber*, *Fagus sylvatica*, *Quercus pyrenaica*, *Quercus robur* and *Quercus faginea*, finding the least pronounced slope for *Quercus petraea* ( $-1,64$ ), with a value closed to Reineke's reference of  $-1,605$  (Table 4). Basic MSDR trajectories are shown for each species in Figure 1.

### 4.2. Climate-dependent MSDR models

The selected climate-dependent MSDR models and  $SDI_{max}$  estimations for the different coniferous and broadleaved species are presented in Table 3 and Table 4, respectively. Results showed that seasonal maximum ( $MXT_i$ ) and mean temperature ( $T_i$ ) were the main climatic variables affecting the MSDR and the  $SDI_{max}$  of the studied species. While *Pinus* and *Fagus* species were affected mainly by temperature and water availability (represented by humidity and evapotranspiration), since temperature was the main climate driver affecting self-thinning in *Quercus* species. Spring and summer seasons were consistently found as key periods where potential climate changes would have a significant effect on the MSDR and the maximum stand carrying capacity. For all of the species, selected climate-dependent MSDR significantly improved the goodness of fit in terms of pseudo- $R^2$  over the basic models. Among the coniferous species, *Pinus pinea* showed the highest pseudo- $R^2$  (40,76%), being this value higher than the basic MSDR model ( $\Delta$  pseudo- $R^2 = +2,92\%$ ). *Pinus halepensis* model was the only coniferous species where the De Martonne Index (M) was significant and showed the highest improvement in terms of pseudo- $R^2$  ( $\Delta$  pseudo- $R^2 = +3,64\%$ ) respect to the basic MSDR model. However, this species showed one of the smallest pseudo- $R^2$  for all the studied species both for the basic (21,8%) and the climate-dependent model (25,44 %). *Pinus nigra*, *Pinus sylvestris* and *Pinus uncinata* were the species for which the inclusion of a climatic variable in the MSDR model was less influential ( $\Delta$  pseudo- $R^2 < 1\%$ ).



**Figure 1:** Maximum Size-Density Relationships (MSDR) for the 15 coniferous and broadleaved species studied plotted on a log-log scale. Self-thinning boundary lines fitted by quantile regression (97<sup>th</sup> quantile) are represented by solid lines. Dashed lines represent the  $SDI_{maxREF}$  (maximum number of trees at a  $D_g$  reference of 25 cm). Gray shaded rectangles represent the upper and lower species-specific diameter thresholds from the plots used in the study.



**Table 3:** Species-specific coefficients,  $SDI_{max}$  estimations and goodness of fits in terms of Akaike's Information Criterion (AIC) and pseudo- $R^2$  coefficient for the basic, the De Martonne and the selected climate-dependent MSDR models fitted by linear quantile regression (quantile 0,97) for coniferous species.

Species	Model	$\alpha_0$	$\alpha_1$	$\beta_0$	$\beta_1$	$SDI_{max}$	AIC	pseudoR <sup>2</sup>
<i>Pinus canariensis</i>	basic	12,948*** (12,345;13,552)		-1,9248*** (-2,1064;1,7432)		856	2233,8	0,3073
	M	-1,122 <sup>ns</sup> (-6,304;4,059)	5,062*** (3,238;6,886)	-0,8901** (-1,4815;-0,2986)	-0,0665*** (-0,0996;-0,0334)	-	2034,1	0,3739
	<b>M4</b>	<b>18,159***</b> <b>(15,986;20,333)</b>	<b>3,462***</b> <b>(2,068;4,856)</b>	<b>-1,1469***</b> <b>(-1,5679;-0,7259)</b>	<b>-3,5330***</b> <b>(-5,3246;-1,7414)</b>	<b>834</b>	<b>2150,3</b>	<b>0,3359</b>
<i>Pinus halepensis</i>	basic	12,191*** (11,89;12,492)		-1,7967*** (-1,8985;-1,6949)		606	14650,5	0,2180
	<b>M</b>	<b>7,477***</b> <b>(5,565;9,389)</b>	<b>1,652***</b> <b>(0,995;2,308)</b>	<b>-1,5526***</b> <b>(-1,7779;-1,3274)</b>	<b>-0,0159**</b> <b>(-0,0269;-0,005)</b>	<b>580</b>	<b>14065,6</b>	<b>0,2544</b>
<i>Pinus nigra</i>	basic	12,504*** (12,144;12,864)		-1,757*** (-1,8787;-1,6353)		942	5309,6	0,2446
	M	12,731*** (10,387;15,074)	-0,133 <sup>ns</sup> (-0,823;0,559)	-1,7922*** (-2,0322;-1,5523)	0,0034 <sup>ns</sup> (-0,0039;0,0106)	-	5280,3	0,2492
	<b>MNT</b>	<b>609,956**</b> <b>(213,95;1005,962)</b>	<b>-106,15**</b> <b>(-176,522;-35,777)</b>	<b>-35,6036**</b> <b>(-59,3271;11,8801)</b>	<b>0,1217**</b> <b>(0,0363;0,207)</b>	<b>976</b>	<b>5285,8</b>	<b>0,2497</b>
<i>Pinus pinaster</i>	basic	13,445*** (13,131;13,759)		-2,0202*** (-2,1167;-1,9237)		1035	10007,7	0,3147
	M	12,214*** (10,843;13,584)	0,411* (0,028;0,793)	-1,9842*** (-2,1521;-1,8162)	-0,0025 <sup>ns</sup> (-0,0056;0,0060)	-	9939,4	0,3209
	<b>TAR</b>	<b>-359,919***</b> <b>(-496,411;-223,427)</b>	<b>65,483***</b> <b>(41,559;89,407)</b>	<b>19,3116***</b> <b>(11,8402;26,783)</b>	<b>-0,0712***</b> <b>(-0,0961;-0,0464)</b>	<b>1086</b>	<b>9900,3</b>	<b>0,3241</b>
<i>Pinus pinea</i>	basic	13,58*** (12,677;14,483)		-2,2055*** (-2,4812;-1,9298)		652	2546,4	0,3784
	M	18,083*** (8,185;27,98)	-1,499 <sup>ns</sup> (-4,805;1,805)	-2,7203*** (-3,6887;-1,7519)	0,0253 <sup>ns</sup> (-0,0214;0,0720)	-	2517,9	0,3883
	<b>M4</b>	<b>13,541***</b> <b>(12,928;14,155)</b>	<b>-0,446**</b> <b>(-0,717;-0,175)</b>	<b>-2,4625***</b> <b>(-2,6352;-2,2899)</b>	<b>0,2958***</b> <b>(0,1695;0,4222)</b>	<b>602</b>	<b>2454,4</b>	<b>0,4076</b>
<i>Pinus radiata</i>	basic	13,18*** (12,377;13,982)		-1,8850*** (-2,1132;-1,6569)		1227	1430,0	0,3730
	M	16,926*** (13,245;20,607)	-1,071* (-2,019;0,123)	-2,1576*** (-2,5244;-1,7908)	0,0079* (0,0010;0,0147)	1168	1415	0,3810
	<b>PET4</b>	<b>62,621***</b> <b>(35,384;89,859)</b>	<b>-10,528***</b> <b>(-16,352;-4,703)</b>	<b>-5,0925***</b> <b>(-6,7268;-3,4582)</b>	<b>0,0292***</b> <b>(0,0141;0,0444)</b>	<b>1195</b>	<b>1396,6</b>	<b>0,3891</b>
<i>Pinus sylvestris</i>	basic	12,633*** (12,342;12,924)		-1,7301*** (-1,8229;-1,6373)		1169	7362,6	0,2689
	M	13,808*** (11,55;16,066)	-0,313 <sup>ns</sup> (-0,905;0,279)	-1,8375*** (-2,0562;-1,6189)	0,0024 <sup>ns</sup> (-0,0017;0,0066)	-	7358,9	0,270
	<b>MXT3</b>	<b>325,181**</b> <b>(125,409;524,953)</b>	<b>-55,169**</b> <b>(-90,442;-19,895)</b>	<b>-16,9605**</b> <b>(-28,1507;-5,7703)</b>	<b>0,0527**</b> <b>(0,0139;0,0916)</b>	<b>1116</b>	<b>7304,5</b>	<b>0,2756</b>
<i>Pinus uncinata</i>	basic	12,861*** (12,164;13,557)		-1,8010*** (-2,0232;-1,5788)		1169	587,8	0,3551
	M	15,495* (3,028;27,963)	-0,516 <sup>ns</sup> (-3,352;2,319)	-2,1320*** (-3,0842;-1,1798)	0,0020 <sup>ns</sup> (-0,008;0,0140)	-	590,1	0,3561
	<b>MXT2</b>	<b>-719,801**</b> <b>(-1195,593;-244,008)</b>	<b>130,277**</b> <b>(45,686;214,868)</b>	<b>41,8256**</b> <b>(14,8029;68,8483)</b>	<b>-0,1576**</b> <b>(-0,2551;-0,0601)</b>	<b>1076</b>	<b>580,4</b>	<b>0,3618</b>

Note:  $SDI_{maxREF}$  corresponds to  $SDI_{max}$  estimations calculated using basic MSDR models.  $SDI_{maxCLIM}$  corresponds to  $SDI_{max}$  estimations calculated using the selected climate-dependent MSDR model.  $SDI_{maxCLIM}$  was only calculated if climate-dependent MSDR model had all coefficients ( $\alpha_0$ ,  $\alpha_1$ ,  $\beta_0$  and  $\beta_1$ ) significant. The best climate-dependent MSDR model by species is in bold.

\*\*\* $p < 0,001$ ; \*\* $p < 0,01$ ; \* $p < 0,05$ ; ns non-significant



**Table 4:** Species-specific coefficients,  $SDI_{max}$  estimations and goodness of fits in terms of Akaike's Information Criterion (AIC) and pseudo- $R^2$  coefficient for the basic, the De Martonne and the selected climate-dependent MSDR models fitted by linear quantile regression (quantile 0.97) for broadleaved species.

