# Maximum stand density strongly depends on species-specific wood stability, shade and drought tolerance

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The abundance of stems in crowded populations and the subsequent self-thinning is a key issue in forest stand dynamics. However, the mechanisms that control self-thinning are challenging to model. Although some attempts to include climate and structural traits like specific gravity (SG) are promising, they remain confined to North American species. In this study we aimed to disentangle how SG along with two major abiotic stress tolerances, i.e. shade- and drought-tolerance, contribute to the maximum density of a forest stand across a climatic gradient in Europe, and thus test the validity of the species-specific trait control over

stand density. We propose a modelling approach that incorporates the tolerance to drought and shade in the determination of maximum relative stocking. Here, relative stocking refers to the degree of tree crowding in forest ecosystems. A relative stocking base model where specific wood density is inversely related to stand density is modified, adding normalized indices of drought and shade stress tolerance. We used available species tolerance rankings modulated by stress intensity to analyze the effects of abiotic stress polytolerance or trade-offs in the study area which represent an environmental gradient from Alpine to Mediterranean climate in northern Spain. Results indicated that the role of drought tolerance in controlling maximum stand density is stronger in warmer sites. The simultaneous tolerance to shade and drought results in less carrying capacity of sites. In those sites where there is no water limitation but minimum temperature is very low the tolerance to bending stress (i.e. specific gravity) explains better the maximum tree occupancy.

**Introduction**

Forest stand density is a key variable in forestry and ecology. Understanding the reasons why tree species occupy an area and the maximum capacity of each site to harbor a certain number of individuals is at the core of management decisions. Early silvicultural studies highlighted the concept that stand density and its control allows managers to keep production within optimum levels to compensate the growth trade-off between stand- and tree-level (Assmann, 1971; Langsaeter, 1941). Long (1985) summarized this hypothesis establishing the density limits between the thresholds of lower full site occupancy and the onset of self-thinning. These limits are based on the maximum stand density of a site that represents the maximum degree of site occupancy (Dean and Baldwin, 1996). The determination of maximum density has largely been explored in terms of maximum size-density relationships (MSDR). Most forestry studies explore MSDR using Reineke's equation (Reineke, 1933) and the associated Stand Density Index (SDI) that relates the number of stems as a function of the size of the trees in relation to a fixed diameter, usually 25 cm (Pretzsch and Biber 2005). Similarly, ecological studies have dealt with the -3/2 self-thinning law postulated by Yoda et al. (1963) that relates the individual mean volume with the number of individuals. Both relationships in their original formulation are based on the assumption that there is a limit in the relationship between size and density and they are equivalent if tree volume is proportional to quadratic mean diameter (Burkhart and Tomé, 2012).

Maximum forest stand density represents an upper limit to the occupancy of a site, and growth is only possible after the death of some individuals. This upper limit on potential site occupancy has been considered to be species- and site-specific by several authors using different variables to characterize the stand. Condés et al. (2017) used de Martonne's aridity index (de Martonne, 1926) for Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) whereas Zhang et al. (2013) included site index to model MSDR for ponderosa pine (*Pinus ponderosa*). The models are fitted for specific species compositions and the results cannot be applied to different compositions. Thus, while potentially useful for well-defined management situations, the ecological inferences from such models remain rather limited.

The simultaneous representation of density boundary lines across many different species, growing in both pure and mixed stands and in different environments is still seldom explored. Site index was also

used in conjunction with other stand-specific attributes like site index, climate, stand purity and origin to fit a MSDR for different forest populations and communities of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and red alder (*Alnus rubra* Bong.) (Weiskittel et al. 2009). Similarly, site quality and species composition were included in modelling maximum density of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss.) stands (Reyes-Hernandez et al., 2013).

Another approach is that based on species-specific traits like specific wood gravity, SG (Ducey and Knapp, 2010; Woodall et al., 2005) or a combination of two traits, like SG and shade tolerance (ST) modulated by climate (Ducey et al., 2017). The hypothesis behind the use of species-specific traits to predict maximum density is based on stress tolerance. Specific wood density is associated with tolerance to bending stress, as developed by Dean and Baldwin (1996) who first postulated that species with light wood would need more stems to support the same foliage mass per unit area than species with harder wood. The inverse relationship between maximum stand density, defined as Reineke's stand density and SG was presented by Woodall et al. (2005) whose relationship can be applied to mixtures as long as specific gravity is known for all component species. Ducey and Knapp (2010) combined Woodall et al's (2005) approach with the summation method to apply the additive stand density index (ASDI) developed by Long and Daniel (1990) in heterogeneous forests along with the Curtis' (1971) modified version of the tree area ratio (Chisman and Schumacher, 1940). The resulting model predicts the relative stocking of a stand based on the specific gravity of tree species. Recently, Ducey et al (2017) added tolerance to low light environments in addition to bending stress. Their results showed how climate variables modulated stress tolerance and provided the improvement to a more mechanistic explanation of site occupancy.

Shade tolerance is a key mechanism shaping forest communities (Valladares and Niinemets, 2008) and it has been used to estimate maximum stand density (Ducey et al., 2017). Other abiotic stresses might be more important, however, in other climatic regions like the Mediterranean where drought events are more harmful than low light levels. Thus, we must test the idea that a single or two-trait approach may be insufficient to characterize maximum density and raise the issue of dealing with polytolerance, i.e. the ability of a species to simultaneously tolerate different abiotic stressors.

In this paper we aimed to identify which trait contributes more to the maximum density of a forest stand, and if the relative contribution of two major types of abiotic stress tolerance, i.e. shade- and drought-tolerance, changes across a climatic gradient. Our working hypotheses are:

1. Mechanical properties, like the wood specific gravity, have an inverse relationship with stocking of forest stands across a climatic gradient.

2. Shade-tolerance value, as modulated by cold temperature, affects maximum density inversely: the more shade tolerant the species and colder the site the less number of individuals needed to occupy the stand.

3. Drought-tolerance is more important in drought-prone areas, like in Mediterranean areas, where fewer individuals are needed to fully occupy the stand due to site conditions.

