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Effects of tree species diversity on early-stage forest dynamics

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Thomas

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List of abbreviations

(G)LMM	(Generalized) Linear Mixed Model
BEF	Biodiversity and Ecosystem Functioning
CE	Complementarity Effect
CWM	Community Weighted Means
DOM	Dominance Effects
DPR	Diversity Productivity Relationship
FD	Functional Diversity
FORBIO	Name of Belgian tree diversity experiment
GED	FORBIO site in Gedinne
Gsmax	Maximum stomatal conductance
HEC	FORBIO site in Hechtel-Eksel
Hmax	Maximum height
IDENT-M	Name of Sardinian tree diversity experiment in Macomer
LA	Leaf Area
LDMC	Leaf Dry Matter Content
Leaf N	Nitrogen content of leaf
LLS	Leaf Life Span
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
N	Sample size
NE	Net diversity Effect
Nm	Leaf Nitrogen content per unit of Mass
PCA	Principle Components Analysis
PLC50	Water potential where 50% of hydraulic conductivity is lost
PMZ	Permanent Monitoring zone
Pnmax	maximum photosynthetic rate per unit area
SDW	Seed Dry Weight
SE	Selection Effect
SGH	Stress-Gradient Hypothesis
SLA	Specific Leaf Area
SR	Species Richness
TDC	Trait-Dependent Complementarity effect
TIDC	Trait-Independent Complementarity effect
WAI	Water Availability Index
WD	Wood Density
ZED	FORBIO site in Zedelgem

Summary

Land-use intensification is often put forward as a key driver of global change, including biodiversity loss. Although intensification has thoroughly helped solving short-term resource deficits, a sustainable delivery of multiple ecosystems services from high-input low-diversity systems is increasingly disbelieved.

Understanding the linkages between biodiversity and ecosystem functioning (BEF) therefore evolved into a pivotal line of ecological research. The research, mostly based on simple experimental set-ups, established broad evidence on strengthening ecosystem functioning at higher diversity. Yet, **how tree species diversity governs function and service in forests is hardly documented**. The research gap contradicts with an apparent position of forests in terms of land cover, repository of biodiversity, carbon sequestration capacity, roles in climate regulation and ability to supply goods and services beneficial to human well-being.

In this thesis we addressed knowledge gaps on mixed-species forest dynamics, shortly after planting. Our central objective was to identify the contribution of species diversity and assembly to tree performance, which was evaluated in terms of survival, vitality, architectural development and growth. The study builds on data gathered at the multi-site **FORBIO** and single-site **IDENT-M** experiments in temperate (Belgium) and Mediterranean (Sardinia) Europe respectively. The experiments are at the frontier of modern ecology because they allow to generalize BEF relationships to forests and to test the mechanistic principles. In both experiments, tree species number and assembly are manipulated in a well-balanced and blocked design.

At FORBIO, diverse stands exhibited **greater insurance against planting failure**. Effects developed through the intimate mixing of tree species with contrasting resistance against natural disturbances. Under harsh conditions, well performing species can locally compensate for the reduced performances of sensitive trees. This knowledge contributes to plantation risk management. We also quantified performance-enhancing effects, representing an increased functioning of organisms, populations or communities at higher diversity. For seedling survival at FORBIO, for instance, we revealed that some species were assisted by mixing, while others were not. Consequently, a performance-enhancing effect of diversity was cancelled-out at the community level. At IDENT-M, the diversity trend was more obvious, as eight out of nine **broadleaved species improved their vitality status in functionally diverse mixtures**. We observed that diversity effects were roughly driven by *Pinus* sp. alleviating environmental stress. Our study therefore suggests that dryland reforestation projects can gain from **seedling facilitation by nurse plants**. We found no radical shift in the

nature of inter-specific interactions when contrasting irrigated with non-irrigated stands. A greater facilitation under drought was nevertheless forecasted based on the stress-gradient theory.

At FORBIO, **83 % of the mixtures demonstrated higher biomass productivity** compared to the weighted-average productivity of monocultures. Although diversity effects are proposed to act at various spatial scale levels, overyielding was mainly underpinned by tree-tree interactions at local neighbourhoods. We also concluded strong context dependency. At the benign ZED site, overyielding was modulated by trait-dependent **complementarity effects**. In other words, only slow growers were facilitated in mixtures. At the harsh GED site, fast growers overyielded at the expense of the poorest. This suggests an alternative **mechanism of competitive dominance**. The functional composition of tree communities contributed to the diversity patterns, notably in terms of species levels of shade tolerance.

Recently planted trees interact with local neighbours, even before canopy closure. This statement was confirmed by studying architectural development. Different attributes of **tree architecture**, such as height-to-diameter ratio, branch insertion angle and branchiness, **responded strongly to neighbourhood competition**. The tendencies were species-specific and could be explained by their strategies to tolerate of avoid light-mediated competition in different neighbourhoods. In contrast, species composition or diversity were weak predictors for architectural plasticity.

It is sometimes believed the early forest stages can be ignored for ecosystem functioning because trees need to grow and develop before relevant interactions appear. In this thesis we demonstrated that interactions in young tree mixtures have a moderate contribution to plantation dynamics in terms of establishment success and growth. We found evidence that, likewise in non-forest experiments, positive BEF relationships can result from the steady influence of some key species (facilitators or dominators) or from niche differentiation in assemblages of well-coexisting species. This result underlies the importance of species selection, which can be done based on functional trait ecology.

The applied value can be summarized by the notion that tree species mixing was never found harmful for seedling or sapling performance. Rather, tree mixing can assist the management by insuring against dramatic die-off after planting, and later-on, by increasing biomass productivity. Further research should target (i) the long-term evolution of BEF relationships over the course of plantation development; (ii) unravel the context-dependency of BEF relationships and finally (iii) further establish a mechanistic BEF framework. All this together will allow to optimize forest ecosystem function and service by playing with tree species interactions.

Samenvatting

Door een intensief landgebruik moeten ecosystemen steeds meer inboeten op biologische complexiteit. Hoewel de korte-termijn voordelen van hoge-input lage-diversiteit systemen duidelijk zijn, wordt de ecologische en economische duurzaamheid ervan in vraag gesteld.

De koppeling tussen biodiversiteit en ecosysteemfunctioneren ontwikkelde zich tot een belangrijke ecologisch onderzoeksdomein. Op basis van resultaten uit kleinschalige experimenten werd het functioneel belang van biodiversiteit reeds overtuigend vastgesteld. Soortgelijk onderzoek in bosecosystemen is veeleer schaars. Nochtans zijn bossen globaal belangrijk voor koolstofopslag, klimaatregulatie en de aanlevering van essentiele ecosysteemdiensten.

In deze thesis **onderzochten we de dynamiek van jonge, gemengde bosaanplantingen**. We bepaalden de functionele rol van soortendiversiteit en -samenstelling voor de overlevingskansen, vitaliteit, vormontwikkeling en groei van jonge bosbomen. Velddata werd verzameld in **FORBIO** en **IDENT-M**, twee diversiteitsexperimenten respectievelijk in gematigd (België) en mediterraan (Sardinië) Europa.

We observeerden dat gemengde opstanden in FORBIO beter **gebufferd** zijn **tegen extreme sterfte na aanplant**. Deze effecten konden zich ontwikkelen door het mengen van boomsoorten met uiteenlopende toleranties voor milieustress. Bij ongunstige omstandigheden kunnen aangepaste boomsoorten lokaal compenseren voor het mogelijk verlies van anderen; een belangrijk inzicht voor risicoanalyse in bosbeheer.

Behalve risicospreiding via buffering onderzochten we ook diversiteitseffecten die de gemiddelde prestaties van bomen, boomsoorten en opstanden verbeteren. Waar de overlevingskansen van sommige boomsoorten verbeterde in menging, werden andere soorten benadeeld (FORBIO). In IDENT-M bleken acht uit negen **loofboomsoorten vitaler in mengingen met hoge functionele diversiteit**. We toonden aan dat dit effect veroorzaakt werd door de aanwezigheid van dennen (*Pinus* sp.), waarschijnlijk dankzij hun microklimaat. De resultaten suggereren dat bebossingsprojecten in semi-aride regio's kunnen baten bij **positieve soorteninteracties (facilitatie)**. Tot slot merkten we geen grote verandering in soorteninteracties tussen geïrrigeerde en niet-geïrrigeerde aanplantingen. Zo'n verandering werd nochtans verwacht op basis van de ecologische stress-gradiënt theorie.

In FORBIO concludeerden we dat **83 % van de mengingen productiever** zijn dan het gewogen gemiddelde van de overeenkomstige monoculturen (overyielding).

Hoewel diversiteitseffecten zich kunnen manifesteren op verschillende schaalniveaus, bleek overyielding het gevolg van interacties tussen nabije buurbomen. We merkten ook een sterke context-afhankelijkheid op. Op het milieu-gunstige ZED proefveld was trait-gebonden **complementariteit** het belangrijkste mechanisme. Dit wil zeggen dat enkel traaggroeiende boomsoorten gefaciliteerd werden in menging. Op het milieu-ongunstige GED proefveld profiteerden snelgroeiende soorten ten koste van de traaggroeiende. Dit suggereert een alternatief mechanisme, genaamd **dominantie in competitieverhouding**. De functionele opstandsamenstelling, vooral inzake lichtbehoefte, had een bepalende invloed op de biodiversiteitseffecten.

Het idee dat jonge bomen snel interageren met buurbomen werd bevestigd in de studie over architecturale plasticiteit in FORBIO. **Boomvormontwikkeling (stam en takken) bleek sterk beïnvloed door de mate van naburige competitie**. De tendensen waren soort-specifiek en konden verklaard worden aan de hand van competitiekracht en -tolerantie in functie van lichtvoorziening. Het verschil in interacties tussen bomen van dezelfde soort of van verschillende soorten bleek niet relevant voor de wijze van architecturale boomontwikkeling.

Het wordt soms aangenomen dat jonge bosbomen eerst voldoende moeten groeien en ontwikkelen alvorens relevante interacties kunnen optreden. In dit onderzoek besluiten we echter **het functioneren van jonge bosopstanden spoedig beïnvloed wordt door soortenmenging**. Net zoals in de vroege graslandexperimenten concluderen we dat BEF relaties het gevolg zijn van de sterke invloed van sleutelsoorten (faciliteren of domineren) en van het complementair gebruik van beperkende hulpbronnen. Dit resultaat bevestigd het belang van soortenkeuze gebaseerd op hun functionele soortkenmerken.

De praktijkwaarde van dit onderzoek kan samengevat worden door te stellen dat het mengen van boomsoorten nooit een algemeen negatief effect had op de prestaties van de jonge bosbomen. Eerder, het beheer kan net ondersteund worden door het beperken van een hoog risico op uitval na aanplanting, en nadien, door het verbeteren van de biomassa productiviteit.

Verder onderzoek zal moeten inzetten op (i) de lange-termijn evolutie van BEF relaties bij het ontwikkelen van de plantages; (ii) het begrijpen van de context-afhankelijkheid en (iii) het verder uitbouwen van een ecologisch-mechanistisch kader voor BEF. Al deze vooruitgangen samen zullen toelaten om ecosysteem functies en diensten uit bossen te verbeteren door gebruik van soorteninteracties.

Chapter 1

Introduction

Cover photo: Birch pruning, FORBIO HEC, 2018 (T. Van de Peer)

1.1 Concerns about global biodiversity loss

The earth is facing enormous environmental challenges, which are principally caused by unsustainable living standards for a vast growing share of the human population. Generally, these well-off people experience an urban life in an highly-globalized world. Also the total number of Earth's inhabitants is expanding, with realistic predictions counting as much as 9.7 billion people by mid-2050 (United nations 2017). The focal point of this population increment is found in the newly industrialized countries such as India, Bangladesh and Brazil. Land area is massively transformed to meet the increased demand for natural resources. For instance, the expansion of land area for intensive agriculture and urban development is globally omnipresent, but particularly so in the tropics (Lambin & Meyfroidt 2011). Industrial activities that our modern civilization depends upon, e.g. mining, traffic and agriculture, trigger a multitude of indirect environmental impacts too. For instance, raising concentrations of atmospheric carbon dioxide (15 %) and methane (10 %) in the period 1984 – 2012 alter global climate systems and induce alarming impacts on ecosystem integrity and functionality (IPCC 2014; Dalsøren *et al.* 2016). Also nitrogen deposition affects abiotic conditions and the outcome of species interactions, so that this form of pollution is ranked among the largest drivers of environmental change (Millennium Ecosystem Assessment 2005a; Rockström *et al.* 2017). Without intending to be exhaustive, the global redistribution of species, and notably the introduction of invasive alien species, is finally modifying many habitats (Early *et al.* 2016).

There is broad evidence that the inherent complexity of biological communities is getting dismantled, with mounting losses of biodiversity in terms of heterogeneity in landscapes, habitat structures, species and genes (Sala *et al.* 2000; Maxwell 2016; Young *et al.* 2016). In agriculture, for instance, 75 % of genetic crop diversity has been lost and 75 % of global food supply comes from just twelve plants and five animal species (FAO 2010). Current species extinction rates – between 200 and 2000 species per year - are about 1 000 times larger than in pre-human eras (Chapin *et al.* 2000). These estimates are based on small, well-studied species groups (e.g. vertebrate animals, vascular plants), so that they likely represent just a tip of the iceberg. Moreover, a conservative scientific emphasis on species extinction pulses is misleading because also the size and range of remaining populations are shrinking rapidly, even for low-concerning species (Ceballos, Ehrlich & Dirzo 2017). Because a clear transition in environmental policy and human behaviour is not near, the decline in biological diversity will likely continue in the near future, prominently so in the 25 global biodiversity hotspots (Cincotta, Wisnewski & Engelman 2000).

Nevertheless the strong scientific basis for an anthropogenic-induced biodiversity crisis, its complexity is begging for nuance. Where some regions (mainly in the tropics) have faced dramatic plant species losses due to the conversion of primary vegetation into intensive agricultural systems (Laurance, Sayer & Cassman 2014), very little changes in biodiversity are found in other regions, and some regions have actually seen a positive trend Figure 1-1. Managed urban green areas, for instance, harbour many plant species (especially neophytes) thanks to accidental and deliberate species introductions and thanks to the human-mediated creation of environmental heterogeneity. In their review study, Vellend *et al.* (2017) indeed conclude that the impacts of temporal biodiversity change drivers (e.g. habitat fragmentation, climate warming, N deposition) are context-dependent, so that biodiversity evolutions vary substantially at local scale and long-term predictions are far from certain (Figure 1-1). This uncertainly also holds at regional scale, where colonisation rates by non-native species are typically greater than the number species that have gone regionally extinct. At global scale, greater species extinction due to anthropogenic pressure are partially balanced by species speciation, although future biodiversity declines are likely due to increased habitat conversion in the tropics and due to extinction debt from current transitions.

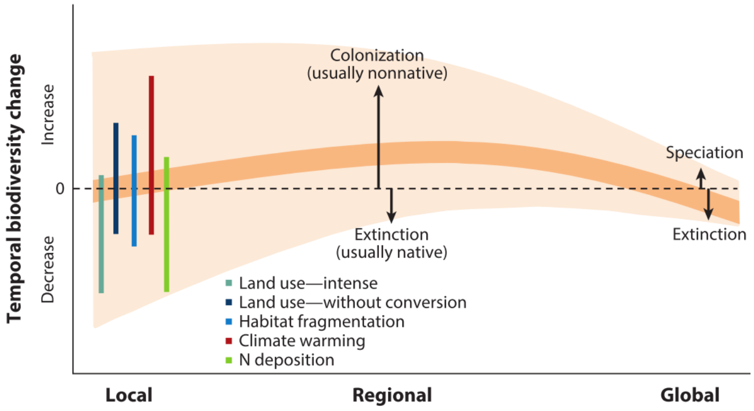


Figure 1-1 Temporal trends of plant biodiversity change during the Anthropocene at different spatial scales. Locally, effects of major drivers of change are highly context-dependent (bars represent variation of possible outcomes). This induces an enormous variation in temporal trends between different localities (light zone), which level out to zero on average (dark zone). At regional scale, establishment of non-native species usually outranges extinction of native species and causes an average increase in plant biodiversity. Global biodiversity trends are a trade-off between extinction and speciation rates, which have both increased owing to human activities. Global extinctions have the potential to, by far, outnumber speciation in the near future (Source: Vellend *et al.* 2017).

Also forest have been modified through overexploitation and simplification of structure and composition. Although the forest area is growing in temperate and boreal zones, it does not compensate for large losses in the tropics due to agricultural expansion (Figure 1-2; FAO 2016). Forests are typified by their geographic cover (i.e. 30 % of terrestrial land area; FAO 2001), prominent carbon sink (i.e. 50 % of earth's terrestrial carbon storage; ICPP 2007) and major reservoir of biodiversity (i.e. over 80 % of terrestrial species; United nations 2011). Forests furthermore play central roles in controlling global carbon and hydrological cycles and at local scale, they regulate essential processes such as soil formation, water purification and nutrient recycling. Forest are thus critically important ecosystems for the existence of life on earth, and altering their extent and natural attributes goes at a certain risks.

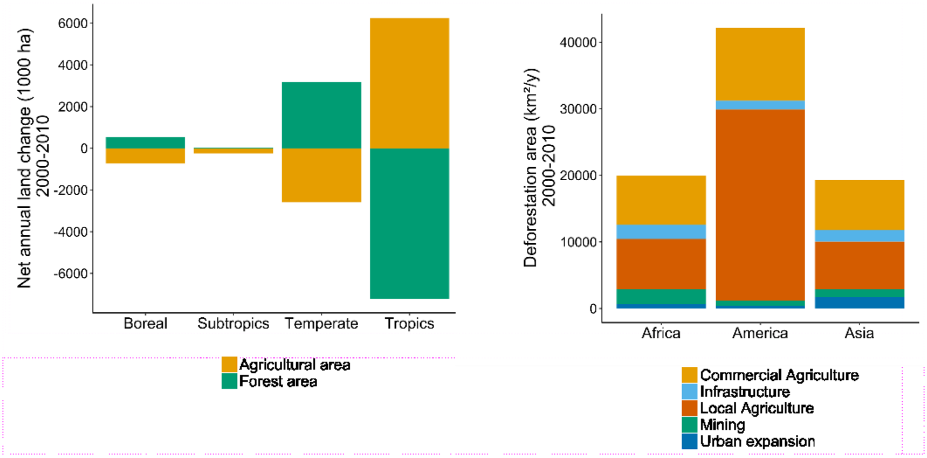


Figure 1-2 Left panel: Net annual land change (x 1000 ha) in agricultural area and forest area between the years 2000 and 2010 by climatic domain. Negative values indicates net land losses and positive values indicates net land gains. Right panel: Deforestation area (km²/year) between the years 2000 and 2010 by proximate drivers in three major (sub) tropical regions. Modified after: State of the world's forests, FAO 2016.

A historical report of Heinrich Cotta revealed that the ecological sustainability of low-diverse forests was already questioned in the beginning of the 19th century*:*

> *"Since not all tree species utilize resources in the same manner, growth is more lively in mixed stands and neither insects nor storms can do as much damage; also, a wider range of timber will be available to satisfy different demands"* (Heinrich Cotta, 1828; translated by Hans Pretzsch, 2014)

Contrary to this reasoning on biodiversity-ecosystem functioning (hereafter BEF) *avant la lettre*, European forest policy of the 20th century still promoted extensive afforestation with monocultures from a small species pool. Many of these species belong to the genera *Pinus*, *Picea, Pseudotsuga, Populus, Quercus and Fagus*. European forests are among the most intensively managed, with even-aged monocultures dominating the forest area, and non-managed protected forests accounting for no more than 0.4 % (MCPFE, 2002).

There are numerous motivations for the historical shift towards forests with low levels of tree species diversity, although supporting economic development and maximizing short-term economic profitability were certainly important. Indeed, only few tree species and genotypes were cultivated, with productive capacity, wood quality and low susceptibility to common infestations as dominant selection criteria (Bauhus, Forrester & Pretzsch 2017a). To further produce at lowest costs, management followed simple and standardized protocols, with trees facing similar growth dynamics in mono-specific and even-aged stands. Finally, a global wood supply chain rapidly developed in the last century, in response to a range of upcoming industries using wood as a raw material (pulp & paper, board materials, saw and veneer timber).

It is questionable if the conventional plantation systems can still meet the socio-economic expectations of forests in the 21th century. First, recent scientific insights prompt concerns about the capacity of low-diverse forests to resist environmental disturbances such as wind, fire and droughts (Jactel *et al.* 2017). Such loss of ecological stability (and gain in financial risk) is recently brought in the context of projected impacts of climate change (Seidl *et al.* 2017). It is clear that future environments will be different from the present. However, since we do not know the specifics of change at local scale, improving forest's inherent adaptive capacity is probably needed (Millar, Stephenson & Stephens 2007; Thompson *et al.* 2009; Messier, Puettmann & Coates 2013). Second, evidence is mounting that ecosystems provide a broad spectrum of supporting and regulating services, which are essential for human well-being, but, which were long time undervalued (Cardinale *et al.* 2012; Ellison *et al.* 2017). If the simplification of forests reduces this natural functionality, it may generate substantial opportunity costs to society (TEEB 2009, Van der Plas *et al.* 2016). Also the recreational and aesthetic value of forests is increasingly appreciated by the people, prominently so in urbanized regions like Western-Europe. To thoroughly fulfil these ecosystem functions, a certain level of tree species diversity at various spatial scales seems to be essential.

1.2 Biodiversity as ecosystem regulator

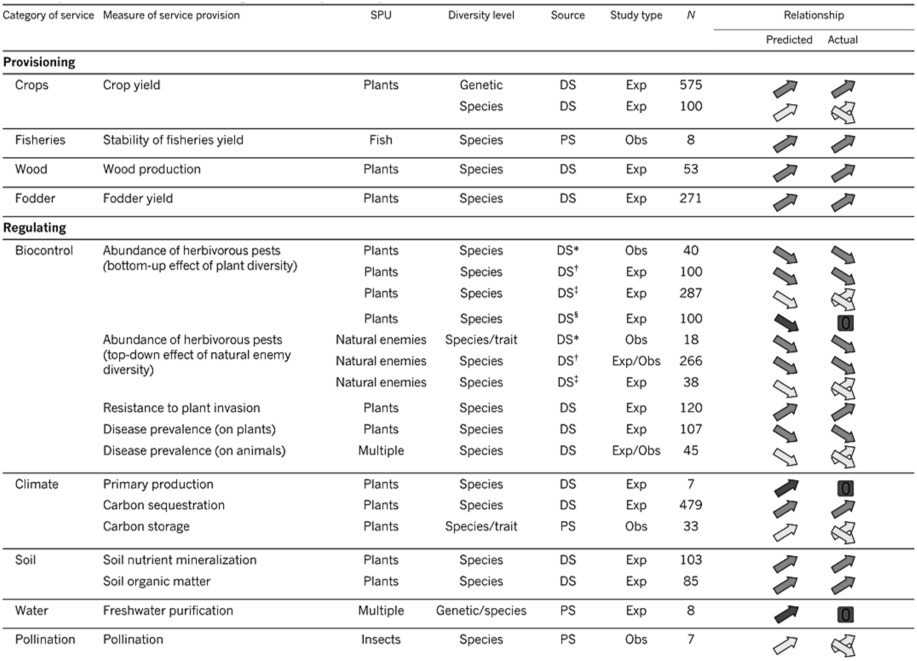
Biodiversity first needs to be specified because the term has been differently interpreted in the past, depending on the research context. In this manuscript, biodiversity (diversity in short) is defined as the variety of organism forms at a given place and time. This way formulated, biodiversity is the result of environmental and ecological filters, shaping biotic communities via an influence on organism fitness and competitive interactions (Duffy *et al.* 2007). Where "variety of organism forms" particularly refers to the taxonomic identity of organisms in a community, we use species richness (SR). Where it refers to organism functional characteristics (traits), functional diversity (FD) will be adopted. In the case we are discussing our own experiments and results, SR and FD always refer to species richness and functional diversity of woody organisms (trees and shrubs), not to organisms in other trophic groups. Variability across organism groups is namely referred to as associational biodiversity. The levels of SR and FD in our experiment are not the result of ecological filters because the tree community assemblages were (randomly) selected and planted (See 1.4. *Research scope*). Because tree species evenness was maximized in the mixed communities, we do not handle this topic in detail.

1.2.1 Emergence of a BEF framework

For a long time, biodiversity conservation efforts were mainly motivated by moral and cultural arguments, i.e., a remarkable aspect of life on Earth is, in itself, worth protecting (Hooper *et al.* 2005). A new conceptual framework evolved during the early 1990's, centring around the idea's that (i) the joint functioning of different life forms regulate essential biological processes through their unique characteristics, behaviour and physiology; (ii) changes in biodiversity or in species composition importantly alter ecosystem functionality and finally (iii) these changes trigger a cascade of adverse impacts on the provisioning of ecosystem services vital to sustaining human society (Naeem *et al.* 1994; Tilman 1999b).

A potential relationship between biodiversity and ecosystem function is inherently appealing and the topic came to dominate ecological sciences through a myriad of theoretical explorations (Tilman, Lehman & Thomson 1997; Yachi & Loreau 1999; Loreau & Hector 2001; Poisot, Mouquet & Gravel 2013), experimental studies (Tilman *et al.* 2001; Healy *et al.* 2008; Hector *et al.* 2009; Scherber *et al.* 2010; Verheyen *et al.* 2015) and quantitative meta-analyses (Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2007, 2011; Quijas, Schmid & Balvanera 2010). From these studies it is now clear that BEF relationships are generally positive, although also neutral and negative effects have been reported. Because a great variety of habitats and taxa have been investigated, it is justified to say that the functional role played by biodiversity is quite general in nature. A global synthesis study even concluded that impacts of biodiversity loss rank among the largest environmental problems of the 21th century, mainly for its contribution to ecosystem functioning (Millennium Ecosystem Assessment 2005a; Hooper *et al.* 2012). Consensus statements on BEF have been compiled in a series of leading articles (Chapin *et al.* 2000; Loreau *et al.* 2001; Schmid, Tilman & Wardle 2001; Hooper *et al.* 2005; Hillebrand & Matthiessen 2009; Cardinale *et al.* 2012; Tilman, Isbell & Cowles 2014). To aid the easy-reading of this PhD manuscript, we briefly introduce some important scientific hypotheses and discoveries.

Table 1-1 Balance of evidence in biodiversity-ecosystem services relationships based on a literature review of Cardinale et al. (2012), evaluating 1700 papers linking biodiversity to services provided by ecosystems. Only provisioning and regulating services were considered because these are most measured and most frequently related to biodiversity changes. For each measure of service provisioning its unit (SPU), diversity level (species, genetic or trait diversity), source (data synthesis DS or primary search PS), study type (experimental or observational) and number of data points (N) is presented. The direction of arrows indicate whether predicted and actual relationships are positive (up), negative (down) or neutral (0). Dark grey arrows reveal service measures where the actual relationship counters the predictions, middle grey arrows indicate service measures with sufficient evidence for the predicted relationships, supported by this literature review. Finally, light grey arrows suggest mixed evidence for the effects of biodiversity on a certain service provision. 13 other ecosystem services were evaluated but are not included in this overview because sufficient data was lacking (N < 5 data points).



Category of service	Measure of service provision	SPU	Diversity level	Source	Study type	N	Relationship	
							Predicted	Actual
Provisioning								
Crops	Crop yield	Plants	Genetic	DS	Exp	575	↗	↗
			Species	DS	Exp	100	↗	⤨
Fisheries	Stability of fisheries yield	Fish	Species	PS	Obs	8	↗	↗
Wood	Wood production	Plants	Species	DS	Exp	53	↗	↗
Fodder	Fodder yield	Plants	Species	DS	Exp	271	↗	↗
Regulating								
Biocontrol	Abundance of herbivorous pests (bottom-up effect of plant diversity)	Plants	Species	DS*	Obs	40	↘	↘
		Plants	Species	DS†	Exp	100	↘	↘
		Plants	Species	DS‡	Exp	287	↘	⤨
		Plants	Species	DS§	Exp	100	↘	0
	Abundance of herbivorous pests (top-down effect of natural enemy diversity)	Natural enemies	Species/trait	DS*	Obs	18	↘	↘
		Natural enemies	Species	DS†	Exp/Obs	266	↘	↘
		Natural enemies	Species	DS‡	Exp	38	↘	⤨
	Resistance to plant invasion	Plants	Species	DS	Exp	120	↗	↗
	Disease prevalence (on plants)	Plants	Species	DS	Exp	107	↘	↘
	Disease prevalence (on animals)	Multiple	Species	DS	Exp/Obs	45	↘	⤨
Climate	Primary production	Plants	Species	DS	Exp	7	↗	0
	Carbon sequestration	Plants	Species	DS	Exp	479	↗	↗
	Carbon storage	Plants	Species/trait	PS	Obs	33	↗	⤨
Soil	Soil nutrient mineralization	Plants	Species	DS	Exp	103	↗	↗
	Soil organic matter	Plants	Species	DS	Exp	85	↗	↗
Water	Freshwater purification	Multiple	Genetic/species	PS	Exp	8	↗	0
Pollination	Pollination	Insects	Species	PS	Obs	7	↗	⤨

1.2.2 Biodiversity and ecosystem functioning

Ecosystems properties and processes related to biogeochemical cycling are intensively investigated, with a predominant focus on primary productivity. From these studies it is well established that different forms of biological diversity mediate the efficiency by which communities capture essential resources, convert these into biomass and release them back to the environment (Cardinale *et al.* 2011, 2012). The effects further translate in a consistently positive relationships between biodiversity and ecosystem service provisioning such as the wood production in plantations, fodder production in grasslands or stability in fisheries yields (Table 1-1). Positive diversity effects have been reported for a broader spectrum of regulating ecosystem processes and services, and according to the extensive meta-analysis of Cardinale *et al.* (2012) this is mainly the case for resistance to invasion by exotic plants, prevalence of plant pathogens such as fungal and viral infections, aboveground carbon sequestration and nutrient mineralization. The BEF trends found by Cardinale *et al.* (2012) give confidence to earlier review studies (Balvanera *et al.* 2006; Quijas, Schmid & Balvanera 2010). We conclude **performance enhancement effects** of biodiversity because biodiversity seems can increase the mean level of ecosystem pools and the mean rate of ecosystem processes. Besides the mean level of ecosystem functioning, **buffering effects** have been reported as well: biodiversity can trigger the spatial-temporal variation of ecosystem functioning (See 1.2.4).

Importantly, not all ecosystem processes and services are equally effected by diversity, and for some the effects come close to zero are can even be negative (lower performance in mixture). For instance, the impacts of plant diversity on pest abundance are highly variable, probably because relationships are shaped by specific traits of and interactions between plants, herbivores and predators (Table 1-1).

1.2.3 Mechanisms of performance enhancement effects

Although it is scientifically challenging to quantify the mechanistic principles giving rise to positive BEF, such quantification is crucial to predict community functioning in many different contexts. The direct monitoring of all possible ecosystem processes involved in species interactions can be labour demanding (e.g. physiological or belowground processes) or practically difficult (i.e. some may operate at large spatial and temporal scales). Even where extensive data is available, disentangling the relative contribution of interrelated processes is not straightforward in complex ecosystems. Without intending to replace direct field measurements, some *post-hoc* methods have been developed to better understand the origin of BEF relationships (Nock *et al.* 2017). The bipartite partitioning of Loreau & Hector (2001) is the best-established framework on this topic. It starts from comparing mixture functioning with the weighted-average functioning of associated monocultures (i.e. net diversity effect). Next, the mathematical procedure separates this net diversity effect in two classes of BEF mechanisms named “complementarity” and “selection” (Figure 1-3); both are operating in combination and possibly with contrasting impacts on net diversity outcomes.

Complementarity effects deal with positive species interactions, including several types of niche differentiation, facilitation and inter-trophic interactions (Loreau & Hector 2001; Petchey 2003). These three types of mechanisms are assembled together under the term “complementarity” because they directly relate to the functional differentiation of participating species based on their specific characteristics, functional position or behaviour.

Niche differentiation is a typical competition-reduction mechanism affecting one or more components of the production ecology equation, i.e. resource supply, fraction of resources acquired or resource use efficiency. Niche differentiation can, for instance, be illustrated by two tree species with differential rooting structures (e.g. shallow *vs.* deep rooting) or nutrient preferences (e.g. NH4+ *vs.* NO3− Jacob et al. 2017). Their coexistence may promote productivity via the improved availability and/or uptake-efficiency of essential resources, causing lower interspecific compared to intraspecific competition (Lei, Scherer-Lorenzen & Bauhus 2012; Lang *et al.* 2014). Temporal niche differentiation is illustrated in assemblages with evergreen (e.g. Norway spruce) and deciduous (e.g. common beech) tree species, where light can penetrate the stand more easily after seasonal leaf shedding and stimulates photosynthesis of evergreens in early spring (Pretzsch 2005). Some tree species also show temporal differentiation in their seasonal growth peaks, which further contribute to temporal niche differentiation by reduced resource competition.

Facilitation includes those biotic interactions that can expand the realised niche of some, but not necessarily all, participating species. The interactions thus permit species persistence in locations that would otherwise, without facilitator, be less optimal (Bulleri *et al.* 2016). The amelioration of microclimatic condition through shading is a classic example of facilitation. Under arid conditions, shading by overstory trees relaxes daily air temperature, wind speed and solar irradiation, with positive impacts on the water regulation of shaded species, particularly those that are on the boundary of their ecological niche (Ren, Yang & Liu 2008). Other examples of facilitation include the improved resource availability via hydraulic lift (water supply), via faster litter decomposition rates (site quality) or via the establishment of mycorrhizal networks (water and nutrient supply) (Pretzsch, Schütze & Uhl 2013; Klein 2016; Fichtner *et al.* 2017). Nitrogen(N)-enrichment effects, for instance, arise where non-N-fixing species are more productive next to N-fixing species in N-deficient environments (Fargione *et al.* 2007).

Within the class of complementarity effects, the improved functioning of diverse ecosystems can finally be related to processes that operate across different trophic levels; in fact a particular form of facilitation. Many studies focused on the **inter-trophic regulation** of herbivory, an ecosystem process that affects plant productivity, vitality and survival and that is therefore crucial to the delivery of ecosystem services in forestry and agriculture. Insect and pest damage from specialist herbivores is often found to be lower in more diverse communities, a pattern called associational resistance. Two mutually non-exclusive mechanisms help explaining the negative herbivory-diversity relationships. First, specialist herbivores tend to accumulate in patches with high host plant density. Indeed, where feeding resources and breeding places are abundantly available, herbivore emigration occurs less frequently. This ecological reasoning provides a basis for the **resource concentration hypothesis** (Haase et al. 2015). Interestingly, effects are not only a simple artefact of reduced host density in mixtures (which also include non-hosts) compared to monocultures (which only include hosts). Different studies confirmed that herbivores face difficulties to locate and reach hosts in a complex vegetation matrix, even after controlling for host density (Castagneyrol, Régolini & Jactel 2014; Damien *et al.* 2016). For instance, tall non-host plants physically disrupt visual or contact cues that some herbivores use to detect suitable habitats. Also the emission of non-host volatiles may reduce chemical apparency and may affect the diversity-herbivory relationship. Besides host density and apparency (together resource concentration), natural herbivore enemies play additional roles in shaping the diversity-herbivory relationships. Species-rich habitats support a higher diversity of prey species, provide better refuges and offer alternative, nutrient-rich feeding sources for predators. This can trigger an effective top-down regulation of ecosystem processes in heterogeneous mixtures compared to homogeneous monocultures (**enemies hypothesis**). The mechanism has been shown for arthropods and birds as herbivory control agents (Poch & Simonetti 2013; Poisot, Mouquet & Gravel 2013; Muiruri, Rainio & Koricheva 2015). Increased herbivory at higher diversity is also observed and is referred to as associational susceptibility. Associational susceptibility occurs where generalist herbivores, rather than specialists, dominantly mediate plant biotic damage. Indeed, generalists can take benefit from the diversified dietary, improved nutrient uptake and diluted secondary plant metabolites in multi-host (mixed) communities. These effects tend to be more important when host plants are phylogenetically similar.

Selection effects are the second class of BEF mechanisms described in the *post-hoc* bipartite partitioning of Loreau & Hector (2001). Selection effects point to an unequal contribution of different species to the observed net diversity effects (Loreau & Hector 2001). More precisely, selection effects occur when changes in the relative yields of species in mixture are non-randomly linked to their yields in monocultures. Yield is often presented in terms of biomass or growth, but it can be proxy for any other ecosystem process as well. The non-random relationship between relative yields and monoculture yields are covered by a covariance function in the partitioning equation.

Although selection effects are sometimes interpreted as a pure stochastic process, i.e. higher probability to sample species with beneficial characteristics in more diverse communities, it is additionally grounded on deterministic processes that allow these well-adapted species, once present, to have a large impact on the ecosystem properties and processes. The deterministic part of a selection effect thus also covers competitive or facilitative interactions when species are brought together in mixture. This way of reasoning, the stochastic sampling process is not exclusively associated to selection effects because it also act on complementarity effects, i.e., in high-diverse communities there are better chances that two or more complementary species will generate positive interactions and positively affect ecosystem functioning.

Selection effects are often described with regard to its positive sign (most productive species taking most advantage from being mixed), however, also negative selection effects occur when species with low (not high) monoculture yields generate strongest relative yields in mixture. In addition, selection effects are often interpreted in the context of competitive dominance: most productive species taking over ecosystem functioning at the expense of other species' functioning, a reasoning that is motivated in the analogy of natural selection in the Price equation (Price 1995). Drawing on the critical reflections of Petchey (2003), Fox (2005) demonstrated that selection effects in the bipartite partitioning of Loreau & Hector 2001 combines processes of competitive dominance with complementarity processes that also scales with species functioning in monoculture. For example, if vitality of slow-growing species is improved in association with fast growing species (e.g. thanks to associational resistance via host apparancy), a negative selection effect will pop-up if vitality of fast growing species is unaffected by mixing. However, this examples clearly demostrates a proces of facilitation, rather than dominance, and there is a risk that negative selection effects will be misinterpreted. To improve the ecological understanding of the partitioning equation, Fox (2005) developed a tripartite partitioning in which selection effects are further split into competitive dominance (improved species functioning is at the expense of other species) and trait-dependent complementarity (improved species functioning is not at the expense of other species functioning).

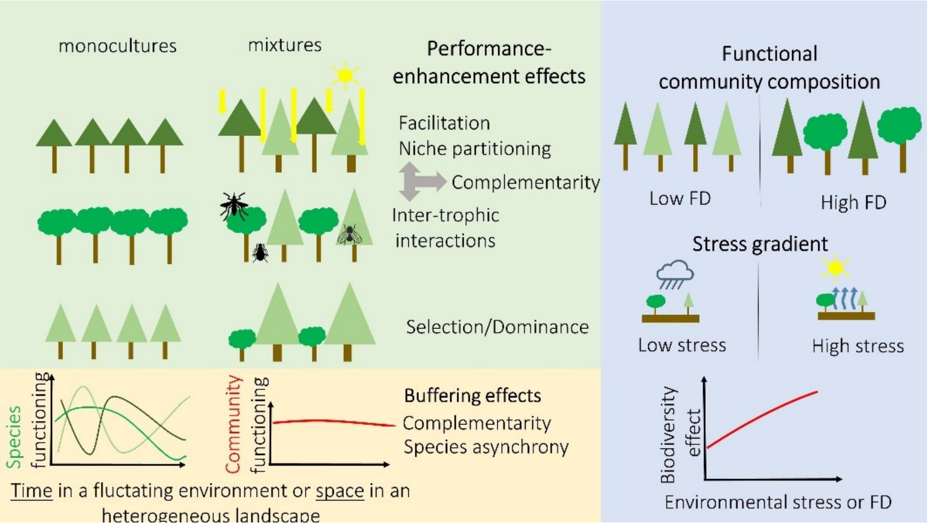


Figure 1-3 Summary of some important ecological mechanisms underpinning a relationship between biodiversity and ecosystem function (EF) when comparing mixtures with the monocultures of associated species. Performance enhancing effects indicate an increased mean-level of EF at higher diversity. Following the additive partitioning of Loreau and Hector (2001), performance enhancing effects are caused by complementarity mechanisms (positive interactions including facilitation, niche partitioning and inter-trophic interactions) and selection effects (dominance by species with extreme trait values (e.g. yield) in monoculture). Buffering effects act on the variance (rather than the mean) of ecosystem functioning, and suggest a decreased variance (increased stability) at higher diversity. Stabilizing forces include probabilistic processes (asynchrony of species' intrinsic responses to environmental fluctuations creates compensatory dynamics) as well as complementarity processes, which reduce or delay impacts environmental stress. The strength of biodiversity effects on EF (performance enhancement and buffering) is predicted to increase at higher functional diversity (closely linked to niche theory) and at higher environmental stress (stress-gradient hypothesis postulating a transition from competition in favourable environments to facilitation in harsher environments).

1.2.4 Ecosystem stability

Besides examining how biodiversity triggers changes in the mean size of ecosystem pools and mean rates of ecosystem processes, biodiversity-stability relationships received considerable attention too. From forests (Thompson *et al.* 2009; Jucker *et al.* 2014a), grasslands (Tilman, Reich & Knops 2006; Hector *et al.* 2010) and aquatic systems (Boyer, Kertesz & Bruno 2009) it is confirmed that diverse ecosystems benefit from higher temporal and spatial stability with environmental stress or with ecological disturbances. For instance, in herbaceous communities it was reported that inter-annual variation in primary productivity is consistently lower at higher diversity (Hautier *et al.* 2014).

Among the mechanisms responsible for this demonstration of ecological stability, statistical averaging (**portfolio effect**) is extremely important. The portfolio effect describes decreased variation in mixture functioning (e.g. productivity) because species differ in their niche preferences and show asynchrony in their responses to environmental perpetuations (Figure 1-3). Thus, in species-rich communities there are better chances that at least some species will survive and therefore, ecosystem functionality is preserved under a wider range of environmental conditions. In herbaceous communities, species relative abundance and composition can easily fluctuate across years in response to environmental variability (e.g. weather, specialist herbivory) and the importance of compensatory effects is large. In forests, shifts in species composition (in terms of biomass) only occur after prolonged stress events or under extreme disturbances. However, in terms of relative growth rates (rather than abundance or survival), compensatory dynamics may still reduce inter-annual variation after droughts, fires, storms or pest outbreaks (Knoke *et al.* 2007; Jucker *et al.* 2014a; Bauhus *et al.* 2017).