Species	Model	$\alpha_0$	$\alpha_1$	$\beta_0$	$\beta_1$	$SDI_{max}$	AIC	pseudoR <sup>2</sup>
<i>Fagus sylvatica</i>	basic	13,162*** (12,969;13,356)		-1,9517*** (-2,0095;-1,894)		972	1869,4	0,5181
	<b>M</b>	<b>18,583***</b> <b>(16,088;21,078)</b>	<b>-1,358***</b> <b>(-1,998;-0,717)</b>	<b>-2,4793***</b> <b>(-2,692;-2,2667)</b>	<b>0,0098***</b> <b>(0,0056;0,0139)</b>	<b>959</b>	<b>1842,3</b>	<b>0,5245</b>
<i>Quercus faginea</i>	basic	11,992*** (11,664;12,319)		-1,6734*** (-1,7954;-1,5514)		739	1103,6	0,2049
	M	8,797*** (6,177;11,418)	0,928* (0,17;1,685)	-1,5316*** (-1,8614;-1,2018)	-0,0050 <sup>ns</sup> (-0,0141;0,0040)	-	1055,3	0,2419
	<b>T4</b>	<b>-883,634***</b> <b>(-1160,672;-606,597)</b>	<b>157,909***</b> <b>(109,103;206,715)</b>	<b>68,0811***</b> <b>(50,1612;86,0011)</b>	<b>-0,2400***</b> <b>(-0,3014;-0,1786)</b>	<b>605</b>	<b>1039,5</b>	<b>0,2557</b>
<i>Quercus ilex</i>	basic	12,585*** (12,419;12,752)		-2,1303*** (-2,1832;-2,0774)		307	8724,9	0,5215
	M	11,609*** (9,862;13,357)	0,265 <sup>ns</sup> (-0,294;0,824)	-2,1581*** (-2,338;-1,9783)	0,0030 <sup>ns</sup> (-0,0047;0,0097)	-	8323,4	0,5451
	<b>T3</b>	<b>-241,048**</b> <b>(-386,804;-95,292)</b>	<b>44,668***</b> <b>(18,935;70,402)</b>	<b>21,6710***</b> <b>(13,0324;30,3096)</b>	<b>-0,0819***</b> <b>(-0,1118;-0,0519)</b>	<b>290</b>	<b>8113,4</b>	<b>0,5578</b>
<i>Quercus petraea</i>	basic	12,148*** (11,701;12,595)		-1,6378*** (-1,7842;-1,4914)		969	431,7	0,4244
	M	24,507*** (21,231;27,783)	-3,194*** (-4,048;-2,339)	-2,5731*** (-2,8483;-2,2978)	0,0193*** (0,0137;0,0250)	943	421,2	0,4499
	<b>MXT3</b>	<b>-213,709***</b> <b>(-339,063;-88,356)</b>	<b>39,947***</b> <b>(17,824;62,069)</b>	<b>18,6637***</b> <b>(11,3061;26,0213)</b>	<b>-0,0709***</b> <b>(-0,0964;-0,0454)</b>	<b>879</b>	<b>369,7</b>	<b>0,5063</b>
<i>Quercus pyrenaica</i>	basic	12,305*** (11,949;12,661)		-1,7346*** (-1,861;-1,6083)		830	3358,7	0,2730
	M	8,022*** (6,81;9,234)	1,200*** (0,866;1,534)	-1,3663*** (-1,5007;-1,2318)	-0,0102*** (-0,0132;-0,0072)	848	3315,5	0,2821
	<b>MXT3</b>	<b>-392,948***</b> <b>(-598,866;-187,03)</b>	<b>71,472***</b> <b>(35,166;107,779)</b>	<b>29,9596***</b> <b>(17,1916;42,7276)</b>	<b>-0,1093***</b> <b>(-0,1532;-0,0653)</b>	<b>776</b>	<b>3236,8</b>	<b>0,3051</b>
<i>Quercus robur</i>	basic	12,147*** (11,711;12,583)		-1,7070*** (-1,8375;-1,5765)		775	1077,7	0,4451
	M	17,014*** (9,609;24,42)	-1,119 <sup>ns</sup> (-2,911;0,672)	-2,1155*** (-2,7079;-1,523)	0,0052 <sup>ns</sup> (-0,0038;0,0143)	-	1074,9	0,4494
	<b>MNT3</b>	<b>-725,556***</b> <b>(-1035,262;-415,849)</b>	<b>130,860***</b> <b>(75,928;185,791)</b>	<b>45,1398***</b> <b>(28,165;62,1146)</b>	<b>-0,1669***</b> <b>(-0,2273;-0,1065)</b>	<b>749</b>	<b>1034,9</b>	<b>0,4675</b>
<i>Quercus suber</i>	basic	12,695*** (12,365;13,024)		-1,9713*** (-2,0667;-1,8759)		572	1455	0,4914
	M	18,576*** (14,922;22,229)	-1,641** (-2,743;-0,539)	-2,8032*** (-3,1424;-2,4641)	0,0249*** (0,0137;0,036)	546	1363,3	0,5245
	<b>MXT4</b>	<b>-808,917***</b> <b>(-1284,838;-332,996)</b>	<b>143,970***</b> <b>(60,530;227,409)</b>	<b>51,6104***</b> <b>(27,016;76,2048)</b>	<b>-0,1782***</b> <b>(-0,2601;-0,0962)</b>	<b>533</b>	<b>1341,6</b>	<b>0,5298</b>

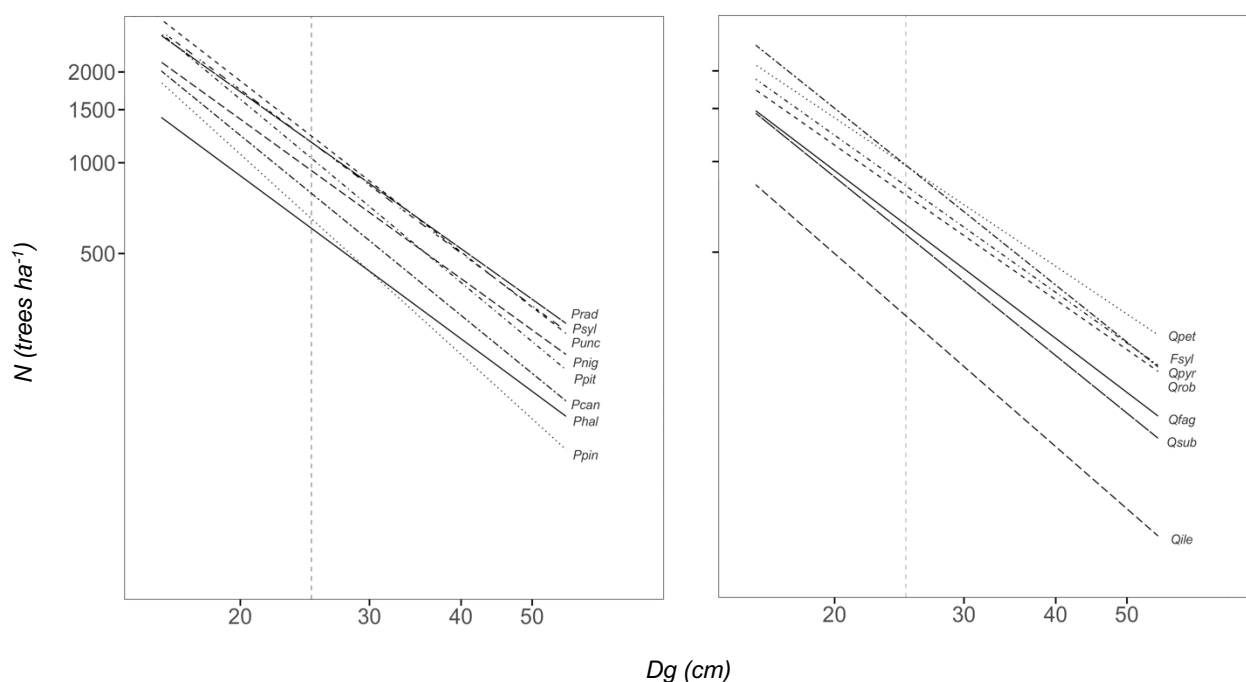
Note:  $SDI_{maxREF}$  corresponds to  $SDI_{max}$  estimations calculated using basic MSDR models.  $SDI_{maxCLIM}$  corresponds to  $SDI_{max}$  estimations calculated using the selected climate-dependent MSDR model.  $SDI_{maxCLIM}$  was only calculated if climate-dependent MSDR model had all coefficients ( $\alpha_0$ ,  $\alpha_1$ ,  $\beta_0$  and  $\beta_1$ ) significant. The best climate-dependent MSDR model by species is in bold.

\*\*\* $p < 0,001$ ; \*\* $p < 0,01$ ; \* $p < 0,05$ ; ns non-significant

## 5.- DISCUSSION

### 5.1. Basic MSDRs and $SDI_{max}$ reference values

Our findings showed significant differences in the coefficients of the basic MSDRs (Tables 3 and 4), confirming the intra and inter-specific variability among the selected coniferous and broadleaved species (Vospernik and Sterba, 2015). The range of the slopes fitted in the basic MSDR models for the coniferous species [-1.730 (*Pinus sylvestris*) and -2.205 (*Pinus pinea*)] agreed with findings reported by Charru et al. (2012) and Aguirre et al. (2018). These authors found shallower slopes for *Pinus sylvestris* than for other pines in Spain and France, showing the great ability of this species to grow and survive under intra-specific competition (Zeide, 1987; Pretzsch and Biber, 2005). The development of wide crown areas at older ages could explain the extreme value of the slope for *Pinus pinea* (Barbeito et al., 2008). In the case of the broadleaved species, *Quercus suber* (-1.971) and *Quercus ilex* (-2.130) presented the steepest MSDRs slopes and the smallest  $SDI_{max}$  estimations. These outputs may be due to the ability of these species to support a great leaf area, being necessary fewer individuals to fully occupy a stand (Woodall et al. 2005).



**Figure 2:** Fits of basic MSDR plotted on a log-log scale for the (a) coniferous and (b) broadleaved species studied.

Note: Pcan - *Pinus canariensis*, Phal - *Pinus halepensis*, Pnig - *Pinus nigra*, Ppit - *Pinus pinaster*, Ppin - *Pinus pinea*, Prad - *Pinus radiata*, Psyl - *Pinus sylvestris*, Punc - *Pinus uncinata*, Fsyl - *Fagus sylvatica*, Qfag - *Quercus faginea*, Qile - *Quercus ilex*, Qpet - *Quercus petraea*, Qpyr - *Quercus pyrenaica*, Qrob - *Quercus robur*, Qsub - *Quercus suber*

Estimated  $SDI_{maxREF}$  values were compared with prior reference values from published studies in similar areas in order to test the consistency of our models (Table 5). In general, good agreement was found between these studies and our results as stands dominated by coniferous showed relatively higher  $SDI_{maxREF}$  values when compared to broadleaved dominated stands. In addition, our findings were consistent with the theory that maximum stand density is known to be positively related to species shade tolerance (Jack and Long 1996, Woodall et al., 2005). However, light-demanding coniferous species such as *Pinus pinaster*, *Pinus uncinata* and *Pinus sylvestris* got unexpected high  $SDI_{maxREF}$  (Table 3) values given their low shade-tolerance (Niinemets and Valladares, 2006). A similar trend was found by Andrews et al. (2018), who obtained  $SDI_{maxREF}$  values for shade-tolerant species such as *Fagus grandifolia* and *Acer saccharum* smaller than other light-demanding species in the Northeast US. Previously, Dixon and Keyser (2017) obtained similar results when analyzing the maximum stand density of 15 coniferous and broadleaved species in the same area. Higher maximum carrying capacities for light-demanding species such as *Pinus sylvestris* than for *Fagus sylvatica* or *Quercus petraea* were also obtained by Charru et al. (2012) and Toigo et al. (2018) in France. These results suggest the existence of other drivers affecting the maximum carrying capacity of the studied species, such as silvicultural objectives, plant phenology, crown allometry, available growing space and, specially, climate.

