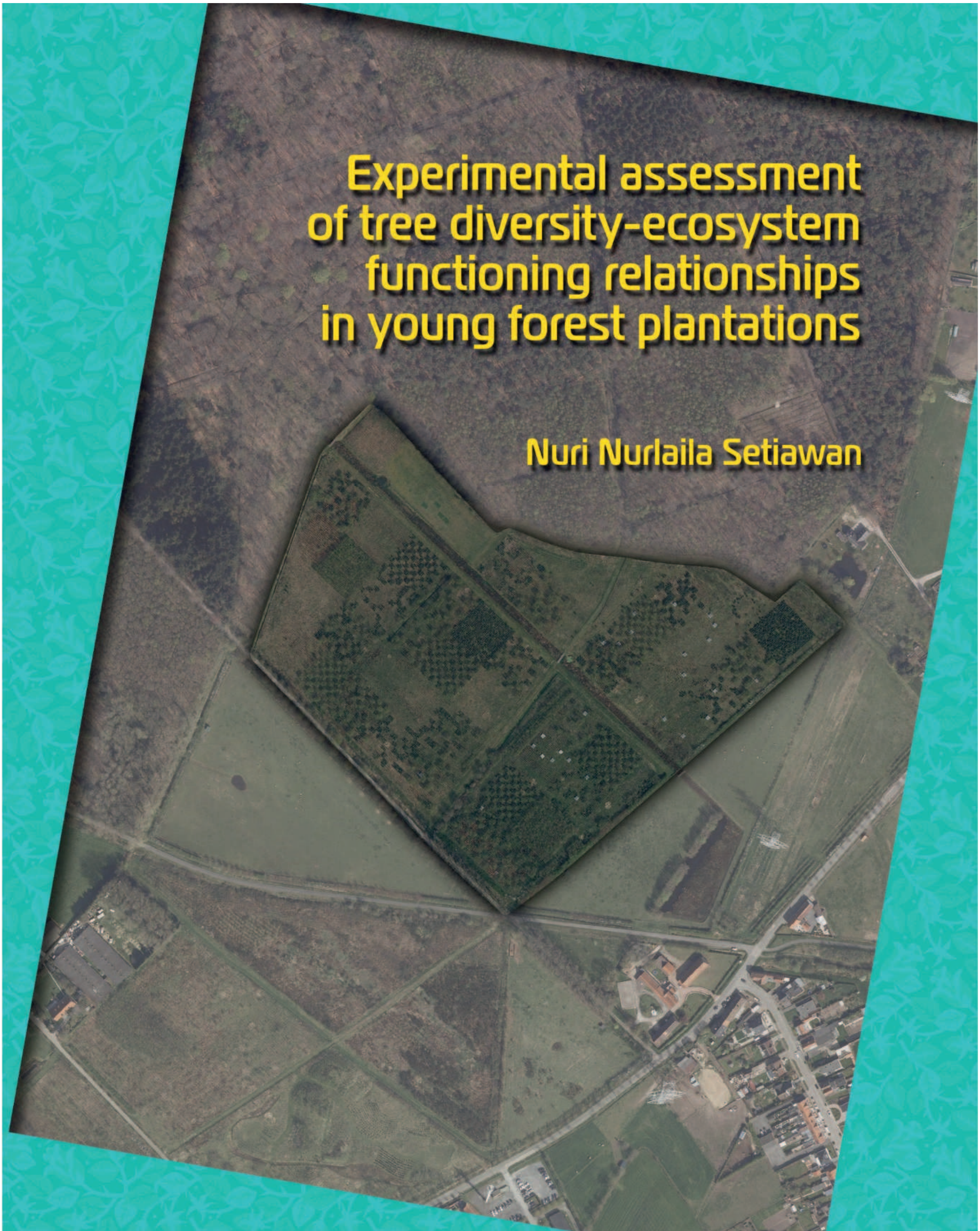

Experimental assessment of tree diversity-ecosystem functioning relationships in young forest plantations

Nuri Nurlaila Setiawan

UNIVERSITEIT GENT

FACULTEIT **BIO-INGENIEURSWETENSCHAPPEN**

In distant travels you learn about yourself

For Apa Ageung Setiawan,
who loved knowledge,
who always wrote in his journals, in sickness and in health

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EXPERIMENTAL ASSESSMENT OF TREE DIVERSITY – ECOSYSTEM FUNCTIONING RELATIONSHIPS IN YOUNG FOREST PLANTATIONS

Thesis submitted in fulfillment of the requirements

For the degree of Doctor (PhD) in Applied Biological Sciences:

Forest and Nature Management

Dutch translation of the title: De relaties tussen boomsoortendiversiteit en ecosysteemfunctioneren in jonge plantages onderzocht in het FORBIO-experiment

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Back: Aerial photograph of Gedinne site (Google Maps, 2016)
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This work is dedicated for all people who initiated and encouraged me to learn, to fall in love with knowledge, and to help me grow as a human being.

Nuri Nurlaila Setiawan

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Summary

Mixed forest plantations, delivering multiple ecosystem services, are generally recognized as more sustainable than monocultures. Mixing different tree species in forest plantations can increase the stand productivity, provide resistance to pests and diseases, and improve nutrient cycling processes. The more heterogeneous habitat created by mixed forests also provides diverse niches for associated biodiversity, such as arthropods. Although numerous studies looked into diversity effects in mature forest, mixing effects in the early stages of mixed forest plantations are still poorly understood. Tree species diversity experiments, such as the FORBIO experiment in Belgium, are a model platform to study the effects of tree species diversity and composition on forest ecosystem functioning throughout the different stages of forest development. The design of FORBIO allows unequivocally exploring the effects of tree species identity and diversity on three ecosystem functions.

The main objective of this thesis was to study early effects of tree species diversity and composition on three related groups of functions: primary production (tree growth), resistance to crown damage (crown damage and crown arthropod community composition), and nutrient cycling (litter decomposition). We focused on 9 different tree species in two study sites of FORBIO, which were planted in 2009 and 2010. We measured the saplings' increment between 2 years, assessed crown damage in 2 seasons, captured crown arthropods in 1 season, and studied litter decomposition rates by using litterbags for 60 weeks.

In our results, tree species identity explained the highest amount of variance in each function. A sapling's growth was additionally related with the characteristics of its local neighbourhood (notably phylogenetic diversity, relative size asymmetry, and ground vegetation cover). The crown damage of a sapling was influenced by the site characteristics and the timing of the assessment. The crown arthropod community differed between the landscapes, sites, and was related to sapling apparency and the phylogenetic diversity of the sapling's local neighbourhood. The decomposition rates of mixed litter were affected more by the identity of the litter species within the mixture than by the diversity of the litter *per se*, but the variability in litter decomposition rates decreased as the litter diversity increased. We expect that the diversity effects will become more apparent as the trees start to interact and develop a closed canopy. Interesting patterns were already developing and some management guidelines can be formulated.

Samenvatting

Gemengde bossen die meerdere ecosysteemdiensten leveren worden algemeen beschouwd als meer duurzaam dan monoculturen. Plantages waarin verschillende boomsoorten samen geplant worden, zouden meer hout kunnen produceren, beter bestand zijn tegen ziekten en plagen en nutriënten beter recycleren binnen het systeem. De grotere habitatheterogeniteit in gemengde bossen kan bovendien veel verschillende niches bieden voor een diverse gemeenschap van geassocieerde soorten. Tot nog toe zijn de effecten van boomsoortenmenging vooral onderzocht in volwassen bossen; over jonge plantages is weinig geweten. Boomsoortendiversiteits-experimenten zoals het Belgische FORBIO-experiment bieden unieke mogelijkheden om de rol van boomsoortendiversiteit en -samenstelling te bestuderen doorheen de verschillende fasen van bosontwikkeling. Het specifieke ontwerp van het FORBIO-experiment maakt het bovendien mogelijk om ondubbelzinnig te bestuderen hoe zowel specifieke boomsoorten als boomsoortendiversiteit het functioneren van een bos beïnvloeden.

De doelstelling van dit doctoraat was het zoeken van relaties tussen de boomsoortendiversiteit en –samenstelling van jonge plantages en hun primaire productie (boomgroei), weerstand tegen schade (kroonschade, geleedpotigen in de kroon) en nutriëntencyclus (strooiselafbraak). Op twee FORBIO-sites, geplant in 2009 en 2010, werden negen verschillende boomsoorten bestudeerd. De groei van de jonge boompjes werd gemeten tussen 2012 en 2014, de kroonschade werd geëvalueerd in twee seizoenen (herfst 2012, zomer 2013), de geleedpotigengemeenschap in de kronen werd bemonsterd in 2012 en de strooiselafbraak werd bestudeerd door het opvolgen van strooiselnetjes gedurende 60 weken.

Het grootste deel van de variatie in de bestudeerde ecosysteemfuncties was toe te schrijven aan de verschillen tussen boomsoorten. De groei van de jonge boompjes werd bijkomend beïnvloed door de fylogenetische diversiteit en relatieve grootte van hun buren en de bedekking van de kruidlaag. De kroonschade verschilde tussen de twee sites en jaren. De samenstelling van de geleedpotigengemeenschap in de kroon verschilde tussen en was gerelateerd aan het omringende landschap, de site, de fylogenetische diversiteit van de buurbomen en de zichtbaarheid t.o.v. de buurbomen. De aanwezigheid van strooisel van bepaalde soorten was belangrijker dan de diversiteit van het strooisel voor de afbraaksnelheid, maar meer divers strooisel vertoonde wel minder variatie in afbraaksnelheid. Naarmate de bomen ouder worden en een gesloten kronendak gaan vormen, zullen diversiteitseffecten wellicht duidelijker worden. We zagen nu al enkele interessante patronen tot ontwikkeling komen en konden ook een aantal richtlijnen voor beheer formuleren.

List of abbreviations and symbols

Abbreviations

BEF	biodiversity and ecosystem functioning (relationships)
CI	confidence interval
df	degrees of freedom
expH	exponent of the Shannon diversity index
ha	hectare
MNTD	mean nearest taxon distance
MPD	mean pairwise phylogenetic distance
SE	standard error of mean

Symbols

k	decomposition rate
N	number of samples
p	significance of statistical test
r	Pearson correlation coefficient
R^2	coefficient of determination

Definition of some terms used in the thesis

deforestation	the direct human-induced conversion of forested land to non-forested land
phylogenetic diversity	measure of diversity which incorporates the species' evolutionary relationships, that is the phylogenetic differences between species
reforestation	re-establishment of forest formations after a temporary condition with less than 10% canopy cover due to human-induced or natural perturbations
trait	any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization (Violle et al. 2007)
tree plantation	Forest sites that have been specifically planted, very often with one tree species that provides the desired commercial output (e.g. construction wood). Spontaneous colonization of other tree species can occur as well, but these species are usually not managed or even removed to avoid competition with the 'target' species.

Zedelgem site after (left) and before (right) ploughed [Photograph: ForNaLab]

Chapter 1

General introduction

Forests have an important role in human health and well-being, by providing multiple benefits to society (Stenger et al. 2009, Bravo-Oviedo et al. 2014). These benefits are called *ecosystem services* and include wood production, CO_2 uptake, water purification, providing habitat to animals and plants, offering recreational areas, and many more. The increase of human activities has an important impact on the present-day forests. In Europe, historical forest clearing for arable land and pasture has often drastically decreased the forest area, and forest exploitation for fuelwood and construction material has changed the forest structure and composition (Williams 2000, Kaplan et al. 2009, Pan et al. 2011). In current forest management plans, foresters generally aim to expand forest areas and utilize resources in more sustainable ways. Recent research has greatly promoted our understanding about how to manage forests in a sustainable way and meet the complexity of societal demands. Planting and maintaining mixed forest has been recognized as an important strategy to create forests with higher levels of resilience and resistance to environmental hazards and a more diverse portfolio of environmental services (Bravo-Oviedo et al. 2014).

Understanding the historical perspectives and the characteristics of mixed forest as a form of sustainable forest management may help to gain a better knowledge on designing and maintaining sustainable forest in the future. The following sections will briefly explain the history of forestry in Europe, which led to the choice of mixed forest as a desirable form of sustainable forest management. Then, the characteristics and mechanism involved in mixed forests are described. Finally, the questions that will be addressed in this dissertation are outlined and related to tree diversity effects on four main ecosystem functions in young forest plantations: growth, damage, arthropod community, and litter decomposition.

1.1 History of forestry in Europe

European landscapes have been largely transformed by anthropogenic deforestation, which started with the establishment of arable land in the mid Holocene era (Kaplan et al. 2009). Since then, forest cover in Europe has been substantially altered (Fig. 1.1). The deforestation in Europe principally occurred in two waves: (1) in the fourth century, during the Roman empire; (2) between the eleventh and twelfth century, following the expansion of arable land due to the growing population and increasing charcoal demand by the iron industry (Powers 1999, Verheyen et al. 1999).

Starting in the fifteenth century, some regions of Europe suffered from timber shortage that led to economic collapse. Advances in the knowledge have raised the collective awareness that forests and timber were not infinite resources (Powers 1999). In his book *Sylvicultura oeconomica*, von Carlowitz (1713) coined the term **sustainable forest management**, which suggests ideas to ensure lasting supply of wood and to create permanent economic wood resources. Some of these ideas were: using energy-efficient smelting furnaces, improving the insulation of the houses, improving agricultural land management practices, and re-planting the forests (Schmithüsen 2013). Reforestation with reliable methods started to flourish, especially in Germany, Austria, France, and Switzerland (Powers 1999).

Since the sustainable forest management concept has started to be widely recognized and implemented, a scientific debate emerged on how planted forests should be established and maintained to fulfill multiple functions. In general, there are two main opinions: the use of monoculture forest plantation versus mixed forest plantation (Knoke et al. 2008). The use of monocultures has been often preferred given the economic advantages related to growth rate and wood quality, such as efficient production of timber and low productivity decline when well-managed (Powers 1999, Cossalter and Pye-Smith 2003, Kelty 2006). However, concerns emerged over several drawbacks of even-aged monocultures. Monoculture forest plantations, especially those planted with conifers, for instance, resulted in a substantial decrease of forest structural diversity and soil degradation (Knoke et al. 2008, Leuschner et al. 2009). Mixed forest, on the other hand, are considered more resistant against biotic and abiotic disturbances (Spiecker 2003). They have the potential to offer a more complex forest structures and wider gradients in ecological conditions, thus providing a variety of habitats for different species and potentially promoting higher biodiversity than monocultures (Tews et al. 2004, Knoke et al. 2008).

Progress in the ecological research at the end of 20th century provided support to the use of mixed forest for sustainable forest management in Europe. Since the 1970s, the increasing loss of biodiversity caused by habitat destruction in the world raised concerns on the potential impacts on the functioning of the ecosystem (Chapin III et al. 2000, Cottingham et al. 2001). Ecologists tried to find the link between the biodiversity loss on ecosystem functioning through experiments

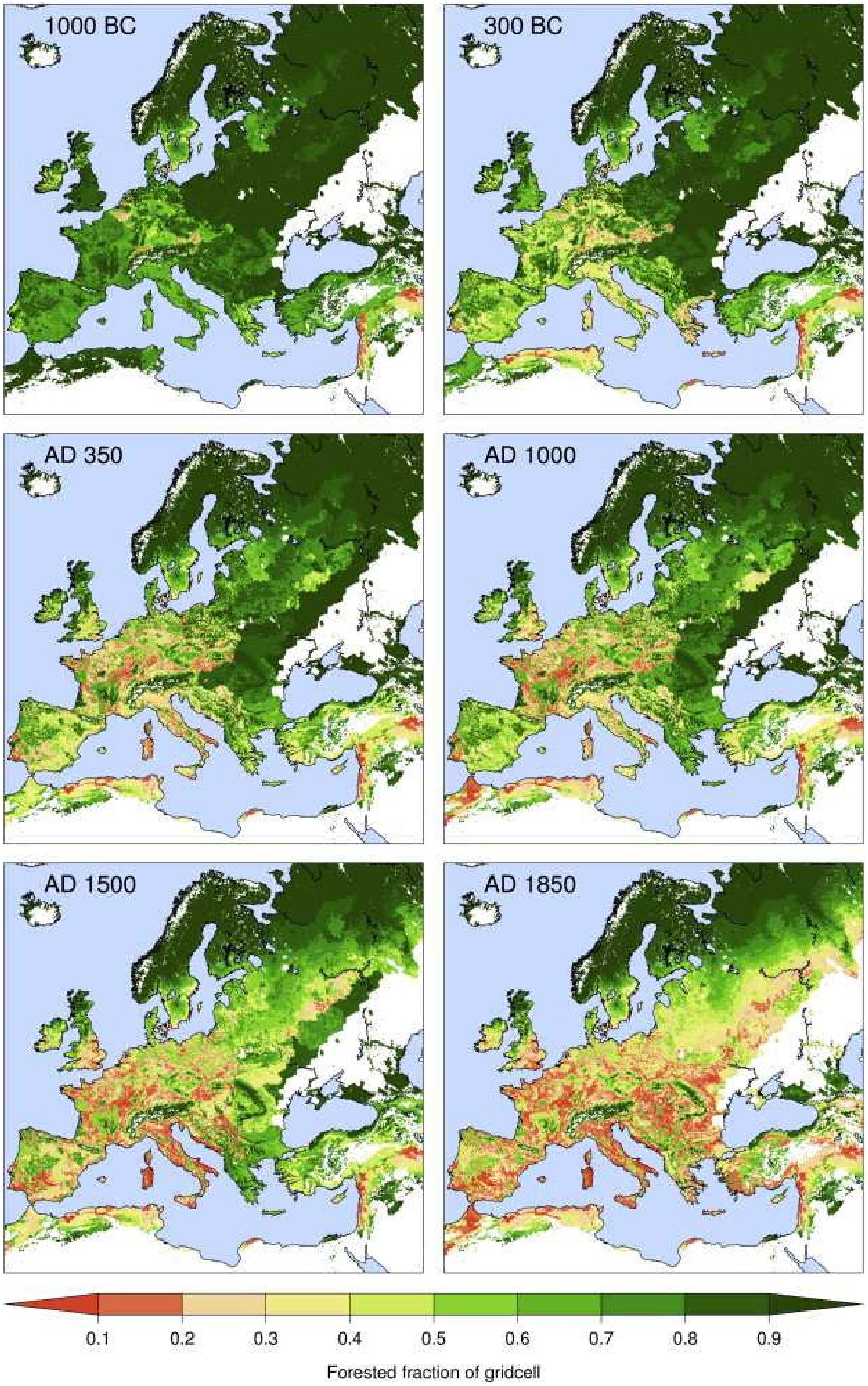


Fig. 1.1 Historical deforestation map of Europe for 1000 BC, 300 BC, AD 350, AD 1000, AD 1500, and AD 1850 generated by the anthropogenic deforestation model by Kaplan et al. (2009). White areas were not considered as forest.

and quantitative measurements on different types of ecosystems. Hypotheses stated that greater diversity would lead to greater primary productivity, more efficient use of resources, decreased susceptibility to herbivory and diseases, more efficient nutrient-cycling, and greater ecosystem stability (Prescott 2000, Cardinale et al. 2012, Tilman et al. 2014). A new paradigm on ecological research called biodiversity-ecosystem function (BEF) emerged (Naeem 2002): biodiversity is no longer considered as a passive consequence of environmental conditions and interactions between species, but it is recognized that differences in biodiversity can largely affect ecosystem functioning (Baeten et al. 2013). More recent studies have started to explore the role of biodiversity for maintaining multiple ecosystem processes and services. Given the functional complementarity of species, different species carry out different functions at any time, the importance of biodiversity for overall ecosystem functioning increases when multiple functions are considered (Hector and Bagchi 2007, Isbell et al. 2011, Gamfeldt et al. 2013).

1.2 Biodiversity and ecosystem functioning

To understand the relationship between tree diversity and forest ecosystem functioning, mixed forest and ecosystem functioning should be first defined carefully. There are different definitions of mixed forest, following a compositional, structural, functional, or developmental approach. Perhaps the most recent and complete definition was the one offered by Bravo-Oviedo et al. (2014):

A mixed forest is a forest unit, excluding linear formations, where at least two tree species coexist at any developmental stage, sharing common resources (light, water, and/or soil nutrients). The presence of each of the component species is normally quantified as a proportion of the number of stems or of basal area, although volume, biomass or canopy cover as well as proportions by occupied stand area may be used for specific objectives. A variety of structures and patterns of mixtures can occur, and the interactions between the component species and their relative proportions may change over time.

Ecosystem functioning is a broad term, which encompasses a variety of phenomena, such as ecosystem properties, ecosystem goods, and ecosystem services (Christensen et al. 1996). In many cases, ecosystem functioning was defined only as ecosystem properties, i.e., stocks of materials (water, minerals, nutrients, carbon, etc.) and rates of processes involving fluxes of materials and energy (Hooper et al. 2005).

In recent years, numerous studies explored tree diversity effects on forest ecosystem functioning. Several studies showed a wide range of benefits gained from mixed forests, such as:

(1) higher productivity than their monoculture counterparts (Kelty 1992, Cardinale et al. 2007, Morin et al. 2011, Vilà et al. 2013, Jucker et al. 2014, Tobner et al. 2016)
(2) higher ecological stability – resulting from more complex structures - and thus higher adaptability to climate change (Wagner et al. 2014)
(3) higher resistance and resilience to disturbances, such as pests and diseases (Spiecker 2003, Jactel et al. 2005, Jactel and Brockerhoff 2007) or storm and snow (Wonn and O'Hara 2001)
(4) multiple niches to be exploited by the associated biodiversity (Tews et al. 2004) of birds (Estades 1997, Berry and Bock 1998), earthworms (Cesarz et al. 2007), mammals (Estrada et al. 1994, Ecke et al. 2002), and arthropods (Siemann et al. 1999, Sobek et al. 2009b, Oxbrough et al. 2012) because of a more complex physical structure with diverse levels of environmental resources
(5) higher leaf litter decomposition rates, which contribute to more efficient nutrient cycling process and ensure soil nutrient availability (Gartner and Cardon 2004, Gessner et al. 2010, Jacob et al. 2010b, Handa et al. 2014)

Since trees of a particular species acquire resources in a similar way, competition within species (intraspecific) is expected to be stronger than between species (interspecific) (Kunstler et al. 2016). The strength of the interactions between trees will depend on the species identity, tree density and age or size differences, distance, and phylogenetic relatedness between trees (Srivastava and Vellend 2005, Barbosa et al. 2009, Ness et al. 2011, Castagneyrol et al. 2014, Kunstler et al. 2016). The positive effects of mixed stands can be explained by two general mechanisms, i.e., **complementarity** and **selection**. The complementarity effect quantifies the combined effects of species interactions on mixture performance after accounting for changes in the relative abundances of species. Positive values result when mixtures do better than expected based on the relative abundance of the present species and the monoculture performances of these species, which is consistent with 'niche differentiation' in terms of resource partitioning, facilitation, or diversity-dependent effects of natural enemies (Baeten et al. 2013). The most common example of complementarity and facilitation in plant communities is overyielding, in which the primary production in the mixtures exceeds the expectations based on the monocultures yields (Hooper et al. 2005, Tobner et al. 2016). An example of facilitation is where the presence of certain species gives benefits to the other species by ameliorating the physical and biotic environment, such as the presence of nitrogen-fixing species in the mixture (Scherer-Lorenzen 2005).

The selection effect occurs when a species with a beneficial trait becomes dominant in the mixture and has a strong (positive or negative) effect on the ecosystem functioning (Loreau and Hector

2001). For example, when a productive species with a higher growth rate compared with the others in the mixture becomes dominant and enhances the overall yield of the mixture. Increasing species richness can promote a mixture's overall ecological functioning because it increases the probability of including a species with beneficial traits that ultimately will dominate the response of the community (Cardinale et al. 2007, Morin et al. 2011).

Irrespective of the two mechanism mentioned, the main underlying cause of tree diversity effects on ecosystem functioning relies on the trait differences among the species in the mixture. Numerous studies have shown that the **identity effect** (identity of the species within a mixture) is more important than the **diversity effect** (number of species) *per se* (Scherer-Lorenzen 2005). The identity of individual trees and their traits will determine the interactions with the neighbouring trees (Kelty 2006). The species' traits control the physiological needs for particular resources and the structural means to obtain these resources (Jose et al. 2006). These trait differences can lead to increased capture of resources (Kelty 1992). Certain traits such as nitrogen-fixing will facilitate the growth of the neighbours by improving soil fertility and increasing the nutrient availability (Forrester et al. 2006). When the needs and physical structure of component species overlap, species will generally compete for resources with their immediate neighbours (Schütz 1999, Yang et al. 2003).

Trees interact in a small local area or neighbourhood and are directly influenced by their neighbours (**neighbour effects**). The presence of certain neighbours might positively affect the trees, such as protecting trees from direct solar radiation, reducing water loss, providing mechanical support, and protecting them from herbivores. Negative neighbour effects can be reductions in growth and survival through competition for resources and allelopathy (Stoll and Weiner 2000). The study of **local neighbourhoods** mainly focuses on describing a tree's performance as influenced by its neighbourhood area (within a certain radius around the tree). Local neighbourhood effects have been shown for tree growth in boreal forest (Kaitaniemi and Lintunen 2010) and tropical forest (Potvin and Dutilleul 2009) and for vulnerability to predation and parasitism (Barbosa et al. 2009). The neighbourhood approach has been considered advantageous since it allows understanding interactions between trees and determining whether the observed functions (e.g., growth, resistance to pests and diseases) are driven by inter- or intraspecific competition or facilitation (Srivastava and Vellend 2005).

1.3 Objectives and outline of the thesis

One way to assess the effect of tree diversity on ecosystem functioning in forests is to compare existing stands of contrasting diversity but similar environmental conditions (Scherer-Lorenzen et al. 2005, Baeten et al. 2013). Ample evidence shows positive diversity effects on ecosystem functioning in forests (Spiecker 2003, Gamfeldt et al. 2008, Vilà et al. 2013, Wagner et al. 2014), but the results are still mostly limited to mature forests. Yet, the early stages of forest plantation development are particularly interesting to study, because of their unique characteristics, such as the vulnerability of young trees to certain biotic (e.g., pests, pathogens) and abiotic (e.g., storm, frost, drought) risks and the competition for light, nutrients, and water with the understory vegetation (Nambiar 1990, Pretzsch 2010). Besides that, some beneficial effects of mixing tree species are only expected in the early development stage, e.g., increased growth through species-specific resource complementarity (Frivold and Frank 2002). This stage is also critical in determining the course of the further forest development.

Tree species diversity experiments, such as the ones in the global network TreeDivNet, (www.treedivnet.ugent.be, Verheyen et al. 2016), are a model platform to study the effects of tree species diversity and composition on forest ecosystem functioning throughout the different stages of forest development. In this PhD thesis, we focused on the FORBIO experiment, the Belgian platform within the global TreeDivNet network. It consists of three forest plantations established in three contrasting sites in Belgium using nine different tree species (see Chapter 2). The experiment was planted between 2009 and 2012, so the plantations were still young at the time of our study.

The main objective of this thesis was to study early effects of tree species diversity and composition on forest ecosystem functioning. We focused on three groups of functions and properties (‘functions’ hereafter): primary production (tree growth), resistance to crown damage (crown damage and crown arthropods), and nutrient cycling (litter decomposition) (see Fig. 1.2). These functions are clearly interrelated. The rate of primary production of the trees reflects the tree’s vitality and the biomass formed. Damage in some parts of the biomass, especially photosynthetic parts, will in turn affect this primary productivity. Arthropods in the tree crowns may potentially cause this damage. In the early development stages of forest plantations, the arthropod community responds rapidly to environmental changes and thus reflects habitat heterogeneity, for instance created by more diverse trees in the local neighbourhood (Kremen et al. 1993, Maleque et al. 2006). Finally, the rate of primary production will also depend on the available nutrients recycled from dead organic matter through litter decomposition.

We expected that tree identity will explain most of the variance in every function studied since the trees were still very young and did not yet interact directly.

The specific objectives of the thesis were to study

(1) the effects of the local neighbourhood (species diversity, species composition and structural diversity) on the growth, crown damage, and the crown arthropod community of individual saplings in two contrasting sites;
(2) the effects of leaf litter diversity and composition on litter decomposition rates.

The thesis is organized in four parts (Fig. 1.2).

The first part of the thesis (Chapter 2) describes the study area: the FORBIO experiment. We describe the design of the experiment, the two sites studied in the thesis, and the traits of the nine tree species planted. The design of FORBIO allowed us to explore the effects of tree species identity and diversity on the ecosystem functions studied in the following parts.

The second part of the thesis discusses sapling growth (Chapter 3). We quantified the growth of individual saplings of the nine study species. We measured diameter and height in two years, and then calculated the relative increment over the two-year period and the height-diameter ratio in the second year. We specifically looked at the effects of the local neighbourhood: the species diversity, phylogenetic diversity, neighbours' species identity and size differences.

The third part of the thesis deals with the pest and disease damage (Chapter 4) and the crown arthropod community (Chapter 5) of individual saplings. In Chapter 4, we discuss three main damage symptoms (branch and shoot damage, defoliation, and crown discolouration) for the nine study species and investigated the effects of local neighbourhood (species diversity, neighbours' species identity), site characteristics and timing of sampling on sapling damage. Chapter 5 shows the guild abundance, order richness, and community composition of the crown arthropods in the nine study species. We discuss whether the local neighbourhood (species diversity, phylogenetic diversity, height differences) affected the crown arthropod community.

In the fourth part, we discuss the leaf litter decomposition (Chapter 6) of five study species in one of the FORBIO sites (Zedelgem). We measured the leaf litter quality and looked for relationships between litter quality and decomposition rate. We also looked into the effects of litter mixing on determining the litter decomposition rate by using 20 different litter compositions with species richness ranging from 1 to 4, and we monitored decomposition for 60 weeks.

In the last chapter (Chapter 7), we will present and discuss an integrated analysis of the main findings. We also discuss the implications for forest management and give recommendation for future research.

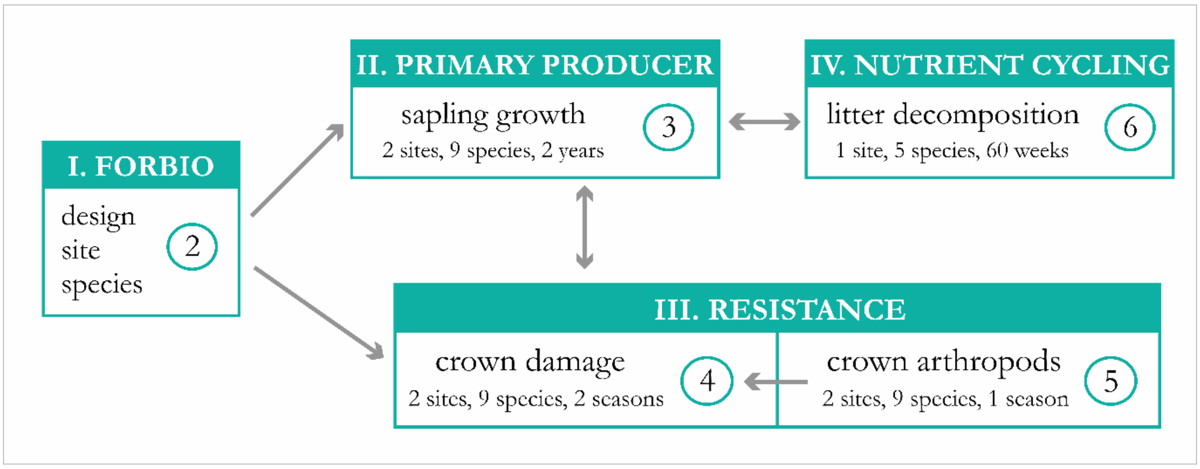


Fig. 1.2 Outline of the thesis. The four main parts of the thesis are indicated with Roman numbers (I–IV); the Arabic numbers represent the individual chapters (2–6)

Planting activities in Zedelgem site [Photograph: ForNaLab]

Chapter 2

FORBIO

After: Verheyen V, Ceunen K, Ampoorter E, Baeten L, Bosman B, Branquart E, Carnol M, De Wandeler H, Grégoire J-C, Lhoir P, Muys B, Setiawan NN, Vanhellemont M, Ponette Q (2013) Assessment of the functional role of tree diversity: the multi-site FORBIO experiment. Plant Ecology and Evolution 146(1), 26-35, doi: 10.5091/plecevo.2013.803

2.1 Abstract

In this chapter, we present the recently established, large-scale FORBIO experiment (FORest BIOdiversity and ecosystem functioning), specifically designed to test the effects of tree species diversity on the functioning of forest ecosystems. FORBIO's design matches with that of other tree diversity experiments worldwide, but at the same time, FORBIO is unique in the sense that it is a multi-site experiment. It consists of a similar experimental set-up at three sites in Belgium (Gedinne, Hechtel-Eksel, and Zedelgem) with contrasting edaphic and climatological characteristics. Such design allows to study some of the most interesting unresolved questions in functional biodiversity research, notably whether the effects of complementarity on ecosystem functioning decrease in less stressful and more productive environments. At each site, FORBIO consists of 41 to 44 plots (127 plots in total) planted with monocultures and mixtures of up to four species, selected from a pool of five site-adapted, functionally different tree species. When allocating the tree species combinations to the plots, any possible covariation with other environmental factors (e.g., soil nutrients) was avoided as much as possible. Not only scientific knowledge, but also forest management will benefit from the results coming from the FORBIO experiment. FORBIO is, for instance, a test case for uncommon, not well-known tree species mixtures and for determining plantation success in the early phases of forest development. To conclude, FORBIO is an important ecosystem experiment that has the potential to deliver badly needed insights into the multiple relationships between biodiversity and ecosystem functioning, which will be valuable for both science and practice.

2.2 Introduction

The FORBIO experiment is designed to study the relationships between FORest BIOdiversity and ecosystem functioning (http://www.treedivbelgium.ugent.be/pl_forbio.html). It is a tree diversity experiment with basic design features that are similar to other experiments across the globe, representing the TreeDivNet network (www.treedivnet.ugent.be). At the same time, the FORBIO experiment is unique as it consists of a similar experimental set-up at three sites with contrasting edaphic and climatological characteristics. Paquette and Messier (2011) stated that one of the most interesting unresolved questions in BEF research is whether the effects of complementarity on ecosystem functioning decrease in favour of competitive exclusions in less stressful and more productive environments (cf. stress-gradient hypothesis of Bertness and Callaway 1994). Several authors (Vilà et al. 2007, Morin et al. 2011, Paquette and Messier 2011) demonstrated that the slope of the richness-complementarity relationship was steeper at the less fertile sites, but also that the absolute complementarity values, calculated following the additive partitioning approach proposed by Loreau and Hector (2001), are larger at the most fertile sites. However, empirical support for the changing BEF relationship along environmental stress gradients in real-world situations is largely confined to studies that used forest inventory data. Such data generally have a low orthogonality and comprehensiveness, i.e. there is almost unavoidably covariation between species diversity and environmental variables (e.g. soil nutrients) and the studies generally focus on only a few functions, including aspects of productivity (Nadrowski et al. 2010). Hence, there is a clear need to build variation in environmental conditions directly into the design of field experiments (cf. Gessner et al. 2010) and to measure multiple ecosystem processes on the same set of plots.

In this chapter, we will first describe the site characteristics, experimental design, tree species characteristics, and understory vegetation survey of the FORBIO experiment. Then we will explain the sites of the FORBIO experiments used in this thesis and the local diversity variables tested.

2.3 FORBIO experiment

2.3.1 Site characteristics

The three FORBIO sites lie in three Belgian regions (Fig. 2.1) and are characterized by contrasting site conditions (Table 2.1).

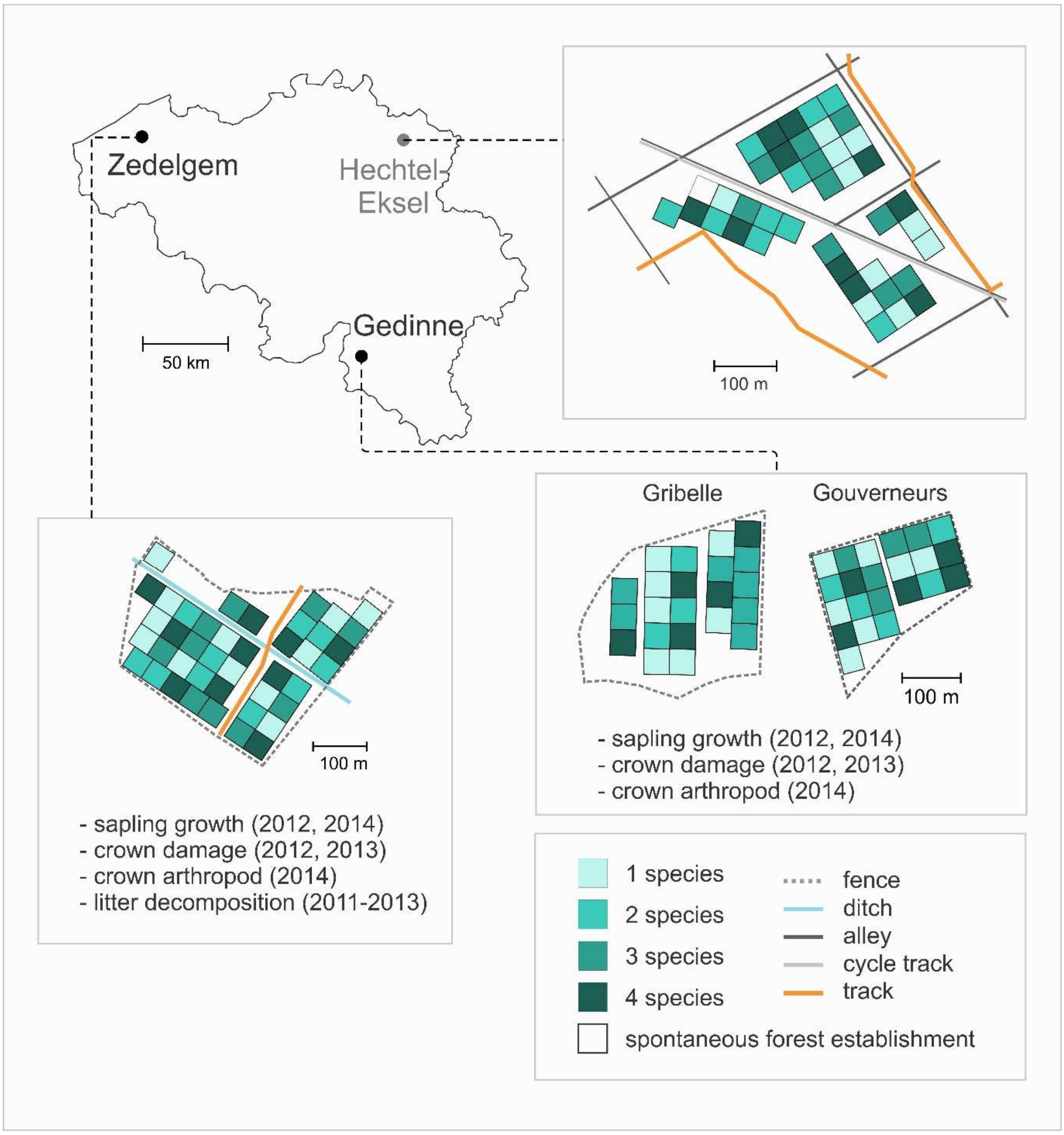


Fig. 2.1 Map of Belgium with the three FORBIO sites and the experimental setup at each site. The tree species richness per plot ranges from one species to four species. In Hechtel-Eksel, one plot (white) was not planted and was left for spontaneous succession

The Gedinne site is located in the Ardennes ecoregion and consists of two subsites c. 2 km apart (‘Gribelle’ and ‘Gouverneurs’). The climate is colder and harsher compared to the other two sites (Table 2.1, more details on weather in Appendix 2.1). The relatively shallow (c. 60 cm) soil has developed in a stony solifluxion sheet in which the weathering products of the bedrock (sandstone and schist) were mixed with periglacial loess. In contrast to the Zedelgem and Hechtel-Eksel sites, the Gedinne site is so-called ‘ancient’ forest (Hermy et al. 1999), that is, it was continuously forested at least since the oldest available map (de Ferraris 1771-1778), and it is not unlikely that, even in the more distant past, it has never been reclaimed for agriculture. The original broadleaved forest had been converted into a spruce plantation in the 1920s (or earlier; exact date not known). This c. 85 year old plantation was clearcut in 2005.

