



Mixing effects along ecological gradients in temperate oak-beech forests: radial growth, drought exposure and stability

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Summary

Mixed species forests are attributed with numerous advantages over pure forests. Though highly dependent on species identity and environmental context, mixing often enhances productivity, resistance and resilience to stresses, and stability of productivity. Additionally, mixed forests are usually richer in biodiversity and provide a wider range in ecosystem services. Diversity-productivity and diversity-stability relationships are shaped by interspecific interactions, which can be facilitative or competitive. Overyielding can happen through complementarity, when interspecific interactions more positive than intraspecific interactions, or through selection effects, when competitively dominant species overyield at the expense of other species. The mixture of sessile oak (*Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.) is common in western and central Europe and is often characterised by a competitive dominance of beech. Oak is more tolerant to drought, and dominates on sites that are too dry for beech.

The goal of this research was to test how mixing impacts several aspects related to the functioning of oak and beech forests. More specifically, we studied mixing effects along different ecological gradients, and on the stability of growth at several hierarchical levels (the individual tree, the population and the mixed community). We also studied potential conflicts between positive diversity effects on productivity and on stability. We selected 8 study sites in Belgium spanning a range in soil conditions. At each site, three forest stands were identified: a mixed oak-beech stand, and one pure stand from each species (triplet sampling). Stands were selected for homogeneity in site and stand conditions, with the exception of species composition. We sampled wood cores on dominant trees on which we measured ring widths. We performed dendrometric measurements on all neighbouring trees within an 18 m radius around each cored tree.

We tested whether positive mixing effects on tree growth in the absence of droughts lead to higher exposure to incidental droughts. If faster growing trees use more water, they may be more strongly dependent on a water supply, and they may exhaust the available soil water reserves more quickly during the early phases of drought. This is especially relevant for beech, which has previously been shown to grow faster in mixture with oak. We measured stable carbon isotopic composition ($\delta^{13}C$) on wood produced in a dry (2003) and in a reference summer (2001). The stable carbon isotope composition is closely related to water use efficiency and, as such, indicative of the water relations during photosynthesis. For each tree we calculated drought exposure as the difference in $\delta^{13}C$ between 2003 and 2001. We also calculated pre-drought growth of each tree as the average ring width in the period 1998-2002. We observed that beech trees had a higher drought exposure in mixtures, and that this was an effect of a faster growth. Oak, however, didn't react significantly to mixing, not in its pre-drought growth, nor in drought exposure. These results indicate that performance benefits of mixed forests in non-drought years can hinder drought resistance.

In a second study, we investigated how the relative importance of dominance and complementarity varies along three different ecological gradients: a spatial and a

temporal water availability gradient, and a temporal gradient in growing conditions. The underlying idea is the stress-gradient hypothesis, which predicts that positive interactions gain importance as growth conditions become harsher. We established a temporal gradient in water availability relevant to tree growth by narrowing down a large set of candidate climate variables to a site- and species-specific precipitation-related variable using lasso models. We used standardised tree growth as a proxy for growing conditions on a temporal scale. We constructed two sets of linear mixed-effects models. Growth models explain ring width directly, whereas mixing index models assess the relative difference in radial growth between trees in mixtures and monocultures. The results confirm the competitive dominance of beech: beech grows faster than oak, and mixing further enhances beech growth at the expense of oak growth. This shifted towards a larger importance of complementarity on dry sites and in years of low growth. Under these conditions, beech still benefitted from mixing, but this did not come at the detriment of oak growth. This pattern was not observed in years of low precipitation, where beech lost part of its mixing benefit.

In a third study, we investigated whether mixing stabilises growth through time at three different organisational levels: the community (the mixed stand), the population (a conspecific fraction of a stand) and the individual tree. We investigated the ways in which mixing-induced stabilisation at the tree level propagates to stabilisation of populations, and further to the community. Previous research has shown that the biodiversity-stability relationship is almost universally positive at the community level, but there is debate on the importance of different mechanisms behind this relationship. We contribute by proposing a methodology for quantifying the stabilising effect of biodiversity (or mixing) on communities and to partition the total stabilisation into effects acting through several pathways. This partitioning helps identifying separate causal mechanisms that act at different organisational levels. We observed a total stabilisation of 21%, half of which happened through pathways that also affect population level stability, half through asynchrony among populations. Community stabilisation through the population level was further partitioned into effects through either mean and standard deviation at the population level. Among effects through asynchrony, we distinguish between asynchrony due to intrinsic species-specific responses to environmental variability and effects of species interactions. We used the partitioning to test several hypotheses related to (de)stabilising mechanisms and found evidence for a signature of interspecific competition. Interspecific competition is believed to destabilise populations by increasing population variability, partly compensated at the community level by increased asynchrony. In the oak-beech mixture, we hypothesised high interspecific competition to affect oak growth especially.

In conclusion, we did find evidence for a mechanism by which increased growth of beech in mixtures poses a risk with regard to its drought resistance, but mixing remained beneficial for beech growth, even under dry conditions. Furthermore, mixing mitigates non-drought related constraints on growth for both species. We found that mixing affected both growth and stability in a positive way, although only beech benefits from increased growth. It was only on the drier sites and during low-growth years that mixing did not affect oak growth negatively. Regarding the role of mixing in mitigating climate-related stresses, our results show that general-

isation is difficult, because buffering effects depend on the nature of the limitation and the gradient over which they are measured. Nevertheless, in mixed forests of oak and beech, mitigation seems to be the rule rather than the exception.

Contents

Acknowledgements	3
Summary	4
1 Introduction	13
1.1 Challenges of the 21st century	14
1.2 Why studying mixed forests?	15
1.3 How does mixing benefit a forest?	17
1.4 When should mixing benefit growth?	21
1.5 Stability	23
1.6 The mixture of sessile oak and European beech	26
1.7 Scope and objectives	29
1.8 Study design	32
1.9 Outline of the thesis	37
1.10 Study sites	38
2 Mixing increases drought exposure through a faster growth in beech, but not in oak	43
Abstract	44
2.1 Introduction	44
2.2 Materials and methods	47
2.2.1 Study sites	47
2.2.2 Stands and target trees	48
2.2.3 Climatic data	49
2.2.4 Wood sampling, treatment and dendrochronological measurements	50

2.2.5	Statistical analysis	51
2.3	Results	52
2.3.1	Pre-drought growth	52
2.3.2	Drought exposure	53
2.3.3	Carbon isotope composition in reference and drought years	57
2.4	Discussion	60
2.4.1	Drivers of drought exposure	60
2.4.2	Selection effect versus complementarity	63
2.4.3	Conclusions and implications for forest management	63
3	Shifts in dominance and complementarity between sessile oak and beech along ecological gradients.	65
	Abstract	67
3.1	Introduction	67
3.2	Materials and methods	70
3.2.1	Study sites	70
3.2.2	Sampling, sample treatment, measuring, cross-dating	73
3.2.3	Statistical analyses	73
3.3	Results	77
3.3.1	Lasso models	77
3.3.2	Growth models	79
3.3.3	Mixing index models	80
3.4	Discussion	80
3.4.1	How does mixing of sessile oak and beech affect the growth of both species?	80
3.4.2	Is the mixing effect influenced by site water availability or interannual variations in growing conditions or in rainfall?	82
3.4.3	Does competitive advantage shift to oak under water limitation?	85
3.4.4	New approaches to assessing mixtures using tree ring widths	85
3.4.5	Conclusions	86

4 Partitioning biodiversity effects on ecosystem stability into stabilisation at population level and asynchrony at community level	89
Abstract	91
4.1 Introduction	91
4.1.1 Different hierarchical levels and asynchrony	92
4.1.2 Competition reduction	93
4.1.3 Overyielding	93
4.1.4 Direct and indirect effects	94
4.1.5 Temporal stability in forests	94
4.1.6 Objectives	95
4.2 Quantifying and partitioning the diversity-stability relationship . . .	95
4.3 Materials and methods	99
4.3.1 Study sites	99
4.3.2 Tree selection, sampling, stand measurements	99
4.3.3 Calculating population level growth	99
4.3.4 Statistical analysis	101
4.4 Results	102
4.4.1 Stabilisation at different levels	102
4.4.2 Partitioning of community stabilisation	102
4.4.3 Competition	103
4.4.4 Indirect effects of asynchrony	104
4.4.5 Stabilising effects of overyielding on populations	104
4.5 Discussion	105
4.5.1 Methodology	105
4.5.2 Stabilisation at hierarchical levels	106
4.5.3 Competition	107
4.5.4 Asynchrony	108
4.5.5 Evenness	110
4.5.6 Overyielding	110
4.5.7 Conclusion	111

5 Discussion	113
5.1 Reminder of main results	116
5.2 Do interspecific interactions increase temporal stability under the stress-gradient hypothesis?	116
5.2.1 Conclusion	120
5.3 Does mixing simultaneously enhance productivity and stability? . . .	120
5.3.1 Trade-off between competitive ability and stress tolerance . .	120
5.3.2 Mitigating limitations	122
5.3.3 Conclusion	124
5.4 Methodological aspects	125
5.4.1 Modeling growth	125
5.4.2 Representing climate	125
5.4.3 Novel approaches to studying stabilisation	127
5.4.4 Substituting space for time	128
5.5 Practical implications	129
5.5.1 Effect of climate change on mixtures	129
5.5.2 Maximising growth or resilience?	129
5.5.3 Is stabilisation through asynchrony among populations a desirable outcome?	130
5.5.4 An ecological niche for the mixture	130
5.6 Prospects	131
5.6.1 Improving climate-growth relationship	131
5.6.2 A better climate-growth relationship could help understanding stabilisation	131
5.7 Conclusion	132
Bibliography	133
A Appendices to chapter 2	157
A.1 Number of trees	157
A.2 Classification of soils according to soil water availability	157
A.3 Tree and neighbourhood variables	158
A.4 Summary of measurements	159
A.5 Model results for $\delta^{13}C$ in oak in 2001 and 2003	160

A.6	Isotopic values	161
A.7	Relationships between $\Delta\delta^{13}C$, mixing and pre-drought growth . . .	162
A.8	Relationships between pre-drought growth, mixing and carbon isotope ratios in both the drought and the reference year	164
A.9	Additional test for the drought exposure model	166
B	Appendices to chapter 3	167
B.1	Classification of sites	167
B.2	Number of trees per site, species and stand	168
B.3	Results of the lasso models	169
B.4	Performance of constructed precipitation variables	174
B.5	Partitioning of variance of growth data	174
B.6	Results of the growth model comparing oak and beech	175
B.7	Plots of data and model predictions arranged per site	177
B.8	Dendrochronological statistics	179
B.9	Plots of dendrochronological master chronologies	180
B.10	Results of growth models	181
B.11	Results of mixing index models	182
C	Appendices to chapter 4	183
C.1	Proof that τ_ρ , τ_μ and τ_σ form a multiplicative partitioning of τ_T . . .	183
C.2	Correction of upscaled population-level σ	184
C.3	Relationship between τ_ρ and φ	185
C.4	Results	186
C.5	Interpreting τ_μ as measure for overyielding	187
C.6	Mixing effects on unevenness in population-level σ	187

Chapter 1

Introduction

1.1 Challenges of the 21st century

A steadily growing and increasingly industrialised human population exerts an unsustainable pressure on the planet, changing the living conditions for biological species, and threatening their existence. In this section we address two important related crises: the worldwide decline in biodiversity and climate change.

Biological evolution has given rise to a large number of species, each adapted to a specific habitat, a range of environmental conditions that allows the species to survive and reproduce. The earth's richness in species partly results from the wide variety of habitats it hosts (Kerr, 2001). Furthermore, species modify the environment, and are thus part of each other's habitat. While some species tolerate far wider ranges in environmental conditions than others, all species are vulnerable when the environment changes beyond their tolerance levels (Saavedra et al., 2013). In such cases, species can still migrate to new environments, or on longer timescales, evolve genetically, leading to populations that are better adapted to prevailing conditions (Feeley, Rehm, and Machovina, 2012). When environmental change is too strong and too abrupt, however, these mechanisms are insufficient and species go extinct (Bridle and Vines, 2007).

Currently, human pressure on the earth's ecosystems has increased the rate of extinction to an estimated 100 to 1000 times the background extinction levels (Pimm et al., 2014; IPBES, 2019). Moreover, many species that do not go extinct suffer losses in genetic diversity, a necessary resource for adapting to changing conditions (Miraldo et al., 2016; Leigh et al., 2019; Hoban et al., 2020). Many consider that we are at the start of the sixth mass extinction event in the history of life on earth (Ceballos and Ehrlich, 2018), which is worrying, if only because of the strong dependence of human well-being on biodiversity (Losey and Vaughan, 2006; Gallai et al., 2009).

The biodiversity crisis is caused by human activity in several ways, including habitat destruction due to land use change (Jantz et al., 2015), exploitation (Branch, Lobo, and Purcell, 2013), and introduction of invasive alien species (Mcneely, 2001). Furthermore, as some species critically depend on others, there are cases where extinctions lead to more extinctions (chains of extinction Colwell, Dunn, and Harris 2012; Turvey and Cress 2019).

Another human factor predicted to become an important driver of species extinction in the future is climate change (Bellard et al., 2012; Urban, 2015). The temperature of the atmosphere is mainly regulated by the equilibrium between incoming solar radiation (warming) and outgoing radiation (cooling). By absorbing some of this outgoing radiation, greenhouse gases such as carbon dioxide (CO_2) shift the equilibrium towards a warmer atmosphere. Mainly through the combustion of fossil fuels, human activity has increased the carbon dioxide concentrations in the atmosphere from approximately 278 parts per million (ppm) in 1750 to 412.4 ppm in 2020 (Friedlingstein et al., 2022), thus increasing the temperature of both atmosphere and

oceans (Arias et al., 2021). These increased temperatures in turn modify weather patterns such as precipitation, increasing both the occurrence of droughts and heavy rains (because warm air can contain more humidity). Despite awareness within the international community about adverse effects on humanity and on the functioning of the earth's ecosystems (IPCC, 2022), worldwide CO_2 emissions continue to increase (Liu et al., 2022).

Forests play a role in slowing down climate change and in mitigating its adverse effects. Trees capture carbon dioxide and many of the carbon atoms end up stored within tree tissues, in other organisms or in the soil. From the 36.4 Gt of yearly human CO_2 emissions (estimate for 2021, Friedlingstein et al. 2022), global forests absorb a net 7.6 Gt (estimate for 2001-2019, Harris et al. 2021). Forests also play a role in the water balance and in the buffering of water (Ellison et al., 2017). Trees in urban areas provide cooling to residents. At the same time there are concerns about the ability of forests to withstand future stresses and disturbances in a changing climate, and fears that forests switch from being carbon sinks to being net carbon sources (Hubau et al., 2020). Trees are expected to suffer from warmth, droughts, increased fire occurrence and storms. Their longevity entails specific vulnerabilities. Individual trees may live up to several centuries, whereas contemporary climate change manifests itself on a timescale of decades. Rooted in the soil, they cannot escape the prevailing conditions. Adult trees find themselves in conditions that differ severely from those in which they grew tall. Long-term decision making on forest management is challenged both by the unpredictability associated with climate change and by uncertainties about the way forests will react to these changes. Among the measures recommended to forest managers, promoting diversity plays a prominent role. Diversity encompasses structural diversity, genetic diversity within conspecific trees and species diversity (Brang et al., 2014).

1.2 Why studying mixed forests?

What do we want from a forest, which functions should it fulfill, and which form should it therefore have? We discuss how different answers to these questions have been proposed and implemented throughout history.

Several formal definitions of mixed forests circulate (Bravo-Oviedo et al., 2014; Forrester and Pretzsch, 2015); we focus on interspecific interactions among trees, which are absent or rare in pure (monospecific) forests. This requires not only that multiple species are present within the same forest stand, but it also implies a spatial arrangement where each tree has close neighbours belonging to different species (intimate mixture). Both pure and mixed forests occur naturally, depending on local conditions such as soil and climate. Contemporary forests in western Europe owe their species composition partially to natural dynamics, and partially to a long

history of forest management with plantations and selective cuttings (Dieler et al., 2017).

Forestry practices and views with respect to mixing in western Europe have shifted throughout history in relation to the socioeconomic expectations from forests. An important concern has been that forests meet the demand for wood. Through tree ring analysis on wooden artifacts we know that import of Baltic timber to western Europe started in the 13th century, indicating that local supply was insufficient (Wazny, 2002; Haneca et al., 2005). During several centuries, the practice of coppicing has been widespread throughout Europe, especially for use as firewood (McGrath et al., 2015; Slach, Volařík, and Maděra, 2021). With industrialisation and the rise of fossil fuels, the economic importance of coppice declined, and many stands were converted into high forests during the 19th or early 20th century (Slach, Volařík, and Maděra, 2021). The 18th century saw the rise of a scientific approach to forestry with the development of theories on how to manage forests so that they produce wood in a sustained manner (Schmithüsen, 2013). This focus has led to forest managers favoring monospecific forest plantations. These provided homogeneous forest products from a small set of profitable species that combine a fast growth with a large market value (Bauhus, Forrester, and Pretzsch, 2017). Additionally, monocultures are easier to manage, and hence practical knowledge on forest management is largely focused on monocultures (Bauhus, Forrester, and Pretzsch, 2017). The trend of fostering monocultures has reversed towards the end of the 20th century. By 2007, the total share of mixed forests in Europe (defined as a forest dominated by two or more species) was estimated at 70% after increasing by 1.0% annually for 15 years (Ministerial Conference on the Protection of Forests in Europe, 2007).

Today, forests that are richer in species are believed to be better at provisioning multiple ecosystem services, and to be more ecologically stable (Puettmann et al., 2015; Bauhus, Forrester, and Pretzsch, 2017; Messier et al., 2021). The moral view that biodiversity has a value on itself plays a role as well, more recently supplemented with the idea that biodiversity is of tremendous economic value through the provisioning of multiple ecosystem services (Hanley and Perrings, 2019). Interestingly, the shift in forestry practice predates the availability of scientific results on the benefits of mixing (Gamborg and Larsen, 2003; Bauhus et al., 2017).

A rise in research interest on mixed forests in the early 21st century led to results on mixing effects on a wide range of ecosystem services. Whether these services are enhanced or weakened has often been shown to depend on environmental context and on the combination of species identities and functional traits, more than on the number of species (species richness) *per se* (Pretzsch, Forrester, and Bauhus, 2017). Functional traits have been defined as morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival (Violle et al., 2007).

Mixing effects on productivity have been found to be variable, but more often positive, with an average of +24% in a global meta-analysis (Zhang, Chen, and Reich, 2012). A very consistent result is the stability of productivity in time, which is higher in mixtures than in monocultures (Jucker et al., 2014; del Río et al., 2017; Schnabel et al., 2021; Xu et al., 2021; del Río et al., 2022). Related with stability is the ability

to cope with disturbances like pests and stresses. This ability is sometimes higher in mixed forests, especially when trees are attacked by specialist insect herbivores (Bauhus et al., 2017; Jactel, Moreira, and Castagneyrol, 2021). There is some evidence that mixed forests store more carbon belowground per hectare, even if species identity (or their functional traits) is a more important predictor than species richness (Dawud et al., 2016; Dawud et al., 2017; Osei et al., 2021). This is relevant given that by storing carbon, forests mitigate climate change (Harris et al., 2021). Finally, mixing enhances biodiversity. A larger number of forest tree species tends to result in a larger number of non-tree forest species as well (Ampoorter et al., 2020).

Apart from improving ecosystem services, the fact that species differ in which functions and services they provide leads to an averaging effect in ecosystem functioning, the jack-of-all-trades effect (van der Plas et al., 2016). As a result, mixed forests ensure a larger number of different ecosystem services (multifunctionality), but rarely at levels as high as monocultures. Under the uncertainties related to climate change, multifunctionality, biodiversity and the ability of forests to maintain functioning over time are often judged more important than the ability to maximise mean growth (Messier et al., 2021).

1.3 How does mixing benefit a forest?

The idea that mixing increases forest growth has intuitive appeal: the whole is more than the sum of its parts. This section deals with mechanisms behind faster growth in mixtures.

It is not self-evident that different tree species can form stable communities at all. As tree species require essentially the same resources, why would the species that is most efficient in using these resources to grow fast not outcompete the others? Generally, it is believed that this principle of **competitive exclusion** is avoided when resource needs of different species do not fully overlap (Hardin, 1960). Some tree species are, for example, more tolerant to shade, others more to drought. These differences among coexisting species may have as extra effect that the community is able to extract more resources from the environment, or to use them more efficiently (**resource partitioning**), which then leads to **competition reduction** and increased functioning and growth of the community (Ammer, 2019). Additionally, species can facilitate each other's growth through positive interactions, when one species benefits from the presence of another. An often cited example of **facilitation** occurs when one species harbours nitrogen-fixing microorganisms, increasing the availability of nitrogen for the complete community (Bellingham, Walker, and Wardle, 2001; Boyden, Binkley, and Senock, 2005). If mixing is beneficial even for the less competitive species, then species diversity can maintain itself in a stable way (Chesson, 2000).

In practice, competition reduction and facilitation are difficult to distinguish (Forrester and Bauhus, 2016) and are commonly considered together under the term

complementarity (also called **relaxation** by Ammer, 2019), and generally lead to **overyielding**. Overyielding is a formal concept for the intuitive notion that mixing increases yield (stand growth, in the case of forests). It occurs when mixed forests grow faster than they would be expected to, if mixing had no effect on growth. Calculating overyielding requires that mixed forests be studied along with comparable monocultures of the component species (Pretzsch and Schutze, 2009; Pretzsch et al., 2010). The expected growth of the mixed forests for a given forest area is then calculated as mean monoculture growth, weighted by the share that each species occupies in the mixture. The expected growth is also called the **additive effect**. The difference between mixed community yield and the additive effect is then the **non-additive effect** (or sometimes multiplicative effect), and can be positive (overyielding) or negative (**underyielding**) (Forrester and Pretzsch, 2015). **Transgressive overyielding** occurs when the mixture grows faster than each of the monocultures (Forrester, 2014).

Typically, overyielding is not evenly distributed over all species within the community, and some species may benefit disproportionately. When the fastest growing species in monoculture contributes most to overyielding, they tend to dominate the mixture. Because this is a form of natural selection that modifies species proportions within the forest stand (the fastest growing species is “selected”), it is called a positive **selection effect** (Loreau and Hector, 2001). A negative selection effect is possible as well. In this case, more slowly growing species in monoculture benefit most from the mixture, which stabilises the species composition.

Loreau and Hector (2001) presented a highly influential statistical technique to partition overyielding into two fractions, one representing the **complementarity effect** (a collective enhancement of productivity) and one representing the selection effect (dominance of the fastest growers). Unfortunately, the relationship between this statistical concept of complementarity and the mechanistic concept (relaxation) is not straightforward, which leads to confusion in terminology (Fox, 2005; Carroll, Cardinale, and Nisbet, 2011; Loreau et al., 2012; Ammer, 2019).

When discussing mixing effects on the growth for trees in a forest, we generally focus on interactions among trees that affect the use of resources. This is not the full story because species impact each other’s growth in non-resource related ways, for example by hosting herbivores. Resources are important, however, because their availability is limited, which creates competition among forest trees.

A key mechanism behind tree growth is **photosynthesis**, a process by which energy and matter are incorporated in the tree’s biomass (Taiz and Zeiger, 2010). Photosynthesis creates biological molecules by combining energy from sunlight (photons) with carbon atoms from atmospheric carbon dioxide. This way, photosynthesis is the basis of all the tree’s needs in terms of biomass and energy (and by extension, for most of life on earth). As sole energy source, the availability of **sunlight** is an important driver of growth (Taiz and Zeiger, 2010). Light, and more specifically competition for light, has played a major role in the evolution of trees. It is not necessarily the case that higher forests capture more light, but the tallest tree in the forest is the best competitor for light. **Carbon** (C) is essential for life, and abundant in the air under the form of carbon dioxide (CO_2). Yet, trees may lack carbon

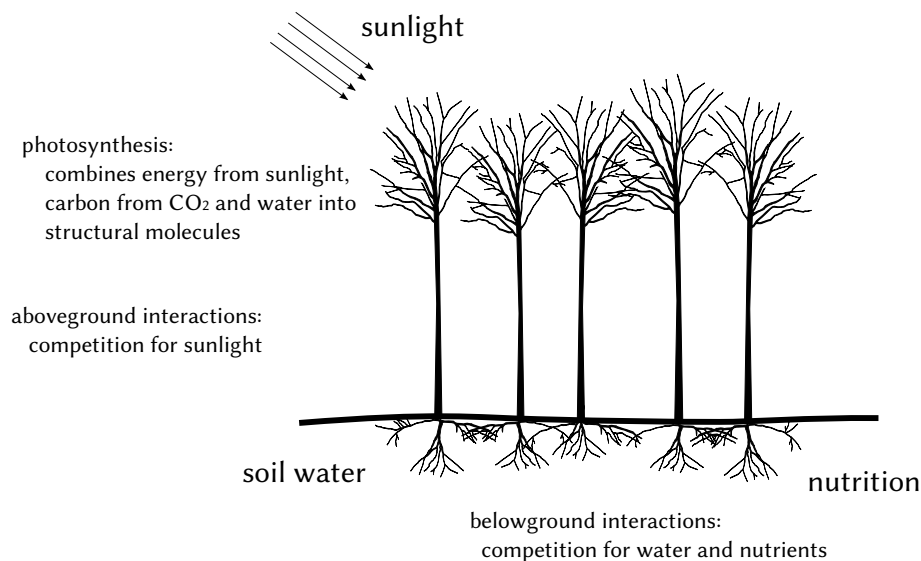


Figure 1.1: Main resources a forest needs to function, along with the most basic interactions among trees.

and may even die from carbon starvation, when other resources necessary for photosynthesis, such as **water**, are scarce (McDowell et al., 2008). The need for carbon and for water are coupled, because carbon uptake is linked to water loss. Stomatal openings in the leaves by which carbon dioxide enters the tree also allow water to evaporate (transpiration). Water lost through transpiration has to be replaced with water taken up through the roots, and transported through stem and branches. When the atmospheric demand for water is too high, and trees are not able to take up enough water, they are able to prevent water loss by closing their stomata (Taiz and Zeiger, 2010). This also prevents the uptake of carbon, and would thus typically decrease the total amount of photosynthesis performed by the tree, but increase the water use efficiency (the ratio between carbon taken up and water lost). Some (anisohydric) species resist closing stomata for longer, decreasing their risk of carbon starvation, but increasing risks of hydraulic failure and desiccation (McDowell et al., 2008; Hartmann, Link, and Schuldt, 2021). Another way to deal with water shortage is to grow more roots. Trees tend to allocate resources to the organ responsible for taking up the resource of which scarcity most limits their functioning (Shipley and Meziane, 2002). As an example, beech has been found to grow more fine roots on sites with less precipitation (Hertel et al., 2013). Carbon dioxide and water provide the three chemical elements that are most abundant in trees (oxygen, carbon and hydrogen). Other vital elements are taken up by the roots, mostly dissolved in the soil water (Taiz and Zeiger, 2010). The presence and availability of **nutrients** depends on a large number of chemical, biological and ecological processes. Nutrients become available through chemical weathering of parent material (Sverdrup and Warfvinge, 1988), atmospheric deposition (van Breemen and van Dijk, 1988), nutrients leaching from the canopy (Cape et al., 1992) or by the recycling of nutrients

from litter through decomposition and mineralisation (Hättenschwiler, Tiunov, and Scheu, 2005). Trees can also recycle their own nutrients internally through retranslocation from senescent tissues (Osman, 2013). Nutrient uptake is usually facilitated by mycorrhizal fungi growing in association with the roots (Hed  nec et al., 2020). Trees provide these fungi with products from photosynthesis, while the fungi supply the trees with nutrients, which they take up more efficiently. The forest floor provides an ecosystem for micro-organisms, fungi and animals that decompose the litter after which the nutrients become available for trees again.

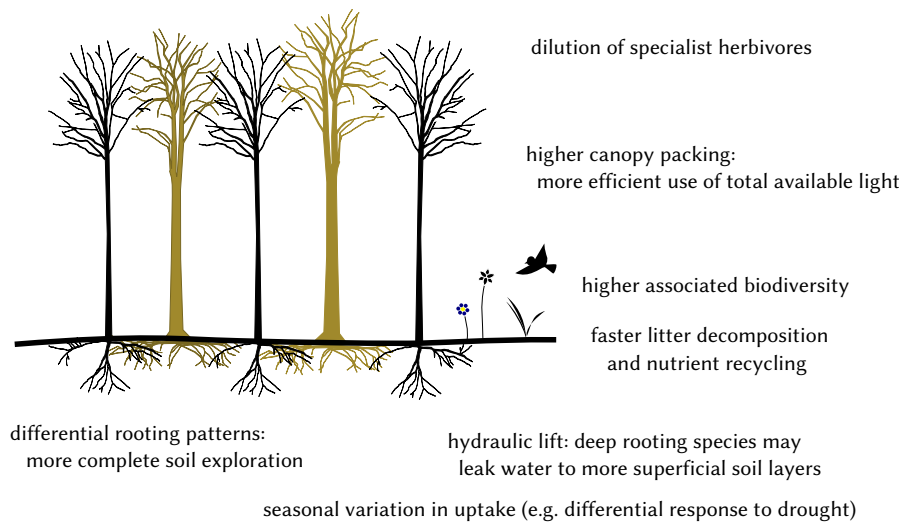


Figure 1.2: Potential mechanisms by which mixing can enhance or alter forest functioning.

Numerous ways have been described by which mixing may affect the availability, uptake or use efficiency of resources. Due to contrasting water uptake patterns in different species, mixed forest stands may better explore the soil compared to pure stands, thereby increase the total availability of water and, release competition for water. Such complementarities among species may be spatial, for example due to different water uptake depths (Schmid, 2002; Schwendenmann et al., 2015) or temporal, due to different seasonal patterns in water extraction (Gebauer, Horna, and Leuschner, 2012; Schwendenmann et al., 2015) or to different responses in stomatal regulation under drought (Schwendenmann et al., 2015). Species also tend to adapt their root systems in reaction to the mixture which can further increase water uptake (Schume, Jost, and Hager, 2004). An often cited example of facilitation by deep-rooting tree species is hydraulic lift, where their hydraulic system spills some water to superficial soil layers, which may benefit neighbouring trees that do not root as deeply (Dawson, 1993).

Mixing generally increases canopy packing (Jucker, Bouriaud, and Coomes, 2015) which should increase the interception of light, and hence photosynthesis (Binkley et al., 2013). One mechanism that has been described is vertical stratification: mixed

canopies can be more densely packed due to differences among species in crown shape and in vertical distribution of leaves. More important than these intrinsic differences seems to be the plasticity of trees to adapt and expand their crown architecture in response to the presence of neighbours (Jucker, Bouriaud, and Coomes, 2015). Why then would mixed forests allow for larger crowns and a denser canopy packing? Often quoted is the ability of shade-tolerant species to grow underneath a canopy of a light demanding species, which could lead to a more efficient use of the total available light (Hardiman et al., 2013; Canham et al., 1994). Additionally, it should be acknowledged that a high total leaf surface for photosynthesis (LAI) also implies a high transpiring surface and thus requires sufficient water supply from the roots. There may be situations where complementarity for water is what finally allows for a denser canopy packing in mixed forests (Ammer, 2019).

Several forms of complementarity have been shown to exist regarding nutrient uptake. Complementarity in root structure can improve nutrient uptake by a more complete exploration of the soil (Bauhus and Messier, 1999; Brassard et al., 2013). Mixing also has an effect on nutrient cycling. The chemical composition of the litter is species-dependent and affects the decomposing ecosystem on the forest floor. While more dependent on species identity than species richness, decomposition is often faster in mixed stands (Hättenschwiler, 2005). An additional complementarity can be provided by chemical stratification: differential preferences in the chemical form in which species take up nutrients (Richards et al., 2010). This may be complemented by a wider variety of mycorrhizal fungi in mixtures, though hard evidence is lacking (Wagg et al., 2015). Facilitation for nutrition has also been described. When a species has access to an extra source for nutrients, these can become available to neighbouring species through decomposition and mineralisation of litterfall. Such sources could be due to deep rooting (e.g. calcium pump, Berger et al., 2006) or due to symbiosis with nitrogen fixing bacteria in soils.

Facilitation may also happen in non-resource-related ways. Mixing can dilute the abundance of specialist herbivores, decreasing the vulnerability of tree species (Bauhus et al., 2017; Wright et al., 2017; Jactel, Moreira, and Castagneyrol, 2021). Additionally by creating shade, species can improve the microclimate of neighbours under heat and drought-induced stress (Wright et al., 2017).

1.4 When should mixing benefit growth?

Complementarities among species can increase growth, but do they also increase resilience to (climate-related) stresses? There are indications that mixing is especially advantageous when resources are scarce. This implies a relief of stress, and a stabilising effect on the growth and functioning of forests through time. The opposite, however, cannot be ruled out. If mixing increases growth, the forest could become more dependent on resources, and more vulnerable to shortages.

In 1994, Bertness and Callaway proposed their stress-gradient hypothesis with which

they predicted that facilitation is especially important in environments of large physical stress. This hypothesis has been very influential and has often been used to explain mixing effects over ecological gradients in forests, far beyond its original definition. For instance, the original manuscript focuses on harsh environments such as deserts where forests do not grow. In forests, competition for resources (negative interactions) is important, and authors often include competition reduction as part of the stress-gradient hypothesis. Additionally, Bertness and Callaway focused on the spatial scale, comparing different ecosystems, whereas we are often interested in mixing to reduce unpredictable climate-related stresses.

A challenge is deciding when organisms experience stress. Generally, stress is defined as an internal state of an organism, occurring when it finds itself outside its fundamental ecological niche (Steinberg, 2012). This, on itself requires a temporal variability in external conditions, because the organism would not survive if it were constantly under stress. Practically, the stress-gradient hypothesis has been tested along ecological gradients (spatial and temporal) on which one end is unfavourable for growth and functioning. Attempts to test the stress-gradient hypotheses on forests have yielded contradictory results, highlighting a need for refinement (Forrester and Bauhus, 2016).

A key aspect that modulates mixing effects is species identity (Maestre et al., 2009; Baeten et al., 2019). The potential of specific complementarities depends on the specific functional traits of the species that make up the mixture (Maestre et al., 2009). Functional diversity has been shown to be a better predictor of mixing benefits than the number of species (species richness) *per se* (Scherer-Lorenzen and Schulze, 2005; Ruiz-Benito et al., 2014). For example hydraulic diversity, diversity in the systems that transport water from roots to leaves, has been shown to buffer the functioning of temperate and boreal forests against drought (Anderegg et al., 2018).

In order to deal with the large number of combinations in species and traits that can appear together in mixture, theoretical papers use the concept of plant strategies. This is based on the observation that functional traits are not randomly distributed over species, but cluster along several axes. Plants developed combinations of traits during their evolutionary history, which together make it adapted to specific environments, but less to others. The term strategy does not imply consciousness in plants (Taiz et al., 2019). Maestre et al. (2009) differentiate between competitive and stress-tolerant species. Contrary to the predictions of the stress-gradient hypothesis, they argue that under high amounts of stress (low resource availability), competition for the scarce resources may be so harsh that there is often no room for facilitation to help. When stress-tolerant species are mixed with competitive species however, the competitive species may decrease its functioning under low resource availability (stress), and hence the amount of competition exerted on the stress-tolerant species (Maestre et al., 2009).

When mixing improves the availability (or the uptake) of a specific resource, we should not automatically expect increased growth. Growth may still be limited by another resource, or condition (Maestre et al., 2009). Forrester and Bauhus (2016) predict that the stress-gradient hypothesis holds when the gradient considered involves a stress that is relieved by interspecific interactions. Thus, under stress,

growth is limited by a specific condition or by shortage of a specific resource. Complementarities lead to increased growth under stress when complementarities relieve this stress factor. Conversely, there are cases where the predictions oppose those of the stress-gradient hypothesis. If we consider, for example, water unavailability as the stress, interspecific interactions that improve light-related processes will only lead to complementarity in the absence of water deficit stress (Forrester and Bauhus, 2016). There are reports from overyielding in forests of *Acacia* and *Eucalyptus* due to increased nutrition (nitrogen fixation). The overyielding leads to higher transpiration and a faster depletion of water reserves under drought in mixtures (Forrester, 2014; Forrester, 2015). Verheyen et al. (2008) observed a very similar mechanism in grasslands, where species diversity led to increased evapotranspiration in reference conditions, but not under drought because the water reserves were more quickly exhausted.

In a 2019 review paper, Ammer proposed a framework for how complementarity for different types of resources should lead to overyielding, based on the central role of photosynthesis as the basis of tree growth. Photosynthesis takes place at the leaves, so total leaf area is a vital aspect of growth. Mixing is not likely to improve productivity, if it does not improve light uptake. This does not mean that below-ground complementarity is not important, but its role is less direct. Following the balanced-growth hypothesis, trees will only increase the size of their crowns if they are able to support it through their roots (Shipley and Meziane, 2002). Large crowns need to be backed up by a sufficient access to water, since they lose a lot through transpiration. If belowground complementarity improves the water relations, trees can shift more of their biomass allocation towards their crown, leading to a higher canopy packing, higher light interception and ultimately higher forest productivity (Ammer, 2019).

1.5 Stability

Biodiversity stabilises ecosystem functioning through time, and this effect is almost universal. This section explores mechanisms behind mixing-induced stabilisation in forests.

Two important aspects of the diversity-ecosystem functioning relationships are the way diversity affects ecosystem productivity, and the way it affects stability of productivity. The diversity-productivity relationship has a strong theoretical and mechanistic base (Ammer, 2019), and its magnitude can be quantified as overyielding, statistically decomposed according to different mechanisms (Loreau and Hector, 2001; Fox, 2005). The diversity-stability debate on the other hand has been plagued by divergence in concepts and terminology (Van Meerbeek, Jucker, and Svenning, 2021). One way of defining stability is the ability of a system to absorb external changes without shifting into a fundamentally different behaviour (resilience *sensu* Holling and Clark, 1975). This has been studied specifically in forests under

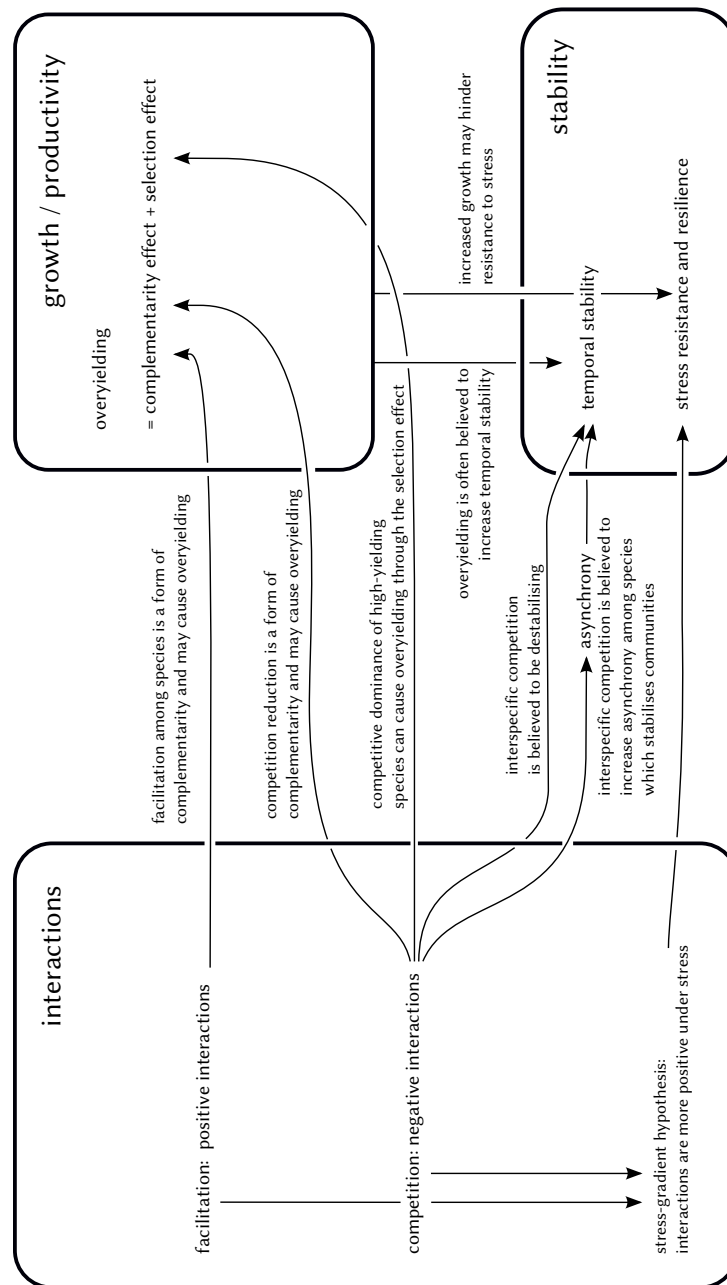


Figure 1.3: Overview of mechanisms by which interactions among species lead to improved growth (or overyielding) and stability.

concepts of resistance, resilience and recovery (Lloret, Keeling, and Sala, 2011). Here, resistance represents the extent to which the tree is able to maintain its growth during the impact, whereas resilience represents the capacity of the tree to return to the growth it had before the impact.