## 5.2. Climatic influence on the maximum stand carrying capacity

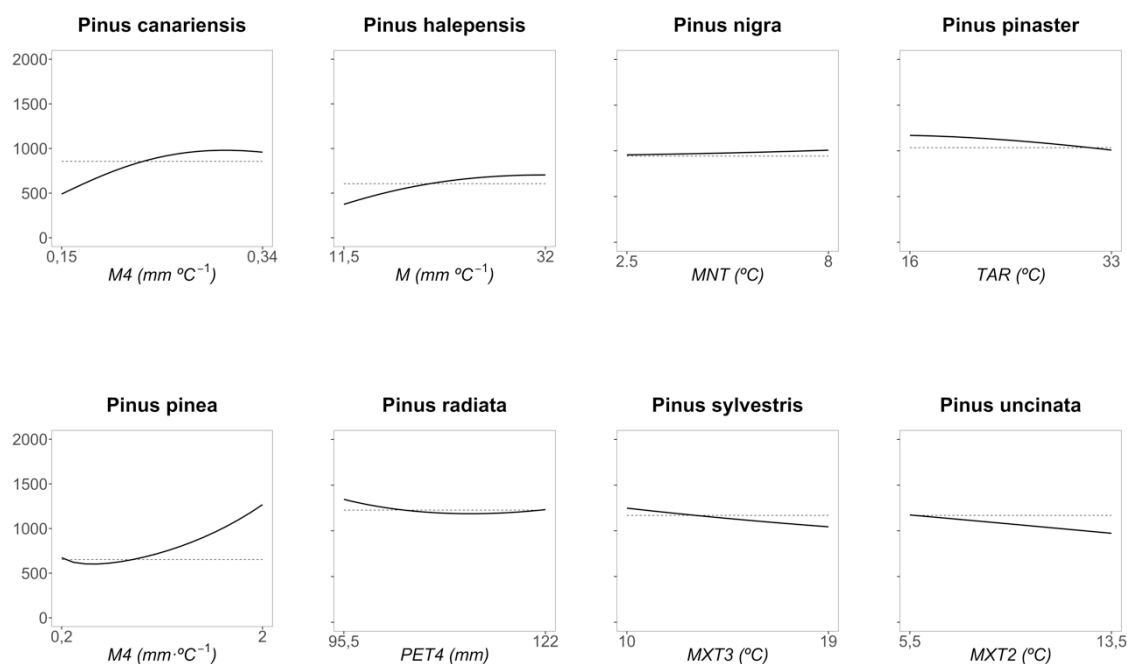
Our results showed that, in general, reductions in the maximum carrying capacity of the studied species were linked to warmer and drier conditions. However, the climatic drivers that best explained the influence of the climate on MSDR and  $SDI_{max}$  varied between the different coniferous (Figure 3) and broadleaved (Figure 4) species of study. Climate change projections for the lower areas of the Mediterranean basin highlight a continuous decrease in precipitation, especially during the warmest season (IPCC, 2018). A pronounced warming is also predicted, giving rise to higher rates of evapotranspiration, with a consequent decrease in the amount of water available in the soil and a greater number of drought episodes. In the face of these scenarios, several authors have shown that these new conditions will drastically affect the growth and vitality of the main conifers (Sabaté et al., 2002; Sanchez-Salguero et al., 2012; Pasho et al., 2012; Gazol et al., 2017; Navarro-Cerillo et al., 2018; Peña-Gallardo et al., 2018) and broadleaved Mediterranean species (Sabaté et al., 2002; Baquedano and Castillo, 2007; Gentilesca et al., 2017; Peña-Gallardo et al., 2018).

### 5.2.1. Climatic influence on the maximum stand carrying capacity for coniferous species

Our models for *Pinus uncinata* and *Pinus sylvestris* indicated that reductions in the carrying capacity of these species are expected as winter and spring maximum temperatures increase (Figure 3).

Recent research focused on climate change and coniferous forest dynamics suggest that cooler temperatures would allow the sustainability of higher densities of species frequently

living at higher altitudes (Kreyling et al., 2015). Opposite to this pattern, similar studies showed that milder winters could also improve the growth and vitality of these conifers (Martin-Benito et al., 2008; Kurz-Besson et al., 2016) enhancing processes such as winter photosynthesis (Rathgeber et al., 2005), cambium and xylem formation (Vieira et al., 2014) or the development of deeper roots during the colder months of the year (Hansen and Beck, 1994). An increase in the minimum temperatures could also boost the growth of individuals in mountain areas, since it has been shown that a smaller snow pack is linked to a greater amount of water available in the soil (Kreyling, 2010), as well as to lower mortality from root damage (Peterson and Peterson, 2001; Gedalof and Smith, 2001) and to foliar erosion by wind-blown snow (Kajimoto et al., 2002). These hidden growth dynamics could explain the unexpected results obtained for *Pinus nigra* in which higher values of  $SDI_{max}$  were linked to increments in the annual minimum temperature (MNT), although the effect of this variable in the  $SDI_{max}$  of this species ( $\Delta SDI_{maxCLIM\_Pnig,MNT} = 9 \text{ trees ha}^{-1} \text{ } ^\circ\text{C}^{-1}$ ) was minimum. A small variation in the  $SDI_{max}$  as effect of temperature changes was also shown for *Pinus pinaster*, denoting the phenotypic plasticity and the adaptation of this species to very diverse climatic conditions (Alía et al., 1995; Corcuera et al., 2010). Two subspecies of *Pinus pinaster* living in Spain (*P.pinaster subsp.maritima* and *P.pinaster subsp.mesogeensis*) were analyzed together, since 3NFI does not differentiate between them. This fact could affect the results obtained in this study for this species. Therefore, further studies analyzing separately these subspecies may be necessary.



**Figure 3:** Climatic influence on the maximum stand carrying capacity (expressed as  $SDI_{max}$ ) for the coniferous species. Solid line corresponds to  $SDI_{max}$  predictions estimations using the best climate-dependent MSDR model by species. Dashed horizontal line represents the reference value of  $SDI_{max}$  obtained from basic MSDR models.

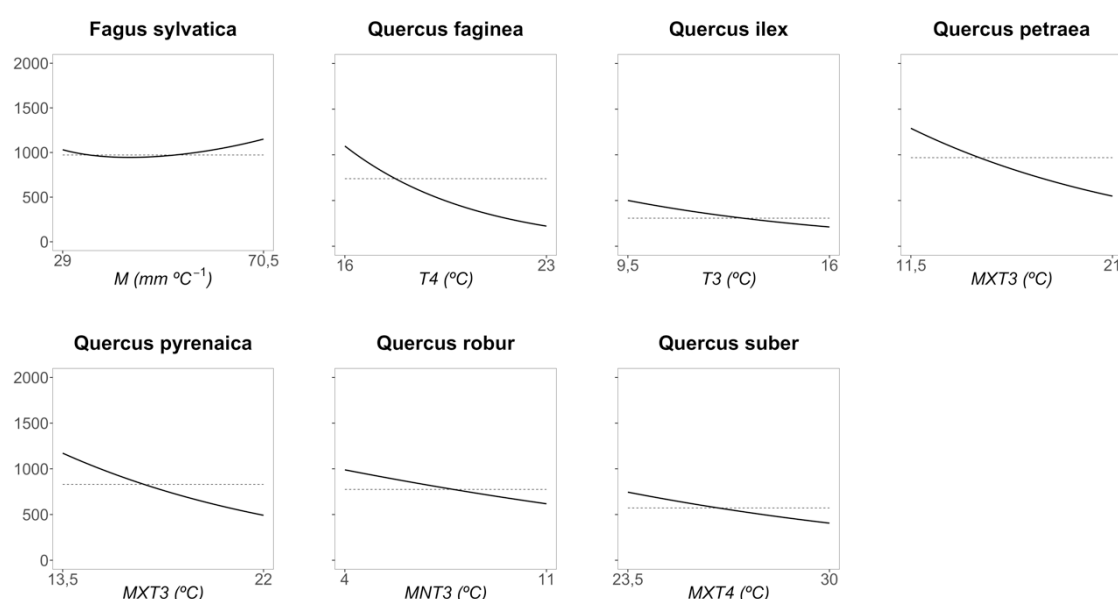
Note: Temperature has been transformed into Celsius degrees ( $^\circ\text{C}$ )

Models for *Pinus pinea* and *Pinus halepensis* indicated that water scarcity (expressed as M) was the key driver explaining differences in the maximum carrying capacity of these species. Nevertheless, *Pinus halepensis* showed the smallest  $SDI_{max}$  variation among the different *Pinus* species. A similar finding was reached by Aguirre et al. 2018, confirming the high resilience and adaptation to extreme drought and heat conditions of this species (Baquedano and Castillo, 2007; Benito-Garzón et al., 2011; de Luis et al., 2013). These results go beyond previous studies (Brunet-Navarro et al., 2016; Freire et al., 2019), showing that drought will be the main driver affecting forest dynamics of Mediterranean species living at low altitudes. Despite being the only species of this study outside the Iberian Peninsula, the close phylogenetic relationship between *Pinus canariensis* and other pines such as *Pinus pinea* or *Pinus halepensis* (Gernandt et al., 2005) was reflected in the variation of its  $SDI_{max}$  estimations. For this species, higher carrying capacities were also found in more humid conditions during summer (Figure 3). Growth reductions (Climent et al., 2006) and even death by xylem embolism (López et al. 2013) by effect of increasing extreme drought events would indirectly influence the maximum number of trees a stand would fully support. Finally, results for *Pinus radiata* showed a slight  $SDI_{max}$  reduction linked to higher rates of potential evapotranspiration during summer (PET4). This species is widely used in afforestations in Spain due to its capacity to adapt to different climatic conditions (Romanyà and Vallejo, 2004). However, higher extreme drought conditions during summer season (Stone et al. 2012) could make this species more vulnerable to pest and disease attacks (McDowell et al. 2008), decreasing its vitality and storage capacity in the future.

