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Article

Disentangling the relationship between tree biomass yield and tree diversity in Mediterranean Mixed Forests

Felipe Bravo[1,2,] *, Ana Martín Ariza[1,2], Narangarav Dugarsuren[1,2], Cristóbal Ordóñez[1,2]

[1] Instituto Universitario de Investigación y Gestión Forestal Sostenible – iuFOR. Universidad de Valladolid - INIA. Avda.Madrid s/n. 34004. Palencia. Spain
[2] Departamento de Producción Vegetal y Recursos Forestales, ETS de Ingenierías Agrarias. Universidad de Valladolid. Palencia, Spain
* Correspondence: fbravo@pvs.uva.es

Abstract: Tree biomass and diversity relationship in mixed forest impacts on forest ecosystem services provisions. Tree biomass yield is driven by several aspects such as species identity, site condition, stand density, tree age as well as tree diversity expressed as species mingling and structural diversity. By comparing diverse degrees of tree mixture in natural forests we can insight on the ecosystem services provision level and dynamic. Two monitoring sites in the Castilian Northern Plateau (Spain) have been analyzed to disentangle the relationships between biodiversity levels and tree biomass yield. Two permanent one ha squared plots were established at Llano de San Marugan and Valdepoza. In each plot all individual trees were measured (diameter and height), georeferenced and its species identity defined. Tree species in the two sites were *Pinus sylvestris, Pinus nigra, Pinus pinea, Quercus pyrenaica, Quercus ilex, Quercus faginea* and *Juniperus thurifera*. From these datasets ten diversity indices that fall in three categories (species richness indices, species compositional/mingling indices and vertical structural indices) were used as predictor variables to fit several candidate models. By merging the trees by site (without considering the species identity) selected models include individual tree basal area as explanatory variable combining by addition or interaction with diversity indices. When species are analyzed independently structural diversity impacts on biomass yield in combination (additive or multiplicative) with tree size is negative *Pinus nigra* and positive for the other species.

Keywords: Modeling, forest structure, silviculture, pine, oaks, juniper

1. Introduction

Mediterranean forests are characterized by a remarkable set of features that make them naturally and aesthetically attractive, but also quite fragile [1]. Mediterranean forestry is focused on a multi-functional approach, 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 [2]. 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 [1]. Dry, hot, harsh climate along with long lasting and frequent droughts, pest, and diseases, increasing the risk of largescale 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 has 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 [3, 4]. 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 [5]. 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 [6]. High biodiversity levels are linked with high forest productivities [7] leading to a general rule of thumb regarding the promotion of mixed versus pure forests. However, forest multifunctionality must include also other components not directly assessed by diversity or biomass yield. Despite this general positive relationship between diversity and productivity for temperate forests has been reported a large variation in terms of species richness leading to stress the importance of species identity in the mixture [8]. Species identity can modify the mixture outcomes so by assessing the impact of different mixtures composition we can insight on the outcomes and delineate adequate management strategies. The loss of biodiversity imposed by anthropogenic and climatic change has stress the importance of diversity worldwide over the last decades [7, 9, 10]. 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 [11]. 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 [7, 12]. 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 such as food production, climate regulation, pest control, pollination [13, 14]. However, contradictory results have been documented for the relationship between species diversity and biomass finding negative impact [10] or no change [15] in biomass yield with species diversity levels. In addition, loss of biodiversity ranks among the most pronounced changes to environment [16], reduction of diversity along with species composition changes alter fluxes of energy and essential services that ecosystem provides to human society such as production of food, pest and disease control or water purification [17]. Biodiversity are largely and irreversibly being degraded and lost globally due to direct drivers, i.e. habitat disturbance, habitat fragmentation, land use change, over-exploitation 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 [18]. 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 [14] and providing required resources and suitable habitat for other forest species [19]. The most 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 [20]. 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 [21].

Two main mechanisms explain the reasons that biodiversity influences 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 [21]. Complementarity between species traits can lead to over or underyielding in mixed forests in relation with monocultures. For instance, tree species that have different root morphologies occupy different soil profile which potentially allowing them to exploit soil resources from different soil depth. Also differences in shade tolerance or in foliage persistence during the year can lead to complementarity. However, it should be noted that these complementarities occur solely when co-existing species exhibits various forms of niche differentiation that allow them to capture resources in different space or time [22, 23]. 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 leads to 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.

Therefore, our main objective was to explore the relationship between tree and structural diversity and forest biomass in Mediterranean mixed forests. To achieve that two intensive sample plots were analyzed in the Spanish northern plateau and all individual trees in each 1-ha plot were recorded their species, measured and geopositioned. With these data different biodiversity metrics and forest biomass values were calculated. Several lineal models were fitted, evaluated, and selected to insight on the diversity and biomass relationship.

2. Materials and Methods

Two one ha squared plots (100 x 100 m) were established in 2015, each plot is part of the regional marteloscopes network and are located in Valladolid and Palencia provinces (northern Plateau in Castile and Leon region) with the latitude and longitude coordinates 41°25'37.1"N, 4°34'15.2"W and 42°36'39.6"N, 4°46'18.7"W, respectively (figure 1). Both marteloscopes are in public forests managed by the regional forest service.

Marteloscopes are silvicultural training sites that in our case (1 ha squared plots) are divided in sixteen permanent subplots, and hereafter referred as quadrats, of 25 x 25 m length. Wooden stakes were placed with GPS subcentimetric to easily access to the plot and its quadrants. Tree positions are determined with headings (in degrees) and distances and they are identified with a number and measured (diameter and height). Different management scenarios and their consequences can be discussed in marteloscopes, thus supporting, and improving the decision-making capacities in a variety of target groups including forest practitioners, forest owners, decision makers and scientists and students from different sectors. Within each quadrat, locations of all trees were recorded in geographic coordinates and their species were identified and corresponding diameter at breast height (dbh, in cm) and, total height (in m). Both marteloscopes are dominated by pines in terms of basal area and biomass (figure 2) with oaks and juniper as associated species but the mixture degree in terms of trees per ha is more evenly distributed. The diameter at breast height (in cm) and total height (in m) for tree with dbh greater than 5 cm. To avoid interferences from past management practices, the sites were established in stands where no silvicultural treatments had been applied during the previous ten years.

