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Neighborhood analysis of tree growth in mixed Mediterranean forests

Doctoral Thesis
by

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Abstract

Understanding how forests respond to disturbances and, more importantly, ensuring that ecosystem services are preserved is crucial under a climate change scenario. In this perspective, biodiversity is fundamental since it is essential for the stability of ecosystem functions and the services they support. First, some of the underlying ecological processes in the link between Biodiversity and Ecosystem Functions (BEF) must be explored. To achieve this, we have integrated the IDENT experiment with neighbourhood analysis to answer specific questions about BEF relationships. In a first case study, we used the Random Forests method to analyse the relative importance of competition and functional diversity in predicting tree growth. The neighbourhood competition index (NCI) characterised competition, whereas the neighbourhood functional dispersion index (FDis) described functional diversity. Both indices were calculated using species functional traits. The same predictors were studied by the linear regression and model selection in a second case study to assess their effect at the species level under the water stress-gradient. Both studies found that: (1) the neighbourhood competition is mediated by functional traits (asymmetric competition) and not dependent on equivalent competitors (symmetric competition), and (2) NCI is a better predictor than FDis. Specifically, the first study found that hierarchical competition based on functional traits related to competition for light best explains the tree growth variation. The second study, in contrast, found that hierarchical competition based on functional traits related to water transport capacity best explains the growth of the target species. Additionally, the second study found that the neighbourhood competition is stronger when species grow in soil with a high water supply. Overall, our findings highlight the importance of functional traits in the BEF relationship study, as these affect interactions between species and, as a result, forest biomass.

Dedicated to my parents.

Acknowledgments

I would like to thank the students and researchers who contributed to the collection of data needed to carry out the research. I would like to thank my supervisor for the advice given during my doctoral experience, and Euro-Mediterranean Center on Climate Change (CMCC) for the funding.

Contents

List of Figures

List of Tables

Chapter 1

Introduction

It is estimated that forest ecosystems can remove nearly 3 billion tonnes of anthropogenic carbon each year through net growth, which represents about 30% of carbon dioxide emissions from fossil fuel burning and deforestation (Canadell et al., 2007; Canadell & Raupach, 2008). Forest ecosystems behave both as a source of atmospheric carbon and as a sink (Sedjo, 1993; Lasco & Pulhin, 2003; Lorenz & Lal, 2009) and the Net Ecosystem Productivity depends on the equilibrium between these two processes, which can be altered by disturbances and climate. Nevertheless, increasing the global forest area will be inevitable if global warming is to be contained. It is thus crucial to understand the internal dynamics of a forest ecosystem. For example, how species in a community interact with each other and how these interactions respond to stress gradients would allow for the engineering of more productive and resilient ecosystems. A forest ecosystem can respond in different ways to disturbances, altering, for example, the taxonomic composition, vegetation structure, and rates of ecosystem processes (Thompson et al., 2009). Many ecologists have widely investigated the relationship between biodiversity and stability, suggesting that biodiversity can be crucial for the stability of ecosystem functions and the services they support (Oliver et al., 2015). Experimental and theoretical studies have investigated the hypothesis that there is a positive relationship between biodiversity and ecosystem functions (BEF). Experimental studies have shown that biodiversity has a positive relationship with aboveground biomass (Hooper & Vitousek, 1997), decomposition rates, invasion susceptibility, CO2 flux, biomass, nitrogen retention, and total cover (Naeem et al., 1994, 1995; Tilman et al., 1996, 1997a; Symstad et al., 1998). Various mixed forests in Europe, for example, are more productive across a wider range of environmental conditions than monocultures (Jucker et al., 2014). Generally, trees that grow faster in mixtures also have higher transpiration, water-use efficiency, and are less susceptible to fire and windstorms than pure conifer forests (Hély et al., 2000; Fernandes, 2009; Catry et al., 2010; Valinger & Fridman, 2011; Forrester, 2015; Jactel et al., 2017). Review articles and meta-analyses clearly show that biodiversity increases forest productivity by an average of 15% compared to monoculture (Jactel et al., 2018). Tilman et al. (1997b) used resource competition models to predict how resource use would change as diversity increased. They found that total resource utilisation is reached at low levels of species richness (SR). However, the changes in functional diversity (FD) that occur because of introducing species to the system, rather than the species themselves, drive the results of such studies. FD, as a measure of diversity, may provide more insight into BEF relationships than SR. To avoid misunderstandings with the term FD, we rely on this definition: 'the value and range of those species and organismal traits that influence ecosystem functioning' (Tilman, 2001). Based on this definition, measuring FD implies first identifying the functional information (traits) of the target species. Plant features (traits) reflect species ecological strategies and determine how plants respond to environmental factors and influence ecosystem properties (Kattge et al., 2011). Functional traits are morphological, biochemical, physiological, structural, phenological, or behavioural characteristics of organisms that carry on ecosystem processes and define species in terms of their ecological role (Violle et al., 2007). According to Conti & Díaz (2013), in a mixed forest, the variety of trait values is a relevant component of FD and contributes to explaining carbon storage. Measuring different components of FD can also help predict ecosystem services (Díaz et al., 2007). However, although FD has significant effects on ecosystem functions, a difficulty is the interpretation of non-significant results, i.e., the absence of relationships. Petchey & Gaston (2006) proposed the potential causes of the absence of significant results: 1) the functional traits considered are functionally irrelevant; 2) inappropriate measures of FD; 3) explanatory variables (such as ecological factors) more important than FD are excluded; 4) experiments with an inappropriate statistical approach; 5) FD has no effect.

However, topics involving functional traits, FD, or more generally, the effect of mixed forests on ecosystem functions have been widely addressed in ecology, including several approaches to investigate them. For example, the International Network of Biodiversity experiments (TreeDivNET - `http://www.treedivnet.ugent.be`) focuses on the relationship between tree species diversity and ecosystem functioning. Within TreeDivNet, the International Diversity Experiment Network with Trees (IDENT) specifically focuses on the role of FD and biodiversity-ecosystem function relationships, and in some cases, stress gradients (Tobner et al., 2014; Van de Peer et al., 2018). The network has already accumulated a large amount of data, which, however, is strongly unbalanced towards boreal and temperate biomes, leaving greater uncertainty for semi-arid biomes such as the Mediterranean one. For this reason, this study investigate the potential of mixed tree communities in the Mediterranean through the IDENT-Macomer experiment. A useful study approach for this purpose is an exploratory study at the individual level following a bottom-up approach, in which system properties emerge from the interactions of individual parts of the system (DeAngelis & Grimm, 2014). The difficulty in linking population and ecosystem behaviour to individual organism traits and environmental factors is becoming increasingly recognised as a major issue in ecology. Models of how individual components interact and respond have had a lot of success in predicting the behaviour of complex physical systems. Here, individual-based models (IBMs) assist us in finding relevant theories for emergent system components without becoming derailed in too much complexity (Grimm & Railsback, 2005; Grimm et al., 2006). For example, IBMs allow us to study plant interactions in a forest community, and a common method for this objective is neighbourhood analysis. Neighbourhood analysis has been widely used for different purposes, and the methodology is now well consolidated and provides a robust reference for analysing the results of diversity manipulation experiments. Many researchers have used neighbourhood models for several purposes, including (i) estimating the amount of interspecific competition between individual trees above and belowground (Bella, 1971); (ii) estimating the amount of intra- and interspecific competition across an environmental gradient (Canham et al., 2004, 2006; Gómez-Aparicio et al., 2011); (iii) testing if interaction strengths are driven by species trait differences (Kunstler et al., 2012; Fortunel et al., 2016). The use of species traits to evaluate individual performance in a competitive context has been an advancement in the study of plant interactions. This study, based on recent research, replicates and tests new hypotheses in the Mediterranean context.

1.1 Research hypotheses

Integrating the IDENT experiment with neighbourhood analysis allows us to answer specific hypotheses concerning BEF relationships by using tree diameter increments (DI) as an output variable, which is a good indicator of individual tree growth (Seidel et al., 2015):

H_1 – The interaction coefficient of the neighbourhood competition is not symmetric but mediated by functional traits (asymmetric).

H_2 – If hypothesis H_1 is correct, asymmetric competition is linked to hierarchical distances of traits related to competition for 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 with similar niches.

H_4 – In addition to the competition, neighbourhood functional diversity may also influence DI. In this last case we used functional dispersion (FDis; Laliberté & Legendre (2010)) as a statistical measure of functional diversity

H_5 – Neighborhood competition has a larger impact on DI of target species in irrigated soils compared to non-irrigated.

STEPS: We used random forest regression and permutation feature importance method to test hypotheses H_1, H_2, H_3, and H_4. The same hypotheses plus H_5 were tested at the species level using linear regression and model selection criterion (AIC).

1.2 Dissertation outline

Chapter 1 provides an overview of the literature, objectives, and results of the research.

Chapter 2 provides a background on the following topics: methods used to investigate BEF relationships; the general concepts of individual-based models (plant IBMs); an overview of neighbourhood analysis research; diversity metrics; and statistical methods.

Chapter 3 shows a case study testing hypotheses H_1, H_2, H_3, and H_4 using random forest regression and permutation feature importance method. The analyses were conducted at the forest level and the results obtained were submitted to *European Journal of Forest Research.*

Chapter 4 shows the results of hypotheses H_1, H_2, H_3, and H_4 at the species level, following the hypothesis H_5, concerning the water stress-gradient. The hypotheses were tested using linear regression and the model selection criterion (AIC).

Chapter 5 summarises important aspects of the thesis and potential recommendations for further research.

