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Climate influences on the maximum size-density relationship in Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) stands

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ABSTRACT

The maximum size-density relationship (MSDR) reflects the boundary site occupancy and the self-thinning line for a given species, being a useful tool in forestry. Studies focusing on the MSDR often do not cover the whole distribution of the studied species, which results in different boundaries for a given species in different regions. A common MSDR is lacking for the increasingly demanded large-scale studies. However, this information is important where silvicultural responses must be prioritized among monospecific stands or where comparisons among maximum and relative stand densities between and within species are required.

For the purposes of this study, we used data from 9911 sample plots located in Scots pine and European beech monospecific stands. Both of these species are of considerable importance and widely distributed throughout Europe. The data came from National or Regional Forest Inventories of five European countries (Austria, Germany, France, Spain and Poland) and therefore were distributed across a wide range of climatic conditions.

The main aim of this study was to determine whether the MSDR of these species depends on environmental variables and to develop a MSDR model for each species that explain this variability along a climate gradient.

The resulting models showed that both parameters of species boundary lines were climate-dependent, but that the pattern of variation differed between species. Hence, the higher the humidity, the steeper the MSDR (more negative exponent) and the higher the intercept for beech, while in the case of pine, the higher the humidity, the straighter the MSDR and the lower the intercept. According to these models, the stand density indices, for a reference diameter of 25 cm, varied with the humidity in a different way for each species. Consequently, the ratio between the two species increases with humidity, although it also depends on stand diameter.

These results are in accordance with the yield level theory and could contribute to the development of more precise silvicultural guidelines and growth models based on the self-thinning line. Moreover, they are of particular importance in the discussion of growth and the effects of mixing on mixed species stands.

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Abbreviations: MSDR, maximum size-density relationship; SDI, stand density index; NFI, National Forest Inventory; RFI, Regional Forest Inventory; M, Martonne aridity index.

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1. Introduction

Maximum site occupancy or carrying capacity is a key concept in both ecology and forestry. In forestry, it indicates the stand density level at which competition-induced mortality occurs at high rates, so that stocking degree no longer increases despite the growth of the remaining trees. Relative indices based on this concept are the most relevant because they make it possible to compare stands at different stages of development (Reineke, 1933).

Reineke (1933) plotted the number of trees per hectare in fully stocked stands (N) against the quadratic mean diameter (dg) and found, in a double logarithmic scale, a linear relationship: $N \propto dg^{-1.605}$. Yoda (1963), in overcrowded populations, found a relationship between mean biomass (w) and stand density: $w \propto N^{-3/2}$. White (1981) linked the Yoda and Reineke's theories using an allometric approach: $w \propto dg^{-1.605(-3/2)}$. In both theories the process is known as self-thinning or decrease of stem density in a population of growing individuals (Begon et al., 2006).

The slope of the self-thinning line, or maximum size-density relationship (MSDR) is often assumed to be independent of species. The assumption of constant slope has been put into question recurrently in forestry literature leading to ambiguous explanations. Divergences from the theoretical slope value and biological interpretation of the intercept variation across species and locations have led to discard the universality of the so-called self-thinning law (Weller, 1987; Lonsdale, 1990). Some of these differences could be associated to the use of different boundary lines. Hann (2014), for example, identifies three types of boundaries: a species boundary line which cannot be exceeded by a given species in any environment; a population boundary line of plants of a given growth form and given environment; and an environmental boundary line which cannot be exceeded by any species in that environment, which represents the interspecific boundary line for all species and embraces all population boundary lines. The environment, species and interspecific boundary represent the upper limits of the population boundary lines constrained by environmental, genetic traits or both (Sackville-Hamilton et al., 1995). The selection of the boundary modelled depends on the type of data, the model form and the parameter estimation method (Hann, 2014). Ultimately, the choice of boundary should reflect the purpose of the investigation or the end use of the boundary for operational guidance.

The coefficients of a given MSDR are most often interpreted as reflecting a dynamic self-thinning relationship: the boundary line itself represents the asymptotic trajectory of a population or stand growing under maximum density (Hann, 2014). In this situation, the slope of the MSDR reflects the dynamic allometry between the size of a tree (expressed in terms of its biomass or diameter) and the growing space it occupies (Pretzsch and Biber, 2005). Alternatively, a theory for the MSDR can be developed in terms of the joint response of tree height and diameter under varying competition and growing space availability (Sterba, 1975, 1987). In the context of monospecific, single-cohort stands, "growing space" is most often interpreted as equal to, or at least closely related to, crown area; but more generally it refers to resource space in the sense described by Oliver and Larson (1996). Thus, the parameters of the MSDR potentially reflect not only the average structural and resource use allometry of a species but also species genetic variability in that allometry, and the plasticity of resource use and growth in response to a varying environment.

Many of the studies focusing on species-specific allometric exponents are based on population boundary lines (Pretzsch, 2006) or when focusing on species boundary lines they often do not cover the whole distribution of the species (VanderSchaaf and Burkhart, 2007). This often results in different intercepts and

slopes of the relationship for a given species in different regions (Charru et al., 2012), which can complicate its use at larger scales and across regions. Additionally, some studies have reported differences in MSDR's among sites, generally pointing to an increase in the elevation of the MSDR as site productivity increases (Weiskittel et al., 2011; Zhang et al., 2013).

Besides the regional variation that can be due to genetic and/or environmental factors, there are other problems which may make the comparison among studies difficult, such as the type of data and the parameter estimation techniques (Hann, 2014). Time-series data from un-thinned permanent plots generally reflect population self-thinning trajectories well, but they frequently represent only a small part of the species distribution to estimate the species boundary line, because long-term permanent plots are relatively rare (Pretzsch, 2006). On the other hand, the disadvantage of using data from temporary plots is that it is difficult to assess whether they really include the maximum stand densities for a given size (Charru et al., 2012). To overcome the limitations of the different types of data sets, specific fitting techniques are required. For instance, frontier analysis or quantile regression techniques are needed to avoid the subjectivity of selecting plots at maximum density in cross-section data from temporary plots (Charru et al., 2012). Nevertheless, methodological approaches differ substantially among studies, which can also influence the reported parameter estimates of MSDR (Zhang et al., 2005).

All of these problems make the use of the concept of maximum stand density challenging, especially in increasingly demanded large-scale studies where a common MSDR is not available. However, this information is important where comparisons among maximum and relative stand densities between and within species are required, or when silvicultural responses must be prioritized among stands of a single species that grows across a wide range of environments. When comparing growth in monospecific and mixed stands, it is important to take into account species-specific potential site occupancy, preferably through relative stand density indices (Huber et al., 2014; Sterba et al., 2014). MSDR provide an excellent tool to calculate those relative stand density indices by species and to estimate competition equivalence coefficients between species (ratios between the maximum densities of the two species), which allows to describe total stand density and species proportion by area (Río et al., 2016). The use of correct species-specific MSDRs for a given site is critical as the results of the equivalence competition coefficient between species depends on them.

We study two species of considerable importance, Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.), which are widely distributed throughout Europe (Pretzsch et al., 2015). Scots pine covers about 12 million ha, European beech 49 million ha, and the potential area for mixtures is 32 million ha (Brus et al., 2012). The MSDR of these species has been studied previously in different European regions with contrasting results (Hynynen, 1993; Río et al., 2001; Charru et al., 2012; Vospernik and Sterba, 2015). However, those results have not yet been compared or analysed taking into account the different environmental conditions of the different study areas.

In this article we hypothesize that both the intercept and the slope of the MSDR of a species varies with environmental conditions and that their pattern of variation is species-specific, which involves variation in the equivalence competition coefficients along environmental gradients.