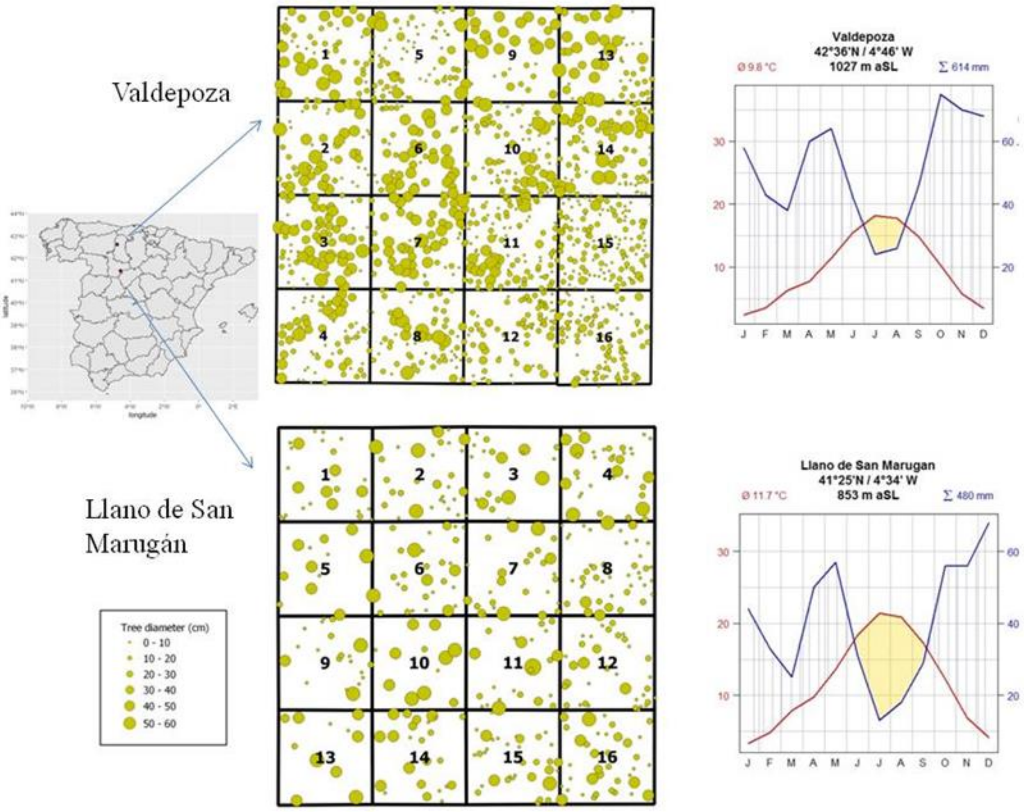

Figure 1. Study sites in Castile and Leon region (Spain) and experimental plot design and tree location for the two experimental sites (size of the circle is proportional to tree diameter (from 0 to 60 every 10 cm). Climate diagram displays monthly average temperature (red line) and precipitation (blue line) by the standards of Walter and Lieth climodiagram. Observations from 1981-2010 from AEMET weather stations and processed by ITACYL.

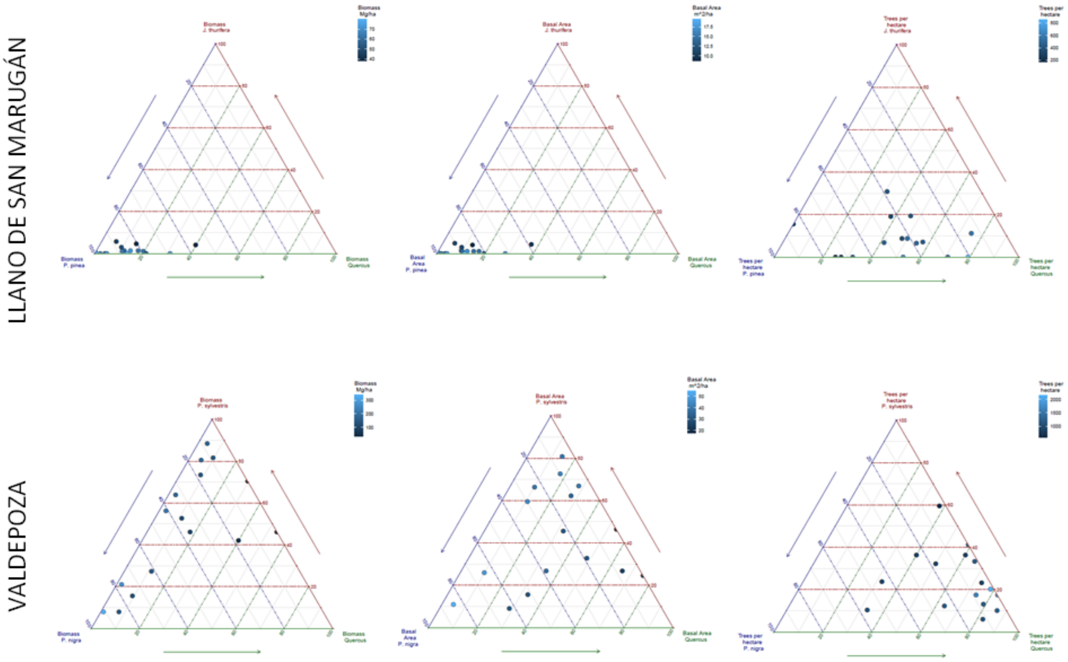

Figure 2. Ternary diagrams (ggtern package, [24]) representing the percentage of species mixture in terms of biomass, basal area, and number of trees per hectare. The representation in the axis is the identity of the species within the marteloscope: *Pinus pinea*, *Juniperus thurifera*, *Quercus* (mixture of *Quercus ilex* and *Quercus faginea*), *Pinus sylvestris*, *Quercus pyrenaica* and *Pinus nigra*. Color of each of the points (quadrats) corresponds to biomass (Mg/ha), basal area (m2/ha) and number of trees per hectare, according to the legend.

