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# Tree biomass and biodiversity relationship in a mixed Mediterranean forest in Spain 

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#### Abstract

RESUMEN

La biomasa de árboles y su relación con la diversidad en bosques mixtos se ha convertido en uno de los temas de investigación más interesantes para los ecólogos en las últimas décadas debido a la importancia de los bosques mixtos para una mejor provisión de servicios ecosistémicos. La pregunta "¿Producen los bosques mixtos más a medida que aumenta la diversidad de árboles?" Ha sido objeto de muchos estudios que llevan a resultados no concluyentes. Este estudio se realizó para contrastar el resultado de estudios anteriores mediante la investigación de la biomasa de árboles y la relación de diversidad en un rodal mixto de bosque mediterráneo (Llano de San Marugan, España), tanto a nivel de masa como de árbol individual. Se analizaron diversos modelos que se ajustaron a partir de ecuaciones de regresión lineal y no lineal para determinar la relación entre la biomasa de los árboles y la diversidad. Se utilizaron 10 índices de diversidad que se pueden clasificar en 3 categorías: índices de riqueza de especies (Sm, Sn, D, E); Índices de composición / mezcla de especies (Mi, MS, S); Los índices estructurales verticales (W, A, TH) como variables predictoras de los modelos con el objeto de caracterizar diferentes estructuras de diversidad en el rodal. Nuestro resultado reveló que la relación entre la biomasa y la diversidad de árboles varía entre las especies. Una combinación de la relación negativa del índice D-Berker-Parker (abundancia de especies dominantes) y la relación positiva de TH (heterogeneidad de la altura) explica la variación de la biomasa a nivel rodal y para Pinus pinea. La biomasa de las especies de Quercus (Quercus faginea y Quercus ilex) se relaciona positivamente con la proporción de especies en área basimétrica ( Gp ); los índices de diversidad probados no mostraron ninguna relación con la biomasa de las especies del género Quercus.


Palabras clave: diversidad de especies arbóreas, índices de diversidad, riqueza específica, composición específica, estructura vertical del rodal.


#### Abstract

Tree biomass and diversity relationship in mixed forest has become one of the attractive research subjects for ecologist in recent decades due to an importance of multicultural mixed forest for better provision of goods and services than monoculture. The questions "Does mixed forest produce more productive and the productivity increase as tree diversity increases?" have been subject of many researches that lead to two contrast results. This study was conducted to contrast the result of previous studies by investigating the tree biomass and diversity relation in Mediterreanean multicultural mixed stand, Llano de San Marugan, Spain, at stand and individual species level. A variety of models that developed from linear and nonlinear regression equations were employed to reveal tree biomass and diversity relation. 10 diversity indices that falls in 3 categories: species richness indices (Sm, Sn, D, E); species compositional/mingling indices (Mi, MS, S); vertical structural indices (W, A, TH) were used as predictor variables for the models to characterize different structure of diversity in the stand. Our result revealed that tree biomass and diversity relation varies among species. A combination of negative relation of D- Berker-Parker index (abundance of dominant species) and positive relation of TH (height heterogeneity) explains the variation of biomass at community level and for Pinus pinea. Biomass of Quercus species (Quercus faginea and Quercus ilex) was positively related with basal area proportion of species $(\mathrm{Gp})$; the tested diversity indices didn't show any relation with biomass of Quercus species and Juniperus thurifera as concerned by metrics and models in this study.


Key words: tree biomass, tree diversity, mixed forest, diversity indices, species richness, species composition, stand vertical structure.

## 1. - INTRODUCTION

Mediterranean forests are characterized by a remarkable set of features that make them naturally and aesthetically attractive, but also quite fragile (ScarasciaMugnozza et al., 2000). Mediterranean forest is a multi-functional, providing a wide range of goods and services for society ranging from products with high market value (fuelwood, cork, mushroom, pinecones etc) and non-market value ecosystem services (soil and landscape protection, water regulation, biodiversity conservation, carbon dioxide fixation, recreation, aesthetic view etc). The latter is more significant than their productive value, especially their significant role for carbon sequestration (del Río et al., 2017). One of notable characteristics of Mediterranean forests is its rich biodiversity, reflected by high genetic variability, exemplified by the large number of tree species in comparison to Nordic forests resulting from the survival of many conifer and broadleaf species during the glacial periods. Long-term exploitation (manipulation) of trees and forestland since ancient times is another feature of Mediterranean forest which results in the dispersion of species as Pinus pinea, Castanea sativa, and Quercus suber all over the Mediterranean basin (Scarascia-Mugnozza et al., 2000). Dry, hot, harsh climate along with long lasting and frequent droughts, pest and decease, increasing the risk of large-scale fires and severe water scarcity are main challenges for the Mediterranean forests which largely impact on forest health, growth and productivity. The role of mixed forest for promoting forest productivity while coping with these challenges has been increased in Mediterranean region in recent decades.

Multicultural mixed forest have been taken a great attention in recent decades due to its greater provision of goods and services, high ecological value in comparison to monoculture forest (Pretzsch \& Schütze, 2014; Riofrío, et al., 2017). Mixed forest is defined as a forest unit of at least 0.5 ha that composes at least two tree species at any developmental stage, shares common resources (water, light, soil nutrients) and its structure and component species are altered over the time (Bravo-Oviedo et al., 2014). Main characterizations of mixed forests are described not only by better protection, preservation, maintaining and monitoring of biodiversity but also have high resistance capacity against both natural and anthropogenic disturbances such as climate change, storm, pest and decease, air pollution and its consequences. Economic importance of mixed forest is un-negligible because of its multi-use, multi-source than pure stands (Knoke et al., 2005).

The loss of biodiversity imposed by anthropogenic and climatic change has brought the importance of diversity under the control worldwide over the past 25 years (Hooper et al., 2012; J. Liang et al., 2016; Szwagrzyk et al., 2007) after the Earth Summit of world governments in Rio de Janeiro in 1992 (Evans, 2016). Since that time, scientists have been taken into account the importance of biodiversity on many ecosystem functioning and service such as productivity, stability, sustainability, sinking carbon dioxide, preserving soil fertility, controlling pest outbreaks, retaining water, and so on (Baskin, 1994). Among them, the importance of tree species diversity on biomass productivity has been studied based on the variety of genes, species, or functional traits of organisms in hundreds of types of ecological communities (Fraser et al., 2015; Jingjing Liang et al., 2016). A series of biodiversity-ecosystem functioning studies have revealed that biodiversity (including taxonomic, functional and phylogenetic diversity) promotes the functionality of ecosystems such as primary production, decomposition, nutrient cycling, trophic interactions and so on) and consequently supports a broad
range of ecosystem services (e.g. food production, climate regulation, pest control, pollination (Gamfeldt et al., 2013; Mori et al., 2017). However, contradictory results have been documented in the findings of previous researchers focused on relationship between species diversity and biomass: biomass decrease (Szwagrzyk et al., 2007) or doesn't change (Grace et al., 2016) with species diversity. In addition, numerous researches justified on loss of biodiversity ranks among the most pronounced changes to environment (Sala et al., 2000), reduction of diversity along with species composition changes alter fluxes of energy and essential services that ecosystem provide to human such as production of food, pest and disease control, water purification and so on (Daily, 1997). Biodiversity are largely and irreversibly being degraded and lost globally due to direct drivers; i.e. habitat disturbance, habitat fragmentation, land use change, overexploitation and the spread of alien species and indirect drivers; i.e. climate change, population growth, economic growth and increasing demand for food, materials, water and energy (Iranah et al., 2018). The loss of biodiversity weakens species connections and impairs the ecosystems, leading to extinction of species and local populations, which will disrupt the capacity of ecosystem to contribute to human well-being and sustain future generations.

Tree diversity plays a fundamental role for forest diversity because it is often linked with major properties of forest ecosystem, leading to the possible enhancement of diversity of other forest assembles (Mori et al., 2017) and providing required resources and suitable habitat for other forest species (Ozcelik, 2009). Diversity is generally defined by the variety of organisms including micro-organisms, plants, and animals in different ecosystems, i.e. deserts, grassland, forests etc. The most commonly used representation of ecological diversity is species diversity, which is defined by the number of species and abundance of each species living within a certain area (Liu et al., 2018). The species coexisting in a certain area are interconnected and dependent on one another for survival, while doing so; they perform important ecosystem functions and offer different ecosystem services for human life and society: provisional service (products obtained from ecosystem: many different type of food, fresh water etc); regulating services (the benefits obtained from the regulation of ecosystem processes: air quality and pollination); cultural service (the non-material benefits that people obtain: spiritual enrichment, recreation and aesthetic experiences); supporting service needed to maintain other services (i.e photosynthesis and nutrient recycling). The provision of ecosystem for such goods and service depends basically on functions performed by living plants (Tilman et al., 1997).