Mechanisms generating ecological stability go beyond this probabilistic perspective of species asynchrony. Also **species interactions** help to buffer impacts of environmental stress and disturbances at higher diversity and help to sustain long-term ecosystem functioning. For instance, facilitative interactions that improve water availability or water-uptake efficiency reduce the onset of severe drought stress, thereby improving ecosystem stability. Among these facilitative interactions is, for instance, hydraulic lift whereby deeper rooting tree species consume water in deep soil layers and redistribute this water to superficial soil layers in mixed forests (Jactel *et al.* 2017). Some mechanisms thus jointly affect performance enhancement effects (section 1.2.3) and buffering effects of biodiversity. Importantly, if species interactions dramatically increase water usage, e.g. due to canopy packing, an even greater drought exposure can be observed at higher diversity (Grossiord *et al.* 2014; Jucker *et al.* 2014b).

Besides resistance to drought, wind damage may be lower in mixed forests, among many other reasons because wind impacts are distributed over multiple forest layers so that wind loading on the tallest trees is relaxed. Finally, the different mechanisms that explain associational resistance are important to explain biotic stability. Indeed, pest populations in homogeneous communities of host plants can rapidly build-up and can dramatically reduce ecosystem functioning. The biodiversity - stability concept offer important management opportunities for improving ecosystem resistance and recuperation from natural disasters in the light of global change. This is particularly the case in forestry, where long timber production periods increases the likelihood that stands will be exposed to numerous risks during their lifetime, possibly affecting ecosystem economics. These risk-spreading benefits of species mixing legitimize to claim an insurance value of biodiversity for ecosystem management (Oliver *et al.* 2015).

1.2.5 Context-dependency

The way biodiversity mediate ecosystem function and service is largely context-dependent (Ratcliffe *et al.* 2017). First, the direction and intensity of ecological interactions depend on organisms involved, their competitive tolerance and ability, ontogenetic stage and functional position within a complete ecosystem' trophic network structure (Duffy *et al.* 2007; Maestre *et al.* 2009; Poisot, Mouquet & Gravel 2013). Second, species interactions show temporal shifts over the course of ecosystem development, with complementarity effects increasing at the cost of selection effects where plant community experiments are running longer (Cardinale *et al.* 2007). Third, the abiotic and biotic environment organisms are living in, including mean conditions and its spatial and temporal variation, determines ecological niches and mediate the way species affect each other via positive and negative interactions. This knowledge formed the basis for a stress-gradient hypothesis (SGH, Figure 1-3), postulating that species in harsher environments rely more on each other to persist (Bertness & Calaway 1994; Maestre *et al.* 2009; He, Bertness & Altieri 2013). For forests in particular, SGH is more challenging to quantify. Forrester & Bauhus (2016) for instance suggest that the direction of BEF in forests depends on how environmental stress and ecosystem processes are interrelated. Finally, land-use legacy effects, which are carry-over effects from land-use history in terms of abiotic (carbon fractions, nutrients and organic matter) and biotic site properties (soil microbial and mycorrhizal communities) may help explaining the context dependency of BEF relationships. In forests, legacy effects can result from the identity and diversity of a former generation of trees (e.g. forest conversion) or from an historical land use different than forest.

1.2.6 Functional diversity

Although BEF research was originally about manipulating the number of species in an ecosystem and monitoring ongoing biological processes, the complex nature of biodiversity does not allow to make accurate inferences based SR alone (Balvanera *et al.* 2006; Hillebrand & Matthiessen 2009). A central conclusion from two decades of BEF research is that functional traits (i.e. organism properties with close linkages to its performance) are fundamental for understanding BEF (Kunstler *et al.* 2015; Li *et al.* 2017). Identifying the functional structure of communities largely improved the explanatory power of statistical models, for instance because species with dissimilar contributions to certain ecosystem function are more likely to achieve ecological benefits through niche differentiation or facilitation (Figure 1-3; Hillebrand &

Matthiessen 2009; Mouillot et al. 2011). Alternative descriptors of biological diversity have been tested, among them various types of functional diversity (FD) measuring variation and abundance distribution of traits in a multidimensional trait space (Petchey & Gaston 2006; Laliberté & Legendre 2010; Milcu *et al.* 2014).

1.3 Methods to investigate BEF

1.3.1 Early-stage experiments

Scientific judgements on how biodiversity is driving ecosystem function are importantly grounded on data from synthetic community experiments. By 2009, literature reports over 600 experiments manipulating > 500 different organisms in freshwater, maritime and terrestrial environments (Cardinale *et al.* 2012). These experiments formed a basis to at least 40 % of all BEF publications (Balvanera *et al.* 2006). For the ease of establishment and monitoring, the creation of small-scale model systems with bacteria, algae or plants in laboratory microcosms received most interest (Hooper *et al.* 2005). Lab work was further complemented by field tests on herbaceous communities, with Jena (Figure 1-4), Cedar Creek and BIODEPTH operating as leading experiments (Tilman 1999a; Hector, Loreau & Schmid 2002; Roscher *et al.* 2004). Nevertheless great variety in organisms and study set-ups, synthetic community experiments share some fundamental design elements. In essence, this covers the direct control of biodiversity under constant extrinsic conditions, often reached by sampling many different compositions from a prescribed species pool. Such rigid design avoids results being confounded by species identity effects (i.e. type of species) and permits to isolate biodiversity effects from compositional effects (i.e. specific set of species; Hector *et al.* 2011; Nock *et al.* 2017). Because heterogeneity is largely avoided or explicitly accounted for in design and analysis, experiments maximize the possibility of quantifying biodiversity effects independent from other influential factors (Nadrowski, Wirth & Scherer-Lorenzen 2010). On the other hand, it has been intensively debated how results translate to complex real-life systems, covering larger temporal scales and more heterogeneous landscapes (Schmid & Hector 2004; Eisenhauer et al. 2016).

Figure 1-4 Aerial photo of the Jena Experiment in Thuringia, Germany. It is one of the largest (10ha) and longest running (15 years) grassland biodiversity experiments (started in 2002), manipulation communities common to the Central European Arrhenatherion grasslands. The 90 plots were sown with between 1 and 16 species (total pool of 60 species) from 1 to 4 functional groups (Roscher et al. 2004). Ecosystem processes such as productivity, root decomposition, nitrogen leaching, water uptake, flooding response, seed predation and pollination are examined along a plant diversity gradients and over long time frames. Photo: www.idiv.de

1.3.2 Towards investigating BEF in forests

It is time to surpass biodiversity experiments with communities of fast-growing organisms and expertise on how BEF apply to forests, one of Earth's dominant terrestrial ecosystems. Besides natural forests, also commercial timber plantations are globally important. Plantations are growing by 5 million ha per year (FAO 2010) and they will provide 50 % of global industrial wood production by 2040 (Kanninen 2010). Surprisingly little is known about the effects of species mixing on forest functioning and how this additional complexity should be dealt with in forest management (Scherer-Lorenzen *et al.* 2007; Bauhus, Forrester & Pretzsch 2017b). Early-stage experiments serve as a good basis of what can be expected. It is nevertheless is crucial to realize that forest are highly-complex systems with the largest and longest living terrestrial plants on Earth embedded in a dense, multi-trophic ecosystem network (Eisenhauer 2012; Messier, Puettmann & Coates 2013). Also, trees are singly identifiable organisms of which biomass is not yearly renewed, allowing biodiversity effects to slowly accumulate with forest aging. It is scientifically challenging to design and test a fundamental ecological framework where diverse forests are able to function superiorly. Nevertheless, such basis is critically important to guide mixed forest management and to strengthen political attention on forest biodiversity conservation.

The question how forest functioning is affected by tree species mixing is certainly not new. An overview of existing evidence is provided by Scherer-Lorenzen et al. (2005) and was more recently updated by Bauhus, Forrester & Pretzsch (2017b). Up-to one decade ago, silvicultural research concentrated on trials with monocultures and two-species mixtures of commercially-important provenances (Pretzsch 2005). These trials produce a wealth of information on inter- and intraspecific interactions modulating productivity and stability (Verheyen *et al.* 2015). Disentangling species identity effects from biodiversity effects is rather problematic due to the short diversity gradient and small species pools. Other scientific advancements are made by analysing forest inventory data (Toïgo *et al.* 2015; Liang *et al.* 2016). Although excellent for reflecting natural conditions in terms of age classes, structure, topic networks and abiotic conditions, diversity gradients are often skewed towards lowest levels of diversity, most notably in European databases. Also the detection of statistical causality is not straightforward because diversity gradients are often confounded with land-use history, management, topography or soil attributes. Variation in local growing conditions, not mediated by varying biodiversity, can be accounted for in the analyses (or even in design of exploratory platforms; Baeten *et al.* 2013), but some of this information may not be available (Paquette & Messier 2011; Vilà *et al.* 2013).

1.3.3 Tree diversity experiments

There are currently at least 25 tree diversity experiments exploring the functional consequences of tree species mixing. Similar as in the conventional model systems, they encompass different species compositions in a replicated and semi-randomized design, with the inclusion of all monocultures as well as mixtures of more than two species. Tree diversity experiments cover a total area of 821 ha in different climates (Figure 1-5). They have been developed through independent initiatives, but they participate in a global network (TreeDivNet) where synthesis work is assisted and field expertise is shared (Verheyen *et al.* 2015). Close affinity with common silvicultural practices is generally objected, but still, experiments differ remarkably in terms of diversity index manipulated (SR, FD, phylogenetic diversity, genetic diversity and evenness), upper-diversity level of SR (from 3 to 18 species), type of tree species mixing (either patch planting or individual-based planting), spatial scale (plots sizes ranging from 0.24 to 12 000 m^2), planting density (between 60 cm and 300 cm, but usually constant within experiments), site heterogeneity (e.g. from flat sites to hilly slopes) and more (Verheyen *et al.* 2015). Only 13 experiments were established before 2010.

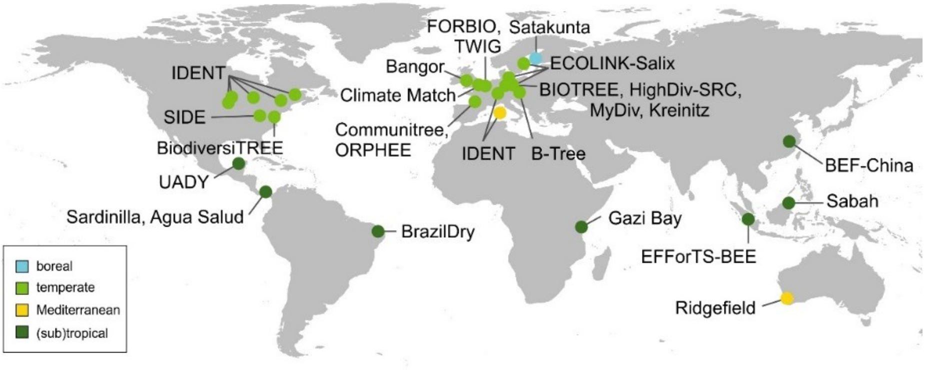


Figure 1-5 Global distribution of tree diversity experiments contributing to TreeDivNet (www.treedivnet.ugent.be). TreeDivNet offers a science-based research platform for discovering the relationships between tree species diversity and ecosystem functioning through experimental approaches (Verheyen *et al.* 2015). The 25 experiments cover dominant ecoregions, including Boreal, Temperate, Mediterranean, and (Sub) tropics. Because of their independent establishment, plantations use various design alternatives and their age ranges between 1 to 15 years old. Source: www.treedivnet.ugent.be

1.4 Research scope

From the literature review above it should be clear that three decades of intensive ecological research generated profound knowledge on how biodiversity controls ecological processes that are fundamental to the functioning of ecosystems. However, almost all manipulative biodiversity experiments carried out so far have used fast-growing and small-scale model systems in laboratory environments. Also the experimental work in the field was mainly limited to grassland systems. This thesis was therefore motivated by a vast call from science, policy and management to test the validity and relevance of BEF relationships and underpinning mechanisms for one of the most important and most complex real-world ecosystems, i.e. the forests. Up to recently, expectations were mainly based on observational data or inferred from the first stage of experiments on non-forest ecosystems.

To do so we capitalized on tree diversity experiments, where a gradient in tree species richness or functional diversity was created under relatively homogeneous site conditions. The experimental design avoid that possible diversity effects become confounded by environmental factors that were not purposely manipulated (Figure 1-7 and Figure 1-9). The approach of manipulating biotic communities of different diversity and composition has rarely been applied with woody species, and certainly not often at relevant spatial scales to plantation forestry. Our study testing the active role of tree species interactions for early plantation dynamics will therefore contribute importantly to the scientific BEF literature. It will allow to bridge mechanistic insights accumulated in a first-generation of biodiversity experiments with the observational insights from inventory data in established forests.

Importantly, this study only handles the initial stage of forest plantation development. Roughly, this initial development stage starts with tree planting and runs up-to the moment where plantation canopy is getting closed. There is mainly a practical reason to singly target these early dynamics: tree diversity experiments have only been establish very recently and therefore, it is currently not possible to investigate later forest stages within this experimental approach. Nevertheless, the focus on early plantation development is extremely interesting from a management perspective. Indeed, ecological processes and tree-tree interactions largely determine the course of forest development. For instance, recently planted seedlings and saplings are extremely vulnerable to certain biotic (e.g., pests, pathogens) and abiotic (e.g., storm, frost, drought) risks and to the competition for light, nutrients, and water with the understory vegetation and with neighbouring trees. From the ecological theory we may expect that seedling performance can be enhanced in some mixed communities where facilitative interactions reduce environmental stress. Planting diverse stands may, for instance, trigger associational resistance towards pest infestation and may therefore more easily pass this critical stage of plantation establishment. However, tree species mixing is still not common in operational management due to critical knowledge gaps. Which species combinations produce facilitative interactions? Are some species combinations harmful for plantation functioning because of strong inter-specific tree competition or associational susceptibility? How relevant are the diversity effects in young plantations compared to other effects? How should trees from different species be spatially arranged to produce beneficial interactions? In this PhD research we aimed to quantify early tree-tree interactions and we aimed to understand their relevance to early plantation management.

To provide management advice, it is not enough to test how ecological processes are affected by tree species mixing. We also strived elucidating underlying biological mechanisms, among others via trait-based approaches (Figure 1-6). Detecting and understanding biological mechanisms will help generalizing the experimental findings. We primarily worked within a tree-centred framework, meaning that we targeted complementarity and competitive interactions between trees, rather than interactions arising from different trophic levels; which are extensively studied by others (Setiawan *et al.* 2016a; Dillen 2017).

1.5 PhD outline

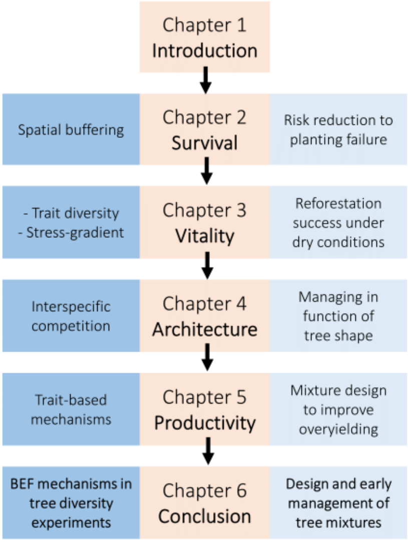


Figure 1-6 Thesis Outline. The left column describes the ecological concept investigated in each chapter and the right column suggest its potential relevance for plantation management.

We dealt with a suite of different tree performance indicators, including seedling survival, seedling vitality, tree architecture and stand productivity (Figure 1-6). These indicators were selected from a plantation management viewpoint. In other words, the tree-level and stand level-level indicators are expected to be relevant in determining the success of plantation establishment and its initial development. The indicators are mainly interesting when provisioning services (woody biomass or timber production) are potential management objectives.

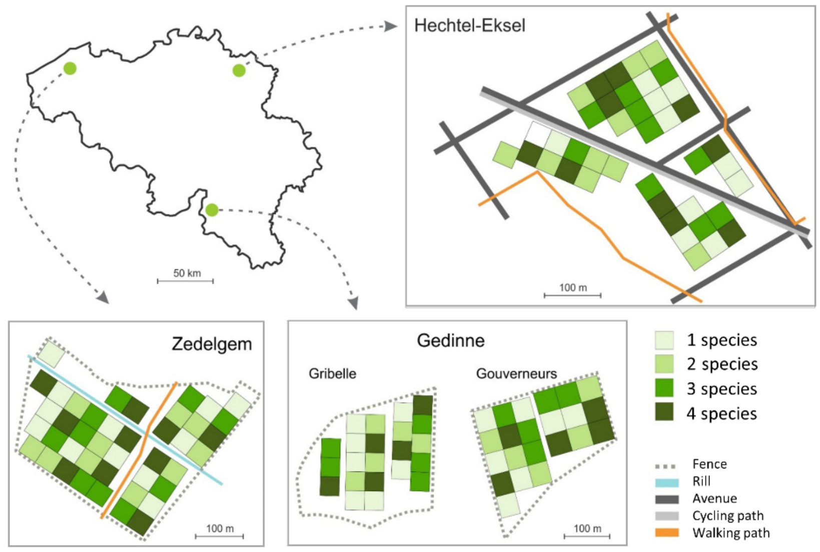
A first step to plantation installation success is that seedlings survive a replanting shock; a topic investigated at the FORBIO experiment (**Chapter 2**, Figure 1-7). Generally, establishing forest plantations is associated with large investment costs, including site preparation, plant material costs, planting and control of competing vegetation. The economic return in forest products comes late in the rotation cycle so that plantation establishment is associated with important management risks. In this study we used data about the survival of seedlings after planting. We hypothesized that tree species mixing can help plantation management via performance-enhancing effects (i.e. mean plot-level seedling survival rates increasing with SR) and buffering effects (i.e. plot-level seedling survival stabilizing at intermediate survival levels or high SR). Only few studies have yet looked into the potential roles species mixing to improve stand installation success and reduce the risks of dramatic planting failure.

Seedlings should not only survive, they also should be vigorous to contribute to plantation functioning. This topic was handled in **Chapter 3**. In a Mediterranean experiment (IDENT-M; Figure 1-9) we explored how facilitative interactions between different tree species affect seedling vitality based on foliage condition. Vitality is very informative in dry areas because even if seedlings are not accumulating much aboveground biomass, healthy foliage indicates that plants are not stressed and likely investing in root development for long-term drought persistence. The IDENT-M experiment is ultimately designed to discover mechanistic insights on BEF. For instance, the large pool of 12 species and the creation of gradients in both SR and FD allowed a trait-based understanding of the relationship between seedling vitality and community composition. Also the inclusion of an irrigation treatment permitted making inferences on how species interactions shift with water availability (i.e. stress-gradient hypothesis). The management objective of this chapter was to discover a potential pathway to improve dryland reforestation success via species mixing.

In **Chapter 4** we studied architectural plasticity in the context of tree species mixing, a topic that is hardly elucidated so far. High-quality logs are made from the lower part of tree stems (Baar 2005), which are essentially shaped during early stages of stand development, including the period before canopy closure. Most knowledge on strategies to manipulate of tree formation comes from experiences in monocultures. Here we assessed architectural development of 400 trees in FORBIO-ZED in both monoculture and mixed stands, five years after planting. We hypothesized that the trees show species-specific architectural plasticity in response to gradients in shading competition and diversity.

In a final study (**Chapter 5**) we explored diversity-productivity relationships (DPR) at FORBIO. In the past, primary productivity is most often used as an integrated metric of ecosystem functioning. Several studies already investigated DPR in tree diversity experiments (Grossman *et al.* 2018), but underpinning biological mechanisms still remain poorly understood. We contributed to the scientific knowledge accumulation by determining how the functional structure of tree communities can shape phenomenological patterns in biomass productivity datasets. Because FORBIO consists of sites at contrasting environmental conditions, context dependency of DPR could be investigated. The results of this study should aid mixture plantation management in function of biomass productivity goals.

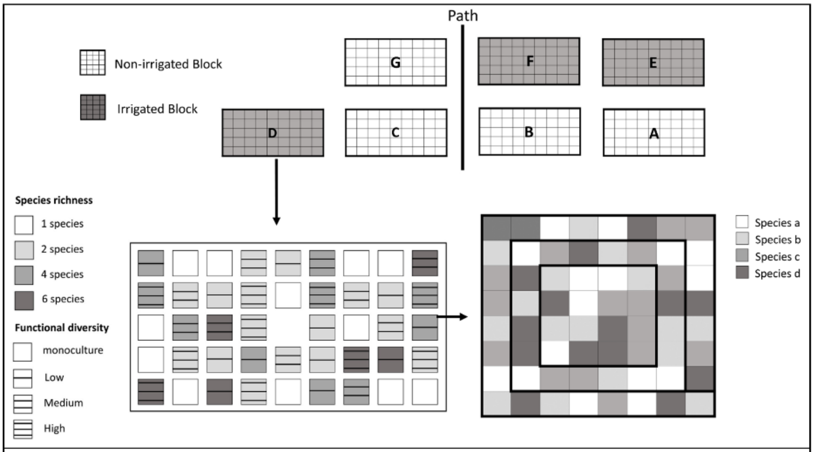
In **Chapter 6** we summarized main scientific discoveries and bring them into perspective of existing literature. We close the chapter by evaluating how results create applied value for early plantation management and by discussing two promising directions for follow-up research.



Zedelgem	**Gedinne**	**Hechtel-Eksel**
Betula pendula	*Fagus sylvatica*	*Betula pendula*
Pinus sylvestris	*Acer pseudoplatanus*	*Pinus sylvestris*
Quercus robur	*Larix* x *marschlinsii*	*Larix kaempferi*
Tilia cordata	*Pseudotsuga menziesii*	*Pseudotsuga menziesii*
Fagus sylvatica	*Quercus petraea*	*Quercus petraea*

Figure 1-7 Experimental design of FORBIO, a Belgian tree diversity experiment planted between 2010 and 2012. The experiment consists of three 9 ha sites (Zedelgem, Gedinne and Hechtel-Eksel) in regions with contrasting soil, land use history and climatic conditions. FORBIO is designed to imitate young plantations in the non-mountainous areas of Western-Europe. Trees from five site-adapted species were planted in different plots. A richness gradient from 1 to 4 functionally different tree species was created via the random sampling of 20 species compositions, well-balanced across the diversity levels. The compositions are replicated twice in a block design and trees are planted in a grid of 1.5 m by 1.5 m. The plot sizes (1269 m² - 1765 m²) are beneficially large to create characteristic microhabitats within each plot.

Figure 1-8 Photos of the FORBIO sites in HEC (left, 2013), GED (middle, 2013) and ZED (right, 2014). Two important management actions were yet undertaken. First, herbaceous vegetation was managed during the summer period (2010-2012 in ZED and 2010 -2014 in GED) to avoid that dominant vegetation would start outgrowing the planted seedlings. At Zedelgem this has been done by mowing a 1 m wide strip between the tree rows. Also spontaneous seeding (mainly Salix sp.) were manually removed. At Gedinne a scythe and a brushcutter were used to control the dominant firn vegetation. The vegetation layer was not a major management issue in HEC. Mowing was only applied in 2016 to control the growth of *Robus* sp. and to limit the spontaneous settlement of *P. sylvestris* seedlings between the rows. The second management action was the replacement of dead or non-vigorous seedling (i.e. those exhibiting uncomplete foliage and/or dead terminal shoot) by new two-year old seedlings. This occurred in winter-spring during the first two years after plantation planting. The replacement of seedling that were not successfully established is important to keep fully-stocked experiments and to maintain equal species balance. More details on seedling survival are found in Chapter 2. Photo: T. Van de Peer (left an right); M. Dillen (Middle).



Conifers	**Deciduous broadleaf**	**Evergreen broadleaf**	
Pinus halepensis	*Acer monspessulanum*	*Arbutus unedo*	*Pistacia lentiscus*
Pinus pinaster	*Fraxinus ornus*	*Olea europea*	*Quercus ilex*
Pinus pinea	*Quercus pubescens*	*Phillyrea latifolia*	*Quercus suber*

Figure 1-9 Experimental design of IDENT-M (Sardinia, Macomer), a single-site tree diversity experiment created in 2014. The experiment is hinges on a high-density planting design (0.4 m by 0.4 m) and small plot sizes (10.2 m²). The planting correspond to densities of regenerating forests and should speed-up the onset of tree-tree interactions (Tobner et al. 2014). The small plot size allows more plot replicates, although it is at the cost of a plot's scientific lifespan. On top of the figure, a site plan is shown with three irrigated (grey) and four non-irrigated (white) blocks, which allows testing the SGH. In the middle left of the figure, the disposition of 44 plots within a block, including orthogonal gradients of SR and FD is shown; In the middle-right there is the arrangement of 64 plants in a four-species plot. Bold lines represent inner, middle and outer frame. Species relative abundances within these frames are alike and the outer frame was not included in the analyses to avoid plot edge effects. A broad species pool of 12 site-adapted Mediterranean species (including conifers, deciduous broadleaved and evergreen broadleaved species) was used to create the monocultures and mixed communities (lower part). All plots were regularly weeded in the first three years to avoid overgrow by herbaceous vegetation.

Chapter 2

Biodiversity As Insurance For Seedling Survival

After: Van de Peer T, Verheyen K, Baeten L, Ponette Q, Muys B (2016) Biodiversity as insurance for sapling survival in experimental tree plantations. Journal of Applied Ecology **53**, 1777—1786. (IF = 5.301).

Author's contributions: TVDP, BM and KV devised the concept of the article; TVDP carried out the data analysis, with statistical advice from LB. TVDP wrote the manuscript text. All co-authors contributed to revising earlier versions of the manuscript and approved the final version.

Cover photo: Young stand with oak and larch, FORBIO HEC, 2014 (T. Van de Peer)

2.1 Summary

Biodiversity can insure ecosystems against declines in their functioning by increasing the mean level of ecosystem processes and decreasing the spatial or temporal variance of these processes. On this basis, mixing tree species is expected to be an effective management strategy to reduce the risk of planting failure in young plantations.

We examined the effects of diversity insurance on seedling survival in three tree diversity experiments across Belgium. Based on the survival scoring of 89 254 seedlings, planted in 126 plots of different SR, we tested two hypotheses: (i) variability in plot-level survival is lower for mixtures compared to monocultures due to compensation among the species (i.e. buffering effect) and (ii) mean survival is higher due to facilitation (i.e. performance-enhancing effect).

Variation in plot-level survival decreased strongly with SR, indicating a buffering effect. The risk of severe planting failure was reduced in mixtures because species exhibit different survival rates; therefore, mixing ensures that not all trees in the plantation are equally susceptible to environmental stressors. In contrast, the mean plot-level survival did not increase with SR, and thus an overall performance-enhancing effect was lacking. However, species-level analyses did show small performance-enhancing effects, where some species profited from mixing while others did not.

We conclude that tree species mixing insures young plantations against planting failure and is therefore highly recommended as a planting management strategy. The risk of large mortality gaps is reduced if tree plantation seedlings are mixed at the scale of individual trees or small cells of trees.

2.2 Introduction

According to the biodiversity insurance hypothesis, diverse ecosystems are more resilient to environmental change because, assuming species-specific responses to such changes, they provide better guarantees that some species will maintain their performance even if others fail (Naeem & Li 1997; Yachi & Loreau 1999; Hector *et al.* 2010). Previous work on the insurance hypothesis has primarily focused on the temporal stability of biomass production (Yachi & Loreau 1999; Tilman, Reich & Knops 2006; Isbell, Polley & Wilsey 2009; Hector *et al.* 2010). This line of research has identified two major stabilizing effects attributable to biodiversity. The first is a buffering effect, which decreases deviation around the long-term mean biomass production through species asynchrony, i.e., species exhibit different temporal dynamics in response to fluctuating environmental conditions, allowing diverse communities to keep stable production levels over time (Doak *et al.* 1998; Hector *et al.* 2010). The second effect is performance enhancing: mean productivity is increased in diverse communities due to facilitation or complementarity effects (Pretzsch & Schütze 2009).

Theoretical studies have shown the general validity of biodiversity insurance for a wide range of ecosystems and ecosystem processes (Yachi & Loreau 1999; Loreau & de Mazancourt 2013). On the other hand, observational studies have mainly focused on biodiversity insurance effects in the context of temporal stabilization of biomass production. This research was mainly conducted in grasslands (Tilman 1999a; Tilman, Reich & Knops 2006), although few studies focused on forests (Thompson *et al.* 2009; Jucker *et al.* 2014a). Other ecosystem responses than productivity are understudied. Seedling survival, for example, has received little attention, despite its importance as a driver for ecosystem structure and functioning and its particular relevance for forest management (Breugel *et al.* 2011; Yang *et al.* 2013). For the first few years after plantation establishment, young trees face a strong planting shock, for instance due to root damage or a shift to harsher environmental conditions than they experienced in the nursery. Mortality occurs when plant stress exceeds certain thresholds: a complex process depending on multiple interrelated factors and mechanisms (O'Brien *et al.* 2014). If planting trees in mixtures rather than monocultures would limit planting failure through insurance, this would serve as a basis for an effective management strategy that reduces investment risks and costs in the early stage of a long forest rotation cycle: typically between 30 and 150 years in a temperate forestry context.

Buffering effects are likely to influence seedling survival due to niche differentiation, i.e., the probability of survival differs among species because they show species-specific adaptations to environmental conditions like droughts, frost and heat, especially in the extremes (Valkonen 2008; Breugel *et al.* 2011; Fonseca, de Figueiredo & Martins 2011). Therefore, monoculture plantings experience the highest risk of planting failure, as individuals are about equally susceptible to present environmental stresses and species compensation is not possible (Knoke *et al.* 2007). This is particularly true for tree species that are sensitive to environmental stresses, e.g., the common European beech (*Fagus sylvatica*), Douglas fir (*Pseudotsuga menziesii*) or sycamore maple (*Acer pseudoplatanus*).

Performance enhancing effects for seedling survival could result from complementarity and facilitation. Due to the relatively large distances between planted seedlings, inter-tree competition for water and light is likely not yet of major importance, thus reducing the importance of complementarity (Yang *et al.* 2013). A facilitative mechanism could result from local environment modification, triggered by neighbouring trees through their specific morphological traits. For instance, fast growing species can provide shelter for more susceptible species by reducing wind, radiation, cold and frost, thus potentially increasing mean survival of those species.

In recent years, large-scale tree diversity experiments have been established in a variety of locations worldwide in order to quantify the relationship between tree species diversity and ecosystem functioning against a background of various other factors and covariates (www.treedivnet.ugent.be and Verheyen et al., 2015). Such experiments allow for an investigation of seedling survival insurance for a wide range of tree species and forest types. In a tropical tree diversity experiment in Panama, Healy et al. (2008) found that environmental heterogeneity and diversity collectively explained 50 % of the total variation in seedling survival. Yang et al. (2013) reported that mean seedling survival was significantly influenced by species identity, diversity and altitude in a tree diversity experiment in China. Both researchers focused on performance enhancing effects of biodiversity, but did not discuss important management consequences derived from buffering effects.

In this study we investigated both buffering and performance enhancing effects on cumulative three-year seedling survival in the Belgian FORBIO tree diversity experiment (Verheyen *et al.* 2013). We explored the spatial aspect of diversity insurance by evaluating mean survival of, and variance between, plots with more or less diverse forest plantings. More specifically, we quantified the relative importance of species identity (i.e., species-specific survival responses due to differences in species ecology), SR, composition (i.e., specific assemblage of different tree species) and the environment for seedling survival. We hypothesized that we would observe: (i) a decreased variability in plot-level survival with increasing SR as a result of species compensation, further referred to as a buffering effect; (ii) an increased mean survival with increasing SR as a result of facilitation, further referred to as a performance enhancing effect.

2.3 Materials and methods

2.3.1 Experimental design

The FORBIO experiment consists of sites at three distinct locations in Belgium, Western Europe (Figure 1-7 and Appendix I. The Zedelgem site (ZED; 51°9’N 3°7’E; 11-16 m; 9.5 ha) was planted on former agricultural land with a nutrient rich, moderately dry sandy soil and a mild Atlantic climate (MAP = 687 mm; MAT = 9.4 °C, WAI = 1.4 %; Appendix I) caused by the proximity of the North Sea coast (16 km). The Gedinne site (GED) is located in the Ardennes highlands and was established after clearcutting a former spruce plantation. It consists of two subsites at two km apart, i.e., Gribelle (49°60’N 4°59’E; 367-376 m; 4.5 ha) and Gouverneurs (49°59’N 4°59’E; 421-426 m; 4.5 ha). Both subsites have well drained stony loam soils and a harsh continental climate (MAP: 1021 mm; MAT: 6.9 °C, WAI: 37.8 %). Finally, the Hechtel-Eksel site (HEC; 51°10’N 5°19’E; 55-56 m; 8 ha) was planted on a former pine plantation in the Campine plains of north-eastern Belgium. This site has a nutrient poor, dry sandy soil with gravel and a slightly Atlantic to continental climate (MAP: 799 mm; MAT: 9.0 °C, WAI : 6.7 %). The region is generally not water deficit (i.e., potential precipitation exceeds evapotranspiration in most months) and weather data did not show any severe drought periods in the first three years after plantations establishment. The experiments in ZED and GED were planted in 2010 and fenced to prevent damage by hare, rabbit and wild boar (ZED) or red deer and wild boar (GED). HEC was planted in 2012 and fencing was not necessary; monitoring game damage during and after planting proved the low browsing intensity. In the first three years, the vegetation between tree rows has been mowed once a year and spontaneously established trees were manually removed. Each site was planted with five tree species from local provenances, bought in commercial nurseries as two or three year old seedlings (Table 2-1; Verheyen et al. 2013). These species are well adapted to local site conditions with regard to climate (MAP, MAT, temperature of coldest and warmest month) and soil (texture, pH KCl, P, N, C/N ratio). Abiotic data was derived from soil surveys taken prior to plantation establishment and from nearby meteorological stations (Appendix I). In addition, site-selected tree species are functionally dissimilar to each other concerning their traits and, as a consequence, their contributions to ecosystem functioning and tolerance to environmental stresses and disturbances (Table 2-1 and Appendix II). An NMDS ordination of the tree species based on Gower distances between trait values shows the clustering of conifer species (*Pinus sylvestris, Pseudotsuga menziesii* and *Larix* ssp.) and broadleaf species (Table 2-1). The latter group is scattered along a gradient that can be related with juvenile growth and light requirement (from high to low: *Betula pendula*, *Quercus* spp., *Tilia cordata*, *Acer pseudoplatanus* and *Fagus sylvatica*, Table 2-1). Most sensitive tree species in open field conditions are *F. sylvatica* (late frost, stagnating water and droughts), *A. pseudoplatanus* (late frost and droughts) and *P. menziessii* (late frost).

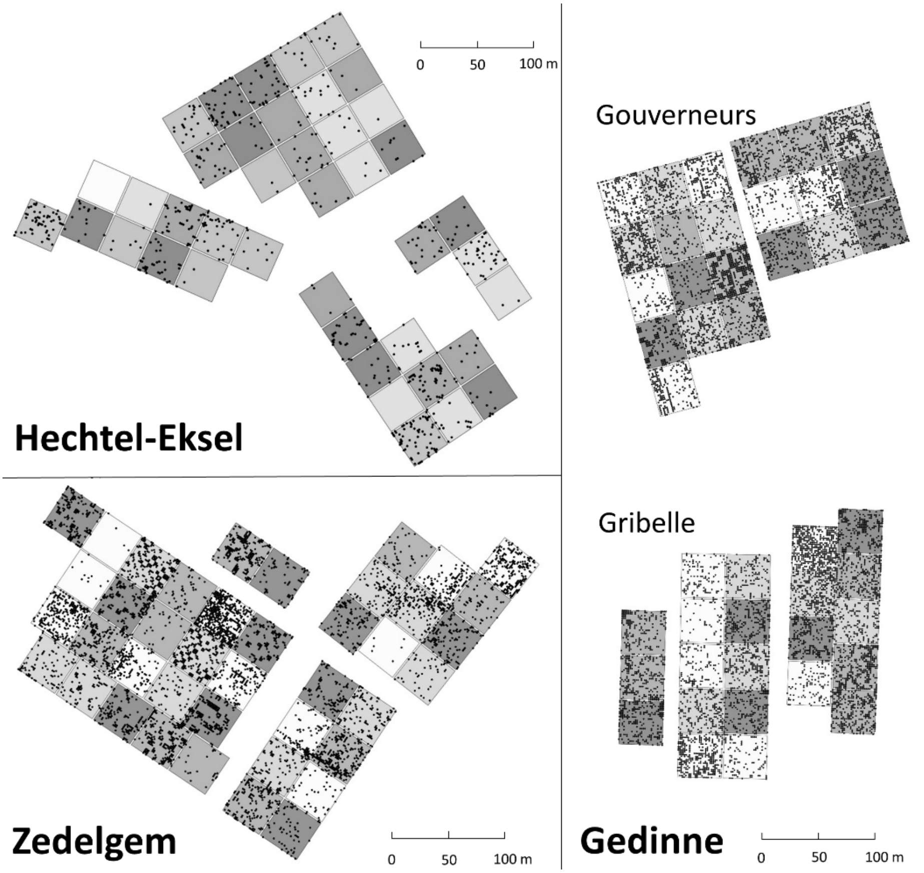


Figure 2-1 Spatial distribution of seedling mortality on the FORBIO sites. Cumulative three-year (ZED and GED) and two-year (HEC) seedling mortality is shown with black dots. Basic experimental design features are monoculture (white) and mixture plots (grey scale) with up to four tree species.

The experimental design is similar among sites and consistent with other manipulative tree diversity experiments (Verheyen *et al.* 2015). Trees were planted in monoculture and mixture plots with up to four species together. Every site consists of 20 different species compositions, all replicated in two blocks (Appendix V). Frequencies of occurrence were similar across the species, both within and across diversity levels. Two additional monocultures of oak (ZED) and four monocultures of beech (GED) with different species provenances were added to the design, resulting in 40, 42 and 44 plots at HEC, ZED and GED respectively. Plots measure 36 m x 36 m in HEC and 42 m x 42 m in ZED and GED, except for thirteen plots in GED that measure 42 m x 37.5 m. Trees were planted in a 1.5 m x 1.5 m grid and in monospecific clusters of 3 x 3 trees (Figure 4-1). As a result, the number of trees per plot is 784 (ZED and GED), 700 (smaller plots in GED) and 56 (HEC). More design details are provided in Verheyen *et al.* (2013)

Table 2-1 Tee species present in FORBIO. Trait data were obtained from different sources, partially modified based on expert knowledge and local growth tables by Dr. Michael Scherer-Lorenzen. Traits matches the ones used by Scherer-Lorenzen *et al.* (2007) and Verheyen *et al.* (2013) to select functionally dissimilar tree species in the BIOTREE and FORBIO experiments respectively.

	Abbreviation	**Scale**	**Source**	***A. pseudoplatanus***	***B. pendula***	***F. sylvatica***	***F. sylvatica***	***L. kaempferi***	***P. sylvestris***	***P. menziesii***	***Q. petraea***	***Q. robur***	***T. cordata***
				GE	ZE	GE	ZE	GE	ZE	GE	GE	ZE	ZE
Family		(1) *Sapindaceae*; (2) *Betulaceae*; (3) *Fagaceae*; (4) *Pinaceae*; (5) *Malvaceae*		1	2	3	3	4	4	4	3	3	5
Taxonomy		(1) gymnosperm, (2) angiosperm		2	2	2	2	1	1	1	2	2	2
Succession		(1) pioneer, (2) intermediate, (3) climax	Burschel and Huss (1997)	2	1	3	3	1	2	2	2	2	3
Root architecture	Root	(1) Flat root, (2) heart root or pile –heart root and strong horizontal root, (3) taproot or vertically with deep root penetration	Thomasius (1978)	2	1	2	2	2	3	2	3	3	2
Shade tolerance	Shade	Tolerance scales range from 0 (no tolerance) to 5 (maximal tolerance)	Niinemets, Ü. And Valladares, F. (2006)	3.73	2.03	4.56	4.56	1.5	1.67	2.78	2.73	2.45	4.18
Specific leaf area	SLA	Metric (cm^2 g^{-1})	FORBIO	105	148	137	129	111	28	56	109	111	163
Leaf dry matter content	LDMC	Metric (mg mg^{-1})	FORBIO	0.44	0.41	0.52	0.48	0.42	0.39	0.49	0.46	0.43	0.39
Leaf nitrogen concentration	N	Metric (%)	FORBIO	2.11	3.16	2.01	2.29	1.39	1.54	1.41	2.04	2.61	2.23
Wood density	WD	Metric g cm^{-3}	FORBIO	0.45	0.43	0.61	0.60	0.35	0.30	0.36	0.51	0.56	0.33

2.3.2 Survival scoring

In the first three years after planting, individual survival of all 89,254 trees was assessed every year at the end of the growing season (September-October). Because of high survival rates (99.8 %) in the second year of HEC, survival scoring on this site was not repeated in the third year. Seedling survival was defined as a binary variable ("0" for dead trees and "1" for living trees), without recording the causes of mortality, as it was impossible to accurately differentiate between them. To keep fully stocked experiments, dead trees were replaced in the winter following every scoring. In this study, we investigated three-year cumulative survival rates, i.e., the survival rates that would be observed if no replacement was done and thus omitting the replaced individuals. For one plot in GED (number 44), these are two-year cumulative survival rates because trees were in deficient stage during planting and all trees are replanted in the next year. In further between-species analyses, we did not distinguish between *Quercus petraea – Q. robur* and between *Larix decidua – L. kaempferi*.

2.3.3 Environmental gradient

A soil analysis based on 165 (ZED), 108 (GED) and 41 (HEC) soil samples (10-20 cm depth), taken prior to plantation establishment, revealed small intra-site variation for pH(KCl), P (mg kg^{-1}), N (%) and C/N ratio (Appendix I and Verheyen *et al.* 2013). Although co-variation between these soil attributes and SR was partly controlled by the experimental design (block design), we further accounted for environmental variation at the plot-level. To do so, we extracted the main axis of environmental variation from Principle Component Analyses (PCA) on soil attributes and elevation measured on the sites (Appendix III). We calculated average PCA scores of the plots and used them as covariate in the survival models. PCA analyses were done with the MASS package of R statistical software (R Core Team 2017).

2.3.4 Statistical analyses

2.3.4.1 Variation in seedling survival

Quantifying the relative importance of different experimental treatments is challenging with e.g. the R function *lmer* in the lme4 package. The differences in R² between two nested models is frequently used as a proxy, however, large difference in degrees of freedom between predictor variables may bias the comparison (Hector *et al.* 2011). Another strategy is to define all variables as random effects, which allows to calculate super population variance components for each variable. The classical least squares or maximum likelihood methodologies are only approximate and understates the uncertainty in variance estimates. Therefore we followed Gelman (2005) by building a multilevel ANOVA model. Here we partitioned the total variance in seedling survival data into finite population variance components within a Bayesian framework (Gelman & Hill 2007). In our model, variance components for site (S, σ_s^2, 3 levels), block (B, σ_b^2, 6 levels), species richness (SR, σ_d^2, 4 levels), composition (C, σ_c^2, 50 levels) and species identities (Sp, σ_{sp}^2, 8 levels) were calculated on the proportion of surviving trees per species and per plot (sample size N = 306; multiplying each of the 126 plots by the number of species in that plot). SR is defined by the number of tree species in the plot and species composition is a categorical variable with 50 levels, one for each species composition containing one or more tree species (Appendix IV). Computation of parameters was done with Markov Chain Monte Carlo sampling (5000 iterations of both warming-up and sampling chains) in Stan C++ language software linked to R (Stan Development core team 2014). The procedure is not fully Bayesian in sense of using informative prior values for the distributions of the random variables (i.e. vague priors were set to a normal distribution with mean zero and variance 1).

