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Functional traits related to competition for light influence tree diameter increments in a biodiversity manipulation experiment

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Abstract

Understanding how functional traits and diversity modulate plant interactions within forests is becoming a widespread research goal in ecology. We applied neighbourhood analysis to a Mediterranean biodiversity manipulation experiment (IDENT-Macomer) to assess the importance of functional traits in predicting tree diameter increments (DI) in a mixed forest. We used tree functional traits to weigh the neighbourhood competition index (NCI) and functional dispersion (FDis), which is a functional diversity metric. We found that functional traits affect competitive performance across species within a mixed forest and that resource acquisition is based primarily on trait hierarchy. We also found that traits related to competition for light, such as maximum plant height (Hmax), are the best predictors of DI. Our results reveal that NCI is a more reliable predictor than FDis, but the combination of both effects helps to better explain differences in DI. Finally, our findings show that gathering functional trait data is a practise that should be prioritised in mixed forest management due to the predictive importance of NCI and FDis in experiments with high density and species diversity.

Keywords: Mixed forest, growth model, competition, functional diversity, functional traits, predictions, IDENT

1 Introduction

Forest ecologists are increasingly concerned about the potential effects of persistent biodiversity loss on ecosystem functioning. As a result, research into the relationships between biodiversity and ecosystem functions (BEF) expanded importantly to cover a large set of ecosystem types, including forests. According to a recent review, biodiversity promotes average biomass production, temporal stability, and pollination success in forest ecosystems, as shown by the results of 258 published research that identified 726 BEF relationships (van der Plas, 2019). In the same line, tree species diversity has proven to increase forest productivity by an average of 15% when compared to monocultures (Jactel et al, 2018). These studies led ecologists to highlight the positive effects of forest management characterised by multi-species trees on ecosystem services, as opposed to the effect of monocultures (Felton et al, 2016).

Previous BEF research used models of interspecific competitive interactions in communities with various combinations of randomly chosen species (Tilman et al, 1997b). The use of plant functional traits – such as the plant size or the leaf, the wood, and seed characteristics – to evaluate individual performance in a competitive context has been an advancement in the study of plant interactions. Traits are morphological, physiological, or phenological characteristics related to the fitness and performance of the individual (Violle et al, 2007). The most commonly used functional traits in these investigations are related primarily to resource use efficiency, the competitive ability for light, carbon accumulation, or the establishment of an individual species, and include specific leaf area (SLA), maximum height (Hmax), wood density (WD), and seed mass (Westoby, 1998; Moles and Westoby, 2006; Wright et al, 2007; Chave et al, 2009; Costa-Saura et al, 2019). Functional traits have been frequently utilised to generate different plant functional diversity (FD) indices (Petchey et al, 2004; Villéger et al, 2008; Schleuter et al, 2010; Laliberté and Legendre, 2010), and have been used as a metric to assess individual performance. Functional diversity has been widely recognized as a hot-topic by the scientific community for being one of the main factors explaining plant productivity (Tilman et al, 1997a), a key driver of ecosystem processes (Lohbeck et al, 2015; Kuebbing et al, 2018) and ecosystem functions (Tobner et al, 2014, 2016). Diversity indices have been researched in a large and growing body of literature in the last years. They are expected to have a relevant predictive power, which should be carefully studied for forest management purposes.

As a common methodology, models or statistical analyses at the community level have been utilised in the majority of BEF studies (Loreau and Hector, 2001; Fox, 2005). Building models at the population or community levels is a common approach to answer ecological questions. Still, it is also particularly insightful to understand how individuals interact with each other and their environment (Grimm and Railsback, 2005). For that reason, individual-based models (IBMs) are an advantageous approach because important insights at the population or community level emerge from the individual-level processes (Grimm et al, 2006; DeAngelis and Grimm, 2014; DeAngelis, 2018). The analysis of distance-dependent competitive interactions with neighbours, a critical aspect of IBMs, explores how a target plant is affected by the sum of effects from all neighbours (Bella, 1971; Uriarte et al, 2004a; Thorpe et al, 2010). One of the first works on neighbourhood analysis was carried out by Bella (1971), implementing the Competitive Influence-Zone Overlap model. This work found that when trees of different sizes compete in a forest stand, they affect each other differently, with large crown trees covering a larger area and overlapping smaller neighbours in the nearest distance. Most early studies tended to oversimplify the mechanics of plant interactions, but more recent models have been upgraded by incorporating details about how neighbouring plants compete for light (Canham et al, 2004; Astrup et al, 2008; Coates et al, 2009; Fichtner et al, 2015), or in response to site and climate change (Canham et al, 2006; Gómez-Aparicio et al, 2011). In this line, other studies highlight the differences in intra- and interspecific competition based on how species acquire resources through competition, i.e., either in an asymmetric or symmetric mode (Cattaneo et al, 2018). Previous studies ascribed the interaction coefficient between a target individual and its neighbour to three different theories: trait similarity, trait hierarchy and phylogenetic similarity (Kunstler et al, 2012, 2016; Fortunel et al, 2016). The trait similarity theory states that species competition decreases with trait distance, without any dominance in the acquisition of resources. In other words, the likelihood that two species can coexist increases with their niche distance. In contrast, the trait hierarchy theory predicts the dominance of superior competitors in the crowding dynamics. For example, in competition for light acquisition, plant species with the greatest maximum height (Hmax) may have more adverse effects on neighbours with low Hmax. On the other hand, the phylogenetic similarity theory is not based on trait distances, but on cophenetic distances. Furthermore, in the context of climate change, it is imperative to understand how abiotic stress (such as water shortage) affects resource competition. Interestingly, the stress-gradient hypothesis holds that when stress levels rise in an ecosystem, mutually beneficial interactions become more important while negative interactions, such as competition, become less relevant (Bertness and Callaway, 1994). However, there is still some uncertainties regarding under which conditions the hypothesis holds true (Forrester and Bauhus, 2016; Belluau et al, 2021).