The Zedelgem site is located in the Cuesta 'ecoregion' (sensu Sevenant et al. 2002), close to the North Sea. The site has a very mild, temperate climate. The soil parent material varies from sand to loamy sand, and the soil moisture regime varies between dry (minimum water table depth 90–120 cm) to moderately wet (minimum water table depth 40–60 cm). Until the plantation establishment in 2009-2010, the site was in agricultural use and both arable crops (potatoes, maize) and grass were grown.

The Hechtel-Eksel site is located in the northeastern part of Belgium, in the Campine ecoregion. The climate is somewhat less mild with higher temperatures in summer and lower temperatures in winter. The soil consists of coarse sand and is dry (minimum water table depth 90–120 cm). The site was converted from heathland to pine plantation in 1908. The site was composed of *Pinus sylvestris* and *Pinus nigra* subsp. *laricio* trees with an age varying between 72 and 96 years before it was clearcut in 2010, just prior to the planting of the experiment.

Prior to the establishment of the experiment, the intra-site variability in soil characteristics was assessed at each of the three sites to avoid any coincidental covariation between diversity levels or the tree species presences and the soil characteristics. Hence, a large number of soil samples were taken at the three sites and analysed for pH, total phosphorus (P_{tot}), total nitrogen (N) and total carbon (C) content (Fig. 2.2). The values at the Zedelgem site still reflect the agricultural history. The pH and P_{tot} were relatively high, whereas the % C, % N and C:N were relatively low. Fairly strong spatial patterns occurred: % C and pH were higher on the more elevated northeastern part of the site, whereas P_{tot} was clearly lower at the southeastern part of the site, which is probably related to the fact that this part of the site has known a longer use as (less intensively fertilized) grassland. The pH and P_{tot} values at the Gedinne site were clearly lower than at the Zedelgem site, whereas % C, % N and C:N were higher. The Gribelle subsite at c. 373 m altitude had a significantly higher pH and P_{tot} and a lower C:N compared to the Gouverneurs subsite (one-way ANOVA, $p < 0.05$), located at c. 424 m altitude. At the Hechtel-Eksel site, the average C:N value is a factor two to three higher and the average P_{tot} value is a factor three to ten lower compared to the Gedinne and Zedelgem site, respectively.

In sum, it can be assumed that the overall growing conditions are most favourable at the Zedelgem site because of its favourable climatic conditions and the higher availability of water and,

Table 2.1 General characteristics of the three FORBIO sites

characteristic	Gedinne	Zedelgem	Hechtel-Eksel
size	2 x c. 4.5 ha	c. 9.5 ha	c. 8 ha
coordinates	49°60'N 4°59'E (Gr) 49°59'N 4°59'E (Go)	51°9'N 3°7'E	51°10'N 5°19'E
altitude (m a.s.l.)	367-376 (Gr) 421-426 (Go)	11-16	55-56
soil type	moderately dry stony loam soil	relatively dry sandy soil	dry sandy soil with gravel
climate[a]			
P (mm)	1254	855	799
MAT (°C)	8.6	10.5	9.0
Tc – Jan (°C)	1.0	6.5	1.4
Tw – Jul (°C)	16.7	14.6	16.7

[a]Annual precipitation (P), mean annual temperature (MAT), mean temperature of the coldest month (Tc; January), mean temperature of the warmest month (Tw; July). Data from nearby meteo stations of the Royal Meteorological Institute of Belgium (RMI): Bièvre (10 km to Gedinne), Lichtervelde (20 km to Zedelgem), Kleine Brogel (12 km to Hechtel-Eksel)

especially, soil nutrients. Water availability and soil fertility are most limiting at the Hechtel-Eksel site, whereas the climatic conditions are less favourable at the Gedinne site.

2.3.2 Tree species selection

At each site, a pool of five tree species was used (Table 2.2), some were shared between the sites but none was present in all three. The species were selected based on the following criteria (ranked in decreasing order of importance): (1) the species must be naturally grown under the prevalent site conditions (see 2.3.1); (2) the species must be (economically) important for forest management, at least in Belgium and preferably also in neighbouring regions, and (3) the trait diversity in the site-specific species pool should be as large as possible (Table 2.3, Table 2.4). The latter criterion was added since species traits link community composition with ecosystem functioning (cf. Suding et al. 2008). It can be assumed that communities exhibiting a higher functional trait diversity can show stronger complementarities in resource use, will display a higher degree of ecosystem multifunctionality (Hector and Bagchi 2007, Gamfeldt et al. 2008) and will deliver a larger range of ecosystem services. We have selected three non-native tree species at the Gedinne and Hechtel-Eksel sites (Table 2.2), which fulfilled the three criteria mentioned. Recently, it has been shown that non-native species may show a different behaviour than native species in biodiversity experiments, among others due to less pronounced plant-soil feedbacks (Wilsey et al. 2009).

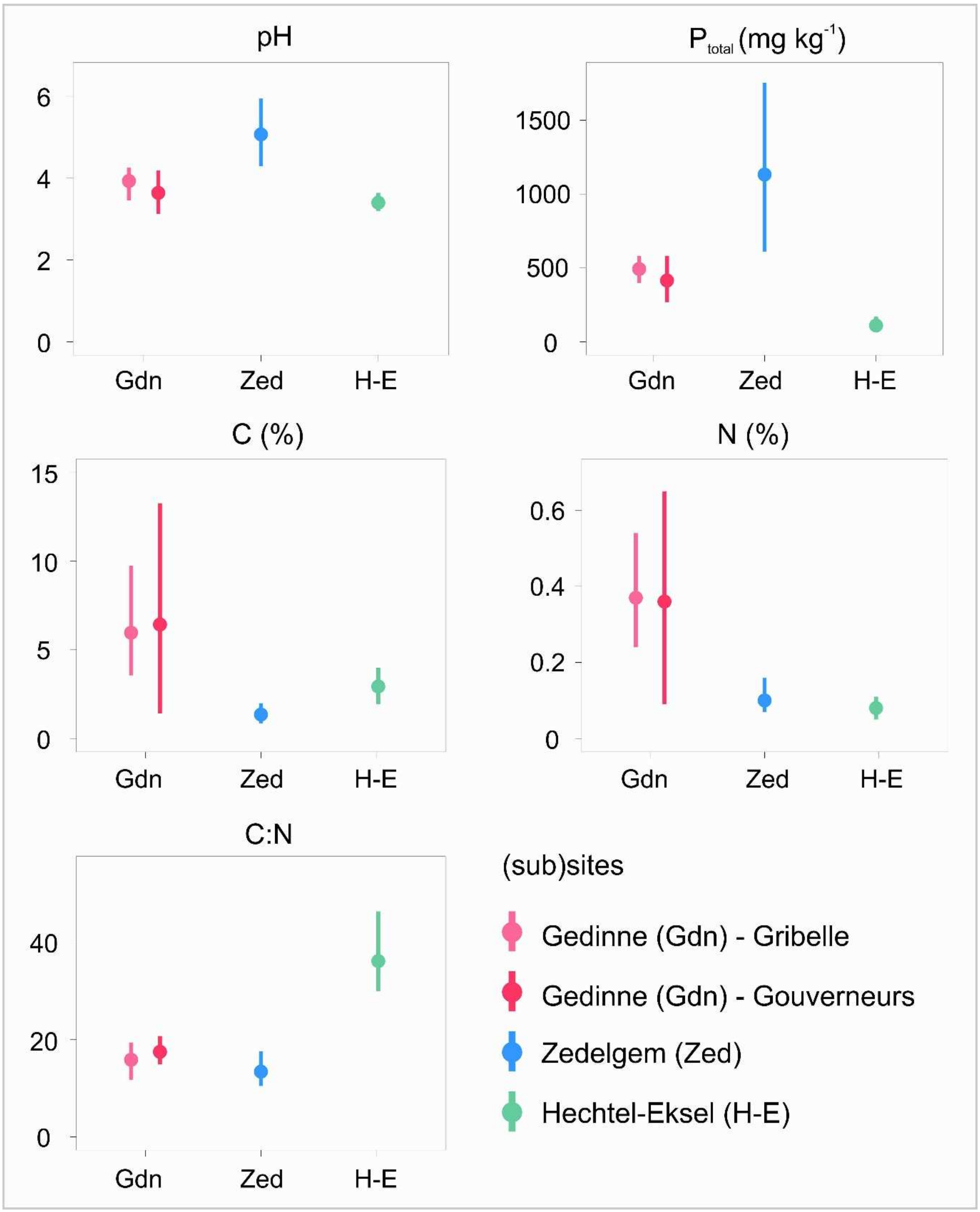


Fig. 2.2 Five chemical soil characteristics (pH (KCl), P - Phosporus, C - Carbon, N – Nitrogen, C:N) of the topsoil layers at the three FORBIO sites (soil samples taken across the entire site; Gedinne: 0-20 cm, *N*: 53-54; Hechtel-Eksel: 10-20 cm, *N:* 40-41; Zedelgem: 10-20 cm, *N:* 152-156). Dots indicate the mean, and lines give the range from the minimum to maximum value.

Table 2.2 Overview of the tree species used in three sites of the FORBIO experiment. Underlined species are non-native in Belgium.

Species	Site		
	Gedinne	Zedelgem	Hechtel-Eksel
Acer pseudoplatanus L.	x		
Betula pendula Roth		x	x
Fagus sylvatica L.	x	x	
Larix eurolepis Henry	x		
Larix kaempferi (Lamb.) Carr.			x
Pinus sylvestris L.		x	x
Pseudotsuga menziesii (Mirb.) Franco	x		x
Quercus robur L.		x	
Quercus petraea (Mattuschka) Liebl.	x		x
Tilia cordata Mill.		x	

Table 2.3 Overview of four morphological functional traits of the tree species used in the three sites of the FORBIO experiment. Data compiled by Scherer-Lorenzen et al. (2007).

species	leaf phenology	leaf morphology	crown form	root type
Acer pseudoplatanus	deciduous	broadleaved	sympodial, wide crown	heart
Betula pendula	deciduous	broadleaved	sympodial, narrow crown	surface
Fagus sylvatica	deciduous	broadleaved	sympodial, wide crown	heart
Larix eurolepis	deciduous	coniferous	monopodial	heart
Larix kaempferi	deciduous	coniferous	monopodial	heart
Pinus sylvestris	evergreen	coniferous	monopodial	tap
Pseudotsuga menziesii	evergreen	coniferous	monopodial	heart
Quercus petraea	deciduous	broadleaved	sympodial, wide crown	tap
Quercus robur	deciduous	broadleaved	sympodial, wide crown	tap
Tilia cordata	deciduous	broadleaved	sympodial, wide crown	heart

2.3.3 Experimental design

The experimental design of the three sites is similar and takes into account the numerous considerations for setting up a proper diversity experiment (cf. Scherer-Lorenzen et al. 2005). Theselected species were used to create a diversity gradient from monocultures up to four-species mixtures. In total, twenty treatments were established, including five monocultures, all five possible four-species combinations and a random selection of five two- and five three-species combinations. Two replicates of each treatment were realized, which resulted in 20 × 2 = 40 plots per site. This will allow testing the significance of particular species combinations and estimating

Table 2.4 The range in maximum height (Jansen et al. 1996) and the sapling shade tolerance (Niinemets and Valladares 2006) of the tree species used in the three sites of the FORBIO experiment.

species	maximum height (m) at[a]		shade tolerance[b]
	30 years	80 years	
Acer pseudoplatanus	10.6 – 16.2	19.8 – 30.3	3.73 ± 0.21
Betula pendula	9.0 – 13.2	17.6 – 25.7	2.03 ± 0.09
Fagus sylvatica	7.2 – 15.9	18.6 – 35.6	4.56 ± 0.11
Larix eurolepis	14.3 – 29.1	20.9 – 32.3	1.5
Larix kaempferi	14.3 – 29.1	20.9 – 32.3	1.38 ± 0.21
Pinus sylvestris	8.5 – 15.2	15.4 – 27.3	1.67 ± 0.33
Pseudotsuga menziesii	14.0 – 21.0	24.0 – 36.1	2.78 ± 0.18
Quercus petraea	8.6 – 15.3	16.0 – 29.8	2.73 ± 0.27
Quercus robur	8.6 – 15.3	16.0 – 29.8	2.45 ± 0.28
Tilia cordata	-	-	4.18 ± 0.16

[a] the height range indicates the maximum height reached at the lowest and highest site index included in the yield tables of Jansen et al. (1996). No yield tables are available for *T. cordata*. For *A. pseudoplatanus* we report the values of *Fraxinus excelsior* L., for *Q. petraea* we report the values of *Q. robur*, for *L. eurolepis* the ones for *L. kaempferi*.
[b] value ranges between 1 (very intolerant) to 5 (very tolerant)

the variation within treatment combinations. When selecting the two- and three-species combinations, it was assured that species were equally represented across all plots, resulting in an overall frequency of each species of 20/40 plots, and an overall frequency of the joint-presence of two species of 10/40 plots. This design will allow making a proper distinction between selection and complementarity effects (cf. Hector et al. 2009), exploring the nature of the interactions within and among particular species along the diversity gradient and estimating the variation within treatment combinations.

The total number of plots in the experiment is not 120 (3 * 40), however, but 127. There is one extra plot left for spontaneous succession at the Hechtel-Eksel site (40 + 1 plots). At the Gedinne and Zedelgem sites, an extra treatment was added to study the effects of provenance diversity for beech (Gedinne) and oak (Zedelgem). At each site, one provenance of beech or oak was planted in the plots of one replicate or block (20 plots) while three provenances were planted in the second replicate or block (20 plots). For the two extra provenances of beech or oak, additional monoculture plots were planted: four additional beech monocultures in Gedinne (2 in Gribelle and 2 in Gouverneurs, 40 + 4 plots in total), and two additional oak monocultures in Zedelgem (40 + 2 plots). Experiments manipulating genetic diversity (here provenances) within tree species are rare (but see Vehviläinen and Koricheva 2006, Castagneyrol et al. 2012). Yet, high levels of genetic diversity may become of vital importance for sustained forest ecosystem functioning, especially in a rapidly changing environment (Aerts and Honnay 2011). This subtreatment will allow testing whether the performance differs between plots with a lower versus higher intraspecific genetic diversity and whether this effect depends on the diversity and identity of the other species present in the plot.

At all three sites, trees are planted on a 1.5 m × 1.5 m grid (Photo 2.1 & 2.2). The plots at the Gedinne site measure 42 m × 42 m (784 trees), except thirteen plots that have a size of 42 m × 37.5 m (700 trees). The plot size is 42 m × 42 m at the Zedelgem site, resulting in a density of 784 trees per plot (4,444 trees.ha^{-1}). The Hechtel-Eksel plots measure 36 m × 36 m and contain 576 trees (also 4,444 trees.ha^{-1}). The total number of planted trees at the three sites is 89,254, with 33,404 in Gedinne, 32,810 trees in Zedelgem, and 23,040 in Hechtel-Eksel, making FORBIO one of the larger tree diversity experiments (see www.treedivnet.ugent.be). Trees were planted in monospecific patches to allow all species in a plot to establish, by avoiding fast-growing species outcompeting slow-growing species, and sustain the intended mixture of the plot in the long run. The patches were kept small (3 × 3 trees, Fig. 2.3) to obtain interspecific interactions as soon as possible within the plots. These cells are arranged in a checkerboard pattern in the two-species mixtures, but were randomly attributed to the species in the three- and four-species mixtures. Before attributing the treatments to the plots, we controlled for any possible covariation between the treatments and the measured soil characteristics (see above). This was done in two steps: (1) by blocking each replication at the sites where there was an obvious gradient in environmental conditions (low-lying southwestern versus more elevated northeastern part of the site in Zedelgem; Gribelle versus Gouverneurs subsite in Gedinne) and (2) by running ANOVA models to test whether there was any significant difference in the soil characteristics between the diversity levels and between plots with and without any of the five selected species. Treatments were randomly attributed to the (blocked) plots until no significant difference ($p > 0.1$) in any of the characteristics was present anymore.

2.3.4 Management practices

The two main management practices applied at the FORBIO sites thus far were vegetation management and replanting. Once every summer, herbaceous vegetation management has taken place at Gedinne and Zedelgem since the herbaceous vegetation was outgrowing the planted saplings (Photo 2.3). In Hechtel-Eksel, vegetation management was considered not necessary. In Zedelgem this has been done in 2010, 2011 and 2012 by mowing a 1 m wide strip between the tree rows; in Gedinne this was done in the years 2010 till 2014 with a scythe and a brushcutter

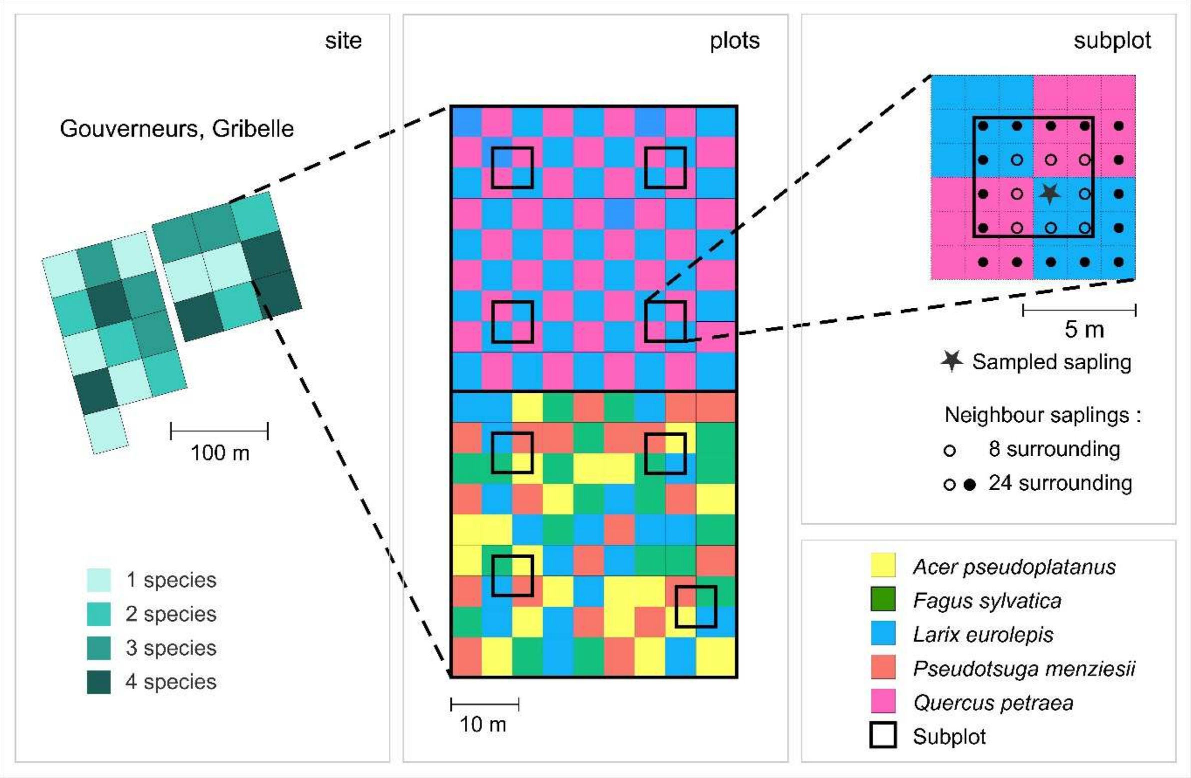


Fig. 2.3 Example of the plot design from one of the FORBIO sites in Gouverneurs, Gedinne. The within-plot design is shown for two- and four- species plot (42 m x 42 m). Four subplots (4.5 m x 4.5 m) was established in every plot, here in a mixed plot with two- species. Each colour represents a different tree species. The 8 or 24 nearest neighbours of the sampled saplings were used to calculate local neighbourhood diversity indices.

Photo 2.1 Planted saplings in Zedelgem site [Photograph: Stephanie Schelfhout]

Photo 2.2 Planting activities in Zedelgem site [Photograph: Stephanie Schelfhout]

Photo 2.3 Ground vegetation outgrowing the saplings in summer 2013 at Gedinne site [Photograph: Mathias Dillen]

around the saplings. In the first years after planting (2010-2012), the survival has been assessed annually using a standardized survival scoring protocol in all sites (see Van de Peer et al. 2016). Replanting was done in both sites in 2011 and 2012, only for plots with total mortality rates higher than 10%. Dead saplings and saplings with less than 2/3 foliage were replaced by new saplings.

2.4 FORBIO in this thesis

2.4.1 Study area

In this thesis, we focused on the Gedinne and Zedelgem sites of FORBIO. In both sites, we measured sapling growth, assessed crown damage, and sampled crown arthropods on selected target saplings in the subplots (Table 2.5). We did a litter decomposition experiment at the Zedelgem site only. Throughout the years of the study, there were no significant differences in weather conditions between years that might have affected the ecosystem functions assessed in the sites (see Appendix 2.1).

2.4.2 Ground vegetation survey

An understory vegetation survey was done in May-June 2011 at the Gedinne and Zedelgem site. Each plot in Gedinne and Zedelgem was subdivided in four equal squares. In each square, one subplot of 4.5 m × 4.5 m was marked (Fig. 2.3), based on the following criteria: (1) the subplot is located at the centre of the square or as close as possible to this centre; (2) the subplot represents the species mixture of the plot; (3) a tree is present at each corner of the subplot (each subplot thus contains 16 trees); (4) the crossing point between four monoculture cells is located at the centre of the subplot (each subplot thus contains four trees of each monoculture cell). The number of subplots is thus 42 × 4 = 168 at the Zedelgem site and 44 × 4 = 176 at the Gedinne site.

In each subplot, the ground vegetation cover (percentage cover per species, total cover of the understorey layer, and cover of bare soil) was recorded. Species richness was higher in Zedelgem compared with Gedinne (Table 2.6). Analysis of the data on ground vegetation confirmed the lack of covariation between environmental parameters.

Table 2.5 List of ecosystem functions measured, methods, and year of measurements in this thesis

ecosystem functions measured	methods	year of measurements	
		Gedinne	Zedelgem
sapling growth	diameter and height measurements	2012 & 2014	2012 & 2014
crown damage	crown damage assessments	2012 & 2013	2012 & 2013
crown arthropod	crown arthropod suction sampling	2014	2013
litter decomposition	litterbags installation	-	2011-2013

Table 2.6 The total number of species for different plant groups and the mean ground vegetation cover of those groups (standard error of mean between brackets) estimated in the 176 and 168 subplots assessed in Gedinne and Zedelgem in May-June 2011. There were no ferns in Zedelgem

	number of species		mean cover (%)	
	Gedinne	Zedelgem	Gedinne	Zedelgem
ferns	1	-	25.0 (2.0)	-
grasses	11	23	9.1 (1.1)	63.5 (1.6)
herbs	20	62	7.9 (0.7)	18.3 (1.2)
legumes	1	11	2.2 (0.2)	16.9 (1.3)
shrub	18	5	26.3 (1.2)	0.03 (0.01)
total	51	101	44.1 (2.1)	98.6 (1.3)

2.4.3 Local neighbourhood characterization

The design of FORBIO is based on a range of plot-scale diversity levels, but since the saplings are expected to be interacting with their immediate neighbours only, the diversity of a tree's local neighbourhood (the 8 and 24 surrounding trees, see Fig. 2.3) probably has a more direct effect (Uriarte et al. 2004, Barbosa et al. 2009). We calculated two different aspects of diversity: species diversity and phylogenetic diversity based on the theoretically present trees in the local neighbourhood (without removing dead trees). The local neighbourhood species diversity was expressed as the exponent of the Shannon diversity index (expH), calculated using the proportional abundances of the species identities of the 8 or 24 trees surrounding the target tree. This measure expresses the effective number of species surrounding a tree, with species weighted precisely by abundance (Jost 2006). Phylogenetic diversity was expressed as mean pairwise phylogenetic distance (MPD) and mean nearest taxon distance (MNTD). The MPD is the mean of all pairwise phylogenetic distances between the species in a sample and allows the analysis of the overall relatedness of the assemblage members (Webb 2000, Webb et al. 2002, Cadotte et al. 2012, Harmon-Threatt and Ackerly 2013); MNTD is the mean of the phylogenetic distances between each species and its closest relative in the assemblage and provides analysis of the phylogenetic clustering of the closest relatives (Webb 2000, Webb et al. 2002, Cadotte et al. 2012, Harmon-Threatt and Ackerly 2013). Both MPD and MNTD were calculated using the *Picante* package in R (Kembel et al. 2010) using the weighted abundance of each species in the local neighbourhood. The phylogeny of the tree species in the FORBIO experiment (Fig. 2.4) was obtained by pruning the DaPhnE tree (Durka and Michalski 2012), a dated phylogeny covering over 4,600 vascular plant species of Central Europe.

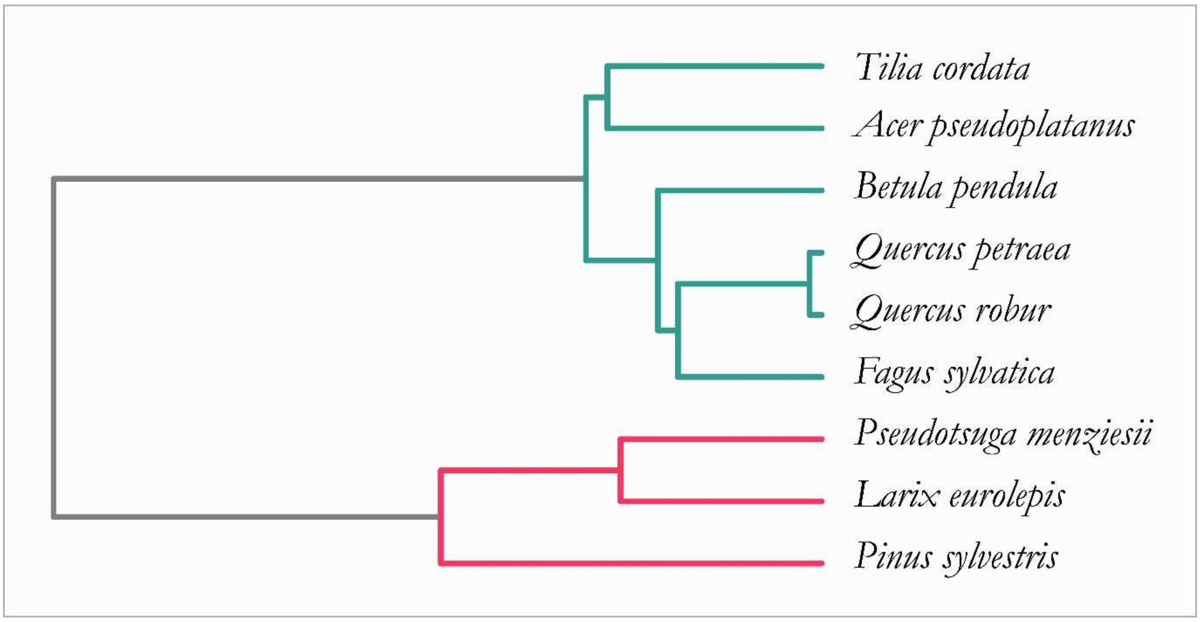


Fig. 2.4 The phylogenetic tree (topology from DaPhnE; see Durka and Michalski 2012) of the nine tree species planted at the Gedinne and Zedelgem sites of the FORBIO experiment. The green lines represent broadleaved species; the pink lines represent coniferous species.

Appendix 2.1 General climatic characteristics of the two FORBIO sites

climate[a]	Gedinne	Zedelgem
2010		
P (mm)	98.2	76.1
MAT (°C)	7.5	9.5
Tc – (°C)	-2.7 (December-Dec)	-0.6 (Dec)
Tw – (°C)	18.2 (July-Jul)	19.8 (Jul)
2011		
P (mm)	89.3	61.9
MAT (°C)	9.4	11.5
Tc – (°C)	1.8 (January-Jan)	3.9 (Jan)
Tw – (°C)	15.9 (August-Aug)	16.4 (June-Jun)
2012		
P (mm)	124.2	90.0
MAT (°C)	8.5	10.5
Tc – (°C)	-2.4 (Jan)	0.8 (Jan)
Tw – (°C)	17.0 (Aug)	18.8 (Aug)
2013		
P (mm)	108.8	71.6
MAT (°C)	8.1	9.9
Tc – (°C)	-0.9 (February)	1.7 (Jan)
Tw – (°C)	18.3 (Aug)	19.3 (Jul)
2014[b]		
P (mm)	97.3	71.5
MAT (°C)	8.4	7.2
Tc – (°C)	3.9 (Jan)	5.8 (Jan)
Tw – (°C)	14.5 (Jun)	9 (March)

[a] Annual precipitation (P), mean annual temperature (MAT), mean temperature of the coldest month (Tc), mean temperature of the warmest month (Tw). Data from nearby meteo stations of the Royal Meteorological Institute of Belgium (RMI): Bièvre (10 km to Gedinne) and Lichtervelde (20 km to Zedelgem).

[a] Data available from January-June for Gedinne and from January-March for Zedelgem.

Pseudotsuga menziesii in summer 2013 at Gedinne site [Photograph: NN Setiawan]

Chapter 3

Local neighbourhood effects on sapling growth

After: Setiawan NN, Vanhellemont M, Baeten L, Van de Peer T, Ampoorter E, Ponette Q, Verheyen K. Local neighbourhood effects on sapling growth in a young experimental forest. *Submitted to Forest Ecology and Management*

3.1 Abstract

Mixing different tree species in forest plantations might increase stand productivity and resilience compared to monocultures, but mixing effects in the early stage of mixed forest plantations are still poorly understood. In general, sapling growth is affected by environmental factors, sapling species identity, direct and indirect interactions with neighbouring saplings, and competition with the ground layer vegetation. We assessed the diameter increment, height increment, and height to diameter ratio of *ca.* 5500 permanently marked saplings growing in local neighbourhoods that differ in number and identity of the sapling species present. We found that sapling growth was related to the sapling's species identity and the characteristics of its local neighbourhood (notably phylogenetic diversity, relative size asymmetry, and ground vegetation cover). The identity of the neighbours only mattered when the species traits, such as light requirements, differed between target and neighbour tree species. The growth of the young saplings was positively affected by tall neighbours and ground vegetation cover. This suggests that careful trait selection when designing mixed forest plantations is important and that ground vegetation can be favourable for sapling growth in the first years of a new plantation.

3.2 Introduction

In terms of forestry practices, the main interest for establishing mixed species plantations was the higher productivity. From a theoretical perspective, mixing different tree species may help to increase the overall stand level growth through different mechanisms called complementarity and selection (Erskine et al. 2006, Vilà et al. 2007, Piotto 2008, Zhang et al. 2012). The complementarity effect occurs when species show niche differentiation, in terms of resource partitioning or facilitation, which enables them to utilize more resources in mixed stands (Kelty 1992, Tilman et al. 2001, Bravo-Oviedo et al. 2014). The selection effect may result in increased productivity because of the higher probability for including a dominant and productive species in the mixture (Cardinale et al. 2007, Morin et al. 2011).

To understand mixing effects, it is crucial to understand the differences between growth in monocultures and mixed plantations at the level of individual trees, since the mixing effects are the result of species-specific interactions between trees (Baeten et al. 2013, del Río et al. 2015). In general, there are three main factors affecting tree growth, i.e., environmental resources (light, soil nutrient), environmental conditions (temperature, humidity), and tree characteristics (species identity, age) (Schulze et al. 2005, Jacob et al. 2010a). These environmental factors are inherent to the site, but are also affected by a tree's interactions – both aboveground and belowground - with the ground vegetation or neighbouring trees (Šebeň et al. 2013). A tree will experience competition (Yang et al. 2003) or facilitation by its neighbours (Vandermeer 1989, Potvin and Dutilleul 2009) depending on their identity, size, and location. Trees also interact with higher trophic levels, such as herbivores, which can have strong effects on tree growth, reproduction, or survival (Maron and Crone 2006).

Most studies on forest productivity have focused on the growth in mature forest plantations. Information on the growth and development of young forest plantations is still limited, impeding the effective design of mixed plantations in forestry practice. To investigate the relation between a sapling's local neighbourhood and its growth, we assessed the diameter increment, height increment, and the resulting height to diameter ratio of *ca.* 5500 permanently marked saplings in local neighbourhoods that differ in the number and identity of the tree species present. We hypothesized that: (1) growth will differ between sapling species, and early-successional species will have a higher growth rate than late-successional species; (2) the growth of a sapling is affected by the species identity of the trees in its local neighbourhood; (3) the growth will be higher in a more diverse or less competitive neighbourhood.

3.3 Materials and methods

3.3.1 Data collection

We measured the growth for all the saplings of each subplot (*N* = 64 saplings/plot, see Fig. 2.2). In total, we measured 2,816 saplings in Gedinne and 2,688 saplings in Zedelgem (Photo 3.1). We only used the data from the saplings that were alive in both measurement years (more details in Appendix 3.1) for further analysis (*N* = 4,868). The stem diameter (20 cm above ground level) and height (ground to highest living bud) were measured for all target saplings in January-April 2012 and February-March 2014. We calculated the growth as relative diameter and height increment (Eq. 3.1):

$$relative\ increment\ (diameter\ or\ height) = \frac{value\ in\ 2014 - value\ in\ 2012}{value\ in\ 2012} \qquad \textbf{(Eq. 3.1)}$$

In addition, we calculated the height to diameter ratio of the 2014 measurements to observe the results of the saplings' growth pattern and as a proxy for a sapling's physical stability to disturbance such as storm damage (Frivold and Frank 2002).

Photo 3.1 The marking and measurement of saplings [Photographs: Sanne Van Den Berge]

3.3.2 Local neighbourhood characterization

To describe the tree diversity of the local neighbourhood around each sampled sapling, we used the tree species identity of its 8 neighbours (Fig. 2.3). We calculated both species diversity (exponent of Shannon index, expH) and phylogenetic diversity (MNTD and MPD) for these local neighbourhoods (see section 2.4.3).

Next to the local neighbourhood diversity, we also calculated a measure for the competition by the 8 surrounding saplings using the distance-dependent competition index introduced by Hegyi (1974). In this chapter, given the small size of the trees, we called it the neighbours' size asymmetry index (NSAI). We used both diameter and height to calculate the NSAI to determine whether size-related competitive effects are better described by the neighbours' diameter or height. The NSAI (Eq. 3.2) of a target tree *i* is calculated as the sum of the diameter or height ratios between living neighbour (neighbour trees alive at the moment of sampling) and target tree (D_j/D_i or H_j/H_i), weighted by the distances ($dist_{ij}$) between the target tree *i* and the 8 close neighbours *j*:

$$NSAI_i = \sum_{j=1}^{n} \frac{X_j/X_i}{dist_{ij}}$$

(Eq. 3.2)

We calculated the NSAI for both measurement years (2012 and 2014) to investigate whether the relative size of the neighbours compared with the target trees affects the growth of the target saplings over time.

At the time of our study, some of the herbaceous plants in the ground vegetation were as tall as the young saplings. Therefore, we used data on the cover of vascular plants < 1.3 m tall available per subplot (vegetation inventory in 2011, see section 2.4.2). For each sampled sapling, we calculated the total cover of the ground vegetation in its subplot as well as the cover of different functional groups (ferns, grasses, herbs, legumes) in the subplot.

3.3.3 Data analysis

We investigated how sapling growth and height to diameter ratio are affected by the species identity of the sapling, the composition and diversity of its local neighbourhood, the relative size of its neighbours, and the ground vegetation cover. We used relative diameter increment, relative height increment, and the height to diameter ratio as our response variables. Due to the differences in growing conditions and planting years between the two study sites, the analyses were done separately for Gedinne and Zedelgem. All analyses were done in R version 3.2.1 (R Core Team 2015); graphs were made with the R package *ggplot2* (Wickham 2009).

3.3.3.1 Effects of admixing a species

In the first analysis, we checked whether the species identity of the neighbours affects sapling growth and the resulting height to diameter ratio growth ratio. As the tree species in our study clearly differed in juvenile growth, the analysis was done separately for the saplings of the different target tree species. We used the entire dataset, consisting of all the saplings measured in the subplots. First, we graphically checked for spatial autocorrelation in our response variables (Borcard et al. 2011). We saw spatial clustering of diameter increment, height increment, and height to diameter ratio for *Quercus* (Appendix 3.2) and other species. Second, we modelled the growth of the target saplings as a function of the abundances (% of stems) of each tree species in their local neighbourhood using *generalized least squares* (*gls* cf. Pinheiro et al. 2014). *Gls* essentially is a weighted linear regression, which allows errors to be correlated and have unequal variances (Crawley 2012). We fitted the models with different spatial autocorrelation structures (i.e., exponential, gaussian, linear, rational quadratic, or spherical) and evaluated the best fit (see Appendix 3.5 for R syntax) using AIC values and variograms (Zuur et al. 2009) from the package *gstat* (Pebesma and Wesseling 1998, Pebesma 2004). Third, we used the coefficients of the fitted models to (1) calculate the expected mean growth and height to diameter ratio, with 95% confidence interval, of a target sapling surrounded by a monoculture of the target tree species and (2) predict the mean growth and height to diameter ratio of the target tree if 50% of the local neighbourhood would consist of another tree species. In short, for each tree species, we predicted the effect of mixing the species with each of the other tree species planted at the site. Even though our models allow us to include different proportions of up to three tree species in the mixture, we only included two species in similar proportions for the sake of simplicity.