Stability can also be studied without explicit reference to specific disturbances or changes in external state. In this regard, the most widespread measure is **temporal stability** $TS = \mu/\sigma$ where μ represents mean yearly growth in time, and σ its standard deviation. When we discuss stability in this manuscript, we refer to temporal stability. The diversity-stability relationship (using temporal stability) has been investigated in many types of ecosystems and is overwhelmingly positive (Tilman, 1999; Ives and Carpenter, 2007; Isbell, Polley, and Wilsey, 2009; Gross et al., 2014; Xu et al., 2021). In recent years a number of publications confirm the stabilising effect of mixing on forests (Jucker et al., 2014; del Río et al., 2017; Schnabel et al., 2021; del Río et al., 2022). An important difference between forests and most other studied ecosystems is the longevity of individuals. Whereas community stability in many ecosystems depends on population dynamics such as recruitment, migration and mortality, in forests it stems from growth trajectories of individual trees. As most of the tree biomass stays unchanged from one year to another, stability in forests is calculated on stand growth (increment), rather than on the amount of biomass, or number of individuals present itself (Jucker et al., 2014). Yet, this literature uses terminology from population dynamics. The mixed stand is called the **community**, species within a stand are referred to as **populations**. As forest stability does not depend on population dynamics, stabilisation may not happen through the same mechanisms as in other ecosystems. Theoretical work aimed at unravelling the mechanistic origins of stabilisation explicitly model community growth as recruitment of individuals (Loreau and de Mazancourt, 2013; de Mazancourt et al., 2013), and it is unclear to which extent these results are applicable to stability in forests.

Asynchrony between populations is usually found to be an important stabilising factor (Isbell, Polley, and Wilsey, 2009; Hector et al., 2010; del Río et al., 2017). If growth is asynchronous, then populations compensate for each others' variability. In the extreme case, mixed stands are less affected when one of their species is hit by high levels of mortality (Van de Peer et al., 2016). This also means that asynchrony stabilises communities, but not populations. Indeed, results on mixing effects on population stability are not consistent, and even often negative (Tilman, 1996; Jiang and Pu, 2009; Hector et al., 2010; Gross et al., 2014; Xu et al., 2021). The diversity-stability relationship at the population level does shine through at community level, but in the cases that it is negative it appears to be compensated by effects of asynchrony which are virtually always positive. In fact, community stabilisation happens through the combination of these two pathways: effects acting at population level, and asynchrony acting among populations (Xu et al., 2021).

Growth is expected to be asynchronous among populations for the reason that species respond differently to environmental fluctuations. On top of this, species interactions can increase asynchrony. When species compete for finite resources, years

of high growth and high resource use for one species may be compensated by low growth and low resource use by another species. Literature does not agree on which of these causes of asynchrony is most important (Gross et al., 2014; Jucker et al., 2014; del Río et al., 2017; del Río et al., 2022).

Several authors have identified overyielding as a stabilising factor, based on a positive statistical relationship between overyielding and community stability but this is not undisputed (Hector et al., 2010; Morin et al., 2014; Cardinale et al., 2013; del Río et al., 2017). Interspecific competition is believed to be both destabilising and growth reducing, and may thus be responsible for a statistical link (Loreau and de Mazancourt, 2013). If stability depends on demographic processes, there is a stochasticity associated to the demographic variability, and this stochasticity is generally destabilising. This is especially important in smaller communities. Overyielding can be stabilising, if it reduces demographic stochasticity by increased population size (de Mazancourt et al., 2013).

1.6 The mixture of sessile oak and European beech

Sessile oak (Quercus petraea (Matt.) Liebl.) and European beech (Fagus sylvatica L.) are two widespread forest tree species in Europe (Eaton et al., 2016; Durrant, de Rigo, and Caudullo, 2016). Both have a cultural, economic and ecological importance, are well-studied and they are often found in mixtures together.

Sessile oak is a deciduous tree from the *Fagaceae* family, native to Europe, and often mentioned together with the closely related pedunculate oak (*Q. robur* L.), with which it shares much of its range. Sessile oak can reach up to 40m of height, and over 1000 years of age. It has a reasonably high morphological variability and hybridises with other oaks within its range such as *Q. robur* and *Q. pubescens* L. (Eaton et al., 2016). Sessile oak is wind-pollinated and is largely dependent on the Eurasian jay (*Garrulus glandarius* L.) for its seed dispersal (Eaton et al., 2016). The species has a large ecological amplitude and tolerates frost, even in spring. Sessile oak prefers fertile and moist soils, but has a certain tolerance for soil drought, to which the deep tap roots certainly contribute (Eaton et al., 2016).

Sessile oak contrasts with pedunculate oak in that it is intolerant for flooding and that it has a certain tolerance for more acidic soils (Jones, 1959). Oaks harbour a high biodiversity in invertebrates, some of which are harmful, such as defoliating caterpillars (Sommerville, 2005). Oaks also suffer from mildew fungi growing on the leaves and blocking sunlight (Jones, 1959).

Oaks are light-demanding and hardy. Their canopies are relatively open and allow light to pass through. They are able to dominate forests, but will rarely do so in the presence of beech. In natural situations, oak dominance is restricted to sites that fall beyond the tolerance of beech. Mixed oak-hornbeam forests, for example,

occur naturally where beech is restricted due to spring frost or insufficient precipitation, whereas oak-birch forests grow on soils that are too poor and acidic for beech (European Environment Agency, 2006).

In reality, sessile and pedunculate oaks grow on many sites where the natural vegetation would be dominated by beech, as a consequence of traditional management. This is partly because traditional coppicing practices favoured oak over beech due to its better resprouting capacity, and partly because oaks were highly desired trees and have had an important cultural significance throughout the centuries. Their acorns have been used to feed livestock, their bark for tanning leather, and their wood among others for construction, ship-building, fuel and the production of charcoal (Eaton et al., 2016).

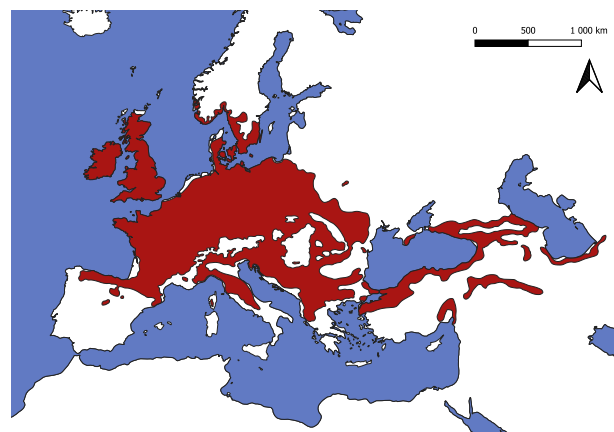


Figure 1.4: The natural range of sessile oak within Europe (Caudullo, Welk, and San-Miguel-Ayaz, 2017).

European beech is one of the largest (more than 40m) and most widespread native tree species in Europe (Packham et al., 2012). Beech trees can have a life span of over 500 years (Piovesan et al., 2003), and start producing seeds at the age of 40 to 50 (Durrant, de Rigo, and Caudullo, 2016). Its natural range spans from southern Scandinavia to Spain, Sicily and Turkey. Towards the southern edge of its range it trades off latitude for altitude and becomes restricted to mountains (1000-2000m). Expectations are that beech will shift its range northwards under climate change (Kramer et al., 2010).

Beech tolerates frost during winter, but not in spring after budburst (Dittmar, Fricke, and Elling, 2006). It also tolerates a wide range of soils and pH (3.5 to 8.5), but because of intolerance to both soil drought and hypoxia, it requires soils to be humid and well-drained (Leuschner and Ellenberg, 2017).

Beech is vulnerable to several types of pests such as aphids, weevils, fungi and water molds (Durrant, de Rigo, and Caudullo, 2016). It tolerates shade better than any other

broadleaved tree species within its range. At the same time it casts a dark shade to which its own seedlings are better adapted than other species. As a result, beech is able to dominate wherever external conditions are inside its range of tolerance, which is a large share of Europe's forests (Leuschner and Ellenberg, 2017).

Beech is an important species for forestry in Europe, not only because of its wide distribution and high abundance, but also because the wood lends itself to a diverse range of applications, such as fuelwood, furniture, staircases, toys and kitchen utensils (Durrant, de Rigo, and Caudullo, 2016).

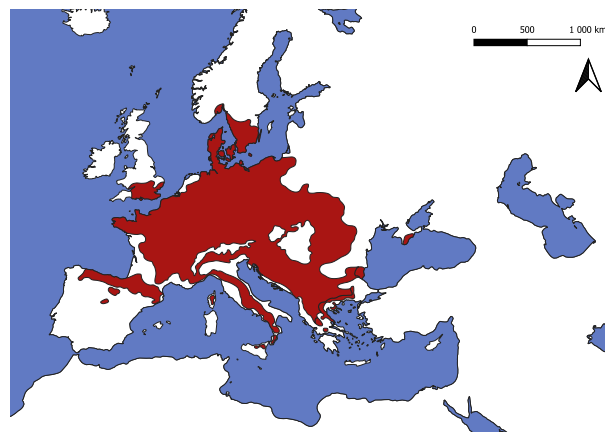


Figure 1.5: The natural range of European beech within Europe (Caudullo, Welk, and San-Miguel-Ayanz, 2017).

Both sessile oak and beech support a wide range of soil conditions, though oak tolerates a larger gradient in water availability. On mesic sites beech has a competitive advantage, suppressing all other species, including oaks, partly by creating shade that only its own seedlings can withstand (von Lüpke, 1998; Hein and Dhôte, 2006; Leuschner et al., 2001b). In a natural situation, beech has a tendency to form monospecific forests, with only a small fraction of other relatively shade-tolerant species (Hobi, Commarmot, and Bugmann, 2015). Oaks will occupy sites that are either too wet (mostly pedunculate oak) or too dry and acidic (sessile oak) for beech (Friedrichs et al., 2009; Leuschner et al., 2001a; Scharnweber et al., 2011; Vanhelle-mont et al., 2019). Mixed forests of oak and beech can occur naturally on sites that are marginally within the range of tolerance of beech, but more often, these mixtures are relics from past management, often coppicing (Ningre and Doussot, 1993; Strandberg, Kristiansen, and Tybirk, 2005; Vandekerkhove et al., 2016; Mölder, Meyer, and Nagel, 2019). Today, selective cutting is necessary in order to avoid beech to outcompete oak completely (Petrutan et al., 2014; Maleki, Zeller, and Pretzsch, 2020). In a warmer climate where droughts are more common, this pattern of dominance is expected to change on many sites (Bontemps et al., 2012; Cavin et al., 2013; Mette et al., 2013).

At the same time, several mechanisms have been described that could lead to complementarities in the mixture of oak and beech. Differential rooting patterns can create complementarities in the use of belowground resources. Beech has more fine roots whereas oak roots more deeply (Büttner and Leuschner, 1994). Hydraulic lift by oak has been observed in mixture with beech, but without evidence that it provided a water source for the admixed beech (Zapater et al., 2011). Differential light requirements have also been hypothesised to lead to a more efficient use of the available sunlight. Finally, differential requirements to water supply could lead to temporal complementarities, as oak may continue functioning under certain levels of soil drought that cause beech to halt its transpiration (Scherrer, Bader, and Körner, 2011).

The general observation is one of overyielding of beech and underyielding of oak (Toïgo et al., 2015). Several results also show that mixing mitigates the climate sensitivity of beech, while no effect on oak is observed. In mixture with oak, beech growth is more resistant to drought and recovers more quickly (Pretzsch, Schütze, and Uhl, 2013) and its stomatal conductance has been shown to react less to extractable water in mixture (Jonard et al., 2011). The competitiveness of beech has been found to decrease on sites with lower precipitation (Scharnweber et al., 2011). Complementarity between oak and beech is not a given. Overyielding in oak-beech mixtures has not been observed in general (Toïgo et al., 2015), but varies from overyielding on poor, to underyielding on fertile sites (Pretzsch et al., 2013).

1.7 Scope and objectives

A concern is that forests provide a wide range of ecosystem services, and continue to do so under climatic hazards and an eroding biodiversity. Of specific importance, considering their role in the global carbon cycle, is the ability to act as carbon sinks. The aim of this thesis is to advance in understanding of how mixing can help to ensure continued functioning of forests under climate-related stresses and disturbances. We focus on the mixture of oak and beech given their importance as native tree species in forests of Western and Central Europe, both from an ecological and an economical point of view.

Chapter 2

Research has shown that mixing effects on forest functioning are highly dependent on the complex interaction between species identity (or functional traits) and abiotic conditions. How mixing effects on productivity, sensitivity and stability interact is not well understood. A relevant question in this regard is how drought response of a tree is affected by its growth rate. As faster growing trees generally need more water, we hypothesise that where mixing increases growth, it also increases drought exposure (chapter 2).

Chapter 3

Sessile oak and beech are well studied, and the mixture has been relatively well characterised before. It has been established that the general dominance of beech over oak is lost at drier sites, because of its lower tolerance to drought. What is less clear is whether beech dominance is then replaced by oak dominance over beech, or by higher complementarity among species. On such sites, beech growth may be hampered by competition from oak, or alternatively, limitations could be mitigated by complementarity. Another aspect that remains largely unexplored is how competitive and facilitative interactions evolve along temporal gradients. In chapter 3, we infer shifts in competitive and facilitative interactions from patterns in mixing effects on tree growth along three ecological gradients (both spatial and temporal). This way we simultaneously study mixing effects on tree growth and sensitivity.

The chapter is based around two research questions. How does mixing of sessile oak and beech affect the growth of both species? And is this mixing effect influenced by water availability, or interannual variations in precipitation.

Chapter 4

Biodiversity has been shown to improve the temporal stability of communities almost universally over a large range of ecosystems, including forests. However, contrasting results have been obtained at the level of populations (species) and individual trees. Within the last decade, theoretical advancements have improved our mechanistic understanding of the diversity-stability relationship at the community level, but distinguishing between several sources of stabilisation in empirical studies remains challenging. In chapter 4, we show how the diversity effect on temporal stability can be quantified and decomposed into different pathways of stabilisation. We use the decomposition to identify a spatial gradient in interspecific competition intensity, thereby demonstrating the relevance of the proposed methodology.

Chapter 5

Research on mixing in forests has used dendrochronology to study the sensitivity of tree growth to climatic factors, and to study the sensitivity of growth to stress. A body of literature on temporal stability of ecosystems has been developed independently, but temporal stability has been studied in forests only recently. In the general discussion (chapter 5), we discuss how patterns compatible with the stress gradient hypothesis can explain both how mixing decreases sensitivity to stress and increases temporal stability (do interspecific interactions increase temporal stability under the stress-gradient hypothesis?).

In chapter 2 we develop the idea that increased growth in mixtures makes beech trees more vulnerable to droughts, suggesting a trade-off between productivity and ecological stability. This contrasts with a hypothesis from community ecology that overyielding drives stability. We discuss by which interspecific interactions, mixing oak and beech can simultaneously enhance productivity and stability on our sites (does mixing simultaneously enhance stability and productivity?).

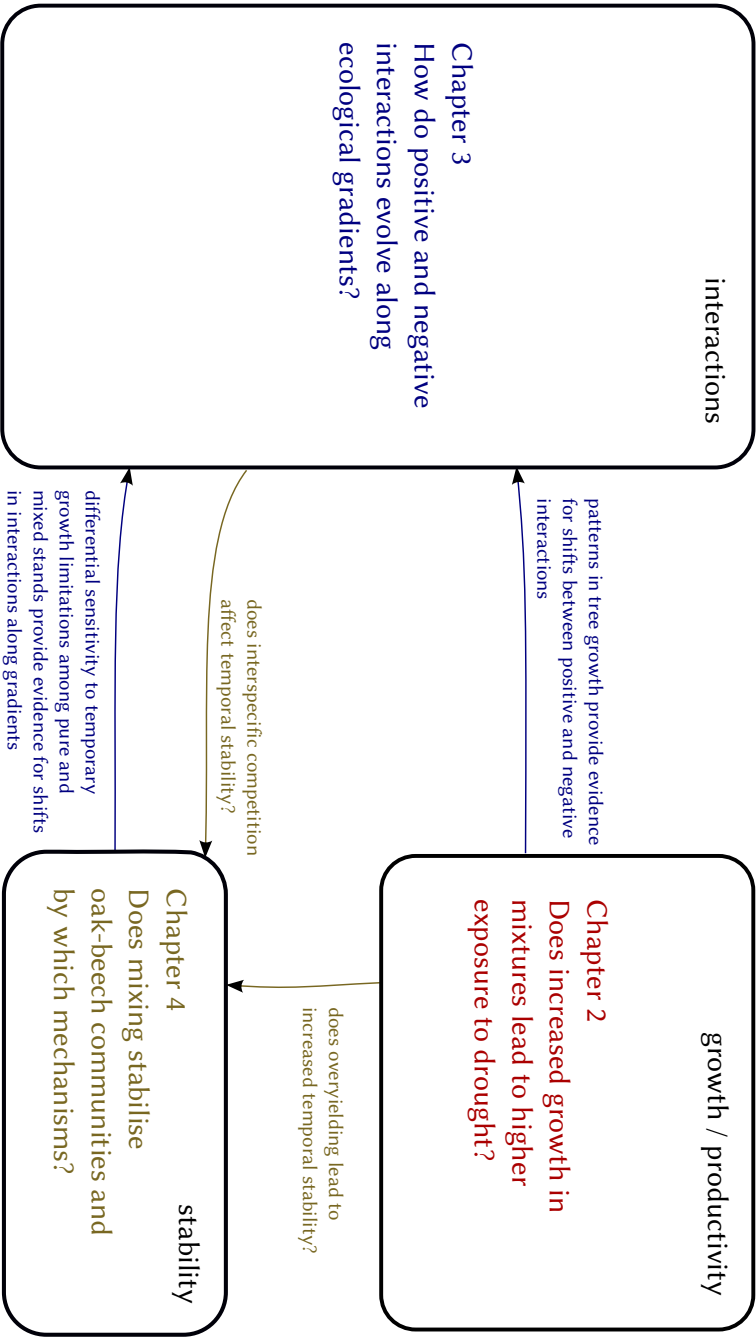


Figure 1.6: Schematic representation of the objectives of the three research chapters.

1.8 Study design

By forming a new growth ring every year, trees in temperate forests record a history of their own growth and functioning. In this section we explain how we use information stored in tree rings to answer ecological questions.



Figure 1.7: Wood cores sampled from oak (above) and beech (below).

This research is based around 8 study sites containing oak and beech in both pure and mixed stands. The study sites are conceived as oak-beech triplets. Concretely, at each study site (triplet), three forest stands are identified: one mixed sessile oak-beech stand, and one pure stand of each species. Except for species composition, these stands are chosen to be as close to identical as possible in terms of site and stand conditions. The underlying hypothesis is that observed differences between pure and mixed forest stands are due to mixing (Pretzsch et al., 2010; Forrester and Pretzsch, 2015). In practice, achieving *ceteris paribus* conditions is challenging because it requires identifying homogeneous sites where such three highly comparable forest stands are found, and obtaining permission for sampling. More fundamentally, the triplet approach carries a potential contradiction when we aim for *ceteris paribus* conditions in stand characteristics. Stand characteristics depend on long-term growth trajectories, which are themselves part of the mixing effect. It should not be expected that pure and mixed stands share the same trajectory in terms of age, size and growth. Triplets are not necessarily expected to occur in natural conditions. If species composition depends on abiotic conditions, triplets should not form within homogeneous site conditions. We benefit from current and past forest management that has favoured oak on sites where it would naturally be excluded by

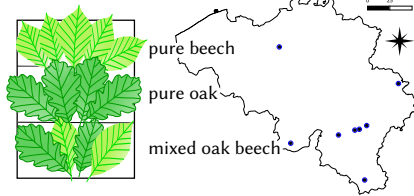
beech dominance. Resulting from management action, oak-beech triplets function as unintendedly created biodiversity experiments.

The study sites are selected along a gradient in soil water availability, though this was not specifically measured. Sites were ranked according to their capacity to store and release water based on information available in the soil map (Bah et al., 2007).

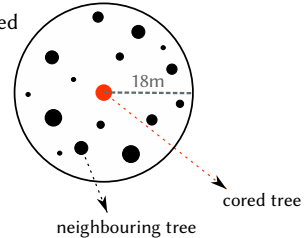
The choice has been to sample (co)dominant trees. As we have no specific information on the social status of the sampled trees throughout the period under study (1953-2014), a focus on dominant trees is the safest bet, as the trees that remain after selective cuttings and potentially mortality are likely the relative dominant trees of the past, even if this is not guaranteed (Cherubini, Dobbertin, and Innes, 1998). This is a choice that may affect the results, as social status is likely to affect climate sensitivity and susceptibility to competition (Lebourgeois et al., 2014; Trouve et al., 2017). From a subset of trees, we sampled wood cores and recorded ring width series. Additionally we mapped all coordinates of the trees within 18m distance of the cored trees and recorded their diameter and height.

Sampling strategy

Triplet approach: three comparable forest stands at 8 contrasted study sites



We identified 10 dominant trees per site, stand and species, and sampled two increment cores per tree



Mapping of tree neighbourhoods within a 18m radius of cored trees

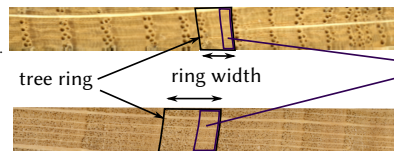
We recorded position and species of trees and measured heights and diameters

Measurements

We measured ring widths on all sampled cores

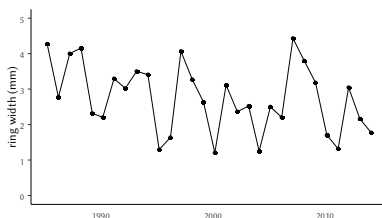
 Sessile oak
Quercus petraea (Matt.) Liebl.

European beech
 *Fagus sylvatica* L.



We extracted latewood produced in the summers of 2003 (drought) and 2001 (reference) and measured carbon isotope ratios ($\delta^{13}\text{C}$) as indicator of drought exposure (chapter 2)

Variability in ring width



1. We studied how weather conditions (specifically precipitation) affect ring width, and whether this is modulated by mixing (chapter 3)
2. We studied whether growing conditions affect mixing effects on growth using ring width as proxy for growing conditions. (chapter 3)
3. Variability is linked to stability of growth. We used ring width to calculate basal area increment at the level of trees, populations and communities and calculated temporal stability at three levels (chapter 4)

Figure 1.8: Overview of study design and methods.

Table 1.1: Overview of research questions and methodology per chapter.

CH 2

Research questions:

- Does increased growth of beech in mixtures lead to higher exposure to drought?

Hypotheses:

- Beech trees benefit from being admixed with oak in reference years in terms of growth, but this increased growth in mixed forests results in increased drought exposure in dry years

Methodology:

- Model pre-drought growth in function of mixing
- Model drought exposure in function of mixing and pre-drought growth
- Model beech $\delta^{13}C$ in both years in function of a mixing coefficient

Main variables:

- Stable carbon isotope ratios $\delta^{13}C_{2003}$ and $\delta^{13}C_{2001}$
- drought exposure
- $\Delta\delta^{13}C = \delta^{13}C_{2003} - \delta^{13}C_{2001}$
- pre-drought growth
- mixing coefficient (degree of mixing)

CH 3

Research questions:

- How does mixing of sessile oak and beech affect the growth of both species?
- Is this mixing effect influenced by site water availability, or interannual variations in precipitation?

Hypotheses:

- On moderately humid sites and in years with average growing conditions, beech will be competitively dominant over oak, leading to an increased growth of beech and a decreased growth of oak in mixed compared to pure stands.
- Under drier conditions (on a temporal or spatial gradient) or in less productive years, complementarity between species will increase, and competitive dominance of beech will become less important.
- Under drier conditions (on a temporal or spatial gradient) or in less productive years, competitive dominance will shift to oak.

Methodology:

- Construct a precipitation variable based on lasso models of growth (master chronology) using candidate climate variables
- Model tree ring width in function of precipitation, mixing, site-level water availability, including long term trends related with time and tree diameter
- Model the mixing index in function of detrended growth (as proxy for growing conditions) site water availability, and precipitation

Main variables:

- Candidate climate variables precipitation and temperature in different time windows
- Constructed precipitation variable
- Mixing
- Site-level water availability (swrank)
- Long term trends: year, tree diameter
- Mean detrended ring width

CH 4	
Research questions: - Does mixing stabilise oak-beech communities, and by which mechanisms?	Hypotheses: - Mixing stabilises oak-beech communities - Stabilising pathways show signature of temporal complementarity and interspecific competition
Methodology: - Calculate basal area increment (BAI) at individual, population and community level - Calculate temporal stability of BAI at three levels - Quantify the total stabilisation in mixtures compared to monocultures. - Decompose total stabilisation in factors acting at the population level, and asynchrony.	Main variables: - Total stabilisation: τ_T - (De)stabilisation through asynchrony τ_ρ, through altered population growth τ_μ and through altered population variability τ_σ
CH 5	
Research questions: - Do interspecific interactions increase temporal stability under the stress-gradient hypothesis? - Does mixing simultaneously enhance productivity and stability?	

1.9 Outline of the thesis

This thesis is organised in three research chapters, preceded by a general introduction (chapter 1), and followed by a discussion (chapter 5).

In chapter 2, we study stable carbon isotopes to estimate the degree to which trees were exposed to summer drought in 2003. Two stable carbon isotopes, ^{12}C and ^{13}C , are found in the atmosphere and in plants, but in different ratios due to a discrimination of ^{13}C during photosynthesis. In C_3 plants such as oak and beech, this discrimination depends on the ratio of intercellular to atmospheric CO_2 concentration (Farquhar, O'Leary, and Berry, 1982; Cernusak et al., 2013), which is linked to stomatal control, and thus to water relations. We use the ratio between ^{13}C and ^{12}C (expressed as $\delta^{13}\text{C}$) within the wood as an indication of the water relations during photosynthesis. We measured $\delta^{13}\text{C}$ on wood formed during a dry (2003) and a reference (2001) summer, and use the difference in $\delta^{13}\text{C}$, because this indicates the extent to which a tree was exposed to the 2003 summer drought. We link this measure with average pre-drought growth of trees to explore the link between mixing, growth and drought exposure.

In chapter 3, we model tree growth (ring width) using linear mixed models in order to test whether mixing has an effect on growth and on the climate sensitivity of trees. We include confounding factors such as tree diameter and site (as random effect) in the models. The variable used to represent the variability in weather conditions is constructed by fitting a large number of climate variables (precipitation and temperature) in a lasso model explaining tree growth per site and per species. The lasso procedure is able to deal with a large number of intercorrelated variables by performing regularisation and variable selection. The precipitation variables selected by the lasso procedure were combined into one site-differentiated climate variable. In a second approach we use tree growth as a proxy for growth conditions, to model the mixing effect on growth. This way we test whether stress or disturbance (low growth) induce mixing benefits. This means we investigate mixing effects on growth along three different gradients: a spatial gradient in water availability (the different study sites), a temporal gradient in precipitation, and a temporal gradient in growth. We use growth patterns in order to infer the context-dependency of positive and negative interspecific interactions.

In chapter 4, we investigate how mixing leads to forest stands with a more stable growth. We first quantify the total mixing effects on temporal stability (TS), by comparing mixed community TS with a reference stability based on growth of the pure stands. Then we partition the total stabilisation in effects through asynchrony in growth among populations (species) and stability at the population (species) level. The effect through stability at population level can further be subdivided into effects through both mean and standard deviation of population-level growth. We use correlations between these pathways in order to detect signatures of stabilising or destabilising mechanisms. In the general discussion we discuss the consistency of the isotope results with the patterns we observe in growth, and how tree responses to temporal gradients in mixtures affect temporal stability. We further discuss whether increased growth due to mixing can coexist with, or rather trades-off with increased

stability. Finally, we discuss strengths and limitations of the used methodologies and address practical implications for forest management.

In the general discussion (chapter 5), we explore which interactions lead to patterns in growth, drought exposure, overyielding and stabilisation, by means of two transversal research questions. We further discuss methodological aspects and practical implications of the results.

1.10 Study sites

We selected eight study sites in Belgium (table 1.3) that cover a range in climatic conditions (table 1.4) and soils (table 1.5). On each site, a triplet is selected consisting of three forest stands (pure oak, pure beech, mixed oak-beech). Stands were selected for homogeneity in site conditions. These stands were usually adjacent, except at the sites in Ave-et-Auffe and Eupen, where the maximum distance between stands was respectively 2 and 5 km.

We use water availability as main site-related gradient, because oak and beech differ in their water requirements more than in their nutritional requirements, and the it is mostly the water-availability gradient that is expected to affect oak-beech interactions. Sites were ranked according to their capacity to store and drain water from driest (1) to most humid (6) (chapter 3), and classified into three categories: dry, optimal, wet (chapter 2). Ellenberg quotients ($EQ: 1000 \cdot \text{mean july temperature} / \text{mean yearly precipitation}$) show that the climate zone is favourable to beech dominance.

The site of Buggenhout was discarded in the analyses of chapters 3 and 4. Some of the trees in this site were relatively young, and showed a strong age trend in growth, which we were not able to filter out completely statistically. For isotopic analysis (chapter 2) these age trends are less relevant.

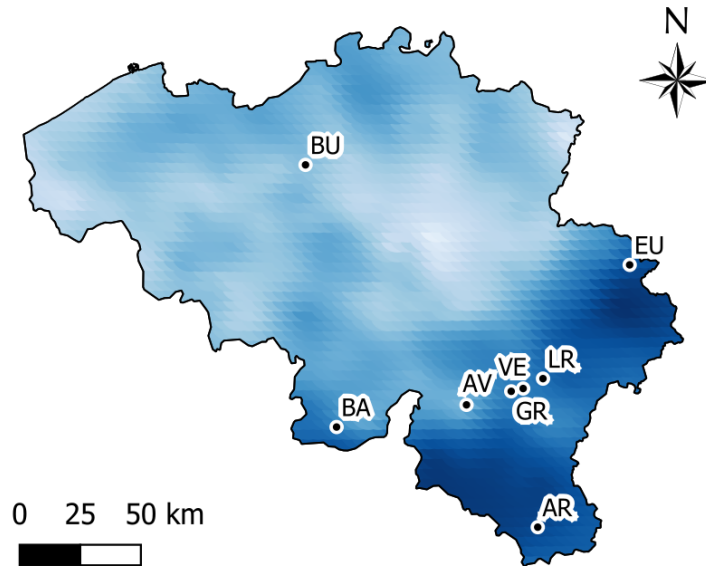


Figure 1.9: Location of the eight study sites in Belgium, plotted against mean yearly precipitation (1980-2016, Delvaux, Journée, and Bertrand 2015) ranging from 731 mm (white) to 1378 mm (dark blue).

Table 1.3: General information on the 8 study sites

	Lat. and long.	Ecoregion	Altitude (m)
Buggenhout (BU)	50° 59' 39" N; 4° 13' 5" E	Mid-Flemish sloping sandy-loamy area	20
Ave-et-Auffe (AV)	50° 06' 9" N; 5° 08' 56" E 50° 7' 3" N; 5° 7' 44" E	Calestienne	250
Baileux (BA)	50° 1' 23" N; 4° 23' 59" E	Atlantic Ardenne and Ardenne basins	300
Arlon (AR)	49° 38' 45" N; 5° 32' 54" E	Cotes de Florenville	340
Grune (GR)	50° 9' 2" N; 5° 24' 28" E	Centro-Eastern Ardenne	420
Eupen (EU)	50° 36' 39" N; 6° 6' 30" E 50° 33' 53" N; 6° 3' 47" E	Centro-Eastern Ardenne	440
La Roche (LR)	50° 11' 45" N; 5° 35' 32" E	Centro-Eastern Ardenne	450
Vecmont (VE)	50° 9' 37" N; 5° 28' 37" E	Centro-Eastern Ardenne	450

Table 1.4: Climatic characteristics of the 8 study sites

	Mean yearly precipitation 1954-2015 (mm)	Mean P-PET Mar-Sept 1954-2015	Mean yearly precipitation 1954-2015 (mm)	Mean yearly temperature 1954-2015 (°C)	Ellenberg quotient
Buggenhout (BU)	800	-97.81	800	10.4	22.5
Ave-et-Auffe (AV)	865	-33.54	865	9.0	19.6
Baileux (BA)	1081	52.09	1081	8.8	15.3
Arlon (AR)	1112	40.78	1112	8.7	15.1
Grune (GR)	1001	54.40	1001	8.1	15.9
Eupen (EU)	1112	127.13	1112	8.5	14.7
La Roche (LR)	967	24.42	967	8.6	17.1
Vecmont (VE)	989	43.16	989	8.2	16.3

Table 1.5: Soil characteristics of the 8 study sites

	Soil type (WRB, 2014)	Texture	Drainage class	Soil depth (cm)	Stoniness (%)	Soil water availability category ¹	Soil water availability ranking ¹
Buggenhout (BU)	Stagnosol fragic	Sandy loam	Poorly drained	> 125	0	wet	
Ave-et-Aurfe (AV)	Cambisol calcareic	Stony loam	Well drained	20-40	5-50	dry	1
Baileux (BA)	Cambisol dystric	Stony loam	Well drained	40-80	5-50	dry	2
Arlon (AR)	Cambisol dystric	Loamy sand	Slightly excessively drained	> 125	0	dry	2
Grune (GR)	Cambisol dystric	Stony loam	Well drained	> 80	< 50	optimal	4
Eupen (EU)	Cambisol dystric skeletal	Stony loam	Well to insufficiently drained	40-80	> 5	optimal	5
La Roche (LR)	Cambisol dystric	Stony loam	Well drained	> 40	< 50	optimal	3
Vecmont (VE)	Stagnosol skeletal	Stony loam	Hydromorphic	40-80	5-50	wet	6

¹ Expert based ranking from driest (1) to most humid (6) or into three categories. See appendices B.1 and A.2 for more information on the classification. Buggenhout is not used in chapter 3 that uses the ranking, but should be placed between Eupen and Vecmont.

Chapter 2

Mixing increases drought exposure through a faster growth in beech, but not in oak

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Abstract

Promoting mixed forests is often seen as a management option to increase the resilience of forests to droughts. However, mixing can also improve tree growth, and if faster-growing trees use more water, they may be exposed to higher risks of drought. Across Belgium, we tested whether increased tree growth in mixed sessile oak/common beech stands results in increased drought exposure of these forests in severe dry summers. We sampled wood cores from 222 trees in mixed and corresponding pure stands at eight different sites and measured ring widths and stable carbon isotope composition ($\delta^{13}C$) in the wood formed during 2001 (wet summer as a reference year) and 2003 (severe dry summer). Pre-drought growth (PG), an index of tree growth in normal climatic conditions, was calculated as the mean ring width in the five years preceding the drought, and drought exposure was assessed as the difference in $\delta^{13}C$ between the dry and the reference year. Growth of individual beech trees was faster in mixtures and both mixing and pre-drought tree growth were positively related to beech drought exposure. These two effects were not independent: the increased drought exposure in mixed stands was an effect of the faster growth. Analysis of $\delta^{13}C$ values suggests that in reference conditions, beech trees in mixtures had a less conservative water use than trees in pure stands, but that they shifted to a functioning similar to that in pure stands under drought. By contrast, growth and drought exposure of oak trees did not differ between pure and mixed stands. Our results emphasize the different strategies of these two species regarding their response to mixing and drought. Beech maximizes its growth as a result of greater resource capture in mixed stands, but this increases the risk of suffering from severe droughts. Oak, on the other hand, exhibits lower variability in growth and in drought exposure across pure and mixed stands. We should stress that if mixing is used as a management strategy to mitigate the negative effects of climate change on temperate forests, forest managers should be aware that the performance benefits of mixed forests in non-drought years could in fact hinder the drought resistance of these forests in severe drought years.

2.1 Introduction

In temperate Europe, drought is a major stress factor for forest ecosystems. This is evidenced by numerous dendrochronological studies showing that annual growth is often correlated with precipitation (see Penninckx et al., 1999; Lebourgeois, Cousseau, and Ducos, 2004; Lebourgeois et al., 2005; Scharnweber et al., 2011 for examples for oak and beech). For a tree, maintaining sap flow is necessary to replace water lost by evapotranspiration at the leaves and this becomes difficult under conditions of soil drought (e.g. Leuzinger et al., 2005). Due to climate change, droughts like those that hit Europe during the summers of 1976 and 2003 are expected to increase in frequency in the 21st century (Dai, 2013), raising concerns over the ability of temperate forests to sustain and recover from these drought events (Allen et al., 2010).

When co-existing species differ in resource usage patterns, interspecific competition may be weaker than intraspecific competition, according to the niche complementarity principle. Available light, for example, may be more efficiently used in a mixture of species showing different degrees of shade tolerance (Forrester, 2014). Differences in rooting patterns (i.e. vertical distribution, maximum depth) may lead to better soil exploration (Schmid, 2002), though it is not clear whether this process often plays an important role (Jacob, Hertel, and Leuschner, 2013). Complementarity may also occur on a temporal scale (del Río et al., 2017). When, under drought-limiting conditions, an isohydric species limits its water usage through stomatal regulation, admixed anisohydric species can have a larger share of the remaining soil water (Pretzsch et al., 2014).

Furthermore, in mixed forests, one species may improve the habitat of another through facilitation of resource acquisition and use (Reiss et al., 2009). The interactions that are possible between a set of species and the ecological relevance of these interactions depend on species identity (ecological traits) in combination with abiotic site conditions (Ammer, 2019).