In this study, we applied the spatially explicit neighbourhood model of growth of twelve saplings of Mediterranean species to an experimental site belonging to the International Diversity Experiment Network with Trees (IDENT; Tobner et al (2014); Verheyen et al (2016)) designed with trees planted 40 cm apart. In particular, our goal was to identify the explanatory variables that contribute the most to the prediction of aboveground tree growth in mixed forests, which might enhance productivity through correct plantation and reforestation plans. This information allows us to deduce which functional traits are most frequently associated with competitive interactions and which resource acquisition mechanism theory is the most prevalent in a highly populated mixed forest. We used tree diameter increments (DI) as an indicator of tree biomass growth (Seidel et al, 2015) to test the following hypotheses: H_1 - The interaction coefficient of the species-specific neighbourhood competition is not symmetric but asymmetric, where this asymmetry is predicted by functional traits. H_2 – If hypothesis H_1 is correct, asymmetric competition is predicted by hierarchical distances of traits related to acquisition of light. In particular, we expect that in a densely populated forest characterised by high diversity in species and canopy structures, architectural traits such as maximum tree height (Hmax) will play a crucial role in competition for light demand (Poorter et al, 2006). H_3 – Asymmetric competition is based on the trait similarity theory. Specifically, this translates into more intense competition for light interception between species occupying similar niche spaces. As a final hypothesis, we assumed (H_4) that neighbourhood functional diversity can predict DI. In this last case we used functional dispersion (FDis; Laliberté and Legendre (2010)) as a statistical measure of functional diversity. Since the experimental site includes a water stress gradient, the hypotheses were evaluated in both control and water-stressed conditions. In this way, we can understand which traits are involved in the competition for water resources and how water availability modulates the effect of the most important variables in tree growth.

2 Material and methods

2.1 IDENT-experiment and field sampling

The experimental site, IDENT-Macomer, is located within the nursery of the "St. Antonio-Sardinian Forest Authority" close to Macomer (40°14'N; 8°42'E; 640 m above sea level) on the island of Sardinia, Italy. The site is part of the International Diversity Experiment Network with Trees (Tobner et al, 2014), a global network of tree diversity manipulation experiments that allows researchers to investigate the relationships between biodiversity and ecosystem functions. The experimental site has a Mediterranean climate with average monthly temperatures ranging from 6.5 °C (January) to 23.9 °C (August), and monthly rainfall ranging from 135 mm (December) to 7 mm (July), for a total annual rainfall of 905 mm. The experiment was established in 2014, and is structured similarly to other IDENT experiments, with trees distributed over 7 blocks (4 irrigated and 3 non-irrigated) and 308 plots (Fig. 1). The blocks are exact replicas in terms of tree species communities in the plot, and each one includes 44 plots of 3.2 m by 3.2 m, distributed randomly within the blocks. Within each plot, 64 seedlings were planted at a distance of 40 cm. The distribution of tree species in each plot was also randomized, but species clumping was prevented. Species relative abundances are similar among plots as well as within the inner, middle, and outer frames (See Fig. 1 of Van de Peer et al (2018)).

In total, 12 native Mediterranean woody species were selected, three of them being shrubs (*A. unedo*, *P. latifolia*, *P. lentiscus*), and nine of them being trees (*A. monspessulanum*, *F. ornus*, *O. europea*, *P. halepensis*, *P. pinea*, *P. pinaster*, *Q. ilex*, *Q. pubescens*, and *Q. suber*). A first diversity gradient was developed within each block by manipulating the species richness (SR) at four levels: one (12 plots), two (17 plots), four (9 plots), and six species (6 plots). A gradient of FD was built for each level of SR using a dataset of 10 functional traits (See Van de Peer et al (2018) for more detailed information). To perform the neighbourhood analysis, a total of six functional traits were used: three of the most commonly used functional traits related to resource use efficiency (SLA, Hmax, and WD), two traits related to water transport capacity (ratio of leaf area to sapwood area (LA/SA); Wright et al (2006) and water potential at which 50% of hydraulic conductivity is lost (PLC50); Pammenter and Van der Willigen (1998)), and one trait related to nutritional status for consumers (nitrogen content per unit of leaf mass (Nm); Wright et al (2004)). Shade tolerance was not included in the analysis, despite it might influence growth and competition (Uriarte et al, 2004b), since it is commonly represented by complex syndrome of traits (Reich et al, 2003).

All functional traits used in this study were measured at species level, and these include: SLA, Nm, WD, LA/SA, Hmax, and PLC50. The traits Hmax and PLC50 are derived from Van de Peer et al (2018). The diameter (at 10 cm above the ground) of 16896 trees was measured annually from 2016 to 2019 for the current study. Due to the young age of the trees (from 2 years in 2016 to 5 years in 2019), diameter at breast height could not be used.

2.2 Predictive variables

A total of 27 predictive variables were used for this study (Table 1). Tree diameter (in cm, D) measured in 2016 represents the tree size (Kunstler et al, 2012; Fichtner et al, 2015). This is followed by seventeen variables representing neighbourhood competition index (NCI), and nine representing functional dispersion index (FDis). The output "DI" (mm year^{-1}) represents the diameter increment from 2016 to 2019, and was calculated as follows:

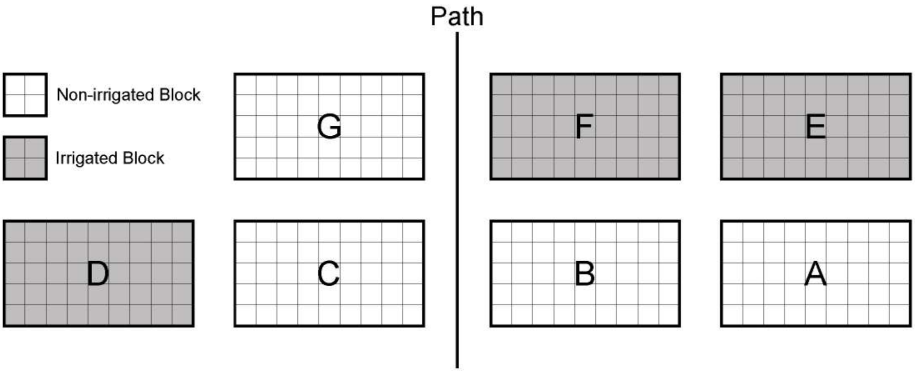

Fig. 1 Experimental design of IDENT-Macomer. The image shows four non-irrigated (white) and three irrigated (grey) blocks. Block A was established to test species response to extreme wet conditions, so it was not considered for this study. Each block includes 44 plots, and within each plot, there are 64 young plants placed at a distance of 40 cm