Llano de San Marugán marteloscope was installed in the municipality of Portillo (Valladolid). The mixed forest is characterized by a plantation of *Pinus pinea* with resprouting of *Quercus* (*Q. faginea* and *Q. ilex*) and natural regeneration of *Juniperus thurifera* (Figure 2). Mean annual temperature is 12 °C and mean annual precipitation is 500 mm, falling irregularly throughout the year with a minimum in the summer with mean precipitation of 64 mm (Figure 1). Fog is frequent in the long, cold winter, while summers are dry and hot with average temperature around 30ºC. The altitude of the experimental site is 853 meters. Köppen classification is defined as warm-summer Mediterranean climate (Csb). Following World Reference Base for Soil Resources classification (WRB) soil belongs to categories, leptosols as dominant and associated with regosols [25]. Leptosols comprise very thin soils over continuous rock and soils that are extremely rich in coarse fragments, while regosols are weakly developed mineral soils in unconsolidated materials that do not have a mollic or umbric horizon [26].

Valdepoza marteloscope installed in the municipality of Saldaña (Palencia), presents the species Pinus sylvestris and Pinus nigra from reforestation during the 1950s and Quercus pyrenaica as coppice (figure 2). Mean annual temperature is 10 °C and mean annual precipitation is 640 mm with summer mean precipitation of 92 mm (figure 1). The altitude of the experimental site is 1027 meters. Köppen classification is defined as temperate oceanic climate (Cfb). Following WRB soil belongs to category of cambisols [25], those soils combine soils with at least an incipient subsurface soil formation [26].

2.1. Biomass estimation

Biomass in the different components of the tree e.g., stem and branches (thick, medium and thin+needles or leaves) and roots were calculated from diameter at breast height (dbh) and total height (h) using existing allometric equations for softwood species [27] and for the hardwood species [28]. From stem diameter at dbh and h, the total biomass value is estimated by the sum of the biomass of stem, thick branch (diameter larger than 7 cm), medium branch (diameter between 2 and 7 cm) and thin branch (diameter smaller than 2 cm) with needles or leaves. Biomass data were transformed from kilograms to tons. Tree component biomass values were computed for individual tree within each quadrat and summed up to derive a summary of tree biomass for each species and marteloscope (Tables 1 and 2).

Table 1. Descriptive statistics of stand variables.

	Llano de San Marugán (437 trees/ha)				Valdepoza (1178 trees/ha)			
Variables	**Mean**	**St.Dev**	**Min**	**Max**	**Mean**	**St.Dev**	**Min**	**Max**
B	134.4	196.7	2.9	1067.5	129.6	223.7	4.4	1139.6
d	16.6	11.7	3.0	50.5	16.5	10.5	4.7	49.3
h	5.8	2.5	2.0	13.0	10.6	5.5	1.5	23.9
V	0.13	0.2	0.001	1.2	0.24	0.37	0.002	1.8
G	14.3				35.6			
Sm	1.0	0.02	0.9	1.0	0.9	0.0	0.9	0.9
Sn	3.3	0.4	2.4	3.9	4.3	0.3	3.5	4.8
E	1.0	0.01	1.0	1.0	0.9	0.01	0.9	0.9
D	2.1	0.4	1.2	2.6	1.5	0.3	1.1	2.5
Mi	0.6	0.3	0.0	1.0	0.2	0.3	0.0	1.0
MS	0.3	0.1	0.0	0.6	0.1	0.1	0.0	0.5
W	0.5	0.2	0.0	1.0	0.6	0.2	0.0	1.0
S	0.3	0.2	0.1	0.9	0.7	0.1	0.5	0.8
A	2.5	0.8	0.0	3.7	3.4	0.7	0.0	4.6
TH	0.3	0.1	0.0	0.7	0.2	0.1	0.02	0.8

Average variable values are presented for stand level: B - total above-ground biomass (kg/ha); d - mean breast height diameter (m); h - mean total height (m), V - mean tree volume (m3/ha), G- total basal area (m2/ha), and mean tree value of: Sm - simpson index; Sn - shannon index; E - evenness index; D - Berger-Parker index, Mi – mingling index; MS - spatial diversity status; W - uniform angle index; S - segregation index; A - vertical profile index; TH - height differentiation index.

Table 2. Tree attributes by species

Species	N	d (cm)	h (m)	v (m3)	g (m2)	B (kg)	Sm	Sn	D	E	Mi	MS	S	W	A	TH
Llano de San Marugán site																
Pinus pinea	177	27.51	8.16	0.25	0.07	290.11	0.95	3.21	1.98	0.98	0.54	0.25	0.19	0.48	1.90	0.36
Quercus faginea	157	9.60	4.18	0.01	0.008	38.75	0.96	3.39	2.14	0.98	0.56	0.26	0.23	0.49	2.96	0.26
Quercus ilex	69	9.10	4.12	0.01	0.007	27.12	0.96	3.54	2.13	0.98	0.55	0.27	0.61	0.44	3.13	0.22
Juniperus thurifera	34	7.62	4.33	0.27	0.005	21.76	0.95	3.20	2.18	0.98	0.76	0.31	0.24	0.50	2.68	0.25
Valdepoza site																
Pinus nigra	139	30.77	19.13	0.74	0.08	518.65	0.98	4.12	1.81	0.98	0.42	0.21	0.60	0.68	3.00	0.25
Pinus sylvestris	266	24.11	14.02	0.49	0.06	259.01	0.98	4.24	1.63	0.99	0.53	0.22	0.65	0.65	3.20	0.24
Quercus pyrenaica	773	11.39	8.02	0.05	0.01	15.14	0.99	4.36	1.45	0.99	0.19	0.09	0.88	0.88	3.63	0.29

Average variable values are presented for tree species level: N- number of trees, B- total above-ground biomass (kg/ha); d –mean tree diameter at breast height (cm); h-mean total height (m); v – mean volume (m^3/per tree); g – mean basal area (m^2/per tree) and tree mean value of: Sm - simpson index; Sn –shannon index; E – evenness index; D – Berger-Parker index, Mi – mingling index; MS – spatial diversity status; W – uniform angle index; S – segregation index; A – vertical profile index; TH – height differentiation index.