3.3.3.2 Effects of identity, diversity, and size asymmetry

In the second analysis, we investigated the effects of neighbourhood diversity, the relative size of the neighbours in both measurement years, and ground vegetation cover on sapling growth and the height to diameter ratio. In this analysis, we used only the four central saplings in every subplot as our target saplings in order to get a proper calculation of the size asymmetry indices: diameter and height data were only available for the 16 target saplings in our subplot, not for the saplings around the subplots (see Fig. 2.3). The three diversity variables calculated for each local neighbourhood were correlated, the two size asymmetry indices (height and diameter) from both years showed clear collinearity, and the ground vegetation cover variables also showed clear collinearity. We therefore selected one diversity variable, one size asymmetry index, and one ground vegetation cover variable for each response variable prior to our analysis. For each response variable, we fitted a series of regression models using the different diversity, size asymmetry, or ground vegetation variables, and we used the variables that gave the lowest AIC (see Appendix 3.3) in the following analyses. In the end, we had six different full model structures (see Appendix 3.4). We modelled sapling growth (diameter, height, and H/D ratio) as a function of the tree species of the target sapling, the diversity of its local neighbourhood, the neighbours' size asymmetry, and the ground vegetation cover using linear mixed effect models and generalized least squares models (Pinheiro et al. 2014), including all two-way interactions between the explanatory variables. Residuals obtained from the models were checked and heterogeneity was corrected by incorporating various weighted variance structures (see Appendix 3.4) in the model. We then selected the best-fit model (see Appendix 3.5 for R syntax) with backwards selection based on likelihood ratio tests (Zuur et al. 2009).

3.4 Results

Growth appeared to be better in Zedelgem than in Gedinne: there was less mortality (Ze 4.4 %, Ge 18.4 %), and the saplings had reached larger diameters (Ze 0.4 – 9.6 cm, Ge 0.3 - 9.1 cm) and heights (Ze 0.4 – 6.1 m, Ge 0.3 - 4.6 m) in 2014. See Appendix 3.1 for more detailed data per species. The relative diameter increment, height increment, and the height to diameter ratio differed significantly between the target tree species (One-way ANOVA of the three growth variables: $p < 0.001$). In both sites, the highest mean relative diameter and height increments were shown by coniferous species: *Larix* in Gedinne, *Pinus* in Zedelgem. The lowest mean diameter and height increments were shown by broadleaved species: *Acer* in Gedinne; *Fagus* (for diameter) and *Quercus* (for height) in Zedelgem (Fig. 3.1a-b). Contrary to the diameter and height increment, the highest height to diameter ratio in both sites was shown by broadleaved species: *Acer* in Gedinne and *Quercus* in Zedelgem; the lowest by coniferous species: *Pseudotsuga* in Gedinne and *Pinus* in Zedelgem (Fig. 3.1c).

3.4.1 Effects of admixing a species

Our results showed that in all monocultures, the relative diameter increment was similar to or higher than the relative height increment (Fig. 3.2). The estimated changes in mean diameter increment, height increment, and height to diameter ratio with the addition of a second tree species in the local neighbourhood were different for every target tree species. We did not see any consistent pattern of increase or decrease in growth with the addition of a second species to the local neighbourhood. However, we saw indications of a lower height increment for some of the target tree species when certain tree species were added to the local neighbourhood, i.e., for *Quercus* in Gedinne if *Acer* was added, *Betula* in Zedelgem if *Tilia* was added, and *Pinus* in Zedelgem

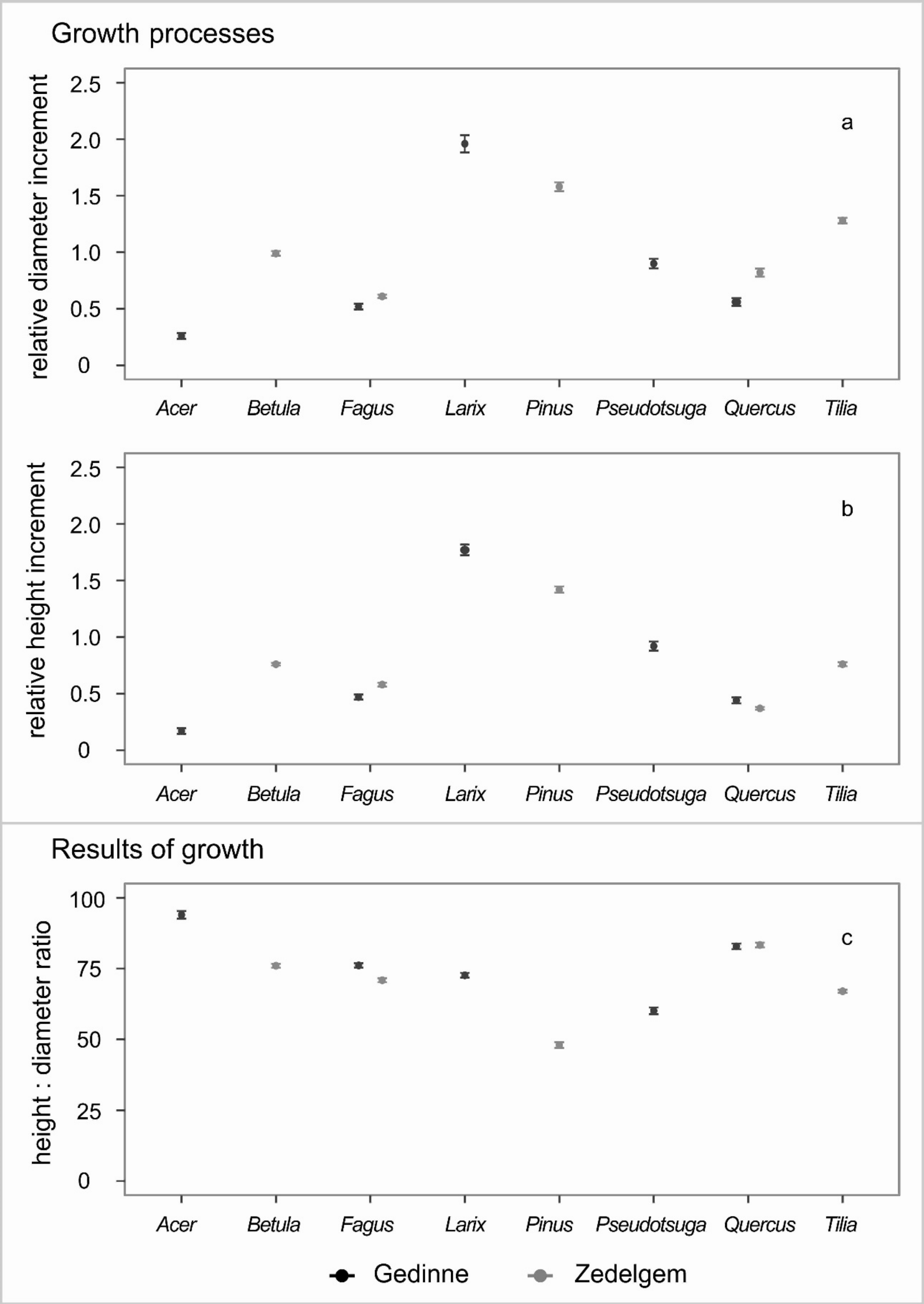


Fig. 3.1 The overall mean (± SE) relative diameter increment (a) and relative height increment (b) between 2012 and 2014 and the overall mean height to diameter ratio in 2014 (c) for the different tree species in Gedinne and Zedelgem (based on all saplings measured in both monoculture and mixture plots).

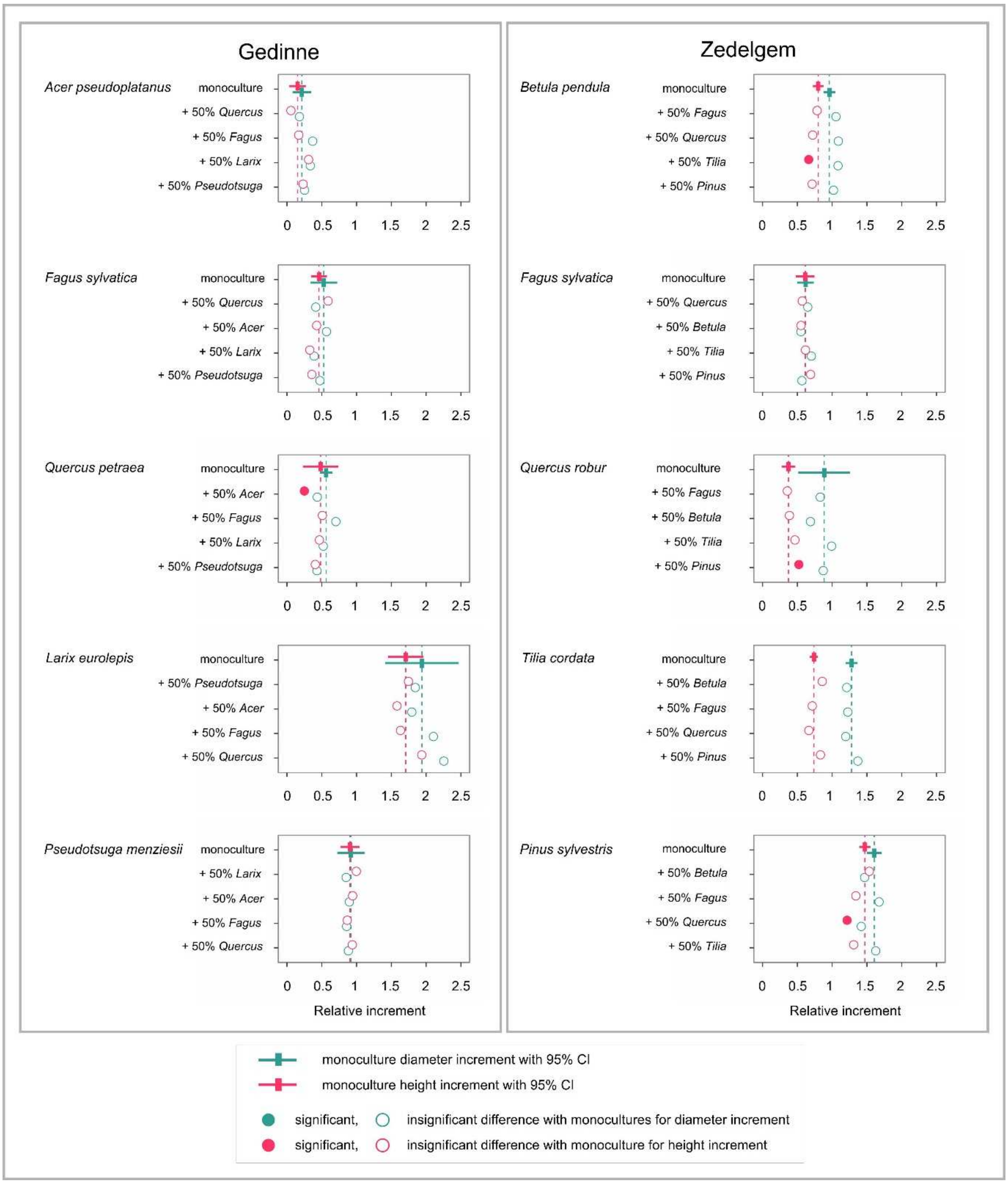


Fig. 3.2 The expected mean increment (diameter and height) for a sapling in a local neighbourhood consisting of its own species (monoculture) or in which saplings of a second species represent 50% of the neighbours (+50%). The expected mean increments were estimated with *gls* models (see 3.3.3.1). The order of the species follows their phylogenetic relatedness (see Fig. 2.4). For the monocultures, the mean increment is given with the 95% confidence interval and also represented by the dashed line. Filled dots indicate species of which the abundance in the local neighbourhood significantly affects the increment of the target sapling, and empty dots indicate that the presence of the second sapling species does not significantly affect the target sapling's increment, compared to the mean increment in a monoculture

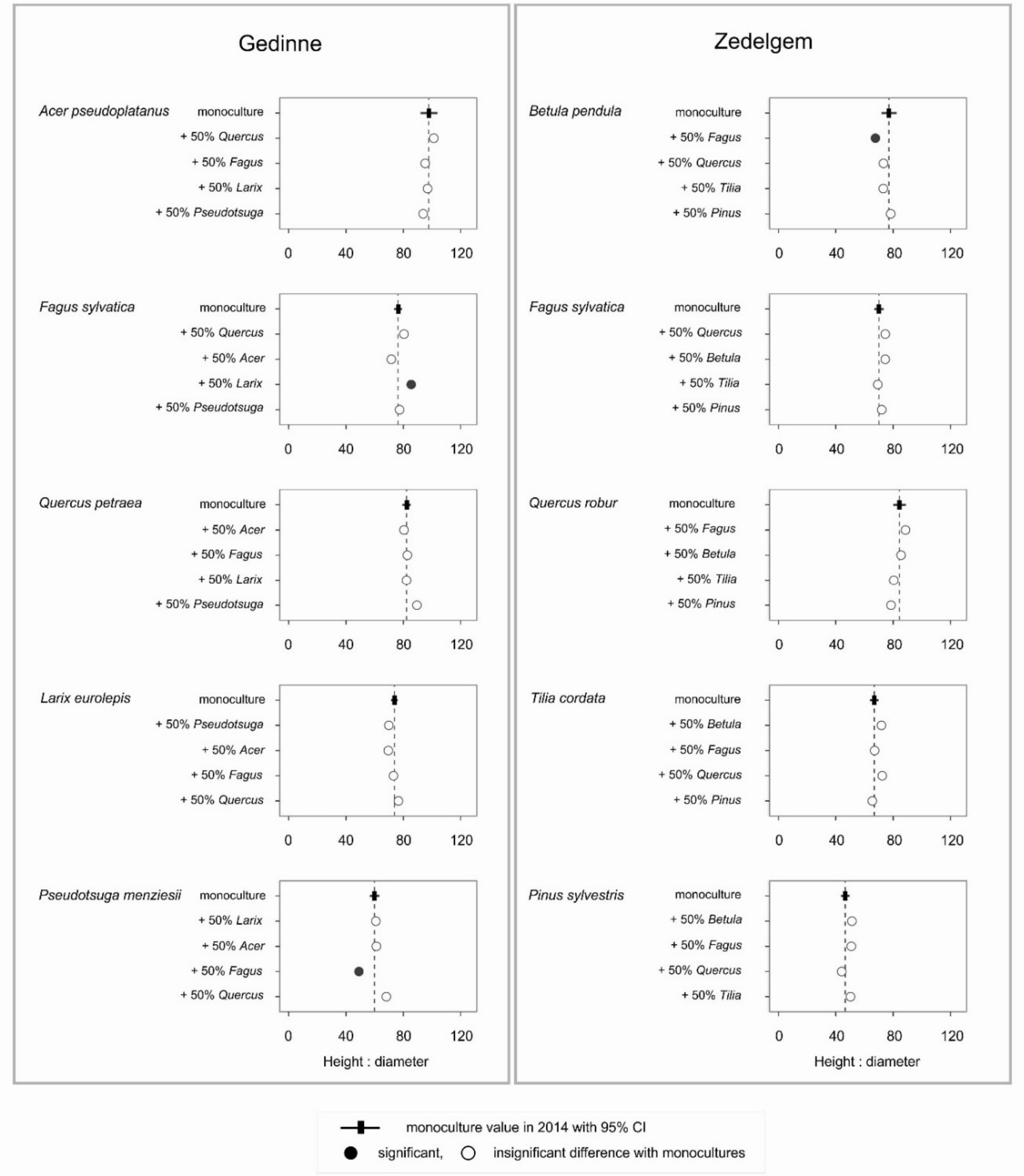


Fig. 3.3 The expected mean height to diameter ratio (H/D) in 2014 for a sapling growing in a local neighbourhood consisting of its own species (monoculture) or in a local neighbourhood in which saplings of a second species represent 50% of the neighbours (+50%) for the Gedinne and Zedelgem site. The expected mean H/D were estimated with *gls* models (see 3.3.3.1). The order of the sapling species in the graphs is linked to their phylogenetic relatedness (see Fig. 2.4). For the monocultures, the mean H/D is given with the 95% confidence interval and also represented by the dashed line. Filled dots indicate species of which the abundance in the local neighbourhood significantly affects the H/D of the target sapling, and empty dots indicate that the presence of the second sapling species does not significantly affect the target sapling's H/D as compared to the H/D in a monoculture.

Table 3.1 The best-fit linear mixed effect or generalized least square models with weighted variance (see Appendix 3.3 for more detail) fitted for the different growth response variables in Gedinne. Significance is based on likelihood ratio tests; id - target sapling species identity, size 2012 or size 2014 - neighbours' size asymmetry 2012 or 2014, veg - ground vegetation cover.

Response variables	Explanatory variables	d.f.	F-value	p-value	% variance explained[a]
diameter increment	intercept	1	433.6	<0.001	
	id	4	187.4	<0.001	32.4
	size 2012	1	205.8	<0.001	4.8
	size 2014	1	821.1	<0.001	23.4
	id x size 2014	4	16.9	<0.001	2.8
height increment	intercept	1	236.7	<0.001	
	id	4	122.7	<0.001	46.3
	size 2012	1	112.5	<0.001	5.1
	size 2014	1	190.3	<0.001	8.3
	id x size 2012	4	13.6	<0.001	3.0
	id x size 2014	4	6.6	<0.001	1.4
height/diameter	intercept	1	14818.8	<0.001	
	id	4	81.4	<0.001	21.6
	size 2012	1	31.4	<0.001	2.8
	size 2014	1	68.8	<0.001	10.9
	veg	1	1.6	0.205	0.6
	id x size 2014	4	11.8	<0.001	5.4
	size 2012 x veg	1	7.0	0.008	0.3

[a] % variance explained was calculated from the *gls* models without the weighted-variance structure

if *Quercus* was added (Fig. 3.2). We also saw indications of a higher height increment in *Quercus* if *Pinus* was added (Fig. 3.2). The height to diameter ratio was lower for *Betula* and *Pseudotsuga* if *Fagus* was added and higher in *Fagus* if *Larix* was admixed (Fig. 3.3).

3.4.2 Effects of species, diversity, and size asymmetry

From the six models tested, three models (diameter & height increment in Gedinne, diameter increment in Zedelgem) were fitted better by a mixed effect model. The results of the three mixed effect models showed that subplot explained 65.9% (Gedinne) and 56.0% (Zedelgem) of variance in diameter increment; plot explained 32.2% of the variance in height increment (Gedinne). The other three models (height to diameter ratio) in Gedinne and Zedelgem, height increment in Zedelgem) showed signs of heterogeneity of variance when fitted with a mixed effect model, and were fitted better by a generalized least squares model with weighted variance (see Table 3.4.3).

Table 3.2 The best-fit linear mixed effect or generalized least square models with weighted variance (see Appendix 3.3 for more detail) fitted for the different growth response variables in Zedelgem. Significance is based on likelihood ratio tests; id - target sapling species identity, div - local neighbourhood diversity, size 2012 or size 2014 - neighbours' size asymmetry 2012 or 2014, veg - ground vegetation cover.

Response variables	Explanatory variables	d.f.	F-value	p-value	% variance explained[a]
diameter increment	intercept	1	3446.6	<0.001	
	id	4	318.2	<0.001	38.5
	div	1	5.4	0.020	0.6
	size 2012	1	67.9	<0.001	1.0
	size 2014	1	1570.2	<0.001	32.3
	veg	1	8.3	0.004	1.0
	id x div	4	4.4	0.002	1.1
	id x size 2014	4	6.3	<0.001	0.8
	div x size 2014	1	16.0	<0.001	0.4
	size 2012 x size 2014	1	15.5	<0.001	0.2
height increment	intercept	1	4701.9	<0.001	
	id	4	159.2	<0.001	51.2
	div	1	2.8	0.095	0.2
	size 2012	1	0.8	0.361	1.0
	size 2014	1	109.6	<0.001	5.6
	veg	1	40.2	<0.001	1.3
	id x div	4	4.8	0.001	1.2
	id x size 2012	4	5.9	<0.001	2.4
	div x size 2014	1	7.4	0.007	0.3
height/diameter	intercept	1	27307.2	<0.001	
	id	4	298.0	<0.001	37.1
	div	1	0.0	0.982	0.0
	size 2012	1	196.8	<0.001	13.5
	size 2014	1	118.5	<0.001	8.9
	veg	1	4.0	0.045	0.2
	id x div	4	3.1	0.015	0.6
	id x size 2014	4	3.9	0.004	0.4
	id x veg	4	4.6	0.001	1.0

[a] % variance explained was calculated from the *gls* models without the weighted-variance structure

In general, the species identity of the target sapling always explained the highest amount of variance in its growth, followed by the relative size of its neighbours (Table 3.1 & 3.2). We saw significant interactions between target sapling identity and neighbourhood diversity, size asymmetry, and ground vegetation cover for several growth response variables. The phylogenetic neighbourhood diversity (MNTD) was the best-performing neighbourhood diversity variable. An effect of neighbourhood diversity on sapling growth was only found in Zedelgem and explained less variability in growth than size asymmetry, sapling species identity, and ground vegetation cover. There were no consistent effects of diversity observed. However, in general, some sapling species surrounded by a more diverse neighbourhood showed a slight increase in their growth and height to diameter ratio (Fig. 3.5).

The effects of size asymmetry were similar in both sites. Using the size asymmetry of 2012 as an explanatory variable showed that saplings surrounded by bigger or taller neighbours during the first measurement campaign grew more in diameter and height (Fig. 3.4a,c & Fig. 3.5b,f). The presence of bigger or taller neighbours influenced the saplings to grow more in height than in diameter (Fig. 3.4e & Fig. 3.5j). The use of the size asymmetry of the year 2014 showed that saplings with a relatively high growth ended up being surrounded by smaller and shorter neighbours; in contrary, saplings with relatively low growth ended up being surrounded by bigger and taller neighbours (Fig. 3.4b,d,f & Fig. 3.5c,g,k). Saplings surrounded by bigger or taller neighbours in 2014 had allocated more to height growth than to diameter growth (Fig. 3.4f & Fig. 3.5k). In both sites, we found a consistent positive effect of ground vegetation cover (Fig. 3.4g & Fig. 3.5d,h,k).

3.5 Discussion

The sapling growth at the two FORBIO sites was related to the sapling's species identity and the characteristics of the local neighbourhood of the sapling, such as the neighbours' identity, the size asymmetry, and the ground vegetation cover. In Zedelgem, the phylogenetic diversity of the local neighbourhood was also related with sapling growth.

3.5.1 Target sapling identity effects

The early-successional, shade-intolerant study species (*Betula, Larix, Pinus, Pseudotsuga*) grew most rapidly. The overall lower growth in Gedinne compared with Zedelgem was probably the result of the different species pool, that is the species identity of the saplings growing in each site, as well as the differences in soil nutrient content and climate. There were more slow-growing tree species planted in Gedinne (*Acer*, *Fagus*) compared with Zedelgem (*Fagus*). The soil nutrient availability (e.g. phosphorus and nitrogen) was higher in Zedelgem and this site has a less harsh climate than the Gedinne site (see Table 2.1). These difference in soil condition affected the growth of *Fagus*, which present in both sites (Fig. 3.1); *Fagus* grew better in Zedelgem compared with Gedinne. The availability of *in-situ* nutrients is a crucial factor in determining growth during the early stages of forest establishment, since there is little or no nutrient input from litterfall yet (Nambiar 1990).

The clear differences in sapling growth among the study species are probably a result of the design of the experiment. The planted tree species were selected to be phylogenetically distant and represent a broad range in trait values (see Verheyen et al., 2013). They differ in, for instance, leaf morphology (coniferous vs. broadleaved), shade tolerance (tolerant vs. intolerant), crown form (monopodial vs. sympodial), and root system type. High growth rates are generally found in species that are coniferous, have low-density wood, and are shade-intolerant (King et al. 2005, Brodribb et al. 2012). Indeed, the highest mean increment values in our study were found in tree species with such traits: *Betula*, *Larix*, and *Pinus*. As also shown by other research (Valladares and Niinemets 2008), shade-intolerant saplings will grow most rapidly in the early stages of plantation development or in resource-rich environments.

The mean height to diameter ratio was higher for the saplings in Gedinne compared with Zedelgem. A sapling with a high ratio of height to diameter will have a high risk of stem breakage by storm, wind, or snow (Niklas 1994, Birot and Gollier 2001, Wonn and O'Hara 2001). Some tree species compensate for this risk by having strong, high-density wood (Kooyman and Westoby 2009). In our study, the saplings of the two *Quercus* species and *Acer* had the highest height to diameter ratio. Sumida et al. (1997) also showed that the height growth of light-demanding species such as *Quercus* is high during the sapling phase. *Quercus* saplings might compensate the stem breakage risk due to growing faster in height by having high-density wood. The high height to diameter ratio of *Acer* in our study might have been due to their high initial height when planted, and may have – in turn – contributed to their high mortality (26.8%).

3.5.2 Neighbours' identity effects

The presence of a second species in a sapling's local neighbourhood can affect its relative height increment and height to diameter ratio. Investing in height growth is a growth strategy for reaching light as one of the most fundamental resources for plant growth. In the early stage of stand development at a clear-cut or post-agricultural site, light is not a limiting factor for sapling growth. Yet, the difference in growth of a sapling in a monoculture and a two-species mixture shows that the race for light has already started. Fast-growing tree species such as *Betula* and *Pinus* showed a relatively lower height increment and height to diameter ratio when grown together

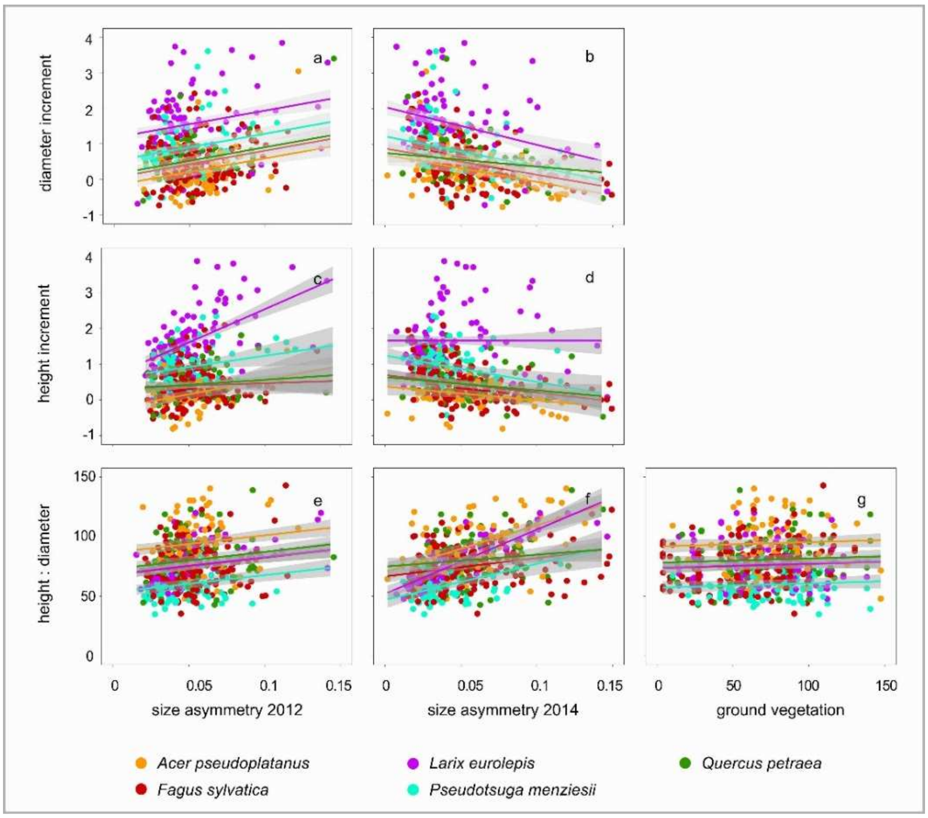


Fig. 3.4 The relationships between relative diameter increment (a-b), relative height increment (c-d), or height to diameter ratio (e-g) and the different explanatory variables (identity, size asymmetry 2012, size asymmetry 2014, ground vegetation) for Gedinne (see Table 3.1). The colours represent tree species, the lines depict model predictions, and the grey areas are the 95 % confidence intervals. All models were corrected for heteroscesdasticity (see 3.3.3.2 for more details).

with slower-growing species such as *Fagus*, *Quercus*, and *Tilia*, compared to their growth in *Betula* or *Pinus* monocultures. In the mixtures, the interspecific competition for light was probably less intense for the fast-growing species so that they could allocate more to secondary growth, or diameter growth. Indeed, mixing fast-growing species with slower-growing ones is an important management practice to allow the fast-growing species to grow into stable saplings (low height to diameter ratio) and reduce the risk of abiotic damage (Bošeľa et al. 2014).

Importantly, as the stands age, the relationships between slow- and fast-growing species (i.e. neighbourhood identity effects) will change. In the beginning, the presence of slow-growing, shade-tolerant *Fagus* altered the dominance of fast-growing, shade-intolerant *Betula* and *Pinus* in the surrounding neighbourhood (cf. Kunstler et al., 2016). Once the canopy closes, the taller, fast-growing trees such as *Betula* and *Pinus* will start to compete for nutrients and light to maintain their positive carbon gain and grow (Messier et al. 1999, Claveau et al. 2002). Over time, litter fall will become an important flux of nutrients. *Pinus* and *Fagus* litters are known to have low decomposition rates (Chapter 6), which may contribute to forest floor build-up and soil

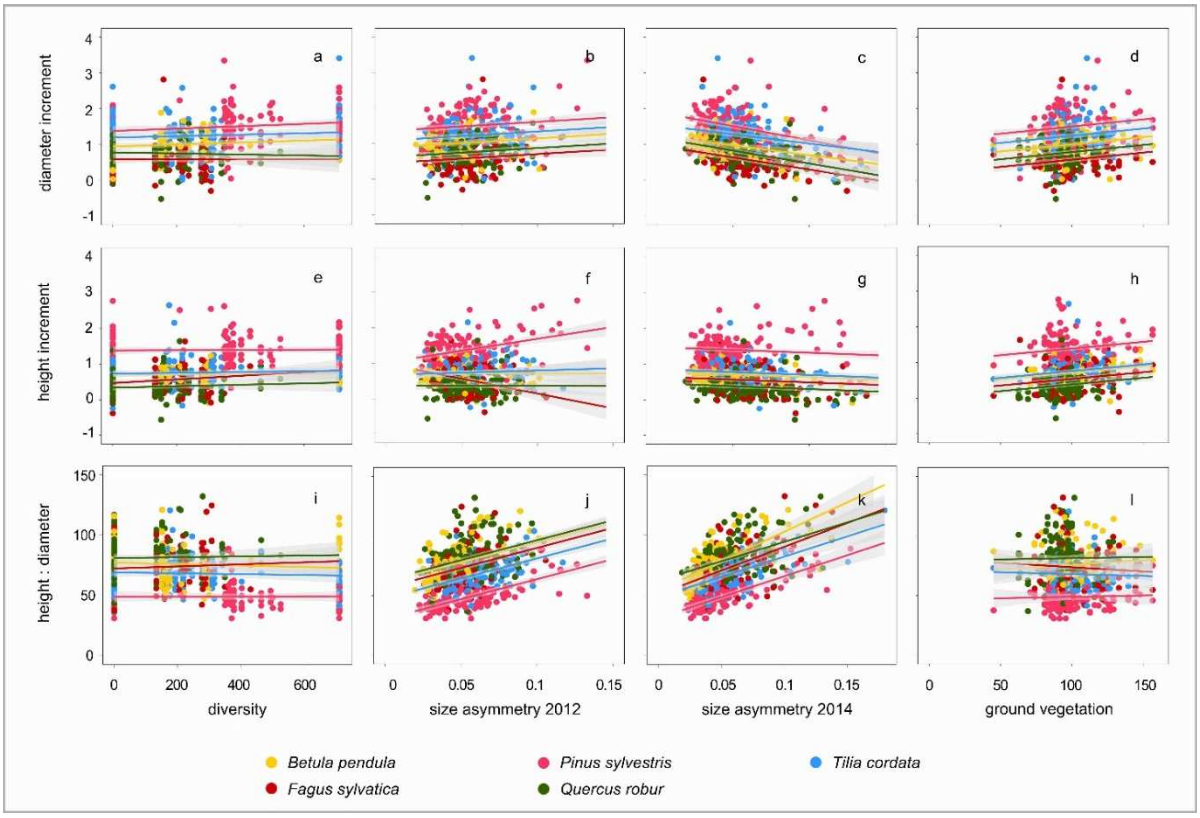


Fig. 3.5 The relationships between relative diameter increment (a-d), relative height increment (e-h), or height to diameter ratio (i-l) and the different explanatory variables (identity, diversity, size asymmetry 2012, size asymmetry 2014, ground vegetation) for Zedelgem (see Table 3.1). The colours represent tree species, the lines depict model predictions, and the grey areas are the 95 % confidence intervals. All models were corrected for heteroscesdasticity (see 3.3.3.2 for more details).

acidification (De Schrijver et al. 2012). As *Fagus* can tolerate deep shade and soils with a low pH (Ellenberg and Leuschner 1996, Von Lüpke 1998), the species is a strong competitor in closed forests in which *Betula* and *Pinus* may suffer from "carbon starvation", a decline in the ratio of photosynthesis to respiration (Gerrish 1990) that eventually may lead to mortality. *Tilia*, with its intermediate growth rate, might outcompete or be outcompeted by its neighbours, depending on their characteristics. Although the species is quite nutrient-demanding (Von Lüpke 1998), its leaf litter has a high decomposition rate (Chapter 6) probably resulting from its high calcium content that attracts decomposers such as earthworms (Reich et al. 2005). Therefore, the presence of *Tilia* may contribute to a stand's nutrient cycling and nutrient availability in the long run.

3.5.3 Neighbours' diversity and size asymmetry effects

The local neighbourhood diversity, size asymmetry, and ground vegetation cover were all important in explaining sapling growth. In Zedelgem, the phylogenetic diversity of the local neighbourhood was related to slight differences in the growth and height to diameter ratio of target species. Research in mature temperate forest found positive diversity effects on tree growth, both at stand level (Jacob et al., 2010a) and at tree level (Ratcliffe et al. 2015) through species-specific complementarity effects. In the studied forest plantations, the canopy was not yet closed, and thus saplings were probably not yet competing strongly for resources. However, indirect interaction between target saplings and their neighbours might have occurred. For instance, more diverse neighbours may have created associational resistance (Tahvanainen and Root 1972) to damage caused by pests and diseases, which can increase sapling growth and vitality. In a previous study, we found that damage caused by pests and diseases in a sapling's crown such as defoliation, discolouration, and branch and shoot damage was indeed negatively affected by the neighbourhood diversity (Chapter 4). Saplings surrounded by more phylogenetically diverse neighbours suffered less from damages, which allowed them to allocate more resources to growth instead of defence or damage recovery.

The relative size of the neighbours also affected the target saplings' growth. In the 2012 situation with high canopy openness, bigger and taller neighbours may have created more beneficial microclimate and thus enhanced the growth of the young saplings. For instance, tall neighbours might be a barrier to wind, hence reducing the risk of stem breakage (Niklas 1995), or provide more shading, reducing the growth of ground layer vegetation and its competition for resources with the saplings (Šebeň et al. 2013). Two years later, the saplings with a high relative growth had become bigger and/or taller than the surrounding neighbours.

Several studies on sapling growth (Örlander et al. 1996, De Luis et al. 1998, Davis et al. 1999, Aussenac 2000, Balandier et al. 2006) found that the ground vegetation layer was negatively correlated with early sapling growth since it competes for the same resources such as nutrients and water. Our results, however, showed the opposite: the ground vegetation cover was positively related to sapling growth. Bertness and Callaway (1994) mentioned that increasing abiotic stress may increase the positive interactions among plants (e.g., facilitation) relative to competitive effects. In other words, a high ground vegetation cover in the early forest establishment stage may help to ameliorate the prevailing harsh abiotic conditions and create a more suitable microclimate for sapling growth. For instance, the saplings in Zedelgem had been planted in the bare soils of a post-agricultural site. In these conditions, a higher ground vegetation cover may reduce the solar radiation that reaches the ground and thus the ground-level temperature, thereby increasing soil moisture and the growth and survival of young saplings (Maher et al. 2005). At a clear-cut forest site such as in Gedinne, the risk of nutrient loss through leaching during the first years after the clear cut is high (Rosén et al. 1996, Palviainen et al. 2005). The presence of ground vegetation helps in buffering the nutrient loss by acting as a nutrient sink in the first few years of stand development (Fahey et al. 1991).

3.6 Conclusions

Our study revealed that sapling growth in the early establishment of plantation forest depended mainly on species identity of the target sapling and to some extent on its local neighbourhood. The target saplings' traits determine its growth rate and height to diameter ratio. The surrounding local neighbourhood properties such as the neighbours' phylogenetic diversity, neighbours' relative size, and ground vegetation cover probably altered the surrounding microclimate, which affected sapling growth. The magnitude of the neighbourhood effects depended on the target saplings' identity. In general, taller neighbours and high ground vegetation cover were beneficial for a sapling's growth during the first years after planting. The diversity effect on early sapling growth was not clearly pronounced yet in our study; identity effects were most important. With regard to forest management, careful trait selection when designing mixed forest plantations thus seems highly important. As a rule of thumb, mixing fast-growing and slow-growing species will decrease the height to diameter ratio of the fast-growing species in these early stages and thus improve their stability.