$$DI = \frac{D_{2019} - D_{2016}}{2019 - 2016} \tag{1}$$

where D is the diameter in the first (2016) and last (2019) sampling years, respectively. A total of 26 combinations of predictors were created for the analyses, e.g., diameter with each type of NCI or diameter with each type of FDis. The diameter or tree size is a mandatory fixed variable (e.g., Fichtner et al (2015)). We avoided mixing NCI and FDis in order to better interpret the effect of these two variables in combination with diameter. However, the best type of NCI and the best type of FDis were combined to assess the predictive gains compared to models with two variables. Predictors were tested on three different datasets: the full experiment (blocks F-E-D-G-C-B; Fig. 1); the irrigated treatment (blocks F-E-D; Fig. 1); and the non-irrigated treatment (blocks G-C-B; Fig. 1). The total number of observations in the full experiment is 16896, with 8448 in each treatment.

2.3 Data pre-processing

Preceding the calculation of the NCI and FDis, functional traits were normalised from 0 to 1, and then a principal component analysis (PCA) was performed, giving explained variances of 47% for the first axis and 33% for the second axis. The coefficients of the first axis are the following: Hmax = -0.31, SLA = 0.56, PLC50 = 0.06, Nm = 0.56, WD = 0.46, LA/SA = 0.24, and for the second axis: Hmax = -0.42, SLA = -0.19, PLC50 = -0.65, Nm = -0.17, WD = 0.43, LA/SA = -0.37. Neighbourhood competition was modelled

Table 1 Brief description of the 27 predictor variables for DI estimation

Abbreviation	Variable
D	Tree species diameter (cm) measured in 2016
NCI_eq	Neighbourhood Competition Index of equivalent competitors
NCI_Hmax	Neighbourhood Competition Index of absolute distance of maximum height
NCI_Hmax_hier	Neighbourhood Competition Index of hierarchical distance of maximum height
NCI_SLA	Neighbourhood Competition Index of absolute distance of specific leaf area
NCI_SLA_hier	Neighbourhood Competition Index of hierarchical distance of specific leaf area
NCI_PLC50	Neighbourhood Competition Index of absolute distance of water potential at which 50% of hydraulic conductivity is lost
NCI_PLC50_hier	Neighbourhood Competition Index of hierarchical distance of water potential at which 50% of hydraulic conductivity is lost
NCI_Nm	Neighbourhood Competition Index of absolute distance of nitrogen content per unit of leaf mass
NCI_Nm_hier	Neighbourhood Competition Index of hierarchical distance of nitrogen content per unit of leaf mass
NCI_WD	Neighbourhood Competition Index of absolute distance of wood density
NCI_WD_hier	Neighbourhood Competition Index of hierarchical distance of wood density
NCI_LA/SA	Neighbourhood Competition Index of absolute distance of ratio of leaf area to sapwood area
NCI_LA/SA_hier	Neighbourhood Competition Index of hierarchical distance of ratio of leaf area to sapwood area
NCI_PC1	Neighbourhood Competition Index of absolute distance of first axis of PCA
NCI_PC1_hier	Neighbourhood Competition Index of hierarchical distance of first axis of PCA
NCI_PC2	Neighbourhood Competition Index of absolute distance of second axis of PCA
NCI_PC2_hier	Neighbourhood Competition Index of hierarchical distance of second axis of PCA
FD_Hmax	Functional dispersion of maximum height
FD_SLA	Functional dispersion of specific leaf area
FD_PLC50	Functional dispersion of water potential at which 50% of hydraulic conductivity is lost
FD_Nm	Functional dispersion of nitrogen content per unit of leaf mass
FD_WD	Functional dispersion of wood density
FD_LA/SA	Functional dispersion of ratio of leaf area to sapwood area
FD_full	Functional dispersion of all traits
FD_PC1	Functional dispersion of first axis of PCA
FD_PC2	Functional dispersion of second axis of PCA

by the neighbourhood competition index (NCI):

$$NCI_z = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_{i,z} \frac{(D_{ij}/100)^{\alpha}}{(distance_{ij})^{\beta}} \tag{2}$$

where $\lambda_{i,z}$ is an interaction coefficient that describes the effect of neighbour of species i on target species z; α and β are estimated parameters and determine the shape of the effects (D_{ij} and $distance_{ij}$) of the neighbours in NCI. The net competitive effect of neighbours on the target tree z is represented by the equation 2, in which the neighbourhood competition is summed between $i = 1, ..., s$ species and $j = 1, ..., n$ neighbours within a radius of 2 m of $distance_{ij}$ between neighbours (Canham et al, 2004, 2006). We performed multiple simulations using the simplest competition model (NCI_eq) with increasing radius measurements, and chose 2 m because there was no performance benefit beyond that. We set $\alpha = 1$ and $\beta = 1$ to provide a basic form of the NCI and reduce complexity. Furthermore, D_{ij} was converted from cm to m so that $distance_{ij}$ could be measured in the same unit. The interaction coefficients $\lambda_{i,z}$ were used to create several types of NCI. In particular, we set $\lambda_{i,z} = 1$, implying the presence of equivalent competitors (NCI_eq, Canham et al (2004)). A set of 8 NCI (NCI_Hmax, NCI_SLA, NCI_PLC50, NCI_Nm, NCI_WD, NCI_LA/SA, NCI_PC1, NCI_PC2) were based on: $\lambda_{i,z} = 1- \mid t_z - t_i \mid$, scaled between 0 and 1 (1 for conspecific), which is the absolute trait distance between the target species trait t_z and the neighbouring species trait t_i (Fortunel et al, 2016). Another set of NCI (NCI_Hmax_hier, NCI_SLA_hier, NCI_PLC50_hier, NCI_Nm_hier, NCI_WD_hier, NCI_LA/SA_hier, NCI_PC1_hier, NCI_PC2_hier) was calculated using the following assumption: $\lambda_{i,z} = 1 - (t_z - t_i)$, 1 for conspecific (less than 1 if $t_z > t_i$, greater than 1 if $t_z < t_i$), which is the hierarchical trait distance between the target species trait t_z and the neighbouring species trait t_i (Kunstler et al, 2012).