**Methods**

*Study area, stand and climate data*

The study is carried out in a transition zone covering Mediterranean, Atlantic, and Alpine climate in Navarra province, northern Spain (Fig. 1). The mean annual temperature is 10.5 ºC, ranging from 4.3 to 14.2 ºC, and annual rainfall ranges from 373 to 2629 mm, averaging 1378 mm (Gonzalo, 2010). Stand information comprising species composition, number of individuals by unit area (N, stems ha$^{-1}$), and quadratic mean diameter (dg, cm) were extracted from the Third Spanish National Forest Inventory (NFI) available at www.mapama.org. Each NFI plot consists of four concentric subplots with radius 5, 10, 15, and 25 m where trees with DBH equal to or over 7.5, 12.5, 22.5 and 42.5 cm were measured respectively. To get the number of stems by unit area an expansion factor is applied for each subplot, i.e., for the 10 m subplot each tree represents $10000/(\pi \times 10^2)$ individuals. We removed from the database plots in fertilized or irrigated *Populus x canadensis* plantations to make sure that intensive management did not affect the intensity of abiotic stress. We retained 2803 plots in four climatic regions built upon Allué-Andrade's (1990) phytoclimatic classification: Mediterranean, Mountainous, Maritime and Transition (see Supplementary Table 1 for description of climatic regions). A species-specific wood gravity for each species were retrieved from Gutiérrez and Plaza (1967) whereas shade- and drought-tolerance (ST and DT respectively) was obtained from Niinemets and Valladares (2006). For those species without a tolerance value we applied the average value for the genus. Table 1 shows main stand-level properties and stress tolerance range by climatic gradient. The dataset comprises 66 species ranging from temperate to Mediterranean-type forests. The most abundant species are European beech (*Fagus sylvatica* L), Scots pine (*Pinus sylvestris* L.), Holm oak (*Quercus ilex* L.), oak (*Q. robur* and *Q. petraea*) and quejigo oak (*Quercus faginea* Lam.) (Supplementary Table 2 describes the main dendrometric characteristic of each species growing in the study region).

*Model structure*

The hypothesis was tested with a modified version of the model structure developed by Ducey et al (2017). This model is based on the tree area ratio proposed by Chisman and Schumacher (1940) who defined the area occupied by the crown projection, i.e. the growing space requirement of a tree, as a quadratic function of stem diameter (eq. 1)

$$A_i = c_0 + c_1 DBH_i + c_2 DBH_i^2 \tag{1}$$

Where $A_i$ is the available growing space and $DBH_i$ is diameter at breast height of tree $i$, $c_0$-$c_2$ are parameters to be estimated.

Summing all individual growing spaces results in the Tree Area Ratio (TAR, eq. 2) which represents the growing space occupied by trees in a stand.

$$TAR = c_0 N + c_1 \sum_i DBH_i + c_2 \sum_i DBH_i^2 \qquad (2)$$

Although Chisman and Schumacher (1940) identified TAR with the potential crown space occupancy of a stand, other researchers have extended the interpretation to reflect a more abstract resource-based growing space requirement (*sensu* Oliver and Larson, 1996). Setting TAR to 1 and estimating parameters $c_0, c_1$ and $c_2$ with data from fully stocked stands, equation 2 can be used to predict the relative density of new stands. Ducey and Knapp (2010) took this approach but changed the growing space requirement to a function of the additive stand density index (Long and Daniel, 1990) combined with wood specific gravity following Woodall et al. (2005). More recently Ducey et al. (2017) modified the approach to accommodate covariates such as climate and functional traits like shade tolerance, e.g.

$$( 3 )$$

$$A_i = \left( b_0 + \sum_{j=1}^{T} b_j T_{ij} \right) \left( \frac{DBH_i}{25} \right)^{1.6}$$

where $A_i$ is the growing space of tree *i*, $T_{ij}$ is any plant trait of tree *i* (such as specific gravity or shade tolerance), $DBH_i$ is diameter at breast height of tree *i* and $b_0$ through $b_j$ are parameters to be estimated. Summing over individual trees provides a relative density similar to TAR (eq. 4)

$$RD = b_0 \sum_{i=1}^{n} \left( \frac{DBH_i}{25} \right)^{1.6} + \sum_{j=1}^{T} b_j T_{ij} \sum_{i=1}^{n} \left( \frac{DBH_i}{25} \right)^{1.6} \qquad (4)$$

Ducey et al. (2017) further extended the model to include climate variables as well as species functional traits. An appropriate fitting procedure is needed to estimate the parameters in Equation 4. If, as in Chisman and Schumacher (1940), RD were set to equal 1 for all stands, and then least-squares regression were used to estimate the parameters, there would be an implicit assumption that the stands included in the data had an average stocking level corresponding to full stocking. Thus, it would be necessary to pre-screen the data to select only fully stocked stands. However, other fitting approaches do not need such pre-screening, as illustrated by Ducey and Knapp (2010) and Ducey et al. (2017) (see below in the Fitting procedure section).

*Stress tolerance and stress intensity*

Testing our hypothesis needs comparable coefficients and a reasonable way to modulate the stress tolerance as a function of the stress intensity. Our modification of Ducey et al.'s (2017) model includes a normalization of Niinemets and Valladares (2006) shade- and drought-tolerance rankings to make them comparable to the specific gravity values found in the dataset. We scaled DT and ST ranked values to a maximum of 1 by dividing the score value by the maximum value found in the dataset, renaming them as *nDT* and *nST* respectively. In so doing, we can assess the relative contribution of each tolerance to the maximum carrying capacity of the stand as all three traits have a maximum value of 1 (e.g. maximum SG is 1 g cm$^{-3}$ for holm oak, *Quercus ilex* L.).

Instead of using continuous climatic variables to assess the climate effect on stress tolerance we built multipliers which reduced the normalized stress tolerance in harsh conditions, hereafter referred as stress tolerance modulators, allowing us to order species tolerance from 0 (no stress and the tolerance

value does not influence the maximum density) to the maximum tolerance, i.e. the maximum normalized tolerance value *nDT* or *nST*.

The contribution of DT to predict the maximum density is regulated by a multiplier that maximizes the tolerance from lower to higher drought stress levels

$$dI = \frac{k}{\max(k)} \qquad (5)$$

where $dI$ is the drought intensity stress modulator of *nDT*, $k$ is the drought intensity, measured for each plot as the area confined between the temperature and precipitation curves in a Walter-Lieth's climodiagram, max($k$) is the maximum drought intensity for the study area, this modulator ranges from 0, i.e. sites without drought period where the contribution of drought tolerance is negligible ($k$=0), to 1, i.e. sites with maximum drought intensity ($k$ = max($k$)).

Analogously, shade tolerance is modulated by minimum temperature, which is correlated with the length of the growing season (Ducey et al., 2017; Laanisto and Niinemets, 2015)

$$cI = 1 - \frac{Tmin - minTmin}{maxTmin - minTmin} \qquad (6)$$

Where $cI$ is the cold-stress modulator of *nST*, *Tmin* is the minimum temperature of the coldest month, *minTmin* and *maxTmin* are the minimum and the maximum of the minimum temperature of the coldest month respectively, this modulator ranges from 1 (minimum *minT*, associated to cold sites where shade tolerance is maximum for the species) to 0 (warmer sites).

