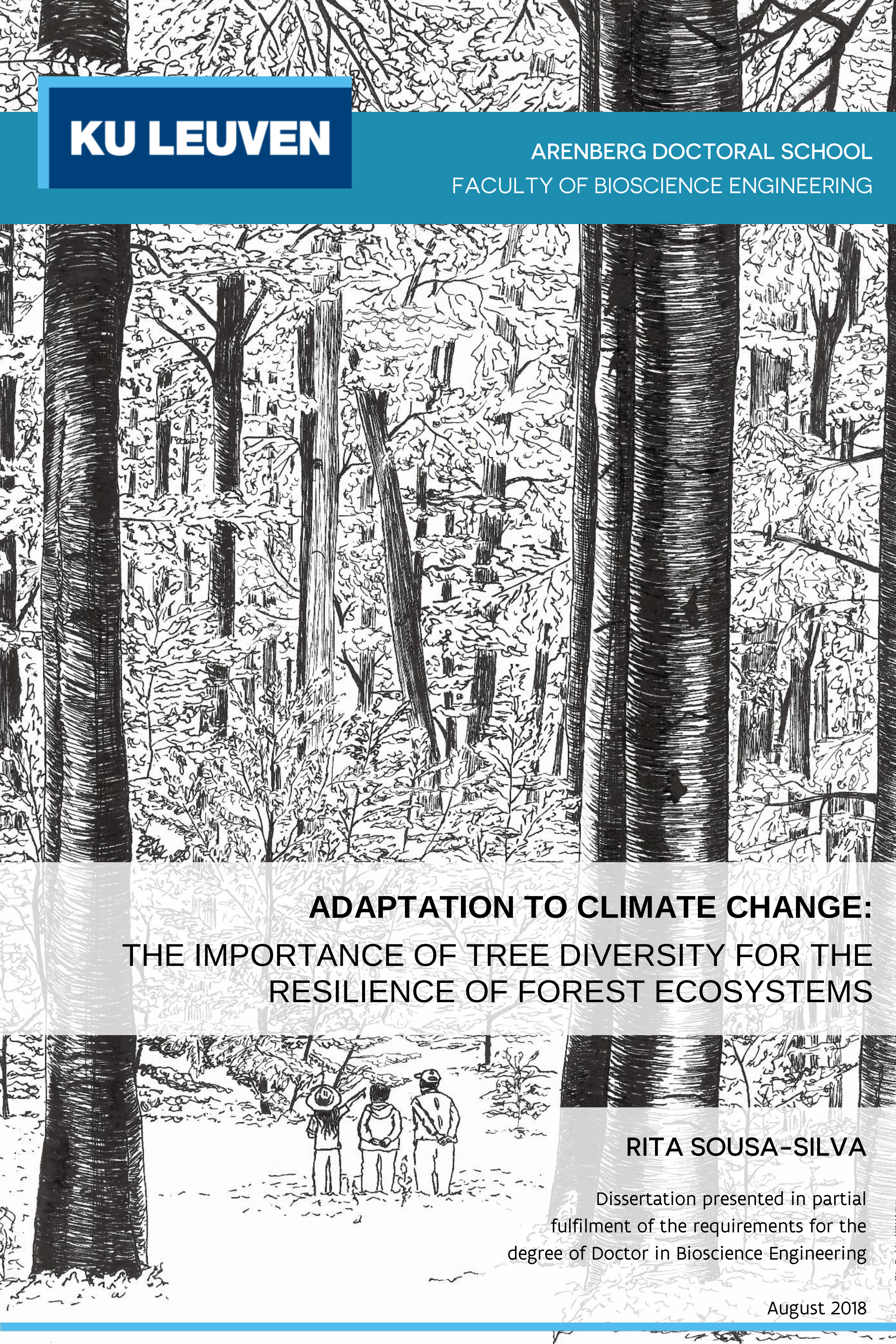

KU LEUVEN

ARENBERG DOCTORAL SCHOOL
FACULTY OF BIOSCIENCE ENGINEERING

ADAPTATION TO CLIMATE CHANGE:

THE IMPORTANCE OF TREE DIVERSITY FOR THE RESILIENCE OF FOREST ECOSYSTEMS

RITA SOUSA-SILVA

Dissertation presented in partial
fulfilment of the requirements for the
degree of Doctor in Bioscience Engineering

August 2018

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To be great, be whole: nothing that's you
Should you exaggerate or exclude.
In each thing, be all. Give all you are
In the least you ever do.
The whole moon, because it rides so high,
Is reflected in each pool.

Odes by Ricardo Reis (Fernando Pessoa)
Translated by Edouard Roditi

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This story started four years ago when I arrived in Leuven with a head full of dreams. I was ten miles from home and I knew no one here. But I was raised to believe that the world can be anything we want it to be, so no matter the circumstances, you always try your best and you never give up. Because that is what you do when you are chasing your dreams. Thank you mum and dad, you gave me roots to grow, and wings to fly. Your love and support, even at a distance, have made a world of a difference. Wherever my story takes me, I will always know the road that will lead me home again.

Home is where memories are created, friends always belong, and laughter never ends. And home then became Leuven. There is something special about this place – the people. Bie, Bjorn, Ellen, Elisa, Eric, Floris, Giuseppe, Hans, Jan, Jeroen, Joana, Koen, Koenraad, Michiel, Pieter, Sam, and so many others: thank you for all the laughs, tears and funny stories that we have shared. What a cracking place to work! Ine, thank you for all the amazing drawings you made. Tatiana, thank you for the family Saturday dinners and Sunday lunches (and the Mondays blues that came along with it). Astrid, what we started together, we will finish together! Thank you for your friendship and for the countless pep talks throughout these four years. And not forgetting your precious help during the finishing and the printing of the thesis. Thomas, thank you for the endless help, the random chats, the endless laughs, and the many great memories. I am sure that without your friendship this PhD would have been a much more difficult and surely less fun endeavor.

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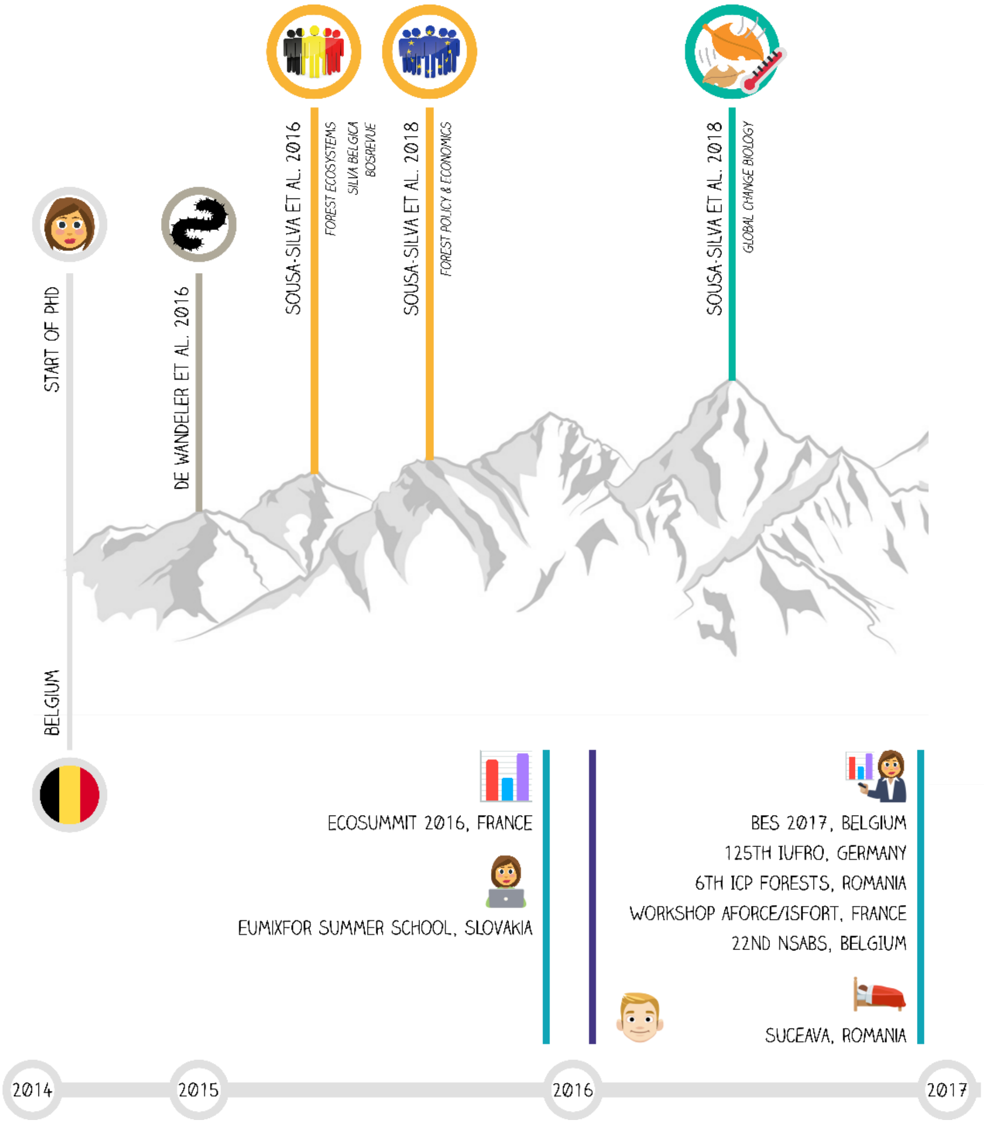
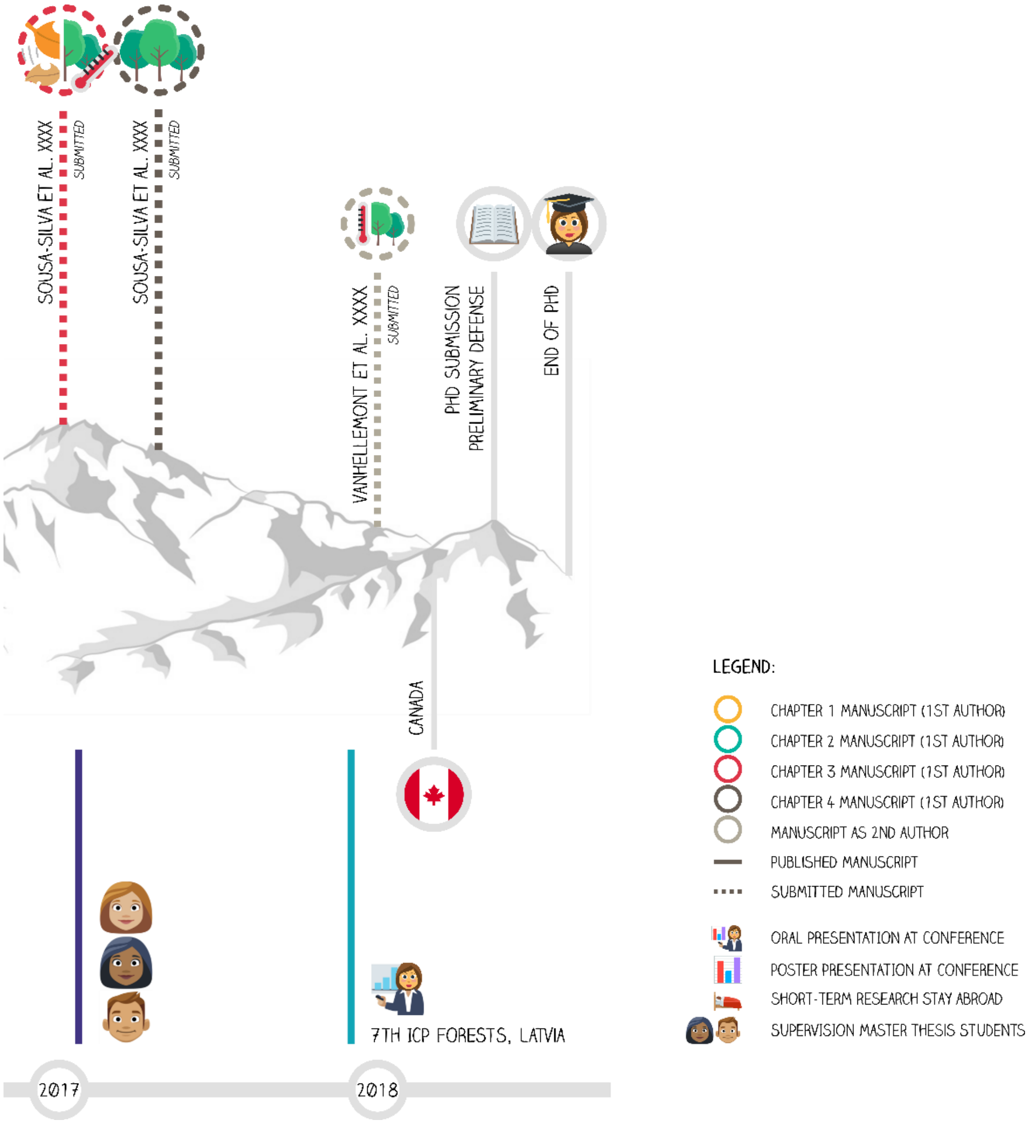
RITA

ROADMAP OF MY PHD

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ABBREVIATIONS

AIC	Akaike's Information Criterion
AICc	small-sample-size corrected version of AIC
BA	Basal Area at stand level
BAI	Basal Area Increment
D	Tjur's coefficient of discrimination
DBH	Diameter at Breast Height
DE	Dominance Effect
ICP Forests	International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests
IPCC	Intergovernmental Panel on Climate Change
N	Sample size
NE	Net diversity Effect
NFI	National Forest Inventory
R^2c	conditional R^2, which is the proportion of the variance explained by both fixed and random effects
R^2m	marginal R^2, which is the proportion of the total variance explained by the fixed effects
RMSE	Root Mean Square Error
SPEI	Standardized Precipitation Evapotranspiration Index
SR	Species Richness
TDC	Trait-Dependent Complementarity effect
TIC	Trait-Independent Complementarity effect
VIF	Variance Inflation Factor

SUMMARY

Resilience is increasingly becoming a guiding principle for forest management, commonly used to describe the ability of a forest to maintain its fundamental structure and functioning despite altered by disturbances. Biotic and abiotic disturbances are an intrinsic element of forest ecosystems. However, climate change is creating substantial new challenges. Forest resilience is closely tied to tree species diversity, anchored in the notion that a wide range of species, which respond in different ways to changes, confers greater ecological stability. Droughts, in particular, are widely recognized as a major threat to forests. Recent drought events have been related to increased defoliation in European forests, as well as to significant reductions in gross primary production. Consequently, with droughts expected to become increasingly more frequent and severe in many regions, including in Belgium, there is a dire need to enhance our understanding of how forests respond to drought and how species dynamics change with major shifts in climate, so as to develop adaptive management strategies to increase the resilience of forest ecosystems.

In this research, we addressed this knowledge gap by providing a comprehensive assessment of drought impacts on forest health and forest growth, as well as of the effects of tree diversity on the resilience of forests to disturbances. To do so, we started by analyzing the temporal variation in the defoliation of *Fagus sylvatica*, *Quercus petraea* and *Quercus robur* trees, using crown defoliation as a proxy for forest health. Next, we investigated the growth dynamics of these species during recent drought events, and across a gradient of site conditions. Special attention was paid to differences between trees growing in mixed and pure stands. This study builds on data from existing forest monitoring networks in Belgium, under ICP Forests programme, and from forest inventory plots in Flanders and Wallonia (Belgium).

To overcome the well-documented mismatch between research and management, in a first step, we conducted a survey with the objective of identifying the extent to which specific adaptation measures to climate change are being implemented and, from the perspective of forest

managers, which impediments limit their ability to prepare and respond to these changes. Our analysis highlighted a lack of adaptation responses so far, despite relatively high awareness of climate change as an issue in forest management. We suggest that providing clear, but detailed, and accessible information on how to manage forests as climate changes is likely to be the most effective strategy to mainstream adaptation.

In a second step, we demonstrate that the crown condition of the three species has declined appreciably over the past decades, in parallel with increasing water stress. This change has triggered a regime shift from healthy monocultures to resilient tree species mixtures. The observed tipping point in the relationship between species richness and the health of forests, suggesting that species interactions shifted from competition to facilitation, though implicit in the literature, has never been previously reported from real ecosystems.

Finally, the well documented, but not yet fully understood, relationship between species diversity and forest productivity was investigated. We describe individual tree and stand level growth rates, and examine how species richness influences tree growth response to drought. On the one hand, a strong and clear link emerged between a decline in tree productivity and the occurrence of drought events, associated with longer recovery times. On the other hand, we found that trees growing in mixtures have greater capacity to recover after drought events than trees growing in monocultures. Similarly, both *F. sylvatica* and *Quercus* spp. trees grew better in mixed stands than in pure stands. However, when we calculated the effect of species mixing on the productivity of each species at stand level, we did not confirm the previous finding. Here, using data from national forest inventories, we found that the positive effect of species mixing on the growth of *F. sylvatica* was counterbalanced by an underyielding of *Quercus* spp., and that the effect was not strong enough to significantly increase overall stand productivity.

Taken together, our results suggest that mixed species forests can better withstand drought stress, which confirms their greater resilience to projected changes in climate extremes and disturbance regimes. Managing forests to retain or increase diversity has the additional potential benefit to provide managers with more options for future stand development.

SAMENVATTING

Stabiliteit in bosecosystemen wordt meer en meer gezien als een hoeksteen van goed bosbeheer. Stabiliteit is de capaciteit van een bos om te blijven functioneren en zijn oorspronkelijke structuur te behouden ondanks verstoringen. Biotische en abiotische verstoringen zijn inherent aan bosecosystemen. Daarenboven zorgt klimaatsverandering voor bijkomende verstoringen. De stabiliteit van bosecosystemen hangt nauw samen met boomsoortendiversiteit aangezien verschillende soorten anders reageren op verstoringen wat resulteert in een grotere stabiliteit van soortenrijke bosecosystemen. Vooral droogte vormt een bedreiging voor bosecosystemen. Zo werden recente droogteperiodes gerelateerd aan een stijging in bladverlies en een daling in houtproductie in Europese bossen. Men voorspelt dat droogteperiodes in de toekomst meer zullen voorkomen en intenser zullen zijn, ook in België. Het is dus cruciaal dat bosbeheer zodanig is dat de stabiliteit van bosecosystemen verhoogd wordt. Om dit te kunnen doen moeten we onze kennis over de reactie van bosecosystemen op droogte verbreden en moeten we meer inzicht krijgen in hoe het klimaat de interacties tussen boomsoorten beïnvloedt.

In deze doctoraatsthesis bestuderen we de impact van droogte op de gezondheid en de groei van bossen, en het effect van boomsoortendiversiteit op de weerstand tegen veranderingen. Hiervoor bestuderen we eerst de temporele variatie in bladval van beuken en eiken. Daarna onderzoeken we het effect van recente droogteperiodes op de groei van beuk en eik langsheen een gradiënt van groeiplaatscondities. Hierbij werd ook het effect van boomsoortendiversiteit bekeken. Voor deze studie werd gebruik gemaakt van data van bosmonitoringnetwerken in België zoals het ICP Forests programme en de bosinventarisatieplots gelegen in Vlaanderen en Wallonië (België).

In een eerste stap werd een enquête opgesteld met als doel de klimaatadaptatiemaatregelen die bosbeheerders momenteel toepassen in kaart te brengen en te identificeren welke informatie bosbeheerders missen om hun bosbeheer adequaat aan te passen aan de voorspelde veranderingen. Onze resultaten tonen aan dat bosbeheerders nog weinig

klimaatadaptatiemaatregelen hebben doorgevoerd ondanks het besef dat dit nodig is. We besluiten dat er een nood is aan duidelijke, toegankelijke en gedetailleerde informatie omtrent klimaatadaptatiemaatregelen voor bosbeheer.

In een tweede stap tonen we aan dat de boomkruin gezondheidsconditie, welke geëvalueerd werd in termen van bladval, van beuken en eiken bomen achteruit is gegaan in de laatste decennia. Dit kan gerelateerd worden aan een stijging in waterstress in de laatste decennia. Deze stijging in waterstress veroorzaakt een overgang van gezonde monoculturen naar stabiele gemengde bossen. Het geobserveerde omslagpunt in de relatie tussen boomsoortdiversiteit en de gezondheidstoestand van bossen suggereert dat de interacties tussen soorten geëvolueerd is van competitie naar positieve soorteninteracties (i.e., facilitatie). Deze observatie is meermaals beschreven in literatuur maar werd tot nog toe niet geïllustreerd met observaties in bestaande ecosystemen.

In een laatste stap werd de, welgekende maar nog niet helemaal begrepen, relatie tussen boomsoortendiversiteit en productiviteit onderzocht. De groei van individuele bomen en bestanden, en het effect van boomsoortendiversiteit op de reactie op droogte werd bestudeerd. Een sterke link tussen droogte en boomgroei werd geobserveerd. Een sterke daling in groei gevolgd door een langere periode van groeiherstel werd waargenomen in periodes van droogte. Daarnaast observeerden we dat boomsoortendiversiteit zorgt voor een sneller herstel van de door droogte geïnduceerde daling in groei. Daarenboven werd een hogere groei geobserveerd voor beuken en eiken die in gemengde bestanden groeien. Wanner we echter het effect van boomsoortendiversiteit op bestandsniveau bestuderen werd er geen hogere groei waargenomen in boomsoortrijke bestanden. Op bestandsniveau wordt het positieve effect van boomsoortendiversiteit op de groei uitgebalanceerd door de underyielding van eik.

We besluiten dat gemengde bossen beter bestand zijn tegen droogte en dat ze dus meer weerstand bieden tegen veranderingen in het klimaat en andere verstoringen. Het diversifiëren van bosbestanden zorgt voor een verhoging van de bosstabiliteit en geeft bosbeheerders meer mogelijkheden voor toekomstige bestandsontwikkelingen.

CHAPTER 1

INTRODUCTION

1.1. THE IMPORTANCE OF FORESTS

> *"Nature is not fragile…*
> *what is fragile are the ecosystems services on which humans depend."*
> ***Simon Levin***

Globally, forests cover nearly one third of the land area and contain more than 75% of terrestrial biodiversity (FAO, 2016). In Europe, forests cover approximately 35% of the terrestrial surface, and their spatial extent has increased over the past 25 years as a result of land abandonment following growing urbanization (Mauri et al., 2017). The understanding that forests are more than trees has been revived in recent decades (Brockerhoff et al., 2017; Gamfeldt et al., 2013; Mori et al., 2017; Thompson et al., 2011). Forests provide food, fuel, timber, and other products for commercial and subsistence use. In forests, microorganisms, soils and vegetative cover interact to purify air and water, regulate the climate, recycle nutrients, and sequester carbon (Kringer, 2001). The importance of forest ecosystems to human well-being cannot, therefore, be underestimated. Without these and many other ecosystem goods and services, life as we know it would not exist.

The ecosystem services concept was introduced in the 1990s by ecological economists as a metaphor of nature as a stock of capital that can sustain a limited flow of ecosystem services (Costanza and Daly, 1992; Norgaard, 2010). This metaphor, however, would soon become a central issue in ecology (Carpenter *et al.*, 2009; but see Gómez-Baggethun (2010) for a critical discussion of ecosystem services valuation). Ecosystem services may, now and then, be seen as a concept that can help redefine perspectives on human–nature relationships towards a more holistic view that highlights the importance of the environment (including forests) in sustaining human livelihoods. Among the different definitions of ecosystem services and interpretations that exist, the Common International Classification for Ecosystem Services (CICES) has become an important frame of reference for classifying ecosystem services that depend on biodiversity (http://www.cices.eu; Haines-Young & Potschin, 2013; Potschin & Haines-Young, 2016). The CICES framework groups ecosystem services into three categories. These include *provisioning services* such as food, water, fuel, and timber; *regulating and maintenance services* including climate, flood, and erosion control, photosynthesis, and nutrient cycling; and *cultural services* that provide recreational, aesthetic, and spiritual benefits (Figure 1.1). However, the loss of biodiversity, alongside climate change, may seriously jeopardize the functioning of forest ecosystems, and consequently the future capability of forests to provide these services (Aerts and Honnay, 2011; Mooney et al., 2009).

Figure 1.1 Ecosystem services provided by forests ecosystems. *Ecological functions and human wellbeing depend on ecosystem services. These include provisional (fiber, food, fuel), regulating and maintenance (flood control, carbon sequestration, air purification; soil formation, photosynthesis, nutrient cycling), and cultural services (aesthetic, spiritual, recreational).*

1.1.1. BIODIVERSITY AND ECOSYSTEM FUNCTIONING

Forests and biodiversity are strongly interlaced. On the one hand, biodiversity depends to a large extent on the health and vitality of forest ecosystems. On the other hand, a reduction in forest biodiversity may translate to losses in forest productivity and its sustainability (Brockerhoff et al., 2017). Moreover, there is a broad consensus that biodiversity promotes the functionality of ecosystems, including the efficiency by which ecological communities capture limited resources, produce biomass, recycle and retain biologically essential nutrients (Cardinale et al., 2012; Hooper et al., 2005).

Increases in ecosystem functioning with increasing diversity mainly arise from two mechanisms: sampling or selection effects and complementarity effects (Loreau and Hector, 2001). A selection effect takes place when species with high productivity are more likely to be present with increasing species diversity, and thus dominate the mixtures through interspecific competition. Complementarity has been proposed as the mechanism through which species use different resources, or the same resources but at different times or different points in space, therefore leading to a better and more extensive use of available resources and an on average higher species biomass production (Hooper et al., 2005; Messier et al., 2013) (for an illustration, see Figure 1.2). Importantly, selection and complementarity effects are not necessarily mutually exclusive (Fargione et al., 2007). These processes can often occur simultaneously, or sequentially, possibly cancelling each other, and it can be difficult to untangle them.

Selection effects are often described with regard to their positive effect on plant growth or survival. In this context, dominant species are those that are most abundant or have the highest biomass (Allan et al., 2011). Furthermore, selection effects are often interpreted in terms of competitive dominance. For example, diverse communities are more likely to contain superior competitors that reduce resources and prevent the establishment of invading species (Jiang et al., 2008).

Conversely, negative selection effects are potentially common for non-biomass functions, for which species competitive ability may often be a poor indictor of its functional impact (Jiang et al., 2008). In this sense, negative selection effects are likely to occur where species with low contributions to ecosystem functioning dominate the mixtures.

Niche partitioning has often been cited as a mechanism to reduce competition and achieve a stable coexistence of multiple species. In forests, this is often said to result from complementary crown architectures and contrasting light requirements (Jucker et al., 2014b; Williams et al., 2017). This is illustrated, for instance, in mixtures of *Fagus sylvatica* and *Picea abies*. *Fagus sylvatica* is a relatively slow-growing, wide-crowned and more laterally expanding species, whereas *P. abies* is a fast-growing, slim-crowned and vertically oriented species (Pretzsch and Schütze, 2005). The mixture of these two species may consequently increase the efficiency of light use due to reduced shading (Bayer et al., 2013). The complementary use of resources can also occur simultaneously in space and time. For example, in early spring, more light can penetrate through the canopy and shorten the dormant period of *P. abies*, thus extending its growing period which is per se longer than that of *F. sylvatica* (Pretzsch, 2014).

Facilitation occurs when one species benefits another species by increasing the availability of resources, such as soil nutrients and water, or by ameliorating microclimatic conditions, such as air temperature and soil moisture (Forrester and Bauhus, 2016). Consequently, facilitation may favor the growth and survival of trees in mixtures over the negative effects caused by their competition for limiting resources (Callaway et al., 2002). In forests, symbiotic nitrogen fixation (Forrester et al., 2006) and hydraulic lift (H. Pretzsch et al., 2013) are among the best examples of facilitative processes shaping species coexistence. For example, facilitation of *F. sylvatica* by hydraulic lift of water by *Quercus petraea* is frequently reported in mixtures of these species (Jonard et al., 2011; Zapater et al., 2011). Hydraulic lift is the passive movement of water from a moist subsoil to a dry topsoil using plant root systems as a conduit (Caldwell et al., 1998;

Dawson, 1993). The term 'hydraulic lift' was originally coined by Richards and Caldwell (1987) to describe this phenomenon since the direction of movement of water is typically upward towards the drier and shallower soil layer. This transfer is driven by root and soil water potential gradients, from the least negative water potentials (usually the deepest layers) to the most negative ones (usually the shallowest layers). Water released from roots at night (when atmospheric demand is low and transpiration ceases) into drier soil layers near the surface is resorbed the following day when transpiration demand exceeds water uptake. Hydraulic lift also involves a reverse water flow in the fine roots located in soils with the most negative water potential and is beneficial to the plant transporting the water, but also to the neighboring plants (Horton and Hart, 1998). Species benefit from this increased water availability both directly, as their water supply increases, and indirectly, as higher soil moisture often increases nutrient availability (Horton and Hart, 1998).

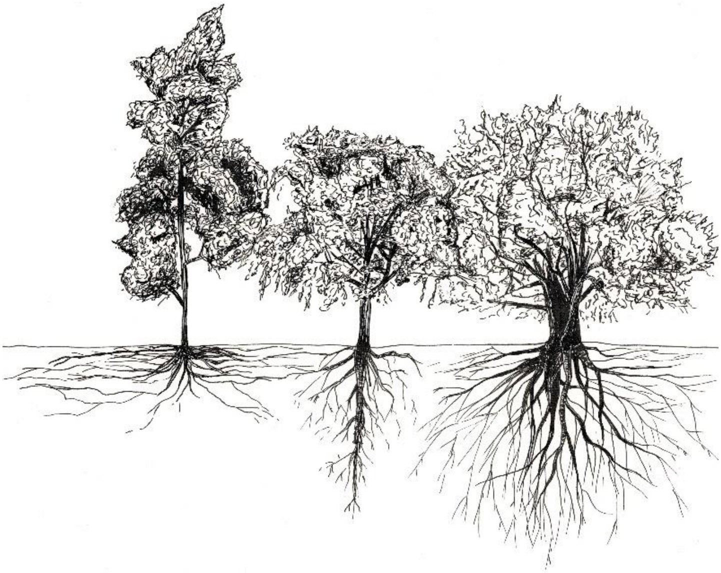

Figure 1.2 Illustration of potential differences between species in terms of crown architecture and root distribution. *For illustrative purposes only, not to scale. It has been hypothesized that ecosystem functioning might increase with diversity because of a better use of resources (Loreau and Hector, 2001). Complementary crown shapes may increase canopy space filling leading to an increase in light interception and use (e.g. Williams et al., 2017). Complementarity in the use of below-ground resources may be achieved by e.g. horizontal and vertical stratification of the root systems of co-occurring species (e.g. Brassard et al., 2013).*

1.1.2. THE EFFECT OF FOREST DIVERSITY ON TREE PRODUCTIVITY AND RESILIENCE

How species richness and forests productivity are interrelated is one of the most studied subjects in ecology (Grace et al., 2016; Willig, 2011). Furthermore, in recent decades, the need to understand this relationship has become increasingly important in response to a growing body of evidence suggesting that the functioning of ecosystems may be considerably impaired by declines in species richness (Liang et al., 2016a). Despite extensive debate (Fraser et al., 2015), fueled in part by insufficient ecosystem-wide evidence and because biodiversity and productivity are jointly controlled by a complex network of processes (Grace et al., 2016), recent studies have shown a consistent positive effect of species richness on tree productivity across forest ecosystems worldwide (Liang et al., 2016a, 2016b; Paquette and Messier, 2011). Species-rich communities are more likely to include a particular combination of species that are complementary (Hooper et al., 2005). Thereby, the accumulating effects of complementarity of resource acquisition and use and of ecosystem feedback effects, over time, stand as a compelling explanation for the positive pattern documented across forest ecosystems worldwide (Reich et al., 2012). Accordingly, more diverse communities, that may appear functionally redundant during early years, are more likely to have higher functioning over time due to turnover in complementary dominant species (Allan et al., 2011).

In addition to increasing productivity, biodiversity also contributes to ecosystem resilience (Folke et al., 2004; Thompson et al., 2009). **Resilience** is a key concept in ecology. It describes the capacity of an ecosystem to persist and maintain its state and functions in the face of disturbance (Ingrisch and Bahn, 2018). A resilient ecosystem is able to minimize the impact of a disturbance and to recover from the impact. The concept of resilience is therefore tightly related to the concept of **resistance** (capacity of a forest to withstand minor disturbances over time) and **recovery** (capacity of a forest to return to its previous state after a disturbance) (Figure 1.3).

Biodiversity can influence the resilience of ecosystems at multiple scales, from genetic to landscape levels (Thompson et al., 2009). For instance, species-rich communities are more likely to contain species that confer resilience to disturbances because as a community accumulates species, there is a higher chance of one of them having traits that enable them to adapt to a changing environment (Oliver et al., 2015). That is, certain species exhibit similar or identical features and manifest asynchronous responses to environmental changes (i.e., ecological redundancy), which helps maintain system stability during disturbance (Elmqvist et al., 2003; Walker, 1992).

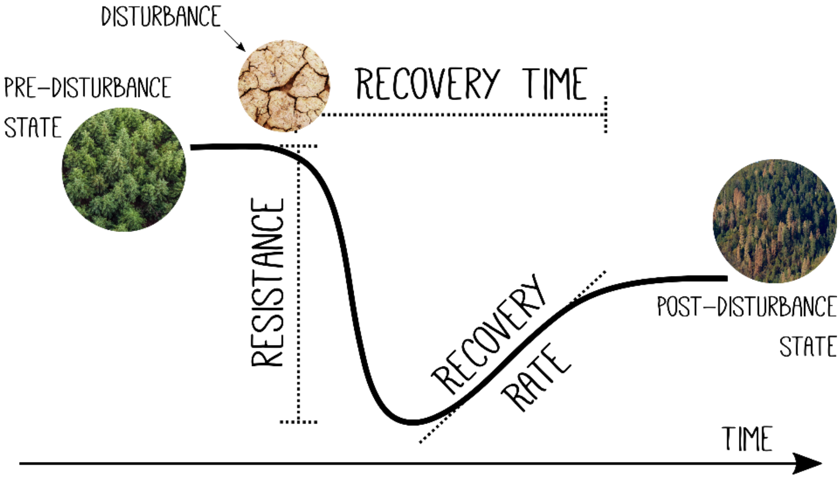

Figure 1.3 Main components of resilience. *Resilience is directly related to both resistance and recovery. The higher the resistance (thus lower disturbance impact), the greater the resilience. In similar fashion, the higher the recovery rate (thus shorter recovery time), the greater the resilience. Adapted from Seddon et al. (2017).*

1.2. THE CLIMATE CHANGE CHALLENGE

"When something is important enough,
you do it even if the odds are not in your favor."

Elon Musk

Climate has always been changing. Geologic evidence shows that Earth's climate has changed regularly over millions of years, likely the result of long-term solar cycles, volcanic eruptions, and sea-surface temperature patterns (Bond et al., 1997; Schurer et al., 2013). However, the current warming trend is particularly significant in that it is proceeding at a rate that is unprecedented over decades to millennia, and that is the result of human activity (IPCC, 2013).

The issue of climate change was first noted by the media in the 1930s (Bazerman, 2006; Boykoff and Roberts, 2007) following a prolonged warm period, which lasted until the end of the 1960s. By the 1980s, as the science of climate change developed, media coverage has increased as well. One of the key events contributing to the rise in coverage was the testimony of the NASA scientist James Hansen to the U.S. Congress in the summer of 1988 (Boykoff and Roberts, 2007). Hansen, a leading expert on climate change, testified that it was 'time to stop waffling' about climate change and that he was '99 percent certain' that warmer temperatures were caused by the burning of fossil fuels and not solely a result of natural variation (Shabecoff, 1988). This widely televised testimony served to generate substantial media coverage, and concomitant with an anomalously warm and dry summer throughout North America, was thought to sensitize many to the issue of climate change (Boykoff and Roberts, 2007). A similar association was observed in Europe, after the heatwave of 2003, which killed more than 70,000 people, and caused more than €13 billion in damage to agriculture and forestry (De Bono et al., 2004).

Ever since then, the IPCC (2014a) has made clear that climate change is accelerating, that changes will continue, and that it poses widespread and serious risks. There will be fewer extreme cold days and increasingly frequent extremely warm days. Extreme precipitation events are also projected to increase in frequency, resulting in more floods (Milly et al., 2002), but also more and longer periods without rainfall, increasing the risk of drought (Dai, 2013).

1.2.1. CLIMATE CHANGE AND FOREST DISTURBANCES

Climate has always provoked changes in forests (Iverson et al., 2014). Disturbances, such as fires and insect outbreaks, are an integral part of forest ecosystem dynamics, and they can affect the structure and function of ecosystems (Figure 1.4). Changes in temperature and precipitation can alter the frequency, intensity, duration, and timing of such disturbances (Dale et al., 2001; Seidl et al., 2017). Moreover, they have the potential to strongly impact the ability of forests to provide ecosystem services to society (Seidl et al., 2017).

Future climate conditions are predicted to further increase the frequency and severity of disturbances, and can dramatically alter the susceptibility of forests to many other disturbances. For instance, when trees are stressed, e.g., because of drought, they may be more susceptible to damage caused by insects and diseases (Anderegg et al., 2015a; Williams et al., 2013).

Natural disturbances having the greatest impact on forests include fire, drought, windstorms, snow and ice storms, insect and pathogen outbreaks (Seidl et al., 2017). Each disturbance affects forests differently. But evidence of recent declines in forest productivity and increases in tree mortality have generally been attributed to water stress at many sites globally (Carnicer et al., 2011; Peng et al., 2011; Phillips et al., 2009; van Mantgem et al., 2009). **Droughts** occur naturally in almost all forest ecosystems. However, projections of future droughts bear a significant increase in the likelihood of drier conditions than that the dominant trees in current forests have adapted to endure (Choat et al., 2012; McDowell and Allen, 2015). The major causes of productivity loss and tree mortality during drought are hydraulic failure and carbon starvation (Figure 1.5) (McDowell et al., 2008). Drought stress induces xylem failure via gas embolism (cavitation) in the water transport system, which reduces the ability of trees to supply water to leaves for photosynthetic gas exchange and can ultimately result in desiccation and mortality (Choat et al., 2012). In contrast, carbon starvation results from avoidance of hydraulic failure through stomatal closure, causing sustained negative carbon balance (McDowell et al., 2008; Sevanto et al., 2014). In addition, warmer droughts facilitate range expansion, growth acceleration and greater tree-infestation success in tree pests such as bark beetles, thereby amplifying risks of tree mortality (Allen et al., 2010; McDowell and Allen, 2015). This further exacerbates risks to ecosystem services, including the loss of carbon currently stored in forests, and associated atmospheric feedbacks.

Figure 1.4 Forest disturbance agents. *Major natural disturbance agents affecting forests, including abiotic (fire, snow and ice, wind and drought) and biotic (insects and pathogens) agents.*

Drought effects are apparent after a long period with a shortage of precipitation, making it difficult to pinpoint the moment when a drought starts and ends and also to quantify its duration, magnitude, and spatial extent (Vicente-Serrano et al., 2010). Therefore, the quantification of drought impacts is usually done by the so-called drought indices, which are proxies based on climatic parameters and assumed to adequately quantify the degree of drought hazard exerted on different types of systems (Vicente-Serrano et al., 2012). Several indices have been proposed to capture the drought impacts. These include the Palmer Drought Severity Index (PDSI,), the Standardized Precipitation Index (SPI), the Standardized Precipitation Evapotranspiration Index (SPEI) and others. In this study, the SPEI was used to assess the frequency (total number of drought events, defined as SPEI ≤ -1) and severity of drought (cumulative water deficiency) after 1980 in Belgium. The SPEI is based on precipitation and temperature data, and it has the advantage of combining its multi-scalar character with the ability to include the effects of temperature variability on drought assessment. First, a climatic water balance is used to calculate the difference between monthly (or weekly) precipitation and potential evapotranspiration. These values represent either a water surplus or deficit for a given month (or week) and are then aggregated over a specific timescale (e.g., 1-, 6-, 12-, and 24-month periods). After aggregation, values are then normalized according to a log-logistic distribution. The resulting standardized value is the SPEI metric, with a mean of zero and standard deviation of unity, where negative values indicate drier conditions. The procedure to calculate the index is detailed in Vicente-Serrano et al. (2010).

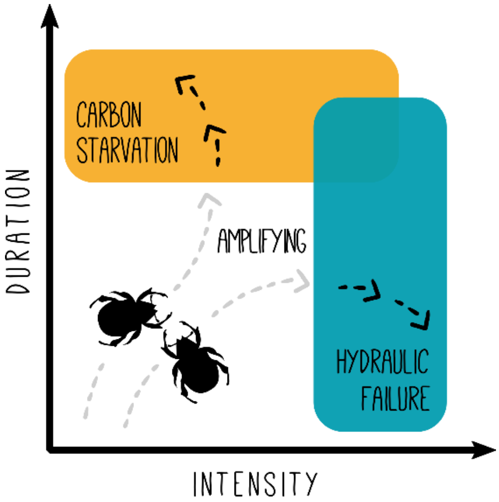

Figure 1.5 Mechanisms of drought-related mortality. *Graphical relationship between the length of drought (duration) and the relative decrease in water availability (intensity). Carbon starvation is hypothesized to occur if drought lasts long enough to reduce photosynthesis and hence the amount of available carbon is less than required for maintenance of metabolism. Hydraulic failure is hypothesized to occur when vulnerability thresholds are exceeded during severe drought leading to the formation of embolisms, xylem damage and desiccation before carbon starvation occurs. Biotic agents, such as insects and pathogens, can amplify or be amplified by these mechanisms. Adapted from McDowell et al. (2008).*

1.2.2. INTEGRATING ADAPTATION IN FOREST MANAGEMENT

Climate change is a challenge for forestry because of the direct and indirect impacts on forests and the long time span between management decisions and achieving desired results (Yousefpour et al., 2017). Forests established today will have to cope with changing climate conditions over the next several decades (Lindner et al., 2010). Consequently, the uncertainties about future climate and forest vulnerability to climate-driven risks mean there is a need to develop flexible and diversified approaches to adaptation.

The IPCC (2014a) defines adaptation as an '*adjustment in natural or human systems in response to actual or expected climatic changes or their effects, which can be taken to reduce the impact of a particular risk or exploit its beneficial opportunities*'. As put forth by Schoene and Bernier (2012), adaptation implies change. In general, these adjustments can be grouped into three categories based on adaptation objectives: passive adaptation, reactive adaptation and planned adaptation (Bolte et al., 2009). Only the last two strategies require active transformation of forest, e.g., by replacing tree species sensitive to climate change with tolerant species. Passive adaptation rests upon spontaneous adaptation processes, i.e., natural succession and species migration, by considerably minimizing the input efforts. However, unfortunately, most current management belongs to the first, or at best to the second category. The most likely reasons for the lack of adaptive responses are the uncertainties inherent to climate and forest dynamics, but also insufficient information or information of poor quality, e.g., about the adaptability of tree species and provenances to future climate conditions (Blennow et al., 2014; Bolte et al., 2009). Consequently, behavioral decision research started to study how forest owners and forest mangers relate to new knowledge, how they form and change perceptions, and how this affects their decision-making behavior (Yousefpour et al., 2017). Studies investigating this are even more important given that fifty one percent of the forest area in Europe is privately owned (Forest Europe et al., 2015). For example, in a recent publication, Sousa-Silva *et al.* (2018a) revealed a strong continent-wide climate change awareness. Yet there is little evidence of the adoption of adaptation strategies.

1.3. FOREST INVENTORIES AND FOREST MONITORING

"If I have seen further than others,
it is by standing upon the shoulders of giants."

Isaac Newton

In Europe, forest monitoring – in the sense of periodic and continuous assessment of forest information in the field – rests largely on two pillars: national forest inventories and ICP Forests monitoring network (Lorenz and Fischer, 2013).