To easily compare the relative importance of the different experimental treatments in the survival data, the results of the multilevel ANOVA are displayed graphically.

2.3.4.2 Plot-level survival

To test performance enhancing and buffering effects on plot-level survival, we fitted generalized least squares models including SR and different variance structures along the SR gradient. A first model assumes residuals ε_i to be normally distributed with constant variance ($Var(\varepsilon_i) = \sigma^2$) and a second model allows residuals to be normally distributed with SR-specific variances ($Var(\varepsilon_i) = \sigma^2 \times SR_i$ with i = 1, ..., 4) (Zuur et al., 2009). When the SR effect in the model increases mean survival, this is interpreted as a performance enhancing effect. When the variance decreases with increasing SR, this is interpreted as a buffering effect. Both models were compared with standardized residual plots and Log-Likelihood Ratio (LLR) tests (Zuur *et al.* 2009). We applied this approach first in an overall analysis where site was included as an additional fixed factor in the models to account for inter-site variability (N_{total} = 126) and second in site-specific analyses (N_{GED} = 44; N_{ZED} = 42, N_{HEC} = 40) where the soil gradient (PCA axis) was included in the models to control for intra-site environmental variation. The models were fit with *gls()* function in the nlme R package, with the variance structure *varIdent* to allow SR-specific variances.

2.3.4.3 Species-level survival

Finally we tested for differences in performing enhancing effects between the species. Here, the survival or mortality (1 and 0, respectively) of all seedling was used as a response (N_{GED} = 28 729 trees, N_{ZED} = 28 177 trees, N_{HEC} = 19 360 trees) in GLM (binomial family, logit-link function).

The model can be written as:

$$\text{logit(tree survival)} \sim SR + Sp + Sp{:}SR + Soil_{PCA} \quad \text{(Eq. 1)}$$

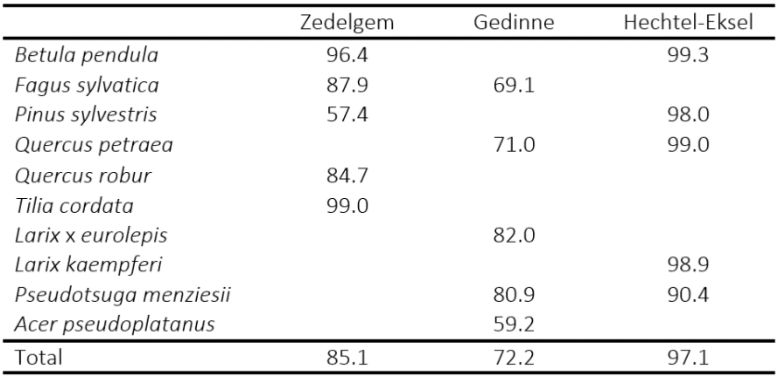
where $Soil_{PCA}$ are plot scores of the first PCA axis to account for intra-site environmental variability (III). We used the parameter estimates of the fitted models to calculate survival probabilities and 95 % confidence intervals for different species along the SR gradient

2.4 Results

2.4.1 Data description

The cumulative three-year seedling survival was 97.1 %, 85.1 % and 72.2 % for HEC, ZED and GED respectively (Table 2-2). GED consists of two sub-sites at 2-km distance, but overall survival was similar apart from some species-specific differences (e.g. *A. pseudoplatanus*: 50.6 % in Gribelle *vs.* 68.8 % Gouverneurs). Survival was above 90 % for all species in HEC and above 80 % for all species in GED and ZED, except for *P. sylvestris* (ZED), *F. sylvatica* (GED)*, Q. petraea* (GED) and *A. pseudoplatanus* (GED). Spatial patterns can be observed in the mortality maps but are caused by the experimental design with monospecific clusters of 3 x 3 trees of the same species (Figure 2-1 and Figure 4-1). There is no indication for spatial survival patterns other than caused by the experimental design.

Table 2-2 Cumulative 3-year seedling survival (%) is calculated on 32 810 (ZED), 33 404 (GED) and 23 040 (HEC) trees. For HEC and for plot 44 of GED a 2-year seedling survival is presented. HEC was not monitored on the third year as mortality events were very rare and seedlings in plot 44 in GED were in deficient stage during planting and all trees were replanted in the next year. Empty cells means that the species was not present at the site.



	Zedelgem	Gedinne	Hechtel-Eksel
Betula pendula	96.4		99.3
Fagus sylvatica	87.9	69.1	
Pinus sylvestris	57.4		98.0
Quercus petraea		71.0	99.0
Quercus robur	84.7		
Tilia cordata	99.0		
Larix x *eurolepis*		82.0	
Larix kaempferi			98.9
Pseudotsuga menziesii		80.9	90.4
Acer pseudoplatanus		59.2	
Total	85.1	72.2	97.1

2.4.2 Variation in seedling survival

Major variation in seedling survival can be attributed to the species (sd = 0.10) and experimental sites (sd = 0.12; Figure 2-2). Much smaller variance components were found for the experimental treatments species richness (sd = 0.01) and species composition (sd = 0.02), indicating that they are relatively of low importance to explain the seedling survival.

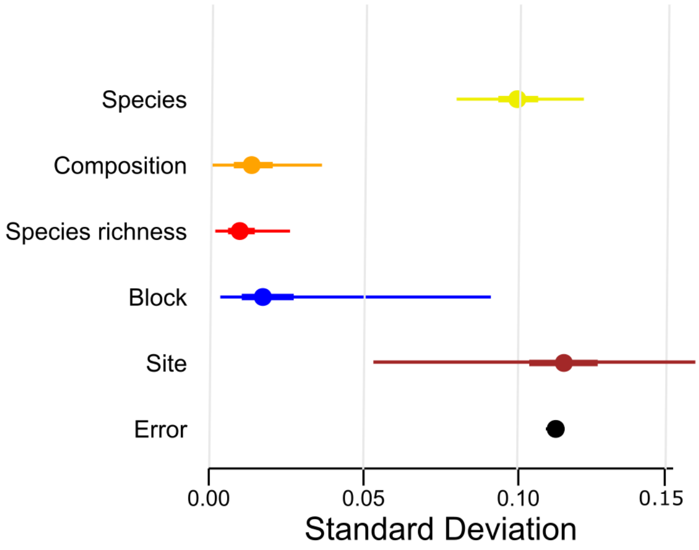


Figure 2-2 Graphical display of the multilevel ANOVA on species-specific plot survival (N=306). Points indicate variance components on a standard deviation scale for different experimental treatments and bars display 95 % (thin) and 68 % (thick) credibility intervals. The point estimates are not always at the interval's centre because of the model restriction that all variance components have to be nonnegative.

2.4.3 Plot-level survival

Scatterplots of observed plot-level survival against SR suggest a decreasing variance with increasing SR (Figure 2-3). The group of four-species plots does not contain survival incidents less than 50 % whereas this is the case for all lower SR levels. LLR tests strongly favour a SR-specific variance structure in the overall analysis (LLR = 31.17, $P < 0.001$) and in ZED (LLR = 15.35, $P = 0.002$), indicating that the variation in plot-level survival changes significantly along the SR gradient. In an analysis across all sites, the residual variance of SR levels 1, 2 and 3 relative to a reference variance of SR level 4 are 7.08, 2.54 and 2.85, respectively (Figure 2-3). In ZED, the corresponding relative variances were 22.46, 3.10 and 6.81 (not presented). The results thus confirm a stabilized plot survival at higher SR levels and indicate that this trend is mainly caused by the large variability within the group of monocultures. Mean survival was not affected by SR in the analysis across all sites (slope = 0.2 %, $P = 0.04$; Figure 2-3) neither in the site-specific analyses (slopes are -0.3 %, 0.8 %, -0.4 % for ZED GED and HEC respectively, all $P > 0.1$). Environmental heterogeneity within a site, measured by soil scores of the first PCA axis, was not important to predict survival in the site-specific analyses.

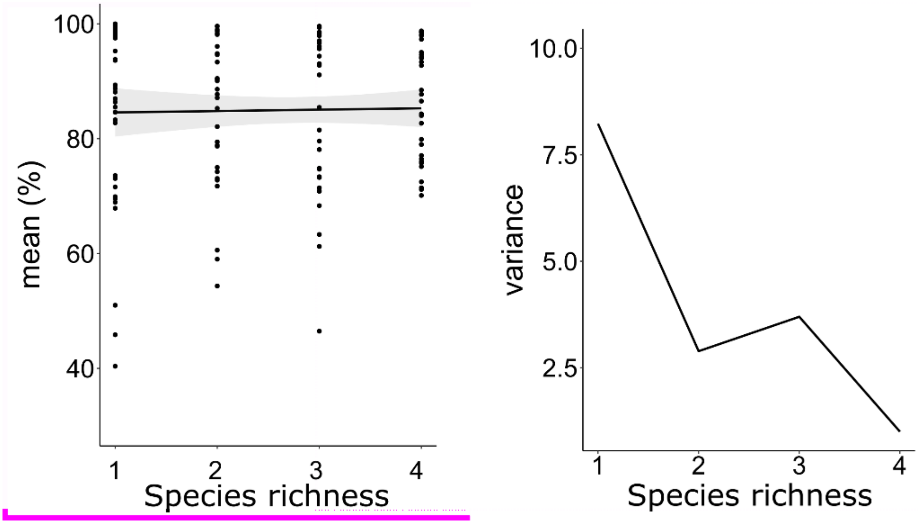


Figure 2-3 Plot-level seedling survival in function of species richness in an analysis across all sites. Left panel: observed (dots) mean plot survival rates (%) and prediction (lines with 95 % confidence intervals as shaded areas) based on a Generalized Least Squares model showing the lack of performance enhancement effect (i.e., constant mean survival along the species richness); right panel: decreasing residual variances ($Var(\varepsilon_i) = \sigma^2$ x species richness with i = 1, ..., 4) of the same gls model showing a buffering along the species richness gradient.

2.4.4 Species-level survival

Consistent with the descriptive statistics (Table 2-2) and the variance components in the multilevel ANOVA (Figure 2-2), the models show strong differences in survival probabilities between the species (Figure 2-4). Wald tests indicate no overall SR effect on mean survival except for HEC ($\chi^2 = 23.3$, $P < 0.001$). However, the interaction term between species and SR is significant in all models, indicating different SR effects between the species. In ZED, a significant SR effect is found for *F. sylvatica* (z = 2.82, *P* = 0.005), in HEC for *P. menziesii* (z = -3.74, *P* < 0.001) and *P. sylvestris* (z = -3.64, *P* < 0.001) and in GED for *F. sylvatica* (z = 2.83, *P* = 0.005), *P. menziesii* (z = -4.09, *P* < 0.001) and *Q. petraea* (z = -3.5, *P* < 0.001). The magnitude and direction of SR effects differ between species, but within species the effects are consistent among the sites (e.g. increasing for *F. sylvatica* and decreasing for *P. menziesii*).

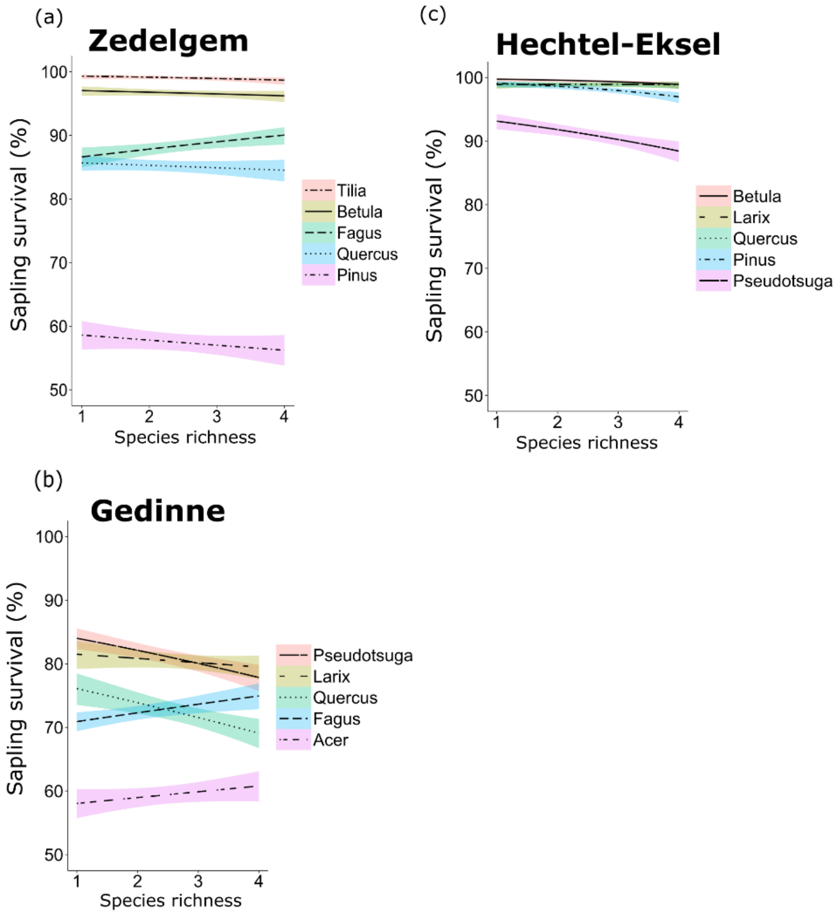


Figure 2-4 Effects of species identity and species richness on the probability of seedling survival in (A) Zedelgem, (B) Gedinne and (C) Hechtel-Eksel. Predicted survival rates (lines) and 95% confidence intervals (shaded areas) are calculated with site-specific GLM (binomial family, logit-link function)

2.5 Discussion

In our three-year study, we examined performance enhancing and buffering effects of SR by comparing seedling survival rates of plots with variable SR. The results show a strongly decreased survival variance with increasing SR, which supports the buffering effect hypothesis. Furthermore, a constant mean survival over the gradient in SR demonstrates that, in this case, performance enhancing effects are not contributing to the insurance. Thus, our results show that the presence of a larger number of tree species stabilizes plot survival by reducing the probability of extreme outcomes, not by increasing net survival probabilities.

2.5.1 Survival rates in the experiment

The observed seedling survival rates (59 % – 99 %) would commonly be considered planting successes, in line with afforestation projects in temperate (Don *et al.* 2007), tropical (Breugel *et al.* 2011), continental (Stanosz & Carlson 1996) and boreal regions (Valkonen 2008). Not only were there differences in establishment success between tree species, but the success rates also differed between experimental sites. Seedling survival was most favourable in HEC, which was likely the result of an intensive site preparation, planting by professional forest workers and the favourable weather conditions during and after planting. In contrast, the less intensive site preparation and harsher weather conditions in GED could explain the lower establishment success there. There is no clear evidence in our study that small-scale environmental variations within sites play a role in explaining seedling survival. In contrast, Healy et al. (2008) reported that intra-site environmental heterogeneity in drainage and topography explained between 35 % and 57 % of the variation in seedling survival and productivity in their tree diversity experiment. This difference is likely the result of the experimental design: our experiment was designed on more homogeneous sites, where topography, soil and other confounding factors were minimized and did not cause additional survival variation.

2.5.2 Buffering effects

Among the mechanisms underpinning temporal insurance (Hector *et al.* 2010), spatial insurance is likely to be generated through differential species responses to environmental conditions. The studied tree species were carefully selected based on relevant silvicultural criteria, including the compatibility with the local climate, soil attributes and regional management experiences (Appendix I and Verheyen *et al.* 2013). In addition, the species were chosen to be functionally dissimilar to each other, according to physiological and morphological traits driving ecosystem properties (effect traits) and responses to biotic and abiotic conditions (response traits) (Díaz *et al.* 2013). Response traits, in particular, build a fundamental link between the environment and seedling fitness. They express the capacity of species to cope with environmental conditions, perturbations in those conditions as well as an initial planting shock (Anderegg & Hillerislambers 2015). Roughly, the species pool in our experiment encompasses early (e.g., *B. pendula* and *Larix* spp.) and late (e.g., *F. sylvatica* and *P. menziesii*) successional tree species, with the former group possessing response traits which optimize fitness in exposed and thus often stressful conditions (Table 2-1). Therefore, despite the fact that all species were well adapted to the average environmental site conditions (climate and soil), inter-species differences in functional traits have led to differences in survival rates between species, species compensation and finally to the observed buffering effects (Loreau, Mouquet & Gonzalez 2003; Isbell, Polley & Wilsey 2009). It is furthermore reasonable that the strength of buffering is a function of (i) intrinsic survival strategies between species, i.e., smaller effects for communities with more closely related response traits, (ii) stochasticity of the environment, i.e., smaller effects under stable and less stressful weather-induced conditions and (iii) spatial heterogeneity, i.e., smaller effects under spatially homogeneous site conditions. The observed buffering effects are clearly a consequence of basic statistical averaging (Doak *et al.* 1998), but to our knowledge, this study is the first to prove biodiversity insurance for seedling survival. The simple effect could have profound implications for the design and management of real-world forest plantations (see 2.5.5).

2.5.3 Performance enhancing effects

In our study, mean plot survival was not influenced by SR, thus performance enhancing effects did not contribute to the insurance. Similar results were found by Liang *et al.* (2007), Potvin & Gotelli (2008) and Healy, Gotelli & Potvin (2008), who concluded that seedling survival differed strongly between species but not between SR treatments. Seedling survival was significantly lower in mixed plots of the BEF China experiment, but according to the authors this negative performance enhancement effect was most likely caused by practical difficulties of planting mixtures of up to 16 uncommon tree species (Yang *et al.* 2013). In our study we performed additional tests to detect SR effects at the species-level. Although mixing did not enhance average plot-level performances, survival of some species was affected by SR, although with various magnitudes and directions. For instance in GED, survival probability in four-species mixtures compared with monocultures is higher for *F. sylvatica* (+5.2 %), lower for *P. menziesii* (-7.6 %) and *Q. petraea* (-8.8 %) and is unaffected for *A. pseudoplatanus* and *L.* x *eurolepis*. Under highly competitive circumstances, performance enhancing effects at the species-level are likely to be explained by interspecific competition, favouring strong competitors such as *F. sylvatica* and disfavouring weak competitors such as *Q. petraea* (Zhao *et al.* 2006; Valkonen 2008). However, we investigated seedling survival in plantations that are far from canopy closure and where the soil is not yet fully occupied with roots. We therefore question whether inter-tree competition is really the main driver of the observed SR effects in this case and suggest facilitative interactions are more plausible (Calder & Clair 2012). For instance, *F. sylvatica* seedlings are susceptible to challenging environmental conditions, such as late-season frosts (Menzel, Helm & Zang 2015), and it is reasonable that they would perform better when mixed with fast growing species, say *P. sylvestris*, *B. pendula* or *Larix* spp., as they provide a buffer against harsh conditions. Not all observed SR effects could be explained in this way, thus facilitative interaction causing SR effects at the species-level is likely but not yet confirmed.

2.5.4 Plantation age and further perspectives

While we focused in this study on the early performance of planted seedlings, performance enhancement effects of SR are expected to increase over time (Cardinale et al. 2012). As trees get older, not only do they interact more directly through physical contact, their environment has also been affected by diversity for several growing seasons, which compounds the effects. Seedlings that initially survive, but suffer from low vitality, are more prone to die as stand development proceeds and inter-tree competition further disfavours these weak individuals. We therefore hypothesize that while mean seedling survival is initially affected by the quality of planting material, planting expertise, environmental site conditions and choices made for specific species and varieties, performance enhancing effects may become more relevant in later development stages. The insurances effect of tree species mixing on seedling survival are expected to be most important right after planting, when seedlings are more vulnerable to environmental disturbances. However, insurance effects remain important in later forest succession stages when vitality or productivity are evaluated. It is generally accepted that mixed forests are more resistant than monocultures to herbivory pressure, soil- borne fungal diseases and specialized insect herbivores (Jactel *et al.* 2017). According to Knoke *et al.* (2007), admixing broadleaves to conifers also improbed the resistance to fire and windstorms. Thus the stabilization effects of species (both spatial and temporal ways) are not singly important to the early plantation stages.

We recognize the importance of site conditions (including climate, soil, site history and weather conditions during and after planting) and management practices (including site preparation, plant quality and planting expertise) for the successful establishment of a tree plantation (Valkonen 2008; Close *et al.* 2009; Breugel *et al.* 2011; Yang *et al.* 2013). However, it is beyond the scope of a single experiment to identity the relative contributions of these factors and to explain differences in overall survival rates between sites. The generic value of our findings could be further explored through meta-analyses, combining survival data across many tree diversity experiments. Global initiatives can contribute to such a synthesis. TreeDivNet, for instance, covers 18 sites, 107 species and more than one million trees across the world's biomes (Verheyen *et al.* 2015). Such synthesis studies should also focus on how species' traits affect seedling survival and on the link between trait dissimilarity in the species pool and survival insurance.

One shortcoming of this study is that the importance of competition by herbaceous ground vegetation was not taken into account in the analyses. Ground vegetation in ZED and GED was controlled by mowing and by removing germinated seedlings between the rows during the first 2-4 summers after planting (Figure 1-8). These management actions strongly reduced any pressure from understory ground vegetation on the planted seedlings, as is proved in many different other studies (Balandier *et al.* 2006; Vandenberghe *et al.* 2006). Setiawan *et al.* (2016b) demonstrated that vegetation cover changed the height/diameter growth ratio of four-year old saplings in FORBIO. This pattern is probably a strategy of the seedlings to avoid light competition. Importantly, Setiawan *et al.* (2016b) found no negative influence of vegetation cover for seedling height increment or diameter increment. This result indicates that survived seedlings were not much hindered by the light, water and nutrient consumption rates of directly surrounding vegetation. We cannot exclude the possibility that understory vegetation competition have influenced initial establishment success rates of planted seedling in ZED and GED. But it is less probable that including vegetation competition would have impacted seedling survival - diversity relationships, which was our main research interest.

2.5.5 Management implications

Even with excellent knowledge of the responses of species to environmental conditions, the early performance of site-adapted seedlings in the field is uncertain. Spatially intimate mixing (i.e., at the level of individual trees or small tree clusters) ensures that well performing species will locally compensate for the mortality of other species. This consequently diminishes the risk for large mortality gaps in the plantation. Other positives are the quick canopy closure, efficient usage of productive site capacity and accelerated natural pruning, i.e., the earlier shading of lower branches in mixtures compared to monocultures of a single, poor performing species (Kubo, Iwasa & Furumoto 1996; Pretzsch & Schütze 2005; Kint *et al.* 2010). These positives should receive more weight in planting design decisions. To date, plantations are still almost exclusively planted with single species, selected for superior growth and stem quality potential rather than for seedling survival (Nichols, Bristow & Vanclay 2006).

When evaluating establishment success at the level of the whole plantation, planting risks are also reduced when tree species are mixed at larger spatial scales, for instance by mixing large monoculture blocks (e.g. of 1 ha size). This system has clear advantages, as it reduces silvicultural complexity and thus offers lower management costs compared to intimate mixing. However, major drawbacks include the risk for group-wise mortality of seedlings, which then requires difficult and cost ineffective replacements, and the lack of complementary effects between different neighbouring species.

According to our results, management will already profit from an insurance effect of diversification in the initial phase of a forest rotation cycle. Due to the long rotation period, cost cutting in the initial stages of a rotation is known to be extremely effective in increasing the profitability of forestry investments at a given interest rate (Bary-Lenger *et al.* 1983). An important finding is that diversification is effective from its lowest level onwards, i.e., two species mixtures. This is particularly relevant for many forestation projects in temperate and boreal regions, where suitable and/or desired species pools are often small (Nichols, Bristow & Vanclay 2006; Kelty 2006). Furthermore, in a study carried out in Central European forests, Knoke & Seifert (2008) showed that a simple two-species mixture, including the less profitable European beech and the more profitable Norway spruce, has the potential for increased yields and, more importantly, for greater economic utility due to insurance against natural disturbances and timber price fluctuations.

The survival insurance policy derived from species mixing is furthermore beneficial for projects applied in regions without a long forestry tradition, as knowledge about best planting techniques is often lacking and tree species have not undergone breeding to optimize plantation performance (Bauhus, Van der Meer & Kanninen 2010; Yang *et al.* 2013). For these projects in particular, species diversification is a preferred option for a risk-averse forest manager (Nichols, Bristow & Vanclay 2006). But similar as the experiment in this study, it always requires certain minimum information on plant ecology (e.g. successional status) based on functional traits (e.g. growth rates, wood density, specific leaf area) in order to select functionally dissimilar tree species with reasonable survival probabilities in the region.

2.5.6 Conclusion

The study shows a plain buffering effect of tree species mixing in sense that severe or clustered seedling mortality is less likely to happen in stands with functionally dissimilar tree species. Mean seedling survival was not higher in mixtures compared to monocultures, thus performance enhancing effects of SR were lacking. Our results support the risk reduction strategy of tree species diversification from the lowest level of mixing (two species) and during the early plantation development stage. The insights are a relevant contribution to the field as the initial investments for planting and replanting trees strongly affect overall financial balances.

Chapter 3

Seedling Vitality Improves with Functional Diversity

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Author’s contributions: TVDP, BM and SM devised the concept of the article; SM, JMCS, LM, JR and MLC collected field data; TVDP carried out the data analysis, with statistical advice from SM and JMCS. TVDP wrote the manuscript text. All co-authors contributed to revising earlier versions of the manuscript and approved the final version.

Cover photo: Weeding IDENT-M, 2015 (S. Mereu)

3.1 Summary

Reforestation with multiple tree species is a promoted strategy to mitigate global change and to improve forest resistance against natural hazards. Dryland reforestation often fails because seedlings suffer from harsh conditions in degraded areas. Positive species interactions can overcome recruitment drawbacks by ameliorating environmental stress, but there is a strong need to advance functional insights from well-designed experiments.

We studied the vitality of 19,712 tree seedlings from 12 species in a Mediterranean common garden experiment (Sardinia). Vitality was assessed as an integrated index of foliage discoloration and defoliation measures, which are in dry areas potential indicators of early plant performance. The experimental design properly replicated all monocultures and a selection of mixed communities with different levels of SR and FD. From the second year onwards, a water availability treatment (irrigated versus non-irrigated) was added to the design.

In the second year, seedling vitality was strongly determined by species identity and irrigation, but ecological interactions between trees were not relevant. In the third year, however, broad-leaved species were significantly more vigorous in mixed assemblages. Importantly, FD was identified as a seven times stronger predictor compared to SR. This suggests that a certain degree of trait diversification is essential to benefit from facilitative interactions. The positive FD effects were principally mediated by the presence of *Pinus* sp. (*P. pinea, P. pinaster* and *P. halepensis*) in the neighborhood of broad-leaved trees. The latter had, on average, a 23 % greater likelihood to have the highest vitality score in mixture with *Pinus* sp.. The creation of a favorable physical and biotic neighborhood by *Pinus* sp. is likely caused by their fast juvenile growth and adequate crown light transmission. FD effects on seedling vitality were positive, but contrary to the stress-gradient hypothesis, they were of similar magnitude in both irrigated and non-irrigated blocks.

We conclude that local neighborhood facilitation provides essential assistance for broad-leaved trees passing a critical seedling stage in semi-arid regions. This knowledge can contribute to increased success rates in forest rehabilitation in these regions.

3.2 Introduction

After the Paris Agreement, the world's nations are committed to undertake sufficient actions for limiting global warming well below 2 °C (UNFCCC 2015; Rockström *et al.* 2017). A substantial role is dedicated to ecosystem-based mitigation actions. For instance, the negative emission potential from reforestation and forest restoration is, without exceeding biophysical constraints, estimated to 480 Gt CO2 by 2100 (IPCC 2014; SEI 2016). Arid, semi-arid and dry-subhumid regions (hereafter: drylands) aggregately represent 41 % of terrestrial land area and provide livelihood to 38 % of the world's human population (Reynolds *et al.* 2007). Excellent opportunities for meeting ecosystem-based mitigation targets are found in these drylands. Due to intensive anthropogenic impacts, approximately 10 to 20 % of land surface is severely affected by degradation (MEA 2005). In the Mediterranean Basin, for instance, native forests once covered extensive areas but are nowadays compromised in their structure and functioning, or evolved to early-successional shrublands (Nocentini & Coll 2013). Via raising temperatures and shifting precipitation patterns, climate change will further accelerate ecosystem vulnerability to desertification (Maestre *et al.* 2012). Many dryland restoration projects failed because seedlings could not pass a critical phase of plant settlement (Gómez-Aparicio 2009; James *et al.* 2013). Such failure weights on financial budgets, but moreover, it demotivates land owners to invest in ecosystem restoration.

Difficulties to re-establish native dryland forest is best understood by considering a system with alternative stable states (Holmgren & Scheffer 2001; Scheffer *et al.* 2001). The dryland forest state is dynamic, but quite inert to environmental modifications (i.e. strong ecosystem resilience). This changes once a critical point is reached, either following gradual stress accumulation or because of a dramatic event such as fire or clear-cut. The dryland forest state collapses and abruptly switches into another alternative state, e.g. a dry landscape dominantly covered by grasses, shrubs and/or bare soil (Holmgren & Scheffer 2001). The backward transition is extremely difficult and requires conditions to be reversed beyond the critical point of ecosystem collapse, a phenomenon known as hysteresis (Scheffer *et al.* 2001). A strong feedback loop between biotic and abiotic components is chiefly stabilizing the degraded vegetation state (Kéfi, Holmgren & Scheffer 2016). For instance, loss of canopy cover increases direct solar irradiation, temperature, evapotranspiration, water runoff and soil erosion. Tree seedlings are highly sensitive to dehydration because of their emerging rooting system and limited capacity to store water and carbohydrates (Valladares & Sánchez-Gómez 2006; Aerts *et al.* 2007; O'Brien *et al.* 2014).

Where negative feedback loops stabilize the degraded vegetation state, positive species interactions can pave a way for transition back into forest. It has been demonstrated that nurse plants, for instance small pioneer shrub species or legumes (Gómez-Aparicio *et al.* 2004), promote native seedling performance via the reduction of environmental stress at microsite scale (Castro & Zamora 2004; Aerts *et al.* 2007; Rey, Alcántara & Ramírez 2008). Besides favouring water and temperature balance of the nursed trees, they also provide protection from grazing, reduce soil erosion and improve nutrient cycling. Conditions generally get better with accumulated biomass (i.e. positive feedback loop) and the thresholds hampering forest succession are surpassed (Kéfi, Holmgren & Scheffer 2016). Once well established, native trees easily withstand harsh conditions.

The interest in restoration pathways via positive nurse plant – seedling interactions aligns with a growing research on the functional significance of biodiversity under climate change (Cardinale *et al.* 2012; Tilman, Isbell & Cowles 2014). It was reported that the adoption of polyculture plantations, instead of conventional large-scale monocultures, provides long-term benefits for dealing with climatic uncertainties (Pawson *et al.* 2013). First, mixed forests benefit from greater spatial and temporal stability; a consequence of asynchrony in species responses to environmental fluctuations (Thompson *et al.* 2009; Jactel *et al.* 2017). Second, ecosystem functioning (e.g. productivity, litter decomposition) is favoured in mixed stands through resource complementarity (Madrigal-gonzález *et al.* 2016) or through the regulation by higher (Castagneyrol, Régolini & Jactel 2014) or lower trophic levels (Laforest-lapointe *et al.* 2017).

As the relationship between biodiversity and forest functioning is primarily explored in mature systems, facilitative interactions in the early forest stages are far less understood, notably in the context of restoration success. To meet these shortcomings, research started manipulating tree species composition and diversity at scales relevant to policy and management (Verheyen *et al.* 2015). In these so-called tree diversity experiments, contrasting results have yet been found about the effects of tree diversity on seedling performance. Negative effects are observed by Yang et al. (2013), neutral effects by Potvin and Gotelli (2008) and Yang (2017), and species-dependent diversity effects (Chapter 2). Also in the IDENT-M experiment (Sardinia, Italy) seedlings are planted in monocultures and mixtures following a well-balanced design (Tobner *et al.* 2014). Interestingly, it is the only tree diversity experiment dealing with dry (Mediterranean) conditions. The experiment comprises 12 woody species assembled in 308 communities at different levels of SR and FD. It furthermore includes an irrigation treatment (irrigated versus non-irrigated) to examine shifts in species interactions with drought stress (Tobner *et al.* 2014). With insights into the autecology of dryland tree species and into mechanisms governing inter-specific interactions, it is possible to merge fundamental biodiversity-ecosystem functioning research with forest restoration ecology.

In this study we explored how tree species interactions are building-up in the Mediterranean IDENT-M experiment and how they have an influence on seedling performance. Because seedling performance cannot be measured directly, growth measures are commonly used as a proxy. However, biomass allocation between aboveground and belowground plant structures differs greatly between species (e.g. the shoot:root biomass ratio is four times larger for seeders compared to resprouters; Verdu 2000) as well as within species. Altered biomass allocation is usually a reaction to abiotic (water, nutrients and salinity) and biotic (vegetation competition) stress. Particularly in drought-prone or nutrient-poor environments, seedlings tend to disproportionally invest in root development to reach deeper and moister soil layers and to withstand droughts (Lloret, Casanovas & Peñuelas 1999; Padilla, Miranda & Pugnaire 2007). Root biomass prioritizing is typical in environments where soil resources, rather than light, are constraining seedling establishment success. Assessing seedling performance with diameter/height measures may thus lead to some error, particularly for seedlings in harsh environments. Combining belowground and aboveground biomass data would be ideal, but belowground biomass is extremely difficult to estimate. The direct monitoring of tree physiological processes (e.g. leaf water potential, stomatal conductance or photosynthetic rate) may also provide valuable information, but these measures require sophisticated instruments and they are quite time consuming to take for many seedlings (Valladares & Sánchez-Gómez 2006; Manzoni 2014).

Foliage condition offers an alternative, time-efficient strategy to compare the performance of plants in different environments. The idea goes back to 1985. Since then, crown condition is annually assessed in the ICP Forests program (International Co-operative Program on Assessment and Monitoring of Air Pollution on Forests, Meining & Fischer 2011). Following this standardized protocol, crown defoliation and discoloration is visually estimated and compared with a healthy reference tree. Intensive training and repeated control systems allow to create an objective vitality indicator. Vitality then reflects the integrated effects of site characteristics, intrinsic factors (e.g., age, phenology), biotic stresses, meteorological conditions and air pollutants (De Marco *et al.* 2014; Bussotti & Pollastrini 2017)

Also in this study, seedling vitality was assessed as a combined index of foliage discoloration and defoliation measures. We hypothesized that (i) seedling vitality is principally determined by species identity and irrigation, because functionally dissimilar tree species respond differently to (drought) stress; (ii) seedling vitality is positively affected by tree species mixing due to facilitative plant interactions or due to the regulation by different trophic levels; (iii) some nurse trees (i.e. species firmly shaping the suitable physical or biotic micro-environment for other trees) substantially improve the vitality of their neighbours and, finally, (iv) positive interactions gain functional relevance under stress (the stress-gradient hypothesis), here tested by comparing irrigated with non-irrigated conditions.

3.3 Material and methods

3.3.1 Description of the experiment

IDENT-M is located on the island of Sardinia (Italy), Macomer (40° 14' N; 8° 42' E; 640m above sea level) and within the nursery “St. Antonio - Sardinian Forest Authority”. It is part of the International Diversity Experiment Network with Trees (IDENT; Tobner et al. 2014). The hot-summer Mediterranean climate (Köppen: Csa) is characterized by warm and dry summers and mild winters with moderate rainfall. More specifically for the plantation site, average monthly temperatures range from 6.5 °C (January) to 23.9 °C (August), and monthly rainfall ranges from 135 mm (December) to 7 mm (July), with an accumulated rainfall of 905 mm over the entire year (Ente Autonomo Flumendosa 1998). The basaltic area was used as a tree nursery for local reforestation projects until 2008. Up to 2014 (the establishment of the experiment) the fields were left unmanaged, although spontaneous vegetation (grasses) was periodically removed. In 2015 a meteorological station was placed in an open field adjacent to the experiment. The station measures precipitation, photosynthetic active radiation, wind speed and wind direction at 2 m height, as well as air temperature and relative humidity at 0.3, 2 and 4 m height. All sensors were connected to a data logger acquiring data every 5 minutes and storing them as 30 minutes averages, or sum for precipitations.

Similar to other IDENT sites, the main experimental design features are hierarchically organized with trees distributed over 308 plots and seven blocks (Figure 1-9). A block comprises 44 plots of 3.2 m by 3.2 m, with in each plot 64 seedlings planted at 40 cm spacing. Blocks are exact replicates in terms of tree species communities in the plots, but the spatial arrangement of plots within blocks is random. All blocks were irrigated during the dry season in the first year (2014). In the following years, three randomly selected blocks were irrigated with 20 mm every 15 days from June to September. For this a pipe system was used to distribute water homogeneously over the soil. The remaining four blocks were not irrigated, thus they serve as controls (Figure 1-9).

From the end of January to mid-April 2014, there were 19,712 containerized one-year-old seedlings (two-year-old for *Fraxinus ornus*) planted by professional foresters. Species selection was based on site requirements and taking into account local availability of seedlings in the nursery. In total, 12 native woody species were selected, of which both shrubs (three species) and trees (nine species), and among them three conifers (all genus *Pinus*), six evergreen broad-leaved species and three deciduous broad-leaved species (). Within each block, a first diversity gradient was created by manipulating SR at four levels: one- (12 plots), two- (17 plots), four- (9 plots) and six-species (6 plots). A second gradient, orthogonal (independent) to the first, was created by manipulating FD.

To do so, species were ranked according to Gower distances (Pavoine *et al.* 2009) in functional ten traits: seed dry weight (SDW), maximum height (Hmax), specific leaf area (SLA), leaf life span (LLS), maximum photosynthetic rate per unit area (Pnmax), maximum stomatal conductance (Gsmax), water potential at which 50 % of hydraulic conductivity is lost (PLC50), nitrogen content per unit of mass (Nm), wood density (WD) and leaf area (LA) using literature-based trait data (Table 3-1). The traits represent important dimensions of plant ecological strategies to tolerate or avoid drought stress (Sánchez-Gómez, Zavala & Valladares 2008; Pivovaroff *et al.* 2016). Because water availability is likely the most constraining resource for seedlings in our Mediterranean experiment, the traits should help explaining variation in species functioning and understanding the mechanisms of species coexistence. It is not an exclusive list of relevant functional traits, but lack of rigorous data (e.g. for seed mass) hindered some other traits to become included. The ranking of species according to their functional relatedness formed the basis for a semi-randomized selection of species assemblages This selection ensured an equal representation of mixed communities with low FD (nearest neighbours in the ranking, 11 plots), medium FD (close neighbours in the ranking, 10 plots) and high FD (far neighbours in the ranking 11 plots). The position of tree species in each plot was randomized, but species clumping was prevented. Within plots, as well as within the inner, middle and outer frame, species relative abundances are alike (Figure 1-9 and Appendix V). Plots were regularly weeded by hand to avoid competition from weeds and unplanted seedlings

Table 3-1 Trait matrix for the 12 species in IDENT-M. Values are derived by averaging from 50 Mediterranean databases and studies. SDW = seed dry weight (mg), Hmax = maximum height (m), SLA = specific leaf area (m2/kg), LLS = leaf life span (days), Pnmax = maximum photosynthetic rate per unit area (µmol CO2/m2 s-1), Gsmax = maximum stomatal conductance (mol H2O/m2 s-1), PLC50= water potential at which 50% of hydraulic conductivity is lost (mp), Nm = leaf nitrogen content per unit of mass (%), WD = wood density (g/cm3), LA = leaf area (cm2).

Species	Leaf habit	Life form	Leaf type	SDW	Hmax	SLA	LLS	Pnmax	Gsmax	PLC50	Nm	WD	LA
Acer monspessulanum	Deciduous	Tree	Broadleaf	46	15.0	15.17	177	17.8	154	-3.3	19.5	0.52	19
Arbutus unedo	Evergreen	Shrub	Broadleaf	3.6	6.8	6.39	330	15.6	292	-1.4	13.8	0.65	16
Fraxinus ornus	Deciduous	Tree	Broadleaf	25	8.5	12.21	190	20.0	200	-2.2	22.0	0.56	70
Olea europea	Evergreen	Tree	Broadleaf	285	12.2	8.62	972	14.0	210	-7.2	19.0	0.81	10
Phillyrea latifolia	Evergreen	Shrub	Broadleaf	16	5.2	6.78	1110	14.9	275	-6.7	17.8	0.85	6
Pinus halepensis	Evergreen	Tree	Needle	23	17.5	3.56	1083	5.0	180	-3.1	12.3	0.46	3
Pinus pinaster	Evergreen	Tree	Needle	52	23.8	3.40	1536	13.8	152	-3.0	10.6	0.41	5
Pinus pinea	Evergreen	Tree	Needle	718	21.3	3.16	1065	10.9	120	-3.7	12.5	0.50	6
Pistacia lentiscus	Evergreen	Shrub	Broadleaf	24	3.7	5.22	735	11.8	298	-5.2	15.0	0.71	20
Quercus ilex	Evergreen	Tree	Broadleaf	2311	16.5	6.43	815	15.1	299	-2.0	14.1	0.82	12
Quercus pubescens	Deciduous	Tree	Broadleaf	634	17.2	14.82	210	18.5	196	-3.3	18.4	0.56	30
Quercus suber	Evergreen	Tree	Broadleaf	3469	12.5	6.76	455	15.0	280	-4.0	16.9	0.77	8

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3.3.2 Vitality scoring

The performance of seedlings was visually assessed in terms of foliage discoloration and defoliation during the end of June 2015 (second growing year) and mid-September 2016 (third growing year). Both indices complement each other because even if defoliation is low, discoloration, may indicated plant vitality issues. The assessment hinged on three criteria: (i) tree survival with 0 = [dead] and 1 = [alive]; (ii) defoliation with 1 = [> 50 % foliage loss], 2 = [5 - 50 % foliage loss] and 3 = [< 5 % foliage loss] and (iii) share of leafs showing discoloration with 1 = [> 50 % discoloration], 2 = [5 - 50 % discoloration] and 3 = [< 5 % discoloration]. Only chlorosis and necrosis were considered as discoloration. These leafs are colouring yellow or white, a typical stress-related phenomenon that affect photosynthesis capacity. The production of accessory pigments, such as anthocyanins or carotenoids, make leafs more reddish or brownish. These pigments often help to protect against excessive sunlight that can damage some leaf tissues. This is one reason why a young, newly developing leaf is often redder than when it reaches its mature size. Red collars is often found for seedlings of *A. unedo, P. lintescus* and *A. monspessulanum*. Because it does not provide information on seedling vitality, it was also not considered in the discoloration assessment.