### 5.2.2. Climatic influence on the maximum stand carrying capacity for broadleaved species

The influence of climate in the MSDR and the maximum stand carrying capacity was also studied for broadleaved species belonging to the *Fagus* and *Quercus* genus. Results for *Fagus sylvatica* showed that higher values of  $SDI_{max}$  were linked to wetter conditions, expressed as increments in the De Martonne Index (Figure 4). A similar trend was found previously by Condés et al. (2017) studying the influence of climate in the MSDR of this species and *Pinus sylvestris* stands across a wide environmental gradient in Europe. Other studies (Friedrichs et al., 2009; Zimmermann et al., 2015) focused on growth dynamics also found similar climatic impacts for this species. In our study, although there was a clear trend in  $SDI_{max}$  increment as M becomes higher, a reduction in  $SDI_{max}$  was found between the minimum (percentile 1%) and the mean (percentile 50%) values of this variable. This effect was also visible for other species such as *Pinus radiata*, which showed a final lift in its function at higher values of evapotranspiration. This artifact could be explained because the link between climate and species traits is often too complex to adequately capture in a linear form (Reich, 2012; Craigmile, 2017). A similar pattern was found in *Quercus* genus where higher temperatures were linked to smaller carrying capacities (Figure 4). This is consistent with what has been found in previous studies (Fernandez-Marin et al., 2017; Gentilesca et al., 2017; Gil-Pelegrín et al., 2017; Kunz et al., 2018) suggesting that future extreme heat and warm-induced drought conditions, especially during spring and summer seasons, will affect the vitality of oak stands in Mediterranean basin.

Among the different *Quercus* species, models for *Quercus petraea* ( $\Delta$  pseudo- $R^2 = +8,19\%$ ) and *Quercus pyrenaica* ( $\Delta$  pseudo- $R^2 = +3,21\%$ ) showed the greatest improvement over the basic MSDR model. For these species, reductions in the carrying capacity were associated with increments in spring maximum temperatures (MXT3). A similar climate impact was also found by Michelot et al. (2012) studying growth dynamics for *Quercus petraea* in France. However, positive impacts in growth (Kellomäki et al., 2008) and seed production (Caignard et al., 2017) are expected in cold and mild areas, such as boreal and temperate forests as an effect of global warming. Our models showed that spring temperature also affected *Quercus robur*, although differences in  $SDI_{max}$  were due to changes in spring minimum temperature for this species. It is important to note that among the studied *Quercus* species, *Quercus ilex* presented the smallest reduction in  $SDI_{max}$  (Figure 4), showing its great adaptation to survive under different extreme conditions (Camarero et al., 2015).



**Figure 4:** Climatic influence on the maximum stand carrying capacity (expressed as  $SDI_{max}$ ) for the broadleaved species. Solid line corresponds to  $SDI_{max}$  predictions estimations using the best climate-dependent MSDR model by species. Dashed horizontal line represents the reference value of  $SDI_{max}$  obtained from basic MSDR models

Note: Temperature has been transformed into Celsius degrees ( $^{\circ}C$ )

In the case of *Quercus faginea* and *Quercus suber*,  $SDI_{max}$  variations were significantly influenced by temperature changes during the summer season. Our results evidenced the high vulnerability of these Mediterranean species to extreme temperatures, being a potential limitation on their vegetative activity in the future (Gea-Izquierdo et al. 2013). Expected reductions of soil water reserves in the distribution area of these species could also potentiate its progressive substitution by more drought-resistant species in the future, such as *Quercus ilex* (Peñuelas et al. 2001). However, leaf area reduction could be a determinant process for these oak species in order to reduce water losses and survive under future drought episodes in the Mediterranean area (Peguero-Pina et al. 2016).



Further studies focused on broadleaved species are needed in order to better understand to what extent the vulnerability of hardwood species will be increased and how climate change will impact on maximum carrying capacity.

**Table 5:** Comparison of the MSDR slope and  $SDI_{maxREF}$  reference values obtained in similar studies and this paper for the studied species.

Functional Group	Species	$\beta_0$	$SDI_{maxREF}$	Area	Reference	
Conifers	<i>Pinus halepensis</i>	-1,881	637	France	Charru et al. 2012	
		-1,777	732	Catalonia	Brunet-Navarro et al. 2016	
		-1,829	619	Spain	Aguirre et al. 2018	
	<i>Pinus nigra</i>	-1,920	780	France	Toigo et al. 2018	
		-1,797	606	Spain	This study	
		-1,653	881	France	Charru et al. 2012	
		-1,787	600	Catalonia	Brunet-Navarro et al. 2016	
		-1,794	960	Spain	Aguirre et al. 2018	
		-1,810	1181	France	Toigo et al. 2018	
		-1,757	942	Spain	This study	
		<i>Pinus pinaster</i>	-1,711	648	France	Charru et al. 2012
			-1,929	1104	Spain	Riofrio et al. 2016
	-1,983		1053	Spain	Aguirre et al. 2018	
	<i>Pinus pinea</i>	-1,860	807	France	Toigo et al. 2018	
		-2,020	1035	Spain	This study	
		-1,857	1040	South Spain	Montero et al. 1998	
	<i>Pinus sylvestris</i>	-2,122	702	Spain	Aguirre et al. 2018	
		-2,205	652	Spain	This study	
		-1,750	1444	Central Spain	Rio et al. 2001	
		-1,615	893	France	Charru et al. 2012	
		-1,750	1297	Navarra, Spain	Condés et al. 2013	
		-1,789	1144	Spain	Riofrio et al. 2016	
		-1,647	579	Catalonia, Spain	Brunet-Navarro et al. 2016	
		-1,630	1079	Europe*	Condés et al. 2017	
		-1,726	1154	Spain	Aguirre et al. 2018	
		-2,020	1000	France	Toigo et al. 2018	
	<i>Pinus uncinata</i>	-1,730	1169	Spain	This study	
		-1,665	581	Catalonia	Brunet-Navarro et al. 2016	
		-1,801	1169	Spain	This study	
		-1,925	856	Spain	This study	
-1,885		1227	Spain	This study		
Broadleaves	<i>Fagus sylvatica</i>	-1,941	814	France	Charru et al. 2012	
		-1,905	1059	Europe*	Condés et al. 2017	
		-1,850	885	Spain	Condés et al. 2017	
	<i>Quercus petraea</i>	-1,790	991	France	Toigo et al. 2018	
		-1,951	972	Spain	This study	
		-1,911	685	France	Charru et al. 2012	
		-2,080	776	France	Toigo et al. 2018	
		-1,638	969	Spain	This study	
	<i>Quercus robur</i>	-1,758	651	France	Charru et al. 2012	
		-1,540	760	France	Toigo et al. 2018	
		-1,707	775	Spain	This study	
	<i>Quercus faginea</i>	-1,673	739	Spain	This study	
	<i>Quercus ilex</i>	-2,130	307	Spain	This study	
	<i>Quercus pyrenaica</i>	-1,735	830	Spain	This study	
	<i>Quercus suber</i>	-1,972	572	Spain	This study	

\* Europe: Austria, France, Spain, Germany and Poland

## 6.- CONCLUSIONS

In this study, a significant climatic influence on the maximum stand carrying capacity (expressed as  $SDI_{max}$ ) was found for the most representative coniferous and broadleaved tree species in Spain. A general trend with higher values of  $SDI_{max}$  in more humid and temperate areas was found, although the climatic variables explaining influences on this index varied among species. Our results showed that future changes in spring and summer temperatures and water availability will limit the maximum stand carrying capacity for the studied species. Climate-dependent MSDR models presented in this study will allow us to obtain more precise estimations of the maximum carrying capacity, providing an advanced tool for managing pure and mixed stands under different scenarios of climate change. In this line, further studies considering more tree species living at a wider range of specific climatic conditions would be necessary to better understand the complex interaction between climate and the potential stocking of Mediterranean forests.



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## **SUPPLEMENTARY MATERIAL**

## ANNEX 1. Climatic variables used in the study for coniferous species

**Supplementary Table 1a:** Mean  $\pm$  standard deviation and range (minimum-maximum) of the climatic variables related to temperature used to fit the climate-dependent MSDR models for the studied coniferous species.