2.2. *Tree species diversity estimation*

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 [2, 29], regeneration pattern, consequent self-thinning and past and present disturbance events [30, 31]. Stand structural diversity leads to increase species richness and contributes to forest stability and integrity [32]. Stand structural diversity combines the concepts of species richness (diversity), species composition (mixture), and spatial diversity (tree positioning) and size differentiation [33]. 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 [34], Shannon index [35], Berger-Parker index [36] and Evenness index [37]; ii) species composition indices -Mingling index [38], Spatial diversity status [39] and Segregation index [40]; iii) tree distributional indices including horizontal and vertical patterns and size differentiation, Uniform Angle Index [41], Vertical Species Profile [42], Height differentiation index [43]. 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 3-dimensionality of mixed forest structures.

The diversity indices used in this study were classified into 3 categories: i) species richness (Simpson index, Sm; Shannon index, Sn; Evenness index, E; Berger -Parker index, D), ii) species composition (Mingling, Mi; Spatial Diversity Status, MS; Segregation index, S) and iii) vertical (Vertical Profile index, A; Height Differentiation index, TH) and horizontal distribution pattern (Uniform Angle Index ,W) .The basic idea behind the diversity indices 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). In this study we extend this definition to include also structural variability in terms of relative size and spatial organization of trees.

The Simpson diversity index (Sm) [34] accounts the number of species and the abundance of each species. The index represents the probability that two individuals randomly selected from a sample belong to different species, therefore this index increases with species diversity. The Shannon index (Sn) [35] as the former, considers the abundance and evenness of the species. When all species are equally common, the value increases until the logarithm of the number of species in the sample, ln (S). On the contrary, if all abundance is concentrated in one species, and the other species are very rare, its value reduces to 0. Species evenness (E) [37] expresses how equally the individuals in the community are distributed over the different species. Low values indicate that one or a few species dominate, and high values indicate that relatively equal numbers of individuals belong to each species. Berger-Parker index (D) [36] is a measure of the numerical importance of the most abundant species in the population. The reciprocal of the index is frequently used, so that an increase in number explains a higher diversity and thus a reduced dominance.

Species spatial mingling index (Mi) describes the proportion of neighbor trees which belong to different species identity as the reference tree [38]. High degree of mingling means that trees are surrounded by different species. However, the number of different species in the structure unit was not considered, and this was a shortcoming of this index. This limitation has fulfilled in spatial diversity status index (MS) [2] which considers not only the spatial mingling, but also the number of tree species [39]. Reference tree of a frequent species is more likely to have the neighbors of the same species, reflecting low index value. On the contrary, rare species have less probability to have same neighbor species, resulting in high value of this index. Thus, spatial diversity status index is considered as a sensitive index for rare species. Segregation index (S) developed by Pielou [40] describes the degree of intermingling of two species groups [44] based on nearest-neighbor method. Values greater than 0 and below 0 indicate a trend towards segregation and association, respectively, while an independent distribution of species will reach values close to 0 [2].

Vertical Profile index (A) [42] calculation is based on the diversity index of Shannon [35]. 'A' considers both proportion of the species within a stand and the presence of each species in different height zones [45] and rises as the vertical profile increases in heterogeneity. Height Differentiation index (TH) [43] measures the variability in the vertical size between the reference tree and neighboring trees, reflecting high differentiation when reaching values close to 1. Increasing values in the Uniform Angle Index (W) indicate a transition from regular to random and then to clumped spatial pattern and defines the degree of spatial dispersion of nearest neighbors around the reference tree based on angles [41].

2.3 Statistical analysis

Different models were fitted to explain how diversity indices impact on individual tree biomass. Three general model structures tested were as follows (eq 1 to 3):

$$\boldsymbol{Y = \beta_0 + \beta_1 x_1 + \cdots + \beta_k x_j} \qquad \text{Eq.1}$$

$$\boldsymbol{Y = \beta_0 + \beta_1 x_1 + \cdots + \beta_k x_j} \qquad \text{Eq.2}$$

$$\boldsymbol{Y = \beta_0 \pi(x_i x_j)(\beta_1)^k} \qquad \text{Eq.3}$$

Where xi and xj represent different explanatory variables and βk represent the estimated parameters. Parameters were estimated by Ordinary Least Squares (OLS) multiple linear regression. When needed the models were transformed by logarithms. Basic assumptions of multiple linear regressions were tested.

Eleven predictor variables were tested: four species richness indices (Sm, Sn, D, E), three species composition indices (Mi, MS, S), four spatial distribution indices (A, TH, W) and the individual basal area per tree (Gi, m2). Different variables combinations, allowing interactions between variables, were tested (table 3) leading to 623 alternative models for each site by species and for the whole tree datasets (without considering species identity) for each marteloscope.

Table 3 Models tested including its general structure and the predictor variables.

#	Fitted models	Predictor variable		
		x_1	x_2	x_3
Single predictor (22 alternative models)				
1.	$B = \beta_0 + \beta_1 x_1$	Gi , Sm, Sn, D, E, Mi, MS, S, A, TH, W		
2.	$lnB = \beta_0 + \beta_1 lnx_1$			
Multivariate models with 2 predictors (413 alternative models)				
3.	$B = \beta_0 + \beta_1 x_1 + \beta_2 x_2$	Gi Sm, Sn, D, E	D, E, Sm, Sn, Mi, MS, S, A, TH, W	
4.	$B = \beta_0 + \beta_1 {x_1}^2 + \beta_2 {x_2}^2$			
5.	$B = \beta_0 + \beta_1 (x_1 * x_2)$			
6.	$lnB = \beta_0 + \beta_1 lnx_1 + \beta_2 lnx_2$			
7.	$lnB = \beta_0 + \beta_1 ln({x_1}^2) + \beta_2 ln({x_2}^2)$	Mi, MS, S	A, TH, W	
8.	$lnB = \beta_0 + \beta_1 ln(x_1 * x_2)$			
9.	$lnB = \beta_0 + \beta_1 \ln ({x_1}^2 * x_2)$			
Multivariate models with 3 predictors (188 alternative models)				
10.	$B = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3$	Gi	TH, A	Sm, Sn, D, E, Mi, MS, S, A, W
11.	$lnB = \beta_0 + \beta_1 lnx_1 + \beta_2 lnx_2 + \beta_3 lnx_3$			
12.	$lnB = \beta_0 + \beta_1 ln(x_1 * x_2 * x_3)$	D, E, A, Sm, S, TH,	MS, S, TH, S, W,	

Where B represents total above biomass; G is individual basal area per tree in m², Sm: Simpson index, Sn: Shannon index, E: Evenness index, D: Berger -Parker index, Mi: Mingling, MS: Spatial Diversity Status, S: Segregation index, A: Vertical Profile index, TH: Height Differentiation index, and W: Uniform Angle Index. x_1, x_2, x_3 represent the predictor variables. β_0, β_1, β_2, β_3 are the parameters of the models; Predictors variables in the same cell are independently analyzed in combination with the variables in other cells.