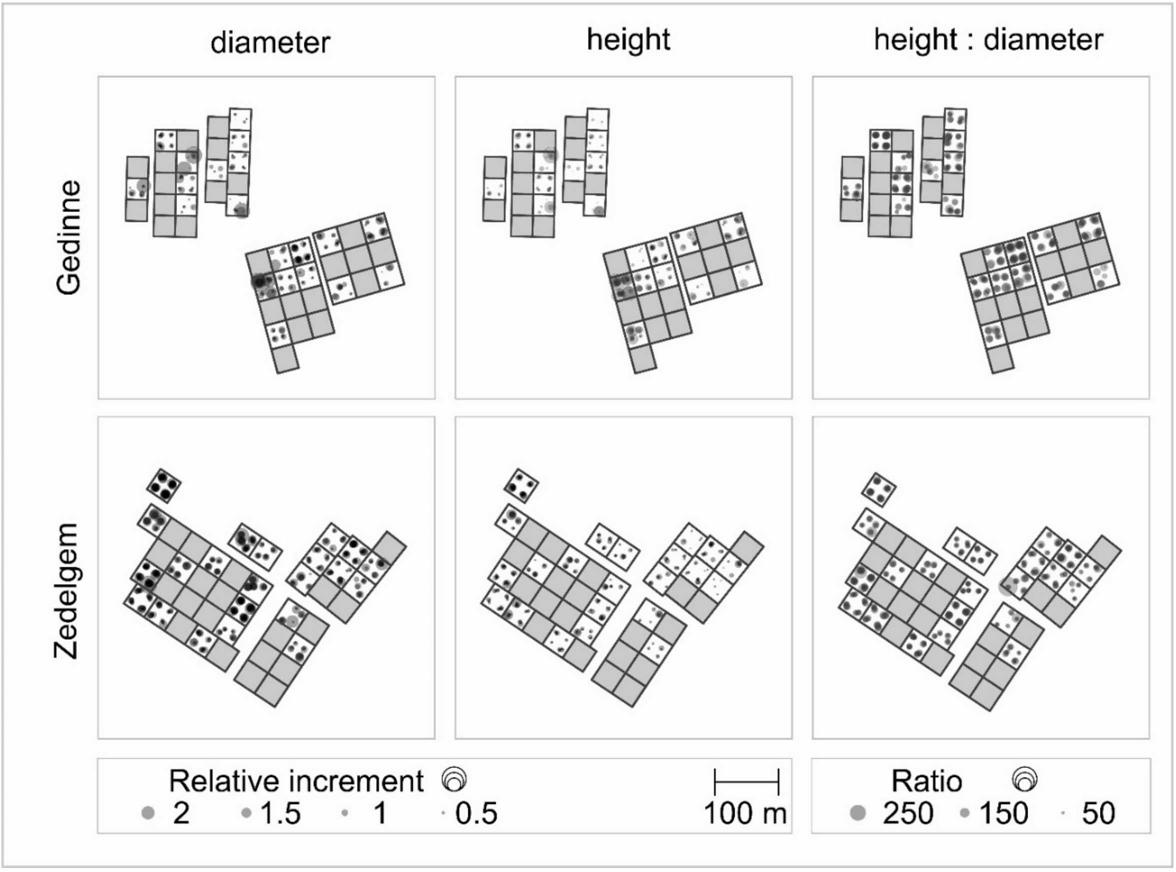
Appendix 3.1 The mean diameter and height (± SEM) of the living saplings taller than 30 cm (min. height at the time of planting) for each tree species out of the 2,816 and 2,688 saplings measured in Gedinne and Zedelgem in winter 2012 and winter 2014. *Quercus* saplings are *Quercus petraea* in Gedinne and *Quercus robur* in Zedelgem.

Variable	Genus	Gedinne	Zedelgem
Number of trees	*Acer*	369	-
	Betula	-	505
	Fagus	660	500
	Larix	443	-
	Pinus	-	477
	Pseudotsuga	420	-
	Quercus	406	595
	Tilia	-	493
	Overall	2,298	2,570
Mean diameter in 2012 (cm)	*Acer*	1.15 (0.02)	-
	Betula	-	2.77 (0.03)
	Fagus	1.03 (0.02)	1.74 (0.02)
	Larix	1.55 (0.04)	-
	Pinus	-	1.82 (0.03)
	Pseudotsuga	1.63 (0.03)	-
	Quercus	1.03 (0.02)	1.47 (0.02)
	Tilia	-	1.23 (0.01)
	Overall	1.26 (0.01)	1.80 (0.01)
Mean diameter in 2014 (cm)	*Acer*	1.35 (0.03)	-
	Betula	-	5.43 (0.07)
	Fagus	1.39 (0.02)	2.78 (0.04)
	Larix	3.97 (0.08)	-
	Pinus	-	4.48 (0.07)
	Pseudotsuga	2.82 (0.06)	-
	Quercus	1.54 (0.03)	2.60 (0.03)
	Tilia	-	2.73 (0.03)
	Overall	2.17 (0.03)	3.56 (0.03)

Appendix 3.1 (continued)

Variable	Genus	Gedinne	Zedelgem
Mean height in 2012 (cm)	*Acer*	113 (2)	-
	Betula	-	228 (2)
	Fagus	74 (1)	124 (1)
	Larix	107 (2)	-
	Pinus	-	86 (1)
	Pseudotsuga	86 (1)	-
	Quercus	88 (1)	154 (1)
	Tilia	-	103 (1)
	Overall	91 (1)	140 (1)
Mean height in 2014 (cm)	*Acer*	121 (2)	-
	Betula	-	396 (4)
	Fagus	101 (1)	191 (3)
	Larix	269 (4)	-
	Pinus	-	199 (2)
	Pseudotsuga	160 (3)	-
	Quercus	122 (2)	209 (2)
	Tilia	-	178 (2)
	Overall	151 (2)	235 (2)

Appendix 3.2 Relative increment (diameter and height) and height to diameter ratio for *Quercus* (*Quercus petraea* in Gedinne and *Quercus robur* in Zedelgem) in the two study sites and years. The size of the dots represents the relative increment or height to diameter ratio of the target saplings in the subplots. Plots without *Quercus* are filled with grey. Clustered dots with a similar size indicate spatial autocorrelation.



Appendix 3.3 Akaike's information criterion (AIC) for *gls* models fitted with relative diameter increment, relative height increment, and height to diameter ratio vs. the different neighbourhood diversity (diversity), neighbours' size asymmetry of year 2012 (size asymmetry 2012), size asymmetry of year 2014 (size asymmetry 2014), and ground vegetation cover (ground vegetation) considered for both study sites (Gedinne: Gdn and Zedelgem: Zed). The lowest AIC values are indicated in bold and correspond to the best models.

	diameter increment		height increment		height to diameter ratio	
	Gdn	Zed	Gdn	Zed	Gdn	Zed
diversity						
null model	1287.9	991.0	1254.2	882.3	**4926.7**	5543.6
exponent Shannon index	1289.9	990.6	1256.0	876.3	4928.5	5542.4
MPD	1287.4	951.9	1254.6	819.3	4928.7	5509.3
MNTD	**1282.6**	**932.5**	**1252.4**	**812.4**	4927.0	**5503.3**
size asymmetry 2012						
null model	1287.9	991.0	1254.2	882.3	4926.7	5543.6
diameter-based	**1266.7**	**976.9**	1251.8	**873.6**	**4903.1**	**5485.0**
height-based	1284.5	**976.9**	**1219.7**	704.2	4928.2	5541.1
size asymmetry 2014						
null model	1287.9	991.0	1254.2	882.3	4926.7	5543.6
diameter-based	**1200.9**	**915.9**	**1207.6**	**869.7**	**4810.0**	**5367.5**
height-based	1246.6	963.1	1246.6	875.4	4926.1	5541.0
ground vegetation						
null model	**1287.9**	991.0	1254.2	882.3	**4926.7**	5543.6
ferns	1289.8	-	1255.3	-	4928.7	-
grass	1288.0	992.6	1252.9	884.3	4926.7	5542.7
herbs	1288.0	983.2	1255.9	872.0	4928.5	5542.7
legumes	1289.3	991.5	1256.1	882.3	4928.7	5542.9
shrub	1289.4	992.6	1256.0	883.9	4927.5	**5534.7**
total cover	1288.3	**981.5**	**1251.0**	**864.2**	**4926.3**	5544.4

Appendix 3.4 Model structure, variance structure, and Akaike's information criterion (AIC) for the *lme* and *gls* full model fitted for relative diameter increment, relative height increment, and height to diameter ratio with different weighted variance structures for both study sites (Gedinne and Zedelgem).

Table 3.4.1 Structure of the six full models fitted by *gls* for both study sites. The explanatory variables used were as follows: sapling species identity (id), neighbourhood diversity (exponent Shannon index – expH, MNTD, MPD), neighbours' size asymmetry (diameter-based size asymmetry 2012 – DSA1, height-based size asymmetry 2012 – HSA1, diameter-based size asymmetry 2014 – DSA2, height-based size asymmetry 2014 – HSA2), and understory cover (ferns – F, grass – G, herbs - H, legumes - L, shrub – S, total cover – T)

	response variables	explanatory variables
Gedinne		
1	diameter increment	~ id + MNTD + DSA1 + DSA2 + id:MNTD + id:DSA1 + id:DSA2 + MNTD:DSA1 + MNTD:DSA2 + DSA1:DSA2
2	height increment	~ id + MNTD + HSA1 + DSA2 + T + id:MNTD + id:HSA1 + id:DSA2 + id:T + MNTD:HSA1+ MNTD:DSA2 + MNTD:T + HSA1:T + DSA2:T + HSA1:DSA2
3	height/diameter	~ id + DSA1 + DSA2 + T + id:DSA1 + id:DSA2 + id:T + DSA1:T + DSA2:T + DSA1:DSA2
Zedelgem		
4	diameter increment	~ id + MNTD + DSA1 + DSA2 + T + id:MNTD + id:DSA1 + id:DSA2 + id:T + MNTD:DSA1+ MNTD:DSA2 + MNTD:T + DSA1:T + DSA2:T + DSA1:DSA2
5	height increment	~ id + MNTD + DSA1 + DSA2 + T + id:MNTD + id:DSA1 + id:DSA2 + id:T + MNTD:DSA1+ MNTD:DSA2 + MNTD:T + DSA1:T + DSA2:T + DSA1:DSA2
6	height/diameter	~ id + MNTD + DSA1 + DSA2 + S + id:MNTD + id:DSA1 + id:DSA2 + id:S + MNTD:DSA1+ MNTD:DSA2 + MNTD:S + DSA1:S + DSA2:S + DSA1:DSA2

Table 3.4.2 The different forms of weighted variance structure used in the *gls* model (based on Zuur et al., 2009)

code	structure
vf1	varFixed (~size asymmetry 2012)
vf2	varIdent (1|~identity)
vf3	varPower (~size asymmetry 2012)
vf4	varExp (~size asymmetry 2012)
vf5	varConstPower (~size asymmetry 2012)
vf6	varConstPower (~size asymmetry 2012|identity)
vf7	varComb (varIdent (1|~identity), varExp (~size asymmetry 2012)
vf8	varFixed (~size asymmetry 2014)
vf9	varPower (~size asymmetry 2014)
vf10	varExp (~size asymmetry 2014)
vf11	varConstPower (~size asymmetry 2014)
vf12	varConstPower (~size asymmetry 2014|identity)
vf13	varComb (varIdent (1|~identity), varExp (~size asymmetry 2014)

Table 3.4.3 Akaike's information criterion (AIC) for the six full models fitted with *lme* and *gls* using different weighted variance structures. The lowest AIC values are indicated in bold and correspond to the best models.

model structure	model 1	model 2	model 3	model 4	model 5	model 6
lme, random: subplot	**657.4**	811.1	4535.2	**130.7**	437.6	4803.5
lme, random: plot	687.6	**802.2**	4539.6	187.3	430.6	4803.8
gls	832.9	863.4	4550.0	319.4	440.3	4822.8
gls + vf1	837.0	832.7	4599.3	304.3	416.8	4812.3
gls + vf2	805.6	837.3	4538.7	265.4	384.9	4781.5
gls + vf3	828.8	834.7	4551.7	303.9	417.5	4810.5
gls + vf4	824.5	829.2	4552.0	300.5	415.2	4808.4
gls + vf5	822.5	830.2	4542.7	302.5	416.8	4810.9
gls + vf6	808.9	816.1	4524.6	260.1	374.0	4764.1
gls + vf7	799.4	820.2	4540.5	256.9	**370.2**	4761.2
gls + vf8	1011.3	968.4	4493.1	359.2	440.3	4758.5
gls + vf9	783.9	860.3	4493.6	321.0	432.7	4758.8
gls + vf10	801.4	861.3	4493.9	321.4	432.2	4752.6
gls + vf11	784.7	862.3	4493.6	322.5	433.7	4754.3
gls + vf12	-	814.1	**4448.4**	-	-	4727.7
gls + vf13	771.0	835.1	4481.7	267.4	378.6	**4720.3**

Appendix 3.5 R syntax of the best-fit models considered in the different analyses. See Appendix 3.4 for more details on the terms.

response variables	R syntax[a]
effects of admixing species	
Gedinne	
diameter increment	
Acer	gls(diameter~P8F+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE),data=AG)
Fagus	gls(diameter~P8A+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE),data=FG)
Larix	gls(diameter~P8A+P8F+P8Ps+P8Q, correlation=corSpher(form=~X+Y,nugget=TRUE),data=LG)
Pseudotsuga	gls(diameter~P8A+P8F+P8L+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE),data=PG)
Quercus	gls(diameter~P8A+P8F+P8L+P8Ps, data=QG)
height increment	
Acer	gls(height~P8F+P8L+P8P+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE),data=AG)
Fagus	gls(height~P8A+P8L+P8Ps+P8Q, correlation=corLin(form=~X+Y,nugget=TRUE),data=FG)
Larix	gls(height~P8A+P8F+P8Ps+P8Q, correlation=corGaus(form=~X+Y,nugget=TRUE),data=LG)
Pseudotsuga	gls(height~P8A+P8F+P8L+P8Q, correlation=corGaus(form=~X+Y,nugget=TRUE),data=PG)
Quercus	gls(height~P8A+P8F+P8L+P8Ps, correlation=corExp(form=~X+Y,nugget=TRUE), data=QG)
height/diameter	
Acer	gls(height/diameter~P8F+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE),data=AG)
Fagus	gls(height/diameter~P8A+P8L+P8Ps+P8Q, correlation=corSpher(form=~X+Y,nugget=TRUE),data=FG)
Larix	gls(height/diameter~P8A+P8F+P8Ps+P8Q, data=LG)
Pseudotsuga	gls(height/diameter~P8A+P8F+P8L+P8Q,data=PG)
Quercus	gls(height/diameter~P8A+P8F+P8L+P8Ps, correlation=corGaus(form=~X+Y,nugget=TRUE),data=QG)
Zedelgem	
diameter increment	
Betula	gls(diameter~P8F+P8P+P8Q+P8T, correlation=corRatio(form=~X+Y,nugget=TRUE), data=BZ)
Fagus	gls(diameter~P8B+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=FZ)
Pinus	gls(diameter~P8B+P8F+P8Q+P8T, data=PZ)
Quercus	gls(diameter~P8B+P8F+P8P+P8T, correlation=corGaus(form=~X+Y,nugget=TRUE), data=QZ)
Tilia	gls(Diameter~P8B+P8F+P8P+P8Q, correlation=corRatio(form=~X+Y,nugget=TRUE), data=TZ)

[a] P8_: proportion of a species (A - *Acer*, B – *Betula*, F – *Fagus*, L – *Larix*, P – *Pinus*, Ps – *Pseudotsuga*, Q – *Quercus*, T - *Tilia*) in the local neighbourhood consisting of the 8 closest neighbours

Appendix 3.5 (continued)

response variables	R syntax[a]
effects of admixing species	
Zedelgem	
height increment	
Betula	gls(height~P8F+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=BZ)
Fagus	gls(height~P8B+P8P+P8Q+P8T, correlation=corSpher(form=~X+Y,nugget=TRUE), data=FZ)
Pinus	gls(height~P8B+P8F+P8Q+P8T, data=PZ)
Quercus	gls(height~P8B+P8F+P8P+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=QZ)
Tilia	gls(Height~P8B+P8F+P8P+P8Q, correlation=corRatio(form=~X+Y,nugget=TRUE), data=TZ)
height/diameter	
Betula	gls(height/diameter~P8F+P8P+P8Q+P8T, correlation=corRatio(form=~X+Y,nugget=TRUE), data=BZ)
Fagus	gls(height/diameter~P8B+P8P+P8Q+P8T, correlation=corGaus(form=~X+Y,nugget=TRUE), data=FZ)
Pinus	gls(height/diameter~P8B+P8F+P8Q+P8T, data=PZ)
Quercus	gls(height/diameter~P8B+P8F+P8P+P8T, correlation=corGaus(form=~X+Y,nugget=TRUE), data=QZ)
Tilia	gls(height/diameter~P8B+P8F+P8P+P8Q, correlation=corGaus(form=~X+Y,nugget=TRUE), data=TZ)

effects of species, diversity, and size asymmetry	
Gedinne	
diameter increment	diameter ~ lme(id + DSA1 + DSA2 + id:DSA2, random=-1| Subplot, method=”REML”, data=Gedinne)
height increment	height ~ lme(id + HSA1 + DSA2 + id:HSA1 + id:DSA2, random=-1| Plot, method=”REML”, data=Gedinne)
height/diameter	height/diameter ~ gls(id + DSA1 + DSA2 + T + id:DSA2 + DSA1:T, weights=vf12, method=”REML”, data=Gedinne)
Zedelgem	
diameter increment	diameter ~ lme(id + MNTD + DSA1 + DSA2 + T + id:MNTD + id:DSA2 + DSA1:DSA2, random=-1| Subplot, method=”REML”, data=Zedelgem)
height increment	height ~ gls(id + MNTD + DSA1 + DSA2 + T + id:MNTD + id:DSA1 + MNTD:DSA2, weights= vf7, method=”REML”, data=Zedelgem)
height/diameter	height/diameter ~ gls(id + MNTD + DSA1 + DSA2 + S + id:MNTD + id:DSA2 + id:S, weights=vf13, method=”REML”, data=Zedelgem)

[a] P8_: proportion of a species (A - *Acer*, B – *Betula*, F – *Fagus*, L – *Larix*, P – *Pinus*, Ps – *Pseudotsuga*, Q – *Quercus*, T - *Tilia*) in the local neighbourhood consisting of the 8 closest neighbours

Shoot dieback of *Quercus robur* at Zedelgem site [Photograph: Mathias Dillen]

Chapter 4

Local neighbourhood effects on pest and disease damage in saplings

After: Setiawan NN, Vanhellemont M, Baeten L, Dillen M, Verheyen K (2014) The effects of local neighbourhood diversity on pest and disease damage of trees in a young experimental forest. Forest Ecology and Management 334, 1–9

4.1 Abstract

Pests and diseases causing defoliation and crown discolouration are important risks threatening the vitality of forests, especially in the early stages of forest development. Mixing different tree species in a forest stand has been described as a possible solution to tackle this problem through the mechanism of associational resistance. However, most research up till now has focused on mature forests. We assessed three different damage symptoms related with tree crown condition, i.e., branch and shoot damage, defoliation, and crown discolouration, for nine common tree species at two sites of a recently established tree species diversity experiment in Belgium. The assessment was done in two subsequent years. A sapling's damage degree was influenced by the site characteristics and the timing of the assessment, and the species identity of the target sapling was more important than the effect of local neighbourhood diversity *per se* in explaining a sapling's damage degree. Our results only partially support the hypothesis that trees in more diverse local neighbourhoods in young plantations show less crown damage. Nevertheless, some particular mixtures resulted in reduced damage degrees.

4.2 Introduction

The crown condition of forest trees is commonly used as an indicator of forest health and vitality, e.g., by the European monitoring network ICP Forests (http://icp-forests.net). Two main crown condition criteria that are commonly assessed are (1) the loss of foliage area or defoliation and (2) crown discolouration. Defoliation and discolouration reduce a tree's photosynthetic capacity (Führer 1998); discolouration may lead to higher herbivore damage due to the increase in soluble nitrogen in the leaf tissues, which attracts invertebrate herbivores (White 1984). Insects are the most common pests causing defoliation in European forests (Becher et al. 2014). Discolouration can be caused by several environmental stresses, e.g., drought or nutrient deficiency, and diseases, e.g., fungi or viruses (Hopkins and Hüner 2009, Taiz and Zeiger 2010). Pests and diseases naturally occur in the forest ecosystem (Ostry and Laflamme 2009) and may serve as one of the key factors shaping the dynamics and diversity of forested landscapes, next to anthropogenic influences, abiotic factors, and large herbivores (Holdenrieder et al. 2004). Diseases may cause tree mortality, which will lead to the formation of canopy gaps in mature forests. Small-scale succession in these canopy gaps helps to maintain tree species and age diversity in the forest (Castello et al. 1995). Yet, for forest management in Europe, the damage caused by insect activities or diseases is considered a threat if it reaches a certain threshold, i.e., affecting 25% crown area of single trees (Eichhorn et al. 2010).

The risk for pest and disease damage is related to the probability of occurrence, the behaviour of populations of damaging agents, and the scale at which the damaging agents actively operate (Hambäck and Beckerman 2003, Jactel et al. 2009, Underwood et al. 2014), which is in turn influenced by the forest stand composition and management. Indeed, the occurrence of most pests and pathogens largely depends on stand density, the presence of host trees, the abundance of non-host trees, and other stand characteristics, such as stand composition and age structure (Hambäck and Beckerman 2003, Vehviläinen et al. 2007, Barbosa et al. 2009, Hambäck et al. 2014). Mixed stands consisting of site-adapted species may be more resistant to pests and diseases compared to monocultures (Spiecker 2003, Jactel et al. 2005). Indeed, a focal tree's vulnerability to predation or parasitism can be altered by the identity, diversity, and abundance of its neighbouring species (Underwood et al. 2014). This phenomenon, also called associational resistance (Tahvanainen and Root 1972), can be explained by the resource concentration theory (Root 1973), i.e., the resources are more concentrated in monocultures and thus more easily found by pathogenic fungi or insect herbivores. Yet, the results of studies on the relation between tree species diversity and crown damage are not consistent and depend on the environmental conditions (Koricheva et al. 2006, Vehviläinen et al. 2007). In mixed stands, populations of specialized herbivores may be reduced, but generalist herbivores (Koricheva et al. 2006) and heteroecious fungal pathogens (Jactel et al. 2009) can be positively affected by tree species diversity. Tree species diversity seems to have less effect than tree species composition. For instance, herbivore damage was less when mixed forests were comprised of taxonomically or phylogenetically more distant tree species or when the host tree species were surrounded by a higher proportion of non-host tree species (Jactel and Brockerhoff 2007, Castagneyrol et al. 2014). The associational resistance in a certain neighbourhood may also change through time, e.g., between seasons, from year to year, or as the trees get older (Montagnini et al. 1995, Vehviläinen et al. 2007). However, most studies on the effect of tree species diversity on the resistance of trees to pests and diseases have been done in mature forests (Vehviläinen et al. 2006, 2007, Koricheva et al. 2006, Jactel and Brockerhoff 2007, Haas et al. 2011, Castagneyrol et al. 2014). Only few studies have focused on the young stages of forest development (Sobek et al. 2009b, Castagneyrol et al. 2012, Hantsch et al. 2013).

To investigate the relation between tree species diversity and pest and disease regulation, we assessed three different damage symptoms related with the crown condition of *ca.* 5500 saplings, i.e., branch and shoot damage, defoliation, and crown discolouration. We assessed branch and shoot damage since it reflects how much of a tree's shoot system is no longer productive. The three hypotheses tested in this chapter were: (1) the damage degree shows significant interspecific variation and different damage symptoms predominate for different species; (2) the damage degree will be lower for saplings growing in a more species-diverse neighbourhood due to associational resistance; (3) the damage degree of a sapling is affected by the species identity of the trees in its local neighbourhood. The results of our study may help in selecting optimal mixtures to reduce damage caused by pests and diseases in new plantations.

4.3 Materials and methods

4.3.1 Data collection

We did the damage assessment for all the saplings of each subplot (*N* = 64 saplings/plot). In total, we assessed 2,816 saplings in Gedinne and 2,688 saplings in Zedelgem. Damage symptoms or a tree's condition due to damaging agents were assessed in three categories, i.e., (1) branch and shoot damage, (2) defoliation, and (3) crown discolouration. The assessment was a modification of the ICP crown condition assessment (Eichhorn et al. 2010) using 5% classes (e.g., 0%, 5%, 10%, 15%, …, 95%, 100%). The scoring was done by only two trained observers to reduce the subjectivity. Prior to the assessment, the protocol used was checked in the field with an ICP expert (ir. Peter Roskams). The branch and shoot damage of a tree was quantified as the estimated percentage of the crown volume that consisted of dead branches and shoots. Defoliation was quantified as the percentage foliage damage in the assessed tree crown as compared to a reference tree, i.e., a healthy tree in the vicinity. The percentage foliage damage was calculated as the multiplication of two estimates, i.e., the incidence and the intensity of the damage, with incidence the percentage of leaves that shows herbivore damage and intensity the percentage of the leaf area of these damaged leaves that is affected. Defoliation was assessed only on broadleaved tree species (Photo 4.1). Crown discolouration was quantified as the estimated percentage of the crown that showed a colour different from the usual leaf colour of the species, caused by environmental stress or pathogens, e.g., necrosis due to fungi (Photo 4.1 & 4.2).

The main causes of defoliation we encountered were insect herbivores, i.e., leaf chewers, leaf miners, and skeletonizers. These three groups of herbivores can be categorized as ectophagous species (leaf chewers), i.e., species consuming plant material by browsing, and endophagous species (leaf miners, skeletonizers), i.e., species disintegrating plant material from within. These insect herbivores mostly emerge following the bud burst of the trees. The leaf damage will accumulate until the second bud burst in early summer or until leaf fall in autumn. Therefore, we performed our assessments when the leaves were fully developed, in early autumn (October 2012). The same target saplings were assessed again in early summer the next year (July-August 2013) to check whether the patterns observed in 2012 were consistent between years and to confirm whether effects were similar in different periods of sampling (e.g., no potential effects of autumnal withering on the discolouration assessment).

4.3.2 Data analysis

Tree identity and local neighbourhood diversity were two factors expected to influence a sapling's damage symptoms. The local neighbourhood diversity was expressed as exponent of Shannon diversity index (expH, see section 2.4.3). The analyses were done separately for the two sampling periods, i.e., early autumn 2012 and early summer 2013, and the two sites, i.e., Gedinne and Zedelgem. All analyses were done in R version 3.0.3 (R Core Team 2013); graphs were made with the R package *ggplot2* (Wickham 2009).

Photo 4.1 Example of defoliation in *Betula* (left) and discolouration in *Fagus* (right) [Photographs: NN Setiawan & Mathias Dillen]

Photo 4.2 Example of mildew infestation (left) and leaf miner (right) in *Quercus* [Photographs: Mathias Dillen & NN Setiawan]

First, we graphically checked for spatial autocorrelation in the damage data (Borcard et al. 2011). Second, correlations between the degrees of damage in the three damage categories and correlations between the degree of damage in each damage category and the total cover of the understory vegetation (see Table 2.6) were calculated using Pearson correlation. Third, we tested the effects of tree species identity and local neighbourhood diversity for each damage category in a generalized least squares model using the *gls* function in the *nlme* package (Pinheiro et al. 2014). The damage percentages of each damage category were used as the response variables; tree species identity, local neighbourhood diversity, and their interaction were used as the explanatory variables (see Appendix 4.1 for R syntax). In order to normalize the data, all damage values were logit-transformed (Warton and Hui 2011). To account for the spatial autocorrelation in the data, we included a spatial correlation structure (i.e., spherical, linear, ratio, gaussian, or exponential) in the model and evaluated the best fit with AIC values and variograms (Zuur et al. 2009).

Last, we tested the effects of the abundance of the different tree species in the local neighbourhood on the damage degree of the target trees for the different damage symptoms. We again used *gls* with spatial autocorrelation, but we now used the abundances (% of stems) of each tree species in the local neighbourhood of the target tree as explanatory variables (see Appendix 4.1 for R syntax). We then used the coefficients of the fitted models to (1) calculate the expected mean damage, with 95% confidence interval, of a target tree surrounded by a monoculture of the target tree species and (2) predict the mean damage of the target tree if 50% of the local neighbourhood would consist of another tree species, i.e., for each tree species, we tested the effect of mixing the species with each of the other tree species planted at the site.

4.4 Results

The number of dead trees was generally low, but higher in Gedinne than in Zedelgem (Table 4.1). Similarly, the number of surviving trees with at least one damage symptom or with more damage than the 25% threshold was higher in Gedinne than in Zedelgem. Overall, damage symptoms were more frequent in early autumn 2012 than in early summer 2013, except for branch & shoot damage (Zedelgem) and defoliation (both sites). For instance, *Fagus* showed lower damage percentages in 2013 than in 2012 (Fig. 4.1). Note the spatial clustering of damage for *Fagus* in Fig. 4.1, a clustering that was also found for the other damage symptoms and species. Based on the AIC values and variograms, an exponential autocorrelation structure provided the best model fit for the data. There were no significant differences in weather conditions between the years that might have caused the differences in damage degrees between sites: temperature did not significantly differ, and there was no drought stress (see Appendix 2.1). The most frequently occurring damage symptoms were crown discolouration (Gedinne, both years; Zedelgem, 2012) and defoliation (Zedelgem, 2013). The species showing the highest mean crown discolouration in Gedinne were *Quercus* (mean damage value with standard deviation: 61.4 ± 28.1%) in 2012 and *Pseudotsuga* (29.9 ± 18.8%) in 2013. In Zedelgem, the species with the highest mean damage were *Fagus* (50.2 ± 28.5%) and *Tilia* (48.7 ± 26.8 %) for crown discolouration in 2012; and *Tilia* (30.8 ± 26.4%) for defoliation in 2013.

In Gedinne, we saw significant differences in damage between the two subsites, i.e., Gribelle and Gouverneurs, in 2013. Branch and shoot damage (Kruskal-Wallis: $p < 0.001$) and crown discolouration ($p < 0.001$) were larger in Gribelle; defoliation ($p < 0.001$) was larger in Gouverneurs. For *Fagus* and *Quercus*, the two species present in Gedinne and Zedelgem, branch and shoot damage (Kruskal-Wallis: $p < 0.001$) and crown discolouration ($p < 0.001$) were higher in Gedinne, while defoliation was higher in Zedelgem ($p < 0.001$). Damage caused by leaf chewers (ectophagous species) was found in all the broadleaved tree species, while damage caused by leaf

Table 4.1 The number of trees (percentage between brackets) out of the 2,816 and 2,688 saplings assessed in Gedinne and Zedelgem that show a certain damage symptom

	Gedinne		Zedelgem	
	2012	2013	2012	2013
branch & shoot damage	893 (*35.3*)	651 (*26.9*)	110 (*4.25*)	192 (*7.41*)
defoliation	845 (*33.4*)	1044 (*43.2*)	1,594 (*61.5*)	2,057 (*79.4*)
crown discolouration	2,234 (*88.2*)	1,854 (*76.7*)	1,867 (*72.1*)	1,328 (*51.3*)
1 or more damage symptoms	2,403 (*94.9*)	2,189 (*90.6*)	2,281 (*88.1*)	2,090 (*80.7*)
overall crown damage > 25%	1,867 (*73.7*)	1,098 (*45.4*)	1,427 (*55.1*)	625 (*24.1*)
dead	284 (*10.1*)	399 (*14.2*)	98 (*3.6*)	98 (*3.6*)

miners and skeletonizers (endophagous species) was only found in two species of *Quercus*. Branch and shoot damage was positively correlated with crown discolouration ($r = 0.14, p < 0.001, N = 10{,}136$) and negatively with defoliation ($r = -0.08, p < 0.001, N = 10{,}136$). Crown discolouration and defoliation showed no correlation ($r = 0.01$, $p = 0.58$, $N = 10{,}136$). In Gedinne, the correlation between branch and shoot damage and understory cover was low ($r = 0.10, p < 0.001$, $N = 4{,}949$); there was no significant correlation between understory cover and defoliation ($r = 0.01, p = 0.44, N = 4{,}949$) or crown discolouration ($r = 0.01, p = 0.46, N = 4{,}949$). In Zedelgem, the correlations between understory cover and the damage categories were also low: branch and shoot damage ($r = 0.03, p < 0.001, N = 5{,}187$), crown discolouration ($r = 0.04, p = 0.001, N = 5{,}187$), and defoliation ($r = -0.08, p = 0.02, N = 5{,}187$).

The damage degrees of all damage symptoms differed significantly between the target tree species (Table 4.2). The diversity of the local neighbourhood was significant only for the branch and shoot damage in Gedinne in 2013, i.e., lower damage percentages in more diverse local neighbourhoods, and for the defoliation in Zedelgem in 2012, i.e., more defoliation in more diverse neighbourhoods. A significant interaction between tree species identity and neighbourhood diversity was only found for the branch and shoot damage at both sites in 2013: the damage percentage was negatively related to the local neighbourhood diversity for some species, e.g., *Acer* and *Quercus* in Gedinne and *Fagus* and *Quercus* in Zedelgem, but there was no correlation for other species, e.g., *Larix* in Gedinne and *Pinus* and *Tilia* in Zedelgem.

Target saplings growing in monocultures showed lower branch and shoot damage in early summer 2013 than in early autumn 2012, except for *Pseudotsuga* in Gedinne (Fig. 4.2a) and *Betula* in Zedelgem (Fig. 4.2b). The defoliation was also lower in 2013 in Gedinne, except for *Acer* (Fig. 4.2a). In Zedelgem, the defoliation was always higher in 2013 than in 2012, except for *Betula* (Fig. 4.2b).

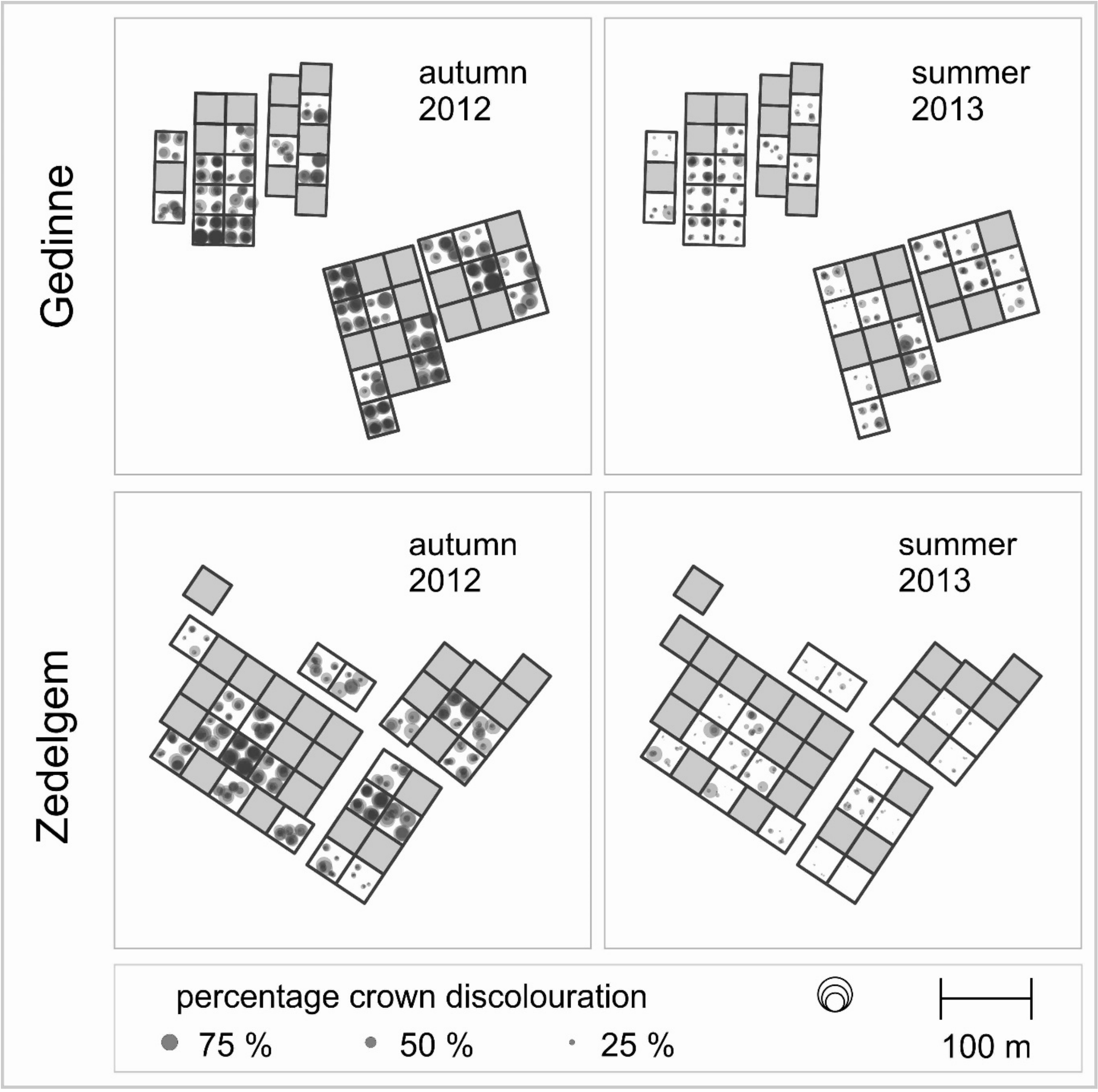


Fig. 4.1 Crown discolouration for *Fagus sylvatica* in the two study sites and years. The size of the dots represents the percentage crown discolouration of the target trees in the subplots. Plots without *Fagus* are filled with grey. Clustered dots with more similar size indicate spatial autocorrelation.

The crown discolouration was also lower in the early summer (2013) compared with the early autumn (2012) survey, except for *Pseudotsuga* in Gedinne (Fig. 4.2a) and *Quercus* in Zedelgem (Fig. 4.2b). The estimated changes in mean damage percentage with the addition of a second tree species in the local neighbourhood were different for every target tree species.

We did not see any consistent pattern of increase or decrease in damage with the addition of a second species to the local neighbourhood, not even when mixing a broadleaved with a coniferous tree species. However, we saw indications of reduction in damage for some of the target tree species when certain tree species were added to the local neighbourhood: (1) *Pseudotsuga* if *Quercus* was added; (2) *Betula* if *Pinus* was added; (3) *Quercus* if *Betula* was added (Fig. 4.2a & b).

Table 4.2 The linear models used to test the effects of tree species identity (id), local neighbourhood diversity (div), and their interaction on the percentage damage for the three damage symptoms, in the two study sites and the two years. P values smaller than 0.05 are indicated in bold.