Although specific gravity might vary, among others, with altitude and dry conditions (Chave et al., 2006; Pompa-García and Venegas-González, 2016) or exposure to stressors, like flooding (Lawson et al., 2015)  we assume, according to our working hypothesis 1, that bending stress is always occurring across the species distribution as it determines the maximum amount of foliage that a stand can support (Dean and Baldwin, 1996). In addition, there is no significant relationship between specific gravity and site aridity measured by de Martonne Index in the study area (see Supplementary Figure 1).

The trade-offs and synergies of stress tolerance modulators were analyzed with dispersion plots of two contrasting broadleaves (*Fagus sylvatica* L. and *Quercus ilex* L.) and conifers (*Pinus sylvestris* L. and *P. halepensis* Mill.). A species with great variability in both multipliers, i.e. large dispersion in both axes, would indicate a large suitable habitat where there could be a shift in the relative importance of shade- or drought-tolerance and even polytolerance, whereas low variability in either of both multipliers would indicate absence of polytolerance and that stress tolerance to a single stressor is more important for the species to occupy the site.

*Hypothesis testing*

We started the fitting procedure from the base model with SG as a single variable as in Ducey and Knapp (2010), eq. 4 (hypothesis 1), and adding one more normalized stress tolerance alternatively

($nST$ and $nDT$) multiplied by its corresponding stress modulator ($cI$ and $dI$ respectively). The subsequent models used for the rest of hypotheses are as follows:

Testing hypothesis 2 expand equation 4 with a term including the tolerance to shade

$$RD = a_0 \sum_i EF_i \left(\frac{DBH_i}{25}\right)^{1.6} + a_1 \sum_i EF_i SG_i \left(\frac{DBH_i}{25}\right)^{1.6}$$
$$+ \; a_2 \sum_i EF_i \cdot (cI \cdot nST_i) \cdot \left(\frac{DBH_i}{25}\right)^{1.6} \tag{7}$$

Where $RD$ is relative density, $EF_i$ is the expansion factor applicable to each individual according to its position in the concentric plot design of the NFI, $DBH_i$ is the diameter of individual, $SG_i$ is the species-specific wood gravity for each individual, $nST_i$ is the species-specific normalized shade tolerance for each individual, $cI$ is the cold temperature stress modulator, and $a_0$, $a_1$ and $a_2$ are parameters to be estimated.

Hypothesis 3 was tested by adding a term for drought tolerance to equation 4

$$RD = a_0 \sum_i EF_i \left(\frac{DBH_i}{25}\right)^{1.6} + a_1 \sum_i EF_i SG_i \left(\frac{DBH_i}{25}\right)^{1.6}$$
$$+ \; a_3 \sum_i EF_i \cdot (dI \cdot nDT_i) \left(\frac{DBH_i}{25}\right)^{1.6} \tag{8}$$

where $D_i$ is the drought stress modulator, $nDT_i$ is the species-specific normalized drought tolerance and the rest of symbols are as in equation 7.

Alternatively, we tested the simultaneous relative importance of tolerance to all stressors

$$RD = a_0 \sum_i EF_i \left(\frac{DBH_i}{25}\right)^{1.6} + a_1 \sum_i EF_i SG_i \left(\frac{DBH_i}{25}\right)^{1.6}$$
$$+ \; a_2 \sum_i EF_i \cdot (cI \cdot nST_i) \cdot \left(\frac{DBH_i}{25}\right)^{1.6} + a_3 \sum_i EF_i \cdot (dI \cdot nDT_i) \left(\frac{DBH_i}{25}\right)^{1.6} \tag{9}$$

where symbols were previously defined.

Model specification described in eq. 5 and eq. 6 does not allow for simultaneous drought- and shade-tolerance values in neither cold nor warm sites (i.e. polytolerance). We also fitted the complementary value in the cold index ($1-cI$) to allow for testing shade-drought tolerance in warmer sites (eq. 10)

$$RD = a_0 \sum_i EF_i \left(\frac{DBH_i}{25}\right)^{1.6} + a_1 \sum_i EF_i SG_i \left(\frac{DBH_i}{25}\right)^{1.6}$$

$$+ a_2 \sum_i EF_i \cdot ((1 - cI) \cdot nST_i) \cdot \left(\frac{DBH_i}{25}\right)^{1.6} + a_3 \sum_i EF_i \cdot (dI \cdot nDT_i) \left(\frac{DBH_i}{25}\right)^{1.6}$$

(10)

where all symbols were previously defined.

*Fitting procedure*

Traditional fitting procedures of maximum stocking need selection of plots at full stocking levels. However, screening data from national forest inventory plots is not efficient and rather subjective as the stocking level for RD = 1 (full site occupancy) is not truly known and there is evidence that plots in the data set do not correspond to RD=1 (Ducey and Knapp, 2010), especially in large areas where environmental conditions and species traits can vary affecting the degree of occupancy. Plantations can be an exception and consequently they were removed from the data set, representing less than 1% of the original dataset.

Fitting models derived from equation 4 by ordinary least squares would require an independent and normal error term, and the regression procedure would select coefficients such that the mean value of the plots included in the dataset corresponded to RD=1. However, our purpose here is to find a combination of coefficients such that the calculated RD value would fall below RD=1 for nearly all plots; in other words, we seek a maximum density relationship at RD=1 that would fall above all observations if the observations were free of measurement errors and other anomalies. To avoid subjective pre-screening procedures when using National Forest Inventory datasets, a default value of RD=1 to all plots is hypothesized, and the models (equations 7 through 10) are fit by quantile regression instead of ordinary least squares. The hypothetical assignment of RD=1 to all plots does not mean that the actual density of all plots is at the maximum. Instead, it is giving a reference value of RD that should be consistent across all plots (no matter what their tree list, species traits, and climate might be). In such case, quantile regression allows the actual density of individual plots to vary freely, but it does enforce a model fit so that the reference RD=1 actually falls at an extreme quantile of the distribution of RD values for individual plots, rather than the mean. By incorporating both species traits and climate variables and predictors, quantile regression ensures that the reference RD=1, taken as a conditional quantile, remains consistently near the upper end of the distribution.

Quantile regression fits a linear model through any value in data as long as the modeler selects a quantile. A quantile is a proportion, $q \in [0,1]$ splitting the data into two proportions where the $q$ observations are below the regression line and the 1-$q$ are above. Maximum density needs a high quantile in order to assure that plots are at maximum density when on the modelled line; occasional observations may fall above the line due to measurement errors or unusual spatial configurations of trees relative to the plot boundaries. We tested four $q$ values leaving 0.5%, 1%, 2.5% and 5% of observations above the maximum density boundary, i.e. we fitted quantiles 0.995, 0.99, 0.975 and 0.95. By setting RD = 1 to all plots and using the quantile regression we are removing all subjectivity associated to plot selection.