To select the best model for dominant tree species and for each marteloscope, five 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 ($P < 0.001$), ii) biological meaning of parameters signs and values, iii) graphical distribution of the residuals (normal Q-Q plot and predicted versus adjusted plot), iv) the adjusted R squared and v) Akaike Information Criteria (AIC). Besides, we checked collinearities between the variables (biodiversity metrics and basal area) (Wei et al., 2017) where it is found higher collinearities in both sites for Simpson and Shannon index, Mi and MS and G and B (see supplementary materials, figure S1). All statistical modeling was carried out with the R software version 3.6.2 and tidyverse package [46]

3. Results

Relationships among biodiversity metrics and forest biomass were broadly examined at stand and species level across the two mixed forest sites (the best three significant models per each site are presented at table 4). In the selected models the response variable is the natural logarithm of the biomass in megagrams per tree (Ln B) while species spatial mingling index (Mi), segregation index (S), uniform angle index (W) and height differentiation index (TH) modify in some cases by Gi (individual tree basal area) are the explanatory variables. These models were selected according to the five criteria and we present them in the table using both the Akaike's Information Criteria (AIC) and the adjusted R2 to determine which model was the most parsimonious while simultaneously explaining most of the information in the data. The significance level is p<0.001. Selected models for the whole plots (not species identity considered) are codified by site and the number (i.e, for Llano de San Marugán are M1, M2 and M3 while for the Valdepoza site are V1, V2 and V3). All the selected models were checked against deviations that prevent the use of multiple linear regressions (see figure S2 for details).

Table 4. Selected models for each site without considering species identity.

Model	M1	M2	M3	V1	V2	V3
Intercept	0.747	1.011	1.303	1.843	0.398	1.414
lnG				1.289	1.057	
ln(Mi+1)				0.509		
ln (G*TH)			0.411			
lnS					-2.398	
ln G*(Mi+1)		0.468				1.224
ln G*(W+1)	0.936					
R adj	0.964	0.976	0.945	0.91	0.956	0.898
AIC	-73.23	-254.38	114.19	1606.42	747.96	1745.14

M1, M2, M3, V1, V2 and V3 represent the three selected models for Llano de San Marugán (M) and Valdepoza (V) sites.

Selected models at stand level for Llano de San Marugán (table 4), three linear models have been highlighted (structure as shown in eq 3): M1 including as explanatory variables Gi and W, M2 including as explanatory variables Gi and Mi and M3 including as explanatory variables Gi and TH. Between these 3 models, M1 was found to be the best model for explaining tree biomass in this site, showing the positive influence of the interaction of individual tree basal area (Gi) and the spatial distribution pattern with the uniform angle index index (W) combined (transformed by logarithms) in one variable (parameter equal to 0.936). For Valdepoza site the three selected models are V1 (structure as shown in eq 1) including as explanatory variables G and Mi, V2 (structure as shown in eq 1) including as explanatory variables Gi and S and V3 (structure as shown in eq 3) including as explanatory variables Gi combined with Mi. In this case, V2 was found to be the best model for understanding the variables relationships in Valdepoza, indicating a positive relationship with tree size expressed by Gi (parameter equal to 1.057) and a negative relationship with the degree of intermingling with other species expressed by the segregation index (S) (parameter equal to -2.398).

The species analysis (table 5 for Llano de San Marugán and table 6 for Valdepoza sites) indicates that biomass (transformed by natural logarithms) is closely related with individual tree size (expressed by Gi) for all the species but modify by diversity indices (mainly vertical and horizontal structure and compositional but also diversity expressed by Simpson index). When the relationship between variables was stronger enough three alternative models were selected. For *Pinus pinea* the relation was so weak that no model was selected. For the other species in Llano de San Marugán site the selected models (table 5) included, beside the tree size (Gi) individually or modifying the other variables, the height differentiation index, TH, (*Quercus faginea*), species segregation, S, (*Quercus ilex*) and uniform angle index, W, expressing the horizontal distribution pattern (*Juniperus thurifera*). We can observe that structural diversity indexes (species composition, i.e S index and distribution pattern, i.e, W and TH) together with tree basal area (Gi) were the strongest independent predictors of forest biomass in Llano de San Marugán and for the species *Quercus faginea* (parameter equal to 0.360), *Quercus ilex* (parameter equal to 1.570) and *Juniperus thurifera* (parameter equal to 0.582),, whereas relationships for *Pinus pinea* were comparatively weak in terms of fulfilling the criteria of the distribution of the residuals (predicted versus adjusted plot). Distributions of the residuals of the selected models are exposed in figure S3.

Table 5. Candidate models by species for Llano de San Marugán site

Models	***Qf1***	***Qf2***	***Qf3***	***Qi1***	***Qi2***	***Qi3***	***Jt1***	***Jt2***	***Jt3***
Intercept	1.502	-1.006	1.28	1.629	1.102	1.57	-1.182	-1.025	-1.887
lnG	0.981								
ln(A+1)	0.029								
ln G*TH		0.36							
lnG^2*(MS+1)			0.475		0.482				
lnG*S)				0.961					
lnG^2*S						0.495			
ln G*(Mi+1)							0.548		
ln G*(W+1)								0.582	
ln G^2*TH									0.158
R adj	0.998	0.364	0.981	0.957	0.975	0.989	0.695	0.758	0.421
AIC	-883.67	113.95	-442.9	-131.35	-168.54	-224.84	-29.02	-36.86	-7.16

*Qf*1, *Qf* 2. *Qf* 3, *Qi*1, *Qi* 2. *Qi* 3, *Jt*1, *Jt* 2 and *Jt* 3 represent the selected models for *Quercus faginea* , *Quercus ilex* and *Juniperus thurifera* respectively in the site Llano de San Marugán.