Variables	Gedinne				Zedelgem			
	2012		2013		2012		2013	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
shoot and branch damage								
id	34.56	**<0.001**	383.45	**<0.001**	12.18	**<0.001**	23.72	**<0.001**
div	1.37	0.242	6.99	**0.008**	3.18	0.075	0.02	0.887
id x div	1.16	0.327	6.70	**<0.001**	1.39	0.233	2.91	**0.020**
defoliation								
id	40.37	**<0.001**	48.6	**<0.001**	78.48	**<0.001**	199.13	**<0.001**
div	3.37	0.067	0.52	0.472	4.61	0.032	0.03	0.860
id x div	1.71	0.182	0.13	0.875	0.78	0.506	1.43	0.234
crown discolouration								
id	74.59	**<0.001**	41.99	**<0.001**	417.0	**<0.001**	538.62	**<0.001**
div	1.13	0.287	0.24	0.626	1.44	0.231	2.09	0.148
id x div	1.56	0.181	1.60	0.172	0.97	0.423	3.32	**0.010**

4.5 Discussion

In our study, the tree species identity of the target saplings was more important than the tree species diversity of the local neighbourhood in influencing a tree's damage degree. Different tree species showed different damage patterns, i.e., differences in damage frequency, mean damage percentage, and the damage symptom. For example, in Gedinne in 2012, crown discolouration was frequent in *Quercus* (438 saplings) and *Larix* (459 saplings), but the mean damage percentage was higher in *Quercus* (64.3 ± 25.2%) than in *Larix* (33.9 ± 20.0%). Similar identity effects have also been found in experiments in temperate grasslands (Scherber et al. 2006), boreal forests (Koricheva et al. 2006), and young temperate forest (Sobek et al. 2009b, Hantsch et al. 2013). The negative correlation between branch and shoot damage, i.e., the percentage of the crown that was dead, and defoliation, i.e., the percentage of living, foliaged crown that was damaged, in our study might reflect that an increased damage on branches and shoots reduces the amount of viable crown that can be affected by defoliators. Most defoliators, e.g., skeletonizers, leaf miners, and leaf chewers, find their host trees based on chemical and visual cues. Trees with less foliage will be less preferential for these defoliators since there is less food available (Matthews and Matthews 2010).

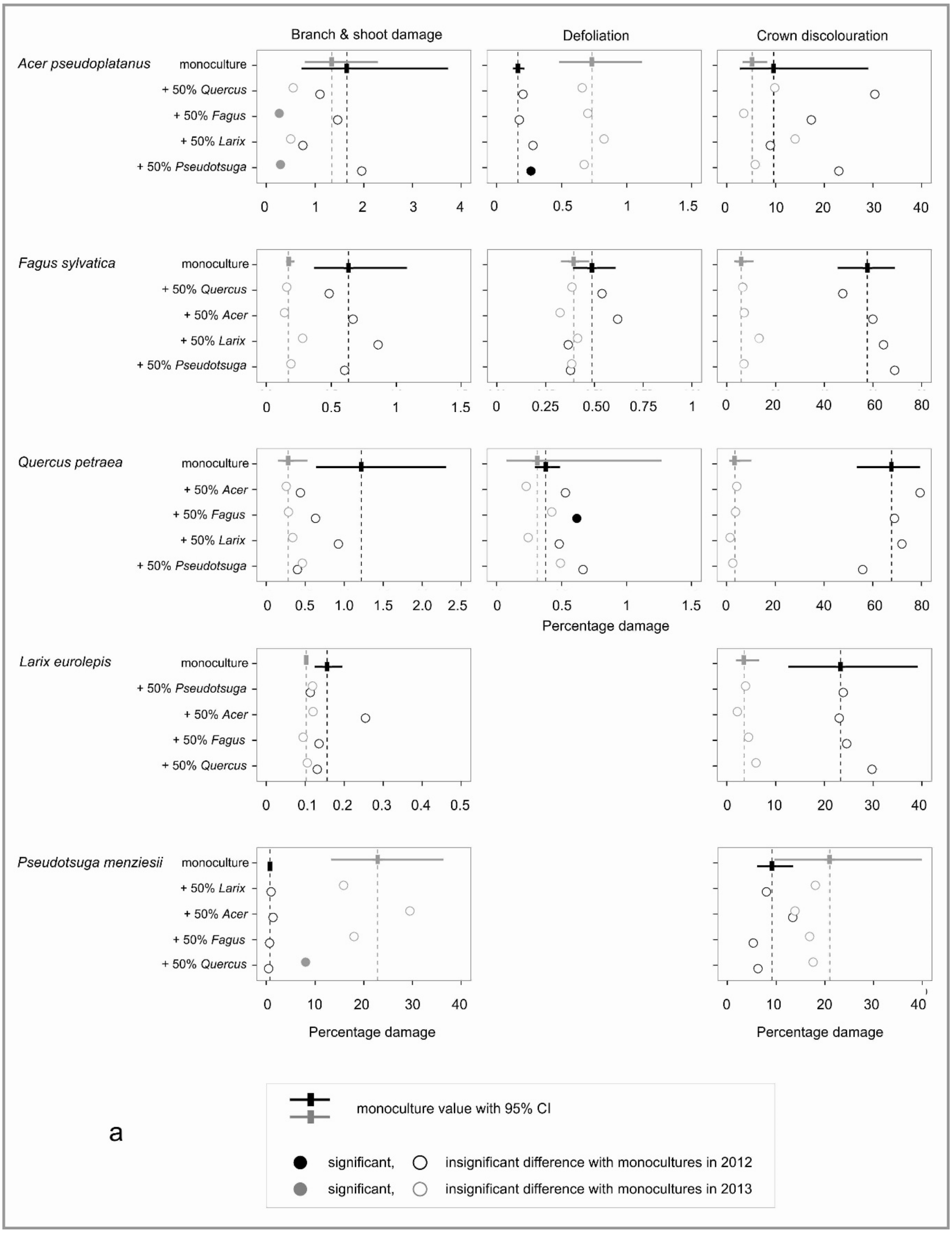


Fig. 4.2 The expected mean damage (%) for a sapling in a local neighbourhood consisting of its own species (monoculture) or in which saplings of a second species represent 50% of the neighbours (+ 50%) for the Gedinne (a) and Zedelgem (b) site. The expected mean damage percentages were estimated with *gls* models (see section 0). The order of the tree species in the graphs is linked to their phylogenetic relatedness (see Fig. 2.4). The mean damage percentages of the monocultures are given with the 95%

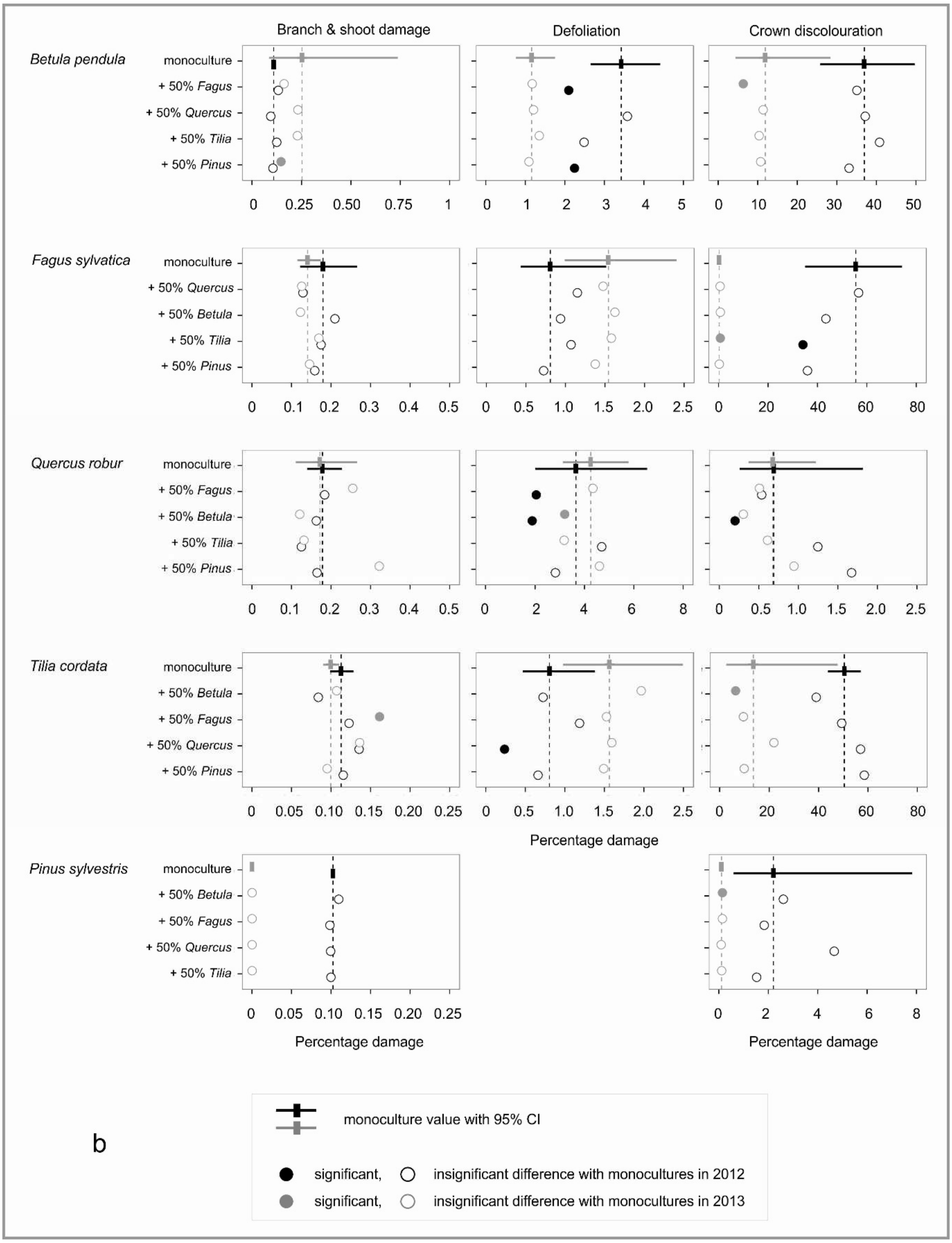


Fig. 4.2 (cont.) confidence interval and are also represented by the dashed lines. Filled dots indicate species of which the abundance in the local neighbourhood significantly affects the damage of the target sapling, and empty dots indicate that the presence of the second tree species does not significantly affect the target sapling's damage level, compared to the damage level in the monoculture. Note that the X axes are scaled differently for the different species and damage symptoms

Although it is widely acknowledged that the identity and abundance of species in the local neighbourhood play a role in the regulation of pests on target trees (associational resistance), only branch and shoot damage (Gedinne, 2013) and defoliation (Zedelgem, 2012) were related to neighbourhood diversity in our study. In young plantations, such as the ones in our study, the understory vegetation may also influence the damage degree of the trees (Giffard et al. 2012).

In the years of our study, some of the saplings were as tall (see Appendix 3.1) as the understory vegetation. In Gedinne, some ferns grew taller than 1.5 m. In such conditions, the effects of small neighbour saplings might be negligible compared to the effect of the understorey vegetation surrounding the target sapling. This surrounding understory vegetation might hinder sapling growth, but may also lower the probability of detection of the saplings by invertebrate herbivores or even provide suitable habitat for natural enemies of the herbivores (Veres et al. 2013). Saplings might also compete with the ground vegetation for water, which might result in drought stress and thus cause specific discolouration patterns in for instance *Tilia* (ir. Peter Roskams, *personal communication*).

Yet, in our study, we did not find any clear correlation between the observed damage degrees and the cover of the understory vegetation or the mean height of the tree species. In young plantations, the height of the understory vegetation might be as important as its cover. Unfortunately, however, we did not have data on the height of the understory vegetation in the years of sampling, nor on the height of the sampled trees in the second year of sampling.

Anyhow, even in our young plantation, we saw some indications that the presence of a second tree species in the local neighbourhood of a sapling can affect its damage degree. For instance, the damage degree of *Quercus* was higher in monocultures than in a two-species mixture with *Betula*. On average, *Betula* was taller than *Quercus* (see Appendix 3.1) and may thus shield *Quercus* from its herbivores (Castagneyrol et al. 2013). We expect the mixture effects to become larger as the stand ages (Montagnini et al. 1995, Vehviläinen et al. 2007, Potvin and Dutilleul 2009, Paul et al. 2011) or if more species are added to the mixture. As the stand ages and the trees grow bigger, the competition for resources will be more intense. For example, when water is limited, dominated trees suffering from drought will be more vulnerable to pest and disease attacks (Bréda et al. 2006, Jactel et al. 2012). Adding more species to a mixture may have two consequences: increasing the damage rate due to the higher probability of including suitable host trees for generalist herbivores, or reducing the damage rate due to diluting the proportion of hosts for specialist herbivores.

The magnitude of a local neighbourhood effect on damage caused by pests and diseases is regulated by factors such as the abundance of neighbour trees, the distance between neighbour and target trees, the season, the age or size difference between the target tree and the neighbour trees, and the phylogenetic relatedness between neighbour and target trees (Srivastava and Vellend 2005, Vehviläinen et al. 2006, Jactel and Brockerhoff 2007, Barbosa et al. 2009, Ness et al. 2011, Castagneyrol et al. 2014). Differences in the sampling season and the phylogenetic relatedness between neighbour and target saplings may be relevant in explaining the results of our study. In general, the damage was less in 2013 than in 2012, most probably due to the difference in timing of the assessment. In 2012, the assessment was done in early autumn, and tree species that generally do not have a second bud burst thus showed the damage that had accumulated during the entire growing season. In 2013, the assessment was done in early summer. Mixing conifers and broadleaved tree species, which are phylogenetically distinct, is considered a rule of thumb for reducing damage caused by pests and diseases (Castagneyrol et al. 2014). Besides that, mixed stands with phylogenetically distant tree species will also provide heterogeneous habitats that allow diverse natural enemies of pests to co-exist. Mixtures of *Pinus* and *Betula*, for instance, can promote associational resistance against European pine sawfly (Kaitaniemi et al. 2007). The pine sawfly survival decreased in mixtures because more sawfly predators (e.g., spiders and predatory heteropterans) were found in mixtures. In our study, we only saw weak indications for a lower damage in mixtures compared to monocultures, e.g., for *Pinus* with *Fagus*. The tree species in FORBIO were selected to represent a broad range of trait values (Chapter 2) and are phylogenetically distant (Fig. 2.4), which may explain the strong tree species identity effect in our results.

Next to differences in season and phylogeny, the difference in former land use, and thus the nutrient concentrations in the soil between the sites (see Table 2.1) may have also influenced the damage degrees. Trees growing in nutrient-rich soil have higher foliar nitrogen concentrations, which is preferred by invertebrate herbivores (Throop and Lerdau 2004). For *Fagus* and *Quercus*, the two species that were present at both sites, we indeed saw more frequent and higher defoliation damage in Zedelgem, formerly used for agriculture, compared with Gedinne, formerly forested. The lower soil nutrient levels and the harsher climatic condition in Gedinne might be linked with the higher frequency and mean percentages of crown discolouration and branch and shoot damage at the site, compared with Zedelgem. Nutrient deficiencies disrupt plant metabolism and functioning, resulting in several symptoms: susceptibility to diseases, chlorosis, and necrosis of a part of the shoots or foliage (Taiz and Zeiger 2010). At each of the two sites, we did also see clear spatial patterns in the damage levels of the sampled trees (see Fig. 4.1 for crown discolouration in *Fagus*). The observed spatial autocorrelations in tree crown damage might have been generated by patterns in nutrient legacies of past land use or understorey vegetation. Yet, more data are needed to explore these relationships.

4.6 Conclusions

To summarise, our results (1) demonstrate that a tree's crown damage degree depends on its species identity and (2) only partially support the hypothesis that trees in more diverse local neighbourhoods show less crown damage. The effect of local neighbourhood diversity varied both spatially and temporally, and the impact of the presence of a certain tree species in the local neighbourhood on the crown condition of target trees was weak in this early stage of stand development. Yet, when planning stand composition in a forest management plan, it might be wise to gather information on specific pests or diseases infecting the target tree species and then select mixture species based on traits that are not preferred by the pests and diseases. The result of our study suggest that some two-species mixtures may reduce the damage degree of target trees: (1) *Pseudotsuga* growing together with *Quercus*, (2) *Betula* with *Pinus*, or (3) *Quercus* with *Betula*. Note, however, that the interrelations in the context of damage reduction might change over time and that other factors related to ecosystem services such as wood production, e.g., light competition between neighbouring trees, might not be maximized in the proposed mixtures.

Appendix 4.1 R syntax of the best-fit models considered in the different analyses

response variables	R syntax[a]
effects of species and diversity	
Gedinne	
shoot and branch damage	
2012	gls(shoot&branch2012 ~ id + div + id:div, correlation=corExp(form=~X+Y,nugget=TRUE), data=Gedinne2012)
2013	gls(shoot&branch2013 ~ id + div + id:div, correlation=corLin(form=~X+Y,nugget=TRUE), data=Gedinne2013)
defoliation	
2012	gls(defoliation2012 ~ id + div + id:div, correlation=corLin(form=~X+Y,nugget=TRUE), data=Gedinne2012)
2013	gls(defoliation2013 ~ id + div + id:div, correlation=corExp(form=~X+Y,nugget=TRUE), data=Gedinne2013)
crown discolouration	
2012	gls(discolouration2012 ~ id + div + id:div, correlation=corLin(form=~X+Y,nugget=TRUE), data=Gedinne2012)
2013	gls(discolouration2012 ~ id + div + id:div, correlation=corExp(form=~X+Y,nugget=TRUE), data=Gedinne2013)
Zedelgem	
shoot and branch damage	
2012	gls(shoot&branch2012 ~ id + div + id:div, correlation=corExp(form=~X+Y,nugget=TRUE), data=Zedelgem2012)
2013	gls(shoot&branch2013 ~ id + div + id:div, correlation=corExp(form=~X+Y,nugget=TRUE), data= Zedelgem2013)
defoliation	
2012	gls(defoliation2012 ~ id + div + id:div, correlation=corLin(form=~X+Y,nugget=TRUE), data= Zedelgem2012)
2013	gls(defoliation2013 ~ id + div + id:div, correlation=corExp(form=~X+Y,nugget=TRUE), data= Zedelgem2013)
crown discolouration	
2012	gls(discolouration2012 ~ id + div + id:div, correlation=corExp(form=~X+Y,nugget=TRUE), data= Zedelgem2012)
2013	gls(discolouration2012 ~ id + div + id:div, correlation=corLin(form=~X+Y,nugget=TRUE), data= Zedelgem2013)
effects of admixing species	
Gedinne	
shoot and branch damage 2012	
Acer	gls(shoot&branch2012~P8F+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=AG2012)
Fagus	gls(shoot&branch2012~P8A+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=FG2012)
Larix	gls(shoot&branch2012~P8A+P8F+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=LG2012)
Pseudotsuga	gls(shoot&branch2012~P8A+P8F+P8L+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=PG2012)
Quercus	gls(shoot&branch2012~P8A+P8F+P8L+P8Ps, correlation=corExp(form=~X+Y,nugget=TRUE), data=QG2012)

[a] tree species identity (id), local neighbourhood diversity (div); P8_: proportion of a species (A - *Acer*, B – *Betula*, F – *Fagus*, L – *Larix*, P – *Pinus*, Ps – *Pseudotsuga*, Q – *Quercus*, T - *Tilia*) in the local neighbourhood consisting of the 8 closest neighbour trees

Appendix 4.1 (continued)

response variables	R syntax[a]
effects of admixing species	
Gedinne	
shoot and branch damage 2013	
Acer	gls(shoot&branch2013~P8F+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data= AG2013)
Fagus	gls(shoot&branch2013~P8A+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=FG2013)
Larix	gls(shoot&branch2013~P8A+P8F+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=LG2013)
Pseudotsuga	gls(shoot&branch2013~P8A+P8F+P8L+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=PG2013)
Quercus	gls(shoot&branch2013~P8A+P8F+P8L+P8Ps, correlation=corExp(form=~X+Y,nugget=TRUE), data=QG2013)
defoliation 2013	
Acer	gls(defoliation2013~P8F+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=AG2013)
Fagus	gls(defoliation2013~P8A+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=FG2013)
Quercus	gls(defoliation2013~P8A+P8F+P8L+P8Ps, correlation=corExp(form=~X+Y,nugget=TRUE), data=QG2013)
crown discolouration 2012	
Acer	gls(discolouration2012~P8F+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=AG2012)
Fagus	gls(discolouration 2012~P8A+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=FG2012)
Larix	gls(discolouration 2012~P8A+P8F+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=LG2012)
Pseudotsuga	gls(discolouration2012~P8A+P8F+P8L+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=PG2012)
Quercus	gls(discolouration2012~P8A+P8F+P8L+P8Ps, correlation=corExp(form=~X+Y,nugget=TRUE), data=QG2012)
crown discolouration 2013	
Acer	gls(discolouration2013~P8F+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=AG2013)
Fagus	gls(discolouration2013~P8A+P8L+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=FG2013)
Larix	gls(discolouration2013~P8A+P8F+P8Ps+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=LG2013)
Pseudotsuga	gls(discolouration2013~P8A+P8F+P8L+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=PG2013)
Quercus	gls(discolouration2013~P8A+P8F+P8L+P8Ps, correlation=corExp(form=~X+Y,nugget=TRUE), data=QG2013)

[a] tree species identity (id), local neighbourhood diversity (div); P8_: proportion of a species (A - *Acer*, B – *Betula*, F – *Fagus*, L – *Larix*, P – *Pinus*, Ps – *Pseudotsuga*, Q – *Quercus*, T - *Tilia*) in the local neighbourhood consisting of the 8 closest neighbour trees

Appendix 4.1 R syntax of the best-fit models considered in the different analyses

response variables	R syntax[a]
effects of admixing species	
Zedelgem	
shoot and branch damage 2012	
Betula	gls(shoot&branch2012~P8F+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=BZ2012)
Fagus	gls(shoot&branch2012~P8B+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=FZ2012)
Pinus	gls(shoot&branch2012~P8B+P8F+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=PZ2012)
Quercus	gls(shoot&branch2012~P8B+P8F+P8P+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=QZ2012)
Tilia	gls(shoot&branch2012~P8B+P8F+P8P+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=TZ2012)
shoot and branch damage 2013	
Betula	gls(shoot&branch2013~P8F+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=BZ2013)
Fagus	gls(shoot&branch2013~P8B+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=FZ2013)
Pinus	gls(shoot&branch2013~P8B+P8F+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=PZ2013)
Quercus	gls(shoot&branch2013~P8B+P8F+P8P+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=QZ2013)
Tilia	gls(shoot&branch2013~P8B+P8F+P8P+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=TZ2013)
defoliation 2012	
Betula	gls(defoliation2012~P8F+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=BZ2012)
Fagus	gls(defoliation2012~P8B+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=FZ2012)
Quercus	gls(defoliation2012~P8B+P8F+P8P+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=QZ2012)
Tilia	gls(defoliation2012~P8B+P8F+P8P+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=TZ2012)
defoliation 2013	
Betula	gls(defoliation2013~P8F+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=BZ2013)
Fagus	gls(defoliation2013~P8B+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=FZ2013)
Quercus	gls(defoliation2013~P8B+P8F+P8P+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=QZ2013)
Tilia	gls(defoliation2013~P8B+P8F+P8P+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=TZ2013)

[a] tree species identity (id), local neighbourhood diversity (div); P8_: proportion of a species (A - *Acer*, B – *Betula*, F – *Fagus*, L – *Larix*, P – *Pinus*, Ps – *Pseudotsuga*, Q – *Quercus*, T - *Tilia*) in the local neighbourhood consisting of the 8 closest neighbour trees

Appendix 4.1 R syntax of the best-fit models considered in the different analyses

response variables	R syntax[a]
effects of admixing species	
Zedelgem	
crown discolouration 2012	
Betula	gls(discolouration2012~P8F+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=BZ2012)
Fagus	gls(discolouration 2012~P8B+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=FZ2012)
Pinus	gls(discolouration2012~P8B+P8F+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=PZ2012)
Quercus	gls(discolouration2012~P8B+P8F+P8P+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=QZ2012)
Tilia	gls(discolouration2012~P8B+P8F+P8P+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=TZ2012)
crown discolouration 2013	
Betula	gls(discolouration2013~P8F+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=BZ2013)
Fagus	gls(discolouration2013~P8B+P8P+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=FZ2013)
Pinus	gls(discolouration2013~P8B+P8F+P8Q+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=PZ2013)
Quercus	gls(discolouration2013~P8B+P8F+P8P+P8T, correlation=corExp(form=~X+Y,nugget=TRUE), data=QZ2013)
Tilia	gls(discolouration2013~P8B+P8F+P8P+P8Q, correlation=corExp(form=~X+Y,nugget=TRUE), data=TZ2013)

[a] tree species identity (id), local neighbourhood diversity (div); P8_: proportion of a species (A - *Acer*, B – *Betula*, F – *Fagus*, L – *Larix*, P – *Pinus*, Ps – *Pseudotsuga*, Q – *Quercus*, T - *Tilia*) in the local neighbourhood consisting of the 8 closest neighbour trees

Aphid infestations in the leaves of *Fagus sylvatica* at Zedelgem site [Photograph: NN Setiawan]

Chapter 5

Local neighbourhood effects on the crown arthropod community

After: Setiawan NN, Vanhellemont M, Baeten L, Gobin R, De Smedt P, Proesmans W, Ampoorter E, Verheyen K (2016) Does neighbourhood tree diversity affect the crown arthropod community in saplings? Biodiversity and conservation 25, 169-185

5.1 Abstract

Mixed forest with multiple tree species is expected to create heterogeneous habitat and diverse niches for the canopy arthropod community. We assessed arthropod abundance, order richness, and community composition in the crowns of saplings of nine temperate tree species in two plantations of a recently established tree diversity experiment in Belgium, and looked for relationships with the diversity and structure of the sapling's local neighbourhood. The crown arthropod community differed between the two study sites, both in terms of abundances and composition. More arthropods were found in the post-agricultural site; the arthropod community was more diverse in the formerly forested site. The tree species identity of a sapling, its apparency, and the phylogenetic diversity of its local neighbourhood all affected the crown arthropod community. Our study suggests that mixing phylogenetically distant tree species creates niches for a diverse crown arthropod community.

5.2 Introduction

Arthropods, the most diverse animal phylum in the world (Kremen et al. 1993, Minelli et al. 2013), are important in the delivery of various ecosystem services, such as plant pollination, decomposition and nutrient cycling, pest regulation, and food source for other animals and humans (Majer 1987, Price et al. 2011). In forest ecosystems, the canopy is an important habitat for arthropods (Lawton 1983, Stork 1988, Basset et al. 2008). The abundance and diversity of herbivorous arthropods present in a certain tree crown are directly affected by a tree's crown characteristics, such as its volume (Ulyshen 2011, Müller et al. 2014) and species-specific leaf traits (Jukes et al. 2002, Schowalter and Zhang 2005, Larrivée and Buddle 2009, Sobek et al. 2009c). Yet, the tree's local neighbourhood is also important: the tree diversity (Underwood et al. 2014) and the overall plant community composition (Andow 1991, Ulyshen 2011) influence a tree's relative apparency or visibility for arthropods (Castagneyrol et al. 2013, Régolini et al. 2014). Furthermore, the herbivore abundance and diversity will control and, in turn, be controlled by the abundance and diversity of higher trophic levels of arthropods such as carnivores and parasites (Haddad et al. 2001, 2009).

Mixed forests, consisting of multiple tree species, are generally characterized by a complex physical structure with diverse levels of environmental resources and hence multiple niches to be exploited by the associated biodiversity (Tews et al. 2004) of birds (Estades 1997, Berry and Bock 1998), earthworms (Cesarz et al. 2007), mammals (Estrada et al. 1994, Ecke et al. 2002), and also the arthropod community (Siemann et al. 1999, Sobek et al. 2009b, Oxbrough et al. 2012). Forest succession and stand development cause changes in the structure of the vegetation, and thus the associated arthropod community (Brown and Southwood 1983, Siemann et al. 1999): a more complex canopy structure leads to a more complex trophic structure in the arthropod community (Brown and Southwood 1983, Schowalter 1989, Jeffries et al. 2006, Price et al. 2011). The early-development stages of young stands are critical in determining the course of forest development and the associated arthropod community, with the resulting mature forests ranging from forest with high pest infestation to forest with high levels of associated biodiversity (Waltz and Whitham 1997). Planting diverse tree stands may trigger associational resistance (Tahvanainen and Root 1972, Root 1973) towards pest infestation (Spiecker 2003, Jactel et al. 2005, Jactel and Brockerhoff 2007) and may therefore result in a more stable and resistant forest.

Arthropods are perfect model organisms to study in the early stage of forest development since their community composition responds rapidly to environmental changes and thus reflects habitat heterogeneity and forest development stage well (Kremen et al. 1993, Maleque et al. 2006). Our main research question was: does the diversity of a tree's local neighbourhood affect its crown arthropod community in the early stage of forest development? Therefore, we studied the abundance, species richness, and composition of the crown arthropod community on saplings of nine tree species and looked for relationships between the arthropod community and different aspects of neighbourhood diversity.

5.3 Materials and methods

5.3.1 Arthropod collection and identification

We did the arthropod collection on one sapling in each of the subplots (N = 4 saplings per plot, see Fig. 2.3.). In total, we collected arthropods from 176 saplings in Gedinne and 168 saplings in Zedelgem. In every mixed plot, the four sampled saplings represented the tree species combination of the plot. The arthropod samples were collected in early summer in Gedinne (July 2014) and Zedelgem (July-August 2013). We sampled in early summer as crown arthropod species richness peaks in summer and most guilds are active in summer (Southwood et al. 2005, Stork and Hammond 2013). Arthropods were collected from the crown and bark by means of suction sampling, using an insect aspirator (model 2820B, BioQuip Products). We used this method for its feasibility, and it enabled us to capture a wide range of arthropods in the crown area. The aspirator is a hand-held vacuum cleaner with a modified nose section: a clear acrylic tube holding a removable collecting chamber (Photo 5.1). Nylon nets with 0.3 mm x 0.3 mm mesh size were used as a filter covering the tube to capture also small arthropods. Each sampled sapling was aspirated for five minutes. The samples were frozen to await further processing; plant material was sorted out of the defrosted samples; and the arthropods were preserved in 70% v/v ethanol. Arthropods were identified to order level (Photo 5.2, Appendix 5.1) according to literature (Kirk 1996, Wheeler 2001, Oosterbroek 2006, Hopkin 2007, Capinera 2008, Chinery 2012).

For a few selected orders containing different feeding guilds (Coleoptera, Diptera, Hemiptera), we identified to a lower taxonomic level to be sure of the specimens' feeding guild whenever possible (family, genus or species). We then assigned all collected arthropods to one of the four guilds (see Appendix 5.1 for definitions): herbivores, carnivores, fungivores (including detritivores), omnivores (Root 1967, Moran and Southwood 1982, Southwood et al. 1982). For further analysis, we only used the abundances of herbivores and carnivores as these are the guilds in which the strongest diversity effects were expected (Scherber et al. 2010) and which are most likely to affect the damage in the trees (Chapter 4). Besides that, omnivores were scarce in our samples and the collected fungivores are not likely to directly affect the trees.

Photo 5.1 The insect aspirator used to collect the crown arthropods in Zedelgem (left) and in Gedinne (right). Each sampled saplings were aspired for five minutes from the bottom to top crown area [photographs: NN Setiawan & Ritchie Gobin]

Photo 5.2 The examples of identified arthropods: Hemiptera - Nabidae (top), Hemiptera - jumping plant lice (middle), and Psocoptera (bottom) [photographs: Ritchie Gobin]

5.3.2 Local neighbourhood characterization

To describe the tree diversity of the local neighbourhood around each individual sampled sapling, we used the tree species identity of the 8 or 24 nearest neighbours of the sampled sapling (Fig. 2.3). We calculated both species diversity (exponent Shannon index, expH) and phylogenetic diversity (MNTD and MPD) for these local neighbourhoods (see section 2.4.3).

Next to the local tree diversity, we also characterized the structural diversity around the sampled saplings. We used data on tree height for the saplings in each local neighbourhood (all saplings in the subplots measured in 2012, see Appendix 3.2) to express how 'visible' the sampled sapling was relative to its local neighbourhood. The tree apparency index (ΔH_d) developed by Castagneyrol et al. (2013) expresses how apparent a target tree (T) is to foraging insect herbivores. It is calculated as the mean difference in height (H) between the target tree and its eight closest neighbours (N_i), weighted by the distances (d_i) between the target tree and these close neighbours:

$$\Delta H_d = \frac{1}{8} \times \sum_{i=1}^{8} \frac{HT - HN_i}{d_i}$$

(Eq. 5.1)

At the time of our study, some of the herbaceous plants in the ground vegetation were as tall as the young trees. Therefore, we used data on the cover of vascular plants < 1.3 m tall available per subplot (vegetation inventory in 2011, see Table 2.6). For each sampled sapling, we calculated the total cover of the ground vegetation in its subplot as well as the cover of different functional groups (ferns, grasses, herbs, legumes) in the subplot. Several studies have shown an increase in the abundance of certain arthropod species with increasing understory cover (Wan et al. 2014, Paredes et al. 2015), legume cover (Smith et al. 1996), or herb cover (Scherber et al. 2014). The calculated cover values should be considered as proxy for the actual ground vegetation as the crown arthropod sampling was done two (Zedelgem) or three (Gedinne) years after the vegetation inventory and the ground vegetation in young forest plantations may change rather quickly as a result of tree growth (see, e.g., Ampoorter et al. (2015) for 6-year vegetation changes in a young German tree diversity experiment).

5.3.3 Data analysis

Our main objective was to investigate the effect of focal tree species identity, local neighbourhood diversity, tree apparency, and ground vegetation cover on the arthropod community diversity and composition in the crown of the sampled saplings. As response variables, we used feeding guild abundance (herbivore or carnivore abundance), arthropod order richness (univariate), and arthropod community composition (multivariate). Arthropod community composition was calculated based on order abundances within the arthropod community. We used thirteen explanatory variables describing the sampled sapling and its local neighbourhood to explain the different response variables used in this study (Appendix 5.2). Due to the differences in site conditions between the two study sites (Table 2.1), the analyses were done separately for Gedinne and Zedelgem. All analyses were done in R version 3.1.3 (R Core Team 2014); graphs were made with the R package *ggplot2* (Wickham 2009).

The different neighbourhood diversity variables were correlated, and the ground vegetation cover variables also showed clear collinearity. We therefore selected one neighbourhood diversity variable and one ground vegetation cover variable for each response variable prior to our analysis (cf. Castagneyrol et al. 2013). For each response variable, we fitted a series of univariate regression models using the different explanatory variables, and we used the explanatory variable that gave the lowest AIC (Appendix 5.3) in the following analyses. The effect of species identity on herbivore and carnivore abundance was tested by comparing the AIC of models with random slopes (linear mixed-effect model, *lme*) and non-random slopes (linear model, Table 5.3.2).

For each of the three response variables, we used a different analysis: (1) linear regressions for the arthropod feeding guild abundances, (2) generalized linear modelling or *glm* (McCullagh and Nelder 1989, Dobson 2002) with Poisson error distribution for the arthropod order richness, and (3) multivariate *glm* with negative binomial error distribution for the arthropod order-level abundances with the package *mvabund* (Wang et al. 2012). For each analysis, we first fitted a full model with the four explanatory variables (tree species identity, neighbourhood diversity, apparency, and ground vegetation cover) and the two-way interactions between them. For the arthropod feeding guilds analysis, we added herbivore or carnivore abundance as extra explanatory variables. We also repeated the analysis for Zedelgem for the dataset without the most dominant herbivore family found (Aphididae, see Appendix 5.1) since the high abundance of this particular family at the time of our sampling might obscure the effects of the explanatory variables tested. We selected the best-fit model (see Appendix 5.6 for R syntax) with backward selection (dropping the most insignificant terms one by one) based on: (1) likelihood ratio tests (Zuur et al. 2009) for the first and second analyses, and (2) a log-likelihood ratio test (Warton et al. 2012) for the third analysis. The residuals of all final models were inspected, and an additional test of overdispersion was done for the final model of the second analysis by comparing the residual deviance with the residual degrees of freedom.

5.4 Results

5.4.1 Abundance

We found 10,948 arthropod individuals on the 344 sampled saplings (Table 5.1), and we were able to assign 96.7% of the individuals into order or family (Appendix 5.1). The mean arthropod abundance was lower in Gedinne (17 ± 1 SE individuals/sapling) compared with Zedelgem (47 ± 4 individuals/sapling), but we found more arthropod orders in Gedinne compared with Zedelgem (Table 5.1). The tree species with the highest mean arthropod abundance were *Pseudotsuga* (22 ± 3 individuals/sapling) and *Fagus* (20 ± 3 individuals/sapling) in Gedinne and *Betula* (110 ± 10 individuals/sapling) in Zedelgem. The lowest mean arthropod abundance was shown by *Acer* (7 ± 1 individuals/sapling) in Gedinne and *Tilia* in Zedelgem (12 ± 2 individuals/sapling). The herbivores were the most abundant guild in both sites: 40.0% of the arthropods in Gedinne, 72.2% in Zedelgem. The high proportion of herbivores in Zedelgem was mainly due to the high abundance of Aphididae (93.7% of the herbivores) found mainly in *Betula.* We found a higher proportion of carnivores and fungivores in Gedinne (carnivores: 26.1%, fungivores: 33.9%) compared with Zedelgem (carnivores: 14.6%, fungivores: 13.0%). The proportion of omnivores was very low in both sites (less than 0.1%).

Table 5.1 The number of arthropod orders (N) and the number of arthropods (Nind) in the different feeding guilds collected on the sampled saplings at the two study sites

	Gedinne (176 trees)	Zedelgem (168 trees)	Both sites (344 trees)
Orders (N)	12	11	13
Herbivores (N_{ind})	1,128	5,603	6,731
Carnivores (N_{ind})	736	1,131	1,868
Fungivores (N_{ind})	956	1,010	1,966
Omnivores (N_{ind})	2	17	18
Total (N_{ind})	2,998	7,950	10,948

In Gedinne, the herbivore abundance increased with decreasing tree apparency and increasing legume cover in the ground vegetation ($p < 0.05$, Fig. 5.1a, b). The carnivore abundance increased with the phylogenetic diversity of the local neighbourhood (MNTD.24) and the herbivore abundance ($p < 0.1$, Fig. 5.1e, f). In Zedelgem, the tree species had a significant effect on the herbivore and carnivore abundances ($p < 0.001$, Fig. 5.1d, g). Herbivore abundance was lowest in *Tilia* (4 ± 1 individuals/sapling) and highest in *Betula* (104 ± 9); carnivore abundance was lowest in *Betula* (5 ± 1) and highest in *Quercus* (9 ± 1) and *Fagus* (8 ± 1). The herbivore and carnivore abundances were, in general, positively related ($p < 0.1$, Fig. 5.1d, g). In addition, herbivore abundance decreased with the phylogenetic diversity of the local neighbourhood (MPD.8, $p < 0.1$, Fig. 5.1c). More results on the model estimates can be found in Appendix 5.4). When the most dominant herbivore family (Aphididae) was removed from the Zedelgem data, results were different (Appendix 5.4).