Chapter 2

Background

2.1 Methods for BEF relationships

Observational studies, experiments, and models are used to investigate the relationships between biodiversity and ecosystem function (BEF). Manipulative experiments have been conducted to investigate the functional relationship between species richness (SR) and ecosystem functions in both semi-natural and artificial communities (Tilman et al., 1996; Symstad et al., 1998). From an experimental perspective, using SR as a measure of biodiversity is straightforward, but the results are often unclear. The size effect of SR on ecosystem functions is already saturated at relatively low SR values, mainly because of redundancy but also because single dominant species seem to be the reason for the importance of SR. High SR levels may not result in high biomass production; a single dominating species might potentially contribute to 80% of the total biomass (Symstad et al., 1998). As a result, it is crucial to assess the nature of the relationship between SR and ecosystem functions. There are two types of ecosystem function responses to changes in SR (Schwartz et al., 2000): 1) species richness is positively correlated with ecosystem function; and 2) ecosystem functions do not saturated at low species richness, but rather there is an improvement in functions at high levels of species richness. In experiments to study BEF relationships, Loreau et al. (2001) has made an additive partitioning of two biodiversity effects: the dominance of species with specific traits has an impact on ecosystem processes, which is known as the "selection effect." Resource partitioning or positive interactions lead to an increase in total resource use in the "complementarity effect". (Loreau et al., 2001).

However, the study of BEF took an important step forward when research began to focus on the mechanism by which species composition affects ecosystem function. One approach is to combine the effects of SR and functional diversity (FD) in a single experiment so that the effect of one can be separated from the effect of the other. In this context, tree mixtures provide a good model for future BEF studies (Tobner et al., 2014). The International Diversity Experiment Network with Trees (IDENT) methodology is being used to evaluate a wide range of tree mixtures, environmental conditions, and hypotheses at different trophic levels. IDENT is part of TreeDivNet (`http://www.treedivnet.ugent.be`), a global network of tree diversity manipulation experiments that provides the opportunity to investigate BEF relationships. The experimental approach isolates the effects of FD and SR through a plot-based replicated random design that includes tree species mixtures that vary in FD independently of SR, as well as exploring underlying processes such as complementarity effect and selection effect (Tobner et al., 2014). The experiment is based on high-density tree plots and focuses on BEF relationships during the first years of tree growth. Furthermore, small changes can be made to the experimental design to evaluate additional hypotheses for each site while maintaining the main hypotheses for all sites.

2.2 Plant IBMs (Individual-based Models)

Behavioral ecology theory focuses primarily on the individual level and not on how individual behaviour explains emergent system behavior, and population ecology theory includes only models created at the population or community level. In individual-based ecology (IBE), a new theory is needed that links the individual to higher levels. The lack of such a theory has significantly hindered both the understanding of ecosystem complexity and the application of individual-based models (IBMs) in practice. However, rather than understanding all aspects of individual behavior, we should focus on developing models that explain key system properties.

Plant IBMs are constructed so that the population-level outcomes of interest (age and size distributions, production rates, species diversity, spatial patterns, etc.) emerge from individual-level processes, including competition among individuals (Grimm & Railsback, 2013). Adaptive traits are almost completely absent from plant IBMs. For example, plants do not show behavioural responses to competition, such as choosing which parts of the plant to develop in which direction. Instead, we assume that competition simply limits growth. The IBMs of the plants directly represent the interaction. Each plant identifies the neighbours with which it interacts, and the effects of each neighbour are represented. It is assumed that competitive interaction with neighbours simply reduces the availability of resources that limit growth.

However, plant IBMs and the IDENT experiment share parts of the same approach, namely, conducting studies and testing hypotheses at two different levels (individual and community). We believe that IDENT is one of the best experiments to exploit the potential of plant growth models to answer questions about BEF relationships. Since the experiment has a high tree density, plant interactions (competition or facilitation) play a key role in this scenario. Models for plant interactions, such as tree neighbourhood models, are now well documented in the literature. In the next section, we provide an overview.

2.3 Neighborhood models overview

Our research was supported by a comprehensive review of recently published articles on tree neighbourhood analysis. One of the first works on neighbourhood analysis was carried out by Bella (1971), with the implementation of a model named Competitive Influence-Zone Overlap (CIO). The basic idea of the work was that when trees of different sizes compete in a forest stand, they affect each other differently. Trees with large crowns cover a larger area and overlap with smaller neighbours in the nearest distance. Most studies of tree neighbourhood analysis are based on the assumption that individual growth rates (or survival in some cases) are affected by multiple effects, including 1) tree size; 2) competition by neighbouring trees (symmetric or asymmetric); 3) soil quality; 4) shading; and 5) climatic conditions. A substantial part of the studies was based on some effects of those just described because of the model complexity and results interpretation. Each of these effects is described by specific equations and has a value ranging from 0 to 1. In mathematical terms, we can summarise the assumption in the following form: $Growth = Max\ Growth \times Size\ Effect \times Crowding\ Effect \times Soil\ Effect \times Shading\ Effect \times Climate\ Effect \times Site\ Effect$. Individual growth is then predicted by adjusting the maximum growth rate ($Max\ Growth$) for the values of the various effects. In some articles (Canham et al., 2004; Uriarte et al., 2004b; Canham et al., 2006), $Max\ Growth$ and $Size\ Effect$ are merged into one equation defined as follows: $PotRG = Max\ Growth \times Size\ Effect$, where $PotRG$ is the potential radial growth.

In general, the functional forms described in the neighbourhood analysis follow a standard but have been modified in some published works. For reasons related to the scope of our study, we will focus on size and crowding effects.

The most common size effect is modelled as a lognormal distribution (Canham et al., 2004; Uriarte et al., 2004b; Canham et al., 2006; Astrup et al., 2008; Coates et al., 2009; Gómez-Aparicio et al., 2011): $\mathit{Size\ Effect} = \exp\left[-0.5\left(\frac{\ln((DBH)/X_0)}{X_b}\right)^2\right]$, where X_0 is the DBH (diameter at breast height) of the target tree at which maximum growth occurs, and X_b describe the breadth of the lognormal function. However, recently, (Canham & Murphy, 2016), a shifted lognormal function has been proposed: $\mathit{Size\ Effect} = \exp\left[-0.5\left(\frac{\ln((DBH+X_p)/X_0)}{X_b}\right)^2\right]$, where X_p allows nonzero intercepts at zero DBH. A functional form different from the lognormal was described in Canham & Murphy (2017), which evaluated sapling and canopy tree survival. The function allows for a U-shaped response: $\mathit{Size\ Effect} = (1 - a \times \exp(b \times DBH)) \times \left(\exp\left(c \times DBH^d\right)\right)$, where a, b, c, and d are estimated parameters, and DBH is the diameter at breast height. Anyway, a linear or non-linear function of tree diameter (DBH; DBH^2) is the simplest form to describe the size effect (Kunstler et al., 2012; Fichtner et al., 2015).

The crowding effect (or neighborhood) is the function that has been most modified from the old articles to the most recent ones. As mentioned at the beginning of this paragraph, the Competitive Influence-Zone Overlap (CIO) was one of the first models describing the competitive effects of the subject tree i. The function is as follows: $CIO_i = \sum_{j=1}^{n} \left[(ZO_{ij}/ZA_i) \left\{ (D_j/D_i)^{EX} \right\} \right]$, where n is the number of competitors, ZO_{ij} the area of zone overlap between subject tree i and competitor j, ZA_i the influence-zone area of subject tree i, D_j the DBH of competitor j, D_i the DBH of the subject tree i, and EX the exponent. After the research of Bella (1971), in several articles (Canham et al., 2004; Uriarte et al., 2004a,b; Canham et al., 2006; Astrup et al., 2008; Coates et al., 2009; Thorpe et al., 2010; Gómez-Aparicio et al., 2011; Fortunel et al., 2016) the crowding effect was modelled with the application of an index, known as the Neighbourhood Competition Index (NCI): $NCI_z = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_{i,z} \frac{(DBH_{ij})^{\alpha}}{(distance_{ij})^{\beta}}$, where $\lambda_{i,z}$ is an interaction coefficient describing the effect of neighbours of species i on target species z, whereas α and β are estimated parameters and determine the magnitude of DBH and $distance$, respectively, on NCI. The result of this function is the cumulative sum over all n individuals of s neighbouring species within a radius (in meters). The NCI just shown is the common form, but in some cases, it has variations according to the study objective. For example, when we assume that all neighbors share resources equally with the target tree (symmetric competition), we set $\lambda_{i,z} = 1$. Different values of $\lambda_{i,z}$ for each species define asymmetric competition, i.e., unequal resource sharing with the target tree as a result of larger individuals having an advantage over smaller ones, or neighbors having a greater ability to capture resources. Neighborhood effects on the target tree growth are typically calculated using a negative exponential function of NCI (Uriarte et al., 2004a,b; Canham et al., 2006; Astrup et al., 2008; Coates et al., 2009; Gómez-Aparicio et al., 2011; Fortunel et al., 2016): $Crowding\ Effect = \exp\left(-C \times NCI^{D}\right)$, where C and D are estimated parameters. A further change to this function is applied to C, that is: $C = C^{'} \times DBH^{\gamma}$, or $C = C^{'} \times Temperature^{\delta} \times Precipitation^{\sigma} \times DBH^{\gamma}$, where γ allows the target species to have differential sensitivity to competition (Canham et al., 2006), whereas δ and σ include a given variation of competition in response to climatic variables (Gómez-Aparicio et al., 2011). However, a function without an exponent was proposed by Canham et al. (2004): $Crowding\ Effect = (-C \times NCI)$. In addition to NCI, basal area (BA) can also be a good predictor for neighbourhood analysis (Canham & Murphy, 2016, 2017): $\textit{Crowding Effect} = \exp\left(-\alpha \times BAratio^{\gamma} \times totalBA^{\beta}\right)$, where α, γ, and β are estimated parameters. Alternative forms of competition index with basal area can be found in Kunstler et al. (2012); Fichtner et al. (2015).

Typically, most of the studies on the neighbourhood effects on the target tree growth share the same methodology, which we can summarise in a few points: i) choice of models, i.e. equations (or functional forms) describing the effects on the target tree growth; ii) parameter estimation; iii) selection of the best model. The choice of functional forms is the most important step and must be consistent as far as possible with the real processes of forest growth. However, already published work facilitates this step, since there is no need to devise new equations for the experiment we intend to carry out.