Historically, forest inventories have focused on assessing the area, the species composition, and the growing stock of forests. Sampling schemes frequently adopted in forest inventories consist of a finite number of sampling units (composed of circular concentric plots), which are randomly selected according to a spatial sampling design as grid points that cover the study area. Sample plots are established with centers at each selected point, and a range of attributes are recorded for the trees included in the plots (Bauhus et al., 2017b; Corona et al., 2011). Mandated periodic surveys are typically conducted every five to ten years, providing the basis for measuring changes in forest condition and satisfying information needs to support forest management plans (Corona et al., 2011; Tomppo et al., 2010). More recently, however, forest inventories have expanded their scope to include information on biodiversity, forest health and vitality, and carbon content (Corona et al., 2011).

Studies on mixed forests can benefit greatly from making use of forest inventory data. The main strength of these datasets is their representativeness (Bauhus et al., 2017b). They often consist of a large number of permanent plots distributed across multiple forest types and large environmental gradients, and because they are conducted in existing mature forests, they can assist in putting results obtained from artificial communities, such as common garden experiments, into perspective (Bauhus et al., 2017b; Vilà et al., 2005). Nevertheless, they often lack orthogonality (Bauhus et al., 2017b), which implies that results must be interpreted carefully. Variables such as edaphic and climatic conditions, stand age, and management practices can influence the diversity–productivity relationship and need to be considered when analyzing inventory data (Vilà et al., 2005). Otherwise cause-and-effect relationships cannot be disentangled from observational data due to unavoidable biological correlations. Importantly, however, when the potential confounding factors are accounted for, forest productivity has been shown to increase with high tree species richness (Paquette and Messier, 2011; Toïgo et al., 2015; Vallet and Pérot, 2011).

The ICP Forests (International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests), one of the largest forest monitoring programs in the world, was established in 1985 with the primary aim of assessing the effects of air pollution on forests. For this purpose, ICP Forests developed a harmonized monitoring approach comprising two complementary monitoring levels (Level I and Level II), which provide a systematic overview of the spatial and temporal variation of forest condition across Europe, on an annual basis, and with regard to anthropogenic and environmental stresses. Data from ICP Forests were further proved to be suitable to answer questions about the impacts of climate change on forest ecosystems as well as to describe the geographical extent and development of damage to forests across Europe (Lorenz and Fischer, 2013). The complete methods of forest monitoring by ICP Forests are described in detail in the ICP Forests Manual (2016).

In the face of rapid environmental change, long-term large-scale forest monitoring embodies a unique opportunity to investigate the role of abiotic and biotic factors on the development of forest conditions over time, and are therefore a powerful tool to inform adaptive management (Ferretti, 1997; Ferretti et al., 2014). The plot network of ICP Forests is a prime example of this, permitting the study of the relationships between forest health, climate change, and biodiversity.

If answering questions about the relationships between species and their environment requires complex data, e.g., multiple predictors for a response variable of interest; these data in turn requires complex mathematical models to adequately represent the system under study. Mixed-effects models have become increasingly popular for fitting models to structured data (Schielzeth and Nakagawa, 2013), as is the case with permanent sample plots data. In permanent plot systems, measurements are nested within a tree (i.e. repeated measurements) and trees are nested within a plot. Furthermore, repeated observations in longitudinal studies are typically correlated. Mixed-effects models explicitly model hierarchical data structures by featuring random effects that allow clustering observations into groups (Gelman and Hill, 2006; Schielzeth and Nakagawa, 2013; Zuur et al., 2009), thus accounting for the potential correlation of trees within plots. In this study, we used mixed-effects models to better understand the interactive effects of tree species richness and drought on crown defoliation and radial growth.

1.4. OBJECTIVES AND OUTLINE OF THE THESIS

"Research is to see what everybody else has seen,
and to think what nobody else has thought."

Albert Szent-Gyorgyi

The overall purpose of this research was to enhance understanding of the effects of tree species diversity to increase the resilience of forests in the face of climate change. The complex interactions among species that affect their responses to environmental changes have been the subject of many published studies, including in forest ecosystems (e.g., Zhang *et al.*, 2012; Forrester & Bauhus, 2016). In addition, several large-scale planted biodiversity experiments have recently been established to investigate the relationship between tree species diversity and ecosystem functionality, i.a. BEF-China (Bruelheide et al., 2014); BIOTREE, Germany (Scherer-Lorenzen et al., 2007); FORBIO, Belgium (Verheyen, 2013); IDENT, North America and Europe (Tobner et al., 2014)). However, these experiments can so far only provide information on the initial phase of stand development and species interactions (Bauhus et al., 2017b). This thesis therefore aims addressing this knowledge gap by using long-term data from a network of permanent forest monitoring plots across Belgium and complemented with data from the national forest inventories. The thesis is structured around the following three research questions:

1. Do perceptions and knowledge on climate change influence the implementation of adaptation practices by forest managers?
2. Does tree species richness increase the resilience of forests to drought-induced defoliation?
3. Are mixed-species forests more productive than monocultures?

To answer these research questions, this thesis is structured in six chapters (Figure 1.6). Chapters 2, 3, 4 and 5 investigate the three main research questions and were written independently from each other, enabling the reader to directly move to any chapter of interest. In chapters 3 to 5, we focused on *Fagus sylvatica*, *Quercus petraea* and *Quercus robur*, as these are, ecologically as well as economically, among the most important tree species both in Belgium and in Europe.

The objective of **Chapter 2** was to assess the perceptions of forest managers in Belgium about the vulnerability of forests to climate change and the extent to which specific actions to enhance the resilience of forest are being implemented in practice. We surveyed 391 individuals, either forest owners or managers of public and private forests, to investigate whether, and how they adapt to climate change. More specifically, we sought to investigate what impacts of climate change have been observed or are expected; what adaptation practices are known and implemented; and what are the barriers and constraints to adaptation.

In **Chapter 3**, we provide a temporal analysis of changes in forest condition caused by sustained drought conditions. Droughts have been associated with regional-scale forest mortality worldwide (McDowell et al., 2008). Moreover, they can have long-term impacts on community dynamics and species interactions. Therefore, we used visual assessments of crown defoliation, an indicator of decline, to examine the influence of tree species richness on forest health. Data acquired from permanent monitoring plots were analyzed for this purpose. These plots were established as a part of the ICP Forests Programme. We hypothesized that the severity of tree defoliation increases with increasing water stress, and that species-rich communities might be less affected by drought, mainly through complementary use of resources.

Chapter 4 continues with the data from the long-term monitoring plots, but the focus shifts to understanding the growth dynamics of mixtures and how resilience of trees relate to tree species diversity and crown defoliation since it has been suggested that negative growth rates and enhanced defoliation tend to be correlated with forest decline. Particular focus is placed on the temporal pattern of drought recovery. We hypothesized that trees growing in mixed-species stands will recover quickly from drought than in monoculture, and that the most defoliated trees will grow less and show the lowest resistance to drought and the lowest post-drought growth rates.

In **Chapter 5**, we examine the mechanisms behind the effects of tree diversity on forest productivity. It has been previously suggested that mixed-species forests can be more productive than monocultures due to complementarity interactions, which reduces competition for water, light, and nutrients (Binkley, 2012; Forrester and Bauhus, 2016; Richards et al., 2010). Following this understanding, biodiversity effects were first assessed by measuring overyielding, which occurs when a mixture of species performs better than its component monocultures. Second, the mechanisms behind the biodiversity effects were explored by partitioning the biodiversity effects using the tripartite equation of Fox (2005). Data from a large number of forest inventory plots were used to estimate the effect of mixing tree species on the yield of different mixtures, as well as the importance of the associated mechanisms.

Finally, **Chapter 6** summarizes the main findings, and outlines implications of the research, particularly for forest management. Furthermore, limitations of this research are discussed, and future research directions are also suggested.

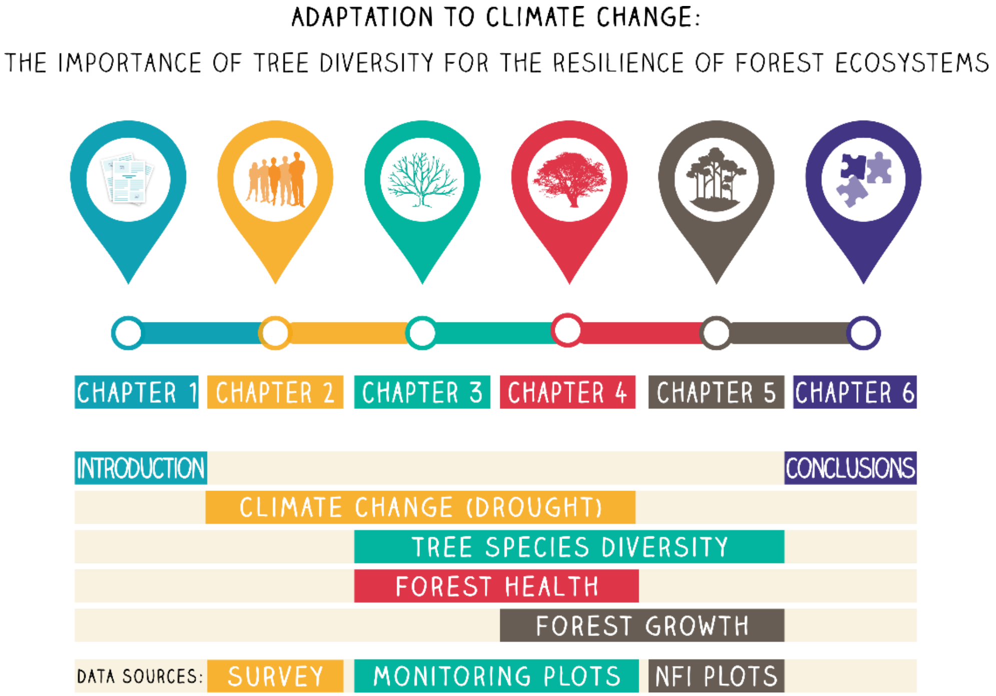

Figure 1.6 Outline of the thesis structure and overview of the contents of each chapter. *The thesis is composed out of six independent, but interconnected, chapters. The thematic link is illustrated in the top five rows. The bottom row details the data sources used in this thesis.*

CHAPTER 2

PERCEPTIONS ABOUT CLIMATE CHANGE ADAPTATION

Based on *Sousa-Silva R, Ponette Q, Verheyen K, Van Herzele A, Muys B. Adaptation of forest management to climate change as perceived by forest owners and managers in Belgium. Forest Ecosystems, 2016.*

2.1. SUMMARY

Climate change is likely to cause significant modifications in forests. Rising to this challenge may require adaptation of forest management, and therefore should trigger proactive measures by forest managers, but it is unclear to what extent this is already happening.

The survey carried out in this research assesses how forest stakeholders in Belgium perceive the role of their forest management in the context of climate change and the impediments that limit their ability to prepare and respond to these changes.

Respondents indicated strong awareness of the changing climate, with more than two-thirds (71%) expressing concern about the impacts of climate change on their forests. However, less than one-third of the respondents (32%) reported modifying their management practices motivated by climate change. Among the major constraints limiting their climate related actions, lack of information was considered the most important for managers of both public and private forests.

Knowledge transfer is an essential condition for research to lead to innovation. Improving the communication and demonstration of possible solutions for climate change adaptation is therefore likely to be the most effective strategy for increasing their adoption.

2.2. INTRODUCTION

Climate change is one of the world's greatest challenges. Despite a number of uncertainties, scientific evidence has led to a general consensus that climate change is occurring and is profoundly influenced by human activity. According to the Intergovernmental Panel on Climate Change (IPCC) fifth assessment report 'it is *extremely likely* that human influence has been the dominant cause of the observed warming since the mid-20th century' (IPCC 2013, p.17). However, even recent extreme weather events have been insufficient to deliver the required change in public and political action. On the contrary, in recent years a decline in public concern and acceptance of climate change has been documented (Capstick and Pidgeon, 2014). The greatest barrier to public recognition of human-made climate change is possibly caused by natural local climate variability (Hansen et al., 2012). Given that climate change cannot be directly experienced or straightforwardly observed, it is difficult for individuals to link local weather events and climate change. Yet, although climate fluctuations are cyclical, rapid global warming in the past decades is highly unusual (Hansen et al., 2012).

Projections of climate change effects for temperate forests are as follows: increased frequency and intensity of tree diseases and pest outbreaks due to a warmer climate, and particularly warmer winters, which increases the survival of parasites that were previously restricted to subtropical forests (Dale et al., 2001); a modification of the potential distribution ranges of tree species, as conditions are shifting far faster than their ability to adapt in place or migrate to more suitable locations (Bell and Collins, 2008); and warmer growing seasons and rising CO_2 concentrations, which, in the short term, will enhance forest production where soil nutrient and water availability allows. However, under nutrient-poor or water-deficient conditions, such as those in the Belgian forest regions of Ardennes and Campine (Campioli et al., 2011), this would not apply. As a result, there is a dire need to raise awareness of climate-related risks (and opportunities) among forest stakeholders, and engage them in adaptation.

The IPCC (2014b) defines adaptation as an ‘adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities’. Actions of climate change adaptation in forestry will have to be taken at different hierarchical levels of decision making, but ultimately the key actors on the field will be the forest owners and managers (CPF 2008). In Belgium, more than half of the forests are privately owned, often divided into parcels as small as 1 ha (2.5 acres) (Ouden et al., 2010; van Gameren and Zaccai, 2015), but whose management is undertaken, in general, by a hired manager or by a cooperative selected by the owners. These stakeholders, defined as people (whether owners or managers) who directly participate in forest management decisions (Locatelli et al., 2010), are particularly sensitive to climate change impacts since the forestry sector is exposed to and directly dependent on climate (Blennow and Persson, 2009), and therefore, insight into their perceptions of climate change risk is crucial. Perceptions are, in this context, defined as the awareness of the occurrence of climate change and the sensitivity to its adverse effects (Clayton et al., 2009).

Existing research suggests that perspectives on climate change are influenced by ethical, social, and political values and attitudes, but also by perceived personal experiences (Blennow et al., 2012; Myers et al., 2012). Indeed, people’s strength of belief in local effects of climate change has been shown to be strongly correlated with their willingness to undertake adaptive practices (Blennow et al., 2012; Lenart and Jones, 2014). Moreover, from a social point of view, climate change belief is an extremely important construct to understand people’s attitudes and actions (Goldman, 1999). In this sense, belief is defined as a personal conviction that is not necessarily supported by science-based evidence – but that is shaped by the overall context in which they occur, including the scientific understanding we have of it.

Several studies have investigated the perceptions of forest sector stakeholders on climate change and the implications for forest management (see for example Blennow et al. 2012; Yousefpour and Hanewinkel 2015; Nelson et al. 2016; Seidl et al. 2016a), using different questions, approaches, and sample sizes, demonstrating a wide general awareness of the issue. In this context, identifying the perceptions of stakeholders can inform us as to their level of knowledge of and degree of concern for climate change impacts, their understanding of risk and vulnerability, and whether they are willing to engage in the adaptation process. Thus, in our study, we attempted to reach this objective through a comprehensive survey involving various forest stakeholders, including forest owners and managers, both public and private.

The research presented here focuses on the perceptions of the vulnerability of forests to climate change and the impediments that limit the ability of forest owners and managers to prepare and respond to climate change. Our specific objectives were to understand (i) if individuals who have direct experience of extreme weather, which they attribute to climate change, are more concerned by and engaged with the issue than those who have not experienced it, (ii) whether they have made changes to their management based on the impacts that climate change may have on forests, and (iii) what are the main constraints to implementing these actions. This approach is in line with the methodology in Blennow et al. (2012) and FAO (2012) who used mailed questionnaires to elicit the perceptions of forest owners and forest managers to prepare and respond to climate change. We thus also test the hypothesis proposed by Blennow et al. (2012) that measurements of belief in local effects of climate change and in having experienced climate change are sufficient for accurately explaining adaptation.

2.3. METHODS

Case study. Belgium is a strongly urbanized country, with a territory of 30 528 km^2. Forests cover roughly 22% of the land area, with near to one third protected as part of the Natura 2000 network. The large majority of the forests (79%) is in the southern Walloon (French speaking) region, whereas the northern Flemish (Dutch speaking) region has a much smaller forest cover. In Wallonia, 50% of forest is publicly owned, while almost 70% of the forest area of Flanders is privately owned (Ouden et al., 2010; van Gameren and Zaccai, 2015). Most private forest owners hold very small properties. Traditionally oriented to timber production, over the last 50 years, the management of forests has become more multifunctional (Rondeux, 2007; Vandekerkhove, 2013).

Research design. The survey was designed to gather evidence from forest stakeholders on the impacts of climate change on their forests and their management. The questionnaire was formulated on the basis of a review of previous studies on perceptions on climate change (Blennow et al., 2012; Blennow and Persson, 2009; FAO, 2012) and recommended adaptation actions (FAO, 2013; Lindner et al., 2008). It was formulated in English, translated into French and Dutch and pilot tested on a sample of ten individuals in March 2015. Following this review, minor revisions were made, and the survey was made available online between April and July 2015. The survey was disseminated by email, newsletters and online media through forest owners' associations and organisations active in the forest sector in Belgium. Finally, survey respondents were encouraged to forward the advertisement to colleagues, creating a snowball effect (Goodman, 1961).

There were a total of 29 questions with dichotomous and multiple-choice answers. The former asked whether the respondents believed in climate change, their experience of the impacts and whether they had made changes to their management. The latter was used for the remaining questions. Risk perception and level of concern were measured on a five-point scale, ranging from 'definitely no' to 'definitely yes'. The questionnaire was divided into five sections, the first of which collected personal information, such as their socio-demographic and forest-related characteristics. Respondents were requested to indicate to which stakeholder group they belonged, owners or managers, and their role in the management of respective forests. Private owners were divided into two categories, depending on whether they manage their own forest (active owners) or not (passive owners). Managers, either in the public sector or private sector, can be understood as the people who assist the forest owner to adapt to climate change or who need to make decisions about whether, how and when to adapt on the owner's behalf. Public administration included Flemish (ANB; 'Agentschap voor Natuur en Bos') and Walloon (DNF; 'Département de la Nature et des Forêts') forest administration and other regional or local authorities. Private managers included non-governmental forestry/nature associations, private forest management organizations and forestry/timber professionals who do not own forest land. The second section asked whether respondents believed in climate change and whether climate change impacts on forests would affect their management. The following section sought to ascertain whether respondents had observed any evidence of climate change on their forests and if so, what was the nature of the impacts. Respondents were also asked about their level of concern about climate change impacts on their forests and the extent to which these risks are considered serious threats to their forests. Questions in the next section focused on assessing whether respondents had made changes to their management practices based on changing climate. Here respondents were presented a list of 17 potential measures to adapt to climate change (Lindner et al., 2008) and they were asked to choose all those that they had carried out in their forests. Respondents were also asked about the main constraints to implementing adaptation actions. Those who indicated not having adapted were assumed to not have taken concrete actions to change their management practices, whereas respondents who reported having made changes in their management were assumed to not have significant hindrances that would prevent them to undertake adaptation actions. Lastly, respondents were asked about their sources of information on climate change.

An online survey was used because of the speed of data collection, anonymity and ability to reach a large and diverse population at low cost (Reips, 2002a). The survey is easily accessible and participation is more voluntary compared to surveys by telephone or door-to-door (Dewaelheyns et al., 2013; Roth, 2006). A drawback of online surveys lies in the potential lack of representativeness (Evans and Mathur, 2005), excluding from the survey those who do not have access to and ability to use the Internet. Nevertheless, within the forest sector in Belgium, it has become common practice for associations to communicate with their members through e.g., newsletters, who are therefore used to this type of interaction. Furthermore, although the representativeness of the sample obtained could not be verified, since reference data on the ownership of private forests in Belgium do not exist, the total number of respondents in our study is comparable or superior to other published findings (e.g., Blennow et al. 2012; Valente et al. 2015; van Gameren and Zaccai 2015; Seidl et al. 2016a). To reduce the problem of dropout, all participants were offered a chance for a small financial reward (2002b, 2002a).

Data analysis. After we collected the data, descriptive statistics were used to summarize the characteristics of the respondents (Table 2.1), and a Pearson's Chi-squared test was applied to examine the relationships among forest owners and forest managers (Table 2.2). Finally, because data involving the relationship between explanatory variables and binary responses is best examined via logistic regression (Stephenson et al., 2001), we used multiple logistic regression to explore how beliefs and experiences affect the intention of forest owners and managers to adapt to climate change. The response variable was a binary variable taking on the value of one if the respondent answered 'yes' to the question about adaptation of management. Responses to other questions were entered either as ranked or binary explanatory variables. Logistic regression models allow us to estimate the probability of the outcome (e.g., yes vs no), based on the values of the explanatory variables. The logit function, $\text{logit}(p) = \ln(p/(1-p))$, where p is the probability of the outcome occurring, is used to determine the corresponding log odds of the outcome which we then model as a linear combination of the explanatory variables. As with standard linear regression analyses, the model coefficients can then be interpreted in order to understand the direction and strength of the relationships between the explanatory variables and the binary response.

The best and most parsimonious model was chosen by means of a stepwise approach using Akaike's Information Criterion (AIC) as a measure of relative goodness of fit, where smaller values represent better fits, and variables remained in the final model if the associated P value was <0.05. Tjur's coefficient of discrimination (D) was used to evaluate and compare the different models, since it is closely related to linear measures of fit and is not based on the likelihood function (Tjur, 2009). Regression coefficients, standard errors, and significance levels are reported for the full model.

Regression analyses were performed using the *brglm* package (Kosmidis, 2013), which addresses issues of near perfect separation in logistic regressions (i.e., when there is perfect correspondence of the response variable for most values of the predictors, but not for all) (Heinze and Schemper, 2002). All statistical analyses were performed in *R* (R Development Core Team, 2017).

2.4. RESULTS

A total of 512 people opened the survey link, of whom 391 (76%) completed the survey before it was closed. Most participants were male (88%) and in the over 50-year-old category (57%), with approximately 80% having at least a higher education degree (Table 2.1). Responses were grouped according to the surveyed respondents groups, i.e., forest owners (both active and passive) and managers (both public and private) (Table 2.2). The majority of respondents are private owners (56%), 91% of them being actively involved in forest management. Amongst managers, representation is fairly evenly divided between the public (93) and private (78) sectors.

Table 2.1 *Characteristics of respondents and samples of forest owners and forest managers.*

	All respondents	**Forest owners**	**Forest managers**
Gender			
Male	88%	87%	90%
Female	12%	13%	10%
Age			
< 30 years	9%	5%	14%
30-39 years	14%	9%	21%
40-49 years	20%	17%	23%
> 50 years	57%	70%	42%
Forest location			
Flanders	55%	58%	51%
Wallonia	40%	37%	43%
Flanders & Wallonia	3%	3%	4%
Abroad	2%	3%	2%
Education			
Basic education	1%	1%	0%
Secondary education	21%	19%	23%
Higher education	79%	80%	77%
Income			
Average gross annual revenue		< 500 €	-
Type of management			
Active / Passive		91 / 9%	-
Public / Private		-	54 / 46%
Forest size			
< 2 ha	22%	32%	9%
2-199 ha	43%	59%	23%
> 200 ha	35%	10%	68%
Member of a forest owners' association			
Yes	52%	61%	40%
No	48%	39%	60%
No. of observations	**391**	**220**	**171**

Forest owners were divided into two categories, depending on whether they manage their own forest (active owners) or not (passive owners). Forest managers, who do not own forest land, were either categorized as being in the public administration (public managers*) or in the private sector (private managers). Revenue represents their self-reported total income received annually, before taking taxes or deductions into account, from the forests they own (considered together). Percentages may not total 100% due to rounding.*

2.4.1. CLIMATE CHANGE AND ADAPTATION

Belief. Almost all the respondents (95%) believe that climate change is already happening and will continue in the future. The degree of belief in climate change did not differ between private forest owners and public or private forest managers. There was also a consensus among forest owners and forest managers that they are worried about climate change. Even 46% of those surveyed reported being 'very worried' or 'extremely worried' about it. Regarding the susceptibility to the risk of climate change of their forests, 71% of all respondents believe that climate change will 'probably' or 'definitely' affect their forests. A perception that is mutually shared between public and private managers (71% vs 67%). In terms of expected impacts, we found that extreme events were the most commonly cited, followed by forest pests and diseases, with the former being indicated by 72% of those respondents who expect to be impacted by climate change (*N* = 358). Species changes are also generally anticipated (Figure 2.1).

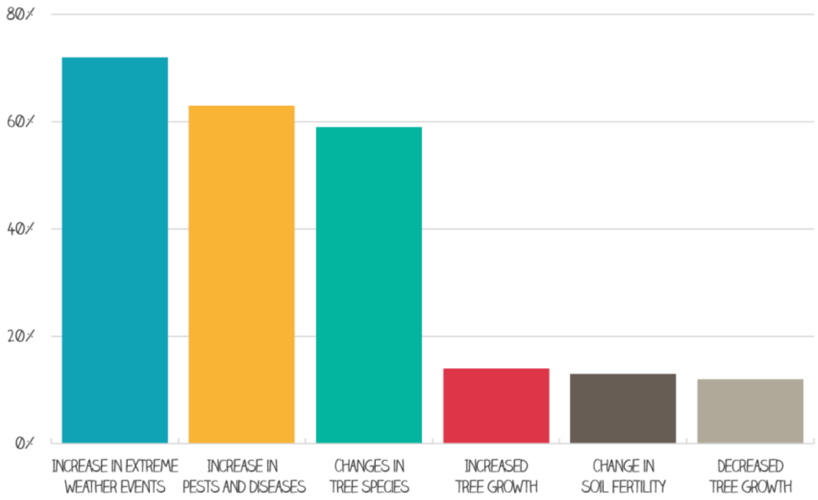

Figure 2.1 Expected impacts of climate change on forests. *Percentage of respondents who answered to the question: How do you think your forests will be affected? (N = 358).*

Experience. Half of the respondents stated that they had already experienced climate change (or phenomena that may be linked to climate change). The most commonly mentioned climate change related experiences were strong winds and storms, drought, and extreme precipitation, followed by heat waves (Figure 2.3). Out of the respondents who said to not believe in climate change, only one reported having had experience of climate change. The proportion of forest owners who reported experiencing local effects of climate change was similar to the forest managers sample, but lower than among private managers ($P < 0.01$; Table 2.2).

Table 2.2 *Descriptive statistics of respondents and samples of forest owners and forest managers (in %).*

	All respondents	**Owners** (O)		**Managers** (M)		***P* values**		
		Active (O1)	Passive (O2)	Public (M1)	Private (M2)	**H_o: O=M**	**H_o: O1=O2**	**H_o: M1=M2**
Belief:								
Do you think that climate change is happening?								
Yes	95	94		98		0.101	1†	0.337†
		93.5	95	99	96			
No	5	6		2				
		6.5	5	1	4			
Experience:								
Have you experienced extreme weather conditions that you interpreted as caused by climate change?								
Yes	50	41		59		<0.001	0.201	0.008
		42.5	25	49	71			
No	50	59		41				
		57.5	75	51	29			
Adaptation:								
Have you adapted your forest management in response to climate change?								
Yes	32	27		37		0.042	0.037	0.137
		29.5	5	43	31			
No	68	73		63				
		70.5	95	57	69			
No. of observations	**391**	**200**	**20**	**93**	**78**			

Forest owners were divided into two categories, depending on whether they manage their own forest (active owners) or not (passive owners). Forest managers, who do not own forest land, were either categorized as being in the public administration (public managers) or in the private sector (private managers). When asked whether they had undertaken climate change adaptation actions, respondents who answered "do not know" were grouped together with those who answered "no". † Pearson's Chi-squared test with simulated P*-value (based on 10,000 replicates) by Monte Carlo test.*

2.4.2. ADAPTATION IN FOREST MANAGEMENT

Adaptation. Respondents were then asked if they had taken measures to adapt the management of their forest to climate change. More than half of the respondents answered negatively. Respondents who answered ‘do not know’ (11%) were grouped together with those who answered ‘no’ (57%) for further analysis, as only those who answered affirmatively were considered having consciously changed their management plans or practices as a result of climate change. Managers of public forests have the highest rate of having adapted their management practices although still lower than 50%. By comparison, private owners are, on average, less likely to have adapted their forest management practices. The percentages of having taken measures to adapt did not differ statistically significantly between groups, but forest managers tended to be slightly more proactive than forest owners ($P < 0.05$; Table 2.2). Those respondents who indicated that they have not taken measures to adapt were further asked to mention the reasons for their inaction (Figure 2.2). Of these 222 respondents, a large majority considered lack of information and technical assistance (64%) as major constraints. The least selected constraint was lack of interest in implementing climate change measures (5%). Respondents also considered lack of conviction that adaptive actions are important as a major constraint.

Following on from the constraints to adopt adaptation measures, respondents were asked what assistance they would require to address climate change. The most selected options were improved access to technical information (47%) and improved public awareness on forests and climate change (46%). Among the respondents who stated that they had made changes to their forest management options to address climate change, 96% said they have promoted the establishment of mixed stands and 92% said they have planted better adapted species or varieties (Figure 2.4). Only 5 respondents said they have purchased an insurance against damage.

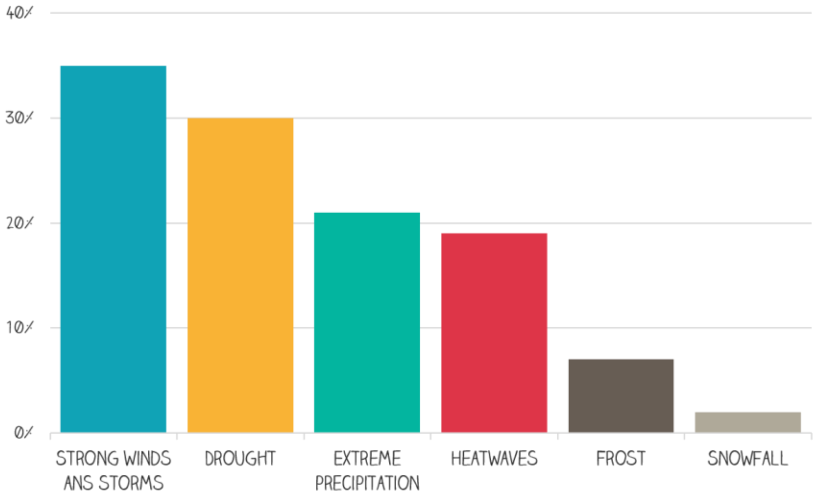

Figure 2.2 Experienced climate change related (or perceived) extreme events. *Percentage of respondents who answered to the question: What are your experiences of extreme weather events in your forests that you interpreted as caused by climate change? (N = 195).*

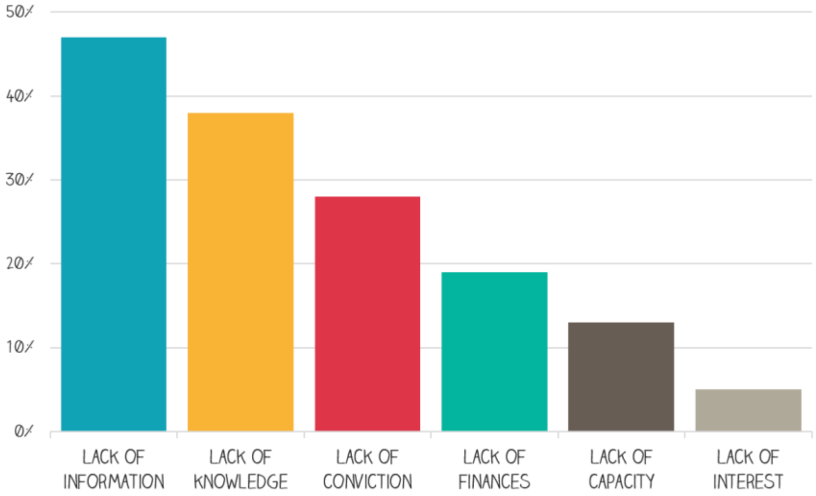

Figure 2.3 Constraints limiting climate change adaptation. *Percentage of respondents who answered to the question: What are the greatest constraints limiting your ability to undertake climate adaptation actions? (N = 222).*

2.4.3. MODELLING ADAPTATION TO CLIMATE CHANGE

Finally, we used logistic regression to investigate if experiences and beliefs in climate change can explain differences in attitudes and motivations for adapting forest management to climate change. We first tested the effect of the belief in climate change on the propensity to adapt, and then we fitted a model based on both beliefs and experiences of respondents with regard to climate change (Table 2.3; see also Blennow et al. 2012). However, the overall explanatory power of both models was poor ($\chi^2 = 7.665$, 1 d.f., $P = 0.006$ and $\chi^2 = 12.448$, 1 d.f., $P = 0.002$, respectively).

Table 2.3 *AIC and coefficients of discrimination (D) values of the different forms of the model fitted to the dataset using logistic regression. The value in bold is the most parsimonious model as selected by AIC comparison (ΔAIC > 2).*

	AIC	D
Adaptation ~ Belief	*484.86*	*0.01*
Adaptation ~ Belief + Experience	*482.12*	*0.03*
Full model	***196.29***	*0.65*

In this final step of the analysis, the model with the best fit included variables describing respondents' belief in climate change and that forest managers need to be proactive in their climate change actions, a positive effect of climate change on tree growth, as well as variables describing constraints to implementing these actions (hereafter referred as full model; Table 2.3). Constraints to responses include lack of knowledge, lack of finances, lack of interest, lack of information and lack of capacity (Table 2.4). This model fitted the data significantly better than the models based on both belief variables (Table 2.4), and was statistically more reliable than the intercept only model ($\chi^2 = 312.80$, 9 d.f., $P < 0.001$).

Figure 2.4 Potential adaptation options for forestry. *Percentage of respondents who answered to the question: How do you think you have adapted your management practices?* (N = *169).*

Table 2.4 *Parameter estimates (Est., with standard error se) and associated statistics (Z-score and* P*-values) of a model for predicting adaptation based on beliefs and constraints associated with adapting forest management to climate change by forest owners and managers.*

	Est. (se)	**z-stat**	***P***
(Intercept)	-0.964 (0.449)	-2.148	0.03
Belief management adapt	2.079 (0.481)	4.325	<0.001
Lack of knowledge	-5.069 (1.635)	-3.101	0.002
Lack of finances	-3.632 (1.555)	-2.336	0.02
Lack of conviction	-4.239 (1.503)	-2.821	0.005
Lack of information	-5.037 (1.669)	-3.019	0.003
Lack of capacity	-3.594 (1.540)	-2.334	0.02
Increased tree growth	2.653 (0.780)	3.400	<0.001
dnk belief climate change	-5.376 (2.053)	-2.619	0.01
dnk how adapt	-1.831 (0.731)	-2.505	0.01

Belief management adapt: belief in the need to adjust forest management practices; *dnk belief climate change*: do not know whether climate change is happening: *dnk how adapt*, *do not know how to adapt forest management. All diagnostic statistics given for the logistic regression model are significant* at $\alpha = 0.05$. The null deviance = 460.49, the degrees of freedom for the null model = 390, the residual deviance = 175.71, and the residual degrees of freedom = 381. The model fits the data significantly better than the null model ($P < 0.001$).

2.5. DISCUSSION

Climate change presents significant risks for forests and challenges for forest stakeholders. Therefore, gleaning their perspective on climate change effects may help policy makers to better assist forest stakeholders to effectively respond to climate change challenges and opportunities over the long term.

Because the belief in local effects of climate change has often been linked to more support for climate change actions (e.g., Blennow et al., 2012; Yousefpour et al., 2013), our study started by asking the stakeholders whether they believed in climate change. Not surprisingly, a large majority (95%) of respondents said that they believe climate change is occurring. Furthermore, they are concerned that it will affect them. This tendency is not new, but it has seldom seen so strong before. But ultimately, as the planet continues to warm, the issue of whether they believe in climate change will become more and more irrelevant.

In this respect, Blennow et al. (2012) suggest considering the combined effect of both personal beliefs and experience to better explain and predict adaptation to climate change. This was also observed by Seidl et al. (2016a) and Ameztegui et al. (2018). Indeed, many forest stakeholders have come to link climate change with recent extreme weather events, such as heat waves and storms, which are expected to become even more pronounced throughout the 21st century (Brouwers et al., 2015; ECORES and TEC, 2011). Yet, although a consensus has been reached, we found that the understanding that climate change is happening and poses a worrisome threat is not synonymous with adjustments to management plans and practices.

2.5.1. ADAPTATION IN FOREST MANAGEMENT

Adaptation to climate change represents new challenges for forest stakeholders, in addition to current economic, social, and political challenges. The implementation of adaptive practices into forest management is best achieved by fostering a shared understanding of the task at hand among the plurality of practitioners (Keenan, 2015). However, what is more startling is that 71% of respondents perceive that their forests are at risk from climate change but are ambivalent about the importance of implementing adaptation measures. Moreover, only just over half of those who said that forest management will need to adapt to climate change have taken measures to adapt. As noted already, the awareness of climate change did not translate into adaptive management practices, which is even more meaningful when considering that those who answered to our questionnaire are mostly well-educated and have an extensive forest management experience (over 15 years). Moreover, even though small forest ownership may be underrepresented in our sample, this reflects the fact that the survey was targeted mainly on those forest owners and managers who are actively engaged in forest management. Therefore, if on the one hand, we may not have reached many of those owners whose residence is in or adjacent to the forest, which is often considered an extension of their garden, and are therefore less engaged in the issue of climate change than those managing their forests; on the other hand, it adds meaning to the results. The owners we indeed reached are expected to be those most strongly affected by the impacts of climate change on forests and who could play a lead role in the implementation of adaptation actions. So, what is preventing them from taking measures to adapt to climate change?

Adaptation is, in essence, about making the best possible decisions for the future, taking into account the implications of climate change (Keenan, 2015). It requires considerable knowledge, competence and commitment for adopting actions, but also embracing risk and uncertainty (Howlett, 2012). As to the later, Hallegatte (2009) proposes to implement ‘no regret’ strategies, which yield benefits even in the absence of climate change. It is implausible that a single ‘right’ decision is ‘right’ for all circumstances, but ‘we can buy time while we learn more’ (Bellassen and Luyssaert, 2014). Accordingly, comparing options from available adaptation measures will be key to successfully adapting forest management to the challenges of climate change (Kolström et al., 2011). But, although much has been written about adaptation strategies in forestry (e.g., Keenan, 2015; Kolström et al., 2011; Lindner et al., 2010), and a number of recent guidance manuals to assist forest managers have been developed (e.g., FAO, 2013; Lindner et al., 2008; Peterson et al., 2011), there is still a major knowledge deficit among forest stakeholders. This is consistent with our results: a higher proportion of Belgian forest owners and managers highlighted the lack of information and technical knowledge to undertake climate change adaptation actions as their main constraints to implement these actions. Furthermore, the minor importance given to the lack of interest when compared to the other constraints indicated that it is not lack of willingness which prevents forest stakeholders from implementing these actions, whereas the lack of conviction in its importance is very likely linked to their lack of knowledge. And although many respondents (20%) consider the future situation too uncertain to undertake adaptation actions, the reason for not having adapted among believers of climate change is most often related to the lack of knowledge on how to adapt rather than to uncertainty about the climate change per se. Blennow and Persson (2009) came to the same conclusion in a study among Swedish private forest owners.

But the view that the problem is merely a knowledge deficit is not correct – it is also a knowledge transfer problem. Climate change has received increased attention by researchers and policy makers (see for example, Spittlehouse and Stewart 2004; Lindner et al. 2010; Keenan 2015; Seidl et al. 2016a), but more knowledge does not necessarily translate into greater acceptance, nor into behavioural change (Kahan et al., 2012). Research and knowledge development must be coupled with effective communication in order to be successful (Morin et al., 2015). For example, regarding the performance of mixed versus pure stands, Carnol et al. (2014) have shown a discrepancy between the perceptions of practitioners and the scientific knowledge on the issue of productivity in mixed species stands, urging to the need to address the lack of scientific data and to improve the communication of the topic towards practitioners through efficient information flow.

Indeed, there has, perhaps, never been a greater need for the sharing of information, knowledge and experience among researchers, policy makers and practitioners than right now. In fact, as pointed out by Keenan (2015), effective climate change adaptation is best achieved by combining scientific and local forest knowledge and by making this knowledge widely accessible. When preferred adaptation options have been identified, which should be done in close consultation with all stakeholders involved in the adaptation process, climate change guidelines for forest managers shall provide descriptions of steps taken or envisaged to implementing these actions to ensure maximum responsiveness to climate change impacts on forests.

2.5.2. ADAPTATION STRATEGIES AND ONGOING MEASURES

In our study only 30% of respondents stated they had already taken action to address climate change. Among the adopted measures, the conversion to mixed species stands better adapted to the prevailing site conditions ranked highest, either between public or private managers. On the other hand, selecting and introducing species better adapted to future warm conditions is preferred by private owners. Many respondents also reported that they have increased the share of natural regeneration of their forests, particularly those who manage public forests. Nevertheless, the current practices are still dominated by even-aged monocultures established by artificial regeneration, e.g., in the Ardennes, where large monocultures of coniferous species occupy sites that would naturally support mixed broadleaved forests.

Recently, a few studies have been published on implementing adaptation within the Belgian forest sector (e.g., Laurent et al. 2009;

Demey et al. 2015; Van der Aa et al. 2015), but to date this has not yet been translated into concrete forest policy, neither have the recommendations contained in these reports pursued further nor implemented. Furthermore, at the time being, a fully comprehensive adaptation plan has yet to be developed, which is urgent considering that even those respondents who recognise the need to adjust their forest management practices to meet the needs for adaptation for climate change, do not know how to adapt to these changes.

As the final step, we have attempted to test the hypothesis proposed by Blennow et al. (2012) that strong beliefs in local effects of climate change and in having experienced climate change are sufficient for accurately explaining and predicting adaptation to climate change. Our results, however, do not support this hypothesis. Unlike the full model, models based only on the two personal belief variables do not account for the variability in predicting adaptation to climate change. There are several plausible reasons for this. Most significantly, European forests are extremely diverse in terms of their biophysical and socio-economic conditions (Kolström et al., 2011). As a result, adaptation in forest management may differ in particular between intensive forestry countries, such as Sweden, and countries where the direct economic output from forestry is less important and forests are managed for ecosystem services other than production (Keskitalo, 2011). In Belgium, where the contribution of forestry to the gross domestic product is very marginal, the importance of sustaining biodiversity and natural ecological processes alongside production-oriented forestry is worth mentioning.

Therefore, we conclude that, to explain and predict adaptation to climate change, the constraints limiting forest management adaptation to climate change must be considered and addressed to make change successful. In particular, there is a need to ensure that all stakeholders have the information and tools they need to make decisions on their forest management options to address climate change.

2.6. CONCLUSIONS

Our findings suggest that there is a marked imbalance between the great awareness about climate change impacts and the adaptation measures put into practice on the ground. In order to tackle climate change challenges, it is important to provide capacities and support to the forest sector. The research presented in this paper provides evidence that despite the many uncertainties associated with climate change, forest stakeholders in Belgium show great awareness of the need to adjust forest management practices to meet the needs for adaptation to climate change. However, this finding contrasts with the perceived lack of knowledge on how to adapt. Improving communication of adaptation challenges and strategies for climate change adaptation is therefore likely to be the most effective approach for increasing action, which should also be the focus of future research.

ACKNOWLEDGMENTS:
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2

CHAPTER 3

THE EFFECT OF TREE DIVERSITY ON DROUGHT-RELATED DEFOLIATION

Based on *Sousa-Silva R, Verheyen K, Ponette Q, Bay E, Sioen G, Titeux H, Van de Peer T, Meerbeek KV, Muys B. Tree diversity mitigates defoliation after a drought-induced tipping point. Global Change Biology, 2018.*

3.1. SUMMARY

Understanding the processes that underlie drought-related tree vitality loss is essential for anticipating future forest dynamics, and for developing management plans aiming at increasing the resilience of forests to climate change. Forest vitality has been continuously monitored in Europe since the acid rain alert in the 1980s, and the intensive monitoring plots of ICP Forests offer the opportunity to investigate the effects of air pollution and climate change on forest condition. By making use of over 100 long-term monitoring plots, where crown defoliation has been assessed extensively since 1990, we discovered a progressive shift from a negative to a positive effect of species richness on forest health. The observed tipping point in the balance of net interactions, from competition to facilitation, has never been reported from real ecosystems outside experimental conditions; and the strong temporal consistency of our observations with increasing drought stress emphasizes its climate change relevance. Furthermore, we show that higher species diversity has reduced the severity of defoliation in the long-term. Our results confirm the greater resilience of diverse forests to future climate change-induced stress. More generally, they add to an accumulating body of evidence on the large potential of tree species mixtures to face manifold disturbances in a changing world.