Tree species identity was only related to carnivore abundance ($p < 0.001$), not to herbivore abundance; and there was no relation between the herbivore and carnivore abundances. Herbivore abundance increased with increasing neighbourhood diversity (expH.8, $p < 0.01$); decreased with increasing apparency ($p < 0.1$) and ground vegetation cover ($p < 0.05$). Herbivore abundance was significantly related to the interaction between neighbourhood diversity and apparency ($p < 0.05$). Carnivore abundance increased with phylogenetic diversity (MPD.8, $p < 0.01$) and was significantly related with the interaction between neighbourhood diversity (MPD.8) and herb cover ($p < 0.05$).

5.4.2 Order richness

The mean arthropod order richness was lower in Gedinne (4.5 ± 0.1 SE orders/sapling) compared with Zedelgem (5.2 ± 0.1). In both sites, tree species identity was the only significant explanatory variable (Table 5.2). In Gedinne, the lowest mean arthropod order richness was found in *Acer* (3.1 ± 0.3 orders/sapling), the highest in *Quercus* (5.2 ± 0.2) (Fig. 5.2). In Zedelgem, the lowest mean arthropod order richness was found in *Tilia* (4.5 ± 0.3), the highest in *Quercus* (6.0 ± 0.2) (Fig. 5.2).

5.4.3 Community composition

The multivariate *glm* analysis with order abundances as response variable showed that tree species identity significantly affected the arthropod community in both sites (Table 5.3). In Gedinne, tree species identity, apparency and the interaction between tree species identity and apparency significantly affected the arthropod community (Table 5.3). In Zedelgem, tree species identity and phylogenetic diversity (of the 24 surrounding trees, MNTD.24) had a significant effect on the arthropod community. The univariate *glm* analyses showed that, in Gedinne, tree species identity significantly affected the abundances of Acari, Araneae, Coleoptera, and Collembola whereas tree apparency significantly affected the abundance of Hemiptera (Appendix 5.5). In Zedelgem, tree

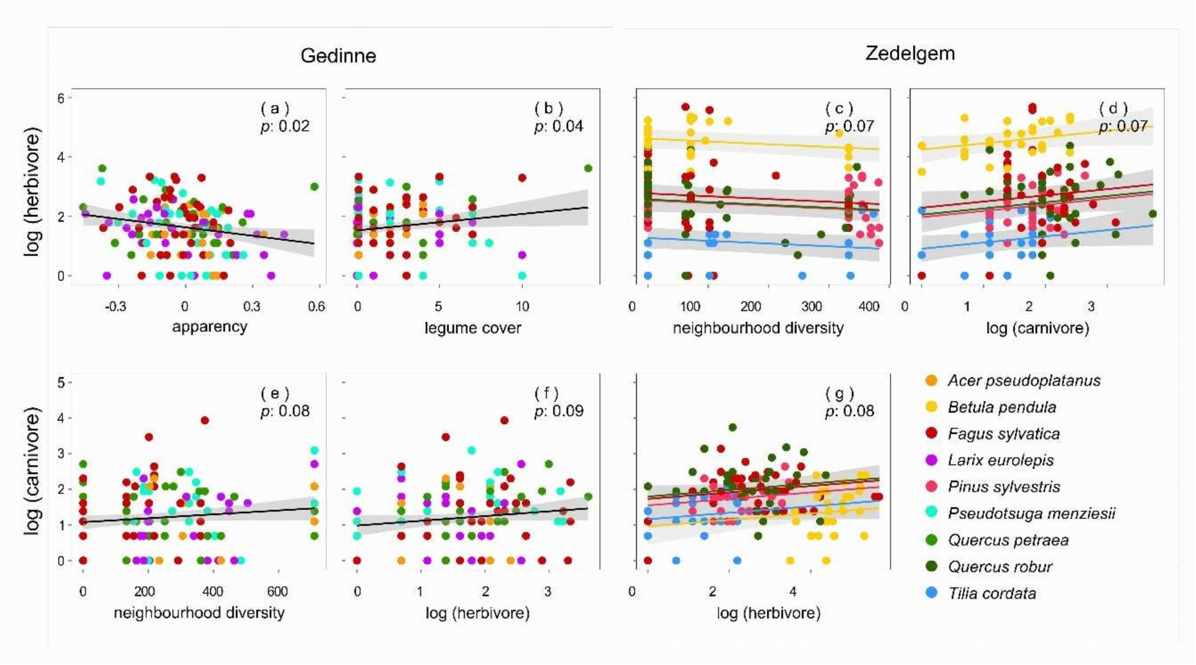


Fig. 5.1 The relationships between herbivore abundance (a-d) or carnivore abundance (e-g) and different explanatory variables for Gedinne (left) and Zedelgem (right). The graphs show the logarithm of the abundances. The colours represent tree species; the lines depict model predictions; and the grey areas are the 95 % CI. Neighbourhood diversity is the mean phylogenetic distance of the 8 neighbours (c) and the mean nearest taxon distance of the 24 neighbours (e).

Table 5.2 The best-fit generalized linear model with Poisson error distribution for order richness in Gedinne and Zedelgem. The intercepts were removed for models with categorical explanatory variables.

Variables[a]	d.f.[b]	Estimate	SE	t-value	p-value
Gedinne					
species (*A. pseudoplatanus*)	1	1.15	0.10	11.55	<0.001
species (*F. sylvatica*)	1	1.54	0.07	23.17	<0.001
species (*L. eurolepis*)	1	1.50	0.08	17.90	<0.001
species (*P. menziesii*)	1	1.63	0.08	20.79	<0.001
species (*Q. petraea*)	1	1.65	0.08	21.35	<0.001
Zedelgem					
species (*B. pendula*)	1	1.55	0.08	18.72	<0.001
species (*F. sylvatica*)	1	1.74	0.07	24.26	<0.001
species (*P. sylvestris*)	1	1.60	0.08	19.75	<0.001
species (*Q. robur*)	1	1.80	0.06	28.00	<0.001
species (*T. cordata*)	1	1.50	0.08	18.05	<0.001

[a] see Appendix 5.2 for variable details

[b] Denominator degrees of freedom 169 for Gedinne, 163 for Zedelgem

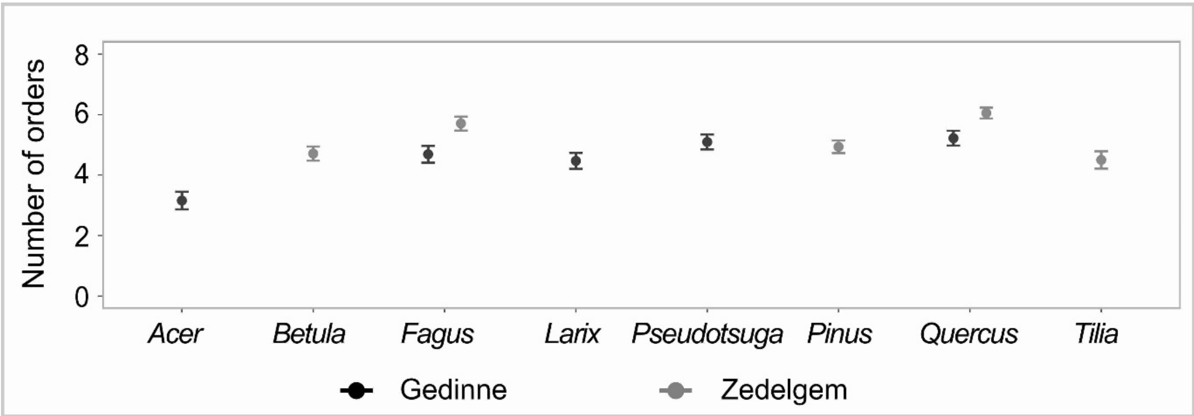


Fig. 5.2 The mean arthropod order richness (± SE) for the different tree species in Gedinne and Zedelgem

Table 5.3 The best-fit generalized linear model with negative binomial error distribution for multivariate order abundances in Gedinne and Zedelgem. Significance was based on log-likelihood ratio test and calculated with 999 resampling iterations.

Variables[a]	d.f.[b]	Deviance	p-value
Gedinne			
intercept			
species	5	136.71	0.001
apparancy	1	26.93	0.016
species:apparency	5	64.97	0.044
Zedelgem			
intercept			
species	5	384.7	0.001
MNTD.24	1	24.0	0.027
species:MNTD.24	5	62.4	0.052

[a] see Appendix 5.2 for variable details
[b] Denominator degrees of freedom 169 for Gedinne, 163 for Zedelgem

species identity significantly affected the abundances of Acari, Araneae, Coleoptera, Collembola, Hemiptera, and Psocoptera whereas phylogenetic diversity (of the 24 surrounding trees) significantly affected Acari.

5.5 Discussion

The crown arthropod community of the saplings sampled at the two FORBIO sites was related to the tree species identity and the characteristics of local neighbourhood of the sapling, such as the phylogenetic diversity of the neighbours and the apparency of the sampled sapling. There were some clear differences between the two study sites, which might be – partly – resulting from (a)biotic legacies of former land use. An indication of bottom-up control of carnivore abundance by herbivore abundance was apparent at both sites: more abundant resources (a higher herbivore abundance) were correlated with more abundant carnivores. In terrestrial ecosystems, bottom-up control has been shown for a plant-based food web (Siemann 1998) as well as a detritus-based food web (Chen and Wise 1999). Note that the results of our study are based on one specific period of sampling, in which we expected to capture the most diverse crown arthropod community. Yet, seasonal patterns in arthropod presence and abundance may differ between guilds, driven by resource availability such as leaf flush for herbivores, high moisture availability for fungivores, and abundance of food for carnivores and omnivores (Wolda 1988, Recher et al. 1996, Southwood et al. 2004, Stork and Hammond 2013). Further observations on seasonal patterns might thus improve our understanding of factors affecting the crown arthropod community.

5.5.1 Tree species effect

We saw a consistent effect of tree species identity on arthropod abundance, order richness, and community composition. The clear differences between species were probably the result of the criteria used in selecting the tree species planted at the FORBIO sites. The tree species had to be phylogenetically distant and represent a broad range in trait values (Verheyen et al. 2013). They differ in, for instance, bark texture, branching structure, leaf area, leaf chemical composition, and leaf abundance. In addition, the juvenile growth potential differs between the species, which resulted in the observed differences in sapling height between the species (see Appendix 3.1). Thus, crown niches differ between the tree species, which may support different species of arthropods (Lawton 1983). Similar species effects on arthropod diversity have been shown before in both forest (Jukes et al. 2002, Schuldt et al. 2008, Sobek et al. 2009a) and grassland experiments (Siemann et al. 1998, Symstad et al. 2000, Koricheva et al. 2000, Woodcock and Pywell 2009).

The arthropod abundance in Gedinne was probably mainly related to crown architecture. A more complex crown architecture results in more niches provided and thus supports more abundant arthropods (Lawton 1983). Although the *Acer* saplings were taller than the other broadleaved saplings such as *Fagus* (Appendix 3.1), their crown architecture (e.g., branching patterns, etc.) was less complex and their crown arthropod abundance was the lowest. In Zedelgem, we mainly saw a '*Betula* effect'. Aphid abundance (and hence herbivore abundance) was very high in *Betula*. These high abundances in *Betula* might be the consequence of the larger crowns of this fast-growing early-successional tree species (the tallest saplings in Zedelgem at the time of sampling, Appendix

3.1). But, *Betula* is known to be a host to different species of phloem-sap sucking aphids throughout the year (Hajek and Dahlsten 1986), which might explain the big difference in aphid abundance between *Betula* and the other tree species.

The mean arthropod order richness at both sites was lowest for species with a simple crown architecture (*Acer* in Gedinne and *Tilia* in Zedelgem). Yet, we should keep in mind that the low arthropod richness in some of our tree species may also be related to the low numbers of arthropods caught in these tree species. On average, the order richness per sapling was highest in *Quercus*, which had a more complex crown architecture. This is not surprising as *Quercus* has been shown to support the highest number of arthropod species among a wide range of temperate broadleaved tree species (Kennedy and Southwood 1984, Southwood et al. 2004). Throughout the year, different herbivore communities - including leaf-chewers, sap-feeders, leaf miners, and gall formers - feed on *Quercus* (Southwood et al. 2004), which ensures a continuous availability of food for the higher trophic levels of arthropods.

Tree species identity affected the abundance of certain orders such as Araneae, Coleoptera, and Collembola, which are known to respond directly to changes in vegetation structure (Uetz 1991, Sousa et al. 2004, Oxbrough et al. 2005, Maleque et al. 2006, 2009, Salamon et al. 2008). Some of the FORBIO tree species had already developed a more complex crown structure (see above), thus providing diverse habitats and food resources for these orders. In addition, host specificity of certain arthropod orders or families can cause tree species identity effects on arthropod community composition, as we saw with the aphids in our *Betula* trees for instance. Similarly, Jukes et al. (2002) and Sobek et al. (2009c) found Coleoptera to be specific to certain tree species.

5.5.2 Local neighbourhood effects

Different aspects of the local neighbourhood were important in explaining arthropod abundances and community composition at the two sites. In Gedinne, the significant local neighbourhood effects were apparency, legume cover in the ground vegetation, and phylogenetic diversity. Tree apparency negatively affected herbivore abundance and also affected arthropod community composition, specifically for Hemiptera (herbivores). Tree apparency is indeed important in determining the rate of herbivore colonization (Moran and Southwood 1982). Trees that are less apparent than their local neighbours experience associational resistance, reducing the rate of herbivore colonization (Castagneyrol et al. 2013, Régolini et al. 2014, Haase et al. 2015). However, we found that more apparent saplings had less herbivores compared with less apparent saplings; probably because the tallest saplings at the Gedinne site were *Larix* (Appendix C), which were found to attract less arthropods compared with the other study species such as *Fagus, Pseudotsuga,* and *Quercus*. Contrary to apparency, legume cover and phylogenetic neighbourhood diversity were positively related to the abundance of certain guilds. Carnivore abundance was higher when saplings were surrounded by phylogenetically distant neighbours, providing a more heterogeneous habitat.

In Zedelgem, we found local neighbourhood diversity effects for herbivore abundance and community composition. Associational resistance to herbivore colonization was shown by saplings surrounded by phylogenetically distant neighbours. A more diverse neighbourhood indeed decreases the likelihood that a tree is detected and attacked by herbivores (Hambäck and Beckerman 2003, Barbosa et al. 2009) as was also shown by studies on herbivore damage (Jactel and Brockerhoff 2007, Castagneyrol et al. 2014). Differences in herbivore populations will also lead to differences in the abundance of higher trophic levels (carnivores) and thus the overall arthropod community composition (Agrawal et al. 2006).

5.5.3 Landscape and legacies of former land use

We saw some clear differences in arthropod abundance and community composition between the sites. The difference in landscape and former land use between the sites might partly explain these findings.

The Gedinne site was surrounded by forest patches and grassland, which may serve as a source of arthropods associated with trees. Besides that, being the stand-replacement site, Gedinne has richer biological legacies, including surviving organisms and organic structures such as wood stumps (Swanson et al. 2011). Even though several studies (Kennedy and Southwood 1984, Ozanne 1999) showed more arthropod species associated with broadleaves compared with conifers, in Gedinne, crown arthropods were most abundant in saplings of the coniferous *Pseudotsuga* and least abundant in the broadleaved *Acer*. *Pseudotsuga* was phylogenetically more similar to the *Picea* of the former forest stand compared with the other tree species in the present experimental site of Gedinne. *Picea* and *Pseudotsuga* may thus share some generalist arthropod species (Goßner and Ammer 2006).

The Zedelgem site was surrounded by forest, arable land, grassland, and rural settlements. Compared with Gedinne, there was less surrounding forest and hence a lower chance of tree-related arthropod input from the forest. As a post-agricultural site, the Zedelgem site was richer in soil nutrients such as phosporus than the Gedinne site (Fig. 2.2). Trees with a higher nutrient concentration are more attractive to herbivores (Ernest 1989, Bird et al. 2000, Price et al. 2011). Herbivore abundance was indeed higher in Zedelgem than in Gedinne, corroborating previous work at these study sites that showed higher levels of herbivore damage at Zedelgem compared to Gedinne (Chapter 4). The herbivore community in Zedelgem was dominated by Aphididae, which were mostly found on *Betula*. Dominance by a particular group of herbivorous arthropods is typical of the early successional stages of post-agricultural forest (Schowalter et al. 1988, Goßner et al. 2008). In nutrient-limited soil conditions such as in Gedinne, the presence of nitrogen-fixing plants such as legumes in their surroundings can help saplings in fulfilling their nitrogen requirements. Indeed, the presence and cover of legumes in the local neighbourhood was more important than tree apparency in determining the herbivore abundance in Gedinne. In addition to the lower soil nutrient availability, the lower number of broadleaved species planted in Gedinne compared with Zedelgem probably also added to the lower arthropod abundance in Gedinne.

5.6 Conclusions

Our study revealed that the crown arthropod community in the early establishment stage of plantation forest depends on the tree species planted, a sapling's local neighbourhood, and the former land use. Local neighbourhood diversity only partially explained the arthropod community composition through its effect on specific guilds. Further research on the short- and long-term temporal variation in the arthropod community will be needed to understand whether the effect of tree species, local neighbourhood, and site landscape and history will persist as the stands develop. As a stand develops, we may expect changes in the arthropod community composition following the changes in the vegetation structure: the trees will grow in biomass and volume, which will suppress the growth of other tree species or eliminate shade-intolerant understory species. The tree crown and understory will become stratified, providing distinct habitats and niches, thus allowing a more diverse and complex arthropod community to exist.

With regard to arthropod diversity conservation efforts, our study shows the importance of planting trait-diverse forests. Plantations of tree species representing a broad range in trait values will enable higher arthropod species diversity as different tree species support distinct arthropod communities. As a rule of thumb, mixing broadleaves with conifers is highly recommended. Broadleaved trees generally have more associated arthropod species, but evergreen coniferous trees provide valuable habitat throughout the year.

Appendix 5.1 The collected arthropods were identified to order level. For some orders (Coleoptera, Diptera, Hemiptera), further identification to family, genus, or species level was done, as these orders contain different feeding guilds. After identification, the arthropods were assigned to a feeding guild. In total, 2,998 and 7,950 arthropods were caught in Gedinne and Zedelgem respectively.

Order - Family	Genus/Species	Guild[a]	Number of individuals in	
			Gedinne	Zedelgem
Acari		U	75	47
Araneae		C	394	714
Coleoptera				
Anthicidae	*Notoxus brachycerus* (Faldermann, 1837)	O	0	1
Cantharidae		C	1	0
Carabidae		C	0	1
Chrysomelidae		H	2	9
Coccinelidae	*Coccinella septempunctata* (Linnaeus, 1758)	C	1	1
Coccinelidae	*Harmonia axyridis* (Pallas, 1773)	C	4	40
Coccinelidae	*Propylea quatuordecimpunctata* (Linnaeus, 1758)	C	0	1
Coccinelidae	*Psyllobora*	F	0	10
Coccinelidae	*Psyllobora vigintiduopunctata* (Linnaeus, 1758)	F	12	7
Coccinelidae juvenile		C	3	0
Curculionidae		H	1	6
Latridiidae		F	13	9
Leiodidae		F	0	1
Staphylinidae		C	1	0
Tenebrionidae	*Lagria hirta* (Linnaeus, 1758)	H	1	0
Coleoptera juvenile		H	8	0
Collembola		F	904	602

[a] Herbivore (H), Carnivore (C), Fungivore (F), Omnivore (O), and u (unidentified)

Appendix 5.1 (continued)

Order - Family	Genus/Species	Guild[a]	Number of individuals in	
			Gedinne	Zedelgem
Diptera				
Asilidae, Phoridae		C	12	0
Culicidae		H	171	264
Dolichopodidae		C	42	35
Drosophilidae, Sepsisdae		H	27	17
Empididae		C	64	19
Hybotidae		C	1	0
Syrphidae		H	2	1
unidentified		u	47	70
Dermaptera		O	0	1
Hemiptera				
Anthocoridae		C	1	3
Aphididae		H	593	5251
Cicadellidae		H	1	1
Cicadidae		H	73	18
Cercopidae		H	1	1
Coreidae	*Coreus marginatus* (Linnaeus, 1758)	H	2	0
Microphysidae		C	0	1
Miridae	*Dicyphus*	O	0	1
Miridae	*Heterotoma planicornis* (Pallas, 1772)	O	0	2
Miridae		H	40	3
Nabidae		C	27	1
Pentatomidae	*Troilus luridus* (Fabricius, 1775)	C	2	0
Pentatomidae		H	2	0
Homoptera		H	33	12
Heteroptera juvenile		H	4	1
Homoptera juvenile		H	0	2

[a] Herbivore (H), Carnivore (C), Fungivore (F), Omnivore (O), and u (unidentified)

Appendix 5.1 (continued)

Order - Family	Genus/Species	Guild[a]	Number of individuals in	
			Gedinne	Zedelgem
Hymenoptera		C	169	315
Lepidoptera				
Lepidoptera juvenile		H	41	0
Neuroptera				
Neuroptera juvenile		C	14	0
Opiliones		O	2	13
Psocoptera		F	27	381
Thysanoptera		H	126	17
unidentified			54	71

[a] Herbivore (H), Carnivore (C), Fungivore (F), Omnivore (O), and u (unidentified)

The identification was done in two steps: identification to order level by NNS and RG; identification to family, genus or species level by PDS and WP. NNS, PDS, and WP have followed basic courses on arthropod identification and biosystematics. PDS and WP have been involved in other projects related with arthropods. The identification keys used were Kirk 1996, Wheeler 2001, Oosterbroek 2006, Hopkin 2007, Capinera 2008, and Chinery 2012.

The identification to order level was done by using a simple dichotomous identification key. The main key steps were as follows:

- The number of legs (6 or 8)
- Presence of wings (well-developed wings, small or missing wings)
- Hind wings reduced to tiny knobs (yes, no)
- Presence of hair covering the wing (yes, no)
- Length of antennae (short, longer than the body)
- Wings covered with cross veins (yes, no)
- Body with narrow waist (yes, no)
- Front legs with spine (yes, no)
- Soft-bodied (yes, no)
- Springlike structure (yes, no)
- Presence of cornicles at the abdomen (yes, no)
- Presence of cerci at the abdomen (yes, no)

The identification to lower level (family, genus, species) was only done for the main orders such as Coleoptera, Diptera, and Hemiptera. When assigning a guild to a family, we carefully considered the literature available, the mouthparts observed in the samples (e.g., rigid beak, sucking, chewing, etc), and (if possible) personal communication with other experts on arthropod identification. Due to the lack of expertise, all Hymenoptera were considered carnivores. The analysis results on carnivore abundance should thus be carefully interpreted. Some remarks on specific families and orders are:

- We considered Culicidae as herbivores since most Culicidae are flower visitors that feed on nectar (herbivore), except for female blood-sucking mosquitoes.
- We considered Syrphidae as herbivores since we only found adults in our samples. Most Syrphidae adults are flower visitors while Syrphidae larvae have different feeding strategies. Some feed on aphids, others live in dead, rotten wood or even in ant nests.

The definitions of the arthropod feeding preferences (guilds) used in this chapter were as follows:

Herbivores – arthropods that consume parts of living plant material (sap, foliage, bark, nectar, etc).

Carnivores – arthropods that consume other arthropods (true carnivore) and/or affect the vitality of other arthropods.

Fungivore – arthropod that consumes fungi and/or parts of dead plant material

Omnivore – arthropod that has a similar diet with herbivores and carnivores in the whole or part of its life cycle

Appendix 5.2 The thirteen explanatory variables used in the study.

Variable and variable codes	Description	Type of variable
Tree species identity		
species	The species of the target tree, i.e., *Acer pseudoplatanus*, *Betula pendula*, *Fagus sylvatica*, *Larix eurolepis*, *Pseudotsuga menziesii*, *Pinus sylvestris*, *Quercus petraea*, *Quercus robur*, *Tilia cordata*	5 categorical values per site
Neighbourhood diversity		
expH.8	Local neighbourhood diversity calculated as the exponent of the Shannon diversity index of the 8 surrounding trees	continuous variable
expH.24	Local neighbourhood diversity calculated as the exponent of the Shannon diversity index of the 24 surrounding trees	continuous variable
MPD.8	The mean phylogenetic distance of the 8 surrounding trees	continuous variable
MPD.24	The mean phylogenetic distance of the 24 surrounding trees	continuous variable
MNTD.8	The mean nearest taxon distance of the 8 surrounding trees	continuous variable
MNTD.24	The mean nearest taxon distance of the 24 surrounding trees	continuous variable
Tree apparency[a]		
apparency	Apparency index	continuous variable
Ground vegetation cover[b]		
ferns	Fern cover in the subplot	continuous variable
grasses	Grass cover in the subplot	continuous variable
herbs	Herb cover in the subplot	continuous variable
legumes	Legume cover in the subplot	continuous variable
total	Total ground vegetation cover in the subplot	continuous variable

[a] based on the tree height data of the year 2012 (cf. Appendix 3.1)
[b] based on vegetation inventory data of the year 2011 (cf. Table 2.6)

Appendix 5.3 Akaike's information criterion (AIC) for every model of a response variable vs. the different neighbourhood diversity and ground vegetation variables considered, for both study sites (Gedinne and Zedelgem). The lowest AIC values are indicated in bold and correspond to the best models (with the lowest AIC). There were no ferns in Zedelgem.

Table 5.3.1 Akaike's information criterion (AIC) for the univariate *lm* of the log herbivore abundance, i.e., log (H), and log carnivore abundance, i.e., log(C), vs. the different neighbourhood diversity and ground vegetation variables considered

	Gedinne	Zedelgem
Log (H)		
Neighbourhood diversity		
expH.8	364.92	560.05
expH.24	364.93	563.68
MNTD.8	364.90	562.55
MPD.8	364.88	**559.85**
MNTD.24	**364.57**	563.73
MPD.24	364.92	563.69
Ground vegetation cover		
ferns	364.11	-
grasses	360.42	563.70
herbs	363.48	**561.02**
legumes	**360.30**	562.85
total	364.94	562.75
Log (C)		
Neighbourhood diversity		
expH.8	361.52	327.14
expH.24	362.34	327.15
MNTD.8	361.25	327.00
MPD.8	360.53	327.00
MNTD.24	**359.73**	327.22
MPD.24	361.50	**326.70**
Ground vegetation cover		
ferns	362.56	-
grasses	361.71	326.87
herbs	361.73	**326.67**
legumes	**361.24**	327.03
total	362.53	326.96

Table 5.3.2 Akaike's information criterion (AIC) for the univariate *lm* and *lme* of the log herbivore abundance, i.e., log (H), and log carnivore abundance, i.e., log(C), vs. identity (id)

	R syntax	Gedinne	Zedelgem
Log (H)			
null model	lm(log(H)~1, method="ML")	**362.9**	561.7
lm	lm(log(H)~id, method="ML")	365.6	**427.7**
lme	lme(log(H)~1, random=1|id, method="ML")	364.9	446.1
Log (C)			
null model	lm(log(H)~1, method="ML")	**360.6**	325.2
lm	lm(log(H)~id, method="ML")	364.6	**292.8**
lme	lme(log(H)~1, random=1|id, method="ML")	362.6	302.9

Table 5.3.3 Akaike's information criterion (AIC) for the univariate glm (with Poisson error distribution) of order richness vs. the different neighbourhood diversity and ground vegetation variables considered

	Gedinne	Zedelgem
Neighbourhood diversity		
expH.8	698.3	655.4
expH.24	697.8	**654.5**
MNTD.8	698.3	657.8
MPD.8	698.3	656.3
MNTD.24	698.0	656.8
MPD.24	**697.7**	655.4
Ground vegetation cover		
ferns	697.8	-
grasses	**697.1**	658.5
herbs	698.3	**658.4**
legumes	697.2	**658.4**
total	698.3	658.5

Table 5.3.4 Akaike's information criterion (AIC) for the multivariate *manyglm* (with negative binomial error distribution) of multivariate abundance based on order level vs. the different neighbourhood diversity and ground vegetation variables considered

	Gedinne	Zedelgem
Neighbourhood diversity		
expH.8	4935.9	5664.2
expH.24	4935.0	5667.6
MNTD.8	**4930.4**	5661.1
MPD.8	4932.6	5671.5
MNTD.24	4930.8	5654.2
MPD.24	4932.1	**5644.9**
Ground vegetation cover		
ferns	4934.2	-
grasses	4930.9	5678.8
herbs	4925.2	**5668.7**
legumes	**4923.0**	5673.7
total	4930.8	5670.3

Appendix 5.4 The best-fit linear models for the log herbivore (H) and log carnivore (C) abundances on the sampled saplings.

Table 5.4.1 The best-fit linear models for the log herbivore (H) and log carnivore (C) abundances on the sampled saplings in Gedinne and Zedelgem. The intercepts were removed for models with categorical explanatory variables.

Response variable	Variables[a]	d.f.[b]	Estimate	SE	t-value	p-value
Gedinne						
log(H)	intercept		1.52	0.08	17.69	<0.001
	apparency	1	-0.89	0.39	-2.32	0.022
	legumes	1	0.05	0.02	2.03	0.044
log(C)	intercept		0.84	0.17	4.95	<0.001
	MNTD.24	1	0.01	0.01	1.78	0.077
	log (H)	1	0.14	0.08	1.72	0.087
Zedelgem						
log(H)	species (*B. pendula*)	1	4.31	0.23	18.75	<0.001
	species (*F. sylvatica*)	1	2.33	0.28	8.28	<0.001
	species (*P. sylvestris*)	1	2.16	0.28	7.64	<0.001
	species (*Q. robur*)	1	2.12	0.28	7.57	<0.001
	species (*T. cordata*)	1	0.99	0.23	4.29	<0.001
	MPD.8	1	-0.01	0.01	-1.82	0.070
	log(C)	1	0.22	0.12	1.83	0.068
log(C)	species (*B. pendula*)	1	0.96	0.26	3.7	<0.001
	species (*F. sylvatica*)	1	1.73	0.17	9.97	<0.001
	species (*P. sylvestris*)	1	1.55	0.16	9.63	<0.001
	species (*Q. robur*)	1	1.79	0.16	11.31	<0.001
	species (*T. cordata*)	1	1.16	0.13	9.09	<0.001
	log (H)	1	0.09	0.05	1.74	0.084

[a] see Appendix 5.2 for variable details

[b] Denominator degrees of freedom Gedinne: 143 for log (H), 143 for log (C); Zedelgem: 155 for log (H), 156 for log (C)

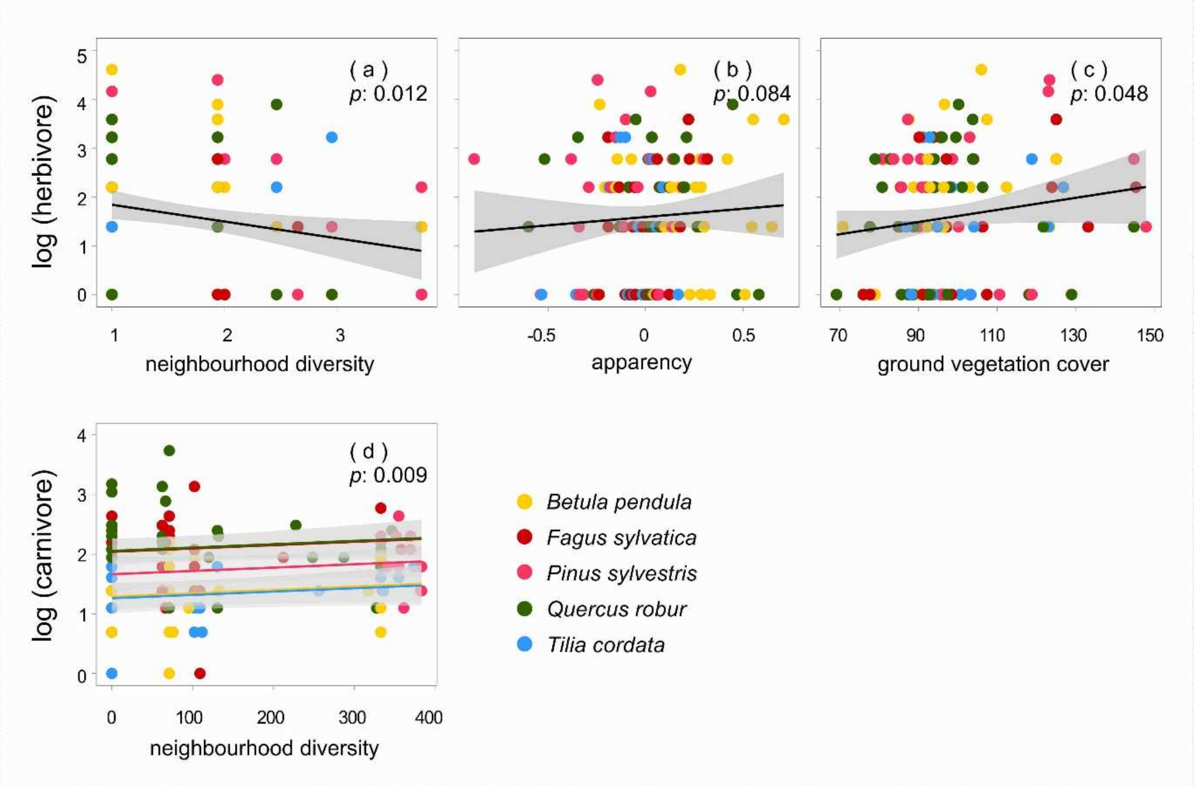
Table 5.4.2 The best-fit linear models for the log herbivore (H) and log carnivore (C) abundances on the sampled saplings in Zedelgem when the most dominant herbivore family (Aphididae) was removed from the dataset. The intercepts were removed for models with categorical explanatory variables.

Response variable	Variables[a]	d.f.[b]	Estimate	SE	t-value	p-value
log(H)	intercept		0.36	0.38	0.96	0.339
	expH.8	1	-0.17	0.07	-2.54	0.012
	apparency	1	-0.69	0.40	-1.74	0.084
	total ground vegetation	1	0.01	0.00	1.99	0.048
	expH.8 : apparency	1	0.48	0.23	2.09	0.038
log(C)	species (*B. pendula*)	1	1.20	0.14	8.49	<0.001
	species (*F. sylvatica*)	1	1.99	0.13	15.64	<0.001
	species (*P. sylvestris*)	1	1.56	0.17	8.96	<0.001
	species (*Q. robur*)	1	1.96	0.13	15.44	<0.001
	species (*T. cordata*)	1	1.19	0.15	7.95	<0.001
	MPD.8	1	<0.001	<0.001	2.65	0.009
	herbs	1	<0.001	<0.001	1.01	0.315
	MPD.8 : herbs	1	<-0.001	<0.001	-2.27	0.025

[a] see Appendix 5.2 for variable details

[b] Denominator degrees of freedom 125 for log (H), 121 for log (C)

Appendix 5.4.3 The relationships between herbivore abundance (a-c) or carnivore abundance (d) and different explanatory variables for Zedelgem for the dataset without the Aphididae. The graphs show the logarithm of the abundances. The colours represent tree species; the lines depict model predictions; and the grey areas are the 95 % CI. Neighbourhood diversity is the exponent of the Shannon diversity index (the effective number of species weighted by their relative abundance) of the 8 nearest neighbours of the sampled sapling (a) or the mean phylogenetic distance of the 8 neighbours (d).



Appendix 5.5 The univariate results from the best-fit generalized linear models with negative binomial error distribution for multivariate order abundances in Gedinne and Zedelgem. Significance was based on log-likelihood ratio tests and calculated with 999 resampling iterations. The significant values are indicated in bold.