2.4 Functional diversity metrics

Three multidimensional functional diversity (FD) indices for continuous functional traits were proposed (Villéger et al., 2008), each exploring a different aspect of FD: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). For our study, we used a new multidimensional FD index, called functional dispersion (FDis) (Laliberté & Legendre, 2010), which is conceptually similar to Rao's quadratic entropy Q (Botta-Dukát, 2005). From the computational point of view, the FDis calculates, for a set of communities, the average distance of individual species in PCoA space from any dissimilarity measure (Anderson, 2006). Weights are species relative abundances. For communities composed of only one species, the FDis is equal to 0 (Laliberté & Legendre, 2010). Euclidean distance and Gower dissimilarity can be used as distance measurements, but the second is more flexible since both quantitative and qualitative variables can be implemented in the dissimilarity matrix (Gower, 1971).

2.5 AIC selection

The Information-Theoretic approach was used to select and infer the model in our statistical analysis (Kullback-Leibler information, K-L). The goal is to develop a candidate model that minimizes the distance between an approximation model g and reality f (Burnham & Anderson, 2002). Akaike (1973) proposed a criterion (Akaike's information criterion – AIC) for estimating relative expected K-L information, which is now widely used in ecology. We calculated the AIC for each candidate model and chose the one with the lowest AIC value. The AIC tells us how well the model fits the data (Burnham & Anderson, 2002).

AIC is calculated as:

$$AIC = -2\ln\left(\mathcal{L}\left(\hat{\theta} \mid data\right)\right) + 2K \tag{2.1}$$

where $\mathcal{L}\left(\hat{\theta} \mid data\right)$ is the maximum likelihood estimate for the model, and K is the number of estimable parameters. The AIC differences ($\Delta_i = AIC_i - AIC_{min}$) over all candidate models in the set give a measure of how much better the approximating models are than the best model (with $\Delta_i = 0$), as suggested by Burnham & Anderson (2002, 2004). In particular, when $\Delta_i < 2$ the degree of empirical support for the model is high, and as Δ_i increases, the level of empirical support for the model decreases.

The Akaike weights (w_i) are useful measurements that normalise the model likelihoods using the following equation:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)} \tag{2.2}$$

where w_i represents the probability that a given candidate model r is the best in a set of R models for the data (Burnham & Anderson, 2004), with values ranging from 0 to 1. If the Akaike weights for the best model are greater than 0.9, then statistical inference should be based only on that model.

The entire set of R models affects the ratios in equation (2.2), however the evidence ratios (ER) provide a more accurate measure:

$$ER = \frac{w_i}{w_j} \tag{2.3}$$

where i is the best model estimated (thus, w_{best} or w_1) and j any other model in the set (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). It basically provides a metric for how likely a model is to be the best candidate over a model j.

2.6 Random Forest (algorithm)

Random forests (RF) are a powerful new statistical tool that has been properly described in multiple studies and is moving into scientific subjects like ecology. Recently, RF has been used for a variety of purposes, including variable selection (Fox et al., 2017), animal and plant species classification (Cutler et al., 2007; Bradter et al., 2011), genetic studies (Brieuc et al., 2015, 2018), groundwater potential mapping (Naghibi et al., 2016), species distribution (Evans et al., 2011), and fire occurrence (Oliveira et al., 2012). With RF, there are numerous advantages. One of these benefits is that generalisation errors are reduced (Breiman, 2001). RF is a similar method to bagging trees (BT; Breiman (1996)), but in the former, each tree is generated with a randomized subset of predictors. A random subset of the original number of predictors is used to find the optimal split at each node. A random forest tree is completely grown and unpruned, and aggregation is done by averaging the trees. Out-of-bag (OOB) data is used to assess the test error of RF models. The test set consists of inputs that were not included in the training bootstrap sample and are then averaged over all trees to result in an estimate of test error (Figure 2-1). Cross-validation can thus be avoided.

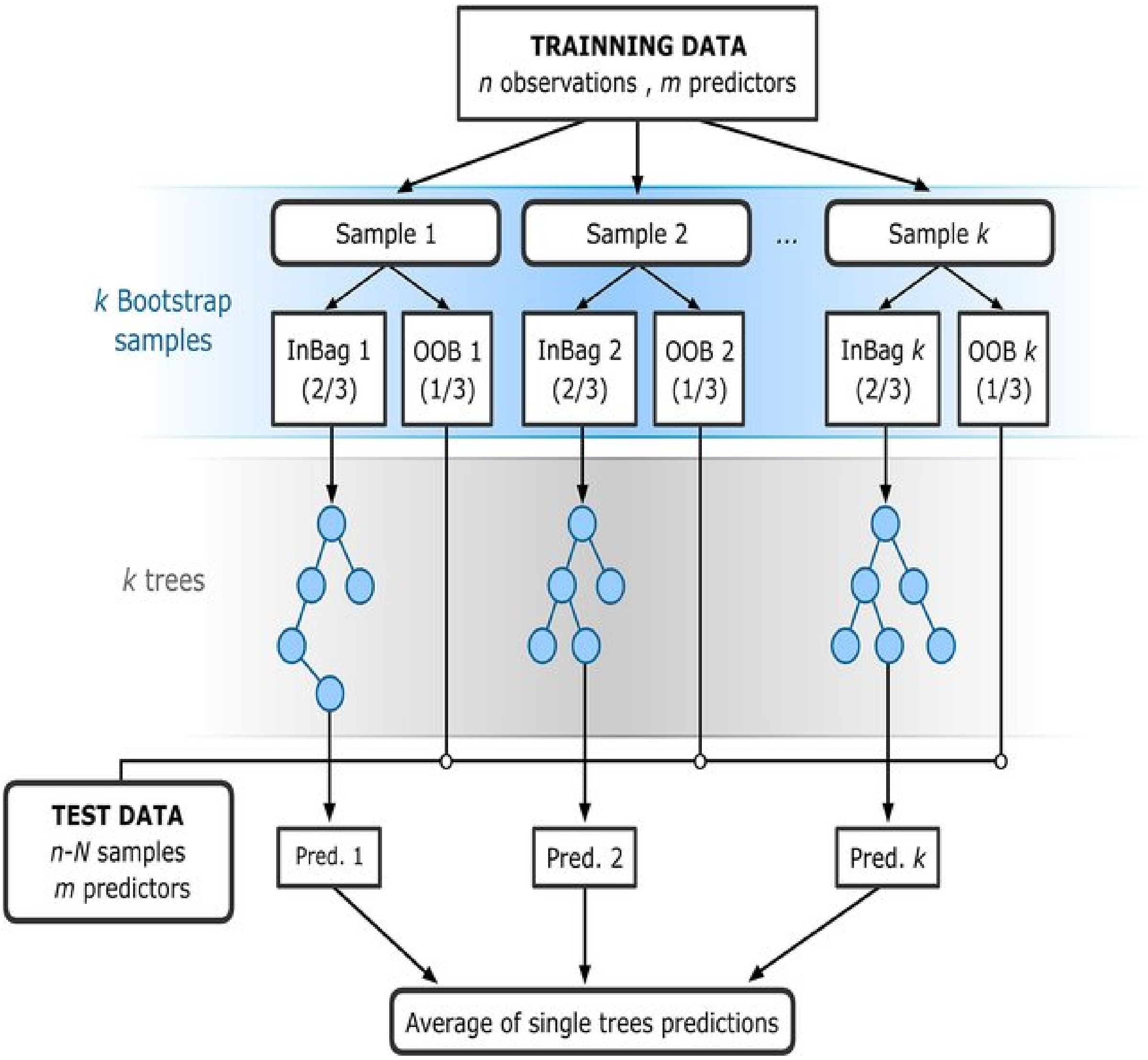

Figure 2-1: RF method synthesized diagram, from Rodriguez-Galiano et al. (2016).

Chapter 3

1st case study

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

3.1 Introduction

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 & 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 & 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 & Hector, 2001; Fox, 2005). Building models at the population or community levels is a common approach to answering ecological questions. Still, it is also particularly insightful to understand how individuals interact with each other and their environment (Grimm & 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 & 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 inter-specific 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 strength 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 the competition strength between two species increases as the distance between their traits decreases, without any dominance in the acquisition of resources. In other words, the likelihood that two species can coexist decreases as their nichia distance decreases. In contrast, the trait hierarchy theory predicts the dominance of superior competitors in the crowding dynamics. On the other hand, the phylogenetic similarity theory is not trait-based, and it assumes that ecologically similar species compete more intensely for resources than dissimilar species (MacArthur & Levins, 1967).

In this study, we applied the spatially explicit neighbourhood model of tree growth of twelve young 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 predictors that contribute the most to the prediction of aboveground tree growth in mixed forests, which might enhance our ability to perform plantations and reforestation plans successfully. 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 individual tree growth (Seidel et al., 2015) to test the following hypotheses: H_1 - The interaction coefficient of the neighbourhood competition is not symmetric but mediated by functional traits (asymmetric). H_2 – If hypothesis H_1 is correct, asymmetric competition is linked to hierarchical distances of traits related to competition for 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 with similar niches. As a final hypothesis, we assumed (H_4) that in addition to the competition, neighbourhood functional diversity may also influence DI. In this last case we used functional dispersion (FDis; Laliberté & 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.

3.2 Materials and Methods

3.2.1 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 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. 3-1). 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. 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 & 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)). 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), the diameter at breast height could not be used.