	<i>Pinus canariensis</i>	<i>Pinus halepensis</i>	<i>Pinus nigra</i>	<i>Pinus pinea</i>	<i>Pinus pinaster</i>	<i>Pinus radiata</i>	<i>Pinus sylvestris</i>	<i>Pinus uncinata</i>
Plots	1000	5887	2297	1051	4563	822	3653	362
T	13,9 $\pm$ 1,7 (10,2-18,4)	14 $\pm$ 1,4 (10,5-18,1)	10,7 $\pm$ 1,1 (5,4-14)	14,6 $\pm$ 2 (11-17,9)	12,3 $\pm$ 1,5 (7,9-17,4)	12,6 $\pm$ 0,8 (10,1-16,8)	8,6 $\pm$ 1,4 (3,6-13,3)	5,1 $\pm$ 1 (1,8-7,7)
MXTWM	23,1 $\pm$ 1,4 (18,7-31,7)	28,8 $\pm$ 1,3 (23,5-32,3)	25,3 $\pm$ 1,8 (17-30)	28,7 $\pm$ 1,9 (25-32,1)	25,4 $\pm$ 2,4 (20-32,1)	22,4 $\pm$ 0,8 (20,2-27,7)	21,4 $\pm$ 1,7 (14,6-27,2)	16,4 $\pm$ 1,6 (11,7-20,3)
MNTCM	5,4 $\pm$ 2,3 (-0,1-12)	-1,2 $\pm$ 2,4 (-6,1-7,6)	-3,9 $\pm$ 1,5 (-8,1-2,9)	0,1 $\pm$ 3,3 (-4,2-8,7)	-1,4 $\pm$ 3,2 (-7,7,8)	2,4 $\pm$ 1,6 (-1,9-10)	-4 $\pm$ 1,4 (-8,2-2,4)	-5,1 $\pm$ 1,2 (-7,8--2,1)
TAR	290,6 $\pm$ 2,1 (285,7-304)	303,1 $\pm$ 2,6 (289,3-307,3)	302,1 $\pm$ 2,3 (291,9-307,2)	301,5 $\pm$ 3,1 (291,9-306,4)	299,8 $\pm$ 4,7 (287,6-307,1)	293 $\pm$ 1,7 (285,9-299,6)	298,4 $\pm$ 1,9 (291-304,8)	294,5 $\pm$ 1,8 (291,4-299,1)
T1	12,9 $\pm$ 2 (8,2-18,4)	10,2 $\pm$ 1,7 (6,6-15,9)	7,3 $\pm$ 1,2 (2,7-10,7)	11,1 $\pm$ 2,5 (7-16,4)	9 $\pm$ 1,9 (4,7-15,2)	10,7 $\pm$ 1,1 (7,5-17)	5,8 $\pm$ 1,4 (1,5-10,4)	3 $\pm$ 0,9 (0,2-5,3)
T2	10,1 $\pm$ 2 (5,5-15,5)	7,5 $\pm$ 1,6 (3,6-12,6)	4,3 $\pm$ 1,2 (-0,4-8)	8,5 $\pm$ 2,3 (4,2-13,1)	6,4 $\pm$ 2 (1,6-12,3)	7,9 $\pm$ 1,1 (4,8-13,9)	2,7 $\pm$ 1,5 (-1,8-7,7)	-0,2 $\pm$ 1 (-2,9-2,5)
T3	13,6 $\pm$ 1,6 (10,4-18,1)	15,8 $\pm$ 1,3 (11,8-19,3)	12,1 $\pm$ 1,3 (6,1-15,8)	16,2 $\pm$ 1,7 (12,7-19)	13,7 $\pm$ 1,5 (8,9-18,5)	13,4 $\pm$ 0,7 (11,2-15,9)	9,6 $\pm$ 1,6 (3,1-15,1)	5,2 $\pm$ 1,3 (0,9-8,4)
T4	18,9 $\pm$ 1,3 (16-25,1)	22,5 $\pm$ 1,3 (18,4-25,4)	19,1 $\pm$ 1,3 (13,2-23,1)	22,7 $\pm$ 1,8 (19,5-25,6)	19,9 $\pm$ 1,8 (15,8-25,3)	18,3 $\pm$ 0,7 (16,3-22)	16,3 $\pm$ 1,3 (11,1-21,1)	12,5 $\pm$ 1,1 (8,7-15,2)
MNT1	9,6 $\pm$ 2,1 (5,1-15,1)	5,3 $\pm$ 2 (1,4-12,6)	2,6 $\pm$ 1,2 (-0,3-7,5)	6,5 $\pm$ 2,6 (2,7-13,1)	4,7 $\pm$ 2,3 (0,2-11,6)	7,3 $\pm$ 1,1 (3,6-13,8)	1,9 $\pm$ 1,2 (-1,6,8)	0,3 $\pm$ 0,7 (-1,9-2,5)
MNT2	6 $\pm$ 2,2 (0,6-12,2)	0,4 $\pm$ 2,2 (-4,6-8,2)	-2,4 $\pm$ 1,7 (-6,8-3,6)	1,8 $\pm$ 3 (-2,7-9,8)	0,1 $\pm$ 2,9 (-5,5-8,7)	3,3 $\pm$ 1,4 (-0,1-10,2)	-2,9 $\pm$ 1,5 (-7,5-3,2)	-4,6 $\pm$ 1,2 (-7,5--1,6)
MNT3	9,6 $\pm$ 1,7 (5,6-14,5)	8,7 $\pm$ 1,7 (4,2-14,3)	5,4 $\pm$ 1,5 (1,3-9,8)	9,6 $\pm$ 2,2 (5,8-15,3)	7,4 $\pm$ 2 (2,1-14,5)	8,8 $\pm$ 0,9 (6,1-12,2)	4,1 $\pm$ 1,5 (-0,6-9,3)	0,8 $\pm$ 1,1 (-2,5-3,2)
MNT4	15,6 $\pm$ 1,3 (13,3-20)	17,6 $\pm$ 1,4 (13,2-20,9)	14,4 $\pm$ 1,2 (10,3-18)	18,1 $\pm$ 1,8 (14,7-20,5)	15,5 $\pm$ 1,7 (12,1-20,2)	14,9 $\pm$ 0,6 (12,9-17,7)	12,5 $\pm$ 1,1 (8,9-16,7)	9,9 $\pm$ 0,8 (7,2-12,2)
MXT1	16,2 $\pm$ 2,1 (11-21,7)	15,1 $\pm$ 1,5 (11,5-20,7)	12 $\pm$ 1,4 (5,6-15,5)	15,8 $\pm$ 2,5 (11,1-20,4)	13,4 $\pm$ 1,7 (8,3-18,9)	14,1 $\pm$ 1,2 (11,1-20,3)	9,7 $\pm$ 1,7 (3,4-14,5)	5,6 $\pm$ 1,3 (1,7-9,1)
MXT2	14,1 $\pm$ 2 (9,2-19,5)	14,5 $\pm$ 1,4 (9,7-18,5)	11 $\pm$ 1,2 (4,3-14,3)	15,1 $\pm$ 1,9 (11,1-19,1)	12,7 $\pm$ 1,5 (7,3-18,2)	12,5 $\pm$ 1 (9,4-17,7)	8,3 $\pm$ 1,7 (1,9-13,4)	4,2 $\pm$ 1,1 (0,9-7,1)
MXT3	17,7 $\pm$ 1,8 (12,9-25,2)	22,8 $\pm$ 1,4 (16,8-26,1)	18,8 $\pm$ 1,5 (10,9-23,4)	22,8 $\pm$ 1,6 (19,2-26,3)	20 $\pm$ 1,9 (14,8-26)	18 $\pm$ 0,9 (15,6-21,7)	15,2 $\pm$ 2 (6,5-20,9)	9,6 $\pm$ 1,8 (4,4-13,7)
MXT4	22,2 $\pm$ 1,5 (17,9-30,2)	27,4 $\pm$ 1,3 (22,4-30,8)	23,8 $\pm$ 1,6 (15,9-28,2)	27,4 $\pm$ 1,9 (24-30,7)	24,2 $\pm$ 2,1 (19,2-30,7)	21,7 $\pm$ 0,8 (19,4-26,5)	20,2 $\pm$ 1,7 (13,1-26,1)	15,1 $\pm$ 1,6 (10,3-19)
MNT	10,2 $\pm$ 1,8 (6,2-15,1)	8 $\pm$ 1,7 (3,9-13,6)	5 $\pm$ 1,3 (1,6-8,9)	9 $\pm$ 2,3 (5,3-14,5)	6,9 $\pm$ 2 (2,4-13,8)	8,6 $\pm$ 0,9 (5,9-13,2)	3,9 $\pm$ 1,2 (0,2-8,3)	1,6 $\pm$ 0,9 (-0,7-3,9)
MXT	17,6 $\pm$ 1,8 (12,9-22,6)	19,9 $\pm$ 1,3 (15,6-23,8)	16,4 $\pm$ 1,3 (9,2-20,1)	20,3 $\pm$ 1,9 (16,5-23,8)	17,6 $\pm$ 1,5 (12,7-23,2)	16,6 $\pm$ 0,9 (14,2-20,2)	13,4 $\pm$ 1,7 (6,2-18,5)	8,6 $\pm$ 1,4 (4,3-12,2)

Note: A complete definition of these climatic variables is available at Table 2

**Supplementary Table 1b:** Mean  $\pm$  standard deviation and range (minimum-maximum) of the climatic variables related to water availability used to fit the climate-dependent MSDR models for the studied coniferous species.