The first assessment was carried out by five observers, which were trained to normalize their scorings by repeated measure and control processes before the start of the survey. In addition, circa 30 % of all seedlings were rescored by a reference observer. If observers were consistently over- or underscoring, their measures (only categories 2 and 3) were a posteriori corrected to eliminate an observer bias (in total 4 % of observations were corrected). The second assessment was exclusively conducted by the reference observer.

Seedlings were grouped in two classes. The first group (value = 1) includes the most vigorous seedlings without any problems rated to foliage discoloration or defoliation (i.e. best scores for both variables). The second group (value = 0) includes the seedlings with indications of foliage discoloration and/or defoliation. This binary vitality index was used in all analyses. The option to include more vitality classes was tested in ordinal regression models. However, a large imbalance in class sizes (in the second-year assessment) caused important analytical complications. A binary reclassification is then considered as the best way forward.

Following Tobner et al. (2016), seedlings in the outer plot frame (Figure 1-9) were omitted from the analyses to minimise plot edge effects. Block A was planted earlier and during extreme wet conditions. As this had great implications on the settlement of all plants, block A is not comparable with the other blocks and it had to be excluded from the experiment. These restrictions led to well-balanced final dataset, including vitality scorings for 9,504 seedlings from 6 blocks (3 control and 3 irrigated), 264 plots and 12 species.

3.3.3 Statistical analyses

All analyses were applied on seedling vitality data from the second and third year. Beforehand the community-level functional dispersion index (FDis) of Laliberte et al. (2010) was used as a more accurate measure of FD compared to the low-medium-high FD classes, which were used to design a well-balanced experiment. FDis is the mean distance of each species to the centre of mass of all species in a multidimensional trait space. The metric produces similar value compared to Rao's quadratic entropy, but it is more flexible because it can handle any number of traits and any trait type (i.e., quantitative, semi-quantitative, and qualitative). Although not relevant in this study, FDis is generally used because the approach allows for missing trait values and the weighting of individual traits. The Pearson correlation coefficient between SR and FDis is 0.58. This means that increasing SR automatically increases FDis, but not necessarily in a similar way for all communities.

The dbFD-function implemented in the FD package (R software) was used for these calculations. This function requires a distance or dissimilarity matrix (Gower distances were used in this study) for all species based on their functional traits (Table 3-1).

The calculations are furthermore based on two formulas: $\mathbf{c} = \frac{\sum a_j x_{ij}}{\sum a_j}$ and $\mathrm{FDis} = \frac{\sum \mathrm{a_j z_j}}{\mathrm{a_j}}$ where vector c represents the weighted centroid in the i-dimensional trait space, taking into account the abundances (aj) and trait values (xij) for all species (j) and traits (i). To compute FDis, distances (zj) between the species position from the centroid c in the multidimensional trait space are weighted by relative species abundances aj in the plots. Species relative abundances do not differ between species in the plot communities (maximum species evenness).

3.3.3.1 Relative importance of explanatory variables

A multilevel ANOVA (Gelman & Hill 2007) on seedling vitality was performed to estimate finite population variance components and confidence intervals for explanatory variables. These include irrigation treatment, species identity, FDis and SR, but also the species-by-FDis interaction and the species-by-irrigation interaction. The multilevel ANOVA is principally designed for comparing the relative contribution of explanatory variables for nested experimental designs (Hector *et al.* 2011). The parameters of the model were computed with Markov Chain Monte Carlo (MCMC) in four chains with 1000 iterations, using Stan C++ language software linked to R (Stan Development core team 2014).

3.3.3.2 Functional diversity and irrigation treatment

Effects of FDis and irrigation treatment on seedling vitality were further explored in Generalized Linear Mixed-effect Models (GLMM, N = 9 505 trees) with binomial distribution and logit-link function (glmer function from the R package “lme4”). A first model, called the diversity model, included species identity, FDis and the pairwise interaction terms irrigation-by-FDis and species-by-FDis as fixed effects. The model allowed testing how FDis effects on seedling vitality differed between irrigated and non-irrigated conditions (stress-gradient hypothesis), and how FDis effects differed across the species. A second model, called the irrigation model, encompassed species identity, irrigation treatment and a pairwise interaction term between both variables as fixed effects. The model allowed testing species-dependent irrigation effects on seedling vitality. Both the diversity model and the irrigation model shared a random effect structure with intercepts for blocks and species composition (i.e. factor with different levels for unique species compositions, Appendix V). Models were fit by maximum likelihood methods and variables were tested for statistical significance by Wald Chi-square tests (Zuur *et al.* 2009). Significant fixed effects were further explored with contrast inferences (Tukey post-hoc tests) available in the R packages “multcomp” and “phia”. Marginal and conditional R^2 values (MuMIn package) were calculated as a measure of model’s goodness-of-fit based on fixed effects (marginal), or the combination of both fixed and random effects (conditional) after Nakagawa & Schielzeth (2013).

3.3.3.3 Buffering effects

In analogy to the hypotheses in Chapter 2, we tested performance enhancing and buffering effects of species mixing at the plot level. To do so we calculated plot-level vitality responses in the third year of the experiment (i.e. percentage of seedlings that were vital in each plot). Similar as before, we used generalized least squares models where residuals are allowed to be normally distributed with SR-specific variances ($Var(\varepsilon_i) = \sigma^2 \times SR_i$ with i = 1, 2,4, 6) (Zuur et al., 2009). When the SR effect in the model increases mean survival, this is interpreted as a performance enhancing effect. When the variance decreases with increasing SR, this is interpreted as a buffering effect.

3.3.3.4 Linking effects with functional traits

In a final step we attempted to functionally understand why vitality differed among species and why the effects of FDis and irrigation differed among species. We extracted fixed-effect intercepts and slopes from the regression models that comprise the species-by-FDis interaction or the species-by-irrigation interaction. If intercepts correlated with traits, it could explain observed differences in vitality among species. If slopes for FDis (or irrigation) correlated with traits, that could explain differences in vitality responses to FDis (or irrigation). To control for species' phylogenetic relatedness, we designed a phylogenetic tree (phylomatic function in the R package branching, Figure 3-1) and we computed phylogenetic independent contrasts (pic function in R package ape). The method transforms mean species values to contrasts (based on branch lengths), which are statistically independent and which can be used in the correlation analyses (Felsenstein 1985; Garland, Harvey & Ives 1992).

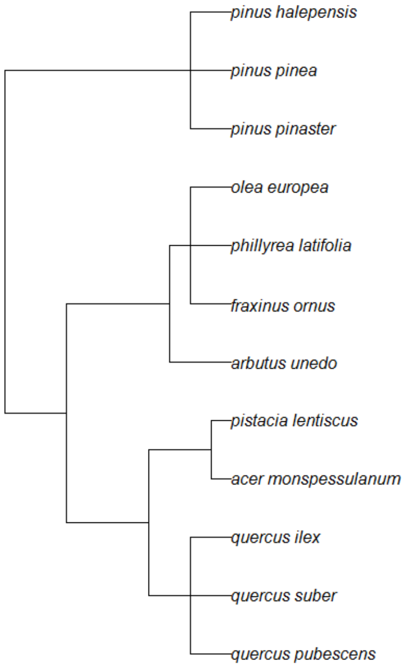


Figure 3-1 Phylogenetic tree of the 12 study species in IDENT-M, with a topology based on Phylomatic (http://phylodiversity.net/phylomatic)

3.4 Results

The two consecutive years in which vitality assessments were performed (2015 and 2016) were comparable in terms of mean annual minimum temperature (8.2 °C and 8.5 °C), mean annual maximum temperature (18.3 °C and 18.5 °C) and annual precipitation (967 mm and 971 mm). In 2016, however, the summer drought began slightly earlier and lasted longer, as is indicated by the monthly climatic data (Appendix VI).

Unfortunately, the difference in soil humidity between control and irrigation treatment was not monitored in the first years. Measuring soil humidity for comparison between plots is challenging because of the huge horizontal and vertical heterogeneity created by species' differences in water conception profiles. In the end we have giving 160 mm (8x20 mm) extra water to the irrigated fields, which was 17 % (2015) and 19 % (2016) of the natural precipitation over the entire year (control fields). Additionally, we are giving that in months where you usually have nearly no rainfall (June to September, Appendix VI). During these month, irrigated fields received about the double amount of water than the control fields, which only relied on natural precipitation. The PET in Macomer over the four summer months was 600 mm (2015) and 585 mm (2016) according to calculation approach of (Hargreaves & Samani 1982)(Appendix I). Assuming a crop coefficient of 0.6, the water requirements for the trees would be around 460 mm. So with the irrigation we are giving about 27% of PET or about 35% of the water requirements. Considering that these are drought adapted species, we are significantly reducing the drought stress.

Seedling survival evaluated in the second year (2015) ranged between 99 % and 99.5 % for all species, except for *P. lentiscus* (80 %). About 63 % of the plants were scored as vital (i.e. no signs of discoloration or defoliation), but there was large variability in vitality between species (Appendix VII). About 75 % of non-vital seedlings did not show recovery, as they were also scored as non-vital trees in the third year (2016). Survival rates in 2016 ranged between 92 % (*P. lentiscus*) and 99 % (*F. ornus*), with 23 % of survived trees being entirely vital.

3.4.1 Relative importance of explanatory variables

A multilevel ANOVA on second-year vitality data revealed species identity (St. Dev. = 0.35) as the most important explanatory variable, followed by species-dependent responses to irrigation (St. Dev. = 0.19, Figure 3-2). Variance components of SR and FDis were roughly similar in magnitude and close to zero. In the third-year vitality data instead, FDis (St. Dev. = 0.07) explained an important part of the variation, but SR (St. Dev. = 0.01) did not. Accordingly, FDis was used in the additional analyses to further inspect diversity patterns. The large variance components for species-by-FDis (St. Dev. = 0.11) and species-by-irrigation (St. Dev. = 0.16) interactions already suggest that effects of FDis and irrigation varied a lot by species.

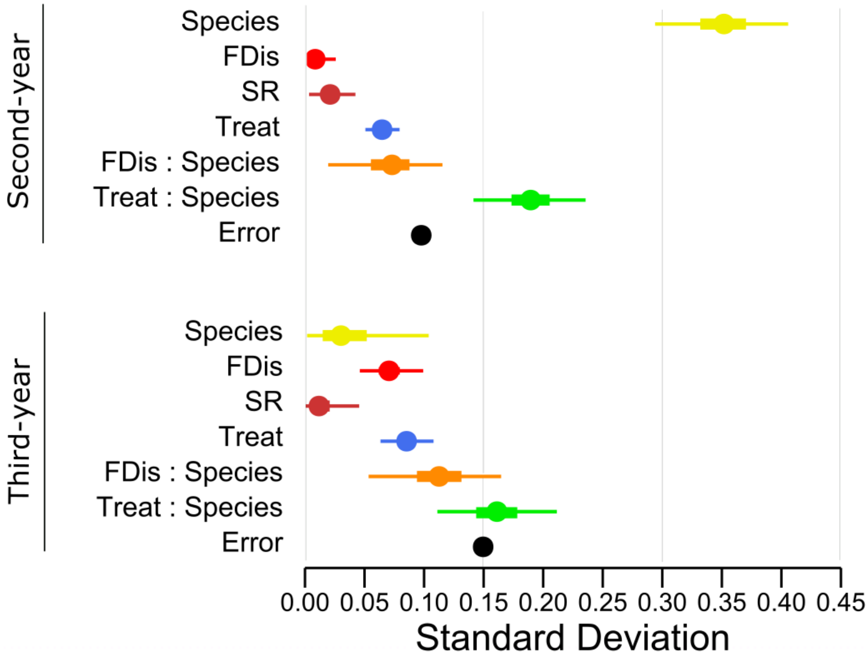


Figure 3-2 Display multilevel ANOVA's showing the variance components of each predictor variable to seedling vitality. The upper panel represents results in the second growing year (2015) and the lower panel represent results in the third growing year (2016). Dots are mean variance components on a standard deviation scale and lines represent 68 % (thick) and 95 % (thin) credible intervals (i.e. Bayesian counterpart of confidence intervals). Species identity (Species), functional diversity (FDis), species richness (SR) and irrigation treatment (Treat), with interactions denoted as a colon between the variables.

3.4.2 Functional diversity and irrigation

Evaluating second-year vitality data, the overall effect of FDis is zero on average and this non-significant effect holds for both irrigated and non-irrigated blocks (Table 3-2, diversity model). A positive FDis effect was found for *Q. pubescens* ($\chi^2 = 38.7$, $P < 0.001$) and a negative effect for *P. pinaster* ($\chi^2 = 11.1$, $P = 0.001$), but the vitality of other species was not affected by FDis.

Table 3-2 Statistical inferences of Generalized Linear Mixed-effect models testing the predictors of seedling vitality (0/1) in the second (2015) and third (2016) growing year. The models include the fixed variables species identity (Species), functional diversity (FDis) and/or irrigation treatment (Treat), as well as pairwise interactions (denoted as a colon sign). Random effects are assigned to species composition (Comp) and replicating blocks (Block), and estimates for their standard deviations (St. Dev) are presented. Goodness-of-fit was evaluated with marginal and conditional R².

		Fixed	**Chi-square**	***P***	**Random**	**St. Dev**	**R²**	
Second-year	Diversity model	Species	1229.6	< 0.001	Comp	0.23	Marginal	0.38
		FDis	0.1	0.70	Block	0.52	Conditional	0.44
		Treat : FDis	0.01	0.96				
		FDis : Species	35.7	0.002				
	Irrigation model	Species	1161.1	<0.001	Comp	0.31	Marginal	0.40
		Treat	10.5	0.001	Block	0.30	Conditional	0.43
		Treat : Species	193.6	<0.0.01				
Third-year	Diversity model	Species	625.0	<0.001	Comp	1.55	Marginal	0.31
		FDis	12.4	<0.001	Block	1.24	Conditional	0.67
		Treat : FDis	0.09	0.77				
		FDis : Species	23.0	0.01				
	Irrigation model	Species	609.8	< 0.001	Comp	1.61	Marginal	0.28
		Treat	4.0	0.04	Block	0.93	Conditional	0.65
		Treat : Species	101.8	< 0.001				

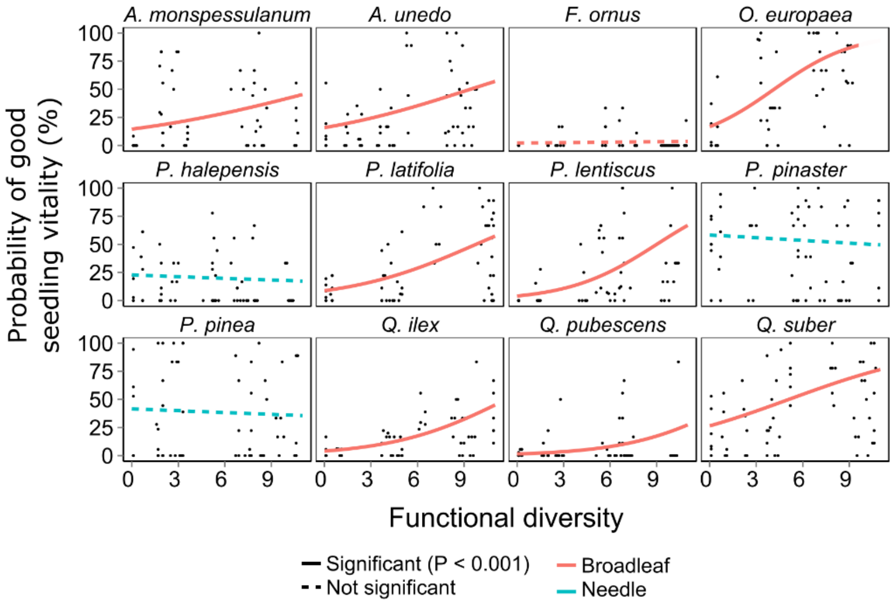


Figure 3-3 Probability of a seedling being vital (vitality index = 1, i.e. no discoloration or defoliation) for the 12 study species along a gradient in functional diversity (FDis). FDis for monoculture plots equals zero. Dots represent observations during the third year of the experiment (2016). Lines represent predictions from the regression models, with full lines for significant trends and dotted lines for non-significant trends based on Chi-square tests and significance level of 0.001. *Pinus* sp. (*P. halepensis, P. pinaster* and *P. pinea*) are colored green and broad-leaved species are colored red. Dots represent observed vitality for the given species.

In the third year, FDis was a positive and significant predictor of vitality in both irrigated and non-irrigated blocks. Broad-leaved species were more vital in plots with higher levels of FDis, except for *F. ornus*, while the vitality of needle-leaved species was not affected by FDis (Figure 3-5). An additional GLMM model was run on a subset of the data exclusively including the broad-leaved trees. Here we could test the effect of presence/absence of *pinus* sp. in the neighbourhood of broad-leaved trees. The results revealed that neighbouring *pinus* sp. substantially improved ($\chi^2 = 807.9$, $P < 0.001$) the vitality of broad-leaved trees, particularly so for *A. monspessulanum, A. unedo, O. europea, P. latifolia, P. lentiscus,* and *Q. suber* (Figure 3-4). On average, broad-leaved trees neighboring *pinus* sp. had a 23 % greater likelihood to be entirely vital. *P. halepensis* ($\chi^2 = 318.1$, $P < 0.001$) and *P. pinaster* ($\chi^2 = 93.2$, $P < 0.001$) contributed most to the faciliation effect, while the influence of *P. pinea* was positive but not significant ($\chi^2 = 2.1$, $P = 0.14$). After controlling for the presence of *pinus* sp., FDis still remained a significant predictor ($\chi^2 = 103.8$, P =0.04), so that a small share of the observed FDis facilitation had a different origin.

3.4.3 Buffering effects

At the plot level, seedling vitality did not change significantly along a gradient in SR, which is in line with the low importance of SR in the mANOVA output (Figure 3-4). Model variances deceased along a gradient in SR, but LLR tests did not favour a SR-specific variance structure (LLR = 2.57, *P* = 0.46, Figure 3-4). This indicates that the decreased plot-level variance in seedling vitality with SR was not significant and that buffering effects were missing.

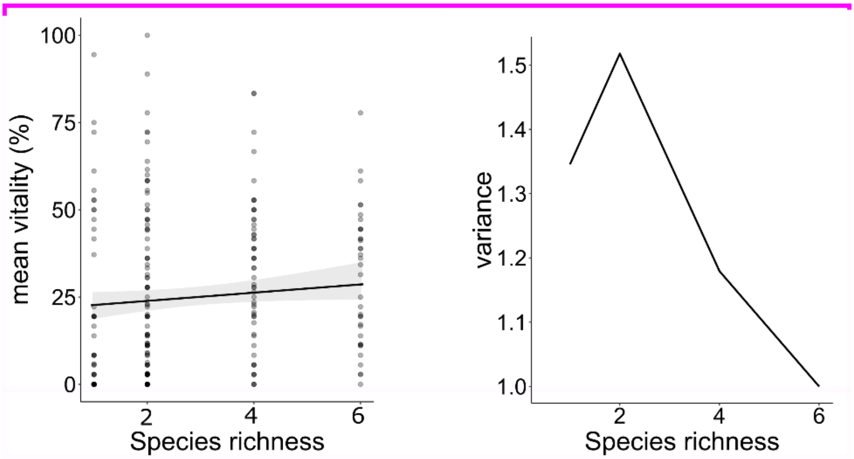


Figure 3-4 Plot-level vitality (third year) in function of species richness (SR). Left panel: observed (dots) plot-level vitality rates (% vigorous plants in a plot) and prediction (lines with 95 % confidence intervals as shaded areas) based on a Generalized Least Squares model. This panel demonstrates the lack of a performance enhancement effect in IDENT-M (i.e., constant mean vitality with SR); right panel: decreasing residual variances ($Var(\varepsilon_i) = \sigma^2 \times SR$ with i = level of SR 1, 2, 4, 6) in the same gls model. Because this decreasing trend was not significant (LLR = 2.57, *P* = 0.46) plot-level vitality is not stabilized with increasing SR (no significant buffering).

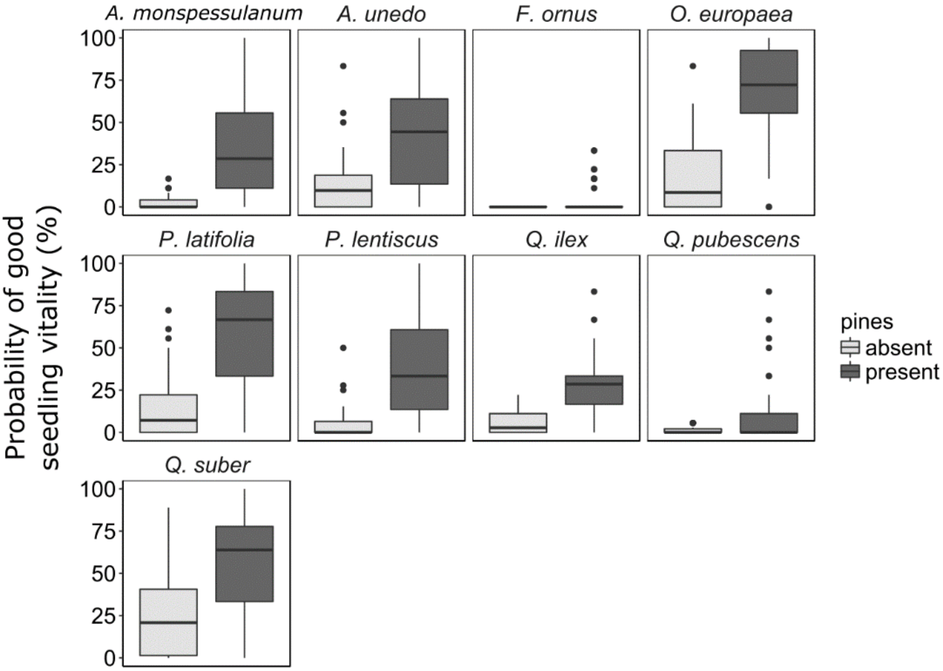


Figure 3-5 Boxplot showing the probability of trees to be vital (%) for broad-leaved species when not admixed (light grey) or admixed (dark grey) with *pinus* sp. (*P. halepensis, P. pinaster* and *P. pinea*) and based on third-year vitality data (2016). A Generalized Linear Mixed-effect model (binomial distribution with 1 = vital seedlings without indications of foliage discoloration or defoliation and 0 = non-vital seedlings) using a data subset of nine broad-leaved species indicated that the presence/absence of *pinus* sp. in the plot is an important predictor for seedling vitality ($\chi^2 = 807.9$, $P < 0.001$).

Based on second-year vitality data, the GLMM displayed an overall positive effect of irrigation as well as species-specific deviations from this average (Table 1, irrigation model). More precisely, seedling vitality improved with irrigation (0.01 level of significance) for *F. ornus, A. unedo, A. monspessulanum, P. latifolia, Q. pubescens* and *Q. suber*, while other species performed equally well under both conditions (Figure 3-7). In the third year, seedling vitality was generally higher in irrigated blocks. However, species-specific responses to irrigation differ from the patterns observed in the second year: *Q. suber, A. unedo, P. halepensis, P. pinea* and *P. pinaster* took most advantage from the additional water.

3.4.4 Relation with functional traits

All trait-related results can be found in Appendix X. Seedling vitality in the second year was the highest for *Pinus* sp. seedlings and scaled negatively with SLA (Pearson Correlation Coefficient, PCC = -0.64) and positively with LLS (PCC = 0.66). After correcting for phylogenetic relatedness, correlations became a bit weaker (PCC = -0.57 and 0.61) and are on the border of being significant (*P* = 0.04 and *P* = 0.07, Figure 3-6). Vitality responses to irrigation (second year) were related to species trait signature and only slightly related to evolutionary species' distances. The irrigation effect became stronger at higher SLA (PCC = 0.7), higher PLC50 (PCC = 0.62) and lower LLS (PCC = -0.82). Finally, vitality responses to FDis were the strongest for broad-leaved species and scaled positively with wood density (WD) in the third year (PCC = 0.83), also after the pic corrections. All other relationships between traits and identity/irrigation effects were not statistically significant.

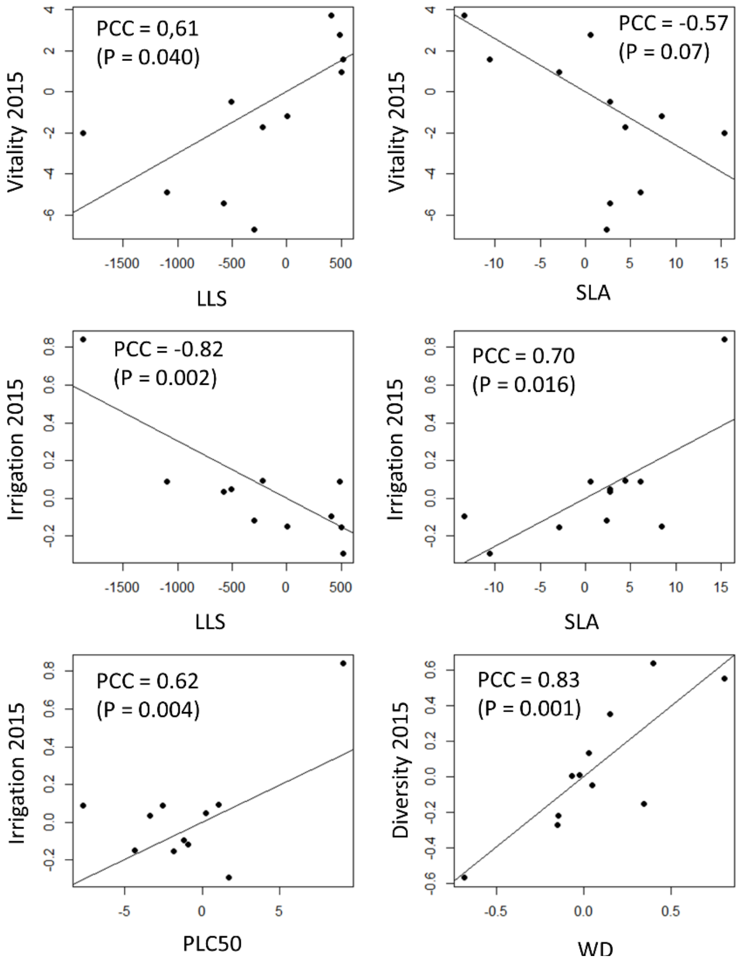


Figure 3-6 Correlation analyses after correcting for species' evolutionary relatedness based on phylogenetic independent contrasts (pic, Felsenstein 1985). Only significant relationships before this pic correction are presented. Pearson correlation coefficients (PCC) between the contrasts are presented in the panel with its level of significance (P). After correcting for evolutionary relatedness, most relationships are still important. SLA = pic for Specific Leaf Area; PLC50 = pic for water potential at which 50% of hydraulic conductivity is lost; LLS = pic for Leaf Life Span, WD = pic for Wood density.

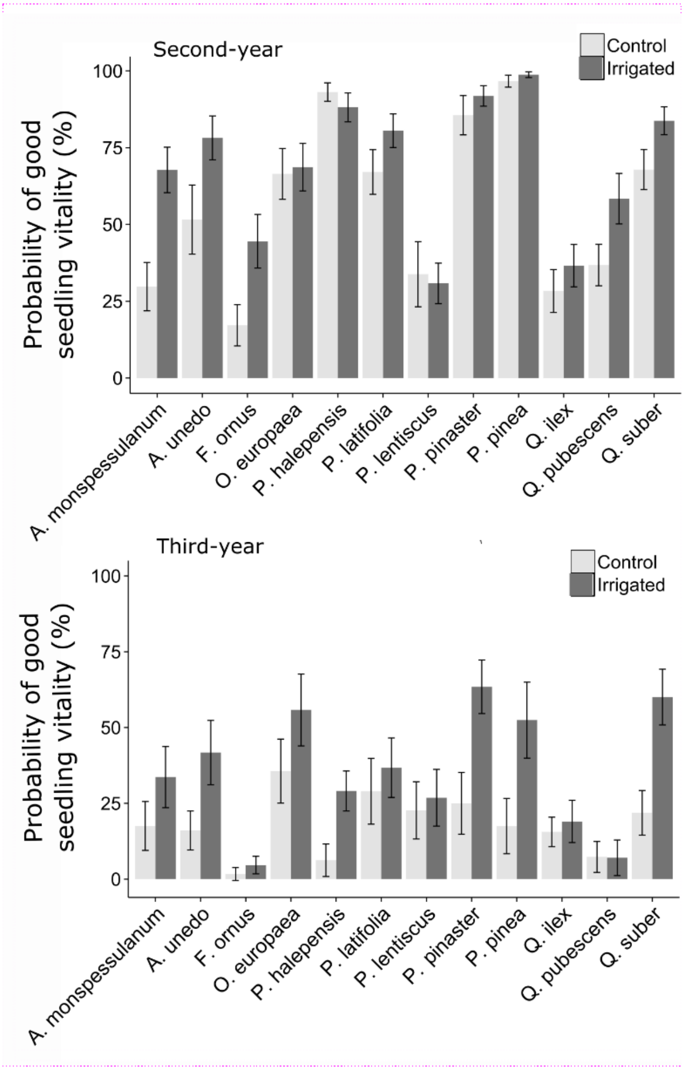


Figure 3-7 Probability of good seedling vitality (vitality index = 1) for the 12 studied species in irrigated and non-irrigated conditions and including standard error bars. The probabilities were derived from in Generalized Linear Mixed-effect Models on seedling vitality, with binomial distribution (1 = vital seedlings without indications of foliage discoloration or defoliation and 0 = non-vital seedlings) and logit-link function. Upper panel represent results obtained in the second year (2015) and lower panel represents results in the third year (2016).

3.5 Discussion

By manipulating SR and FD in a three-year-old Mediterranean common garden experiment, we tested how species interactions drive seedling vitality. The study revealed higher vitality in functionally diverse mixtures for eight out of nine broad-leaved species, but not for the three *pinus* sp. The analyses furthermore demonstrate that effects were principally mediated by fast-growing *pinus* sp. facilitating the vitality of broad-leaved seedlings.

3.5.1 Species identity and irrigation effects are prevalent

Vitality was strongly species-dependent (i.e. some species were more vigorous than others), notably in the second growing season of 2015. This effect prevailed in comparison with irrigation or diversity (both SR and FDis). The major role of species identity corroborates other studies where seedling survival (Chapter 2, Yang *et al.* 2017), growth (Li *et al.* 2014; Lübbe *et al.* 2016) and herbivory (Sobek *et al.* 2009; Setiawan *et al.* 2014; Wein *et al.* 2017) was investigated for a wide range of species. Traits are fundamental to understand differences in the functioning among species. For instance, vitality scaled negative with specific leaf area (SLA), as low SLA prevents extensive water loss and mechanical damage, and it increases leaf tolerance to xylem tensions during droughts (Mitchell *et al.* 2008; Anderegg & Hillerislambers 2015). Leaf life span (LLS) correlated positively with vitality. Species with low LLS (e.g. the deciduous species *A. monpessulanum, F. ornus* and *Q. pubescens*) have low leaf construction costs but therefore also low resistance against heat and drought. The decline in the importance of species identity effects from the second to the third growing years can be explained by the planting shock that seedlings have experienced. All seedlings are site-adapted, but not all seedlings deal equally well when replanted at an openly-exposed reforestation site. Therefore, species identity effects, mediated by their trait structure, are most important under stressful conditions, i.e. when seedlings are not yet completely settled after planting.

Seedling vitality was generally higher in irrigated blocks, but not all species were equally 151 affected. In the second year, species that do not occur in very dry regions, according to 152 Spanish plant distribution models (Costa-Saura et al., 2016, Appendix VIII), benefitted most 153 from the additional water (i.e. *A. monspessulanum, Q. pubescens, F. ornus, A. unedo* and *Q.* 154 *suber*). Similar as for the identity effects, seedling responses to irrigation correlated negative with SLA and positive with LLS. This result supports the importance of drought for seedling vitality in our experiment. Besides SLA and LLS, also PLC50 scaled with seedling' responses to irrigation. PLC50 is the water potential at which a species loses 50% of xylem hydraulic conductivity due to cavitation. In agreement with our findings, PLC50 is known to be higher for drought-intolerant species (Costa-Saura *et al.* 2016). Most trait-related patterns are not biased by the evolutionary difference between angiosperms and gymnosperms. Indeed, in the correlation analyses we controlled for phylogenetic relatedness via phylogenetic independent contrasts (Felsenstein 1985). So although LLS is larger (and SLA is lower) for gymnosperms, this was not the only reason for the trait-based results.

The correspondence between species life-history and their response to irrigation was lost in the third year. For instance, drought-tolerant *Pinus* sp. were more vigorous in irrigated blocks. *Pinus* sp. perhaps increasingly relied on irrigation because their water consumption rates scaled positive with aboveground biomass (Appendix XI). Also in 2016, some drought-susceptible deciduous species suffered in both irrigated and non-irrigated blocks. At the end of the dry summer (September), irrigated and non-irrigated deciduous seedlings might have both reached a degree of stress, albeit with a different timing, sufficient to trigger drought avoidance strategies such as leaf shedding. None of the species is a summer deciduous, thus they typically don't lose leaves before the end of October. As vitality was assessed in September, we conclude that higher defoliation and discoloration was triggered by environmental stress, not by a seasonal pattern. Nevertheless, the time difference of assessment (i.e. before (2015) and after (2016) a peak in summer drought) likely contributed to the observed vitality patterns.

3.5.2 Buffering effects were not relevant

In Chapter 2 we presented stabilized plot-level survival rates at higher levels of SR, a trend that was mainly caused by large variability in planting success within the group of monoculture plots. Variability in third-year plot-level vitality also degreased with SR in IDENT-M, but contrary to our expectations, this potential buffering effect was not statistically important. One possible reason is that species vitality rates were quite similar, as confirmed by the low variance components for species identity in Figure 3-2. Differential vitality responses namely form a fundamental basis for species compensation and for buffering. A similar gls model was run on a subset including only non-irrigated plots, where growing condition were a bit harsher. But also on this subset, the trend of decreasing variability in plot-level vitality with SR was only marginally important. The results do not hinder our conclusions on biodiversity insurance in Chapter 2. It is logic that buffering effects will only be visible under certain specific conditions where some, but not all, species failed in their functioning. Our analysis in Chapter 1 dealt with cumulative survival rates that ranged strongly between the species, i.e. 57% for *P. sylvestris vs.* 99% for *T. cordata* in ZED and 59% for *A. pseudoplatanus vs.* 82 % for *Larix x eurolepis* in Gedinne. In IDENT-M, seedling survival was above 99%, indicating for 11 of 12 species, indicating that most species established extremely well.

3.5.3 Functional diversity improves seedling vitality

Second-year seedling performance was not affected by the identity or diversity of neighboring trees. Indeed, although two species showed contrasting responses to FDis (positive for *Q. pubescens* and negative for *P. pinaster*), these effects were marginally important to explain over vitality patterns. In the third year we found higher vitality in functionally diverse communities. This result indicates that interspecific competition was lower than intraspecific competition, or that a more favorable environment (biotic or abiotic) was established in diverse neighborhoods. In agreement, Tobner et al. (2016) demonstrated positive species mixing effects on the performance of four-year-old seedlings in IDENT-Québec. These signals even became stronger over time (Laforest-lapointe *et al.* 2017).

The positive effects of FDis on seedling vitality were generally observed in the group of broad-leaved species (besides F. ornus facing lowest vitality) while it was not observed in the group of *Pinus* sp.. In addition, species with high wood density (WD) were more strongly affected by FDis, also after controlling for evolutionary relatedness (PCC FDis effect - WD = 0.83). Contrasting to the significant effect of FDis, almost no variation in seedling vitality was attributable to SR per se. SR implicitly assumes that all species are equally dissimilar. Because FDis reflects spatial-temporal differences in resource acquisition strategies, it leads to better predictions of ecosystem dynamics (Petchey, Hector, & Gaston, 2004).

3.5.4 Large-sized *Pinus* sp. mediate diversity effects

Further analyses revealed that *pinus* sp. were important in explaining FDis effects because all broad-leaved species, excluding *F. ornus*, performed better if surrounded by *pinus* sp. Diversity effects generated via the identity of neighbouring trees have been described before (Hantsch *et al.* 2014; Damien *et al.* 2016; Dillen, Verheyen & Smit 2016). In our experiment, neighbourhood identity effects (and thus FDis effects) were most likely mediated by the structural properties of heterospecific neighbours, as aboveground biomass was approximately eight times larger for *Pinus sp.* compared to the average of broad-leaved species (Appendix IX). Aboveground biomass is a property associated to shading capacity. But besides seeing this as a resource-limiting factor, it also reduces environmental stress for shaded seedling through a facilitation effect (Lübbe, Schuldt & Leuschner 2015; Yang *et al.* 2017). Indeed, shading by fast-growing (*Pinus sp.*) neighbours relaxes daily air temperature, solar radiation and wind speed. Consequently, it diminishes the transpirative demand of shaded trees, favours a higher leaf hydration, and avoids damage from excess radiation. In agreement, other studies have shown the improved water and temperature balance of evergreen *Quercus* sp. seedlings (Quero *et al.* 2006) and of several other species (Castro & Zamora 2004; Gómez-Aparicio *et al.* 2004; Aerts *et al.* 2007) when planted under larger nurse shrubs. Shading may furthermore provide positive effects during winter by buffering low temperatures and frost events.

The favourable impact of *Pinus sp.*on the performance of broad-leaved trees may be generalized to other species with fast resource acquisition in early ontogenetic stage. However, apart from size-related properties, the amelioration of abiotic conditions also rests on traits such as density and distribution of leaves (Sapijanskas *et al.* 2014; Williams *et al.* 2017). From this viewpoint, *Pinus sp.*allow fair levels of light transmission for neighboring or understory trees. So the creation of a buffered microclimate is at the expense of only a limited loss of light. The facilitation effects can be generalized to other ecosystems where evaporative demand is the key constrain on seedling vitality.

Indeed, the concept of nurse-plant facilitation is gaining importance in dryland reforestation studies, including those in arid desert, savanna, semi-arid shrub-lands, alpine habitat, northern dry forest and tropical sub-humid forests (Callaway *et al.* 2002; Aerts *et al.* 2007; Ren, Yang & Liu 2008). Most research focus was on pre-existing vegetation (often shrubs) acting as nurse plants. In this study we proved that nurse-plant syndromes can also be created by the direct planting of nurse trees (here *Pinus sp.*).

The provision of a favorable microclimate by *Pinus sp.* is not necessarily an exclusive foundation for the positive FDis effects. Underlying mechanisms could have operated across different trophic levels. For instance, seedlings are restricted in their ability to tolerate pathogen infections, compromising tree growth and competitive capacity (Barton & Hanley 2013). Seedlings in mixtures may have experienced reduced herbivory impacts as we observed -although not quantified for *P. lentiscus* and *P. latifolia*. Associational resistance can be underpinned by multiple means, including resource concentration, host appearance or effective top-down control (Haase et al., 2015; Mathias et al., 2016; Zhang et al., 2017). In our study, broad-leaved trees in the vicinity of large-sized *Pinus sp.* could be masked for specialist herbivores (in line with the host appearance hypothesis, Castagneyrol et al., 2014). Alternatively, *Pinus sp.* could have attracted fewer generalist herbivores, thereby reducing herbivory pressure on broad-leaved seedlings (in line with the resource concentration hypothesis, Hantsch et al., 2014). A final mechanism explaining the observed FDis effect is complementarity in aboveground or belowground resource-use strategies. However, as canopies were not yet closed, the mechanism is likely less relevant at this early stage of the experiment.

The design of IDENT-M provided a good framework to detect effects of SR, FD and other influential on species/traits on seedling performance, at a background of many other potential covariates. However, the design does not directly allow for causal inferences to the underpinning biological mechanisms. This study would therefore advance from the directly measuring water stress for a sample of the trees, from the monitoring of microclimate conditions (humidity, light availability, temperature) in neighbourhoods that included or exclude *Pinus* sp., from the survey of leaf damage patterns in relation to its herbivory agent, from the identification of mycorrhizal associations and finally, but not exclusively, from measuring aboveground and belowground growth patterns that allow complementarity in resource usage. Because this additional information was missing, we could only hypothesize on the most probable mechanism behind the correlation seedling vitality and FD (i.e. microclimate facilitation through *Pinus* sp.). High confidence on the underlying cause of BEF relationships will help to design planting schemes for reforestation and restoration in semi-arid environments.

3.5.5 Stress-gradient hypothesis is not supported

We hypothesized that diversity effects are stronger under harsh conditions, for instance on low-productive sites or in environments with frequent droughts or frosts.

The reasoning behind this stress-gradient hypothesis is that facilitation operates as a stress reduction process, which is particularly contributing to ecosystem functioning in less favorable environments (Paquette & Messier 2011). However, the significance of FDis for seedling vitality did not differ between irrigated and non-irrigated blocks during dry Mediterranean summer months. Our findings are in line with a related study of Lübbe et al. (2015) where productivity of artificially assembled tree communities was examined under ample and water-limited conditions. In addition, Grossiord et al. (2014) found that SR had a positive effect on drought tolerance in some biomes, but not in the Mediterranean. Our results contrast with a global meta-analysis on plant community experiments (sample size = 727 studies) in which a clear shift towards facilitation with drought stress was concluded (He, Bertness & Altieri 2013). The stress gradient hypothesis was recently discussed within a more generalized framework that considers the complex interplay between resource availability and climatic conditions for shaping biodiversity-ecosystem functioning relationships in forests (Forrester & Bauhus 2016). Applying their model to our results, different mechanisms could explain FDis effects in both treatments, with water-based facilitation being more likely under non-irrigated conditions and light-based complementarity being more likely under irrigated conditions.

3.5.6 Foliage vitality as seedling performance indicator

In water-stressed environments, seedlings will remarkably invest in root development to reach moister soil layers and explore larger soil volumes (Padilla, Miranda & Pugnaire 2007). The vitality status of leaves was therefore analysed in this study because it may better reflect the physiological status of plants compared to conventional growth measures (diameter/height). With biomass data from a subset of seedlings, we demonstrated that foliage vitality is positively correlated with aboveground biomass growth (Appendix XI). Importantly, there is an enormous growth variation within the category of healthy trees (i.e. no defoliation, no discoloration). Thus, the healthy foliage of slow-growing seedlings indicate they are not suffering from environmental stress.