Managing forests toward species mixtures has been promoted with several objectives. Mixed forests often show increased growth compared with monocultures of the constituent species (i.e. overyielding; Ammer, 2019). Higher resistance to drought has also been hypothesized to be the result of mixing. This is important in regions where drought is expected to increase with climate change, yet there are conflicting empirical results. Pretzsch, Schütze, and Uhl (2013) observed that the resistance and resilience of European beech (*Fagus sylvatica* L.) growth during the summer droughts of 1976 and 2003 were higher in mixtures with oak than in pure stands. Lebourgeois et al. (2013) found a similar increase in drought resistance for *Abies alba* in mixtures. However, Grossiord et al. (2014b) found higher drought exposure, expressed as the increase in $\delta^{13}C$ from a wet to a dry year, of trees in mixtures for several tree species in the boreal zone, and no positive effects of mixing in hemiboreal, mountainous beech, or Mediterranean forests (Grossiord et al., 2014a). Metz et al. (2016) observed that beech trees that grew in mixtures with different combinations of species, while generally growing faster than beech in pure stands, had higher growth reductions during the drought years of 1976 and 2003.

Although faster growth is considered a potential benefit of mixing, it may be accompanied by higher demand for water (Ammer, 2019), which in turn could increase susceptibility to drought in mixtures compared with pure stands, unless compensated for by higher availability of water through facilitation mechanisms or by an increase in water-use efficiency. Forrester (2015) observed that some but not all trees in mixtures had higher growth than trees in corresponding pure stands. Those trees growing faster in mixtures had higher water-use efficiency than trees in pure stands, while the trees in mixtures that did not show faster growth did not increase their water-use efficiency either. If higher growth is accompanied by higher water consumption, this may negatively impact water availability under drought conditions. In grasslands, species diversity has been observed to be positively related to evapotranspiration in reference conditions, but not under drought, because the higher water consumption of the most diverse grasslands led to faster depletion of the water reserves (Verheyen et al., 2008).

Increased growth, resulting from complementary interactions, could increase tree susceptibility to drought if optimizing for growth trades off against optimizing for stress resistance. Under conditions that are not water-limited, trees can, for example, shift carbon allocation away from belowground fine roots towards aboveground shoots, or optimize their wood anatomy towards efficient water transport that may be less tolerant to water deficits (Schuldt et al., 2016).

Drought is expected to become a major stress factor for forest ecosystems and mixing is increasingly being used by forest managers as a potential strategy to improve drought resistance of forests to future severe droughts. In this context, it is essential to gain a better understanding of the possible trade-offs between mixing effects on growth and mixing effects on drought resistance. While some studies have examined mixing effects on productivity (Pretzsch et al., 2013) and on drought resilience (Pretzsch, Schütze, and Uhl, 2013; Lebourgeois et al., 2013) separately, little is known about the relationship between performance enhancement and buffering effects of mixing. In this study, we investigated this relationship in pure and mixed sessile oak (*Quercus petraea* (Matt.) Liebl.) - beech (*Fagus sylvatica* L.) forests across Belgium. These two species, which frequently co-occur in Western and Central Europe, differ in a number of ecological traits, leaving room for complementarity processes (Pretzsch et al., 2013). One important such trait is shade tolerance (Toigo et al., 2018), which is higher in beech than in oak. Regarding water, sessile oak is better adapted to drought-limiting situations, partly due to its ability to develop deeper roots than beech (Leuschner et al., 2001a). Sessile oak is also able to maintain high photosynthesis and transpiration under lower leaf water potentials than beech (Leuzinger et al., 2005) potentially allowing temporal complementarity of soil water use among species. Finally, while sessile oak is more stress tolerant, beech appears to be a much stronger competitor in less stressful conditions. As a result, beech often grows faster in mixed than in pure stands (see for example del Río, Condés, and Pretzsch 2014).

Our main hypothesis was that beech trees would benefit (in terms of growth) from being admixed with oak in reference years, but that increased growth in mixed forests would result in increased drought exposure of beech in dry years. For oak, we expected the opposite pattern, namely that growth would be lower in mixed forests, resulting in a decreased exposure to the 2003 drought. To test this hypothesis, we sampled oak and beech trees in pure and mixed stands, using a triplet approach (Forrester and Pretzsch, 2015), at eight different sites. The response to summer drought was assessed as the difference in wood carbon isotope composition ($\delta^{13}C$) between a wet (2001) and a dry (2003) year. This was introduced by Grossiord et al. (2014b) as a way to extract the effect of drought exposure from the $\delta^{13}C$ measurements. We used pre-drought growth (ring width averaged over five years) as an indicator of growth under normal conditions. We first tested for a mixing effect on drought exposure. We then analysed whether this mixing effect was related to the impact of mixing on growth by looking successively at the relationship between mixing and growth, and between growth and drought exposure, while accounting for effects at tree level, such as local neighbourhood and tree dimensions, in addition to stand

Table 2.1: Selected site characteristics of the eight triplets. In addition to long-term (1954-2015) averaged climate indices (total P, P-PET over the vegetation period), P-PET and SPEI values over the summer period (July-September) are given for the two years under study (2001, 2003). The sites are ranked according to elevation.

	Long. and lat.	Ecoregion	Altitude	Soil type
			(m)	(WRB, 2014)
Buggenhout (BU)	4° 13' 5"; 50° 59' 39"	Mid-Flemish sloping sandy-loamy area	20	Stagnosol fragic
Ave-et-Auffe (AV)	5° 8' 56"; 50° 6' 9" 5° 7' 44"; 50° 7' 3"	Calestienne	250	Cambisol calcaric
Baileux (BA)	4° 23' 59"; 50° 1' 23"	Atlantic Ardenne and Ardenne basins	300	Cambisol dystric
Arlon (AR)	5° 32' 54"; 49° 38' 45"	Cotes de Florenville	340	Cambisol dystric
Grune (GR)	5° 24' 28"; 50° 9' 2"	Centro-Eastern Ardenne	420	Cambisol dystric
Eupen (EU)	6° 6' 30"; 50° 36' 39" 6° 3' 47"; 50° 33' 53"	Centro-Eastern Ardenne	440	Cambisol dystric skeletal
La Roche (LR)	5° 35' 32"; 50° 11' 45"	Centro-Eastern Ardenne	450	Cambisol dystric
Vecmont (VE)	5° 28' 37"; 50° 9' 37"	Centro-Eastern Ardenne	450	Stagnosol skeletal

	Soil water	Mean yearly	Mean P-PET	P-PET	SPEI
	availability	precipitation	Mar-Sept	Jul-Sept	Jul-Sept
	category ^a	1954-2015 (mm)	1954-2015	2001 2003	2001 2003
Buggenhout (BU)	wet	800	-97.81	85.37 -138.07	1.92 -0.83
Ave-et-Auffe (AV)	dry	865	-33.54	40.72 -163.73	1.46 -1.49
Baileux (BA)	dry	1081	52.09	82.64 -142.38	1.35 -1.44
Arlon (AR)	dry	1112	40.78	75.11 -138.94	1.31 -1.28
Grune (GR)	optimal	1001	54.40	61.32 -102.44	1.11 -1.07
Eupen (EU)	optimal	1112	127.13	62.84 -141.22	0.56 -1.76
La Roche (LR)	optimal	967	24.42	34.32 -128.37	0.97 -1.25
Vecmont (VE)	wet	989	43.16	50.78 -116.57	1.04 -1.17

^aSee description in appendix A.2.

and site effects.

2.2 Materials and methods

2.2.1 Study sites

Eight study sites were selected in Belgium, spanning a range of climate and soil conditions. Five sites are located in the Ardennes region (Table 2.1) on acid loamy soils with a high stone content but contrasting soil depth and drainage. Three other sites have soils ranging from sandy to loamy, and from excessive to insufficient drainage.

We divided the study sites into three categories of water availability (see appendix A.2 for more details).

At each site, a triplet of stands was selected: a mixed stand consisting of sessile oak and common beech and a pure forest stand of each of the two species. The three stands were selected for homogeneity in site and stand conditions. With the exception of the Ave-et-Auffe and Eupen sites, where the maximum distance between stands was 2 and 5 km, respectively (Table 2.1), all three stands within one triplet were located next to each other.

2.2.2 Stands and target trees

In each triplet we aimed for seven dominant target trees of each species in both the pure and the mixed stands. The exact number of target trees deviates slightly and is given in Table A.1 in the appendix.

Dendrometric measurements were performed in the winter of 2015-2016. We measured total height, trunk diameter and location of all trees with a circumference at breast height greater than 50 cm within an 18 m radius of each target tree (Table 2.2). On each target tree we measured at least four crown radii. For each target tree, we calculated Hegyi's competition index, ci , based on the circumference of neighbouring trees within the 18 m radius (Hegyi, 1974; Contreras, Affleck, and Chung, 2011).

$$ci = \frac{1}{C130_{target}} \sum \frac{C130_{neighbour}}{dist_{target,neighbour}}$$

where $C130_{target}$ (cm) represents the circumference of the target tree at the height of 130cm, $C130_{neighbour}$ (cm) the circumference of each neighbour at 130 cm, and $dist_{target,neighbour}$ (m) the distance from the neighbour to the target tree. For each target tree, we calculated the basal area BA_{target} (m^2ha^{-1}) of its neighbours as the sum of the basal area of each neighbouring tree (the target tree not included) divided by the area of the circle described by the 18 m radius. While each target tree was selected in either a pure or a mixed stand, the proportion of species in each target tree's neighbourhood is variable within stands. We quantified this variability using a mixing coefficient:

$$mixing = \frac{BA_{target,heterospecific}}{BA_{target}}, \quad (2.1)$$

where $BA_{target,heterospecific}$ (m^2ha^{-1}) is calculated using the same formula as the general basal area but summing over only heterospecific neighbours. We also calculated D/d as the ratio of the arithmetic mean crown diameter (m) to the trunk diameter at 130 cm height (m), a variable that reflects past competition. A summary of the dendrometric measurements is shown in Table A.2 of the appendix.

Table 2.2: Mean and ranges of stand characteristics across the eight selected triplets. Stand age is based on mean age of the cored trees in 2014. Tree number (N) and stand basal area are based on all trees within 18 m of any of the cored trees. Partial tree number and stand basal area are calculated for both species separately in the mixed stand.

Stand	Stand age (years)	N (trees ha^{-1})	Stand basal area ($m^2 ha^{-1}$)
Mixed stand		220 (139 - 286)	32.2 (24.8 - 46.2)
Oak in mixed stand	154 (113 - 213)	86 (46 - 131)	15.0 (8.2 - 23.9)
Beech in mixed stand	109 (86 - 172)	125 (79 - 155)	16.6 (12 - 22)
Pure oak stand	134 (89 - 187)	239 (180 - 313)	29.3 (22 - 39)
Pure beech stand	113 (54 - 175)	152 (102 - 234)	25.2 (16 - 30)

2.2.3 Climatic data

Grid-based daily precipitation and mean daily temperature were obtained from the RMI (Royal Meteorological Institute of Belgium). We calculated the potential evapotranspiration (PET) on a monthly basis using the Thornthwaite method (Thornthwaite, 1948). The standardized precipitation-evapotranspiration index (SPEI) was calculated using the R SPEI package (Vicente-Serrano, Beguería, and López-Moreno, 2009; Beguería and Vicente-Serrano, 2017). SPEI is a drought index that can be calculated over different time frames and represents a standardized deviation from the usual P-PET of the time frame considered.

In order to test the effect of drought on trees, we selected two different years: a drought year (2003) and a reference year without drought (2001). The main criterion for the choice of drought year was a meteorological drought occurring in summer at all sites (Fig. 2.1), based on both absolute and relative (SPEI) indices of precipitation deficit on several timescales. The reason we focused on summer is that wood formed at the beginning of the growing season is dependent on carbon that was assimilated in the previous year and temporarily stored in the tree tissues. This confounds the relationship between the climatic conditions and wood $\delta^{13}C$ (Offermann et al., 2011). Hence, we limited the isotopic measurements to latewood.

In order to select a year with summer drought and a reference year, we calculated several indices based on the P-PET from July to September: a site-specific average of P-PET over the years 1954-2015, and the corresponding SPEI-values for the years 2001 and 2003. In 2003, the three-month SPEI from July to September was below or near -1 for all sites, which we consider an indicator of drought (Table 2.1). Monthly values for P-PET were consistently negative from June to September. As reference year we selected 2001 because the complete growing season was average to wet. It is very close in time to 2003, and changes in stand structure and atmospheric isotopic composition can therefore be ignored. The year 2002 was excluded as a reference year because of the occurrence of a minor precipitation deficit.

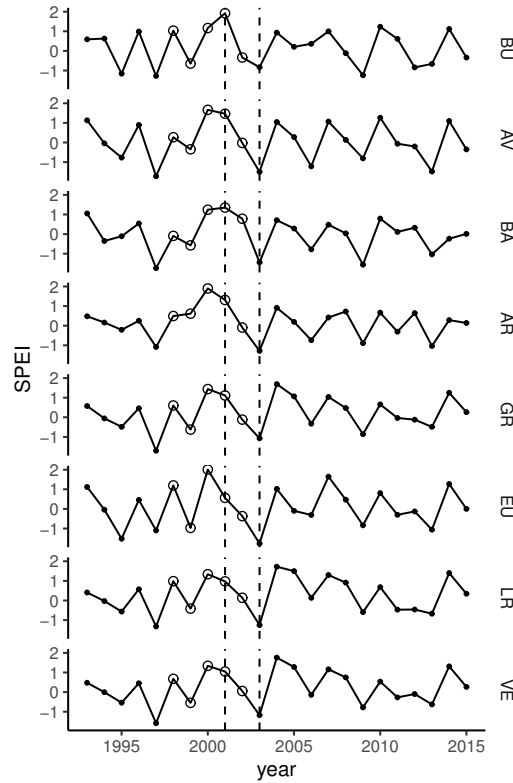


Figure 2.1: SPEI values for each site calculated during the period July-September at all sites. Vertical dashed lines represent the reference year (2001) and the drought year (2003). Open circles represent years used for calculating pre-drought growth (1998-2002). See Table 2.1 for site names.

2.2.4 Wood sampling, treatment and dendrochronological measurements

Two wood cores were obtained from each target tree at breast height (130 cm) in winter 2014-2015, using an increment borer, from the northern and eastern side of the tree towards the centre. Cores were prepared using a sliding microtome, oven-dried and scanned at high resolution. We then measured ring widths using ImageJ (Schneider, Rasband, and Eliceiri, 2012) with the ObjectJ plug-in. The measurements were cross-dated with the COFECHA software (Holmes, 1983). We averaged the results of two cores from each tree in order to obtain one ring width per tree and per year.

We then calculated for each tree the pre-drought growth (PG, $mm\ yr^{-1}$) as the average radial growth for the years 1998 to 2002. We thus obtained a general indicator of tree growth during the period under study while excluding any potential influence of the 2003 drought. From each tree, one core was chosen for isotopic measurements.

This choice was essentially random, except when the selected core was discarded for practical reasons, for example when the rings were too narrow. From the tree rings corresponding to the years 2001 and 2003, the last third was cut out with a scalpel. Wood produced at the beginning of the growing season was not used because it is dependent on photosynthates of the previous summer, which complicates the relationship with climate. The wood samples obtained were then ground, weighed and analysed by mass spectrometry. Stable carbon isotope compositions ($\delta^{13}C$) were calculated as $\left(\frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{standard}} - 1\right) * \frac{1}{1000}$. These are studied because they show a clear link with the availability of water that trees were exposed to during tree growth (Saurer, Siegenthaler, and Schweingruber, 1995).

$\delta^{13}C$ is higher (less negative) under drought conditions, and tends to be closely correlated with water-use efficiency (the ratio of carbon assimilation to transpiration), to the extent that differences in $\delta^{13}C$ can be interpreted as differences in water-use efficiency (Farquhar, Ehleringer, and Hubick, 1989). A summary of these measurements is given in Table A.3 in the appendix.

2.2.5 Statistical analysis

Pre-drought growth

We constructed linear mixed models explaining pre-drought growth of trees (1998-2002) for both species separately, using trees from both mixed and pure stands. The effect of mixing was integrated through the mixing coefficient.

$$PG_{i,j} = \alpha + \beta \cdot mixing_{i,j} + a_i + e_{i,j} \quad (2.2)$$

for tree j at site i , where α represents the intercept, β the fixed parameter corresponding to the mixing effect, a_i the random parameter corresponding to the site effect and $e_{i,j}$ the residual term. We used AIC to test for additional variables: competition index $ci_{i,j}$, crown-to-trunk diameter ratio $((D/d)_{i,j})$ and trunk circumference $C130_{i,j}$ as a substitute for tree age.

Drivers of drought exposure

For each tree we calculated the difference in $\delta^{13}C$ between the two sampled years ($\Delta\delta^{13}C = \delta^{13}C_{2003} - \delta^{13}C_{2001}$). This enabled us to distinguish between natural variation in $\delta^{13}C$ between trees and the effects of drought. $\Delta\delta^{13}C$ represents the drought exposure of a tree as the increase in $\delta^{13}C$ from the reference to the drought year, and should be positive if the 2003 summer drought is reflected in the tree's physiology and recorded in the stable carbon isotope signature. In order to test whether this is the case we constructed for each species separately a mixed model including only an intercept in $\Delta\delta^{13}C$ integrating site as a random effect. Firstly, no distinction was made between trees from pure and mixed stands.

$$\Delta\delta^{13}C_{i,j} = \alpha + a_i + e_{i,j} \quad (2.3)$$

for tree j at site i , using the same parameter names as in the previous equation.

Secondly, we tested the impact of mixing on drought exposure by adding the mixing coefficient as a fixed effect to this model.

$$\Delta\delta^{13}C_{i,j} = \alpha + \beta \cdot mixing_{i,j} + a_i + e_{i,j} \quad (2.4)$$

where β represents the fixed parameter corresponding to the mixing coefficient. The other parameter names are the same as those used in previous equations. This model was extended by adding additional fixed variables. Site-level water availability was modelled using two dummy variables dry_i and wet_i which take a value of 1 (for sites in the wet and dry categories respectively) or 0, sites in the optimal water availability category are modelled by a 0 for both variables. The other variables were $(P - PET)_i$ for long-term average P-PET, $ci_{i,j}$ for the competition index, pre-drought growth $PG_{i,j}$, trunk circumference $C130_{i,j}$ and $(D/d)_{i,j}$ for the crown-to-trunk diameter ratio. We used AIC to test for the inclusion or exclusion of each of these variables and removed any insignificant variable from the model.

$\delta^{13}C$ in reference and drought years

In order to better understand the results of the drought exposure ($\Delta\delta^{13}C$) models, we tested whether growth and mixing act on the $\delta^{13}C$ of either 2001 or 2003. Hence, for each species two models were constructed explaining $\delta^{13}C$ in 2001 and 2003, respectively.

$$\delta^{13}C_{i,j} = \alpha + \beta \cdot mixing_{i,j} + \gamma \cdot PG_{i,j} + a_i + e_{i,j} \quad (2.5)$$

where γ represents the fixed parameter corresponding to the pre-drought growth effect and the other variables are taken from previous equations. Again, we used AIC to test for the inclusion or exclusion of the fixed variables.

We assessed all mixed models for the inclusion of the fixed effects as random slopes, but likelihood ratio tests indicated that this did not improve the models.

All statistical analyses were performed in R (R Core Team, 2017) using lme4 (Bates et al., 2015), nlme (Pinheiro et al., 2017) and MuMIn (Barton, 2017) packages.

2.3 Results

2.3.1 Pre-drought growth

Pre-drought growth varied between 0.49 mm yr^{-1} and 4.21 mm yr^{-1} for oak and between 0.66 mm yr^{-1} and 5.45 mm yr^{-1} for beech with considerable differences between sites (see Table A.3 in the appendix). The pre-drought growth model resulted in a positive effect of mixing that was significant in the case of beech, but not in oak (Table 2.3). For both species, the ratio of crown diameter to stem diameter

was positively and significantly related to growth. No other fixed variables were selected for the pre-drought growth model using AIC.

Table 2.3: Model results for pre-drought growth (PG) of beech and oak. Models test for (i) mixing, (ii) the crown-to-trunk diameter ratio (D/d) and (in the case of beech) mixing. In each case, the site effect was added as a random intercept. For models (ii), variables not shown were removed from the models based on significance or AIC. Marginal R^2 (R^2_m) represents the variance explained by fixed factors, while conditional R^2 (R^2_c) represents the variance explained by both fixed and random factors (Nakagawa and Schielzeth, 2013).

	estimate	SE	Pr(> t)		
Beech					
(i)					
intercept	2.23	0.27	1.71×10^{-5}	R^2_m	0.05
mixing	0.93	0.30	0.0021	R^2_c	0.43
				AIC	299.02
(ii)					
intercept	1.72	0.29	8.44×10^{-5}	R^2_m	0.16
D/d	0.02	0.0050	1.00×10^{-5}	R^2_c	0.54
mixing	0.81	0.27	0.0035	AIC	290.07
Oak					
(i)					
intercept	1.73	0.19	5.96×10^{-6}	R^2_m	0.01
mixing	-0.29	0.19	0.13	R^2_c	0.47
				AIC	204.91
(ii)					
intercept	0.86	0.33	0.012	R^2_m	0.05
D/d	0.04	0.015	0.010	R^2_c	0.44
				AIC	201.53

2.3.2 Drought exposure

For both species, the simple intercept model yielded a significantly positive $\Delta\delta^{13}C$ (Table 2.4 [i]), which indicates an overall effect of the summer drought of 2003. While $\Delta\delta^{13}C$ values were on average positive (Fig. 2.2), there was a large variability in $\Delta\delta^{13}C$ among trees of both species, with values ranging from -1.24‰ to 1.76‰ for oak, and from -0.98‰ and 3.28‰ for beech (Fig. 2.2). For the Ave-et-Auffe site, $\Delta\delta^{13}C$ was negative on average (Table A.3 in the appendix), though not significantly different from 0 ($p = 0.38$ using a t-test on pooled $\Delta\delta^{13}C$ values for both species). For beech, mixing had a significantly positive effect on $\Delta\delta^{13}C$, which means beech trees were more exposed to the 2003 drought when growing in mixtures; for oak, there was no effect of mixing (Table 2.4 [ii]).

The addition of other explanatory variables in these statistical models resulted for beech in three distinct models that were comparable in AIC. One includes only a mixing effect, the second only pre-drought growth (mean ring width 1998-2002) and

the third contains both effects together. While effects of both pre-drought growth and mixing were significantly positive when used separately (Table 2.4, Fig. 2.3b, c), mixing lost its significance in the model when these two variables were combined. Pre-drought growth explained $\Delta\delta^{13}C$ better in beech than mixing (in terms of R^2m). The combined model barely explained more variation than pre-drought growth alone. We verified that pre-drought growth captures within-site variability in growth, and not variability among sites (appendix A.9). Minimizing the AIC of the drought exposure model for oak resulted in a simple intercept model without any fixed variables (Table 2.4). Unlike in beech, neither mixing nor pre-drought growth was clearly related to $\Delta\delta^{13}C$ in oak (Table 2.4, Fig. 2.4). For neither species, substituting the mixing coefficient with a binary stand variable (pure versus mixed) improved the drought exposure model.

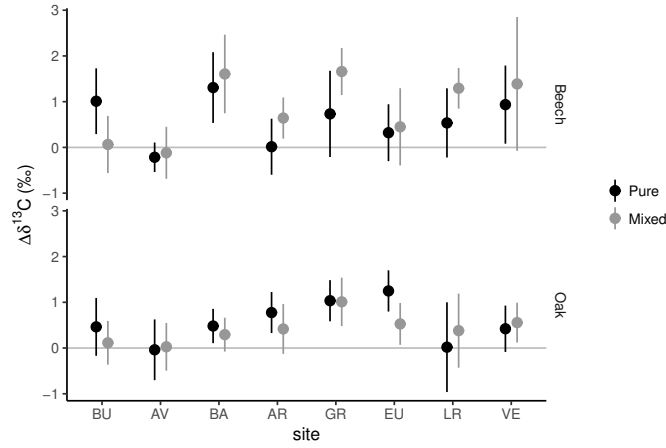


Figure 2.2: Mean and standard deviations of tree drought exposure ($\Delta\delta^{13}C = \delta^{13}C_{2003} - \delta^{13}C_{2001}$) values grouped by species, site and stand. See Table 2.1 for site names.

Table 2.4: Model results for drought exposure ($\Delta\delta^{13}C$) of beech and oak. The models tested for (i) intercept, (ii) mixing, (iii) pre-drought growth (PG) and (iv) both mixing and pre-drought growth. In each case, the site effect was added as a random intercept. For models (iii) and (iv), variables not shown were removed from the models based on significance or AIC (no significant models for oak). Marginal R^2 (R^2m) represents the variance explained by fixed factors, while conditional R^2 (R^2c) represents the variance explained by both fixed and random factors (Nakagawa and Schielzeth, 2013).

Beech					
(i)	est.	SE	Pr(> t)		
intercept	0.73	0.19	3×10^{-4}	R^2m	0
				R^2c	0.28
				AIC	283.35
(ii)					
intercept	0.54	0.22	0.035	R^2m	0.03
mixing	0.59	0.28	0.034	R^2c	0.34
				AIC	281.62
(iii)					
intercept	0.16	0.29	0.57	R^2m	0.06
PG	0.22	0.08	0.0090	R^2c	0.34
				AIC	281.56
(iv)					
intercept	0.12	0.29	0.67	R^2m	0.07
mixing	0.44	0.28	0.14	R^2c	0.37
PG	0.19	0.087	0.034	AIC	282.11
Oak					
(i)	est.	SE	Pr(> t)		
intercept	0.49	0.12	2×10^{-4}	R^2m	0
				R^2c	0.22
				AIC	214.87
(ii)					
intercept	0.58	0.14	0.0012	R^2m	0.01
mixing	-0.26	0.21	0.21	R^2c	0.23
				AIC	216.59

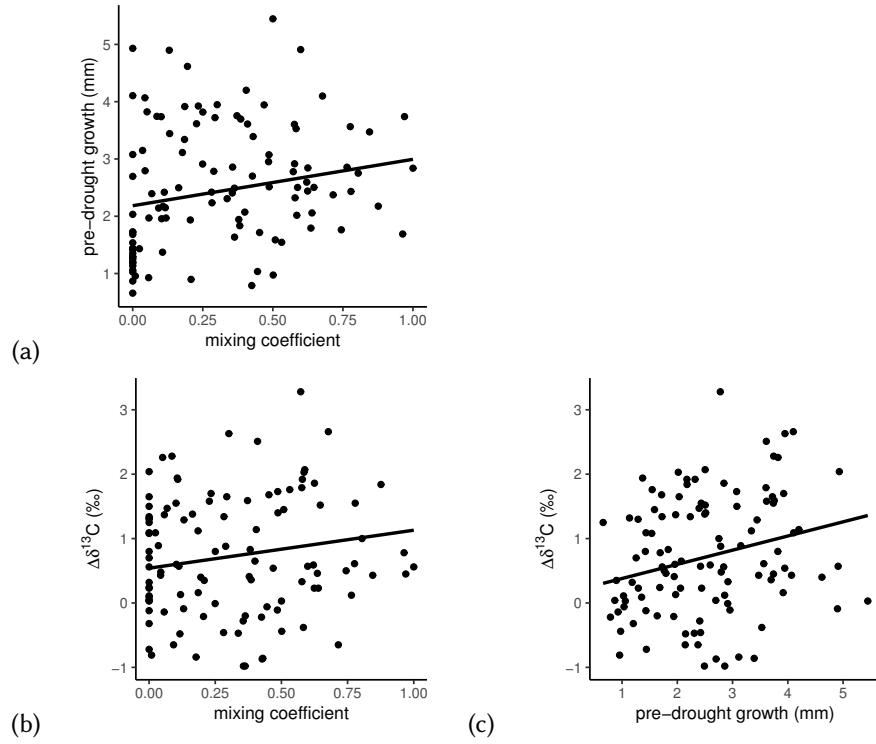


Figure 2.3: Relationships between $\Delta\delta^{13}C$, mixing and pre-drought growth for beech, across all sites. Solid lines represent values predicted by the linear models documented in Tables 2.3 (ii) and 2.4 (ii and iii). A similar plot, grouped by site is shown in Figure A.1 in the appendix.

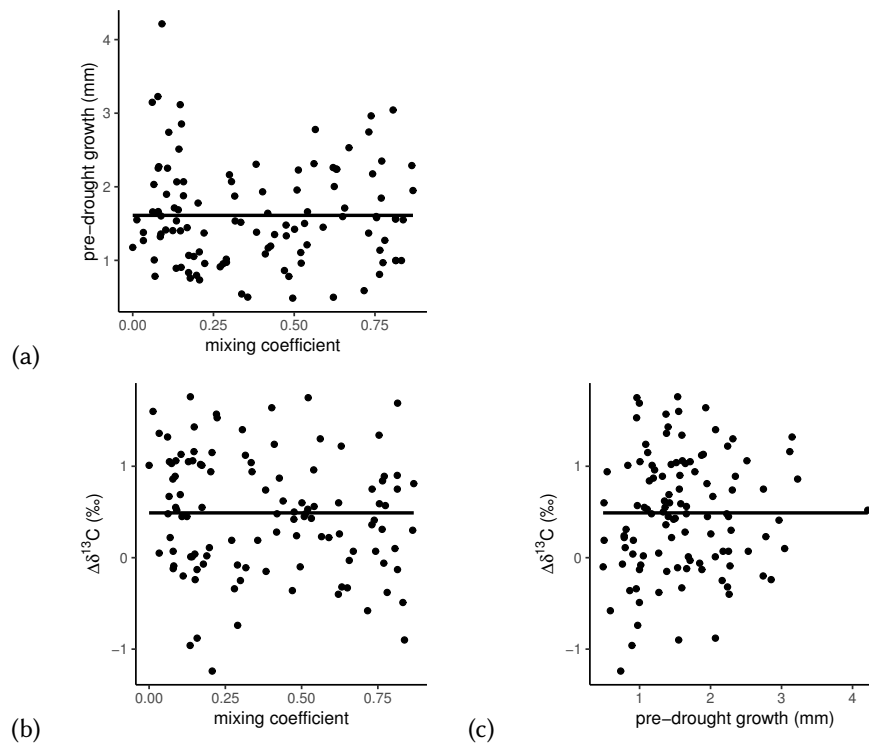


Figure 2.4: Relationships between $\Delta\delta^{13}C$, mixing and pre-drought growth for oak across all sites. Solid lines represent values predicted by the linear models documented in Tables 2.3 (ii) and 2.4 (i). A similar plot, grouped by site, is shown in Figure A.2 in the appendix.

2.3.3 Carbon isotope composition in reference and drought years

In order to better understand the observations for the beech drought exposure model, we tested whether these effects were related to an effect on $\delta^{13}C$ in either 2001 or 2003. The trends were less clear than they were for $\Delta\delta^{13}C$ and may be site-specific (Fig. 2.5). Nevertheless, $\delta^{13}C$ was negatively related to both pre-drought growth (significantly) and mixing (not significantly) in 2001, while there was no effect in the drought year (Table 2.5, Fig. 2.5).

For oak, neither mixing nor pre-drought growth had a significant effect on $\delta^{13}C$ in either 2001 or 2003 (Table A.4 in the appendix).

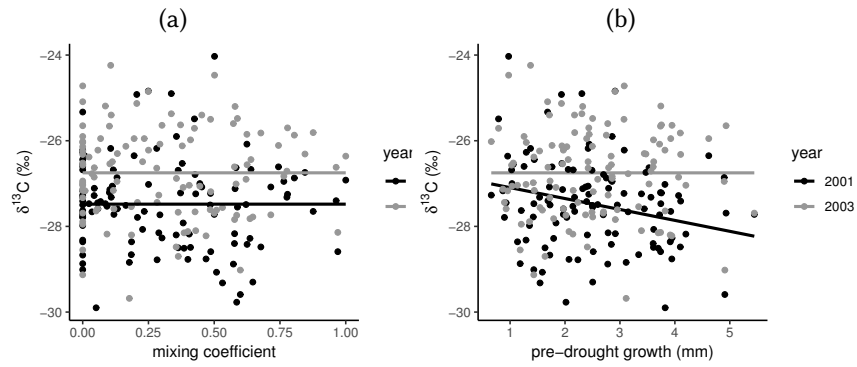


Figure 2.5: Beech $\delta^{13}\text{C}$ in 2001 and 2003 plotted against mixing (a) or pre-drought growth (b). Statistical tests are given in Table 2.5. Solid lines represent values predicted by the linear models documented in Table 5 (i and iii) for 2001 and 2003. A similar plot, grouped by site, is shown in Figure A.3 in the appendix.

Table 2.5: Model results for $\delta^{13}C$ in beech in 2001 and 2003. In addition to the intercept (i), the models test for (ii) mixing, (iii) pre-drought growth (PG) and (iv) both mixing and pre-drought growth. In each case, the site effect was added as a random intercept. Marginal R (R^2_m) represents the variance explained by fixed factors, while conditional R (R^2_c) represents the variance explained by both fixed and random factors (Nakagawa and Schielzeth, 2013). See Table A.4 in the appendix for results for *oak*.

2001					
(i)	estimate	SE	Pr(> t)	R^2_m	
intercept	-27.48	0.20	0	R^2_m	0
				R^2_c	0.23
				AIC	317.95
(ii)					
intercept	-27.29	0.24	$< 2 \times 10^{-16}$	R^2_m	0.024
mixing	-0.61	0.33	0.064	R^2_c	0.28
				AIC	316.93
(iii)					
intercept	-26.84	0.3233	$< 2 \times 10^{-16}$	R^2_m	0.06
PG	-0.255	0.09825	0.01	R^2_c	0.30
				AIC	316.19
(iv)					
intercept	-26.8	0.33	$< 2 \times 10^{-16}$	R^2_m	0.07
mixing	-0.41	0.33	0.23	R^2_c	0.31
PG	-0.22	0.10	0.033	AIC	317.07

2003					
(i)	estimate	SE	Pr(> t)	R^2_m	
intercept	-26.75	0.14	0	R^2_m	0
				R^2_c	0.080
				AIC	329.11
(ii)					
intercept	-26.74	0.18	$< 2 \times 10^{-16}$	R^2_m	5.9×10^{-5}
mixing	-0.030	0.36	0.93	R^2_c	0.080
				AIC	331.33
(iii)					
intercept	-26.7	0.30	$< 2 \times 10^{-16}$	R^2_m	5.4×10^{-4}
PG	-0.023	0.10	0.82	R^2_c	0.085
				AIC	333.79
(iv)					
intercept	-26.69	0.30	$< 2 \times 10^{-16}$	R^2_m	5.3×10^{-4}
mixing	-0.0095	0.37	0.98	R^2_c	0.085
PG	-0.022	0.11	0.84	AIC	335.93

2.4 Discussion

The increase in wood $\delta^{13}C$ from 2001 to 2003 (values were on average less negative in 2003; Table 2.4 [i]) indicates that most trees from both species adapted their physiology as expected in response to the meteorological summer drought of 2003, in both pure and mixed stands (Ehleringer and Cooper, 1988; Farquhar, Ehleringer, and Hubick, 1989). The Ave-et-Auffe site is however, an exception as both oak and beech showed lower $\delta^{13}C$ values on average in 2003 than in 2001, though not significantly so (Fig. 2.2). Several hypotheses can be put forward to explain this local pattern. First, it could indicate either that there was no summer drought in 2003, or that the reference year (2001) may have actually been dry. However the climatic data does not support either hypothesis (Fig. 2.1). The 2003 summer drought hit Ave-et-Auffe at least as much as it did the other sites, and was markedly drier than in 2001. Second, site-specific soil characteristics could explain the observed pattern. Ave-et-Auffe is indeed specific among the sites because of its superficial soil and calcareous bedrock. This, in combination with a low yearly precipitation, classifies Ave-et-Auffe as a dry site (Table 2.1). This is supported by the relatively high (less negative) values of $\delta^{13}C$ in 2001 (Table A.3 in the appendix). Even during a reference summer, trees at this site have to limit their evapotranspiration by stomatal regulation, more than at other sites. Why, then, did the precipitation deficit of 2003 not lead to extreme exposure to drought at this site? The type of calcareous bedrock found on this site is typically highly fissured and water-permeable, and roots can penetrate very deep down. We suspect that this acted as an additional water source that is only slightly affected by temporary precipitation deficits. The additional water source is not sufficient to avoid a water shortage in typical summers, but it does protect the trees against more extreme precipitation deficits. Furthermore, trees growing in drier sites build a hydraulic architecture that is adapted to deal with water shortage (Schuldt et al., 2016). This may have proven beneficial during the 2003 drought.

2.4.1 Drivers of drought exposure

Our primary objective was to investigate the effect of mixing on drought exposure ($\Delta\delta^{13}C$) and how tree growth mediates this effect. In beech, mixing enhanced pre-drought growth, while at the same time both mixing and pre-drought growth had a significant positive effect on drought exposure (Fig. 2.3). The effects of these two variables are not independent, because when both were introduced into one model, the mixing effect on drought exposure was replaced by the effect of pre-drought growth. This indicates that the positive effect of mixing on $\Delta\delta^{13}C$ in beech is essentially caused by the increased growth of beech observed in mixtures.

It is interesting to note that at the Buggenhout site, where the relationship for beech between pure and mixed stands for pre-drought growth is reversed (trees in mixtures grow more slowly), the relationship between pure and mixed stands for $\Delta\delta^{13}C$ is also reversed (trees in mixtures were less exposed to the 2003 drought, see Fig. 2.3 in the appendix). Though we don't have any clear explanation for the particular

pattern at this site, this provides additional evidence for the hypothesis that mixing influences $\Delta\delta^{13}C$ due to its impact on growth.

Differences in $\delta^{13}C$ can be interpreted as differences in water use efficiency of the trees during the two summers (Farquhar, Ehleringer, and Hubick, 1989). For beech, drought exposure ($\Delta\delta^{13}C$), and thus the increase in water-use-efficiency under drought conditions, was more pronounced as trees grew faster (Fig. 2.3c). This could suggest that fast growth led to higher water-use-efficiencies than low growth under drought conditions; however this was not the case. Instead, fast growth was associated with lower water-use-efficiencies in the reference year but not in the drought year (Fig. 2.5b). Water-use efficiency is defined as the ratio of carbon assimilation to transpiration. The observed pattern then suggests that beech trees must use more water, as they grow faster. Indeed, in reference years, the faster-growing trees showed a combination of lower water-use efficiency and higher carbon assimilation (necessary for growth) relative to slow growing beeches. Why would faster-growing trees have higher water use and lower water-use efficiency than more slowly growing ones in the reference year? Could water availability be a common driver of water use, water-use efficiency and growth? This is unlikely, as we don't expect water availability to limit growth in reference conditions, irrespective of mixing degree. Hence, this relationship requires a different explanation. At species level, fast growth is associated with a competitive strategy, which trades off against stress tolerance (Grime et al., 1997; Ouédraogo et al., 2013). Fast-growing species often use resources at a high rate, giving them a competitive edge in environments where these resources are available. Slow-growing species, on the other hand, are adapted to less productive environments and are better able to cope with resource shortages, such as droughts. Beech is more competitive than oak and grows faster, and therefore needs more resources to maintain this growth. We assume that those beech trees that benefit from higher resource availability adapt their structure and functioning to assimilate resources more quickly. Wood anatomical traits associated with efficient water transport have been found to be more evident in faster-growing beech branches (Schuldt et al., 2016). The faster-growing beech trees in our study may thus have had higher water use in reference conditions, not necessarily because they had more soil water available, but because they developed more efficient systems for accessing it and transporting it up to the leaves. The higher drought exposure then results from these trees not being able to maintain their high water use under conditions of drought during the summer of 2003. The faster growth observed for beech in mixtures was related to higher water use, but may also indicate higher use or use efficiency of other resources (see section on selection effect versus complementarity). A high resource-using strategy is possible in mixtures, either because resources are more available, or because beech is more efficient than oak in accessing and using them. Mixed with oak, beech can, for example, benefit from lower light interception of oak crowns (Leuschner et al., 2001a; Meier and Leuschner, 2008). Regarding nutrient acquisition, beech could benefit from its tendency to dominate the most superficial soil layer when mixed with oak (Leuschner et al., 2001b; Zapater et al., 2011). Positive mixing effects on growth in reference conditions seem to have the drawback that trees are less adapted to dealing with water deficits and are thus less resistant to drought. Ammer (2019) points out a possible adverse effect of higher productivity in mixtures, i.e. that this can lead to increased transpiration.