3.2. INTRODUCTION

Disturbances are inherent to forest dynamics and contribute to forest resilience (Seidl et al., 2014). Drought, fire, insect and disease outbreaks are all predisposing factors that weaken or kill trees but at the same time can favor tree regeneration and foster diversity, pulling forests toward a shifting mosaic steady state (Bormann and Likens, 1979). Notwithstanding this, anthropogenic climate change is likely to alter this regime in ways that can push ecosystems past tipping points (Dale et al., 2001; Millar and Stephenson, 2015). Recently, widespread drought-induced die-off events have been observed in forests around the world (Allen et al., 2010), resulting in decreased productivity and ecosystem uptake of atmospheric carbon. For instance, the extreme drought that parched Europe in 2003 led to the lowest productivity of and carbon storage in Europe's forests during the last century (Ciais et al., 2005). This underlines the urgent need to detect, understand, and predict potential declines in the health and productivity of forest ecosystems (Trumbore et al., 2015).

Previous experimental (Williams et al., 2017) and observational (Liang et al., 2016a) research has demonstrated the importance of tree species mixtures for increasing ecosystem productivity. Tree diversity has also been shown to enhance resistance to pest outbreaks (Guyot et al., 2016; Jactel and Brockerhoff, 2007), but whether or not diverse forests are also better adapted to address drought stress is less clear. Extreme or prolonged droughts can trigger a variety of forest physiological responses, such as reduced radial growth and increased crown defoliation, potentially leading to extensive tree mortality (Carnicer et al., 2011). Some studies have reported that mixed-species forests are more resistant and resilient to drought stress (Gazol et al., 2016; H. Pretzsch et al., 2013), but this is not a general pattern (Forrester et al., 2016; Grossiord et al., 2014). In fact, multiple types of interactions can occur simultaneously in mixtures, and these interactions are dynamic, changing through space and time (Forrester, 2014). Most studies have considered a switch in the net interactions from competition to facilitation with increasing environmental stress as primary evidence supporting the stress-gradient hypothesis (Bertness and Callaway, 1994; Maestre et al., 2009), but few studies have considered the duration or frequency of the stress factor over time. Our analysis is, to our knowledge, the first to test the importance of species diversity for the maintenance of the health and vitality of forest ecosystems along a temporal stress gradient.

Here, we present a temporal analysis of changes in forest condition based on annual assessments of crown defoliation of *Fagus sylvatica*, *Quercus petraea* and *Quercus robur*. We aimed to test the influence of tree species richness on tree defoliation in relation to drought stress. We hypothesized that (i) the severity of tree defoliation increases with increasing water stress and that (ii) an increase of species richness is able to mitigate the negative impact of drought on forest vitality, mainly through the complementary use of resources. We tested these hypotheses using data from the Belgian plots of the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests). ICP Forests is the largest forest monitoring network in Europe dedicated to assessing the status and development of forest condition at the European scale (Lorenz, 1995; Lorenz and Fischer, 2013).

3.3. METHODS

Study area and crown condition assessment. In this study, we analyzed the temporal variation in the defoliation of *Fagus sylvatica*, *Quercus petraea*, and *Quercus robur*. The study was carried out in Belgium using data from the European ICP Forests program. In ICP Forests, crown condition is annually assessed using harmonized methods (Eichhorn et al., 2016), which includes assessments of defoliation, damage causes and mortality as well as stem diameter. Defoliation is defined as the loss of foliage in relation to a reference tree, according to a scale with 5% intervals from 0 to 100%, regardless of the cause of foliage loss. Due to the subjectivity associated with the visual assessment of defoliation (Ferretti, 1998; Innes et al., 1993), training courses are organized every year in order to ensure spatial and temporal data consistency. The annual training courses take place before commencing the field data collection, during the summer months, and the results are discussed in the field (see SM for details). Regular training courses are believed to minimize the subjectivity of the assessments and the variation among individual observers (Eickenscheidt and Wellbrock, 2014).

The network of ICP Forests plots is organized into two levels of monitoring (Level I and Level II) (Ferretti, 2013). Level I involves large-scale monitoring of the spatial and temporal variation of forest condition. Level II aims at understanding the cause-effect relationships between the condition of forest ecosystems and stress factors. In Belgium, the Level I survey was originally conducted on a 4 km x 4 km and 8 km x 8 km grid. In each plot, a cross-cluster sampling was used to select 4 groups with 6 trees. If a monitored tree died, due to either anthropogenic or natural causes, it was replaced within the plot to ensure a continuous sample size over the time period of assessment. In 2009, circular plots (radius 18 m) were installed and from 2012 on, sample trees have been selected only in these circles. Level II plots consist of a fenced core area of 0.5 ha surrounded by a 20 m buffer area. In the Level I network, defoliation has been assessed since 1987, whereas in the Level II network, defoliation assessments started in 1995. The initial dataset consisted of 114 Level I plots and 5 Level II plots (Table 3.1). Plots were selected according to the following criteria: the presence of the study species (i.e. *F. sylvatica, Q. petraea* or *Q. robur* trees); having been assessed at least five times over the study period. Percentage of plot defoliation was estimated by averaging the values of percentage of defoliation determined for the plot trees. Only plots with a minimum of five assessed individuals per tree species were considered for the determination of defoliation at the plot level. Using the abovementioned criteria, we studied 2,710 trees during the 26-year study period, from 1990 to 2015, resulting in a total of 37,800 observations (trees × years) available for analysis (see **Table A.1** for the number of plots and trees monitored in each year).

Stand attributes and drought index. In each plot, the stem diameter at 1.3 m was measured for all trees with diameter ≥ 7 cm. These diameters were used to calculate the basal area (m^2 ha^{-1}) of each species in each plot and hence the total plot basal area (BA). Most stands (approximately 90%) are even-aged with limited (10-year thinning cycle) or no management activity (Table 3.1). Species richness (SR) was determined as the number of tree species in each plot, ranging from monocultures to a maximum of five species. To avoid class imbalance, mixtures of four and five species were grouped together and a gradient of species richness with four levels was used for all the plots.

Table 3.1 Main characteristics of the study plots. *Number of observations; age class*[a] *(median); mean (with standard deviation between brackets) of stand basal area*[b]*, defoliation, elevation, annual mean temperature and total annual precipitation*[c] *for the monoculture and mixed plots in which* Fagus sylvatica *and* Quercus *spp. grew.*

	Fagus sylvatica		***Quercus petraea***		***Quercus robur***	
	Monocultures	Mixtures	Monocultures	Mixtures	Monocultures	Mixtures
No. plots	*16*	*39*	*7*	*24*	*16*	*47*
No. trees	*401*	*431*	*143*	*223*	*470*	*627*
Age class	*5*	*6*	*7*	*4*	*5*	*5*
Stand basal area (m^2 ha^{-1})	*41.0 (32.4)*	*54.9 (24.4)*	*31.7 (13.7)*	*34.1 (18.0)*	*34.5 (18.0)*	*47.8 (24.0)*
Crown defoliation (%)	*18.4 (16.0)*	*19.8 (17.2)*	*12.0 (15.1)*	*13.3 (14.6)*	*20.9 (15.1)*	*22.2 (13.4)*
Elevation (m)	*287 (216)*	*250 (155)*	*306 (149)*	*259 (146)*	*113 (146)*	*86 (105)*
Annual temperature (°C)	*9.4 (1.1)*	*9.7 (0.9)*	*9.2 (0.8)*	*9.5 (0.8)*	*10.4 (0.8)*	*10.5 (0.6)*
Annual precipitation (mm)	*1038 (145)*	*990 (120)*	*941 (92)*	*1054 (153)*	*933 (152)*	*883 (112)*

[a] *The mean age class of the dominant storey is reported in 20-year classes, as follows: '1' = 0–20 years; '2' = 21–40 years; '3' = 41–60 years; '4' = 61–80 years; '5' = 81–100 years; '6' = 101–120 years; '7' > 120 years. The age class was unknown or could not be determined for 21 study plots.*

[b] *Tree diameter measurements (and hence basal area) were not available for 20 study plots. These plots were not included in the regression analysis.*

[c] *Meteorological data were averaged from daily means over the period 1990-2015.*

Species diversity (SD) was quantified using Shannon's index, which combines both species richness and evenness, based on the basal area of each target species within a plot. It is noteworthy that not all plots were monitored since the beginning of the program, nor were they revisited every year. Hence 2011, when most of the plots (89%) were simultaneously surveyed, was used as a reference year to describe the structure and diversity of each plot. Functional diversity (FD) was measured as functional dispersion, using leaf dry matter content (LDMC), specific leaf area (SLA) and xylem vulnerability to cavitation of the tree species present in a plot. Trait values were obtained from the TRY database (Kattge et al., 2011). FD was calculated as the mean distance of each species, weighted by its relative abundance, to the centroid of all species in a multidimensional trait space (Laliberté and Legendre, 2010).

Climate data were obtained from the FORBIO Climate dataset. Details of the data quality procedures applied to the meteorological observations to generate this climate data set are described in Delvaux et al. (2015). Daily temperature and precipitation were summarized at monthly intervals from 1980 to 2015. Potential evapotranspiration was calculated according to Hargreaves equation (Hargreaves, 1994), using mean monthly temperature and monthly temperature range. Based on the difference between precipitation and potential evapotranspiration, we calculated the Standardized Precipitation Evapotranspiration Index (SPEI) using the SPEI-package in R (Vicente-Serrano et al., 2010). SPEI is a multi-scalar drought index that accounts for the influences of precipitation deficit and atmospheric evaporative demand on drought severity and can be used to identify water deficits and surplus conditions for a given period of time at monthly intervals. The average value of SPEI is 0, meaning that for a certain period of time (e.g., from June to August) the climatic water balance (precipitation – potential evapotranspiration) is equal to the long-term average of the 1980-2015 base period. Positive values indicate conditions of above-normal wet conditions, whereas negative values identify dry situations. SPEI values between 0.67 and −0.67 are considered normal, whereas values < -0.67 indicate drought and values < -1.28 indicate severe drought (Isbell et al., 2015).

Soil characteristics were retrieved from the digital soil map of Belgium (Dondeyne et al., 2014). The data set covers the two ecoregions of Belgium: the lowlands (41 plots) located to the north of the Sambre and Meuse rivers in the maritime climate zone and the uplands (78 plots) to the south of this axis, with hilly topography in the sub-continental climate zone. In the lowlands, soils are deeper (>1 m) and composed of silt loam and/or sand in different proportions. In the uplands, soils are shallow and can be sandy, loamy or clayey with a high stone content. Topographic variables (terrain aspect, curvature, elevation and slope) were extracted from a LiDAR-derived digital terrain model at a spatial resolution of 1 m (AGIV, 2015; SPW, 2015). LiDAR point clouds were subjected to a strict geometric quality control, planimetrically (RMSExy = 1 m) and altimetrically (RMSEz = 0.1 m). For more details, see Supplementary Note A.1.

Statistical analysis. We used linear mixed-effects models to test the hypothesized relationships between tree species richness and drought effects on crown defoliation. The mean percentage of defoliation per plot per species was used as response variable (after log transformation). Since the log-transformation is not capable of handling the values 0% (not defoliated) and 100% (dead), these values were treated as 1.0 and 99.9%, respectively (the value 99% was already reserved for trees that were completely defoliated but not dead). Defoliation was then modeled as a function of (i) species identity (accounting for variation in defoliation among species); (ii) species richness; (iii) stand basal area (to account for the effects of stem density and competition on tree defoliation), age class distribution (even-aged, uneven-aged), and management type (high forest, coppice without standards, coppice with standards); (iv) drought severity (quantified using the Standardized Precipitation Evapotranspiration Index, *SPEI*); (v) an interaction term between species identity, species richness, and the year of observation (to determine whether species richness effects on tree defoliation vary among species over the years); and (vi) an interaction term between species identity and SPEI (testing whether drought impacts on defoliation vary among species):

$$
\begin{aligned}
log(DFL_{i,j}) = \beta_0 + \beta_1\,SP_i + \beta_2\,SR_j + \beta_3\,BA_j + \beta_4\,Age_j \\
+ \beta_5\,Management_j + \beta_6\,SPEI_j \\
+\ \beta_8\,[SP_i \times SR_j \times Year_j] + \beta_9\,[SP_i \times SPEI_j] + \varepsilon_{i,j}
\end{aligned}
$$

where DFL_{ij} is the defoliation of species i in plot j; SP is a categorical variable encoding for the identity of species i in plot j; SR_j is the species richness of plot j; BA_j, Age_j and $Management_j$ are, respectively, the stand basal area, the stand age structure and their management type; $SPEI_j$ is a measure of drought in plot j; $Year_i$ is a continuous variable and is interpreted as the underlying annual change in defoliation rate during the study period within each of the j plots; β_0-β_9 are parameters to be estimated from the data (i.e., intercept and slope coefficients); and ε_i is the residual error.

In all models, *plot identity* and *plot cluster* were included as random factors to account for the nested structure of the data (several trees located within each plot, which are themselves clustered together within known forest management units). Plot cluster is a categorical grouping variable that has four levels, used to identify the more or less homogeneous clusters of plots with respect to who carried out the assessment of crown condition (survey teams). Hence, this variable also accounts for systematic differences between the two levels of the monitoring network (Level I and Level II) and differences within the network of plots in Belgium (Flanders and Wallonia). To address the potential temporal autocorrelation in the data, we specified an autoregressive correlation structure [ARMA(2,0)], by inspecting the autocorrelation function (ACF) of the residuals (Zuur et al., 2009). We also fit models in which we accounted for a number of confounding factors that could conceivably alter the response of trees to mixing and drought (precipitation, minimum and maximum temperature during the growing season, soil type and topography), with effectively no change in the findings (see Table A.2 for a full list of models that were compared). Additionally, we fitted models that included species diversity and functional diversity indices as factors in the model. As these models yielded a worse fit to the data, but led to similar results, we focused on the parameter estimates obtained from the model including species richness.

We started by fitting a null model (i.e., an intercept-only model) and then observed how progressively increasing model complexity, by adding each predictor in turn, affected AIC values (Table A.2). Model selection was then done by ranking the models by their AICc (Akaike's Information Criterion with small sample size correction), and the AICc weight (wAICc), which varies from 0 (no support) to 1 (complete support). Goodness of fit was estimated using marginal and conditional R^2, which allow for assessing the predictive capacity of mixed-effects models (Nakagawa and Schielzeth, 2013).

Analyses were conducted in R 3.4.3 (R Development Core Team, 2017), using the following libraries: *vegan* (Oksanen et al., 2017), *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2016), *nlme* (Pinheiro et al., 2018), and *MuMIn* (Barton, 2016). The predicted interactions were plotted using the *sjPlot* package (Lüdecke, 2016).

3.4. RESULTS

3.4.1. CROWN DEFOLIATION AND DROUGHT STRESS

An increasing trend in defoliation was observed over the period 1990-2015 in the forest stands studied (Figure 3.1). The overall upward trend was particularly pronounced at the end of the period of assessment. The increase in defoliation was statistically significant for all three species examined ($P < 0.001$), with peak values occurring in 2012 for *Q. petraea* and *Q. robur* and in 2014 for *F. sylvatica*. Another yet smaller peak is evident between 2003 and 2005, likely connected with the dry hot summer of 2003.

Next, we tested the occurrence and magnitude of drought effects using the multiscalar SPEI metric (Vicente-Serrano et al., 2010). We observed an increase in the number of dry years since 1980 ($R^2 = 0.073$, 1 d.f., $P < 0.001$), as well as an increase in the frequency of months classified as moderate or extreme drought events (Figure 3.2). To assess the statistical significance of this increase, we fitted a simple linear regression model (SPEI ~ YEAR). The regression line showed a statistically significant positive slope ($P < 0.001$). Considering the possible lag in the response of tree defoliation to drought (Anderegg et al., 2013; Vicente-Serrano et al., 2013), we carried out a correlation analysis between the annual mean defoliation at plot level and the SPEI calculated at time scales between 1 and 24 months for the months prior to the survey (crown condition surveys are carried out every year in July and August). In this study, the highest correlations were found for the months of March, April and May for SPEI scales longer than 12 months, spanning nearly 2 years (Figure A.1). The relationship between crown defoliation and SPEI reached the strongest negative correlation by May and when accounting for the water balance of the previous 21 months (hereafter $\text{SPEI}_{21\text{-May}}$). This correlation was weak but significant ($r = -0.15$, $P < 0.001$; Figure A.1).

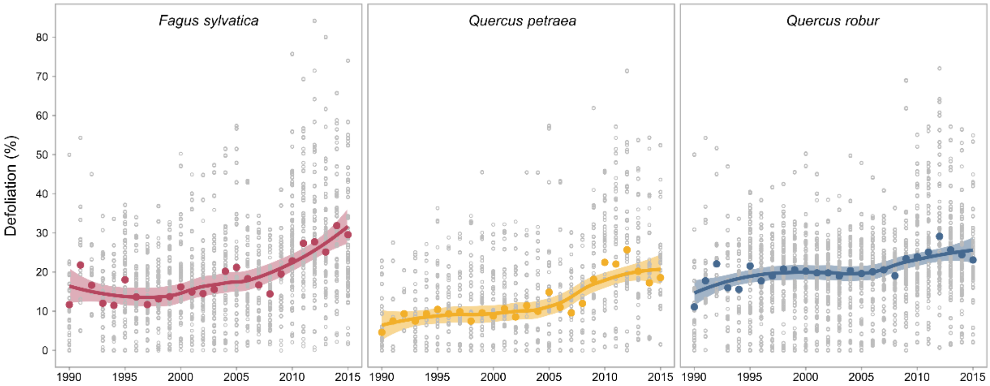

Figure 3.1 Temporal pattern of defoliation of the three studied species,* Fagus sylvatica, Quercus petraea *and* Quercus robur*, using 25 years of data on crown defoliation in temperate deciduous forests. *Defoliation severity was expressed as the proportion (percentage 0-100%, with intervals of 5%) of leaf loss, and a mean annual value was calculated for each* species. *Gray dots indicate annual defoliation averaged over all trees of a monitoring plot. Solid lines represent the smoothed trend and shaded areas denote 95% confidence intervals.*

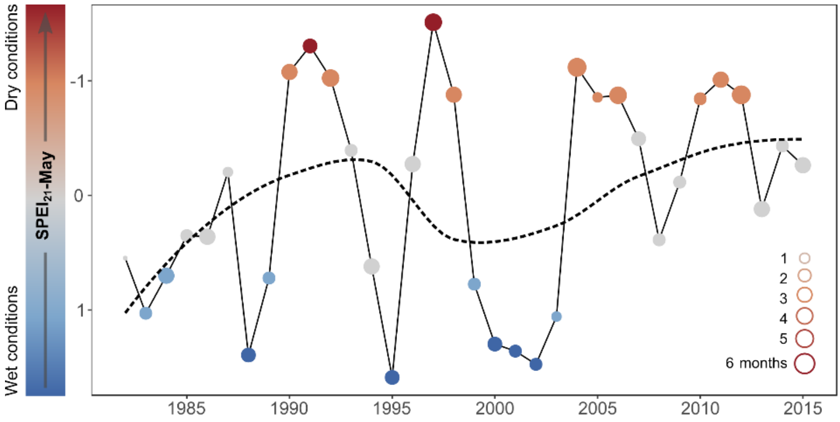

Figure 3.2 Temporal trend of drought conditions averaged over all monitored plots according to the SPEI values. *The trend shown here was calculated on a 21-month time interval for May* ($\text{SPEI}_{21\text{-May}}$)*, which corresponds to the month and the SPEI time lag at which the maximum SPEI/crown defoliation correlation was identified.* $\text{SPEI}_{21\text{-May}}$ *is calculated using the water balance of the 20 months prior to May and the month itself. The blue and red colors denote conditions, respectively, wetter or drier than the median of the 1980–2015 base period. Size of dots denotes the number of months per year classified as dry and the dashed line represents a loess smoother. Note that the y-axis has been reversed for convenience (i.e. negative SPEI values indicate dry conditions and positive SPEI values correspond to wet conditions).*

3.4.2. DIVERSITY EFFECTS ON DROUGHT-INDUCED DEFOLIATION

Species interactions are dynamic and can change through time. Accordingly, we examined the temporal pattern of defoliation along the tree species richness gradient present in the data (Figure 3.3). Our results show that, at the beginning of the study period, defoliation levels were significantly higher in mixtures than in pure stands. However, this trend has progressively shifted towards lower defoliation levels at higher species richness levels. The turning point occurred around the year 2010, following a period of steady increase in defoliation. For example, the average of annual values increased from 16% in 2008 to 31% in 2012. Furthermore, before 2010, the average defoliation in monocultures (SR = 1; *N* = 38 plots) was 15%, whereas in mixtures (SR ≥ 4; *N* = 16) was 18%. After 2010, the average defoliation in monocultures rose to 26%, whereas in mixtures this dropped to 19%. This pattern is consistent among the three studied species, with minor differences in the timing and magnitude of the shift (Figure A.2).

To further quantify the factors associated with the observed patterns of defoliation, we modeled crown defoliation as a function of tree species richness and drought stress from 1990–2015 (Table 3.2). Including stand-level variables as covariates in the regression model, such as the stand basal area, age class distribution and the type of management, improved the variance explained (see AIC values in Table A.2), though not all of them reached statistical significance. This may reflect the homogeneity of management practices, or lack of them, among the study plots at both temporal and spatial level (see Supplementary Note A.2 for a discussion on the role of age). Conversely, both species richness and species identity were found to be significant predictors of crown defoliation ($P < 0.05$). The severity of defoliation may thus depend on the identity of the tree species concerned, including its competitive ability and drought tolerance. Additionally, the effect of drought on crown defoliation differed substantially between the three species (i.e., interaction between species identity and $\text{SPEI}_{21\text{-May}}$). For *F. sylvatica* and *Q. petraea*, the mean defoliation level is, respectively, 38% and 39% higher following dry years than wet years (Figure 3.4a). These differences are statistically significant ($P < 0.001$). The highest average defoliation was found in trees of *Q. robur* in both monocultures and mixtures. For *F. sylvatica* and *Q. petraea*, the overall increase in defoliation level during the study period was markedly more pronounced in the low-diversity plots ($\text{SR} \leq 2$) than in high-diversity plots ($\text{SR} \geq 3$) (Figure 3.4b).

Figure 3.3 Annual trends in plot-averaged tree defoliation along a tree species richness gradient in temperate deciduous forests. *Defoliation severity was expressed as the proportion (percentage 0-100%, with intervals of 5%) of leaf loss. Solid lines and shaded areas represent the mean and 95% confidence intervals for each year of the study. Positive slopes (red) indicate an increase in defoliation with increased species richness (ranging from 1 to 5), whereas negative slopes (green) denote a decrease in defoliation in more diverse stands. Non-significant slopes are shaded gray (P ≥ 0.05).* N = *37,800 observations.*

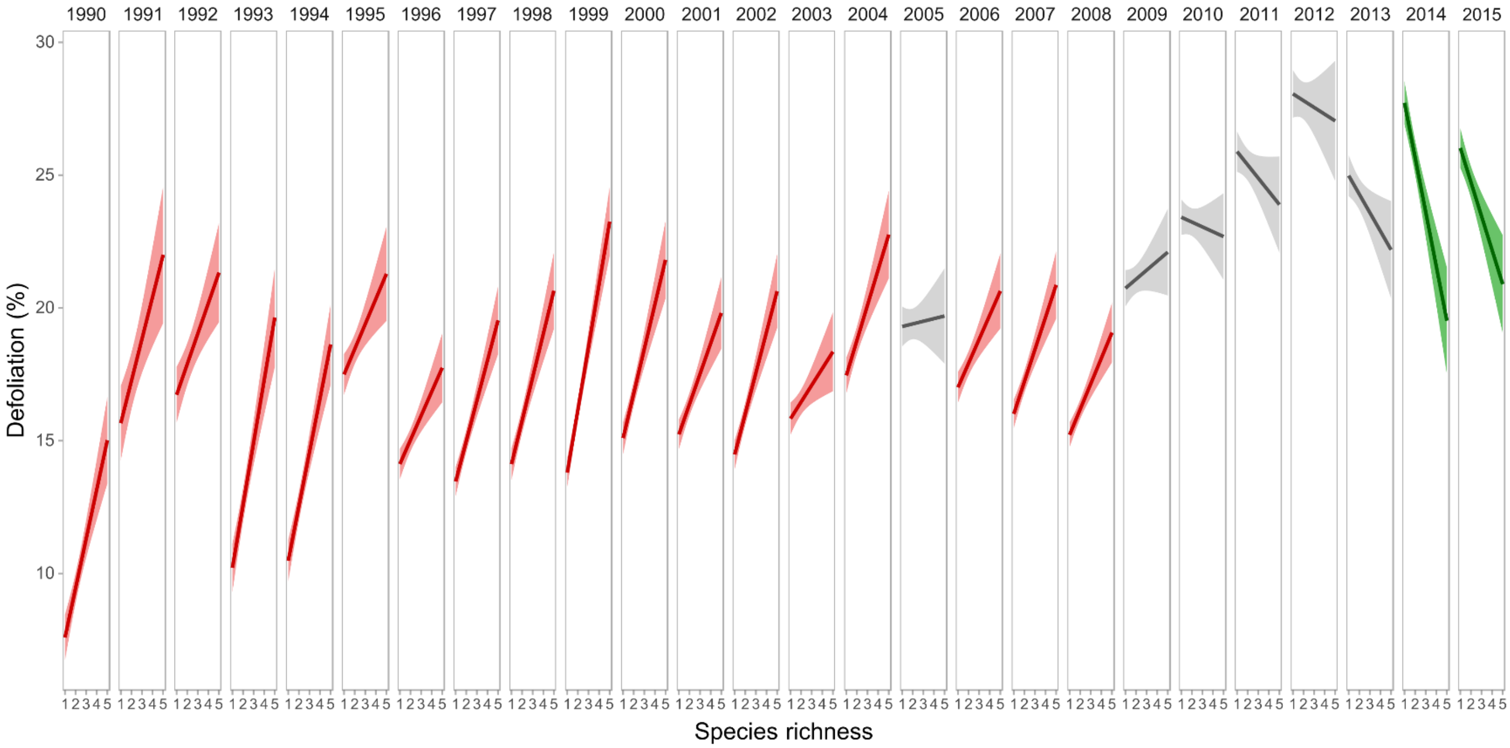

Table 3.2 Summary of the linear mixed-effects model to test the effects of species richness and drought over time on annual crown defoliation. *Best-fit parameter estimates (Est, with standard error SE), the estimated auto-regressive parameters of the ARMA(2,0) autocorrelation structure, the standard deviation of the random terms, and the marginal and conditional* R^2 *are shown for* N = *99 plots.*

Fixed effects	**Est.**	**se**	***P***
(Intercept)	-120.6	(10.040)	<0.001
Plot basal area	0.010	(0.003)	0.004
Fagus sylvatica	-120.6	(10.040)	<0.001
Quercus petraea	-120.7	(10.040)	<0.001
Quercus robur	-120.1	(10.040)	<0.001
Species Richness (SR)	24.850	(4.115)	<0.001
SPEI	-0.122	(0.024)	<0.001
Year of defoliation (YEAR)	0.059	(0.005)	<0.001
Fagus sylvatica : SPEI	*reference*		
Quercus petraea : SPEI	0.010	(0.041)	0.807
Quercus robur : SPEI	0.137	(0.030)	<0.001
SR:YEAR	-0.012	(0.002)	<0.001
Random effects			
sd plot		0.635	
sd level of network		0.652	
sd residuals		0.604	
Model statistics			
marginal R^2		0.13	
conditional R^2		0.73	

Response variable ('tree defoliation') was log-transformed prior to model fitting to normalize variance in the residuals. Drought was expressed by the SPEI (Standardized Precipitation Evapotranspiration Index) for May calculated at 21-month lags ($SPEI_{21\text{-}May}$)*.*

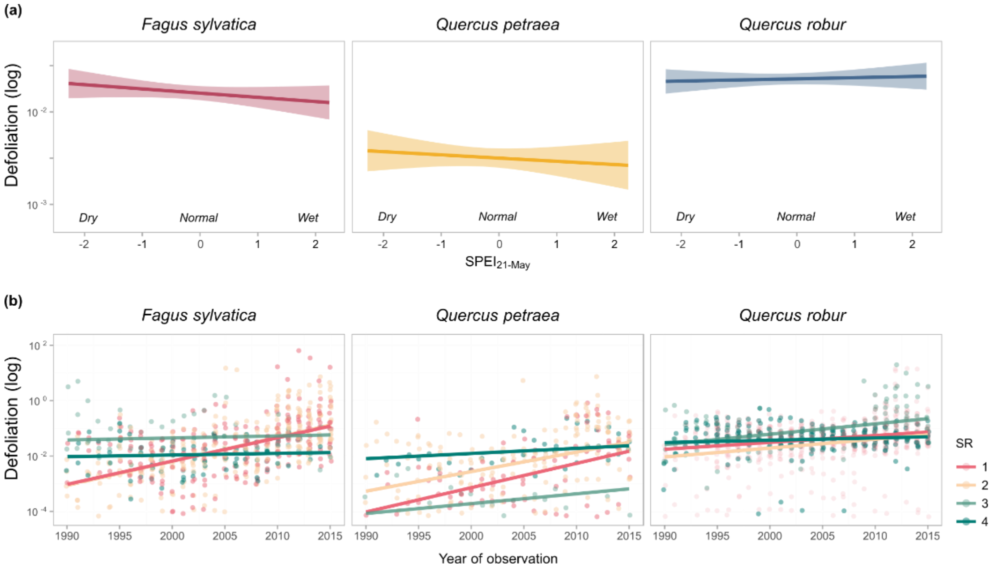

Figure 3.4 Estimated interaction effects of drought and species richness on defoliation of* Fagus sylvatica *(left panel),* Quercus petraea *(middle panel), and* Quercus robur *(right panel). *(a) Species defoliation response to drought (represented by $SPEI_{21\text{-}May}$). Shaded areas represent 95% confidence intervals (for parameter estimates, see Table 3.2). Negative values indicate drier than normal conditions, whereas positive values represent wetter than normal conditions. (b) Defoliation for trees growing in monocultures and mixtures (ranging from 1 to 5 species, with plots with 4 or more species grouped into class 4), over time. The dots show the raw data points and lines the regression lines. SR is species richness.* N = *99 plots.*

3.5. DISCUSSION

3.5.1. DROUGHT STRESS AS A TRIGGER FOR INCREASED LEVELS OF DEFOLIATION

Crown defoliation has been found to vary considerably across species and environments (Michel and Seidling, 2017). Furthermore, the visual assessment of tree defoliation is susceptible to a number of different sources of error, e.g. observer bias, which could influence the reliability of the results (Ferretti, 1998). To counteract this limitation, regular training courses and quality assurance and control procedures have been progressively implemented (in Belgium as elsewhere) to improve the quality of the data and maximize the temporal and spatial comparability of results (see Bussotti *et al.*(2009) and Eickenscheidt & Wellbrock (2014) for examples of these). In the present study, we observed an increasing trend in defoliation over the period of assessment, which coincides with the trend observed in other European countries, especially in southern Europe (Bussotti et al., 2018; Carnicer et al., 2011; de la Cruz et al., 2014). As such, although we cannot completely rule out the possibility of bias due to subjectivity in the visual assessment, these long-term trends are unlikely to be due to the effects of observer errors in assessed defoliation data. Another potential limitation of this study is that the available water capacity of soils was not determined. During drought, reduced precipitation leads to decline in soil moisture, often in combination with higher temperatures and increased evaporative demand from the atmosphere, which ultimately induces water stress in trees (Choat et al., 2018). However, soil moisture profiles – ideally, their spatio-temporal evolution – are generally difficult to obtain or are not readily available, as is the case in this study. In future studies, it would be interesting to examine the temporal dynamics of soil water content (e.g., by means of a soil water balance model) to further understand the mechanisms that control the physiological responses of trees to drought (e.g., hydraulic redistribution; Neumann and Cardon, 2012).

In fact, among the biotic and abiotic factors that drive forest defoliation, water availability is often the most limiting factor in many forest ecosystems (Bréda et al., 2006). Drought is a natural phenomenon characterized by the prevalence of low water availability during longer periods as a consequence of reduced precipitation, increased atmospheric evaporative demand or both (Trenberth et al., 2013). There is growing evidence that drought impacts have increased considerably in recent decades (Schwalm et al., 2017). In addition, projected changes in both precipitation and temperature over the 21st century suggest a general decrease in available water for the summer period, in Belgium (Tabari et al., 2015), as elsewhere (Dai, 2013; Kumar et al., 2013), which implies that many forests will become increasingly vulnerable to drought and associated disturbances (Allen et al., 2010; Choat et al., 2012; Neumann et al., 2017). For Belgium, for instance, the cumulative water shortage during the summer season is projected to go up to about 200 mm in the late 21st century, suggesting an increased risk of summer drought (Tabari et al., 2015). Drought induces short-term physiological disorders by decreasing carbon and nutrient assimilation and can cause hydraulic failure (xylem embolism) in more extreme cases or carbon starvation (exhaustion of stored soluble carbohydrates in sapwood) after long exposure (Bréda et al., 2006). Trees may recover from these symptoms and restore their crowns, but in the long term, the accumulation of these processes is more likely to result in progressive decline and eventual death of the tree. Such lagged susceptibility has been widely reported (Anderegg et al., 2013; Bréda et al., 2006; Camarero et al., 2015). Anderegg *et al.* (2013), for example, found that hydraulic damage persisted and increased in dying trees over multiple years and exhibited few signs of repair.

Here, based on the SPEI index, representing drought conditions in the previous 16 months, we observed a significant increase in the number of dry years, as well as a decrease in the occurrence of wet years, obviously important to restore ecosystem health after dry periods. For instance, the year with the lowest SPEI value was 1997. Yet, it was followed by relatively wet years, which are likely to have alleviated the adverse effects of drought stress on trees, thus not causing serious damage. Conversely, 2004 marked the beginning of a period of successive relatively dry years, with a peak in defoliation in 2005 (in response to the drought of 2003), and particularly the period between 2010 and 2012, when we observed the highest levels of defoliation. Such repeated drought events suggest that the studied stands may suffer chronic stress, making it plausible to conclude that the observed increase in defoliation was triggered by successive droughts. Our results correlate well with the literature in the sense that shorter drought recovery times have been shown to cause lasting damage to forests (Schwalm et al., 2017). Furthermore, we found that the highest correlations between the SPEI and tree defoliation occur at timescales longer than 12 months. These results are consistent with those of previous studies, which have observed that tree vitality in Europe's forests is substantially driven by climate variability in both the current and preceding years (Neumann et al., 2017). Defoliation of *F. sylvatica* in a given year, for instance, has been consistently associated with low precipitation and high evapotranspiration rates in the year before (e.g., Seidling, 2007; de la Cruz *et al.*, 2014; Ferretti *et al.*, 2014). The previous year's defoliation has also been suggested to enhance the process of defoliation in the current year (de la Cruz et al., 2014; Ferretti et al., 2007).

3.5.2. TREE SPECIES RICHNESS INCREASES RESISTANCE TO DROUGHT

In mixed forests, interactions between species strongly influence ecosystem properties. Positive biodiversity-ecosystem functioning relationships are commonly attributed to a combination of selection and complementarity effects (Hooper et al., 2005; Loreau and Hector, 2001). In contrast, a negative effect of diversity on ecosystem functioning can result from direct competition for resources between species when ecological niches overlap (Naeem, 1998). Among the many studies that have investigated these processes, several have reported conflicting results (Forrester et al., 2016; Jactel and Brockerhoff, 2007; Jucker et al., 2014b; H. Pretzsch et al., 2013). This apparent incongruence can at least partially be explained by the facts that facilitation and competition always occur simultaneously and that the net effect is strongly species- and context-dependent and subject to change through time. Such context dependency derives in part from changes in the availability of resources, and the dissimilarity in both species composition and species interactions, over space and time. These dynamics may also help to explain why the models retained large portions of unexplained variability. As for the influence of age on defoliation, there is a tendency for increased defoliation with age, but both young and older trees showed similar responses with respect to species richness (see Supplementary Note A.2 for a detailed discussion).

Our results suggest that not only species interactions may involve a complex balance of competition and facilitation, but also demonstrate a complex interplay between tree species richness and the longer-term responses of forest ecosystems to drought-induced stress. Initially, defoliation levels were significantly lower in monoculture stands. However, following a progressive shift, the balance between tree species diversity and drought responses was reversed by approximately 2010, which is well consistent with the increased drought stress, after which defoliation decreased with increasing tree species richness. While the positive effect of diversity on the vitality of young experimental tree plantations has been previously demonstrated (Van de Peer et al., 2016), our findings highlight for the first time the close link between species richness and repeated defoliation in a large systematic sample of mature (managed and unmanaged) forests. Regarding the role of management, it has been suggested that forest management can be used to reduce the incidence of defoliation, in particular caused by insects (Jactel et al., 2009; Muzika and Liebhold, 2000). This can be done, for instance, by selectively harvesting high-risk trees to reduce the susceptibility (likelihood of defoliation) and vulnerability (likelihood of mortality following defoliation) of the stand. Thinning also modifies the structure of forest stands, and reducing stand density through silvicultural thinning has been proposed as a strategy for improving resistance and resilience to drought via increased soil water availability (D’Amato et al., 2013). In our case, however, as many plots have not been subjected to thinning or other management since the beginning of the 1990s, or when thinning has been applied, we have no indication that treatments were different between monocultures and mixtures, nor did it change over time, the management effect seems highly unlikely as an explanation of our observations. The observed tipping point in the relationship between species richness and the health and vitality of forests, suggesting that species interactions shifted from competition to facilitation, though implicit in the literature, has never been reported from real ecosystems outside experimental conditions. Furthermore, the strong temporal consistency of our observations with increasing drought stress emphasizes its climate change relevance. Natural systems are variable not only in space but also in time. However, due to the lack of long-term studies, empirical evidence for temporal shifts in the balance between facilitation and competition in long-lived systems is extremely limited (but see (2000). Here, we show that this relationship is not immutable and can even flip from overperforming monocultures to overperforming mixtures with increasing environmental stress, as more diverse communities are able to maintain relatively higher levels of functioning than less diverse ones under stressful conditions (Isbell et al., 2011).

3.5.3. MECHANISMS OF RESISTANCE OF MIXTURES TO WATER STRESS

The fact that, for both *F. sylvatica* and *Q. petraea*, the mean defoliation level was highest after dry years than wet years confirms the results of earlier studies (e.g., Seidling, 2007; Carnicer *et al.*, 2011; Sánchez-Salguero *et al.*, 2016), as well as our hypothesis, that drought can trigger and expedite defoliation in deciduous forests. But perhaps more importantly, our results reveal that the negative impact of drought on the crown defoliation of the three studied species in deciduous temperate forests was mitigated by species mixing through time (i.e., interaction between species richness and year of observation; Figure 3.4b). This was particularly evident in *F. sylvatica* and *Q. petraea*. In the fullness of time (i.e., within the study period), the two species experienced the largest decline in vitality when growing in a monoculture (Figure 3.4b), which was further corroborated by the observed shift in the relationship between tree species richness and crown defoliation. It is also noteworthy that the positive effect of species richness on crown condition arose after a period of steady increase in defoliation, which adds further support to our observation that increased stress had a stronger negative effect on less diverse plots.

This positive relationship between biodiversity and stability is often assumed to result from compensatory dynamics between species, mostly through strong complementarity between species (Morin et al., 2011). The superior performance (i.e., lower defoliation levels) of monocultures compared to stands with higher species richness at the beginning of the monitoring period might be explained by differences in resource use efficiency. On the one hand, with high resource availability, and in the absence of significant disturbances, interspecific competition might outweigh the positive effects of species facilitation and complementarity (Maestre et al., 2009); thus, this might enhance the performance of trees growing in monocultures. On the other hand, in the short-term, drought may cause trees in a mixed forest to compete more fiercely for resources, leaving less room for complementarity and causing positive diversity effects to weaken (Jucker et al., 2014b). However, as we have shown here, under increasing environmental stress, increasing species richness reduced drought-induced defoliation in the long term. The overall pattern we found corroborates the stress-gradient hypothesis (Bertness and Callaway, 1994; Maestre et al., 2009), which posits that the net outcome of biotic interactions (facilitation and competition) shifts from negative to positive along gradients of increasing stress. Recurrent drought periods, such as those observed in recent years, may produce a rapid loss of resilience by carbon starvation and embolism, particularly when new disturbances occur before the reserves are fully recovered (Bréda et al., 2006). Conversely, increasing tree species diversity may mitigate the impact of disturbances, as more complementary interactions are expected. Water uptake efficiency likely increases in mixed forests because a greater volume of soil can be exploited in space and time by species with complementary root stratification (Brassard et al., 2013). This can arise from root plasticity or differences in root foraging strategies among species. For example, in dry years, available water might be better used in mixed stands due to facilitation mechanisms such as hydraulic lift whereby deeper rooting tree species take up water and redistribute it via their root system to drier superficial soil layers, thus favouring shallower rooting species (H. Pretzsch et al., 2013; Hans Pretzsch et al., 2013). Resistance to insect defoliators has also been reported to be positively affected by tree species richness (Guyot et al., 2016).

In addition, previous studies have also described strong species identity effects on crown defoliation (e.g., Pollastrini *et al.*, 2016; Bussotti *et al.*, 2018). Thus, identity and diversity may affect tree defoliation. Surprisingly, among the three studied tree species, *Q. robur* exhibited the highest average defoliation in both pure and mixed stands. *Quercus robur* is known to be less tolerant of water shortages than *Q. petraea* (Hans Pretzsch et al., 2013). However, both species are believed to suffer less than *F. sylvatica*, partly because they can maintain photosynthesis at low water potential (Raftoyannis and Radoglou, 2002). This somewhat unexpected finding can, at least to some extent, be linked with the widespread occurrence of oak decline across Europe. Oak decline is a slow-acting disease complex in which several damaging agents interact and result in the mortality of *Quercus* spp. (Thomas et al., 2002). Both *Q. petraea* and *Q. robur* are subject to decline, but on average, here and in other studies, *Q. robur* has been more severely affected than *Q. petraea* (Thomas et al., 2002). These examples may show that the current process of *Q. robur* decline is not necessarily triggered by drought, but risk is associated with increased stress. In this study, identifiable causes of defoliation and damage symptoms (as assessed according to the ICP Forests criteria) were not consistently available for analysis or were unreliable. Future research that examine particular causes of stem and crown damages, and their influence on crown condition, may provide valuable information to disentangle the cause-effect relationship of forest decline.

3.6. CONCLUSIONS

We found that the crown condition of *F. sylvatica*, *Q. petraea* and *Q. robur* trees in temperate deciduous forests has deteriorated over the past quarter century, closely connected to increasing drought stress. This change has triggered a regime shift from healthy monocultures to resilient tree species mixtures. For the first time, we document a tipping point beyond which a drought stress-induced positive diversity-stability relationship in mature forest ecosystems emerged. Our results show that standardized, large-scale, long-term monitoring of forest health, such as that performed in Europe by ICP Forests, is an effective method to detect climate change-induced and tree diversity-mediated trends in forest vitality. Despite repeated criticism due to subjectivity in the visual assessment and a number of limitations have been associated with the monitoring approach (Ferretti and Chiarucci, 2003; Innes et al., 1993), the very high representativeness over space and time of the ICP Forests monitoring program, and the continuous improvement in the quality of data that has been achieved so far (Bussotti et al., 2009; Eickenscheidt and Wellbrock, 2014), has proven to be an effort that merits improved and extended continuation. We recommend further investigation of longitudinal data sets of forest vitality to corroborate the trends we observed for other species and in different climatological contexts.