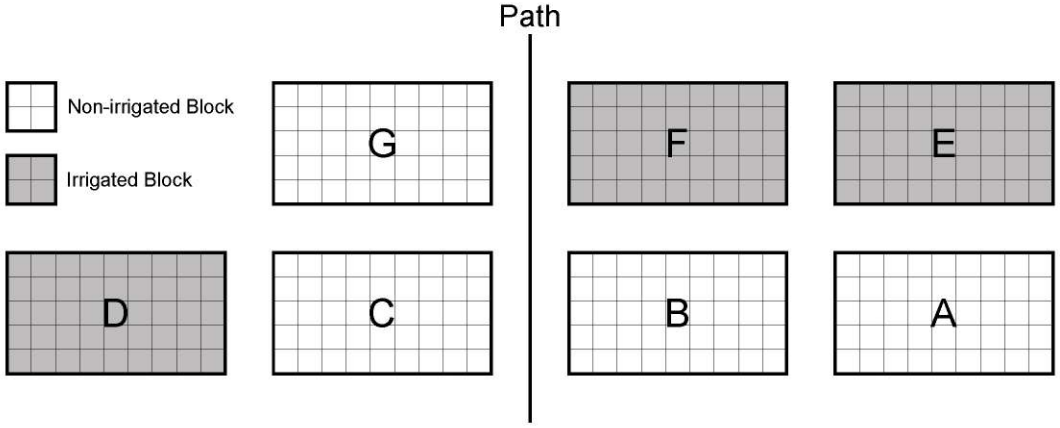

Figure 3-1: Experimental design of IDENT-Macomer. The image shows four non-irrigated (white) and three irrigated (grey) blocks. Block A was established to test species response to extreme wet conditions, so it was not considered for this study. Each block includes 44 plots, and within each plot, there are 64 young plants placed at a distance of 40 cm

3.2.2 Predictive variables

A total of 27 predictive variables were used for this study (Table 3.1). 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 eighteen representing functional dispersion index (FDis). The output "DI" (mm year^{-1}) represents the diameter increment from 2016 to 2019, and was calculated as follows:

$$DI = \frac{D_{2019} - D_{2016}}{2019 - 2016} \tag{3.1}$$

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. 3-1); the irrigated treatment (blocks F-E-D; Fig. 3-1); and the non-irrigated treatment (blocks G-C-B; Fig. 3-1). The total number of observations in the full experiment is 16896, with 8448 in each treatment.

Table 3.1: 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

3.2.3 Calculations

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 (Table 3.2), 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 by the neighbourhood competition index (NCI):

$$NCI_z = \sum_{i=1}^{s}\sum_{j=1}^{n} \lambda_{i,z} \frac{(D_{ij}/100)^{\alpha}}{(distance_{ij})^{\beta}} \tag{3.2}$$

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 3.2, 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). With $\alpha = 1$ and $\beta = 1$, we modified the NCI to focus more on the regression coefficient estimation. 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 & Legendre, 2010). Following Laliberté & Legendre (2010), we used two simple formulas to calculate neighbourhood FDis:

$$\mathbf{c} = \frac{\sum a_j x_{ij}}{\sum a_j} \tag{3.3}$$

$$FDis = \frac{\sum a_j z_j}{a_j} \tag{3.4}$$

where $\mathbf{c}$ 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 3.2 – z_j represents the distance between species j and centroid $\mathbf{c}$, 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).

Table 3.2: Principal component analysis based on six functional traits

	PCA axes	
Functional traits	PC1	PC2
Hmax	-0.31	-0.42
SLA	0.56	-0.19
PLC50	0.06	-0.65
Nm	0.56	-0.17
WD	0.46	0.43
LA/SA	0.24	-0.37
Variance explained (%)	47	33

Hmax, maximum height; SLA, specific leaf area; PLC50, water potential at which 50% of hydraulic conductivity is lost; Nm, nitrogen content per unit of leaf mass; WD, wood density; LA/SA, ratio of leaf area to sapwood area

3.2.4 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 advantage 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.

3.3 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 (Fig. 3-2) 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 (Fig. 3-3) 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 (Fig. 3-3) than those in the full experiment (Fig. 3-2). In contrast, the impact in the 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 (Fig. 3-4). 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 3.3. 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 45% less performance than the best combination (Fig. 3-2), 30% less in the irrigated treatment (Fig. 3-3), and 65% percent less in the non-irrigated condition (Fig. 3-4). Furthermore, the R^2 and RMSE values of the second-best combination are not considerably different from the model accounting only for D (Table 3.3), especially in the non-irrigate treatment. The scatter plots shown in Fig. 3-5 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. 3-5). The best NCI type and the best FDis type were combined with D to generate a combination of three variables with higher accuracy compared to models with two variables (Table 3.3). The scatter plots shown in Fig. 3-6 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.

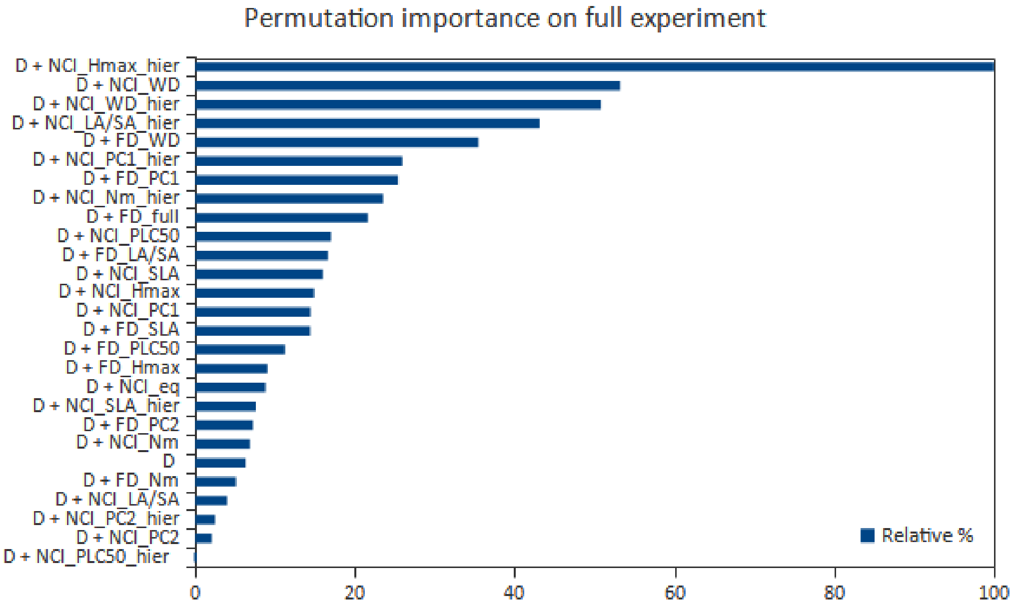

Figure 3-2: Bar plot ranking predictors according to their relative importance in predicting tree diameter increments on the test set (4224 observations) of the full experiment, irrigated treatment, and non-irrigated treatment. Acronyms for each variable are listed in Table 3.1

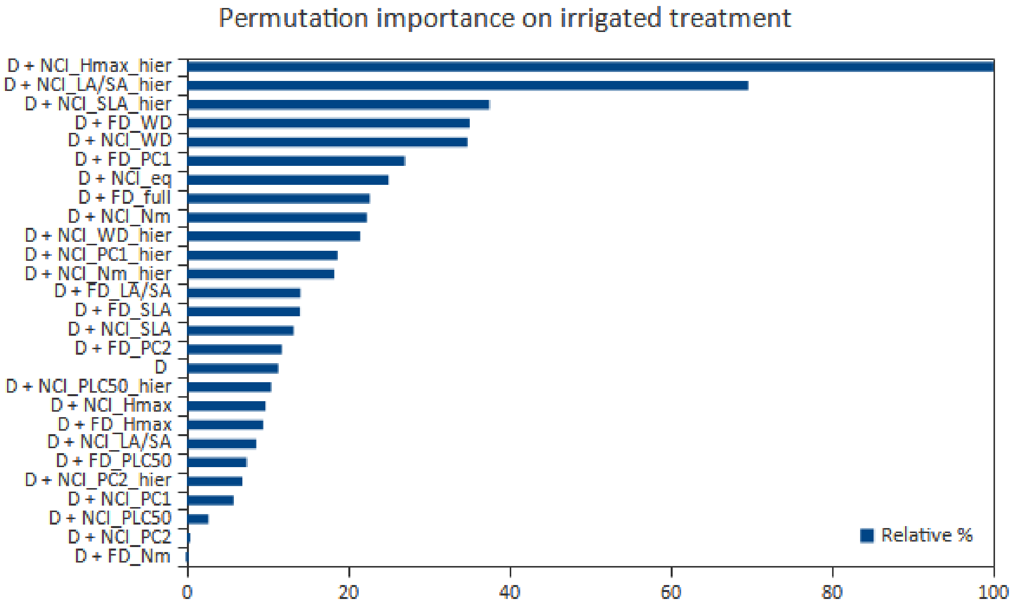

Figure 3-3: Bar plot ranking predictors according to their relative importance in predicting tree diameter increments on the test set (2112 observations) of the full experiment, irrigated treatment, and non-irrigated treatment. Acronyms for each variable are listed in Table 3.1