This relationship was found in young forest plantations in Panama by Kunert et al. (2012), who observed higher growth, more sapwood and higher stand transpiration with increasing species diversity. If, under reference conditions, increased growth in mixed stands is related to increased water usage, then this can be expected to affect water relations during drought as well. Some authors argue that, as a result of higher transpiration, water resources are more quickly depleted when droughts build up (e.g. Verheyen et al., 2008). This was observed in grasslands, for instance, where evapotranspiration was higher in diverse than in monospecific grasslands. Yet this pattern was not observed under drought conditions, because the higher water use of biodiverse grasslands caused faster depletion of the water reserves. Higher drought exposure ($\Delta\delta^{13}C$) of mixed forest stands, linked with faster tree growth, has also been observed by Grossiord et al. (2014b). Contrary to our findings, this resulted from a positive relationship between growth and $\delta^{13}C$ in the drought year, which could indicate that the trees in mixtures had less water available than those in monocultures under drought conditions, because their faster growth prior to the drought was linked with faster depletion of the water reserves. Forrester (2015) also observed higher water use, in combination with higher water-use efficiency for trees in mixtures, but only for the subset of individual trees that grew faster due to mixing. Since, in our case, we did not observe higher $\delta^{13}C$ for fast-growing beech trees, we cannot conclude that under drought conditions, the faster-growing trees had less water available (per unit of carbon assimilated) than the more slowly growing ones. There is thus no evidence for faster depletion of the water reserves (Fig. 2.5). However, for beech, fast-growing trees had to reduce their water use during drought more so than did trees that grew more slowly, which means they were not able to maintain their higher water consumption under conditions of drought. We do not have the necessary data to assess whether or not beech trees halted their growth during the peak of the summer drought of 2003, but this may have been the case (van der Werf, Sass-Klaassen, and Mohren, 2007). If so, no more carbon allocation has taken place and further drought is undetected by $\delta^{13}C$ measurements in the tree rings. The lack of significant difference in $\delta^{13}C$ between trees that differ in degree of mixing or pre-drought growth could indicate that trees reached a common site-specific threshold above which they were no longer able to allow photosynthesis by regulating water use.

We did not find a similar mechanism in oak. We hypothesized that oak growth would decrease due to mixing which, however, was not the case (Fig. 2.4a). Hence, we are not able to test the hypothesis that as a consequence of a lower growth, the oaks would be less exposed to the drought in mixture. While not universal, a lack of mixing effects on $\delta^{13}C$ has previously been reported for sessile oak specifically (Bonal et al., 2017) and in mixtures in general (Grossiord et al., 2014a; Forrester et al., 2016). This does not rule out that tree growth mediates the mixing effect on drought exposure, since we found no mixture effect on oak growth (Fig 2.3). Although a tendency towards increasing drought exposure with higher pre-drought growth was observed at some sites (Fig. A.2 in the appendix), this was not statistically significant on average (Fig. 2.4c). The lack of significance might be explained by the range in pre-drought growth, which was smaller for oak (Fig. 2.4c) than for beech (Fig. 2.3c). Conservative but stable growth can be an adaptation to water stress (Ouédraogo et al., 2013). Compared with beech, sessile oak combines lower growth (see, for

example, the growth of pure stands in Figures 3a and 4a) with higher tolerance to drought stress. Another hypothesis for the absence of mixing effects may be the fact that we sampled dominant oaks in mature forests, which minimizes the effects of beech domination on oak in the dataset. This could explain why oak was not affected by the presence of beech in the vicinity, either in its growth or in its exposure to drought.

2.4.2 Selection effect versus complementarity

Loreau and Hector (2001) consider two types of mechanisms between species in mixed forests: selection and complementarity. The results of this study are compatible with the selection effect, which implies that the fastest-growing species in pure stands (beech) benefits most from the mixture in terms of growth. This is linked with the competitiveness of beech. Its shade tolerance, together with its ability to grow faster and higher, is responsible for its ability to invade pure oak forests and to become dominant (Hein and Dhôte, 2006). Mixing has also been observed to increase beech growth with different admixed species (for example del Río, Condés, and Pretzsch, 2014). This does not mean, however, that complementary interactions do not play any role. The combination of a shade-tolerant and a heliophilous species can lead to more efficient use of available light (Forrester, 2014), which would especially benefit the shade-tolerant beech. Such complementarity could explain why the increase in beech growth due to mixing is not compensated for by a decrease in oak growth, as we would have expected. On the other hand, the negative effects of beech on oak may be minimized by the oak selection criteria used in this study, as previously stated (dominant oaks in mature forests). The increased water use of beech due to mixing in reference conditions (as evidenced by increased pre-drought growth in combination with lower water-use efficiency) did not affect oak $\delta^{13}C$, probably because water was sufficiently available and beech did not reduce it below oak demand. Complementarity could improve water relations during droughts, though we did not observe this for either oak or beech. Hydraulic lift (Moreira et al., 2003) probably plays no role at most of our study sites because many have shallow soils and lack a water table, but vertical stratification of the roots in mixtures could still improve the exploitation of the soil and ease competition for water in mixtures during drought. However, complementarity for water appears to have been too weak to significantly affect water relations. Alternatively, high water use by beech trees preceding the precipitation deficit could have contributed to the soil drought, cancelling out any effects of complementarity in water use between oak and beech.

2.4.3 Conclusions and implications for forest management

Mixing species is often advocated as a strategy to mitigate the negative effects of climate change (Jactel et al., 2009). There may be benefits in terms of performance and drought resistance, although this varies according to species combination and site (Ammer, 2019). In our case, we observed faster growth for beech trees in mixtures, but this resulted in higher drought exposure during a severe drought. The

fact that the $\delta^{13}C$ during the 2003 drought was not higher in mixtures than in pure stands suggests that the trees in mixtures shift to a functioning similar to that in pure stands. However, it is not clear whether this would still be the case under more extreme and/or more frequent droughts, as are expected in the future. While managing forests towards greater productivity may reduce risk exposure due to shorter rotation times, faster growth could also increase drought sensitivity, leaving the forest more vulnerable overall when shifting to a climate with recurrent drought events. In the absence of any water limitation, trees may indeed optimize their structure towards faster growth by, for example, increasing their above- to below-ground ratio, which could in turn put them at higher risk under conditions of reduced water availability. Any possible complementarity for water that could have benefited beech in this mixture seems to have played at most only a minor role during the 2003 drought. Our results thus emphasize the need for managers to consider whether for a combination of species, there is a complementarity for water that acts during drought and whether complementary mechanisms in non-drought conditions could hinder the ability of those trees to withstand droughts.

Chapter 3

Shifts in dominance and complementarity between sessile oak and beech along ecological gradients.

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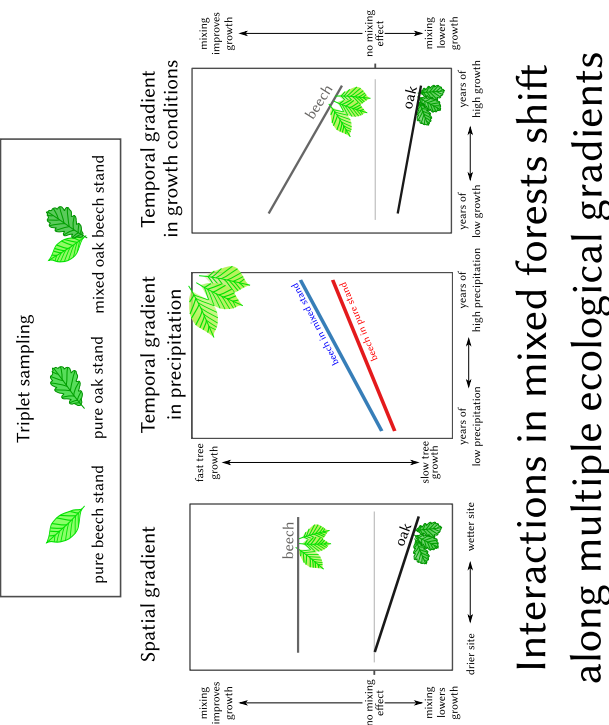


Figure 3.1: Graphical abstract of chapter 3

Abstract

1. Whether tree species benefit from growing in a mixed forest depends on the relative importance of positive versus negative interactions, which varies according to abiotic conditions. In mixture with sessile oak (*Quercus petraea* (Matt.) Liebl.), European beech (*Fagus sylvatica* L.) is often competitively dominant. Sessile oak, however, is more resistant to water deficit stress. Under water-limiting conditions, facilitation or even competition exerted by oak may gain in importance.
2. We investigated the relative importance of dominance and complementarity in 7 triplets of pure and mixed forests in Belgium's temperate oceanic climate. We analysed ring width data of 145 oaks and 138 beech trees along three distinct gradients: a spatial (i) and a temporal (ii) water availability gradient and a temporal gradient in growing conditions (iii). Gradient (ii) was represented by a precipitation variable, obtained by defining a large set of candidate climate variables over variable time frames, narrowed down using a species and site-specific lasso model. Growing conditions on a temporal gradient (iii) were represented by standardized tree growth. Two sets of linear mixed-effects models were used. Growth models assess mixing effects on ring width along gradients (i) and (ii). Mixing index models test for all three gradients how they affect the relative difference in average ring width of trees in mixed and pure stands.
3. Beech trees grew faster than oak trees, and mixing further increased beech growth while decreasing oak growth, except on drier sites where the negative effect on oak growth disappeared. Low precipitation years, in contrast, reduced the beneficial effect of mixing on beech. In years of low growth, the positive mixing effect on beech growth was reinforced, and the negative mixing effect on oak growth decreased.
4. **Synthesis** Mixing buffered against growth limitations in general, though this depends on the nature of the limitation and the gradient over which it is measured. On dry sites, competitive dominance of beech was replaced by higher complementarity between species. During dry years, however, oak did not profit from a decreased mixing benefit of beech.

3.1 Introduction

Patterns of dominance and complementarity among tree species are to a large extent shaped by interactions among species, which on their turn depend on species-specific functional traits and on the abiotic environment (Forrester and Bauhus, 2016). Consequently, climate change is expected to lead to shifts in species interactions and to modified forest dynamics (Ammer, 2019). Such interactions can be either synergistic (facilitation) or antagonistic (competition) and tree growth patterns are widely used to study the net outcome of species interactions, at least those

interactions that modify the partitioning and allocation of resources (Pretzsch, Forrester, and Rötzer, 2015). Yet, mechanisms that lead to increased and decreased growth in mixing usually occur together and remain difficult to disentangle (Callaway and Walker, 1997; Larocque et al., 2013). With respect to mixing effects on growth, a distinction is made between the complementarity and selection effects (Loreau, 2000). Under species complementarity, we understand that the community is able to increase its growth as a result of increased resource uptake or use efficiency due to mixing (Forrester and Bauhus, 2016). Complementarity can arise from positive interactions among species (facilitation), or from the relaxation of negative interactions (competition reduction Reiss et al., 2009). The selection effect occurs when the increased growth due to mixing is not distributed over the constituent species in an even manner, but according to their specific ecology and traits. Effects of complementarity and selection can occur at the same time, yet careful assessment of mixing effects on growth can distinguish between these two effects (Loreau and Hector, 2001). Fox (2005) argues that the selection effect (*sensu* Loreau and Hector, 2001) should further be partitioned into trait-dependent complementarity and a dominance effect. While for trait-dependent complementarity, one species profits without affecting the growth of the other, the dominance effect, which we will call here “competitive dominance”, occurs when species with specific traits dominate the mixture at the expense of others. When considering growth as the response, this means that the mixing effect is related to the growth of those species in pure stands. This relation may be positive (when faster growing species benefit from mixing at the expense of those growing more slowly) or negative (when slower growing species benefit from mixing at the expense of those growing faster).

Tree species mixing is frequently proposed as a management tool to increase not only growth, but also the resistance and resilience of forests to global change (Ammer, 2017; Bauhus, Forrester, and Pretzsch, 2017). However, the available studies report contrasting results regarding the impact of mixing on the buffering of adverse effects such as droughts (see Forrester and Bauhus, 2016 for a review). In this regard, the stress gradient hypothesis, proposed by Bertness and Callaway (1994) has been influential. This hypothesis predicts that facilitative interactions among species are higher in ecosystems of low productivity. In ecosystems of higher productivity, the dynamics is then expected to be mainly dominated by competitive interactions.

As the stress gradient hypothesis is not unequivocally supported in mixed forests, Forrester and Bauhus (2016) proposed a refined framework focused towards forests and applicable at both spatial and temporal scales. It predicts variation in complementarity along spatial and temporal gradients in resource availability and climate. The framework’s hypothesis is that complementarity increases with a declining availability of a specific resource, provided that species interactions improve the availability, uptake or use efficiency of that resource. The direction and magnitude of the net mixing effect appear thus to be highly context-dependent as they result from (i) the local or current growing conditions, (ii) the peculiar combination of species traits, and (iii) the impacts that both growing conditions and interspecific interactions have on the expression of the species traits.

The mixture of European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) is usually characterized by a dominance of beech. Many authors have noted a competitive dominance of beech on oak (von Lüpke, 1998; Leuschner et al., 2001b; Hein and Dhôte, 2006). Responsible for this pattern is on the one hand a higher competitive power of beech and on the other hand a higher sensitivity to competition of oak. Beech grows faster and is more tolerant for shade, while sessile oak is known to have a higher tolerance for water deficit stress (Leuschner et al., 2001a; Friedrichs et al., 2009; Scharnweber et al., 2011; Vanhellemont et al., 2019) and a higher sensitivity to low light conditions (Eaton et al., 2016). Maintaining mixed forests of oak and beech, often requires intensive management to prevent oak to be outcompeted by beech (Petritan et al., 2014). If, however, under climate change, droughts become more prevalent, beech may become less competitive (Scharnweber et al., 2011), and the patterns of dominance may shift in favour of oak (Bontemps et al., 2012; Cavin et al., 2013; Mette et al., 2013).

While sessile oak is a native tree species in Western Europe, historical management in favour of oak, rather than natural dynamics has led to its current distribution (Strandberg, Kristiansen, and Tybirk, 2005; Ningre and Doussot, 1993; Vandekerckhove et al., 2016; Mölder, Meyer, and Nagel, 2019). Many of the sessile oak forests remaining today are naturally evolving towards pure beech forests, only delayed by management actions focused on preserving oak. Under climate change, water availability is expected to become much more important as a limiting factor for tree growth. As a result, the balance could shift towards a natural dominance of oak on some sites. It is not clear whether the management practice of species mixing will protect the drought sensitive beech from the most severe droughts, or whether beech will in fact suffer from an increased competitiveness of the more drought-resistant sessile oak.

The objective of this paper is to analyse how mixing effects change along spatial and temporal gradients of growing conditions, with an emphasis on water availability, using a network of triplets spanning a range of environmental conditions. We consider the mixture between European beech and sessile oak as those two species frequently co-occur in low to mid-elevation forests of Western and Central Europe. We focus on a region where the current climate is favourable to beech dominance, but where the patterns of complementarity and dominance may change along variation in soil conditions and yearly precipitation, and possibly shift under climate change.

More specifically, we want to answer two research questions: (1) how does mixing of sessile oak and beech affect the growth of both species? and (2) is this mixing effect influenced by site water availability, or interannual variations in growing conditions, particularly in rainfall?

This leads to the following three hypotheses.

1. On moderately humid sites and in years with average growing conditions, beech will be competitively dominant over oak, leading to an increased growth of beech and a decreased growth of oak in mixed compared to pure stands.

2. Under drier conditions (on a temporal or spatial gradient) or in less productive years, complementarity between species will increase, and competitive dominance of beech will become less important.
3. Under drier conditions (on a temporal or spatial gradient) or in less productive years, competitive dominance will shift to oak.

We assessed the impact of mixing on growth over a range of conditions following two complementary approaches. The first approach tests whether mixing affected the climate-growth relationship, using multi-level regression models. We test how interactions between stand composition (pure versus mixed) and site-specific climatic drivers impact radial growth of each component species. Because growth does not respond to exactly the same drivers on different sites, we use lasso models (Tibshirani, 1996) in order to summarize variation in precipitation into one site-specific variable that best explains growth. In a second approach we create an index that represents the mixing effect on growth and assessed drivers behind this effect. This allows us to detect mixing effects without relying on a climate-growth relationship. In contrast to the first approach, where growth is the response variable, we can now use growth (detrended and averaged over both species) as an explanatory variable representing temporal changes in growing conditions. This way, we can test whether unspecified environmental constraints impact the interactions and dominance patterns in mixtures.

3.2 Materials and methods

3.2.1 Study sites

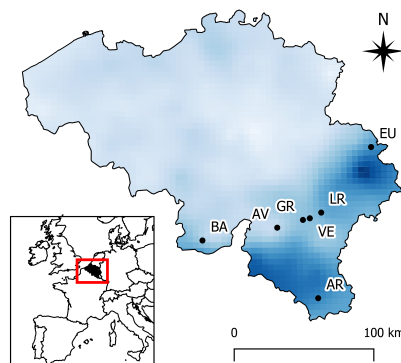


Figure 3.2: Location of the study sites in Belgium and western Europe, plotted against mean yearly precipitation (1980-2016, Delvaux, Journée, and Bertrand 2015) ranging from 731 mm (white) to 1378 mm (dark blue).

Table 3.1: Site characteristics of the 7 triplets.

	Lat. and long.	Ecoregion	Altitude (m)	Soil type (WRB, 2014)	Soil water	Mean yearly	Mean yearly	Ellenberg quotient
					availability ranking ¹	precipitation 1954-2015 (mm)	temperature 1954-2015 (°C)	
Ave-et-Auffe (AV) ²	50° 06' 9" N; 5° 08' 56" E 50° 7' 3" N; 5° 7' 44" E	Castellane	250	Calcareic Cambisol	1	865	9.0	19.6
Baileux (BA)	50° 1' 23" N; 4° 23' 59" E	Atlantic Ardenne and Ardenne basins	300	Dystic Cambisol	2	1081	8.8	15.3
Arton (AR)	49° 38' 45" N; 5° 32' 54" E	Côtes de Florenville	340	Dystic Cambisol	2	1112	8.7	15.1
Grune (GR)	50° 9' 2" N; 5° 24' 28" E	Centro-Eastern Ardenne	420	Dystic Cambisol	4	1001	8.1	15.9
Eupen (EU) ²	50° 36' 39" N; 6° 6' 30" E 50° 33' 53" N; 6° 3' 47" E	Centro-Eastern Ardenne	440	Dystic Skeletic Cambisol	5	1112	8.5	14.7
La Roche (LR)	50° 11' 45" N; 5° 35' 32" E	Centro-Eastern Ardenne	450	Dystic Cambisol	3	967	8.6	17.1
Vecmont (VE)	50° 9' 37" N; 5° 28' 37" E	Centro-Eastern Ardenne	450	Skeletal Stagnosol	6	989	8.2	16.3

¹ Expert based ranking from driest (1) to most humid (6). See appendix B. 1 for more information on the classification.
² At the sites of Ave et Auffe and Eupen, we found no suitable adjacent stands, the maximum distance between stands on these sites is 2 and 5 kilometres respectively.

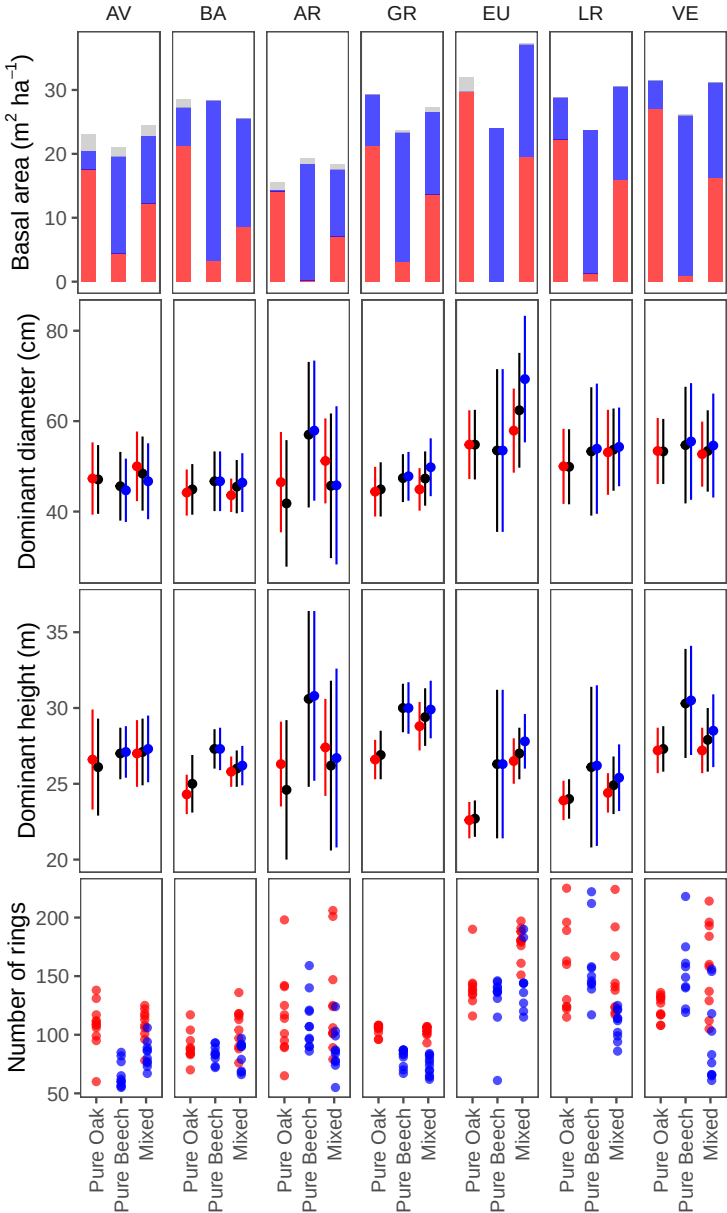


Figure 3.3: Stand characteristics for total stands (black), oak fraction (red), beech fraction (blue) and other species (grey, upper panel only). Dominant diameter (or height) is calculated as the mean diameter (or height) of the 100 largest (in diameter resp. height) trees per hectare, and is plotted together with the standard deviation around the mean. Dominant diameter and height of individual species were calculated on the subset of trees belonging to the respective species. As stands are generally uneven-aged, we report the number of rings measured on the cores as an underestimate of tree age. Stand information was collected in the winter 2015-2016, except number of rings which is based on tree cores collected during the winter 2014-2015.

We selected seven study sites in Belgium covering a range in soils and climatic conditions (table 3.1). The study sites are selected as triplets of sessile oak and beech. This means that each study site contains a pure stand of each species and a stand where both species co-occur in an intimate mixture. Within a triplet, these tree stands are selected for homogeneity in both site (soil, aspect, slope, climate) and comparability of stand characteristics (average tree height and diameter). We only selected mixed stands where both species were present in the dominant layer. Another requirement was that stands were of sufficient size so that at least 10 (in pure stands) or 20 (in mixed stands) dominant trees could be selected from the relevant species, while avoiding sampling neighbouring trees, especially when they belonged to the same species. This led to stand sizes of approximately 1 to 2 hectare (pure) and 3 to 6 ha (mixed). Sites were selected in a climate zone favourable to beech dominance (as evidenced by the Ellenberg Quotient below 20, see Table 3.1), in order to test whether variation in soil conditions and yearly weather conditions would shift the patterns of competition and complementarity between both species.

The sites were ranked according to the capacity of the soil to store and drain water based on the Belgian soil map (Bah et al., 2007). The ranking procedure follows (Weissen, Bronchart, and Piret, 1994) and is explained in appendix B.1.

3.2.2 Sampling, sample treatment, measuring, cross-dating

In total we selected 145 dominant oak trees (of which 73 in pure and 72 in mixed stands), and 138 dominant beech trees (of which 69 in pure and 69 in mixed stands). Numbers of trees per site are found in appendix B.2. Permission for sampling was granted by the Walloon forest service (Département de la Nature et des Forêts, Service Public de Wallonie – DNF, SPW). Using an increment borer, each of these trees was cored at a height of 130 cm during the winter of 2014-2015. Coring happened from both the eastern and northern side of the bark towards the pith. The obtained wood cores were cut with a microtome along the transverse plane and oven-dried at 28°C. The prepared cores were then scanned at high resolution (ranging from 1200 to 5000 dpi). Ring widths were then measured using ImageJ (Schneider, Rasband, and Eliceiri, 2012) with the ObjectJ plugin. The resulting ring width series were then cross-dated using COFECHA (Holmes, 1983). At the moment of coring we also measured the tree circumferences at the height of 130 cm.

3.2.3 Statistical analyses

We used two separate sets of statistical models to test for mixing effects on growth. Firstly, we tested whether mixing affected the climate-growth relationship, and in particular the precipitation-growth relation. Secondly, we created an index that represents the mixing effect on growth, and assessed possible drivers behind this mixing index. A summary of the models used in this study can be found in table 3.2.

Construction of climatic variables

We obtained grid based ($10 \text{ km} \times 10 \text{ km}$) meteorologic data from the Royal Meteorologic Institute of Belgium covering the time period 1954-2014. For each site, we selected the geographically closest grid point. The variables we used were daily mean temperature and daily precipitation.

In order to be able to test whether mixing influences climate-growth relationships we started by isolating climatic variables that are related with tree growth. First we defined a large set of candidate variables, from which to select from. The candidate climate variables were cumulated precipitation (P), averages of daily mean temperatures (T) and precipitation minus potential evapotranspiration (P-PET) over variable time intervals. The selected time frames start at either the 1st or the 16th of each month and span multiples of 15 days, with a maximum of 180 days. Because trees can grow using assimilates from the previous year, we included intervals from both the growth year and the preceding year. Each candidate climatic variable (a time series 1954-2014) was standardised: from each series, its mean was subtracted, and then it was divided by its standard deviation. The selection of variables was carried out by a series of lasso-models (Tibshirani, 1996). The lasso procedure allows to include a large number of intercorrelated climatic variables and avoids overfitting by a penalty (L1) on the parameter values. This performs a shrinkage of the parameters, and at the same time a selection of variables by setting some parameters to 0. As the climate-growth relationship is expected to vary among species and sites, a lasso model was constructed for each combination of species and site separately. Each model uses the complete set of candidate climatic variables corresponding to the particular site to explain tree growth in the form of the master chronology. For this, the two cross-dated ring width series per tree were first averaged into one tree series. The tree series were then detrended using a modified negative exponential followed by smoothing splines (Cook and Peters, 1981; Bunn, 2008). The master chronologies were constructed by averaging these detrended tree series per site and per species. The lambda values of the lasso model, which regulate the magnitude of the lasso shrinkage, were chosen using a 10-fold cross-validation procedure using the Glmnet R package (Friedman, Hastie, and Tibshirani, 2010). Per site and per species, this resulted in one model, and in a selection of climatic variables. In most cases, precipitation gave a better fit than P-PET. Moreover, models that contain both P-PET, T and P are complicated to interpret, so we decided to refit the models with P-PET omitted from the explanatory variables. In some cases an empty model was selected (i.e. parameter values for all candidate climatic variables were zero), in which cases we relaxed the lasso penalty until at least one variable was selected. This yielded in each case a positive relation between growth and precipitation, which was consistent with the other lasso models (see appendix B.3), and can easily be interpreted as a dependence of growth on water supply. This convinced us that relaxing the lasso penalty did not result in overfitting. On specific combinations of site and species, temperature variables were also present, as well as negative relations between growth and certain precipitation variables. From the lasso models, we selected those precipitation variables for which the corresponding parameter values were positive (at least one was selected in each lasso model), averaged them using these parameters as weighting factors, and standardized the

result. This way we constructed one variable that models the growth reaction to yearly variation in water availability for each site and species separately. We left out precipitation variables for which the corresponding parameter values were negative, because they may reflect either waterlogged conditions or conditions where rainfall is associated with conditions of low sunlight, rather than a gradient in water availability. An overview of the explicative power of these variables per site and species is given in appendix B.4. Given that this constructed precipitation variable is site-specific, when used in hierarchical models it cannot be interpreted as precipitation in a specific period. Instead, it should be interpreted as the precipitation needed for enhancing growth in the respective site.

Growth models

We tested whether the climate-growth relationships are modified by species mixing using hierarchical mixed effects models for growth (tree ring width, mm) that contain (1) long-term trends in tree growth using second degree polynomial curves based on trunk diameter and calendar year, (2) climatic variables and (3) interactions between mixing, climate and soil variables. As response variable, we used raw, undetrended dendrochronological series, to avoid removing mixing effects by detrending. Detrending is replaced by modelling long-term trends using quadratic terms for calendar year and tree diameter. These should also account for the tree age effect, for which we have no precise measurement.

For each of the two species, we constructed a linear mixed effects model explaining undetrended tree ring width, using variables at site, stand, tree and year-level. Because no reliable climatic data prior to 1954 was available for our sites, and the constructed climatic variable depends on the precipitation of both the growth year and the preceding year, we only used dendrochronological measurements starting in 1955.

We constructed a full model as follows:

$$\begin{aligned}
 RW_{i,j,k} = & s_i + s_i \times t_{i,j} + \\
 & \beta_0 + \beta_1 \cdot (year_k - 1984) + \beta_2 \cdot 1/40 \cdot (year_k - 1984)^2 + \\
 & \beta_3 \cdot D_{i,j,k} + \beta_4 \cdot 1/10 \cdot D_{i,j,k}^2 + \beta_5 \cdot mixing_{i,j} + \beta_6 \cdot prec_{i,k} + \beta_7 \cdot swrank_i + \\
 & \beta_8 \cdot mixing_{i,j} \cdot prec_{i,k} + \beta_9 \cdot prec_{i,k} \cdot swrank_i + \\
 & \beta_{10} \cdot mixing_{i,j} \cdot swrank_i + \beta_{11} \cdot swrank_i \cdot mixing_{i,j} \cdot prec_{i,k} + e_{i,j,k} \quad (3.1)
 \end{aligned}$$

where $RW_{i,j,k}$ (mm) is the ring width of tree j on site i for year k , calculated as the mean of the two ring width measurements taken per tree. The random effects, s_i and $t_{i,j}$ correspond to respectively site i and tree j on site i . Fixed variables, $year_k$ is offset at 1984. $D_{i,j,k}$ (m), tree diameter of tree j on site i before the start of the growing season k , is estimated based on the measurements of tree diameter at the time of sampling, and the measured ring widths. $year_k^2$ and $D_{i,j,k}^2$ were divided by 40 and 10 in order to avoid too large differences in scale between variables that may cause convergence problems when fitting the models. $mixing_{i,j}$ is a dummy

variable, that takes the value of 0 for pure and 1 for mixed stands. $prec_{i,k}$ represents the constructed climate variable obtained with the lasso models. Swrank is a variable that ranks sites according to the capacity of the soil to store and drain water (appendix B.1), originally ranging from 1 (driest site) to 6 (most humid site), but standardised by subtracting the mean rank and dividing by its standard deviation, in order to ease the interpretation of the model results. $e_{i,j,k}$ represents the residuals.

In order to test whether mixing influenced the tree responses to drought, we tested for the addition of the interactions between $swrank_i$, $mixing_{i,j}$ and $prec_{i,k}$. This resulted in one full model per species. These full models were then reduced, first by likelihood ratio tests to discard random effects if necessary, then by omitting fixed variables one by one, provided this decreases the AIC of the model.

Because the growth models above are built for each species separately, they do not allow for comparison between the species. In order to test whether beech grows faster than oak, whether beech has a higher sensitivity to precipitation, and whether beech benefits more from mixing than oak, we modelled growth rings for the two species together as

$$\begin{aligned}
 RW_{i,j,k} = & s_i + s_i \times t_{i,j} + \\
 & \beta_0 + \beta_1 \cdot mixing_{i,j} \cdot (year_k - 1984) + \beta_2 \cdot mixing_{i,j} \cdot \\
 & 1/40 \cdot (year_k - 1984)^2 + \\
 & \beta_3 \cdot mixing_{i,j} \cdot D_{i,j,k} + \beta_4 \cdot 1/10 \cdot D_{i,j,k}^2 + \beta_5 \cdot beech + \\
 & \beta_6 \cdot mixing_{i,j} + \beta_7 \cdot prec_{i,k} + \\
 & \beta_8 \cdot beech \cdot mixing_{i,j} + \beta_9 \cdot beech \cdot prec_{i,k} + e_{i,j,k} \quad (3.2)
 \end{aligned}$$

where the variables are same as in the other growth models, but we added a dummy variable *beech* that takes 1 for rings of beech, and 0 for rings of oak. The long-term trends are modelled in the same way as in the species-specific growth models, with separate parameter values for each species.

Mixing index models

In a second approach, we define a mixing index

$$\frac{M_{i,k} - P_{i,k}}{M_{i,k} + P_{i,k}} \quad (3.3)$$

where, for a given species, $M_{i,k}$ is calculated as the average ring width of all trees from the mixed stand of site i in year k . $P_{i,k}$, accordingly is defined as the average ring width of all trees from the pure stand of site i in year k . Subtracting the mean growth of the pure stand from that of the mixed stand allows us to extract the effect of mixing on tree growth. This value is divided by the sum, thereby removing the variability caused by years and sites with different growth rates.

For each species separately, this index was modelled as:

$$\begin{aligned} \frac{M_{i,k} - P_{i,k}}{M_{i,k} + P_{i,k}} = & s_i + y_{1,i} \cdot (k - 1984) + y_{2,i} \cdot (k - 1984)^2 / 40 + \\ & \beta_0 + \beta_1 \cdot (M_{det,i,k} + P_{det,i,k}) + \beta_2 \cdot swrank_i + \\ & \beta_3 \cdot (M_{det,i,k} + P_{det,i,k}) \cdot swrank_i + e_{i,k} \end{aligned} \quad (3.4)$$

for site i in year k , where $swrank_i$ is the same standardised variable as in the previous models. We used detrended growth to represent environmental conditions, i.e. deviations from the trend are indicators of temporarily beneficial or unbeneficial growing conditions. Tree series (average of two cross-dated ring width series per tree) were detrended using the approach explained earlier, and centred around 0 by subtracting 1 from each series. The resulting ring width indices were then averaged per species, site, year and stand, and finally averaged over the two species, resulting in two variables: $M_{det,i,k}$ for the averages of all ring width indices on site i for year k in the mixed stand, and $P_{det,i,k}$ accordingly for the pure stand. The mixing index may be biased by divergent long term trends between pure and mixed stands. We account for this bias by modelling year as a quadratic function, using random slopes with parameters $y_{1,i}$ and $y_{2,i}$. $year_k$ was offset at 1984 (central within the measurements) in order to be able to interpret the intercept. For numerical accuracy, the $year_k^2$ was divided by 10.

These full models were then reduced using likelihood ratio tests and AIC, using the same approach as in the growth models. Afterwards, we fitted the model again, but we substituted the species-specific constructed precipitation variable $prec_{i,k}$ for the effect of $(M_{det,i,k} + P_{det,i,k})$, in order to test whether precipitation is in part responsible for the effect of growing conditions on the mixing index.

An overview of the different models with the main response variables is found in table 3.2. All analyses were performed using R (R Core Team, 2017) with packages ciTools (Haman and Avery, 2020) dplR (Bunn, 2008), ggplot2 (Wickham, 2016), Glmnet (Friedman, Hastie, and Tibshirani, 2010), lme4 (Bates et al., 2015), lmerTest (Kuznetsova, Brockhoff, and Christensen, 2017), MuMIn (Barton, 2017).

3.3 Results

3.3.1 Lasso models

The lasso selected both temperature and precipitation variables, both in positive and negative relation with ring width. Common between all lasso models was the positive relationship between spring precipitation and ring width. Results of the lasso-procedure are given in detail in appendices. See appendix B.4 for the variability of detrended growth explained by the lasso models, and appendix B.3 for lists of candidate variables retained.

Table 3.2: Summary of the models used in this study. The climatic variable (precipitation) is the output of the lasso models and is further used as regressor in the two other models.

Model	Number of models	Model type	Response variable	Main regressors
Climate variable	One per site and per species	lasso model	master chronology (based on detrended ring widths)	candidate variables
Growth model	One per species, one for both species together	mixed model	ring width (raw undetrended)	- climate variable (precipitation) - mixing - site water availability (swrank) - long term trends: year, tree diameter
Mixing index model	One per species	mixed model	mixing index $\frac{M_{t,k} - P_{t,k}}{M_{t,k} + P_{t,k}}$ (based on undetrended ring width series)	- $M_{det} + P_{det}$ based on detr. ring width series - site water availability (swrank) - climate variable (precipitation)

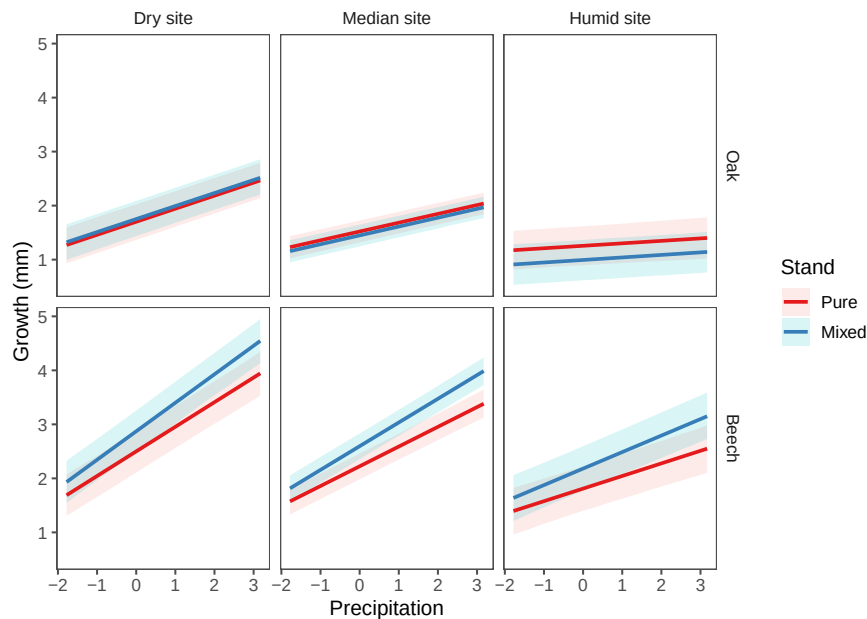


Figure 3.4: Predictions of the growth models using fixed effects only, representing the relationships between growth (ring width) and precipitation (constructed variable) at yearly resolution for both oak and beech in pure versus mixed stands. Random parameters were set to 0, fixed variables not shown were set to their average value. Three different levels of site water availability are presented, corresponding to the driest, the median and the most humid site. Shaded areas represent 95% confidence intervals for the fixed effects in pure and mixed stands. See appendix B.10 for significances of mixing effects.