Two main mechanisms explain the reasons that biodiversity influence on productivity: selection effects and complementary effects. Different plant species in a mixture have different physiologies, morphologies and life history traits might allow them to fully utilize limiting resources at different space and time than a monoculture of any species (Tilman 1997). For instance, some tree species have more ability to adapt and grow better in cooler and wetter environmental condition while others grow better in hotter and drier environment. If these species grow together in a mixture, these complementary characteristics of both species lead to greater productivity across the whole grown season than either species grows alone. Similarly, tree species that have different root morphologies occupy different soil profile which potentially allowing them to exploit soil resources from different soil depth. However it should be noted that these complementary occur solely when co-existing species exhibits various forms of niche differentiation that allow them to capture resources in different space or time (Cardinale
et al., 2007; David Tilman, 1999). Another mechanism that diversity effects on productivity is selection effect (sampling effect) which describes species specific effect on biomass: a greater productivity in more diverse communities is due to the most productive species which become dominant in the community due to competition. The likelihood of becoming a high productive species increases as diversity increases. Thus this causes in the increment of the total productivity of the community. Such considerations have led to the general perception of having higher productivity in an area where more plant species co-exist.

Forest is 3 -dimensional system whose structure is a key element in ecosystem functioning and biological diversity by regulating resource related forest functioning (light, water, soil nutrients supply, capture, use), intra and inter specific interactions (Brockerhoff et al., 2017a; del Río et al., 2018), regeneration pattern, consequent selfthinning and past and present disturbance events (Bohn \& Huth, 2017; Zhang et al., 2018). Stand structural diversity leads to increase species richness and contributes to forest stability and integrity (Wang et al., 2016). Stand structural diversity combines the concepts of species richness (diversity), species composition (mixture), and spatial diversity (tree positioning) and size differentiation (Bravo \& Guerra, 2002). Accordingly three distinct types of stand structural indices and methods have frequently been purposed in preceding literature for explaining the influence of stand structural diversity on productivity and functioning of forest stand: i) species richness - Simpson index (1949), Shannon index (1948), Berger-Parker index (Berger et al., 1970) and Evenness index (Kohn, 1977); ii) species composition indices - Mingling index (Füldner, 1995), Spatial diversity status (Gadow \& Hui, 2002) and Segregation index (Pielou, 1977); iii) tree distributional indices including horizontal and vertical patterns and size differentiation - Aggregation Index (Clark et al., 1954), Uniform Angle Index (Gadow et al., 1998), Vertical Species Profile (Pretzch 1995b), Height differentiation index (Gadow 1993). Since forest structure is determined in 3 dimensions, it is appropriate to analyze the effect of tree diversity on biomass by the metrics that can fully address 3dimensionality of mixed forest structures.

## 2. - OBJECTIVES

In this study, we addressed the question "Does stand diversity impact on biomass?" by examining the relationship between tree biomass and diversity indices (species richness, species compositional, horizontal and vertical structural indices) in the Mediterranean multi-species mixed forest, Llano de San Marugan, Valladolid, Spain. The specific aims were:

- To calculate biomass of individual trees by different compartments (stem, thin branches + needles, medium and thick branches) and in total
- To compute the tree diversity indices to represent the diversity of the stand
- To determine the relationship between tree biomass and diversity.


## 3. - MATERIAL AND METHODS

### 3.1. Study site

The study was conducted in a Mediterranean mixed forest stand, located in Llano de San Marugan, Valladolid, Castile and Leon, Spain. Valladolid has a continental

Mediterranean climate with cold winters and hot summers. The average annual temperature ranges between 11 and $12^{\circ} \mathrm{C}$. Fog is frequent in the long, cold winter, while summers are dry and hot with average temperature around $30^{\circ} \mathrm{C}$. Precipitation falls irregularly throughout the year with a minimum in the summer and a maximum in spring and autumn, with maximum of 400 mm . In a mixed forest stand, a marteloscope was installed in 2015 covering 1 hectare (ha). The marteloscope (a square of 100 by 100 m ) was divided into 16 subplots (hereafter referred as quadrants), $25 \times 25 \mathrm{~m}$ length, as shown in Figure 1. Within each quadrant, locations of all trees were recorded in $4.55728^{\circ} \mathrm{W}$ and $41.43948^{\circ} \mathrm{N}$ geographic coordinates and their species were identified and corresponding diameter at breast height ( dbh , in cm ) and, total height (in m ). The diameter at breast height and total height were measured from trees whose diameters were greater than 5 cm . The study workflow is shown in Figure 2 and detailed explanations are given in following sub-sections.


Figure 1. Study area location of Marteloscope of Llano de San Marugan (Valladolid, Spain)


Figure 2. Workflow for the study of tree biomass and diversity relationship

### 3.2. Biomass estimation

Biomass in the different components of the tree e.g., stem and branches (thick, medium and thin+needles) and roots were calculated from dbh and height using existing relative allometric equations (Table 1) developed by (Ruiz-Peinado Gertrudix, Montero, \& del Rio, 2012; Ruiz-Peinado, del Rio, \& Montero, 2011). Tree component biomass values were computed for individual tree within each quadrat, and summed up to derive a summary of tree biomass for each quadrat. Total biomass obtained from sum of the biomass of all components.

Table 1. Biomass allometric equations by species

| Species | Components | Model |
| :---: | :---: | :---: |
| Juniperus thuriferia L. | Stem | $W_{s}=0.0132 \times d^{2} \times h+0.217 \times d \times h$ |
|  | Thick branches | $\begin{gathered} \text { if }\left\{\begin{array}{l} d \leq 22.5 \mathrm{~cm} \text { then } Z=0 \\ d \geq 22.5 \mathrm{~cm} \text { then } Z=1 \end{array}\right. \\ W_{b 7}=\left[0.107 \times(d-22.5)^{2}\right] \times Z \end{gathered}$ |
|  | Medium branches | $W_{b 2-7}=0.00792 \times d^{2} \times h$ |
|  | Thin branches +needles | $W_{b 2+n}=0.273 \times d \times h$ |
|  | Roots | $W_{r}=0.0767 \times d^{2}$ |
| Pinus pinea | Stem | $W_{s}=0.0224 \times d^{1.923} \times h^{1.0193}$ |
|  | Thick branches | $\begin{gathered} \text { if }\left\{\begin{array}{l} d \leq 22.5 \mathrm{~cm} \text { then } Z=0 \\ d \geq 22.5 \mathrm{~cm} \text { then } Z=1 \end{array}\right. \\ W_{b 7}=\left[0.247 \times(d-22.5)^{2}\right] \times Z \end{gathered}$ |
|  | Medium branches | $W_{b 2-7}=0.0525 \times d^{2}$ |
|  | Thin branches +needles | $W_{b 2+n}=21.927+0.0707 \times d^{2}-2.827 \times h$ |
|  | Roots | $W_{r}=0.117 \times d^{2}$ |
| Quercus faginea | Stem | $W_{s}=0.154 \times d^{2}$ |
|  | Thick branches | $W_{b 7}=0.0861 \times d^{2}$ |
|  | Medium branches | $W_{b 2-7}=0.127 \times d^{2}-0.00598 \times d^{2} \times h$ |
|  | Thin branches + leaves | $W_{b 2+1}=0.0726 \times d^{2}-0.00275 \times d^{2} \times h$ |
|  | Roots | $W_{r}=0.169 \times d^{2}$ |
| Quercus ilex | Stem | $W_{s}=0.143 \times d^{2}$ |
|  | Thick branches | $\begin{gathered} \text { if }\left\{\begin{array}{l} d \leq 12.5 \mathrm{~cm} \text { then } Z=0 \\ d \geq 12.5 \mathrm{~cm} \text { then } Z=1 \end{array}\right. \\ W_{b 7}=\left[0.0684 \times(d-12.5)^{2} \times h\right] \times Z \end{gathered}$ |
|  | Medium branches | $W_{b 2-7}=0.0898 \times d^{2}$ |
|  | Thin branches + leaves | $W_{b 2+1}=0.0824 \times d^{2}$ |
|  | Roots | $W_{r}=0.254 \times d^{2}$ |

[^0]
### 3.3. Tree species diversity estimation

The diversity indices used in this study were classified into 3 categories (Table 2). The basic idea of a diversity index is to obtain a quantitative estimate of biological variability that can be used to compare biological entities, composed of discrete components, in space or in time (Morris et al., 2014).