We used the functional dispersion index (FDis), which is a multidimensional functional diversity (FD) metric (Laliberté and Legendre, 2010). FDis is the multivariate analogue of the weighted mean absolute deviation, which makes this index independent of species richness by construction (Laliberté and Legendre, 2010). FDis can be computed from any distance or dissimilarity measure (Anderson, 2006), and can take into account species relative abundances. Following Laliberté and Legendre (2010), we used two simple formulas to calculate neighbourhood FDis:

$$\mathbf{c} = \frac{\sum a_j x_{ij}}{\sum a_j} \tag{3}$$

$$FDis = \frac{\sum a_j z_j}{a_j} \tag{4}$$

where **c** is the weighted centroid in the i-dimensional space, a_j the abundance of species j – which includes the target tree's neighbours within the distance radius of equation 2 – z_j represents the distance between species j and centroid **c**, and x_{ij} is the value of trait i for species j. For the calculations, the dbFD-function from the FD package of R software was utilised. Several types of FDis were obtained; one for each functional trait (FD_Hmax, FD_SLA, FD_PLC50, FD_Nm, FD_WD, FD_LA/SA), one grouping all six traits (FD_full), and two with the principal components resulting from the previous PCA (FD_PC1, FD_PC2).

2.4 Random forest regression and permutation feature importance

We used the "sklearn" (Pedregosa et al, 2011) and "rfpimp" (Parr et al, 2018) Python libraries for random forest (RF) regression and permutation feature importance, respectively. RF algorithm has the advantages of providing accurate predictions without overfitting the data (Breiman, 2001). For the analyses, we used three different datasets: the full dataset including both treatments, the dataset with the irrigated treatment, and the dataset with the non-irrigated treatment. The datasets were split into a training set (75% of the dataset) and a test set (25% of the dataset). The following parameters were established: min_samples_leaf = 10 and oob_score = True. The first is the minimal number of samples that must be in a leaf node, while the second is the score of the training set obtained using an out-of-bag estimate. The out-of-bag sample is a portion of data that was not chosen for model training and is used to validate the model. The remaining parameters were kept at their default values. After fitting the model, we calculated the permutation importance for the test set. The permutation feature importance is defined as the drop in a model score when a single feature value is randomly shuffled, and the best variable in terms of performance is the one that is less affected by the shuffle. Each feature combination was permuted as a feature or meta-feature, and the loss in overall model accuracy indicates the relative importance. After determining the permutation importance on the test set, the best variables or variable combinations were selected and retrained with RF regression to estimate the coefficient of determination (R^2), the root mean square error (RMSE), the slope, and the intercept.

3 Results

The diameter increments (DI) of 16896 young Mediterranean trees (full experiment) were predicted using random forest (RF) regression. Performance results were as follows: $R^2 = 0.86$ on the training set (12672 observations), $R^2 = 0.76$ on the out-of-bag (OOB) set (a subset of data that was not chosen for model training), and $R^2 = 0.77$ on the test set (4224 observations). Tree diameters (D) and the neighbourhood competition index of the hierarchical distance of maximum height (NCI_Hmax_hier) was found to be the most relevant combination of variables in the full experiment as a result of the permutation importance (Table 2) performed on the test set after the model fitting. This combination of variables was used to retrain the model with RF regression, and the results were as follows: $R^2 = 0.73$ on the training set, $R^2 = 0.66$ on the OOB set, and $R^2 = 0.69$ on the test set. The same routine was used to predict DI in the irrigated treatment, and the performance results were as follows: $R^2 = 0.86$ on the training set (6336 observations), $R^2 = 0.76$ on the OOB set, and $R^2 = 0.76$ on the test set (2112 observations). The combination of D and NCI_Hmax_hier was also the most relevant under irrigated conditions due to the permutation importance (Table 2) performed on the test set after the model fitting. The results in performance after retraining the model were: $R^2 = 0.76$ on the training set, $R^2 = 0.69$ on the OOB set, and $R^2 = 0.71$ on the test set. The combination of variables of D and the neighbourhood competition index of the hierarchical distance of the ratio of leaf area to sapwood area (NCI_LA/SA_hier), showed a higher impact in predictions than those in the full experiment (Table 2). In contrast, the impact in prediction of the combination of D and NCI_WD dropped significantly.

We also predicted DI in the non-irrigated treatment as a final RF regression analysis. The results in performance were as follows: $R^2 = 0.85$ on the training set (6336 observations), $R^2 = 0.74$ on the OOB set, and $R^2 = 0.77$ on the test set (2112 observations). The combination of variables of D and NCI_Hmax_hier was also influential in the non-irrigated conditions (Table 2). The second-best combination of variables included D and NCI_LA/SA_hier. After retraining the model with the best combination, the results in performance were: $R^2 = 0.71$ on the training set, $R^2 = 0.63$ on the OOB set, and $R^2 = 0.66$ on the test set. Regarding functional dispersion, D with FD_WD was the best combination in the full dataset and each subset type (irrigated treatment and non-irrigated treatment). The combination of variables of D and the neighbourhood competition index of equivalent competitors (NCI_eq) showed significantly lower predictive importance than the best combination in the full experiment dataset and each water-treatment. The accuracy indicators (R^2 and RMSE) of the above mentioned simulations are presented in Table 3. The combination of variables of D with NCI_Hmax_hier reduced RMSE compared to the model accounting only for D, and in particular in the non-irrigated treatment, where this value varied from RMSE = 3.05 to RMSE = 3.42. The second best combination of variables in the full experiment dataset shows about 47% less performance than the best combination (Table 2), 30% less in the irrigated treatment, and 66% percent less in the non-irrigated condition. Furthermore, the R^2 and RMSE values of the second best combination are not considerably different from the model accounting only for D (Table 3), especially in the non-irrigated treatment. The partial dependence plot shown in Fig. 2 describes how the predictions of tree diameter increments depend on values of D and NCI_Hmax_hier in each water treatment. The scatter plots shown in Fig. 3 illustrate the relationships between predicted and observed DI of the best combination on the test set of the full experiment, irrigated treatment, and non-irrigated treatment. Except for the smallest values of DI, the model generated overestimations of DI for each dataset (Fig. 3). The best NCI type and the best FDis type was combined with D to generate a combination of three variables with higher accuracy compared to models with two variables (Table 3). The scatter plots shown in Fig. 4 illustrate the relationships between predicted and observed DI of the latter combination on the test set of the full experiment, irrigated treatment, and non-irrigated treatment.