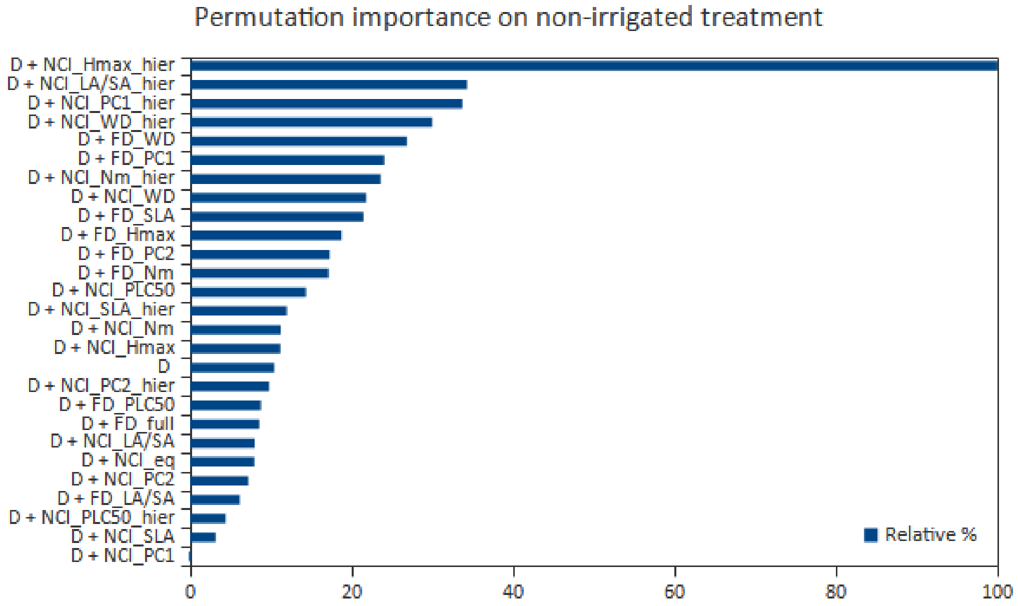

Figure 3-4: Bar plot ranking predictors according to their relative importance in predicting tree diameter increments on the test set (2112 observations) of the full experiment, irrigated treatment, and non-irrigated treatment. Acronyms for each variable are listed in Table 3.1

Table 3.3: Diameter increments (DI) estimation accuracy assessment on the test set with random forest regression. Acronyms for each variable are listed in Table 3.1

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
		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
		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
		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

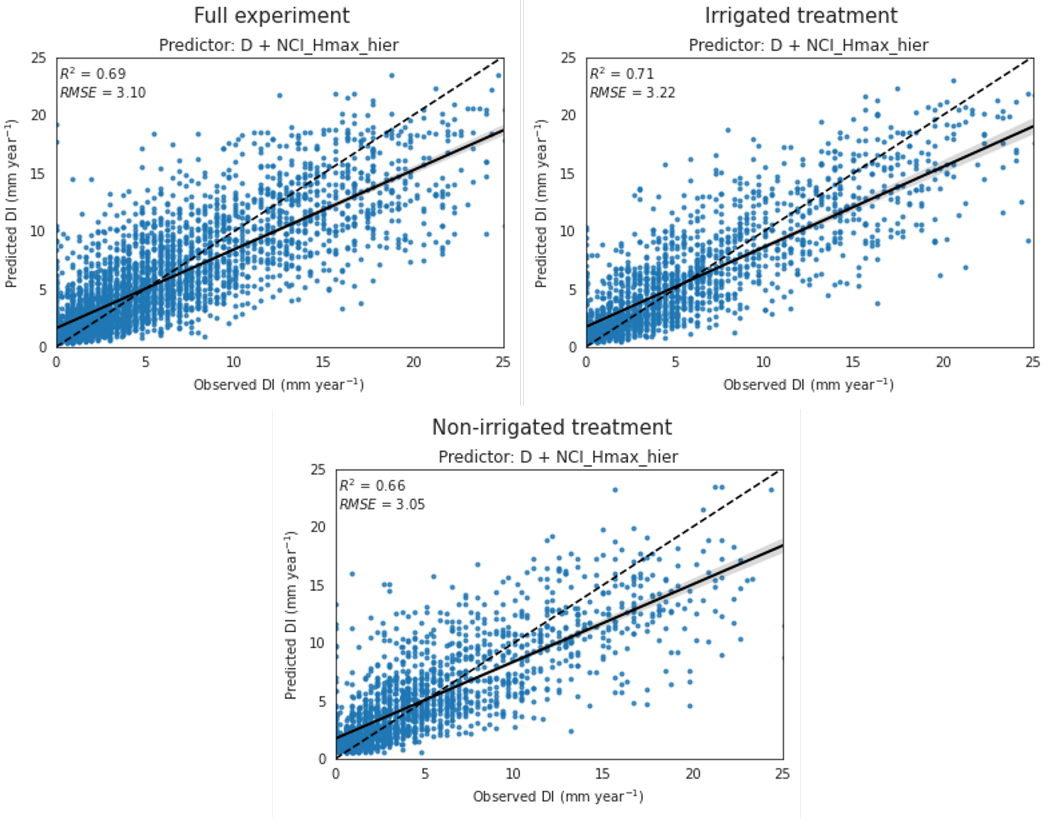

Figure 3-5: Scatter plots of the predicted and observed DI of the best combination on the test set of the full experiment, irrigated treatment, and non-irrigated treatment. Dotted lines indicate the identity line (1:1)

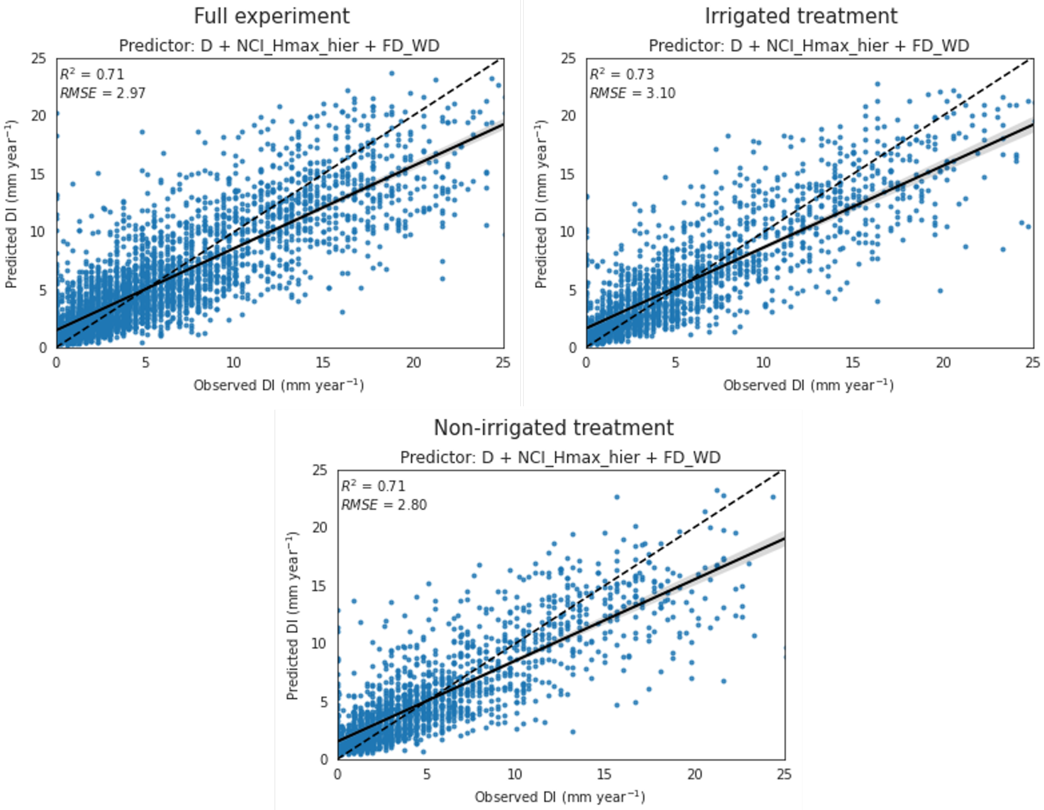

Figure 3-6: Scatter plots of the predicted and observed DI of the combination of three variables on the test set of the full experiment, irrigated treatment, and non-irrigated treatment. Compared to the combination of two variables, the inclusion of FDis increased the predictive power (See Fig. 3-5). Dotted lines indicate the identity line (1:1)

3.4 Discussion

We found strong support for the hypothesis that the interaction coefficient of the neighbourhood competition of twelve young Mediterranean species is asymmetric, i.e. mediated by the functional traits (H_1). In comparison to the top models depicting asymmetric competition, the symmetric competition represented by NCI_eq gained less relative importance. However, symmetric competition is commonly representative of belowground rather than aboveground competition (Schwinning & Weiner, 1998; Cahill & Casper, 2000; Bartelheimer et al., 2008). 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. Our ability to find support for the symmetric competition hypothesis is constrained by the lack of variables related to belowground competition (e.g. root competition) within our dataset, which may have supported this theory.

We found strong support for the hypothesis that asymmetric competition is linked to hierarchical distances of traits related to competition for light (H_2), i.e., individuals with the greater hierarchical distance of maximum height (NCI_Hmax_hier) compete for more for this resource. 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 3.3). In contrast, the nichia similarity hypothesis (H_3) was less supported by our results compared to the trait hierarchy hypothesis. The combination of variables supporting this theory is represented by D and NCI_WD in the full experiment dataset, with a relative importance of about 50%, which declines in the irrigated and non-irrigated treatment. In the latter case, individuals with the greater absolute distance of wood density compete for less for shared resources. Our results align with recent evidence that trait hierarchy plays a key role in determining competitive outcomes (Goldberg

& 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 & Wayne, 1996; Law et al., 1997; Schwinning & Weiner, 1998; Weiner & Damgaard, 2006; Brown & 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 & 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 & 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.

The effects of water use strategies on plant interactions have received less attention to date. However, our results indicate that in well-watered soil, functional traits related to water transport capacity, such as LA/SA (Wright et al., 2006; Buckley & Roberts, 2006), showed 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 70% (Fig. 3-3), and in the non-irrigated treatment the relative importance is less than 40% (Fig. 3-4). 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, the 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.

Our results support the hypothesis that functional dispersion can be used as a diversity metric to predict DI (H_4). Among all functional dispersion indexes, FD_WD was the best predictor of DI in all datasets (Figs. 3-2, 3-3, and 3-4). 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 the 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 than FDis. 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. 3-6). 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. 3-5). 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.

3.5 Conclusion

The results of this research, conducted in a high diversity experiment of young Mediterranean species, suggest that: (1) the neighbourhood competition is asymmetric; (2) the neighbourhood competition based on trait hierarchy related to competition for light more accurately explains tree diameter increments than 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 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 managing a Mediterranean forest, which has received little attention compared to other biomes in terms of competitive neighbourhood analysis. 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 neighborhood competition and functional dispersion indexes, 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.