Table 2. Categorization of indices

| Richness \& diversity | Species composition | Distribution pattern |  |
| :---: | :---: | :---: | :---: |
|  |  | Vertical | Horizontal |
| Simpson index (Sm) | Mingling (Mi) | Vertical Profile index (A) | Aggregation index (R) |
| Shannon index (Sn) | Spatial Diversity Status (MS) | Height Differentiation | Uniform Angle Index (W |
| Evenness index (E) | Segregation index (S) | index (TH) |  |
| Berker-Parker index (D) |  |  |  |

### 3.3.1. Species richness indices

Two different aspects are generally used to conceptualize the diversity in a community: species richness and evenness. Species richness represents the number of species or attributes present in a community which is the simplest and most commonly applied metric. The distribution of individuals over species is called evenness. Additionally, species or trait abundance is also important for diversity, and the proportional abundance of species can be incorporated into indices that represent diversity.

### 3.3.1.1. Simpson Diversity index (1-D)

The Simpson diversity index (Eq. 1) was introduced by Edward H. Simpson (Simpson, 1949) to measure species diversity in a community by taking into account the number of species present and the abundance of each species. The index represents the probability that two individuals that are randomly selected from a sample will belong to different species.

$$
\begin{equation*}
1-D=1-\frac{\sum_{i=1}^{R} n i(n i-1)}{N(N-1)} \tag{Eq. 1}
\end{equation*}
$$

where $n_{i}$ is the number of individuals belonging to $i$-th type, $N$ is total number of individuals in the dataset, $R$ - richness ( total number of species types in dataset).
It ranges $0 \leq \mathrm{D} \leq 1$. The value increases with species diversity. The higher the diversity, the greater the value of $D$.

### 3.3.1.2. Shannon index

Shannon index ( $H^{\prime}$ ) by Shannon and Weaver (Shannon, 1948) is distance independent index to characterize the species diversity in a given stand. It takes into account both abundance and evenness of the existing species (Eq. 2).

$$
H^{\mathrm{\prime}}=-\sum_{i=1}^{S} p_{i} \ln p_{i}
$$

Eq. 2
where S is the number of species, $p_{i}$ - proportion of $i$-th species in the total number of individuals of all species and calculated from individuals of $i$-th species divided by total number of individuals present $(\mathrm{n} / \mathrm{N}), \ln p_{i}$ is natural logarithm of this proportion. Its value
ranges from 0 to $\ln (S)$. When all species in the dataset are equally common, all pi values equal $1 / S$, and the Shannon index hence takes the value $\ln (S)$. When all abundance is concentrated in one species, and the other species are very rare (even if there are many of them), its value reduces to 0 . The value is 0 when only one species in the dataset.

### 3.3.1.3. Berker-Parker index (D)

Berker-Parker index (Berger \& Parker, 1970) is a measure of the numerical importance of the most abundant species in the population (Eq. 3). It has an analytical relationship with the geometric series of the species abundance model and represents the proportional abundance of only the most abundant species in the population (Morris et al., 2014).

$$
D=\frac{N_{\max }}{N}
$$

Eq. 3
where $N_{\max }$ is the number of individuals is in the most abundant species and $N$ is the total number of individuals in the sample. The reciprocal of the index, 1/D, is often used, so that an increase in the value of the index corresponds an increase in diversity and a reduction in dominance.

### 3.3.1.4. Evenness index (E)

Species evenness (E) (Pielou, 1975) refers to how species are close to each other in numbers (del Río et al., 2018). It represents the degree to which individuals disturb closely among species in terms of number. E is not calculated independently, but rather derived from compound diversity measures such as, D indices, as they inherently contain richness and evenness components. In Eq. 3, $H^{\prime}$ is the number derived from the Shannon diversity index and $H^{1}{ }_{\max }$ is the maximum possible value of $H^{\prime}$ (if every species was equally likely). $E$ is supposed to be independent of a measure of species richness.

$$
\begin{equation*}
E=\frac{H^{\urcorner}}{\ln S} \tag{Eq. 4}
\end{equation*}
$$

where $H^{\prime}$ is a value of Shannon diversity index, $\ln S$ is natural logarithm of the number of species which equals to $H^{\prime}{ }_{\max }$. Its value falls between 0 and 1 ( 1 demonstrates complete evenness). Low values indicate that one or a few species dominate, and high values indicate that relatively equal numbers of individuals belong to each species.

### 3.3.2. Species intermingling

The spatial relationships between two groups of individuals play important role for many components of a species' population biology. A numerous different types of tests indices have been designed to seek for an answer to the question whether two species are spatially segregated (individuals occur near the same species), associated (individuals occur near the other species), or neither.

### 3.3.2.1. Species segregation (S) index

Segregation index (S) developed by Pielou (1977) describes the degree of intermingling of two species groups based on nearest-neighbor method. S considers the ratio of the observed probability ( $\mathrm{p}_{\mathrm{i}}$ ) that reference tree $i$ and its nearest-neighbor $j$ belong to different species along with the same probability for completely randomly distributed or independent species attributes (del Río et al., 2018) (Eq. 5). There are 2 main procedures to calculate $S$ index: 1) calculation between distances between reference
trees $i$ to every tree in the plot which derived from Euclidean distance calculation. Once the distances were computed, trees were ranked from nearest to farthest to reference tree and the first $n$-th number of neighboring trees (which are user dependent) were selected, 2) computation of $S$ index: which was computed based on the nearestneighbor tree distances calculated in $1^{\text {st }}$ step. S is originally designed for being applied to a two-species mixture (Biber \& Weyerhaeuser, 1998). In Pielou's approach, a contingency table is constructed in form described in Table 3.

$$
S=1-\frac{p_{i j}}{E\left(p_{i j}\right)}=1-\frac{\text { Observed number of mixed pairs }}{\text { Expected number of mixed pairs }}
$$

$P_{i j}$ and $E\left(p_{i j}\right)$ can be solved by Eq. 6:

$$
S=1-\frac{N *(b+c)}{m w+n v}
$$

Eq. 6
where: $m$ and $n$ are the observed number of individual trees of species 1 and 2 respectively. $N$ can easily be extracted from sum of $m$ and $n$ as described in the table. The $v$ and $w$ are the number of individual trees of species 1 and 2 that are found as the nearest-neighbors of a reference tree. These variables are clearly described in a contingency table (Table 3).

Table 3. Descriptions of variables for $S$ index calculation

|  | Nearest-neighbor species (j) |  |  |  |
| :--- | :--- | :--- | :--- | :--- |
|  |  | species.1 | species.2 | Total (i) |
| Reference | species.1 | species.2 | $c$ | $b$ |
|  | Total (j) | $\mathrm{v}=\mathrm{a}+\mathrm{c}$ | d | $\mathrm{w}=\mathrm{b}+\mathrm{d}$ |

If the nearest-neighbors are always the same species as the reference trees, then $S=1$ which implies that the reference tree is associated with itself. There is a segregation of reference species from others. If all neighbors are different species, $\mathrm{S}=-1$ which indicates that the reference tree is associated with other species. There is association between 2 species. Independent distribution of species is indicated by value near to 0 .

$$
S=\left\{\begin{array}{c}
1, \text { all nearest neighbors }(j) \text { are the same species with reference tree }(i) \\
-1, \text { all nearest neighbors are the different than reference tree }(i)
\end{array} \quad 1 \geq S \geq-1\right.
$$

### 3.3.2.2. Mingling (Mi) index

Species spatial mingling (Mi) index is a measure of species diversity within a structure unit (neighbor trees plus reference tree) which describes the proportion of neighbor trees which don't belong to same species as the reference tree. The Mi by Füldner (1995) is defined as in Eq. 7 :

$$
\begin{equation*}
M_{i}=\frac{1}{n} \sum_{i}^{n} V_{i j} \tag{Eq. 7}
\end{equation*}
$$

where n is the number of nearest neighbor trees considered, $V_{i j}$ produces binary output which equals to 1 if the $j$-th neighbouring tree is not the same species as the $i$-th reference tree and $V_{i j}=0$ otherwise.
$V_{i j}=\left\{\begin{array}{c}0, \text { neighbour }(j) \text { belong to the sampe species as reference tree ( } i \text { ) } \\ 1, \text { neighbour }(j) \text { belong to different species from reference tree ( } i \text { ) }\end{array} \quad 0 \leq M_{i} \leq 1\right.$
A low degree of mingling indicates that trees of a particular species occur together with few or no trees of different species in the same area. High degree of mingling means that trees are surrounded by different species. Assume there are 4 neighbor trees to a reference tree, 5 different outputs are possible to derive as shown in Figure 3. The distribution of the Mi values, in conjunction with the species proportions within a given tree population, allows a detailed study of the spatial diversity within a forest. However, the number of different species in the structure unit was not taken into account, and this was a shortcoming of the Mi index. This shortcoming has fulfilled in spatial diversity status index.