3.3.2 Growth models

For both species, a growth model was constructed. No random effect or slope was dropped based on likelihood ratio tests in both the model for beech or oak (model results can be found in appendix B.10).

Growth tended to be higher on drier sites, though this effect was not significant. In general, beech growth was higher in mixed stands than in corresponding pure stands ($p < 10^{-4}$), while for oak there was no general trend. The effect of mixing on oak growth varied from nearly non-existent on dry sites to negative on humid sites ($p = 0.044$, Fig. 3.4). Growth of both oak and beech responded positively to increased precipitation, expressed as the constructed precipitation variable ($p < 10^{-4}$). This sensitivity of growth to precipitation was lower in humid sites, for both species ($p < 10^{-4}$). The sensitivity of beech growth to precipitation was higher in mixed than in pure stands ($p = 0.0007$).

The growth model using both species together showed that (i) beech growth was on average higher than oak growth ($p=0.0013$), (ii) the mixing effect on growth was

significantly higher for beech than for oak ($p=0.0028$) and (iii) while both oak and beech growth respond positively to precipitation, beech growth was more sensitive to precipitation than oak growth ($p < 10^{-4}$). The model results are available in appendix B.6.

3.3.3 Mixing index models

One model was constructed per species, explaining the mixing index $\frac{M_{i,k}-P_{i,k}}{M_{i,k}+P_{i,k}}$. No random effect or slope was dropped based on likelihood ratio tests in either the model of beech or of oak (model results can be found in appendix B.11). The mixing index was positive for beech throughout both the spatial and the temporal gradient, indicating that beech grows faster in mixtures compared to pure stands (Fig. 3.5). The mixing index of oak ranged from negative on humid sites to indistinguishable from 0 on the dryer sites. The slope of $(M+P)_{det}$ was negative for both species (oak: $p = 0.027$, beech: $p < 10^{-4}$). This means that the mixing effect was highest (most positive or least negative) in years of reduced growth, and lowest (least negative or most positive) in years in which growth is highest. This effect was consistent over both species and over the site gradient in water availability.

As there was a positive effect of precipitation on growth (see growth models, appendix B.10), we tested whether the effect of $(M+P)_{det}$ would be to some extent due to variations in precipitation by substituting the constructed precipitation variable for $(M+P)_{det}$, but this effect was not significant for either oak or beech (model results can be found in appendix B.11).

3.4 Discussion

3.4.1 How does mixing of sessile oak and beech affect the growth of both species?

In line with hypothesis 1, beech exhibits a competitive dominance over oak, at least under moderate conditions on the water availability and productivity gradients that were assessed. The dominance of beech does not only express itself in superior growth compared to oak (appendix B.6), but also in a positive mixing effect on growth for beech, and a negative for oak (Fig. 3.5). Both the growth models and mixing index models show this pattern, though in the growth model, the negative mixing effect in oak on moderate and humid sites is not significant (Fig. 3.4). The competitive dominance of beech was expected in Belgium's temperate oceanic climate, given previous literature highlighting the tendency of beech to dominate mixed oak-beech forests. There are previous reports of the superior growth of beech (see for example Scharnweber et al. (2011) for the mixture of *Quercus robur* with *F. sylvatica*), as well as of the competitive dominance of beech (Hein and Dhôte, 2006; Metz et al., 2016). At stand scale, Toïgo et al. (2015) observed an overyielding of beech in mixed sessile oak-beech forests, compensated by an underyielding of sessile oak. Mölder and Leuschner (2014) confirmed this growth benefit of beech mixed with several

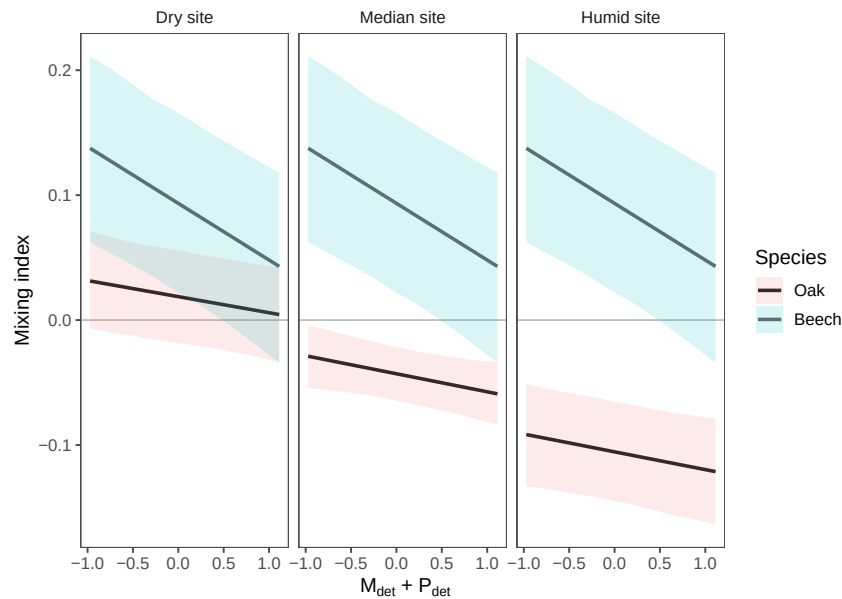


Figure 3.5: Predictions of the mixing index models (appendix B.11) using fixed effects only, representing the relationships between the mixing index and detrended growth of trees in both mixed (M_{det}) and pure (P_{det}) stands (averaged over all trees per stand and over both species). Random parameters were set to 0, fixed variables not shown were set to their average value. Three different levels of site water availability are presented, corresponding to the driest, the median and the most humid site. Shaded areas represent 95% confidence intervals for the fixed effects.

other tree species (*Tilia*, *Fraxinus* and *Acer*), but surprisingly not in those with oak (*Q. robur* and *Q. petraea*).

The fastest grower benefitting most from the mixture in terms of growth is consistent with the selection effect (*sensu* Loreau, 2000) and with the dominance effect (*sensu* Fox, 2005). This suggests that functional traits related with growth in monoculture could be responsible for the capability of beech to exert a competition onto oak. Could a more acquisitive uptake strategy of beech (Diaz et al., 2004) compared to oak be able to explain its competitive dominance? This would mean that resource uptake of beech is higher than proportional to its size, leaving less resources for competitors. The faster growth certainly suggests such a higher resource uptake (unless compensated by a lower resource use efficiency). When it comes to light, beech's more acquisitive strategy is well known, and particularly harmful to the shade intolerant oak. When it comes to belowground resources, the acquisitive nature of beech is less clear. Beech seems to be able to gain dominance belowground as well (Leuschner et al., 2001b), although oak is usually assumed to root more deeply, and thus able to access extra water sources (Zapater et al., 2011). Deep rooting should be seen as an adaptation to drought stress for oak, rather than as a way to gain dominance. First, because the mechanism is less useful when water is sufficiently

present. Second, because there is no competition between species for water in the deeper soil layers and oaks adds water to the ecosystem that would otherwise not be available to beech.

3.4.2 Is the mixing effect influenced by site water availability or interannual variations in growing conditions or in rainfall?

It is well established that environmental conditions shape mixing effects, though the mechanisms in which this happens, and the direction of the effects vary (see Forrester and Bauhus (2016) for a review). For sessile oak and beech, increased droughts could result in both a shift in dominance from beech to oak (Scharnweber et al., 2011; Cavin et al., 2013; Mette et al., 2013) or in increased complementarity in mixtures (Pretzsch et al., 2013; Sousa-Silva et al., 2018). We explored three different gradients to test for such changes in complementarity and competitive dominance (hypotheses 2 and 3), and we indeed observed shifts along these three gradients. Using ring width data, we are unable to assess tree-to-tree interactions directly, and we cannot test whether these interactions are facilitative or competitive in nature. We are, however, able to infer whether the relative importance of facilitative versus competitive interactions shift along ecological gradients. If mixing effects on growth become more positive under certain conditions, then this must stem from either increased facilitative interactions, or reduced competitive interactions.

Water availability on a spatial scale

At the spatial scale, our data confirms hypothesis 2 (a shift from competitive dominance towards complementarity). We observe the pattern of competitive dominance of beech only on average to humid sites. On the driest sites however, beech still benefits from the mixture, but no longer at the expense of oak growth. (Figs 3.4 and 3.5), this despite of the local climate which is favourable to beech dominance. We expected sessile oak to be more competitive in dry sites because it is better able to cope with drought (Leuschner et al., 2001a; Friedrichs et al., 2009; Scharnweber et al., 2011; Vanhellefont et al., 2019). Such a shift in competitiveness towards oak is evident from our data, but not to the extent that oak would gain the competitive advantage (hypothesis 3). Beech remains competitive given that it maintains its growth and manages to benefit from mixing, but as this is no longer at the expense of oak growth, it is no longer a competitive dominance. Instead, the complementarity between these two species is higher on dry sites. This means that, either facilitative interactions improve resource availability, or that niche complementarity reduces overall competition.

Following the framework of Forrester and Bauhus (2016), species interactions that improve the availability of water could lead to increased complementarity under conditions where water availability is low. If so, water related interactions could explain the higher complementarity on the driest sites. Several studies have shown that contrasting rooting patterns lead to a better soil exploration (Lei, Scherer-Lorenzen,

and Bauhus, 2012; Brassard et al., 2013; Sun et al., 2017) and even belowground overyielding, though this seems to depend on functional diversity and does not apply to all mixtures (Meinen et al., 2009; Jacob, Hertel, and Leuschner, 2013). Root stratification (Schmid and Kazda, 2001; Bolte and Villanueva, 2006), where oak roots occupy deeper soil layers than beech (Zapater et al., 2011) could lead to complementarity for water when these two species grow in mixture.

Another often-cited mechanism of facilitation related to the deeper rooting of oak is hydraulic redistribution. This requires that oak is able to access a deeper water source and leak some of that water to more superficial soil layers. While it has been shown that hydraulic redistribution can facilitate neighbouring species (Mora et al., 2003; Hafner, Hesse, and Grams, 2021), it is not certain that in oak-beech mixtures, beech actually uses water lifted by oak (Zapater et al., 2011). Our results do not provide clear evidence of a facilitative effect of oak on beech when it comes to water availability. This contrasts with the results of Pretzsch, Schütze, and Uhl (2013) who observed enhanced resistance and recovery of beech to drought in mixture with oak which could be expected if hydraulic redistribution plays a role. As many of our sites have less than 80 cm of soil available, according to the Belgian soil map (Bah et al., 2007) they may not be suitable for hydraulic lift.

Contrary to our expectation, growth (at least when expressed as ring width) was not lower on the drier sites, not even for beech, which is more sensitive to water deficit. The water limitation that trees on the driest sites face is not necessarily harsher than other limitations (e.g. nutritional) on other sites. We suspect that none of our sites is really harsh in terms of water unavailability, and that sampling a broader geographical area would yield sites where water limitation is more pronounced.

Water availability on a temporal scale

While, in general, beech grows faster in mixed versus pure stands, this mixing benefit is highest in years of high precipitation, and (to some extent) lost in the drier years (Fig 3.4). Given that we consider the general benefit of mixing on beech growth to result from a competitive dominance of beech, an increased mixing benefit in years of abundant precipitation would imply that the competitive ability of beech is stronger in those years. This is conceivable, as this species is more sensitive to drought and its radial growth reacts more strongly to precipitation (appendix B.6).

If competitive ability of beech was on its own responsible for the positive effect on beech growth, however, we would expect this to be accompanied by a negative effect on oak, which we did not observe (no significant interaction between mixing and precipitation for oak; Fig. 3.4, appendix B.10). This implies that increased complementarity must be at play as well in years of high precipitation. It appears that oak and beech can partition the water during years of high availability in such a way that beech benefits without additional cost to oak growth. This is probably related to a conservative water usage of oak, whose uptake and growth reacts less than beech to temporarily higher water availability, in either pure or mixed stands (appendix B.6). In contrast to the growth models, the mixing index models do not show a higher mixing benefit for beech in wetter years (appendix B.11). This should

probably be explained by the fact that the mixing index represents the mixing benefit (or disadvantage) relative to growth. Not only does the mixing benefit increase with higher precipitation, growth increases as well (Fig 3.4). It appears that the increase in mixing benefit is somehow proportional to the increase in growth, hence this does not affect the mixing index significantly.

We do not observe a shift from competitive dominance towards more complementarity in drier years, as predicted by hypothesis 2. This contrasts with the spatial scale, where such a shift was observed at the drier end of the gradient. It appears that interactions enhancing productivity during drought act especially on the long term, i.e. structural adaptations (such as root partitioning) while mechanisms that cope with drought on a short term, such as stomatal closure seem to play a lesser role in creating complementarities. A differential isohydric behaviour, by which beech closes its stomata earlier than oak, halting its water use and photosynthesis (see for example Scherrer, Bader, and Körner 2011) should benefit admixed oak in dry periods, but we find no evidence for such a mechanism in our data. We suspect that on wet sites, beech can adapt its crown so to capture more light, and that this comes at the expense of oak. Temporary high water availability due to higher precipitation inputs means that beech trees can make better use of their larger crowns, but the timescale of a year is too short for beech to develop structural changes that would increase its competitive dominance and affect oak growth negatively.

Growing conditions on a temporal scale

We use radial growth (detrended ring width, summed over both stands and averaged over both species) as a proxy for growing conditions. Growing conditions are thus assessed at the temporal scale and do not, as is more usual, represent site quality. Among conditions that impact growth on a yearly scale are variations in weather conditions (either directly being more or less favourable for growth, or indirectly through their effect on masting) and pathogen attack.

For both species, the mixing index is higher in low growth years than in years of high growth (Fig 3.5). This means that trees benefit more from mixing (or are less negatively affected by mixing) in harsh years, at least in relative terms. As this trend is similar for both species, the shift does not stem from a changed competitiveness pattern, but instead from a higher complementarity between species in harsher years. This indicates either that facilitation becomes more important, or that the mixture is better able to capture resources or to use them efficiently. It is remarkable that complementarity is negatively related with growth, but positively with precipitation, given that precipitation enhances growth. This is not necessarily contradictory, as the relatively higher complementarity we observe in years of reduced growth was not explained by precipitation, and was thus mostly unrelated to water availability (appendix B.11). This indicates that other factors beyond water availability must be at play in the complementarity between oak and beech. Possible candidates are diseases and pathogen attacks. Most likely, mixing protects against a variety of constraints, though our methods do not allow to investigate which in particular. Light

limitation could, for example, be alleviated in mixed stands, due to a more efficient canopy packing and differential light requirements of both species.

3.4.3 Does competitive advantage shift to oak under water limitation?

Mette et al. (2013) predict a climatic turning point where, as the climate becomes drier, oak will become more competitive than beech, and many sites where beech forests are now the climax vegetation will have a natural tendency to turn into oak forests. Such shifts towards oak dominance have been noted by other authors. Scharnweber et al. (2011), for example, observed a trend in growth superiority with declining precipitation. Bontemps et al. (2012) reported increased competitiveness of sessile oak relative to beech in terms of height growth related with increased temperatures. Our observations, however, do not support such a shift towards dominance of oak (hypothesis 3). Beech remained the faster grower, even in dry or low-productive conditions (Fig. 3.4, appendix B.6), likely due to the prevailing climate, which remains favourable for beech. Instead, we observe shifts towards a lower dominance of beech and towards more complementarity (hypothesis 2). Mixing has thus the ability to stabilize primary productivity in oak-beech forests and protect both species from harsh conditions. So, while oak dominance is possible under a changing climate, on sites that are now very favourable for beech dominance, we expect in the first place a shift towards more complementarity. This could have consequences for the dynamics of the forest ecosystem. Whereas beech dominance currently leads to a loss of oak in these mixed forests, a higher importance of complementary interactions may have a stabilising effect on species composition.

3.4.4 New approaches to assessing mixtures using tree ring widths

Several methodological issues arise when trying to investigate the outcome of species interactions in mixtures along spatial or temporal gradients. A first challenge is related to the characterization of the gradient itself.

Dendrochronological techniques have been developed to identify ecologically relevant variation in weather conditions. However, much of the variation within growth series has other origins (for example age and cutting cycles), and the climate-growth relationship is typically not very strong. Detrending techniques are often used in dendrochronological studies in order to remove unwanted variation in the growth series (Cook and Kairiūkštis, 1990). Our approach was to avoid detrending and to account for medium to long-term trends by constructing models containing polynomials that represent time and tree size (similar to, for example, Kint et al., 2012). The rationale was that detrending could remove ecologically relevant signals from the growth series, and would thus not be appropriate here. The growth models are dependent on a good representation of the climate-growth relationships on each site, hence the attention we paid to constructing appropriate climatic variables. The approach of constructing a single precipitation variable from a selection of a large

range of candidate variables using lasso models is a trade-off between several objectives. The first is to represent the climate-growth relationship as well as possible, which is challenging in Belgium's temperate climate lacking extremes in either drought or temperature. Other authors have used variable time frames to allow for more freedom in defining climate variables (Beck, Sanders, and Pofahl, 2013) and report a better representation of the climate-growth relationship (Jevšenak, 2019). The second objective is that the representation should be sufficiently simple, in order to be able to study the interactions with mixing and site-specific variables. Third, the variables used should have an ecological interpretation. No climatic variable will completely capture the precipitation-growth relationship, and the statistical model used is not able to distinguish between a low dependence of growth on precipitation and an inadequate representation of this precipitation dependence. An analysis crossing several sites is particularly challenging, as the climatic drivers on growth are site specific, mediated by the local climate, the water buffering capacity of the soil, tree-soil interactions, and tree adaptations to the local situation. A uniformly defined climatic variable would thus not necessarily allow for a good comparison among different sites. If the constructed variable explains growth better on certain sites than on others, then we can reasonably assume that this represents real differences in precipitation-growth relationships between sites, rather than an inadequate fit of the variable to some sites.

Mixing index models have as added value that they bypass the dependence on climatic growth drivers, which limits the growth models. Additionally, because growth is no longer the response variable, it can be used as a predictor, which, while not informative about the specific drivers at play, is interesting as it represents a productivity gradient beyond those related to precipitation.

3.4.5 Conclusions

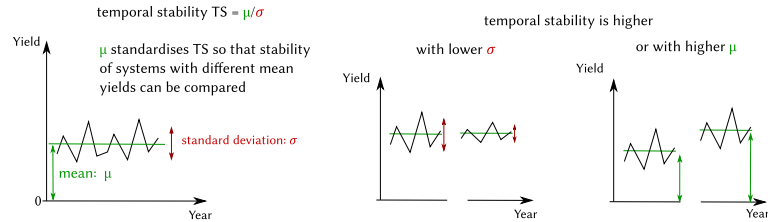
While on many sites in West and Central Europe beech is nowadays the most efficient competitor, able to outcompete other species such as sessile oak, increase in frequency and intensity of droughts under climate change can make the position of beech more vulnerable. This could be mitigated by species mixing. In our study, mixing effectively buffered against constraints, but this depends on the nature of the constraint and the gradient over which it is measured. The general tendency is that mixing increased complementarity under harsh conditions. For water availability, which we investigated in more detail, complementarity increased on dry sites, but not in dry years. Interactions between species in mixed forests can thus provide beech with a protection from droughts. On the other hand, it has been projected that, under severe drought, beech will lose its competitive dominance over oak, and beech could even suffer from an increased competitiveness of oak (Mette et al., 2013). We observed a decrease in the competitive dominance of beech on the drier sites, but not to the extent that it shifted towards domination of oak. Beech remained the fastest grower overall. In part, a natural domination of oak usually requires a failure of beech at the site, a situation that is excluded from the study by the triplet sampling strategy we used. Furthermore, it looks like in the area of study, with a relatively cool climate and evenly distributed rainfall, the drought events may so far

not have been sufficient to reverse the relationship between beech and oak.

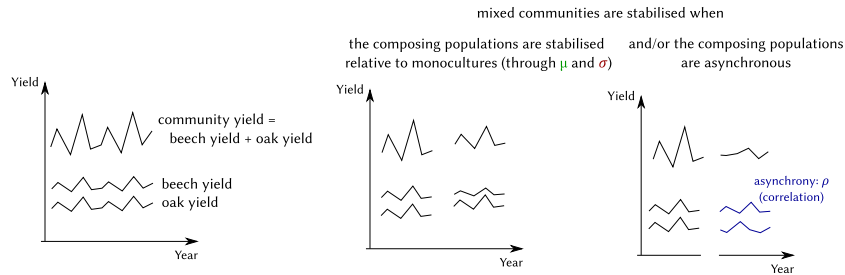
Chapter 4

Partitioning biodiversity effects on ecosystem stability into stabilisation at population level and asynchrony at community level

Yield of a population or a community is variable through time



In mixed communities, total yield is the sum of the yield of the composing populations



Mixed communities have been found to be more stable than monocultures

We quantify stabilisation relative to monocultures as τ_T

How does community stabilisation depend on μ and σ of populations, and ρ ?

We quantify this through τ_μ , τ_σ and τ_ρ so that $\tau_T = \tau_\mu \cdot \tau_\sigma \cdot \tau_\rho$

=> These variables act as pathways through which any (de)stabilising mechanism must act

Asynchrony stems from two sources

- additive asynchrony, present in monocultures ($\tau'_{\rho_{mono}}$)
- species interactions in mixed communities ($\tau'_\rho - \tau'_{\rho_{mono}}$)

Indirect effects of overyielding and asynchrony on stability

- asynchrony ρ could lead to overyielding (increased μ)
- if mixing leads to increased μ , σ may also increase naturally

Competition release in mixtures should affect stability

- through ρ : compensatory dynamics
- through μ : less overyielding under high interspecific competition
- through σ : temporal variability in competitive pressure

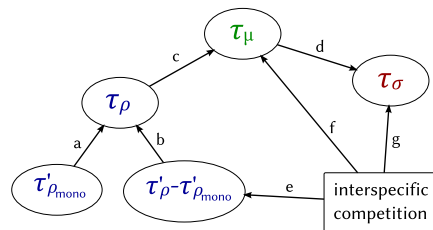


Figure 4.1: Graphical abstract of chapter 4

Abstract

1. The biodiversity-stability relationship is found to be close to universally positive, but the importance of different mechanisms behind this relationship is unresolved. Identifying and quantifying such mechanisms is complicated because causal pathways from diversity to stabilisation involve multiple ecological interactions and statistical effects acting simultaneously at multiple organisational levels (individual, population, community).
2. We propose a new method to quantify the total biodiversity effect on community stability in biodiversity experiments, and to partition this into effects acting through several pathways.
3. We distinguish between asynchrony among populations and pathways that also affect population level stability. We can further differentiate between effects of asynchrony as caused by intrinsic differences among species responses to environmental fluctuations and asynchrony caused by species interactions. Within population level (de)stabilisation, we further distinguish between the diversity effect on mean yield of populations and those on standard deviation of population yield.
4. We apply this method to a forest triplet study on sessile oak and European beech, confirming the importance of asynchrony in stabilising mixed communities. Effect through population-level stabilisation can be large, but highly variable and not consistently positive.
5. We find evidence for a signature of interspecific competition that increases the fraction of asynchrony due to species interactions, decreases oak yield and increases variability at the population level.

4.1 Introduction

Positive biodiversity-stability-relations

Concerns on the long-term functioning of ecosystems under both a climate and a biodiversity crisis raise the interest in the biodiversity-ecosystem stability relationship. An overwhelming amount of evidence has shown that biodiversity stabilises the functioning of communities in time, at least when trophic interactions can be ignored (Tilman, 1999; Ives and Carpenter, 2007; Isbell, Polley, and Wilsey, 2009; Gross et al., 2014) and focus has shifted to unraveling the underlying mechanisms (Loreau and de Mazancourt, 2013). This has proven complicated for several reasons. Biodiversity stabilises communities through both species interactions and statistical effects, with multiple stabilising and destabilising mechanisms acting simultaneously. As an example, population dynamics models have shown that interspecific competition can have a negative effect on yield stability of individual species (the population level), and at the same time a positive effect at the community level by

increasing asynchrony among species (Loreau and de Mazancourt, 2013). A number of experimental design and sampling strategies have been used to isolate biodiversity effects from confounding factors. Additionally, partitioning techniques enable separating different contributors to diversity-productivity relationships (Loreau and Hector, 2001; Fox, 2005). Distinguishing among effects of different mechanisms acting on stability, however, is an open challenge. Recent observational and experimental studies have used structural equation modeling because of its ability to assess complex causal paths from diversity to stabilisation (Morin et al., 2014; Schnabel et al., 2021; del Río et al., 2022), while theoretical modeling approaches have been complementary in identifying mechanisms that may play a role in biodiversity-stability relationships.

Stability is frequently measured as temporal stability (further called stability in this paper) $TS = \mu/\sigma$, with μ and σ mean and standard deviation of community yield over time (Tilman, 1999). Temporal stability is defined independently from any environmental driver of stability, in contrast to other measures such as engineering resilience (Lloret, Keeling, and Sala, 2011), which are defined as response to specific stresses.

4.1.1 Different hierarchical levels and asynchrony

While diversity effects on stability are virtually always positive at the community level, at population level they are often, but not always, negative (Tilman, 1996; Jiang and Pu, 2009; Hector et al., 2010; Gross et al., 2014; Xu et al., 2021). This could appear counter-intuitive, because community yield is defined as the sum of population yields. If populations are destabilised by diversity, then the community should inherit to some extent this destabilisation. In fact, if biodiversity stabilises communities, this must happen either through stabilisation of individual populations, or through species asynchrony (Thibaut and Connolly, 2013; Xu et al., 2021). When fluctuations in growth are asynchronous among different populations, species neutralise to a certain extent each other's fluctuations, thereby stabilising community productivity. On theoretical grounds, some authors have argued that a stabilising effect of asynchrony is unavoidable (Doak et al., 1998; Loreau and de Mazancourt, 2013), and empirical studies have identified asynchrony as an important stabilising factor in diverse communities (Isbell, Polley, and Wilsey, 2009; Hector et al., 2010; del Río et al., 2017). The question on how asynchrony among populations arises, however, is still under discussion (Gross et al., 2014; Tredennick et al., 2017; del Río et al., 2017; del Río et al., 2022). A first source of asynchrony consists of intrinsic differences in the way different species react to environmental fluctuations (Yachi and Loreau, 1999). While this effect is a statistical consequence and does not stem from interspecific interactions, the mechanism remains important because it buffers the productivity of communities against environmental vulnerabilities of individual species. It has been noted that if monocultures were used to calculate expected yield series as the additive effect (similar to the practice for calculating overyielding), this will be stabilised through the asynchrony among the monocultures (Jourdan et al., 2021; del Río et al., 2022). This form of asynchrony constitutes thus an additive fraction of total asynchrony. The relevance of this mechanism is

tested in studies where monocultures are paired with mixtures, because asynchrony among monocultures should reflect the intrinsic differences in species response to environmental variability. However, some authors report that asynchrony between monocultures predicts the stability of mixtures poorly (Gross et al., 2014; del Río et al., 2017), providing evidence to the importance of the second source of asynchrony, that is, species interactions (del Río et al., 2017). Interspecific competition, specifically, is often attributed with compensatory dynamics, which increases asynchrony among populations (Tilman, Lehman, and Bristow, 1998; Lehman and Tilman, 2000; Gross et al., 2014). Temporarily high yield of one population under certain environmental conditions comes with a higher competitive pressure onto other populations, which on its turn reduces their yield.

4.1.2 Competition reduction

Due to functional complementarities, competition is often lower among than within species. According to theoretical models, competition reduction should increase stability, mainly because interspecific competition is destabilising (Loreau and de Mazancourt, 2013; Wang et al., 2021). Variability in population yield is induced by the species specific growth responses to environmental variability. As competition induces a growth response, temporal variability in the functioning of competitors should likewise be a source of variability in population yield. On top of that, positive interactions among species stabilise the species composition and maintain or increase species evenness, whereas dominance of one species would lead decrease biodiversity through selection effects. Maintaining biodiversity, including the aspect of evenness, is necessary to benefit from diversity-related stabilisation (Thibaut and Connolly, 2013). To the extent that species trade off stability for performance, complementarity should also help maintaining the share of more stable species in community yield, whereas selection effects favour the best performing (Wang et al., 2021).

4.1.3 Overyielding

Overyielding is often seen as a driver of stabilisation (Hector et al., 2010; Jucker et al., 2014), although by some, both are considered to result independently from diversity (Cardinale et al., 2013; Morin et al., 2014). Overyielding occurs when the productivity of a mixed community is higher than the predicted additive effect. This is typically calculated as average of monoculture yields, weighted by the abundance of the respective species in the mixed community (Tilman, 1999). A positive effect of overyielding (increased mean yield μ) on stability is suggested by the definition of temporal stability $TS = \mu/\sigma$, in so far that increased μ is not completely compensated for by increased σ . Such compensation is to be expected as μ could be seen as a standardisation factor for σ (which represents the variability) allowing stability to be compared across large ranges of productivity, and ensuring that TS is independent of the units of measurement (Tilman, 1996). Standard deviation is too dependent on the mean in order to be useful as universal measure for temporal stability, but standardising by μ may overshoot its aim of removing that dependence, because σ

and μ do not necessarily scale linearly in ecosystems. More often, they follow Taylor's power law, by which σ does not compensate completely for increased mean yield (Taylor, Woiwod, and Perry, 1978; Kilpatrick and Ives, 2003). Demographic stochasticity is a source of variability (σ) that does not scale linearly with the mean (Anderson et al., 1982; de Mazancourt et al., 2013). If overyielding translates into a higher number of individuals, stochasticity at the individual level (recruitment, mortality, migration) becomes relatively less important.

4.1.4 Direct and indirect effects

Giving the position of mean yield (μ) in the definition of TS, overyielding must unavoidably be stabilising when considered in isolation. In reality, it is reasonable to assume that increased yield would be accompanied by increased variability (σ), through which the direct stabilising effect is at least partly neutralised. In order to assess the total effect, many authors test for a statistical relationship between overyielding and stability, rather than relying on the presence of overyielding alone (Hector et al., 2010; Cardinale et al., 2013; Morin et al., 2014; del Río et al., 2017; Jourdan et al., 2021; del Río et al., 2022). However, a statistical relationship does not guarantee a causal effect. An example is competition reduction, which could be responsible for the statistical link between overyielding and stability that is sometimes observed, if it is responsible for both (Wang et al., 2021). In a similar way, asynchrony has an unavoidable stabilising aspect (Doak et al., 1998; Loreau and de Mazancourt, 2013), but may affect stability indirectly if it drives overyielding through temporal complementarities (Allan et al., 2011; del Río et al., 2017). This means that we can distinguish between (1) direct effects of overyielding and asynchrony, which are mathematically self-evident (2) indirect effects, which stem from interactions between several components of stability and (3) more complex mechanisms that affect stability through different pathways.

4.1.5 Temporal stability in forests

In the last decades, temporal stability has been studied in forests, either in biodiversity experiment studies (Jucker et al., 2014; Schnabel et al., 2021), forest triplet studies (del Río et al., 2017; del Río et al., 2022) using forest inventories (Yuan et al., 2019) or exploratory platforms (Jing et al., 2022). Specific to forests is that they are characterised by the presence of long-lived individuals, which has consequences for the biodiversity-stability relationships. Species composition tends to evolve slowly, which may have a stabilising effect relative to ecosystems with a high turnover in individuals. Rather than studying the stability of abundance or total biomass, we study the stability of growth (increment). This also means that stability of growth in mature forests depends less on demographic variability, and more on the stability of individual trees (see e.g. Jourdan, Kunstler, and Morin, 2020), a level that is less relevant in communities of short-lived species. Literature on stability of growth in forests uses terminology consistent with community ecology, even if demographic population dynamics are considered slow and ignored. Community yield is represented by mixed stand growth, population yield by the growth of one specific species

within a stand. Monocultures are pure forest stands, thus consisting of one population.

4.1.6 Objectives

We present a method to quantify the total biodiversity effect on temporal stability of yield in biological communities based on a reference stability calculated from yield series of monocultures of the component species. We also show how the biodiversity effect can be partitioned into (1) effects acting through population-level stability, and (2) asynchrony among populations. Effects (de)stabilising through the population level must affect either mean (μ) or standard deviation (σ) of population-level yield.

We use seven triplets of sessile oak (*Quercus petraea*) and beech (*Fagus sylvatica*) as a model. Oak and beech are well-studied tree species from temperate forests that form a mixture where interspecific competition is asymmetric (benefitting beech) and context-dependent (Mette et al., 2013). In these triplets, we quantify and partition effects of species mixing on stability. Additionally, we calculate temporal stability at the individual and population levels to study the ways in which stability in mixed forests is shaped by effects within and among populations. We make use of the fact that all mechanisms acting on stability must do so through the three defined pathways, and leave a signature there. This way, we use statistical relations among the three pathways to detect signatures of temporal complementarity and interspecific competition as stabilising factors (Fig. 4.1).

4.2 Quantifying and partitioning the diversity-stability relationship

We quantify the effect of species diversity on temporal stability of yield in biological communities, based on time series of yield of the populations within the community and in comparable monocultures. We decompose this diversity effect into different pathways through which biodiversity can affect stability: asynchrony among populations (ρ), mean population yield (μ) and population yield standard deviation (σ). We start by defining observed community yield Y_O as a time series, as the sum of the observed yield of each species i ($Y_{O,i}$) in the community (because all yield variables are time series, we omit the index for time in all variables). We can now decompose the observed stability of community yield $TS_O = \mu_{Y_O} / \sigma_{Y_O}$ into quantities defined at the population level.

$$\begin{aligned}
TS_O &= \frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sigma_{Y_O}^2}} \\
&= \frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j cov(Y_{O,i}, Y_{O,j})}} \\
&= \frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}} \quad (4.1)
\end{aligned}$$

where $\rho(Y_{O,i}, Y_{O,j})$ stands for the Pearson correlation between the observed yield for species i and j , and $\mu_{Y_{O,i}}$ and $\sigma_{Y_{O,i}}$ respectively as the temporal mean and standard deviation of the growth of species i . We make use of the decomposition of variance (σ^2) of a sum into the sum of covariances between all combinations of the terms that make up the sum.

Reference stability

We compare observed community TS with a reference TS of community yield composed of the same species, calculated under a set of assumptions that replicate conditions and properties of monocultures. These assumptions are (1) the absence of diversity effects on the mean yield of individual populations, (2) the absence of diversity effects on the standard deviation of individual species yield and (3) the absence of asynchrony in yield among populations. We meet assumptions (1) and (2) by defining the expected population-level yield for species i ($Y_{E,i}$) in function of the yield of that species in a comparable monoculture ($Y_{mono,i}$) and the proportion of that species in mixture (p_i) as $Y_{E,i} = p_i \cdot Y_{mono,i}$. It is important that p_i is a constant (for example the mean proportion over time) and does not represent the temporal variability of this proportion, to guarantee assumption (2). In order to satisfy assumption (3), we consider all correlations in yield series among the different species to equal 1. This is reasonable in large populations, but may need to be corrected for demographic stochasticity otherwise.

Reference stability can be calculated as

$$TS_{ref} = \frac{\sum \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}} \quad (4.2)$$

TS_O is defined under the simultaneous negation of all three assumptions, respectively (1'), (2') and (3'). We can now quantify the total diversity effect on temporal stability as $\tau_T = TS_O / TS_{ref}$. By calculating TS under alternative sets of assumptions we can quantify specific biodiversity effects in isolation.

Temporal stability at the population level

Temporal stability at the population level is defined as $\mu_{Y_{O,i}}/\sigma_{Y_{O,i}}$. Diversity effects on either mean (μ) or standard deviation (σ) of population yield affect both population and community stability. We estimate the effects on community stability through μ and σ separately, and together.

In order to single out effects of altered mean yield, we calculate TS under the assumptions (1'), (2) and (3). We divide this by TS_{ref} in order to quantify the direct effect on temporal stability.

$$\tau_{\mu} = \frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}} / TS_{ref} \quad (4.3)$$

This definition can be simplified to $\tau_{\mu} = \sum \mu_{Y_{O,i}} / \sum \mu_{Y_{E,i}}$, which means that the index can also be interpreted as a measure foroveryielding (appendix C.5). For diversity effects acting through σ , we calculate temporal stability under the assumptions (1), (2') and (3), and standardise it through division by TS_{ref} .

$$\tau_{\sigma} = \frac{\sum \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}} / TS_{ref} \quad (4.4)$$

Similarly, combined biodiversity effects through population-level μ and σ can be quantified by calculating TS under the assumptions (1'), (2') and (3).

$$\tau_{\mu,\sigma} = \frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}} / TS_{ref} \quad (4.5)$$

From these definitions, it follows that $\tau_{\mu,\sigma} = \tau_{\mu} \cdot \tau_{\sigma}$ (see appendix C.1).

Asynchrony

Asynchrony stabilises communities to the extent that the variability of different populations neutralise each other. This means that the stabilising potential of asynchrony depends on the population variability (σ), which is also impacted by mixing. Therefore we calculate the effect of asynchrony (assumption 3 versus 3') in the presence of diversity effects at the population level (assumptions 1' and 2'). This leads to the following definition

$$\tau_{\rho} = TS_O / \frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}} \quad (4.6)$$

and a multiplicative partitioning of the total mixing effect on temporal stability $\tau_T = \tau_\mu \cdot \tau_\sigma \cdot \tau_\rho$ (see appendix C.1). Note that τ_ρ is related to the measure of asynchrony φ defined by Loreau and de Mazancourt (2008), in fact $\tau_\rho = \sqrt{1/\varphi}$ (see appendix C.3).

As τ_ρ is calculated under the assumption of diversity effects at the population level, it contains effects of the interaction between diversity effects on population-level σ and diversity effects on the correlations among populations. For a more complete decomposition, we define an alternative τ'_ρ , representing the the stabilising effect of asynchrony, had there been no diversity effects on either population-level μ or σ (assumptions 1, 2 and 3').

$$\tau'_\rho = \frac{\sum \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \sigma_{E,i} \sigma_{E,j}}} / TS_{ref} \quad (4.7)$$

It can be shown that the difference between τ_ρ and τ'_ρ is entirely due to diversity effects on unevenness among σ of different populations (appendix C.6).

We can distinguish between asynchrony due to intrinsic differences in species responses to temporal environmental variability (additive effect) and asynchrony due to species interactions. Asynchrony due to intrinsic species differences occurs between monocultures, we can thus estimate this fraction using ρ between the expected yields, rather than the observed yields.

$$\tau'_{\rho_{mono}} = \frac{\sum \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j \rho(Y_{E,i}, Y_{E,j}) \sigma_{E,i} \sigma_{E,j}}} / TS_{ref} \quad (4.8)$$

The effect of asynchrony due to species interactions is then simply $\tau'_\rho - \tau'_{\rho_{mono}}$.

Conclusion

We calculate total diversity-induced stabilisation in mixed communities by comparing temporal stability of the community with a reference stability based on monocultures. We establish a multiplicative partitioning of total stabilisation τ_T into effects through asynchrony τ_ρ , overyielding τ_μ and altered population variability τ_σ .

The stabilising effect through asynchrony depends on the correlation in yield among populations, but also on the evenness in population-level σ . In order to avoid mixing up effects of diversity effects on unevenness with effects of correlation, we calculate τ'_ρ , in which the effects of unevenness are filtered out. We use τ'_ρ for further decomposition into an effect of asynchrony due to intrinsic differences among species in response to environmental variability and into effects of species interactions on asynchrony.