Similar as in Chapter 3, also survival rates (dead/alive) could have been used to quantify the effects of environmental conditions on the performance of planted seedlings. Although seedling mortality can be objectively identified, this response variable is not very informative under moderate stress. Because seedling survival in IDENT-M ranged between 99 % and 99.5 % for (except for *P. lentiscus* 80 %, Appendix VII), it cannot be used to compare seedling performance between treatments. The high plant settlement success is thanked to the professionality of the planting team, but also because the complete site was irrigated during the first summer droughts. Importantly, by estimating foliage condition we proved that not all survived seedlings were equally vigorous, that the irrigation treatment was beneficial for some species and that deciduous trees profited from growing in mixtures. All of this information would not have been available by singly evaluating seedling survival. If stress continues, irreversible damage may occur and plant survival may also become a reliable indicator for long-term plant persistence.

3.5.7 Conclusion

In a Mediterranean common garden experiment we found evidence that higher FD enhanced the vitality status for broad-leaved seedlings in IDENT-M. We proposed some alternative, but not inherently exclusive, mechanisms underpinning the diversity effects. *Pinus sp.* served well as nurse plants, most likely thanks to their fast juvenile growth and sufficient crown light transmission. We conclude that manipulating tree species composition can overcome barriers of plant settlement in dry habitats. When compared to irrigation or artificial sheltering, it is likely a cost-effective management action in large reforestation projects, potentially with additional long-term benefits in terms of productivity and resilience.

Chapter 4

Plasticity Of Tree Architecture

Van de Peer T, Verheyen K, Kint V, Van Cleemput E, Muys B (2017) Plasticity of tree architecture through interspecific and intraspecific competition in a young experimental plantation. Forest Ecology and Management **385**, 1-9. (IF = 3.062)

Author's contributions: TVDP, BM and KV devised the concept of the article; EVC and TVDP collected field data; TVDP carried out the data analysis, with statistical advice from VK. TVDP wrote the manuscript text. All co-authors contributed to revising earlier versions of the manuscript and approved the final version.

Cover photo: tree architecture measurements, FORBIO ZED, 2014 (E. Van Cleemput)

4.1 Summary

It is acknowledged that trees behave plastic in response to environmental conditions. Even so, knowledge on how tree architecture in pure and mixed stands compare is largely underexplored. The main objective of this work was to test the effects of competition, diversity and species identity of neighbouring trees on the architecture of five important European tree species (*Quercus robur, Betula pendula, Fagus sylvatica, Pinus sylvestris* and *Tilia cordata)* in a temperate plantation before and during canopy closure.

Data were collected in the five-year-old FORBIO-Zedelgem. For 396 trees we measured architectural properties including branchiness, tree height-to-diameter (HD) ratio, branch diameter and branch insertion angle, and we investigated how these properties were shaped in different competitive neighbourhoods using mixed models.

Species showed contrasting architectural responses to neighbourhood competition, in line with species life-history strategies. In more competitive environments, trees of *Q. robur* (slow growing and light-demanding) increased HD ratio and branch insertion angle to optimize light foraging in the upper canopy; trees of *B. pendula* (fast growing and light-demanding) increased HD ratio and decreased branching following the branch autonomy principle; trees of *F. sylvatica* (slow growing and shade tolerant) increased branching to improve light uptake under shading and finally, trees of *P. sylvestris* (fast growing and light-demanding) and *T. cordata* (slow growing and shade tolerant) were not shaped in response to competition. Diversity and identity of species in a trees' neighbourhood did not contribute to the architectural plasticity, although competitive differences between pure and mixed stands underpinned such effects for *B. pendula,* with lower branching in the highly competitive monocultures.

We conclude that competition between trees, but not diversity, influences the architecture of young plantation trees before and during canopy closure.

4.2 Introduction

The growing interest in mixed species silviculture is motivated by awareness that forest functioning is under threat at low biodiversity (Balvanera *et al.* 2006; Nadrowski, Wirth & Scherer-Lorenzen 2010; Carnol *et al.* 2014). Understanding mixed forest dynamics is crucial in this context, particularly with regard to the complex interspecific interactions that may occur (Forrester 2014). Tree-tree competition -hereafter referred to as competition- is an interaction between trees in a common growing space, with the purpose of individual trees to maximize capturing of limited resources (i.e. water, light and nutrients) by their growth and development and this at the expense of other trees' resource availability (Craine & Dybzinski 2013). Competition is thus an ecosystem process that largely shapes environmental conditions and that triggers architectural and physiological plasticity, which is the continuous acclimation of a trees' structure and functioning to the dynamic environment (Longuetaud *et al.* 2013). Such plasticity expresses the capacity of, and the need for, species to optimize fitness and furthermore, it is an important aspect in the feedback system between tree functioning, tree structure and the environment (Schröter, Härdtle & von Oheimb 2012; Pretzsch 2014). Among all different types of plasticity, aboveground architectural plasticity is acknowledged as a proper process to study forest dynamics when tree growth and development is mainly driven by competition for light (Thorpe *et al.* 2010).

Previous studies focused on light-mediated crown plasticity by simple measures of crown size and shape (Schröter, Härdtle & von Oheimb 2012; Longuetaud *et al.* 2013). They concluded that crown development differs among trees due to genotypic variation, with strong species-specific trends that relates with species strategies to tolerate or avoid shading. Furthermore, some studies showed that crown plasticity stimulate light complementarity and overyielding in mixed forests and is therefore a key component to understand BED relationships (Dieler & Pretzsch 2013; Pretzsch 2014).

Crown plasticity is the result of complex mechanisms operating at lower levels of organization, i.e., the dynamic development of twigs and branches (Niinemets 2010; Lang *et al.* 2012). Architectural plasticity at the level of branches has rarely been elucidated so far, in particularly not for young forest trees. Nevertheless, such study would give detailed information on light acquisition strategies and biomass allocation to optimize tree functioning in contrasting competitive environments (Lintunen & Kaitaniemi 2010; Lang *et al.* 2012). So far, only few predictive models for conifer (Mäkinen & Hein 2006; Hein *et al.* 2007; Kantola, Mäkinen & Mäkelä 2007; Duchateau *et al.* 2015) and broadleaved species (Hein 2008; Kint *et al.* 2010) relate branch development to environmental factors (such as nutrient status, water availability and climate) and management (such as species choice and stand density control).

Nevertheless, tree architecture has been a topic of interest for a long time (Heikinheino 1953; Curry & Endersby 1965; Persson 1976). It determines the growth and the stem quality of trees, two key factors for the provisioning service of forests (Duchateau *et al.* 2015). Prevailing silvicultural strategies focus on stand density control to guide tree architectural development (Kint *et al.* 2010). Generally, these strategies aim at the early shedding and occlusion of lower branches, the development of strait stems and desirable height-to-diameter ratio's (HD) to ensure physical stability (Kantola, Mäkinen & Mäkelä 2007). As most studies were executed in monoculture stands, they did not specifically address the influence of species mixing (but see Bayer et al., 2013; Rozenbergar and Diaci, 2014). Such knowledge is relevant from an economical point of view, given the increasing interest in optimizing financial returns from species diverse plantations through high-quality timber production (Pretzsch & Rais 2016).

In this study we investigated tree architecture within a framework that is novel in two ways. First, an experimental set-up on mixed forest functioning allows studying architectural plasticity in the context of tree species mixing. Monocultures and mixtures were planted in synthetic communities, at the same time, at constant density and on a homogeneous site to exclude confounding environmental factors. Second, our study addresses the underexplored young forest stage before and during canopy closure. As young trees are expected to be sensitive and respond quickly to competition, it is most interesting to investigate inter-tree interactions in this stage.

We measured the architecture of 396 trees from five temperate species in a young experimental plantation. With this data we wanted to test following hypotheses: (i) light-mediated competition triggers architectural plasticity at the tree level (number of branches and stem diameter-to-height ratio) and at the branch level (branch diameter and insertion angle); (ii) plastic responses differ among species and can be explained with species autecology; and (iii) architectural plasticity is influenced by the diversity and identity of neighbouring trees, in particular concerning competitive differences between inter- *vs.* intra-specific neighbours and light-demanding *vs.* shade-tolerant neighbours.

4.3 Materials and methods

4.3.1 Experimental design

Data were collected at FORBIO-Zedelgem, five year after the planting in 2010 (See Chapter 2 and Appendices I and II). We considered the option to also collect data at the HEC and GED site. However, both were at the time of measurement in an earlier stage of plantation development, either because of the young plantation age (HEC was two years old) or because sapling growth occurred more slowly (less favourable abiotic conditions at GED). Because architectural plasticity requires a certain degree of tree development and eventually also crown contact, this study was only conducted at ZED.

The site was planted with five well-adapted tree species from local provenances, seeded in commercial nurseries and planted as two or three year old saplings (Verheyen et al. 2013). The species pool consists of one conifer, *P. sylvestris,* and four broadleaved species, *B. pendula, F. sylvatica, Q. robur* and *T. cordata*. They are common species in west European forests and functionally, they are strongly dissimilar to each other concerning morphological and physiological traits (Table 2-1). Most relevant differences for the competition in this study are shade tolerance (ST) according to the index of Niinemets and Valladares (2006) and average height growth rates (HGR) according to data from the FORBIO experiment : *P. sylvestris* (ST = 1.67, HGR= 57 cm year^{-1})*, B. pendula* (ST = 1.54, HGR = 85 cm year^{-1})*, F. sylvatica* (ST = 4.56, HGR = 34 cm year^{-1})*, Q. robur* (ST = 2.45, HGR = 28 cm year^{-1}) and *T. cordata* (ST = 4.18, HGR = 38 cm/year).

In the plots, 32 810 saplings were planted in a regular grid (1.5 m x 1.5 m) with monospecific clusters of 3 x 3 individuals (Figure 4-1). Four permanent monitoring zones (PMZ) in the central area of each plot were marked to monitor ecosystem functioning over the long run. The PMZs consist of 16 trees each and reflect the species composition of the associated plot (Figure 4-1).

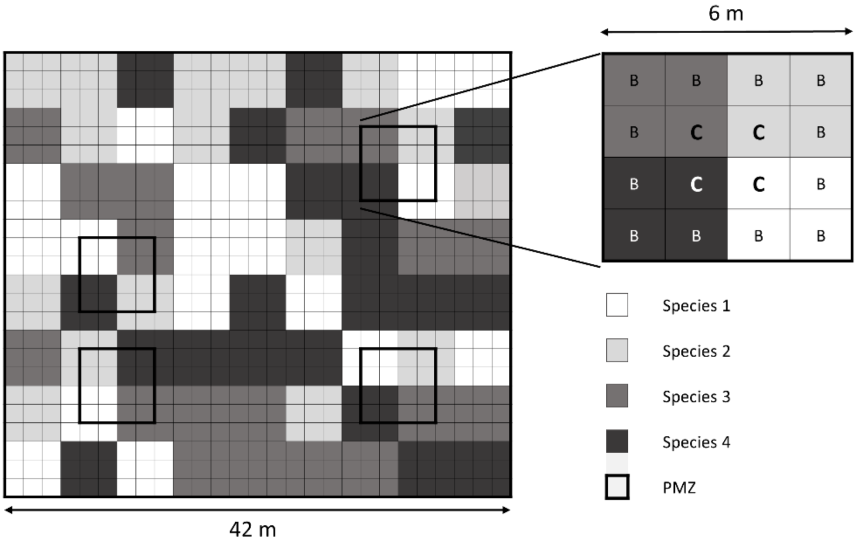


Figure 4-1 Example of an experimental plot (42 m x 42 m) containing 764 trees (squares) from 4 species (grey scale) arranged in monospecific clusters of 3 x 3 trees. Four Permanent Monitoring Zones (PMZ, indicated with bold lines) with 16 trees each were defined to measure tree architecture of central trees (C) and tree size (stem diameter, tree height and crown projection area) of border trees (B).

The site was fenced to prevent browsing damage by hare, rabbit and wild boar. Sapling mortality occurred at rates of 12 %, 4 % and 2 % in the first three years after planting respectively and replanting was done during wintertime using saplings of two years old (Chapter 2). Furthermore, sapling mortality was, on average, not related with SR and also not affected by environmental heterogeneity. Data furthermore revealed an additional 3 % mortality in the fifth year (2014, when tree architecture was measured), which was taken into account in the design of the competition index we used (see 4.3.3.1).

The vegetation between planted trees was mown in the first three years and spontaneously established trees were manually removed from the fourth year onwards. As pruning and thinning have not been conducted yet, the outcomes of this study reflect tree development and competitive interactions in a young quasi-unmanaged plantation.

4.3.2 Data sampling

Data were sampled between July and September 2014 (except for stem diameter and tree height that were measured in January 2014) in 103 randomly selected PMZs. In each PMZ, the tree architecture of four central trees (in total 396 when excluding dead trees) was characterized in detail. Size measures of the 12 surrounding trees (in total 1236 when excluding dead trees) were used to describe the competitive neighbourhood of central trees, but no branch attributes were measured (Figure 4-1). Tree species identity and position were known from the experimental design. Measurements were taken in a non-destructive way.

4.3.2.1 Tree level measurements

For all selected trees, we measured stem diameter (Td) at 20 cm above the ground with a digital caliper, and tree height (Th) with a telescopic measuring rod in vertical position from soil surface to the highest living bud. Crown projected area (Tcpa) was derived from crown radii measured from ground basis in eight sub-cardinal direction classes. The horizontal distance between stem (at 1.3m) and the furthest living twig or leaf was measured recorded with a ruler. The total area of this irregular octagon was calculated via triangulation and used as Tcpa.

4.3.2.2 Branch level measurements

For the central trees, living first-order branches, i.e. branches directly attached to the main stem, were sampled if two criteria were met: (i) minimum branch diameter is larger than 10 mm (*B. pendula*) or 7 mm (other species) and (ii) branch insertion height was lower than 75 % of the total tree height. The criteria were set to avoid the time-intense measurement of many small branches and twigs in the upper part of tree crowns. For these branches, diameter at 5 cm from the main stem, height and azimuth (as a class variable expressed in eight sub-cardinal directions) were measured. Branch insertion angle, defined as the angle between the first 5 cm branch part and the 5 cm part of the main stem above the branch, was measured with a standard manual protractor at 5° accuracy.

4.3.3 Data analyses

4.3.3.1 Characterization of local neighbourhood

The local neighbourhood of each central tree was given by the eight directly surrounding trees and characterized with indices for competition, diversity and species identity (Figure 4-1).

A competition index (CI) was calculated for each central tree, representing the limitation of available growing space. We designed this CI *a priori* to capture main important features of light competition (shading) in young forest plantations (i.e. size, distance and cardinal direction of neighbouring trees) such as described by Pukkala (1987) and Contreras et al. (2011).

The CI of a central tree i can be written as: $CI_i = \sum_{j=1}^{8} \frac{Th_j .Tcpa_j .c_j}{l_{ij}}$ with, for each neighbour j (1-8): Th_j is the tree height; $Tcpa_j$ is the tree crown projection area; c_j is a weight variable that depends on the compass direction of neighbour j [0.5 (north) - 1.5 (south-east)] to correct for the direction of incoming sunlight (Pukkala & Kolström 1987) and finally l_{ij} is distance between the central tree i and the jth neighbour. The continuous and multi-trait functional dispersion index (FDis) of Laliberte et al. (2010) was used to describe the FD of the local neighbourhood (Laliberté & Legendre 2010). FDis is defined as the mean species distance to the centre of mass of all species in a multidimensional trait space. The metric uses species-specific trait values indicative for their life-history strategy, which are derived from literature (Scherer-Lorenzen et al., 2007; Table 2-1). FDis is similar to Rao's quadratic entropy but it allows to use species relative abundances in the calculations and to deal with quantitative and qualitative data types. A structural diversity index, slightly modified from von Gadow et al. (2012), was calculated to represent the structural heterogeneity around the central tree i: $SDiv_i = \frac{StDev\ (Th_j .Tcpa_j)}{Mean\ (Th_j .Tcpa_j)}$ with index j representing the jth neighbor and StDev the standard deviation.

The CI was partitioned in (i) competition caused by interspecific ($CI_{\text{interspecific}}$) and intraspecific ($CI_{\text{intraspecific}}$) neighbours and (ii) shade tolerant (*F. sylvatica* and *T. cordata;* CI_{Shade}) and light-demanding (*P. sylvestris* and *Q. robur;* CI_{Light}) neighbors, such as previously done by Ratcliffe et al. (2015).

4.3.3.2 Modelling tree architecture

We used regression techniques to estimate the effects of local neighbourhood competition, FDis and species identities on tree architectural development. As data were hierarchically organized with blocs, plots, PMZ's, trees and branches all nested within each other, a mixed model approach was used to test the random correlation structure. Two response variables at the tree level (branchiness and HD ratio) and two response variables at the branch level (diameter and insertion angle) were regressed against candidate predictor variables in linear (mixed) models, except for the non-negative integer values of branchiness that assumed a Poisson distribution and log-link function in generalized linear (mixed) models (Table 4-1). We tested for overdispersion in the model (i.e. variance larger than mean) by comparing the residual deviance with the residual degrees of freedom (overdispersion factor ϕ in Zuur *et al.* 2009) and we refitted the model with quasi-Poisson parameterization if $\phi > 1$. All analyses were performed in R 3.0.1 (R Foundation for Statistical Computing, Vienna, AT) using lme4 package (lmer and glmer) for fitting mixed models.

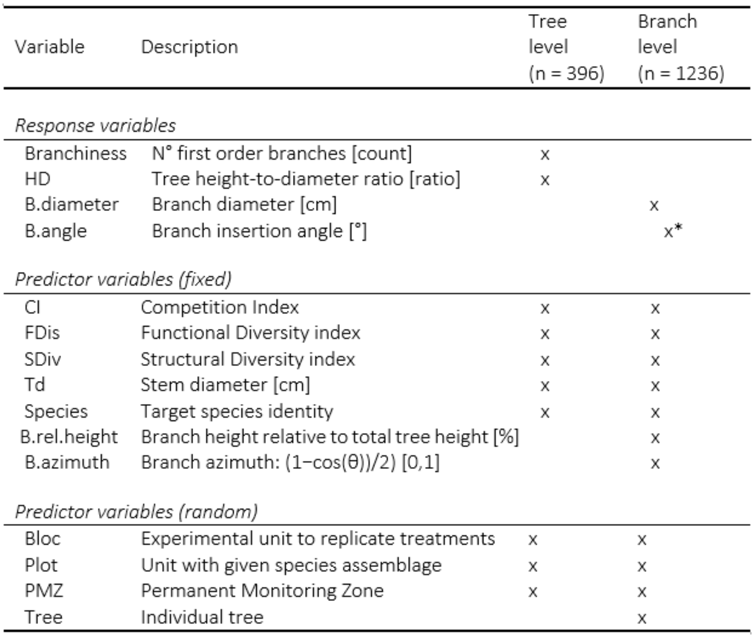
Searching for model parsimony, we optimized the random structure first and the fixed structure second, as advised in the model selection procedure of Zuur et al. (2009). First, random design features were stepwise included as nested effects in *beyond optimal* mixed models (Zuur *et al.* 2009), i.e. models that contain all fixed effects and reasonable interactions (such as: Species:CI, B.rel.height:CI and B.rel.height:B.angle). The most appropriate random structure (if one) was kept on the basis of likelihood ratio tests for REML-fitted models. In case of weak evidence (*P*-value close to 0.05) for one selected random structure, confirmation was given with a simulated Chi-square based *P*-value. Second, fixed-effect structure was optimized in maximum likelihood-fitted models via backward elimination at a 0.01 level of significance. For LMM, this procedure was automatized using the StepLmer function, with F-tests for parameter estimates calculated from a Satterthwaite's approximation. The selection procedure was redone manually with AIC comparison and likelihood ratio tests between competing models to confirm the results. For all response variables, the most parsimonious model was refitted with restricted maximum likelihood criteria (Eq. 1).

Two additional models with same predictor variables (base) but partitioned CI were fitted (Eq. 2-3) if the CI was retained before:

$$\text{Response} \sim \left[\begin{array}{ll} \text{base} + \beta_0 \text{CI}_{\text{Total}} & (\text{Eq.}\,1) \\ \text{base} + \beta_1 \text{CI}_{\text{Intra}} + \beta_2 \text{CI}_{\text{Inter}} & (\text{Eq.}\,2) \\ \text{base} + \beta_3 \text{CI}_{\text{Light}} + \beta_4 \text{CI}_{\text{Shade}} & (\text{Eq.}\,3) \end{array} \right.$$

with CI_{Total} the competition index from all neighbours and CI_{Intra}, CI_{Inter}, CI_{Light}, CI_{Shade}, the partitioned competition index for relevant species groups (see section: *2.3.1.Characterization of local neighbourhood*). The model parameter estimates (β_1 – β_4) are comparable within but not between models and can be interpreted as the intensity of competition caused by the corresponding species or functional types. As tree sizes of *B. pendula* trees felt outside the size ranges observed by the other species (Appendix XII), they were excluded from the partitioning in Eq. 2 and Eq. 3 as it would bias the comparison.

Table 4-1 Description of response variables and candidate predictor variables used to model branch architecture in tree level and branch level (mixed) regression models. Variables used as fixed predictor variable in the branch diameter model are marked *.



Variable	Description	Tree level (n = 396)	Branch level (n = 1236)
Response variables			
Branchiness	N° first order branches [count]	x	
HD	Tree height-to-diameter ratio [ratio]	x	
B.diameter	Branch diameter [cm]		x
B.angle	Branch insertion angle [°]		x*
Predictor variables (fixed)			
CI	Competition Index	x	x
FDis	Functional Diversity index	x	x
SDiv	Structural Diversity index	x	x
Td	Stem diameter [cm]	x	x
Species	Target species identity	x	x
B.rel.height	Branch height relative to total tree height [%]		x
B.azimuth	Branch azimuth: (1−cos(θ))/2) [0,1]		x
Predictor variables (random)			
Bloc	Experimental unit to replicate treatments	x	x
Plot	Unit with given species assemblage	x	x
PMZ	Permanent Monitoring Zone	x	x
Tree	Individual tree		x

4.4 Results

4.4.1 Tree species characteristics

Trees of *B. pendula* are the tallest (481 ± 111 cm) and they have the largest crown projected area (3.6 ± 1.6 m²) compared to the other studied species (Table 4-2 and Appendix XII). As a result, *B. pendula* will strongly contribute to the competition, which is in this study calculated with tree height and crown projection area. Tree height of *P. sylvestris* (233 ± 53 cm) is on average lower than *B. pendula,* although stem diameters are of similar size (4.4 ± 1.4 cm and 5.3 ± 1.4 cm respectively). The average dimensions (tree height, stem diameter and crown projection area) of other species have the same order of magnitude (Table 4-2 and Appendix XII).

Table 4-2 Mean and standard deviation (StDev) of architectural characteristics of the seven-year old (5 year in plantation) tree species in FORBIO-Zedelgem (summer 2014) with d: stem diameter; h: tree height; HD: tree height-to-diameter ratio; Cpa: crown projected area; Branchiness: number of first order branches

	d (cm)		h (cm)		HD		Cpa (m^2)		Branchiness	
Species	mean	StDev	mean	StDev	mean	StDev	Mean	StDev	mean	StDev
Betula pendula	5.3	1.4	480	111	93	19	3.57	1.52	12.6	6.9
Fagus sylvatica	2.7	0.9	215	70	83	24	0.64	0.49	8.0	6.5
Pinus sylvestris	4.3	1.4	232	53	58	18	1.62	0.76	17.0	6.9
Quercus robur	2.7	0.9	227	86	84	18	1.03	0.79	6.5	5.4
Tilia cordata	2.7	0.7	205	39	78	16	0.95	0.62	8.6	3.5

4.4.2 Tree- and branch level models

A summary of parameter estimates and significance tests can be found in Appendix XIII. A generalized linear mixed model ($R^2_{conditional} = 0.57$) for branchiness ($n = 396$) was fitted with a quasi-Poisson parameterization (overdispersion factor = 2.9). The model includes a random intercept at the PMZ-level (StDev = 0.069), a negative stem diameter term and different competition terms of each target species as fixed predictors. A linear model ($R^2 = 0.46$) was used to describe HD ($n = 396$) and the model includes a negative stem diameter effect and species-specific competition effects. For branch diameter ($n = 1236$), a linear mixed model ($R^2_{conditional} = 0.43$) was fitted with nested random effects at the tree-level (StDev = 0.12) and plot-level (StDev = 0.02), a negative fixed effect for branch relative height, a positive fixed effect for stem diameter and species-specific fixed effects for branch insertion angle. Finally a linear mixed model ($R^2_{conditional} = 0.39$) for branch insertion angle ($n = 1236$) includes random effects at tree level (StDev = 6.58) and plot-level (StDev = 3.14), a negative fixed effect for branch relative height and a positive fixed effect for both stem diameter and branch azimuth.

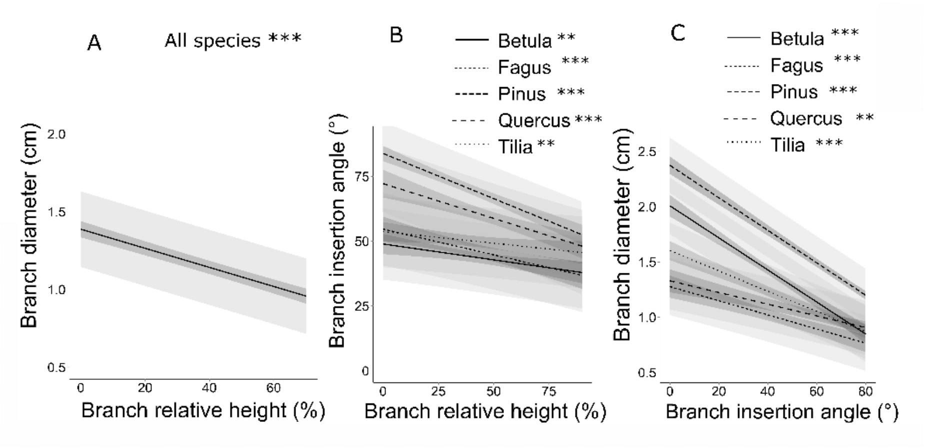


Figure 4-2 Allometric relationships between: (A) branch diameter (cm) and branch relative height (%); (B) branch insertion angle (°) and branch relative height (%); and (C) branch diameter (cm) and branch insertion angle (°). Predictions were made with the regression models on branch diameter and branch insertion angle, while keeping other variables at their observed mean values (Eq. 1). Shaded areas represent 95 % confidence intervals when including (light grey) and excluding (dark grey) random effect uncertainty. Significance with χ^2-test for model parameters: single asterisk ($P < 0.05$); double asterisk ($P < 0.01$); triple asterisk $5P < 0.001$).

4.4.3 Competition

Branchiness, HD and branch insertion angle were under influence of neighborhood competition because the regression models include the CI and an interaction between CI and the target tree species (Appendix XIII and Figure 4-3). More specifically, branchiness decreases significantly with neighbourhood competition for the target species *B. pendula* ($\chi^2 = 7.94$, $P = 0.004$), whereas it increases for *F. sylvatica* ($\chi^2 = 3.77$, $P = 0.02$) and *Q. robur* ($\chi^2 = 2.28$, $P = 0.07$). HD ratio increases with competition for the target species *B. pendula* (F = 11.5, $P < 0.001$), *Q. robur* (F = 5.21, $P < 0.001$) and *T. cordata* (F = 5.21, $P = 0.02$). Finally, branch insertion angle decreases with competition for target species *Q. robur* ($\chi^2 = 15.03$, $P < 0.001$), which means that branches are more sharply attached to the stem in competitive neighbourhoods.

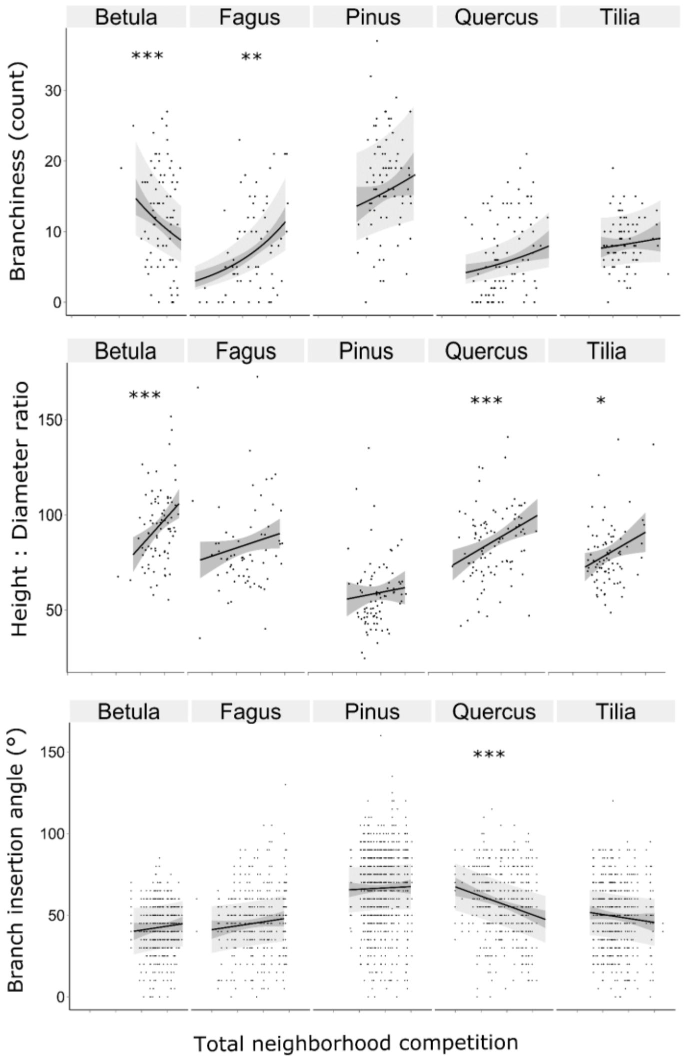


Figure 4-3 Relationship between total neighbourhood competition and branchiness (upper panel); tree height-diameter ratio (cm/cm) (middle panel); or branch insertion angle (°) (lower panel). Results for branch diameter are not presented as the competition index was not retained in the final model. The graphs show observed (dots) and predicted (lines) values against competition, while setting other predictor variables at their observed species-specific mean values (Eq. 1). Shaded areas represent 95% confidence intervals when including (light grey) and excluding (dark grey) random effects uncertainty. Significance with χ^2-test for model parameters: single asterisk ($P < 0.05$); double asterisk ($P < 0.01$); triple asterisk ($P < 0.001$).

4.4.4 Diversity and species identity

Functional and structural diversity indices were not retained in the final models for branchiness, HD and branch diameter and branch insertion angle. The partitioning of CI’s revealed one significant effect for *Q. robur*, i.e., parameter estimates (± 2 SE) for CI$_{\text{Inter}}$ and CI$_{\text{Intra}}$ in Eq. 2 show stronger competitive effects by intraspecific neighbours compared to interspecific neighbours for branchiness (0.13 ± 0.10 vs. 0.39 ± 0.17) (Figure 4-4).

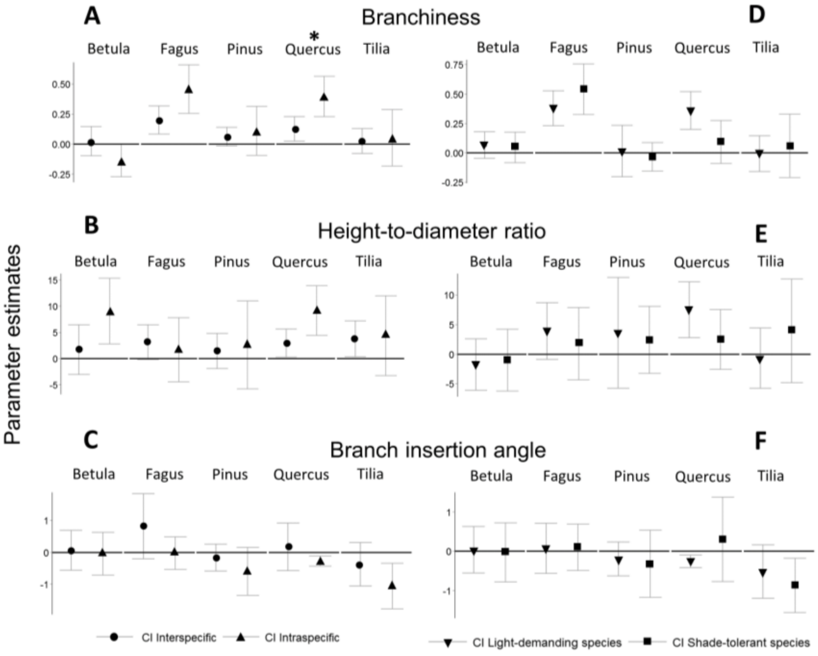


Figure 4-4 Effects of neighbourhood competition on branchiness (A, D), height-to-diameter ratio (cm/cm) (B, E) and branch insertion angle (°) (C, F). Parameter estimates (β) ± SE for the partitioned competition indices present the change in response variable for one unit change in CI, keeping all other predictor variables in the regression model fixed. Panels A, B and C display competitive effects caused by interspecific *vs.* intraspecific neighbours (Eq. 2); panels D, E and F display competitive effects caused by light-demanding *vs.* shade tolerant neighbours (Eq. 3). For a significant competition effect, the confidence interval of a parameter estimate should not touch the zero line; for a significant ($P < 0.05$) difference between two types of competition, the associated confidence intervals should not overlap (indicated with * above the species name). Parameter estimates are comparable within but not between models.

4.5 Discussion

Beside inherited genotypic variation, the architecture of young plantation trees results from an interaction with the local environment. Focusing on this latter, we showed that structural properties, such as HD ratio, branchiness and branch insertion angle, respond plastically to neighbourhood competition for *F. sylvatica, Q. robur* and *B. pendula*. The species-specific trends are in accordance with species' strategies to tolerate or avoid competition. Mixing tree species did not change the competitive environment, and consequently, also tree architecture did not differ between pure and mixed neighbourhoods for most species.

4.5.1 Allometric relationships

Branch attributes showed strong interdependencies that can be captured in four allometric relationships. First, lower branches are thicker than higher branches, a consequence of the age gradient in branch development from top to down (Figure 4-2A). Second, branches that are positioned on the north-facing stem side are shaded more intensively by the foliage. These branches are stimulated to grow steeper (i.e., significant azimuth effect for branch insertion angle), which is likely an adaptation to mediate the shading. If so, the adaptation was successful, as branch growth was irrespective to its cardinal direction (i.e., non-significant azimuth effect for branch diameter). The observation of steeper branches on the north-facing stem side confirms the findings of Kint et al. (2010) for beech trees. It thus presents a more generic effect, which is also valid for the species we studied. Third, branch diameter is strongly related with branch insertion angle: the steeper the branch, the thicker it is (Figure 4-2C). In literature such observation is named *gravimorphism* and is cause by the large auxin production in the apex of steep branches, stimulating apical dominance (Wareing & Nasr 1961; Wilson 2000). Fourth, branches positioned at higher stem parts tend to be more sharply attached to the main stem (Figure 4-2B). Lower (and thus older) branches are under stronger gravitational forces and the shading of upper branches further stimulates a horizontal branch development to capture a satisfactory amount of light. From all of this, it should be clear that allometric relationships are complex: branch diameter seems to result from a trade-off between stem position (age effect) and branch insertion angle (effect of photosynthesis and apical dominance/suppression). The four allometric relationships are shared between the study species but follow some species-specific trends as well. For instance, the negative relationship between branch diameter and branch insertion angle is most clear for *B. pendula* and *P. sylvestris* and the relationship between branch insertion angle and branch relative height is most clear for *Q. robur* and *P. sylvestris* (Figure 4-2B and Figure 4-2C).

4.5.2 Competition

Tree architecture in the young plantation has been strongly shaped in response to neighbourhood competition. Proposed mechanisms are physiological processes to optimize photosynthesis at the level of a whole tree and at the level of individual branches (Sachs 2004; Mäkinen & Hein 2006). The species showed various architectural responses to neighbourhood competition that can be linked to species-specific light requirements and growth rates, and thus, to species strategies to tolerate or avoid competition.

First, *Q. robur* is a slow growing (HGR = 28 cm year^{-1}) and moderately light-demanding species (shade-tolerance index of 2.45 on a scale between 0 and 5; Niinemets & Valladares 2006). If competition for light increases, *Q. robur* has to keep foliage at high position in order gain from photosynthesis. To do so, two types of morphological adaptation, one at the tree level and one at the level of individual branches, can improve foliage positioning. At the tree level, stronger investments in tree height increment relative to stem diameter increment will remedy the competition. At the level of individual branches, upwards lifting facilitates photosynthesis of *Q. robur* without additional resource allocation to the branches.

A completely different competitive strategy is observed for *F. sylvatica,* a slow growing (HGR = 34 cm year^{-1}) and highly shade-tolerant tree species, according to the STI of 4.56 (Niinemets & Valladares 2006). In this study, the species is intensively branched in more competitive environments. Following literature, *F. sylvatica* saplings are indeed highly capable to alter growth and architecture because of low epinastic control (Dieler & Pretzsch 2013). In shaded environments this results in branchy and plagiotropic tree shapes, with positive effects on competitive ability but potentially also with negative effects on timber quality (Rozenbergar & Diaci 2014).

With increased neighborhood competition, saplings of *B. pendula* reallocate resources to the upper crown parts by increasing HD ratio and by decreasing the number of first order branches. It is typical for a light-demanding (STI = 1.54) and fast growing (HGR = 85 cm year^{-1}) species to largely avoid competition by the continuous exploration of light-abundant zones at the upper canopy. The investment in new branches in the upper canopy is associated with an increased shading of lower branches. According to the branch autonomy principle, these lower branches die once energy balance becomes negative, that is, when respiration costs to maintain leafs and branch structures exceed their energy capturing capacity (Lacointe *et al.* 2004). By their fast growth, trees of *B. pendula* are the first to reach the phase of natural pruning, more particularly at five years after plantation establishment.

Finally, *P. sylvestris* and *T. cordata* does not respond to neighbourhood competition. We assume that light availability did not yet drop below a threshold that is required for the species to stimulate internal resource allocation. Pretzsch (2014) studied crown morphology in mature plantations and found lowest levels of crown plasticity for *P. sylvestris* when compared to *F. sylvatica* and *Q. robur,* which is in line with our results from an immature plantation.

Competition was measured by measuring aboveground tree structures, and the competition index therefore directly related to aboveground competition for space and light. Although we have no data on the importance of belowground competition to architectural plasticity, we think that it plays minor roles. Rather, belowground competition for water and nutrients is extremely important to biomass productivity. I believe that the formation of branches in a certain position, as well as the processes that trigger natural stem pruning, are mainly determined by total light availability and by the spatial distribution (horizontal and vertical) of this light because of their importance to photosynthesis and carbon balances at the levels of leafs, twigs and branches. Light availability is mainly covered by the intensity of aboveground competition and may be dependent on the different types of neighbours that change light transmission through canopy. Light distribution was not directly measured here and is subject to further research, for instance by defining light-gradients through the canopy layer. Of course, both water and light play roles in the photosynthesis process, so that competition for both resources are anyway related. Thus, by measuring the size of neighbours, we not only have a direct proxy for aboveground competition but also an indirect proxy for belowground completion. Separating these effects is not possible given our data.

4.5.3 Diversity and species identity

B. pendula faced a competitive release in mixtures, because sapling growth rates differed largely between the studied species, with *B. pendula* being most productive. As competition is an important driver of architectural plasticity, *B. pendula* obtained less branches and higher HD ratios in monocultures to mediate the strong intraspecific competition. Although studied in mature forests, also Lintunen & Kaitaniemi (2010) have shown strong responses of *B. pendula* trees to mixing, for instance by investing in longer and steeper branches if surrounded by heterospecifics. No competitive differences between mixtures and monocultures were found for the other species, and consequently, their architecture was not affected by FDis. Also in a subtropical plantation of four years old, tree diversity was a poor indicator for aboveground biomass allocation (Lang *et al.* 2012). However, apart from tree diversity *per se,* Lang *et al.* (2012) reported that species composition and species identities in a sapling's local neighbourhood were important determinants of foliage structure and branch demography. These morphological rearrangement may suggest that competition is not solely driven by the size and distance of neighbours, but that other species characteristics are important too. Various traits are known to influence quantity and quality of light transmission through tree crowns, among them branch density, foliage density, leaf petiole length, leaf surface, leaf thickness and leaf shape (Mark, Bart & Meir 1999; Lintunen *et al.* 2013). Species-specific differences in such traits may explain contrasting competitive effects of species and functional groups, at least as it is shown in mature forests (Sumida *et al.* 2002; Valkonen & Ruuska 2003; Bayer, Seifert & Pretzsch 2013; Longuetaud *et al.* 2013). When examining branchiness of *Q. robur* in our experiment, intraspecific neighbours seem to be stronger competitors than interspecific neighbours. However, these findings were not observed for other species and other architectural attributes. This may imply that such competitive differences are rather exceptional at FORBIO. Importantly, as trees get older, not only do they interact more directly through physical contact, their environment has also been affected by diversity for several growing seasons, which may compound the effects on tree architecture (Pretzsch *et al.* 2016).

4.5.4 Management implications

Veneer and saw timber industries strongly rely on high-quality logs from the lower part (± 25%) of tree stems (Baar 2005). These stem parts have been shaped in the early stages of stand development, including the period before canopy closure. Already before canopy closure, silvicultural strategies should focus on two key factors influencing timber quality. First, to develop an appropriate tree architecture (e.g. single straight spill), because architectural failures in young plantation trees may cause irreversible quality loss. Second, to develop branch-free stems of 3-6 m needed to produce knotless wood. For these reasons, pruning activities including formative pruning (tree shape) before and shortly after canopy closure, and stem raising (branch-free stem) often in different interventions after canopy closure can improve the wood quality, but it seldom offers an economically attractive solution (Valkonen & Ruuska 2003; Kerr & Morgan 2006).

In this study we focused on natural processes that may positively affect tree shaping. More particularly, we considered the relationship between species mixing and architectural development because it closely relates with two current trends in forestry, i.e., a trend to revalue forest biodiversity and a trend to reduce operation costs by avoiding pricey management interventions such as pruning. In this study we could demonstrate with statistical significance that even at low age and density, interaction between tree individuals takes place, and has an effect on tree architecture in the area of the lower trunk. Clearly, tree-tree interactions establish earlier than generally considered, but see Setiawan *et al.* (2016), Lang *et al.* (2010, 2012) & Haase *et al.* (2015) for more evidence from juvenile plantations. Furthermore, the large differences in initial height growth rate and crown expansion between species can cause increased asymmetric competition and strong architectural responses in mixture, with potential relevance for tree quality. This is for instance shown by the delayed process of natural pruning of *B. pendula* if surrounded by slow growing species. However, the young plantation stage is dynamic and effects might shift over time. Thus, before silvicultural learnings can be drawn from this exercise, more studies are required to monitor species mixing over all subsequent stages of plantation development.