The objectives of this study are therefore: (i) to determine whether MSDR for pure Scots pine and European beech depends on environmental variables; (ii) to develop a model for these two species to estimate MSDR along a climate gradient in Europe; (iii) to study the equivalence competition coefficients along a climate gradient.

2. Materials and methods

2.1. Forest inventory data

We used data from National Forest Inventories (NFI) and regional forest inventories (RFI) across five countries - Austria, France, Spain (Spanish NFI and Catalanian RFI separately), Germany (RFI Bavaria) and Poland (Fig. 1). Together with the inventory data, mean annual temperature (T, °C) and annual precipitation (P, mm) were provided for each plot.

The Austrian NFI was based on clusters, with spacing between the clusters of 3.89 km. The clusters themselves were squares with 200 m side length. Each corner of the square was the centre of an angle count sample with basal area factor 4 m²/ha and a minimum breast height diameter of 10.5 cm. Trees with a diameter larger than 5 cm and less than 10.5 cm were measured in a fixed circle of 2.6 m radius. Site and stand description was performed within a circle of 300 m². From all sampled trees, i.e. those within the angle count and those within the 2.6 m circle, the species, diameter and height were recorded (see further details in Gabler and Schadauer, 2008). For this investigation the data of the survey from 2000 to 2002 were used. The climate data came from climate maps developed for the period 1971–2000 specifically for Austria (Hiebl et al., 2011).

The forest inventory of Catalonia was based on circular sampling plots of 10 m radius randomly distributed throughout the forest area of the region. Sampling was conducted from 1988 to 1998 at a density of one plot per km² of forest. For each tree with

a diameter at breast height above 5 cm, its species identity was annotated and the height and DBH measured. More detailed information about methodology can be found in Gracia et al. (2004) and on the web site: <http://www.creaf.uab.es/iefc>. Climatic data was obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al., 2005), a collection of digital maps at 200 × 200 m resolution with average annual and monthly data for total rainfall and maximum, mean, and minimum temperatures (period 1950–1999).

Data from Germany came from RFIs, carried out between 2001 and 2011, for five forest enterprises (Allersberg, Burglengenfeld, Forchheim, Nürnberg, and Roding in Bavaria). The width of the grid on which the plots were located varied between 100 m × 100 m (Allersberg) and 300 m × 300 m (Nürnberg). The measurements were based on the concept of concentric circles with radii of 3.15, 6.31 and 12.62 m, where trees with breast height diameters larger than 0, 10 and 30 cm respectively were inventoried (Bayerische Staatsforsten, 2011). The climate data came from Arbeitskreis Standortkartierung (1985).

The French NFI consisted of plots randomly located around the nodes of a systematic one-kilometer grid. About one tenth of the plots were measured every year. For this study data from the 2005 to 2012 measurements were used. In each plot, dendrometric measurements were carried out in three concentric circles of 6, 9, and 15 m radii, for all trees with diameters at breast height over 7.5, 22.5, and 37.5 cm respectively. Monthly temperature and precipitation data came from the Aurelhy model from MétéoFrance (Bénichou and le Breton, 1987) calibrated on the 1961–1990 period.

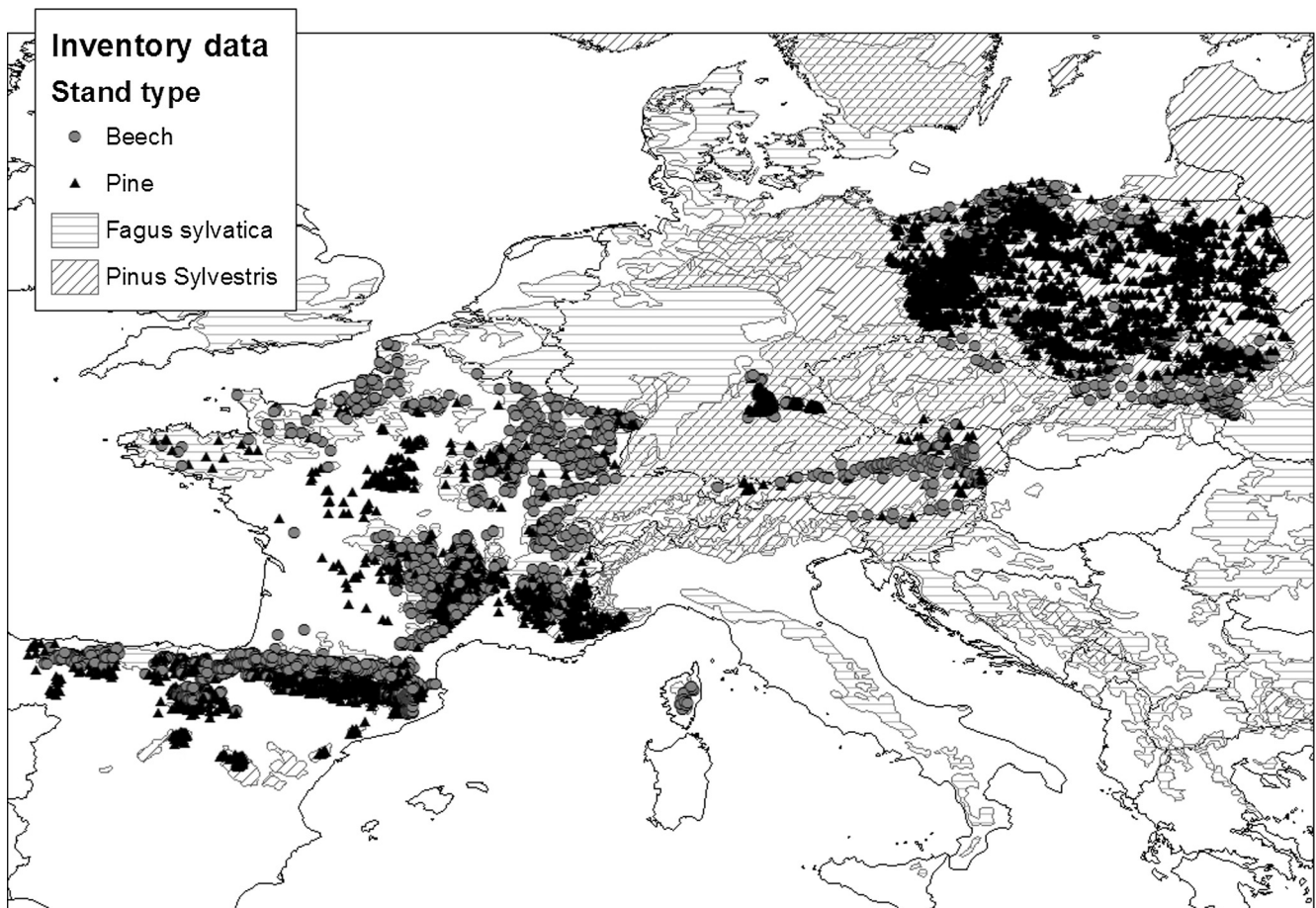


Fig. 1. Location of the sample plots in monospecific pine stands (triangles), and monospecific beech stands (circles) used in this study together with the natural range of both tree species according to EUFORGEN (2009).

Spanish NFI plots were permanent concentric sample plots of 5, 10, 15 and 25 m radii, located at the nodes of a one kilometre square grid, re-measured in an inventory cycle of ten years. Trees with breast height diameters of over 7.5, 12.5, 22.5 and 42.5 cm respectively were measured. Data used in this study came from the period between 1988 and 1998. Climatic data came from raster maps with a 1 km resolution for the Iberian Peninsula, obtained from a functional phytoclimatic model based on raw data (period 1951–1999) from meteorological stations (Gonzalo Jiménez, 2010).