The more humid site of Valdepoza (table 6) shows the main results for *Pinus sylvestris, Pinus nigra* and *Quercus pyrenaica*. In this plot for the pines four models were selected as candidates because all of them are very close in terms of normality assessment but the evaluation criteria allow us to select the best one. The selected models for Valdepoza site always include tree size (Gi) in combination with structural diversity indices (height structure, TH; for *Quercus pyrenaica* (parameter equal to 0.433) and segregation index, S, for *Pinus sylvestris* (parameters equal to 1.145 for Gi and to -0.225 for S, this trend is the same as show the model selected by Valdepoza site) or Simpson index for *Pinus nigra* (parameter equal to 6.830 for Gi and to -5.190 for Sm). All the selected models were checked against deviations that prevent the use of multiple linear regressions (see figure S4 for details).

Table 6. Candidate models by species in Valdepoza site

Models	***Qp1***	***Qp2***	***Qp3***	***Ps1***	***Ps2***	***Ps3***	***Ps4***	***Pn1***	***Pn2***	***Pn3***	***Pn4***
Intercept	-1.718	-1.367	-1.304	1.74	2.21	1.199	1.612	-0.09	1.515	5.076	0.307
lnG				1.145							
lnG*(W+1)		0.712									
lnS				-0.225							
lnG*TH	0.433										
lnG^2*(A+1)			0.387			0.603					
lnG^2*(MS+1)					0.587						
lnG^2*(W+1)							*0.58*				
G								6.868	6.85	6.83	6.81
D								0.036			
E									-1.573		
Sm										-5.19	
Sn											-0.08
R adj	0.539	0.907	0.9272	0.99	0.982	0.984	0.984	0.967	0.967	0.969	0.968
AIC	693.28	-544.98	-732.77	-284.42	-119.63	-144.31	-148.94	-471.22	-472.14	-479.02	-475.85

*Qp*1, *Qp*2. *Qp*3, (*Ps*1, *Ps*2. *Ps*3, *Ps*4, *Pn*1, *Pn*2. *Pn*3, and *Pn4* 3 represent the selected models for *Quercus pyrenaica, Pinus sylvestris* and *Pinus nigra* respectively in Valdepoza.

4. Discussion

Our main findings supported the importance of structural and spatial diversity, in combination with tree identity and size to assess biomass yield in Mediterranean mixed forests. Individual basal area, as a tree size proxy, is included in all the models both by species and without considering species identity. Our results agree with the findings from Bohn & Huth [30], who examined the 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. On the contrary, Aponte et al [46] found that forest structure diversity is the key variable to explain carbon storage in Australian forests while species- and functional-diversity indices hold a weak impact. Interestingly, Hime and Puettman [47] found no influence of tree mixture on biomass while the understory diversity was positively associated with biomass. Our team analyzing pine mixed forests in northern Spain [4] also found the positive impact of species combination on forest yield. Size heterogeneity enables bigger trees to obtain greater amount of a certain resource and use them more efficiently than small trees [29] while species complementarity due to differential traits leads to a more efficient resources use [48, 49]. These facts are reflected in the models for our drier site (Llano de San Marugán) where mixture of *Pinus pinea, Quercus faginea, Quercus ilex* and *Juniperus thurifera* create a multilayered open canopy strata where top layer is occupied by *Pinus pinea*, enabling the light-demanding species (pine) to capture more light and grow better than the other cohabitant species and become dominant in the stand.

Positive relation between productivity (biomass accumulation) and tree diversity largely depends on presenting highly productivity species in multispecific communities [23] In our case this role of highly productivity species is played by pine (*Pinus pinea* in Llano de San Marugán and *Pinus sylvestris* and *Pinus nigra* in Valdepoza). In both site pine species also facilitate the development of a low layer of oaks than in areas where pine density is lower can dominate at microsite level because pines may facilitate oak development by increasing seed protections, enhancing habitat to facilitate seedling establishment. Although there is an opposition between suitable condition for recruitment and suitable condition for further oak growth and development after seedlings and saplings stages [50], the open in the mixed pinewoods are adequate sites for the development of oak patches that enhance the mixture by including species with differential traits.

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 [5, 52] which might not be reflected by the metrics considered in this analysis.

5. Conclusions

After thoughtful examination of 623 models with 10 predictor tree diversity indices (grouped as proxies of species richness, species composition and size distribution pattern) plus a tree size proxy (individual basal area), we found out that there is a relation between tree biomass and diversity although this relation varies among the analyzed species. As expected, all the selected models include individual tree basal area as explanatory variable combining by addition or interaction with diversity indices. When data of each site is analyzed without considering the species identity the spatial dispersion results in a positive outcome in terms of biomass in our drier site (Llano de San Marugán) exposing the importance of the effect site selection in the dominance of the two similar species (*Quercus faginea* and *Quercus ilex*) and thus more productive. On the mesic site (Valdepoza) the spatial segregation shows a negative effect on yield that can be explained by the cohabitation of two pines with similar traits (*Pinus sylvestris* and *Pinus nigra*). Structural diversity shows a positive impact on biomass yield in combination (additive or multiplicative) with tree size. Only in *Pinus nigra* structural diversity (segregation index) is negatively related with biomass. Operational forestry by selection thinning can modify structural and specific diversity impacting on biomass yield and carbon sequestration. Local studies, where a careful analysis of the species composition, structural and spatial arrangement jointly with site conditions is done, are needed to orientate operational forestry to obtain diverse ecosystem services under multifunctional forest management.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1,

Figure S1. Correlation matrix using corrplot package in R (Wei and Simko, 2017). The correlation number is presented at significance level 0.05 for both experimental sites.

Figure S2. Residual graphs are referred in the first column to Llano de San Marugán (models M1, M2 and M3), and in the second column to Valdepoza (models V1,V2 y V3). On the left we examine the predicted versus residual plot with the predicted values on the x-axis and the residuals on the y-axis. On the right, quantile-quantile plot (q-q plot). Notice the x-axis for the theoretical quantiles and the y-axis for sample quantiles.