Quantile regression has been successfully applied to model maximum boundary lines (Ducey et al., 2017; Ducey and Knapp, 2010; Vospernik and Sterba, 2014; Zhang et al., 2005). Schwarz's Bayesian Information Criteria (BIC) within each quantile was used to assess fitting performance

$$BIC = -2 \cdot \ln(L) - k \cdot \ln(n) \tag{11}$$

where $L$ is the log-likelihood of the data, $k$ is the number of parameters and $n$ the number of observations. The lower BIC the better the fit. The significance level for parameter estimation was set to 0.05. All models were fitted using *quantreg* package of R (Koenker, 2016; R Core Team, 2016).

*Evaluation of maximum SDI for pure and mixed stands*

Maximum density predictions were evaluated graphically across environmental stress gradients (cold temperature and drought) between and within functional groups and species composition (broadleaves vs. conifers and pure vs. mixed-species stands).

The maximum stand density relationship for two important commercial species, Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.), has been previously assessed in the study area by Condés et al. (2017, 2013). Their maximum SDI was used as benchmark against to discuss our model's output. In order to contrast results against climatic regions we also included comparisons of two Mediterranean species Aleppo pine (*Pinus halepensis* Mill.) and Holm oak (*Quercus ilex* L.) Additionally, we compared the SDI predicted by our model with information of SDI retrieved in the literature for species also found in our database: Pedunculate and Sessile oak (*Quercus robur* and *Quercus petraea)*, black pine (*Pinus nigra* Arn.*)* and Silver fir (A*bies alba* L.) using values published by Pretzsch and Biber (2005) and Vospernik and Sterba (2014).

**Results**

*Relationship and variability between normalized stress tolerance values.*

Simultaneous variation in tolerance to drought and cold would indicate that a species or group of species can be found in a wider environmental range. Differences in polytolerance to shade and drought were detected by functional groups (Figure 2a and 2b). Plots of broadleaves growing in pure and mixed stands showed the highest variability for simultaneous normalized drought- and shade-tolerance whereas conifers did not show polytolerance either in pure or in mixed stands.

A graphical analysis of stress modulators for two contrasting species per functional group showed that Scots pine and European beech are located mostly on drought free sites but with a large variability of minimum temperatures indicating that both species are not drought tolerant, whereas Holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.) can be found over both a large range of drought intensity values and minimum temperature range (Figures 3a and 3b).

*Best model selection*

SG as the only explanatory variable (Table 2) was significant at all quantiles (eq. 4, hypothesis 1 accepted) leading to an implied maximum density for Scots pine ranging from 1427 stems ha$^{-1}$ at quantile 0.995 to 1121 stems ha$^{-1}$ at quantile 0.95. European beech showed a maximum density between 1233 stems ha$^{-1}$ and 945 stems ha$^{-1}$ for the same quantiles respectively. The addition of shade

tolerance alone led to non-significant parameters at 0.05 significant level (eq. 7, hypothesis 2 rejected), whereas drought tolerance alone led to significant models at all quantiles (eq. 8, hypothesis 3 accepted). The full model with ST acting in cold sites and DT in warm sites (eq. 9) led to non-significant parameters for ST at all quantiles. The best fitted model in terms of BIC includes both normalized stress tolerance values modulated by temperature and drought intensity in warmer sites (eq. 10). This model at quantile 0.975 will be used for further SDI predictions as it represents the best fitted upper boundary line.

According to the best model, the relative contribution of shade and drought tolerance to explain the maximum density for a given species increases in warm sites. Specific wood gravity and its relation to bending stress contributes more to explain maximum density in colder sites.

*Predicted maximum SDI values*

Differences were found in maximum density between phylogenetic groups. Gymnosperms showed higher maximum number of stems per unit area at a given diameter than angiosperms. Within each phylogenetic group drought tolerant species had lower density than drought intolerant species whereas shade intolerant species had higher density. The maximum density is reduced across the environmental stress gradient with the abiotic stress factor changing from the south where drought is more intense to north, where cold temperatures is the limiting factor. The maximum SDI for Scots pine ranges from 1244 to 1416 stems ha$^{-1}$, whereas European beech maximum density ranged from 826 to 1191 stems ha$^{-1}$ (Figure 4a). Drought tolerant species needed fewer stems to full occupy the stand. Aleppo pine ranged from 473 to 1225 stems ha$^{-1}$ and Holm oak ranged from 725 to 946 stems ha$^{-1}$ (Figure 4b).

## Discussion

Maximum density is important to our understanding of species stand dynamics as it indicates the maximum occupancy or full-resource use by trees. This relationship has been described as the link between forestry and ecology (Jack and Long, 1996; Long et al., 2004) and it relies in the constancy of leaf area index (LAI) during self-thinning (Long and Smith, 1984). The assumption of constancy of LAI has helped to build the hypothesis that tolerance to bending stress is driven by structural traits like specific wood density. Woodall et al. (2005) demonstrated that under this assumption trees with lower wood density would need fewer individuals to support the same amount of foliage than species with higher wood density. This hypothesis could be behind the evidence that Scots pine and beech mixed stands in Europe have greater densities than pure stands (Pretzsch et al., 2015; Pretzsch and Schütze, 2015) as this type of mixture also has lower wood density (Zeller et al., 2017).

So far, this hypothesis has been tested for North America species and we present here the first test of this hypothesis for European tree species expanding the validity of the stress-bending stress control over stand density. However, whether LAI remains constant during self-thinning has been put into question as foliar mass development is age-dependent indicating that the leaf mass that a stand can support is a function of stand development (Holdaway et al., 2008). These authors pointed that the change in leaf mass can be attributable to changes in crown vertical structure. On the other hand, Pretzsch and Mette (2008) found constant LAI in self-thinned stands of Norway spruce and beech but variable specific leaf area (SLA) with increasing diameter attributed to losses of shade leaves from suppressed dead trees. Self-thinning implies redistribution of the same amount of foliage in less and

larger individuals (Long et al. 2004). However, the non-constancy of LAI is more evident in old stands where large aged trees cannot occupied the space available after mortality or thinning events leading to departures from a linear size-density trajectory (Long and Vacchiano, 2014). In general, the older the individual tree the less the foliage in high dense stands (Long et al. 2004)

To reconcile the LAI constancy hypothesis with observations of age-dependent LAI, self-thinning boundary line modelling must combine the abiotic stress intensity and tolerance approach, as done in our model, and the existing relationship between crown plasticity and shade-tolerance (Jucker et al., 2015; Pretzsch, 2014) or the competitive advantage of species with higher crown plasticity (Vincent and Harja, 2008). Equation 10 predicts a change in the relative contribution of stress tolerance from specific wood gravity in cold sites to increasing contribution of drought- and shade-tolerance in dry sites. This is in line with the finding of Condés et al. (2017) who suggested that plasticity in hydraulic structure outweighs mechanical control over stand density in arid environments. However, tree hydraulics might not be only relevant in dry areas as water transport has been also proposed to explain the inverse relationship between wood density and leaf mass in Neotropical forests (Wright et al., 2007).