Table 2 Ranking of variables according to their relative importance in predicting tree diameter increments on the test set of the full experiment (4224 observations), irrigated treatment (2112 observations), and non-irrigated treatment (2112 observations). Acronyms for each variable are listed in Table 1.

Full experiment		Irrigated treatment		Non-irrigated treatment	
Predictors	Importance (%)	Predictors	Importance (%)	Predictors	Importance (%)
D + NCI_Hmax_hier	100	D + NCI_Hmax_hier	100	D + NCI_Hmax_hier	100
D + NCI_WD	53.2	D + NCI_LA/SA_hier	69.6	D + NCI_LA/SA_hier	34.3
D + NCI_WD_hier	50.8	D + NCI_SLA_hier	37.5	D + NCI_PC1_hier	33.7
D + NCI_LA/SA_hier	43.1	D + FD_WD	35.1	D + NCI_WD_hier	30.0
D + FD_WD	35.4	D + NCI_WD	34.8	D + FD_WD	26.8
D + NCI_PC1_hier	25.9	D + FD_PC1	27.0	D + FD_PC1	24.0
D + FD_PC1	25.4	D + NCI_eq	25.0	D + NCI_Nm_hier	23.6
D + NCI_Nm_hier	23.5	D + FD_full	22.7	D + NCI_WD	21.8
D + FD_full	21.6	D + NCI_Nm	22.3	D + FD_SLA	21.5
D + NCI_PLC50	17.0	D + NCI_WD_hier	21.5	D + FD_Hmax	18.8
D + FD_LA/SA	16.6	D + NCI_PC1_hier	18.7	D + FD_PC2	17.3
D + NCI_SLA	16.0	D + NCI_Nm_hier	18.3	D + FD_Nm	17.2
D + NCI_Hmax	14.9	D + FD_LA/SA	14.1	D + NCI_PLC50	14.3
D + NCI_PC1	14.4	D + FD_SLA	14.0	D + NCI_SLA_hier	12.0
D + FD_SLA	14.4	D + NCI_SLA	13.2	D + NCI_Nm	11.2
D + FD_PLC50	11.2	D + FD_PC2	11.8	D + NCI_Hmax	11.2
D + FD_Hmax	9.0	D	11.3	D	10.4
D + NCI_eq	8.8	D + NCI_PLC50_hier	10.4	D + NCI_PC2_hier	9.7
D + NCI_SLA_hier	7.6	D + NCI_Hmax	9.7	D + FD_PLC50	8.7
D + FD_PC2	7.2	D + FD_Hmax	9.4	D + FD_full	8.6
D + NCI_Nm	6.8	D + NCI_LA/SA	8.6	D + NCI_LA/SA	8.0
D	6.3	D + FD_PLC50	7.4	D + NCI_eq	7.9
D + FD_Nm	5.1	D + NCI_PC2_hier	6.9	D + NCI_PC2	7.2
D + NCI_LA/SA	4.0	D + NCI_PC1	5.8	D + FD_LA/SA	6.1
D + NCI_PC2_hier	2.4	D + NCI_PLC50	2.7	D + NCI_PLC50_hier	4.4
D + NCI_PC2	2.0	D + NCI_PC2	0.4	D + NCI_SLA	3.2
D + NCI_PLC50_hier	0	D + FD_Nm	0	D + NCI_PC1	0

Table 3 Diameter increments (DI) estimation accuracy assessment on the test set with random forest regression. Acronyms for each variable are listed in Table 1.

Dataset	Test set	Predictors	R^2	RMSE	Slope	Intercept
Full experiment	4224 observations	All predictors (n = 27)	0.77	2.66	0.74	1.30
		D	0.62	3.42	0.60	2.03
		D + NCI_eq	0.63	3.35	0.63	1.87
		Second-best combination				
		D + NCI_WD	0.65	3.30	0.65	1.77
		Best combination				
		D + NCI_Hmax_hier	0.69	3.10	0.68	1.62
		Best NCI and FDis combination				
		D + NCI_Hmax_hier + FD_WD	0.71	2.97	0.71	1.48
Irrigated treatment	2112 observations	All predictors (n = 27)	0.76	2.93	0.72	1.55
		D	0.65	3.56	0.62	2.09
		D + NCI_eq	0.69	3.36	0.66	1.86
		Second-best combination				
		D + NCI_LA/SA_hier	0.66	3.49	0.65	1.94
		Best combination				
		D + NCI_Hmax_hier	0.71	3.22	0.69	1.73
		Best NCI and FDis combination				
		D + NCI_Hmax_hier + FD_WD	0.73	3.10	0.70	1.64
Non-irrigated treatment	2112 observations	All predictors (n = 27)	0.77	2.53	0.74	1.33
		D	0.57	3.42	0.57	2.22
		D + NCI_eq	0.60	3.31	0.62	1.99
		Second-best combination				
		D + NCI_LA/SA_hier	0.58	3.41	0.60	2.09
		Best combination				
		D + NCI_Hmax_hier	0.66	3.05	0.66	1.74
		Best NCI and FDis combination				
		D + NCI_Hmax_hier + FD_WD	0.71	2.80	0.70	1.52