Figure S3. Residual graphs are referred in the first column to *Quercus faginea* (Qf1, Qf 2. Qf 3), the second column to *Quercus ilex* (Qi1, Qi 2. Qi 3), and the third to *Juniperus thurifera* (Jt1, Jt 2. Jt 3). On the left we examine the predicted versus residual plot with the predicted values on the x-axis and the residuals on the y-axis. On the right, quantile-quantile plot (q-q plot). Notice the x-axis for the theoretical quantiles and the y-axis for sample quantiles.

Figure S4. Residual graphs are referred in the first column to *Quercus pyrenaica* (Qp1, Qp2. Qp3), the second column to *Pinus sylvestris* (Ps1, Ps2. Ps3, Ps4) and the third to *Pinus nigra* (Pn1, Pn2. Pn3, Pn4). On the left we examine the predicted versus residual plot with the predicted values on the x-axis and the residuals on the y-axis. On the right, quantile-quantile plot (q-q plot). Notice the x-axis for the theoretical quantiles and the y-axis for sample quantiles.

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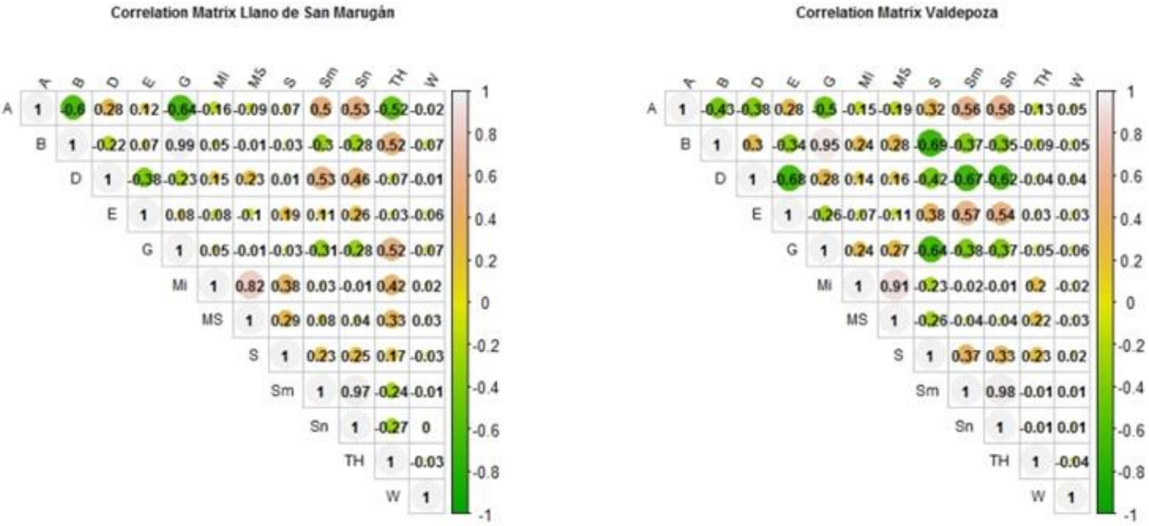
Supplementary material

Figure S1. Correlation matrix using corrplot package in R (Wei and Simko, 2017). The correlation number is presented at significance level 0.05 for both experimental sites.



Correlation Matrix Llano de San Marugán

	A	B	D	E	G	Mi	MS	S	Sm	Sn	TH	W
A	1	-0.6	0.28	0.12	-0.64	-0.16	-0.09	0.07	0.5	0.53	-0.52	-0.02
B		1	-0.22	0.07	0.99	0.05	-0.01	-0.03	-0.3	-0.28	0.52	-0.07
D			1	-0.38	-0.23	0.15	0.23	0.01	0.53	0.46	-0.07	-0.01
E				1	0.08	-0.08	-0.1	0.19	0.11	0.26	-0.03	-0.06
G					1	0.05	-0.01	-0.03	-0.31	-0.28	0.52	-0.07
Mi						1	0.82	0.38	0.03	-0.01	0.42	0.02
MS							1	0.29	0.08	0.04	0.33	0.03
S								1	0.23	0.25	0.17	-0.03
Sm									1	0.97	-0.24	-0.01
Sn										1	-0.27	0
TH											1	-0.03
W												1

Correlation Matrix Valdepoza

	A	B	D	E	G	Mi	MS	S	Sm	Sn	TH	W
A	1	-0.43	-0.38	0.28	-0.5	-0.15	-0.19	0.32	0.56	0.58	-0.13	0.05
B		1	0.3	-0.34	0.95	0.24	0.28	-0.69	-0.37	-0.35	-0.09	-0.05
D			1	-0.68	0.28	0.14	0.16	-0.42	-0.67	-0.62	-0.04	0.04
E				1	-0.26	-0.07	-0.11	0.38	0.57	0.54	0.03	-0.03
G					1	0.24	0.27	-0.64	-0.38	-0.37	-0.05	-0.06
Mi						1	0.91	-0.23	-0.02	-0.01	0.2	-0.02
MS							1	-0.26	-0.04	-0.04	0.22	-0.03
S								1	0.37	0.33	0.23	0.02
Sm									1	0.98	-0.01	0.01
Sn										1	-0.01	0.01
TH											1	-0.04
W												1

Figure S2. Residual graphs are referred in the first column to Llano de San Marugán (models M1, M2 and M3), and in the second column to Valdepoza (models V1,V2 y V3). On the left we examine the predicted versus residual plot with the predicted values on the x-axis and the residuals on the y-axis. On the right, quantile-quantile plot (q-q plot). Notice the x-axis for the theoretical quantiles and the y-axis for sample quantiles.