Abiotic stress tolerance is an important driver of woody plant distribution and productivity, as negative changes of environmental conditions may reduce the realized niche and potential biomass growth of a species (Laanisto and Niinemets, 2015). Polytolerance to stress is considered rare in nature leading to a trade-off between shade- and drought-tolerance (Niinemets and Valladares, 2006). Equation 9 in table 2 would have yielded a lack of simultaneous effect of shade- and drought tolerance in maximum density at both ends of a cold-warm spectrum (supplementary figure 2a). However, the lack of statistical significance for shade-tolerance in equation 9 and the significance of its complementary value in equation 10 indicates that the relative importance of shade- and drought-tolerance increases in warmer sites (supplementary figure 2b). Tolerance to both stressors result in a reduction of the number of individuals needed to make full use of resources. However, species growing in warm sites are usually more drought-tolerant than shade-tolerant and the predicted reduction is mainly driven by drought stress, as it was reflected by the relative contribution of drought tolerance which is 2.7 higher than shade tolerance (table 2). In contrast, species growing in cold sites showed an increasing effect of tolerance to bending stress on the number of individuals as compared to tolerance to shade and drought. Cold sites are expected to have a shorter growing season which has been pointed out to be a main reason for shade-drought trade-offs (Laanisto and Niinemets, 2015; Valladares and Niinemets, 2008).

Equation 10 does not predict the presence or absence of polytolerance but it can be used to make inferences on maximum density about the effect of observed shade-drought trade-offs or polytolerance in a cold-warm spectrum. Warm sites would support less trees per unit area irrespective of tolerance ranking whereas a suite of polytolerant species would need fewer individuals than species with stronger trade-offs (supplementary figure 3). Linking this finding with the fact that polytolerance is associated with a higher probability of survival in harsh conditions, as suggested by Laanisto and Niinemets (2015), would have to be assessed in terms of constancy or stress tolerance dependence of the slope parameter in the density-size relationship. The basic model used in our approach keeps a constant slope in the density-size relationship (eq. 4). The constancy of slope in forestry and ecology has been a subject of intense debate (Lonsdale, 1990; Zeide, 2004, 1987) and findings suggest that the 1.6 constant slope is much more an exception than a rule (del Río et al., 2001; Pretzsch and Biber,

2005). The mathematical computation of a variable slope according to environmental filters or stress tolerances in our model is challenging but it would improve our understanding of the mechanisms behind site occupancy. Nevertheless, our SDI predictions using stress intensity and tolerance are realistic and do not dramatically depart from predictions using a variable slope (Condés et al., 2017; del Río et al., 2001; Pretzsch and Biber, 2005; Vospernik and Sterba, 2014).

SDI for Scots pine in our study, 1307 stems ha$^{-1}$, is consistent with 1297 stems ha$^{-1}$ found in Condés et al., (2013) for the same region and slightly less than the 1442 stems ha$^{-1}$ found by Río et al (2008) for Spain. For European beech our model predicted less individuals, 966 stems ha$^{-1}$, as compared with 1042 stems ha$^{-1}$ found by Condés et al (2013), nevertheless the range of our predictions embraced that of Condés' as it ranged from 826 in colder sites to 1191 stems ha$^{-1}$ in warmer sites. Our model predictions are closer to other estimations for beech in Europe (Figure 5), whereas SDI values for Silver fir (1134 stems ha$^{-1}$) and Black pine (1246 stems ha$^{-1}$) in Navarra are sightless less from those found in Austria, 1278 and 1424 stems ha$^{-1}$ respectively (Vospernik and Sterba, 2014).

Stress tolerance to shade is an important driver in shaping species distribution and community composition whereas structural traits, like wood density predict species' competitive response (Kunstler et al., 2016). However, tolerance is not constant for a given species and it varies across genotypes and environmental conditions (Barnes et al., 1997). For example, shade tolerance is affected by nutrient and water availability (Valladares and Niinemets, 2008 and reference therein) and it decreases for Douglas-fir, western redcedar and hemlock with increasing soil moisture. Stress tolerance differs both with species ontogeny being more important in juvenile stages than in mature forests, and might differ during the same stage within a gradient of stress and species with a large distribution area. For example, Scots pine does not show the same shade tolerance across its distribution in Europe, being more shade intolerant in Central Europe than in the South. This variation in stress tolerance allows species to survive and grow in a wide range of light conditions. This gives a clue that scoring species according to stress tolerance is not an absolute value and the tolerance might be modulated by climatic factors as tested by Ducey et al (2017) and normalized in this paper.

Our model cannot be used to test the over- or under-density of mixed vs. pure stands as the contribution of stress tolerance to maximum density is averaged across species, i.e. the resulting density cannot be higher that the individual contribution of each species. This is a caveat as long as several studies have shown higher density in mixed stands than in single-species ones (Pretzsch et al., 2015; Pretzsch and Biber, 2016) in association to changes in specific wood density in mixed stands (Zeller et al., 2017).

A practical use of the model presented here is the substitution of stand density measures in empirical growth and yield model to include stress tolerance in the prediction of timber production. In so doing, the stand-level management models will capture differences in yield production according to differences in stress tolerances. Silviculture aims to maintain density below the maximum density to keep stocking between the onset of competition and the onset of the density-dependent mortality where growth is constrained by resource competition and production loss due to mortality is not economically important. When management objectives promote individual tree growth the density is kept near the lower limit but if higher stand-level yield is expected then the density is kept near the upper limit. These limits are set between 35 and 65% of maximum density based on the seminal paper by Long (1985) and have been used in silvicultural prescriptions (Valbuena et al., 2008), however these

values remain empirical and a mechanistic explanation is still lacking. Although our model does not provide mechanistic information about the exact limits it helps to accommodate the density taking into account the abiotic stress intensity and the species tolerance. For example, in the case of managed Scots pine stands in the study area the SDI limits should be set between 868 and 467 stems ha$^{-1}$ in cold sites and between 544 and 293 stems ha$^{-1}$ in the warmest sites.