### 3.3.2.3. Spatial diversity status (MS)

$M S_{i}$ is improvement of mingling index. It considers not only the spatial mingling, but also the number of tree species. $M S_{i}$ is determined by the relative species richness within the structure unit $i$ and the degree of mingling of the reference tree and expressed by Eq. 8 (Gadow \& Hui, 2002). The structural unit is defined by the neighborhoods that consisting a reference tree and its nearest neighbors (Zhang et al., 2018).

$$
M S_{i}=\frac{S_{i}}{n_{\max }} \times M_{i}
$$

Eq. 8.
Where $S_{i}$ is the number of tree species in the neighborhood of the reference tree $i$, including tree $i$, and $n_{\max }$ is the maximum number of species in this structure unit. $M_{i}$ is the species mingling value. MS measures the tree species richness as well as an important species characteristic within a structure unit. Reference tree of a common species is more likely to have the neighbors of the same species, reflecting low MS value. R rare species have less probability to have same neighbor species, resulting in high value of MS. Thus, MS is considered as an index that sensitive to rare species.

Determinations of $S_{i}$ and $n_{\max }$ for MS are given in Figure 3 where explanation are based on example images of Mi. For 4 nearest neighbors, the structural unit is considered to be 5 ( 4 neighbors plus reference tree). There are 4 different species $(a, b, c, d)$ in the structure unit. So $n_{\max }$ is defined by $4 . S_{i}$ can be calculated as a number of species within the structure unit as exemplified in Figure 3.

|  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | $M_{i}=0 / 4=0$ | $\begin{aligned} & M_{i}=1 / 4 \\ & =0.25 \end{aligned}$ | $M_{i}=2 / 4=0.5$ | $M_{i}=3 / 4=0.75$ | $M_{i}=04 / 4=1$ |
|  | None of the neighbor tree is different species than reference tree | One of the neighbor tree is different species than reference tree | Two of the neighbor tree are different species than reference tree | Three of the neighbor trees are different species than reference tree | All 4 neighbor trees are different species than reference tree |
|  | No mixture | Low mixture | Medium mixture | High mixture | Complete mixture |
|  | $S_{i} / n_{\max }=1 / 4$ | $S_{i}=2 / 4$ | $S_{i}=2 / 4$ | $S_{i}=4 / 4$ | $S_{i}=4 / 4$ |
|  | Ther is 1 species (a) in the structure unit/max number of species in this structure unit is 4. | There are 2 species ( $a, b$ ) in the structure unit/ max number of species in this structure unit is 4. | There are 2 species $(a, b)$ in the structure unit/ max number of species in this structure unit is 4. | There are 4 species $(a, b, c, d)$ in the structure unit/ max number of species in this structure unit is 4. | There are 4 species ( $a, b, c, d$ ) in the structure unit/ max number of species in this structure unit is 4. |
| $\begin{aligned} & \times \\ & \stackrel{\times}{0} \\ & \vdots \\ & 3 \end{aligned}$ |  |  |  |  |  |
|  | $W_{i}=0 / 4=0$ | $\begin{aligned} & W_{i}=1 / 4 \\ & =0.25 \end{aligned}$ | $W_{i}=2 / 4=0.5$ | $W_{i}=3 / 4=0.75$ | $W_{i}=04 / 4=1$ |
|  | None of the angles $(\theta)$ is smaller than standard angle $\left(\theta_{s}\right)$ | One of the angles $(\theta)$ is smaller than standard angle $\left(\theta_{s}\right)$ | Two of the angles $(\theta)$ are smaller than standard angle $\left(\theta_{s}\right)$ | Three of the angles $(\theta)$ are smaller than standard angle $\left(\theta_{s}\right)$ | All of the angles $(\theta)$ is smaller than standard angle $\left(\theta_{s}\right)$ |
|  | Very regular | Regular | Random | Clumped | Very clumped |

Figure 3. Description and calculation of Mingling index (Mi), Spatial diversity status (MS) and Uniform Angle index ( Wi ) and corresponding likelihood values for structure unit of 4 neighbors around the reference $i$ tree: a, b, c, d are the tree species types ; $\boldsymbol{\theta}$ are angles between adjacent neighbor trees; $\boldsymbol{\theta}_{\boldsymbol{s}}$ is a standard angle (which is equal to $360 / 4$ for 4 neighbor trees) (Adapted from Gadow \& Hui, 2002)

### 3.3.3. Spatial structural indices

The concept of spatial distribution consist vertical and horizontal spatial distributions which refer to the spatial arrangements (positioning) of different tree species along the
vertical or horizontal axis (del Río et al., 2018). The horizontal spatial distribution gives an idea of the variation of tree positioning (Bravo \& Guerra, 2002). The indices that measure the horizontal spatial distribution quantifies the degree of regularity of the trees which are typically classified into regular, random, and clustered patterns and linked to processes of tree mortality, competitive interaction, regeneration and gap creation and so on. Vertical spatial distribution is most commonly described in terms of layers that refer to distinct classes or stratification of the canopy corresponding to height-related differentiation between trees.

### 3.3.3.1. Uniform Angle Index (W)

The Uniform Angle Index (W) formulates the degree of spatial dispersion of nearest neighbors around the reference tree based on angles between adjusting nearest neighbor trees defined as vectors from reference tree to each neighbors as shown in Figure 3 (Gadow et al., 1998). W is determined as the proportion of the angles that are smaller than the standard angle $\alpha_{0}(360 / n)$ and calculated as (Eq. 9):

$$
W_{i}=\frac{1}{n} \sum_{j=1}^{n} v_{j} \text { where } v_{j}=\left\{\begin{array}{c}
1, \alpha_{j}<\alpha_{0}  \tag{Eq. 9}\\
0, \text { otherwise }
\end{array}\right.
$$

where $n$ is number of nearest neighbours

$$
0 \leq \mathrm{W} \leq 1 ; \quad \text { If }\left\{\begin{array}{c}
W<0.5, \text { regular tree distributoin } \\
0.5<W<0.6, \text { random distribution } \\
W>0.6, \text { clumped }
\end{array}\right.
$$

The value of W ranges from 0 to 1 . The value of W increases from regular to clumped pattern (regular < random < clumped).