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CHAPTER 4

THE EFFECT OF TREE DIVERSITY ON GROWTH RESPONSES TO DROUGHT

Based on *Sousa-Silva R, Verheyen K, Bay E, Sioen G, Titeux H, Vanhellemont M, Ponette Q, Muys B. Unveiling the role of forest diversity for tree growth and recovery to drough (submitted).*

4.1. SUMMARY

Droughts have become increasingly more common worldwide. For forests, drier conditions have been linked to reduced primary production and mortality. Complementarity among species for resource use may lead to reduced competition and increased facilitation, resulting in higher growth rates and higher resilience to drought. Therefore, mixed-species forests have been proposed as a strategic approach for managing forests under future climate change. Yet, whether or not mixed forests are more capable of withstanding drought conditions remains unclear.

In this study, we investigated how the growth and resilience to drought of *Fagus sylvatica*, *Quercus petraea*, and *Q. robur* relate to forest diversity, across three distinct drought events, and additionally examined whether declining growth was correlated with increased defoliation. We monitored over 1,900 individual trees across 90 long-term forest vitality monitoring plots between 1990 and 2016. Trees growing in mixtures were more resilient to drought compared to those growing in monocultures, and recovery after drought was also faster and more pronounced in mixtures than in monocultures. In addition, we found a tendency towards lower resilience to drought in defoliated trees. Reductions in growth during drought years were more pronounced for *F. sylvatica*.

Our results demonstrate a clear link between more frequent droughts and a reduction in tree productivity, associated with longer recovery times. Moreover, these findings indicate that higher tree species diversity allows for higher growth resilience to drought, which adds further evidence to the overall positive impact of diversity on forest productivity under the anticipated warmer and drier conditions.

4.2. INTRODUCTION

The importance of forests in providing valuable ecosystem services to society has been increasingly recognized (Mori et al., 2017). Under rapidly changing environmental conditions, the importance of gaining knowledge about the responses of forests to global change is therefore also growing. Natural disturbances are an integral part of forest ecosystem dynamics (Thom and Seidl, 2016; Turner, 2010). However, disturbance regimes are changing, and the implications of such changes for forests and the services they provide to society are still uncertain (Seidl et al., 2017; Thom and Seidl, 2016). An increase in disturbance frequency may exceed the resilience of forests and trigger transitions to alternative ecosystem states when tipping points are crossed (Buma and Wessman, 2011; Reyer et al., 2015; Seidl et al., 2016b). Consequently, changing disturbance regimes, such as repeated or prolonged droughts, are assumed to be amongst the most severe impacts that climate change will impose on forests in the next decades (Lindner et al., 2010). Drought can have major impacts on both human and natural systems (Schwalm et al., 2017). In forests, drought has been associated with large-scale die-off and decreases in productivity (Cavin et al., 2013; Grossiord et al., 2014). Furthermore, because of climate warming, droughts are expected to become more frequent due to decreasing regional precipitation and increasing evapotranspiration (Seneviratne et al., 2012). Thus, the time between droughts may become shorter than the time needed for forests to recover from them, pushing some ecosystems into an alternative, less desirable state in a sudden and hardly reversible manner (Anderegg et al., 2015b; Caldeira et al., 2015; Schwalm et al., 2017).

The enhancement and maintenance of species diversity have been advocated as means to increase forest resilience to climate change (Elmqvist et al., 2003; Folke et al., 2004). If multiple co-occurring species contribute to the same ecosystem function yet exhibit a variety of responses to environmental changes, increased diversity might provide insurance against ecosystem regime shifts, i.e. transition to a less productive or otherwise less desired ecosystem state (Cavin et al., 2013; Folke et al., 2004). Monocultures can be notoriously vulnerable to sudden ecosystem regime shifts to a lower functional state, when critical thresholds in climate conditions are exceeded (Scheffer and Carpenter, 2003). This is especially true for forests; the long lifespan of trees implies that their establishment may have occurred under climatic conditions different from those they now occupy, but also that they are more likely to experience extreme events within their lifetimes (Petit and Hampe, 2006).

Forest decline has been related to two main processes: a progressive growth reduction and a sharp increase in defoliation (Sánchez-Salguero et al., 2012). It has been further suggested that negative growth rates and enhanced defoliation tend to be correlated in a decline process (Drobyshev et al., 2007; Guada et al., 2016; Sánchez-Salguero et al., 2012). Defoliation depends on many stress factors, especially drought (Carnicer et al., 2011), and is a key parameter for monitoring forest health describing a loss of foliage compared to a reference standard tree (Michel and Seidling, 2017). We previously examined the influence of drought on the relationship between tree species richness and crown condition decline in deciduous temperate forests (Sousa-Silva et al., 2018b). Higher species richness was shown to reduce the severity of crown defoliation in the long term and under conditions of increasing drought stress. In the present study, we extend our analysis to drought impacts on tree growth.

The beneficial effect of forest diversity on ecosystem functioning, in particular on tree productivity, is determined by mechanisms arising from species interactions (Liang et al., 2016a; Paquette and Messier, 2011). For instance, complementary use of resources through niche differentiation and facilitative processes increases ecosystem performance. Because of the differences in resource use and acquisition among neighboring species, the available resources can potentially be fully exploited, thereby reducing competition among neighboring trees (Loreau et al., 2001). More diverse forests are also more likely to be more resilient to biotic stresses such as insects and disease outbreaks due to mechanisms of associational resistance (Guyot et al., 2016; Haas et al., 2011). However, the question remains as to whether a higher species diversity in forests also leads to a higher resilience of trees to drought (Dai, 2011; Sheffield and Wood, 2008). So far, published studies have shown inconsistent results (del Río et al., 2013; Forrester et al., 2016; Grossiord et al., 2014; H. Pretzsch et al., 2013).

Therefore, here we sought to compare the growth responses to drought of *Fagus sylvatica*, and native *Quercus* spp. (*Q. petraea* and *Q. robur*) growing in neighborhoods differing in tree species richness. Mixtures of *F. sylvatica* and *Quercus* spp. are common in Europe, and have been suggested to serve as a source of resilience in the event of disturbances (del Río et al., 2013; H. Pretzsch et al., 2013; Hans Pretzsch et al., 2013). We hypothesized that: (i) trees growing in more diverse stands will have a stronger resistance and recover more quickly from drought events than trees in monocultures; and (ii) defoliated trees will grow less and show the lowest resilience (including both resistance and recovery) to drought. We also expected to detect significant differences in the effect of, and recovery from drought on tree growth, between successive droughts, regardless of the stand diversity and crown condition.

4.3. METHODS

Sampling network and tree selection criteria. This study was carried out in Belgium using data from the European ICP Forests program. The network of ICP Forests plots is organised in two levels that differ in the intensity of monitoring (Level I and Level II), but crown condition and tree diameter increment are assessed in both levels (Ferretti, 2013). Level I involves monitoring of the spatial and temporal variation of forest condition across a broad geographic range; Level II aims at in-depth understanding of the cause-effect relationships between stress factors and the condition of forest ecosystems. In Belgium, the Level I survey was originally conducted on a 4 km x 4 km grid (Flanders) and 8 km x 8 km grid (Wallonia). In each plot, a cross-cluster sampling was used to select four groups with six trees (Ferretti et al., 2017). If a monitored tree died, due to either anthropogenic or natural causes, it was replaced within the plot to ensure a constant sample size over the time period of assessment. In 2009, circular plots (radius 18 m) were installed and from 2012 on, sample trees have been selected only in these circles. Level II plots consist of a fenced core area of 0.5 ha surrounded by a 20 m buffer area.

Periodic measurements of tree diameter are mandatory for Level II plots, but optional in Level I plots. In each plot, stem diameter (at 1.3 m above the ground) was measured for all trees with diameter ≥7 cm. We used all *Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl., and *Quercus robur* L. trees from the Level I and Level II crown condition assessment for which at least three diameter measurements were available between the years 1990 and 2016. Since not all the individual trees were measured every year, we filled gaps in the diameter time series using linear interpolation between the before-gap and after-gap year to preserve monotonicity. Gap-filling was done only by interpolation at the middle of a series, never by extrapolation at the beginning or end of a series. For each tree, we then transformed the diameter time series into basal area and basal area increment time series. This resulted in a total of 30,049 observations (1,926 trees x 27 years), of which 18% were interpolated observations.

For the 91 study plots (see Table 4.1), we calculated the total basal area of the plot based on the tree diameters. Plot species richness was determined as the number of tree species in each plot, ranging from monocultures to a maximum of five species. A plot was considered *monospecific* when the corresponding species accounted for ≥ 90% of the total basal area (Pretzsch et al., 2017). Similarly, a plot was classified as *mixed* when the considered species together represented ≥ 90% of the total basal area and each of the species contributed at least 5% to the basal area. Tree defoliation was assessed in 5% steps in accordance to the ICP Forests criteria (Eichhorn et al., 2016). A tree is considered defoliated if the crown defoliation exceeds 25% (Michel and Seidling, 2017).

__Table 4.1 Main characteristics of the study plots__. Number of observations; age class^{a} (median); mean (with standard deviation between brackets) of tree diameter and defoliation, plot elevation, annual mean temperature and total annual precipitation^{b} for the monoculture and mixed plots in which Fagus sylvatica, Querucs *spp. grew.*

	Fagus sylvatica		***Quercus petraea***		***Quercus robur***	
	Monocultures	Mixtures	Monocultures	Mixtures	Monocultures	Mixtures
Np. plots	*16*	*32*	*6*	*19*	*16*	*42*
No. trees	*384*	*320*	*120*	*171*	*405*	*525*
Age class	*5*	*6*	*7*	*4*	*5*	*5*
Diameter (cm)	*47.0 (15.6)*	*56.0 (17.9)*	*50.2 (11.3)*	*46.2 (15.3)*	*38.4 (13.1)*	*48.0 (15.6)*
Crown defoliation (%)	*18.9 (16.3)*	*19.5 (15.0)*	*13.5 (14.4)*	*13.9 (14.0)*	*20.4 (13.6)*	*21.3 (11.6)*
Elevation (m)	*299 (213)*	*240 (150)*	*347 (92)*	*224 (146)*	*127 (152)*	*83 (109)*
Annual temperature (°C)	*9.4 (1.0)*	*9.7 (1.0)*	*9.3 (0.8)*	*9.5 (0.8)*	*10.4 (0.8)*	*10.5 (0.6)*
Annual precipitation (mm)	*1042 (143)*	*994 (125)*	*913 (89)*	*1056 (154)*	*939 (153)*	*881 (113)*

[a] *The age class of the dominant storey is reported in 20-year classes, as follows: '1' = 0-20 years; '2' = 21-40 years; '3' = 41-60 years; '4' = 61-80 years; '5' = 81-100 years; '6' = 101-120 years; '7' > 120 years. The age class was unknown or could not be determined for 11 study plots.*

[b] *Metereological data were averagaed from daily means over the period 1990-2016.*

The data set covers the two ecoregions of Belgium: the lowlands located to the north of the Sambre and Meuse rivers in the maritime climate zone and the uplands with hilly topography south of this axis, in the sub-continental climate zone. In the lowlands, soils are deeper (>1 m) and mainly composed of silt loam and sand in different proportions. In the uplands, soils are shallow and can be sandy, loamy or clayey with a high stone content. Soil properties (including fertility, drainage and texture) were retrieved from the digital soil map of Belgium (Dondeyne et al., 2014), and described in detail in Supplementary Note A.2.

Drought years and disturbance responses. In order to explore the relationship between climate and tree growth, daily weather variables were obtained for all plots from the high-resolution FORBIO Climate dataset: maximum temperature, minimum temperature and precipitation. This data set has a 4 km × 4 km resolution and covers the period from 1980 to 2016. Details on interpolation methods and data quality control procedures applied to the meteorological observations to generate this climate data set are described in Delvaux et al. (2015).

Drought severity was quantified using the multiscalar standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al., 2010). SPEI is a drought index with flexible temporal integration from 1 up to 24 months and has been demonstrated to be effective in the study of tree growth responses to climate (Cavin and Jump, 2017; Schwalm et al., 2017). SPEI is calculated as the difference between monthly precipitation and potential evapotranspiration, thus accounting for both temperature and precipitation, with potential evapotranspiration derived from the Hargreaves equation (Vicente-Serrano et al., 2010). These values represent either a water surplus or deficit for a given month and are then aggregated over the desired integration timescale. Typically, SPEI takes negative or positive values in the range between -2.5 and +2.5, indicating dry- or wet-conditions (Beguería et al., 2010; Vicente-Serrano et al., 2010). Following Merlin et al. (2015), we calculated SPEI for the growing season (April to October; $\text{SPEI}_{7\text{–Oct}}$), and the threshold of –1 (Merlin et al., 2015; Schwalm et al., 2017) was used to identify individual drought events between 1990 and 2016. We categorized the years 1995, 2003, 2009, and 2011 as drought years (SPEI of -1.12, -1.57, -1.17, and -1.31; Figure 4.1), and combined the 2009 and 2011 droughts into a single event. We did not consider the 1990, 1991, and 2015 droughts in our analysis given that the pre-drought and post-drought periods for these years were not fully contained within the period of study.

Differences in basal area increment between pre-drought, drought, and post-drought periods were compared using one-way ANOVA with a Tukey's *post hoc* test for multiple comparisons ($P < 0.05$). Recovery after drought was analysed by comparing the basal area increment during the year(s) before the drought (pre-drought growth) with the basal area increment of the after-drought years (post-drought growth) (Anderegg et al., 2015b). We accounted for background differences between stand types (e.g. monocultures versus mixtures) using baseline-normalization, i.e., by expressing the state after disturbance relative to its state pre-disturbance (baseline state, at time t_0) as recommended by Ingrisch and Bahn (2018). To rule out any possible bias caused by differences in tree size between mixtures and

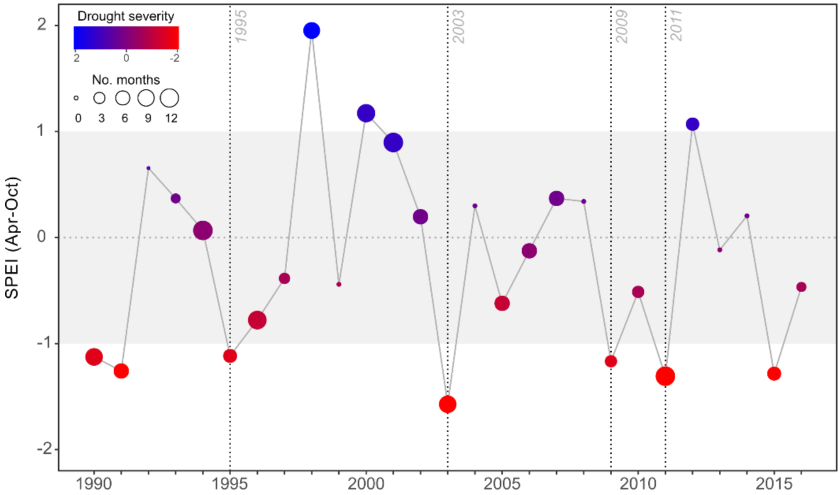

Figure 4.1. Drought years since 1990. *Drought severity represented by SPEI calculated for the growing season (April–October;* $SPEI_{7\text{–}Oct}$*) from 1990 to 2016. The red and blue colors denote conditions respectively drier or wetter than the median of the 1990–2016 period. The size of the dots denotes the number of months per year classified as dry (SPEI ≤ -1) or wet (SPEI ≥ 1). Vertical dotted grey lines indicate the drought years discussed in the text.*

monocultures (e.g., *F. sylvatica* trees had a somewhat larger diameter in mixtures), we first checked for differences in basal area increment at time t_0 (baseline state), and found no significant differences between stand types at the time immediately before disturbance. For each drought, three disturbance responses – resistance, recovery, and recovery time – were examined separately for each species, stand type (monoculture/mixture), and tree crown condition (defoliated/non-defoliated). Resistance is the capacity to reduce the impact of disturbance; recovery is the capacity to recover from the impact of disturbance; and recovery time is defined as the time from when recovery begins time is defined as the time from when recovery begins (first year after the drought) until it is completed (when post-drought growth returns to its pre-drought level) (Schwalm et al., 2017). Resilience combines tree resistance to and recovery from drought, and is defined as the capacity to persist and maintain its functioning under drought stress (Ingrisch and Bahn, 2018).

Modelling framework. We used basal area increment as response variable to model the influence of species identity, species diversity, and defoliation on individual tree growth. First, we modelled the basal area increment for each tree (BAI) over the 1991-2016 period as a function of species identity (SP, i.e., *F. sylvatica*, *Q. petraea*, *Q. robur*), species richness (SR) and crown defoliation in the previous year (DFL of t_{-1}), also accounting for tree *size* (i.e., diameter at breast height in the previous year, t_{-1}), *age* class, stand *management* (even-aged, uneven-aged), *climate* (i.e., mean annual temperature and annual precipitation during the study period, and drought severity quantified by SPEI computed for the growing season), and *soil* variables. We additionally included two interaction terms to account for potential differences between species in their responses to increased diversity and increased defoliation: (species identity x species richness) and (species identity x tree defoliation). Tree identity nested within plot was specified as a random effect in the model. Potential temporal autocorrelation in the data was accounted for by using an autoregressive correlation structure [ARMA(2,0)]. The annual basal area increment, diameter, and crown defoliation were tree-level data (i); the other variables were available at plot level (j); and ε_i is the residual error.

Eq. 1:

$$
\begin{aligned}
sqrt(BAI_{i,j}) = \beta_0 &+ \beta_1 size_{i,t_{-1}} + \beta_2 DFL_{i,t_{-1}} + \beta_3 SP_i + \beta_4 SR_j \\
&+ \beta_5 (SP_i : DFL_i) + \beta_6 (SP_i : SR_j) + \beta_7 age_j + \beta_8 mgmt_j \\
&+ \beta_9 clim_j + \beta_{10} soil_j + \varepsilon_{i,j}
\end{aligned}
$$

Second, to investigate the effects of drought on the relationship between tree growth, species diversity and crown defoliation, we fitted the same model using only the growth observations from during the post-drought recovery time, and using a fixed post-drought time horizon of 4 years. We included additional interaction terms to account for potential differences between species in their responses to drought across diversity and defoliation levels for each drought event: (species identity x species richness x drought event) and (species identity x tree defoliation x drought event).

For both models, the goodness of fit was estimated using marginal and conditional *R*-squared, which allow for assessing the predictive capacity of mixed-effects models (Nakagawa and Schielzeth, 2013). Prior to the inclusion of any variables in the models, we tested for collinearity using variance inflation factors (VIF), and no variable had to be removed (all VIF < 4). Variables that were not significantly related to the tree growth were dropped (drought index SPEI, soil fertility and texture). Analyses were conducted in R 3.4.3 (R Development Core Team, 2017), using the following libraries: *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2016) and *MuMIn* (Barton, 2016).

4.4. RESULTS

4.4.1. GENERAL PATTERNS OF POST-DROUGHT GROWTH

An increase in drought conditions was synchronous with a reduction in tree productivity, although we found no relationship between drought severity and tree growth. The basal area increment dropped for the three species during the drought events of 1995, 2003, and 2009-2011 (Figure 4.2). *Quercus petraea* was an exception, with the drop in growth rate for the 2009-2011 drought occurring in 2011 only. The decreases in basal area increment were largest for *F. sylvatica*, whose growth was reduced by 20% after the first drought (1996) and by 30% for the following droughts (Figure 4.3). By comparison, *Q. robur* suffered only a 10% reduction in 1996 and 20% in 2012; whereas *Q. petraea* experienced a 10% reduction in response to the 2011 drought (Figure 4.3). After the growth suppressions of 1995 and 2011, growth recovery started almost immediately; after 2003, though, growth rates continued to decrease until 2005 for *F. sylvatica*, and 2006 for *Quercus* spp. By 2016, *F. sylvatica* and *Q. robur* had not yet fully recovered from the 2009-2011 drought event (Figure 4.3).

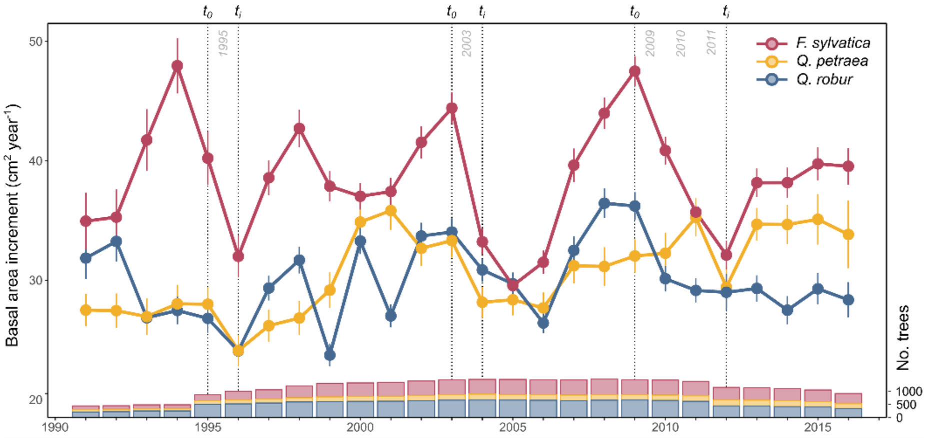

Figure 4.2 Annual basal area increment from 1991 to 2016 for the three studied tree species. *Values are means with standard errors (left y axis), and the bars show the sample depth, i.e., the annual number of assessed trees (right y axis) for* Fagus sylvatica *(red),* Quercus petraea *(yellow), and* Quercus robur *(blue). Vertical dotted lines encompass the immediate effect of the drought event;* t_o *and* t_i *correspond to the time immediately before and immediately after the main disturbance effect.*

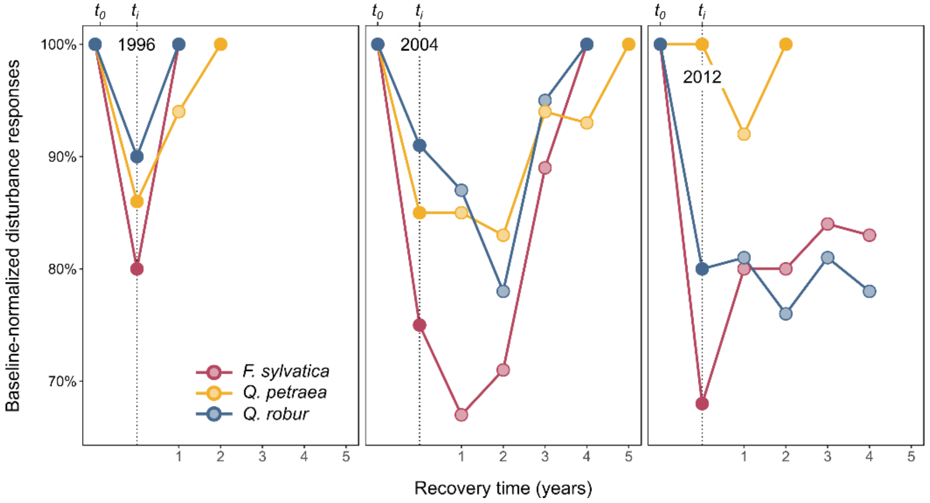

Figure 4.3 Relative growth responses and recovery time of the three studied tree species for the three drought events. *The three drought events are shown in three separate panels, and* t_o *and* t_i *correspond to the time immediately before and immediately after the main disturbance effect for* Fagus sylvatica *(red),* Quercus petraea *(yellow), and* Quercus robur *(blue). Both the impact (at time* t_i*) and the annual growth rates afterwards are expressed as a percentage of the baseline state (at time* t_o*). Recovery time starts the first post-drought year and is assumed to be complete once post-drought growth returns to its baseline state (filled dark circles).*

The three drought events, and associated recovery periods, differed in their duration and severity. For instance, the drought of 2003 had the lowest SPEI scores for the whole period 1991-2016 ($SPEI_{7–Oct}$ =-1.57; Figure 4.1). The 2009–2011 drought, on the other hand, was followed by a relative wet year in 2012 ($SPEI_{7–Oct}$>1; Figure 4.1), which initiated the recovery in tree growth. The recovery time became longer as the time between droughts became shorter. For *Q. petraea*, the post-drought recovery time of the 2003 drought event even overlapped with the pre-drought baseline period of 2009-2011 drought event.

4.4.2. THE INFLUENCE OF DIVERSITY ON TREE GROWTH

Species richness was significantly and positively related to basal area increment (P < 0.001; Figure B.1-B.3). Trees in mixtures grew faster than those in monocultures (Figure 4.4, top) and had a greater capacity to recover after drought. This tendency was consistent across species, although not always significant (Figure B.4-B.6). Consequently, the post-drought growth was also higher in mixtures than in monocultures (P < 0.05;). Monocultures were more strongly affected by drought than mixtures, which was particularly evident for the first drought event (1995) during which the trees in monocultures experienced the greatest growth decline. Similarly, in 2012, the drop in growth was ~1.2 times more pronounced for *F. sylvatica* trees growing in monocultures (37% reduction) than in mixtures (27%), and ~1.3 times for *Q. robur* trees between monocultures (30% reduction) and mixtures (20%). The trees in monocultures also had the longest post-drought recovery time; they required two to four years to regain the pre-drought levels of growth (Figure 4.5). By contrast, trees in mixtures were able to recover to pre-drought growth levels within a year. For *F. sylvatica* and *Q. robur*, this pattern was consistent across the three drought events, but *Q. petraea* showed a higher resistance to drought and a higher recovery rate in monocultures than in mixtures, although statistically non-significant, for the 2003 and 2009-2011 drought events.

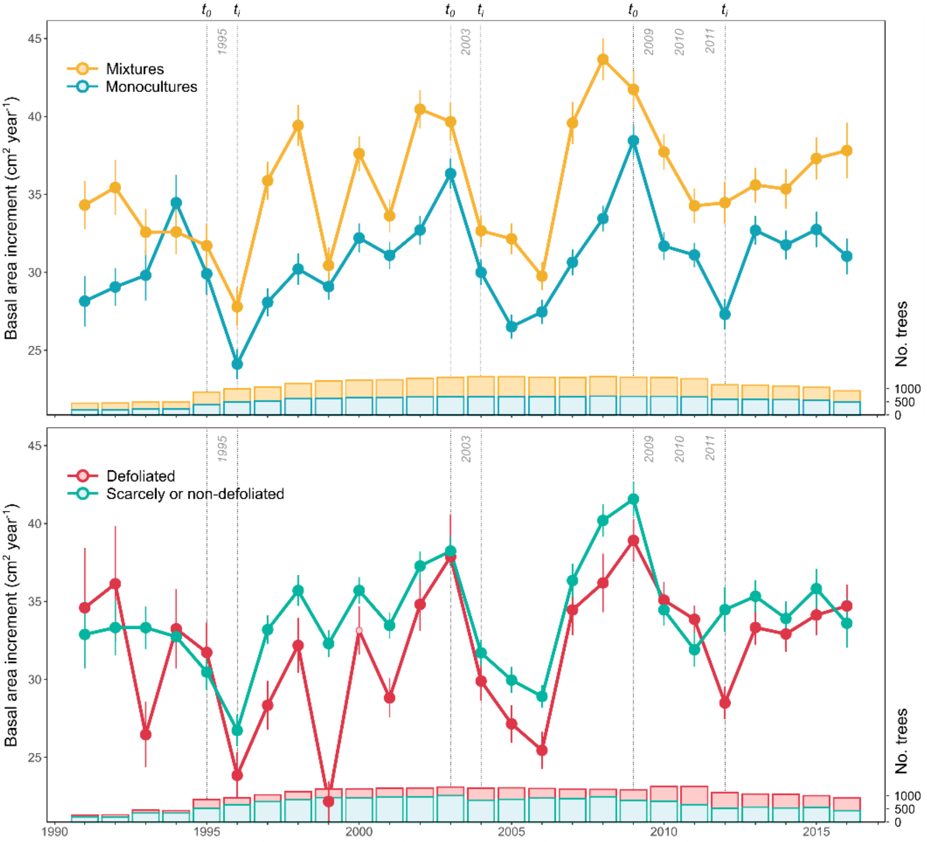

__Figure 4.4 Basal area increment for trees in mixtures and monocultures (top) and for defoliated and non-defoliated trees (bottom).__ Values are means with standard errors (left y axis), and the bars show the sample depth, i.e., the annual number of assessed trees (right y axis). Vertical dotted lines encompass the immediate effect of the drought event; t_0 *and* t_i *correspond to the time immediately before and immediately after the main disturbance effect. Mixtures are stands composed of two or more tree species, and trees were considered defoliated when their defoliation was higher than 25% at time* t_0*.*

For species-specific growth, see Figure B.4-B.6.

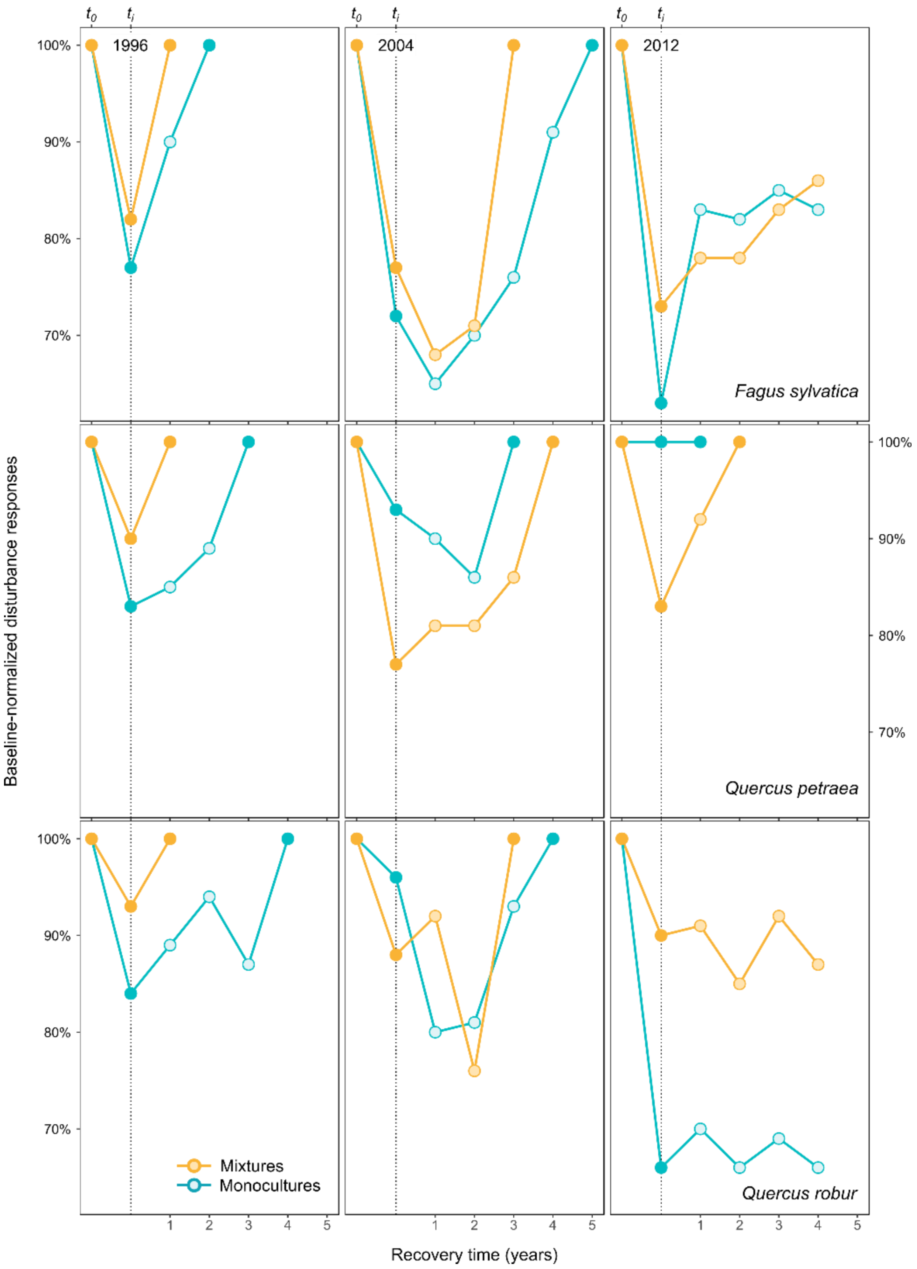

Figure 4.5 Relative growth responses and recovery time of the three studied tree species in mixtures and monocultures. *The three drought events are shown in the three separate panels, and t_0 and t_i correspond to the time immediately before and immediately after the main disturbance effect. Both the impact (at time t_i) and the annual growth rates after the drought event are expressed as a percentage of the baseline state (at time t_0). Recovery time starts the first post-drought year and is assumed to be complete once post-drought growth returns to its baseline state (filled dark circles). Mixtures are stands composed of two or more tree species. For test results, see Table B.1.*

4.4.3. THE EFFECT OF CROWN DEFOLIATION ON GROWTH RATES

There was a negative association between defoliation and productivity ($P < 0.001$; Figure B.1-B.3), and this association was significant for both *F. sylvatica* and *Q. robur*. *Fagus sylvatica* showed an abrupt growth reduction in both defoliated and non-defoliated trees during the three drought events, except for 1995, when the non-defoliated trees showed a significantly higher resistance than the defoliated trees (Tukey's HSD test, $P < 0.05$; Table B.1-B.3). Likewise, the growth after the 2003 and 2009-2011 drought events was significantly lower than that observed before the drought events for both defoliated and non-defoliated trees (Table B.3).

Overall, both defoliated and non-defoliated trees had a marked growth reduction during the three studied drought events, and the resilience to drought (i.e., the capacity to again reach the pre-drought growth values) decreased progressively in both defoliated and non-defoliated trees (Figure 4.6). For instance, for non-defoliated trees, *F. sylvatica* showed a ~1.3 times higher drop in growth in 2009-2011 (27% reduction) than in 1995 (6%), and *Q. robur* a ~1.1 times higher drop (23% in 2009-2011, 12% in 1995). The decrease in resilience was even more noticeable among defoliated trees for the 2009-2011 drought (47% reduction for defoliated *F. sylvatica* trees and 29% for defoliated *Q. robur* trees). No statistically significant differences between defoliated and non-defoliated trees were observed for *Q. petraea*.

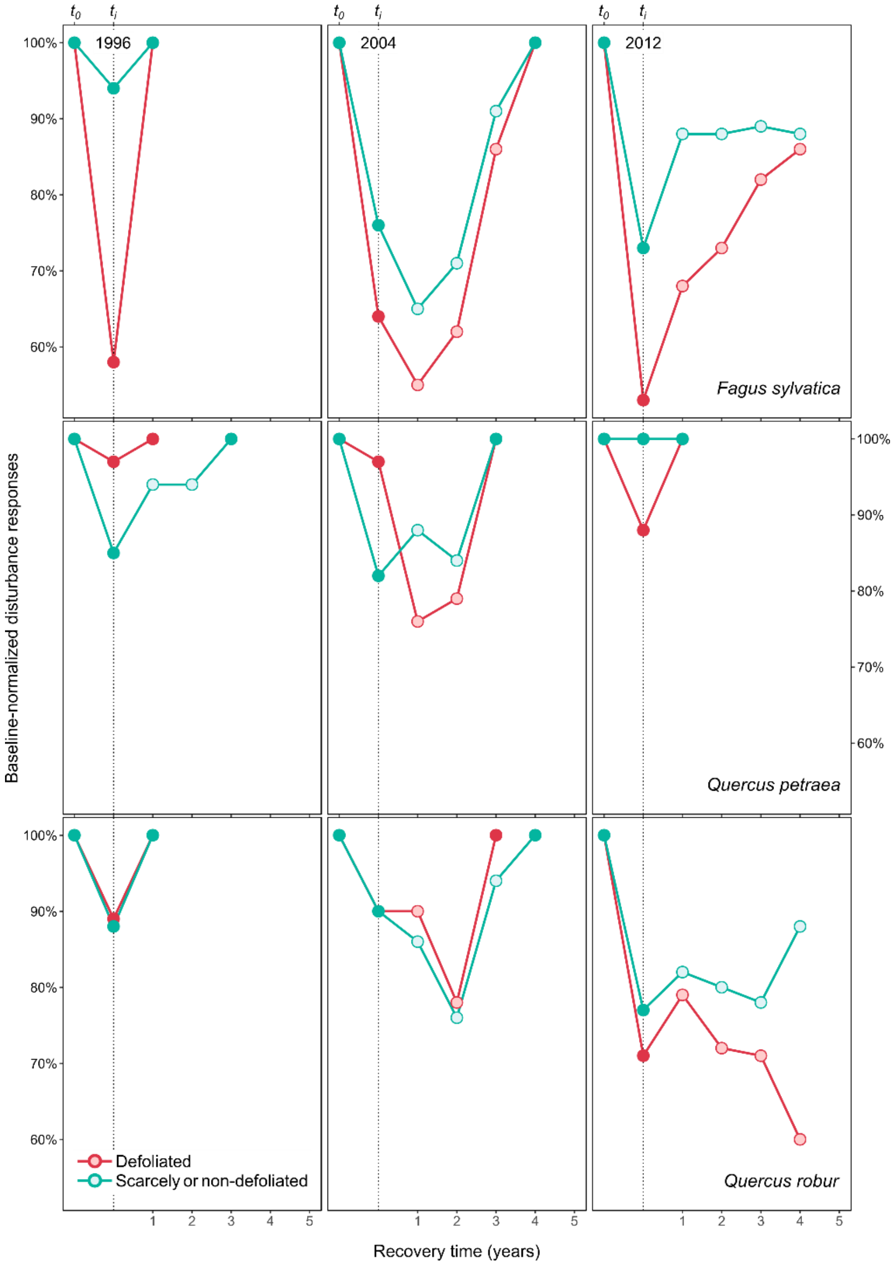

Figure 4.6 Relative growth responses and recovery time of the three studied tree species considering defoliation. *The three drought events are shown in the three separate panels, and t_0 and t_i correspond to the time immediately before and immediately after the main disturbance effect. Both the impact (at time ti) and the annual growth rates after the drought event are expressed as a percentage of the baseline state (at time t0). Recovery time starts the first post-drought year and is assumed to be complete once post-drought growth returns to its baseline state (filled dark circles). Trees were considered defoliated when their defoliation was higher than 25% at time t_0. For test results, see Table B.3.*

4.5. DISCUSSION

4.5.1. DROUGHT STRESS AND ITS INFLUENCE ON INDIVIDUAL TREE GROWTH

Our results provide compelling evidence that drought induces a sharp decline in tree growth. This pattern is not unexpected, as drought-driven declines in forest productivity and widespread increases in tree mortality have been observed at the global scale and across different biomes (Allen et al., 2010), a trend that is expected to continue into the future as climate warms (Schwalm et al., 2017). Trees have evolved many strategies to sustain drought stress. For example, stomatal closure may limit water stress when conditions are not favorable, and restricted shoot growth may result in trees having higher root-to-shoot ratios and greater capacity to take up water relative to the shoots that must be supported (Brunner et al., 2015). In addition, trees have extensive secondary growth, which allows them to increase the thickness of their cell walls and results in increased resistance against cavitation in the vascular tissues (Jacobsen et al., 2005).

From the three studied drought events, the 2003 drought was the most severe, causing a marked reduction in tree growth in the three years following the episode (2004-2006). The drought of summer 2003 was particularly severe in Central Europe and resulted in substantial loss of forest productivity (Bréda et al., 2006; Ciais et al., 2005), followed by increased mortality in 2004 and 2005 in areas where weather conditions remained unfavorable (Bréda et al., 2006). In our case, the growth decline was most evident in 2004, which is consistent with results of other studies (Cavin and Jump, 2017; Pichler and Oberhuber, 2007). Growth recovery lasted from 2005 to 2008 for *F. sylvatica* and *Q. robur*, and until 2009 for *Q. petraea*. This result may seem contradictory to many other examples found in the literature, in which *Q. petraea* is commonly considered more tolerant to drought than *F. sylvatica* and *Q. robur*. However, despite longer recovery times, *Q. petraea* showed a higher resistance to drought, particularly evident for the 2009-2011 drought. The overall impact caused by the 2009-2011 drought was smallest for *Q. petraea* trees, which continued to grow after the 2009 dry year, and only in 2011 the drought event led to a reduction of tree growth. The third and final drought event investigated here (2009-2011) might be considered a succession of unusually dry years, reaching a peak in 2011. Unlike the previous drought events, trees appeared slow to recover pre-drought growth levels, especially in the case of *F. sylvatica* and *Q. robur*, and the marked drop in growth was prolonged at least until the most recent data available (2016).

The recovery time after drought events increased progressively in our study, which points to legacy effects of drought on growth that can last for several years. On the one hand, drought-induced leaf shedding reduces the amount of assimilated carbon allotted to growth during the drought event, which can affect the tree growth during several years following a severe drought (Bréda et al., 2006; Huang et al., 2018). On the other hand, under drier conditions, trees tend to increase below-ground biomass allocation to improve their water foraging capacity to maintain an efficient water transfer from soil to leaves (Brunner et al., 2015; Sala et al., 2012). This process requires substantial metabolic energy, since tree transpiration is largely reduced during drought (Huang et al., 2018). As a result, drought forces trees to invest large amounts of carbohydrates in metabolism, rather than in radial growth (Brunner et al., 2015; Huang et al., 2018). This also suggests that if, as expected, droughts become more frequent, the time between droughts may become shorter than the time it takes for trees to recover from previous drought events, which may then lead to a decline in growth and an increasing vulnerability to subsequent stresses (Schwalm et al., 2017).

Drought severity was not related to the post-drought growth responses in our data. This may indicate that the severity of drought can cause a sharp growth drop, but does not impede a full recovery afterwards, albeit with some delay. A possible reason why there was no significant relationship between tree growth and severity of drought could be the narrow range of SPEI values included in the analysis.

4.5.2. GROWTH RECOVERY AFTER DROUGHT IS STRONGER IN DIVERSE FORESTS

In line with a number of recent studies, we found a positive relationship between stand diversity and tree growth (Jucker et al., 2016; Liang et al., 2016a; Morin et al., 2011; Hans Pretzsch et al., 2013). Our results indicate that trees growing in mixtures showed significantly higher increments than trees growing in monocultures, and this was more evident in *F. sylvatica* and *Q. robur*. Furthermore, the difference in BAI between mixtures and monocultures was not only significantly larger in mixtures in the post-drought period, but also the overall impact caused by drought was smaller: both the impact of drought and the recovery rate were lower in mixtures than in monocultures (Figure 4.5). Nevertheless, the greater resilience of mixtures does not necessarily mean that species will be less sensitive to drought. Indeed, our results also revealed that the growth reduction was observed in both mixtures and monocultures, but our findings do clearly indicate that higher diversity promotes a higher resistance (and thus lower disturbance impact) and a higher recovery rate than monospecific stands do.