	<i>Pinus canariensis</i>	<i>Pinus halepensis</i>	<i>Pinus nigra</i>	<i>Pinus pinea</i>	<i>Pinus pinaster</i>	<i>Pinus radiata</i>	<i>Pinus sylvestris</i>	<i>Pinus uncinata</i>
Plots	1000	5887	2297	1051	4563	822	3653	362
P	408,1 $\pm$ 44,8 (262-590)	451,6 $\pm$ 98,6 (273-868)	595,1 $\pm$ 125,4 (373-1364)	482,2 $\pm$ 104,2 (326-884)	723,7 $\pm$ 423,5 (329-1988)	1131,2 $\pm$ 191,7 (360-1802)	797,7 $\pm$ 193,7 (393-1597)	1223,2 $\pm$ 107,5 (683-1540)
PWM	73,5 $\pm$ 8,6 (47-96)	58,4 $\pm$ 13,9 (37-128)	72,6 $\pm$ 12,5 (43-178)	69,1 $\pm$ 21,7 (38-145)	97,4 $\pm$ 62,6 (38-303)	130,1 $\pm$ 26,5 (67-251)	94,5 $\pm$ 23,1 (43-220)	132 $\pm$ 11,7 (91-173)
PDM	1,2 $\pm$ 0,6 (0-4)	13,7 $\pm$ 7,7 (0-44)	23,8 $\pm$ 11,4 (5-79)	9,5 $\pm$ 7,4 (0-42)	18,9 $\pm$ 10,5 (0-71)	54,6 $\pm$ 13,8 (0-86)	36,4 $\pm$ 13,7 (5-72)	66 $\pm$ 4,3 (38-74)
MT1	2,5 $\pm$ 0,4 (1,3-3,9)	2,4 $\pm$ 0,6 (1,3-6)	3,6 $\pm$ 0,9 (1,5-8,9)	2,9 $\pm$ 0,6 (1,8-5,3)	4,4 $\pm$ 2,5 (1,7-12,5)	5,8 $\pm$ 1,2 (2-10,4)	5,4 $\pm$ 1,8 (1,8-13,4)	9,8 $\pm$ 1,6 (4,3-16,2)
MT2	3,1 $\pm$ 0,6 (1,5-4,5)	2 $\pm$ 0,7 (1-7,8)	3,3 $\pm$ 1,1 (1,1-9)	2,4 $\pm$ 0,7 (1,4-6,2)	4,2 $\pm$ 2,7 (1,2-12,4)	5,7 $\pm$ 1,2 (2,3-11,4)	5,1 $\pm$ 1,8 (1,5-12,9)	10 $\pm$ 1,9 (4,5-17,9)
MT3	0,7 $\pm$ 0,1 (0,4-1,6)	1,7 $\pm$ 0,4 (0,7-3,6)	2,8 $\pm$ 0,5 (1,6-6,5)	1,6 $\pm$ 0,3 (1-3)	2,6 $\pm$ 1 (1,1-5,5)	4,1 $\pm$ 0,7 (0,5-5,3)	4,1 $\pm$ 1 (1,7-10,1)	7,7 $\pm$ 1,4 (4,6-13,3)
MT4	0,2 $\pm$ 0 (0,1-0,4)	0,8 $\pm$ 0,4 (0,2-2,5)	1,2 $\pm$ 0,5 (0,4-3,2)	0,5 $\pm$ 0,3 (0,2-2,1)	1 $\pm$ 0,6 (0,2-3)	2,3 $\pm$ 0,5 (0,2-3,5)	1,8 $\pm$ 0,7 (0,4-4)	3,6 $\pm$ 0,4 (1,8-4,8)
P1	54,3 $\pm$ 6,6 (35,3-83)	47,7 $\pm$ 12,5 (28-109,7)	59,4 $\pm$ 13,6 (28,3-149,7)	60,4 $\pm$ 17,5 (36,3-120,7)	84,1 $\pm$ 53,9 (30-252)	117,7 $\pm$ 23,1 (50,7-211,3)	80,9 $\pm$ 24,2 (31-190,7)	122,2 $\pm$ 12,3 (59-161,7)
P2	59,9 $\pm$ 7 (37,3-75,7)	35,1 $\pm$ 12 (18-119,7)	45,6 $\pm$ 13,6 (17-128)	44,9 $\pm$ 16,5 (24-131)	70,1 $\pm$ 51,8 (20-236,7)	101,4 $\pm$ 20,9 (51,3-213)	62,9 $\pm$ 20,6 (21,7-171,3)	96,7 $\pm$ 11,5 (47,7-132,3)
P3	15,6 $\pm$ 2 (10,3-41,3)	43,2 $\pm$ 8,7 (15,7-81,7)	59,4 $\pm$ 10,9 (37,3-115,3)	39,3 $\pm$ 6,7 (27,3-72,7)	58,2 $\pm$ 22,5 (30-128,3)	92,4 $\pm$ 15,8 (12-119,3)	76 $\pm$ 13,8 (38,7-122)	109,8 $\pm$ 8,6 (77-131)
P4	6,2 $\pm$ 0,8 (4,3-10,7)	24,6 $\pm$ 12,4 (6-71)	34 $\pm$ 16 (10,7-90,3)	16,1 $\pm$ 10,4 (6,3-65,3)	28,9 $\pm$ 16,4 (7,3-86,3)	65,6 $\pm$ 14,2 (4,7-99,3)	46,1 $\pm$ 16,7 (12-84,7)	79 $\pm$ 4,6 (44-88,3)
PET1	55,7 $\pm$ 3,4 (48-65,7)	45,6 $\pm$ 5,6 (33,3-59,7)	38,5 $\pm$ 3,8 (27,7-49)	46,1 $\pm$ 6 (34,3-57,3)	39,6 $\pm$ 4,8 (31-54,7)	35,7 $\pm$ 4,1 (32-61)	32,4 $\pm$ 3 (22-46,7)	24,1 $\pm$ 1,8 (19-32,3)
PET2	54,9 $\pm$ 3,6 (46,7-65,7)	47,4 $\pm$ 5 (35,3-62)	39,6 $\pm$ 3,4 (28,3-50,7)	47,8 $\pm$ 5,2 (36,7-58,7)	41,6 $\pm$ 4,5 (32,7-56,3)	38,3 $\pm$ 3,6 (33,7-60,3)	33,7 $\pm$ 3,1 (22-46,7)	24,2 $\pm$ 2,1 (18-31)
PET3	95,7 $\pm$ 5,3 (83,7-149,7)	122,3 $\pm$ 8,8 (97,7-145,7)	112,3 $\pm$ 7,4 (89-132,3)	130,2 $\pm$ 11,1 (99-154,3)	117,5 $\pm$ 13,2 (89-152)	97,2 $\pm$ 4,9 (87,7-122)	100,1 $\pm$ 8,4 (69-128,3)	74,9 $\pm$ 5,3 (60-91,3)
PET4	114,3 $\pm$ 5,1 (104,7-182,7)	142,1 $\pm$ 15 (108,3-178,7)	135,2 $\pm$ 14,5 (101-166,3)	153,7 $\pm$ 17,8 (108,7-186)	139,4 $\pm$ 21 (94-184,7)	108,2 $\pm$ 6,9 (92,3-148,7)	120,9 $\pm$ 13,2 (84,3-161)	89,6 $\pm$ 5,1 (75,3-111,7)
M	17,3 $\pm$ 2,8 (9,3-24,9)	18,9 $\pm$ 4,5 (10,1-39,8)	28,9 $\pm$ 6,3 (16,7-65,1)	19,5 $\pm$ 3,7 (13,4-35,2)	32,3 $\pm$ 18,1 (13,3-84,4)	50,2 $\pm$ 8,7 (14,2-77,7)	43,3 $\pm$ 12 (18-98,6)	81,6 $\pm$ 12,3 (40,9-130,1)
PET	961,9 $\pm$ 47,7 (849-1319)	1072,3 $\pm$ 96,7 (825-1298)	976,6 $\pm$ 84,2 (747-1183)	1133,5 $\pm$ 106,5 (836-1369)	1014,4 $\pm$ 125,3 (754-1340)	837,9 $\pm$ 49 (752-1116)	861 $\pm$ 79,9 (592-1132)	638,4 $\pm$ 42,8 (519-799)

## ANNEX 2. Climatic variables used in the study for broadleaved species

**Supplementary Table 2a:** Mean  $\pm$  standard deviation and range (minimum-maximum) of the climatic variables related to temperature used to fit the climate-dependent MSDR models for the studied broadleaved species

	<i>Fagus sylvatica</i>	<i>Quercus faginea</i>	<i>Quercus ilex</i>	<i>Quercus petraea</i>	<i>Quercus pyrenaica</i>	<i>Quercus robur</i>	<i>Quercus suber</i>
Plots	1348	498	3911	229	1442	591	732
T	9,4 $\pm$ 1,3 (5,1-14)	11 $\pm$ 1,1 (8,2-16,3)	14,1 $\pm$ 2,2 (6,6-17,8)	9,7 $\pm$ 1,5 (5,6-14,6)	10,5 $\pm$ 1,5 (6-15,6)	12,1 $\pm$ 1,2 (6,1-14,5)	15,6 $\pm$ 1,3 (11,4-18)
MXTWM	20,9 $\pm$ 1,4 (15,9-25,4)	24,4 $\pm$ 1,9 (20,8-31,7)	28,5 $\pm$ 2,5 (19,4-32,7)	21,4 $\pm$ 2,1 (16,3-28,7)	23,2 $\pm$ 1,8 (17,6-30)	22,2 $\pm$ 1,1 (17,5-25,5)	28,3 $\pm$ 1,5 (22,9-32,2)
MNTCM	-2,1 $\pm$ 1,3 (-5,7-5,2)	-2,7 $\pm$ 1,3 (-6-2,7)	-0,8 $\pm$ 2,2 (-7,2-6,6)	-2 $\pm$ 1,2 (-5,1-1,6)	-2,3 $\pm$ 1,7 (-5,8-2,6)	1,5 $\pm$ 1,6 (-5,1-6,8)	2,7 $\pm$ 2,5 (-3,2-8,9)
TAR	296 $\pm$ 1,7 (290,9-300,6)	300,1 $\pm$ 2,4 (294-305,4)	302,3 $\pm$ 1,9 (290,4-307,4)	296,4 $\pm$ 2 (292,2-301,7)	298,5 $\pm$ 2,1 (292,1-303,9)	293,6 $\pm$ 1,5 (288-298)	298,6 $\pm$ 3,1 (292,6-304,8)
T1	6,9 $\pm$ 1,3 (2,9-12,4)	7,9 $\pm$ 1 (5,3-12,4)	10,6 $\pm$ 2,2 (3,4-15,2)	7,2 $\pm$ 1,4 (3,4-11,3)	7,5 $\pm$ 1,5 (3,2-12)	10 $\pm$ 1,4 (3,8-13,5)	12,7 $\pm$ 1,7 (7,8-16,2)
T2	4 $\pm$ 1,4 (-0,3-9,6)	5,1 $\pm$ 1,1 (2,1-9,9)	7,8 $\pm$ 2,2 (0,1-12)	4,2 $\pm$ 1,5 (0,8-8,7)	4,8 $\pm$ 1,6 (0,1-9,5)	7,5 $\pm$ 1,5 (0,8-11)	9,8 $\pm$ 1,6 (5,3-13,1)
T3	10,5 $\pm$ 1,4 (5,2-14,5)	12,4 $\pm$ 1,3 (9,1-18)	15,6 $\pm$ 2,1 (7,6-19,3)	10,8 $\pm$ 1,7 (5,4-16,2)	11,7 $\pm$ 1,5 (6,9-17)	12,9 $\pm$ 1,2 (6,2-15,8)	16,7 $\pm$ 1,1 (12,9-18,9)
T4	16,3 $\pm$ 1,1 (12,5-19,8)	18,7 $\pm$ 1,5 (15,7-25)	22,5 $\pm$ 2,3 (14,5-25,8)	16,6 $\pm$ 1,6 (12,7-22,3)	18 $\pm$ 1,6 (13,7-24,3)	17,8 $\pm$ 1 (13,5-20,5)	23 $\pm$ 1,2 (18,3-25,9)
MNT1	3,3 $\pm$ 1,3 (0,1-8,8)	3,4 $\pm$ 1,2 (0,6-8,1)	5,9 $\pm$ 2,2 (0,4-11,4)	3,4 $\pm$ 1,1 (0,8-6,4)	3,4 $\pm$ 1,6 (0,1-8)	6,4 $\pm$ 1,3 (0,9-10,5)	8,5 $\pm$ 1,8 (3,9-12,3)
MNT2	-0,9 $\pm$ 1,4 (-4,9-5,9)	-1,1 $\pm$ 1,3 (-4,9-3,9)	0,9 $\pm$ 2,1 (-6,4-7,7)	-0,9 $\pm$ 1,3 (-4-3,2)	-0,9 $\pm$ 1,7 (-5-3,9)	2,6 $\pm$ 1,5 (-4-7,5)	4 $\pm$ 2,3 (-1,3-9,9)
MNT3	5,6 $\pm$ 1,3 (0,9-10,7)	6,2 $\pm$ 1,2 (2,5-10,5)	8,7 $\pm$ 2 (1,3-13,9)	5,8 $\pm$ 1,4 (1,2-10,6)	6 $\pm$ 1,4 (1,8-10,7)	8 $\pm$ 1,2 (1,8-11,3)	10,9 $\pm$ 1,6 (6,3-15,2)
MNT4	12,7 $\pm$ 0,9 (10,1-15,8)	14,2 $\pm$ 1,4 (11,5-19,9)	17,8 $\pm$ 2,2 (10,8-20,6)	12,8 $\pm$ 1,2 (10,5-17,3)	14 $\pm$ 1,6 (10,7-20)	14,2 $\pm$ 0,8 (10,9-16,2)	18,8 $\pm$ 1,1 (14,3-20,7)
MXT1	10,5 $\pm$ 1,5 (5,4-16)	12,4 $\pm$ 1,1 (9,7-17,6)	15,2 $\pm$ 2,3 (6,3-20,5)	10,9 $\pm$ 1,8 (5,6-16,6)	11,5 $\pm$ 1,5 (6,3-16,3)	13,7 $\pm$ 1,6 (6,4-16,8)	17 $\pm$ 1,7 (11,7-20,1)
MXT2	8,8 $\pm$ 1,5 (4-14,3)	11,3 $\pm$ 1,3 (7,8-17,4)	14,8 $\pm$ 2,4 (6,4-19,1)	9,3 $\pm$ 1,9 (4,9-14,2)	10,5 $\pm$ 1,8 (5,1-16,1)	12,4 $\pm$ 1,6 (5,3-15,3)	15,7 $\pm$ 1,5 (11,8-19,4)
MXT3	15,3 $\pm$ 1,7 (9,4-20)	18,6 $\pm$ 1,6 (14,5-25,6)	22,6 $\pm$ 2,4 (13,1-26,7)	15,9 $\pm$ 2,2 (9,5-21,8)	17,4 $\pm$ 1,9 (11,8-23,7)	17,9 $\pm$ 1,4 (10,7-21,5)	22,5 $\pm$ 1,6 (19,1-26,5)
MXT4	19,9 $\pm$ 1,5 (14,8-24,4)	23,2 $\pm$ 1,8 (19,6-30,2)	27,2 $\pm$ 2,4 (18,1-31,2)	20,4 $\pm$ 2,1 (14,9-27,6)	22,1 $\pm$ 1,8 (16,5-28,6)	21,4 $\pm$ 1,2 (16,2-24,8)	27,3 $\pm$ 1,5 (22,3-31,1)
MNT	5,2 $\pm$ 1,2 (1,6-10,3)	5,7 $\pm$ 1,2 (2,5-10,1)	8,3 $\pm$ 2,1 (2-13,3)	5,3 $\pm$ 1,2 (2,4-9,4)	5,6 $\pm$ 1,5 (1,9-10,3)	7,8 $\pm$ 1,2 (2,5-11,2)	10,5 $\pm$ 1,5 (6,1-14,4)
MXT	13,7 $\pm$ 1,5 (8,6-18,3)	16,4 $\pm$ 1,4 (12,9-22,7)	19,9 $\pm$ 2,4 (11,2-24)	14,1 $\pm$ 2 (8,7-20)	15,4 $\pm$ 1,7 (10,1-21,1)	16,4 $\pm$ 1,4 (9,6-19,2)	20,6 $\pm$ 1,4 (16,6-24,2)