### 3.3.3.2. Aggregation index $R$

Aggregation index (R) by Clark \& Evans (1954) is a single value index that is designed to describe aspects of variability of tree locations in forest stands (Eq. 10).

$$
R=\frac{\bar{r}_{\text {observed }}}{E(r)} \text { where } E(r)=\sqrt{\frac{A}{N}}
$$

Eq. 10

Where $\bar{r}_{\text {observed }}$ is an average distance to their nearest neighbours in a given forest stand while $E(r)$ is an average nearest neighbor distance when trees completely random distributed, A is area of the plot, N is the total number of trees in the plot. The edge effect arising from the spatial limitations of experiment plots has minimized by applying the boundary correction factor by Donnelly (1978). Interpretation of R values is as follows:

$$
0 \leq R \leq 2.149: R\left\{\begin{array}{l}
<1 ; \text { then pattern shows clustering } \\
\approx 1 ; \text { then pattern is random distribution } \\
>1 ; \text { then pattern is regular distribution }
\end{array}\right.
$$

### 3.3.3.3. Height Differentiation index (TH)

Height differentiation index (TH) is size differentiation index, developed by Gadow (1993) which measures the variability in height between $i$-th reference tree to each neighboring trees ( $j-1 \ldots n$ ) and describes vertical distribution of tree height (Eq. 11).

$$
T H_{i j}=1-\frac{\operatorname{MIN}\left(H_{i}, H_{j}\right)}{\operatorname{MAX}\left(H_{i}, H_{j}\right)}
$$

where $H_{i}, \& H_{j}$ are the height of reference tree and neighbor tree respectively.

$$
0 \leq \mathrm{TH} \leq 1 . \text { If }\left\{\begin{array}{c}
T H=1, \\
\quad \text { neighbour trees have high differentiation in height } \\
T H=0, \text { neightbour trees have equal height }
\end{array}\right.
$$

### 3.3.3.4. Vertical species profile (A)

Vertical species profile (A) (Pretzsch, 1995) is outlined in Eq. 12. Calculation is based on the Shannon and Weaver (Shannon, 1948) diversity index. A considers both proportion of the species within a stand and the presence of each species in different height zones (Eq. 12). Height zones were determined as a same way as Pretzsch (2009).

$$
\begin{equation*}
A=-\sum_{i=1}^{S} \sum_{i=1}^{Z} p_{i j} \times \ln \left(p_{i j}\right) \tag{Eq. 12}
\end{equation*}
$$

where $S$ represents the number of species present, $Z$ is the number of height zones (three in this case), $p_{i j}$ is the proportion of a species in the height zone $p_{i j}=\frac{n_{i j}}{N}, \mathrm{~N}$ is the total number of individuals, $n_{i j}$ is the number of individuals of the species $i$ in the zone $j$. Standardization of $A$ can be done by dividing $A$ value by the maximum value of the $A$ index, i.e. $A_{\max }=\ln (S \times Z)$. Its value is greater than 0 . For a pure stand with single layer, A equals to 0 . Its value is increases as heterogeneous the vertical profile increases.

### 3.4. Statistical analysis

We used multiple linear regressions to evaluate the relationship between tree biomass and diversity indices in the stand, where total biomass (B) per tree was the dependent variable, and species richness, composition and species distribution indices were covariates of interest. Following previous researches that have developed a various regression models for estimating total-tree and tree compartment biomass, we utilized following three general forms of linear and non-linear regression equations (Eq. 13 to Eq. 15) for development of different forms of prediction models.

$$
\begin{gather*}
Y=\beta_{0}+\beta_{1} x_{1}+\cdots+\beta_{k} x_{j}+\varepsilon  \tag{Eq. 13}\\
Y=\beta_{0} x_{1}{ }_{1} x_{2}{ }^{\beta_{2}} \ldots x_{j}^{\beta_{k}}+\varepsilon  \tag{Eq. 14}\\
Y=\beta_{0} \pi\left(x_{i} x_{j}\right)^{\beta_{k}}
\end{gather*}
$$

Eq. 15

Two different approaches of regression analysis were used to find the coefficients: the first approach was to apply, whenever possible, multiple linear regressions to the original equations; the second approach was to transform the above equations to the logarithmical form and then apply multiple linear regressions to the transformed equations. Eq. 13 used to develop multiple linear regressions that can be fitted by standard least squares estimation. Non-linear models (Eq. 14 and Eq. 15) were transformed into linear models (Eq. 16 and Eq. 17) by taking the logarithm of both sides of the equation. In this form, the equation parameters can easily be estimated by least squares procedures.

$$
\begin{gather*}
\ln Y=\ln \beta_{0}+\beta_{1} \ln x_{i}+\cdots \beta_{2} \ln x_{j}+\varepsilon  \tag{Eq. 16}\\
\ln Y=\ln \beta_{0}+\beta_{1} \ln \left(x_{i} * x_{j}\right)+\varepsilon \tag{Eq. 17}
\end{gather*}
$$

where $\ln$ is the natural logarithm. $\varepsilon$ is the random error term which is assumed to be normally distributed with mean zero and variance constant.

The models structures and their corresponding predictor variables are given in Table 4. 11 predictor variables: four species richness indices ( $\mathrm{Sm}, \mathrm{Sn}, \mathrm{D}, \mathrm{E}$ ), three species composition indices (Mi, MS, S), four spatial distribution indices: A, TH, W and G were used as predictor variables for fitting models. Several different ways were implemented in variable selection process for the fitting models in order to avoid a problem of collinearity. First, all the variables were used as a single predictor variable for the models with single term. Second, basal area, species richness indices and species composition indices were utilized as state variables individually and each one of the spatial distribution indices were added into the multivariable models with two terms as secondary predictor variable. Third, we tested G, TH or A as a second, other individual indices as a third predictor variable for the multivariable models with three terms. Finally all possible combinations of indices are examined for multivariable models as well. In total, 537 alternative models were examined for each individual species and community level. For the community level analyze, basal area per quadrant $G$ ( $\mathrm{m} 2 / \mathrm{ha}$ ), for the species level analyze, species proportion of basal area $G_{p}$ per quadrant were explored.

For the best models selection, four criteria were employed: i) significance of variables (in the ANOVA analysis, an effect is concerned to be significant when its coefficients have a probability less than or equal to the significant probability ( $P<0.05$ ), ii) biological meaning of parameters, iii) the normality of the residuals with $\mathrm{Q}-\mathrm{Q}$ plots and iv) Akaike Information Criteria (AIC).

Table 4. Fitting models and their predictor variable reference

where $B$ represents total biomass; $x_{1}, x_{2}, x_{3}$ represent the predictor variables; $\beta_{0}, \beta_{1}, \beta_{2}$, $\beta_{3}$ are the parameters of the models; For the species level analyze, basal area proportion of each species in each quadrant, for the whole community level analyze, basal area of each quadrant ( $\mathrm{m} 2 / \mathrm{ha}$ ) were explored along with other indices.

## 4. - RESULTS

From the result of 537 investigated models, 11 significant models for community level are summarized in Table 5. Parameters of all models were statistically significant at ( $p<0.01$ ). TH alone or in combination with species richness or composition indices i.e Sm+TH, Sm*TH, Sn*TH, D+TH, E+TH, E*TH, Mi+TH, MS+TH, S+TH, G+TH+Sm, G+TH+MS was a main explanatory variable in all models except model 10 demonstrating the importance of vertical structural on tree biomass. According to parameter estimation, negative parameters were associated to species richness and compositional indices ( Sm in model 1 and 4 ; MS in model 2 and 10 ; Mi in model 9 ; S in model 11 in logarithmic form) while positive parameters were correspond to TH in all the models excluding models 5 and 8 which implies that biomass increases as species richness or species composition decreases and height heterogeneity increases. From the selected 11 models, model 6 (Eq. 18) was found to be the best model for predicting community level tree biomass, showing negatively influence of $D$ and positively influence of TH on tree biomass of the stand.

$$
\begin{equation*}
\operatorname{Ln} B=6.594-1.349 \ln D+0.841 \ln T H \tag{Eq. 18}
\end{equation*}
$$

Where $B$ is total biomass per tree (kg), D is Berker-Parker index, TH is height differentiation index.

Table 6 showed that the parameter estimates of selected models by species based on models in Table 4. Similar trend that had observed at community level occur for Pinus pinea: TH alone or in combination with species richness or composition indices such as $\mathrm{Sm}+\mathrm{TH}$; $\mathrm{Sm}^{*} \mathrm{TH} ; \mathrm{Sn}+\mathrm{TH}$; $\mathrm{Sn}^{*} \mathrm{TH} ; \mathrm{D}+\mathrm{TH} ; \mathrm{D}^{*} \mathrm{TH} ; \mathrm{E}^{*} \mathrm{TH}, \mathrm{Mi}^{*} \mathrm{TH}$ was a main explanatory variable for all the models. The strength of the relationship ranges from 0.02 to $0.16\left(0.16<R^{2}<0.2\right)$. The highest statistically significant and the lowest AIC value belong to Eq. 19 (model 6, Table 6). The same form of model as community level analysis has been chosen as a best model for Pinus pinea as well. The reciprocal interactive effect of D and TH had the best prediction power on biomass. Gp has been shown to be the best explanatory variable for the biomass for both Quercus faginea (Eq. 20) and Quercus ilex (Eq. 21). None of the model was significant for Juniperus thurifera as concerned by models in this study.