4.5.5 Conclusion

We studied competitive interactions in a young plantation with 66 % canopy closure. Although many trees were not yet in full crown contact with neighbours, competition for light is already a principle determinant for sapling architectural development. The morphological responses were species-specific and could be related to species autecology. Diversity and identity of species in a trees’ neighbourhood did not contribute to the architectural plasticity, but competitive differences between pure and mixed stands underpinned such effects for *B. pendula*, with lower branching in the highly competitive monocultures. Long-term monitoring into the thicket and pole stages is advised to get the full picture of what tree architecture in mixed stands will yield compared to pure stands, how this will depend on the species choice and how this will finally determine the quantity and quality of produced wood.

Chapter 5

Overyielding Is Driven By Complementarity And Selection

Van de Peer T, Verheyen K, Ponette Q, Setiawan NN, Muys B (2017) Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. Journal of Ecology (in press) (IF = 5.813)

Author's contributions: TVDP, BM and KV devised the concept of the article; NNS and TVDP collected field data; TVDP carried out the data analysis and wrote the manuscript text. All co-authors contributed to revising earlier versions of the manuscript and approved the final version.

Cover photo: Birch in mixture, FORBIO ZED, 2017 (H. Bruelheide)

5.1 Summary

Overyielding in mixed-species forests has been demonstrated in a vast body of literature, and the focus of functional biodiversity research is now shifting towards a mechanistic understanding of these observations.

We explored diversity-productivity relationships (DPRs) at two sites of a large-scale tree diversity experiment, with harsh (GED) and benign (ZED) environmental conditions for plantation establishment. Additive partitioning methodologies were adopted to detect phenomenological patterns in the productivity data, and the trait structure of mixed communities was used to advance insights into compositional effects.

After six years of plantation development, biomass productivity was significantly higher in mixtures compared to the monocultures of component species. We observed that processes operated through direct tree-tree interactions, since the diversity signal disappeared where trees in mixed stands were surrounded by conspecific neighbours only. This result is particularly relevant for mixed-species planation systems, as trees are commonly planted in monospecific clusters to simplify management.

Partitioning unveiled strong selection effects at both plantation sites. However, at the harsh GED-site this was caused by competitive dominance of species with fast young growth whereas at the benign ZED-site, species with slow young growth improved their performances but not at the expense of others (i.e., trait-dependent complementarity). Species tolerance to shading is an influential trait for predicting biodiversity effects, with community-weighted means in shade tolerance mediating dominance effects (GED) and functional diversity in shade tolerance mediating (trait-dependent) complementarity effects (ZED).

This study highlights that biodiversity effects in young tree plantations could be explained by the functional composition of mixed communities, with a key role for species levels of shade tolerance. As contrasting results between plantation sites were observed, future research should target the context-dependency of DPRs.

5.2 Introduction

Many studies have examined the significance of biodiversity for ecosystem functioning, with a strong focus on biomass productivity (Balvanera *et al.* 2006; Cardinale *et al.* 2011; Liang *et al.* 2016). Biodiversity is thought to promote productivity via complex mechanisms that involve organism-organism and organism-environment interactions and that may be grouped in two major classes: complementarity and selection (Loreau & Hector 2001).

Complementarity accounts for various types of interspecific interactions, most notably niche partitioning and facilitation. Niche partitioning arises if species obtain greater access to available resources or if they improve resource-use efficiency through functional differences in, for example, shade tolerance (Morin *et al.* 2011; Toïgo *et al.* 2017), foliar phenology (Bayer, Seifert & Pretzsch 2013) or rooting architecture (Jucker *et al.* 2014b). Facilitation may improve plant performance by enhancing resource supply, or climatic or biotic conditions for some of the species involved (Bulleri *et al.* 2016; Forrester & Bauhus 2016). A stronger intraspecific compared to interspecific competition is shared between niche partitioning and facilitation, and both attributes of complementarity are often difficult to distinguish (Montès *et al.* 2008). Selection effects indicate that overyielding is attributable to species with particular monoculture traits, often considering monoculture biomass (Loreau & Hector 2001; Jiang, Pu & Nemergut 2008). Positive effects are best known and arise if, across all species, mainly those species with high monoculture biomass demonstrate superior performance. Complementarity and selection can simultaneously affect productivity, even in opposite ways (Loreau & Hector 2001).

The direct quantification of biological processes often requires methodologically challenging approaches. As an alternative, the *post hoc* additive partitioning of Loreau & Hector (2001) allows the detection of phenomenological patterns in productivity datasets (Fridley, 2002; Lübbe et al., 2015; Wang et al., 2013). Very briefly, a net biodiversity effect is calculated by comparing the observed yield in mixture with the expected yield derived from monocultures of component species, and next, the mathematical procedure teases apart how much of this net biodiversity effect is attributable either to complementarity or to selection effect. Fox (2005) provided a further split of the selection effect in order to differentiate between conditions where the improved functioning of species with particular traits occurs at the expense of other species functioning (competitive dominance), or where it does not affect the others (trait-dependent complementarity). Applied to plant diversity experiments, complementarity came out as the strongest determinant of overyielding, especially when evaluated over longer times frames (Cardinale *et al.* 2007; Fargione *et al.* 2007; Jiang, Wan & Li 2009).

The expression of diversity effects and underlying mechanisms depends on how species contribute to ecosystem processes in diverse communities. Functional traits can accurately predict plant growth, and at the community-level they can drive competitive interactions between different species (Kunstler *et al.* 2015). Two attributes of community composition, i.e. functional identity (mean trait values) and functional diversity (variation in trait values), can provide mechanistic insights into DPRs (Shipley, Vile & Garnier 2007; Mouillot *et al.* 2011). However, only a few studies to date have performed a unified analysis of partitioned biodiversity effects and trait-based attributes of community composition (Roscher et al. 2012; Kröber et al. 2015). In addition, although forest covers about 30% of land area and provides fundamental ecosystem services (Thompson *et al.* 2005; Jiang, Wan & Li 2009), they are critically underrepresented in functional biodiversity literature, mainly for pragmatic reasons associated with its experimental manipulation (Scherer-Lorenzen 2013). As a matter of fact, forests are dominated by large, long-lived and singly-identifiable organisms and as woody biomass is not renewed annually, complementarity effects may easily accumulate over time (Forrester & Bauhus 2016). Processes of recruitment, replacement and mortality also occur over much longer time frames, so that studies encompass only a small fraction of a system’s functioning. It is therefore reasonable that biological processes and functional traits mediating DPRs in forests differ from those found in earlier experimental studies on grasslands or aquatic microcosms.

In the last decade, research facilities manipulating tree species composition across a tree diversity gradient have been established to advance the functional biodiversity research in forest ecosystems (Verheyen et al. 2015). Our work hinges on data from a West European tree diversity experiment that mimics current forest practices in terms of planting densities and species use, and that is well buffered against edge effects thanks to large plot sizes. As the experiment was planted six years ago, our study handles the early stage of plantation development, characterized by the emergence of tree-tree interactions and closing canopies. We sought to test (i) if mixtures are more productive compared to monocultures of component species; (ii) at what spatial scale diversity effects operate (tree neighbourhood-level or stand-level) (ii) how diversity effects relate to the community trait composition and finally (iii) if findings are similar at two sites with contrasting environmental conditions and species pools.

5.3 Materials and methods

5.3.1 Site information and experimental set-up

The study was conducted at the Belgian FORBIO experiment (Verheyen et al. 2013), accommodating two experimental sites with relatively benign (ZED) or harsh (GED) environmental conditions for plantation establishment in terms of soil water, nutrient availability, soil acidity and climate (Appendix I and Chapter 2). The third site (HEC) was not included in this study because the site was planted later and six-year productivity data was not yet available.

5.3.2 Biomass data

Biomass data were collected in wintertime after two, four and six growing seasons. This data encompass 5502 (ZED) and 5657 (GED) permanent monitoring trees representing the established communities. Monitoring trees in the monoculture plots were randomly selected. In the mixtures, monitoring trees consist of two groups of similar size. The first group represents center trees of monospecific clusters and are directly surrounded by conspecific neighbours only. The second group represents edge trees of monospecific clusters and are directly surrounded by both conspecifics and heterospecifics (Figure 5-1). Stem diameters were measured with a digital caliper at 20 cm above ground level and tree height with a vertically positioned telefix from the ground to the highest living bud.

Aboveground biomass of individual trees was derived from biomass equations for seedlings and saplings of common European tree species (Annighöfer *et al.* 2016). These equations are irrespective to site conditions or diversity levels, but they do include species-specific expansion factors. Specific expansion factors are not available for *Larix* x *marschlinsii* and generic factors for conifer species had to be used (Annighöfer *et al.* 2016). Biomass productivity (expressed in kg dry matter per ha per year) after four and six growing years were considered in the analyses, with second year's biomass serving as reference data to correct for initial differences in tree size (Appendix XV). We further refer to these measures as 'four-year productivity' and 'six-year productivity'.

5.3.3 Diversity effects

Net diversity effect (NE) is defined as the deviation in yield (i.e. aboveground biomass productivity in this study) between what is observed in mixture (Y_O) and what is expected from the monocultures of component species (Y_E, Loreau & Hector 2001), or mathematically:

$$\mathrm{NE} = \mathrm{Y_O} - \mathrm{Y_E} = \textstyle\sum_i \mathrm{M_i}\Delta\mathrm{RY_i} \qquad \text{(Eq. 1)}$$

In this equation, M_i represents the yield of species *i* in monoculture and ΔRY_i the deviation between observed and expected relative yield of species *i*. The two-way partitioning of Loreau & Hector (2001) allows us to additively partition NE into complementarity (CE) and selection effects (SE):

$$\mathrm{NE} = \mathrm{CE} + \mathrm{SE} = \mathrm{N}\,\overline{\Delta\mathrm{RY}}\,\overline{\mathrm{M}} + \mathrm{N}\,\mathrm{cov}[\mathrm{M}, \Delta\mathrm{RY}] \qquad \text{(Eq. 2)}$$

To quantify CE, the number of species in mixture (N) is multiplied by the average, across all component species, monoculture yield ($\overline{\mathrm{M}}$) and the average, across all component species, deviation from expected relative yield ($\overline{\Delta\mathrm{RY}}$). Positive CE are at work if species' relative yields are positive on average, indicating patterns of niche partitioning or facilitation. SE are calculated by multiplying the number of species in mixture with the covariance (cov) between monoculture yields and species' deviations from expected relative yield (ΔRY_i). Positive (negative) SE indicate that overyielding is controlled by one or a few species with fast (slow) monoculture growth. In fact, the SE term combines processes that allow species with particular monoculture growth to dominate mixtures, with complementarity processes that likewise scale with these growth rates, but, that does not imply dominance. Fox (2005) therefore suggested a further partitioning of the SE term:

$$\mathrm{SE} = \mathrm{DOM} + \mathrm{TDC} = \mathrm{N}\,\mathrm{cov}\left(\mathrm{M}, \frac{\mathrm{RY_O}}{\mathrm{RYT_O}} - \mathrm{RY_E}\right) + \mathrm{N}\,\mathrm{cov}\left(\mathrm{M}, \mathrm{RY_O} - \frac{\mathrm{RY_O}}{\mathrm{RYT_O}}\right)$$

(Eq. 3)

With RY_O and RY_E the observed and expected relative yields respectively. RYT_O and RYT_E are the sums of observed and expected relative yield.

Both components (DOM and TDC) define a larger yield in mixture compared to monocultures thanks to the deviating performance of species with relatively fast/slow growth (i.e. selection effect *sensu* Loreau & Hector 2001). However, a deviation in yield may result either at the expense of other species' performances (competitive dominance, DOM) or not (trait-dependent complementarity, TDC). In contrast to observed relative yields, the RY_{Oi}/RYT_O ratios are species 'frequencies', with values between 0 and 1 and all species' frequencies summing–up to 1. These frequency characteristics are crucial differences between the bipartite (Loreau & Hector 2001) and tripartite (Fox 2005) partitioning. Indeed, increased RY_{Oi}/RYT_O for a certain species i necessarily comes at the expense of other species ratio's. A simple example of the different partitioning techniques is available in Appendix IV.

5.3.4 Trait data and calculation of functional composition

Six functional traits were selected based on their relevance to plant productivity and on data availability. They include SLA, Leaf Dry Matter Content (LDMC), Leaf Nitrogen concentration (leaf N), WD, Shade tolerance (Shade) and Root architecture (Root). Besides shade tolerance and root architecture, which are derived from literature, all trait data were collected from *in situ* measurements taken in the monoculture plots (Table 2-1 and Appendix II). The functional composition of plots was quantified by two indices with different conceptual meaning. On the one hand, community-weighted means (CWM_{trait}) identify the dominant trait values of a community. CWM are the mean values of each trait after weighting by species' biomass proportions (Roscher *et al.* 2012). On the other hand, functional trait diversity (FD_{trait}) describes the dissimilarity of trait values across all species in a community. It was computed as a univariate functional dissimilarity index (Laliberté *et al.* 2010), measuring the average biomass-weighted distance of species to the centroid of a single-trait space. The *dbFD*-function in the R package FD was used to calculate CWM and FD (Laliberté & Shipley 2014).

5.3.5 Statistical analyses

NE were evaluated in mixed-effect regression models ($N_{mixture\ plots} = 60$). These models include species composition and block as random effects, and site (ZED and GED), SR (two, three or four species) and site-by-SR interaction as fixed effects. Site-specific grand means of NE (t-tests) and site-specific influences of SR (Chi-square tests) were inspected to deviate from a zero contribution, with degrees of freedom approximated after Satterthwaite (Kuznetsova, Brockhoff & Christensen 2014). Five such models were built to investigate the outcome of NE when computed from different datasets. The main conditions to calculate NE are six-year productivity, exclusion of sapling mortality and including all sampled trees (Model 1). The other datasets used the same conditions, but four-year productivity (Model 2), inclusion of sapling mortality (Model 3), only sampled trees in diverse local neighbourhoods (Model 4, Figure 5-1) and only sampled trees in monospecific local neighbourhoods (Model 5, Figure 5-1). Next, we evaluated CE, SE, DOM and TDC from the partitioning approaches, with the same model structure and post-hoc analyses as before. Similarly, to define how species contributed to NE, species' deviation from expected relative yields (ΔRY) were tested against zero. In a final analysis, productivity and additive biodiversity effects (calculated on the main conditions) were predicted by community-wide measures of functional trait composition. These variables were first standardized to estimate their relative importance. For all response variables, a global mixed-effect model included the six FD_{trait} and the six CWM_{trait} indices as fixed effects, while treating block and species composition as random effects. The most-parsimonious model was found by a procedure that computes all candidate models with subsets of the fixed effects (2^{12} = 4096 combinations) and that ranks these models based on lowest AICc (corrected Akaike Information Criterion) with the *dredge*-function available in the MuMIn package. Top-ranked models with similar likelihood (ΔAICc < 2) were further evaluated to provide a final model with significant predictors only. Variance inflation factors (VIF) were calculated to address potential collinearity, but the results confirmed that collinearity is of little concern in our data (all VIF < 4). All statistical analyses were conducted with R software, version 3.3.3 (R Development Core team, 2017).

5.4 Results

Aboveground productivity is 1597 kg/ha/y in GED and 2961 kg/ha/y in ZED, and this difference reflects site-specific environmental conditions and species pools. Productivity also varied substantially between the species, for instance with high values for *B. pendula* (6292 kg/ha/y), *P. sylvestris* (5688 kg/ha/y) and *Larix* x *marschlinsii* (5409 kg/ha/y), and low values for *Quercus* sp. (344 kg/ha/y in GED and 974 kg/ha/y in ZED) and *F. sylvatica* (302 kg/ha/y in GED and 929 kg/ha/y in ZED, Appendix XV). Species with fast, intermediate or slow juvenile tree growth are further referred to as fast, intermediate or slow growing species respectively (Appendix XV).

A positive NE was observed in 83% of all mixtures, with NE based on six-year productivity, excluding sapling mortality and including all sampled trees. Consequently, the grand means of NE are significantly positive and of similar magnitude at both sites (Figure 5-2

Table 5-1). Transgressive overyielding, a greater yield in mixture as compared to the most productive monoculture, was never observed in this experiment. The productivity of the best growing species (*Larix* x *marschlinsii* in GED and *B. pendula* in ZED) was 341 % (GED) and 110 % (ZED) of the productivity of the second best growing species. These large values (especially in ZED) placed ecological limitations for the detection of transgressive overyielding.

NE effects do not become stronger at higher levels of SR (either two, three or four species). Additional models were built to test a difference between four-year *vs.* six-year productivity, including *vs.* excluding mortality and low *vs.* high neighbourhood diversity. First, NE evaluated after four growing years was slightly negative on average, but did not significantly differ from zero. Second, the option to include sapling mortality in the analyses yielded NE effects of similar size as the main procedure. Indeed, sapling mortality (15.8 % in GED and 5.6 % in ZED) seemed to be homogeneously distributed across the experiment and not related with SR. Third, if a trees' local neighbourhood only consists of conspecifics (centre trees of monospecific clusters), NE effects are non-significant in GED and only slightly significant in ZED. In contrast, if a trees' local neighbourhood is more diverse, NE are large and significant at both sites.

The partitioning approach revealed that CE are positive on average, although the effect is only significant at ZED. Contrasting patterns appeared for SE, with a positive value in GED mainly originating from positive DOM (mean = 296 kg/ha/y, *P* = 0.008), and a negative value in ZED mainly originating from negative TDC (mean = -219 kg/ha/y, *P* = 0.001). Species deviations in relative yield (ΔRY) support the positive dominance effect in GED by showing overyielding of fast (*Larix* x *marschlinsii*, *P* < 0.001) and intermediate (*P. menziesii, P* = 0.001) growing species, but also underyielding of slow growing species (*Q. petraea, P* = 0.02 and *A. pseudoplatanus, P* = 0.008, Figure 5-3). In ZED, ΔRY's confirm the negative trait dependent complementarity effect by showing overyielding of slow growing species (*F. sylvatica*, *P* < 0.001 and *T. cordata, P* = 0.002) but equal monoculture to-mixture performances for the other species (Figure 5-3).

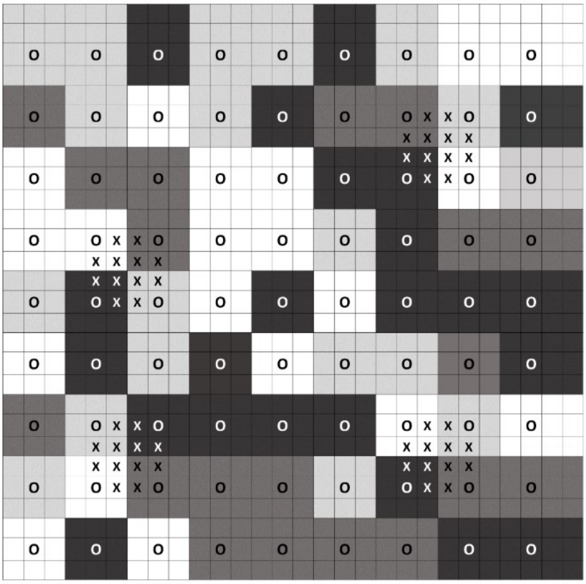


Figure 5-1 Example of the sampling design in a four-species plot. Squares represent the 784 trees and grey scaling was used to differentiate between the four species. Approximately 15 % of the trees were beforehand selected for long-term monitoring (stem diameter and tree height measures at a two-year interval), including center trees of monospecific clusters (indicated by O and referred to as trees in monospecific local neighbourhoods) and trees in the edge of monospecific clusters (indicated by X and referred to as trees in diverse local neighbourhoods).

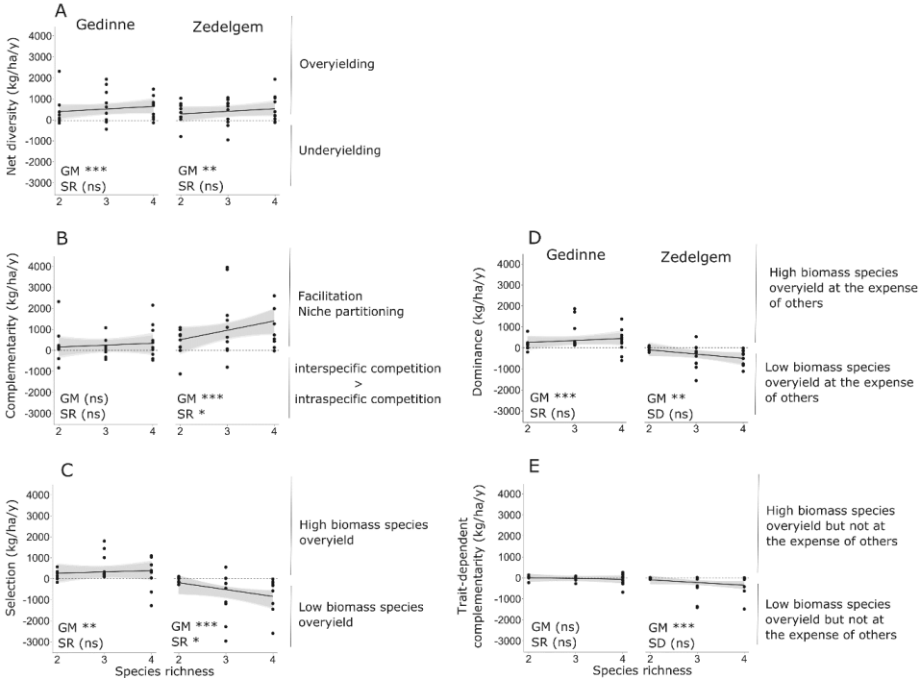


Figure 5-2 Partitioning net diversity effects on biomass productivity (kg/ha/y) evaluated at main conditions, i.e. six-year productivity, all sampled trees, and excluding sampling mortality. The analyses include the two-way partitioning methodology of Loreau and Hector (2001) and the extended version of Fox (2005). Net diversity (A), complementarity (B), selection (C), dominance (D) and trait-dependent complementarity (E) effects (all presented in kilogram dry matter per hectare per year) are plotted against species richness. Solid lines represent predictions from mixed regression models fitted to the data (dots). Significance of parameters (i.e. grand mean GM and species richness SR) are indicated with a single asterisk (P < 0.05); double asterisk (P < 0.01), triple asterisk (P < 0.001) or ns for non-significance (P > 0.05). The interpretation of positive and negative values is given on the right side of the panels.

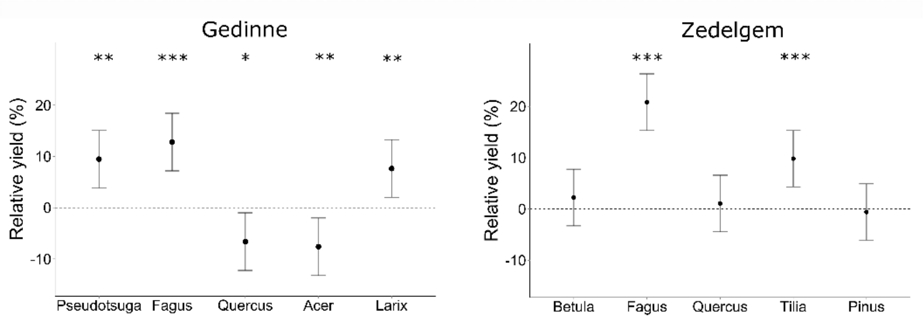


Figure 5-3 Means (± SE) of species' deviation from expected relative yield (**Δ**RY term in Eq. 1 but converted to percentages). Mean values that significantly differ from zero (t -tests) are denoted with asterisks as in Figure 5-2

Table 5-1 Statistical inferences of linear mixed-effect models testing net biodiversity effects (NE) on different productivity datasets. The main conditions to calculate NE are six-year productivity of all trees, excluding sapling mortality (Model 1). All other models used the same conditions but four-year productivity (Model 2), including sapling mortality (Model 3), only trees in diverse local neighbourhoods (Model 4) and only trees in monospecific local neighbourhoods (Model 5). The difference between monospecific and diverse local neighbourhoods is illustrated in Figure 4-1. Random effects were assigned to species composition and to the blocking design. Post-hoc tests were used to check the grand means of NE (t-tests) and the influence of species richness (SR, Chi-square tests) at both sites Gedinne and Zedelgem.

		Overall			Gedinne			Zedelgem		
		F	*P*		Estimate	test	*P*	Estimate	test	*P*
Model 1 Main conditions	Site	0.01	0.95	Grand mean	**518**	**4.30**	**< 0.001**	**398**	**3.25**	**0.002**
	SR	1.40	0.24	SR	112	0.54	0.463	139	0.89	0.343
	Site x SR	0.02	0.89							
Model 2 Four-year productivity	Site	0.01	0.96	Grand mean	-161	-1.89	0.063	-33	-0.47	0.639
	SR	0.01	0.95	SR	27	0.18	0.667	-32	0.25	0.623
	Site x SR	0.47	0.49							
Model 3 Including mortality	Site	0.01	0.91	Grand mean	**514**	**4.43**	**< 0.001**	**417**	**3.54**	**0.001**
	SR	1.21	0.28	SR	108	0.55	0.465	119	0.69	0.416
	Site x SR	0.01	0.96							
Model 4 Diverse neighbourhoods	Site	0.02	0.90	Grand mean	**900**	**5.32**	**< 0.001**	**511**	**3.98**	**0.006**
	SR	2.62	0.11	SR	151	0.53	0.461	322	2.53	0.119
	Site x SR	0.35	0.55							
Model 5 Monospecific neighbourhoods	Site	0.06	0.81	Grand mean	144	1.16	0.251	300	2.38	0.034
	SR	0.02	0.89	SR	67	0.19	0.672	-39	0.06	0.794
	Site x SR	0.23	0.63							

Out of six functional traits selected, the most powerful one to predict productivity and biodiversity effects in this experiment is shade tolerance (Table 5-2). These values range from 1.50 (*Larix* x *marschlinsii*) to 4.45 (*F. sylvatica*) after the 1-5 ranking of Niinemets & Valladares (2006). Mean trait values and their diversity both describe patterns in the data. At GED, 72 % of variation in productivity was explained by the combination of CWM_{Shade} and FD_{SLA}, and at ZED, 68 % of variation was explained by CWM_{Shade}, CWM_{WD}, CWM_{LDMC} and FD_{Root}. When NE effects were present in GED, they were negatively associated with CWM_{Shade}. This indicates that communities dominated by species with lowest levels of shade tolerance are most strongly overyielding. In line with this result, also DOM effects were found in communities with a high mean and a low variation in levels of shade tolerance. Importantly, the relationship between NE and traits only captures 15 % of observed variation in GED. The proportion of NE explained by traits is larger in ZED (28 %), with NE scaling positively to FD_{Shade} and CWM_{SLA}. Because TDC and DOM are both negative on average, the negative association with FD_{Shade} should be interpreted as stronger effect sizes in more diverse communities.

Table 5-2 Summary table of optimized mixed-effect models relating plot-level productivity, net biodiversity effects (NE), complementarity effects (CE), trait dependent-complementarity effects (TDC) and dominance effects (DOM) with the functional diversity (FD) and community-weighted means (CWM) of specific leaf area (SLA), shade tolerance (Shade), wood density (WD), leaf dry matter content (LDMC), nitrogen concentration (N) and root form (root). Models included species composition and block as random terms, and a model selection based on AIC ensured that only significant effects are included. The variance explained by traits (marginal R²) is computed for each model following Nakagawa & Schielzeth (2013).

	Gedinne (Ged)					Zedelgem (Zed)				
	R²	Trait	Estimate	t	*P*	R²	Trait	Estimate	t	*P*
Productivity	0.72	Intercept	58.9	2.3	0.029	0.68	Intercept	1064	2.9	0.005
		FD SLA	82	3.4	0.002		CWM WD	-199	-5.7	< 0.001
		CWM shade	-176	-8.5	< 0.001		FD Root	97	4.3	< 0.001
							CWM shade	-1229	-2.6	0.015
							CWM LDMC	112	2.7	0.018
NE	0.15	Intercept	25	1.3	0.207	0.29	Intercept	16	1.1	0.262
		CWM shade	-37	-2.3	0.021		FD shade	39	3.1	0.004
							CWM SLA	22	2.1	0.050
CE	0.20	Intercept	16	1.2	0.221	0.34	Intercept	38	1.4	0.170
		FD shade	46	2.6	0.013		FD shade	91	3.8	< 0.001
TDC	NA	Intercept	-3	1.0	NA	0.28	Intercept	-5.2	-0.5	0.607
							FD shade	-28	-3.2	0.005
DOM	0.63	Intercept	14	0.9	0.405	0.61	Intercept	19	1.3	0.251
		FD shade	-54	-4.5	< 0.001		FD shade	-75	-8.4	< 0.001
		CWM shade	-37	-2.9	0.011					

5.5 Discussion

5.5.1 Higher productivity in diverse local neighbourhoods

Our results provide insights into DPRs of young forest plantations encompassing functionally dissimilar tree species. After six years of stand development, net diversity effects were significantly positive and observed in 83% of the mixtures. This result corroborates seminal synthesis reports on higher levels of ecosystem functioning in biodiverse communities (Hooper *et al.* 2005; Cardinale *et al.* 2007; Hector *et al.* 2011). Focusing on forest productivity, positive relationships along wide climatic gradients have frequently been found, although relationships typically hinge on complex interactions between resource availability, climatic conditions and stand structures (Morin *et al.* 2011; Paquette & Messier 2011; Hulvey *et al.* 2013; Forrester & Bauhus 2016; Liang *et al.* 2016).

When consulting the relatively scarce literature available on tree experiments, diversity seems not to, or only marginally, influence productivity (Healy, Gotelli & Potvin 2008; Li *et al.* 2014; Domisch *et al.* 2015; Haase *et al.* 2015; Setiawan *et al.* 2016b; Tobner *et al.* 2016). The limited experimental demonstration of DPRs could be due to the early stage of plantation development, i.e., most data comes from sites that are less than five years old. Several years are required before trees reach certain sizes and before considerable differences in species architecture allow them to benefit from above- and underground niche separation (Tilman *et al.* 2001; Cardinale *et al.* 2007; Fargione *et al.* 2007). It is also probable that light-mediated complementary promotes tree productivity, but that such influence only gradually amplifies with canopy closure (i.e., with increased competition for light). Also in our experiments we observed that overyielding was not yet significantly important after four growing years, both for GED and ZED. HEC was not included in this research because data on six-year productivity was not yet available. A quick check of four-year productivity data provided us net diversity effects that were zero on average, a result that is in line with ZED and GED after the same period.

The mixture design based on small clusters of a single species allowed us to test at what spatial scale diversity effects emerge. Trees at the centre of clusters are surrounded by eight immediate conspecifics, representing neighbourhood-level monocultures within plot-level mixtures. These centre trees were equally productive as trees in monoculture plots. Consequently, plot-level overyielding of mixtures is exclusively motivated by trees growing in diverse local neighbourhoods. We conclude that processes driving DPRs in young plantations operate at small spatial scales, i.e. trees interacting with direct neighbours. Previous studies have described the functional growing space of individual trees as fundamental for explaining community-level performance (Getzin *et al.* 2008; Fichtner *et al.* 2017). For instance, Potvin & Dutilleul (2009) observed DPRs were driven by shifting biomass allocation patterns in response to the size and identity of immediate competitors. Also Williams *et al.* (2017) concluded that spatial crown complementarity, attributable to both species' inherent differences and neighbourhood-driven plasticity, relates to patterns of stem biomass overyielding. The spatial scaling aspect of diversity may reflect substantial trade-offs in plantation management. Mixing species on a tree-by-tree basis speeds up the early expression of diversity effects on productivity and enhances insurance against planting failure (Chapter 2). On the other hand, competition is also at play and may quickly eliminate shade intolerant, slow growing species from the mixtures. For the purpose of simplifying management, tree planting in conventional silvicultural systems typically occurs in large monospecific patches (Nichols, Bristow & Vanclay 2006; Puettmann *et al.* 2015). However, our analyses elucidated that trees may draw ecological benefits, in terms of increased biomass productivity, if they are mixed at finer spatial scales.

5.5.2 Mechanisms of diversity effects from additive partitioning

The exploration of productivity data with additive partitioning methods unveiled a positive complementarity effect in ZED, which became even stronger at higher levels of SR. This result supports a classical hypothesis that niche differentiation, facilitation and/or trophic interactions reduce interspecific competition compared to intraspecific competition (Hooper *et al.* 2005). An influential role was furthermore given to selection effects. Importantly, these effects differed in sign between the two plantation sites (positive in GED and negative in ZED) and even reflected contrasting biological processes. In GED, positive selection effects indicated patterns of competitive dominance, because in mixture, fast and intermediate growing species (*Larix x marschlinsii* and *P. menziesii*) tended to increase productivity at the expense of other species performance (*Q. petraea* and *A. pseudoplatanus*). This observation is likely related to successful establishment and rapid development of species that are well-adapted to harsh environmental conditions at GED. When these trees grow together with less adapted species, they may capture a disproportionate amount of resources (e.g. by overtopping) and possibly further disfavour the growing conditions of others (Potvin & Dutilleul 2009). In ZED, negative selection effects indicate that slow growing species (*F. sylvatica* and *T. cordata*) were overyielding, but this occurred without diminishing the performance of other species (*B. pendula* and *P. sylvestris*). Slow growing trees indeed capture resources in lower canopy strata, so that their improved performance leads to size-dependent complementarity, rather than competitive dominance (Fox 2005). In a recent study of Fichtner *et al.* (2017) it is clarified that overyielding of species with conservative resource strategies (i.e., slow growing and shade tolerant) is generally driven by facilitative interactions, for instance those brought about by mitigating microclimate conditions.

Contrasting observations between the experimental sites suggest a strong context-dependency of DPRs regarding the interdependent effects of soil, climate and species pools (Forrester & Bauhus 2016). For instance in GED, microclimate-mediated facilitation could have been expected for conservative species surrounded by fast growing trees. However, responses represent a trade-off between facilitative and competitive interactions. The harsh environmental site conditions at GED disproportionately favoured species with rapid resource acquisition strategies, thereby setting the context for competitive dominance to prevail over facilitation. Soil resources are less limited and climatic conditions more favourable at the post-agricultural site ZED, and all species settled easily after planting. Under these circumstances, competitive dominance is likely to have been avoided and conservative species in mixtures were able to benefit from facilitation.

5.5.3 A trait-based investigation of the diversity effects

To further advance a functional understanding of DPRs, we tested how the compositional structure of tree communities contributed to observed diversity effects. For this we used six traits reflecting variation in resource-use strategies between tree species in early ontogenetic stages. The procedure rests on quantifying the abundance (functional identity, CWM) and dissimilarity (functional diversity, FD) of individual traits, in that we expect these functional attributes to be causally linked to selection (dominance) and complementarity (Mouillot *et al.* 2011).

CWM are based on the mass-ratio hypothesis and the associated traits therefore characterize species with large or even dominant impacts on ecosystem functioning (Grime 1998). Our analyses revealed that most productive communities chiefly included species with low WD and low levels of shade tolerance. Both trait values characterize acquisitive species, which are typically driving ecosystem functioning in young forests (Kunstler *et al.* 2015; Fichtner *et al.* 2017). However, the positive effect of CWM in LDMC, a measure of leaf tissue density, on mixture productivity is inconsistent with such an interpretation. Acquisitive species experience high biomass turnover rates and are therefore typified by low LDMC (Poorter & Markesteijn 2008). It is unclear as to why the opposite (positive) relationship was found. In addition to the strong influence of CWMs, productivity in mixtures was promoted by variation in specific leaf area and rooting architecture. This result suggests that different attributes of community composition (i.e., mean and variation in trait values) are both affecting ecosystem functioning, although not necessarily at equal weights (Mouillot *et al.* 2011; Roscher *et al.* 2012).

There was a wide range of tolerance to shading between the species and it was a leading trait in the prediction of net diversity effects. Tobner *et al.* (2016) also carried out research based on the functional trait structure of young tree communities, and in agreement with our results, they revealed that overyielding was caused by selection effects related to $\text{CWM}_{\text{shade}}$, and additionally to $\text{CWM}_{\text{leaf nitrogen}}$ and $\text{CWM}_{\text{branch intensity}}$. The importance of shade tolerance is not unique to young tree communities. Also in a recent study based on French National Forest Inventory databases, overyielding of mature *Q. petraea* trees was sufficiently explained by species differences in shade tolerance (Toïgo *et al.* 2017).

In GED, overyielding was mainly found in communities including shade-intolerant tree species (negative $\text{CWM}_{\text{shade}}$). This result corresponds to the identification of positive dominance effects, because the dominant species in GED are indeed shade-intolerant. Following our expectations, DOM also scaled negatively to $\text{CWM}_{\text{shade}}$. In ZED, the additive partitioning approach indicated that NE were driven by CE and TDC. The trait-based approach now clarifies that NE and CE scale positively to FD_{shade} and that TDC (negative values) scaled negatively to FD_{shade}. This all indicates that slow growing species (often shade tolerant) performed best in mixed communities including shade intolerant (often fast growing) species.

5.5.4 Conclusions

Species mixing significantly increased biomass productivity in six-year-old tree plantations, a result that is in line with worldwide observations in forests (Liang *et al.* 2016) and other biological systems (Cardinale *et al.* 2011). The underpinning mechanisms are site-specific, operate at the small scale of a trees' local neighbourhood, and relate to the functional trait composition of communities, with an essential role for species levels in shade tolerance. Indeed, functional identity in shade tolerance mediated dominance effects (GED-site) and functional diversity in shade tolerance mediated (trait-dependent) complementarity effects (ZED-site). The contrasting mechanisms between sites with harsh (GED) or benign (ZED) environmental conditions for plantation establishment emphasize the need to further explore the context-dependency of DPRs. Such advancements could be made within comparative research platforms such as TreeDivNet or FunDivEUROPE (Baeten *et al.* 2013). Finally, despite the long-term perspectives of tree diversity experiments, only the early developing phase could be investigated at this time. Tree-tree interactions are dynamic, for instance because conservative species increase competitive ability with time, but also because complementarity effects likely change with plantation development (Eisenhauer, Reich & Scheu 2012). Hence, monitoring across all forest stages would help to quantify the long-term impacts of biodiversity on biomass productivity.

Chapter 6

General Discussion

Cover photo: mixture with oak, pine and larch, FORBIO HEC, 2015 (T. Van de Peer)

6.1 Overall goal, methodology and key findings

We monitored the performance of seedlings and saplings after reforestation to assess the functional roles played by tree diversity and assembly in this early stage of plantation development. This research focus is much decisive, given a current global transition towards multi-species plantations and given the incomplete understanding of tree-tree interactions in forest stands. Indeed, 20 years of intensive BEF research, mainly in grasslands and mesocosms, already provided consensus that biodiversity supports ecosystem functionality. The research also revealed mechanisms and environmental factors that can importantly modify BEF relationships. Today, ecologists agree upon one more thing: we need to move forward and test the validity and generalizability of early BEF findings across different ecosystem types. Among these ecosystems are also the structurally complex and long-lived forests that provide essential services to humanity.

We dealt with tree performance as a multi-faceted barometer that includes survival (Chapter 2), vitality (Chapter 3), architectural development (Chapter 4) and growth (Chapter 5). All these indicators are relevant to judge on the success of plantation development and to guide the management. For instance, one of the most initial objectives is to achieve high rates of plant survival, by making right decisions on site preparation, plant material sources, species selection and planting design, including species mixing. At this point, sapling growth and architectural tree formation are of lower concern, but both success indicators become relevant once trees have passed the critical planting phase. Our choice to measure seedling vitality, rather than survival, in Chapter 3 is motivated by the high plantation establishment success (99 %) in IDENT-M. Measuring seedling vitality based on foliage condition allowed to further differentiate between stressed and non-stressed seedlings.

Some interesting patterns emerged from undertaking our study and we briefly report main findings of individual chapters before bridging between them (Table 6-1). We discuss relevant ecological insights and we evaluate how results create applied value for plantation design and management. We finalize by discussing two central directions for follow-up research. First there is a necessity to establish better insights into the context-dependence of BEF relationships and second, causal mechanistic linkages underlying BEF should be further explored.

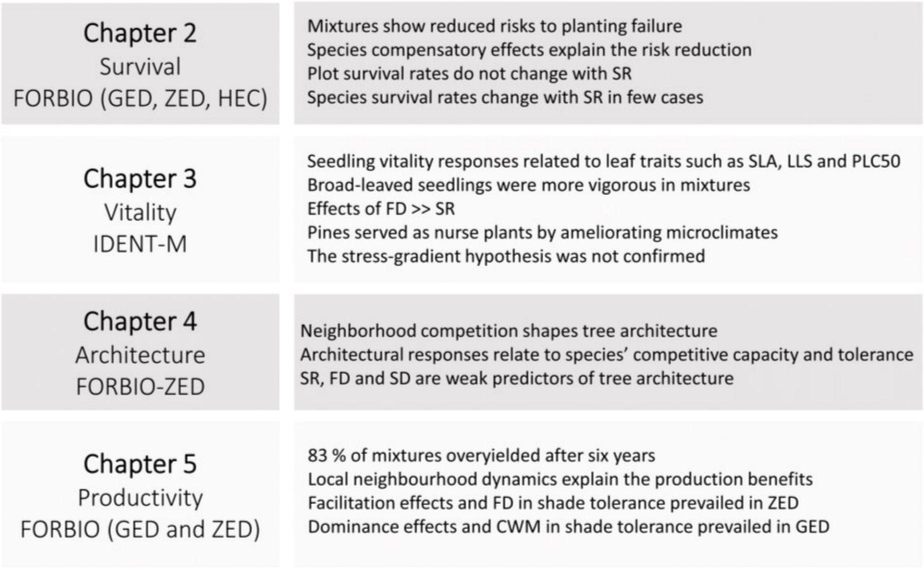
Via analysing patterns of seedling survival in FORBIO (**Chapter 2**), we tested two functional effects attributable to tree species mixing. First, we found evidence for plain buffering effects, owing to differences in species functioning and their tolerance levels to environmental stressors. Second, we tested a change in mean plot survival along a gradient in SR (i.e. performance enhancement effect), but we concluded that this effect was not at play in FORBIO. Few species showed variation in survival rates with SR, but the ecological or applied value of these species-specific effects was marginal.

In **Chapter 3** we shed light on the early functioning of seedlings that survived the planting at the Mediterranean IDENT-M site. Species identity and irrigation were prime determinants of seedling vitality, but we also observed higher vitality probabilities for eight out of nine broad-leaved species planted in functionally diverse mixtures. *Pinus sp.* (*P. pinaster, P. halepensis* and *P. pinea*) were not affected by mixing, but some had a firm positive impact on the vitality of broad-leaved seedlings. A facilitation effect likely appeared by creating gentle microclimates for seedlings that are otherwise heavy exposed to solar irradiation. The stress gradient hypothesis, a shift in species interactions with water availability under dry conditions, could not be confirmed in this study.

From **Chapter 4** we learned that tree-tree interactions took place after only four growing years, even though the plantation trees were not yet in full crown contact. We came to this conclusion after discovering aboveground architectural plasticity in response to neighbourhood competition for the species *B. pendula, F. sylvatica* and *Q. robur*. In contrast with our second hypothesis, tree species mixing did not importantly affect competitive environments (besides for the fast-growing *B. pendula*) and therefore, architectural development was not affected by tree species composition or diversity.