## Conclusions

We built a normalized approach to explain the maximum density needed to make full use of resources in terms of variability of the stress tolerance ranking according to Niinemets and Valladares (2006) modulated by the intensity of drought and low temperature stress. The model is based on the assumption that bending stress is concomitant to all sites in the study area assuming a constant LAI during self-thinning. A basic model of stocking degree inversely related to specific wood density is found significant in the study area showing an inverse relationship (hypothesis 1 accepted). The addition of normalized tolerance shade showed to be non-significant (hypothesis 2 rejected) whereas the combination of drought-tolerance reduces the number of individuals that a site can support being this reduction stronger in warm sites (hypothesis 3 accepted). A species or group of species with high capacity to tolerate several abiotic stresses simultaneously, i.e. polytolerance, need far less individuals to fully occupy a site than species showing tolerance trade-offs. Linking polytolerance/trade-offs with a mechanistic explanation of survival at the stand level needs further investigation that should include variation due to stress tolerance in the slope parameter of the density-size relationship.

## Conflict of interest statement

None declared

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**Table 1.** Descriptive stand variables, specific gravity and stress-tolerances by bioregions in the study area.

| Bioregion | # plots | Hdom (m) | BA ($m^2$ $ha^{-1}$) | dg (cm) | N (stems $ha^{-1}$) | SG | ST | DT |
|---|---|---|---|---|---|---|---|---|
| Maritime | 1044 | 17 (5.3) 3.5-33 | 28.1 (10.6) 0.7-78.2 | 26.1 (11.5) 8-111.5 | 755.6 (577) 5.1-3738.4 | 0.7 (0.1) 0.4-1 | 3.4 (1.1) 1.2-4.6 | 3 (0.8) 1.2-5 |
| Mediterranean | 374 | 12.4 (6) 3-27.6 | 22.8 (11.5) 0.4-52.6 | 19 (7) 7.6-81.3 | 998.8 (677.9) 10.2-2910.8 | 0.7 (0.2) 0.4-1 | 2.4 (0.8) 1.4-4.6 | 3.6 (1.1) 1.2-5 |
| Mountainous | 1121 | 17.8 (6) 2.5-36.5 | 31.5 (13.8) 0.4-82.7 | 25.6 (10) 7.6-95.5 | 808.2 (561.8) 5.1-3243.2 | 0.7 (0.1) 0.4-1 | 3.2 (1.4) 1.2-4.6 | 3.3 (0.9) 1.7-5 |
| Transition | 264 | 10 (4.1) 3-28.3 | 22.6 (10.4) 0.6-56.1 | 17.7 (8.7) 7.7-113.9 | 1214.2 (775.2) 10.2-3448.4 | 0.9 (0.2) 0.4-1 | 2.9 (0.8) 1.4-4.6 | 3.9 (0.9) 1.7-5 |

Average, standard deviation in parenthesis and range, minimum-maximum for Hdom: Dominant height, BA: basal area, dg: quadratic mean diameter, N: number of stems per hectare, SG: specific gravity according to Gutierrez Oliva and Plaza Pulgar (1967), ST: averaged shade tolerance, and DT: drought tolerance according to Niinimets and Valladares (2008). The dominant species and its respective SG, ST and DT values by bioregions are European beech (0.75, 4.56, 2.4) and Scots pine (0.50, 1.67, 4.34) in Maritime and Mountainous regions, Black pine (0.58, 2.1, 4.38) and Aleppo pine (0.55, 1.35, 4.97) in the Mediterranean region and Holm oak (1.00, 3.02, 4.72) and Faginea oak (0.95, 2.73, 3.02) in the Transition bioregion.

**Table 2**. Estimates of relative density models including functional traits (SG specific gravity, DT drought tolerance and ST, shade tolerance) and abiotic stress modulators (iC cold temperature modulator and iD drought modulator)

| Model | Variable | $q_{0.995}$ Estimate (s.e.) | BIC | $q_{0.99}$ Estimate (s.e.) | BIC | $q_{0.975}$ Estimate (s.e.) | BIC | $q_{0.95}$ Estimate (s.e.) | BIC |
|---|---|---|---|---|---|---|---|---|---|
| (4) | Intercept | 0.00048 (0.00009) | 3364.3 | 0.00043 (0.0001) | 3305.9 | 0.00044 (0.00011) | 3206.57 | 0.00051 (0.0001) | 3113.18 |
| | SG | 0.00044 (0.00013) | | 0.00059 (0.00016) | | 0.00068 (0.00015) | | 0.00073 (0.00013) | |
| (7) | Intercept | 0.00048 (0.00009) | | 0.0004 (0.0001) | | 0.00044 (0.00012) | | 0.00051 (0.0001) | |
| | SG | 0.00044 (0.00013) | | 0.00061 (0.00017) | | 0.00068 (0.00015) | | 0.00078 (0.00014) | |
| | iC x ST | n.s. | | n.s. | | n.s. | | n.s. | |
| (8) | Intercept | 0.00048 (0.00008) | 3317.44 | 0.00043 (0.0001) | 3273.17 | 0.00044 (0.00011) | 3171.97 | 0.00051 (0.00009) | 3077.7 |
| | SG | 0.00044 (0.00013) | | 0.00059 (0.00016) | | 0.00068 (0.00016) | | 0.00071 (0.00013) | |
| | iD x DT | 0.00129 (0.00033) | | 0.00126 (0.00022) | | 0.0012 (0.00022) | | 0.00121 (0.00028) | |
| (9) | Intercept | 0.00048 (0.00008) | | 0.0004 (0.0001) | | 0.00014 (0.00012) | | 0.00051 (0.00009) | |
| | SG | 0.0044 (0.00011) | | 0.00061 (0.00018) | | 0.00068 (0.00015) | | 0.00076 (0.00013) | |
| | iC x ST | n.s. | | n.s. | | n.s. | | n.s. | |
| | iD x DT | 0.00129 (0.00039) | | 0.00127 (0.00023) | | 0.0012 (0.00025) | | 0.00115 (0.00026) | |
| (10) | Intercept | 0.00049 (0.00008) | | 0.00051 (0.00011) | | 0.00052 (0.0001) | 3116.91 | 0.00054 (0.00009) | 3035.1 |
| | SG | n.s. | | n.s. | | 0.00033 (0.00016) | | 0.00045 (0.00014) | |
| | (1-iC) x ST | 0.00029 (0.00013) | | n.s. | | 0.00046 (0.00015) | | 0.00041 (0.00011) | |
| | iD x DT | 0.0013 (0.00021) | | 0.00128 (0.00023) | | 0.00122 (0.0002) | | 0.00115 (0.00029) | |

**Figure 1.** Study area (Navarra, Spain), biogeoclimatic zones and National Forest Inventory plots used in this study.

**Figure 2.** Relationship between drought- and shade-tolerance ranking modulated by drought and cold temperature stress intensity ($dI$ and $cI$). Large variability in both axes would indicate polytolerance