$$
\begin{gathered}
\ln B=7.249-0.935 \ln D+0.988 \ln T H \\
\ln B=4.278+0.156 \ln G_{p} \\
\ln B=4.241+0.168 \ln G_{p}
\end{gathered}
$$

Eq. 20
Eq. 21

Table 5. Parameter estimates for biomass from selected models at community level

| Model | Explainatory variable |  |  |  |  |  |  |  |  |  |  | N | Adj.R2 | AIC | RSE | F.value |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Intercept | $\log G$ | $\log D$ | $\operatorname{logTH}$ | $\operatorname{logSm}$ | $\log M S$ | $\log (\mathrm{Sm} * \mathrm{TH})$ | $\log E$ | $\operatorname{logMi}$ | $\log 5$ | $\log \left(E^{\star} T H\right)$ |  |  |  |  |  |
| 1 | $\begin{array}{r} \hline 2.929 * * * \\ (0.638) \end{array}$ | $\begin{array}{r} \hline 0.812^{* * *} \\ (0.217) \end{array}$ |  | $\begin{array}{r} \hline 0.763^{* * *} \\ (0.098) \end{array}$ | $\begin{array}{r} \hline-11.142^{* * *} \\ (2.953) \end{array}$ |  |  |  |  |  |  | 437 | 0.20 | 1264.2 | 1.02 | 37.809*** |
| 2 | $\begin{array}{r} 4.426^{* * *} \\ (0.594) \end{array}$ | $\begin{array}{r} 0.706^{* *} * \\ (0.213) \end{array}$ |  | $\begin{array}{r} 0.990^{* * *} \\ (0.097) \end{array}$ |  | $\begin{array}{r} -2.028^{* * *} \\ (0.465) \end{array}$ |  |  |  |  |  | 437 | 0.21 | 1259.6 | 1.02 | 39.746*** |
| 3 | $\begin{array}{r} 5.684^{* * *} \\ (0.137) \end{array}$ |  |  | $\begin{array}{r} 0.883^{* * *} \\ (0.096) \end{array}$ |  |  |  |  |  |  |  | 437 | 0.16 | 1283.9 | 1.05 | 84.958*** |
| 4 | $\begin{array}{r} 5.191^{* * *} \\ (0.207) \end{array}$ |  |  | $\begin{array}{r} 0.797^{* * *} \\ (0.099) \end{array}$ | $\begin{array}{r} -9.264^{\star * *} \\ (2.954) \end{array}$ |  |  |  |  |  |  | 437 | 0.18 | 1276.1 | 1.04 | 48.260*** |
| 5 | $\begin{gathered} 5.717^{* * *} \\ (0.142) \end{gathered}$ |  |  |  |  |  | $\begin{gathered} 0.881^{* * *} \\ (0.097) \end{gathered}$ |  |  |  |  | 437 | 0.16 | 1285.8 | 1.05 | 82.659*** |
| 6 | $\begin{array}{r} 6.594^{* * *} \\ (0.218) \end{array}$ |  | $\begin{array}{r} -1.349^{* * *} \\ (0.257) \end{array}$ | $\begin{array}{r} 0.841^{* * *} \\ (0.093) \end{array}$ |  |  |  |  |  |  |  | 437 | 0.21 | 1258.9 | 1.02 | 58.877*** |
| 7 | $\begin{array}{r} 6.149^{* * *} \\ (0.185) \end{array}$ |  |  | $\begin{array}{r} 0.894^{* * *} \\ (0.095) \end{array}$ |  |  |  | $\begin{array}{r} 32.906 * * * \\ (8.965) \end{array}$ |  |  |  | 437 | 0.19 | 1272.5 | 1.03 | 50.434*** |
| 8 | $\begin{array}{r} 5.701^{* * *} \\ (0.138) \end{array}$ |  |  |  |  |  |  |  |  |  | $0.887^{* * *}(0.096)$ | 437 | 0.16 | 1283.2 | 1.05 | 85.791*** |
| 9 | $\begin{array}{r} 6.466^{* * *} \\ (0.217) \end{array}$ |  |  | $\begin{array}{r} 1.038^{* * *} \\ (0.100) \end{array}$ |  |  |  |  | $\begin{array}{r} -1.319^{* * *} \\ (0.288) \end{array}$ |  |  | 437 | 0.20 | 1265.2 | 1.02 | 54.926*** |
| 10 | $\begin{array}{r} 6.288^{* * *} \\ (0.197) \end{array}$ |  |  | $\begin{array}{r} 1.001^{* * *} \\ (0.098) \end{array}$ |  | $\begin{array}{r} -1.973^{* * *} \\ (0.470) \end{array}$ |  |  |  |  |  | 437 | 0.19 | 1268.5 | 1.03 | 52.898*** |
| 11 | $\begin{array}{r} 5.963^{* * *} \\ (0.146) \\ \hline \end{array}$ |  |  | $\begin{array}{r} 0.710^{* * *} \\ (0.101) \\ \hline \end{array}$ |  |  |  |  |  | $\begin{array}{r} -2.125^{* * *} \\ (0.452) \\ \hline \end{array}$ |  | 437 | 0.20 | 1264.2 | 1.02 | 55.575*** |

Table 6. Parameter estimates for biomass from selected models at species level

| Model | Explanotory variable |  |  |  |  |  |  |  |  |  |  |  |  |  |  | N | Adj.R2 | AIC |  | RSE | F.value |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Intercept | logTH | logSm | $\log \left(\mathrm{Sm}^{*}{ }^{\text {TH }}\right.$ ) | $\log S$ | $\log \left(S^{*}{ }^{*}{ }^{\text {H }}\right.$ ) | $\log D$ | $\log \left(D^{*} T H\right)$ | $\log \left(E^{\star} T H\right)$ | $\log \left(\mathrm{Mi}^{*} T \mathrm{~T}+1\right)$ | $\log G$ | $\log (E+1)$ | $\log (E+1)^{\wedge} 2$ | $\log (\mathrm{D}+1)$ | $\log (D+1)^{\wedge} 2$ |  |  |  |  |  |  |
| Pinus pinea |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1 | $\begin{gathered} \hline 6.575^{* * *} \\ (0.191) \end{gathered}$ | $\begin{aligned} & \hline 0.937^{* * *} \\ & (0.163) \end{aligned}$ |  |  |  |  |  |  |  |  |  |  |  |  |  | 177 | 0.16 |  | 488.5 | 0.95 | 33.191*** |
| 2 | $\begin{aligned} & 6.158^{* * *} \\ & (0.249) \end{aligned}$ | $\begin{gathered} 0.926^{* * *} \\ (0.160) \end{gathered}$ | $\begin{gathered} -8.738^{* *} \\ (3.391) \end{gathered}$ |  |  |  |  |  |  |  |  |  |  |  |  | 177 | 0.18 |  | 483.8 | 0.94 | $20.452^{* * *}$ |
| 3 | $\begin{gathered} 6.596^{* * *} \\ (0.199) \end{gathered}$ |  |  | $\begin{aligned} & 0.917^{* * *} \\ & (0.163) \end{aligned}$ |  |  |  |  |  |  |  |  |  |  |  | 177 | 0.15 |  | 489.9 | 0.96 | 31.494*** |
| 4 | $\begin{array}{r} 7.986^{* * *} \\ (0.662) \end{array}$ | $\begin{gathered} 0.923^{* * *} \\ (0.161) \end{gathered}$ |  |  | $\begin{gathered} -1.230^{* *} \\ (0.553) \end{gathered}$ |  |  |  |  |  |  |  |  |  |  | 177 | 0.17 |  | 485.5 | 0.94 | 19.444*** |
| 5 | $\begin{array}{r} 5.500^{* * *} \\ (0.074) \end{array}$ |  |  |  |  | $\begin{array}{r} 0.774^{* * *} \\ (0.162) \end{array}$ |  |  |  |  |  |  |  |  |  | 177 | 0.11 |  | 497.5 | 0.98 | 22.873 *** |
| 6 | $\begin{gathered} 7.249^{* * *} \\ (0.289) \end{gathered}$ | $\begin{gathered} 0.988^{* * *} \\ (0.160) \end{gathered}$ |  |  |  |  | $\begin{array}{r} -0.935^{* * *} \\ (0.306) \end{array}$ |  |  |  |  |  |  |  |  | 177 | 0.19 |  | 481.2 | 0.93 | $22.060^{* * *}$ |
| 7 | $\begin{gathered} 5.782^{* * *} \\ (0.098) \end{gathered}$ |  |  |  |  |  |  | $\begin{gathered} 0.532^{* * *} \\ (0.145) \end{gathered}$ |  |  |  |  |  |  |  | 177 | 0.07 |  | 506.2 | 1.00 | 13.398*** |
| 8 | $\begin{gathered} 6.594^{* * *} \\ (0.193) \end{gathered}$ |  |  |  |  |  |  |  | $\begin{aligned} & 0.943^{* * *} \\ & (0.163) \end{aligned}$ |  |  |  |  |  |  | 177 | 0.16 |  | 488.1 | 0.95 | $33.613^{* * *}$ |
| 9 | $\begin{gathered} 5.004^{* * *} \\ (0.129) \\ \hline \end{gathered}$ |  |  |  |  |  |  |  |  | $\begin{array}{r} 2.864^{* \star}{ }^{1} \\ (0.556 \end{array}$ |  |  |  |  |  | 177 | 0.13 |  | 494.3 | 0.97 | 26.489*** |
| Quercus faginea |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1 | $\begin{array}{r} 4.278^{* * *} \\ (0.170) \\ \hline \end{array}$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 157 | 0.023 |  | 183.2 | 0.43 | 4.632** |
| Quercus ilex |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1 | $\begin{array}{r} 4.241^{* * *} \\ (0.126) \\ \hline \hline \end{array}$ |  |  |  |  |  |  |  |  |  | 0.168 $(0.0$ |  |  |  |  | 69 | 0.157 |  | 74.3 | 0.403 | 13.702*** |