Increased species richness can insure against a decline in ecosystem functioning (here productivity), as the long-term resilience of forest ecosystems is increased when species exhibit a diversity of responses to a disturbance (here drought) (Elmqvist et al., 2003; Folke et al., 2004). Species interactions may reduce susceptibility to drought stress via facilitative mechanisms, such as hydraulic lift and canopy shading, or via a reduction in competition due to spatial and temporal partitioning of water resources (Forrester and Bauhus, 2016). This occurs, for instance, when species that extend their root systems toward deeper soil layers coexist with others that occupy the superficial layers, taking up significantly more soil water from deeper layers and redistributing it through their roots to dry surface soil layers (Brunner et al., 2015). Yet, because fast-growing stands typically have greater evapotranspiration than slow-growing stands, these interactions can also cause an increase in tree transpiration in mixtures, thus exacerbating the water stress during drought periods (Forrester et al., 2016; Grossiord et al., 2014). Responses of trees to drought are therefore highly context-dependent. For example, *F. sylvatica* has been shown to be significantly more resistant and resilient against drought (Metz et al., 2016; H. Pretzsch et al., 2013) and to exhibit higher growth rates (Condés et al., 2013; Hans Pretzsch et al., 2013) when growing in mixtures than in monocultures. This positive effect of mixing on *F. sylvatica* has been attributed to its low self-tolerance (Del Río et al., 2014), superior space sequestration efficiency (Dieler and Pretzsch, 2013), and specific root system architecture (Leuschner et al., 2001), which give the species a competitive advantage in mixtures. For *Q. petraea*, studies have provided mixed evidence, with either a positive, a negative, or an insignificant effect of species diversity on tree growth (Hans Pretzsch et al., 2013; Toïgo et al., 2018). The mixture effect on *Q. petraea* growth has been found to depend on the shade tolerance of the surrounding species, i.e. positive effects when the surrounding species are shade-intolerant and negative effects when the surrounding species are highly shade-tolerant (Toïgo et al., 2018). *Quercus petraea* is a light-demanding species with low shade tolerance, thus the more shade-intolerant the surrounding species, the more *Q. petraea* may benefit from the mixture. Similarly, we observed no significant differences in the growth rates of *Q. petraea* trees between mixtures and monocultures, neither before, during, nor after the drought events. The reverse holds for *F. sylvatica* and *Q. robur*; these species displayed significantly higher post-drought growth in mixtures than in monocultures.

4.5.3. COMBINED EFFECTS OF DROUGHT AND DEFOLIATION ON TREE GROWTH

The combination of drought and defoliation resulted in markedly reduced growth rates, consistent with other studies in which the growth decline induced by successive droughts was more evident in defoliated trees than in non-defoliated trees (Galiano et al., 2011; Guada et al., 2016; Julio Camarero et al., 2018). Crown defoliation is commonly used to assess tree health and forest decline as defoliation may predispose trees to decline via a reduction in carbohydrate, due to the reduced leaf area, which limits root production and the capacity to access to deeper soil water under drought conditions (Jacquet et al., 2014). In addition, as non-structural carbohydrates are vital to maintain plant metabolism and hydraulic processes, their depletion under defoliation may exacerbate water stress (Jacquet et al., 2014; Sala et al., 2012). This strongly suggests that tree growth and crown defoliation can complement each other as stress indicators, as has been noted by earlier studies (Dobbertin, 2005; Guada et al., 2016). In general, defoliated trees grew less than non-defoliated trees, which, however, does not allow us to conclude whether growth reduction is caused by defoliation or whether growth reduction and defoliation are manifestations of the same underlying process (e.g., hydraulic failure or carbon starvation).

In previous work, we showed that the crown defoliation for the three study species increased in the past 25 years, with a peak in average defoliation in 2012 (see Chapter 3 for details), and we documented a change from healthy monocultures to resilient tree species mixtures around the year 2010, concurrent with the marked growth decline in trees in monocultures in the current study during the 2009-2011 drought event. Together, this suggests that trees growing in monocultures not only grew less, but also showed high defoliation levels.

4.5.4. CONCLUSIONS AND IMPLICATIONS FOR FOREST MANAGEMENT

In this study, we presented strong evidence that drought caused a sharp growth reduction in deciduous trees, and this was particularly marked for *F. sylvatica*. However, the magnitude of this growth decline, as well as the associated legacy effects, differed depending on the drought event. We observed that trees growing in mixtures were more resilient to drought than those growing in monocultures: they displayed a lower disturbance impact (higher resistance) and they returned faster to their pre-disturbance state (higher recovery rate). Moreover, defoliated trees showed a higher susceptibility to drought-induced growth decline, which was most evident after the 2009-2011 drought.

Maintaining high tree species diversity in forests has, therefore, a large potential in forest management practices and efforts to mitigate the vulnerability of forests to drought under a warmer climate. In our study, we found that mixed species forests could better withstand drought stress. Further work should seek to elucidate the physiological mechanisms involved in drought-induced growth decline and how they can be influenced by specific species combinations. This will ultimately allow us to more confidently predict which combinations of species, in terms of their water use strategies, and depending on site-specific climatic and edaphic characteristics, will be most beneficial for increasing the resistance of forest stands to drought.

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CHAPTER 5

THE MIXTURE EFFECT ON TREE SPECIES PRODUCTIVITY

Based on *Sousa-Silva R, Boggers S, Verheyen K, Muys B.*
Partitioning of tree biodiversity effects on forest growth using national forest
inventory data (submitted).

5.1. SUMMARY

The conversion of forests from monocultures to mixed-species forests is considered as a promising management strategy for maintaining high productivity, while enhancing other ecosystem services. Recent studies using data from tree diversity experiments have shown that species diversity can increase forest productivity, but the limited number of studied species compositions and the small gradient in site conditions used does not allow generalizing these findings and hampers knowledge transfer to forestry practice.

Here, we use data from permanent national forest inventory plots to investigate whether mixed-species stands can overyield monospecific stands. We did so by applying the tripartite partitioning method (Fox 2005) to inventory plots. Our analyses were based on data from 970 plots made up of pure beech (*Fagus sylvatica*) stands, pure oak (*Quercus robur* and *Quercus petraea*) stands, and mixed stands in which these species were present.

We found that the mixture effect was not significant for overall stand productivity possibly due to an overyielding of beech counterbalanced by an underyielding of oak. This is consistent with the observed negative values of the complementarity effect when diversity effects were partitioned into a selection effect and a complementarity effect. In addition to beech-oak mixtures, the effect of mixing on growth was either positive (overyielding), neutral, or negative (underyielding), depending on the component species. These findings are consistent with studies where species identity has been regarded as a key in the relationship between productivity and tree diversity. Finally, we discussed how differences in light requirements and leaf phenology between the species in the mixture may influence this relationship.

5.2. INTRODUCTION

Maintaining forest diversity is key in providing ecosystem services in the context of future environmental change. Mixed-species forests have been shown to harbor higher biodiversity (Felton et al., 2010; Hua et al., 2016), exhibit fewer pest and disease outbreaks (Guyot et al., 2016; Jactel and Brockerhoff, 2007), store more carbon (Gamfeldt et al., 2013; Ruiz-Benito et al., 2014), and cycle nutrients more efficiently (Prescott, 2002; Richards et al., 2010). Importantly, various studies have demonstrated that mixed forests can be more productive than monocultures (Liang et al., 2016a; Paquette and Messier, 2011; Pretzsch and Schütze, 2009).

Nevertheless, most forest plantations are monocultures (Kelty, 2006; Verheyen et al., 2016). There are several factors leading to this situation, such as the possibility to deploy their resources on the growth of a particular species, the ease of stand management and especially mechanized harvesting, and predictability of yield (Kelty et al., 1992; Piotto, 2008). However, this market-oriented approach, which excels at providing large quantities of wood in a relatively small area, is almost always in detriment of other ecosystem services (Felton et al., 2010; Griess and Knoke, 2011). Conversely, mixed forests are less prone to such tradeoffs. On the one hand, the diversity of species means mixtures may be better suited to hedge against changes in market prices, as they can provide a higher financial return both in the short- (from harvesting faster growing species) and in the long term (from harvesting slower-growing but more valuable species) (Nguyen et al., 2015). On the other hand, mixed-species stands offer managers with alternative ways of future stand development, which may be key in effectively tackling climate change (Gamfeldt et al., 2013; Millar et al., 2007; Seidl et al., 2017).

Biodiversity effects on ecosystem functioning are driven by species interactions. When inter- and intraspecific interactions differ in strength, biodiversity affects ecosystem functions as species will function differently in the presence of other species compared to their monocultures (Loreau and Hector, 2001). The mechanisms behind the biodiversity effects can be partitioned into three statistically additive components: *trait-independent complementarity, trait-dependent complementarity*, and *dominance effect*. Fox's (2005) tripartite equation is a modification of the additive partition of Loreau & Hector's (2001), which defines net biodiversity effect as the difference between the observed yield of a mixture and that of the average monoculture yield, assuming that there was no selection or complementarity effects. Both the bi- (Loreau and Hector, 2001) and tripartite (Fox, 2005) partitioning methods have been extensively used to identify the mechanisms by which species diversity influences forest dynamics. However, previous studies have mostly focused on data from biodiversity experiments (e.g., Fargione *et al.* 2007; Tobner *et al.* 2014; Van de Peer *et al.* 2017). Such experiments usually consist of spatially restricted, replicated plantations with different species compositions and levels of tree species diversity that show minimal variation in site conditions (Bauhus et al., 2017b). As a result, experimentally controlled conditions may differ from real ecosystems characterized by a large degree of variability in abiotic and biotic conditions. Using inventory plots is an alternative for filling the knowledge gaps on mixed forest dynamics (Vallet and Pérot, 2011). Ideally, to assess the effects of biodiversity on ecosystem functioning, studies should optimize three basic criteria: orthogonality, comprehensiveness, and representativeness (Pretzsch et al., 2017), but this is seldom achievable in practice. The strength of inventory datasets is their representativeness. Forest inventories typically cover large numbers of sample plots systematically distributed across multiple forest types and large environmental gradients (Bauhus et al., 2017b), thus representing effective tools to assess the extent and condition of forest resources over large areas (Corona et al., 2011). In addition, because they are implemented in existing mature forests, they can help to put results obtained from artificial communities, such as created in experiments, into perspective (Vilà et al., 2005).

Therefore, in this study, we applied the tripartite partition approach to examine whether mixtures are more productive than monocultures, using data from national forest inventories. Our analysis encompassed 7 two-species mixtures, as well as their corresponding monocultures, whose species differ in growth strategies and shade tolerance, and where beech (*Fagus sylvatica* L.) or oaks (*Q. petraea* (Matt.) Liebl. and *Quercus robur* L.) were present (Figure 5.1). These species were selected for their ecological and economic importance in Europe and because they display different characteristics, including contrasting root types (Leuschner et al., 2001) and light requirements (Dieler and Pretzsch, 2013; Toïgo et al., 2018). Herein, we hypothesized that (i) oak and beech would be complementary for below- and above-ground resources; and (ii) the mixture of these species would result in higher productivity at both species and stand level. Finally, we discussed our findings in the light of the methodological and ecological implications.

5.3. METHODS

Forest inventory data. We combined the National Forest Inventory (NFI) database of Flanders (Northern Belgium) and Wallonia (Southern Belgium) to study the effects of tree species diversity on stand-level tree growth. Both territories developed their own inventory procedures independently, but strong similarities can be identified among the two regions (Rondeux et al., 2010), which enable generally reliable estimates of changes in forest cover, stand density, and net annual increment in Belgian forests over time. For a discussion on addressing the harmonisation of data collected regionally, and a comparison of datasets, see Supplementary Note C.1.

Forest plots (three concentric circular plots with a radius of 18 m, 9 m and 4.5 m according to the type of data collected; Figure C.1) are centred on the intersections of a 500 m (north-south) by 1000 m (east-west) grid. Each year, one-tenth of the permanent sample plots are revisited and remeasured according to a predefined scheme ensuring that the whole territory is uniformly covered. Within a sampling plot, stand level data and tree level data are collected in a similar fashion for both inventories. The measured variables include within-plot coordinates, tree species and diameter at breast height (1.5 m above ground) for each tree with circumference ≥ 20 cm. A total of 3883 permanent plots with two consecutive surveys were available within the study area.

Plot selection. To compare the productivity of monocultures versus mixed stands, we performed five steps to ensure data were comparable within and between plots (Figure 5.1; Table 5.1). First, we categorized the plots according to species composition. We considered *monospecific* those plots where a single dominant species accounted for 85% or more of the basal area (N = 2104). A plot was categorized as a *two-species mixture* when the two species contributed at least 85% of the total basal area and each of the two species represented 20% or more of the basal area (N = 1020). Plots that did not fall into one of these categories were categorized as *multi-mixed* (N = 448) and were excluded from the dataset. Second, we filtered out those mixtures that did not contain either beech or oak trees and monocultures of species not included in the targeted mixtures (N = 2238). Because of their contrasting characteristics (deciduous/coniferous) and different shade tolerance strategies (light-demanding/shade-tolerant), we considered three main European tree species: Scots pine (*Pinus sylvestris* L.), European ash (*Fraxinus excelsior* L.), and Norway spruce (*Picea abies* (L.) H. Karst). Third, to avoid confounding effects from distinct abiotic growing conditions, the study area was split into ecoregions, i.e., areas with major physiographic and minor macroclimatic variation, with limits that mimic the original extent of natural communities, and that are suited to study ecosystem functioning and community-level processes (Olson et al., 2001). Belgium can be roughly divided into two physiographic domains separated by the rectilinear northeast-oriented Sambre-Meuse river line (National Committee of Geography of Belgium, 2012). These regions differ mainly with respect to their climate and relief: the lowlands in the north (below 200 m a.s.l.) contrast with the Ardennes heights to the south (200–700 m a.s.l.), and the climate becomes colder and wetter as elevation rises. Therefore, we used these domains to define our ecoregions, 'North SM' and 'South

SM', but with an additional distinction between the higher zones in the Ardennes ('Cold Ardennes', *sensu* Van der Perre et al. [2015]) and the other zones in southern Belgium (Figure 5.2 and Figure C.2). Subsequently, mixed-species plots and corresponding monocultures were selected within the same ecoregion to avoid excessive discrepancies among the abiotic conditions, even though they were taken into account in the models (see Toïgo et al. (2015) for a similar exercise). And from these plots, we discarded any two-species mixture represented by less than five plots per ecoregion (N = 2235). From these plots, in a fourth step, only those that contained at least 5 trees and had a minimum plot basal area of 10 $m^2\ ha^{-1}$ (N = 1192) were maintained in the dataset to standardise the number and density of trees in each plot. This arises because diversity effects, as well as relative yields, are sensitive to absolute values and may strongly outweigh the contribution of higher-yielding monocultures (Tobner et al., 2016). Finally, because of the data availability, mixtures of beech and oak with other species were considered for analysis if they were sampled in the ecoregion south of the Sambre and Meuse valley (Figure 5.1b and Table 5.2). Plots of pure beech, pure oak and beech-oak mixtures were analysed across the entire study area. We thus obtained a final selection of 970 plots, accounting for 27% of the initial dataset (Table 5.1 and Table 5.2).

Biodiversity effects. Biodiversity effects were calculated using the tripartite partition method (Fox, 2005). This method allows comparison of the observed yield of a mixture to the average of monoculture yields of its constituent species. The net biodiversity effect is positive when species grow better in mixture than in monoculture. The partitioning splits the net biodiversity effect (NE) in *trait-independent complementarity* (TIC), *trait-dependent complementarity* (TDC), and *dominance effect* (DE):

$$\Delta Y = \sum_{i=1}^{n} \Delta Y_i = TIC + TDC + DE$$

$$= N\overline{\Delta RY}\,\overline{M} + Ncov\left(M, \frac{RY_O}{RYT_O} - RY_E\right)$$

$$+ Ncov\left(M, RY_O - \frac{RY_O}{RYT_O}\right)$$

where ΔY is the net biodiversity effect, N is the number of species in the mixture (here, $N = 2$), $\overline{M}$ is the average monoculture yield of each species present in the mixture, and $\overline{\Delta RY}$ is the average difference between species observed (RY_O) and expected (RY_E) relative yields. RY_O is calculated as mixture yield divided by monoculture yield, whereas RY_E is the expected relative abundance of each species in mixture. RYT_O is the sum of the observed relative yields across all species. All parameters were calculated separately for each ecoregion (e.g., $\overline{M}_{ij}$ is the average yield of of species i in monoculture throughout ecoregion j).

The first two terms (TIC and TDC) refer to niche differentiation, a mechanism by which competing species use the environment differently in a way that allows them to coexist. Positive values of TIC indicate better growth in mixture than in monoculture, independent of their traits and not at the cost of other species. TDC is positive when species with high monoculture yield attain high yield in mixture, but also not at the cost of other (less productive) species. Finally, DE is positive if species with higher monoculture yields dominate a mixture at the cost of species with low monoculture biomass. The sum of the TDC and DE terms equals the selection effect *sensu* Loreau & Hector (2001), whereas TIC is similar to the complementarity effect.

Data analysis. Biodiversity effects were evaluated using linear models and linear mixed-effects models. Three models were built based on data availability: one full model on the overall productivity of beech-oak mixtures across the ecoregions studied (M1; $N_{\text{mixtures}} = 250$); and two additional models fitted to the data for each mixture of beech (M2; $N_{\text{mixtures}} = 208$) and oak (M3; $N_{\text{mixtures}} = 249$) in the South SM ecoregion (Table C.2).

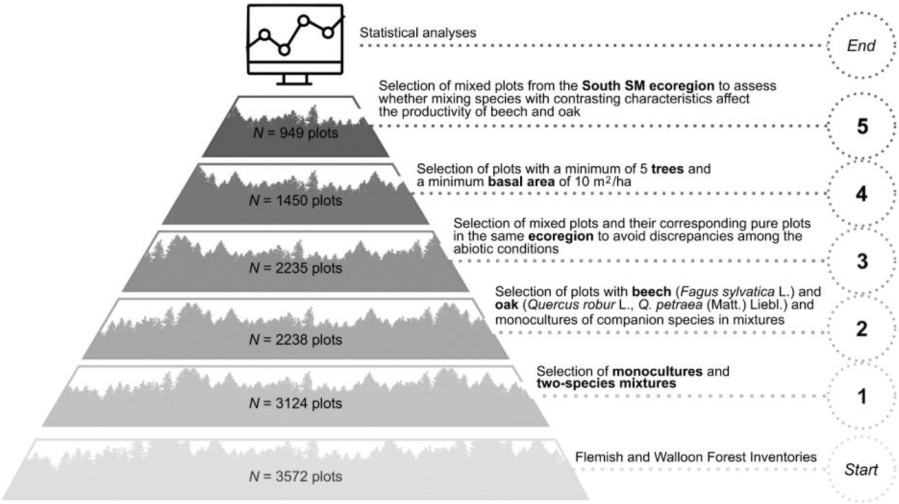

Figure 5.1 Schematic representation of the steps involved in the plot selection procedure. N *is the total number of plots.*

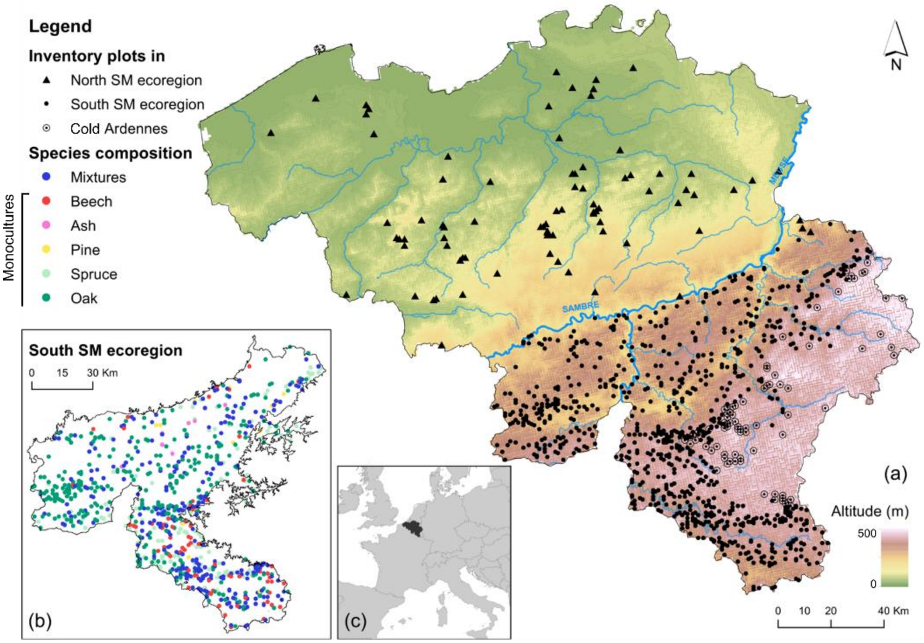

Figure 5.2 Location of the studied inventory plots across Belgium. *(a) We distinguished plots sampled in the region north (shown as triangles) and south (shown as dots) of the Sambre and Meuse valley, and in the High Ardennes (shown as open circles). (b) Mixtures and pure stands of European beech, European ash, Scots pine, Norway spruce, and oak are included in this study. (c) Study area in the European context.*

We used the calculated net biodiversity effect as a response variable to model the effect of species mixing on the productivity of each species (beech and oak) in mixture. Models included stand attributes, such as the stand density (based on the number of trees per area) and the species developmental stage (quadratic mean diameter), climate (growing-season temperature and precipitation), soil (texture, drainage and fertility; see Supplementary Note C.2 for details), and topographic factors (slope and elevation; Supplementary Note C.2). In M1, ecoregion was included as random factor and the variance explained by the fixed factors (marginal R^2) and that incorporating the random factors (conditional R^2) was computed following Nakagawa & Schielzeth (2013). In M2-M3, the identity of the companion species was included as fixed factor and the goodness- of-fit was assessed by the adjusted R-square statistics ($adjR^2$) and the root mean squared error (RMSE). For each model, residuals were inspected by plotting predicted versus observed values. Further, variance inflation factors (VIF) were examined to prevent multicollinearity, and variables with a VIF > 10 were removed. The remaining variables were retained in the models due to ecological significance, regardless of their statistical significance. All calculations were performed in R version 3.4.1 (R Development Core Team, 2017).

5.4. RESULTS

5.4.1. NET DIVERSITY EFFECTS

When calculated across the three ecoregions, the grand mean effect size of the net biodiversity effect in beech-oak mixtures was close to zero (NE = -0.01 m^2 ha^{-1} $year^{-1}$; P = 0.08; N = 250) (Figure 5.3), implying that we cannot reject the null hypothesis of no biodiversity effect. This null mixture effect partly arises from an asymmetry between the overyielding of beech (2%; P = 0.1) and the underyielding of oak (-7%; P < 0.001) (Figure C.3).

Table 5.1 Main characteristics of the study plots with beech and oak. *Mean (standard deviation) of dendrometric characteristics and climatic conditions for the forest inventory plots in which beech and oak trees grew in the three ecoregions considered.*

	North Sambre-Meuse			**South Sambre-Meuse**			**High Ardennes**		
	Pure stands		Mixed stands	Pure stands		Mixed stands	Pure stands		Mixed stands
	Beech	Oak		Beech	Oak		Beech	Oak	
No. plots	*26*	*30*	*25*	*69*	*310*	*193*	*39*	*10*	*32*
Basal area (m^2 ha^{-1})	*22.1 (7.7)*	*18.6 (6.7)*	*20.4 (4.4)*	*17.7 (5.1)*	*15.7 (4.0)*	*16.3 (4.5)*	*16.3 (3.9)*	*15.2 (2.2)*	*18.4 (5.6)*
Stand density (trees ha^{-1})	*336.4 (97.3)*	*289.5 (96.7)*	*299.0 (63.4)*	*276.0 (77.9)*	*250.4 (58.2)*	*258.0 (67.4)*	*257.7 (60.4)*	*244.8 (30.4)*	*291.2 (77.9)*
Quadratic diameter (cm)	*48.7 (13.2)*	*44.7 (8.9)*	*47.2 (7.9)*	*45.2 (7.8)*	*41.8 (6.4)*	*43.5 (7.0)*	*44.6 (7.5)*	*39.6 (5.5)*	*44.3 (6.9)*
Basal area increment (m^{2}ha^{-1}yr^{-1})	*0.40 (0.1)*	*0.40 (0.2)*	*0.43 (0.1)*	*0.32 (0.1)*	*0.26 (0.1)*	*0.29 (0.1)*	*0.30 (0.1)*	*0.26 (0.1)*	*0.28 (0.1)*
Elevation (m)	*92 (49)*	*58 (49)*	*74 (43)*	*354 (72)*	*276 (67)*	*336 (74)*	*488 (52)*	*454 (39)*	*458 (35)*
Mean annual temperature (°C)	*10.3 (0.2)*	*10.3 (0.2)*	*10.3 (0.2)*	*8.7 (0.5)*	*9.1 (0.4)*	*8.8 (0.5)*	*8.0 (0.3)*	*8.2 (0.2)*	*8.1 (0.3)*
Mean annual precipitation (mm)	*909 (35)*	*885 (43)*	*908 (34)*	*1230 (133)*	*1103 (137)*	*1197 (149)*	*1192 (90)*	*1164 (86)*	*1246 (89)*

Table 5.2 Main characteristics of the study plots with pine, ash, and spruce. *Mean (standard deviation) of dendrometric characteristics and climatic conditions for the forest inventory plots in which the respective species grew in the ecoregion south of the Sambre and Meuse valley.*

	Pine			**Ash**			**Spruce**		
	Pure stands	Mixed stands		Pure stands	Mixed stands		Pure stands	Mixed stands	
		Beech	Oak		Beech	Oak		Beech	Oak
No. plots	*12*	*5*	*12*	*7*	*5*	*23*	*124*	*6*	*21*
Basal area (m^2 ha^{-1})	*14.2 (3.4)*	*14.1 (2.6)*	*15.3 (6.7)*	*14.7 (4.2)*	*20.2 (10.6)*	*15.2 (14.7)*	*20.1 (7.4)*	*15.1 (2.1)*	*16.0 (4.1)*
Stand density (trees ha^{-1})	*242.1 (54.1)*	*232.2 (31.6)*	*254.0 (50.7)*	*225.6 (52.9)*	*262.9 (120.4)*	*237.4 (58.8)*	*325.5 (112.1)*	*249.8 (41.0)*	*256.3 (55.7)*
Quadratic diameter (cm)	*34.0 (3.1)*	*35.4 (5.9)*	*38.5 (4.8)*	*40.3 (3.8)*	*51.5 (6.2)*	*39.7 (6.7)*	*34.8 (5.4)*	*43.0 (5.5)*	*35.2 (6.0)*
Basal area increment (m^{2}ha^{-1}yr^{-1})	*0.28 (0.1)*	*0.32 (0.1)*	*0.26 (0.1)*	*0.27 (0.1)*	*0.32 (0.1)*	*0.29 (0.1)*	*0.58 (0.2)*	*0.36 (0.1)*	*0.40 (0.1)*
Elevation (m)	*300 (60)*	*367 (21)*	*286 (77)*	*246 (24)*	*249 (82)*	*234 (60)*	*349 (66)*	*424 (42)*	*293 (87)*
Mean annual temperature (°C)	*9.1 (0.5)*	*8.4 (0.1)*	*9.0 (0.4)*	*9.2 (0.2)*	*9.3 (0.3)*	*9.3 (0.3)*	*8.7 (0.4)*	*8.3 (0.1)*	*9.0 (0.4)*
Mean annual precipitation (mm)	*1337 (374)*	*1304 (32)*	*1116 (127)*	*1533 (491)*	*997 (75)*	*994 (58)*	*1797 (668)*	*1339 (62)*	*1135 (154)*

A negative NE was observed in the three ecoregions under study, although results were not significant. The tripartite partitioning approach revealed that TIC was negative on average (i.e., species compete more intensely with individuals of other species than they do amongst themselves), and selection effects were positive (i.e., the best-performing species in mixture are not the species with higher monoculture yields). Nevertheless, none of these terms was significantly different from zero.

Furthermore, for beech-oak mixtures, we also tested to what extent differences in biodiversity effects depended on the stand density and development stage, climate, soil and topographic factors of each site. Results from the regression analysis (Table C.2) revealed that the net diversity effect on the productivity of these mixtures was significantly positively associated with a higher density of stems and, less strongly, negatively correlated with large trees (Figure 5.4). Climate and soil properties were not found to be significant predictors.

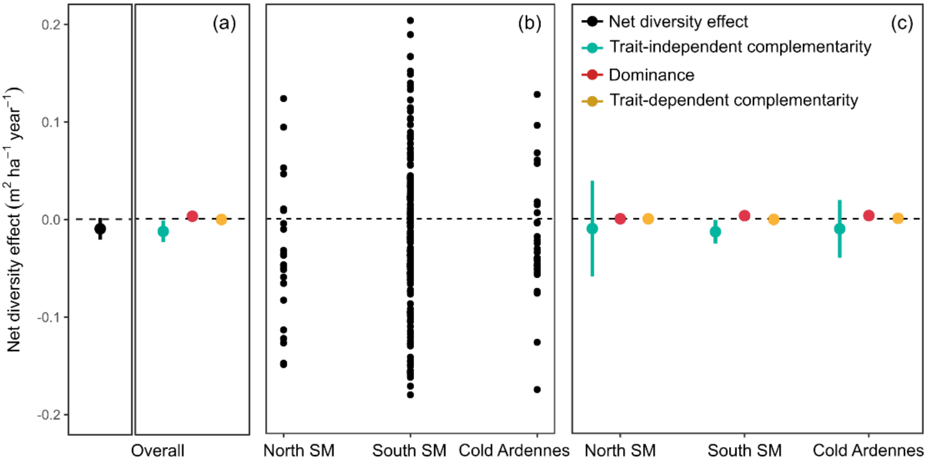

Figure 5.3 Partitioning of the net diversity effect on basal area increment (m^2 ha^{-1} $year^{-1}$). *Net diversity effect in beech-oak mixtures averaged across the study area (a) and split by ecoregion (b). The solid line is a smooth regression line fitted to the data (dots). The partitioned effects – trait-independent complementarity, dominance, and trait-dependent complementarity – are shown as the means with error bars representing upper and lower bounds of a 95% confidence interval for the three ecoregions (c).*

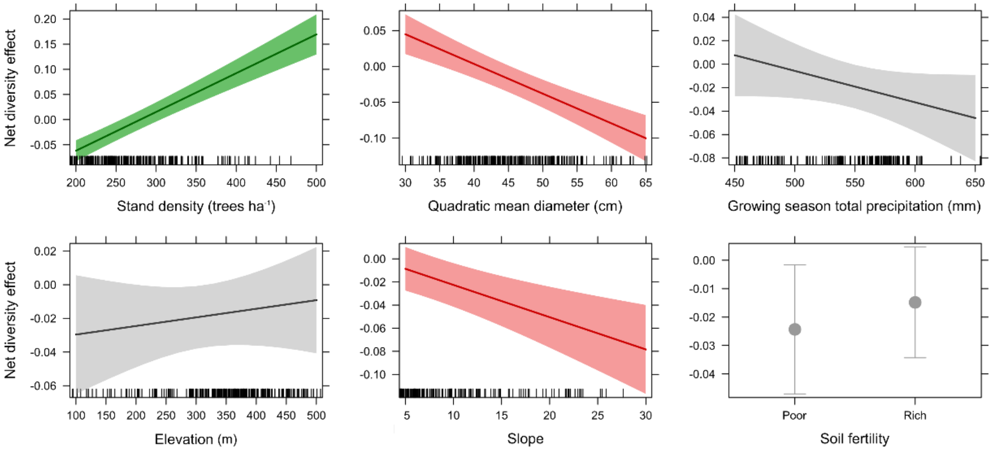

Figure 5.4 Fitted relationships from linear mixed-effects models. *Variation in the net biodiversity effect as a function of stand density, species developmental stage (quadratic mean diameter), and site conditions (climate and soil) for beech-oak mixtures across the ecoregions studied. For model coefficients, see Table C.2. Shading represents the 95% confidence interval. Positive slopes (green) indicate a positive influence on the net diversity effect, whereas negative slopes (red) denote a negative relationship. Non-significant slopes are shaded grey ($P > 0.05$). $N_{mixtures} = 250$.*

5.4.2. SPECIES RELATIVE YIELDS IN MIXTURES

In addition to beech-oak mixtures, we examined the effect of species mixing on the productivity of beech and oak when mixed with other species with contrasting characteristics such as ash, pine and spruce.

We found there is a large variability in mixture effect depending on the companion species, and within a given companion species (NE = -0.01 m^2 ha^{-1} $year^{-1}$; P = 0.001). The relationship between the net, complementarity and selection effects, for each mixture studied, is illustrated in Figure C.4. Overall, the mixture effect on total stand productivity was mostly slightly negative or close to zero, due to negative values of TIC. Models fitted to these data showed consistent results with the full model (Table C.2 and Figure C.5).

Overall, when we examined the effect of mixtures on the productivity of both species, we found overyielding in the case of *F. sylvatica* (1%; P = 0.456), and underyielding for *Quercus* spp. (-6%;

$P < 0.001$). The mixture effect, whether positive or negative, was generally not significant except for overall productivity of beech–spruce (-10%; $P = 0.039$) and oak–spruce (-8%; $P = 0.013$) mixtures. Nevertheless, responses to mixing were similar across species combinations: *F. sylvatica* and *Quercus* spp. overyielded (positive mixture effect, but again not significant) when mixed with Scots pine, and underyielded (negative mixture effect) when mixed with Norway spruce and ash (Figure 5.5).

5.5. DISCUSSION

5.5.1. METHODOLOGICAL STRENGTHS AND LIMITATIONS

The tripartite partitioning approach described by Fox (2005), following Loreau & Hector (2001), has been frequently used to compare the relative yield of mixtures to monocultures. This methodology was initially applied only to grassland experiments but has since been extended to other systems such as forests. Invariably, however, this approach has been applied in biodiversity-ecosystem functioning experiments. The main reason for this is the greater orthogonality of controlled experiments (Baeten et al., 2013; Bauhus et al., 2017b). By using planted experiments, it is possible to carefully control species compositions and proportions, functional diversity, stand density, and edaphic and climatic factors (Bauhus et al., 2017b). However, in comparison to the lifespan of trees, these planted experiments are still relatively young, and the results might therefore be different from those found in mature forests, dominated by large, old trees which have been influenced, at least in part, by species diversity over time (Baeten et al., 2013).

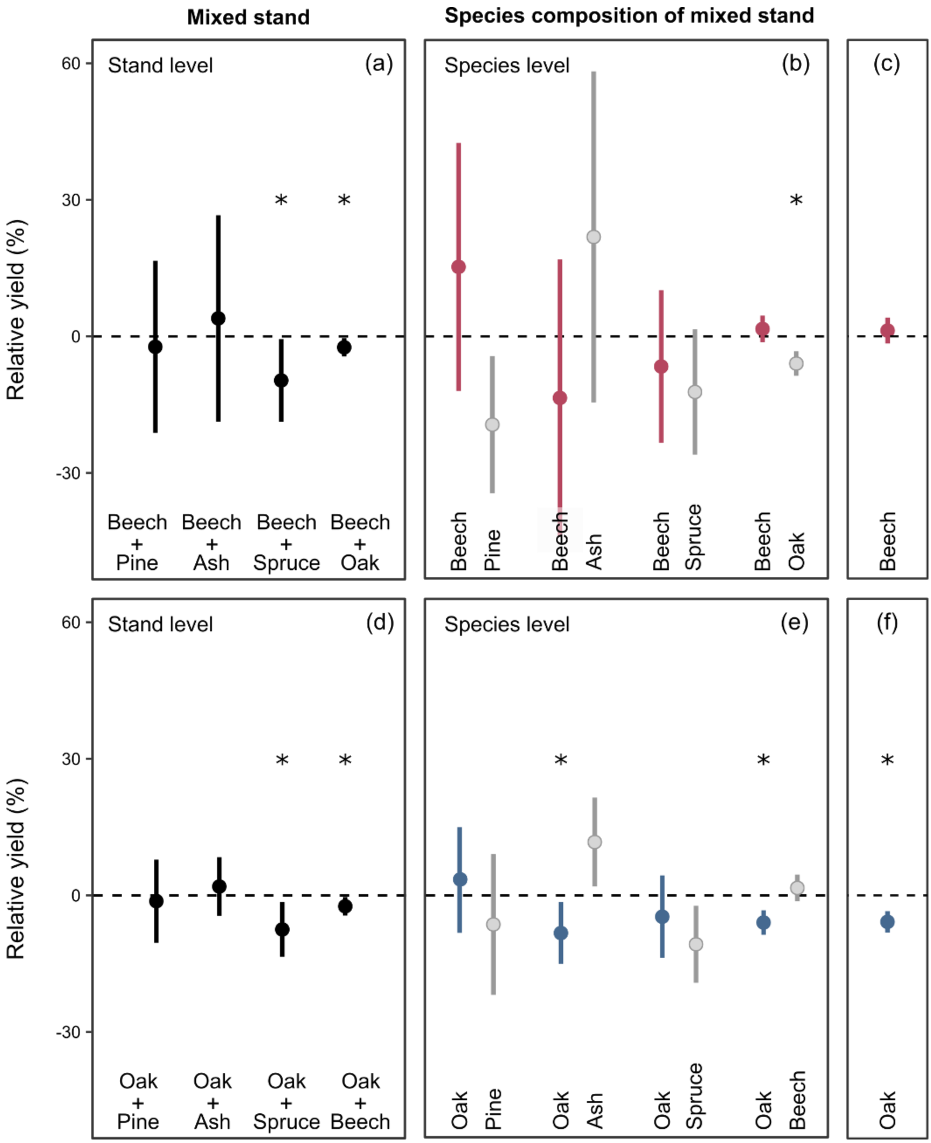

Figure 5.5 Effect of species mixing on productivity. *Mean (±95% confidence interval) of the mixture effect on the overall stand productivity (a, d), and on the productivity of each species in mixture (b, e), for plots with beech (upper panel) and oak, (lower panel), in the South SM ecoregion. The average mixture effect on beech (c) and oak (f) productivity is also depicted. Relative yield is the yield of a species in mixture divided by its yield in monoculture* (Loreau and Hector, 2001). *Asterisk denotes significant differences (P < 0.05; t-test).*

Conversely, forest inventories are ready-to-use databases that typically include a large variety of environmental conditions, ages, densities, species compositions, and management regimes. Yet, we are unaware of any literature that applied either the bi- (Loreau and Hector, 2001) or tripartite (Fox, 2005) partitioning methods to forest inventory data. This may reflect the fact that forest inventories have certain limitations and potential caveats that should be considered when studying the relationship between tree diversity and forest productivity (Vilà et al., 2005). For example, the fact that the plots are distributed across various soil types might level out this relationship. In this study, we addressed this issue using ecoregions as a proxy for relatively homogeneous site conditions (i.e., abiotic factors limiting species growth). The rationale behind this approach has previously been applied to data from the French National Forest Inventory to account for potential confounding effects from different abiotic growing conditions before comparing species productivity in monocultures and mixtures (Toïgo et al., 2015). However, their approach is conceptually different from ours as the productivity of species *i* in mixed stands was calculated as the relative difference between the observed productivity of the species *i* in mixed stands and its expected productivity in a mixture as predicted from models of species productivity in a monoculture. Here, we directly compared the observed yields in mixtures with those observed in monocultures, all things being equal (i.e., within ecoregions). Differences in abiotic conditions, such as climate and soil, were accounted for in the model by including them as explanatory variables. In addition, ecoregion was included as random effect to control for the non-independence of multiple plots from each ecoregion. The fact that these terms were not retained in the best fit model and were non-significant when added individually to the best fit model (Table C.2) provides further support to the selection procedure. Nevertheless, a direct consequence of these procedures was the loss of many inventory plots, which caused a loss of explanatory power in the analysis as it is only possible to make comparisons between the productivity of pure and mixed stands in the same ecoregion (and not all species were found in pure and mixed stands within each ecoregion). In the end, we obtained a selection of 970 plots, which corresponds to about 27% of the initial dataset.

Finally, another point to consider when studying forest dynamics based on inventory data is management history – notably thinning – that keeps stands below a maximum stand basal area and density, thus broadening the opportunities for complementary use of resources within a site (Lu et al., 2016). In this study, we found that both stand density and species developmental stage were significantly correlated with NE ($P < 0.001$). Regarding the relationship between stand density and net stand productivity, our results are in agreement with previous studies that have shown that tree species mixing can modify crown morphology, towards higher space filling of the crown volume, and that the resulting canopy structure may increase stand productivity (Dieler and Pretzsch, 2013; Pretzsch, 2014; Pretzsch and Dieler, 2012). Denser canopy space filling causes increase light interception, which in turn leads to increased growth. A negative effect of progressing development stage (mean quadratic diameter) on stand productivity has also been reported elsewhere (Bourdier et al., 2016; Pretzsch, 2014; Toïgo et al., 2015) and appeared related to both a decrease in total light interception and a decrease in the conversion of light into basal area increment and volume. Management can both directly and indirectly enhance the positive relationship between stand diversity and productivity, e.g., via the presence and growth of some tree species and not others (Vilà et al., 2005), or by creating gaps in the canopy, through selective harvesting, increasing light availability in the understory possibly favoring the growth of the remaining trees (Muscolo et al., 2014). However, this information is often not readily available in forest inventories. We therefore strongly recommend future inventory assessments to include information on silvicultural practices such as planting, thinning and harvesting operations, to increase the utility of their data for biodiversity research.

Provided these caveats are respected, additive partitioning methods can also be applied to forest inventory data to untangle the mechanisms behind the biodiversity effects for a much broader range of site conditions, species assemblages, mixing proportions, mixing patterns, and stand densities.

5.5.2. BIODIVERSITY EFFECTS ON THE PRODUCTIVITY OF BEECH AND OAK IN MIXED STANDS

Previous studies based on forest inventory data have mostly focused on the relationship between species richness and productivity, with most large-scale analyses describing a positive relationship between diversity and productivity (e.g., Paquette & Messier 2011; Vilà et al. 2013; Toïgo et al. 2015). Here, we report on net biodiversity effects for mixtures of oak and beech and the average change in relative yield for all species in each mixture; and, contrary to expectation, we found little evidence of differences in relative yield between pure and mixed stands. Averaged across all sites, mixtures of oak and beech had a lower productivity than their monoculture yield would predict. This is primarily because the positive effect of species mixing on the growth of beech is counterbalanced by an underyielding of oak. Our findings therefore do not support the hypothesis that in oak-beech mixed stands both species would increase their productivity compared to monocultures. Furthermore, this pattern is common to the three regions under study.

The observed positive mixture effect for beech when mixed with oak has been attributed to facilitation processes such as hydraulic lift and complementary crown morphologies (H. Pretzsch et al., 2013). Hydraulic lift results in increased surface soil moisture, because water is transported from deep moister soil layers, where root density is generally small, to shallow drier soil layers, where neighboring trees can utilize this excess of water. Oak is a mid-successional species, deep-rooted, that has a moderate shade-tolerance. Beech is a late-successional species, shallow-rooted, that is very shade-tolerant. Therefore, because both species have contrasting canopies and rooting systems, they are often mixed together, potentially reducing competition for light and below-ground resources (nutrients and water) for both species (Leuschner et al., 2001). However, as reported in previous studies, beech is deemed to be a better competitor than oak for both above- and belowground resources (Bolte et al., 2013; Toïgo et al., 2015). This often results in a negative effect of beech on oak, especially when the environmental conditions are more favorable for beech. Accordingly, mixtures of these two species tend to be maintained only under conditions (e.g., frost, heat, wetness, and drought) in which the competitive ability of beech is significantly reduced, thereby allowing oak to compete effectively with beech (Hans Pretzsch et al., 2013), or, more often, in managed forests, where thinning at appropriate intervals largely eliminates strong intraspecific competition and helps to maintain or even favor oak over beech. In line with this, the exploration of productivity with the tripartite partitioning method unveiled negative values of TIC and estimates of TDC and DE towards zero. On the one hand, a negative TIC indicates that the relative yields in mixture were lower than expected based on their monoculture yields. On the other hand, considering that we did not observe a large selection effect, these findings may suggest that the dominance of beech over oak is somewhat mediated by intended management practices.

In addition to oak-beech mixtures, we found that mixtures achieved greater, or lower, yields than monocultures (but not always significant) depending on its constituent species (Figure 5.5). This observation is consistent with studies where species identity has been used to explain the association between tree diversity and forest productivity (Pretzsch, 2005). Light interception and light use efficiency have been proposed as plausible mechanisms that contribute to diversity-enhanced productivity in forests (Jucker et al., 2015, 2014b; Williams et al., 2017). Multi-layered stands that combine fast-growing overstory species with slow-growing and shade-tolerant species might benefit from reduced competition due to higher light interception (because more canopy space is occupied allowing more leaf area to intercept light) and light use efficiency (because different species show different light response curves). Nonetheless, as shade-tolerant species have a large leaf area, they are also more likely to compete more fiercely for below-ground resources (Valladares et al., 2016). In fact, facilitation and competition are not mutually exclusive and may act together or one after the other (Holmgren et al., 1997).