Table 5.5.1 The univariate results from the best-fit generalized linear model with negative binomial error distribution for multivariate order abundances in Gedinne

Variables[a]	Deviance	p-value	Deviance	p-value	Deviance	p-value
	Acari		Araneae		Coleoptera	
species	18.3	**0.036**	20.3	**0.036**	19.8	**0.036**
apparency	0.6	0.833	1.2	0.833	4.4	0.325
species:apparency	6.3	0.826	13.2	0.169	6.0	0.826
	Collembola		Diptera		Hemiptera	
species	42.3	**0.002**	3.8	0.960	12.1	0.172
apparancy	6.0	0.197	1.4	0.833	8.9	0.057
species:apparency	2.4	0.956	3.8	0.943	5.9	0.826
	Hymenoptera		Lepidoptera		Neuroptera	
species	7.5	0.605	2.9	0.960	1.9	0.960
apparancy	1.6	0.833	0.9	0.833	0.02	0.894
species:apparency	10.5	0.338	1.9	0.956	9.4	0.434
	Psocoptera		Thysanoptera			
species	3.7	0.960	3.9	0.960		
apparancy	0.3	0.833	1.6	0.833		
species:apparency	3.3	0.943	2.2	0.956		

[a]see Appendix 5.2 for variable details

Table 5.5.2 The univariate results from the best-fit generalized linear model with negative binomial error distribution for multivariate order abundances in Zedelgem

Variables[a]	Deviance	p-value	Deviance	p-value	Deviance	p-value
	Acari		Araneae		Coleoptera	
species	15.7	**0.020**	71.4	**0.001**	29.7	**0.003**
MNTD.24	8.9	**0.054**	2.7	0.583	0.07	0.953
species:MNTD.24	16.2	0.068	4.2	0.934	3.7	0.938
	Collembola		Diptera		Hemiptera	
species	28.8	**0.003**	8.2	0.354	144.0	**0.001**
MNTD.24	1.5	0.753	2.9	0.583	0.817	0.868
species:MNTD.24	14.3	0.127	1.6	0.986	7.0	0.779
	Hymenoptera		Opiliones		Psocoptera	
species	3.8	0.859	2.1	0.918	79.8	**0.001**
MNTD.24	0.01	0.953	0.4	0.893	2.9	0.583
species:MNTD.24	1.4	0.986	6.9	0.779	1.9	0.986
	Thysanoptera					
species	1.2	0.918				
MNTD.24	3.7	0.457				
species:MNTD.24	5.0	0.898				

[a]see Appendix 5.2 for variable detail

Appendix 5.6 R syntax of the best-fit models considered in the different analyses

response variables	R syntax[a]
abundance	
Gedinne	
herbivore abundance	lm(log(H) ~ apparency + legumes, method=”REML”, data=ArthropodG)
carnivore abundance	lm(log(C) ~ MNTD.24 + log(H), method=”REML”, data=ArthropodG)
Zedelgem	
herbivore abundance	lm(log(H) ~ id + MPD.8 + log(C), method=”REML”, data=ArthropodZ)
carnivore abundance	lm(log(C) ~ id + log(H), method=”REML”, data=ArthropodZ)
herbivore abundance (withoud Aphididae)	lm(log(H) ~ expH.8 + apparency + total ground vegetation + expH.8:apparency, method=”REML”, data=ArthropodZA)
carnivore abundance (without Aphididae)	lm(log(C) ~ id + MPD.8 + herbs + MPD.8:herbs, method=”REML”, data=ArthropodZA)
order richness	
Gedinne	
order richness	glm(Order ~ -1 + id, family=poisson, data=ArthropodG
Zedelgem	
order richness	glm(Order ~ -1 + id, family=poisson, data=ArthropodZ
community composition	
Gedinne	
community composition	ArtmvabundG<-mvabund(ArthropodG) manyglm(ArtmvabundG ~id + apparency + id:apparency, family=”negative.binomial”)
Zedelgem	
community composition	ArtmvabundZ<-mvabund(ArthropodZ) manyglm(ArtmvabundZ ~id + MNTD.24 + id:MNTD.24, family=”negative.binomial”)

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[a] see Appendix 5.2 for variable details

Litterbags installed in *Pinus sylvestris* monoculture at Zedelgem site [Photograph: NN Setiawan]

Chapter 6

Mixing effects on leaf-litter decomposition rates

After: Setiawan NN, Vanhellemont M, Deschrijver A, Schelfhout S, Baeten L, Verheyen K (2016) Mixing effect on litter decomposition rate in a young tree diversity experiment. Acta Oecologica 70, 79-86

6.1 Abstract

Litter decomposition is an essential process for biogeochemical cycling and for the formation of new soil organic matter. Mixing litter from different tree species has been reported to increase litter decomposition rates through synergistic effects. We assessed the decomposition rates of leaf litter from five tree species in a recently established tree diversity experiment on a post-agriculture site in Belgium. We used 20 different leaf litter compositions with diversity levels ranging from 1 up to 4 species. Litter mass loss in litterbags was assessed 10, 20, 25, 35, and 60 weeks after installation in the field. We found that litter decomposition rates were higher for high-quality litters, i.e., with high nitrogen content and low lignin content. The decomposition rates of mixed litter were more affected by the identity of the litter species within the mixture than by the diversity of the litter *per se*, but the variability in litter decomposition rates decreased as the litter diversity increased. Among the 15 different mixed litter compositions in our study, only three litter combinations showed synergistic effects. Our study suggests that admixing tree species with high-quality litter in post-agricultural plantations helps in increasing the mixture's early-stage litter decomposition rate.

6.2 Introduction

Every ecosystem in the world depends on decomposition to convert dead organic matter to inorganic nutrients and CO_2 usable for plant and microbial production (Chapin et al. 2011). Decomposition is an essential process in the ecosystem, next to photosynthesis, since only a small part of the produced plant biomass will enter the trophic system. During decomposition, litter changes physically and chemically through several processes that vary in duration, i.e., leaching, fragmentation, and degradation of simple molecules (early decomposition stages), and degradation of large molecules such as lignin (later decomposition stages) (Berg and Matzner 1997, Adl 2003). The overall decomposition rate is controlled by three main factors, i.e., the physicochemical environment, the litter quality, and the composition of the decomposer community (Daubenmire and Prusso 1963, Swift et al. 1979).

In forest ecosystems, tree leaves are the main component of the aboveground plant litter (Berg and McClaugherty 2008, Gessner et al. 2010). As tree species differ in their leaf litter quality, the tree species composition of a forest influences the overall quality of the litter that reaches the forest floor (Hobbie 1992, Hättenschwiler 2005). In general, high decomposition rates are expected for high-quality litter: litter with a low carbon:nitrogen (C:N) and low lignin:nitrogen (L:N) ratio, which promotes microbial decomposer activity, and high calcium (Ca) concentration, which promotes earthworm activity (Gartner and Cardon 2004; Reich et al. 2005; Hobbie et al. 2006; Gessner et al. 2010). The quality and structure of mixed-species litter can differ from monospecific litter, which may affect the physicochemical environment (e.g., soil chemical composition) as well as the decomposer abundance, composition, and activity (Blair et al. 1990, Chapman and Newman 2010, Chapman et al. 2013), and thus the decomposition rate. Numerous studies do indeed show significant tree diversity effects on the rate of litter decomposition (Gartner and Cardon 2004, 2006, Vivanco and Austin 2008, Gessner et al. 2010, Jacob et al. 2010b, Vos et al. 2013, Handa et al. 2014). When the required decomposer organisms were present, higher decomposition rates in mixed litter compared to monospecific litter were more commonly found than the opposite (Gartner and Cardon 2004, Hättenschwiler and Gasser 2005, Cuchietti et al. 2014). However, litter mixture effects on decomposition rates are not yet predictable in forests (Hättenschwiler 2005) and inconsistent among ecosystems (Cardinale et al. 2011). Recent research in forests suggests that the identity of the litter species within the mixture affects the decomposition rate of mixed litter more than the diversity of the litter *per se* (Wu et al. 2013, Cuchietti et al. 2014).

Mixing litter of different species may have an additive or non-additive effect on the decomposition rate. Purely additive effects occur when the decomposition rate of a litter species is not affected by the other litter species present in the mixture. The decomposition rate of the litter mixture can then be predicted from the monospecific decomposition rates of the component litter species. Non-additive effects, on the other hand, occur when different litter species do influence each other, which leads to a higher (synergistic effects) or lower (antagonistic effects) decomposition rate in the mixed litter than expected based on the decomposition rates of the component species (Hättenschwiler 2005). These non-additive effects may be the result of chemical effects brought about by one or more of the litter species in the mixture, which will affect the decomposer activity. A transfer of nitrogen (N) from litter of nitrogen-fixing plants to the co-occurring litter will accelerate decomposition (Hobbie 2000; Schimel and Hättenschwiler 2007); a release of inhibitory compounds such as phenols and tannins by one of the litter species will dampen the decomposition rate of the adjacent litter (Salamanca et al. 1998, Gartner and Cardon 2004).

Up till now, most studies about tree diversity effects on litter decomposition have focused on mature forest. Yet, litter decomposition rates may differ between forest development stages (Coleman and Crossley 2004). The early stages of forest development, especially in post-agricultural forests, are important in producing soil organic matter and nutrient input into the soil (Chapin et al. 2011). In addition, the soil nutrient concentrations (e.g., N, phosphorus) and the soil pH are generally much higher and less limiting in young post-agricultural forests than in mature forests. Hence, differences in the effects of litter mixing on decomposition rates can be expected between young and mature forests. To investigate the relation between leaf litter diversity and decomposition, we assessed the decomposition rate for 20 different leaf litter compositions with diversity levels ranging from 1 to 4 species. In the present chapter, we address three main questions: (1) Are there differences between the litter decomposition rates of the tree species in the FORBIO experiment and is there a link with chemical litter quality?; (2) Are there differences in litter decomposition rate between litter mixtures and are these differences related to litter diversity and composition?; (3) Do the observed decomposition rates of the litter mixtures differ from the decomposition rates predicted based on the component litter species, i.e., is there evidence for non-additive effects? We hypothesize that: (1) high-quality leaf litter (high in N and Ca, and with low C:N ratio and lignin content) will decompose faster than low-quality leaf litter; (2) the decomposition rate will differ between leaf litter mixtures, and the composition of the leaf litter mixture will be more important than the number of species in the litter mixture; (3) litter mixtures that include high-quality leaf litter will decompose faster than predicted based on the abundances of the component species and their monospecific (unmixed) decomposition rates.

6.3 Materials and methods

The study of litter decomposition was only done at the Zedelgem site.

6.3.1 Leaf litter collection

Litter was collected from the five different tree species at the site in November 2011. Since the trees were still young, with small crowns, we could not collect enough freshly fallen litter. We used senescing leaves (i.e., withering-yellowish leaves that were still attached to the trees) for the broadleaved species and green needles formed during the last growing season for *Pinus* (no brown needles were present yet). Thus, the nutrient reabsorption was probably not yet completed for the leaves and needles we used as litter in our litter bags. For each tree species, leaves were collected throughout the site (in both monocultures and mixtures) and then mixed. The collected litter was first air-dried for 1-2 weeks and then dried in a forced air oven at room temperature (25ºC) for 24 hours.

For each species, the collected litter was analysed for its chemical composition: from each big bag, we randomly took three samples to analyse for total concentrations of C, N, P, Ca, Mg, and K; one sample per species was analysed for concentrations of lignin, cellulose, and hemicellulose. Prior to the chemical analysis, the litter was oven-dried (70ºC) until it reached constant weight and then ground using a centrifugal mill (Retsch ZM1, Germany). The Ca, K, and Mg concentrations were measured with flame atomic absorption spectrophotometry (Varian SpectrAA-240) after digestion with $HClO_4$ (65%) and HNO_3 (70%) in Teflon bombs for 4 h at 140°C. The concentrations of C and N were measured by combustion at 1,150°C using an elemental analyzer (Vario MACRO cube CNS, Elementar, Germany). The lignin, cellulose, and hemicellulose contents were determined using acid detergent fibre analysis (Van Soest et al. 1991).

6.3.2 Litterbags

The litterbags used in this experiment were constructed from 50 cm x 20 cm nylon nets with a 0.7 cm x 0.7 cm mesh size (Photo 6.1). This mesh size was chosen to ensure the accessibility of the litter for soil fauna that can help the decomposition process. Each bag was filled with 20 grams dry weight of litter. We used 20 different litter compositions (i.e., five different compositions for each litter richness level from monospecific to four species), corresponding to the 20 tree species compositions planted at the site (see Verheyen et al., 2013), i.e., B, F, P, Q, T, BP, BQ, FQ, TF, TP, BFP, FQP, TBF, TBQ, TQP, BFQP, TBFP, TBFQ, TBQP, and TFQP – with B being *B. pendula*, F for *F. sylvatica*, P for *P. sylvestris*, Q for *Q. robur*, and T for *T. cordata*. In the mixed litter composition, litter of each of the component species was present in equal amounts (2 x 10 g, 3 x 6.6 g, 4 x 5 g). For each litter composition, six bags were installed *in situ* to follow the decomposition over time, representing a time series. This set-up was replicated five times: five time series of six bags were used for each litter composition. As we were interested in litter-mixing effects on decomposition rather than in stand mixture effects (expected to be still small in the young FORBIO experiment), we installed the five replicates in five different monoculture plots within the western part of the site (Fig. 6.1). Each of the five plots thus received 120 litter bags (20 litter compositions x 6 bags per composition), for a total of 600 litter bags. Before installation, the grasses growing between the trees were mown till ground level to ensure direct contact between litter and soil. The litterbags were installed in December 2011 (Photo 6.2).

Litterbags were collected 10, 20, 35, 60, 75, and 100 weeks after the installation (Photo 6.3). At every collection date, 100 litterbags were collected (20 litter compositions x 5 plots). For the monospecific litterbags of *Betula* and *Tilia*, we did an additional collection in week 25 since the data from the two first collections showed that these litters were decomposing faster than the other litter compositions. The collected litterbags were air-dried for 1-2 weeks and then dried in a forced air oven at room temperature (25°C) for 24 hours. The litter remaining in the litterbag was separated from soil and unwanted organic material (e.g., grasses, moss) using a sieve (mesh size 0.5 mm) and then weighed. In spring 2012, grasses and mosses had started to grow through the litterbags, which caused the litter remaining in the litterbags to be strongly contaminated with soil and unwanted organic material. From week 75 onwards, the brittle remaining litter could no longer be sorted out accurately. Thus, we only used the litterbags collected in week 10, 20, 25, 35, and 60 (410 litterbags in total) for further analysis.

6.3.3 Data analysis

Litter diversity and composition are two important factors expected to influence the decomposition rate. We defined litter diversity as the number of leaf litter species present in a litterbag (i.e., 1-4 species), and litter composition as the 20 different litter compositions used in the experiment. The decomposition rate was defined as the decomposition rate k in the exponential decay model as described by Olson (1963):

$$W_t = W_o e^{-kt} \qquad \textbf{(Eq. 6.1)}$$

Where W_t is the weight of the litter remaining at time t, W_o is the initial litter weight, k is the decomposition rate (expressed as week^{-1} in our study), and t is the time of collection (i.e., the week

Photo 6.1 Litterbags before installation (left) and after collection (right) [Photographs: NN Setiawan]

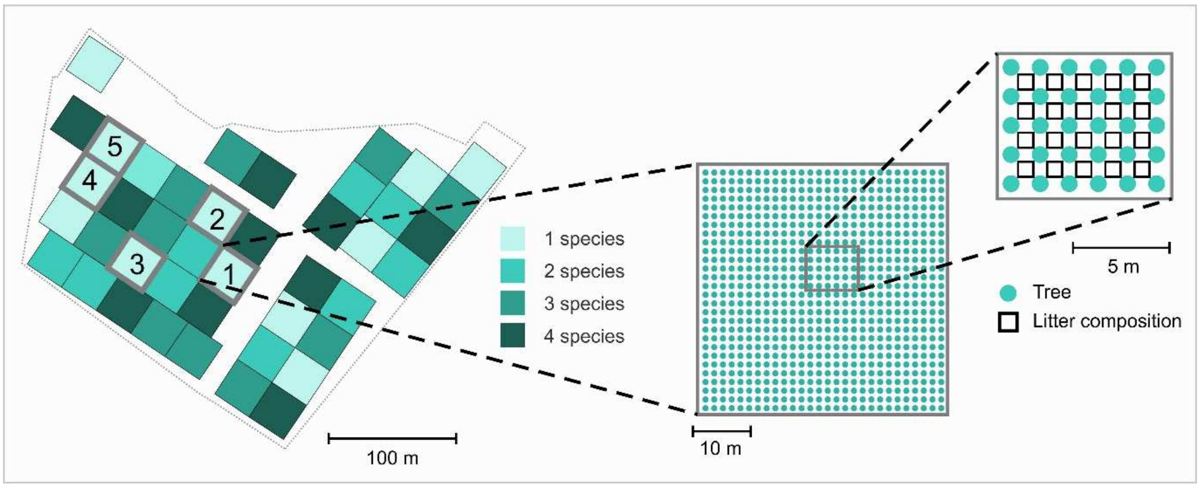

Fig. 6.1 (Left) the 42 plots at the Zedelgem site of the FORBIO experiment. The numbers indicate the five monoculture plots in which the litterbags were installed; (right) a monoculture plot with the 28 x 28 planted trees. The litterbags were installed in the open areas between the trees in the central part of the plot. For each of the 20 different litter compositions, six litterbags were installed to enable constructing a time series of litter decomposition.

number in our study). All analyses were done in R version 3.0.3 (R Core Team 2014); graphs were made with the R package *ggplot2* (Wickham 2009).

First, Principal Component Analysis (PCA) was used to visualize the initial chemical composition of the leaf litter we used for the five study species. Second, we calculated the decomposition rate (*k*) for each of the 100 time series (20 litter compositions x 5 plot replications), using the initial weight and the remaining weights of the 4 (or 5) collection dates in each time series (see Appendix 6.1 for R syntax). The fits of the exponential decay models were evaluated by visual inspection (plotting weight against time) and by inspecting the *R*-square (R^2) of the models. Third, we looked for differences in litter decomposition rates between the five study species by comparing the mean decomposition rates of the monospecific litter compositions ($n = 5$ per composition). We also calculated the correlation between the initial nutrient concentrations and the decomposition rates of the monospecific litter with a multilevel model using the *lme* function in the *nlme* package (Pinheiro et al. 2014). The decomposition rate of the monospecific litters were used as response

Photo 6.2 The litterbags installed in a *Pinus* monoculture (left) and one time series of litterbags (right)[Photographs: NN Setiawan]

Photo 6.3 The ground vegetation cutting before the litterbags collection [Photographs: Mathias Dillen]

variable, the first and second PCA axes as fixed effects, and the litter species as a random factor (see Appendix 6.1 for R syntax). Fourth, we investigated whether litter diversity and composition influenced the variance among the decomposition rates for the 20 litter compositions with a multilevel model using the *lmer* function in the *lme4* package (Bates et al. 2014; *n* = 100, i.e., 20 litter compositions x 5 plots). Decomposition rate was used as the response variable; litter diversity, litter composition, and plot were fitted as random effects; and the optimal model was selected by comparing the Akaike Information Criterion (AIC) of each model (see Appendix 6.1 for R syntax). Last, for the mixed litters, we looked for synergistic or antagonistic effects. We calculated an expected litter decomposition rate (k_{exp}) for each of the 75 time series (15 mixed litter compositions x 5 plots) as follows: (1) for each litter composition and plot, we calculated the expected remaining biomass at each of the 4 collection dates based on the weights remaining in the monospecific litter bags in the plot at that particular collection date, (2) based on these expected time series of remaining litter biomasses, we then calculated the 'expected' decomposition rate as described above, for each litter composition and plot. We compared the expected decomposition rates with the observed mixed litter decomposition rates (k_{obs}) using the log-ratio of k_{obs} to k_{exp} (see Appendix 6.1 for R syntax). A positive value of the ratio indicates a synergistic effect, i.e., the litter mixture decomposes faster than expected; a negative value indicates an antagonistic effect, i.e., the litter mixture decomposes slower than expected. To test for differences in the log-ratio between the litter compositions, we used a multilevel model (*lme* function) with the log-ratio as the response variable, litter composition as fixed effect, and plot as random effect ($n = 75$). As the five replicates of each litter composition time series were installed in five different plots and the local site conditions in these plots might also affect the decomposition rate, we included plot as a random effect in the last two models.

6.4 Results

6.4.1 Litter quality: the five study species

The initial nutrient concentrations of the litter we collected (Table 6.1) differed significantly among the five tree species (One-way ANOVA: $p < 0.001$). The first two principal components of the PCA on the leaf litter nutrient concentrations captured 74.3% of the variation in chemical composition. *Betula*, *Pinus*, and *Tilia* were quite distinct with regard to the chemical composition of their litter, while *Fagus* and *Quercus* showed a similar chemical composition (Fig. 6.2). The first three species showed significantly higher nutrient concentrations: mainly K, Mg, P, N for *Betula*; N for *Pinus*; and Ca, N for *Tilia*. Compared with the other species in our study, we found significantly higher lignin and hemicellulose concentrations in *Betula* and higher cellulose and lower lignin concentrations in *Pinus* needles. The *Fagus* and *Quercus* litter was fairly low in nutrients (mainly Mg and N) and high in lignin. Consequently, the C:N and L:N ratios of the *Fagus* and *Quercus* litter were significantly higher than for the other species. *Betula* showed the highest L:N ratio of all five species, N:P was significantly highest for *Pinus*, and C:N was significantly lowest for *Tilia*.

6.4.2 Monospecific and mixed litter: decomposition rates

After 60 weeks, the remaining mass of all litters varied between less than 1% until 75.3% of the initial weight. The highest mass loss occurred during spring-summer 2012 (i.e., between week 20 and 35). The negative exponential decay model described our litter weight loss data very well; for all 100 model fits (monospecific and mixed litters), the (adjusted) R-square ranged between 0.701 and 0.999.

The highest mean decomposition rates of monospecific litter were shown by *Tilia* (k = 0.046 week^{-1} ± 0.004 SE), followed by *Betula* (k = 0.041 ± 0.004). A moderate decomposition rate was shown by *Pinus* (k = 0.023 ± 0.001). The monospecific litters of *Quercus* (k = 0.014 ± 0.001) and *Fagus* (k = 0.008 ± 0.001) showed the lowest decomposition rate (Fig. 6.3a). The monospecific litter decomposition rates were positively correlated with the first axis of the PCA on the initial chemical composition of the leaf litter (p = 0.005).

Table 6.1 The chemical composition of the collected leaf litter for the five tree species at the start of the decomposition experiment: mean nutrient concentrations (standard error between brackets, N = 3), the different C fractions (n = 1), and ratios between some important components (for details on the chemical analysis see 6.3.1)

Nutrients (mg/g) [a]					C fraction (mg/g)[b]			Ratios		
N	Ca	K	P	Mg	Cls	Hm	L	C:N	N:P	L:N
Betula pendula										
19.6	13.3	10.6	6.5	3.1	103	213	252	26.6	3.0	12.9
(0.2)	(0.2)	(0.6)	(0.2)	(0.1)				(0.2)	(0.6)	
Fagus sylvatica										
16.3	17.1	3.7	3.1	1.1	172	184	206	30.4	5.3	12.7
(0.4)	(0.2)	(0.2)	(0.1)	(0.1)				(0.7)	(0.2)	
Pinus sylvestris										
19.9	4.8	7.7	1.8	1.3	267	185	151	25.4	11.4	7.6
(0.7)	(0.1)	(0.2)	(0.1)	(0.0)				(0.9)	(0.9)	
Quercus robur										
16.2	12.4	5.6	3.5	1.3	136	151	198	30.5	4.7	12.3
(0.3)	(0.1)	(0.2)	(0.2)	(0.1)				(0.4)	(0.2)	
Tilia cordata										
22.5	25.9	6.5	4.9	2.5	116	187	178	21.7	4.6	7.9
(0.3)	(0.7)	(0.5)	(0.2)	(0.1)				(0.3)	(0.2)	

[a]Nitrogen (N), Calcium (Ca), Potassium (K), Phosphor (P), Magnesium (Mg)
[a]Cellulose (Cls), Hemicellulose (Hm), Lignin (L)

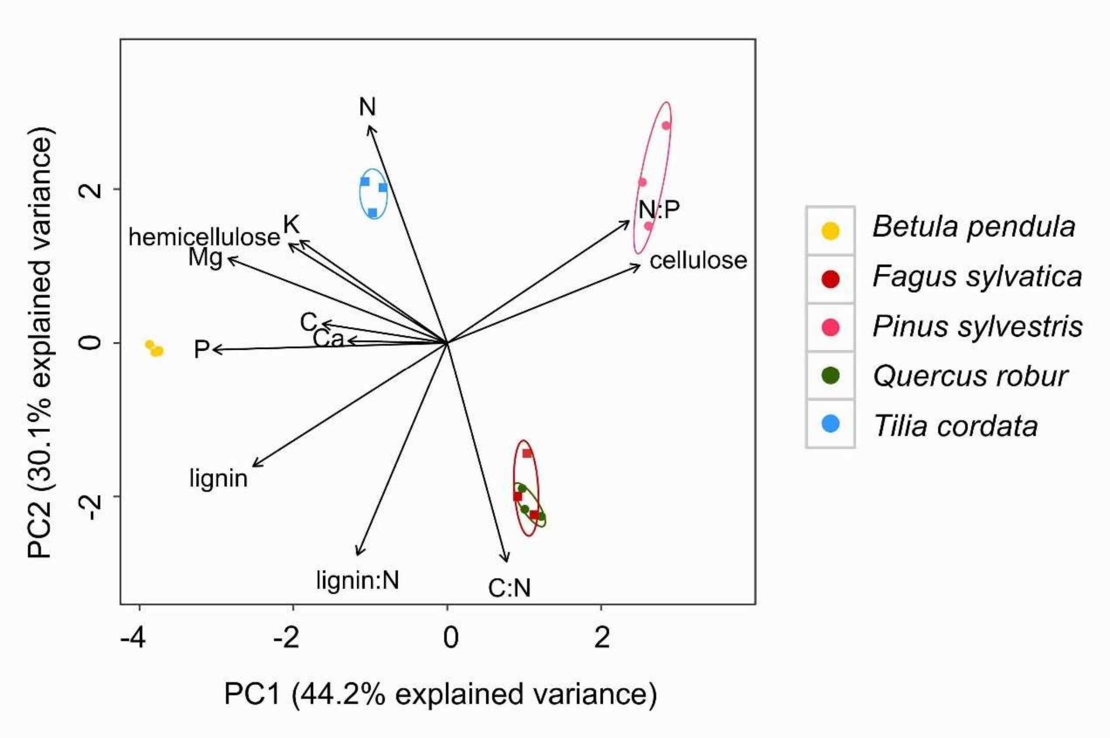

Fig. 6.2 PCA biplot of the initial leaf litter chemical composition of the five tree species. The proportion of variance explained by the first two components (PC1 and PC2) was 44.2 and 30.1%.

The mean *k* values (in week^{-1}, ± SE) of the four litter diversity levels were 0.026 (± 0.003) for the monospecific litters, 0.027 (± 0.003) for the two-species mixtures, 0.021 (± 0.001) for the three-species mixtures, and 0.025 (± 0.001) for the four-species mixtures. The variability in decomposition rate was smaller in the three-species and four-species litter mixtures compared with the monospecific and two-species litter mixtures. Using decomposition rate as a response variable, the most optimal multilevel model contained litter composition and plot as variance terms. Litter composition explained 67.5% of the variance in *k*; plot only 3.2%.

In general, mixtures containing *Tilia, Betula*, and *Pinus* decomposed faster than mixtures containing *Fagus* and *Quercus* (Fig. 6.3b-d). For mixed two-species litter, the highest mean *k* (in week^{-1}, ± SE) was shown by the combination *Tilia* - *Pinus* (0.047 ± 0.008) and the lowest by the combination *Fagus* - *Quercus* (0.009 ± 0.002). The highest mean *k* values in mixed three-species litter was shown by the combination *Betula* – *Quercus* – *Tilia* (0.026 ± 0.003) and the lowest was *Fagus* – *Pinus* – *Quercus* (0.013 ± 0.001). In mixed four-species litter, the two highest mean *k* values were shown by the combination without *Quercus* (0.032 ± 0.002) and the one without *Fagus* (0.031 ± 0.003).

6.4.3 Mixed litter: synergistic or antagonistic effects?

For five out of the fifteen studied litter mixtures, the mean observed decomposition rate was clearly higher than the mean expected decomposition rate (synergistic effect); for one of the fifteen mixtures, the mean observed decomposition rate was lower than the mean expected one antagonistic effect) (Fig. 6.4b-d). Mixtures containing at least 50 percent of low-quality litter (*Fagus, Quercus*) tended to have a lower decomposition rate (mean k 0.042 - 0.107 week^{-1}) compared with mixtures containing at least 50 percent of high-quality litter (*Betula, Pinus, Tilia*: mean k 0.106 - 0.234 week^{-1}). The multilevel modelling showed a significant effect of litter composition ($F = 2.50$, $p = 0.007$) in explaining the log-ratio of k_{obs} to k_{exp}, and plot explained 13.4% of the variance in the log-ratio. Three out of the fifteen different mixtures showed significant synergistic effects, i.e., the two-species mixtures *Betula – Pinus* (t-value = 2.57, p = 0.013) and *Pinus – Tilia* ($t = 2.89$, $p = 0.005$), and the four-species mixtures *Betula – Fagus – Pinus – Tilia* ($t = 2.39$, $p = 0.019$).

6.5 Discussion

The decomposition rates during the early litter decomposition stage (60-week period) significantly differed between the monospecific litters of the five studied tree species, and between the fifteen different litter mixtures. These differences appeared to be not related to litter diversity; litter composition was determining. Mixing specific litter species may lead to significant synergistic effects during the early decomposition stage.

6.5.1 Monospecific litters: the five study species

The differences in litter decomposition rate between the studied species were related to differences in initial litter quality, as shown by the results of the multilevel modelling. High-quality litter species with high N concentration, low C:N ratio, high P concentration, and high to moderate Ca concentration, such as *Tilia* and *Betula*, decomposed faster than low-quality litter species with low N concentration, high C:N ratio, low P concentration, and moderate to low Ca concentration such as *Fagus* and *Quercus*. The intermediate litter quality and decomposition rate of the *Pinus* needles in our study are exceptional for coniferous tree species, which are, in general, less rich in nutrients such as N, P, Ca, and K than broadleaved tree species (Berg and McClaugherty, 2008). Of course, we used green needles that were still attached to the *Pinus* trees at the time of 'litter' sampling, and living leaves have higher nutrient concentrations than senescing leaves as trees reabsorb nutrients from senescing leaves and translocate the nutrients into the

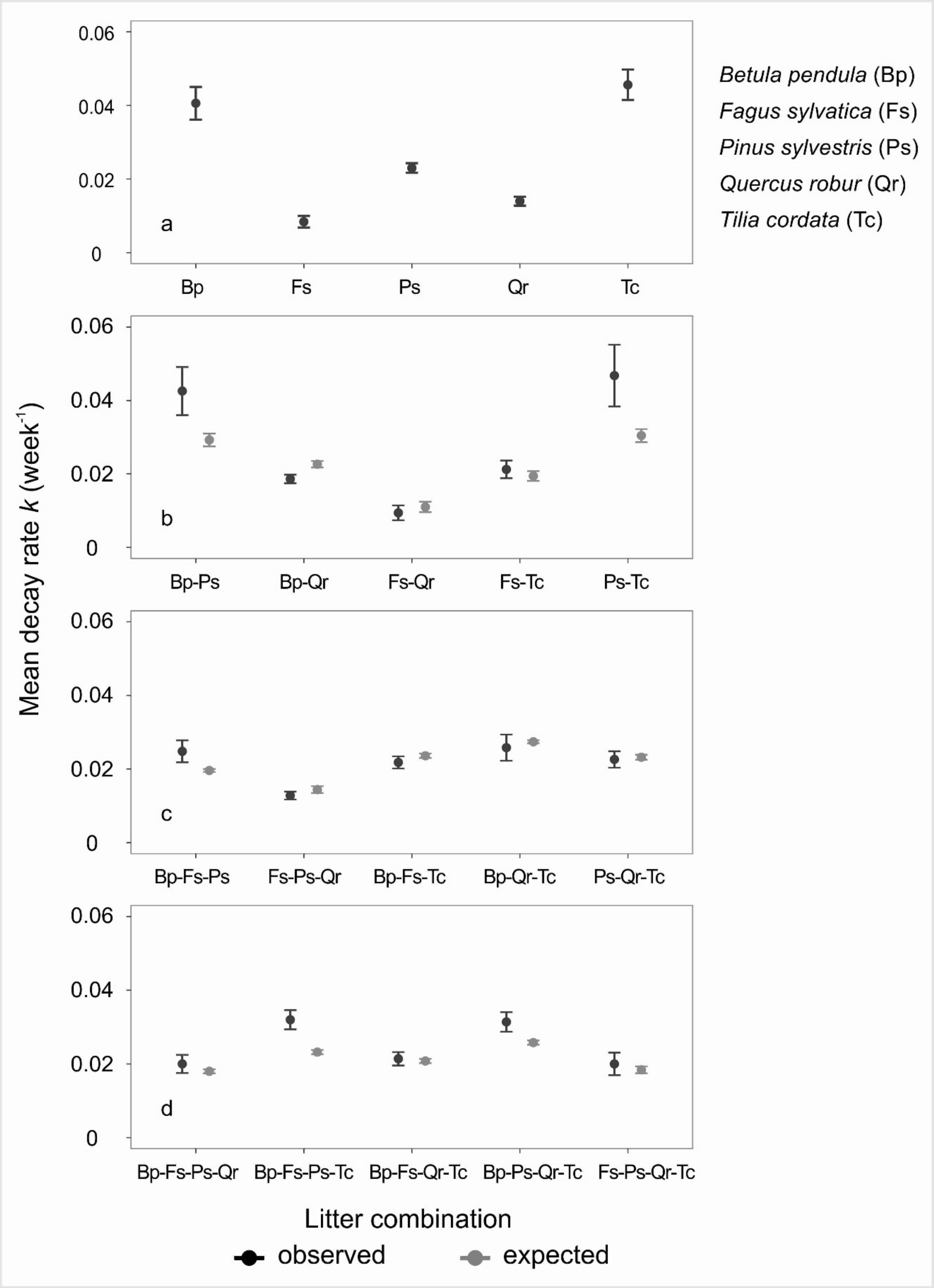

Fig. 6.3 The mean observed and expected decomposition rates (± SE) for the 20 different litter compositions: (a) monospecific litter, (b) two-species mixtures, (c) three-species mixtures, and (d) four-species mixtures.

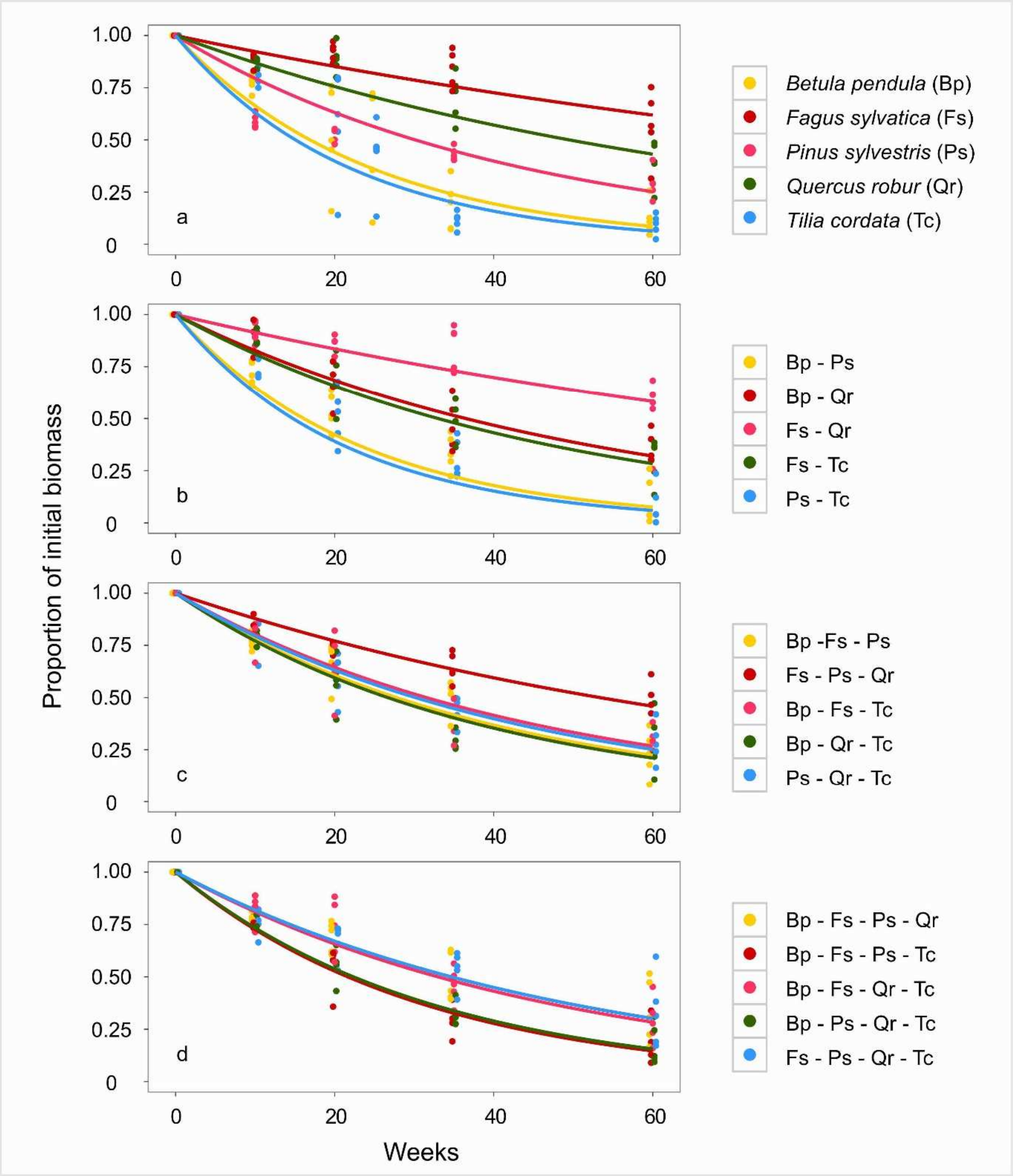

Fig. 6.4 The litter biomass remaining at 10, 20 (+25), 35, and 60 weeks for the different litter compositions: (a) monospecific litter, (b) two-species mixtures, (c) three-species mixtures, and (d) four-species mixtures. The lines show the exponential decay model for each litter composition, based on the mean decomposition rate (*k*) for the five replicates of this composition.

growing parts of the trees during the process of leaf shedding (Adl 2003). Girisha et al. (2003) indeed found significant differences in chemical composition (i.e., for C, Mg, and holocellulose) between green needles and freshly fallen (brown) needles of *Pinus* and a three-times higher decomposition rate for the green *Pinus* needles. Even in green needles, there is a difference in nutrient concentrations between needles from former growing seasons and fresh needles of the current growing season due to nutrient retranslocation into the youngest shoots (Oleksyn et al. 2003). The *Pinus* needles of our study had an even higher N and P content and a two times lower lignin content than the green *Pinus* needles from the study of Girisha et al. (2003). The high N and P content and the low lignin content in our *Pinus* litter explain its exceptionally high decomposition rate.

In general, the nutrient concentrations of the litter in our study were higher than in other Belgian studies that also looked into some of our study species, i.e., *Betula*, *Fagus*, and *Quercus*. Leaf litter concentrations of P, K, and Ca were lower than in our study (but N was slightly higher) for *Betula* and *Quercus* in a mature forest on a nutrient-poor sandy loam soil without agricultural legacy (Staelens et al. 2011). Leaf litter N, P, K, and Ca were lower (but Mg, lignin, cellulose, and hemicellulose were higher) for *Fagus* and *Quercus* in a mature forest on acid brown earth soil (Jonard et al. 2008). In a young post-agricultural forest on well-drained sandy soil, the leaf litter Ca and N concentrations were lower and the C:N was higher than in our study for *Betula*, *Fagus*, and *Quercus* (Van Nevel et al. 2014). The high nutrient concentrations of the litter in our study might be the result of the litter collection (withering leaves and fresh needles still attached to the trees) and the high soil nutrient availability (P from the agricultural legacy of the site and N mostly due to atmospheric deposition). The availability of nutrients, especially N (Hobbie 2000), in the soil can influence the nutrient content of leaves and thus the leaf litter in some tree species (Berg and McClaugherty 2008, Chapin et al. 2011). The high N and P content of the soil at our post-agricultural site may have led to an input of leaf litter with higher quality to the soil. But, even in this high-nutrient, post-agricultural environment, early-stage litter decomposition rates were higher in the tree species with high-quality litter.