The Polish NFI was based on permanent circular plots, with four supplementary subplots, performed with an inventory cycle interval of five years, located at the nodes of a 4 km grid. The radius of the plots ranged from 0.02 to 0.05 ha depending on the stand age and stand structural components (see Talarczyk, 2014, for methodological details). Data for this study came from the first inventory cycle (2005–2009). Climatic data came from the CRU database. To calculate annual mean temperature and sum of precipitation, a data-set with the highest available spatial resolution, i.e. 10' gridded climatology of 1961–1990 monthly means (New et al., 2002), was used.

2.2. Data selection

Sample plots located in monospecific stands of *Pinus sylvestris* and *Fagus sylvatica* were selected from the complete dataset. We considered that a plot belonged to a monospecific stand when the main species accounted for more than 90% of the total basal area. This threshold was a compromise between keeping a high number of plots for the study and being as near as possible to the strict criteria (100%).

As a measure of climatic conditions we used the Martonne aridity index (M) (Martonne, 1926), i.e. $P/(T + 10)$ (being P annual precipitation in mm and T mean annual temperature in °C) which, due to its minimal data requirement, has been widely used in modern studies to describe the drought condition or aridity in a given region (Rötzer et al., 2012; Pretzsch et al., 2013; Quan et al., 2013; Bielak et al., 2014).

The database was further debugged by discarding plots located in open forests that would be of no interest for the purpose of estimating MSDR (see Supplementary Fig. 1 for data before discarding plots). Under the hypothesis that the MSDR depends on the climatic conditions, and in order to avoid biasing the sample by removing more plots in some conditions than in others, we fitted two quantile regressions ($\tau = 0.5$), one between the basal area and the M, and the other between the ratio of dominant height-quadratic mean diameter and the M. All plots which, for a given M, presented values for basal area or ratio dominant height-quadratic mean diameter ratio of less than half of those expected (according to the fitted regression), were removed from the sample (i.e. they represented plots growing at low densities). The use of the quantile regression in this step was determined by the subsequent use of quantile regression with τ close to one for describing the upper limit of the observed densities.

We also restricted the sample to plots with quadratic mean diameters between 10 and 55 cm, in order to avoid including data from very young stands that may be underrepresented or flawed as they were not completely inventoried due to threshold diameters, as well as old stands, which may also be underrepresented due to harvesting, especially on better sites where forest harvests are more frequent. Furthermore, younger stands have often not reached canopy closure, so their apparent self-thinning line is shallower while older stands may have reached constant final standing volume, so their slope should be steeper (around -2.0).

Summary statistics of the sample plots used in this study are given in Table 1.

Table 1 Summary of the data used, provided by the national forest inventories or the regional inventories in different countries.

	AT		CAT		DE		ES		FR		PL		All	
	N	M	N	M	N	M	N	M	N	M	N	M	N	M
<i>Pinus</i>														
# plots	49	49.5	1088	1082	1596	1412	1412	1412	1003	2629	2629	7777	7777	7777
Mean	987	24.8	1069	19.0	502	51.1	838	39.7	797	910	910	821	821	821
Sd	686	5.9	578	5.3	449	8.3	544	1.4	538	625	625	589	589	589
Min	247	11.2	144	10.1	80	29.1	59	36.0	42	80	80	42	42	42
Max	3656	37.6	4317	50.1	5363	77.6	3533	48.7	3836	4000	4000	5363	5363	5363
<i>Beech</i>														
# plots	83	88.0	133	133	23	916	916	916	828	151	151	2134	2134	2134
Mean	947	29.9	1082	19.2	898	57.9	659	43.6	844	541	541	763	763	763
Sd	1042	11.8	528	5.9	896	6.9	512	4.2	732	402	402	646	646	646
Min	70	10.2	242	10.4	100	44.3	61	36.0	57	75	75	57	57	57
Max	4730	54.7	2913	44.7	3623	85.7	4838	49.7	6057	2600	2600	6057	6057	6057
<i>dg</i>														
Mean	43.1	24.0	44.8	27.4	27.2	27.4	27.4	27.4	50.7	23.6	23.6	23.8	23.8	23.8
Sd	7.7	7.7	9.4	9.5	10.3	10.3	10.3	10.3	11.3	7.3	7.3	7.6	7.6	7.6
Min	26.7	10.0	35.0	10.1	48.7	48.7	48.7	48.7	29.7	54.9	54.9	10.0	10.0	10.0
Max	89.9	54.9	118.4	54.7	118.4	54.7	4838	49.7	88.3	52.5	52.5	52.5	52.5	52.5

N = number of trees per ha; dg = quadratic mean diameter; M = Martonne aridity index; sd = standard deviation; Min = minimum value; Max = maximum value; AT = Austria, CAT = Catalonia (Spain), DE = Bavaria (Germany), FR = France, ES = Spain, PL = Poland, All = All countries together.

2.3. Maximum stand density relationship and model parametrization

In a first step, Reineke's MSDR (Reineke, 1933) (Eq. (1)) for Scots pine and European beech were fitted independently to each inventory data, i.e. the NFI or RFI for each country, and to all countries together.

$$N_{\max} = C \cdot d_g^E \quad (1)$$

where N_{\max} is the maximum number of stems per hectare, d_g the quadratic mean diameter and C and E the coefficients which depend on the species.

The values of C and E were obtained by using a non-linear quantile regression of the R package "quantreg" (Koenker, 2013) using tau values of 0.95, 0.975 and 0.99, which were selected following similar studies (Ducey and Knapp, 2010; Vospernik and Sterba, 2015).

In a second step, data were classified according the M, with a value of 5 as class width. Considering a minimum of 30 plots per class, there were 13 classes for pine, with M values varying from 25 to 85, while for beech there were 16 classes with M values from 35 to 110.

MSDRs were then fitted independently for each class and each species by using linear quantile regression with tau 0.95 (higher quantiles were not used because the small number of plots in some classes made the results unstable). For each species a set of C and E coefficients (Eq. (1)) was obtained. These values were plotted against the M values in order to determine whether there were any relationships between them.

Finally, Eq. (1) was generalized by expanding coefficients as a function of the M. Some different options were tested by changing the relationship between the coefficients and the index.

After testing different structures for expanding the coefficients with M, the most appropriate Martonne-dependent models were the following:

$$N_{\max} = (C_0 + C_1 \cdot M) \cdot d_g^{(E_0 + E_1 M)} \quad (2)$$

$$N_{\max} = (C_0 + C_1 \cdot \log(M)) \cdot d_g^{(E_0 + E_1 M)} \quad (3)$$

$$N_{\max} = (C_0 + C_1 \cdot \log(M)) \cdot d_g^{(E_0 + E_1 \log(M))} \quad (4)$$

$$N_{\max} = (C_0 + C_1 \cdot M) \cdot d_g^{(E_0 + E_1 \log(M))} \quad (5)$$

$$N_{\max} = \exp(C_0 + C_1 \cdot M) \cdot d_g^{(E_0 + E_1 M)} \quad (6)$$

$$N_{\max} = \exp(C_0 + C_1 \cdot M) \cdot d_g^{(E_0 + E_1 \log(M))} \quad (7)$$

$$N_{\max} = (C_1 \cdot M) \cdot d_g^{(E_0 + E_1 M)} \quad (8)$$

$$N_{\max} = (C_1 \cdot M) \cdot d_g^{(E_0 + E_1 \log(M))} \quad (9)$$

where log is the natural logarithm, N_{\max} is the number stems per hectare, d_g the quadratic mean diameter, M the Martonne aridity index and C_0 , C_1 , E_0 and E_1 the parameters which depend on the species.

The parameter values in Eqs. (2)–(9) were obtained by using a non-linear quantile regression because it is well adapted for a non-linear framework. As these equations cannot be linearized, the starting values used for initializing C_0 and E_0 were obtained from the basic model (Eq. (1)), while C_1 and E_1 were initialized to 0.