Chapter 4

2nd case study

Neighbourhood analysis of tree growth at the species level

4.1 Introduction

Traits are morphological, physiological, or phenological features measurable at the individual level and are fitness- and performance-related (Violle et al., 2007). Functional traits provide a deterministic relationship between basic biological processes and community dynamics (Westoby & Wright, 2006). Several studies have used functional traits to determine different indices of functional diversity, such as functional richness, functional evenness, functional divergence, and more recently functional dispersion (FDis) (Villéger et al., 2008; Laliberté & Legendre, 2010).

However, trait influences on individual plant physiology and functions are becoming well understood, but the role of traits in competitive interactions between species is still limited (Kunstler et al., 2016). Only recently, functional traits have been included in neighbourhood competitive analysis by assuming that the intensity of competition is related to the distance of traits between species (Uriarte et al., 2010; Kunstler et al., 2012; Fortunel et al., 2016). Generally, competitive neighbourhood analysis describes the influence of neighbouring trees on the growth of a target tree by using competition indexes (Canham et al., 2004; Uriarte et al., 2004a,b; Canham et al., 2006; Astrup et al., 2008; Coates et al., 2009; Thorpe et al., 2010; Gómez-Aparicio et al., 2011). However, the intensity of competition reflects how species use resources. For example, when we assume that all neighbours share resources equally with the target tree, the competition is symmetric. In contrast, unequal resource sharing with the target tree defines an asymmetric competition.

Different theories have been associated with asymmetric competition: trait similarity, trait hierarchy, and phylogenetic similarity (MacArthur & Levins, 1967; Uriarte et al., 2010; Kunstler et al., 2012, 2016; Fortunel et al., 2016). According to the theory of trait similarity, competition between two species is stronger as the distance between them gets smaller, yet there is no dominance in resource acquisition. In other words, when the nichia distance between two species gets reduced, the possibility that they can cohabit becomes smaller. For example, species with a high maximum height (Hmax) compete more with neighbours of the same Hmax, but less with smaller neighbours. The trait hierarchy theory, in contrast, suggests that superior competitors will predominate in the crowding dynamics. For example, species with high Hmax may have more adverse effects on neighbours with low Hmax than the opposite. The phylogenetic similarity theory, on the other hand, is not trait-based and makes the assumption that ecologically related species compete in more severe resource competition than dissimilar ones.

In the context of climate change, it is imperative to understand how abiotic stress affects resource acquisition intensity. This follows the stress-gradient hypothesis (SGH), which 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 & Callaway, 1994). Another point to consider in the SGH hypothesis is the age of the plants. For example, Siles et al. (2010) discovered that in a Mediterranean habitat, the survival rate of larger plants (2-year-old) was higher than that of smaller plants (1-year-old) in numerous species. This is likely related to the fact that some older plants have larger and more efficient root systems that quantitatively increase the absorption of the water resource. But, what impact does a water stress-gradient have if the plantation is formed of a high density and diversity of species of the same age? Water demand and species adaptations (e.g., drought tolerance) are the variables at play in this context.

The overall aim of this research was to investigate how functional traits drive the competitive performance and FDis of 12 young Mediterranean species by including the water stress-gradient effect. Specifically, we used tree diameter increments (DI) as an indicator of individual tree growth (Seidel et al., 2015) to test the same hypotheses (H_1, H_2, H_3, and H_4) as the previous case study (See Chapter 3), but at the species level. In addition to these hypotheses, we tested (H_5) whether neighbourhood competition has a larger impact on DI of target species in irrigated soils compared to non-irrigated. We predict that when water stress decreases, the influence of neighbouring trees on the growth of the target species increases due to the high water demands of young plants.

4.2 Methods

4.2.1 Linear regression models and AIC selection

To test our study hypotheses a simple linear regression was used, as the random forest (RF) regression applied in Chapter 3 presents some limitations: (i) the lack of coefficients, which would allow for a more accurate interpretation of the results; and (ii) the inability to assess the interaction effect of several independent variables on output. The same predictors from Table 3.1 were used for these analyses, but the model fitting was applied to the twelve study species (See Section 3.2.1).

In total, 106 models were created, with 27 models having no treatment effect and 79 models having a treatment effect on predictors (Table 4.1). Because tree diameters (D) represent the size of the target species at the beginning of sampling, it was the only fixed variable for each combination. The combination of variables was D with the neighbourhood competition index (NCI) or the functional dispersion (FDis). To make the interpretation of the data easier, the combination of NCI and FDis was omitted. To analyse the regression models, the "statsmodels" module in Python (Seabold & Perktold, 2010) was used. Regression coefficients with related statistical significance, residual sum of squares (RSS), the goodness of fit (R^2 or adjusted R^2), and AIC were among the metrics supplied by the method for assessing regression models. The AIC values were used to compute the ranking measures (AIC differences (Δ_i), Akaike weights (w_i), and the evidence ratios (ER)). For models with $\Delta_i = 0$, the coefficient estimation results were reported.

Table 4.1: List of combinations of predictors with the corresponding number of generated models and variables

Combinations of predictors	No. models	No. variables	Treatment effect
DI = D	1	1	No
DI = D + NCI	17	2	No
DI = D + FDis	9	2	No
DI = T:D	1	2	Yes
DI = T:D + NCI	17	3	Yes
DI = T:D + FDis	9	3	Yes
DI = D + T:NCI	17	3	Yes
DI = D + T:FDis	9	3	Yes
DI = T:D + T:NCI	17	4	Yes
DI = T:D + T:FDis	9	4	Yes

T, treatment (irrigated vs non-irrigated); symbol " : " denotes the interaction term.

4.3 Results and Discussion

The simulation results allowed us to determine the best variable combination for predicting tree diameter increments (DI) from 2016 to 2019, including the influence of irrigation on these variables, species by species. For each species, only models with strong empirical support ($\Delta_i < 2$) were reported (See Additional Resources A). Models including the variable combination of tree diameters (D) and neighbourhood competition index (NCI) were found to be consistently the best models for the twelve species studied (Table 4.2). In contrast, there was no support for models accounting only for D and for models including the variable combination of D and functional dispersion (FDis). In particular, the watering treatment affected (Table 4.2) tree diameters of ten species (83% of our full experiment dataset), and the neighbourhood competition of seven species (58% of our full experiment dataset). For nine out of the ten species affected by the watering treatment, the diameter regression coefficients were more positive in the irrigated treatment (IR) than in the non-irrigated treatment (NIR), indicating the importance of water resources in young species growth (Figure 4-1). For two species (*A. monspessulanum* and *Q. pubescens*), no treatment effect was observed, probably due to the drought tolerance of the latter. An experiment conducted in urban environments showed that species of the *Acer* genus exhibit high tolerance to water deficit, measured by the leaf water potential at turgor loss (Sjöman et al., 2015). Negative water potential values can retain physiological function over a wider range of leaf water potentials. Similarly, *Q. pubescens* focuses its physiological activity when moisture conditions are most favourable, exhibiting a high tolerance to water scarcity (Weber et al., 2007). However, the response of tree diameters to irrigated treatment was not significant ($P > 0.05$) for *P. lentiscus* (See Table A.7). This result could be an artefact due to the difficulties of this species in growing in our experimental design because of its slow-growing rate and small size compared to the other species. Our results agree with the well-known beneficial properties of water for plant physiology; water transports the nutrients required for plant growth and has been identified as the primary abiotic element affecting regeneration and restoration success in the

Mediterranean-type climate region (Siles et al., 2010; Becerra et al., 2013).

The trait-based models best described the DI of ten out of the twelve species, whereas the model with equivalent competitors (NCI_{eq}) best explained the DI of *P. pinea* and *Q. suber*. We confirmed the hypothesis (H_1) that the neighbourhood competition is asymmetric, i.e., mediated by functional traits. This is consistent with the findings of Fortunel et al. (2016) and the previous case study (See Chapter 3. The hierarchical trait distance models were supported for seven out of the ten species best described by trait-based models, and the second axis of PCA (PC2) was the most frequently selected multivariate trait, followed by the univariate traits LA/SA, Hmax, and PLC50 (Table 4.2). Plant height (Hmax) is related to competitive ability for light (Weiher et al., 1999; Perez-Harguindeguy et al., 2013; Maracahipes et al., 2018), and was the best predictor of DI in the random forest regression results performed on three different datasets (full experiment, irrigated treatment, and non-irrigated treatment) from the previous case study (See Chapter 3). The species-level analysis of this study also gives importance to physiological traits such as LA/SA and PLC50. The trait LA/SA is strongly associated with the water transport capacity of plants (Medhurst & Beadle, 2002; Perez-Harguindeguy et al., 2013), and links photosynthesis to transpiration (Togashi et al., 2015). Regarding PLC50, this is an essential plant physiological parameter about a threshold or hydraulic safety margin of tree species (Delzon & Cochard, 2014) and is directly related to mortality in most climatic zones (Anderegg et al., 2016). Rosner et al. (2019) found that species-specific relative water loss is a strong predictor of PLC50. The trait with the highest weight in PC2 was PLC50, followed by Hmax and WD, highlighting the importance of traits related to competition for light and water. Mechanical resistance, the storage capacity of woody tissues, and tree development are all related to WD (King et al., 2005; Chave et al., 2009). Additionally, species with high WD are frequently the most shade-tolerant (Nock et al., 2009).