Furthermore, conclusions on the different mechanisms of species interactions remain somewhat speculative because changes in environmental conditions, such as the concentration of carbon dioxide in the atmosphere, can alter the outcome of competitive interactions between species (Ainsworth and Rogers, 2007; Lu et al., 2016). For example, mixtures of deciduous and evergreen trees may benefit from high atmospheric inputs of major ions (André et al., 2008), an increase in litterfall which fuels rapid turnover of nutrients (Richards et al., 2010), and have greater stability over time (Jucker et al., 2014a). This spatial and temporal variation in interactions even within the same mixture makes it difficult to generalize and predict the outcomes of specific tree species mixtures. In our study, we observed that oak productivity was higher in the vicinity of light-demanding species such as pine than near shade-tolerant species like beech or spruce. Since previous studies have shown that, in oak-pine mixtures, pine growth appears not to be influenced by competition from oak (e.g., Perot & Picard 2012), the observed overyielding of oak in mixtures with a light-demanding coniferous species like pine was likely due to complementarity effects. Conversely, the decrease in mixture effect with more shade-tolerant species was likely due to an increase in interspecific competition. However, we could not confirm these assumptions. In our analyses, neither trait-independent complementarity nor dominance effects were significantly different from zero.

Similar trends were also observed in mixtures with beech driven, although not exclusively, by competitive dominance. The high competitiveness of beech has been reported before and is thought to result from partitioning resources above or belowground, or both (Dieler and Pretzsch, 2013; Rewald and Leuschner, 2009).

5.5.3. CONCLUSIONS AND IMPLICATIONS FOR FOREST MANAGEMENT

Positive effects of tree diversity on forest productivity have been commonly observed (Liang et al., 2016a). However, in our study, we did not find evidence of a significant effect, positive or negative, of mixing on stand productivity of beech-oak mixtures. Potentially important but unaccounted context variables, such as soil type and management operations, may have possibly levelled out the diversity effects (Vilà et al., 2005). A shortcoming of this study is that we were unable to find comparative data about the soil characteristics, especially soil type, of the forest inventory plots (i.e., for the Flemish and Walloon inventories). Alternatively, we used drainage, texture and fertility status as proxy indicators of forest soil quality, but the results could have been confounded by factors other than those included. That, coupled with the fact that it is likely that the different mixtures we studied have been altered by forest management and would otherwise have been replaced by monospecific stands of the most competitive species may help explain this lack of evidence.

Here, we aimed to demonstrate how the tripartite partitioning method (Fox, 2005) can potentially be used to describe the mechanisms behind the diversity-productivity relationship using forest inventory data, and that a degree of disentanglement of this relationship from all confounding co-factors is indeed possible using such data. This has never been applied in inventory plots as far as we know. Future in-depth research on the context-dependency of mixing specific tree species might provide the key to enable forest managers to establish and maintain forests of high tree species diversity and thereby high levels of forest multifunctionality. Yet for such efforts to succeed, forest inventories should be updated to include clear information on past management practices (e.g., thinning and harvesting), as well as the primary motivation behind them, since management may play a key part in the relationship between stand diversity and productivity.

Finally, our results should not discourage forest managers from adopting mixtures but rather show that mixtures are not always expected to attain higher yields, as they strongly depend on the component tree species and on site characteristics. Although here we did not find a significant effect of tree species diversity on forest productivity, growing evidence indicates that managing forests to retain or increase diversity provides multiple additional benefits relative to monocultures. Mixed forest have been shown to sustain forest productivity in the face of multiple disturbances (Jucker et al., 2014a), and to produce positive outcomes for forest biodiversity, water quality, and aesthetic and recreational values (Felton et al., 2016). Moreover, mixed forests give forest managers more options to adapt their tending and thinning operations according to the prevailing price differences for the component tree species (Lu and Gong, 2005). On the basis of these findings, the conversion of coniferous monocultures, consisting mainly of pine (*Pinus* spp.) and spruce (*Picea* spp.), into more stable deciduous and coniferous mixed-species stands is therefore strongly encouraged (Gérard, 2008; Lust et al., 2000).

ACKNOWLEDGMENTS:

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CHAPTER 6

CONCLUSIONS

6.1. ADAPTING TO CLIMATE CHANGE: WHY AND HOW

"Now, here, you see,
it takes all the running you can do, to keep in the same place."
Lewis Carroll

In evolutionary ecology, the Red Queen hypothesis, after Lewis Carrol's classic "*Through the Looking Glass*" in which Alice meets the Red Queen and learns to keep running fast enough to stay in the same place, postulates that organisms must constantly adapt, evolve, and thrive in order to survive against ever-evolving opposing organisms in an ever-changing environment (Van Valen, 1973). Today, in the face of an uncertain climate and rapid changes in many biophysical and socioeconomic aspects of their work, forest managers are faced with a similar challenge.

Minimizing the risks and impacts that climate change will have on forest outcomes (such as timber production) and forest management (such as thinning and harvesting practices) requires adaptation. Therefore, developing adaptive forest management strategies to cope with climate change is of great importance and urgency (Lindner et al., 2014; Spittlehouse and Stewart, 2003). In agriculture, for example, where rotations are short, it is assumed that crops may adapt fast enough to respond to possible changes in climate (Reilly et al., 1996). But this is unlikely to occur in forestry, where adaptation measures need to account for the long time lags between the establishment and maturity of trees (Lindner et al., 2010; Messier et al., 2016).

Awareness of climate change is increasing as an important issue for forest management (Keenan, 2015; Lindner et al., 2014; Peterson et al., 2014). However, only recently has the relevance of perceptions and concerns of forest managers on matters related to climate change received substantial attention (e.g., Blennow et al. 2012; Yousefpour & Hanewinkel 2015; Ameztegui et al. 2018). Efforts to bridge this gap are, therefore, still needed to provide useful insights into the state of knowledge and practice on climate adaptation as well as how to build science-management partnerships that recognize local management needs and can facilitate improved decision making (Keenan, 2015). In this study, we addressed this issue in Chapter 2.

By means of a questionnaire that was completed by 391 forest owners and forest managers across Belgium (Figure 6.1), we showed that their level of awareness of vulnerability to climate change effects is high, and relates to already experienced climate change impacts, although only a third of respondents reported having undertaken adaptation measures. In our study, the establishment of more mixed-species stands, and selecting site adapted species and varieties were the most often cited practices already implemented to adapt to the challenges associated with climate change. This may reflect the efforts being made, on sector specific level, in awareness-raising and communication on climate change adaptation. For approximately the last 20 years, the regional administrations in charge of forest management in Belgium started to encourage the replacement of coniferous monocultures – notably, *Picea abies* (Norway spruce) in Wallonia and *Pinus sylvestris* (Scots pine) in Flanders – with broadleaved or mixed-species stands (Gérard, 2008; Lust et al., 2000). Management practices should therefore attempt to favor species best adapted to (current) local conditions, which constitutes a first step towards adaptation to future changes. Regulatory and financial incentives are used, in particular subsidies for planting in accordance with a guide to species adapted to the present climate (National Climate Commission, 2010).

Figure 6.1 †

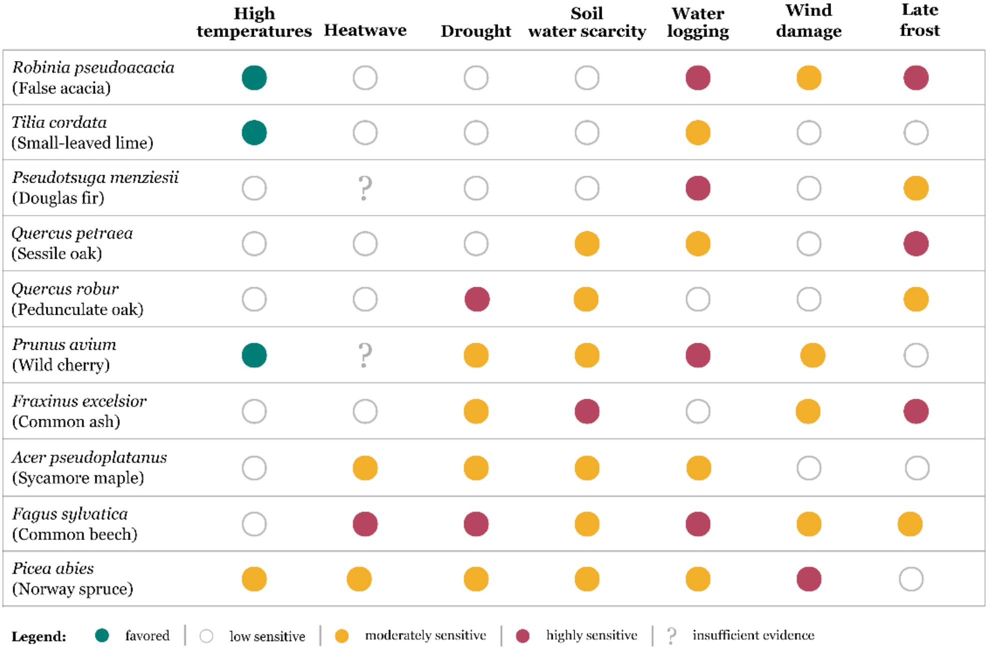
† *Forest manager filling in a questionnaire at the Libramont forestry fair, 2015.*

In fact, it is noteworthy that a number of adaptation initiatives, mostly at local and regional levels, are already taking place in Belgium (National Climate Commission, 2010). At the national level, the first initiative has been taken with the formulation of a national climate policy by the National Climate Commission in 2009, though still mainly focusing on mitigation. The Belgian National Climate Change Adaptation Strategy (2010) describes the potential threats posed by climate change per sector in Belgium, highlights the existing adaptation responses, and frames a roadmap to a comprehensive national adaptation plan, which was later adopted in April 2017. The National Adaptation Plan (2017-2020) proposes a set of measures that need to be taken at national level in order to strengthen cooperation and develop synergies between the different entities in Belgium on adaptation (National Climate Commission, 2016). Furthermore, a number of research projects dealing with adaptation to climate change are currently running or have recently been finished, including the 'FORBIO Climate' project (Belgian Research Action through Interdisciplinary Networks) in which framework this work has been carried out.

Among the initiatives developed to address adaptation needs, especially in the areas of monitoring, research and the sharing of information, the Walloon region has taken a leading role through the new Forest Code (2008) and the creation of a working group of experts to study the impacts of climate change in forest ecosystems. Of particular relevance is the report produced by this group, entitled *'Le changement climatique et ses impacts sur les forêts wallonnes - Recommandations aux décideurs, propriétaires et gestionnaires'* (2017; 2009), which contains recommendations for policy makers and a good practice guide for forest managers (see Figure 6.1 for an example). And even though the recommendations are not detailed enough to be entirely satisfactory, e.g., guidelines on which species are vulnerable to which disturbance and the type of actions that are most needed in order to facilitate the species adaptation to climate change; the report represents a significant step forward towards building capacity to adapt to climate change and to encourage forest managers to take a proactive approach to climate change adaptation.

The recently launched *'Fichier écologique des essences'* (https://fichierecologique.be/; Petit et al. 2017), a web tool to help forest managers with choice of tree species and for assessing the adequacy of a site to support the growth of a particular species or group of species, is another big step in the right direction (Figure 6.2).

Figure 6.2 Sensitivity to forest disturbances caused by climate change for the main tree species in Wallonia. *Data extracted from the Walloon 'Ecological file of species' (https://fichierecologique.be/). Adapted from Himpens et al. (2017).*



	High temperatures	Heatwave	Drought	Soil water scarcity	Water logging	Wind damage	Late frost
Robinia pseudoacacia (False acacia)	🟢	○	○	○	🔴	🟡	🔴
Tilia cordata (Small-leaved lime)	🟢	○	○	○	🟡	○	○
Pseudotsuga menziesii (Douglas fir)	○	?	○	○	🔴	○	🟡
Quercus petraea (Sessile oak)	○	○	○	🟡	🟡	○	🔴
Quercus robur (Pedunculate oak)	○	○	🔴	🟡	○	○	🟡
Prunus avium (Wild cherry)	🟢	?	🟡	🟡	🔴	🟡	○
Fraxinus excelsior (Common ash)	○	○	🟡	🔴	○	🟡	🔴
Acer pseudoplatanus (Sycamore maple)	○	🟡	🟡	🟡	🟡	○	○
Fagus sylvatica (Common beech)	○	🔴	🔴	🟡	🔴	🟡	🟡
Picea abies (Norway spruce)	🟡	🟡	🟡	🟡	🟡	🔴	○

Legend: 🟢 favored | ○ low sensitive | 🟡 moderately sensitive | 🔴 highly sensitive | ? insufficient evidence

It would therefore be highly desirable to develop similar initiatives in Flanders, i.e., to produce evidence-informed content and site-specific recommendations for advancing adaptation goals in forest management.

6.2. DIVERSIFYING FORESTS TO ENHANCE ECOSYSTEM RESILIENCE

> *“Biodiversity starts in the distant past*
> *and it points toward the future.”*
> ***Frans Lanting***

The concept of resilience was first introduced in ecology by Holling in the early 1970s to describe the capacity of a system to resist change in the face of disturbances (Holling, 1973). Since then, resilience has been defined in various ways and terms. These include *engineering resilience* (return to a previous steady-state; Pimm, 1984; Holling, 1996), *ecological resilience* (degree to which a system withstands disturbances and still retains the same function and structure [Walker et al. 2004], or changes in order to maintain the same identity [Folke et al. 2004]), and *socio-ecological resilience* (ability to reorganize and adapt through social, political and environmental change [Carpenter *et al.*, 2001]). In a world facing global change, promoting resilience through management is especially relevant to the long-term persistence of forests and the maintenance of their functional processes (Hodgson et al., 2015; Seidl et al., 2016b).

Disturbances are important drivers of forest dynamics. However, as climate warms, an increase in the occurrence and severity of disturbances, such as drought, fire, and insects outbreaks, will have a profound impact on forests (Seidl et al., 2017). In particular, drought has emerged as a major threat to forests worldwide (Anderegg et al., 2015b). Higher temperatures increase evapotranspiration from trees, while the trees themselves are left with less water. Therefore, as the climate continues to warm, studying how drought affects the growth and vitality of trees becomes ever more important to identify suitable adaptive strategies. Hot summers like the one of 2003 are becoming the new normal (Brouwers et al., 2015). Under projected future climate conditions for Belgium (for 2071-2100), potential evapotranspiration is expected to increase during both winter and summer seasons, and water availability is expected to decrease for summer and increase for winter (Tabari et al., 2015). These climatic changes reflect the changes from the reference period 1961–1990 to the future scenario period 1971–2100. In other words, winters will get wetter and summers drier, resulting in increasingly frequent (summer) droughts. Since the beginning of the measurements in Uccle (1833), the years 2014, 2011 and 2007 went on record as the top three warmest years, but 2018 is on the track to be the absolute warmest year on record; and furthermore, at the beginning of August, 2018, almost the entire northern part of Belgium (north of the Sambre-Meuse river line) was affected by severe drought (IRM, 2018).

In this study, we focused on the period between 1980 and 2016, during which we observed a significant increase in the number of dry years (Appendix B1), as well as a decrease in the occurrence of wet years, obviously important to restore ecosystem health after dry periods. Indeed, if the time between drought events becomes shorter than the time needed for trees to recover from them, trees are likely to become increasingly prone to water stress and insect attacks (Schwalm et al., 2017). We assessed the severity and trends of drought using the multiscalar drought index SPEI (Vicente-Serrano et al., 2010). Although computed at different time scales, to adapt to the different response times of tree defoliation ($\mathrm{SPEI}_{21\text{–}\mathrm{May}}$) and tree growth ($\mathrm{SPEI}_{7\text{–}\mathrm{Oct}}$) to the precipitation deficit, both SPEI indices revealed a similar pattern of increased frequency of dry years over the past three decades (cf. Figure 3.2 and Figure 4.1). It is also important to stress that, even though we used different SPEI thresholds to define drought (-0.67 in Chapter 3 and -1 in Chapter 4), the significance and comparability between study results were not affected by choice of thresholds since they lead to the same conclusions in the statistical analyses. The years 1995, 2003 and 2009-2011 stood out as drought years (as quantified by low SPEI), suggesting that the main results reported are robust and reliable. In Chapter 3, the SPEI was calculated over the previous 21 months, and as such, negative SPEI values indicate dry conditions in previous year. For instance, with regard to the 2003 drought, the SPEI value in Chapter 3 was -1.12 (observed in 2004), and -1.57 in Chapter 4 (observed in 2003).

6.2.1. TREE SPECIES RICHNESS SUSTAINS HIGHER RESISTANCE OVER TIME

Drought limits how much trees can grow and store carbon (e.g., Anderegg et al., 2015b). An indispensable requirement for assessing the long-term impact of drought events on trees is the availability of long-term records (Bräuning et al., 2017). In this study, we used data from over 100 long-term monitoring plots, where crown defoliation and radial growth have been assessed extensively since 1990, and we showed that trees growing in mixtures were more resilient to drought compared to those growing in monocultures. Furthermore, we were able to demonstrate that the impacts of drought differ considerably among species and from event to event, and that species interactions are dynamic and can change through time (Chapter 3 and Chapter 4).

The encouragement for mixed forests has gained increased attention in recent years (e.g., Gérard 2008; Messier et al. 2013), owing to their importance under changing societal demands on functions and services, and because of their higher resilience to disturbances such as drought and insect outbreaks (e.g., Lebourgeois *et al.*, 2013; Pretzsch *et al.*, 2013; Jactel *et al.*, 2017), because if more species are present, then there is a greater chance that at least one of the species will maintain functioning under stress, compensating for other species that experience declines (Yachi and Loreau, 1999). In Chapter 3, we demonstrated how the complex interplay between tree species richness and the responses of forests to drought stress evolves over time; we showed that higher species diversity has reduced the severity of defoliation in the long-term, and that the positive effect of species richness on crown defoliation arose after a period of steady increase in defoliation. Our study thus adds to the weight of evidence that more diverse forests are more likely to display higher levels of functioning than less diverse ones under stressful conditions.

This positive relationship between species richness and ecosystem functioning is usually interpreted in terms of complementarity and selection effects (Hooper et al., 2005; Loreau and Hector, 2001). The complementarity effect includes both niche partitioning and facilitative processes, and is based on the assumption that different species complement each other in the acquisition of resources, thereby decreasing interspecific competition and increasing total resource use in space and time. Our results further suggest that the likelihood for the complementarity use of resources increases when resources are limited, such as under water-limited conditions. This may explain the regime shift from healthy monocultures to resilient tree species mixtures, considering that facilitation and competition always occur simultaneously and that the balance of these counteracting mechanisms is strongly context-dependent and subject to change through time.

6.2.2. TREE GROWTH AND DIFFERENT RESPONSES TO DROUGHT

Traditionally in Europe, as elsewhere, the main purpose of forest management is to enhance forest productivity and to maximize economic returns from the production of wood (Bastrup-Birk et al., 2016; Bauhus et al., 2010). Achieving this goal requires knowledge of the growth potential of various tree species, stand-specific conditions, as well as of stand dynamics. Furthermore, understanding how these dynamics are altered in response to disturbances, such as drought, becomes increasingly important for forest management as climate change forces them to adjust.

In Chapter 4, we described a strong and convincing link between the decline in tree productivity and an increase in drought conditions, associated with longer recovery times. Trees growing in mixtures had significantly higher increments compared with trees growing in monocultures, and recovery after drought was also faster and more pronounced in mixtures than in monocultures. In addition, we found a tendency towards lower resilience to drought in defoliated trees. It is however noteworthy that the marked decline in growth during drought years was observed for both defoliated and non-defoliated trees, regardless their defoliation level. Indeed, although a significant correlation was observed between decrease in radial growth and increase in crown defoliation, our results do not allow to conclude whether slower growth is caused by defoliation, or whether growth reduction and defoliation result from co-varying responses to the same underlying process(es) (e.g., hydraulic failure or carbon starvation). For instance, defoliation induced by drought may predispose trees to decline via a reduction in carbohydrates supply, since the reduced leaf area contributes to less photosynthesis, thus limiting further root production and its ability to exploit deeper soil water (Jacquet et al., 2014). As water deficits increase, moisture stress results in stomatal closure, which ultimately decreases growth because of reduced carbon uptake (Chaves, 1991).

Nevertheless, taken together, the results from Chapters 3 and 4 clearly indicated that trees growing in mixtures not only grew more quickly, but also showed lower defoliation levels, and that the positive effect of diversity became stronger with time. The observed tipping point in the relationship between species richness and tree vitality, beyond which a drought stress-induced positive diversity-stability relationship emerged, as described in Chapter 3, was concurrent with the marked growth decline in trees in monocultures during the 2009-2011 drought event investigated in Chapter 4, after which tree growth was significantly higher in mixtures than in monocultures.

Species interactions may reduce susceptibility to water stress through facilitative mechanisms, such as hydraulic lift and canopy shading, but also via a reduction in competition due to spatial and temporal partitioning of water resources (Forrester and Bauhus, 2016). Hydraulic lift is a phenomenon whereby trees with deep root systems take in water from lower soil layers and distribute that water through their roots to upper, drier soil layers (Horton and Hart, 1998). Hydraulically lifted water can benefit the plant that lifts it but might also benefit neighboring trees, because of the better buffering ability against water stress during drought. This is the case of *Fagus sylvatica*, which is facilitated significantly when mixed with, e.g., *Quercus* spp. This positive effect of species mixing on growth has been attributed to the low self-tolerance (Del Río et al., 2014), superior space sequestration efficiency (Dieler and Pretzsch, 2013), and specific root system architecture (Leuschner et al., 2001) of *F. sylvatica*, which give the species a competitive advantage in mixtures. For comparison, no significant differences were found between the growth *of Q. petraea* trees in mixtures and monocultures. This might result from the fact that *Q. petraea* is a light-demanding species with low shade tolerance, thus their response to mixing has been found to depend on the shade tolerance of the surrounding species, i.e. positive effects when the surrounding species are shade-intolerant and negative effects when the surrounding species are highly shade-tolerant (Toïgo et al., 2018).

6.3. FOREST MANAGEMENT: CHALLENGES AND RECOMMENDATIONS

“Sadly, it's much easier to create a desert than a forest.”

James Lovelock

Ultimately, science is about bettering society – whether it is to deepen our understanding of the natural world or to solve the problems and challenges of today and tomorrow. Accordingly, the overarching goal of this research was to advance our understanding on the dynamics of *F. sylvatica* and *Quercus* spp. forests, and in particular to assess the effect of tree species diversity on the productivity and resilience of forests in the face of increasing drought stress.

Fagus sylvatica, *Q. petraea* and *Q. robur* are three of the most widespread broadleaved species in Europe. These species are not only of great ecological importance, e.g., as habitat and food sources for a variety of wildlife species, but also of considerable economic value for forestry and the timber industry (e.g., Dittmar *et al.*, 2003; Annighöfer *et al.*, 2015). *Quercus petraea* and *Q. robur* are mid-successional species, deep-rooted, that have a moderate shade-tolerance, whereas *F. sylvatica* is a late-successional species, shallow-rooted, that is very shade-tolerant. As a result, together they may compete less (e.g., for light), potentially leading to a more complete use of resources (e.g., water and nutrients). However, as described in earlier studies, *F. sylvatica* is a better competitor than *Quercus* spp. for both above- and belowground resources (Bolte et al., 2013; Toïgo et al., 2015). Silvicultural treatments have therefore a prominent role in maintaining the equilibrium between *F. sylvatica* and *Quercus* spp. trees to counteract the competitive advantage of *F. sylvatica*. In fact, mixtures of these two species tend to develop naturally only under conditions in which the competitive ability of *F. sylvatica* is significantly reduced (Hans Pretzsch et al., 2013). This is often the case in managed forests, where thinning at appropriate intervals may reduce or eliminate strong intraspecific competition and help to maintain or even favor *Quercus* spp. over *F. sylvatica*.

There are also concerns regarding the successful regeneration of *Quercus* spp., which is complicated by many factors including the amount of viable seeds available for germination (Annighöfer et al., 2015). Successful oak (*Quercus* spp.) regeneration is possible in unshaded sites (gaps), such as under the canopy of a mature stand in *shelterwood* and *group selection* harvesting methods. *Quercus* spp. can be grown successfully under a *shelterwood system* due to an increased photosynthetic potential and water-use efficiency (Annighöfer et al., 2015); and *group selection* harvesting methods have proven to be appropriate regeneration methods for mixed stands (Bartsch and Röhrig, 2009). *Group selection* permits to selectively remove clusters of adjacent trees, more or less even-aged, thus creating larger openings needed to regenerate shade-intolerant species such as *Q. petraea* and *Q. robur*. After harvest, the control of herbaceous vegetation and undesirable tree species may be necessary to encourage oak regeneration.

A summary list of recommended management adaptation actions, as reported elsewhere in the literature (FAO, 2013; Himpens et al., 2017), is provided in Supplementary Table D.1.

6.3.1. THE IMPORTANCE OF TREE SPECIES IDENTITY ON STAND-LEVEL PRODUCTIVITY

Although frequent, the advantages and benefits of mixed-species stands should not be overgeneralized. For example, in Chapter 5, using data from national forest inventories, we showed that the positive effect of species mixing on the growth of *F. sylvatica* was counterbalanced by an underyielding of *Quercus* spp., and that the effect was not strong enough to significantly increase overall stand productivity. In this respect, Forey et al. (2016) have argued that *F. sylvatica* and *Quercus* spp. are too similar to be ideal for mixing and have suggested to mix *F. sylvatica* with other tree species (e.g., ash, hornbeam, maple or lime trees), and so to enhance complementarity effects and to reduce competition within stands.

We also note that the findings from Chapters 3, 4 and 5 are somewhat contradictory. There are several possible explanations for this apparent contradiction. The first, and most obvious reason, is that these studies were based on different data sets that were analyzed for each research question using different approaches. Second, within the monitoring plots of ICP Forests, trees are measured every year, whereas in the regional forest inventories, plots are revisited approximately every 10 years. The continuous measurements on ICP Forests plots (1990-2016) allowed us, for instance, to unveil a progressive shift from a negative to a positive effect of species richness on forest health (Chapter 3), but such inferences cannot be drawn using inventory plots. Third, and perhaps most important, in Chapter 4, we analyzed how species diversity affects tree growth across a gradient of tree species richness ranging from monocultures to mixtures of five species. However, in Chapter 5, productivity was derived from measurements in monocultures and *two-species* mixtures, and plots that did not fall into one of these two categories were excluded from the analysis as we were aiming at investigating not only the diversity effect, but also the neighbor identity effect. This may strongly suggest that the more diverse a stand is, the higher is the overall growth rate of each species. These conclusions are consistent with our observations that tree health and productivity increased at high tree species richness (Chapters 3 and 4), as well as those described in the literature for multiple ecosystem services (Gamfeldt et al., 2013; van der Plas et al., 2016).

Mixing tree species is not a zero-sum game, where one species' gain is another's loss. Although the primary aim of this work was to investigate the effect of species diversity on vitality, growth, and resilience of forests, the importance of species identity cannot be dismissed. In fact, species identity has been suggested to explain the effect of tree species diversity on forest productivity (e.g., Pretzsch, 2005; Lubbe *et al.*, 2015; Tobner *et al.*, 2016). Thus, decisions about mixing species should be made with due consideration for the identity of the species, species traits, and the environmental characteristics of forest sites. In this regard, a proper choice of tree species and provenances should take precedence in forest planning. For instance, as climate becomes hotter and drier, forest management should consider the selection of climate-tolerant species and the use of a mixture of genotypes, or seed sources, from ecologically different sites whose environments match most closely those of the planting site (Breed et al., 2013; Crowe and Parker, 2008). Maximizing the genetic variation of trees within a forest (e.g., for drought tolerance), and enhancing the likelihood of plant establishment and persistence in stressful environments are likely to confer greater resilience to climate variability. For example, the genus *Quercus* comprises hundreds of deciduous evergreen tree and shrub species distributed over a wide range of environments (Nixon, 2006). Thus, seeds from provenances or species originating from drier habitats may provide a superior seed source for future plant establishment (Hu et al., 2013).

Nevertheless, growing evidence supports the notion that managing forests to retain or increase diversity has the additional potential benefit of sustaining forest productivity in the face of multiple disturbances (Bauhus et al., 2017a; Jucker et al., 2014a), as mixed forests provide managers with more options for future stand development, as well as better outcomes in terms of biodiversity, water quality, esthetic and recreational values (Felton et al., 2016). For example, the conversion of coniferous monocultures, which still cover large areas in Europe, into more stable mixed conifer-deciduous forest stands can provide additional benefits such as increased biodiversity, ecosystem services, and economic flexibility (Felton et al., 2016; Zerbe, 2002). In addition, resistance to herbivory and to pathogens might be higher in mixed stands because hosts are less abundant and enemies of forest pests may be more common (Kaitaniemi *et al.*, 2007; Guyot *et al.*, 2015; Jactel *et al.*, 2017; but see Haase *et al.*, 2015). But despite its benefits, several limitations still hinder the adoption of tree species mixtures, including increased management complexity and a continued uncertainty regarding their economic and production outcomes (Felton et al., 2016). If from an academic point of view the recent advances in our understanding of mixed forest functioning are of unquestionable value (Forrester and Bauhus, 2016), the challenge for the future will be to translate this knowledge into better management decisions.

6.4. LIMITATIONS AND DIRECTIONS FOR FUTURE RESEARCH

"The important thing is not to stop questioning."
Albert Einstein

This study benefited from existing data from the European-wide ICP Forests monitoring network (Chapter 3 and Chapter 4), and from the Regional Forest Inventory of Flanders and Wallonia (Chapter 5). These data are of paramount importance, especially given the longevity of trees, because they provide information on the status of forests and a continuous record of forest change (Chirici et al., 2012). On the one hand, inventories typically cover a large range of environmental conditions, stand ages, densities, species compositions, and management regimes, thus showing a high degree of representativeness (Figure 6.3; cf. Nadrowski *et al.*, 2010; Bauhus *et al.*, 2017b). On the other hand, their comprehensiveness and orthogonality are limited. In general, inventories include a quantification of only a few ecosystem properties and processes (e.g., growth, biomass production, and carbon sequestration), and confounding factors may mask the effect of species diversity in the data. For example, one might conclude that higher productive sites that support high productive stands simply permit the coexistence of more species (Bauhus et al., 2017b). In particular, management practices can affect the relationship between stand diversity and productivity via the presence and growth of some tree species and not others (Vilà et al., 2005), but this information is often not readily available in forest inventories. We recommend that future inventory assessments aim to reduce this major knowledge gap by including clear information on past management practices (e.g., thinning and harvesting), as well as the primary motivation behind them (e.g., a desire to derive financial value from threatened or wind-thrown trees). Thinning, for instance, can be broadly described by type (systematic or selective), frequency (recurrence interval), and intensity,

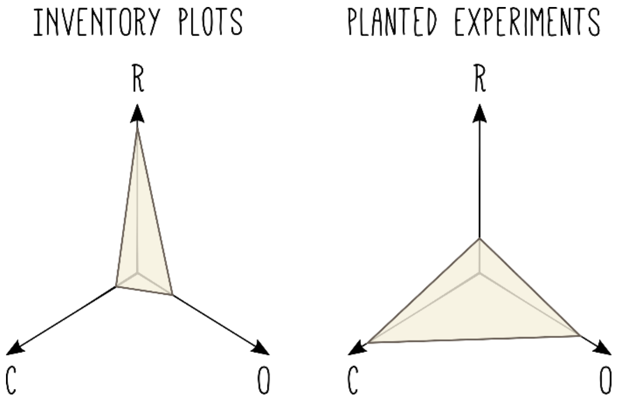


Figure 6.3 Relative differences in representativeness, comprehensiveness, and orthogonality between permanent inventory plots and controlled experiments in forests to quantify the effect of biodiversity. *Representativeness (R) refers to the relevance of analyzed results for real-world forests. Comprehensiveness (C) refers to the spectrum of ecosystem functions and services quantified in a study. Orthogonality (O) refers to the statistical independence of the effects of species diversity from other influencing factors and covariates. Ideally, tree diversity studies should optimize these three criteria. Adapted from Bauhus et al.* (2017b).

the aims of which include decreasing the competition of neighboring trees, thus enhancing the growth of the remaining trees; creating harvest opportunities; and influencing the tree species composition and vertical structure of the stand (Nabuurs et al., 2008).

Another inherent limitation of our work is the lack of information about the soil and site quality of each forest stand and therefore, which could have potentially confounded the results (Vilà et al., 2005). In the case of drought stress, the prevailing soil conditions, and in particularly the soil water content, can strongly influence the response of trees (Brunner et al., 2015; Gaul et al., 2008). However, the lack of fine-scale soil data at the stand level prevents a better understanding of the influence of site conditions on tree growth. For instance, while the ICP Forests Level II plots include detailed information on forest soil quality, including soil hydraulic properties, this is not the case either for the Level I plots, or for the inventory plots. Therefore, we used coarse soil map data (Dondeyne et al., 2014), together with DEM-derived data (AGIV, 2015; SPW, 2015), to characterize each study plot. And although we acknowledge that these data may not fully capture the different soil properties that can be observed in the field, as the present study covered the whole of Belgium (and both monocultures and mixed-species plots are widely distributed across the landscape), we are convinced that these data have not compromised the main findings of this research. We do, however, acknowledge its limitations with regard to soil moisture dynamics and the access of trees to subsurface water during drought. A cross-disciplinary study using other relevant metrics, such as the temporal dynamics of soil water content, would certainly be a valuable follow-up to this work.

Regarding the ICP Forests program, forest monitoring has focused on crown defoliation and discoloration as indicators of forest health and vitality (Eichhorn *et al.*, 2016). Crown defoliation expresses the relative amount of foliage on the tree crown compared to an ideal healthy tree, and is assessed visually by trained field teams (Pollastrini et al., 2016). Therefore, although strict international guidelines and intensive training programs exist for assessing crown defoliation (Eichhorn et al., 2016), a subjective component still subsists (e.g., Ferretti, 1998; De Vries *et al.*, 2000; Metzger & Oren, 2001). For example, the perception of the observers might cause observation bias (Solberg and Strand, 1999), which might in turn be increased by weather and lighting conditions, the visibility of the crown, tree species, tree age and social position (Muukkonen et al., 2014; Wulff, 2002). Consequently, regular training courses and the adoption of a quality assurance system (e.g., Ferretti *et al.*, 1999) to improve and to document the consistency and reproducibility of visually assessed defoliation data are of utmost importance to ensure the reliability and reproducibility of the results For instance, Bussotti *et al.* (2009) reported a rapid and steady improvement of defoliation data consistency in Italy following the adoption of the quality assurance system. Eickenscheidt & Wellbrock (2014) have also reported a trend towards increasing defoliation data consistency in Germany following national training courses. In Belgium, training courses are organized every year aiming at ensuring spatial and temporal data comparability, but separately for Flanders and Wallonia. These training courses take place before commencing the field data collection, and results are discussed in the field. Participation in international intercalibration and intercomparison courses is also a common practice. Yet, paradoxically, a national training and intercalibration course has so far been neglected. Nevertheless, and despite its inherent limitations, the very high representativeness over space and time of the ICP Forests monitoring program has proven to be an effort that merits improved and extended continuation.

6.5. CONCLUSIONS AND PERSPECTIVES

"The past, like the future, is indefinite
and exists only as a spectrum of possibilities."

Stephen Hawking

Monitoring the condition of forests is of great importance because insights from monitoring can directly inform adaptive management options, and also because decisions made by managers over whether and how to intervene could prove decisive to secure the future health and productivity of forest systems. In this research, we showed that standardized, long-term monitoring of forest vitality is an effective method to detect climate change-induced and tree diversity-mediated trends in forest health and productivity. Furthermore, our results point to a pivotal role of tree species diversity in an increased growth resilience to drought events, which adds further evidence to the overall positive impact of diversity on forest productivity under anticipated warmer and drier conditions.

Revisiting our research hypotheses,

1. Do perceptions and knowledge on climate change influence the implementation of adaptation practices by forest managers?
2. Does tree species richness increase the resilience of forests to drought-induced defoliation?
3. Are mixed-species forests more productive than monocultures?

we may conclude that:

1. There is a marked imbalance between the great awareness about climate change impacts and the adaptation practices put in place by forest managers for coping with it (**Chapter 2**). A lack of locally relevant and practical information about

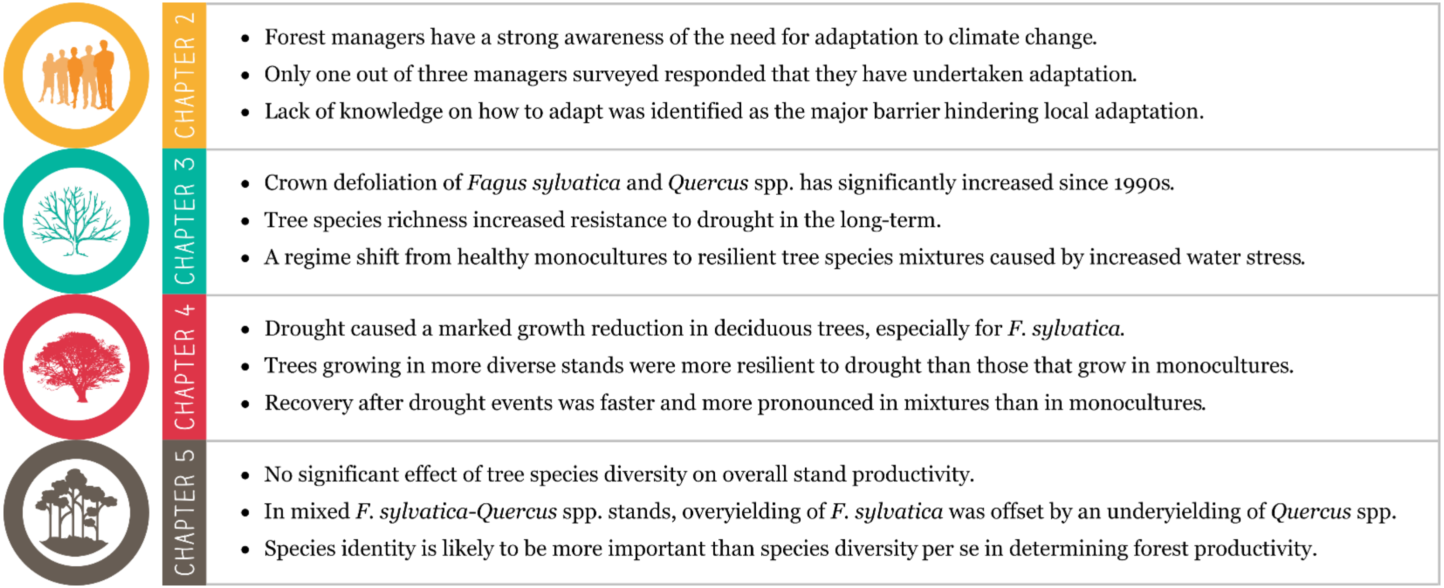
potential climate impacts and a lack of technical expertise on how to adapt were identified as barriers to adaptation, but significant progresses have been recently made in increasing and improving the information available.

2. The severity of defoliation is lower at higher tree species richness levels when considering long-term responses to changes in temperature and precipitation (**Chapter 3**). The observed shift from a negative to a positive effect of species richness on forest condition, although implicit in previous studies, has never been reported from real ecosystems outside experimental conditions.

3. There is mixed evidence regarding the effect of species mixing on tree growth. On the one hand, we showed that trees in mixture grew better and faster than those in monoculture (**Chapter 4**). On the other hand, we found no significant effect of mixture on the overall stand productivity of *F. sylvatica*-*Quercus* spp. mixtures (**Chapter 5**). This null mixture effect on stand productivity conceals an overyielding of *F. sylvatica* offset by an underyielding of o *Quercus* spp. Differences in study design and methodologies may partly account for differences in the reported results.

Main results of individual chapters are summarized in Figure 6.4. Taken together, we found that mixed species forests could better withstand drought stress, which confirms the greater resilience of diverse forests to anticipated climate change-induced water constraints. Maintaining forest diversity has, therefore, major implications for forest management practices and efforts to mitigate the vulnerability of forests to drought under changing climate conditions.

Further work is needed to clarify the physiological mechanisms involved in drought-induced canopy and growth decline and how they can be influenced by species interactions and forest management. Hence, further efforts are required to identify which combinations of species mixtures, in terms of their water use strategies, and depending on site specific climatic and edaphic characteristics, will be most beneficial for increasing the resilience of forests to drought. This will enable us to provide answers to the frequently asked questions: *Which mixtures of species provide the best resilience to climate change?* and *Are mixed-forests more efficient in using resources than monocultures?* (Coll et al., 2018). Ultimately, such efforts could prove pivotal for forest managers to establish and maintain forests of high tree species diversity and thereby high levels of forest multifunctionality.



CHAPTER 2

- Forest managers have a strong awareness of the need for adaptation to climate change.
- Only one out of three managers surveyed responded that they have undertaken adaptation.
- Lack of knowledge on how to adapt was identified as the major barrier hindering local adaptation.

CHAPTER 3

- Crown defoliation of *Fagus sylvatica* and *Quercus* spp. has significantly increased since 1990s.
- Tree species richness increased resistance to drought in the long-term.
- A regime shift from healthy monocultures to resilient tree species mixtures caused by increased water stress.

CHAPTER 4

- Drought caused a marked growth reduction in deciduous trees, especially for *F. sylvatica*.
- Trees growing in more diverse stands were more resilient to drought than those that grow in monocultures.
- Recovery after drought events was faster and more pronounced in mixtures than in monocultures.

CHAPTER 5

- No significant effect of tree species diversity on overall stand productivity.
- In mixed *F. sylvatica-Quercus* spp. stands, overyielding of *F. sylvatica* was offset by an underyielding of *Quercus* spp.
- Species identity is likely to be more important than species diversity per se in determining forest productivity.

Figure 6.4 Overview of the key findings from each individual chapter.