All models were fitted with the nlrq procedure from the R package "quantreg" (R Core Team, 2014) with tau equal to 0.95, 0.975 and 0.99. A level of $p = 0.05$ was used for significance testing of the variables in the model, and Akaike's information criterion

(AIC) and pseudo- R^2 for quantile regression (Koenker and Machado, 1999) were used for comparing results.

These Martonne-dependent models were compared with the basic model obtained by fitting Eq. (1). The best models were selected taking into account the significance of the coefficients and the AIC.

3. Results

The results of the basic MSDR (Eq. (1)) fitted using tau = 0.95, including coefficients, pseudo- R^2 values and maximum stand density indices (SDI_{\max}), i.e. the maximum number of stems per ha for a reference diameter of 25 cm according Eq. (1), obtained for each country and for all countries together, are presented in Table 2 (see results for tau 0.975 and 0.99 in Supplementary Table 1). Table 2 shows a large variation between slopes (E) and intercepts (C) depending on the country. For instance, for quantile 0.95 the slopes varied for pine between -1.494 and -2.226 and for beech between -1.469 and -2.244 . In Fig. 2 the MSDRs for all countries together were represented for pine and beech. In this figure the lines for quantiles 0.95, 0.975 and 0.99 show that the three lines are almost parallel (with slopes around -1.6 for pine and -1.9 for beech) and fit correctly to the data.

Moreover, it should be noted that when comparing the pine and beech maximum SDIs obtained for all countries together for the same quantile, the result was contrary to other authors' findings (Condés et al., 2013; Pretzsch et al., 2015), i.e. the maximum density in beech stands was greater than in pine stands.

Table 2

Coefficients, and their standard errors in parenthesis, of Reineke's maximum density lines (basic model according Eq. (1)) by countries, for the quantile 0.95.

	ndata	C	E	SDI_{\max}	R^2
<i>Pine</i>					
AT	49	190,722 (280,375)	-1.545 (0.473)	1320	0.8237
CAT	1088	154,611 (31,620)	-1.539 (0.071)	1090	0.6876
DE	1596	1,213,554 (627,931)	-2.226 (0.162)	939	0.8554
ES	1412	127,071 (19,765)	-1.494 (0.052)	1038	0.7177
FR	1003	185,631 (67,803)	-1.592 (0.120)	1105	0.7195
PL	2629	210,150 (14,762)	-1.704 (0.024)	871	0.8781
ALL	7777	210,209 (21,311)	-1.670 (0.033)	972	0.7943
<i>Beech</i>					
AT	83	577,162 (428,400)	-1.918 (0.276)	1201	0.8729
CAT	133	110,800 (54,368)	-1.469 (0.168)	980	0.7097
DE	23	1,615,685 (3,975,857)	-2.244 (0.893)	1179	0.7919
ES	916	341,925 (105,765)	-1.850 (0.099)	885	0.8250
FR	828	428,430 (150,740)	-1.831 (0.111)	1182	0.7859
PL	151	254,156 (268,856)	-1.720 (0.308)	1001	0.8218
ALL	2134	486,988 (124,932)	-1.905 (0.081)	1059	0.7924

C and E – Maximum density line coefficients (Eq. (1)); SDI_{\max} – Maximum stand density index, i.e. maximum number of stems per hectare calculated for a reference quadratic mean diameter of 25 cm.; R^2 – pseudo- R^2 for nonlinear quantile regression; AT – Austria, CAT – Catalonia (Spain), DE – Bavaria (Germany), FR – France, ES – Spain, PL – Poland, ALL – All countries together.

Global model using data from all countries together in bold font.

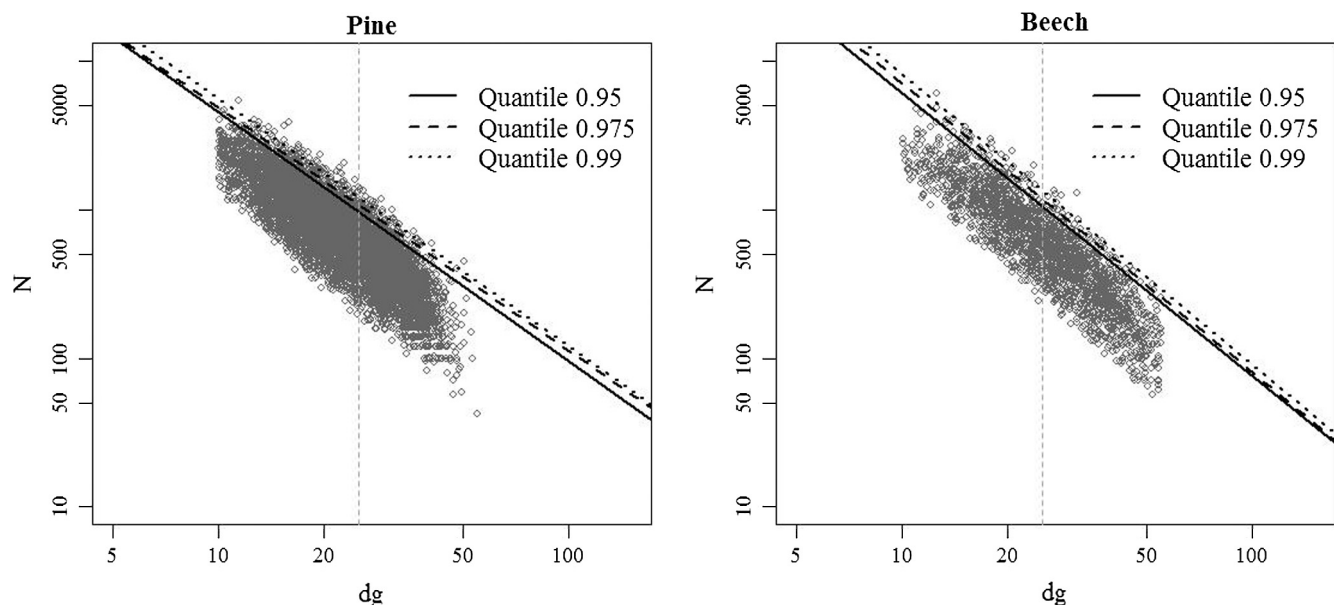


Fig. 2. Maximum stand density relationships according to Eq. (1) for all countries together. N – number of trees per ha; dg – quadratic mean diameter.