In comparison, no species selected the multivariate distance of functional traits represented by PC1 as the best model. Leaf traits such as SLA and Nm mainly represent the latter axis, as opposed to PC2. SLA is frequently used in growth analysis because it is often positively related to potential radial growth across species and is strongly related to Nm (Westoby et al., 2002; Wright et al., 2007; Poorter et al., 2009). However, both these traits are indicators of the nutritional status of plants. The lack of relevance of leaf traits in these species-by-species neighbourhood competition models is consistent with the previous case study results (See Chapter 3). A similar result was found in a recent study (Fortunel et al., 2016), where SLA was the least representative functional trait of the neighbourhood competition models. However, considering both multivariate and univariate traits, those related to water transport capacity are more represented, so we cannot confirm hypothesis H_2. For example, excluding multivariate traits, Hmax best described the growth of one species (*Q. ilex*), while traits related to water transport capacity (LA/SA and PLC50) best described the growth of three species (*A. monspessulanum*, *O. europaea*, and *Q. suber*). The absolute trait distance models were supported for three species, with the traits chosen including SLA and LA/SA (Table 4.2). Therefore, even at the species level, the trait hierarchy theory outperforms the trait similarity theory (hypothesis H_3).

Overall, the neighbourhood competition of seven species was affected by irrigation, and six of them experienced greater competition in the irrigated treatment (Figure 4-2), confirming hypothesis H_5. Different studies state that a given plant species competes with its neighbours for water and nutrients by acquiring a large amount of these resources, or through resource use efficiency strategies to increase biomass production (Nambiar & Sands, 1993). Successful competitors optimise stomatal conductance and water loss on soils with high water availability while reducing water loss and increasing water use efficiency on soils with low water availability (Balandier et al., 2006). These observations imply that soils with abundant water resources may experience more competition than soils with limited water resources because the dominant species have immediate access to them. Previous studies have discovered that the environmental stress gradient affects plant interactions, leading to a shift to facilitation or a reduction in competition (He et al., 2013). Although neighbourhood competition is decreased for some species in the non-irrigated condition, we cannot speculate on potential facilitative effects because the NCI only measures the negative impacts of neighbours on the target species.

Our results do not support the hypothesis (H_4) that the neighbourhood FDis influences DI. The Neighbourhood competition proved to be a stronger predictor of DI than FDis, which confirmed the finding of the previous case study (See Chapter 3). However, the FDis simply provides information on species traits, in contrast to the NCI, which describes the neighbourhood competition with information on species tree size and functional traits.

Table 4.2: The best model for each of the twelve study species

Species	Best model (for $\Delta_i = 0$; See Additional Resources A)	No. variables	RSS	R^2_{adj}
ACMO	DI = D + NCI_LA/SA_hier	2	1.175	0.358
ARUN	DI = T:D + T:NCI_LA/SA	4	4.802	0.312
FROR	DI = T:D + T:NCI_PC2_hier	4	3.489	0.309
OLEU	DI = T:D + T:NCI_LA/SA_hier	4	1.225	0.218
PHLA	DI = T:D + T:NCI_SLA	4	0.934	0.222
PIHA	DI = T:D + NCI_PC2_hier	3	21.846	0.369
PILE	DI = T:D + NCI_SLA	3	0.373	0.071
PIPA	DI = T:D + NCI_eq	3	16.991	0.581
PIPE	DI = T:D + T:NCI_PC2_hier	4	15.842	0.417
QUIL	DI = T:D + T:NCI_Hmax_hier	4	3.639	0.416
QUPU	DI = D + NCI_eq	2	3.125	0.345
QUSU	DI = T:D + T:NCI_PLC50_hier	4	5.184	0.430

ACMO, *A. monspessulanum*; ARUN, *A. unedo*; FROR, *F. ornus*; OLEU, *O. europaea*; PHLA, *P. latifolia*; PIHA, *P. halepensis*; PILE, *P. lentiscus*; PIPA, *P. pinea*; PIPE, *P. pinaster*; QUIL, *Q. ilex*; QUPU, *Q. pubescens*; QUSU, *Q. suber.* T, treatment (irrigated vs non-irrigated); symbol : denotes the interaction term.

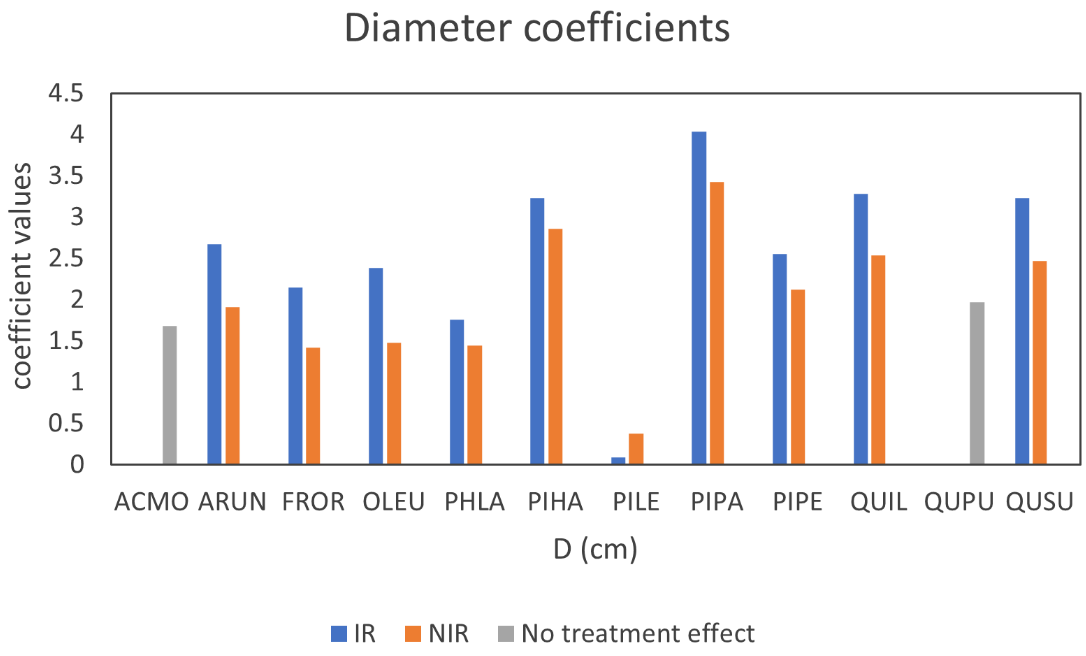

Figure 4-1: ACMO, *A. monspessulanum*; ARUN, *A. unedo*; FROR, *F. ornus*; OLEU, *O. europaea*; PHLA, *P. latifolia*; PIHA, *P. halepensis*; PILE, *P. lentiscus*; PIPA, *P. pinea*; PIPE, *P. pinaster*; QUIL, *Q. ilex*; QUPU, *Q. pubescens*; QUSU, *Q. suber*. IR, irrigated treatment; NIR, non-irrigated treatment.

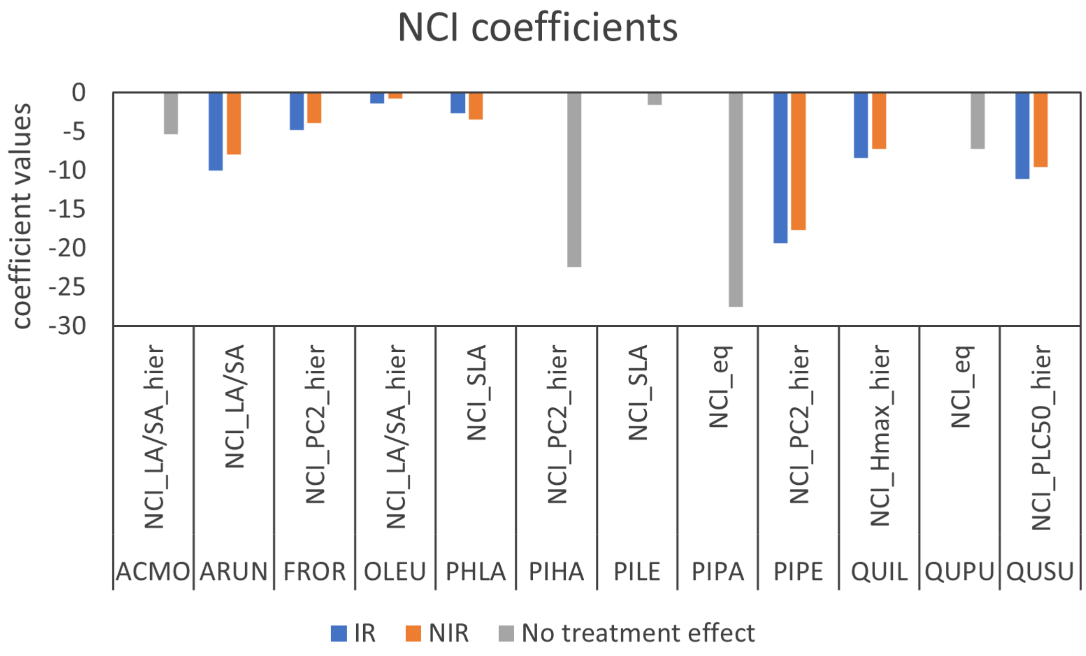

Figure 4-2: ACMO, *A. monspessulanum*; ARUN, *A. unedo*; FROR, *F. ornus*; OLEU, *O. europaea*; PHLA, *P. latifolia*; PIHA, *P. halepensis*; PILE, *P. lentiscus*; PIPA, *P. pinea*; PIPE, *P. pinaster*; QUIL, *Q. ilex*; QUPU, *Q. pubescens*; QUSU, *Q. suber*. IR, irrigated treatment; NIR, non-irrigated treatment.

Chapter 5

Conclusion

The general objective of the thesis was to unravel some underlying ecological processes in Biodiversity and Ecosystem Functions relationships (BEF) to advance our understanding of BEF research. This thesis focuses on individual-level interactions rather than on an ecosystem-level approach. The entire research was carried out at the IDENT (International Diversity Experiment Network with Trees), located in Italy, an experimental site specialised in the study of BEF relationships. Individual-based models are a modelling approach that allows researchers to analyse individual-level processes in detail. Neighbourhood analysis, at the heart of individual-based models, allows for the study of competitive interactions – expressed by the neighbourhood competition index (NCI) – between individuals, where this interaction is defined as a reduction in resource availability that limits the growth of the target plant and, consequently, the ecosystem function of the mixed forest. In addition to competitive interactions, the novelty of this thesis was the evaluation of the effect of neighbourhood functional diversity – expressed by the functional dispersion (FDis) – on species growth.