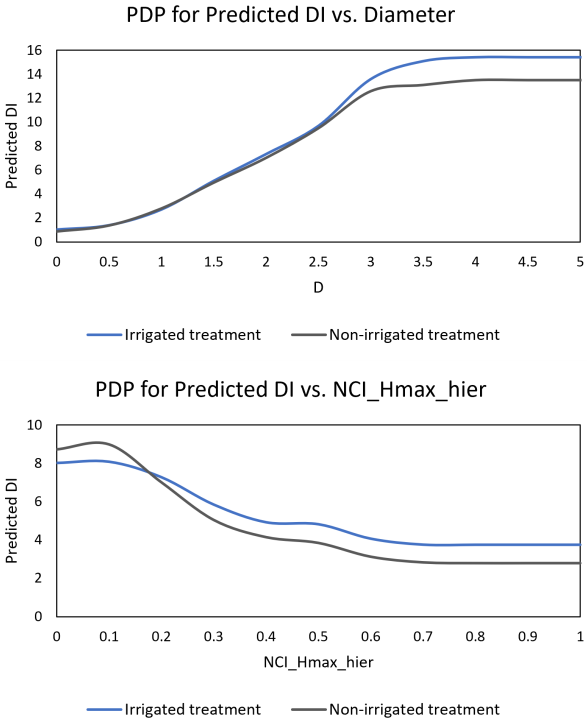

Fig. 2 Partial dependence plot (PDP) of the best combination in the irrigated and non-irrigated treatment. The upper panel shows that larger tree diameters correspond to higher values of the predicted DI, but for diameters above 2.5 cm, the predicted DI values are higher under conditions of water availability. The lower panel shows that the effects of competition for light acquisition on predicted DI are more limiting under water shortage conditions, but for low competition values (NCI_Hmax_hier ranging between 0 and 0.2), the effects are opposite.

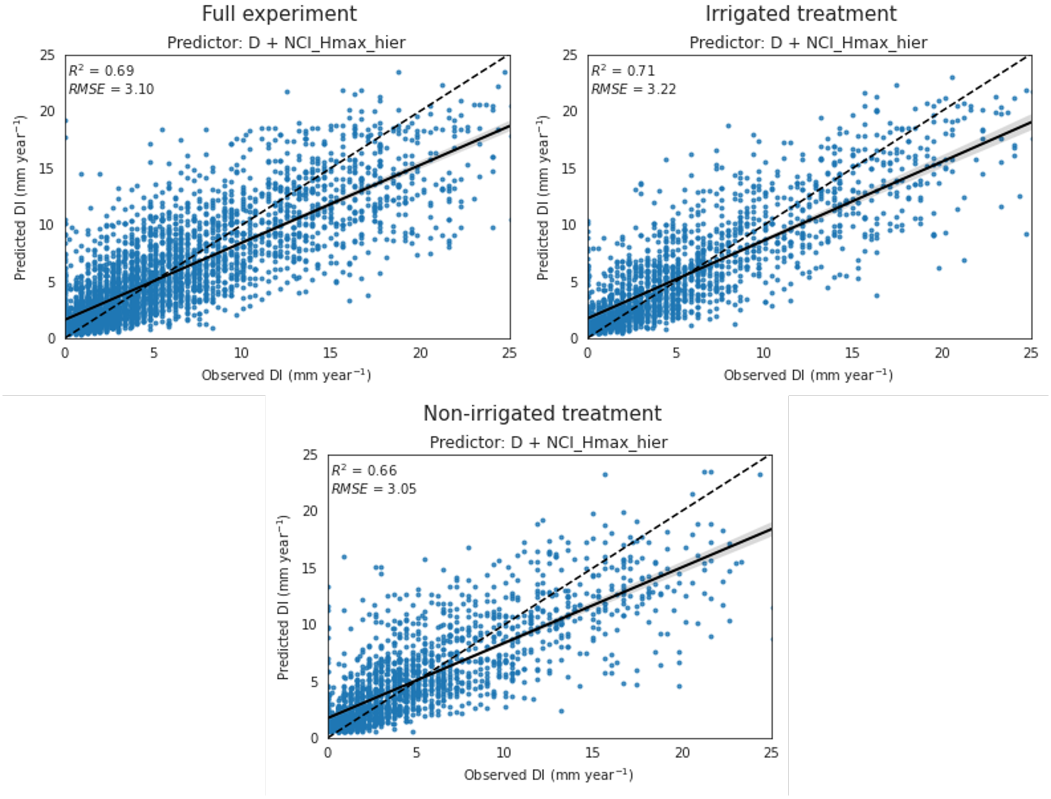

Fig. 3 Scatter plots of the predicted and observed DI of the best combination on the test set of the full experiment, irrigated treatment, and non-irrigated treatment. Dotted lines indicate the identity line (1:1)