In **Chapter 5** we finally observed that 83 % of the mixed communities in FORBIO overyielded after six years; an effect that was evidently significant. Cross comparing results between sites unveiled that overyielding was mediated by two different biological mechanisms. Competitive dominance of tree species with acquisitive resource strategies prevailed at GED, and this effect scaled positive with community-weighted means in shade tolerance. On the other hand, trait-dependent complementarity effects, caused by the improved functioning of species with conservative resource strategies, underlined overyielding at ZED. Complementarity effects at ZED scaled positive with functional diversity in shade tolerance.

Table 6-1 Overview of main findings from the individual research chapters



Chapter 2 Survival FORBIO (GED, ZED, HEC)	Mixtures show reduced risks to planting failure Species compensatory effects explain the risk reduction Plot survival rates do not change with SR Species survival rates change with SR in few cases
Chapter 3 Vitality IDENT-M	Seedling vitality responses related to leaf traits such as SLA, LLS and PLC50 Broad-leaved seedlings were more vigorous in mixtures Effects of FD >> SR Pines served as nurse plants by ameliorating microclimates The stress-gradient hypothesis was not confirmed
Chapter 4 Architecture FORBIO-ZED	Neighborhood competition shapes tree architecture Architectural responses relate to species' competitive capacity and tolerance SR, FD and SD are weak predictors of tree architecture
Chapter 5 Productivity FORBIO (GED and ZED)	83 % of mixtures overyielded after six years Local neighbourhood dynamics explain the production benefits Facilitation effects and FD in shade tolerance prevailed in ZED Dominance effects and CWM in shade tolerance prevailed in GED

6.2 Diversity matters for forest functioning

6.2.1 The potential for early diversity effects

There are consistent signals that tree diversity exerts strong impacts on biological processes in mature forests, including those processes affecting tree performance (Zhang, Chen & Reich 2012; Gamfeldt *et al.* 2013; Longuetaud *et al.* 2013; Guyot *et al.* 2016; Pollastrini *et al.* 2016). In younger plantations, however, fewer opportunities for diversity effects exist, simply owing to large planting distances relative to small plant sizes. For instance, a complete multi-layered exploitation of light is proposed to explain biomass production benefits in mixtures, but such process of light partitioning is not evident for young stands with yet underdeveloped canopies (Sapijanskas *et al.* 2014, but see Williams 2017). Another example is leaf litter decomposition, which is assumed to occur faster and stimulate mixture productivity (Chapman *et al.* 2013; Jewell *et al.* 2016). Setiawan *et al.* (2016b) found that decomposition rates in the young FORBIO mixtures did not significantly deviate from the weighted-average decomposition rates of component species in monocultures (i.e. no synergistic interaction). Among other reasons, this may be due to an incomplete establishment of biotic decomposer communities, so that litter mixing effects can still develop with plantation maturation (Sapijanskas, Potvin & Loreau 2013).

Neutral (i.e. non- significant) or weak BEF relationships observed in young experiments would stimulate the perception that the early forest stages can be ignored for ecosystem monitoring. Trees first need to develop, both aboveground and belowground, before interactions are meaningful to investigate. In this PhD research we focussed on the early stages of plantation development and we proved that forest dynamics quickly start to differentiate between stands of different composition, potentially with decisive implications for management. Because the framework of this thesis is the development of a plantation from planting to six growing years, only short-term processes could be assessed. Therefore, it should be underlined that our conclusions and discussions cannot simply be translated to long-term trends or to mature forest functioning. The continuation of monitoring ecosystem functioning in TreeDivNet should provide quantitative data on temporal shifts in forest dynamics as a function of tree species diversity or composition. While waiting for such long-term data, the available data from inventory or observatory platforms should be analysed and linked with the experimental results. The issue of shifting forest dynamics is topic of more discussion in 6.4. *Further research perspectives.*

6.2.2 Insurance effects were most important

From our study we conclude that buffering effects on seedling survival can rapidly unfold in mixed plantations because such effects do not singly rely on ecological interactions or associated biotic communities building-up. Rather, buffering effects are also generated through averaging contrasting seedling survival probabilities (portfolio effects). This way, buffering simply requires species or genotypes with dissimilar response traits and thus, with dissimilar vulnerabilities to environmental stresses. Although not tested here, the insurance value of tree species mixing is likely extendable to other plant fitness indicators, including vitality and growth. However, when examining buffering effects on seedling vitality data from the Mediterranean IDENT-M experiment (Chapter 3), we only found little confirmation for the results in FORBIO (Chapter 2). Variation in plot-level vitality, measured as an average vitality scoring from all seedlings in the plot, only slightly (non-significantly) decreased at higher diversity. In Chapter 2 we hypothesized that the strength of buffering effects will be higher in communities where species have more distant response traits. We also suggested that buffering effects become stronger in more stressful environments due to intense ecological filtering. The contrasting results between Chapter 2 and Chapter 3 seems to indicate that buffering effects can contribute to reduce plantation establishment risks (see section 6.3 Applied perspectives), but, that these effects strongly rely on the species pool and their connection with the environmental conditions at the time of evaluation.

Besides buffering, also performance-enhancing effects were observed. However, their contribution to early plantation functioning should not be overvalued. For instance, plot-level survival in FORBIO did not change with diversity and effects at the level of populations were limited and inconsistently linked with species life-history strategies. We also found that mixtures in ZED and GED significantly overyielded after six, but not yet after four growing years. This drastic temporal shift in ecosystem functioning corresponds to the fast ecosystem dynamics of early-developing forests. A similar temporal shift was found at IDENT-M. Higher FD led to higher seedling vitality in the third growing year, but not yet in the second. These results proves our statement that we can only evaluate the early forest dynamics. Both competitive and facilitative interactions are building-up and can lead to quickly switches in ecosystem functioning.

Transgressive over-performing of mixtures (i.e. survival, vitality or productivity rates better than the best-performing monoculture) was not displayed in our research. But importantly, also mixtures rarely performed very badly. This suggest that mixing tree species was at least not harmful for plantation functioning.

6.2.3 Functional diversity or species richness?

It is interesting to discuss what aspect of tree diversity is most influential to the functioning of young stands. In Chapter 3 we found that broadleaf seedlings in IDENT-M improved their vitality status along a gradient of FD, but that such trend was not apparent for SR. The fact that both diversity measures (FD and SR) generated different trends could be explained by the facilitation of *Pinus* sp. Communities with high FD mostly include a combination of gymnosperms and angiosperms because species from both groups usually show strong trait dissimilarity. A correlation between seedling vitality and FD is then evident if *Pines* sp. are important facilitators for broadleaved seedlings. Communities with high SR can either include *Pinus sp.*, or not (i.e. because only three out of 12 species are *Pinus sp.*). If Pinus are important facilitators, the correlation between seedling vitality and SR will be lower.

The results align with a growing body of literature that points to the importance of community trait structures, community species assembly and the presence of key facilitator species to understand the functioning of biodiverse ecosystems (Mouchet *et al.* 2010; Flynn *et al.* 2011; Mouillot *et al.* 2011; Milcu *et al.* 2014). Based on this literature information and on our own insights from Chapter 3, it may look antagonistic to continue testing SR, rather than FD, in the other chapters. In FORBIO, however, the species pool only contains five site-adapted species, which are deliberately chosen to have little niche overlap (Verheyen *et al.* 2013). If the inclusion of species with comparable functional roles or resource requirements is avoided by the experimental design, the trends of ecosystem functioning should be very similar for SR and FD. We decided to stick with SR because it was directly manipulated in FORBIO. To meet the scientific calls for analysing community functional composition, we calculated CWM and FD of individual traits in Chapter 5.

6.2.4 Stand density and mixing type

Several processes causing improved mixture functioning compared to monoculture functioning rely on a certain degree of tree contact. For this reason, planting density and spatial mixing type will influence the speed by which interactions manifest.

Trees in FORBIO are planted at 1.5 m by 1.5 m and performance-enhancing effects became meaningful after six growing years. Trees at IDENT-M are planted more densely (0.4 m by 0.4 m) and diversity effects were detectable after just three growing years (Figure 6-1). Obviously, we did not directly test for a density-dependence of diversity effects because experiments differ in many more ways. Tree density is also hold constant within the experiments. This allows an easy and unbiased comparison between plots of different diversity, but it also limits our capacity to investigate a potential role played by stand density. In literature it is reported that net diversity effects, defined as the balance between complementarity and competitive interactions, are importantly modulated by stand density (He et al., 2005; Amoroso and Turnblom, 2006). Generally, complementarity effects increase with density because individuals become close enough to interact and facilitate each other. But at very high densities, complementarity is often outweighed by intense competition by the dominant species. The density-diversity interplay is probably even more complex. Indeed, the diversity-density relationships seems to depend on how essential resources are affected by the density and how species can tolerate resource limitations. For instance, Fichtner *et al.* (2017) showed that acquisitive species mainly overyielded under low competition intensity, whereas conservative species took most advantage under high competition intensity. This conclusion was also made in the study of Condés, Del & Sterba (2013) where complementarity effects decreased with stand density for *P. sylvestris* (acquisitive species, weak competitor) but increased for *F. sylvatica* (conservative species, strong competitor). Because of the important forest management consequences, there is a strong need to further explore how stand density modifies species competitive and facilitative interactions (Forrester 2014). Some new tree diversity experiments with orthogonal diversity-density gradients are now being established (e.g. TWIG - Tree Wheels In Geerbos, Belgium, www.treedivnet.ugent.be). The TWIG design is based on Nelder wheels, which are circular plots containing concentric rings and spokes connecting the centre with the largest ring. If trees are planted on the intersections, this creates a tree density gradient from the plot edge towards the centre. Because plots differ in number and type of tree species, it will be possible to discover the complex interplay between tree density, tree diversity and plantation functioning.

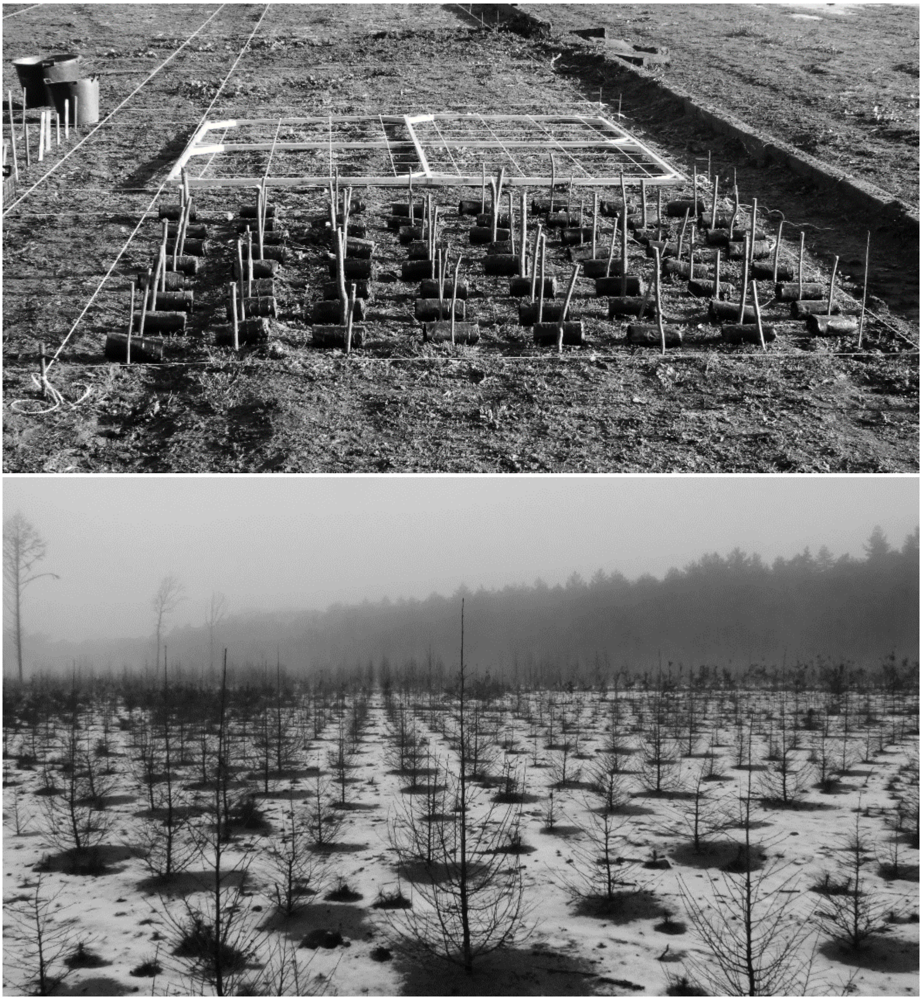


Figure 6-1 Planting densities of 62 500 seedlings/ha in IDENT-M (top) and of 4 444 seedlings/ha in FORBIO (bottom). Photo's: T. Van de Peer

The spatial scale of species interactions could be investigated because trees in FORBIO mixtures were planted in small mono-species cells (Figure 6-2). As only trees with diverse local neighbourhoods (edge trees of the cells) outperformed compared to the trees in monoculture plots, we assumed that underpinning biological mechanisms operated at local spatial scale. Also in literature it is often concluded that competition and facilitation are spatially explicit processes on the scale of trees' local neighbourhood (Thorpe *et al.* 2010; Schröter, Härdtle & von Oheimb 2012; Li *et al.* 2014). Therefore, local dynamics are crucial for understanding individual tree functioning and for predicting stand development in complex mixed-species forests. At FORBIO, Setiawan *et al.* (2014) demonstrated that local neighbourhood structure, partially mediated by tree species composition, is critical in understanding crown arthropod community composition (GED and ZED), branch and shoot herbivory damage (GED) and defoliation (ZED). Similar signals come from the Satakunta experiment (Finland) where bird predation, as part of an effective herbivory top-down-control, increased with neighbourhood-level diversity but not with stand-level diversity (Muiruri, Rainio & Koricheva 2015). Over larger time frames, the radius of influence (neighbourhood) will grow, so that also trees inside monospecific clusters of FORBIO will start responding to the unique conditions in mixtures.

In Chapter 3, FDis in IDENT-M was calculated on plot-level composition, but based on our insights on the importance of local neighbourhood dynamics, it would have been better to calculate FDis at a scale of local neighbourhoods. In IDENT-M trees of different species have been mixed at a tree-by-tree basis (no cluster planting) and accidental species clumping was also not allowed. Furthermore, plots are also smaller than in FORBIO, including just 64 seedlings. We can fairly assume that neighbourhood-level FDis will be very similar to plot-level FDis and that similar results would appear from each analysis. Even better than calculating FDis for all species present in a certain neighbourhood or plot, it is interesting to consider a tree-centralized approach. This approach should allow to estimate trait dissimilarity between a target tree and its neighbouring trees.

Figure 6-2 Tree planting in FORBIO was done in clusters of 3 × 3 trees of the same species. Because interaction mainly occurred at the scale of local neighbourhood, productivity of the centre trees was similar as the trees in plot-level monocultures. Cluster planting helps to sustain mixtures in the long run, a common practice mixed plantation systems. Photo: T. Van de Peer

6.2.5 Comparison with other experiments

Grossman *et al.* (2018) recently scanned all the research that uses data from TreeDivNet experiments and they found 143 peer-reviewed publications and 15 doctoral theses. Inspecting these studies, our conclusion is approved that very young trees have yet the capacity to modify its local environment, and therefore, that tree species interactions play some modest roles at the beginning of plantation development. Grossman *et al.* (2018) inspected tree survival, growth and herbivory and pathogen damage, which are usually considered as critical diversity-dependent ecosystem processes. Generally they concluded that tree diversity improves the survival and above- and belowground growth of young trees, but that damaging patterns are far less conclusive without further context.

Starting with seedling **survival**, Yang et al. (2013) documented higher plantation establishment success in monocultures compared to mixed-species plots in BEF China. Shrub survival in the same experiment was not affected by species mixing (Yang *et al.* 2017) and also Potvin and Gotelli (2008) concluded no steady survival differences at Sardinillia (Panama). We partially agree, because although plot-level survival did not change with mixing, we demonstrated a need to perform analyses for individual species or functional groups. Furthermore, from IDENT-M we revealed that mixing had a beneficial effect on seedling vitality during the dry Mediterranean summers. Although reduced vitality in monocultures did not cause severe mortality, it is possible that accumulation of drought stress over longer time frames may eventually cause higher mortality rates in monocultures compared mixtures.

We assessed seedling **vitality** as an integrated index of crown condition, independent from the origin of a possible deficiency. Many experimental work on seedling vitality handled about specific insect and fungal pathogen damages, rather than overall crown vitality condition. From these studies we learned that the presence of disease-prone species usually overrules the influence of diversity (Hantsch *et al.* 2013 in BIOTREE, Germany; Setiawan *et al.* 2014 in FORBIO, Belgium; Haase *et al.* 2015 in various experiments). Both associational resistances and associational susceptibility (Haase *et al.* 2015; Wein *et al.* 2017 in IDENT, Canada) have been reported and the effects are influenced by phylogenetic relatedness of trees (Setiawan *et al.* 2014; Damien *et al.* 2016 in ORPHEE, France), herbivore specialization (Castagneyrol *et al.* 2014), tree appearance (Castagneyrol, Régolini & Jactel 2014) and biological control (Zhang *et al.* 2017 in BEF China).

For tree **architecture** we agree with Lang *et al.* (2010) and Lang *et al.* (2012) that although saplings adapt their morphology to boost light harvesting efficiency, diversity is a poor indicator of plasticity. Only for *B. pendula* we observed an architectural shift with diversity. This appeared in a way that trees in monoculture had larger height-to-diameter ratios and faster rates of natural stem pruning. Effects were surely driven by a competitive release for the large-sized *B. pendula* when growing in mixture with smaller-sized trees of *Q. robur, T. cordata* or *F. sylvatica*. We nevertheless believe that architectural development and canopy structure will reveal valuable insights on BEF relationships in the coming years of FORBIO. This confidence comes from Williams (2017) who concluded that neighbourhood-driven crown plasticity enhanced canopy stratification and explained overyielding at IDENT (Canada) with almost closed canopies.

Finally, we found that neighbourhood diversity promotes stand **productivity**, a result that is in line with many other tree diversity experiments that run for several years (Sapijanskas *et al.* 2014; Tobner *et al.* 2016; Fichtner *et al.* 2017; Grossman *et al.* 2017; Williams *et al.* 2017). However, studies that analysed growth shortly after planting found that diversity is of little importance (Li *et al.* 2014; Haase *et al.* 2015; Setiawan *et al.* 2016b). Interestingly, the latter studies separated diversity effects on tree height and stem diameter, but trees in their early life stage experience a strong trade-off between height and diameter increment. So although competitive interactions among tree species can be explored through separate analyses of primary (height) and secondary (diameter) growth, trade-off hinders overyielding tests in immature stands.

6.3 Applied perspectives

Our overarching goal was to generate evidence-based recommendations on the establishment and initial management of species-mixed plantation systems. But before discussing advantages of species interactions, it is important to realize that the performance of planted seedlings primary depends on species identity characteristics and on local environment. Confirmation is given by the large variance components for species identity (FORBIO and in IDENT-M) and water availability (IDENT-M) in this thesis and by many more TreeDivNet reports (Healy, Gotelli & Potvin 2008; Hantsch *et al.* 2013; Tobner *et al.* 2014; Lübbe *et al.* 2016; Dillen 2017; Yang *et al.* 2017). Thus, species selection based on finding a match between niche requirements (from functional traits or silvicultural experience) and abiotic environment remains a fundamental precondition to achieve high establishment success. Because stress-tolerance levels vary remarkably over plant ontogenetic stages, this selection should partially rest on seedling niche requirements.

In Chapter 3 we stated that forest restoration projects often have a preference for native, late-successional species. Many of these are prone to stress, thus presenting low fitness at unsheltered and climatically tough planting sites. We demonstrated that nurse trees can contribute to forest rehabilitation success via mitigating environmental harshness and improving the persistence of mid- to late-successionals. In IDENT-M, facilitation was likely driven by *Pinus sp.* broadening the physical niche of broadleaved trees. Restoration pathways via positive nurse plant – seedling interactions should also work for other species combinations, depending on a local species pool (Bulleri *et al.* 2016). However, we suggested that *Pinus sp.* function superiorly as nurse plants because they combine fast juvenile growth with strong foliage clumping (Lintunen *et al.* 2013). This allows appropriately high levels of radiation transmission per unit crown area, which in turn allows facilitation to prevail over competition. The nurse trees can be planted like it is the case in IDENT-M, but may also be part of the spontaneously-established shrub vegetation in degraded areas.

Even if seedling ecology coordinates with local environment, there are no guaranties for success because weather and pest outbreaks unreliably fluctuate over time and space. We proved that planting tree mixtures can buffer a financial hangover under worst-case scenarios. If mixing occurs at small spatial scales, widespread mortality gaps will be less apparent. Apart from lowering replanting costs after serious events, a spatially regular seedling survival pattern allows optimal use of productive site capacity by advancing canopy closure. Shading under closed canopy limits spontaneous tree settlement, some of the invaded tree species may otherwise disturb management schemes. In the Sabah Biodiversity Experiment (Malaysia), Tuck et al. (2016) reported a second type of management insurance associated to planting mixtures. Relatively high rates of self-thinning in the best-performing monocultures can be wasteful if seedlings are costly or scarcely available. Early thinning operations before the stage of self-thinning are usually fruitless because trees have not yet reached minimum dimensions for commercial usability. Our last management notion on insurance is that buffering effects show an increasing but flattening trend with SR, likely due to functional niche overlap. Hence, management may profit from insurance after mixing just two tree species with different stress profiles. This result is essentially important in regions with small species pools or where other motivations play against the installation of highly-diverse stands.

Where trees settled well, more attention can be attributed to tree architectural development in function of local neighbourhood conditions. The creation of straight, branch-free stems is indeed crucial when the production of high-quality timber is targeted. Importantly, the valuable lower stem part is shaped in the beginning of plantation development. Some of the initially-developed stem irregularities are difficult to correct afterwards.

Similar as for planting success, a critical baseline for architectural development is a deliberate choice of tree species and provenances in function of the local context. Besides this, in Chapter 4 we demonstrated a general tendency that light competition triggers architectural plasticity. This result confirms that trees in a four-year old and so far unclosed plantation are controlling each other's development and functioning via direct tree-tree interactions. In contrast to competition intensity, diversity and composition did not yet matter.

In the next summer we organized an extra field campaign (Figure 6-3) to study managers' perceptions on tree quality in monocultures and mixtures (Van de peer *et al.* 2017, not part of the PhD thesis). In contrast to our expectations, tree quality was not defined by the morphological characteristics we initially investigated (height-to-diameter ration, number of thick branches, number of steep branches and branchiness), but rather by irregularities in stem spill, loss of apical dominance and tree lending. Particularly the latter two characteristics can cause permanent misshapes, unless actions are taken soon. Importantly, tree quality (and also its mediators: stem spill, apical dominance and tree lending) was not affected by neighbourhood diversity or composition. Among the 21 managers contributing to our field survey, a majority believed that tree quality is difficult to inspect at this plantation stage. Furthermore, many participants were not convinced about the economic profitability of early management interventions, like a preliminary selection and form-pruning of end-harvest trees. They nevertheless acknowledged that management actions to maintain species balances will be rapidly needed because large differences in species competitive tolerance and ability may stimulate competitive dominance. Planting in larger mono-species clusters reduces this need. But as seen before, it also slows down neighbourhood-mediated complementarity effects (Chapter 5) and it limits biodiversity insurance benefits to management (Chapter 2).

Figure 6-3 Discussion at the Pro-Silva excursion to study managers' perceptions on tree quality in monocultures and mixtures in the early stage of stand development. Photo: T. Van de Peer

Productivity scaled positive with tree diversity after six-growing years (Chapter 5), an important finding because primary productivity is an ecosystem service supporting many more. It is attractive to interpret results in the context of optimizing wood production objectives or carbon sequestration goals through mixed-species afforestation. However, because ecosystem dynamics may seriously shift throughout the course of plantation development, our study should be seen a first attempt to test if tree mixing is an appropriate strategy to combat biodiversity losses without substituting productive capacity. Only few tree diversity experiments are yet able to investigate temporal changes in DPR. In the Sardinellia experiment, for instance, it became clear that the magnitude of overyielding increased substantially over the years (Sapijanskas, Potvin & Loreau 2013). This shift was also found in grassland experiments (Cardinale *et al.* 2007). The positive DPR's are not unique to young stands or experimental set-ups, as is showed by forest inventory studies in Europe (Morin *et al.* 2011) and worldwide (Liang *et al.* 2016). In the latter study it was even quantified that a conversion of currently diverse forests to monocultures would reduce global wood productivity by 26 % - 66 %. This corresponds with a direct biodiversity value between $166 billion to $490 billion per year.

We presented some management advantages of planting mixtures instead of monocultures, most of these were brought about by ecological mechanisms like complementarity, selection and insurance. We finally need to reflect on their significance in the promotion of mixed-species plantations. However, this is extremely ambitious since the study covered six years of a 40 - 150 years plantation rotation cycle. Also in literature there is an enormous focus on evaluating ecological processes over short periods, rather than on quantifying what tree mixing means for long-term financial balances (Knoke *et al.* 2007; Knoke & Seifert 2008). Though, a large barrier to the adoption of plantation polycultures are additional costs, throughout the course of plantation development, induced by management complexity. Indeed, the conventional monoculture systems still function well in many production-oriented forest enterprises (Carnol *et al.* 2014), so why making things more complicated? Even where species mixing shortens plantation rotation periods or where it generates timber of higher quality, it is arguable whether diversity benefits can financially offset additional investments. For instance, if tree species face contrasting growth dynamics, such as *B. pendula* - *Q. robur* in ZED or *L. marschlinsii* - *F. sylvatica* in GED, pruning requires different intervention moments. Intermediate thinning of early-peaking species is also technically sophisticated. More time and well-skilled labour should avoid damaging of high-quality trees that needs be preserved (Puettmann *et al.* 2015). Other difficulties include advanced planning and administration for maintaining heterogeneous, species-diverse stands. The development of decision support tools to assist mixture design, planning and operational management should help minimizing extra costs. Also practical training programmes should promote the efficiency and effectiveness of mixed-species forestry schemes.

Moving beyond direct economic profitability, the picture of biodiverse forests presented in recent literature is anyway positive for their contribution to multifunctionality and ecosystem sustainability goals (Messier, Puettmann & Coates 2013; Puettmann *et al.* 2015). When a whole society benefits from a better provisioning of essential ecosystem services (i.e. regulating, supporting and cultural services), tree species mixing may be worth to be promoted, e.g. via governmental subsidy programmes (Millennium Ecosystem Assessment 2005b; Gamfeldt *et al.* 2013). In wealthy countries with low forest cover and many forests owners, Flanders is an excellent example, wood production is often a secondary household income, if one.

Notably these forest owners may be willing to leave conventional monoculture systems if they are well-informed, guided and acknowledged for their contribution to public services (Urquhart & Courtney 2011). Non-profit forest associations (e.g. regional forest groups In Flanders) are well-positioned to assist small-scale forest owners having insufficient silvicultural background for a sustainable, multifunctional management. Besides developing well-functioning ecosystems in terms of water use efficiency, litter decomposition, nutrient retention and biomass productivity, tree species mixing can be adopted as a risk-management strategy in the light of global change (Loreau *et al.* 2001). Research agrees that the conversion of conifer monocultures into conifer-broadleaved mixtures, a current policy objective in many European countries, is effective to improve stability. Mixed forests cope better with abiotic disturbance regimes (e.g. storm, fire and drought), pest outbreaks and wood markets price fluctuations (Knoke *et al.* 2007; Jucker *et al.* 2014a; Jactel *et al.* 2017). Sousa-Silva *et al.* (2016) unveiled that forest stability can be an important incentive for Belgian foresters to adapt their management. However, many feel constrained by their knowledge about forest conversion.

6.4 Future research perspectives

We close this general discussion chapter by reflecting on two emerging areas of scientific interest in the context of forest BEF.

6.4.1 Context-dependency

In literature it is often stated that patterns of BEF vary tremendously across different forest types and climatic zones, and that this variation is generally underpinned by resource availability, biotic growing space and trait dissimilarity (Jucker *et al.* 2016; Ratcliffe *et al.* 2017). Ratcliffe *et al.* (2016) for instance, demonstrated that water availability strongly modulate diversity effects in mature forests across Europe, with niche complementarity and trait differentiation being most relevant at latitudinal extreme (e.g. the Mediterranean). In accordance with postulations on context dependency of BEF, we found that the relative importance of mechanisms mediating mixture functioning was the same at all sites. The most obvious case was overyielding at the contrasting sites of FORBIO. Due to low site preparation investments, high vegetation pressure (mainly ferns) and harsh weather impacts at the clear-cut areas of GED, some mid- to late-successional species performed badly right after planting. This situation led to intense asymmetric competition between species in mixtures, with fast-growing trees dominating productivity and driving overyielding at the expense of others. A similar process was observed at the German BIOTREE site, where dominant conifers showed belowground productivity benefits next to inferior competitors (Lei, Scherer-Lorenzen & Bauhus 2012). At ZED, where all species settled quite easily, slow-growing species increased mixture productivity through complementarity interactions with fast growing neighbours. Dillen (2017) found that growth of oaks planted in pots and placed at the FORBIO sites were either positively (GED) or negatively (ZED) affected by shading. They therefore suggested that facilitation was more favourable at the harsh GED site, a conclusion that corresponds to the SGH but that opposes our findings. Most experimental studies handling context-dependency of BEF indeed built around a SGH, but often they only target one component of environmental stress (Forrester 2014). We believe, however, that the interplay between the environment (e.g. herbivory, soil fertility, water availability, climate, species environmental niches and management disturbances) and ecosystem responses to tree diversity is complex and hard to capture by focussing on one critical stress factor. Evaluating a complete picture of context-dependency is extremely challenging though, and it will require many more site replications.

Merging data from tree diversity experiments across important ecological gradients will likely generate essential insights, at least if the environmental and experimental contrasts between sites are accurately captured in the analyses. Some authors yet took first steps into the idea of multi-site comparison (Haase *et al.* 2015; Verheyen *et al.* 2015 and Dillen 2017) but they often merged data from few experiments along short ecological gradients. Large quantitative meta-analyses including a majority of the 25 TreeDivNet experiments are still lacking, although data on tree mortality, productivity and litter decomposition is available at nearly all sites. First initiatives are being undertaken (e.g. sampling mortality, tea bag litter decomposition and bird predation), and results can be expected in near future. Also, two critical ecosystem responses and functions, tree growth/survival and herbivore/pathogen damage, have been recently evaluated by scanning of all TreeDivNet papers before half 2017 (Grossman *et al.* 2018). This synthesis work demonstrated great variety of BEF relationships that emerged from these experiments. The outcomes can provide essential assistance to design future research about factors shaping BEF relationships. Importantly, synthesis work and quantitative meta-analyses are substantially more powerful if consistent protocols are used across the sites.

Environmental drivers of BEF can also be explored by incorporating them wisely into the design of a single experiment. One option is to statistically evaluate how within-site heterogeneity affect ecosystem responses to diversity. Although successful at some experiments with clear environmental gradients (Healy, Gotelli & Potvin 2008;

Bruelheide *et al.* 2014), site heterogeneity was unimportant to shape diversity-functioning relationships at FORBIO. An alternative strategy is to artificially create contrasting abiotic conditions at a certain site. The water irrigation treatment at IDENT-M is an obvious example, but species interactions did not delayed the onset of seedling drought stress. At FORBIO there is a tendency to *a posteriori* incorporate additional treatments to better understand context-dependency. For example, some saplings were made subject to drought by installing rainfall-exclusion shelters (Rahman *et al.* 2017). A last interesting option to better understand context dependency is to incorporate alternative management strategies into design. The most straightforward management interference in forestry is selective thinning. For instance, in GED it is plausible that competitive dominance of pioneer species will be reduced after selective thinning, opening the door for facilitative interactions and species coexistence. In conclusion, context-dependency can be scientifically tacked by many scientifically means. The insights will help overcoming a serious obstacle to generalize forest BEF relationships and to forecast mixed-species plantations dynamics in different settings.

6.4.2 Mechanistic framework

The second topic grounding follow-up research is the identification of biological processes stimulating greater forest functioning in mixtures. We discovered that trait-(in)dependent complementarity and competitive dominance effects play essential roles in FORBIO. But details on the ecology behind partitioning mathematics are seldom identified with direct evidence, surely not for forests. We went one step further, though, by relating partitioning outcomes with the functional composition of tree communities. We concluded that community-weighted means and functional diversity in shade tolerance alleviated competitive and facilitative interactions in mixtures. Still, our study faced many difficulties in its move towards a process-based understanding of BEF relationships.

The use of trait-base approaches is hinder by practical obstacles, with the first one being a lack of accurate trait data. Intra-species trait variability is often large due to inherent genetic variation and environmentally (diversity)-mediated trait plasticity. Therefore, trait data ideally needs to be directly measured at the focal trees. Some traits are labour-intensive to measure (e.g. root traits), others needs to be measured with sophisticated instruments (WD on saplings) and sometimes the protocol face problems to handle large within-organism trait variability (e.g. SLA at different crown parts). A second conceptual problem is that traits are underpinned by globally consistent trade-offs to create evolutionary successful plant functions and forms (Díaz *et al.* 2015; Kunstler *et al.* 2015). Shade tolerance, for instance, often negatively correlates with plant juvenile growth rates, both below and above the ground. In this perspective, it is difficult to link trait-based results with competitive processes for either light, nutrients, water, space or other resources. A last complicating factor, quite related with the second, is that biological processes occur simultaneously and at different spatial scales or trophic levels. Although we are certain that increasing CWM (GED) and FD (ZED) in shade tolerance stimulated overyielding, we may have overlooked a possible influences of e.g. decomposition improving nutrient availability, symbiotic associations improving water and nutrient uptake, or associational resistance causing lower herbivory pressure/pest infestations. These processes could not all be monitored within the PhD project.

To cope with the challenges, a next-generation of experimental research needs to design robust mechanistic-based protocols where a broad set of relevant pools/fluxes of energy/matter should be monitored. The idea of intensive monitoring is already successfully applied in the explorative platform FunDivEurope (Baeten *et al.* 2013), but tree diversity experiments have the additional advantage that initial conditions are known. Thus, stands can be easily evaluated for gradual changes in biotic and abiotic environment due to tree species diversity, identity and composition. Importantly, there is little empirical evidence regarding species belowground interactions and how they affect aboveground processes. We therefore finalize with the recommendation to thoroughly investigate BEF within a complete aboveground-belowground framework and across different trophic levels. Doing this will likely yield deeper mechanistic insights into the drivers of forest BEF.

6.4.3 Data collection in tree diversity experiments

This thesis research required many data that were collected with a simple instrumentation, mainly including ruler, telescopic measurement pole and calliper. Although we could define relevant tree architectural properties of 400 sapling within a timeframe of 2 months, the field campaigns will become more difficult when trees get larger and more complex. Also the direct measurement of tree diameter and heights to estimate biomass will be more complicated when foliage and branch get dens, which hinders the work efficiency. With the fast scientific developments in the field of remote sensing, data acquisition in tree diversity experiments can be substantially improved. Terrestrial laser scanning, for instance, uses laser pulses that are reflected on ground surfaces and vegetation layers canopies. After constructing a highly detailed three-dimensional (3D) surface model of individual crowns from neighbouring trees, productivity, biomass allocation, crown plasticity and canopy packing can be assed (Purves, Lichstein & Pacala 2007). Such data provide a solid basis to explore the mechanisms that ground mixed forest dynamics and biodiversity effects via aboveground tree-tree interactions. Another promising method to obtain 3D data of forest stands is with the use of digital photogrammetry based on multiple high-resolution aerial images with stereoscopic coverage obtained with UAV (Bohlin, Wallerman & Fransson 2012; Maes, Huete & Steppe 2017). Besides structural properties, a UAV equipped with visual, infrared and thermal camera furthermore allows to monitor forest health, evapotranspiration and thermal buffering of the different experimental plots. This data allows researchers to test the hypothesis that more diverse communities use water more efficiently and that these communities show better resilience against disturbances. First initiatives to quantify tree physiology and forest functioning using sensors on UAV are ongoing in FORBIO and in IDENT-M. Finally, the complications of trait data collection (section 6.4.2), which are critically important sources of information to quantify plant functioning, can be partially overcome with remote sensing technique. Indeed, in the area of specific near infrared, many leaf characteristics (e.g. C and N content) have unique reflectance spectra. This trait information can thus be derived from UAV flights with hyperspectral cameras. In conclusion, although conventional ground data methods will always remain essential, remote sensing also provide opportunities to efficiently monitor ecosystem functioning in the next stages of tree diversity experiments.

Larch trees in FORBIO HEC, 2018 (T. Van de Peer)

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Appendix I

General characteristics of the FORBIO experimental sites in Zedelgem, Hechtel-Eksel and Gedinne.

Soil types according to the Belgian Soil map are derived from Van Ranst and Sys (2000) and Bock et al (2007) and WRB codes are derived from IUSS Working Group WRB (2006).

MAP: Mean Annual Precipitation (mm/year); MAT: Mean Annual Temperature (°C); Tc: mean temperature of coldest month (°C); Tw: mean temperature of warmest month (°C); WAI: Water Availability Index (%)

Climate data from nearby meteo stations (KMI, 1981-2010, www.meteo.be): Lichtervelde (10 km to Zedelgem), Kleine-Brogel (12 km to Hechtel-Eksel), Bièvre (10 km to Gedinne).

WAI is defined as difference between precipitation and evapotranspiration relative to evapotranspiration (%) according to Vayreda et al. (2012):

$$\boldsymbol{WAI = \frac{MAP - PET}{PET}\, 100}$$

Potential evapotranspiration (mm/year) is calculated with monthly climate data according to Hargreaves & Samani (1982):

$$\boldsymbol{PET = \sum_{i=1}^{12} 0.0023\, (T_{max\,(i)} - T_{min\,(i)})^{0.5}\, (T_{mean\,(i)} + 17.8\,) R_{a\,(i)}}$$

where T_{mean}, T_{max} and T_{min} refer to mean, maximum and minimum temperatures of month i (°C); and R_a is the extra-terrestrial radiation of the crop surface (mm/month).

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Table I-1 General characteristics of the FORBIO experimental sites in Zedelgem, Hechtel-Eksel and Gedinne.

		Zedelgem	Gedinne	
Blocks		At the same field	**Gouverneurs**	**Gribelle**
Coordinates		51°9’N 3°7’E	49°59’N 4°59’E	49°60’N 4°59’E
Geographical region		Flanders plain	Ardennes highlands	
Elevation (m)		11-16	421-426	367-376
Area (ha)		9.5	4.5	4.5
Climate	MAP (mm)	687	1021	
	MAT (°C)	9.4	6.9	
	Tc (°C)	2.9	-1.0	
	Tw (°C)	16.3	14.4	
	WAI (%)	1.37	37.79	
Soil type	Belgian Soil map code / WRB code	Relatively dry sandy soil to moderately wet loamy sand soil	Moderately dry stony loam soils	
Former land use		Agriculture (mainly arable)	Broadleaved forest converted to spruce plantation in 1920	
Surrounding landscape		Mature deciduous forest (north – west) and pasture land (south – east)	Mixture of mature forest and agricultural land	
Timing of planting		Winter 2009- spring 2010	Early spring 2010	
Fencing		80 cm above ground and 20 cm below	2 m above ground	
Soil survey	Timing of sampling	June-July 2009	October 2009	
	Sampling protocol	156 sample points, with 78 points located on a circa 40 m × 40 m grid and 78 points randomly located within a c. 20 m radius around the sampled grid points. Samples were taken with a 3 cm diameter gouge auger	54 (Gribelle) & 54 (Gouverneurs) points, with 54 points located on a c. 40 m × 40m grid and 54 points randomly located within a c. 20 m radius around the sampled grid points. Samples were taken with a 3 cm diameter gouge auger at five spots: at the sampling point and at 0.5 m distance in all four cardinal directions. Samples were pooled per sampling depth.	

		at five spots: at the sampling point and at 0.5 m distance in all four cardinal directions. Samples were pooled per sampling depth.								
	Sampling depth	0-10 cm								
	Chemical analyses	Soil samples were dried for 48 h at 40 °C before sieving over a 2 mm mesh. The pH was measured using a glass electrode (Orion, model 920A) after extracting 14 ml soil in a 70 ml KCl (1 M) solution, respectively. Total P concentration was determined according to the colorimetric method of Scheel (1936) with molybdenum vanadate as colour reagent after acid wet digestion ($HClO_4$:HNO_3 in a 1:5 ratio). Carbon and nitrogen concentrations were determined by elemental analysis (Variomax CNS, Germany).								
	Soil variables	n (1)	Mean	CV (2)	n(1)	Mean Gouverneur	CV (2)	n(1)	Mean Gribelle	CV (2)
	pH KCl	156	5.07	6.71	54	3.64	6.64	54	3.93	4.72
	P_{tot} (mg kg^{-1})	156	1132	15.76	54	415	17.95	54	493	9.57
	N (%)	152	0.10	23.28	53	0.36	33.39	54	0.37	19.92
	C (%)	152	1.35	23.45	53	6.42	39.40	54	5.96	25.66
	C/N	152	13.41	12.34	53	17.5	9.17	54	15.86	9.15

(1) n = Sample size

(2) CV = Coefficient of variation (%)

Appendix II

Details on trait data measurement

Specific Leaf Area (SLA) is defined as the ratio of leaf area (cm^2) to dry mass (g) and Leaf Dry Matter Content (LDMC) is defined as the ratio of leaf dry mass (mg) to fresh mass (mg). Consistent with the trait-measurement handbook of Pérez-Harguindeguy (2013), we sampled for every species 12 outer canopy leaves in direct sunlight from trees in all monoculture plots (summer 2016). After collection, leaves were sealed in plastic bags and transported to the laboratory in cool boxes to prevent weight (or turgor) loss. In the lab, leafs were dried with towel and leaf petiole was removed. Fresh leaf weight was defined with micro-balance (Sartorius TE214S) and leaf area with ImageJ-software Rasband (n.d.) The leaves were stored in labelled paper envelopes, openly dried for 48 hours at 60°C and re-weighted. Another sample of 9 leaves per species was used to determine leaf nitrogen concentration (%), following the same criteria for leaf collection (summer of 2014). For this we used an elementar analyser, type Vario Macro Cube in configuration CNS, with Argon as carrier gas. A Trephor instrument (Rossi, Anfodillo, & Menardi, 2006) was used to collect high-quality wood samples for Wood Density (WD) estimations (summer of 2016). A Trephor allows to extract cylindrical microcores of 2 mm in diameter and 15 mm in length and was preferred to minimize damage to small-sized trees. The microcores were transported in Eppendorf microtubes in an ethanol solution (0.5 in water) and stored at 5°C. After removing bark, the volume of the microcores was determined following the suspension technique of Huges (2005). The technique is based on suspending an object in a water-filled container placed on electronic scales and is in accordance with the Archimedes principle. Samples were dried for 72 hours at 60°C and wood density (WD, g/cm^3) was calculated by dividing the oven-dry mass by the fresh volume of the wood samples.