4.3 Materials and methods

4.3.1 Study sites

We used an exploratory platform for biodiversity function research in temperate broadleaved forests, consisting of 7 triplets in southern Belgium. On each study site, an intimate mixture of sessile oak (*Quercus petraea*) and European beech (*Fagus sylvatica*) was selected alongside a comparable monoculture of each species. Within a site, the three stands were selected for homogeneity in site conditions (elevation, slope, soil) and stand characteristics (fully stocked, similar in height), and we avoided mixtures where one species clearly dominates the other. The sites were chosen to cross a range in site conditions.

4.3.2 Tree selection, sampling, stand measurements

From each site, we selected at least 20 oaks and 20 beech trees for coring, half of which in the pure and half of which in the mixed stand. Only dominant trees were selected. We ended up with 145 oaks and 138 beech trees in total after removing trees of which tree rings were unreadable, or cross-dating failed (see appendix B.2 for the exact numbers per site).

During the winter of 2014-2015, each selected tree was cored twice using an increment borer at a height of 1.30m, once from the northern and once from the eastern side of the bark inwards. Cores were prepared using a microtome, oven dried and scanned at high resolution (1200 to 5000 dpi). On these scans, we measured ring widths using imageJ (Schneider, Rasband, and Eliceiri, 2012) with the objectJ plugin. The cross-dating of ring widths was verified using COFECHA (Holmes, 1983).

We delineated stands as the total area within 18m of any of the cored trees. From each tree with a circumference larger than 50 cm within these stands, we recorded the circumference and species in the winter of 2015-2016.

4.3.3 Calculating population level growth

In order to perform the different calculations of temporal stability and τ , we need to calculate $Y_{O,i}$ and $Y_{E,i}$ (defined in section 4.2) for both species at each study site. We represent yield by basal area increment (BAI) at community (stand), population (species within stand) and individual tree level. Tree level BAI series (m^2y^{-1}) were calculated based on tree ring series and tree diameters at the time of sampling, assuming tree rings form concentric circles. Population-level BAI series ($m^2ha^{-1}y^{-1}$) were calculated as average of tree-level BAI series ($BAI_{i,k}$ in m^2y^{-1} for tree k in stand i), after rescaling them to a per-hectare basis. For this scaling, we used stand measurements within a circular plot of 18m radius around each cored tree's stem. We divided BAI values by a fraction of the plot surface, proportional to the tree's share in the plot basal area ($share_k$).

$$BAI_i = \frac{1}{n_i} \cdot \sum_k^{n_i} \frac{1}{share_k \cdot \pi \cdot 18^2 \cdot 10^{-4} ha} \cdot BAI_{i,k} \quad (4.9)$$

where n_i is the number of cored trees of species i within the stand and $\pi \cdot 18^2 \cdot 10^{-4} ha$ is the surface of the circular plot.

In order to comply with the requirements that oak and beech population growth in mixed stands sum to community growth, we scale these values according to the share (in basal area) of the species in the mixed stand p_i .

$$Y_{O,i} = p_i \cdot BAI_i \quad (4.10)$$

p_i is calculated as the share of species i in the mixed community basal area as measured during the field campaign. For monocultures, $Y_{mono,i}$ is defined as BAI_i . For the expected yield, we use the same formulas but based on the trees in pure stands. Because we consider p_i constant in time, we can use this value to scale monoculture yield series without introducing variability from the mixed community: $Y_{E,i} = p_i \cdot Y_{P,i}$.

Correction for σ and ρ for bias due to a limited sample size

We use the resulting yield series $Y_{O,i}$ and $Y_{E,i}$ directly for calculating mean population yield. For the standard deviation (σ) and the correlations (ρ) however, we apply a correction to avoid bias associated with incomplete sampling. In the same way that asynchrony in growth among populations stabilises communities, asynchrony in growth among trees stabilises populations (by reducing population level σ). If population-level BAI is estimated from a limited number of trees (about 10 in this case), we do not fully capture this stabilising effect, and the standard deviations of $Y_{O,i}$ and $Y_{E,i}$ will overestimate population standard deviations. Technically, population-level σ depends on the variances at individual level and covariances at the between-individual level. In large stands, the relative importance of variances compared to covariances is negligible, and ignoring the variances removes the bias associated with limited sample sizes. We make use of the fact that we can separate the contribution of each cored tree k to $Y_{O,i}$ (or $Y_{E,i}$) and calculate the covariances among these contributions. The contributions are calculated as $Y_{O,i} = \sum_k contr_{i,k}$ where $contr_{i,k} = p_i \cdot \frac{1}{n_i} \cdot \frac{1}{\pi \cdot 18^2 \cdot 10^{-4} ha \cdot share_k} \cdot BAI_{i,k}$ (or equivalent for $Y_{E,i}$). We estimate σ for $Y_{O,i}$ (resp. $Y_{E,i}$) as $\sqrt{n_i^2 \mu_{cov}}$, where μ_{cov} is the mean covariance between any two different series of $contr_{i,k}$ that make up $Y_{O,i}$ (resp. $Y_{E,i}$). An argumentation is found in appendix C.2. Additionally, we calculate correlations using the definition $\rho(a, b) = \frac{cov(a, b)}{\sigma(a) \cdot \sigma(b)}$ with corrected standard deviations. $cov(a, b)$ is not corrected, except in the case where $a = b$ (then, $cov(a, b) = \sigma^2(a)$ and the correlation is 1).

$$\rho(Y_{O,i}, Y_{O,k}) = \frac{cov(Y_{O,i}, Y_{O,k})}{\sigma_{Y_{O,i}} \sigma_{Y_{O,k}}} \quad (4.11)$$

Temporal stability at different levels

We calculated observed and expected temporal stability at population level as $TS_{O,i} = \frac{\mu_{Y_{O,i}}}{\sigma_{Y_{O,i}}}$ and $TS_{E,i} = \frac{\mu_{Y_{E,i}}}{\sigma_{Y_{E,i}}}$ for both species i . Stability was calculated for each individual tree k as $\frac{\mu_{BAI_k}}{\sigma_{BAI_k}}$. These values were averaged per species and stand into $TS_{tree,O,i}$ for the mixed community and $TS_{tree,E,i}$ for trees growing in monocultures.

4.3.4 Statistical analysis

Stabilisation at different organisational levels

We test for mixing effects on stability at three different organisational levels.

1. We test whether mixing affects community stability over all sites, using a one-way t-test on total stabilisation ($\tau_T \neq 1$).
2. For either species i , we use $TS_{O,i}/TS_{E,i}$ to inspect the effects of mixing on stability at the population level. We use t-tests to test whether these indices differ from 1 over all sites.
3. We test whether mixing increased temporal stability at the individual level using the mean tree-level stability. We calculated the ratio $TS_{tree,O,i}/TS_{tree,E,i}$ for each species in each stand. For each species we tested whether this differed from 1 over all sites using one-way t-tests.

Pattern of competition

We expect that competition release in mixture affects several aspects of stability. Therefore, we test for a pattern whereby competition intensity (a) increases asynchrony due to compensatory dynamics, (b) reduces growth, especially for oak since beech could actually benefit under high competition and (c) increases variability at the population level.

We used the fraction of asynchrony due to interspecific interactions $\tau'_\rho - \tau'_{\rho_{mono}}$ as measure for (a), τ'_μ for overyielding, $\mu_{Y_{O,oak}}/\mu_{Y_{E,oak}}$ for overyielding of oak and $\mu_{Y_{O,beech}}/\mu_{Y_{E,beech}}$ for overyielding of beech (b), and τ'_σ for variability at the population level (c).

We test correlations between (a) and (b) (total overyielding and both species separately), and between (a) and (c). Testing between (b) and (c) is not useful because it risks being confounded by a strong natural positive link between mean and standard deviation of population growth.

Indirect effects of asynchrony

As discussed, the direct mathematical effect of asynchrony is unavoidably stabilising. We test whether these would be either reinforced or compensated for by indirect effects through other pathways by testing for correlations between τ'_ρ and either τ_μ or τ_σ . In order to gain insight in the causality we differentiate between the additive and the non-additive fraction of τ'_ρ . The additive fraction can only be a driver for other diversity effects, but can not itself be driven by diversity, whereas the non-additive part is caused by species interactions. A correlation between $\tau'_{\rho_{mono}}$ and τ_μ would provide evidence for temporal niche complementarity.

Stabilising effect of overyielding on populations

Even if overyielding has a direct positive effect on temporal stability (or negative, in the case of underyielding), we expect that it is at least partially compensated for by an indirect effect through increased (or decreased) population-level σ . We test whether overyielding is behind a potential population-level (de)stabilisation, using the correlation between τ_μ and $\tau_{\mu,\sigma}$.

4.4 Results

4.4.1 Stabilisation at different levels

Over all sites, mixing had a significant positive effect on the temporal stability of communities (21% on average, $p=0.018$). This effect was consistently positive at all sites, though ranging from 3% to 52%. Temporal stability of populations was higher in mixed than in pure stands on most sites for either species, though this was insignificant in both oak (+8% on average, $p=0.24$) and beech (+20% on average, $p=0.06$). At the tree level, temporal stability was significantly higher in mixtures for beech (16% on average, $p=0.0048$), whereas in oak the increase was marginal and insignificant (4% on average, $p=0.33$).

4.4.2 Partitioning of community stabilisation

The positive mixing effect on temporal stability at community level can be partitioned multiplicatively in effects of asynchrony (τ_ρ) and effects expressed at the population level ($\tau_{\mu,\sigma}$). Both had on average a positive effect of 10%, but the direct effect of asynchrony was stabilising at each forest site (4% - 17%), whereas $\tau_{\mu,\sigma}$ ranged from a 4% destabilising to a 43% stabilising effect (see Fig. 4.2). Mixing effects through the population level are composed of effects through either altered mean or altered standard deviation of population growth. τ_μ , which represents both overyielding and its direct effect on community stability, was on average 25% (ranging from 3% to 41%, see Fig. 4.3). τ_σ , which represents the effect of altered population

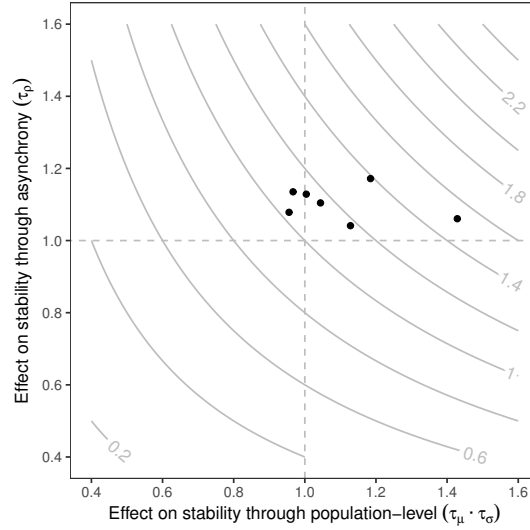


Figure 4.2: Multiplicative partitioning of mixing effects on stability (τ_T) through asynchrony (τ_ρ) and through effects at the population level ($\tau_{\mu,\sigma}$). Isolines represent equal (de)stabilisation. Effects through asynchrony are consistently stabilising, while effects at the population level are stabilising in 5 out of 7 sites.

standard deviations on community stability is mostly destabilising (on average -11%, ranging from -31% to +2%).

τ'_ρ showed a stabilisation of 12% on average (4% to 18%), of which 9% (3% to 14%) represents the additive effect ($\tau'_{\rho_{mono}}$), and 3% the additional fraction due to species interactions ($\tau'_\rho - \tau'_{\rho_{mono}}$). The additive effect is unavoidably positive and ranged from a 3% to a 14% stabilisation, whereas the effect of species interactions varied between a 6% destabilisation and a 8% stabilisation.

4.4.3 Competition

We tested for statistical relationships between the different stabilising or destabilising pathways, for two reasons. First, they allow us to test whether asynchrony and overyielding have indirect effects on stability, other than the direct effects through respectively τ_ρ and τ_μ . Second, these relations are indicative of mechanisms that cause stabilisation through the different pathways.

In our test for evidence of a gradient in competition intensity, we compared the (de)stabilising effect of species interactions through asynchrony $\tau'_\rho - \tau'_{\rho_{mono}}$ with effects through the population level. The correlation with τ_σ was significantly negative ($r=-0.76$, $p=0.048$), as well as the correlation with oak overyielding $Y_{Oak,O}/Y_{Oak,E}$ ($r=-0.80$, $p=0.029$). Correlation with τ_μ ($r=0.11$, $p=0.81$) and with beech overyielding $Y_{Beech,O}/Y_{Beech,E}$ ($r=0.46$, $p=0.30$) were insignificant.

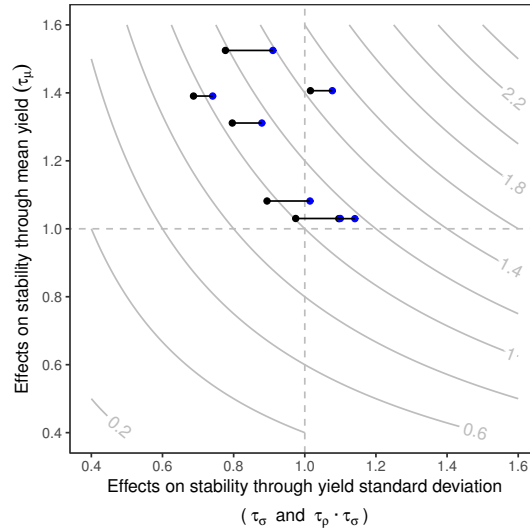


Figure 4.3: Mixing effects on stability through overyielding (τ_μ) versus through population level σ (τ_σ , black) or community level σ ($\tau_\rho \cdot \tau_\sigma$, blue). Isolines represent equal (de)stabilisation. The blue dots form a multiplicative partitioning of total stabilisation τ_T . The figure shows the consistent stabilising direct effect of overyielding throughout the study sites, whereas population-level σ is destabilising at 5 out of 7 sites. The combination of τ_ρ and τ_σ , which together form the effects through community-level σ is positive at 4 out of 7 sites. Blue and black dots from the same site are connected.

4.4.4 Indirect effects of asynchrony

We tested for potential indirect effects of asynchrony. These could occur when asynchrony affects either mean or standard deviation at population level, but we found no correlations between τ'_ρ and either τ_μ ($r=0.27$, $p=0.54$) or τ_σ ($r=-0.68$, $p=0.09$). We tested whether asynchrony is a causal driver of overyielding (temporal complementarity). We used the additive part of asynchrony because it is better suited to assess causality, but we find no significant correlation between $\tau'_{\rho_{mono}}$ and τ_μ ($r=0.18$; $p=0.70$).

4.4.5 Stabilising effects of overyielding on populations

There was no evidence for a stabilising effect of overyielding at the population level (no significant correlation between τ_μ and $\tau_{\mu,\sigma}$, $r=0.43$, $p=0.33$).

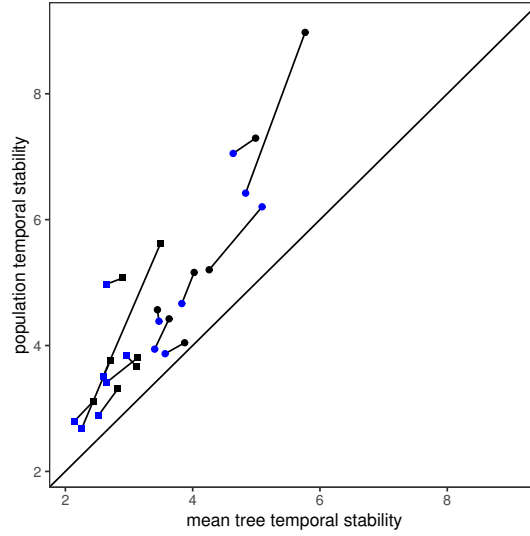


Figure 4.4: Mean tree temporal stability versus population-level temporal stability for oak (circles) and beech (squares) in monocultures (blue) and mixed communities (black). The population level is more stable than the tree level due to asynchrony among individuals. Mixing can affect population-level stability either by modifying tree-level stability or asynchrony among conspecific individuals. Marks from the same species within a site are connected.

4.5 Discussion

4.5.1 Methodology

Given formula (4.1) for temporal stability, any biodiversity effect on temporal stability must be expressed through at least one of the three variables μ , σ , and ρ . These variables can thus be seen as pathways through which diversity effects affect ecosystem stability. We calculated the total biodiversity effect as τ_T , which can be partitioned based on effects through these three pathways as $\tau_T = \tau_\mu \cdot \tau_\sigma \cdot \tau_\rho$, or alternatively based on the distinction between asynchrony and population level stability as $\tau_T = \tau_\rho \cdot \tau_{\mu,\sigma}$. This distinction is justified by the fact that asynchrony is the only way in which community-level stability is decoupled from population-level stability (Thibaut and Connolly, 2013; Xu et al., 2021). All diversity effects that modify population level stability should also impact community level, and this is quantified by $\tau_{\mu,\sigma}$.

These pathways have a direct effect on community stability, which makes them obvious candidates for being causal drivers of stabilisation, but they must not necessarily be so. τ_μ for example represents a direct effect from overyielding on stability, however it could be expected that overyielding also negatively affects τ_σ , which

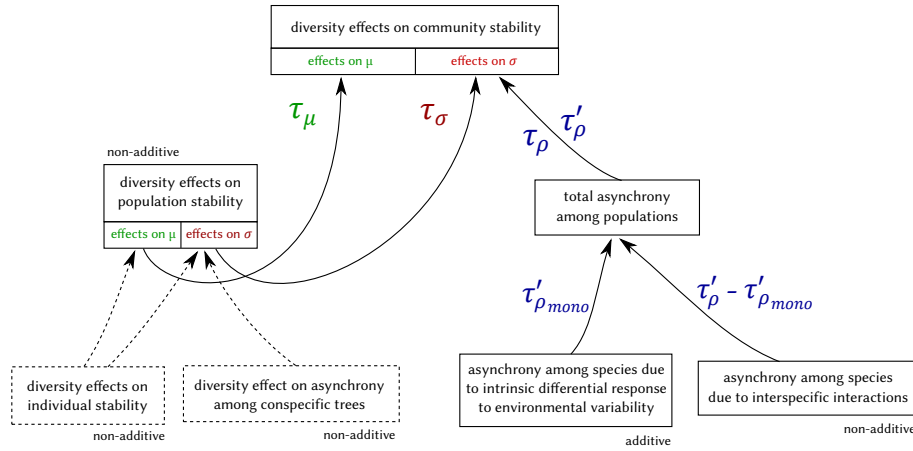


Figure 4.5: Scheme indicating the different pathways through which diversity effects at the individual level and asynchrony affect community stability. This scheme represents only direct, mathematically unavoidable effects, not indirect effects or statistical relationships. Diversity effects on population stability have to act at the community stability as well. Diversity effects on population-level μ also affect community-level μ , and this is quantified as τ_μ . Diversity effects on population-level σ affect community-level σ , quantified as τ_σ . Asynchrony among populations is quantified as τ_ρ or τ'_ρ and is subdivided in two different sources. Asynchrony among species due to intrinsic differential response to environmental variability is quantified as $\tau'_{\rho mono}$, asynchrony among species due to interspecific interactions as $\tau'_\rho - \tau'_{\rho mono}$. Of all effects, asynchrony due to intrinsic differences among species is the only diversity effect that is also present in monocultures and not dependent on species interactions, which is why we consider it to be an additive effect. For the case of forests, where we ignore demographic effects like recruitment and mortality, diversity effects on population-level stability stem from stability of individual trees, and asynchrony among them (indicated with dotted lines).

would counteract this stabilisation. Some systems may even exhibit a trade-off between mean growth and stability (Wang et al., 2021; Loreau et al., 2021). These different components of stabilisation are themselves driven by mechanisms that may affect asynchrony through different paths at the same time, sometimes at different levels.

We explore how we can use the decomposition of τ_T in order to shed light on interactions and mechanisms behind stabilisation.

4.5.2 Stabilisation at hierarchical levels

We explore in detail how community stability is made up from elements of stability at the population level and asynchrony between populations. It is to be expected that the stability of growth of individual trees should also have an impact on population and community stability.

In many communities, (in)stability stems from population dynamics such as recruitment of individuals, mortality and migration. Because such dynamics are slow in mature forests, and perhaps absent on smaller time frames, we consider that over the studied period, population-level stability depends only on the dynamics of individual trees, and interactions between them. This creates a symmetry in the setup of our study, just as growth of populations sum to growth of communities, growth of individual trees sum to population growth (admittedly expressed per ha, but this is only a linear scaling and does not affect temporal stability). This means that population stability depends on elements of stability (μ and σ) at the tree level, and on asynchrony between individual trees. There are reasons for why we cannot use the same partitioning to decompose population (de)stabilisation into effects at the tree-level. Our partitioning relies on a sampling strategy where each population in the mixed community has a corresponding monoculture, whereas individual trees in mixture are not paired with a corresponding tree in monoculture. An overview of how communities are stabilised through effects at individual and population level, and through asynchrony among individuals and populations is given in Fig. 4.5.

Numerically, effects through asynchrony and population-level stability were equally important in stabilising community growth, both responsible for a 10% increase in stability. An important difference is that the effect through population-level stability is highly variable, and even destabilising on two sites, whereas asynchrony is consistently stabilising (Fig. 4.2). This is consistent with a large body of literature that shows that asynchrony is behind the near-universally positive diversity-stability relationship, whereas effects at the population-level may also destabilise (Xu et al., 2021). At the tree level, stabilisation due to mixing is obvious for beech, but less so for oak (appendix C.4). Stabilisation at the individual level means that increased (resp. decreased) growth due to mixing is not evenly distributed over the different years, but that it is relatively higher (resp. lower) in years of low growth. This could arise when diversity buffers against certain stresses or disturbances, such as drought, insect attacks or pathogens.

4.5.3 Competition

Competition for finite resources creates compensatory dynamics between species as resources used for growth by one population cannot be used by other populations (Tilman, Lehman, and Bristow, 1998; Gonzalez and Loreau, 2009; Morin et al., 2014). Higher than usual growth for one species in some years tend to be compensated by a lower growth for other species. This effect is generally believed to be stabilising, because it creates asynchrony among populations. Some authors note that compensatory dynamics depend on fluctuating population densities, which can happen in communities with a fast turnover of individuals (for example annual plants), but less in forests (Jucker et al., 2014), which would mean that asynchrony through species interactions is unimportant in forests. An increase in density of one species means also an increase in competition exerted onto other species which decreases yield of other species. However, in a forest triplet study, del Río et al. (2017) identified species interactions to be the most important mechanism by which asynchrony stabilises communities of *Pinus sylvestris* and *Fagus sylvatica*. It is conceivable that temporal

variability in tree functioning (such as stomatal closure, water uptake or defoliation) can also lead to temporal variability in competitive ability of species, and could also increase asynchrony in the absence of fluctuating population densities.

However, theoretical results predict that competition also amplifies the variability in population-level growth, which would cancel out the stabilising effect of increased asynchrony, and that the total effect of competition on community stability is more likely negative than positive (Ives, Gross, and Klug, 1999; Loreau and de Mazancourt, 2013).

We obtained two lines of evidence for a pattern of interspecific competition on community stability. The first is the negative correlation between $\tau'_\rho - \tau'_{\rho_{mono}}$ and τ_σ . This is to be expected when competition has a stabilising effect through asynchrony ($\tau'_\rho - \tau'_{\rho_{mono}}$) and at the same time a destabilising effect through population-level σ (τ_σ). The second one is based on patterns in overyielding among sites. In general, competition release in mixtures should lead to overyielding (Ammer, 2019). However, high level of interspecific competition could result in selection effects and dominance which may also lead to overyielding (Loreau, 2001; Fox, 2005). As dominance of beech over oak is commonly observed in forests of oak and beech (von Lüpke, 1998; Leuschner et al., 2001a; Hein and Dhôte, 2006), we cannot rely on overyielding as a measure of competition release. Overyielding in oak specifically, at the other hand should follow from both reduced competitiveness of beech and of complementarity. The fact that $\tau'_\rho - \tau'_{\rho_{mono}}$ was negatively correlated with overyielding for oak, but not for beech nor with overyielding in general (τ_μ), provides further evidence that $\tau'_\rho - \tau'_{\rho_{mono}}$ represents a gradient in intensity of interspecific competition.

These correlations do not reveal the mechanism behind the decreased τ_σ under competition release. Competition release could entail relaxation of competition as a growth driver, and hence as a source of variability (σ). At the same time, intense competition would favour beech, whereas complementarity can protect the share of oak in community yield and in its variability (see Wang et al. 2021). This would also stabilise the community, as growth is more stable in oak than in beech (appendix C.4).

4.5.4 Asynchrony

The importance of asynchrony between populations has been predicted using modeling approaches (Loreau and de Mazancourt, 2013; Morin et al., 2014) and is consistent with empirical literature results, both in forests (Jucker et al., 2014; del Río et al., 2017; Schnabel et al., 2019; Schnabel et al., 2021) and in other ecosystems (Hector et al., 2010; Thibaut, Connolly, and Sweatman, 2012; Hautier et al., 2014; Craven et al., 2018; Kigel et al., 2021). It is also consistent with the observation that diversity consistently stabilises communities, but not always populations (del Río et al., 2017; Xu et al., 2021; Schnabel et al., 2021), since asynchrony is the only mechanism that can stabilise communities without stabilising individual populations (Xu et al., 2021).

An important argument for the importance of asynchrony as stabilising factor is that it is statistically unavoidable (Doak et al., 1998; Loreau and de Mazancourt, 2013). It

can easily be shown that τ_ρ cannot be lower than 1 (it would require correlation values above 1), which means that there is a direct mathematical and causal stabilising effect. We observe a direct stabilisation due to asynchrony of 10% on average (τ_ρ).

This does not necessarily equal the total effect, as long as we can't exclude the possibility of indirect effects, when asynchrony acts as a causal driver for mechanisms that affect population stability. Asynchrony (in the form of τ'_ρ) was not significantly correlated with either τ_μ or τ_ρ , though with a small number of study sites (7), we can't interpret this as evidence for the absence of indirect effects. We did find a relationship between the fraction of asynchrony due to species interactions ($\tau'_\rho - \tau'_{\rho_{mono}}$) and τ_σ , which we interpret as a gradient in interspecific competition, rather than as a causal effect of asynchrony. The additive fraction of asynchrony ($\tau'_{\rho_{mono}}$), which can be interpreted as driver for diversity effects was not significantly related with τ_σ .

There is no consensus on the relative importance of the two origins of asynchrony. Our results show that species differences in response to environmental variability are the most important source of stabilisation through asynchrony on our study sites (table 1). Species interactions can potentially be an important source of additional asynchrony on some sites, but the effect was highly variable among sites and sometimes even decreased asynchrony.

This seems to contrast with previous studies that found that asynchrony in monocultures are poor predictors of the stabilising effect of diversity (Gross et al., 2014 for grasslands and algal communities, (del Río et al., 2017) in forests), suggesting a higher importance for temporal variation in species interactions. Species interactions tend to depend on both species identity and environmental context (Maestre et al., 2009; Ammer, 2019; Baeten et al., 2019), so contrasting results among studies are not unexpected. However, there may be a methodological aspect as well, as calculating the magnitude of the direct stabilising effect is not the same thing as testing for statistical significance, if only because statistical analysis includes both direct and indirect effects. In our case, the effect of species interactions on asynchrony was not large numerically (+3% on average), but it did show an important variability (from -6% to +8%) with ecological relevance (intensity of interspecific competition).

It has been established that asynchrony is always stabilising, while the effect of population stability is context-dependent (Xu et al., 2021). We hypothesise that it is the stabilising effect of asynchrony due to intrinsic differences in environmental response (the additive fraction) which is unavoidable. It has been pointed out that if an expected yield series would be calculated as mean yield of monocultures, weighted by the proportions of each species in the mixed community, then this fraction of asynchrony would stabilise expected yield relative to monoculture yield series (Jourdan et al., 2021; del Río et al., 2022). It should also be noted that the remaining non-additive fraction of asynchrony was highly variable within our sample and sometimes destabilising. It appears thus that, as is assumed in literature on overyielding, additive effects are unavoidable, and non-additive effects, related to species interactions are context-dependent. The reason why diversity is near-to-universally stabilising, is that the effect includes an unavoidable additive fraction.

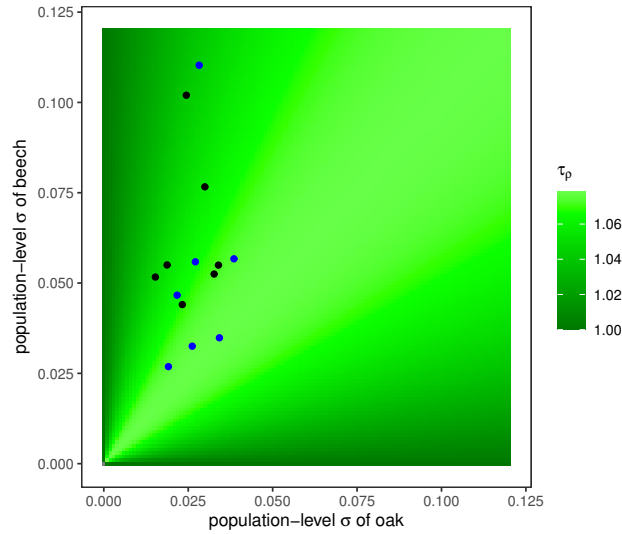


Figure 4.6: Population-level σ of oak versus beech in monocultures (blue) and mixed communities (black) plotted against a hypothetical value of τ_ρ given a fixed correlation value of 0.58 (the mean throughout the 7 mixed communities). This plot shows that the stabilising effect of asynchrony depends on the evenness in σ between populations of both species.

4.5.5 Evenness

It has been shown that the stabilising effect of asynchrony is mediated by evenness (Thibaut and Connolly, 2013), and this hinders the full separation of stabilisation into effects through asynchrony and effects at the population level. τ_ρ depends on the correlation in yield among populations, but for equal correlation values, τ_ρ will be higher when population-level σ values are more equal (Fig. 4.6). Evenness on itself can also be impacted by mixing. Overyielding through selection effects, for example, would increase the unevenness in species yield. If this also increases the unevenness in species σ , then that would affect the stabilising potential of asynchrony negatively. Using τ'_ρ rather than τ_ρ allows us to study the stabilising effect of asynchrony excluding the diversity effect of unevenness (see appendix C.6). τ_ρ will be lower than τ'_ρ (on average 10% versus 12%) when population-level values for σ are more uneven in mixture than in monoculture. Fig. 4.6 demonstrates how evenness in σ modifies stabilisation through asynchrony.

4.5.6 Overyielding

While it has been established that biodiversity induces both overyielding and stabilisation, the question whether overyielding is one of the driving forces behind stabilisation is under debate (Hector et al., 2010; Jucker et al., 2014; Cardinale et al., 2013; Morin et al., 2014). Overyielding (in the form of τ_μ) provides a pathway by

which diversity can stabilise a community, but this does not mean that overyielding itself is the driver. In fact, it is realistic to expect increased mean to be accompanied with an increased σ of growth, which would counteract the stabilisation. Several authors have tested for statistical relationships between overyielding and community stability over study sites or biodiversity experiments. These relationships have been found to be positive (Hector et al., 2010), weakly positive (Morin et al., 2014) or absent (Cardinale et al., 2013; del Río et al., 2017). Even when positive, such statistical links do not necessarily indicate a causal relationship. They may also result, for example, from patterns in species interactions related to interspecific competition.

If overyielding caused stabilisation, this should be either through an effect on asynchrony, or through an effect at the population level. We didn't find a significant correlation between overyielding (τ_μ) and stabilisation through the population-level ($\tau_{\mu,\sigma}$). With a small number of data points, this should not be interpreted as evidence against an effect at the population level.

We also tested for a statistical link between asynchrony (τ'_ρ) and overyielding (τ_μ). There is some evidence that asynchrony in diverse communities can cause overyielding through temporal complementarity (Allan et al., 2011). The rationale is that reductions in one species yield constitute a reduction in competitiveness of that species, allowing increased yield in other species. If such a mechanism depends on fluctuating species densities, however, it is unexpected in forests (Jucker et al., 2014). However, a positive relationship between overyielding and asynchrony was detected in forests by (del Río et al., 2017), suggesting that also individual trees can benefit from a temporary growth decline of neighbours. This mechanism is interesting, because if asynchrony drives both stability and overyielding, this would induce a non-causal statistical link between overyielding and stability. Our results do not confirm such a mechanism in the mixture of sessile oak and beech. Of course, this does not exclude the possibility that such a mechanism could act on a smaller temporal resolution.

4.5.7 Conclusion

We quantify biodiversity-driven stabilisation, taking into account both additive and non-additive aspects. By partitioning diversity-driven stabilisation, we are able to separate effects through the different pathways. In our example case, community stabilisation happened both through asynchrony (10%) and population-level stabilisation (10%). We detected a pattern of interspecific competition, affecting stability positively through asynchrony and mean oak growth, and negatively through population-level σ .

The proposed partitioning can help with establishing causality. First, because direct effects are causal. Second, because the fraction of asynchrony caused by intrinsic differences in environmental response is an additive effect and cannot be caused by other diversity effects. The partitioning of diversity effects on stability allows us to distinguish between relations that are mathematical in nature and that

can be explained analytically from ecological interactions which require a statistical approach. This should help bridging the gap between theoretical and empirical research on the diversity-stability relationship.

Chapter 5

Discussion

Glossary

asynchrony Imperfect correlation ($r < 1$) among yield series of different populations. This leads to a temporal stabilisation of communities relative to populations, as extremes of one population are leveled out by other populations within the community.

community Group of populations of several species that live or grow together and interact. Here: mixed forest stand.

compensatory dynamics The phenomenon by which temporarily high yield of one species is compensated for by low growth of another, expected under competition for limited resources. This increases asynchrony and is therefore often described as stabilising. A strict definition requires that covariances (or correlations) among population yield series are negative, but this is rare in nature.

competition Interaction among individuals or populations by which at least one negatively affects the growth or functioning of another by reducing resource availability.

competitive dominance Here: the situation where one species is able to increase its growth in mixture at the expense of the other species. Dominance has been formalised in a more general way by Fox (2005).

complementarity occurs when mixed communities are able to take up more resources than monocultures, or to use them more efficiently. This can happen through competition reduction or through facilitation.

constructed climate variable Variable used to represent precipitation relevant to growth for each combination of site and species specifically (see section 3.2.3).

direct vs indirect effects Here: direct effects of asynchrony and overyielding on community stability (represented by respectively τ_ρ and τ_μ) are effects that can be derived mathematically from the definition of temporal stability; indirect effects stem from interactions between several components of stability.

drought exposure $\Delta\delta^{13}C = \delta^{13}C_{2003} - \delta^{13}C_{2001}$. Represents the amount of drought a tree was exposed to during the 2003 summer.

facilitation Improvement of one species' habitat by another.

growth models Linear mixed models we use to test for growth responses to mixing along spatial and temporal gradients in water availability (see section 3.2.3, Fig. 3.4).

lasso models Linear models that allow using a large number of possibly intercorrelated regressors, and that prevent overfitting by implementing a penalty on the model coefficients. This performs shrinkage of the coefficients, but also variable selection when coefficients are shrunk to 0. Here, lasso models are used to prune within a large set of climate variables, and to construct a precipitation variable relevant for growth (see section 3.2.3).

mixing index models Linear mixed models that explain the relative difference in growth between trees in mixed and pure forests (mixing index) using detrended growth as a proxy for growing conditions (see section 3.2.3, Fig. 3.5).

overyielding Non-additive diversity effects on community yield. Typically calculated as the difference between observed yield of mixed communities, and expected growth. The latter is based on average growth in monocultures, weighted by species proportions in the mixed community. τ_p can be seen as an alternative measure for overyielding, as its definition can be simplified to the ratio of observed to expected growth.

population Group of conspecific individuals that live or grow together and interact. Here: conspecific trees within a stand.

pre-drought growth Mean ring width of a tree in the 5 years preceding 2003 (see section 2.2.5).

resistance Here: the ability of an individual (or population or community) to maintain its growth or functioning during a period of stress or disturbance.

resilience The ability of a system to absorb external changes without shifting into a fundamentally different behaviour.

stabilisation Here: the degree to which temporal stability in mixed communities is more stable than a reference based on monocultures. We measure total stabilisation as τ_T .

stress-gradient hypothesis The hypothesis that the relative importance of positive versus negative interactions become more important along gradients of increasing stress.

temporal stability (TS) A measure for the stability of ecological properties through time defined as $TS = \mu/\sigma$, where μ represents the temporal mean and σ the standard deviation of a performance measure. Here measured over basal area increment at the level of the individual, population and community.

water use efficiency Ratio of carbon assimilation to water use.

$\delta^{13}C$ A measure for the ratio between the stable carbon isotope ratios ^{13}C and ^{12}C , measured against a standard and calculated as $(\frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{standard}} - 1) * \frac{1}{1000}$. The value of $\delta^{13}C$ within photosynthates depends on the ratio of intercellular to atmospheric carbon dioxide concentration during photosynthesis. Hence, it is dependent on stomatal regulation and correlates well with water use efficiency.

μ Here: temporal mean of basal area increment at individual, population or community level

σ Here: temporal standard deviation of basal area increment at individual, population or community level

5.1 Reminder of main results

The main result of chapter 2 is that beech exposure to drought is higher in mixtures, and that this is the result of an increased growth of beech (Fig. 2). Oak drought exposure was not affected by mixing.

Using patterns in tree ring width, we observed a general growth increase for beech in mixtures, at the expense of oak growth. However, next to beech dominance, complementarity occurs in this mixture as well, and we observed that the relative importance of complementarity is higher on dry sites, and in less productive years. Precipitation is an important driver of temporal variability in tree growth at our sites. Depending on the site, precipitation explains between 13% and 44% of the high-frequency variability in growth (master chronology) of oak, and between 17% and 55% in beech (appendix B.4). The effect is larger for beech than for oak, and larger on drier sites. On drier sites, beech ring widths may be twice as large in years of high precipitation compared to years of low precipitation (as estimated by the growth models, Fig. 3.4). We can interpret this as confirmation that beech is more prone to drought, although the regression analysis does not indicate whether trees are stressed by drought or merely constrained by limited water availability.

We used detrended growth as a measure for growth conditions (section 3.2.3, Fig. 3.5). Along this gradient, mixing effects became more beneficial in years where growth was lower than usual. In years of stronger growth limitation, the positive mixing effect on beech growth further increased, while the negative mixing effect on oak growth was mitigated. We concluded that mixing provides protection against strong limitation, stress or disturbance.

The results are to a certain extent in agreement with predictions of the stress-gradient hypothesis, with a larger importance of complementarity under higher physical stress, at least for water unavailability on a spatial scale, and for general growth conditions on a temporal scale (Bertness and Callaway, 1994; Maestre et al., 2009; Forrester and Bauhus, 2016).

Furthermore, we observed an average 21% increase in community stability due to mixing, equally distributed over asynchrony (10%) and stabilisation at the population level (10%). Overyielding was on average 25%.

5.2 Do interspecific interactions increase temporal stability under the stress-gradient hypothesis?

In this section, we revisit the effects observed along the different ecological gradients. We discuss how patterns in growth along temporal gradients lead to increased temporal stability.