Note: A complete definition of these climatic variables is available at Table 2

**Supplementary Table 2b:** Mean  $\pm$  standard deviation and range (minimum-maximum) of the climatic variables related to water availability used to fit the climate-dependent MSDR models for the studied broadleaved species

	<i>Fagus sylvatica</i>	<i>Quercus faginea</i>	<i>Quercus ilex</i>	<i>Quercus petraea</i>	<i>Quercus pyrenaica</i>	<i>Quercus robur</i>	<i>Quercus suber</i>
Plots	1348	498	3911	229	1442	591	732
P	962,4 $\pm$ 163,4 (525-1396)	663 $\pm$ 174,7 (387-1036)	557,2 $\pm$ 139,8 (317-1567)	910,4 $\pm$ 130,7 (492-1405)	755,5 $\pm$ 239,60 (339-1738)	1372,3 $\pm$ 276,5 (753-1827)	681,3 $\pm$ 136 (359-1665)
PWM	104,8 $\pm$ 15,4 (61-174)	76,8 $\pm$ 17,6 (45-158)	78,9 $\pm$ 23,2 (38-216)	102,1 $\pm$ 15,5 (58-176)	97,9 $\pm$ 37,2 (40-251)	179,2 $\pm$ 52,1 (88-268)	105,7 $\pm$ 25,3 (44-240)
PDM	49,2 $\pm$ 10,1 (21-80)	30,8 $\pm$ 12,5 (1-59)	11,5 $\pm$ 10,6 (1-64)	45,8 $\pm$ 8,2 (18-70)	23,7 $\pm$ 10,3 (5-53)	43,5 $\pm$ 11,3 (22-87)	7,9 $\pm$ 10,6 (0-42)
MT1	5,9 $\pm$ 1,1 (3-10,4)	3,8 $\pm$ 1 (1,8-7)	3,4 $\pm$ 1 (1,6-9,6)	5,5 $\pm$ 1,3 (2,9-11,4)	5,1 $\pm$ 1,8 (1,8-11)	8,1 $\pm$ 2,1 (4,3-11,8)	4 $\pm$ 0,9 (2-10)
MT2	5,9 $\pm$ 1,2 (2,8-11)	3,5 $\pm$ 1,1 (1,4-7,2)	3 $\pm$ 1,1 (1,3-9,9)	5,3 $\pm$ 1,4 (2,6-11,5)	4,8 $\pm$ 1,9 (1,5-11,4)	8,1 $\pm$ 2,3 (4-12,1)	3,9 $\pm$ 1,3 (1,4-10)
MT3	4,5 $\pm$ 0,6 (2,6-8,2)	3 $\pm$ 0,7 (1,5-4,8)	1,9 $\pm$ 0,6 (1,1-5,3)	4,1 $\pm$ 0,7 (2,5-7,8)	3,1 $\pm$ 0,7 (1,3-6,4)	4,5 $\pm$ 0,5 (2,5-7,1)	1,7 $\pm$ 0,4 (1,1-4,7)
MT4	2,1 $\pm$ 0,4 (1-3,7)	1,4 $\pm$ 0,5 (0,3-2,9)	0,6 $\pm$ 0,5 (0,2-3)	2,1 $\pm$ 0,4 (0,9-3,6)	1,1 $\pm$ 0,4 (0,4-2,6)	2,2 $\pm$ 0,3 (1,5-3,6)	0,6 $\pm$ 0,5 (0,2-2,3)
P1	96,2 $\pm$ 17,2 (49,7-161,3)	66,9 $\pm$ 17,6 (32,3-129)	68,3 $\pm$ 19,2 (30,7-199,7)	91,6 $\pm$ 17,5 (47,3-162,7)	85,9 $\pm$ 33,4 (37-216)	158,1 $\pm$ 41 (80,3-220,7)	89,3 $\pm$ 20,8 (40-205)
P2	81,1 $\pm$ 16,3 (40,3-135)	52,4 $\pm$ 17,3 (22,7-116,7)	52,9 $\pm$ 18,3 (20,7-169,7)	73,8 $\pm$ 16,9 (39,3-138,3)	70,3 $\pm$ 30,3 (26,7-193)	139,7 $\pm$ 41,4 (64,3-216,7)	76,6 $\pm$ 27,5 (25,3-182,7)
P3	87,3 $\pm$ 11,5 (55-117,7)	63,5 $\pm$ 14,1 (37-92)	45,6 $\pm$ 11,2 (30,3-99,7)	81,6 $\pm$ 9,4 (51-114)	64,6 $\pm$ 13,1 (33,3-112)	98,5 $\pm$ 10,8 (62,3-122,3)	43,4 $\pm$ 10,2 (29,7-108)
P4	56,2 $\pm$ 11,6 (27,7-93,7)	38,1 $\pm$ 14,5 (8-76)	18,9 $\pm$ 12,8 (7,3-77)	56,4 $\pm$ 11,1 (26-84,3)	31 $\pm$ 10,7 (11-64,7)	61,2 $\pm$ 8,7 (39,7-102)	17,8 $\pm$ 16,2 (7-65)
PET1	32,9 $\pm$ 2 (24,3-38)	36,1 $\pm$ 3,4 (29,3-52,7)	45,1 $\pm$ 6,4 (27-57)	32,7 $\pm$ 2,2 (24-38,3)	36,1 $\pm$ 3,2 (28,3-48,3)	35,1 $\pm$ 1,7 (25,3-39,3)	48 $\pm$ 5,7 (34-58)
PET2	34,2 $\pm$ 2,3 (24,3-41)	37,8 $\pm$ 3,4 (31,3-54,7)	46,9 $\pm$ 6 (28,3-59)	34 $\pm$ 2,5 (24-40)	37,8 $\pm$ 3,4 (29-49,3)	37,9 $\pm$ 2,2 (26-42,7)	49,6 $\pm$ 5,4 (36-59,7)
PET3	99,9 $\pm$ 5 (76-111,7)	109,3 $\pm$ 9,9 (92,7-148,3)	130,8 $\pm$ 13,7 (85-154,7)	99,5 $\pm$ 5,5 (75,3-121,3)	112,5 $\pm$ 8,7 (91,7-139)	100,9 $\pm$ 5,8 (79,7-117)	124,1 $\pm$ 13,7 (99,3-155)
PET4	118,5 $\pm$ 6,9 (90,3-135,7)	128,9 $\pm$ 14,3 (102,7-182,3)	157,1 $\pm$ 18,8 (99,3-187)	115,9 $\pm$ 7,4 (90-147)	136,4 $\pm$ 11,8 (103-172,3)	112,6 $\pm$ 7,7 (91-131)	144,9 $\pm$ 21,8 (109,3-187)
M	49,7 $\pm$ 8,5 (25,8-82,7)	31,7 $\pm$ 8,7 (16,9-53,8)	23,4 $\pm$ 7 (12,5-65,8)	46,6 $\pm$ 8,4 (24,7-81,3)	36,9 $\pm$ 11,4 (14,1-80,2)	62,2 $\pm$ 12,1 (37,3-83,9)	26,7 $\pm$ 5,7 (14-72,9)
PET	856,4 $\pm$ 44 (645-961)	936,6 $\pm$ 90,3 (782-1313)	1139,7 $\pm$ 131,4 (719-1373)	846,3 $\pm$ 48,8 (640-1040)	968,1 $\pm$ 79,2 (788-1215)	859,6 $\pm$ 47,1 (674-982)	1099,4 $\pm$ 124,7 (837-1379)

Note: A complete definition of these climatic variables is available at Table 2

### ANNEX 3. Basic MSDR models fits for the 95<sup>th</sup> and the 99<sup>th</sup> quantiles

**Supplementary Table 3:** Species-specific coefficients, goodness of fits in terms of Akaike's Information Criterion (AIC) and pseudo-R<sup>2</sup> coefficient and SDI<sub>max</sub> estimations for the basic MSDR models fitted by linear quantile regression at the 95<sup>th</sup> and 99<sup>th</sup> quantiles.