We demonstrated, using tree diameter increments as an indicator of individual tree growth, that: (1) competitive performance, defined as differences in resource use, is driven by functional traits and, in particular, by hierarchical distances of traits related to competition for light; (2) at the species level, the neighbourhood competition is driven mostly by trait hierarchy theory, but the functional traits are related especially to water transport capacity; (3) neighbourhood competition compared to functional dispersion is a better predictor of tree diameter increments; and (4) environmental factors (for example, water stress-gradient) influence both growth in diameter and the outcome of competition across species. In particular, species grow more in irrigated soils, but competition between species is also stronger.

Although the findings mainly confirm the assumptions of our study, more research is needed to compensate for the limitations of our experiment. Tree diameter increments, for example, reflect aboveground tree growth in our models, omitting belowground interactions. Root interactions might be included in a more comprehensive model. Additionally, the relationship between functional traits involved in neighbourhood competition and target species has been difficult to decipher, probably due to the limitations of the statistical methods used in the study, or the small number of species. Additionally, we only considered blocks (irrigated and non-irrigated) and removed plots within the blocks to decrease the number of variables considered in the models. Including the plots would have improved the ecological interpretation of the findings. Another drawback is the distance of the competition radius between species; in particular, we only examined a distance of 2 metres in our models. We are conscious that considering alternative distances (e.g., 1, 1.5, 2, and 2.5 metres) might have resulted in a more accurate analysis, but to avoid getting lost in many results, we chose 2 metres as the appropriate distance.

In conclusion, at the local scale, trait-based ecology has proven to be a powerful approach to understanding and predicting complex dynamics within a mixed forest. We recommend the inclusion of functional traits in BEF relationship research and use the modelling approach to extend investigations across different spatial and temporal scales.

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Appendix A

Additional Resources

Table A.1: Best models for *A. monspessulanum* with coefficient estimation result

ACMO								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = D + NCI_LA/SA_hier	2	1.175	0.358	4328.342	0	0.250	0.250	1
DI = D + NCI_eq	2	1.176	0.357	4328.696	0.353	0.209	0.459	1.196
DI = T:D + NCI_LA/SA_hier	3	1.176	0.357	4330.006	1.663	0.109	0.568	2.294
DI = T:D + NCI_eq	3	1.176	0.357	4330.234	1.892	0.097	0.665	2.577
DI = D + T:NCI_PC1	3	1.176	0.357	4330.326	1.984	0.093	0.758	2.688

coefficients result (for $\Delta_i = 0$)			
Predictor	Estimate	Std. error	*P*-value
Intercept	2.776	0.141	0
D	1.684	0.133	0
NCI_LASA_hier	-5.314	0.219	0

Table A.2: Best models for *A. unedo* with coefficient estimation result.

ARUN								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + T:NCI_LA/SA	4	4.802	0.312	6355.419	0	0.852	0.852	1

coefficients result (for $\Delta_i = 0$)			
Predictor	Estimate	Std. error	P-value
Intercept	4.474	0.314	0
NIR:D	1.912	0.156	0
IR:D	2.672	0.147	0
NIR:NCI_LA/SA	-7.898	0.755	0
IR:NCI_LA/SA	-9.955	0.721	0

Table A.3: Best models for *F. ornus* with coefficient estimation result.

FROR								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + T:NCI_PC2_hier	4	3.489	0.309	5890.978	0	0.599	0.599	1
DI = T:D + NCI_PC2_hier	3	3.493	0.308	5891.789	0.811	0.399	0.998	1.501

coefficients result (for $\Delta_i = 0$)			
Predictor	Estimate	Std. error	P-value
Intercept	2.016	0.234	0
NIR:D	1.415	0.120	0
IR:D	2.146	0.104	0
NIR:NCI_PC2_hier	-3.870	0.489	0
IR:NCI_PC2_hier	-4.765	0.469	0

Table A.4: Best model for *O. europea* with coefficient estimation result.

OLEU								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + T:NCI_LA/SA_hier	4	1.225	0.218	3802.575	0	0.6	0.6	1

coefficients result (for $\Delta_i = 0$)			
Predictor	Estimate	Std. error	P-value
Intercept	0.362	0.111	0
NIR:D	1.479	0.139	0
IR:D	2.384	0.143	0
NIR:NCI_LA/SA_hier	-0.754	0.201	0
IR:NCI_LA/SA_hier	-1.362	0.211	0

Table A.5: Best models for *P. latifolia* with coefficient estimation result.

PHLA								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + T:NCI_SLA	4	0.934	0.222	3990.764	0	0.376	0.376	1
DI = T:D + NCI_SLA	3	0.935	0.221	3991.379	0.615	0.276	0.652	1.362
coefficients result (for $\Delta_i = 0$)								
Predictor	Estimate	Std. error	P-value					
Intercept	1.405	0.113	0					
NIR:D	1.440	0.131	0					
IR:D	1.760	0.122	0					
NIR:NCI_SLA	-3.432	0.445	0					
IR:NCI_SLA	-2.667	0.426	0					

Table A.6: Best models for *P. halepensis* with coefficient estimation result.

PIHA								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + NCI_PC2_hier	3	21.846	0.369	8513.752	0	0.515	0.515	1
DI = T:D + T:NCI_PC2_hier	4	21.836	0.369	8514.109	0.357	0.431	0.946	1.195
coefficients result (for $\Delta_i = 0$)								
Predictor	Estimate	Std. error	P-value					
Intercept	12.942	0.790	0					
NIR:D	2.861	0.226	0					
IR:D	3.232	0.213	0					
NCI_PC2_hier	-22.362	1.119	0					

Table A.7: Best models for *P. lentiscus* with coefficient estimation result.

PILE								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + NCI_SLA	3	0.373	0.071	2314.137	0	0.458	0.458	1
DI = D + T:NCI_SLA	3	0.374	0.071	2315.166	1.028	0.274	0.732	1.672
DI = T:D + T:NCI_SLA	4	0.374	0.071	2315.794	1.657	0.2	0.932	2.290
coefficients result (for $\Delta_i = 0$)								
Predictor	Estimate	Std. error	P-value					
Intercept	0.929	0.058	0					
NIR:D	0.379	0.114	0					
IR:D	0.093	0.136	0.495					
NCI_SLA	-1.522	0.170	0					

Table A.8: Best models for *P. pinea* with coefficient estimation result.

PIPA								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + NCI_eq	3	16.991	0.581	8163.890	0	0.433	0.433	1
DI = T:D + NCI_PLC50	3	17.003	0.581	8164.920	1.030	0.259	0.692	1.672
DI = T:D + T:NCI_eq	4	17.002	0.581	8165.838	1.948	0.164	0.856	2.640
coefficients result (for $\Delta_i = 0$)								
Predictor	Estimate	Std. error	P-value					
Intercept	15.995	0.598	0					
NIR:D	3.424	0.195	0					
IR:D	4.035	0.175	0					
NCI_eq	-27.574	0.737	0					

Table A.9: Best models for *P. pinaster* with coefficient estimation result.

PIPE								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + T:NCI_PC2_hier	4	15.842	0.417	8080.992	0	0.479	0.479	1
DI = T:D + NCI_PC2_hier	3	15.858	0.416	8081.444	0.452	0.382	0.861	1.254

coefficients result (for $\Delta_i = 0$)			
Predictor	Estimate	Std. error	P-value
Intercept	15.320	0.696	0
NIR:D	2.124	0.212	0
IR:D	2.557	0.209	0
NIR:NCI_PC2_hier	-17.664	0.842	0
IR:NCI_PC2_hier	-19.380	0.920	0

Table A.10: Best models for *Q. ilex* with coefficient estimation result.

QUIL								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + T:NCI_Hmax_hier	4	3.639	0.416	5951.614	0	0.65	0.65	1
DI = T:D + NCI_Hmax_hier	3	3.645	0.416	5952.884	1.270	0.344	0.994	1.89

coefficients result (for $\Delta_i = 0$)			
Predictor	Estimate	Std. error	P-value
Intercept	2.763	0.224	0
NIR:D	2.539	0.145	0
IR:D	3.285	0.148	0
NIR:NCI_Hmax_hier	-7.249	0.573	0
IR:NCI_Hmax_hier	-8.421	0.519	0

Table A.11: Best model for *Q. pubescens* with coefficient estimation result.

QUPU								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = D + NCI_eq	2	3.125	0.345	5730.284	0	0.436	0.436	1
DI = D + T:NCI_eq	3	3.127	0.345	5732.185	1.901	0.168	0.604	2.595
DI = T:D + NCI_eq	3	3.127	0.345	5732.283	1.999	0.16	0.764	2.725

coefficients result (for $\Delta_i = 0$)			
Predictor	Estimate	Std. error	P-value
Intercept	3.626	0.189	0
D	1.965	0.105	0
NCI_eq	-7.238	0.386	0

Table A.12: Best model for *Q. suber* with coefficient estimation result.

QUSU								
Candidate models	No. variables	RSS	R^2_{adj}	AIC	Δ_i	w_i	acc w_i	ER
DI = T:D + T:NCI_PLC50_hier	4	5.184	0.430	6461.115	0	0.792	0.792	1

coefficients result (for $\Delta_i = 0$)			
Predictor	Estimate	Std. error	P-value
Intercept	3.739	0.309	0
NIR:D	2.473	0.139	0
IR:D	3.227	0.142	0
NIR:NCI_PLC50_hier	-9.546	0.748	0
IR:NCI_PLC50_hier	-11.059	0.735	0