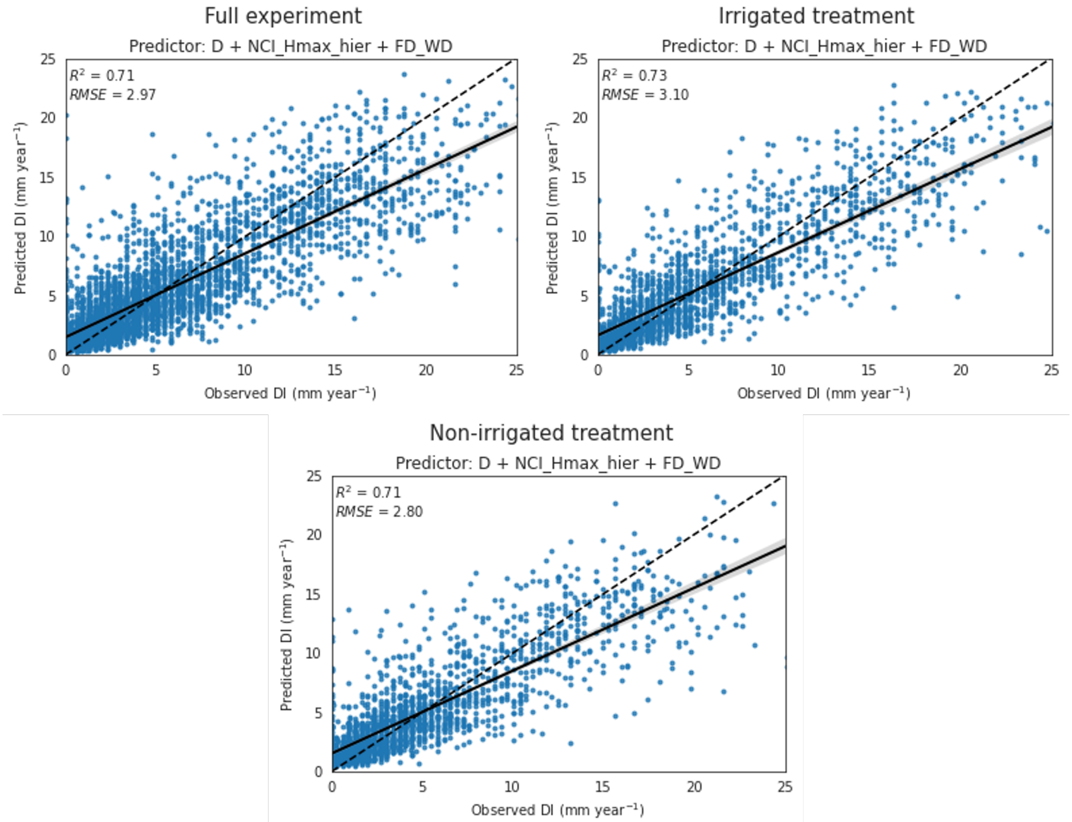

Fig. 4 Scatter plots of the predicted and observed DI of the combination of three variables on the test set of the full experiment, irrigated treatment, and non-irrigated treatment. Compared to the combination of two variables, the inclusion of FDis increased the predictive power (See Fig. 3). Dotted lines indicate the identity line (1:1)

4 Discussion

We found strong support for the hypothesis that the interaction coefficient of the neighbourhood competition of twelve young Mediterranean species is asymmetric (H_1). In comparison to the top models depicting asymmetric competition, the symmetric competition represented by NCI_eq gained less relative importance. Fortunel et al (2016) found that only four out of the 315 target tree species were best described by the neighbourhood competition models with equivalent competitors in a tropical ecosystem. In addition, Canham et al (2006) found that only one out of the 14 target tree species supported the symmetric competition theory in a temperate ecosystem.

We found strong support for the hypothesis that asymmetric competition is predicted by hierarchical distances of traits related to acquisition of light (H_2), i.e., individuals with the greater hierarchical distance of maximum height (NCI_Hmax_hier) compete more for light acquisition. Hypothesis H_2 was supported by the results of the permutation importance performed in the three datasets (full experiment, irrigated treatment, and non-irrigated treatment), and was later confirmed by the accuracy indicators (R^2 and RMSE). The combination of variables of D and NCI_Hmax_hier performed better than the second-best combination in each dataset (Table 3). In contrast, the hypothesis that asymmetric competition is based on the trait similarity theory (H_3) was less supported by our results compared to the trait hierarchy theory. The combination of variables supporting this theory is represented by D and NCI_WD in the full experiment dataset, with a relative importance of 53.2%, which declines in the irrigated and non-irrigated treatment. In the latter case, individuals with the greater absolute distance of wood density compete less for shared resources. Our results align with recent evidence that trait hierarchy plays a key role in determining competitive outcomes (Goldberg and Landa, 1991; Kunstler et al, 2012; Fort et al, 2014; Carmona et al, 2019; Pan et al, 2021). From the ecological point of view, the differential ability of tree species to occupy higher positions in the competitive hierarchy results in asymmetric competition between species (Weiner, 1990; Connolly and Wayne, 1996; Law et al, 1997; Schwinning and Weiner, 1998; Weiner and Damgaard, 2006; Brown and Cahill Jr, 2022), and size-asymmetric competition appears as a structuring component in the plantation (Del Río et al, 2014; Kunstler et al, 2016). In this scenario, the dominant species in the hierarchy can extract more resources than those dominated. Under conditions of asymmetric exploitation of the light resource, the dominant species can have a negative impact on the performance of the slow-growing species, decreasing their diameter and height growth (Weiner, 1990). With plant height differences across species, one species can overtake another and prevent access to light (Freckleton and Watkinson, 2001). Kunstler et al (2012) found evidence for a link between competition and hierarchical distance of WD and leaf mass per unit area, but not for Hmax. Leaf mass per unit area is understood as the leaf cost of photosynthetic activity and is therefore related to competition for light (Poorter et al, 2009). The relationship between WD and light interception is less known, but species with high WD are often the most shade-tolerant (Nock et al, 2009), and species with low WD require more light to allocate resources to the development of the central trunk and reach higher heights (Poorter et al, 2012). Still, there is good evidence related to mechanical resistance, the storage capacity of woody tissues (Chave et al, 2009), and tree growth (King et al, 2005). Fortunel et al (2016) found support for both absolute and hierarchical trait distances in a study of 315 tropical tree species. In the latter study, maximum diameter at breast height was a strong predictor of tree growth, a size trait allometrically related to height and indicative of asymmetric competition for light (Westoby et al, 2002). However, maximum height is regarded as a globally important size trait since it represents the core of the plant life cycle (Grime et al, 1997; Westoby, 1998) and is related to biomass production and climate regulation through carbon sequestration (Hanisch et al, 2020; Singh and Verma, 2020). This result also emphasises the vital role of tree architecture, which refers to the overall shape of a tree and the spatial position of its components (Poorter et al, 2006). Tall species, for example, have access to light and develop narrow crowns in height to achieve reproductive size, while small species improve light interception by developing long and wide crowns (Poorter et al, 2003). Also, in trials, neighbouring height has been demonstrated to be significantly related to light shortage on target trees; for example, Violle et al (2009) found that light depletion affects phytometer performance in an experiment done on 18 different monocultures. In addition, measuring maximum plant height is a relatively straightforward procedure compared to measuring other traits (such as SLA), which is relevant from the practical point of view of taking forest management decisions. Further work is needed to define if the growth-trait relationships we observed only apply to the early stages of development or if their effect persists in mature trees. Furthermore, a future species-by-species analysis might give important information about the competitive influence of shade-tolerant species on pioneer species (shade-intolerant). Uriarte et al (2004b) found, for example, that in late successional stages of subtropical forests, the development of pioneer species decreases with increasing shade-tolerant neighbours. However, we cannot yet evaluate these effects due to the early age of our plantations.