Leaf litter quality is mainly determined by certain essential nutrients (i.e., N, P, and Ca) and lignin, which influence the decomposition rate (Hättenschwiler 2005, Vos et al. 2013). The leaf litter decomposition process starts with the degradation of soluble and low-molecular-weight compounds (e.g., cellulose, hemicellulose, carbohydrates) into more simple organic matter through microbial decomposer activity (Berg and McClaugherty 2008). High concentrations of N and P in the leaf litter will support microbial decomposer growth and activity, thus resulting in a high initial decomposition rate (Berg and McClaugherty 2008). Partially degraded organic matter can be fragmented and eaten by earthworms and soil arthropods, which will result in smaller fragments available for other saprotrophs to utilize and degrade (Adl 2003). Soil decomposer activities such as earthworms and arthropods were related to the litter structure and nutrient content, and can be specifically related with certain tree species (Bultman and Uetz 1984, Hansen

1999). A high concentration of leaf litter Ca, such as in *Tilia*, will provide a more palatable substrate for earthworms and support earthworm activity (Reich et al. 2005); thus resulting in a high leaf litter decomposition rate. Indeed, the leaf litter of *Tilia* in our study had the highest initial Ca concentration and also showed the highest decomposition rate. Other decomposer such as oribatid mite has shown to be species-specific (Hansen 1999). The degradation of lignin and the highly stable polymers of plant cell walls (Dence and Lin 1992) happens in the later stages of decomposition. Several studies have mentioned that high lignin concentrations limit the decomposition rate since lignin is difficult to degrade and lignin-degrading organisms are tree species-specific (Eriksson and Bermek 2009) and scarce in many cases (Melillo et al. 1982). In our study, *Betula* had the highest lignin concentration in its initial litter, and yet, it was one of the two species showing a high early-stage decomposition rate (next to *Tilia*). Berg and Matzner (1997) also saw a rapid mass loss in the early decomposition stages of *B. pendula* litter, related to the high N and P concentration in the *Betula* leaves, and found the later decomposition stages to be independent of the initial lignin concentration.

6.5.2 Litter mixing effects

Our study is one of the first tree litter decomposition studies to use up to four litter diversity levels (1-4 litter species), many species combinations and an equal number of combinations at every diversity level. We saw that the identity of the litter species present in the mixtures (litter composition) was more important than the number of litter species in the mixtures (litter diversity) in determining their early-stage decomposition rates. Significant species identity effects have been reported before in biodiversity – ecosystem functioning studies, for litter decomposition rates (Gartner and Cardon 2004, 2006, Hättenschwiler 2005, Hättenschwiler et al. 2005, Vivanco and Austin 2008, Gessner et al. 2010, Jacob et al. 2010b, Vos et al. 2013, Handa et al. 2014) as well as other ecosystem processes and functions in forests, e.g., resistance to pests and diseases (Chapter 4, Haase et al. 2015), soil nutrient retention (Ewel and Bigelow 2011), and tree biomass production (Healy et al. 2008, Ratcliffe et al. 2015).

The early-stage decomposition rates of the litter mixtures in our study were clearly linked to the initial litter quality of the component species, a finding that has been reported before. The positive effects of high-quality litter in litter mixtures have been stressed often (Cuchietti et al. 2014), and synergistic effects seem to be more common than antagonistic ones (Gartner and Cardon 2004, Hättenschwiler and Gasser 2005, Cuchietti et al. 2014). We also saw significant synergistic effects for three mixtures, containing our fast-decomposing study species *Betula, Pinus*, and *Tilia*. The nutrient-rich soils of our post-agricultural site might be responsible for the low number of clear litter mixture effects. Transfer of N between N-rich and N-poor litter, causing synergistic effects, may not happen at sites where the N availability does not limit decomposition. In addition, the lignin content of the litter might not limit early-stage decomposition rates at sites with soils rich in N (Hobbie 2000). Synergistic or antagonistic effects may be more apparent in nutrient-limited soils.

6.6 Conclusions

In the context of forest management practices in post-agricultural plantations, our study showed that mixing tree species, and carefully selecting which species to mix, can affect the nutrient cycling process by altering the early-stage leaf litter decomposition rate. Current management practices for tree species selection are mainly based on the commercial value of the timber, which results in planting *Fagus*, *Pinus*, or *Quercus*. In the long term, the poor leaf litter quality of these species may cause the absence of a burrowing earthworm community, which will slow down leaf litter decomposition and result in forest-floor buildup and soil acidification (De Schrijver et al. 2012). Our study suggests that admixing tree species with high-quality litter in post-agricultural plantations might increase the early-stage decomposition rates of the mixture's litter. As a result, more organic matter will be incorporated in the mineral soil, and more nutrients will become available for plant growth through mineralization and mycorrhizal activity. Planting more diverse stands might thus be a wise option to ensure sustained nutrient availability that will support long-term tree growth, even though the overall mixing effect cannot be predicted in most cases. To investigate whether the early-stage litter decomposition effects observed in our study also hold in the later decomposition stages, further research, over a longer time period, will be necessary.

Appendix 6.1 R syntax of the best-fit models considered in the different analyses

response variables	R syntax
decomposition rate (*k*)	lm(proportion of the remaining litter ~ -1 + incubation weeks, data=DecompositionZ)
k of monospecific litter	lme(k~PC1 + PC2, random= ~1|Species, data=Decomposition_K_mono, method="ML")
k of overall litter	lmer(k~1 + (1|diversity) + (1|composition) + (1|plot), data=Decomposition_K)

Overview of Zedelgem site in summer 2015 [Photograph: NN Setiawan]

Chapter 7

General discussion & conclusions

Positive tree diversity effects on ecosystem functioning in mature forests have been recognized widely (Spiecker 2003, Gamfeldt et al. 2008, Vilà et al. 2013, Wagner et al. 2014), but knowledge on the effects in the early development stages of forest plantations is still limited. Seeing the unique characteristics of these young plantations compared with mature forests, it is relevant to determine the potential role of tree diversity in the early stages of forest development. Tree diversity experiments, such as FORBIO, offer a promising approach to study tree diversity effects on different ecosystem functions throughout the different stages of forest development.

The main objective of this thesis was to study the early effects of tree diversity and composition on forest ecosystem functioning and explore the context-dependency of these effects, by studying experimental sites in contrasting environmental conditions. For the four ecosystem functions that we studied in this thesis (i.e., sapling growth, crown damage, crown arthropod community, and litter decomposition), we saw different effects of the different explanatory variables. In the following sections, we will first discuss the relative importance of site, neighbourhood diversity and species composition on the different ecosystem functions. Second, we will discuss the tree identity effects and the driving mechanism behind them. Third, we will compare the results with findings in mature forests. Finally, we will present possible management consequences and discuss the limitations of this study, thereby suggesting options for future research.

7.1 Relative importance of site, neighbourhood diversity, and composition

We studied the effects of three main experimental design elements on the different response variables in this thesis: site, neighbourhood diversity, and composition. To quantify and visualize the relative importance of these three experimental design elements, we did an additional variance partitioning analysis in which the total variation in a response is partitioned among the different elements ('variance components').

We analysed the relative importance of site, neighbourhood diversity, and composition on nine of the ecosystem function variables studied in this thesis, using a multilevel analysis of variance approach (see Appendix 7.1 for more detail) (Gelman 2005; Hector et al. 2011). We did not include litter decomposition in this analysis since we only measured it at the Zedelgem site. In this summarizing analysis, we focused only on the main experimental factors of the FORBIO experiment (site, diversity, composition), even though we found a consistent effect of tree species identity throughout the four chapters of the thesis. Obviously, the tree species identity and neighbour identity effects are partially captured by the composition effect that we included in the model.

The results of this additional analysis showed that site and composition were more important than diversity in determining the ecosystem functions tested. For five out of the nine response variables, the largest part of the variation was explained by site (i.e., diameter increment, height increment, height to diameter ratio, branch & shoot damage, discolouration); for the other four response variables (i.e., defoliation, herbivore abundance, total abundance, order richness), the relative importance of composition was the highest (Fig. 7.1).

The **site differences** accounted for most of the variation in four of the response variables related with herbivorous arthropods: the abundance of herbivores and overall arthropod abundance in the crowns of the saplings, arthropod order richness, and defoliation of the saplings. Indeed, we saw that the total number of herbivore individuals in Gedinne was five times lower (1,128) compared with Zedelgem (5,603). The herbivore abundance was positively correlated with the abundance of the higher trophic level (carnivores), which resulted in a higher total arthropod abundance (see Table 5.1). The higher number of herbivores as damaging agents (e.g., leaf chewer, skeletonizer, leaf miner) was also related with higher defoliation rates in Zedelgem (see Table 4.1). The high abundance of Aphididae found in Zedegem (93.7%, Appendix 5.1) might have biased our results on herbivore abundance and total arthropod abundance, thus obscuring a true site effect. The interaction between site and diversity in the herbivore abundance and total abundance models represented the *Betula* effect in Zedelgem (the Aphididae being abundant in *Betula*). However, the neighbourhood diversity effect was consistent even when the Aphididae were removed from the analysis (Chapter 5).

The arthropod order richness, on the other hand, was slightly higher at the Gedinne site than in Zedelgem (see Table 5.1). The high amount of variation in order richness explained by the site might be – partly - resulting from (a)biotic legacies of former land use and the surrounding landscape. The Gedinne site is surrounded by forest patches and grassland, which may serve as a

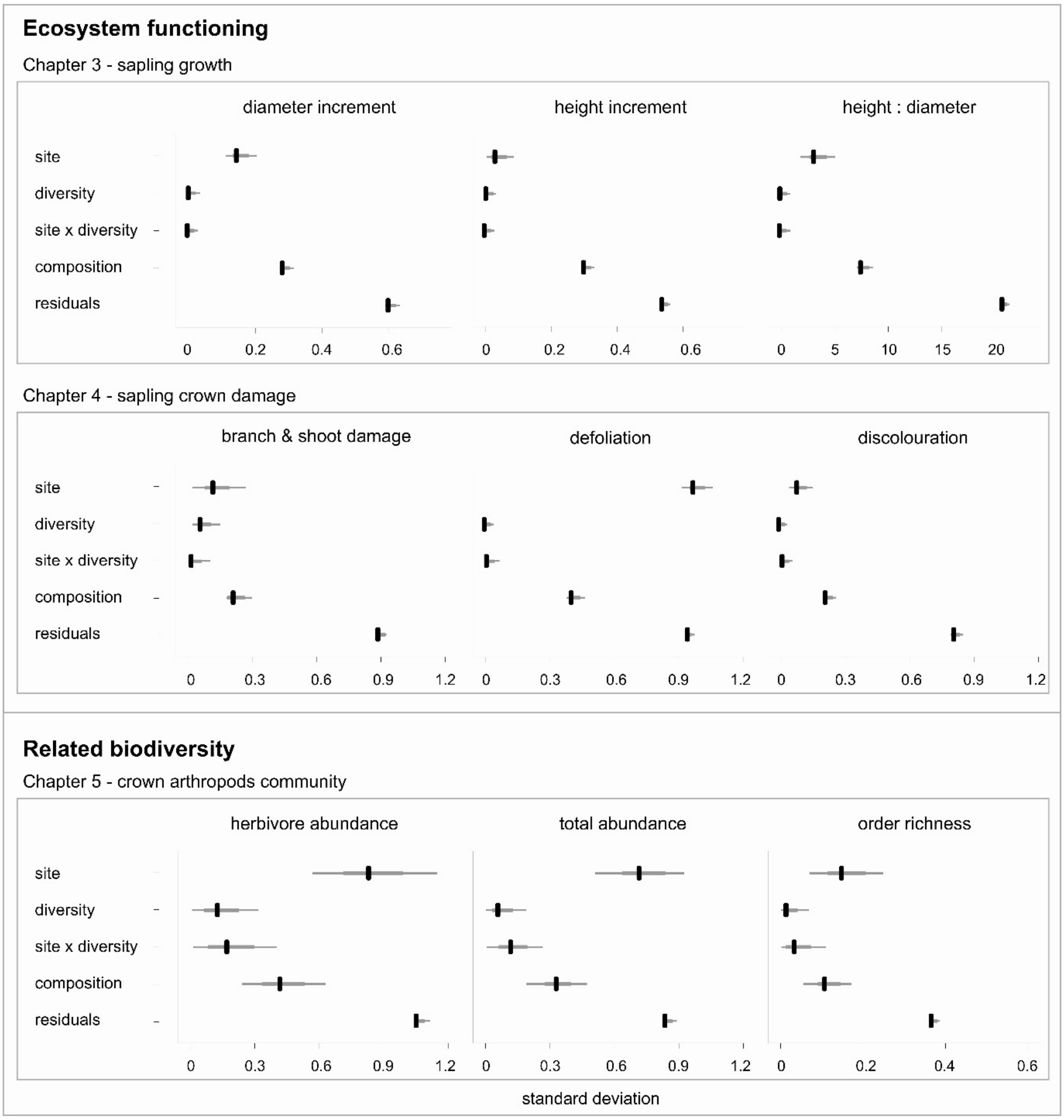

Fig. 7.1 Results of a multilevel analysis of variance using MCMC sampling, presented as graphical ANOVA. The vertical black lines represent medians of the the variance components on the standard deviation scale and can be used to compare the relative importance of the different factors. The credibility intervals are presented in grey horizontal lines: 95% (wide line) and 68% (narrow line).

source of arthropods associated with trees. As a stand-replacement site, biotic legacies with an effect on arthropods may be important here, including surviving organisms and organic structures such as wood stumps (Swanson et al. 2011). The order richness in Gedinne was probably also higher since one of the tree species planted in the present experiment (*Pseudotsuga*) was closely related (phylogenetically) to the tree species of the former stand (*Picea*). *Picea* and *Pseudotsuga* may thus share some generalist arthropod species (Goßner and Ammer 2006). The post-agricultural Zedelgem site was surrounded by arable land, grassland, rural settlements, and less mature forests than Gedinne. The arthropod community in Zedelgem was thus probably less diverse than in Gedinne due to the lower chance of tree-related arthropod input from the surrounding forest.

The defoliation of saplings in Zedelgem was two times higher than in Gedinne in both measurement years. The differences in the soil condition of the sites might explain this. The post-agricultural Zedelgem site was richer in soil nutrients such as phosphorus than the Gedinne site (Fig. 2.2). Trees with a higher nutrient concentration are more attractive to herbivores (Ernest 1989, Bird et al. 2000, Price et al. 2011).

Composition explained most of the variation of the response variables that were directly related with tree species traits and local neighbourhood identity. The differences in tree species traits governed the differences in several of the studied responses, and the presence of certain neighbours only mattered when the trait values differed between target and neighbour saplings. For instance, the sapling growth rate (diameter and heigh increment) and growth allocation pattern (height to diameter ratio) differed between tree species with different light requirements. Early-successional species, which are light-demanding, grow faster than shade-tolerant, late-successional species in this early stage of young plantation establishment. The identity of the neighbours of a sapling becomes important when the neighbours' light requirements differ from those of the target tree species.

The effects of composition on crown damage and herbivore abundance were probably related with the phylogenetic relatedness and the relative size of the neighbours. Two of the crown damage symptoms (i.e., branch and shoot damage, discolouration), which were positively correlated with each other ($r = 0.14$, $p < 0.001$, $N = 10{,}136$), differed between the tree species. The identity of the neighbours becomes important in determining sapling damage when the neighbours are phylogenetically distant from and bigger or taller than the target sapling. The more phylogenetically distant the tree species, the less likely they will share pests or diseases due to differences in traits that affect susceptibility to pests or diseases, e.g., leaf toughness, presence of secondary metabolites, or foliar trichome density. For instance, the trichomes in *Betula* leaves protect leaves from arthropod herbivores by interfering with their movement, and glandular trichome secretion in *Betula* also negatively affects fungal pathogen infestation and arthropod herbivore load (Valkama et al. 2004, 2005, Tian et al. 2012). Bigger and taller neighbours can shield trees from harsh climate and thus reduce the risks of branch and shoot damage caused by abiotic factors. Bigger and taller neighbours also reduce the target trees' apparency, making them less visible to herbivores (associational resistance).

7.2 Tree identity effects

For every response variable studied in this thesis, tree identity always explained the highest variance. The different tree species performed differently for the different responses; no single species exceeded the others for every response. For example, the fast-growing *Betula* grew well in the open, high-light condition of early plantation establishment, but the *Betula* saplings were highly infested by phloem-sucking Aphididae, which may have reduced their vitality and contributed to their high branch and shoot dieback in summer 2013. There was a trade-off between growing fast and dominating the canopy and being more exposed to pests and diseases.

In some of the studied response variables, the tree species identity effect could be directly related with tree species traits. Growth and litter decomposition were mainly affected by certain tree species traits, such as high juvenile growth, shade tolerance, and high-quality litter (high N and Ca, low lignin content).

While several tree traits are related with herbivory (high foliar N content for example), the crown damage response variable involving herbivores in this thesis (i.e., defoliation) seemed to be more related with the host-specificity of herbivores. The specific relation between trees and herbivores has been known as the "evolutionary arms race", in which sets of traits in trees and herbivores co-evolved due herbivores competing to feed on trees and trees developing defenses against herbivores.

Changes in the local microclimate may alter the responses of the trees depending on their traits. For example, the growth of slow-growing, shade-tolerant *Fagus* is low in the beginning. When the canopy closes, *Fagus* can tolerate the low light and continue to grow while other species might not be able to survive.

7.3 Early stage of forest plantations vs mature forests

Research focusing on mature temperate forests has reported significant relationships between tree diversity and the ecosystem functions that we tested in this thesis, as follows:

- tree diversity positively affects tree growth through species-specific complementarity effects, both at stand level (Jacob et al. 2010a, Morin et al. 2011) and individual tree level (Ratcliffe et al. 2015)
- a higher tree diversity increases the resistance to pests and diseases through associational resistance (Spiecker 2003, Jactel et al. 2005, Jactel and Brockerhoff 2007)

- a higher tree diversity provides a more complex vegetation structure, which supports a trophically more complex arthropod community through niche complementarity effects (Brown and Southwood 1983, Schowalter 1989, Jeffries et al. 2006, Price et al. 2011)
- tree diversity affects litter decomposition rates through non-additive synergistic or antagonistic effects (Gartner and Cardon 2004, 2006, Vivanco and Austin 2008, Gessner et al. 2010, Jacob et al. 2010b, Vos et al. 2013, Handa et al. 2014)

In the early stage of the forest plantations we studied, we saw that the studied ecosystem functions were mostly affected by the **species identity** of the target sapling. The clear differences between the study species were probably the result of the criteria used in selecting the tree species planted at the FORBIO sites. The selected tree species had to be phylogenetically distant and represent a broad range in trait values and ecological strategies (Chapter 2). The differences in leaf morphology (coniferous vs. broadleaved), sapling light requirement (low vs. high), crown form (monopodial vs. sympodial), root system type, and litter quality led to different species performances for the different ecosystem functions studied.

We saw indications of **diversity** effects, especially phylogenetic diversity, on ecosystem functions such as diameter increment in Zedelgem, branch and shoot damage in Gedinne (year 2013), crown arthropod order richness in Zedelgem, crown herbivore abundance in Zedelgem, and litter decomposition rate in Zedelgem. The diversity effects were not always consistent or larger than the identity effect. In this young forest plantation, in which no closed canopy had yet established, the saplings were unlikely to already have direct interactions, thus lowering the chance for neighbourhood diversity effects to occur. Indirect interaction between target and neighbour saplings, however, seemed to occur. For example, more diverse neighbours may have created a more heterogeneous, suitable microclimate that supported the growth of target saplings (Chapter 3) and a more complex arthropod community structure (Chapter 5). We expect that direct interaction between the trees will occur as the trees grow, a closed canopy is formed and stands become structurally more complex (Leuschner et al. 2009). The trees will start to compete for resources, and taller trees will start to outcompete smaller trees. Big trees will shade out the understory vegetation and provide a suitable microclimate for shade-tolerant tree species.

In comparation with results found in mature forests, the tree diversity effects in our young forest plantations were rather weak. Next to the lack of interactions between individual trees in our young forest plantations, some general limitations of tree diversity experiments might partly explain the weak diversity effects that we found. Natural or near-natural mature forests are predominantly self-sustaining systems with more complex structures (e.g., uneven-aged trees with random locations, stratified canopy) and more associated biota, which are more stable compared with tree diversity experiments. The ecosystem processes and interactions in mature forest are the result of long-term diversity effects (Baeten et al. 2013), which might be impossible to already capture in tree diversity experiments plots. It might be more relevant to compare results of tree diversity experiments with tree plantations and young intensively managed forests, instead of mature natural or near-natural and managed stands (Leuschner et al. 2009).

To translate the results from this thesis into actual management planning or to compare them with natural forests, careful interpretation is needed. Several functions investigated in this study rely on an experimental set-up within a limited period of time. Therefore, there might be differences with the conditions in natural forests. For example, the saplings in the FORBIO experiment were planted in uniform spacing, whereas in natural forest conditions, the spacing is not uniform. The distances between target trees and their neighbors will influence tree growth and the spread of diseases. The crown damage and arthropods captured only represent a glimpse of the continuously changing damage rates and the population dynamics in arthropod communities. Next, the arthropod sampling method used might have introduced a bias in the results since we only captured the arthropods that are active during daytime and during the sampling period. Last, the litter structure in real situations differs with litter inside litterbags. Litterbags may press and compact the litter, which results in a reduced litter volume and surface area. Yet, the exposed surface is essential for the contact with microbial decomposers.

7.4 Management consequences

Planting tree plantations that consist of several species or different genotypes and will lead to complex canopy structures has been recognized as an important strategy to create sustainable forests (Verheyen et al. 2016). In spite of this scientific consensus, one of the main challenges is to convince foresters to establish mixed forests. Indeed, mixed forest plantations are still perceived to have lower yields and require more complicated management (Carnol et al. 2014). Global networks of tree diversity experiments (TreeDivNet, including the FORBIO experiment) may play an important role in providing a science-based framework for documenting and understanding the advantages and drawbacks of mixed forest plantations. The results from this research network will provide useful insights worldwide on the functioning and management of mixed forest plantations throughout the different forest development stages.

In the context of this thesis, we translated our main findings on the early stage of mixed forest plantations to field practices in the following general recommendations:

(1) Carefully select the tree species in the mixtures, based on their species traits.

We found consistent species identity effects in all the ecosystem functions that we studied, which shows that every tree species performs differently based on their specific trait values. However, no tree species was excellent in all studied ecosystem functions, which is referred to as the jack-of-all-trades mechanism that leads to positive effects of biodiversity on ecosystem multifunctionality (Van der Plas et al. 2016). There are always trade-offs between different functions for a given species. For example, *Betula* is an early-successional species that grows fast in the early stage of forest plantations. *Betula* also produces high-quality leaf litter, which decomposes fast. However, the species experiences a high sap-feeder (Aphididae) pest infestation throughout the year.

(2) Mix phylogenetically distant tree species (e.g. different families) to increase sapling growth in the first years.

We showed that the species identity of the neighbours played a minor role in determining the growth rate and pest and disease damage of saplings. Distantly related neighbours usually have different ecological traits and may show lower interspecific competition compared with close relatives or conspecifics (intraspecific competition) (Kunstler et al. 2016). Neighbours that grow fast can create a supporting microclimate for the growth of target saplings in the first years.

(3) Mix phylogenetically distant tree species to reduce pest and disease damage.

Besides supporting the target sapling growth in the first years, phylogenetically diverse neighbourhoods also reduce the risk of pest and disease infestation in target saplings. Therefore, we suggest to gather information on specific pests and diseases that might affect target tree species before planting. A careful selection of neighbour species should focus on selecting traits that are not preferred by the pests and diseases of the target tree species to reduce the spread of the risk.

(4) Plant forests with tree species that differ in traits to enhance arthropod diversity conservation.

We saw that even in the early stage, plantations of tree species that represent a broad range in traits will enable higher crown arthropod species diversity as different tree species support distinct arthropod communities. We expect that an even more complex arthropod community will develop during further forest development because of the development of a more complex and stratified canopy layer, which will provide diverse niches for different arthropods. In the context of arthropod diversity conservation, mixed plantations with broadleaved and coniferous species are highly recommended. Broadleaved trees generally have more associated arthropod species, but evergreen coniferous trees provide valuable habitat throughout the year.

(5) Admix tree species with high-quality litter to increase the decomposition rates in the early stages of litter decomposition.

High-quality leaf litter might help to increase the overall litter mixture decomposition rate. This is particularly important since the current forest management practices are based on species that produce commercially valuable timber, such as *Fagus*, *Pinus*, or *Quercus,* which produce low-quality litter. If plantations only contain these species, the poor leaf litter quality of these species may cause the absence of a burrowing earthworm community, which will slow down leaf litter decomposition and result in forest-floor buildup and soil acidification in the long term (De Schrijver et al. 2012). Mixing species with high-quality litter with these poor-quality litter species might help to increase litter decomposition rates and ensure nutrient availability to support long-term tree growth.

According to the results of this study, there are a few specific suggestions that can be made:

(1) Mix *Betula* with fast-growing, phylogenetically distant species, such as conifers.

The main problem with *Betula* seems to be related with the high pest infestation. To create associational resistance, *Betula* should have bigger and/or taller neighbour that reduce its apparency but still allow *Betula* leaves to receive light. Fast-growing conifers such as *Larix* trees generally have high growth rates and their crown and foliage structure will still allow light to penetrate into the canopy layer (Chapin et al. 2011). The high-quality litter of *Betula* might counter the effects of slowly-decomposing litter produced by conifers.

(2) Mix *Quercus* with *Fagus* and *Tilia*.

Mixing *Quercus* and *Fagus* can enhance the wood quality of *Quercus*, but the low-quality litter of these species can be a problem. By adding *Tilia* into the mixture, the overall decomposition rate will be enhanced since *Tilia* produces high-quality litter. *Tilia* trees also grew relatively fast and can produce shade for *Fagus* and create associational resistance for *Quercus*. *Quercus* is known for its high degrees of pest infestation.

7.5 Suggestions for further research

Based on our results, several recommendations can be made for future research. We saw the effects of species identity, neighbourhood diversity and composition in our experiments. As trees grow and start to interact more intensely, the local environment will definitely change. We expect that the diversity effect will become more pronounced as the stands age.

Continuing research on the ecosystem functions studied in this thesis is definitely needed to understand whether the effects of tree species identity, local neighbourhood diversity, and site will persist as the stands develop. The research also needs to be expanded to the broader network of experiments in TreeDivNet. Besides that, other response variables might be interesting to explore, such as:

(1) Litter decomposition using actual litters (i.e., dead, fallen leaves), litterbags with a finer mesh size or a microcosm

Studies using actual litter will give a better insight into the actual litter decomposition rates. A finer mesh will exclude the macro-decomposers such as earthworms, which will allow us to see the impact of these organisms on the litter decomposition rate. In a microcosm, an apparatus with a simplified analogue to the actual ecosystem (cf. Taylor et al. 1989, Salamanca et al. 1998, Barantal et al. 2011, Meyer III et al. 2013), the litter will not be compacted and thus have its actual volume and surface area.

(2) Soil arthropod community

Soil arthropods greatly assist in litter decomposition processes. It will be interesting to see whether the quality of litter will influence the abundance of certain decomposer arthropods or affect the soil arthropod community composition.

(3) Fungal infection in *Quercus*

Quercus (oak) is known for its economical importance in producing high-quality wood. In the past decades, *Quercus* forests in Europe have suffered from decline phenomena caused mainly by fungal infections (Führer 1998). Fungal infections such as mildew cause shoot dieback and foliage necrosis. During our damage assessment, the fungal infestation was really high. The high crown discolouration and branch and shoot damage of *Quercus* in Chapter 4 were probably caused by fungi. It would be interesting to see the relationships between fungal cover in the foliage and the actual crown damage. Specific research focusing on the effects of local neighbourhood diversity on mildew infection in *Quercus* at two FORBIO sites (Gedinne and Zedelgem) is currently being done by Mathias Dillen. Our colleagues of the FunDivEUROPE project have also published research focusing on fungal pathogen infestations (Hantsch et al. 2013, Nguyen et al. 2016) and *Quercus* (Castagneyrol et al. 2012, Alalouni et al. 2014)

(4) The provenance effect on growth and resistance to pests and diseases in *Quercus* (Zedelgem) and *Fagus* (Gedinne)

It will be interesting to see whether growth differs between different provenances and whether genotype diversity will create associational resistance to pests and diseases.

(5) Drought effects on growth and resistance to pests and diseases

Drought is a form of environmental stress that can decrease growth and increase the trees susceptibility to pests and diseases. It will be interesting to see the effects of drought stress on tree growth and the resistance to pests and diseases. Specific research focusing on the effects of drought on pest and disease damage at two FORBIO sites (Gedinne and Zedelgem) is currently being done by Mathias Dillen and Masudur Rahman.

(6) The effects of management (e.g., pruning/thinning) on growth

When a closed canopy is formed, trees will be in more direct competition for light. It will be interesting to see the effect of, for example, thinning on tree growth and crown plasticity.

(7) Growth affected by the growth of the neighbours

It would be interesting to see whether the growth of the neighbours affects the growth of target saplings, especially when resources start to be limited.

The consistent identity effect found in this thesis (Chapter 3-6) also revealed the importance of the trait selection in determining the species performances in delivering ecosystem functions. The trait values we used so far came from other experiments or available databases. Traits need to be measured *in situ* to better characterize the species in the three FORBIO sites since differences in the site conditions might influence the traits. Thus, for a species that grows in all sites, the intraspecific variation in trait values can be compared.

Appendix 7.1 Methods used to calculate variation partitioning between different explanatory variables

We used a multilevel analysis of variance, with parameters estimated using a Bayesian approach (Gelman et al. 2005, Hector et al. 2011). To perform the analysis, we used the probabilistic programming language *Stan* (Carpenter et al. 2014), called from the *RStan* package in R version 3.2.3 (R Core Team 2015). Posterior distributions were derived from 500 MCMC sampling iterations. Variance components were calculated as finite-population standard deviations with 95 and 68% credibility intervals (the Bayesian counterparts of confidence intervals (Gelman et al. 2005)). The importance of the explanatory variables was visualized using a graphical ANOVA table (shown in 7.1).

Table 7.1.1 List of explanatory variables used in the Bayesian multilevel modelling

explanatory variable	description	number of levels	levels
site	experimental sites	2	Gedinne, Zedelgem
diversity	number of species in the surrounding neighbourhood	12	0, 0.82, 0.94, 1, 1.22, 1.46, 1.60, 1.65, 1.83, 1.95, 2.75, 2.93
composition	all the possible combinations of species (mixtures and monocultures); partially captures tree identity and neighbour identity	38	*Acer* (A), *Betula* (B), *Fagus* (F), *Larix* (L), *Pinus* (P), *Pseudotsuga* (Ps), *Quercus* (Q), *Tilia* (T), AF, APs, BP, BQ, FL, FQ, FT, LP, LQ, PT, AFL, ALQ, APsQ, BFP, BFT, BQT, FLPs, FPsQ, FQP, PQT, AFLP, AFLQ, AFPsQ, ALPsQ, BFPQ, BFPT, BFQT, BPQT, FLPsQ, FPsQT

Table 7.1.2 List of response variables used in the multilevel anova

ecosystem function	variable	description
sapling growth	diameter increment	relative diameter increment between 2012-2014
	height increment	relative height increment between 2012-2014
	height : diameter ratio	height to diameter ratio in the year 2014
crown damage	branch and shoot damage	percentage of crown volume that consisted of dead branches and shoots
	defoliation	percentage foliage damage in the assessed tree crown compared with a reference tree
	discolouration	percentage of the crown that showed a colour different from the usual colour of the species
crown arthropods	herbivore abundance	number of herbivore arthropods
	total abundance	total number of arthropods
	order richness	number of arthropod orders

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Curriculum vitae

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Education

2009–2011	MSc in Environmental Biology, School of Life Sciences and Technology, Bandung Institute of Technology (ITB) - GPA 4.00/4.00
2003–2008	BSc in Biology, School of Life Sciences and Technology, Bandung Institute of Technology (ITB) - GPA 3.40/4.00

Professional experience on research

September 2011–present	PhD researcher at Scientific worker at Ghent University, Faculty of Bioscience Engineering, Department of Forest and Water Management, Forest and Nature Laboratory
2010 – 2011	Research assistant at collaborative program of ITB and and Islamic Development Bank on the program 'enhancement of global carbon sequestration from Indonesian tropical rain forest'
January - December 2010	Research assistant at School of Life Sciences and technology, ITB on the project 'Species availability and the performance of native tree species in mount Papandayan, West Java, Indonesia'
January - December 2009	Research assistant at School of Life Sciences and technology, ITB on the project 'Study of native tree species for reforestation with local community in mount Papandayan, West Java, Indonesia'
2009 - 2010	Research assistant at The Indonesian Institute of Sciences (LIPI) on the project 'Estimating carbon stock of mount Gede Pangrango National Park, Indonesia'

January - December 2009	Research assistant at ITB on the project 'Estimating carbon stock of Gayo Lues, Nanggroe Aceh Darussalam, Indonesia'
January - December 2009	Research assistant at School of Life Sciences and technology, ITB on the project 'Constructing web-based genetic resources database of Gowa, Sulawesi, Indonesia'
2008	Research assistant at West Java Environmental Organization Government Agency (BPLHD Jabar) on the project 'Estimation of marine quality status of West Java coastal area'
2007	Student Internship at world agroforestry center (ICRAF) Southeast Asia on the project 'Baseline study on farmer preferences in agroforestry system'

Professional experience on education

August 2009–February 2010	Coordinator assistant in the course 'Project ecology' at School of Life Sciences and Technology, ITB
August 2006–February 2009	Field and laboratory assistant in the course 'Project ecology' at School of Life Sciences and Technology, ITB
August 2006–February 2007	Laboratory assistant in the course 'Biostatistics' at Department of Mathematics, ITB
August 2005–February 2006	Field and laboratory assistant in the course 'General biology' at School of Life Sciences and Technology, ITB

Scientific publications

Publications in international journals with peer review cited in the Science Citation Index (IF: impact factor in 2014)

Ampoorter E, Federico S, Auge H, Baeten L, Berger S, Carrari E, Coppi A, Fotelli M, Kalliopi R, **Setiawan NN**, Vanhellemont M, Verheyen K (2016) Driving mechanism of overstorey-understorey diversity relationships in European forest. Perspectives in Plant Ecology Evolution and Systematics 19, 21-29, doi: 10.1016/j.ppees.2016.02.001 (IF 3.606)

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Verheyen V, Ceunen K, Ampoorter E, Baeten L, Bosman B, Branquart E, Carnol M, De Wandeler H, Grégoire J-C, Lhoir P, Muys B, **Setiawan NN**, Vanhellemont M, Ponette Q (2013) Assessment of the functional role of tree diversity: the multi-site FORBIO experiment. Plant Ecology and Evolution 146(1), 26-35, doi: 10.5091/plecevo.2013.803 (IF 0.986)

Publications in national journals with peer review

Sulistyawati E, Mashita N, **Setiawan NN**, Choesin DN, Suryana P (2012) Flowering and fruiting phenology of tree species in Mount Papandayan Nature Reserve, West Java, Indonesia. Tropical Life Sciences Research. 23, 81–95

MSc, BSc thesis, report

Setiawan NN (2011) Seed rain, seed germination, and seedling performance of native tree species on early reforestation stage at Mount Papandayan Nature Reserve, West Java. MSc thesis, Bandung Institute of Technology, Bandung, Indonesia.

Setiawan NN (2008) Vegetation structure and composition on reforested abandoned field at Mount Papandayan Nature Reserve, West Java. BSc thesis, Bandung Institute of Technology, Bandung, Indonesia.

Setiawan NN (2007) Baseline study on vegetable priority species, current practices, and gender role in Nanggung subdistrict agroforestry system. Internship report, Bandung Institute of Technology, Bandung, Indonesia.

Scientific activities

Participation in congresses, symposia or meetings

Participation with oral presentation

26 January 2015. Experimental assessment of early tree diversity effegcts on tree growth, litter decomposition, and herbivory: research design, FORBIO bi-annual meeting, Hechtel-Eksel, Belgium

28 March 2014. Assessment of pest and pathogen attack on trees in more or less diverse forest stands. Startersdag in het natuur en bosonderzoek, Brussels, Belgium

29 November 2013. Experimental assessment of early tree diversity effegcts on tree growth, litter decomposition, and herbivory: progress, FORBIO bi-annual meeting, Loppem, Belgium

16 December 2011. Litter-mixing effects on decomposition rates: the story of five tree species in a young tree diversity experiment, FORBIO bi-annual meeting, Brussels, Belgium

20-21 December 2010. Seed rain, seed germination, and seedling performance of native tree species on early reforestation period at Mount Papandayan, West Java. The First Joint Symposium: ITB-Universiti Sains Malaysia, Bandung, Indonesia

28-30 May 2008. Succession following reforestation on abandoned fields in Mount Papandayan, West Java. International Conference of Environmental Research and Technology: University Sains Malaysia, Penang, Malaysia

Participation with poster presentation

18-23 August 2013. Does tree diversity increase resistance against pest and disease attacks? INTECOL Congress: British Ecological Society, London, United Kingdom

9-12 November 2010. Seedling performance of five native tree species on early reforestation period at Mount Papandayan Nature Reserve. Abstract of poster presentation. International Conference of Environmental and Natural Resources: Mahidol University, Salaya, Thailand

Participation without presentation

27 March 2015. Startersdag in het natuur en bosonderzoek, Brussels, Belgium

29-31 January 2014. Annual FunDiv meeting, FunDiv Europe, Kopenhagen, Denmark

15 March 2013. Startersdag in het natuur en bosonderzoek, Brussels, Belgium

25 February – 1 March 2013. Annual FunDiv meeting, FunDiv Europe, Firenze, Italy

7 December 2012. Symposium of Entomology in Belgium 2012. The Royal Belgian Entomological Society, Royal Belgian Institute of Natural Sciences (KBIN), Brussel, Belgium

16-18 January 2012. Annual FunDiv meeting, FunDiv Europe, Vantaa, Finland

23-25 November 2010. International Conference on Mathematics and Natural Sciences, Bandung Institute of Technology (ITB), Bandung, Indonesia

Supervision of MSc thesis students

2014-2015	Ritchie Gobin. Effects of forest stand diversity on arthropod diversity. Supervisor: Prof. dr. ir. Jan Mertens and Prof. dr. ir. Kris Verheyen

Post-graduate courses

June 2014. FLAMES workshop ‘Graphics in R’, University of Antwerp, Antwerp, Belgium

March 2014. Impact & Research Communication Skills, Ghent University, Ghent, Belgium

September 2013. International Summer School on the functional significance of forest biodiversity, FunDiv Europe project, Bialowieza National Park, Poland

May-June 2013. Effective Graphic Display, Ghent University, Ghent, Belgium

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