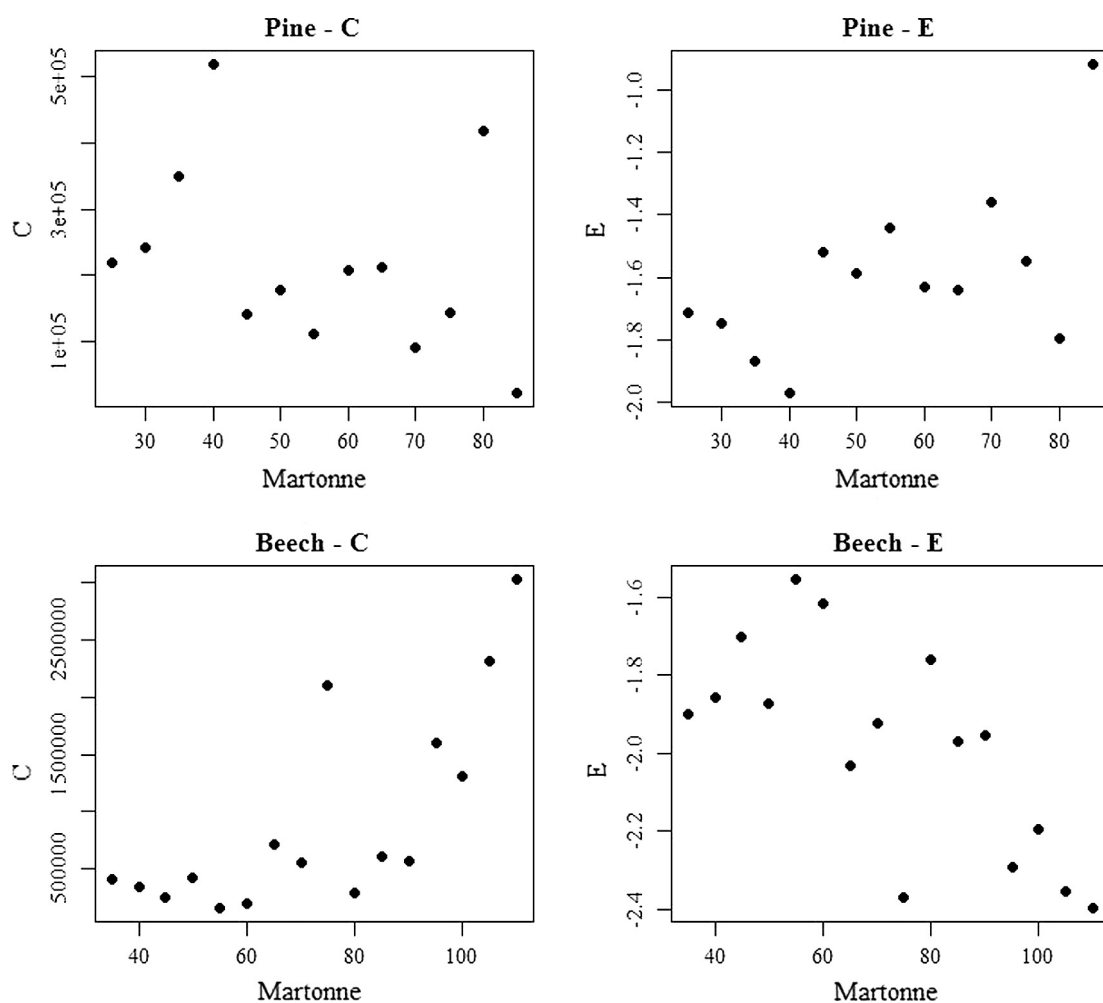


Fig. 3. Relationships between the Reineke's MSDR coefficients (C and E), estimated by linear regression for quantile 0.95, and the Martonne aridity index for pine and beech species.

Table 3

Martonne-dependent MSDR coefficients estimation by nonlinear quantile regression (quantile 0.95) and comparison in terms of Akaike's Information Criterion (AIC) and pseudo R^2 coefficient. Best models in bold font.

Model	C0	C1	E0	E1	AIC	R^2
<i>Pine</i>						
1	210,209 (***)		−1.6704 (***)		118,516	0.7943
2	339,979 (***)	−2764.14 (***)	−1.9662 (***)	0.0065 (***)	117,945	0.8018
3	158,957 (*)	18114.88 (ns)	−1.7528 (***)	0.0012 (.)	117,993	0.8012
4	518,734 (**)	−80063.73 (ns)	−2.4763 (***)	0.2116 (**)	117,961	0.8016
5	256,536 (***)	−775.84 (ns)	−2.2024 (***)	0.1365 (**)	117,970	0.8015
6	12.58 (***)	−0.01 (ns)	−1.8621 (***)	0.0038 (.)	117,992	0.8012
7	12.5 (***)	0 (ns)	−2.2496 (***)	0.1496 (*)	117,969	0.8015
8		6273.34 (***)	−1.5069 (***)	−0.0054 (***)	118,399	0.7959
9		6048.9 (***)	−0.7953 (***)	−0.251 (***)	118,162	0.7990
<i>Beech</i>						
1	486,988 (***)		−1.9047 (***)		33,025	0.7924
2	146,538 (ns)	4850.15 (*)	−1.7518 (***)	−0.0022 (.)	32,854	0.8007
3	−108,391 (ns)	137731.03 (ns)	−1.872 (***)	−0.0004 (ns)	32,872	0.7998
4	−905,891 (.)	332788.4 (*)	−1.2552 (***)	−0.155 (*)	32,859	0.8004
5	−73,802 (ns)	8163.71 (***)	−0.6259 (*)	−0.303 (***)	32,827	0.8020
6	10.9 (***)	0.03 (**)	−1.2716 (***)	−0.0091 (**)	32,805	0.8030
7	12.56 (***)	0.01 (ns)	−1.3962 (.)	−0.1302 (ns)	32,861	0.8004
8		6945.85 (***)	−1.6413 (***)	−0.0036 (***)	32,870	0.7999
9		7208.94 (***)	−0.8536 (***)	−0.2507 (***)	32,828	0.8018

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' 1.

However, when classifying sample plots according to the M values before fitting MSDRs, the slopes and intercepts varied in a different way for each species (Fig. 3). While for pine the intercepts C decreased and the exponents E increased with more humid conditions, for beech the opposite relationships were found, that is, the higher the humidity the steeper the MSDR (more negative exponent) and the higher the intercept. In the case of pine, the higher the humidity the straighter the MSDR and the lower the intercept.

Both species MSDRs were improved by including the M in the model (Table 3). However, for each species some of the model parameters could not be estimated reliably, such that the coefficients were not significantly different from zero ($p > 0.05$). These models, which were poorly constrained, were excluded from further analysis. For pine, the best results for quantile 0.95 were obtained when fitting Eq. (2), improving the pseudo- R^2 from 0.7943 to 0.8018 for that Martonne-dependent model (Table 3). For other quantiles (Supplementary Table 2) the best models can vary, for instance for quantile 0.975 models 4 and 5 provide better results than model 2, although the differences are very slight.

For beech, the best results were obtained when fitting models 6 or 9, while fitting other models resulted in non-significant coefficients. The expansion of the C coefficient by using an exponential relationship with M, i.e. model 6, also agreed with the result presented in Fig. 3. The pseudo- R^2 for this Martonne-dependent model was 0.8030, while for the basic model it was 0.7924, both for quantile 0.95 (Table 3).

Although the differences between Martonne-dependent models were very small, we selected models 2 and 6 for pine and beech respectively due to their lower AIC. According to these models the stand density indices for a reference diameter of 25 cm were not constant but varied with the humidity for each species (Fig. 4).

3.1. Equivalence competition coefficients

Fig. 4 shows that the more humid the conditions the higher the density for both studied species, but the pattern of this variation differs between them which reflects different equivalence competition coefficients between species with humidity. It should also be

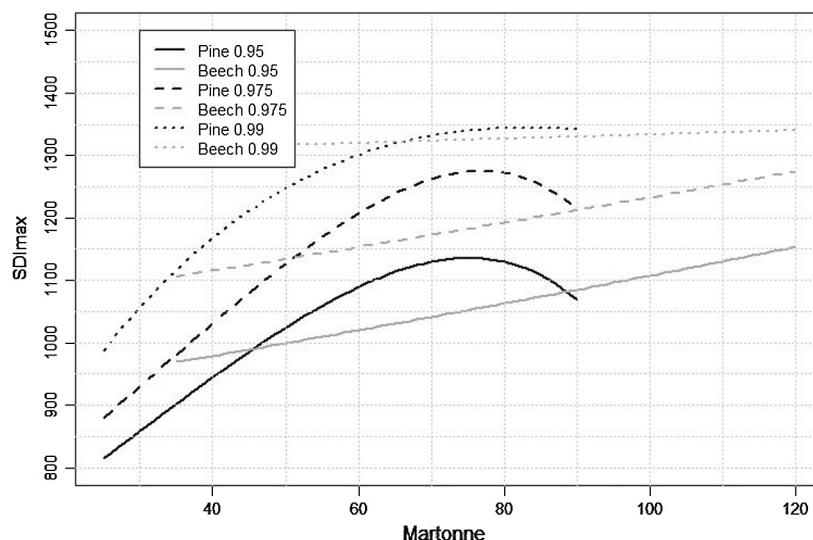


Fig. 4. Variation of maximum stand density index (SDI_{max}), for a reference diameter of 25 cm, with the Martonne aridity index, according to model 2 for Scots pine and 6 for European beech.