## 5. - DISCUSSION

Our finding revealed that the variation of tree biomass can be accounted by negative influence of $D$ and positive influence of TH indicating that specific dominance in the stand influenced negatively and height heterogeneity influenced positively on biomass at community level. For the species level analysis, the variation of biomass of Pinus pinea can be explained by the same model as community level analysis which highlighted the negative impact of $D$ and the positive impact of TH on biomass. This results is agreement with Bohn \& Huth, (2017) who examined an influence of species diversity and forest structure on aboveground biomass over a broad range of forest stands and found out a positive relation between forest structural diversity and forest productivity. The same result was found in Riofrío et al., (2017). Size heterogeneity enables bigger trees to obtain greater amount of a certain resource and use them more efficiently than small trees (Brockerhoff et al., 2017b). In our stand, mixture of the Pine, Quercus faginea, Quercus ilex and Juniperus thurifera might create a different canopy strata; top layer occupied by Pinus pinea, enabling the light-demanding species - Pine to capture more light and grow better than other species and become dominant in the stand.

The variation of biomass for Quercus faginea and Quercus ilex were predicted by basal area proportion of species (Gp). The examined diversity indices such as $\mathrm{Sm}, \mathrm{Sn}$, D, E, Mi, MS, S, W, A, TH were found not significant relation with biomass of Quercus. This might be explained by abundance of Pinus pinea. The abundance of Pine have an strong inhibitory effect on the abundance and richness of understory species through light, water, and soil nutrients and thus reversely influences on biomass productivity of understory species (Laughlin \& Grace, 2006). Moreover, biomass of individual tree in a given stand is not only the reflection of diversity (species richness, composition and structure) but also various internal and external factors such as age, stand density, site productivity, competition at the tree level, climate, soil (texture, moisture content), geographical location, and length of grown season (Con et al., 2013; Poudel \& Hailemariam, 2015) which might not be reflected by the available metrics or models that we are considered in this study.

One notable thing is that almost all the predictor variables of significant models (except model 1 in Table 6) for Pinus pinea were identical with the community level models in Table 5. This might be fact that community level analysis may be influenced by characteristic of Pinus pinea due to its dominance in the stand. This can be explained by "selection effect" which describes the impact of the most productive species on relationship between species richness and productivity. Positive relation between productivity (biomass accumulation) and tree diversity largely depends on presenting highly productivity species in multi-cultural communities (Tilman, 1999). However, in our case the proportion of the most productive, dominant species (Pinus pinea) showed a negative effect on biomass stand as represented by D in Eq. 18 \& Eq. 19. As stresstolerant and pioneer species, Pinus has the ability to become a dominant tree species in the mixed forest and accumulate biomass in a short time and it is considered as a strong competitor species with relatively high production due to its prolonged photosynthetic activity (coniferous evergreen tree) and high nutrient uptake through the rapid turnover of nutrients (Li, Su, Lang, Liu, \& Ou, 2018). In old growth stand, Pinus with large diameter have a greater contribution to the stand biomass than small diameter trees (Baishya \& Barik, 2011). In terms of complementarity of the species in this stand, Pinus pinea may facilitate development of Quercus by increasing seed protections, enhancing habitat condition which promote the recruitment of Quercus (Sheffer, 2012). Nevertheless, the facilitation of Pine for Quercus colonization depends on many factors such as stand density, development stage of Quercus, and environmental conditions. Pine forests with intermediate density enhance the site conditions for successful colonization of Quercus by reducing light intensity, creating partial shading and
improving the soil moisture status for Quercus seedlings. However, there is an opposition between suitable condition for recruitment and suitable condition for further growth and development of Quercus species that after seedlings and saplings stages (Puerta-Piñero, Gómez, \& Valladares, 2007). In dense forest with poor environmental condition, although Pinus improved soil properties during a short period (a decade), it causes in decrement of soil moisture which may reduce recruitment of Quercus in their subcanopy. Low light interception levels and competition for water with Pinus reduces Quercus colonization in poor environmental condition. Maestre \& Cortina, (2004) emphasized that Pine plantation in semi-arid environment don't facilitate the establishment of Quercus and causes in reduction of species richness and all plant cover. Therefore, based on these reviews, we can say that Pinus pinea might be a main contributor for biomass of the stand whereas its abundance has negatively impact on biomass of coexisting species i.e Quercus faginea, Quercus ilex and Juniperus thurifera.

## 6. - CONCLUSIONS

In this study, we examined the relationship between tree biomass and diversity in Llano de San Marugan, Valladolid, Spain at stand and individual species level by a various linear and non-linear models. After thoughtful examination of 537 models with 11 predictor tree diversity indices, we found out that there is a relation between tree biomass and diversity although this relation varies among the species. A stand level analyze revealed that tree biomass-diversity relation can be explained by an interaction of negative affect of abundance of dominant species and positive effect of tree' height heterogeneity which indicates that tree biomass increases as abundance of dominant species decreases and height heterogeneity increases. This result was identical for Pinus pinea. For Quercus faginea and Quercus ilex, only the species proportion of basal area $\left(G_{p}\right)$ has a positive relation with biomass. The examined diversity indices were found not to have significant explanatory power for the explanation of biomass variation for Quercus species and Juniperus thurifera.

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## ANNEX

Annex 1. Descriptive statistics of stand variables (437 trees in the one hectare plot)

| Variables | Mean | St.Dev | Min | Pctl(25) | Pctl(75) | Max |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| B | 137.4 | 196.7 | 2.9 | 26.2 | 128.4 | 1.067 .5 |
| d | 16.6 | 11.7 | 3.0 | 8.6 | 23.1 | 50.5 |
| h | 5.8 | 2.5 | 2.0 | 4.0 | 7.6 | 13.0 |
| V | 0.1 | 0.2 | 0.001 | 0.01 | 0.1 | 1.2 |
| $\mathrm{Gi}(\mathrm{m} 2 / \mathrm{ha})$ | 14.3 | 3.1 | 8.8 | 12.5 | 16.8 | 19.4 |
| Sm | 1.0 | 0.02 | 0.9 | 1.0 | 1.0 | 1.0 |
| Sn | 3.3 | 0.4 | 2.4 | 3.2 | 3.5 | 3.9 |
| E | 1.0 | 0.01 | 1.0 | 1.0 | 1.0 | 1.0 |
| D | 2.1 | 0.4 | 1.2 | 1.9 | 2.3 | 2.6 |
| Mi | 0.6 | 0.3 | 0.0 | 0.5 | 0.8 | 1.0 |
| MS | 0.3 | 0.1 | 0.0 | 0.2 | 0.4 | 0.6 |
| W | 0.5 | 0.2 | 0.0 | 0.2 | 0.8 | 1.0 |
| S | 0.3 | 0.2 | 0.1 | 0.2 | 0.3 | 0.9 |
| A | 2.5 | 0.8 | 0.0 | 1.9 | 3.1 | 3.7 |
| TH | 0.3 | 0.1 | 0.0 | 0.2 | 0.4 | 0.7 |

$B$ - total biomass (kg); d - breast height diameter ( m ); h - total height ( m ), V - volume $\left(\mathrm{m}^{3}\right), \mathrm{Sm}$ - simson index; Sn - shannon index; E - evenness index; G- basal area (m2/ha), D - barker Parker index, Mi - mingling index; MS - spatial diversity status; W uniform angle index; S - segregation index; A - vertical profile index; TH - height differentiation index.