**Figure 3a.** Relationship between cold and drought multipliers for broadleaves in Navarra (Spain). Large point dispersion in both axes would indicate simultaneous tolerance for cold and drought-stress. Filled circles for *Fagus sylvatica*, void circles for *Quercus ilex.*

**Figure 3b**. Relationship between cold and drought multipliers for conifers in Navarra (Spain). Large point dispersion in both axes would indicate simultaneous tolerance for cold and drought-stress. Filled circles for *Pinus sylvestris*, void circles for *Pinus halepensis.*

**Figure 4a**. Predicted maximum stand density index (stems ha$^{-1}$) across temperature stress gradient in Navarra, Spain, for cold-tolerant / drought-intolerant species. Grey circles for *Pinus sylvestris* and black circles for *Fagus sylvatica*

**Figure 4b**. Predicted maximum stand density index (stems ha$^{-1}$) across drought stress gradient in Navarra, Spain, for cold-intolerant / drought-tolerant species. Grey circles for *Pinus halepensis* and black circles for *Quercus ilex*

**Figure 5.** Mean SDI (bars), standard error (whiskers), maximum SDI (triangles) found in the literature search for the species in the x-axis. Black points are predictions in Navarra using model 4 in table 2.
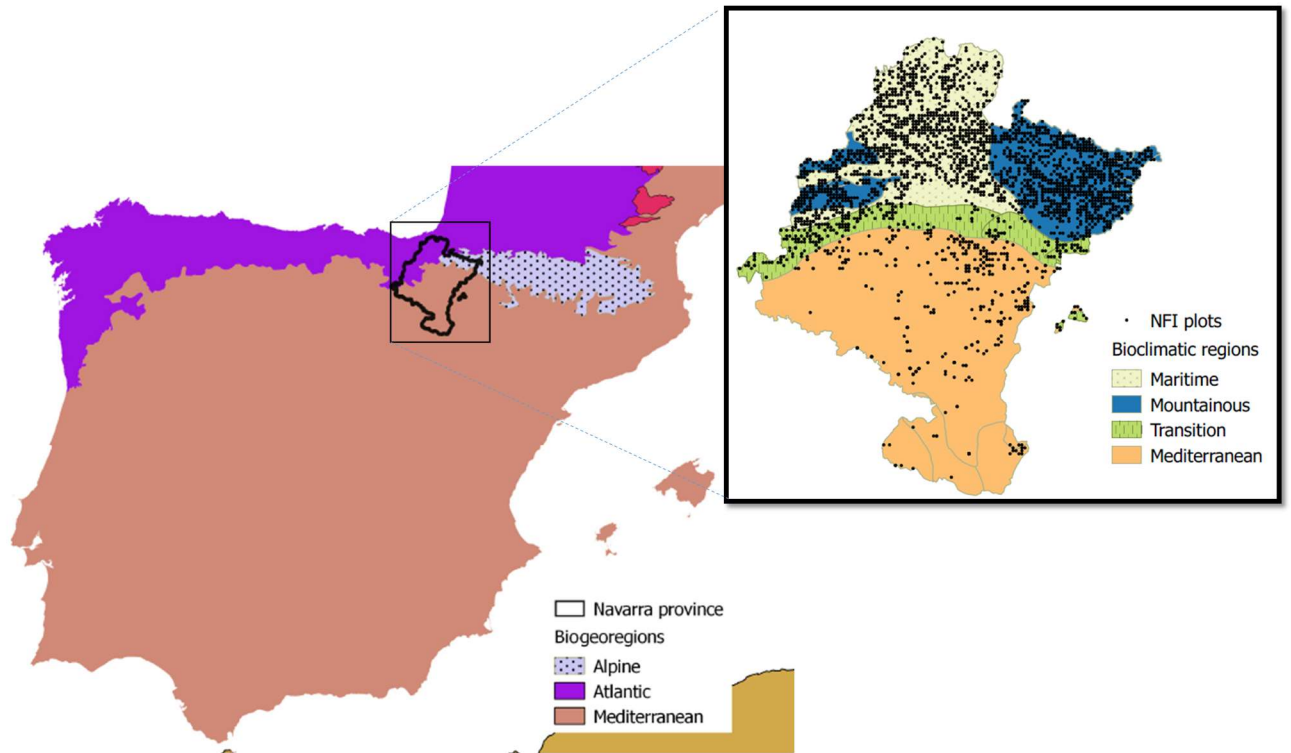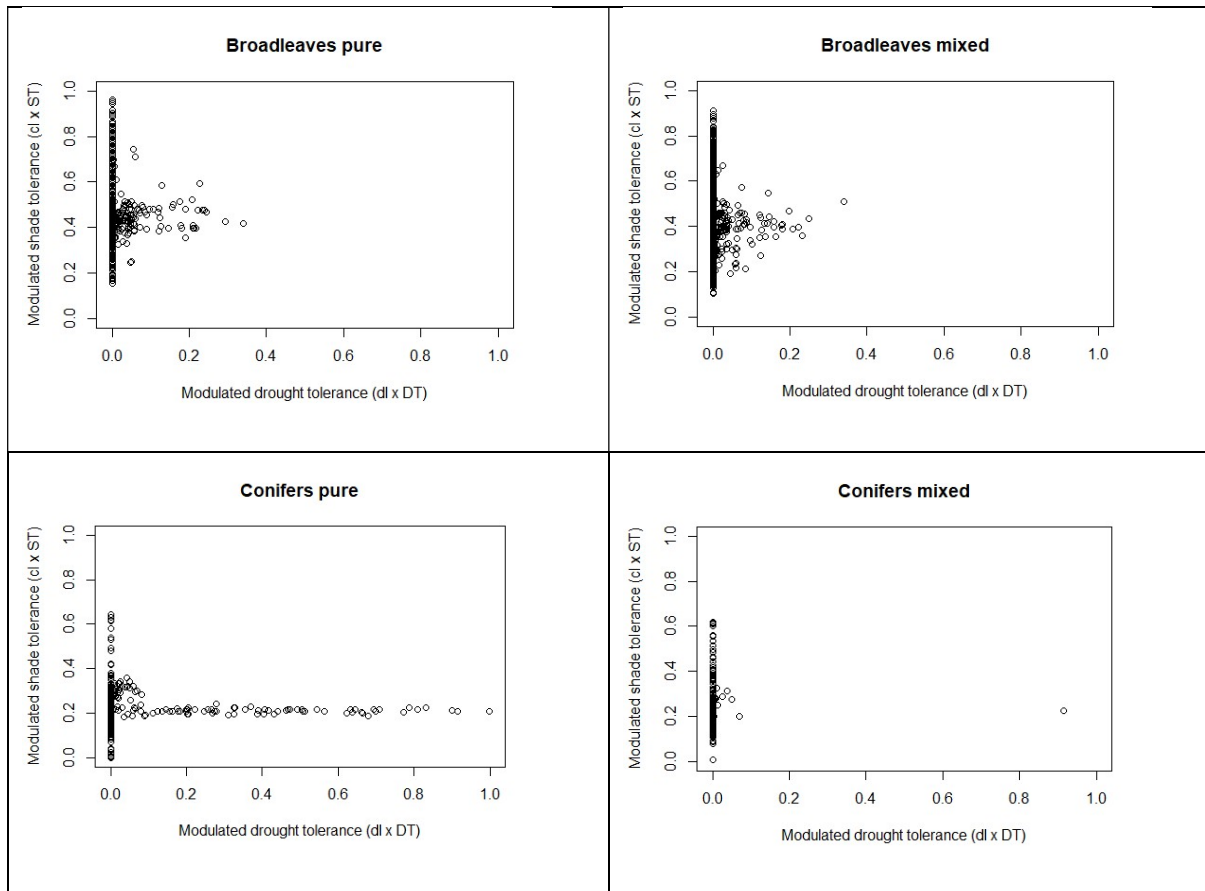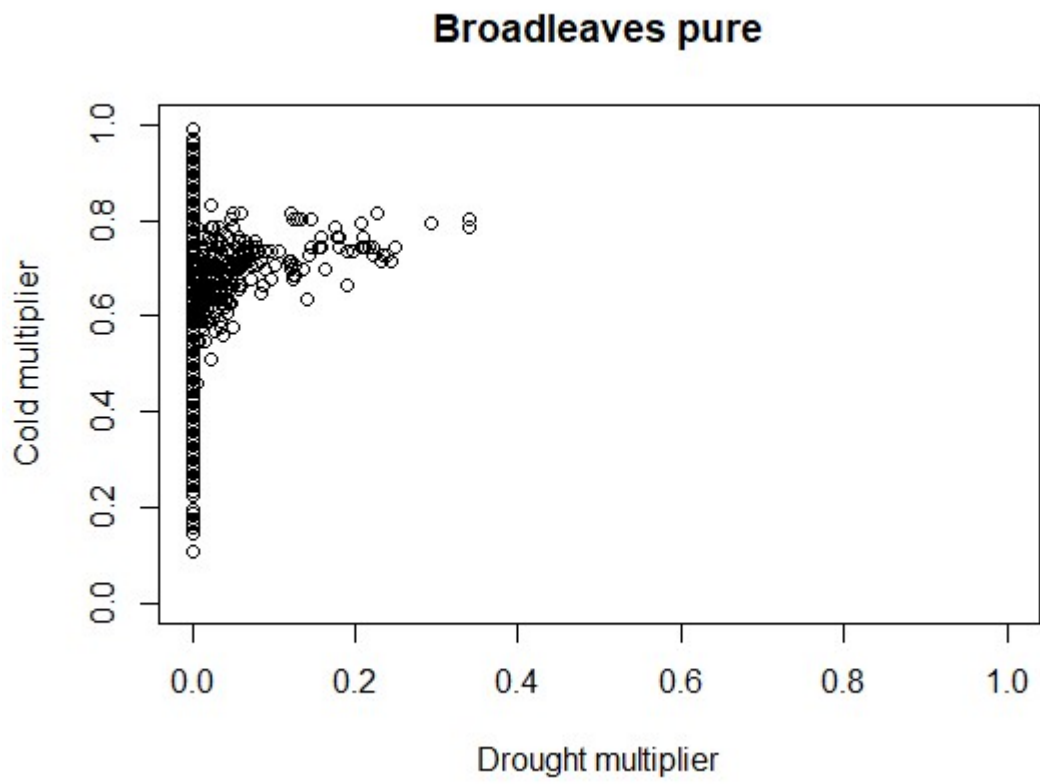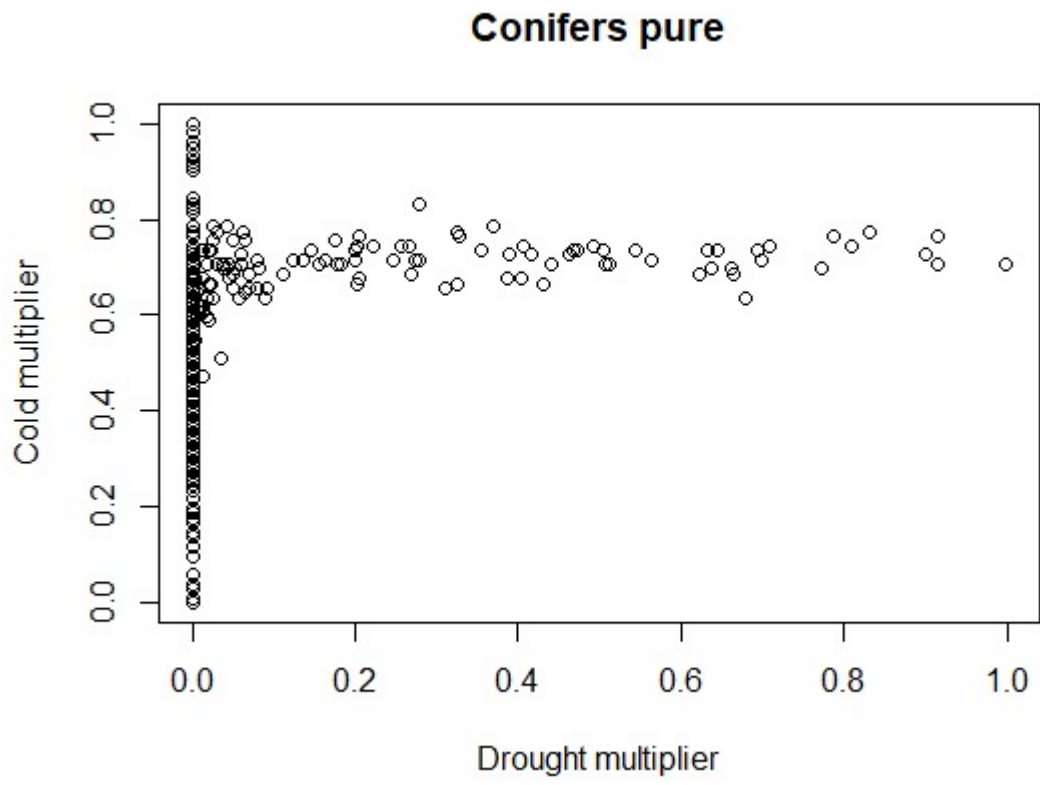
Figure 1.

Figure 2.

Figure 3a.



**Broadleaves pure**

Figure 3b



**Conifers pure**

Figure 4a.

Figure 4b

Figure 5