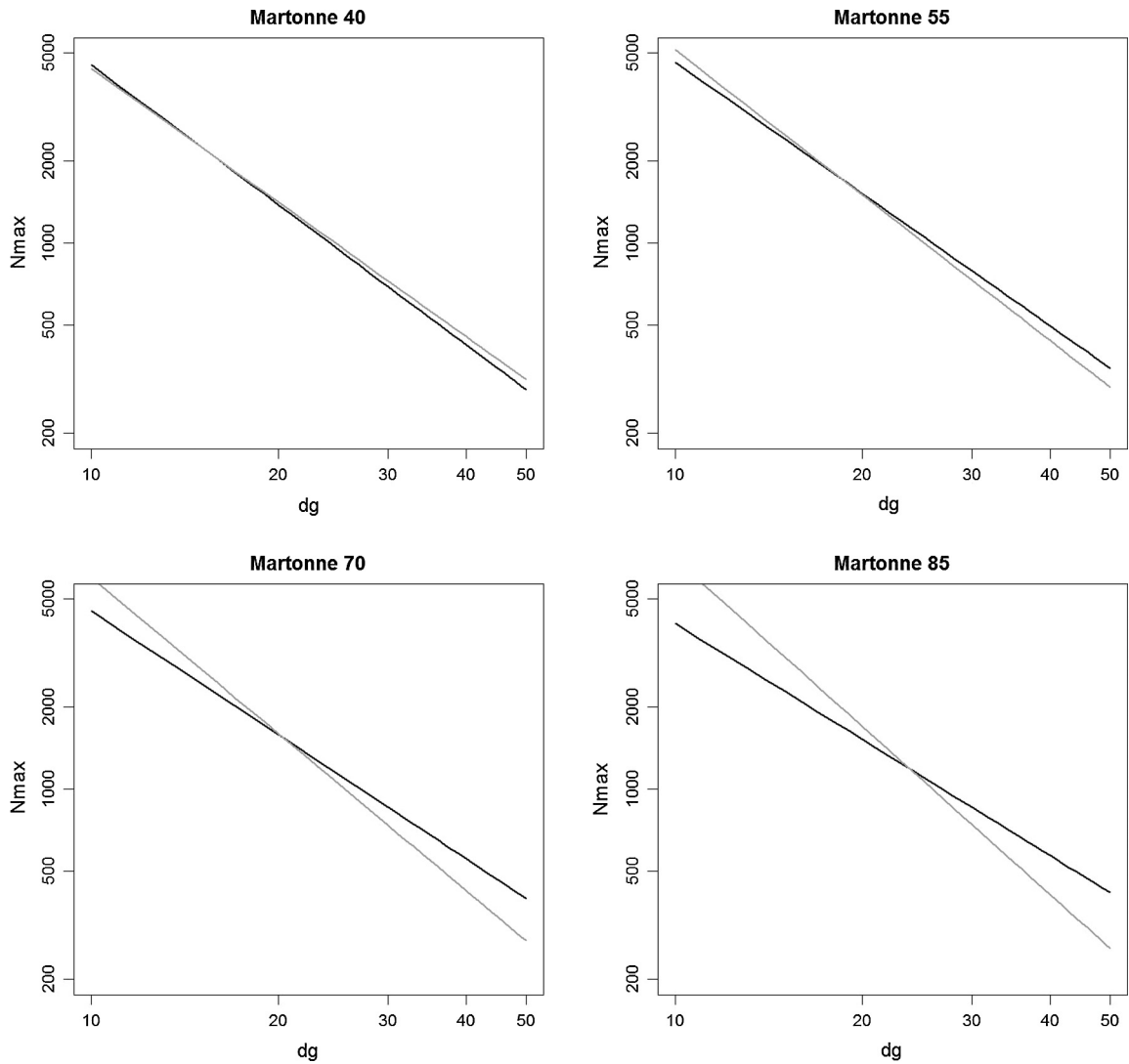


Fig. 5. Variation of the ratio between Scots pine (black) and European beech (grey) MSDR with stage of development for different Martonne values.

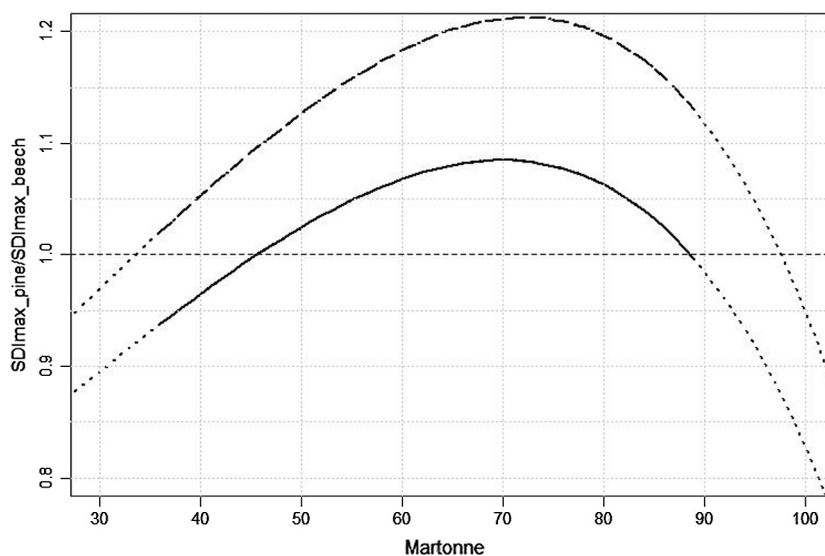


Fig. 6. Variation of the relationship between pine and beech maximum stand density indices, for a reference diameter of 25 cm, with the Martonne aridity index, according to model 2 for pine and 6 for beech, with the same 0.95 quantile for both species (solid line) and with quantiles 0.975 and 0.95 for pine and beech respectively (dashed line). Dotted line for values of Martonne index where one of the species was underrepresented.

highlighted that the competition equivalence coefficients depend not only on climatic conditions but also on the mean tree size (Fig. 5). Thus, when the quadratic mean diameter is taken as a proxy for the stage of development of a stand (Pretzsch, 2005), there was a clear variation in the different potentials of the two species depending on both aridity and stand age. So, while for low humidity conditions ($M = 40$ in Fig. 5) the maximum density of both species was similar along the stage development of a stand, in the more humid sites ($M = 85$ in Fig. 5), the maximum density of pine in younger stands was clearly above that of beech whereas in older stands the relationship was inverse.

It is important to consider that the mean quadratic mean diameter for both species might differ as a specific species trait, and therefore that differences would also depend on M . The solid line in Fig. 6 shows the relationship between the pine and beech maximum densities for the same reference quadratic mean diameter of 25 cm according to the selected models 2 and 6 for pine and beech, estimated with $\tau = 0.95$.

4. Discussion

The MSDR is a very useful concept in forestry. When applying MSDR many studies have used one single line per species for all the conditions at a regional or national scale (Toigo et al., 2015). However, the population boundary lines can vary considerably among sites or regions for a given species (Hynynen, 1993; Río et al., 2001; Pretzsch and Biber, 2005; Charru et al., 2012; Vospernik and Sterba, 2015). Generally, the data range on a small geographical scale may be not large enough to justify a varying MSDR with site conditions. In this study we fitted MSDR models that explain this variability at large scales, providing a climate-dependent species boundary line.