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Appendix III

FORBIO site heterogeneity: PCA on the soil attributes and elevation.

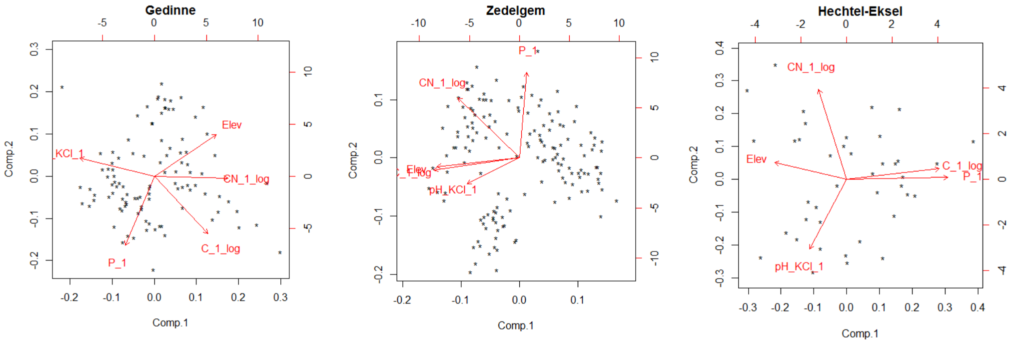


Figure III-1 Principal Component Analysis (PCA) on the soil attributes and elevation based on 108, 165 and 41 soil samples taken prior to plantation establishment in GED, ZED and HEC respectively (See Appendix 1 for mean attribute values and for more details on the soil sampling design). Stars refer to the soil samples and arrows to environmental variables. “C”: Carbon content (%); “P”: Phosphorus content (%); “pH_KCl”: pH measured in KCl solution; “Elev”: elevation (m); “CN”: Carbon to Nitrogen ratio. Skewed variables were log transformed to improve normality. For Gedinne, 51.7% of the variance was explained by PCA axis 1, which was positively correlated with log transformed C/N ratio and negatively with pH(KCl). For Zedelgem, the first PCA axis explained 42.6% of the total variance and was negatively correlated with elevation and log transformed C content. Finally for Hechtel-Eksel, PCA axis 1 was positively correlated with C and P contents and negatively with elevation, while accounting for 39.6% of the total variance. Axis 1 was used to reduce dimensionality of environmental variables in the regression models on sapling survival.

Appendix IV

Species compositions in FORBIO

Table IV-1 Presence of different species in each composition and different compositions on each site (Zedelgem, Hechtel-Eksel and Gedinne) are indicated with x. The species composition term is used as categorical variable with 50 different composition levels in a nested ANOVA.

Species composition	*A. pseudoplatanus*	*B. pendula*	*F. sylvatica*	*Larix* spp.	*P. sylvestris*	*P. menziesii*	*Quercus* spp.	*T. cordata*	Species diversity	Zedelgem	Hechtel-Eksel	Gedinne
1			x						1	x		x
2							x		1	x	x	x
3		x							1	x	x	
4								x	1	x		
5					x				1	x	x	
6						x			1		x	x
7				x					1		x	x
8	x								1			x
9	x		x						2			x
10					x	x			2		x	
11				x		x			2		x	x
12			x					x	2	x		
13			x				x		2	x		x
14	x					x			2			x
15					x		x		2		x	
16					x			x	2	x		
17		x					x		2	x	x	
18		x		x					2		x	
19				x			x		2			x

20		x			x				2	x		
21	x		x	x					3			x
22					x		x	x	3		x	
23	x			x			x		3			x
26	x					x	x		3			x
24		x					x	x	3	x		
27			x	x		x			3			x
25				x	x		x		3		x	
28			x			x	x		3			x
29				x		x	x		3		x	
30		x		x	x				3		x	
31			x		x		x		3	x		
33		x			x	x			3		x	
32		x	x					x	3	x		
34		x				x	x		3		x	
35		x	x		x				3	x		
37	x		x	x		x			4			x
36	x		x	x			x		4			x
39	x		x			x	x		4			x
38				x	x	x	x		4		x	
41	x			x		x	x		4			x
40			x		x		x	x	4	x		
44		x			x		x	x	4	x		
43		x		x	x	x			4		x	
45			x	x		x	x		4			x
42		x	x				x	x	4	x		
46		x		x	x		x		4		x	
47		x			x	x	x		4		x	
49		x		x		x	x		4		x	
48		x	x		x			x	4	x		
50		x	x		x		x		4	x		

Appendix V

Tree species compositions in IDENT-M.

Table V-1 Tree species compositions in IDENT-M. FD stands for the functional diversity gradient used to design to experiment. The presence of species in each composition is indicated by X.

Composition	FD	Species richness (SR)	*Quercus ilex*	*Quercus suber*	*Olea europea L.*	*Phillyrea latifolia L.*	*Arbutus unedo L.*	*Pistacia lentiscus*	*Pinus pinaster L.*	*Pinus halepensis L.*	*Pinus pinea L.*	*Fraxinus ornus L.*	*Acer monspessulanum L.*	*Quercus pubescens*
1	Monoculture	1	X											
2	Monoculture	1		X										
3	Monoculture	1			X									
4	Monoculture	1				X								
5	Monoculture	1					X							
6	Monoculture	1						X						
7	Monoculture	1							X					
8	Monoculture	1								X				
9	Monoculture	1									X			
10	Monoculture	1										X		
11	Monoculture	1											X	
12	Monoculture	1												X
13	Low	2											X	X
14	Low	2					X	X						
15	Low	2									X	X		
16	Low	2			X	X								
17	Low	2							X	X				
18	Low	2	X	X										
19	Medium	2								X			X	
20	Medium	2		X			X							
21	Medium	2							X			X		
22	Medium	2	X			X								
23	Medium	2									X			X
24	High	2			X						X			
25	High	2					X						X	
26	High	2				X						X		
27	High	2		X						X				
28	High	2						X						X
29	High	2	X						X					
30	Low	4									X	X	X	X
31	Low	4					X	X	X	X				
32	Low	4	X	X	X	X								
33	Medium	4		X		X					X		X	
34	Medium	4	X		X		X		X					
35	Medium	4						X		X		X		X
36	High	4		X			X			X			X	
37	High	4	X			X			X			X		
38	High	4			X			X			X			X
39	Low	6							X	X	X	X	X	X
40	Low	6	X	X	X	X	X	X						
41	Medium	6			X	X			X	X			X	X
42	Medium	6	X	X			X	X			X	X		
43	High	6	X		X		X		X		X		X	
44	High	6		X		X		X		X		X		X

Appendix VI

Meteo data IDENT

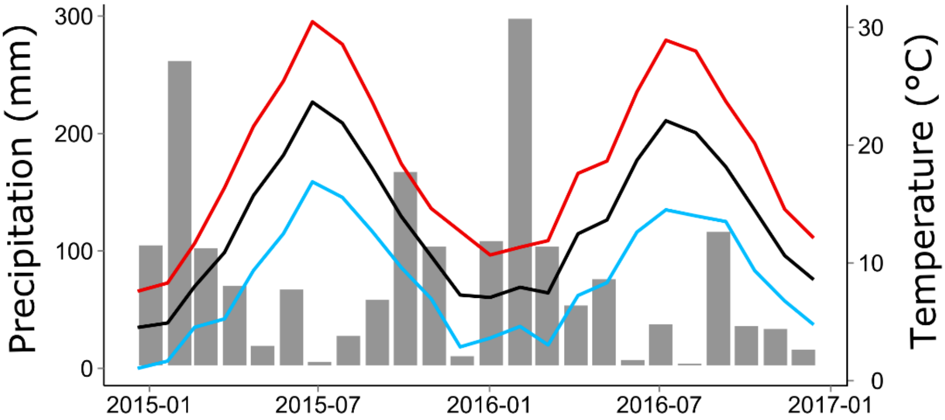


Figure VI-1 Summary of weather condition in 2015 and 2016 based on a meteo station on the IDENT-M site. Lines represent monthly-averaged maximum temperature (top), mean temperature (middle) and minimum temperature (bottom). Bars represent total precipitation at monthly intervals.

Appendix VII

Sapling mortality and vitality at IDENT-M

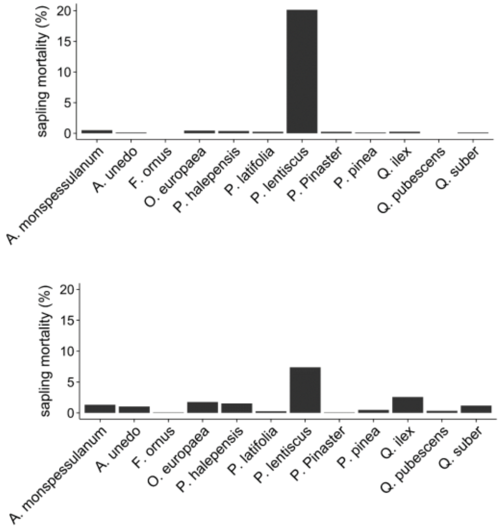


Figure VII-1 Species mortality rates observed in June 2015 (second year) and September 2016 (third year) are presented in upper and lower panel respectively.

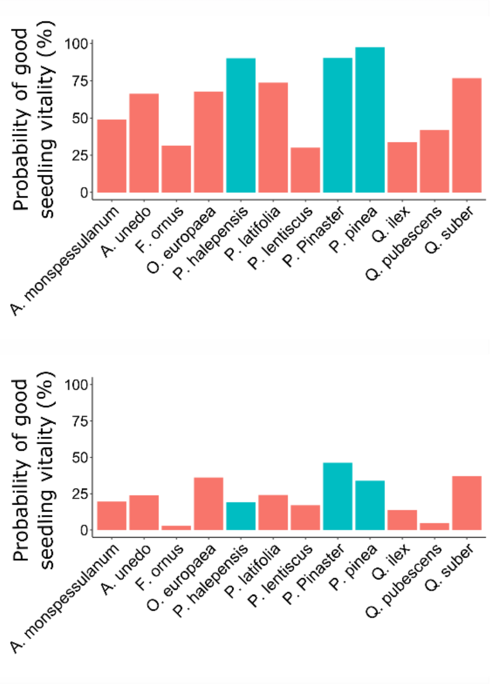


Figure VII-2 Species vitality observed in June 2015 (second year) and September 2016 (third year) are presented in upper and lower panel respectively. *Pinus sp.* are presented in blue and broad-leaved species are presented in red.

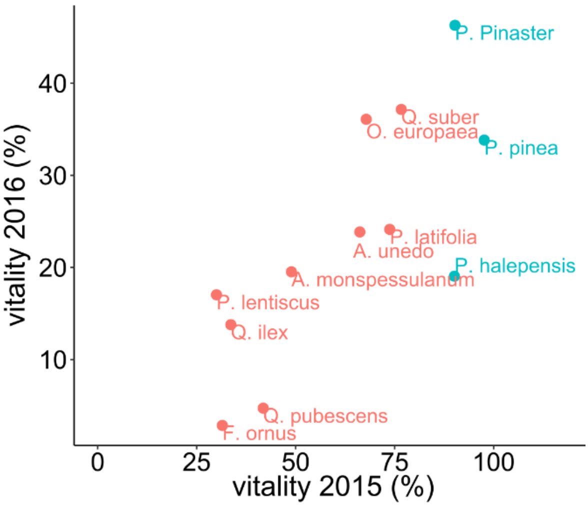


Figure VII-3 Species probability of good vitality (%) observed in June 2015 (second year) and September 2016 (third year). *Pinus sp.* are presented in blue and broad-leaved species are presented in red. Both vitality datasets have a Pearson correlation coefficient of 0.76 ($P = 0.004$).

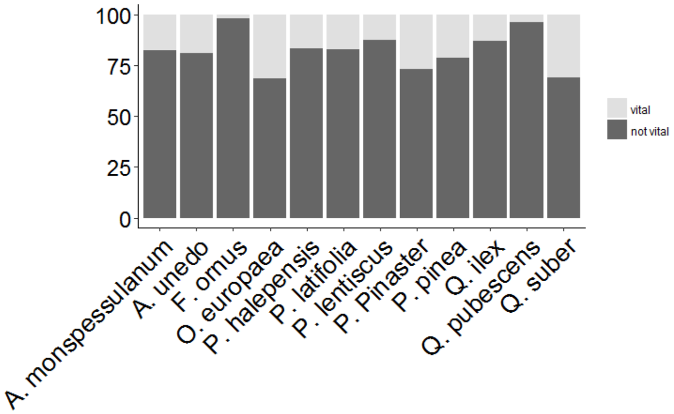


Figure VII-4 The figure shows how plants classified as not vital (vitality class zero) in June 2015 were performing in September 2016 in (%). *Circa* 25 % recovered during this period, and were scored as vital plants in September 2016. The other way around, circa 75 % did not completely recover during this period, and were still scored as non-vital trees in September 2016.

Appendix VIII

Aridity niches IDENT

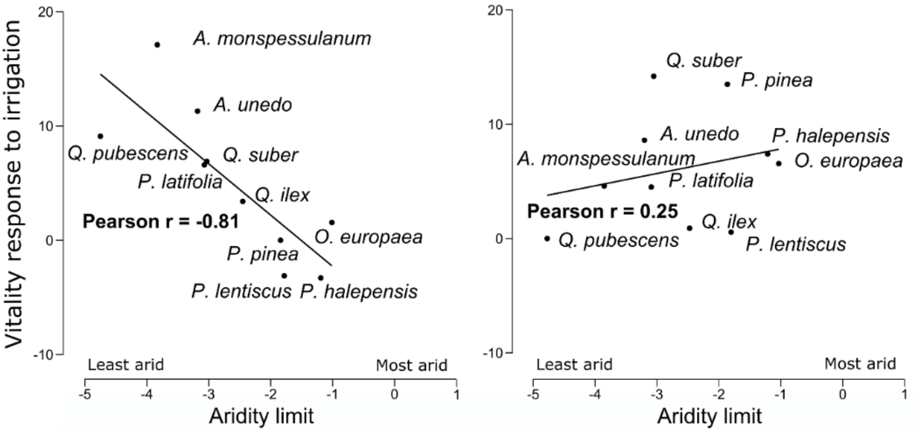


Figure VIII-1 Species response to irrigation (i.e. difference in vitality for species in irrigated compared to controlled conditions) regressed against species aridity limits (most arid locations species occur based on plant distribution models from the Spanish Mediterranean region, Costa-Saura et al., 2016). Left panel is the result from two-year vitality and the right panel is the result of three-year vitality. No aridity limits were available for the species *P. pinaster* and *F. ornus*.

Appendix IX

Biomass data IDENT-M

Table IX-1 Aboveground biomass (gram dry matter) in the second year was calculated based on biomass equations for seedlings of European tree species (Annighöfer et al 2016). AGB= B1(RCD²H)^B2, with AGB = aboveground biomass (g), RCD = root-collar diameter (mm), H = seedling height (cm), B1 and B2 are specific parameters for conifers and broadleaves.

Species	Height (cm)	Stem diameter (cm)
Acer monspessulanum	62.8	0.8
Arbutus unedo	93.0	1.8
Fraxinus ornus	81.2	1.7
Olea europea	40.9	0.8
Phillyrea latifolia	43.8	0.7
Pinus halepensis	110.8	2.4
Pinus Pinaster	100.6	2.5
Pinus pinea	73.3	2.9
Pistacia lentiscus	19.9	0.5
Quercus ilex	67.1	1.3
Quercus pubescens	62.8	1.3
Quercus suber	81.2	1.5
Total	71.0	1.5

	Stem diameter (cm)	Height (cm)	Aboveground biomass (g)
Broadleaved	1.1	63	102.5
Conifers	2.6	94.7	817.4

Annighöfer, P., Ameztegui, A., Ammer, C. *et al.* (2016) Species-specific and generic biomass equations for seedlings and saplings of European tree species. European Journal of Forest Research, 135, 313–329.

Appendix X

Trait correlations vitality IDENT-M

Table X-1 Pearson correlations between species traits and species-specific intercepts (vitality) and slopes for FDis and irrigation treatment from regression models 1 and 2 (see *material and methods* section of Chapter 3). Significant correlations (P < 0.05) are indicated in bold. SDW = seed dry weight (mg), Hmax = maximum height (m), SLA = specific leaf area (m^2/kg), LLS = leaf life span (days), Pnmax = maximum photosynthetic rate per unit area (µmol CO_2/m2 s^{-1}), Gsmax = maximum stomatal conductance (mol H_2O/m2 s^{-1}), PLC50 = water potential at which 50% of hydraulic conductivity is lost (mp), Nm = leaf nitrogen content per unit of mass (%), WD = wood density (g/cm^3), LA = leaf area (cm^2).

	Vitality data second-year (2015)			**Vitality data third-year (2016)**		
	Vitality	FDis	Irrigation	Vitality	FDis	Irrigation
SDW	0.01	-0.17	-0.03	0.04	0.18	-0.01
Hmax	0.57	-0.13	-0.18	0.51	-0.56	-0.25
SLA	**-0.64**	0.28	**0.77**	-0.61	0.32	0.37
LLS	**0.66**	-0.28	**-0.77**	0.61	-0.28	-0.18
Pnmax	-0.53	-0.22	**0.81**	-0.50	0.31	0.21
Gsmax	-0.52	-0.02	-0.02	-0.42	0.65	0.40
PLC50	-0.04	-0.17	0.39	-0.05	-0.50	-0.27
Nm	-0.61	0.17	0.59	-0.62	0.42	0.23
WD	-0.37	-0.10	-0.07	-0.34	**0.78**	0.43
LA	-0.58	0.11	0.51	-0.66	0.00	0.01

Appendix XI

Biomass correlations vitality IDENT-M

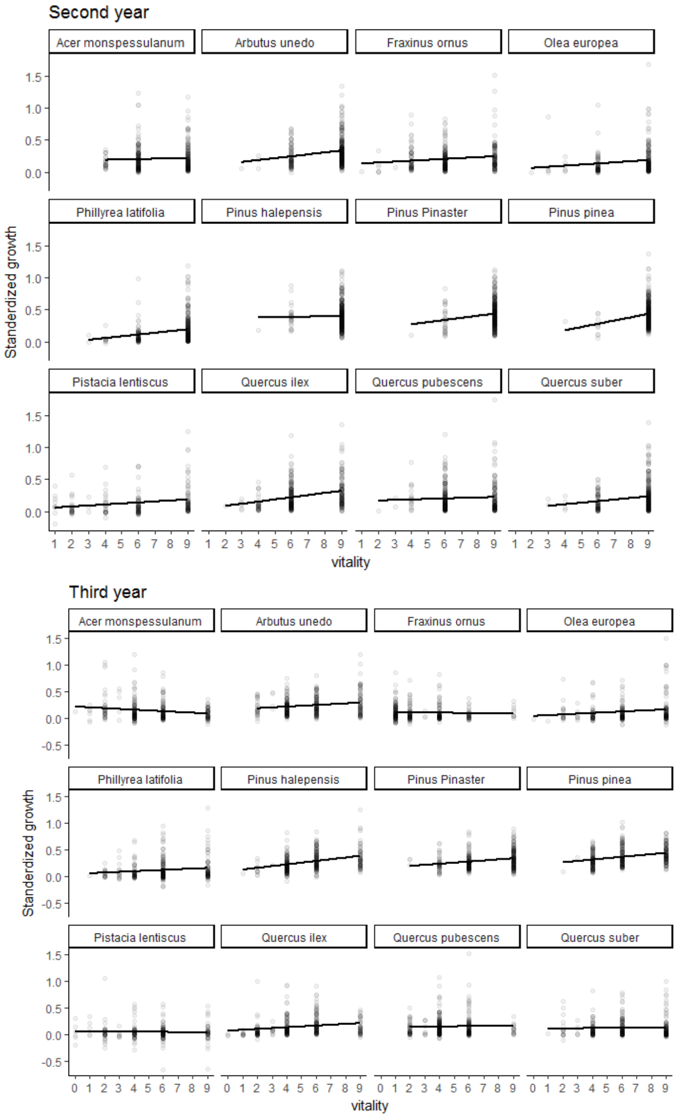


Fig XI 1 Relationship between Standardized seedling growth (%) and seedling vitality. Standardized seedling growth is defined as the annual aboveground biomass increment divided by the 99th percentile of each species. For a representative sample (N = 3802) of trees across all species and treatments, annual diameter and height data were available. Aboveground biomass data (in dry matter content) could be calculated based on the generic metrics described in Table VIII1. Seedling vitality was calculated by multiplying the scores of discoloration (1-3) and defoliation (1-3). Due to the imbalanced sample size in the second year, a binary vitality index was used in the main analyses of the manuscript.

Table XI 1 correlation coefficients between seedling vitality and standardized growth rates, as described in Figure XI 1

Species	Year 2	Year 3
Acer monspessulanum	0.07	-0.08
Arbutus unedo	0.21	0.17
Fraxinus ornus	0.17	0.05
Olea europea	0.14	0.19
Phillyrea latifolia	0.2	0.1
Pinus halepensis	0.04	0.31
Pistacia lentiscus	0.16	0.09
Pinus Pinaster	0.15	0.26
Pinus pinea	0.15	0.23
Quercus ilex	0.28	0.21
Quercus pubescens	0.06	0.02
Quercus suber	0.16	0.05

Appendix XII

Tree height distribution of species in FORBIO-ZED

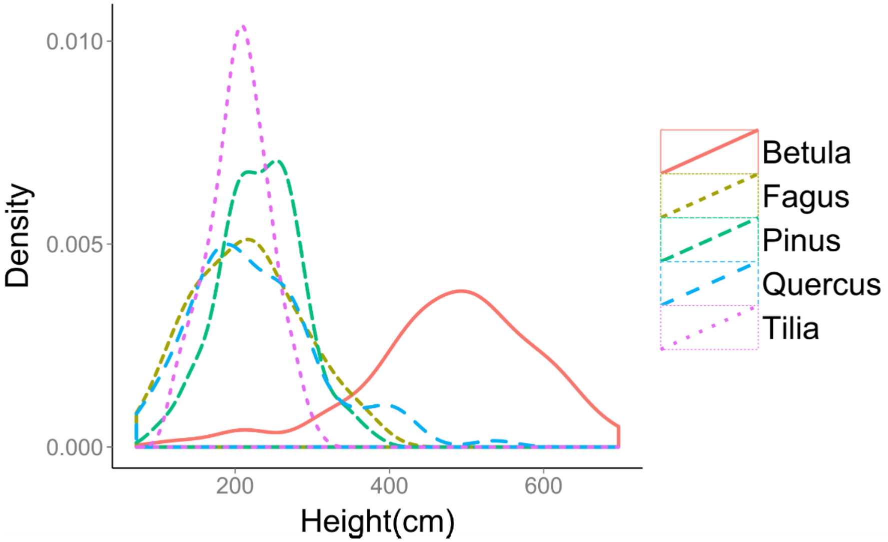


Figure XII-1 Density curves of the tree heights (cm) of the five study species in FORBIO-Zedelgem after five growing years

Appendix XIII

Branch architecture models

Table XIII-1 Parameter estimates and test statistics of tree level models (N=396) for branchiness (total branch number) and HD (tree height-to-diameter ratio) from summary output in R statistics; Td= stem diameter of target tree (cm); CI = competition index; FDis = functional diversity index; SDiv= structural diversity index; ":" indicates interaction.

	Branchiness Generalized linear mixed model				**HD** Linear model			
Variable	Estimate	SE	z-value	p (>|z|)	Estimate	SE	t-value	p (>|t|)
Intercept	2.62	0.38	6.87	**< 0.001**	68.78	15.07	4.56	**< 0.001**
Td	0.38	0.02	13.28	**< 0.001**	-12.19	1.13	-10.72	**< 0.001**
Species_Fagus	-1.81	0.45	-4.04	**< 0.001**	12.01	16.14	0.74	0.457
Species_Pinus	0.88	0.45	-1.97	**0.048**	2.44	17.82	0.14	0.891
Species_Quercus	-1.96	0.46	-4.26	**< 0.001**	3.96	16.21	0.24	0.807
Species_Tilia	-0.83	0.46	-1.81	0.071	-0.60	17.10	-0.04	0.972
CI	-0.28	0.10	-2.82	**0.004**	14.15	3.94	3.59	**< 0.001**
CI : Fagus	0.38	0.08	4.50	**< 0.001**	-9.92	4.56	-2.17	**0.030**
CI : Pinus	0.14	0.0	1.69	0.091	-11.66	5.19	-2.25	**0.025**
CI : Quercus	0.32	0.09	3.79	**< 0.001**	-6.68	4.49	-1.49	0.137
CI : Tilia	0.07	0.10	0.66	0.511	-6.81	5.08	-1.34	0.181
FDis								
SDiv								
	Random intercepts (StDev)		R^2					R^2
	PMZ	Residual	Conditional	Marginal				Conditional
	0.069	0.232	0.57	0.55				0.46

Table XIII-2 Parameter estimates and test statistics of branch level models (N= 1236 branches from 396 trees) for branch diameter and branch insertion angle; B.$_{rel.height}$ = branch height relative to total tree height (%); Td = stem diameter of target tree (cm); B.$_{angle}$ = branch insertion angle (°); CI = competition index; B.$_{azimuth}$ = (1−cos(θ))/2) with θ directional angle from north (°); FDis = functional diversity index; SDiv = structural diversity index.

FVariable	**Branch diameter**				**Branch insertion angle**			
	Linear mixed model				Linear mixed model			
	Estimate	SE	t-value	p (>|t|)	Estimate	SE	t-value	p (>|t|)
Intercept	1.89	0.060	31.45	**< 0.001**	35.57	8.75	4.07	**< 0.001**
B.$_{rel.height}$	-0.06	0.004	-15.96	**< 0.001**				
Td	0.14	0.012	11.90	**< 0.001**	1.15	0.62	1.85	**0.050**
B.$_{angle}$	-0.02	0.001	-14.08	**< 0.001**				
Species_Fagus	-0.44	0.073	-5.99	**< 0.001**	11.25	9.96	1.13	0.259
Species_Pinus	0.54	0.063	8.49	**< 0.001**	43.29	10.06	4.31	**< 0.001**
Species_Quercus	-0.37	0.073	-5.99	**< 0.001**	49.20	10.04	4.90	**< 0.001**
Species_Tilia	-0.10	0.068	-5.04	0.156	22.51	9.96	2.26	**0.024**
B.$_{angle}$: Fagus	0.01	0.001	5.82	**< 0.001**				
B.$_{angle}$: Pinus	0.01	0.001	-0.17	0.863				
B.$_{angle}$: Quercus	0.01	0.001	7.05	**< 0.001**				
B.$_{angle}$: Tilia	0.01	0.001	4.20	**< 0.001**				
B.$_{rel.height}$: Betula					-1.22	0.39	-3.16	**0.002**
B.$_{rel.height}$: Fagus					-1.98	0.48	-4.16	**< 0.001**
B.$_{rel.height}$: Pinus					-3.48	0.32	-10.96	**< 0.001**
B.$_{rel.height}$: Quercus					-2.68	0.49	-5.47	**< 0.001**
B.$_{rel.height}$: Tilia					-0.89	0.39	-2.30	**0.021**
CI					2.41	2.30	1.05	0.296
B.$_{azimuth}$					1.91	0.78	2.45	**0.015**
CI : Fagus					0.01	2.77	0.00	0.997

CI : Pinus					-1.61	2.84	-0.57	0.572
CI : Quercus					-8.11	2.69	-3.01	**0.003**
CI : Tilia					-4.84	2.89	-1.67	0.096
FDis								
SDiv								
$B_{rel.height}$: CI								
	Random intercepts (St Dev)				Random intercepts (St Dev)			
	Tree(Plot)	Plot	Residual		Tree(Plot)	Plot	Residual	
	0.117	0.016	0.373		6.588	3.146	17.440	
	$R^2_{Conditional}$	$R^2_{Marginal}$			$R^2_{Conditional}$	$R^2_{Marginal}$		
	0.43	0.37			0.39	0.31		

Appendix XIV

Example of additive partitioning approaches on net biodiversity effects

M_i	Yield of species i in monoculture
N	Number of species in mixture
Y_{oi}	Observed yield of species i in mixture
RY_{ei}	Expected relative yield of species i in mixture; This is the proportion of species i planted in mixture
RY_{oi}	Observed relative yield of species i in mixture; This is the ratio between yield of species i in mixture and monoculture
Y_{ei}	Expected yield of species i in mixture; This is the yield of species i without mixing effects
Y_e	Expected yield of the mixture; This is the mixture yield theoretically derived from monoculture yields
ΔRY_i	Rate of relative overyielding of species i; This is the difference between observed relative yield and expected relative yield for species i
$\overline{\Delta RY}$	Average level of relative overyielding across all species
$\overline{M}$	Average level of monoculture yield across all species
$Cov\,[x, y]$	Covariance between x and y = $\sum_{i=1}^{n} \frac{(x_i-\overline{x})(y_i-\overline{y})}{n-1}$

Y_{oP} = 342 kg
Y_{oT} = 63 kg
$Y_o = Y_{oP} + Y_{oT}$ = 405 kg
N = 2 species

RY_{eP} = 50 %
RY_{eT} = 50 %
$RY_{oP} = Y_{oP} / M_P$ = 63.5 %
$RY_{oT} = Y_{oT} / M_T$ = 65.6 %

$Y_{eP} = RY_{eP} \times M_P$ = 268.5 kg
$Y_{eT} = RY_{eT} \times M_T$ = 48 kg
$Y_e = Y_{eP} + Y_{eT}$ = 316.5 kg

$\Delta RY_P = RY_{oP} - RY_{eP}$ = 63.5 % - 50 % = 13.5 %
$\Delta RY_T = RY_{oT} - RY_{eT}$ = 65.6 % - 50 % = 15.6 %

$\text{NET DIVERSITY EFFECT} = Y_o - Y_e = 405\ \text{kg} - 316\ \text{kg} = 89\ \text{kg}$

Additive bipartite partitioning of Loreau and Hector (2001)

$\text{NE} = \text{CE} + \text{SE} = \text{N}\,\overline{\Delta \text{RY}}\,\overline{\text{M}} + \text{N cov}[\text{M}, \Delta\text{RY}]$

$\text{CE} = \text{complementarity effecvt} = \text{N}\,\overline{\Delta \text{RYM}} = 2 \text{ x } 15\% \text{ x } 316\ \text{kg} = 94\ \text{kg}$
$\text{SE} = \text{selection effect} = \text{N cov}\left[\text{M},\ \Delta\text{RY}\right] = 2 \text{ x } (-2{,}5\ \text{kg}) = -5\ \text{kg}$

Additive tripartite partitioning of Fox (2005)

$\text{NE} = \text{CE} + \text{DOM} + \text{TDC}$

$\text{CE} = \text{complementarity effect} = \text{N}\,\overline{\Delta \text{RY}}\,\overline{\text{M}} = 2 \text{ x } 15\% \text{ x } 316\ \text{kg} = 94\ \text{kg}$
$\text{TDC} = \text{trait-dependent complementarity} = \text{N cov}\left(\text{M}, \text{RY}_\text{O} - \frac{\text{RY}_\text{O}}{\text{RYT}_\text{O}}\right) = 2 \text{ x } (-0.48) = -1$
$\text{DOM} = \text{dominance} = \text{N cov}\left(\text{M}, \frac{\text{RY}_\text{O}}{\text{RYT}_\text{O}} - \text{RY}_\text{E}\right) = 2 \text{ x } (-1.835) = -4$

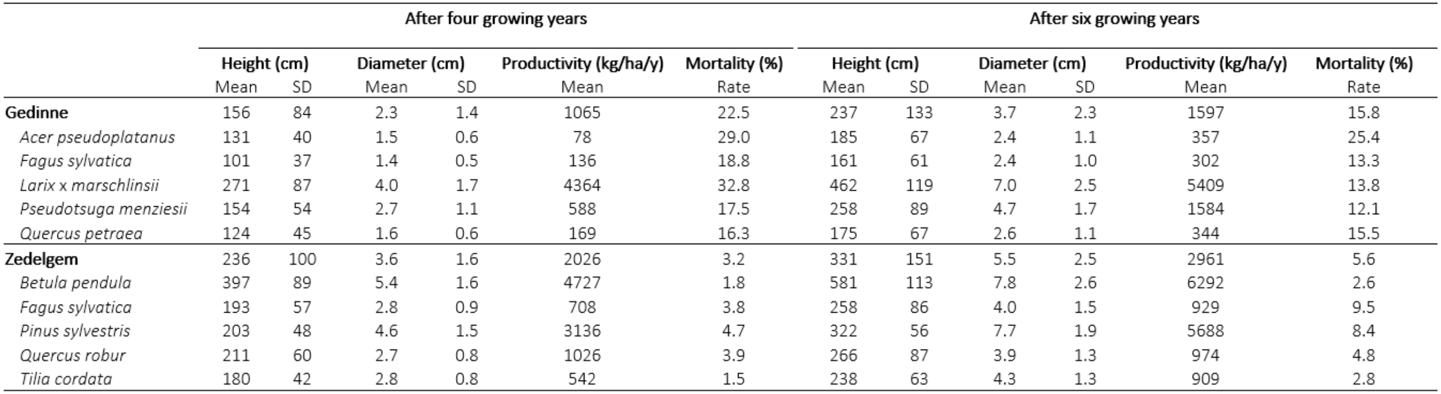
Fox, J.W., 2005. Interpreting the “selection effect” of biodiversity on ecosystem function. Ecol. Lett. 8, 846–856. doi:10.1111/j.1461-0248.2005.00795.x

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76. doi:10.1038/35083573

Appendix XV

Biomass data FORBIO

Table XV-1 Summary (Mean ± Standard Deviation) of tree height, stem diameter at 20 cm above ground level and biomass productivity for species in Gedinne, and Zedelgem evaluated after four and six growing years. Biomass productivity after four (six) years is defined as the yearly difference in standing biomass between the fourth (sixth) year and the second year. Mortality represents the percentage of trees that were dead or that could not be identified during the field visits in the fourth or sixth year, thus after the replanting period. A decrease in mortality between the years may be caused by trees that resprouted after being scored as dead. Growth rates are relative categories for species within the each site. As it is based on FORBIO data, represent growth of saplings under given environmental conditions at the sites. The categories are in the main text used to group species based on biomass/growth rate relative to each other.



	After four growing years						**After six growing years**					
	Height (cm)		**Diameter (cm)**		**Productivity (kg/ha/y)**	**Mortality (%)**	**Height (cm)**		**Diameter (cm)**		**Productivity (kg/ha/y)**	**Mortality (%)**
	Mean	SD	Mean	SD	Mean	Rate	Mean	SD	Mean	SD	Mean	Rate
Gedinne	156	84	2.3	1.4	1065	22.5	237	133	3.7	2.3	1597	15.8
Acer pseudoplatanus	131	40	1.5	0.6	78	29.0	185	67	2.4	1.1	357	25.4
Fagus sylvatica	101	37	1.4	0.5	136	18.8	161	61	2.4	1.0	302	13.3
Larix x marschlinsii	271	87	4.0	1.7	4364	32.8	462	119	7.0	2.5	5409	13.8
Pseudotsuga menziesii	154	54	2.7	1.1	588	17.5	258	89	4.7	1.7	1584	12.1
Quercus petraea	124	45	1.6	0.6	169	16.3	175	67	2.6	1.1	344	15.5
Zedelgem	236	100	3.6	1.6	2026	3.2	331	151	5.5	2.5	2961	5.6
Betula pendula	397	89	5.4	1.6	4727	1.8	581	113	7.8	2.6	6292	2.6
Fagus sylvatica	193	57	2.8	0.9	708	3.8	258	86	4.0	1.5	929	9.5
Pinus sylvestris	203	48	4.6	1.5	3136	4.7	322	56	7.7	1.9	5688	8.4
Quercus robur	211	60	2.7	0.8	1026	3.9	266	87	3.9	1.3	974	4.8
Tilia cordata	180	42	2.8	0.8	542	1.5	238	63	4.3	1.3	909	2.8

Curriculum Vitae

Personal Information

Name	Van de Peer Thomas
Date and place of birth	25/04/1990; Lier (Belgium)
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Education

2011 - 2013	Master in the Bioscience Engineering: Land- and Forest Management. Major: Forest and Nature; Minor: Agriculture *(Magna cum laude)*	KU Leuven, Belgium
2008-2011	Bachelor in the Bioscience Engineering : Land- and Forest Management (C*um laude*)	University of Antwerp, Belgium
2002-2008	Secondary education: Science-Mathematics	Sint-Ursula Lier, Belgium

Research experience

PhD research

- "Effects of tree species diversity on early-stage forest dynamics"
  Joint PhD KU Leuven Department Earth and Environmental Sciences – Ghent University Department of Forest & Water Management (2014 - present) Supervisors: Prof. Bart Muys and Prof Kris Verheyen

Publications in international journals with peer review cited in the Science Citation Index (IF: impact factor in 2016)

- **Van de Peer T**, Verheyen K, Baeten L, Ponette Q, Muys B (2016) Biodiversity as insurance for sapling survival in experimental tree plantations. Journal of Applied Ecology 53: 1777—1786. http://onlinelibrary.wiley.com/doi/10.1111/1365-2745.12839/full (IF = 5.301)

- **Van de Peer T**, Verheyen K, Kint V, Van Cleemput E, Muys B (**2017**) Plasticity of tree architecture through interspecific and intraspecific competition in a young experimental plantation. Forest Ecology and Management 385: 1-9. http://dx.doi.org/10.1016/j.foreco.2016.11.015 (IF = 3.062)

- Setiawan N, Vanhellemont M, Baeten L, **Van de Peer T**, Ampoorter E, Ponette Q, Verheyen K (2017). Local neighbourhood effects on sapling growth in a young experimental forest. Forest Ecology and Management, 384, 424-443. https://www.sciencedirect.com/science/article/pii/S0378112716307344 (IF = 3.062)

- **Van de Peer T**, Verheyen K, Ponette Q, Setiawan, NN, Muys B (**2017**) Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. Journal of Ecology (in press) http://onlinelibrary.wiley.com/doi/10.1111/1365-2745.12839/full (IF = 5.813)

- **Van de Peer T.,** Mereu S., Verheyen K., María J., Costa-Saura J., Morillas L., Roales J., Lo Cascio M., Spano D., Paquette A. & Muys B. (2018) Tree seedling vitality improves with functional diversity in a Mediterranean common garden experiment. Forest Ecology and Management, 409, 614–633 https://www.sciencedirect.com/science/article/pii/S0378112717314950 (IF = 3.062)

Publications in national journals or external reports

- Borremans L, Jacxsens P, Dalemans F, **Van de Peer T**, Aertsen W, Aerts R, Van Orshoven J, Muys B (2014). Verdere ontwikkeling van de Sim4Tree tool. Eindrapport na fase 5a. KOBE-rapport, 80 pp. Brussels, Belgium: Agentschap voor Natuur en Bos en Inverde.

- **Van de Peer T**, Vanhellemont M, Ampoorter E, Baeten L, Muys B, Ponette Q, Verheyen K (2015). 5 jaar FORBIO-Een tussentijdse update van het Belgische boomsoortendiversiteitsexperiment. Bosrevue, 54, 5-9.

- **Van de Peer T**, Verheyen K, Kint V, Muys B (2017). Boomvorm en kwaliteitsbeoordeling in jonge gemengde opstanden. Bosrevue, 62a, 1-9.

Theses

- **Van de Peer T** and Inge Van den Berg "Mitigation and adaptation strategies for global change: possibility's for wastewater treatment systems" (2011) BSc thesis University of Antwerp, Belgium
- **Van de Peer T "**Nest-site selection of Canabanis's Greenbul (*Phyllastrephus cabanisi*) in the Afromontane cloud forest of Taita Hills (Kenya)" (2013) MSc thesis KU Leuven, Belgium

Participation in congresses, symposia or meetings

- "Nest-site selection of Cabanis's Greenbul (*Phyllastrephus cabanisi*) in the afromontane forests of Taita Hills (Kenya)". **Van de Peer T**, Thijs K, Aerts R and Muys B"
Studiedag Starters in het Natuuronderzoek, Brussels, 15/03/2013

- "Effects of tree species diversity on vitality, growth and tree quality of young forest stands" **Van de Peer T**, Verheyen K, Muys B
EuMIXFOR training school, Solsona, 28/10/2013 – 31/10/2013

- "Tree mortality in a young diversity experiment", **Van de Peer T,** Verheyen K, Ponette, Q, Muys B
FORBIO annual meeting, Hechtel-Eksel, 26/01/2015

- "Response of branch architecture to neighbourhood competition in a young tree diversity experiment" **Van de Peer T**, Verheyen K, Muys B.
EEF conference Ecology at the interface, Rome, 21/09/2015 - 25/09/2015.

- "Response of branch architecture to neighborhood competition in a young tree diversity experiment" **Van de Peer T**, Verheyen K, Kint V, Van Cleemput, E, Muys B.
FORBIO annual meeting, Louvin-la-Neuve, 10/02/2016

- "Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance" **Van de Peer T**, Verheyen K, Ponette Q, Setiawan, NN, Muys B
TreeDivNet Workshop, Bordeaux, 31/01/2017 – 01/02/2017

- "Partitioning selection and complementarity to understand overyielding in tree diversity experiments" **Van de Peer T**, Verheyen K, Ponette Q, Setiawan, NN, Muys B
National Symposium for Applied Biological Sciences 7/02/2017

- “The relative contribution of species identity, diversity and irrigation to the vitality of Mediterranean saplings”, Van de Peer et al.
  FORBIO annual meeting, Brussels, 16/02/2017

- “Waarom soortenrijke bossen beter groeien” Van de Peer T and Boogers S
  Studiedag Starters in het Natuuronderzoek, Brussels, 24/03/2017

Scientific missions:

- Short Term Scientific Mission for COST Action FP1206 to Euro-Mediterranean Center on Climate Change (Dr. Simone Mereu)
  Sassari, Italy, 30/03/2016 to 08/04/2016

Post graduate courses

- Concepts of Multilevel, Longitudinal and Mixed Models; Academic year 2014-2015
- Intensive Academic Writing Course; Academic year 2016-2017
-

Supervision MSC thesis studens

- Elisa Van Cleemput; “Diversity and timber quality: tree morphology and branch architecture in a young experimental forest” Academic year 2014-2015
- Corinne Deffontaine; “Tree diversity can enhance biomass productivity in a young experimental forest” Academic year 2015-2016
- Valérie Adriaensen; “Effects of aboveground competition on the crown morphology of young trees in an biodiversity experiment” Academic year 2015-2016
- Frederik Gerits; “How are functional tree traits related to productivity in a young biodiversity experiment?” Academic year 2016-2017