We observed that mixing effects become more positive (or less negative) in years of low growth, consistent with the stress-gradient hypothesis. We discuss how this

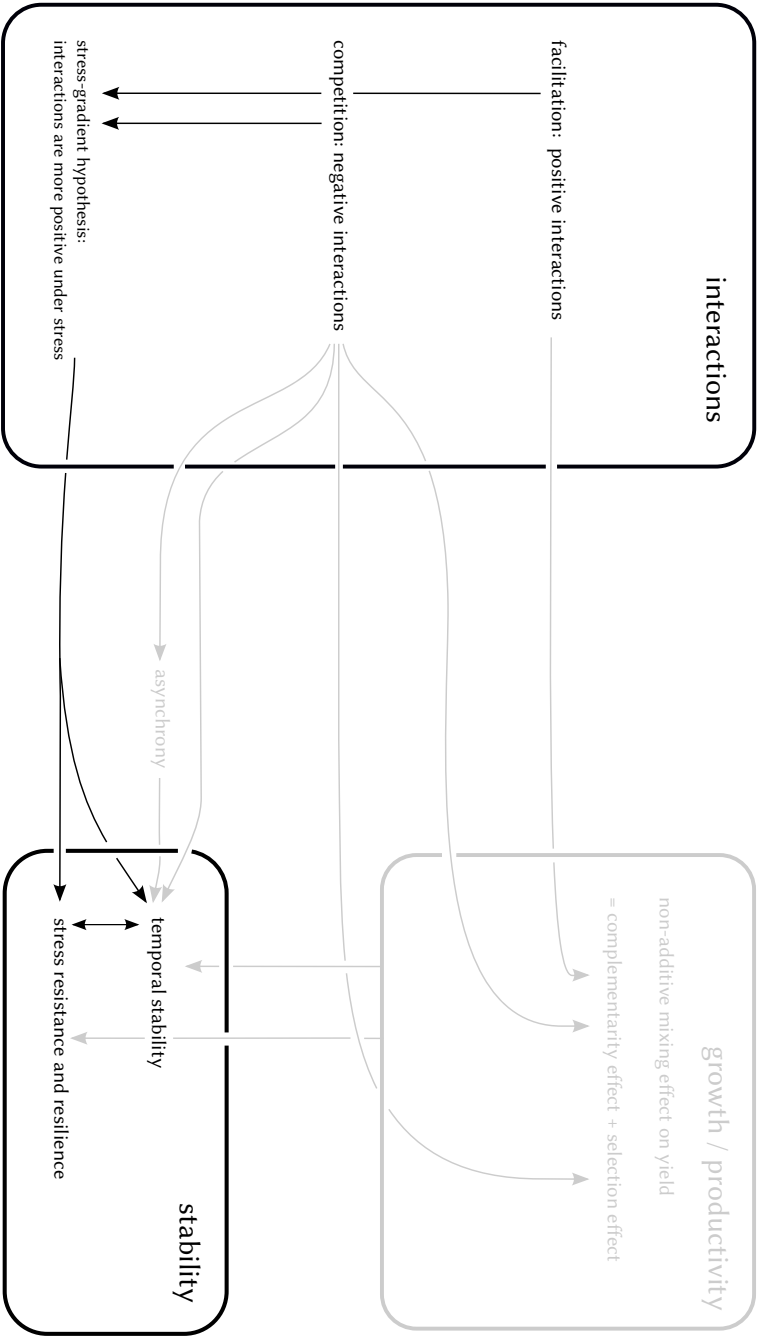


Figure 5.1: In chapter 3, we discussed how mixing improves tree stress resistance and resilience. Here, we discuss how this relates to the stress-gradient hypothesis and leads to temporal stability.

relates to temporal stability. Mixing decreases the temporal variability in growth if it has as an effect that yearly growth values are closer to their temporal mean. Because TS is standardised by mean growth ($TS = \mu/\sigma$), closer to the temporal mean should be interpreted in relative terms, i.e. relative to the mean itself (see Fig. 5.2 for a conceptual scheme). This means that mixing should generally increase growth in years of low growth (below the temporal mean) more than it increases mean growth (or decrease growth in low growth years less than it decreases mean growth). This is exactly what has been observed in the mixing index models (Fig. 3.5). Beech trees grow faster overall due to mixing (μ), but this effect is stronger in slow-growth years. Oak trees grew more slowly in mixed stands overall, but this effect was weaker in slow-growth years. This means that the mixing index models are a way of studying temporal stability. They are, however, not explicit about the hierarchical level they are defined at. The mixing index ($\frac{M-P}{M+P}$) is defined at a mean-tree level. This is different from true population level since it does not take into account stand density. Yet the explanatory variable used in the mixing index models ($P_{det} + M_{det}$) is averaged over both species. To some extent the signal may thus contain effects of one species benefitting from temporarily low functioning of the other (compensatory dynamics), which should increase asynchrony among species and as such stabilise at the community level.

The stress-gradient hypothesis, considered on a temporal level, would predict higher complementarity as growth conditions worsen (Bertness and Callaway, 1994), which is what we observe in the mixing index models. This means that the stress-gradient hypothesis can also be related to temporal stability: higher complementarity (when manifested as growth increase) in stressful years (when represented by low growth) leads to stabilisation.

Does this mean that the increased stability at community level should also be a form of the stress-gradient hypothesis? An important part of the stabilisation of communities was due to asynchrony (see Fig. 4.2). Asynchrony has been identified as unavoidably stabilising, also when populations and individual trees are destabilised (its direct effect). We tested whether asynchrony could have an indirect stabilising effect, acting at population level. This could happen through overyielding due to temporal complementarities (Allan et al., 2011; del Río et al., 2017), but we did not find evidence for such an effect. Asynchrony acts in the first place because trees have different tolerances and differential responses to environmental variability. Through asynchrony, growth reductions in response to unfavorable environmental conditions are not alleviated (as is the case under the stress-gradient hypothesis), but averaged out over different species. Hence, stabilisation through effects at population level can be related to the stress-gradient hypothesis, while stabilisation through asynchrony is not.

In beech, there was a relationship between pre-drought growth and $\delta^{13}C$ in the reference (wet) summer. Faster growing trees had a lower $\delta^{13}C$, and hence a lower water use efficiency in the reference summer (Figs. 2.4, 2.5). Faster growth of beech due to mixing is thus likely partially linked to a higher water availability. Having more water does not directly lead to increased growth, but it allows trees to build more canopy through which water is lost (Ammer, 2019). As a consequence, the increased growth is not sustainable during drier years. In principle, this could be a

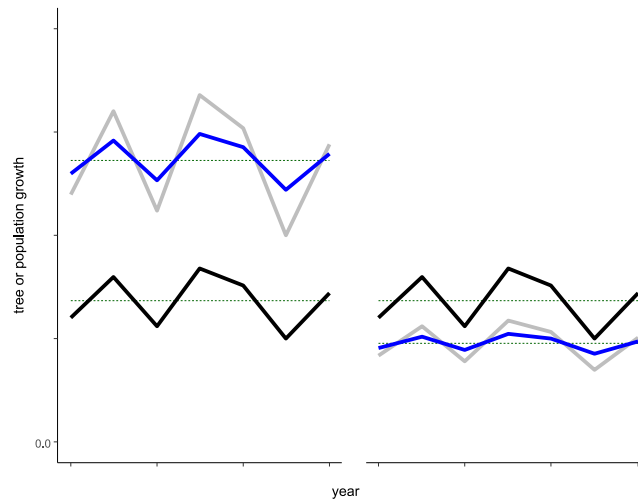


Figure 5.2: Conceptual scheme of how mixing effects on growth can increase stability at tree or population level. Black curves represent growth in monoculture. Dashed lines represent temporal means. Grey curves represent the case where mixing increases (left) or decreases growth (right) in a way that mean growth and standard deviation are scaled with the same factor, so that temporal stability (μ/σ) is unaffected by mixing. Blue curves represent cases where the standard deviation is scaled with a smaller factor than the mean, creating stabilisation due to mixing. Stabilisation happens when mixing increases growth in low growth years (lower than average) more than it increases average growth (left panel), or when mixing decreases growth in low growth years less than it decreases average growth (right panel).

handicap for beech trees in mixture. If they use more water, they may more quickly exhaust the reserves during a drought. In our data this does not seem to become problematic for beech, as mixing did not significantly affect $\delta^{13}C$ during drought (Fig. 2.5), and the mixing increased beech growth, also in dry years. It may, however, be the reason for why we don't observe the stress-gradient hypothesis on the temporal precipitation gradient.

As evident from the lasso models (appendix B.3) and the growth models (Fig. 3.4), variability in precipitation is a driver for variability in growth within individual trees, which implies it should also be a destabilising factor at the individual level. For beech this effect is even stronger in mixtures, where trees respond more strongly to the temporal precipitation gradient. This is thus a source for mixing-induced destabilisation in mixtures. Yet, stability of individual trees was higher in mixture than in monocultures (Fig. 4.4). One source of stabilisation is increased mean growth (Fig. 3.4) at least when measured as temporal stability). Additionally, it is clear

that there are other sources of variability in growth unrelated to the precipitation gradient (appendix B.5), and these tend to be reduced in mixture (Fig. 3.5).

5.2.1 Conclusion

In chapter 4, we observed that half of the stabilisation of mixed communities is due to stabilisation at population level, and that competition release plays a role, but we did not investigate which interactions in mixture stabilise the trees and populations. In this section we explored the link between stability and the stress-gradient hypothesis, under the assumption that stress can be measured by a slowdown in growth. We showed that stabilisation at the lower levels (individual tree, population) should be expected when interspecific interactions follow the stress-gradient hypothesis.

5.3 Does mixing simultaneously enhance productivity and stability?

Mixing is credited with two important benefits regarding its effects on growth. Mixing would increase mean growth, and mixing would protect growth against limitations, stress or disturbance, hence decreasing the temporal variability of growth. Several mutually exclusive hypotheses have been put forward on how and whether these two are compatible. We investigate how mixing would lead to either, or to both.

5.3.1 Trade-off between competitive ability and stress tolerance

Why are temperate forests not dominated by species that combine fast growth and dominating traits with tolerance to various stresses? The usual answer is that functional traits of species represent trade-offs (Laanisto and Niinemets, 2015), and one such well-described trade-off is the one between stress-tolerance and competitiveness (Grime, 1988; Grime et al., 1997; Reich, 2014). Beech tends to dominate on mesic sites, sessile oak can dominate sites where water unavailability is beyond beech stress-tolerance.

It is less clear whether this trade-off extends to mixing effects. Does it imply that mixing can either improve productivity or stress tolerance, but not both? There are arguments for such a trade-off in mixing effects (Loreau et al., 2021; chapter 2). As overyielding is dependent on resource acquisition, it could lead to forests that are more sensitive to resource scarcity (Forrester, 2015; Forrester and Bauhus, 2016; Ammer, 2019).

The idea of a trade-off between performance and stability (see for example Fririon et al., 2023) contrasts with the commonly-held assumption in population ecology that overyielding drives temporal stability of biological communities (Hector et al.,

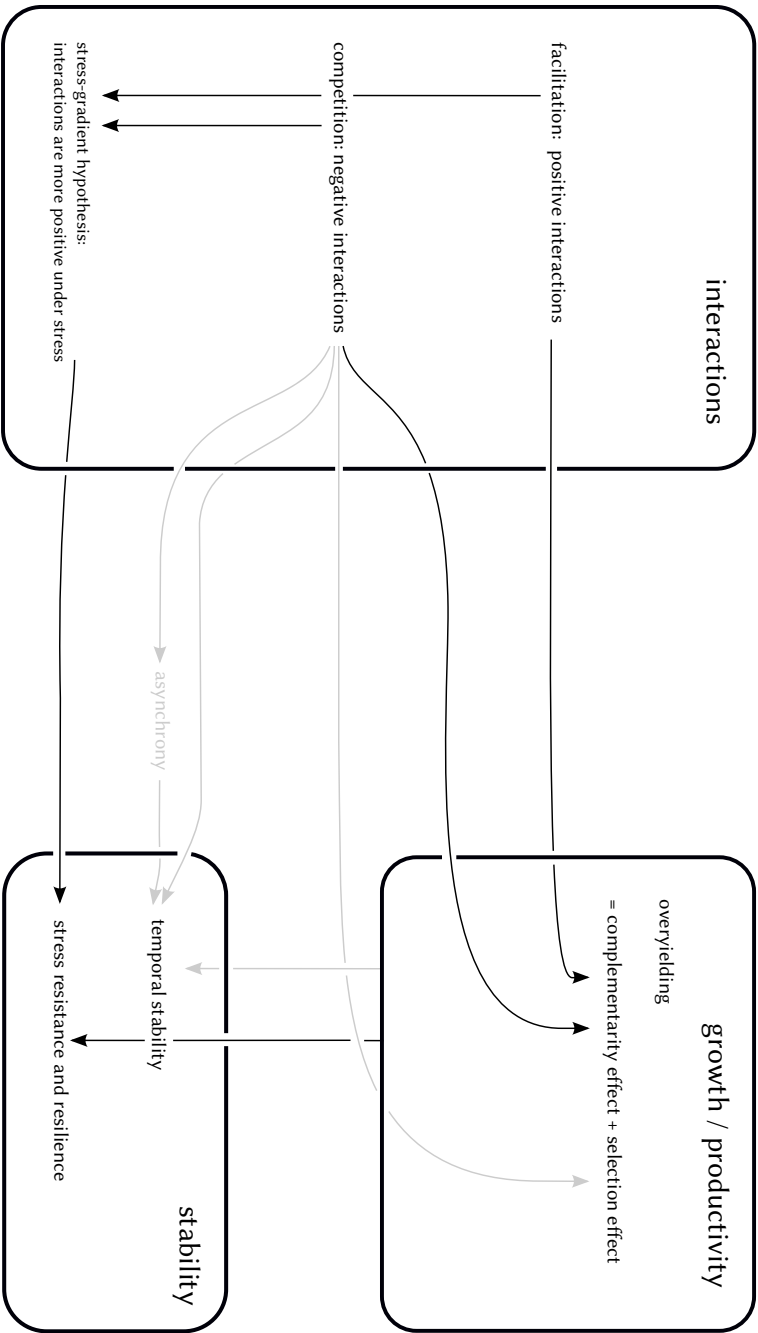


Figure 5.3: Stable carbon isotope analysis shows that positive effects on growth may hamper resistance to stress (chapter 2). Yet, by studying growth patterns, we observe positive effects on growth (for beech, chapter 3), productivity (overyielding, chapter 4), resistance (chapter 3) and stability (chapter 4). In this section we try to solve the contradiction and discuss which mechanisms can lead to both enhanced productivity and stability.

2010; Jucker et al., 2014). This assumption is not universally accepted (Cardinale et al., 2013; Morin et al., 2014), but it has a theoretical base nevertheless. Stochasticity is one source of instability, and overyielding may lead to larger communities where stochasticity is minimised (de Mazancourt et al., 2013). Overyielding and stabilisation can also co-occur as both may result from competition reduction in mixtures (Loreau and de Mazancourt, 2013; Fig. 4.1).

We observed both overyielding and stabilisation (Fig. 4.3) and investigate the mechanisms that lead to both.

Overyielding requires that mixtures perform more photosynthesis than monocultures, so light relations must be improved, and this often happens through a higher canopy packing (Pretzsch, 2014; Jucker, Bouriaud, and Coomes, 2015). This does not mean that the interactions behind overyielding necessarily take place in the canopy. Higher canopy packing requires access to soil resources (nutrition to build leaves and water to meet the demand of transpiration). It may be belowground complementarity which allows the forest to increase the canopy packing (Shipley and Meziane, 2002; Ammer, 2019). Theory has been developed to answer why mixing sometimes but not always leads to better resistance to stress. Mixing should improve resilience to resource unavailability (or unfavourable condition) in cases where there is complementarity for that specific resource (or when mixing improves the condition). Complementarity for a resource that is not limiting may not be of any importance (Forrester and Bauhus, 2016). This means that we must distinguish between complementarities that improve functioning under specific strong temporary constraints (for example droughts), and complementarities that improve functioning in absence of such constraints. The first category should increase resilience and stability of growth, while the latter should lead to faster mean growth and overyielding.

5.3.2 Mitigating limitations

Although the general idea behind limiting factors is that there can only be one, resources and conditions are variable through time, so there can be multiple limiting factors throughout a growing season, or even throughout a single day. Not only are limitations variable over time, they may differ among trees and sites. We investigate which factors are limiting, whether complementarities are likely, and whether these would rather lead to increased growth (and overyielding) or increased resilience (and stability).

Light is essential to forest growth, but we did not test for gradients in light availability, because historical data of incoming solar radiation were not available for dendrochronological analysis. Nevertheless, light relations play an important role in competition among trees, given that the ability of beech to cast shade on oak is a major contributor to its dominance (von Lüpke, 1998; Hein and Dhôte, 2006; Leuschner et al., 2001b). Dominance (see for example Fox, 2005) can be part of the selection effect, and thus lead to overyielding, even in the absence of complementarity. Light relations have been shown to play an important role in overyielding, in particular when species differ in shade tolerance (Zhang, Chen, and Reich, 2012; Toïgo et al., 2018; Van de Peer et al., 2018)

We have evidence that **water** unavailability limits growth, at least under low levels of precipitation. Temporal variability in precipitation explains growth for both species at each site (Fig. 3.4), with precipitation in spring as most important and consistent driver (appendix B.3). The effect of precipitation is stronger at the driest sites, but is present even on sites where we expect water excess to be more problematic than shortage (e.g. Vecmont). The importance of spring precipitation is not self-evident. In the region of the study sites, soils dry out during the growing season, but are replenished during winter. For this reason, precipitation should not be expected to really improve water availability in spring. Precipitation in spring can, however, delay the gradual drying out of the soil. It could also be that soil saturation has an effect on some process, for example to restore xylem conductivity after winter. Spring precipitation has been linked to earlywood vessel size in sessile oak (González and Eckstein, 2003; Fonti and García-González, 2008), and could thus result in higher xylem conductivity that year.

Beyond temporal variability in precipitation, there is evidence for a more structural water limitation of growth in the observation that individual beech growth (pre-drought) is negatively related to $\delta^{13}C$ in the reference year (and thus to water use efficiency). This is consistent with the idea that the more slowly growing trees are more strongly limited by water. Such a structural water limitation was unexpected, given the relatively high precipitation at our sites, and the fact that growth was not lower at the drier sites (at least in the analysis where the site of Buggenhout is excluded). It cannot be excluded that variability in water availability for individual trees is linked to variability in nutrition. In the Ardennes, growth may be limited by the amount of available soil, which can vary greatly locally due to variability in soil depth and stoniness, and which should affect both water availability and nutrition at the same time.

In chapter 3 we concluded that there is an effect of increased complementarity for water with lower water availability, and this acted on the spatial scale only, not on the temporal. Complementarity was higher on dry sites (because there, mixing benefitted beech growth without negatively affecting oak growth), but it did not seem to provide relief during drought stress (the positive effects of mixing on beech growth were reduced in drier years).

Belowground complementarities in mixture (among others improved water relations) could enable trees to invest more resources aboveground and lead to increased canopy packing, which in turn leads to higher photosynthesis and overyielding (Ammer, 2019). But this does not necessarily benefit trees under drought, because faster growing trees may be more dependent on water for their functioning (Forrester, 2015).

It appears that mechanisms leading to complementarity specifically under drought play no important role at our sites. One example is hydraulic lift, which can be performed by deep oak roots (Zapater et al., 2011). This would facilitate beech under drought, and is hypothesised as mechanism by Pretzsch, Schütze, and Uhl (2013), who did observe a release from drought stress in mixture with sessile oak. Hydraulic lift may however not be very important here because most of our study sites have relatively shallow soils. Another often quoted mechanism that probably plays no role of importance here is a differential isohydric behaviour, where the the most

isohydric species (beech in this case) halts its functioning earlier under low water availability which may then benefit the other species (Scherrer, Bader, and Körner, 2011).

As water availability is probably not an important factor that explains variability in growth among sites, **nutrition** is a likely candidate. Complementarity for nutrients could partly explain overyielding, as oak and beech have differential rooting patterns which can lead to a better exploration of the soil. An additional mechanism could be a differential preference for the form in which nitrogen is taken up, though evidence for this is scarce (Schulz, Härtling, and Stange, 2011). If complementarities for nutrition are part of the cause of overyielding, they could also be part of the reason for why mixing did not improve tolerance to drought. Improving growth, without improving water relations would lead to trees that are more dependent on a stable water supply (Dziedek et al., 2016).

From the lasso models we observe that **temperature** matters, but generally less and less consistently than precipitation (appendix B.3). Interpreting the temperature-growth relationship is more complicated because it can include winter frost, late frost, and high summer temperatures aggravating droughts. Sessile oak tends to suffer more from cold temperatures (positive relations between temperature and growth), whereas beech suffers more from warm temperatures (negative relations). Differences in temperature sensitivity between the species, should add to asynchrony and thus to community stability.

Masting affects growth, because reproduction requires resources that could otherwise be used for wood formation (Hacket-Pain et al., 2015), and its irregular nature should have a destabilising impact. Because masting is generally synchronised within, but not among species, this destabilising effect would be a cause of asynchrony among populations, and thus partially neutralised at the community level. The same could be said about **insect attack and pathogens**, to the extent that these are species specific. Unfortunately, we do not have the historical data on masting and herbivory or pests that would allow testing this hypothesis, but on other sites, mixing has been found to provide protection to specialist herbivores (Bauhus et al., 2017; Jactel, Moreira, and Castagneyrol, 2021).

5.3.3 Conclusion

A trade-off between productivity and sensitivity to stress exists, and this entails a risk that overyielding jeopardises resistance and resilience of trees. We observed this principle for beech, where faster growth in mixtures led to a higher exposure to the 2003 summer drought (chapter 2). Yet, we observe positive mixing effects on both productivity and stability. We address the different mechanisms that can affect mixing effects on growth, and discuss how they would lead to overyielding, stabilisation or both. Precipitation was an important driver of temporal variability in growth, and became even more important in mixture, at least for beech. This is consistent with the idea that faster growth harms ecological stability. We con-

clude that stabilisation must come from other drivers of growth variability, which are mitigated by mixing (such as for example insect attack and pathogens).

5.4 Methodological aspects

5.4.1 Modeling growth

Dendrochronology has been applied to a wide variety of domains such as climatology and archaeology (Büntgen, 2019). Adapting the methodology to suit our specific needs, required solving several challenges. For instance, we study mixing effects on both mean and variability in growth rings. Many dendrochronological studies use detrending to remove unwanted variability, typically leaving only short-term variability in weather conditions (McPartland et al., 2020), thus potentially removing mixing effects that act at lower frequencies. Detrending techniques have been developed that are more sensitive, for example regional curve standardisation, applicable in millenium-length time series, that removes age-trends while preserving lower-frequency variability (Esper et al., 2003; Briffa et al., 2013). Our choice for the growth models has been to use linear mixed models to explain undetrended ring width. Variability that would typically be filtered out by detrending is modeled through random (site, tree) and fixed (time, tree diameter) effects. Fixed effects are then used to model the climate-ring width relationship, and the mixing effects. One important advantage of this approach is that we avoid risking detrending to filter out mixing effects of interest (and possibly interactions) beforehand. A potential drawback is that it was difficult to take into account a potential relationship between mean growth rate and amplitude of high-frequency variability. Tree response to climatic events or disturbances (high frequency) is usually assumed to be proportional to the absolute growth rate (low frequency). Hence detrending typically happens by dividing ring width by the detrending curve, rather than by subtraction (Cook, 1987; Bunn, 2008), whereas in the growth models, high and low frequency variability are treated as additive.

The mixing index models are complementary to the growth models in the sense that by studying the mixing effect on growth, rather than growth itself, we can use growth as an explanatory variable. This way we have a temporal gradient in growth conditions without relying on the climate-growth relationship which can only be incompletely captured in variables, and which ignores non-climatic drivers. The observation that precipitation was unable to explain the mixing index illustrates the added value of the mixing index models. Growth as explanatory variable for the mixing index is detrended in a classical way, because some longer-term trends in growth may well be unrelated to growth conditions, but rather to age or tree size.

5.4.2 Representing climate

When studying climate-growth relationships, an important consideration is how to represent climate. The climate-growth relationship is often not very strong in tem-

perate climates, certainly not for oak which is relatively tolerant to climatic variability (Lebourgeois, Cousseau, and Ducos, 2004). Dendrochronologists have several options to amplify the climate-growth relationship. Often, trees would be selected at marginal sites where tree growth is limited by a specific climatic stressor (Trouet, 2020), but also detrending serves that purpose.

Weather conditions (precipitation and temperature) are often recorded on a daily base, and aggregated to a monthly resolution for use in dendrochronological analysis (Fritts, 2012; Zang and Biondi, 2015). The monthly resolution is to some extent arbitrary and unrelated to tree functioning. Weather events (such as droughts) may be better represented by the climatic variables when they, by chance, align with the calendar. Calendar months present a compromise between representing climate with sufficiently fine grain while avoiding statistical issues related to a large number of explanatory variables, but many other choices could be made.

A specific challenge is that we are interested in how mixing affects the climate-growth relationship, in a situation where this relationship is not very strong. A finer-grained representation is thus useful. This motivates the approach of generating a large number of candidate variables, even if it required solving and to some extent accepting the statistical consequences. Linear regression models do not generally cope well with a large number of inter-correlated predictor variables. One issue is that too many degrees of freedom in fitting a model leads to overfitting, and this is solved by regularisation (the lasso procedure, Tibshirani 1996). Rather than restricting the number of explanatory variables in the model as is typically done in multiple regression, the coefficients associated to these variables are restricted (shrinkage). A second issue related to the large number of variables, is that any unrelated climate variable may show a statistical relationship with growth, just by chance. The probability of this happening increases with the number of variables. Indeed, some selected variables represent conditions after the growing season, albeit with low (close to 0) coefficients (appendix B.3). The statistical relationship may occur by chance, but there could also be an effect of autocorrelation within the climatic data. This could arise when atmospheric conditions at continental scale (for example the north Atlantic oscillation) persist for several months and affect local weather conditions. Tree growth may be linked to such persistent atmospheric conditions (Trouet, 2020). On the other hand, there is an argument for why the procedure is sufficiently conservative. In the few cases where no variable was selected using cross-validation and we relaxed the lasso-penalty in order to obtain a variable at all, the chosen variable represented spring precipitation, which is consistent with the results at other sites. The potential noise added by non-causal variables is a price to pay for a more fine-grained representation of the climate-growth relationship, necessary to find mixing effects. Among related regularisation techniques such as elastic net and ridge regression, lasso is the one who has the largest tendency to prune in the available variables (Zou and Hastie, 2005). Ridge regression for example will perform shrinkage of coefficients but no selection. When two climatic variables explain the same variability in growth, the lasso will have the tendency to choose the strongest, which is more likely to be causal.

Another advantage of the method for constructing a precipitation variable, is that its definition differs among sites. If climate variables are not site-differentiated it

is difficult to distinguish between a weak climate response of growth on particular sites, and an insufficient representation of the climate response.

5.4.3 Novel approaches to studying stabilisation

Progress has been made in understanding processes behind the diversity-stability relationships over the last decades (for example Loreau and de Mazancourt, 2013), but a method for quantifying the magnitude of the stabilisation is lacking. Quantifying biodiversity-induced stability is more complex than quantifying overyielding, because some additive effects are stabilising (Jourdan et al., 2021; del Río et al., 2022). We could construct expected growth series as weighted mean of monoculture series, but its stability (expected stability) would not be intermediate to those of the monocultures. The reason is that expected stability would be impacted by asynchrony due to intrinsic species-specific responses to climate (Jourdan et al., 2021; del Río et al., 2022). This is why we use a reference stability, rather than expected stability in order to calculate total stabilisation τ_T (section 4.2).

The proposed partitioning of total stabilisation is aimed at improving mechanistic understanding, but it requires interpretation. While τ_μ and τ_ρ represent the direct (mathematical) stabilising effect of overyielding and asynchrony respectively, the total effect may differ, due to indirect effects. An important advantage of the partitioning ($\tau_T = \tau_\mu \cdot \tau_\sigma \cdot \tau_\rho$) is that it guarantees that every effect on stability passes through one of the pathways. This means that, if overyielding would have indirect effects on stability, these must pass through either τ_σ or τ_ρ . Analogously, indirect effects of asynchrony must pass through either τ_μ or τ_σ . Indirect effects can thus be assessed through statistical relationship between the three components of stability.

Temporal stability is defined as μ/σ , where μ is mean growth (of an individual tree, population or community) over time and σ the associated standard deviation. The underlying idea is that stability remains constant when change in σ is proportional to change in μ . This is a reasonable assumption in the sense that it results in a measure that is independent of the choice of unit, but it is not without consequence. It implies that any effect that decouples μ from σ is recorded as (de)stabilising, including stochastic effects and measurement error. Demographic stochasticity (associated with recruitment, mortality and migration), should be not so important in forests, where we consider stability of growth, rather than the stability in number of individuals. In forests, however, we can expect stochasticity associated with individual trees. This exposes an issue when comparing stability among systems of different sizes. As a source of variability, stochasticity should become relatively less important in larger systems (de Mazancourt et al., 2013). When calculating overyielding, estimating expected yield as weighted mean of monoculture yield depends on the assumption that yield per hectare is independent of the plot size. The equivalent assumption, that stability should be independent of plot size is less obvious. In chapter 4, this issue was avoided by estimating values for stand size $n \rightarrow \infty$. This solution relies on the fact that, in forests, population yield series is calculated as sum of the growth of individual trees, and is thus not readily applicable in different ecosystems.

Next to stochasticity, observer error is a mechanism through which large systems would be measured as more stable (de Mazancourt et al., 2013). This could be an

important factor, but we assume that the precision of tree ring measurements should minimise this effect in our data.

Another issue with temporal stability is that it assumes a stable mean. An issue at the site of Buggenhout (and the main reason for removing its data in two chapters) is that some of the trees were still relatively young and showed an important age trend.

A limitation of the use of temporal stability is that it considers mean yield (μ) and the associated standard deviation (σ), but it does not distinguish between high-frequency and low-frequency variability. This means that age trends are included in σ , and thus interpreted as instability, but it could be argued that long-term age trends in forest growth should rather be interpreted as a change in the average over time. Age trends in a subset of trees at the site of Buggenhout were the main reason for not including them in the analyses of chapters 2 and 3.

5.4.4 Substituting space for time

Time for space substitution is often used for predicting how biological systems will perform in the future under a changed climate. However, there are concerns that trees respond differently to variability at a spatial or at a temporal scale (Klesse et al., 2020; Wu et al., 2022), and our data confirm that there is reason for this concern. We observe that complementarity in mixture increases with water unavailability at the spatial scale, but not at the temporal scale. Trees have multiple ways of dealing with water shortage. When this condition is structural, trees can react structurally (balancing root and shoot), whereas temporal variability needs to be accommodated for physiologically, for example through stomatal or osmotic regulation (Chaves, Maroco, and Pereira, 2003). The longevity of trees is a weakness, as some structural features (for example tree height) cannot easily be reversed in adult trees when climatic conditions harshen. Other properties, such as wood anatomy can change because trees grow a new layer of wood each year, and the hydraulic system can be built to favour safety over efficiency of water transport, trading off potential higher mean functioning for resilience (Lens et al., 2011).

Another uncertainty regarding the ability of trees to remain functional in the future is related to the nature of future stressors or disturbances. Mixing became more beneficial under stronger growth limitation in general, but not for beech when this limitation is water unavailability. This means that mixing has the capacity of buffering future stresses, but to a lesser extent future droughts. Mixing could buffer against pathogen attack (Jactel, Moreira, and Castagneyrol, 2021), which is also expected to increase under climate change (La Porta et al., 2008).

5.5 Practical implications

5.5.1 Effect of climate change on mixtures

The mixture of oak and beech may increase in importance in Europe (Pretzsch et al., 2013), given that climate change may leave some common species such as *Pinus sylvestris* and *Picea abies* too vulnerable (Sáenz-Romero et al., 2019).

Under moderate amounts of climate change, species ranges tend to evolve, as both local extinctions and range expansions are part of the natural dynamics. Climate change nowadays is too fast for species ranges to expand naturally, and introducing non-native species may be helpful (Zhu, Woodall, and Clark, 2012; Corlett and Westcott, 2013; Dumroese et al., 2015). However, there is a reluctance in introducing non-native species because of the risk that they become invasive, or host invasive associate species (Richardson and Rejmánek, 2011; Ormsby and Brenton-Rule, 2017). Another argument for preserving native species is the higher biodiversity associated with them (Ennos et al., 2019).

Beech is expected to be vulnerable to future climate change, due to its limited drought tolerance (Leuschner, 2020) and its competitiveness is expected to diminish in mixtures with oak. We observed shifts in competitiveness, but without evidence that beech suffers from oak competition on our sites. Instead, complementarity seems to protect the mixture against growth limitations, and to stabilise productivity of beech trees. Benefits do depend on the nature of the stressors, and mixing was less potent against incidental drought than against other types of stressors, even if we were not able to pin-point which stresses or disturbances exactly were mitigated. Other potential climate-related vulnerabilities are increasingly frequent late spring frosts (Zohner et al., 2020) and insect attacks or pests (Dukes et al., 2009; Jactel, Koricheva, and Castagneyrol, 2019).

5.5.2 Maximising growth or resilience?

The management choice of species or species combination affects many forest functions and ecosystem services, and requires a balance between various objectives such as increasing biodiversity, maximising carbon uptake and storage and maximising stability of the forest and resistance to future climatic hazards. Often included is the expected net financial return, which depends on forest growth rates but also on the future evolution in economical value of forest products (Hildebrandt and Knoke, 2011; Friedrich et al., 2021). Community ecology has adapted concepts from analogies with economical theory, where a trade-off between performance and risk-avoidance is well-studied. One such example is the insurance effect, which is commonly understood as asynchrony: because temporarily low growth of a specific species is compensated by higher growth of another, mixing provides an insurance against weaknesses of individual species. But the analogy can be extended to include the trade-off between maximising expected performance and avoiding risks, which is central to the concept of insurances (Loreau et al., 2021). Entities would

purchase an insurance cover in order to reduce financial risks, knowingly that it represents an expected net cost. Risks to forests associated with rapid climate change force forest managers to place a higher value on resilience and stability (thus reducing risks), even if that means accepting lower growth or lower expected financial returns (Knoke et al., 2005).

Regardless of mixing, risk avoidance today could mean promoting drought or stress-tolerant species such as sessile oak on sites that would naturally be dominated by more competitive species such as beech. Such choice is not self-evident from a practical point of view, because in many situations it requires forest managers to counter-act the natural succession towards beech (Petritan et al., 2014).

A trade-off between performance and risk-avoidance must not necessarily be the case. An inherent stabilising aspect of fast growth is that it allows for shorter rotation times (overyielding was on average 25%, appendix C.4). As disturbances such as wind throw and fire are stochastic, certain risks can be reduced by shortening life times (Schelhaas, 2008; Cosofret and Bouriaud, 2019). We showed that in the mixture of oak and beech, mixing is capable of increasing growth, without jeopardising stability. Hence, mixing can be key to combining growth with resilience.

5.5.3 Is stabilisation through asynchrony among populations a desirable outcome?

Half the stabilisation associated with mixing happened through asynchrony among species, the other half through stabilisation of species growth (appendix C.4, Figs. 4.2, 4.1). Are both sources of stabilisation equally desirable? Do we settle for stable forest stands, even if individual trees are destabilised? Asynchrony may even be associated with variability at the species level. Indeed, asynchrony requires variability in order to act, and species interactions that enhance asynchrony often destabilise populations (Loreau and de Mazancourt, 2013). To the extent that forest health depends on the vitality of individuals, stability effects at the individual level are to be preferred. If mortality is among the risks, growth stabilisation of individual trees should be expected to be linked to a protection against stresses, and thus against mortality. However, there are aspects of forest resilience that cannot be assessed at the level of individual trees, for example regeneration and nutrient cycling (Trumbore, Brando, and Hartmann, 2015). One specific example of diversity-related stability that plays at higher levels is that a high degree of mortality in one specific species does not cause a loss of the complete stand (Van de Peer et al., 2016).

5.5.4 An ecological niche for the mixture

Theory predicts that species can coexist when interspecific competition is lower than intraspecific competition, and this seems to be backed up by experimental data (Chesson, 2000). Interspecific competition is often not symmetrical, and for coexistence it is necessary that both species experience competition release (Chesson, 2000). This is often not the case in mixtures of oak and beech, which, due to beech dominance, evolve naturally into beech forests, only delayed by management

action favoring oak (Petritan et al., 2014; Maleki, Zeller, and Pretzsch, 2020). We observed that this dominance diminishes on drier sites, and may even disappear, while complementarity increases. Both complementarity and dominance can lead to overyielding, but complementarity helps in maintaining the species composition, whereas dominance tends to steer forest stands towards monocultures. This means that a stable coexistence of sessile oak and beech can be expected in natural conditions towards the drier end of the spectrum, where complementarities gain and dominance loses in importance. So even if mixing leads to overyielding and growth stabilisation throughout the range of study sites, maintaining a mixture with a stable species composition is easier towards the drier end of the spectrum.

5.6 Prospects

5.6.1 Improving climate-growth relationship

Using dendrochronology for ecological questions, we refrained from several dendrochronological approaches that would help obtaining a strong climatic signal.

The procedures of detrending and building master chronologies are specifically designed to amplify the climatic signal (Cook et al., 1990), but we preferred to model growth on undetrended ring width, because detrending would remove signals of mixing along with growth trends. In addition, it would be unreasonable to sample only the extremest of sites, where climatic signals are stronger. Likewise, we did not replace ring width by alternative tree-ring related proxies known to show stronger climatic signals, because we are interested in the ecological relevance of tree growth itself. A potential improvement to our methodology could be to measure wood density of the tree rings so that we can calculate biomass increase, rather than radial increment (Vannoppen et al., 2018).

Using precipitation as measure of temporal variability in water availability does not explicitly acknowledge the role of the soil in buffering water. The methodology could be refined by using estimates of drought based on output from soil water budget models (Brédoire et al., 2020). Non-climatic related drivers such as insect outbreaks and pests would be valuable information, if such information could be found over long time series (Rolland, Baltensweiler, and Petitcolas, 2001).

5.6.2 A better climate-growth relationship could help understanding stabilisation

With the growth models, we model and explain mean and variability of the tree ring widths of individual trees. The extent to which certain effects affect variability (σ^2) within the data can be estimated through several forms of R^2 (partial R^2 , R^2m , R^2c , see appendix, B.5). In chapter 4, we quantify the impact of mixing effects on community stability through mean (μ) and variability (σ) of growth at a population level. We formulate hypotheses about which environmental factors would be behind

altered μ and σ of populations. Such effects could be tested for and even quantified (using R^2 -related measures) using growth models at the population-level. This requires of course that temporal variability in the growth models is sufficiently well explained.

5.7 Conclusion

In general, mixing increases beech growth, at the expense of oak growth, due a dominance of beech over oak. This dominance shifts towards complementarity between species on the drier sites. Over all sites, mixing increases productivity with 25% on average at the stand level (overyielding in terms of basal area increment). An adverse effect of the faster growth of beech is that also its exposure to the 2003 summer drought increased. Beech in mixture is also more dependent on precipitation to maintain the faster growth. Yet, mixing improves the stress-resistance of both species. In years of low growth, the mixing effect on growth becomes even more beneficial for beech, and less detrimental for oak. These effects lead to a temporal stabilisation of both oak and beech populations, which in turn translates to a 10% increase in stability of the mixture compared to a reference based on pure stands. In combination with effects on asynchrony between oak and beech populations, total stabilisation is 21%.

Our results confirm the general idea that beech has higher productivity, whereas oak has higher stability. In this regard, the mixture can be seen as a compromise between these two desirable qualities. But we also show that mixing is more than a compromise. Mixing oak and beech eases the tension between productivity and stability by enhancing both.