Annex 2. Tree attributes by species

| $\#$ | Species | N | $\mathrm{d}(\mathrm{cm})$ | $\mathrm{h}(\mathrm{m})$ | $\mathrm{v}(\mathrm{m} 3)$ | $\mathrm{g}(\mathrm{m} 2)$ | $\mathrm{B}(\mathrm{kg})$ | Sm | Sn | D | E | Mi | MS | S | W | A | TH |
| :--- | :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 1 | Pinus pinea | 177 | 27.512 | 8.163 | 0.256 | 0.070 | 290.110 | 0.955 | 3.215 | 1.985 | 0.987 | 0.549 | 0.251 | 0.194 | 0.489 | 1.900 | 0.366 |
| 2 | Quercus faginea | 157 | 9.604 | 4.183 | 0.019 | 0.008 | 38.757 | 0.963 | 3.390 | 2.141 | 0.987 | 0.562 | 0.260 | 0.239 | 0.497 | 2.965 | 0.263 |
| 3 | Quercus ilex | 69 | 9.100 | 4.122 | 0.013 | 0.007 | 27.122 | 0.969 | 3.548 | 2.130 | 0.987 | 0.558 | 0.270 | 0.612 | 0.446 | 3.137 | 0.226 |
| 4 | Juniperus thurifera | 34 | 7.626 | 4.331 | 0.271 | 0.005 | 21.764 | 0.956 | 3.202 | 2.189 | 0.981 | 0.765 | 0.312 | 0.241 | 0.507 | 2.683 | 0.251 |

Average values are presented for the tree species variables: B - above-ground biomass (kg); d -tree diameter at breast height ( cm ); h - total height $(m)$; v - volume $\left(\mathrm{m}^{3}\right)$; g - basal area per tree ( $\mathrm{m}^{2}$ ), Mi - Mingling index; MS - Spatial diversity status; A - vertical profile Index; W - Uniform angle index; S - segregation index; TH - height differentiate index; G - basal area per quadrant ( $\mathrm{m}^{2} / \mathrm{ha}$ ); Sm - simpson index; Sn - shannon index; D -Berker- Parker index; E - evennes index; R - aggregation index, respectively.

Annex 3. Main attributes of tree by quadrant.

|  |  | Tree variables |  |  |  |  |  |  |  |  |  |  | Stand variables |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| number | of trees | $B$ | $d$ | $h$ | $v$ | $g$ | Mi | MS | A | W | $S$ | TH | G | Sm | $S n$ | D | $E$ | $R$ |
| 1 | 26 | 110.4 | 14.1 | 5.4 | 0.18 | 0.027 | 0.55 | 0.25 | 2.29 | 0.47 | 0.21 | 0.29 | 11.06 | 0.96 | 3.18 | 2.60 | 0.98 | 1.02 |
| 2 | 31 | 127.5 | 16.0 | 5.7 | 0.14 | 0.030 | 0.65 | 0.27 | 2.56 | 0.52 | 0.21 | 0.29 | 14.73 | 0.97 | 3.40 | 1.94 | 0.99 | 1.27 |
| 3 | 21 | 152.0 | 16.5 | 6.0 | 0.19 | 0.034 | 0.73 | 0.35 | 2.25 | 0.48 | 0.22 | 0.36 | 11.36 | 0.95 | 2.97 | 2.33 | 0.97 | 1.00 |
| 4 | 34 | 132.8 | 16.4 | 5.6 | 0.18 | 0.032 | 0.71 | 0.34 | 2.57 | 0.54 | 0.22 | 0.30 | 16.81 | 0.97 | 3.41 | 2.29 | 0.98 | 0.92 |
| 5 | 12 | 272.9 | 25.8 | 7.5 | 0.38 | 0.065 | 0.50 | 0.18 | 1.59 | 0.52 | 0.17 | 0.41 | 12.55 | 0.91 | 2.47 | 1.33 | 0.99 | 0.99 |
| 6 | 29 | 130.3 | 16.5 | 5.6 | 0.25 | 0.031 | 0.59 | 0.26 | 2.62 | 0.45 | 0.18 | 0.33 | 14.27 | 0.96 | 3.33 | 1.93 | 0.99 | 1.15 |
| 7 | 28 | 140.6 | 17.5 | 5.9 | 0.11 | 0.033 | 0.65 | 0.29 | 2.41 | 0.54 | 0.24 | 0.33 | 14.80 | 0.96 | 3.29 | 2.15 | 0.99 | 1.00 |
| 8 | 53 | 83.4 | 13.1 | 5.0 | 0.07 | 0.020 | 0.53 | 0.24 | 3.35 | 0.53 | 0.39 | 0.21 | 16.63 | 0.98 | 3.94 | 2.21 | 0.99 | 1.06 |
| 9 | 26 | 93.5 | 12.9 | 5.0 | 0.17 | 0.021 | 0.64 | 0.29 | 2.52 | 0.49 | 0.21 | 0.28 | 8.76 | 0.96 | 3.20 | 2.17 | 0.98 | 1.12 |
| 10 | 13 | 353.7 | 28.6 | 8.0 | 0.21 | 0.081 | 0.31 | 0.12 | 1.56 | 0.38 | 0.18 | 0.36 | 16.89 | 0.92 | 2.54 | 1.18 | 0.99 | 1.08 |
| 11 | 23 | 173.9 | 17.8 | 6.0 | 0.04 | 0.038 | 0.60 | 0.30 | 2.42 | 0.38 | 0.29 | 0.33 | 14.14 | 0.95 | 3.08 | 2.30 | 0.98 | 0.89 |
| 12 | 36 | 66.7 | 12.6 | 5.0 | 0.09 | 0.016 | 0.39 | 0.18 | 2.81 | 0.53 | 0.53 | 0.22 | 9.46 | 0.97 | 3.52 | 1.89 | 0.98 | 0.97 |
| 13 | 11 | 365.9 | 29.9 | 8.3 | 0.36 | 0.085 | 0.55 | 0.22 | 1.54 | 0.45 | 0.16 | 0.37 | 14.93 | 0.91 | 2.38 | 1.38 | 0.99 | 1.21 |
| 14 | 25 | 175.8 | 20.8 | 7.1 | 0.18 | 0.044 | 0.41 | 0.16 | 2.13 | 0.49 | 0.29 | 0.31 | 17.48 | 0.96 | 3.18 | 1.47 | 0.99 | 1.03 |
| 15 | 31 | 105.5 | 14.8 | 5.3 | 0.01 | 0.025 | 0.60 | 0.29 | 2.71 | 0.36 | 0.34 | 0.33 | 12.46 | 0.97 | 3.40 | 2.58 | 0.99 | 1.02 |
| 16 | 38 | 131.3 | 17.1 | 6.2 | 0.02 | 0.032 | 0.62 | 0.32 | 2.61 | 0.51 | 0.28 | 0.30 | 19.44 | 0.97 | 3.60 | 2.11 | 0.99 | 1.22 |

Average values are presented for the tree stand variables: B- above-ground biomass (kg); d - tree diameter at breast height ( cm ); h - total height $(m)$; v - volume $\left(m^{3}\right) ; g$ - Basal area per tree $\left(m^{2}\right)$, Mi - mingling index; MS - spatial diversity status; $A$ - vertical profile Index; $W$ - uniform angle index; S - segregation index; TH - height differentiate index; G - basal area per quadrant ( $\mathrm{m}^{2} / \mathrm{ha}$ ); Sm - simpson index; Sn - shannon index; D -Berker-Parker index; E - evennes index; R - aggregation index, respectively.

Annex 4. R scripts































[^0]:    Source: (Ruiz-Peinado Gertrudix et al., 2012; Ruiz-Peinado et al., 2011).