Functional group	Species	tau	$\alpha_0$	$\beta_0$	SDI <sub>max</sub>	AIC	pseudoR <sup>2</sup>	
Conifers	<i>Pinus canariensis</i>	0,95	13,058*** (12,467;13,649)	-1,983*** (-2,161; -1,805)	792	2173,2	0,2937	
		0,99	12,465*** (12,046;12,885)	-1,734*** (-1,866; -1,614)	958	2326,4	0,3440	
	<i>Pinus halepensis</i>	0,95	12,137*** (11,812;12,462)	-1,8166*** (-1,927; -1,701)	539	14188,7	0,2089	
		0,99	12,05*** (11,723;12,371)	-1,6904*** (-1,800; -1,582)	742	15397,2	0,2329	
	<i>Pinus nigra</i>	0,95	12,26*** (11,784;12,736)	-1,707*** (-1,868; -1,546)	867	5109,8	0,2416	
		0,99	12,615*** (12,209;13,021)	-1,7359*** (-1,873; -1,599)	1127	5649,9	0,2486	
	<i>Pinus pinaster</i>	0,95	13,378*** (13,071;13,685)	-2,0237*** (-2,118; -1,929)	957	9568,0	0,3140	
		0,99	13,354*** (13,060;13,649)	-1,9402*** (-2,031; -1,849)	1223	10842,5	0,3113	
	<i>Pinus pinea</i>	0,95	13,591*** (12,891;14,290)	-2,2363*** (-2,450; -2,023)	597	2403,6	0,3798	
		0,99	13,443*** (12,231;14,660)	-2,0919*** (-2,462; -1,722)	820	2829,8	0,3789	
	<i>Pinus radiata</i>	0,95	12,916*** (12,430;13,401)	-1,8256*** (-1,964; -1,688)	1141	1326,5	0,3785	
		0,99	13,888*** (13,029;14,748)	-2,0372*** (-2,282; -1,793)	1526	1574,8	0,3834	
	<i>Pinus sylvestris</i>	0,95	12,457*** (12,241;12,672)	-1,6949*** (-1,763; -1,626)	1098	7038,7	0,2602	
		0,99	12,88*** (12,577;13,184)	-1,7664*** (-1,863; -1,669)	1332	8019,8	0,2771	
	<i>Pinus uncinata</i>	0,95	13,506*** (12,639;14,374)	-2,0369*** (-2,314; -1,760)	1043	570,9	0,3141	
		0,99	12,599*** (11,987;13,211)	-1,7038*** (-1,900; -1,508)	1230	603,1	0,3997	
	Broadleaves	<i>Fagus sylvatica</i>	0,95	13,323*** (13,059;13,586)	-2,0178*** (-2,097; -1,939)	923	1759,0	0,5208
			0,99	12,939*** (12,264;13,613)	-1,8530*** (-2,055; -1,651)	1069	2149,7	0,5039
		<i>Quercus faginea</i>	0,95	12,300*** (11,400;13,199)	-1,8171*** (-2,152; -1,482)	633	1085,2	0,1836
			0,99	11,589*** (10,735;12,443)	-1,4855*** (-1,804; -1,167)	904	1140,6	0,2227
<i>Quercus ilex</i>		0,95	12,644*** (12,487;12,800)	-2,1832*** (-2,233; -2,133)	275	8391,6	0,5307	
		0,99	12,558*** (12,294;12,823)	-2,0734*** (-2,157; -1,989)	359	9306,2	0,5092	
<i>Quercus petraea</i>		0,95	12,358*** (11,775;12,941)	-1,7256*** (-1,917; -1,535)	901	411,7	0,4205	
		0,99	13,312*** (13,048;13,576)	-1,9571*** (-2,044; -1,871)	1110	475,1	0,4089	
<i>Quercus pyrenaica</i>		0,95	12,364*** (11,929;12,799)	-1,792*** (-1,946; -1,638)	732	3265,4	0,2712	
		0,99	11,893*** (11,586;12,201)	-1,5409*** (-1,650; -1,432)	1026	3510,3	0,2765	
<i>Quercus robur</i>		0,95	12,343*** (12,054;12,631)	-1,7802*** (-1,866; -1,694)	745	1039,7	0,4326	
		0,99	12,066*** (11,476;12,656)	-1,6576*** (-1,834; -1,481)	837	1180,4	0,4253	
<i>Quercus suber</i>		0,95	13,036*** (12,627;13,444)	-2,0922*** (-2,210; -1,974)	545	1402,8	0,4931	
		0,99	12,369*** (11,286;13,452)	-1,8333*** (-2,146; -1,520)	644	1573,8	0,4789	

\*\*\* $p < 0,001$ ; \*\* $p < 0,01$ ; \* $p < 0,05$



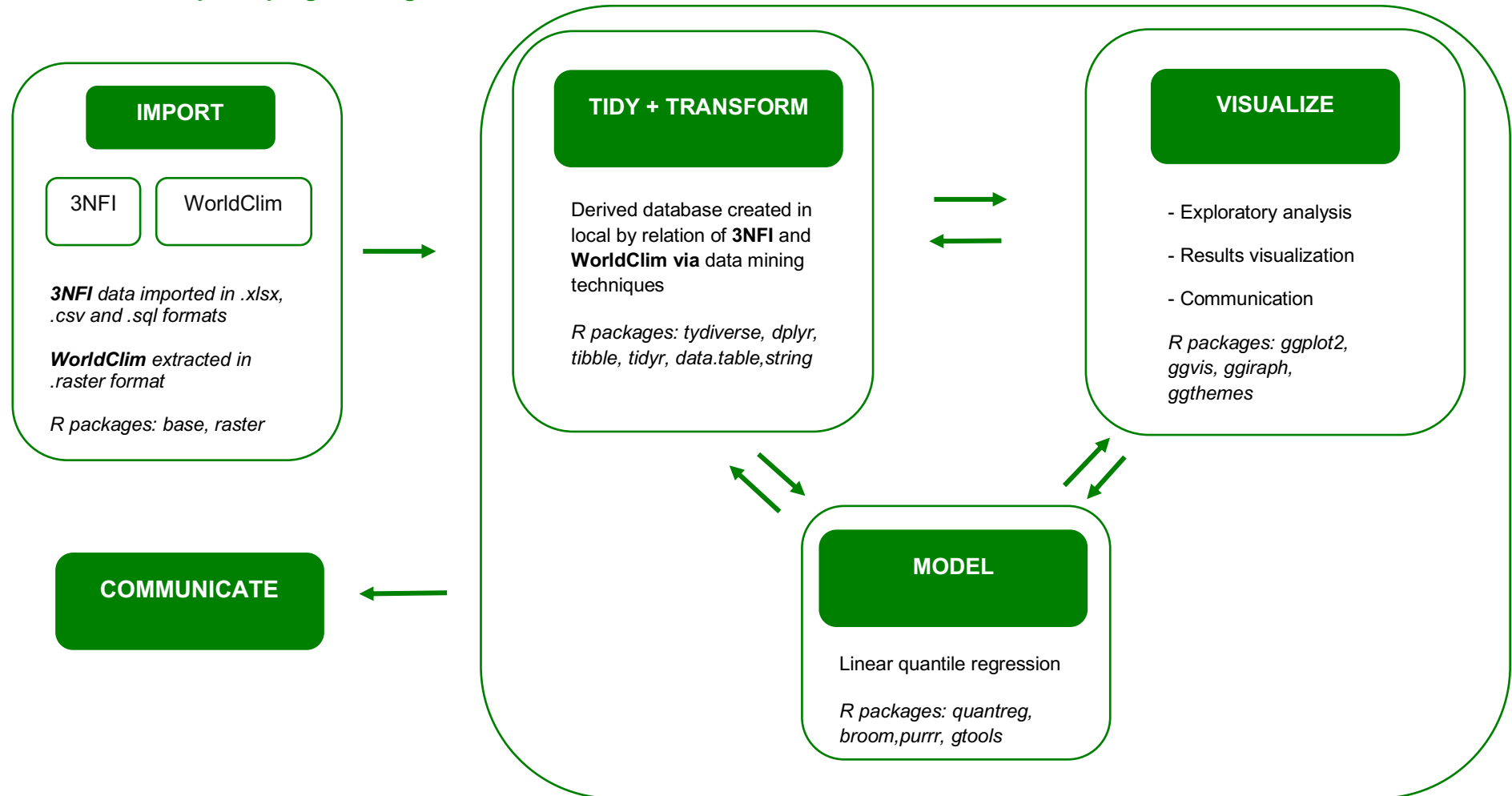
## ANNEX 4. Functional traits and climatic requirements for the studied species

**Supplementary Table 4:** Functional traits and climatic requirements for the 15 studied species

Functional group	Species	ST	T	MTWM	MTCM	P	RSP
Coniferous	<i>Pinus canariensis</i>	1	13-17	18-25	7-14	400-1000	No limit
	<i>Pinus halepensis</i>	1,35	12-16	21-26	3-8	300-700	20-132
	<i>Pinus nigra</i>	2,1	9-12	20-23	1-4	600-1200	60-130
	<i>Pinus pinaster</i>	1,89	12-16	18-27	1-7	400-1600	70-150
	<i>Pinus pinea</i>	1	11-18	21-16	3-11	430-800	15-125
	<i>Pinus radiata</i>	2,97	10-13	16-20	4-8	1000-2000	100-290
	<i>Pinus sylvestris</i>	1,67	6-12	15-20	0-3	600-1200	> 100
	<i>Pinus uncinata</i>	1,2	4	< 15	< 0	> 800	> 200
Broadleaved	<i>Fagus sylvatica</i>	4,56	7,3-10	18	0	600-900	150-200
	<i>Quercus faginea</i>	-	8-16	15-26	(-3)-5	350-1400	> 100
	<i>Quercus ilex</i>	3,02	10-18	14-28	(-3)-11	> 450	75-100
	<i>Quercus petraea</i>	2,73	5-15	15-25	(-3)-7	600	150
	<i>Quercus pyrenaica</i>	2,55	11-16	12-22	(-5)-7	600	> 125
	<i>Quercus robur</i>	2,45	10	14-25	-10	600	200
	<i>Quercus suber</i>	-	13-16	20-26	4-5	> 500	23-165

Note: ST - Shade Tolerance, T - Mean Annual Temperature (°C), MTWM - Mean Temperature of the Warmest Month (°C), MTCM - Mean Temperature of the Coldest Month (°C), P - Mean Annual Precipitation (mm), and RSP - Required Summer Precipitation (mm). Data obtained from Niinemets and Valladares (2006) and Serrada et al. (2008). Shade tolerance is ranked as proposed by Baker (1949): 1 = Very intolerant, 2 = intolerant, 3 = moderately tolerant, 4 = tolerant, 5 = very tolerant.

## ANNEX 5. Datamap and programming



Based on the book "R for Data Science" (2017)

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