4.1. Methodological considerations

The combination of NFI and RFI data from five European countries provided us with an opportunity to investigate the variation in the MSDR over a large climate range, and to refine the hypotheses of the MSDR concept. M ranged from 26.7 to 89.9 for pine and from 35.0 to 119.7 for beech, for a total of 9911 plots (Table 1). This kind of analysis is considerably strengthened by the inclusion of not only a wide range of climates but also the large number of plots provided by NFI data, which are far superior to that available at national or regional level, particularly where experimental data is used.

However, two kinds of problems arose through the use of NFI data for MSDR study. The first was linked to the nature of NFI protocols. Most of the NFI protocols (Spanish, German, and French) use concentric circles or even angle count sampling (Austria) where trees were measured depending on their diameter. The radius of the Polish plots depended on age and stand structure components. As a result, in all the NFI protocols the estimation of stand level variables such as the stem number or the mean quadratic diameter relied on smaller circles for smaller mean quadratic diameter, leading to higher variability. Therefore, the estimation of maximum value could be biased for smaller quadratic diameter; possibly leading to steeper slopes for MSDR fitted with NFI data in comparison to results obtained using monitored untreated permanent plots. Moreover, old stands, especially on rich sites may be underrepresented due to harvesting. Nevertheless it should be noted that M and the mean quadratic diameters were not correlated variables (correlation of -0.06 for pine, and -0.02 for beech) and therefore, the climate effect found in this study remains, despite this possible bias.

The second kind of problem is associated with differences in protocol between countries. Even if the NFI protocols differ from

one country to another, they all provide unbiased estimations of stem numbers and mean quadratic diameters at stand level. However, the variances of these estimates are not the same, which could lead to confounding factors between climate and protocol. We avoided this risk by discarding plots with extreme mean quadratic diameters and extreme M values, to ensure that each climatic condition can be found in several countries. Some other analyses, such as linear mixed quantile regressions with the country as random factor, were explored with the same aim of correcting, at least partially, the above mentioned differences between NFI protocols, although poor results were obtained.

Several methods exist to assess MSDR (Hann, 2014). In this study, we used quantile regression because it is well adapted for a nonlinear framework (Koenker, 2013). Quantile regression is sensitive to the tau level, which defines the number of plots above the fitted line. For tau values close to 1, the fitting is very sensitive to extreme values, especially for small datasets or if there are several co-variables in the models, as in our case. The choice of the tau value for the quantile regression is arbitrary, especially in the absence of an external reference value for the MSDR (Ducey and Knapp, 2010). One could choose a high tau value to be close to an absolute line that could not be crossed by natural dynamics. On the other hand, mortality usually occurs before reaching the self-thinning boundary. Moreover, NFI data consist of plots much smaller than one hectare, and local density can be higher than that which could be reached with one hectare stands, prompting a drop in the tau value. As a consequence, MSDR provides a basis for stand comparisons, and several tau values may be legitimate as long as they are precisely defined and kept the same for stand comparisons, such as stands in various climatic contexts (as in this article), comparisons between species, or pure versus mixed stands. However, from a methodological perspective, it is better to use the same tau for comparing species (solid line in Fig. 6). In our study, between-species differences in the number of plots used in the analysis (three times larger for pine than for beech) and in density distributions (larger amount of plots with lower basal areas for pine than for beech) suggest that the use of a larger tau for pine than for beech (dashed line in Fig. 6) might be recommendable. However, the main result, concerning the variation of the MSDR with climate, is again stable for the different tau values, even if the form of the best model can differ for a given species (Table 3 and Supplementary Table 2).

4.2. Dependence of MSDR on environmental conditions

A number of authors (e.g. Tang et al., 1995; de Montigny and Nigh, 2007; Poage et al., 2007) support the notion that Reineke's MSDR is independent of site conditions, but this has also been called into question by many authors. At species level, for example, the intercept of the self-thinning boundary has been reported to increase with the site index in different conifer species (Hynynen, 1993; Palahí et al., 2003; Pittman and Turnbull, 2003; Weiskittel et al., 2009) and broadleaves (Weiskittel et al., 2009). Some authors have also found the slope of the boundary line to increase at better sites (Zeide, 1987) and others such as Bi (2001) have even proposed a new formulation of MSDR that explicitly includes site productivity. In our study, we found higher MSDR intercepts and steeper slopes for Scots pine growing in less humid areas. This unexpected result could be explained by differences in site index between the plots with low M values (which interestingly corresponded to Central European regions) and those with higher values (i.e. Southern European regions) (see Table 1). In the latter, the effects of climatic variables on MSDR parameters might be counterbalanced by lower site quality, since Scots pine mainly grows on south-facing slopes of mountainous areas in those regions. In contrast to Scots pine, we found that the intercept and

the slope of the MSDR for beech decrease in sites with low M values (i.e. less humid ones). The use of other drought indices that better describe the water availability for trees might improve these results and must be the object of further studies. Nevertheless, among other environmental factors species genetic variability might also influence on the climate effect on MSDR. Broad range provenance studies have detected intraspecific genetic differences in growth for the two studied species (e.g. Rehfeldt et al., 2002; Alía et al., 2011), showing that there is a climatic adaptive component in this genetic variation. But also, other factors as genetic differences in the abilities of trees (or populations) to compete for resources (Costa e Silva and Kerr, 2013), or the genetic differences in functional traits (Robson et al., 2012) can determine these differences among populations.

The variation of the MSDR with the aridity index is in accordance with the yield level theory. In thinning experiments of Norway spruce, Assmann (1970) found that stands with equal height growth and no thinning at all, could have very different total volume growth. He attributed these growth differences to site factors, such as soil nutrition and humidity and called this second dimension of site quality “yield level”. Sterba (1985, 1987) showed that these differences in volume growth and thus the yield levels can be identified by the maximum stand density index according to Reineke (1933). In our study, we showed that the response of maximum stand density, and consequently the yield level, to aridity sensu Martonne, differs between species, in accordance with yield tables that consider yield levels (Schmidt, 1971; Dittmar et al., 1986; Halaj et al., 1987). However, the pattern between species depends on the stage of development, with higher densities for pine than for beech at younger ages and the opposite at older ages, particularly for more humid sites. This trend agrees with the findings of Pretzsch et al. (2016), who indicated that in the long term, pine-beech mixture might lead to a beech monoculture at more humid sites. In our study, when comparing pine and beech stands with the same quadratic mean diameter of 25 cm, this ratio varies from 0.9 to less than 1.1 (solid line in Fig. 6). However, ratios obtained in other previously published studies tend to be slightly higher, for example 1.14 in Austria (Vospernik and Sterba, 2015), 1.10 in France (Charru et al., 2012), or 1.24 in Spain (Condés et al., 2013). Our results would be closer to those values if different τ values were used to define both species MSDR (dashed line in Fig. 6).

4.3. Interpretation of coefficients and mechanistic considerations

The difference between the species boundary lines (Fig. 2) and the SDI_{max} as a reflection of the population boundary lines after accounting for the M (Fig. 4), illustrates the challenges for inference that arise when environment is not taken into account (Hann, 2014). Table 2 shows that, when comparing the results on a large scale, i.e. for all countries together, the relative position of species' SDI_{max} is opposite to other authors findings (Condés et al., 2013; Pretzsch et al., 2015). However, Fig. 4 reveals that when environment is considered, the maximum density of pine is greater than that of beech across most of the climate range where both species can be found. This is consistent with what would be expected using, for example, species-specific wood gravity as a functional trait to describe the competitive ability of each species (Dean and Baldwin, 1996; Ducey and Knapp, 2010). Since *Fagus sylvatica* has a higher wood specific gravity than *Pinus sylvestris*, in terms of stem mechanics it should be capable of fully occupying a site with a smaller average stem diameter for a given density of stems. For the 0.95 quantile models, which reflect the most stable estimates across the full environmental gradient, this relationship is only reversed at values of M below about 45. At

those levels of aridity, changes in overall stem form as well as species plasticity in hydraulic structure are likely to outweigh the stem mechanical considerations which may dominate in more mesic sites.