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APPENDICES

APPENDIX A

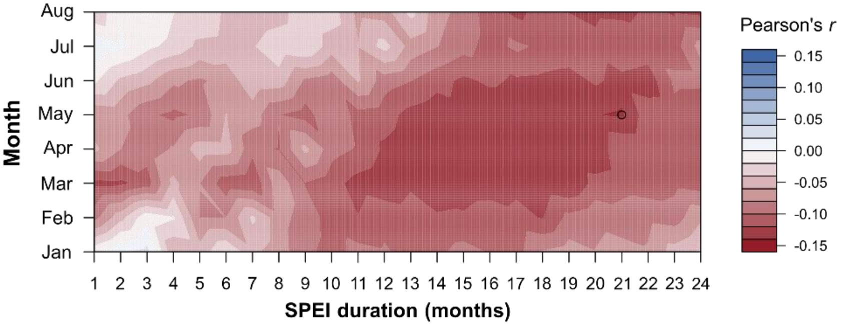


Figure A.1 Correlation heat map between the mean annual defoliation and the SPEI (Standardized Precipitation Evapotranspiration Index) for the targeted forest plots. *The SPEI duration on the x-axis represents the number of months used to calculate the index (e.g., a 3-month SPEI makes use of the previous 2 months and the month being considered). The y-axis is the month in which the calculation of SPEI ends. The panel on the right indicates the correspondence of the colors in the heat map with the Pearson's correlation between SPEI and defoliation. The monthly values for the SPEI were averaged across plots (N = 119) over the period 1990-2015.*

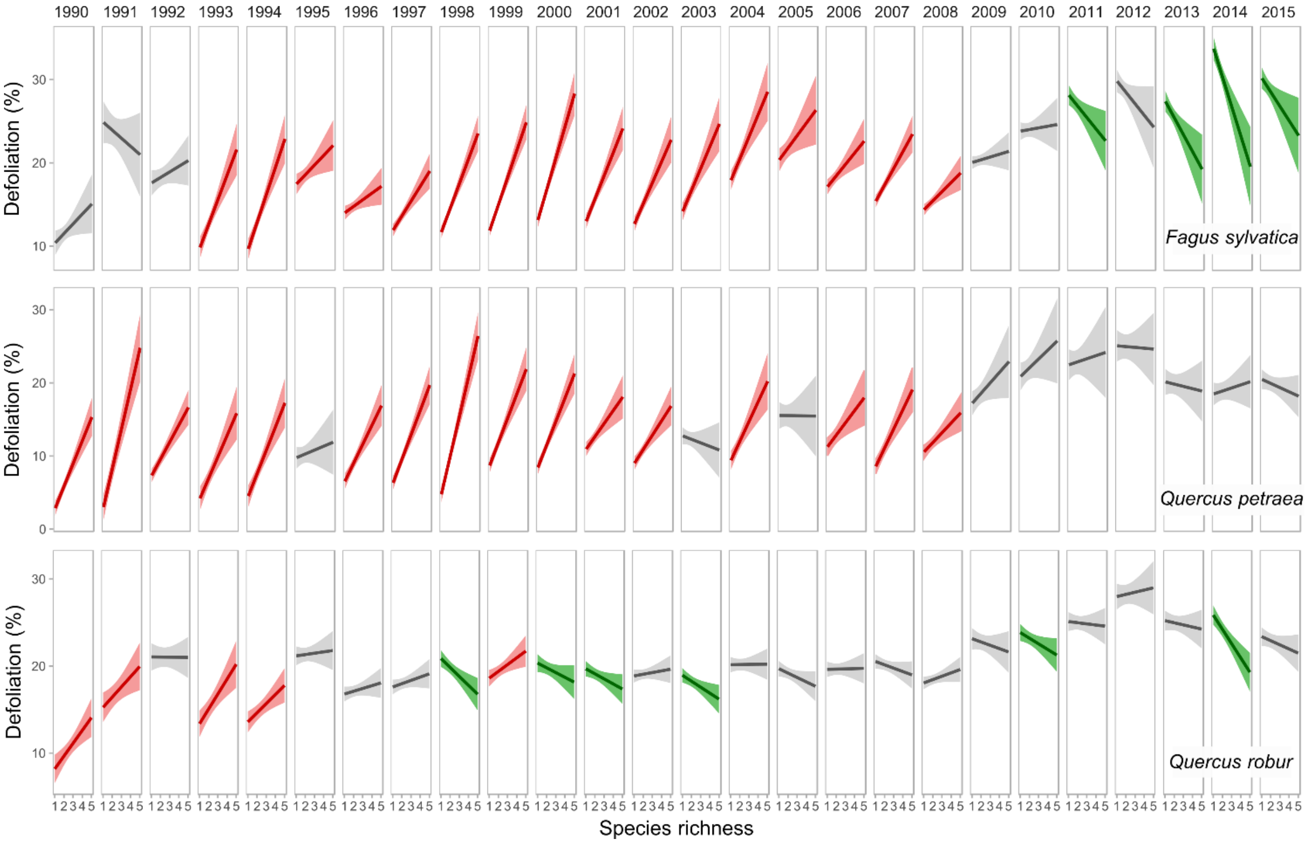


Figure A.2 Annual trends in plot averaged tree defoliation along a tree species richness gradient in temperate deciduous forests*. Crown condition assessments of* F. sylvatica *(upper panel; N = 14618 observations),* Q. petraea *(middle panel; N = 6583 obs.) and* Q. robur *(lower panel; N = 16528 obs.) trees growing in pure and mixed stands. Defoliation severity was expressed as the proportion (percentage 0-100%, with intervals of 5%) of leaf loss. Solid lines and shaded areas represent the mean and 95% confidence intervals for each year of the study. Positive slopes (red) indicate an increase in defoliation with increased species richness (ranging from 1 to 5), whereas negative slopes (green) denote a decrease in defoliation in more diverse stands. Non-significant slopes are shaded gray ($P \geq 0.05$).*

Table A.1 *Temporal variation of number of plots and trees assessed from 1990 to 2015 as part of the surveys of the ICP Forests monitoring programme in Belgium.*

	Fagus sylvatica		***Quercus petraea***		***Quercus robur***		**Total**
	No. plots	No. trees	No. plots	No. trees	No. plots	No. trees	No. trees
1990	28	318	22	184	29	288	790
1991	13	140	7	68	19	227	435
1992	13	141	7	68	17	200	409
1993	27	319	21	170	31	358	847
1994	28	322	21	172	33	364	858
1995	41	477	27	277	56	755	1509
1996	43	547	24	228	56	740	1515
1997	43	574	24	245	56	746	1565
1998	45	664	25	266	55	723	1653
1999	45	735	28	310	57	771	1816
2000	44	728	28	317	56	760	1805
2001	46	720	28	314	58	777	1811
2002	44	684	25	281	54	731	1696
2003	42	658	24	291	56	764	1713
2004	43	657	22	267	55	732	1656
2005	44	672	26	304	58	780	1756
2006	44	659	25	297	54	747	1703
2007	41	651	26	295	53	717	1663
2008	43	665	24	256	52	721	1642
2009	41	618	25	277	54	744	1639
2010	60	714	32	272	65	764	1750
2011	57	672	33	297	68	776	1745
2012	54	630	35	322	64	620	1572
2013	55	617	33	304	65	629	1550
2014	49	551	26	270	62	587	1408
2015	51	544	26	242	56	507	1293

In Flanders, surveys are carried out by INBO (Research Institute for Nature and Forest). Survey teams are trained before each field survey and quality control assessments on data have been conducted annually (results not published). The core survey crew did not change over time. In Wallonia, survey teams changed throughout the study period. Surveys were carried out by DNF (Département de la Nature et des Forêts), DEMNA (Département de l'Etude du Milieu Naturel et Agricole), and UCL (Université catholique de Louvain). UCL is currently performing and supervising the field assessment of the forest condition survey in Wallonia. Regular training courses have been in place since 1990 and assessments of the quality of the assessed defoliation data (e.g. field checks) are carried out since 2010 (results not published).

Table A.2. Model comparisons and variation explained. *The table shows the covariates examined in the analyses, the goodness-of-fit (R^2), and the Akaike Information Criterion (AIC) of the respective regression models. M0 is the intercept-only model. In the baseline model (M1), defoliation (DFL) is expressed as a function of target species identity (SP) and plot attributes [species richness (SR), stand basal area (BA), age class distribution (AGE) and management type (MGM)]. 'SPEI' indicates a model that accounts for the impact of drought conditions on DFL (represented by the SPEI calculated at 21-month lag in May; M2), and model M3 tests whether the effects of drought on DFL varies among species (i.e., the interaction between SP and SPEI). Model M4 further allows SR effects to vary among years (i.e., the interaction between SR and YEAR), and model M5 tests whether this effect increased or decreased over time for each species separately (i.e., the interaction between SP, SR and YEAR). Additionally, models that incorporated data relating to climate (mean temperature (TA) and precipitation (PP) during the growing season; M6), soil and topographic conditions (e.g., elevation and aspect; M7), as well as the Shannon (SD; M8) and functional diversity (FD; M9) indices were also considered.*
Model structure follows lme4 syntax in R, including the random effect of plot nested within level of monitoring (categorical grouping variable), which is normally distributed and affects the intercept. ΔAIC represents the difference between models, and Akaike weights (wAICc) are interpreted as the probability that the associated model is the best in the set. Marginal and conditional R^2 relate to the variance explained by the fixed effects and the full model (fixed plus random effects), respectively. Note that DFL was log-transformed prior to model fitting. Best fitting model (M5, shown in bold) was fitted with an autocorrelation structure [ARMA(2,0)] to account for temporal autocorrelation in the data.

Table A.2 Comparison of mixed-effects models of crown defoliation.

Model	Structure	AICc	wAICc	R^2 conditional (marginal)
M0	DFL ~ 1 + (1 | Plot/Cluster)	4326	0	0.74 (0.08)
M1	DFL ~ SP + SR + BA + AGE + MGM + (1 | Plot/Cluster)	4289	0	0.68 (0.14)
M2	DFL ~ SP + SR + BA + AGE + MGM + SPEI + (1 | Plot/Cluster)	4268	0	0.68 (0.14)
M3	DFL ~ SP + SR + BA + AGE + MGM + SPEI + (SP*SPEI) + (1 | Plot/Cluster)	4292	0	0.73 (0.09)
M4	DFL ~ SP + SR + BA + AGE + MGM + SPEI + (SP*SPEI) + (SR*YEAR) + (1 | Plot/Cluster)	4292	0	0.73 (0.09)
M5	**DFL ~ SP + SR + BA + AGE + MGM + SPEI + (SP*SPEI) + (SP*SR*YEAR) + (1 | Plot/Cluster)**	**3916**	**1**	**0.72 (0.24)**
M6	DFL ~ SP + SR + BA + AGE + MGM + SPEI + (SP*SPEI) + (SR*YEAR) + Soil + Aspect + Elevation + Slope + (1 | Plot/Cluster)	4077	0	0.73 (0.17)
M7	DFL ~ SP + SR + BA + AGE + MGM + SPEI + (SP*SPEI) + (SR*YEAR) + TA_{GS} + PP_{GS} + (1 | Plot/Cluster)	4056	0	0.73 (0.14)
M8	DFL ~ SP + SR + BA + AGE + MGM + SD + SPEI + (SR*YEAR) + (1 | Plot/Cluster)	4328	0	0.73 (0.09)
M9	DFL ~ SP + SR + BA + AGE + MGM + FD + SPEI + (SR*YEAR) + (1 | Plot/Cluster)	4328	0	0.73 (0.09)

Supplementary Note A.1

The soil variables included in this study were: reference soil group, drainage status, texture class, and chemical soil fertility. These variables were derived from the soil map of Belgium, which has recently been revised and complemented for the Flemish region by Dondeyne et al. (2014). In their work, Dondeyne et al. converted the legend of the soil map of Belgium to a legend according to the international soil classification system of the World Reference Base for Soil Resources (WRB) for the Flemish region, at a 1 : 250 000 scale. Later, this was extended to cover all the plots in the Walloon region (Dondeyne, 2017). Information on drainage, soil texture, and chemical soil fertility was extracted using the *Supplementary Qualifiers*, which are meant for presenting properties that are not specific to a particular *Reference Soil Group*.

In this study, the reference soil groups with the hight incidence were *Cambisols* (45%), followed by *Anthrosols*, *Luvisols*, *Podzols*, *Retisols*, and *Stagnosols*, which together constituted about 85% of the studied plots.

Drainage classes (from *well drained* to *very poorly drained*) are defined according to the depth at which redoximorphic mottling and/or reduction colours occur. *Textural* classes (*Arenic*, *Loamic*, *Siltic*, and *Clayic*) are defined based on the relative content of clay, silt and sand. For additional details on drainage and textural classes, see Dondeyne et al. (2014). For example, in the soil series Zcg, Zdg and Zeg, the first capital means the soil texture is sand (Z), the second symbol means the drainage status is moderately well drained (.c.), imperfectly drained (.d.), or poorly drained (.e.), and the third symbol (..g) indicates that the soil profile development corresponds to a spodic horizon, with a well-developed iron and/or humus B horizon. Such Podzols can be commonly found in the Campine region of Flanders, sampled in this study.

The chemical soil *fertility* status (*Dystric*, *Eutric*, *Calcaric*) is defined for each soil type and according to the various soil districts.

Dystric implies that the base saturation of the soil between 20-100 cm depth is less than 50%; while *Eutric* implies that it is more than 50%. A soil is *Calcaric* when it has calcaric material (>2%) throughout between 20-100 cm from the soil surface (Dondeyne et al., 2014).

All variables were treated as categorical variables.

Supplementary Note A.2

Age is known to be an important factor influencing defoliation. For instance, it has been shown in the literature that stands composed of younger trees are at low risk of insect defoliation, regardless of species composition or stand structure (Gast et al., 1991; Tenow et al., 2004), because they offer more places for oviposition (e.g., cracks, lichens, scarred surfaces), increasing the survival rate of the eggs (Babst et al., 2010). In this study, however, stand age could not be included in the main analysis due to the incomplete data – age class was unknown or could not be determined for 21 study plots. Nevertheless, the influence of age on defoliation was tested on a subset of plots for which we had complete data (*N* = 85), as shown next.

According to the ICP Forests Manual (Eichhorn et al., 2016), stand age is defined as the mean age of the dominant storey, which is reported in 20-year classes ('1' = 0-20 years; '2' = 21-40 years; '3' = 41-60 years; '4' = 61-80 years; '5' = 81-100 years; '6' = 101-120 years; '7' = >120 years). In our case, the 5th, 6th and 7th age classes dominate the age structure of the monitoring plots (Table A.3). This higher representation of older stands is likely the result of the intentional selection of these stands at the beginning of the programme motivated by the then existing practice and experience with the assessment of damage on mature forest stands.

As for the influence of age on defoliation, there is a tendency for increased defoliation with age (Figure A.3), but both young and older trees showed similar responses with respect to species richness (Figure A.4). For instance, at the end of the study period, defoliation was higher in monospecific stands (SR = 1) than in more diverse ones (SR ≥ 2) for all stands in age classes 4, 5, 6 and 7.

Table A.3 *Defoliation according to age class.*

	No. plots	**No. trees**	**Mean defoliation (%)**
2	1	51	12.82
3	8	224	16.74
4	10	315	14.71
5	24	599	19.21
6	20	377	23.32
7	22	509	20.25

We have also fitted an additional mixed-effects model that included the effect of age on defoliation. The coefficients of the model and their significance are reported in Table A.4. Adding *age* as a predictor did not increase model accuracy (0.18 vs 0.23 R^2_m). All data are in agreement with previous findings described in the main text, and the main conclusions remain unchanged.

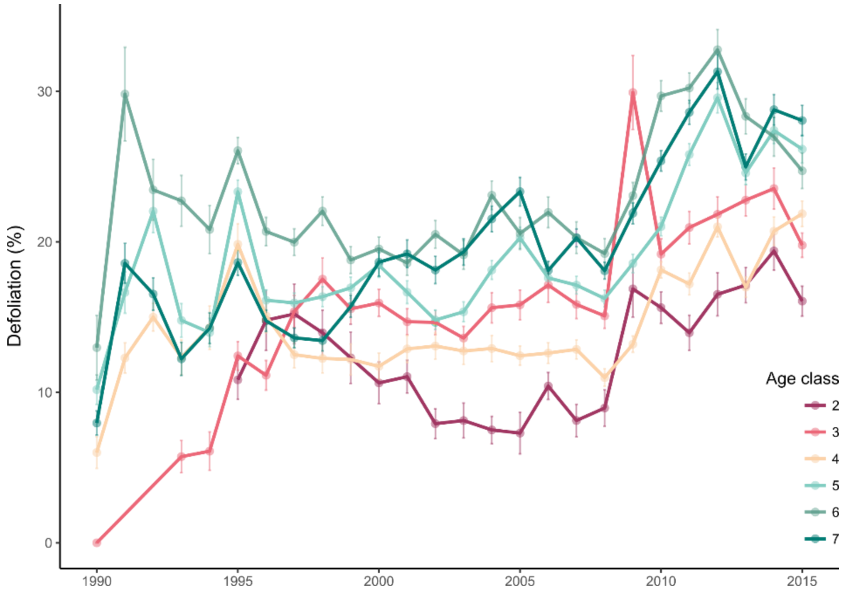


Figure A.3 Temporal trends in defoliation for plots with differently-aged dominant trees. N = *85.*

Figure A.4 Differences in defoliation levels for plots with differently-aged dominant trees through time.

Mean defoliation for monospecific plots is shown in blue, and for mixed-species plots (SR ≥ 2) in yellow. Solid lines represent the linear trend and shaded areas denote 95% confidence intervals. N = *85.*

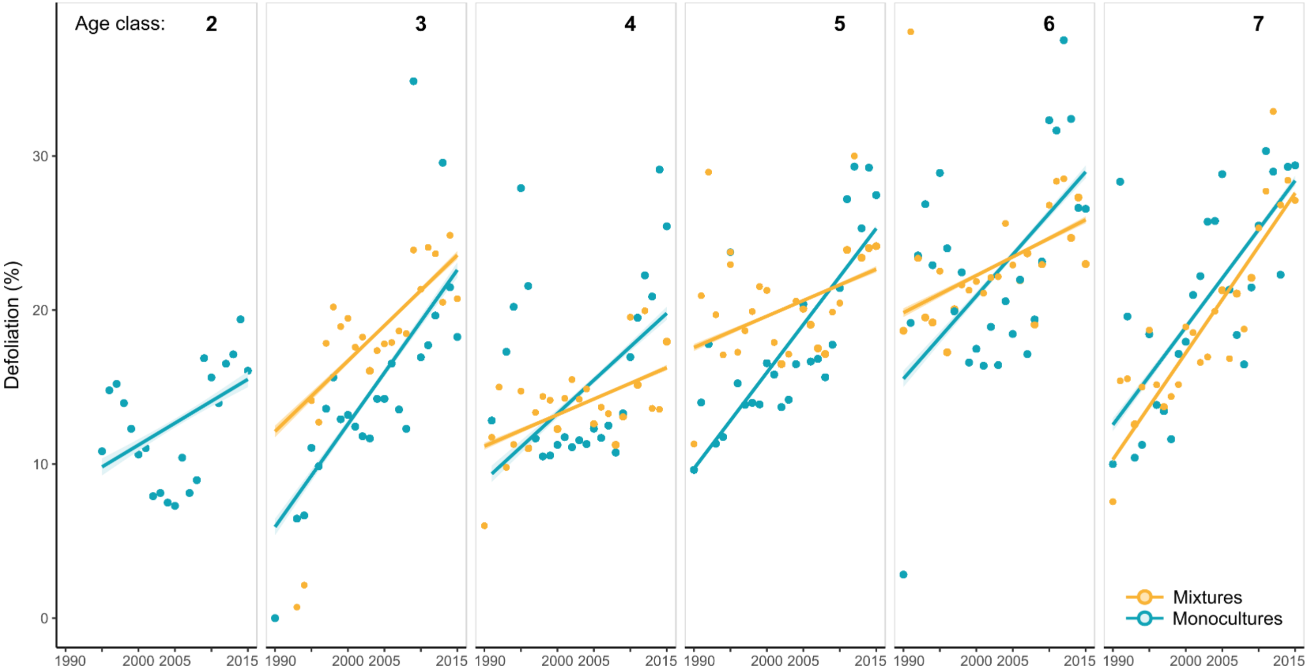


Table A.4 *Summary of the linear mixed-effects model including age as a fixed effect (in bold) to test for the effects of species richness and drought on tree defoliation*[†]*. Best-fit parameter estimates (Est, with standard error se), and the marginal and conditional* R^2 *are shown for* N = *85 plots.*

Fixed effects	**Est.**	**se**	***P***
Fagus sylvatica	*-178.4*	*(35.457)*	*<0.001*
Quercus petraea	*-111.3*	*(78.355)*	*0.159*
Quercus robur	*-48.375*	*(28.246)*	*0.090*
Stand basal area	*0.001*	*(0.003)*	*0.787*
Age	***0.185***	***(0.071)***	***0.010***
Management type	*-0.736*	*(0.328)*	*0.027*
Species Richness (SR)	*40.496*	*(16.343)*	*0.015*
$\text{SPEI}_{\text{21-May}}$	*-0.045*	*(0.020)*	*0.027*
Fagus sylvatica : $\text{SPEI}_{\text{21-May}}$	*-0.078*	*(0.023)*	*0.001*
Quercus petraea : $\text{SPEI}_{\text{21-May}}$	*-0.121*	*(0.039)*	*0.002*
Quercus robur : $\text{SPEI}_{\text{21-May}}$	*0.013*	*(0.017)*	*0.442*
Fagus sylvatica : SR : YEAR	*-0.021*	*(0.004)*	*<0.001*
Quercus petraea : SR : YEAR	*-0.001*	*(0.011)*	*0.899*
Quercus robur : SR : YEAR	*-0.005*	*(0.002)*	*0.031*

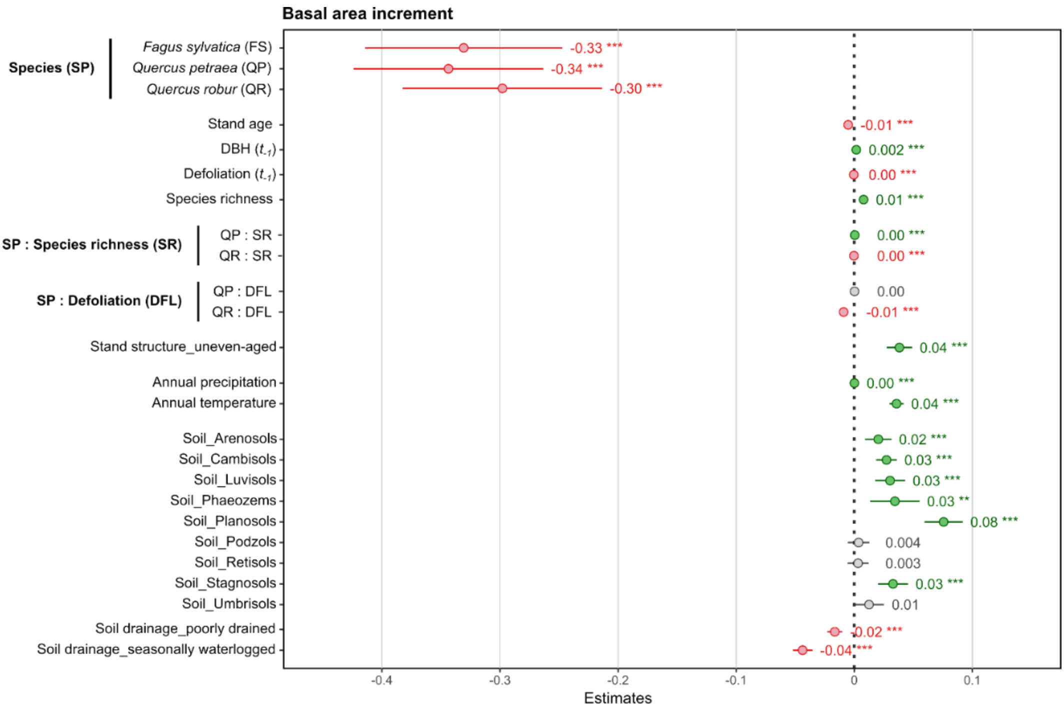
Model statistics		
marginal R^2		*0.18*
conditional R^2		*0.61*

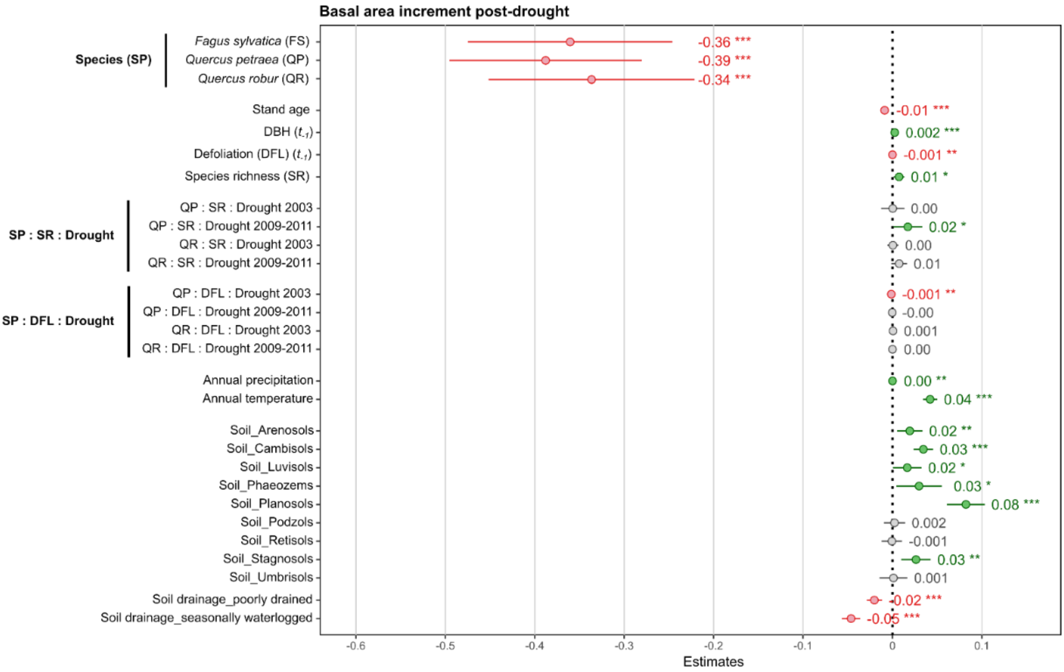
Response variable ('tree defoliation') was log-transformed prior to model fitting to normalize variance in the residuals. Drought was expressed by the SPEI (Standardized Precipitation Evapotranspiration Index) for May calculated at 21-month lags (SPEI21-May).

APPENDIX B

***Figure B.1 Graphical display of the parameter estimates of the linear mixed effects model of tree growth (top) and post-drought growth (bottom) for* Fagus sylvatica, Quercus petraea *and* Quercus robur.** *Dots indicate the estimated means and bars display 95% confidence interval. Positive effects are shown in green, negative effects in red, non-significant effects in grey ($P < 0.05$). The vertical dotted line is the model intercept that indicates no effect. Asterisks indicate the significance level of the P-values. Model statistics: marginal $R^2 = 0.22$, conditional $R^2 = 045$, N = 23,278 observation (top); marginal $R^2 = 0.27$, conditional $R^2 = 049$, N = 9,586 observations (bottom).*

▶


Basal area increment
Species (SP)
Fagus sylvatica (FS)
Quercus petraea (QP)
Quercus robur (QR)
Stand age
DBH (t_{-1})
Defoliation (t_{-1})
Species richness
SP : Species richness (SR)
QP : SR
QR : SR
SP : Defoliation (DFL)
QP : DFL
QR : DFL
Stand structure_uneven-aged
Annual precipitation
Annual temperature
Soil_Arenosols
Soil_Cambisols
Soil_Luvisols
Soil_Phaeozems
Soil_Planosols
Soil_Podzols
Soil_Retisols
Soil_Stagnosols
Soil_Umbrisols
Soil drainage_poorly drained
Soil drainage_seasonally waterlogged
-0.33 ***
-0.34 ***
-0.30 ***
-0.01 ***
0.002 ***
0.00 ***
0.01 ***
0.00 ***
0.00 ***
0.00
-0.01 ***
0.04 ***
0.00 ***
0.04 ***
0.02 ***
0.03 ***
0.03 ***
0.03 **
0.08 ***
0.004
0.003
0.03 ***
0.01
-0.02 ***
-0.04 ***
-0.4
-0.3
-0.2
-0.1
0
0.1
Estimates


Basal area increment post-drought
Species (SP)
Fagus sylvatica (FS)
Quercus petraea (QP)
Quercus robur (QR)
Stand age
DBH (t_{-1})
Defoliation (DFL) (t_{-1})
Species richness (SR)
SP : SR : Drought
QP : SR : Drought 2003
QP : SR : Drought 2009-2011
QR : SR : Drought 2003
QR : SR : Drought 2009-2011
SP : DFL : Drought
QP : DFL : Drought 2003
QP : DFL : Drought 2009-2011
QR : DFL : Drought 2003
QR : DFL : Drought 2009-2011
Annual precipitation
Annual temperature
Soil_Arenosols
Soil_Cambisols
Soil_Luvisols
Soil_Phaeozems
Soil_Planosols
Soil_Podzols
Soil_Retisols
Soil_Stagnosols
Soil_Umbrisols
Soil drainage_poorly drained
Soil drainage_seasonally waterlogged
-0.36 ***
-0.39 ***
-0.34 ***
-0.01 ***
0.002 ***
-0.001 **
0.01 *
0.00
0.02 *
0.00
0.01
-0.001 **
-0.00
0.001
0.00
0.00 **
0.04 ***
0.02 **
0.03 ***
0.02 *
0.03 *
0.08 ***
0.002
-0.001
0.03 **
0.001
-0.02 ***
-0.05 ***
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
Estimates

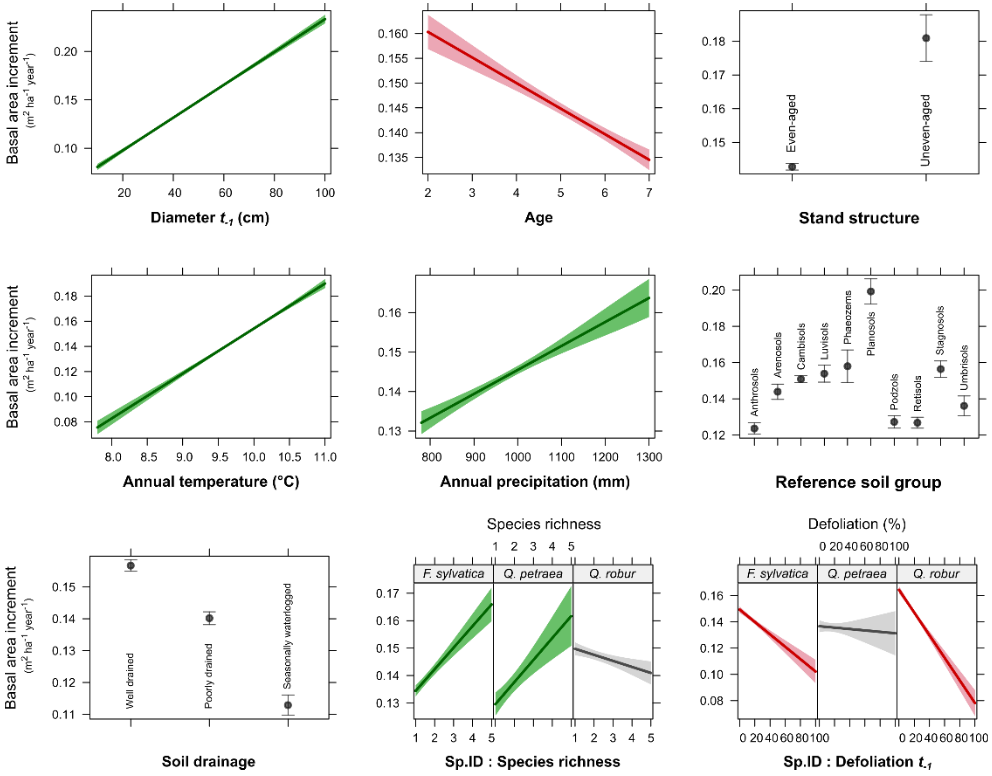
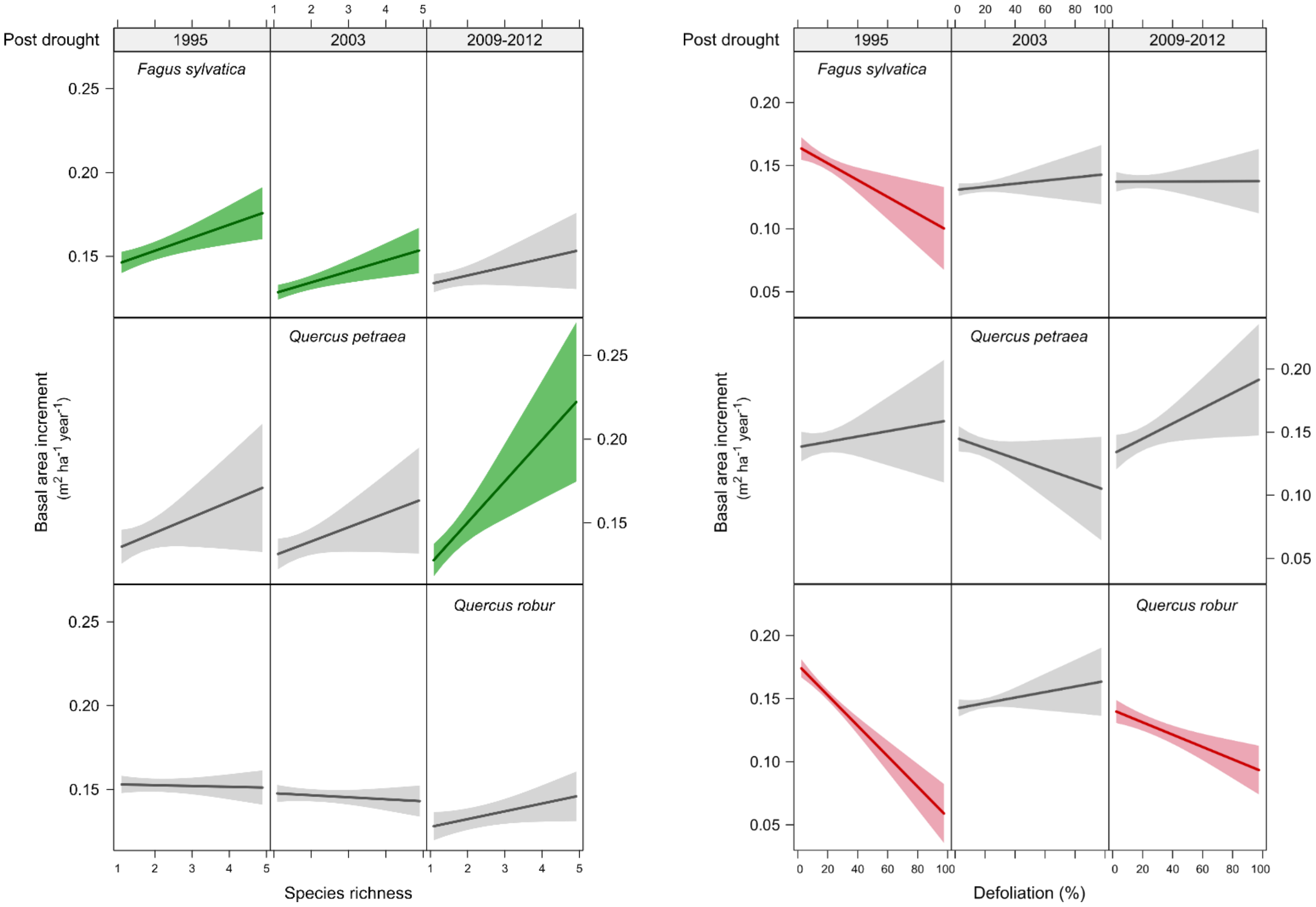


***Figure B.2 Fitted relationships from the linear mixed effects model of tree growth for* Fagus sylvatica, Quercus petraea *and* Quercus robur.** *Shading represents the 95% confidence interval; positive slopes (green) indicate a positive effect, negative slopes (red) denote a negative relationship; non-significant slopes are shaded grey ($P < 0.05$). Sp.ID is species identity. Parameter estimates are displayed in Figure B.1 (top).*

***Figure B.3 Estimated interaction effects of species richness (left) and defoliation (right) on post-drought growth for* Fagus sylvatica, Quercus petraea *and* Quercus robur.** *Shading represents the 95% confidence interval; positive slopes (green) indicate a positive effect, negative slopes (red) denote a negative relationship; non-significant slopes are shaded grey ($P < 0.05$). Parameter estimates are displayed in Figure B.1 (bottom).*

▶


Post drought
1995
2003
2009-2012
Fagus sylvatica
Quercus petraea
Quercus robur
Basal area increment
(m^2 ha^{-1} $year^{-1}$)
0.25
0.20
0.15
1
2
3
4
5
Species richness
Post drought
1995
2003
2009-2012
Fagus sylvatica
Quercus petraea
Quercus robur
Basal area increment
(m^2 ha^{-1} $year^{-1}$)
0.20
0.15
0.10
0.05
0
20
40
60
80
100
Defoliation (%)

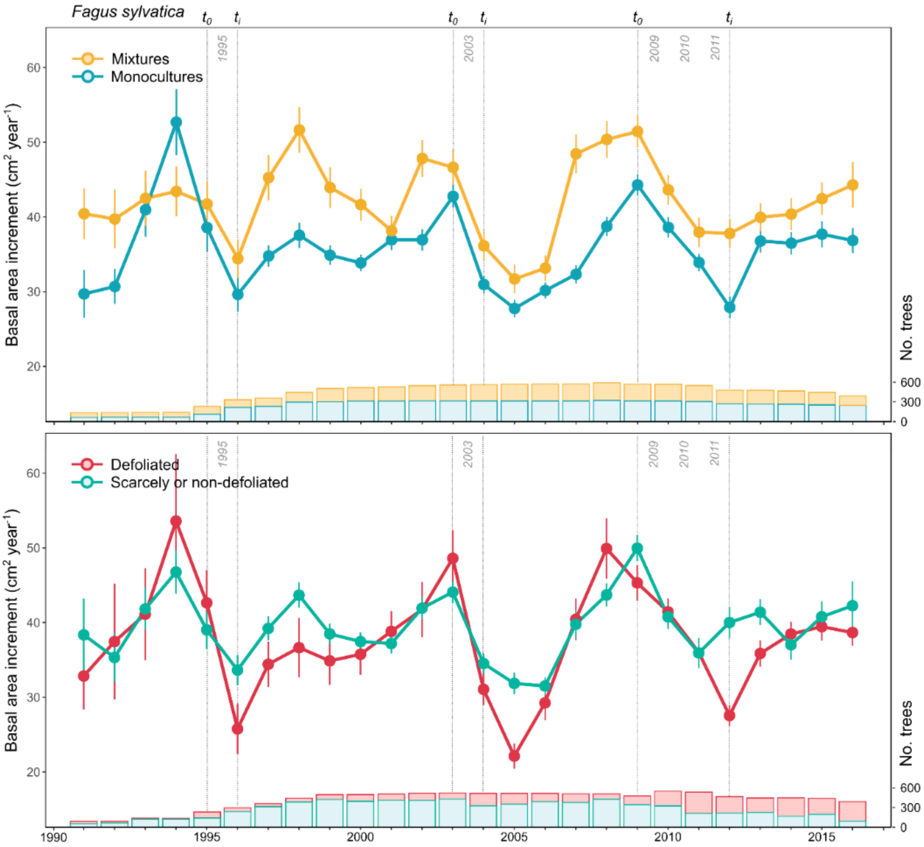


Figure B.4 Basal area increment for* Fagus sylvatica *in mixtures and monocultures (top) and for defoliated and non-defoliated trees (bottom). *Values are means with standard errors (left y axis), and the bars show the sample depth, i.e., the annual number of assessed trees (right y axis). Vertical dotted lines encompass the immediate effect of the drought event;* t_0 *and* t_i *correspond to the time immediately before and immediately after the main disturbance effect. Mixtures are stands composed of two or more tree species, and trees were considered defoliated when their defoliation was higher than 25% at time* t_0*.*

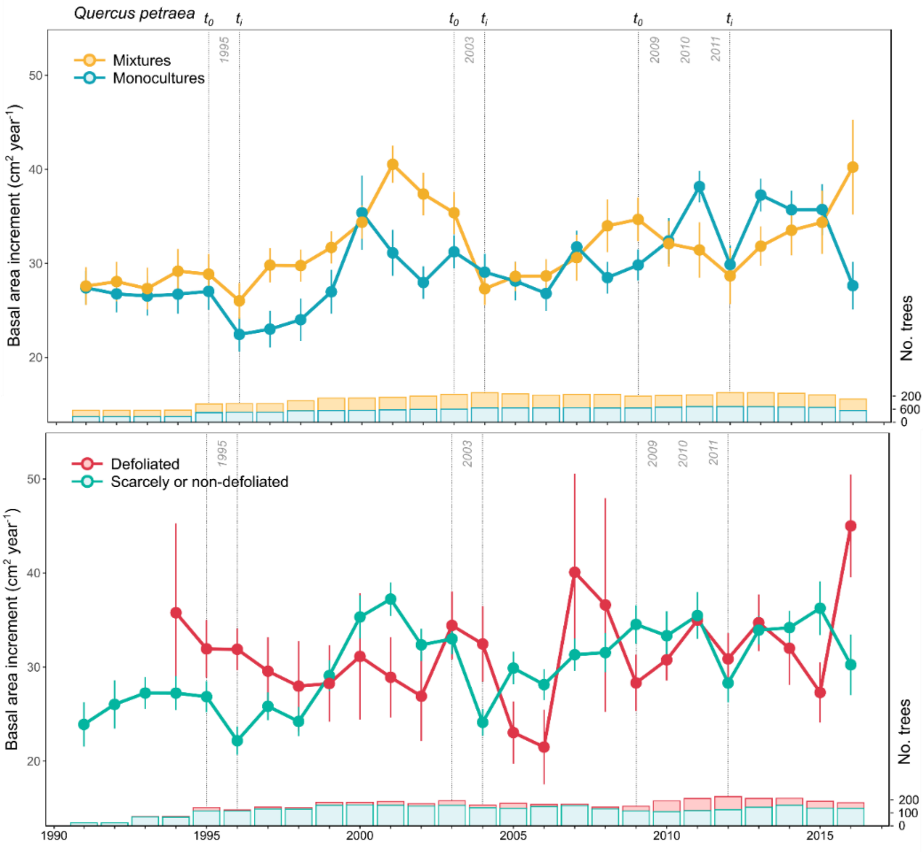


Figure B.5 Basal area increment for* Quercus petraea *in mixtures and monocultures (top) and for defoliated and non-defoliated trees (bottom). *Values are means with standard errors (left y axis), and the bars show the sample depth, i.e., the annual number of assessed trees (right y axis). Vertical dotted lines encompass the immediate effect of the drought event;* t_o *and* t_i *correspond to the time immediately before and immediately after the main disturbance effect. Mixtures are stands composed of two or more tree species, and trees were considered defoliated when their defoliation was higher than 25% at time* t_o*.*

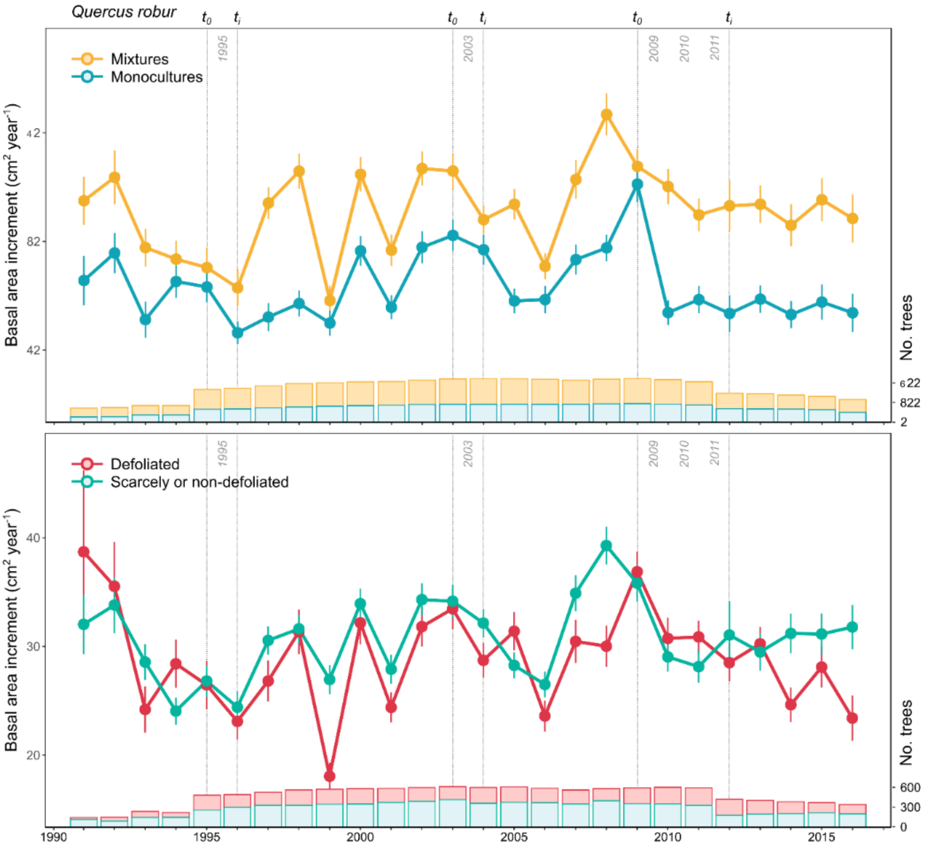


Figure B.6 Basal area increment for* Quercus robur *in mixtures and monocultures (top) and for defoliated and non-defoliated trees (bottom). *Values are means with standard errors (left y axis), and the bars show the sample depth, i.e., the annual number of assessed trees (right y axis). Vertical dotted lines encompass the immediate effect of the drought event;* t_o *and* t_i *correspond to the time immediately before and immediately after the main disturbance effect. Mixtures are stands composed of two or more tree species, and trees were considered defoliated when their defoliation was higher than 25% at time* t_o*.*

Table B.1 *Summary table of the statistically significant differences in growth responses of the three studied tree species when growing in mixtures as compared to monocultures (top half) and between defoliated and non-defoliated trees (bottom half) for the pre-drought, drought, and post-drought periods across the three drought events. The results were analyzed according to ANOVA followed by post hoc analysis using Tukey's test with P < 0.05 as the minimum level of significance, and test scores are shown in Table B.2-B.3. Statistically significant differences are shown in bold, colored in red for* Fagus sylvatica *(FS), in yellow for* Quercus petraea *(QP), and in blue for* Quercus robur *(QR). Shaded cells denote significant differences when the three species were pooled together. Mixtures are stands composed of two or more tree species, and trees were considered defoliated when their defoliation was higher than 25% at time* t_0.