The effects of water use strategies on plant interactions have received less attention to date. Our results indicate that from a condition of water availability to one of water shortage, competition for light acquisition is still the best predictive variable (Table 2). However, the results suggest that in a well-watered soil, functional traits related to water transport capacity, such as LA/SA (Wright et al, 2006; Buckley and Roberts, 2006), showed a higher importance in predicting DI. For example, the second-best combination in the irrigated treatment is the coupling of D and NCI_LA/SA_hier, with a relative importance of 69.6% (Table 2), and in the non-irrigated treatment the relative importance is 34.3%. In a study of different Australian vegetation types, the LA/SA trait was positively correlated with site rainfall (Wright et al, 2006). Togashi et al (2015) observed that, compared to species in drier conditions, species in wetter conditions have greater LA/SA at a given xylem-specific hydraulic conductivity. However, we argue that including belowground processes into competition models is the best strategy to assess how water use strategies affect competition, but also the most complex due to the separation of biotic and abiotic factors (e.g. evaporation). Furthermore, belowground competitive ability is correlated with root-related traits such as root length density, surface area and root plasticity (Jose et al, 2006), all variables absent in our model.

The dependence relationship between the predictions and the best input variables (D + NCI_Hmax_hier) suggests that competition for light acquisition is more restrictive for tree growth under water-stressed conditions (Fig. 2). However, with low levels of competition (NCI_Hmax_hier between 0 and 0.2), the effects are opposite, and the competition is stronger in conditions of water availability. One possible interpretation is that irrigation provides enough resources for tree growth, thus limiting competition for light acquisition. A recent experiment showed that increased water availability, rather than the stress-gradient hypothesis, favoured young tree aboveground productivity (Belluau et al, 2021).

Our results support the hypothesis that functional dispersion can be used as a diversity metric to predict DI (H_4). Among the nine functional dispersion variables, FD_WD was the best predictor of DI in all datasets (Table 2). This is consistent with the findings of Ziter et al (2013), which suggested that functional dispersion is a significant predictor of aboveground carbon stock in unmanaged forest stands. These findings are echoed more recently by Wondimu et al (2021), where functional dispersion was the best predictor of aboveground carbon stock compared to functional richness, functional evenness, and functional divergence. Our study indicates that functional dispersion is a less important predictor of DI than neighbourhood competition. This result was not surprising as NCI holds much more information about the neighbourhood than FDis. The FDis (equation 3) was calculated using species functional traits and species relative abundances, but the NCI (equation 2) incorporates species functional traits and diameters of each individual tree. In other words, FDis shows less variability than NCI.

However, to facilitate the ecological interpretation of the results, we chose to evaluate the effect of NCI separately from FDis, but combining NCI with FDis resulted in higher performance for merely predictive purposes. For example, combining D with NCI_Hmax_hier and FD_WD produced better results in R^2 and RMSE in all datasets (Fig. 4). Overall, the latter combination explained 71–73% of the variance of DI, compared to 66–71% of the variance explained by the combination of two variables (Fig. 3). Therefore, from a practical point of view regarding forest management, which aims to maximise the tree growth prediction in a structured forest like our experimental site, the spotlight should be put on the combined effect of NCI and FDis.

5 Conclusion

The results of this research, conducted in a high diversity experiment of young Mediterranean species, suggest that: (1) the aboveground resource competition is asymmetric; (2) the asymmetry in resource competition is based on trait hierarchy related to acquisition of light, which more accurately explains tree diameter increments than resource competition based on trait similarity; (3) under different water resource conditions, size-related traits are favoured over water transport capacity-related traits, but in the irrigated treatment the latter traits have a higher importance in predictions compared to the non-irrigated treatment; (3) functional dispersion has a lower predictive power than neighbourhood competition; (4) functional dispersion combined with the neighbourhood competition increases prediction accuracy. Our results emphasize the importance of trait-based ecology and IBMs in understanding complex mechanisms (such as competition) in mixed forests. Our work using a machine learning approach has determined which predictor variables are most influential in assessing the behaviour of the response variable. The key contribution of this work is the solution it provides for the management of a Mediterranean forest, which has received little attention in comparison to other biomes in terms of competitive neighbourhood analysis. Since the results suggest that the maximum height (Hmax) is the trait most strongly associated with competition, a practical solution could be to design multiple virtual forests (with combinations of different heights) and predict tree growth using our best model (D + NCI_Hmax_hier). With this approach, we can estimate the productivity of different virtual forests and design a plantation based on the results.

A forest manager in a densely mixed forest with high species diversity could focus on gathering minimal useful information to predict species growth. For instance, it should prioritise traits related to plant size or some traits related to water transport capacity instead of allocating resources to gathering data on leaf traits. The striking element of using functional traits is that they allow for the calculation of the neighbourhood competition and functional dispersion indexes, both of which significantly improve predictive performance. However, the next step in this research is determining the functional relationships between the predictors and the response variable at the species level or how the predictors respond to environmental stress.

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Author contributions. The article was written by RM with assistance from all authors. The entire experiment was supervised by SM. The study hypotheses were developed by RM and MS. Sampling was done by SM, LM, JR, MLC, and RM. LM contributed to all sections of the manuscript. The statistical approach was chosen by RM, and JMCS was active in its refinement.

LM, JR, and MLC revised the writing and text exposition. MLC was active in the funding acquisition process. SM motivated RM to improve the discussion. SM and DS provided final input on the manuscript's final version.

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Declarations

The authors have no competing interests to declare that are relevant to the content of this article.

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