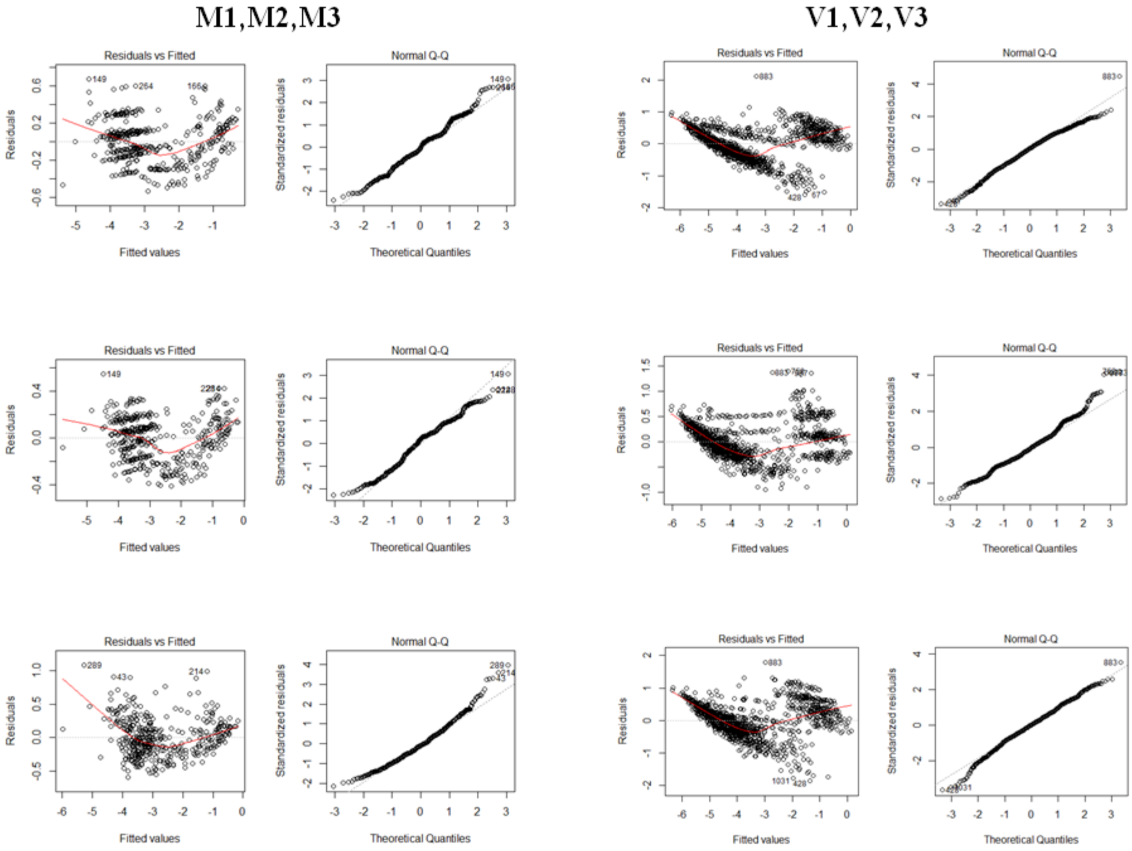


Figure S3. Residual graphs are referred in the first column to *Quercus faginea* (*Qf*1, *Qf* 2. *Qf* 3), the second column to *Quercus ilex* (*Qi*1, *Qi* 2. *Qi* 3), and the third to *Juniperus thurifera* (*Jt*1, *Jt* 2. *Jt* 3). On the left we examine the predicted versus residual plot with the predicted values on the x-axis and the residuals on the y-axis. On the right, quantile-quantile plot (q-q plot). Notice the x-axis for the theoretical quantiles and the y-axis for sample quantiles.

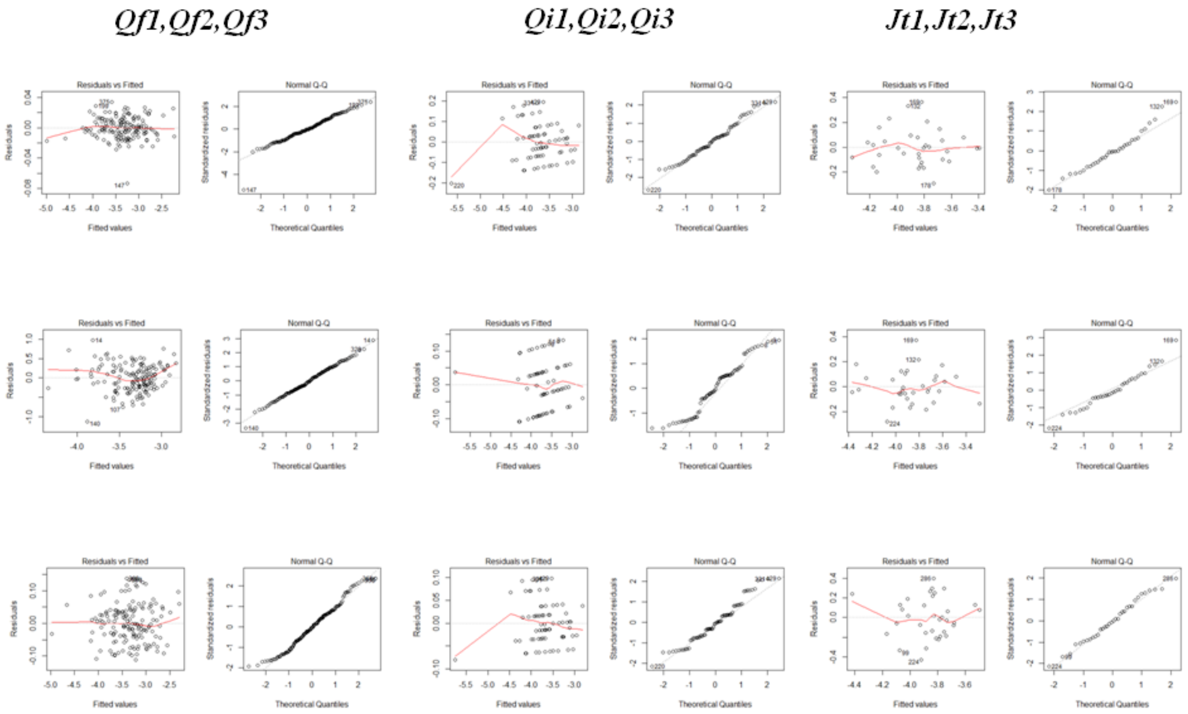


Figure S4. Residual graphs are referred in the first column to *Quercus pyrenaica* (*Qp*1, *Qp*2. *Qp*3), the second column to *Pinus sylvestris* (*Ps*1, *Ps*2. *Ps*3, *Ps*4) and the third to *Pinus nigra* (*Pn*1, *Pn*2. *Pn*3, *Pn*4). On the left we examine the predicted versus residual plot with the predicted values on the x-axis and the residuals on the y-axis. On the right, quantile-quantile plot (q-q plot). Notice the x-axis for the theoretical quantiles and the y-axis for sample quantiles.