While the MSDR slope for pine remains relatively close to Reineke's (1933) canonical value of -1.6 , it deviates quite strongly from that value for beech, reaching a value less than -2.0 even in moderately humid environments. It can be challenging to interpret such values if we believe that the MSDR represents an asymptotic self-thinning trajectory, because they run counter to conventional thinking on forest growth and yield. Since $N_{max} = Cd_g^E$ (Eq. (1)), and stand basal area $G = N\pi/4d_g^2$, we have $G_{max} = C\pi/4d_g^{E+2}$. Slope values (E) greater than -2 imply an increase in maximum basal area with increasing d_g . This is consistent with many normal yield tables, as well as with theories of forest growth based on the pipe model (Shinozaki et al., 1964; Mäkelä and Valentine, 2006). In principle, if the total biomass of foliage (or of physiologically active roots) approaches a constant dictated by the resource limitations of a given site and that biomass is proportional to the cross-sectional area of sapwood (and thus to total stand basal area), then the conventional result should hold across all climates (although the exponent E could vary with changes in crown allometry, hydraulic architecture, or other climate-related factors). However, when $E < -2$, the maximum basal area declines with increasing d_g . This could only occur endogenously if there is a concomitant change in the functional allometry of the trees (e.g. a substantial change in hydraulic architecture), a decline in resource availability with increasing tree size, and/or a decline in the efficiency of use of a limiting resource with increasing tree size. In the case of beech, where E declines past -2 as humidity (expressed using M) increases, this would require such size-dependent changes to be more pronounced in mesic than xeric sites.

Such a result could be an artifact of unobserved variables, or of assumptions in fitting the model that change in their applicability across climate (or in ways that turn out to be correlated with climate because of political geography) or of NFI protocol differences between countries. The assertion that a constant quantile reflects similar levels of stand density, across a range of d_g , rests on the assumption that unobserved factors that also influence the MSDR are distributed more or less independently of d_g . A similar challenge has long been recognized in the literature on site index (Spurr, 1955; Curtis, 1964), where differences in the distribution of site quality with stand age due to land use history or harvesting behavior have been shown to affect site index models, although this has not been widely studied in the context of stand density. Alternatively, the assumption that the maximum or near-maximum observed density actually reflects self-thinning or biological potential may not always hold. For example, if the intensity of tending varies, such that some stands with small d_g are in maximum density conditions, but others nearby have been thinned in ways that reduce density below the maximum, then estimates of E could be artificially depressed. Again, these factors might only explain the results we found for beech if they had varied in a manner associated (through cause or coincidence) with variation in humidity. Ultimately, disentangling the abovementioned hypotheses about the role of: (i) endogenous change in allometry, resource availability, or resource efficiency; (ii) the influence of unobserved site factors and (iii) the influence of management differences, is probably impossible using NFI data alone, and might require synthesis across multiple types and sources of data. However, a key first step is to recognize that the MSDR and its coefficients vary with climate and perhaps with other factors as indicated in this study, and to identify the overall pattern.

4.4. Implications for analysing mixed effects and designing silvicultural guidelines

A good estimation of potential densities per species is essential to the discussion of growth and the effects of mixing on mixed species stands. To compare density and growth in mixed and pure stands, “reference stands” are established in a way that allows the expected density or growth of mixed stands without mixing effects (competition, facilitation) to be calculated as a function of potential density measures in pure stands (Río and Sterba, 2009; Condés et al., 2013). Thus, the species proportion and relative density depend directly on equivalence competition coefficients (Río et al., 2016). The species-specific MSDRs from large data sets are an excellent and more objective estimator of potential density if their dependence on site variables is sufficiently considered. The dependence of the MSDR on M, as determined from the large European dataset, allows us to better describe the potential densities of pine and beech whereas not considering the aridity of the site would lead to erroneous estimations of the relative density of the stand, in turn affecting the estimations of under or overyielding either for each species or for the total yield in the mixed stand.

Determining maximum stocking density is crucial for both silviculture practices and forest modelling. Clear information regarding size-density relationships under given climatic conditions can contribute significantly to the development of regionally appropriate and more precise silvicultural guidelines for shaping stand density management diagrams (Castedo-Dorado et al., 2009; Burkhart, 2013). The results obtained in this study can help to design thinning regimes in pine and beech stands since they provide the site adapted reference values for maximum densities. For example, Figs. 3 and 6 indicate that under highly arid or humid climatic conditions, more beech than pine trees can be retained in a fully occupied stand, due to the higher intraspecific competition of beech. In contrast, under temperate climatic conditions more pine than beech trees can grow within the same stand. The results concerning the influence of climate on the maximum stand density relationship in pine and beech stands, and thus their different yield levels, should also be taken into account in constructing yield tables (Assmann and Franz, 1965; Assmann, 1970). The self-thinning rule has already been extensively employed for forest management purposes as a reference line in stand density management diagrams and stocking guides (Drew and Flewelling, 1979; Newton, 1997; Halligan and Nyland, 1999; Spathelf and Schneider, 2000), yield tables (Mesfin and Sterba, 1996; Eckmüllner and Vospernik, 2005; Lhotka and Loewenstein, 2008) and individual tree growth models, where the actual stem numbers are compared to the maximum theoretical number given by the self-thinning line (Mäkelä et al., 2000; Hansen and Nagel, 2014). In contrast to previous studies, here we shed light on an additional aspect which is a very important modulator of maximal stocking density i.e. climatic conditions, which might have important implications in the framework of climate change. Additionally, our results regarding the potential stocking level can be used in (1) formulating tree planting densities for pine and beech, which should reflect the “carrying capacity” of a site and approach the stockability of a planting site, defined as the maximum number of trees that can grow to a given size at a site with specific conditions (DeBell et al., 1989; Harms et al., 1994); (2) avoidance of stagnation in dense natural regeneration which can be prone to insect and fungus outbreaks for example; (3) maintenance of optimal stand stability, i.e. a balanced height to diameter ratio (slenderness coefficient), which, if too high, can lead to damage from wind and snow; (4) production of merchantable timber volume, which depends, to a large extent on the density of a stand (Powell, 1999).

5. Conclusions

Common MSDR for a given species on a large scale are not currently available. However, the use of correct species-specific MSDRs is critical when comparisons between current and maximum stand densities are required, when silvicultural responses must be prioritized among stands of a single species that grows across a wide range of environments, or even when studying mixed effects, because the equivalence competition coefficient between species depends on them.

This paper showed that the MSDRs for pure Scots pine and European beech at large scales depends on climatic variables. The fitted climate-dependent boundary lines for these species throughout Europe indicate that the variation of MSDR with climate is species-specific.

The equivalence competition coefficient for a reference quadratic mean diameter of 25 cm, i.e. the ratio between maximum densities of pine and beech, increases with humidity, reaching a maximum and rapidly decreasing from it. However, the competition equivalence coefficients depend not only on climatic conditions but also on the stage of development of the species. The use of the climate-dependent MSDR allows us to better describe the potential densities of pine and beech whereas not considering the site humidity would lead to erroneous estimation of the stand stocking degrees.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.10.059>.

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