	Drought 1995			***Drought 2003***			***Drought 2009-2011***		
	Monocultures	**Mixtures**	**Monocultures/ Mixtures**	**Monocultures**	**Mixtures**	**Monocultures/ Mixtures**	**Monocultures**	**Mixtures**	**Monocultures/ Mixtures**
Prior D – D			–	**FS**	**FS QP**	–	**FS QR**	**FS**	–
D – Post D		**FS QR**	–			–	**FS**		–
Prior D – Post D			–	**FS**	**FS QR**	–	**FS QR**	**FS**	–
Prior D	–	–		–	–		–	–	**FS**
D	–	–		–	–		–	–	**FS QR**
Post D	–	–	**FS QR**	–	–	**FS QR**	–	–	**FS QR**
	Defoliated	**Non-defoliated**	**Defoliated/ Non-defoliated**	**Defoliated**	**Non-defoliated**	**Defoliated/ Non-defoliated**	**Defoliated**	**Non-defoliated**	**Defoliated/ Non-defoliated**
Prior D – D	**FS**		–	**FS**	**FS**	–	**FS QR**	**FS**	–
D – Post D	**FS**		–			–			–
Prior D – Post D			–	**FS**	**FS QR**	–	**FS**	**FS**	–
Prior D	–	–		–	–		–	–	
D	–	–	**FS**	–	–		–	–	
Post D	–	–		–	–		–	–	

Abbreviations:

Prior D = growth immediately before drought (at time t0); D = growth immediately after drought (at time ti); Post D = average growth rates after the drought event.

t_0 *and* t_i *correspond to the time immediately before and immediately after the main disturbance effect.*

dash = test not applicable to data.

Table B.2 *Differences in growth responses of the three studied tree species when growing in mixtures as compared to monocultures between pre-drought, drought, and post-drought periods for the three drought events. The results were analyzed according to ANOVA followed by post hoc analysis using Tukey's test with* $P < 0.05$ *as the minimum level of significance. P-values are shown in bold where statistically significant. Mixtures are stands composed of two or more tree species. For instance, for* Fagus sylvatica *trees growing in monocultures, the difference in basal area increment before and during the 2003 drought event was 11.80 (Prior D – D), i.e., the pre-drought growth was 11.80* cm^2 *higher than growth during the drought. The 95% confidence interval of that difference is between 5.42* cm^2 *and 18.19* cm^2*. In a similar fashion, the basal area increment for* F. sylvatica *trees after the 2003 drought (Post D) was -4.88* cm^2 *lower in monocultures than in mixtures. These differences were highly significant* ($P \leq 0.005$)*.*

		Drought 1995				***Drought 2003***				***Drought 2009-2011***			
		diff.	*lwr*	*upr*	*P-value*	*diff.*	*lwr*	*upr*	*P-value*	*diff.*	*lwr*	*upr*	*P-value*
Fagus sylvatica	**Monocultures**												
	Prior D – D	8.964	-2.666	20.593	0.238	11.803	5.415	18.192	**<0.001**	16.407	9.764	23.050	**<0.001**
	D – Post D	5.152	-3.530	13.835	0.535	1.477	-3.628	6.582	0.963	8.849	1.828	15.870	**0.004**
	Prior D – Post D	3.811	-6.753	14.375	0.908	10.326	5.260	15.393	**<0.001**	7.558	0.968	14.147	**0.014**
	Mixtures												
	Prior D – D	7.308	-4.121	18.736	0.449	10.507	3.161	17.853	**0.001**	13.652	6.089	21.215	**<0.001**
	D – Post D	10.836	1.017	20.656	**0.021**	1.184	-4.847	7.215	0.994	3.343	-4.682	11.368	0.842
	Prior D – Post D	-3.529	-14.725	7.668	0.946	9.323	3.235	15.410	**<0.001**	10.309	2.941	17.676	**0.001**
	Monocultures/Mixtures												
	Prior D	-3.143	-16.008	9.722	0.982	-3.875	-10.769	3.020	0.597	-7.144	-13.676	-0.613	**0.023**
	D	-4.799	-14.816	5.219	0.746	-5.171	-12.045	1.702	0.264	-9.899	-17.558	-2.240	**0.003**
	Post D	-10.483	-18.936	-2.029	**0.006**	-4.878	-8.776	-0.981	**0.005**	-4.393	-11.812	3.025	0.539
Quercus petraea	**Monocultures**												
	Prior D – D	4.586	-3.812	12.983	0.623	2.160	-5.879	10.198	0.973	-0.054	-8.074	7.966	1.000
	D – Post D	0.563	-6.628	7.755	1.000	-0.128	-6.522	6.266	1.000	7.150	-0.890	15.189	0.114
	Prior D – Post D	4.022	-4.375	12.420	0.744	2.288	-4.106	8.682	0.911	-7.204	-15.417	1.010	0.123
	Mixtures												
	Prior D – D	2.840	-5.520	11.199	0.926	8.082	0.196	15.968	**0.041**	6.007	-3.534	15.548	0.466
	D – Post D	3.796	-3.893	11.484	0.718	2.069	-4.733	8.871	0.954	2.504	-6.807	11.815	0.973
	Prior D – Post D	-0.956	-9.289	7.377	0.999	6.013	-0.920	12.946	0.132	3.503	-5.220	12.226	0.861
	Monocultures/Mixtures												
	Prior D	-1.828	-11.035	7.379	0.993	-4.155	-12.173	3.864	0.678	-4.857	-13.447	3.733	0.588
	D	-3.574	-11.033	3.885	0.743	1.767	-6.139	9.673	0.988	1.204	-7.828	10.235	0.999
	Post D	-6.806	-14.235	0.623	0.094	-0.430	-5.394	4.535	1.000	5.849	-2.503	14.202	0.342

		Drought 1995				*Drought 2003*				*Drought 2009-2011*			
		diff.	*lwr*	*upr*	*P-value*	*diff.*	*lwr*	*upr*	*P-value*	*diff.*	*lwr*	*upr*	*P-value*
Quercus robur	**Monocultures**												
	Prior D – D	4.215	-3.623	12.053	0.642	1.321	-5.084	7.726	0.992	11.902	3.294	20.510	**0.001**
	D – Post D	1.448	-5.028	7.924	0.988	-2.282	-7.354	2.791	0.795	1.988	-7.297	11.272	0.990
	Prior D – Post D	2.767	-4.975	10.509	0.911	3.603	-1.523	8.728	0.340	9.914	2.539	17.289	**0.002**
	Mixtures												
	Prior D – D	1.865	-4.890	8.620	0.970	4.478	-0.886	9.842	0.163	3.629	-3.864	11.122	0.738
	D – Post D	7.729	2.379	13.079	**0.001**	-0.351	-4.767	4.065	1.000	0.144	-8.008	8.295	1.000
	Prior D – Post D	-5.864	-12.612	0.884	0.131	4.829	0.375	9.284	**0.025**	3.485	-2.974	9.945	0.638
	Monocultures/Mixtures												
	Prior D	-1.786	-10.211	6.639	0.991	-5.927	-11.871	0.017	0.051	-1.636	-7.707	4.434	0.973
	D	-4.136	-10.143	1.870	0.363	-2.770	-8.640	3.100	0.759	-9.910	-19.573	-0.246	**0.041**
	Post D	-10.417	-16.290	-4.545	**<0.001**	-4.700	-7.984	-1.417	**0.001**	-8.065	-15.764	-0.367	**0.034**
All species	**Monocultures**												
	Prior D – D	5.792	0.150	11.434	**0.040**	6.339	2.357	10.320	**<0.001**	11.143	6.738	15.548	**<0.001**
	D – Post D	3.448	-0.922	7.818	0.215	-0.453	-3.581	2.675	0.998	4.785	0.996	8.573	**0.004**
	Prior D – Post D	2.344	-2.949	7.637	0.805	6.792	3.662	9.921	**<0.001**	6.358	3.117	9.600	**<0.001**
	Mixtures												
	Prior D – D	3.926	-1.229	9.081	0.251	7.001	3.134	10.867	**<0.001**	7.269	2.649	11.888	**<0.001**
	D – Post D	8.093	3.854	12.333	**<0.001**	1.096	-2.039	4.231	0.919	1.136	-3.748	6.021	0.986
	Prior D – Post D	-4.167	-9.260	0.925	0.181	5.905	2.735	9.074	**<0.001**	6.133	1.934	10.331	**<0.001**
	Monocultures/Mixtures												
	Prior D	-1.808	-7.943	4.327	0.960	-3.332	-7.271	0.608	0.152	-3.287	-7.203	0.629	0.159
	D	-3.674	-8.231	0.882	0.194	-2.670	-6.579	1.240	0.374	-7.161	-12.202	-2.120	**0.001**
	Post D	-8.319	-12.357	-4.281	**<0.001**	-4.219	-6.298	-2.139	**<0.001**	-3.513	-7.091	0.065	0.058

Abbreviations:

Prior D = growth immediately before drought (at time t0); D = growth immediately after drought (at time ti); Post D = average growth rates after the drought event. *t_0 and t_i correspond to the time immediately before and immediately after the main disturbance effect.*

diff. = difference between pair of mean; lwr = lower limit of 95% confidence interval for difference between pair of means; upr = upper limit of 95% confidence interval for difference between pair of mean.

Table B.3 *Comparison of differences in growth responses of the three studied tree species for defoliated (>25% defoliation) and non-defoliated trees between pre-drought, drought, and post-drought periods for the three drought events. The results were analyzed according to ANOVA followed by post hoc analysis using Tukey's test with P<0.05 as the minimum level of significance.* P*-values are shown in bold where statistically significant. For instance, for* Fagus sylvatica*, the difference in basal area increment of defoliated trees before and during the 2003 drought was 10.59 (Prior D – D), i.e., the pre-drought growth was 10.59* cm^2 *higher than growth during the drought. The 95% confidence interval of that difference is between 5.02* cm^2 *and 16.16* cm^2*, and hence the difference is statistically significant (P<0.01). In a similar fashion, the difference in basal area increment between defoliated and non-defoliated trees after that drought (Post D) was -1.44* cm^2 *lower in defoliated trees. This difference, though, was not significant (P=0.969).*

		Drought 1995				***Drought 2003***				***Drought 2009-2011***			
		diff.	*lwr*	*upr*	*P-value*	*diff.*	*lwr*	*upr*	*P-value*	*diff.*	*lwr*	*upr*	*P-value*
Fagus sylvatica	**Defoliated**												
	Prior D – D	2.397	-8.274	13.068	0.988	10.588	5.016	16.160	**<0.001**	17.048	10.309	23.787	**<0.001**
	D – Post D	4.349	-5.227	13.924	0.786	0.621	-3.885	5.126	0.999	7.141	-0.424	14.706	0.077
	Prior D – Post D	-1.952	-12.623	8.719	0.995	9.967	5.507	14.428	**<0.001**	9.907	2.994	16.821	**0.001**
	Non-defoliated												
	Prior D – D	17.792	3.376	32.209	**0.006**	17.558	5.603	29.513	**<0.001**	21.126	10.849	31.402	**<0.001**
	D – Post D	19.820	7.963	31.677	**<0.001**	4.510	-5.125	14.144	0.766	6.530	-4.497	17.558	0.538
	Prior D – Post D	-2.027	-16.444	12.389	0.999	13.049	3.334	22.763	**0.002**	14.595	4.232	24.959	**0.001**
	Defoliated /Non-defoliated												
	Prior D	-3.622	-17.960	10.715	0.979	-4.518	-13.875	4.839	0.741	4.651	-3.330	12.631	0.556
	D	11.774	0.997	22.550	**0.023**	2.452	-6.844	11.748	0.975	8.728	-0.617	18.073	0.083
	Post D	-3.697	-14.474	7.079	0.924	-1.437	-6.604	3.731	0.969	9.339	-0.227	18.905	0.060
Quercus petraea	**Defoliated**												
	Prior D – D	3.973	-2.659	10.605	0.522	6.044	-0.503	12.591	0.090	5.247	-4.003	14.496	0.583
	D – Post D	2.285	-3.535	8.104	0.871	2.308	-3.092	7.708	0.827	7.511	-2.457	17.480	0.260
	Prior D – Post D	1.688	-4.944	8.320	0.978	3.736	-1.546	9.018	0.332	-2.265	-11.862	7.333	0.985
	Non-defoliated												
	Prior D – D	1.053	-12.009	14.116	1.000	1.193	-12.567	14.953	1.000	3.326	-12.713	19.364	0.991
	D – Post D	2.030	-10.451	14.512	0.997	-4.812	-16.037	6.413	0.825	9.768	-6.271	25.806	0.503
	Prior D – Post D	-0.977	-14.040	12.085	1.000	6.005	-5.097	17.107	0.635	-6.442	-22.481	9.597	0.860
	Defoliated /Non-defoliated												
	Prior D	-5.084	-16.029	5.860	0.768	-1.425	-12.107	9.256	0.999	6.221	-6.732	19.173	0.742
	D	-8.004	-17.742	1.734	0.175	-6.276	-17.144	4.591	0.566	4.300	-8.930	17.529	0.938
	Post D	-7.749	-17.487	1.989	0.205	0.844	-5.244	6.931	0.999	2.043	-11.432	15.518	0.998

		Drought 1995				***Drought 2003***				***Drought 2009-2011***			
		diff.	*lwr*	*upr*	*P-value*	*diff.*	*lwr*	*upr*	*P-value*	*diff.*	*lwr*	*upr*	*P-value*
Quercus robur	**Defoliated**												
	Prior D – D	3.306	-3.664	10.275	0.755	3.443	-1.747	8.634	0.407	7.285	-1.836	16.405	0.203
	D – Post D	5.442	-0.502	11.386	0.095	-1.604	-5.818	2.610	0.887	2.451	-9.225	14.126	0.991
	Prior D – Post D	-2.136	-9.116	4.843	0.953	5.047	0.848	9.246	**0.008**	4.834	-4.690	14.358	0.697
	Non-defoliated												
	Prior D – D	2.791	-5.380	10.963	0.926	3.193	-4.409	10.796	0.838	10.833	0.549	21.118	**0.032**
	D – Post D	4.453	-1.846	10.752	0.333	0.001	-6.177	6.179	1.000	5.688	-7.735	19.110	0.832
	Prior D – Post D	-1.662	-9.855	6.531	0.992	3.192	-2.949	9.334	0.676	5.145	-6.278	16.569	0.793
	Defoliated /Non-defoliated												
	Prior D	0.363	-8.474	9.199	1.000	0.698	-5.789	7.184	1.000	-1.049	-7.893	5.795	0.998
	D	-0.152	-6.256	5.952	1.000	0.447	-6.084	6.979	1.000	2.500	-9.421	14.421	0.991
	Post D	0.837	-5.307	6.981	0.999	-1.157	-4.800	2.486	0.945	-0.737	-13.943	12.468	1.000
All species	**Defoliated**												
	Prior D – D	3.557	-1.433	8.548	0.324	6.895	3.492	10.298	**<0.001**	10.557	5.827	15.288	**<0.001**
	D – Post D	4.444	0.096	8.792	**0.042**	0.037	-2.727	2.802	1.000	6.116	0.551	11.681	**0.022**
	Prior D – Post D	-0.886	-5.880	4.108	0.996	6.858	4.119	9.597	**<0.001**	4.441	-0.452	9.335	0.100
	Non-defoliated												
	Prior D – D	7.232	0.640	13.824	**0.022**	7.060	1.069	13.052	**0.010**	13.889	7.318	20.461	**<0.001**
	D – Post D	8.341	3.044	13.638	**<0.001**	0.797	-4.063	5.656	0.997	6.724	-0.967	14.414	0.126
	Prior D – Post D	-1.109	-7.714	5.496	0.997	6.264	1.416	11.112	**0.003**	7.165	0.345	13.985	**0.033**
	Defoliated /Non-defoliated												
	Prior D	-1.256	-7.963	5.451	0.995	0.357	-4.503	5.216	1.000	2.655	-2.136	7.446	0.612
	D	2.418	-2.417	7.253	0.711	0.522	-4.363	5.408	1.000	5.986	-0.541	12.514	0.094
	Post D	-1.479	-6.335	3.377	0.954	-0.238	-2.956	2.481	1.000	5.378	-1.514	12.271	0.226

Abbreviations:

Prior D = growth immediately before drought (at time t0); D = growth immediately after drought (at time ti); Post D = average growth rates after the drought event. t_0 *and* t_i *correspond to the time immediately before and immediately after the main disturbance effect.*

diff. = difference between pair of mean; lwr = lower limit of 95% confidence interval for difference between pair of means; upr = upper limit of 95% confidence interval for difference between pair of mean.

APPENDIX C

Supplementary Note C.1

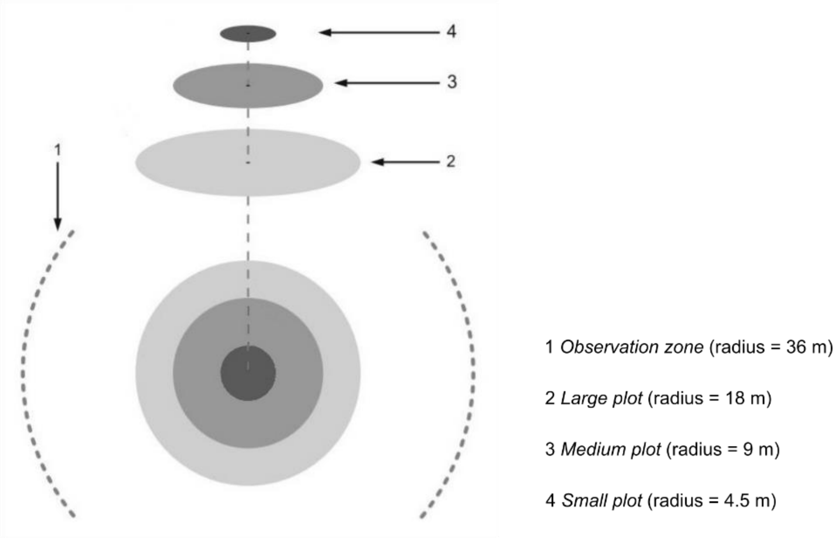


Figure C.1 General scheme of a sampling unit and size variation for the sample plots. *Adapted from Rondeux, Sanchez & Latte (2010).*

Belgium is a federal state comprising three regions (Flanders, Wallonia, and Brussels Capital) and forest inventories are conducted both in the Flemish and the Walloon regions. Both inventories have strong methodological similarities because the first Walloon forest inventory was used as basis for subsequent sampling design and attributes to be measured (Rondeux et al., 2010).

Sampling units consist of three concentric circular plots, which are used for measuring living trees of, respectively, 20, 70 and 120 cm according to the different plot sizes, ranging from small to large (Rondeux et al., 2010). In Flanders, diameter (*D*) thresholds are as follows: trees with $D \geq 39$ cm are measured on a plot with radius of 18 m; trees with 7 cm $\leq D \leq 39$ cm are measured on a plot with radius of 9 m; and trees with $D < 7$ cm and under 2 m are measured on a plot with radius of 4.5 m (Wouters et al., 2008).

Girth is measured at breast height at 1.50 m above ground and its increment is determined through the comparison of the two measurements. Plots which, at the first measurement, changed their location, were not forest, or were privately owned and not accessible, but become forest land at the second measurement were excluded from the analyses.

Tree species identification was not always possible at the species level. For instance, distinguishing sessile oak (*Quercus petraea* (Matt.) Liebl.) from pedunculate oak (*Quercus robur* L.) is often difficult to achieve since these taxa are interfertile and the number of individuals with intermediate morphology is high (Gömöry et al., 2001). *Q. robur* and *Q. petraea* trees were defined here as indigenous oak. A similar procedure was used for *Larix* species and *Populus* species.

Supplementary Note C.2

Soil variables. The soil variables included in this study were: drainage status, texture class, and chemical soil fertility.

For Flanders, these variables were derived from the soil map of Flanders, which has recently been revised by Dondeyne et al. (2014). In their work, Dondeyne et al. converted the legend of the soil map of Belgium to a legend according to the international soil classification system of the World Reference Base for Soil Resources (WRB) for the Flemish region, at a 1 : 250 000 scale. Information on drainage, soil texture, and chemical soil fertility was extracted using the *Supplementary Qualifiers*, which are meant for presenting properties that are not specific to a particular *Reference Soil Group*.

Drainage classes (from *well drained* to *very poorly drained*) are defined according to the depth at which redoximorphic mottling and/or reduction colours occur. Textural classes (*Arenic*, *Loamic*, *Siltic*, and *Clayic*) are defined based on the relative content of clay, silt and sand. For additional details on drainage and textural classes, please see Dondeyne et al. (2014). For example, in the soil series Zcg, Zdg and Zeg, the first capital means the soil texture is sand (Z), the second symbol means the drainage status is moderately well drained (.c.), imperfectly drained (.d.), or poorly drained (.e.), and the third symbol (..g) indicates that the soil profile development corresponds to a spodic horizon, with a well-developed iron and/or humus B horizon. Such Podzols can be commonly found in the Campine region of Flanders, sampled in this study.

The chemical soil fertility status (*Dystric*, *Eutric*, *Calcaric*) is defined for each soil type and according to the various soil districts. *Dystric* implies that the base saturation of the soil between 20-100 cm depth is less than 50%; while *Eutric* implies that it is more than 50%. A soil is *Calcaric* when it has calcaric material (>2%) throughout between 20-100 cm from the soil surface (Dondeyne et al., 2014). For the purpose of this study, inventory plots on soil classified as *Eutric* or *Calcaric* were described as being in *rich* soils, whereas those from a soil classified as *Dystric* were described as being in *poor* soils.

For Wallonia, drainage status and soil texture were obtained directly from the Walloon forest inventory database (Rondeux and Lecomte, 2010). During the field surveys, for each sampling unit, soil samples were collected and the associated soil type, along with the soil properties, were determined. The classification of soil profiles (including drainage and texture classes) was done according to the legend of the soil map of Belgium. Therefore, a direct relationship can be established between observations made *in situ* and information derived from the soil map of Belgium.

The soil fertility status was derived by combining information on the topsoil humus content and the depth of the sampled soil layer. First, the humus content of the soil (eight classes in total; Rondeux and Lecomte, 2010) was reclassified into six classes (1-6; Table C.1). Second, the values of this index (humic index) were multiplied by the index value of soil depth (1-5; Table C.1), resulting in a score of 1 to 30 (soil quality index). Third, the eventual distinction between *rich* and *poor* soils was done using the median as threshold.

These assessments were performed in consultation with a soil expert.

All soil variables (texture, drainage and fertility status) were extracted using ArcGIS 10.3 Spatial Join tool within the Spatial Analyst Toolbox, and were treated as categorical variables in the model.

Table C.1 *Soil classification indices (soil depth index and humic index) for Wallonia, according to the Walloon forest inventory methodological guidelines (Rondeux and Lecomte, 2010).*

Soil depth index	**Soil depth**	**Humic index**	**Humus type**	**Humic index reclassified**	**Humus type**
1	0-19 cm	*1*	Mor	*1*	Mor Anmmor Peat
2	20-39 cm	*2*	Anmmor	*2*	Dysmoder
3	40-59 cm	*3*	Peat	*3*	Moder
4	60-79 cm	*4*	Dysmoder	*4*	Mull-like moder
5	≥ 80 cm	*5*	Moder	*5*	Mull
		6	Mull-like moder	*6*	Calciferous mull
		7	Mull		
		8	Calciferous mull		

Topographic variables. The topographic variables included in this study were: elevation and slope

These two variables were extracted from a LiDAR-derived digital terrain model at a spatial resolution of 1 m (AGIV, 2015; SPW, 2015). LiDAR point clouds were subjected to a strict geometric quality control, planimetrically (RMSExy = 1 m) and altimetrically (RMSEz = 0.1 m).

Raster values were extracted using ArcGIS 10.3 Extract Values to Points tool within the Spatial Analyst Toolbox, and were treated as continuous variables in the model.

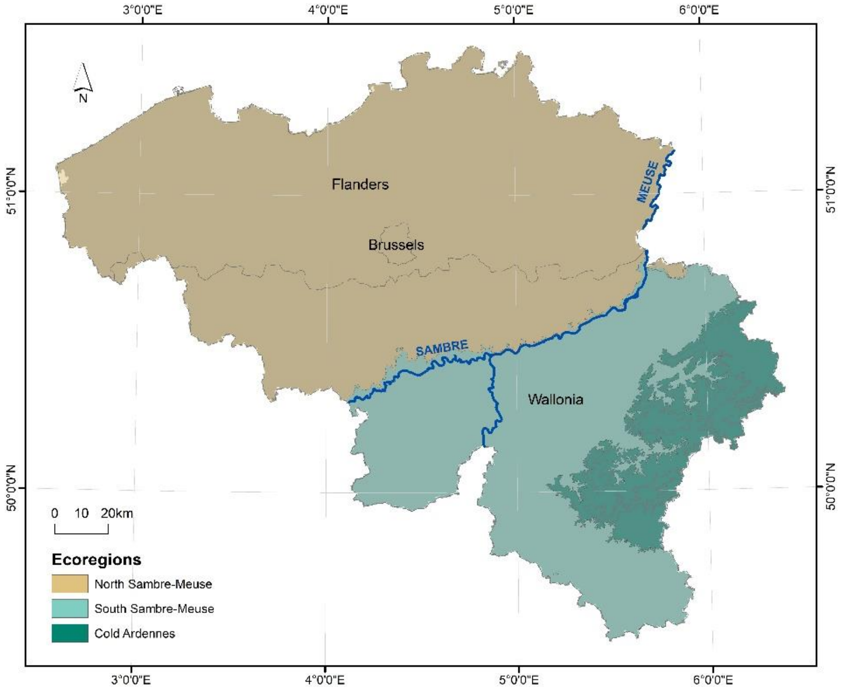


Figure C.2 *Ecoregions in Belgium, as defined in our study, with boundaries supported by previous work in Wallonia* (Van der Perre et al., 2015).

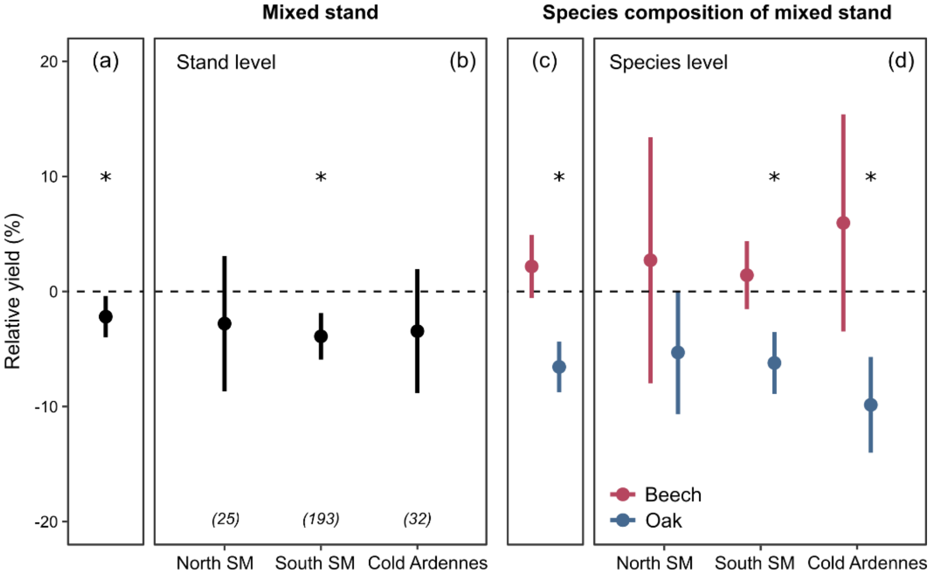


Figure C.3 Relate yielding for beech-oak mixtures. *Mean (±95% confidence interval) of the mixture effect on the overall stand productivity for the beech-oak stands (a, c), and on the productivity of each species in mixture (b, d) averaged across the study area and split by ecoregion. Relative yield is the yield of a species in mixture divided by its yield in monoculture* (Loreau and Hector, 2001). *Numbers in brackets represent the number of plots. Asterisk denotes significant differences (P < 0.05; t-test).*

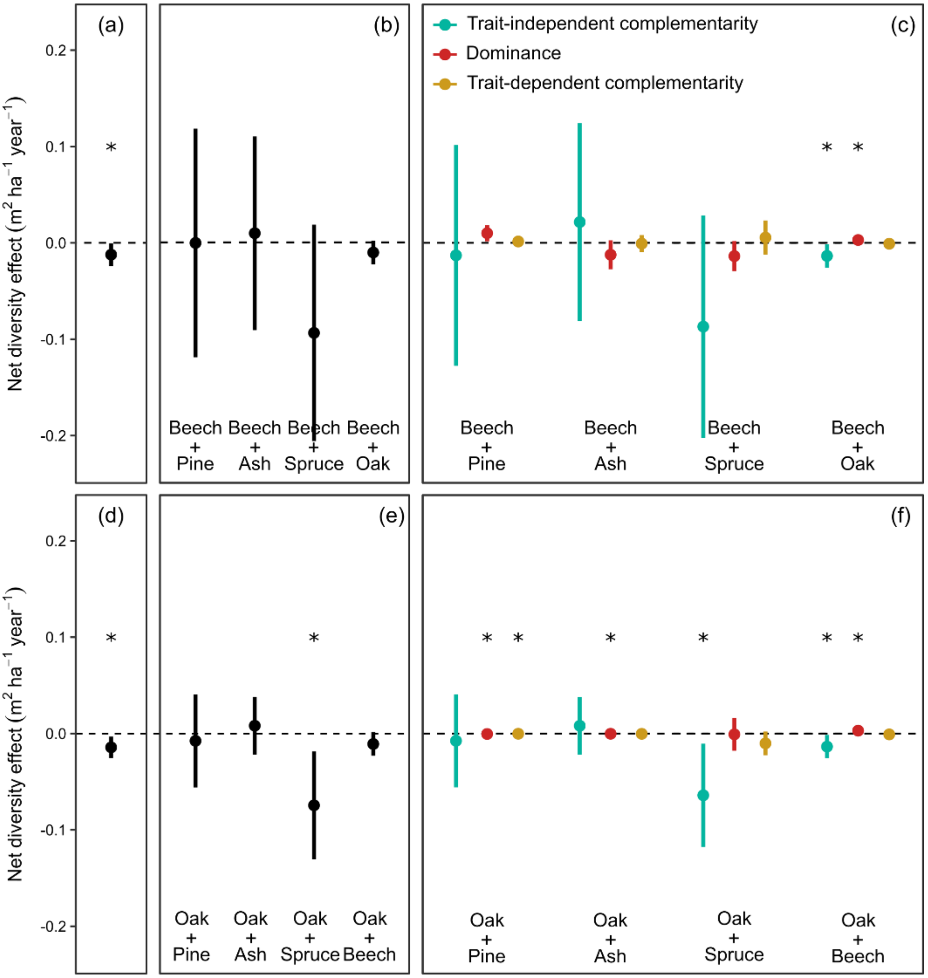


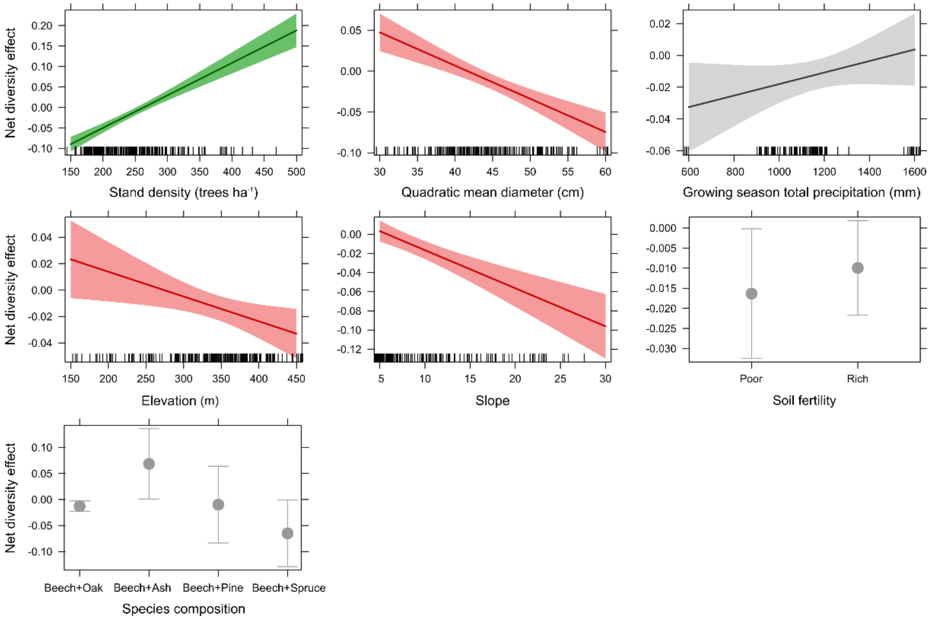
Figure C.4 Partitioning of the net diversity effect on basal area increment (m² ha⁻¹ year⁻¹). *Net diversity effect (difference between mixture and average monoculture yield) for beech (upper panel) and oak (lower panel) averaged across the mixtures studied (a, d) and split by species composition (b, e) in the South SM region. The partitioned effects – trait-independent complementarity, dominance, and trait-dependent complementarity – are shown as the means with error bars representing upper and lower bounds of a 95% confidence interval for each species assemblage (c, f). The analyses followed the tripartite partitioning method of Fox (2005). Asterisk denotes significant differences (P < 0.05; t-test).*

Table C.2 *Coefficients (Est.), standard deviations (SD) and* P*-values (*P*) of the net diversity effect models according to abiotic factors, stand density, species developmental stage and composition of the mixtures. In M1, a mixed-effects model was fitted to the data from all plots (*N *= 250) with beech-oak mixtures in the three ecoregions studied. In M2-M3, linear regression models were fitted to the data from all mixed plots with beech (*N *= 208) and oak (*N *= 249), respectively, located in the South SM ecoregion. All the abiotic factors tested are included in the table. Only the parameters of the selected best model are specified. In M1, ecoregion was included as random factor and the variance explained by the fixed factors (marginal* R^2*) and that incorporating the random factors (conditional* R^2*) was computed following Nakagawa & Schielzeth (2013). In M2-M3, the goodness-of-fit was assessed by the adjusted R-square statistics (adj*R^2*) and the root mean squared error (RMSE).*

	M1: Net diversity effect for beech-oak mixtures			**M2: Net diversity effect for mixed stands with beech**			**M3: Net diversity effect for mixed stands with oak**		
Factors	Est.	SD	*P*	Est.	SD	*P*	Est.	SD	*P*
Intercept	0.118	0.078	0.132	-0.017	0.045	0.715	0.025	0.047	0.588
Abiotic factors									
TMED									
PRCP	0.001	0.001	0.087	0.001	0.001	0.061	0.001	0.001	0.130
Soil drainage									
Soil texture									
Soil fertility	0.009	0.001	0.332	0.006	0.01	0.539	-0.001	0.010	0.937
Elevation	0.001	0.001	0.724	0.001	0.001	0.013	0.001	0.001	0.003
Slope	-0.003	0.001	<0.001	-0.004	0.001	<0.001	-0.004	0.001	<0.001
Stand density	0.001	0.001	<0.001	0.001	0.001	<0.001	0.001	0.001	<0.001
QMD	-0.004	0.001	<0.001	-0.004	0.001	<0.001	-0.003	0.001	<0.001
Mixed stands									
Pine				0.003	0.038	0.938	0.016	0.026	0.553
Ash				0.081	0.035	0.021	0.042	0.023	0.075
Spruce				-0.052	0.033	0.119	-0.074	0.024	0.002
Model statistics									
	marginal R^2	0.35		adjusted R^2	0.40		adjusted R^2	0.37	
	conditional R^2	0.37		RMSE	0.07		RMSE	0.07	

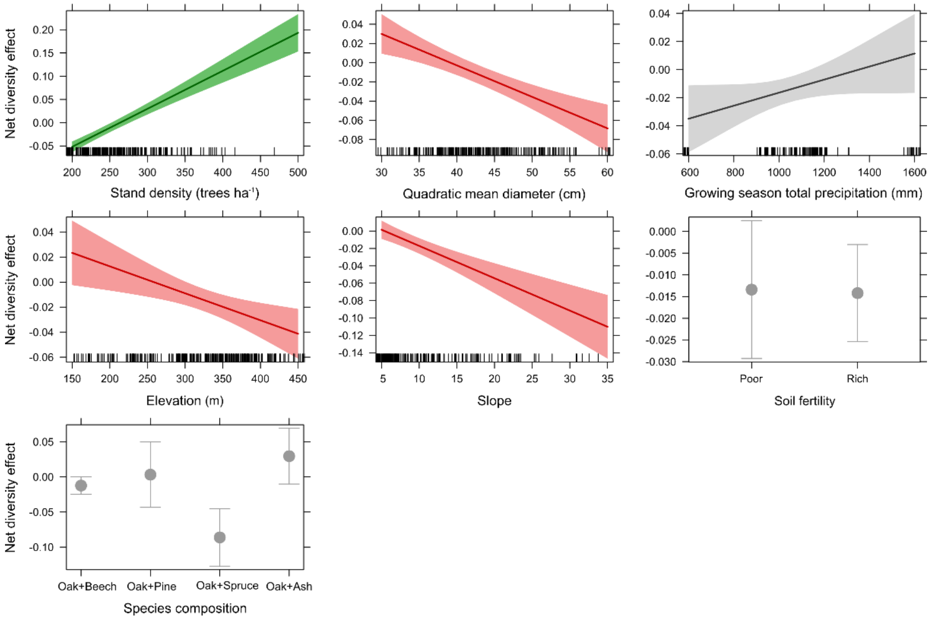
TMED, mean temperature for the growing season (April-September); PRCP, total precipitation for the growing season (April-September); QMD, quadratic mean diameter. Climate data were obtained from the FORBIO Climate dataset (Delvaux et al., 2015). Soil properties were retrieved from the digital soil map of Flanders (Dondeyne et al., 2014) and the Walloon forest inventory (for details, see Supplementary Note C.1). Topographic variables (elevation and slope) were extracted from a LiDAR-derived digital terrain model at a spatial resolution of 1 m (AGIV, 2015; SPW, 2015)

Figure C.5 Linear regression models. *Variation in the net biodiversity effect as a function of stand density, species developmental stage (quadratic mean diameter), site conditions (climate and soil), and composition of tree species mixtures for stands with beech (a; N = 208) and oak (b; N = 249) in the South SM ecoregion. Shading represents the 95% confidence interval. Positive slopes (green) indicate a positive influence on the net diversity effect, whereas negative slopes (red) denote a negative relationship. Non-significant slopes are shaded grey (P > 0.05). Model structure and parameter estimates are presented in Table C.2.*



(a) Net diversity effect for mixed stands with beech

(b) Net diversity effect for mixed stands with oak



APPENDIX D

Table D.1 Examples of recommended actions for integrating climate change adaptation and mitigation measures into forest management plans and practices. *These actions, drawn from a document prepared by FAO (2013), are intended to support forest managers (whether individual forest owners, private forest enterprises, forest organizations or public-sector agencies) in responding to the challenges (and opportunities) of adapting to climate change.* ▶

CLIMATE CHANGE IMPACTS	RECOMMENDED ADAPTATION ACTIONS
Water scarcity and increased drought	Select heat-tolerant and drought-resistant species and varieties for afforestation and reforestation Reduce evapotranspiration and competition for water by vegetation management (e.g. thinning, pruning and planting deciduous species) Invest in measures (e.g. maintain organic matter) to improve soil structure and reduce water stress Manage vegetation (e.g. control understorey vegetation) to reduce drought stress
Changes in temperature and precipitation	Adjust silvicultural treatments accordingly (e.g. thinning and harvesting) Adapt primary management objectives to allow the use of the existing or affected crop for other purposes (e.g. switching from timber production to pulp, wood fuel or poles) Manage for diverse tree composition, age and structure and understorey vegetation at the stand and landscape levels Plant or promote the use of climate-adapted species and varieties
Increased outbreaks of insects, pathogens and invasive plant species	Conduct regular surveys to facilitate the early detection and assessment of outbreaks Adjust harvesting schedules to harvest affected or vulnerable stands to reduce the risk of pest outbreaks Encourage the introduction and maintenance of mixed-species stands to increase resistance to pest invasion and resilience In forest stands, introduce and retain genotypes and varieties that are resistant and resilient to pest attack

Increase in the frequency and intensity of storms	Modify harvesting regimes to improve species and stand stability Avoid clear-cutting in vulnerable areas Maintain or increase species and structural diversity in ecosystems to promote resistance to storm damage and resilience following damage Select wind-resistant species and promote the development of multilayered canopies
Increase in the frequency, size and severity of wildfire	Obtain available information on the increased risk of fire due to climate change (e.g. from research organizations, forestry associations and agencies, and regional and national governments) Integrate fire management considerations with forest management planning (e.g. assess the quantities of potential fuel during monitoring to assess fire risk) Modify landscape structure to impede fire spread (e.g. establish networks of fire breaks; manage for a mix of stand ages and stocking densities; thin stands; create mosaics of controlled burns; select fire-tolerant species) Reduce or avoid the burning of logging residues in fire-prone areas
Heightened risk of economic loss	Adjust forest management plans to avoid or minimize financial losses Identify markets for new products and alternative opportunities for current products Explore market opportunities for species affected by pests, diseases, fire, storms and other climate change-related disturbances Explore opportunities for forest insurance to offset the risk of damage from climate change-related disturbances

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Sousa-Silva, R., Van Meerbeek, K., Van de Peer, T., Sioen, G., Laurent, C., Ponette, Q., Verheyen, K., & Muys, B. 2017. *Contrasting vulnerability and resilience to drought-induced defoliation in mixed versus pure stands*. IUFRO 125th Anniversary Congress. Freiburg, Germany, 18-22 September 2017. *Oral presentation.*

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Sousa-Silva, R., Verbist, B., Ponette, Q., Verheyen, K., & Muys, B. 2017. *A line made by walking: adaptation to climate change in forestry across Europe*. International Workshop on Forests and Climate Change: adaptation initiatives and new management practices. Nancy, France, 8-9 March 2017. ***Invited oral presentation***.

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AWARDS

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Start again…
If you can,
No anguish, no rush.
And the steps you walk,
In that tough way
Of future,
Walk them in freedom
While you don’t achieve,
Do not give up.
From any fruit you should accept only half.

And, never satiated,
Keep picking
Followed illusions in the orchard.
And seeing
Woken up,
The bluff of the adventure,
You are a man, don’t forget!
It is only your madness,
Where, with lucidity, you’ll know yourself…

Sísifo by Miguel Torga