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Appendix A

Appendices to chapter 2

A.1 Number of trees

The number of trees deviates from the intended 7 per site, stand and species, due to safety margins and the discarding of unreliable results (Table A.1)

Table A.1: Number of trees for which two valid measurements ($\delta^{13}C_{2001}$ and $\delta^{13}C_{2003}$) were obtained

	Oak		Beech	
	Pure	Mixed	Pure	Mixed
Buggenhout	7	7	7	7
Ave-et-Auffe	7	7	7	7
Baileux	7	7	7	7
Arlon	7	7	6	7
Grune	6	7	7	7
Eupen	7	7	7	7
La Roche	8	7	7	6
Vecmont	7	7	7	7

A.2 Classification of soils according to soil water availability

We classified the study sites into categories of water availability using the following classifiers from the Belgian soil map (Bah et al., 2007): soil texture, drainage class, soil depth and stoniness. We used the classification scheme from Weissen, Bronchart, and Piret (1994), but simplified the numerical scale so that only three classes remain: wet (tendency towards a water excess), dry (tendency towards a water deficit), and optimal.

A.3 Tree and neighbourhood variables

Table A.2: Average values and standard deviations (between brackets) of tree and neighbourhood variables by species, site and stand. M and P stand for respectively mixed and pure stands. D/d: crown to trunk diameter ratio. C130: circumference at 130 cm. ci: Hegyi competition index. See Table 2.1 for site names.

species	site	stand	D/d	C130 (cm)	ci
Beech	BU	M	21.94 (2.41)	172.16 (17.96)	1.14 (0.35)
		P	18.26 (1.84)	140.38 (13.85)	1.69 (0.22)
	AV	M	22.37 (1.46)	146.24 (15.76)	1.31 (0.22)
		P	24.77 (4.70)	132.44 (16.03)	1.33 (0.34)
	BA	M	20.21 (3.00)	152.00 (19.67)	1.69 (0.70)
		P	18.29 (2.67)	147.57 (27.69)	1.89 (0.68)
	AR	M	53.91 (55.95)	183.56 (38.76)	0.75 (0.29)
		P	22.37 (2.72)	198.60 (11.14)	0.53 (0.20)
	GR	M	22.95 (4.59)	151.87 (21.21)	1.57 (0.23)
		P	22.61 (1.85)	140.71 (19.97)	1.46 (0.36)
	EU	M	19.56 (1.97)	203.93 (21.26)	1.08 (0.30)
		P	21.86 (3.12)	193.68 (15.85)	0.61 (0.06)
	LR	M	22.41 (2.77)	171.06 (22.82)	1.35 (0.24)
		P	19.24 (3.79)	187.60 (12.50)	0.63 (0.16)
	VE	M	20.10 (2.67)	157.98 (22.41)	1.64 (0.42)
		P	20.04 (2.63)	175.44 (29.21)	1.05 (0.50)
Oak	BU	M	18.57 (4.08)	173.24 (18.68)	1.16 (0.37)
		P	18.24 (2.83)	169.29 (21.35)	1.34 (0.36)
	AV	M	17.70 (1.30)	164.44 (15.24)	1.19 (0.11)
		P	17.90 (2.06)	168.12 (22.51)	1.16 (0.16)
	BA	M	16.88 (3.14)	130.14 (26.53)	2.13 (0.61)
		P	17.94 (2.20)	115.21 (13.70)	3.01 (0.58)
	AR	M	22.48 (2.50)	176.68 (29.14)	0.74 (0.23)
		P	26.25 (2.86)	169.64 (23.52)	0.63 (0.16)
	GR	M	17.92 (4.86)	135.36 (8.14)	1.79 (0.33)
		P	21.34 (1.18)	131.42 (17.71)	2.11 (0.32)
	EU	M	16.69 (3.28)	180.69 (22.70)	1.23 (0.25)
		P	17.20 (2.64)	164.44 (12.72)	1.33 (0.17)
	LR	M	19.43 (4.10)	142.16 (18.29)	1.72 (0.45)
		P	18.05 (3.32)	163.28 (26.98)	1.46 (0.30)
	VE	M	15.95 (1.59)	157.13 (14.99)	1.56 (0.41)
		P	18.40 (4.46)	167.49 (21.44)	1.51 (0.31)

A.4 Summary of measurements

Table A.3: Average values and standard deviations (in brackets) of measurement results by species, site and stand. M and P stand for respectively mixed and pure stands. $\Delta\delta^{13}C = \delta^{13}C_{2003} - \delta^{13}C_{2001}$, PG: pre-drought growth (mean over 1998-2002). See Table 2.1 for site names.

species	site	stand	$\delta^{13}C_{2001}$ (‰)	$\delta^{13}C_{2003}$ (‰)	$\Delta\delta^{13}C$ (‰)	PG (mm)
Beech	BU	M	-27.69 (0.82)	-27.62 (0.65)	0.06 (0.62)	2.88 (0.73)
		P	-27.78 (0.47)	-26.77 (1.03)	1.01 (0.72)	4.01 (0.47)
	AV	M	-26.44 (1.31)	-26.56 (1.16)	-0.12 (0.57)	2.40 (0.81)
		P	-26.01 (1.24)	-26.23 (1.29)	-0.22 (0.32)	2.68 (0.91)
	BA	M	-27.85 (0.55)	-26.25 (0.77)	1.61 (0.86)	3.70 (0.38)
		P	-27.35 (0.76)	-26.04 (1.13)	1.31 (0.77)	3.23 (1.12)
	AR	M	-28.04 (1.07)	-27.40 (1.01)	0.64 (0.45)	3.62 (1.33)
		P	-27.34 (0.53)	-27.33 (0.58)	0.01 (0.61)	1.73 (0.70)
	GR	M	-28.00 (0.97)	-26.34 (0.97)	1.66 (0.51)	2.69 (0.51)
		P	-27.41 (0.80)	-26.68 (1.61)	0.73 (0.94)	2.50 (0.50)
	EU	M	-26.90 (0.28)	-26.45 (0.76)	0.45 (0.84)	1.93 (0.57)
		P	-27.29 (1.17)	-26.97 (1.25)	0.32 (0.62)	1.37 (0.38)
	LR	M	-28.61 (0.84)	-27.31 (0.86)	1.29 (0.44)	2.00 (0.41)
		P	-27.03 (0.67)	-26.49 (0.48)	0.54 (0.76)	1.18 (0.30)
	VE	M	-27.67 (1.13)	-26.28 (0.87)	1.39 (1.46)	2.69 (1.01)
		P	-28.38 (0.90)	-27.44 (0.86)	0.94 (0.85)	1.70 (0.97)
Oak	BU	M	-27.03 (0.52)	-26.91 (0.59)	0.11 (0.48)	1.78 (0.92)
		P	-26.72 (0.52)	-26.26 (0.32)	0.46 (0.63)	2.58 (0.85)
	AV	M	-26.60 (0.52)	-26.58 (0.48)	0.03 (0.52)	1.91 (0.48)
		P	-25.62 (1.12)	-25.66 (0.62)	-0.04 (0.66)	1.79 (0.55)
	BA	M	-26.62 (0.74)	-26.33 (0.70)	0.29 (0.37)	1.77 (0.37)
		P	-27.00 (0.99)	-26.52 (1.26)	0.48 (0.38)	1.94 (0.46)
	AR	M	-26.34 (0.64)	-25.92 (0.69)	0.42 (0.54)	2.28 (0.41)
		P	-27.12 (0.83)	-26.35 (0.51)	0.78 (0.45)	2.27 (0.89)
	GR	M	-27.40 (0.75)	-26.39 (0.62)	1.01 (0.53)	1.34 (0.31)
		P	-27.34 (0.66)	-26.31 (0.71)	1.04 (0.45)	1.57 (0.41)
	EU	M	-27.14 (1.29)	-26.62 (1.01)	0.53 (0.46)	1.41 (0.56)
		P	-27.84 (1.41)	-26.59 (1.07)	1.25 (0.45)	1.38 (0.24)
	LR	M	-27.16 (1.03)	-26.78 (0.95)	0.38 (0.81)	0.94 (0.32)
		P	-26.39 (1.44)	-26.37 (0.71)	0.02 (0.98)	0.97 (0.21)
	VE	M	-27.60 (1.13)	-27.05 (1.01)	0.56 (0.44)	1.06 (0.45)
		P	-27.56 (0.48)	-27.14 (0.65)	0.42 (0.51)	1.05 (0.31)

A.5 Model results for $\delta^{13}C$ in oak in 2001 and 2003

Table A.4: Model results for $\delta^{13}C$ in oak in 2001 and 2003. In addition to the intercept (i), models test for (ii) mixing, (iii) pre-drought growth (PG) and (iv) both mixing and pre-drought growth. In each case, the site effect was added as a random intercept. Marginal R^2 (R^2_m) represents the variance explained by fixed factors, while conditional R^2 (R^2_c) represents the variance explained by both fixed and random factors (Nakagawa and Schielzeth, 2013).

2001					
(i)	estimate	SE	Pr(> t)	R^2_m	0
intercept	-26.96	0.17	$< 2 \cdot 10^{-16}$	R^2_c	0.16
				AIC	325.61
(ii)					
intercept	-26.96	0.22	$< 2 \cdot 10^{-16}$	R^2_m	4.32×10^{-7}
mixing	-0.0026	0.35	0.99	R^2_c	0.15
				AIC	327.89
(iii)					
intercept	-26.78	0.32	$< 2 \cdot 10^{-16}$	R^2_m	5.3×10^{-3}
PG	-0.11	0.16	0.49	R^2_c	0.19
				AIC	329.00
(iv)					
intercept	-26.76	0.36	$< 2 \cdot 10^{-16}$	R^2_m	5.6×10^{-3}
mixing	-0.04	0.35	0.91	R^2_c	0.19
PG	-0.11	0.16	0.49	AIC	331.25
2003					
(i)	estimate	SE	Pr(> t)	R^2_m	0
intercept	-26.49	0.11	$< 2 \cdot 10^{-16}$	R^2_c	0.07
				AIC	280.88
(ii)					
intercept	-26.40	0.16	$< 2 \cdot 10^{-16}$	R^2_m	5.2×10^{-3}
mixing	-0.23	0.28	0.43	R^2_c	0.09
				AIC	282.93
(iii)					
intercept	-26.7	0.22	$< 2 \cdot 10^{-16}$	R^2_m	0.01
PG	0.13	0.12	0.29	R^2_c	0.06
				AIC	284.28
(iv)					
intercept	-26.61	0.25	$< 2 \cdot 10^{-16}$	R^2_m	0.01
mixing	-0.19	0.29	0.51	R^2_c	0.07
PG	0.12	0.12	0.34	AIC	286.52

A.6 Isotopic values

We obtained tree $\delta^{13}C$ values between -29.73‰ and -24.71‰ for oak, and between -29.90‰ and -24.03‰ for beech, except for two outliers (-30.93‰ and -31.92‰ , both measurements on beech in 2001, respectively on the sites of La Roche and Arlon). These were discarded because the corresponding values measured for the same trees in 2003 were in the range of the other trees. The strong difference in $\delta^{13}C$ between 2001 and 2003 for these trees can be explained either by an erroneous measurement, or by a major change in tree neighbourhood between the two growing seasons. A summary of these measurements is given in Table A.3.

A.7 Relationships between $\Delta\delta^{13}C$, mixing and pre-drought growth

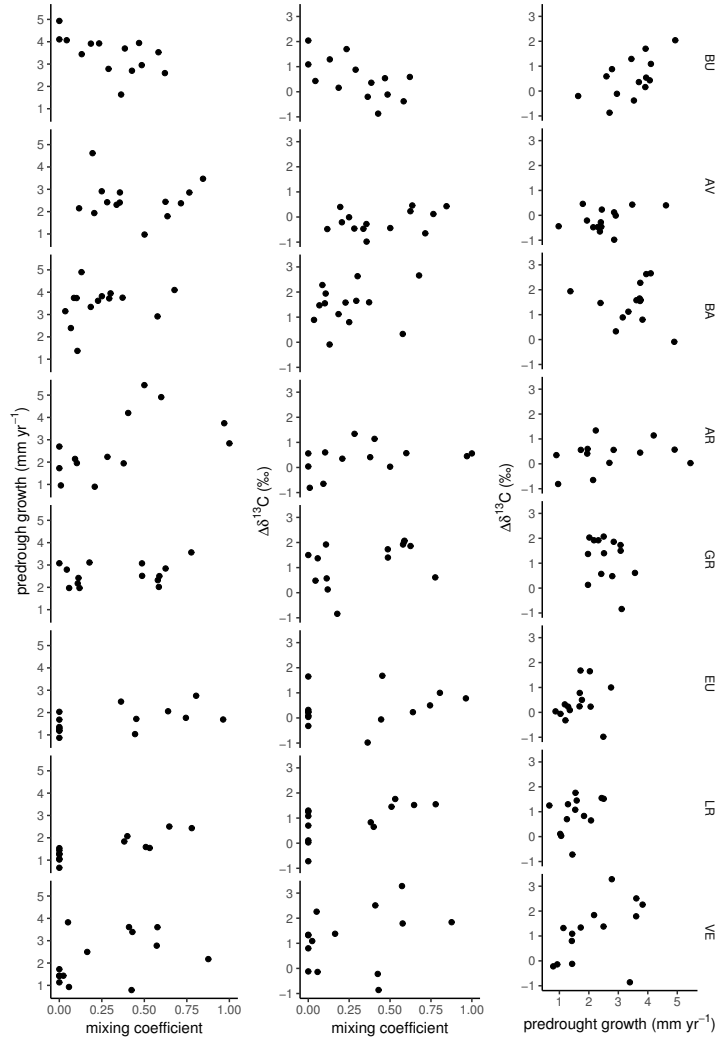


Figure A.1: Relationships between $\Delta\delta^{13}C$, mixing and pre-drought growth for beech, grouped by site. See Table 2.1 for site names.

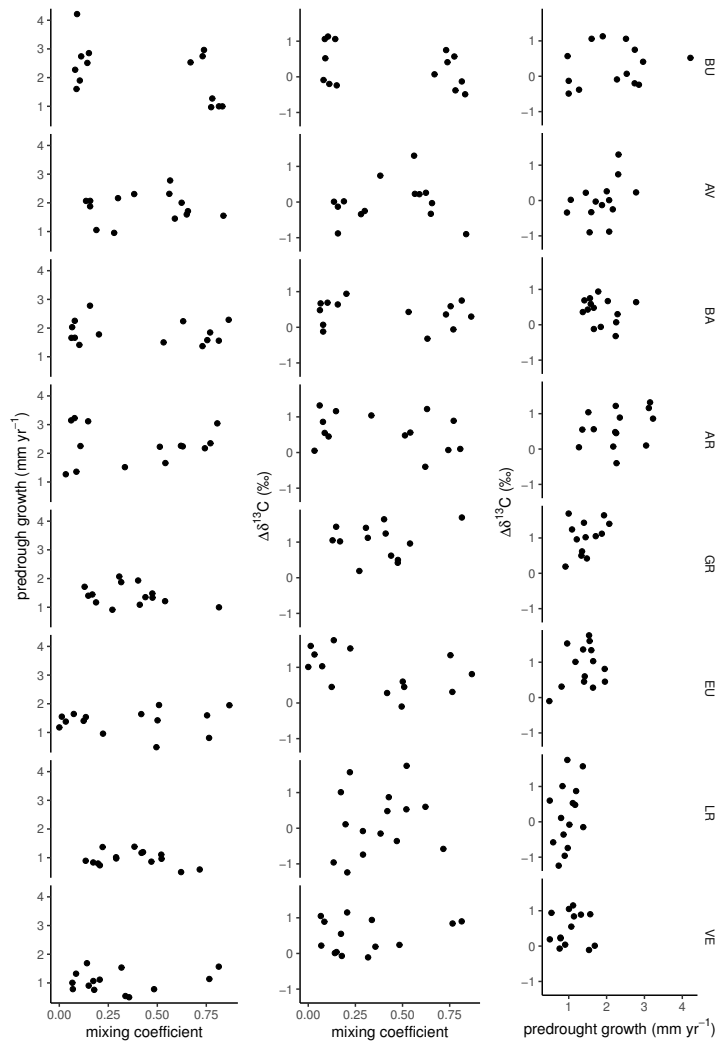


Figure A.2: Relationships between $\Delta\delta^{13}C$, mixing and pre-drought growth for oak, grouped by site. See Table 2.1 for site names.

A.8 Relationships between pre-drought growth, mixing and carbon isotope ratios in both the drought and the reference year

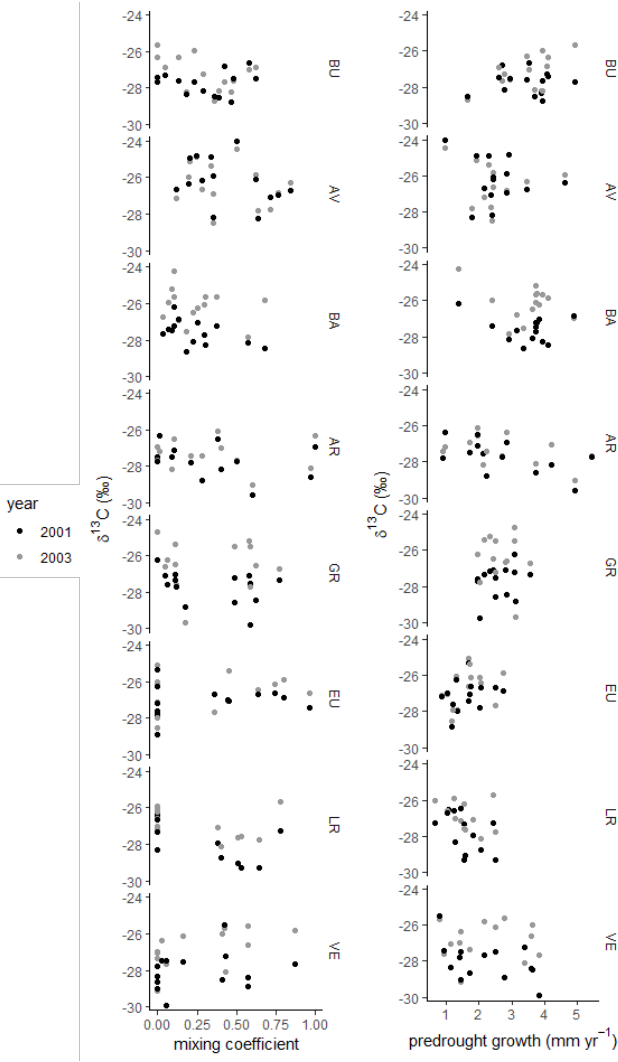


Figure A.3: Beech $\delta^{13}C$ in 2001 and 2003 plotted against both pre-drought growth and mixing, grouped by site. See Table 2.1 for site names.

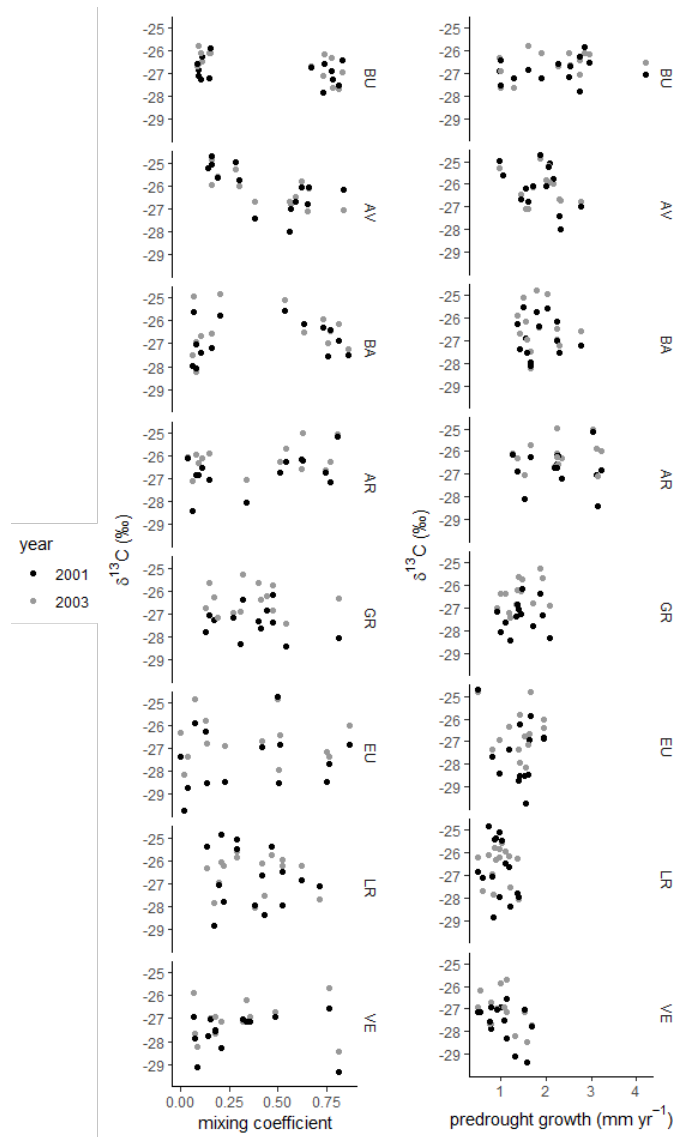


Figure A.4: Oak $\delta^{13}C$ in 2001 and 2003 plotted against both pre-drought growth and mixing, grouped by site. See table 2.1 for site names.

A.9 Additional test for the drought exposure model

Though the models for drought exposure ($\Delta\delta^{13}C$) include a random site effect, this does not exclude the possibility that the site effect may be partially captured by predrought growth (PG) instead, since PG varies among the study sites. The risk is that through the variable PG, site effects would be incorrectly interpreted as effects of predrought growth. As a verification, we refitted the drought exposure models for beech, splitting predrought growth (PG) in a mean per site ($\overline{PG}_{site}$) and a rest that represents intra-site variability ($PG - \overline{PG}_{site}$). We can conclude that the observed effects of PG stem from differences within, rather than between sites, consistent with the intended interpretation.

Beech					
(iii)	est	SE	Pr(< t)		
intercept	0.40	0.80	0.61	R^2_m	0.05
$PG - \overline{PG}_{site}$	0.23	0.09	0.0094	R^2_c	0.36
$\overline{PG}_{site}$	0.13	0.31	0.69	AIC	283.96
(iv)					
intercept	0.28	0.84	0.74	R^2_m	0.06
mixing	0.42	0.28	0.14	R^2_c	0.39
$PG - \overline{PG}_{site}$	0.19	0.09	0.038	AIC	284.50
$\overline{PG}_{site}$	0.13	0.32	0.70		

Appendix B

Appendices to chapter 3

B.1 Classification of sites

The sites were classified according to water availability using the classification scheme from Weissen, Bronchart, and Piret 1994. This scheme is based on the following classifiers from the Belgian soil map (Bah et al., 2007): soil texture, drainage class, soil depth and stoniness. The indices resulting from the classification scheme were used to rank the sites from 1 (driest) to 6 (most humid).

Table B.1: Soil information based on classifiers from the Belgian soil map. Soil depth and stoniness are estimated from map symbols and should be interpreted as indicative only (Bah et al., 2007).

Site	Texture	Drainage class	Soil depth (cm)	Stoniness (%)
Arlon (AR)	Loamy sand	Slightly excessively drained	> 125	0
Ave-et-Auffe (AV)	Stony loam	Well drained	20-40	5-50
Baileux (BA)	Stony loam	Well drained	40-80	5-50
Eupen (EU)	Stony loam	Well to insufficiently drained	40-80	> 5
Grune (GR)	Stony loam	Well drained	> 80	< 50
La Roche (LR)	Stony loam	Well drained	> 40	< 50
Vecmont (VE)	Stony loam	Hydromorphic	40-80	5-50

B.2 Number of trees per site, species and stand

Table B.2: Number of trees cored per site, species and stand.

Site	Stand	Number of trees	
		Oak	Beech
Arlon (AR)	Pure	11	11
	Mixed	11	10
Ave-et-Auffe (AV)	Pure	11	10
	Mixed	10	10
Baileux (BA)	Pure	10	9
	Mixed	10	9
Eupen (EU)	Pure	10	10
	Mixed	11	9
Grune (GR)	Pure	10	10
	Mixed	10	11
La Roche (LR)	Pure	10	10
	Mixed	10	10
Vecmont (VE)	Pure	11	9
	Mixed	10	10
Total	Pure	73	69
	Mixed	72	69

B.3 Results of the lasso models

Climatic variables that were selected (i.e. have a parameter value different from 0) by the lasso models to affect ring width. Each variable represents either total precipitation (P) or mean temperature (average of daily mean temperatures, T) over time frame with the starting date and duration given. When indicated, the variable represents weather conditions of the previous year. From these, only precipitation variables with a positive parameter value were used in constructing the climate variable, used in subsequent models.

Arlon Oak

Month	Day	Duration (days)	year	variable	included	parameter
1	1	135		P	yes	0.0035

Ave et Auffe Oak

Month	Day	Duration (days)	year	variable	included	parameter
1	1	180		P	yes	0.044
6	1	45		P	yes	0.0119
11	16	150		P	yes	0.0094
8	16	165	previous	P	yes	0.0083
5	16	60		P	yes	0.0073
10	1	45	previous	P	yes	0.0032
10	1	180	previous	P	yes	0.0013
6	1	180	previous	P	yes	3e-04

Baileux Oak

Month	Day	Duration (days)	year	variable	included	parameter
3	16	120		P	yes	0.0354
2	16	30	previous	T		0.0308
10	16	60	previous	P	yes	0.0277
4	1	30	previous	P	yes	0.0163
11	1	90		P	yes	0.014
2	1	135	previous	T		0.0094
2	16	120	previous	T		0.0058
5	1	30		T		0.0042
5	1	45	previous	T		0.0039
2	16	75	previous	P	yes	0.0033
11	1	45		P	yes	0.0027
11	16	45		P	yes	0.0027
11	16	30		T		0.0022
11	1	60		P	yes	0.0022
11	16	30		P	yes	3e-04
8	16	30	previous	P		-7e-04

Eupen Oak

Month	Day	Duration (days)	year	variable	included	parameter
3	16	90		P	yes	0.0178
11	16	15		P	yes	0.0012
7	16	45		P		-0.0175

Grune Oak

Month	Day	Duration (days)	year	variable	included	parameter
3	16	45		P	yes	0.0041

La Roche Oak

Month	Day	Duration (days)	year	variable	included	parameter
3	16	15		P	yes	0.0042

Vecmont Oak

Month	Day	Duration (days)	year	variable	included	parameter
4	1	45	previous	T	yes	0.0185
3	16	15		P		0.0153
7	16	15		T		0.0096
7	16	45		T		0.0036
7	16	30		T		0.0012
3	16	45	previous	P	yes	8e-04
4	1	75		T		8e-04
7	16	15		P		-0.002
7	16	120		P		-0.0063

Arlon Beech

Month	Day	Duration (days)	year	variable	included	parameter
3	1	90		P	yes	0.0035

Ave et Auffe Beech

Month	Day	Duration (days)	year	variable	included	parameter
5	1	90		P	yes	0.0799
3	1	15		P	yes	0.0326
3	1	165		P	yes	0.0254
5	1	165		P	yes	0.0201
5	1	180	previous	P	yes	0.0162
5	16	30	previous	P	yes	0.0119
5	1	105		P	yes	0.004
5	1	45	previous	P	yes	0.0033
5	1	60		P	yes	0.0015
8	1	45	previous	T		-0.002
10	1	60		T		-0.0031
6	1	30		T		-0.006
7	16	60	previous	T		-0.0071
2	16	60		T		-0.0098
10	16	45		T		-0.0108

Baileux Beech

Month	Day	Duration (days)	year	variable	included	parameter
3	1	150		P	yes	0.0332
4	1	120		P	yes	0.0309
10	16	60	previous	P	yes	0.0224
2	16	165		P	yes	0.0114
3	1	165		P	yes	0.0055
6	16	180	previous	P	yes	0.0034
5	16	75	previous	P	yes	9e-04
7	1	45	previous	T		< 0.0001
10	1	60		T		-0.007
6	16	60	previous	T		-0.0136

Eupen Beech

Month	Day	Duration (days)	year	variable	included	parameter
5	16	180	previous	P	yes	0.0412
5	1	180	previous	P	yes	0.0408
5	1	105	previous	P	yes	0.0301
3	1	90		P	yes	0.0254
5	1	15	previous	T		0.0186
3	1	15		P	yes	0.0157
4	16	30	previous	T		0.0119
7	1	150	previous	P	yes	0.009
9	16	75	previous	P	yes	0.0066
3	1	30		P	yes	0.0052
12	16	60	previous	P	yes	-7e-04
7	16	105	previous	T		-0.0027
7	16	30	previous	T		-0.0036
12	1	75	previous	P		-0.008
10	16	15		T		-0.0088
3	16	15		T		-0.0103
1	1	45		P		-0.0154
8	1	15	previous	T		-0.0177
9	1	60		T		-0.0545

Grune Beech

Month	Day	Duration (days)	year	variable	included	parameter
2	16	165		P	yes	0.0549
5	16	60	previous	P	yes	0.0147
5	1	75		P	yes	0.0124
5	16	45	previous	P	yes	0.0025
3	1	15		P	yes	1e-04
6	16	165		T		-0.0034
6	16	30		T		-0.0048
6	16	15		T		-0.0051
1	16	15	previous	P		-0.0143

La Roche Beech

Month	Day	Duration (days)	year	variable	included	parameter
5	1	105	previous	P	yes	0.0549
3	1	90		P	yes	0.0409
9	16	75	previous	P	yes	0.0071
5	1	30	previous	P	yes	0.0011
12	16	30	previous	P		-0.014

Vecmont Beech

Month	Day	Duration (days)	year	variable	included	parameter
5	16	90	previous	P	yes	0.0424
2	16	105		P	yes	0.0208
5	16	180	previous	P	yes	1e-04
12	16	15	previous	P		-3e-04
10	1	105		T		-0.0041
6	16	135	previous	T		-0.014

B.4 Performance of constructed precipitation variables

Table B.3: Performance of constructed precipitation variables in terms of R^2 of the linear models $MC_i = \alpha + \beta \cdot prec_i + \epsilon$ (1955-2014), with MC_i (ring width index) the site and species specific master chronology, α the intercept and β the parameter associated to the constructed precipitation variable $prec_i$.

	Oak	Beech
Arlon (AR)	0.15	0.17
Ave-et-Auffe (AV)	0.44	0.55
Baileux (BA)	0.41	0.48
Eupen (EU)	0.16	0.45
Grune (GR)	0.16	0.39
La Roche (LR)	0.15	0.38
Vecmont (VE)	0.13	0.33

B.5 Partitioning of variance of growth data

The total variance in ring widths stems from several sources, which complicates the interpretation of R^2_c and R^2_m values of the growth models. Therefore, we assessed the partitioning of variance of the ring widths among these levels by constructing a series of random effects models for each species.

$$RW_{i,j,k} = s_i + e_{i,j,k} \quad (\text{B.1})$$

$$RW_{i,j,k} = s_i + s_i \times t_{i,j} + e_{i,j,k} \quad (\text{B.2})$$

$$RW_{i,j,k} = s_i + s_i \times t_{i,j} + y_k + e_{i,j,k} \quad (\text{B.3})$$

$$RW_{i,j,k} = y_k + e_{i,j,k} \quad (\text{B.4})$$

$$RW_{i,j,k} = s_i \times y_k \quad (\text{B.5})$$

where $RW_{i,j,k}$ is the ring width of tree j on site i for year k , calculated as the mean of the two ring width measurements taken per tree. s_i , $t_{i,j}$ and y_k are the random effects corresponding to respectively site i , tree j on site i and year k . $s_i \times y_k$ represents the interaction between s_i and y_k .

Table B.4: Partitioning of variance of ring width over sites using the conditional R^2 of random effects models

random effects	Oak R^2_c	AIC	Beech R^2_c	AIC
site	0.234	15082	0.128	24130
site + site×tree	0.460	12494	0.340	22241
site + site×tree+year ¹	0.615	9874	0.508	20112
year ¹	0.154	15847	0.166	23800
site x year ¹	0.443	13178	0.368	22359

¹ in these random effects models, year is used as a categorical variable

B.6 Results of the growth model comparing oak and beech

Table B.5: Results for the model comparing oak and beech growth. Marginal R^2 (R^2_m) and conditional R^2 (R^2_c) represent the variance explained by fixed factors and the variance explained by both fixed and random factors respectively (Nakagawa and Schielzeth, 2013). Significant parameter estimates ($p < 0.05$) are indicated in bold. D: tree diameter at the start of the growing season; mixing: dummy variable that takes 1 for trees in mixed stands and 0 for trees in pure stands; swrank: soil-related variable ranking sites according to water availability (higher values for wetter sites); precipitation: precipitation variable constructed using lasso models.

	Estimate	Std. Error	Pr(> t)
Intercept	1.149	0.1448	< 0.0001
beech	-0.1066	0.1786	0.5505
mixing (oak)	-0.2074	0.09913	0.03728
precipitation (oak)	0.1568	0.008009	< 0.0001
year - 1984 (oak)	-0.006121	0.001048	< 0.0001
year - 1984 (beech)	-0.007787	0.001278	< 0.0001
$(year - 1984)^2/40$ (oak)	-0.001448	0.001102	0.1889
$(year - 1984)^2/40$ (beech)	-0.001493	0.001108	0.1778
D (m) (oak)	0.2014	0.05307	0.0001483
D (m) (beech)	1.033	0.02892	< 0.0001
$D^2(m^2)$ (oak)	-0.452	0.1872	0.01577
$D^2(m^2)$ (beech)	-4.368	0.1079	< 0.0001
beech x mixing	0.3612	0.1415	0.01122
beech x precipitation	0.1944	0.01173	< 0.0001
(difference oak and beech)			
	AIC	R^2_m	R^2_c
	41330	0.2977	0.6203

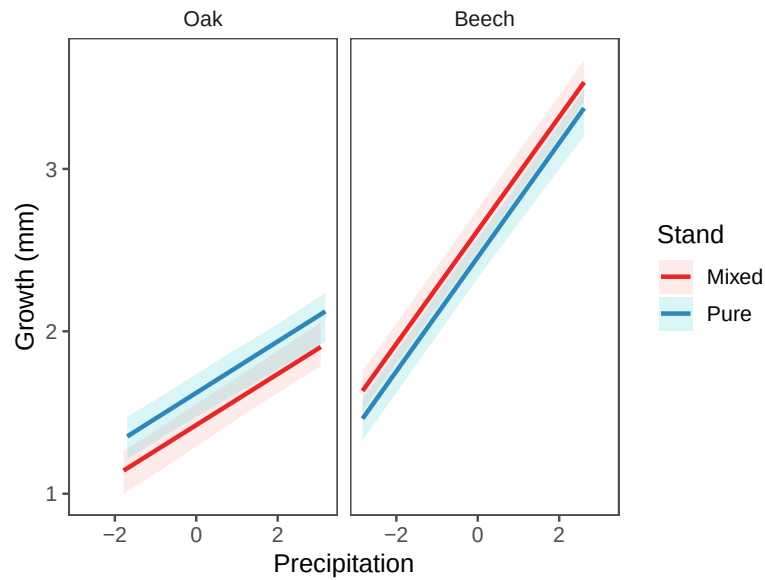


Figure B.1: Predictions of the growth models for oak and beech together using fixed effects only, representing the relationships between growth and precipitation (constructed variable) at yearly resolution for both oak and beech in pure versus mixed stands. Random parameters were set to 0, fixed variables not shown were set to their average value. Shaded areas represent 95% confidence intervals for the fixed effects in pure and mixed stands. See table in appendix B.6 for significances of mixing effects.

B.7 Plots of data and model predictions arranged per site



Figure B.2: Relationships between growth and precipitation (constructed variable) at yearly resolution for both oak and beech in pure versus mixed stands. Regression lines show predictions of the growth models where random parameters (except site) were set to 0. Fixed variables not shown were set to their average value.

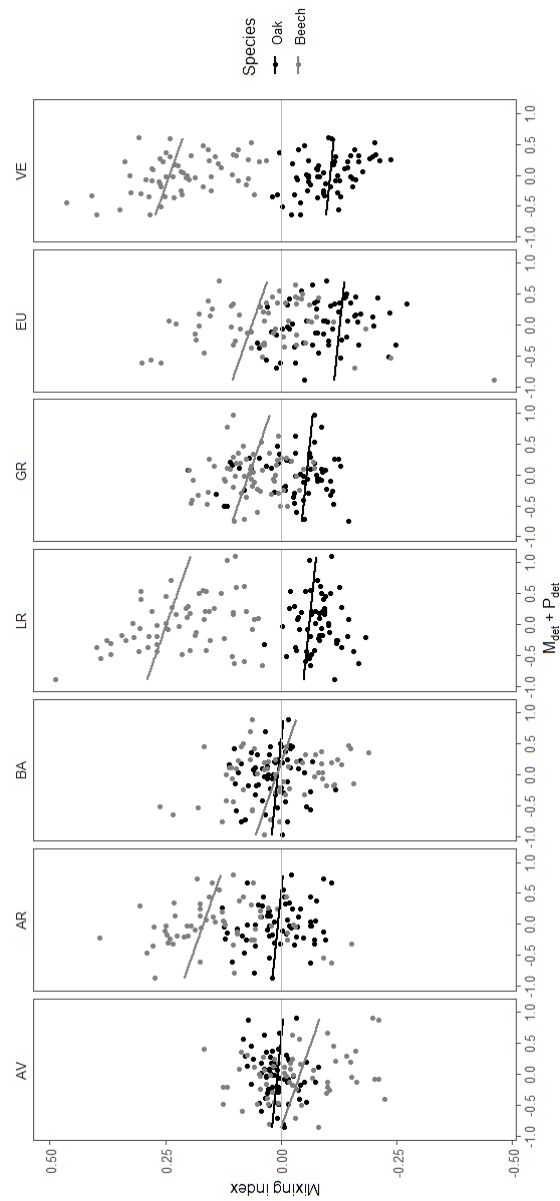


Figure B.3: Relationship between mixing index and detrended growth of trees in both mixed (M_{det}) and pure (P_{det}) stands. Regression lines show predictions of the mixing index models where random parameters (except site) were set to 0. Fixed variables not shown were set to their average value.

B.8 Dendrochronological statistics

Table B.6: Dendrochronological statistics for the period 1955-2014. Mean ring width, first order autocorrelation and mean sensitivity were calculated for individual tree series and averaged over all trees per site and per species.

Site	Species	Mean ring width (mm)	First order autocorrelation	Mean sensitivity	Series intercorrelation	Expressed population signal	Signal-to-noise ratio
AV	Oak	1.63	0.42	0.22	0.75	0.97	30.93
BA	Oak	1.62	0.55	0.24	0.69	0.96	21.79
AR	Oak	2.02	0.53	0.23	0.63	0.96	22.17
GR	Oak	1.26	0.53	0.25	0.74	0.97	33.26
EU	Oak	1.34	0.55	0.21	0.65	0.96	21.93
LR	Oak	1.16	0.55	0.23	0.73	0.97	36.03
VE	Oak	1.16	0.55	0.24	0.66	0.95	19.2
AV	Beech	2.65	0.53	0.32	0.72	0.96	21.47
BA	Beech	2.64	0.48	0.30	0.74	0.96	22.85
AR	Beech	2.84	0.57	0.26	0.58	0.92	11.17
GR	Beech	2.61	0.50	0.25	0.69	0.96	21.09
EU	Beech	1.90	0.63	0.31	0.72	0.94	15.81
LR	Beech	1.96	0.61	0.31	0.69	0.95	20.34
VE	Beech	1.99	0.64	0.27	0.54	0.90	8.68

B.9 Plots of dendrochronological master chronologies

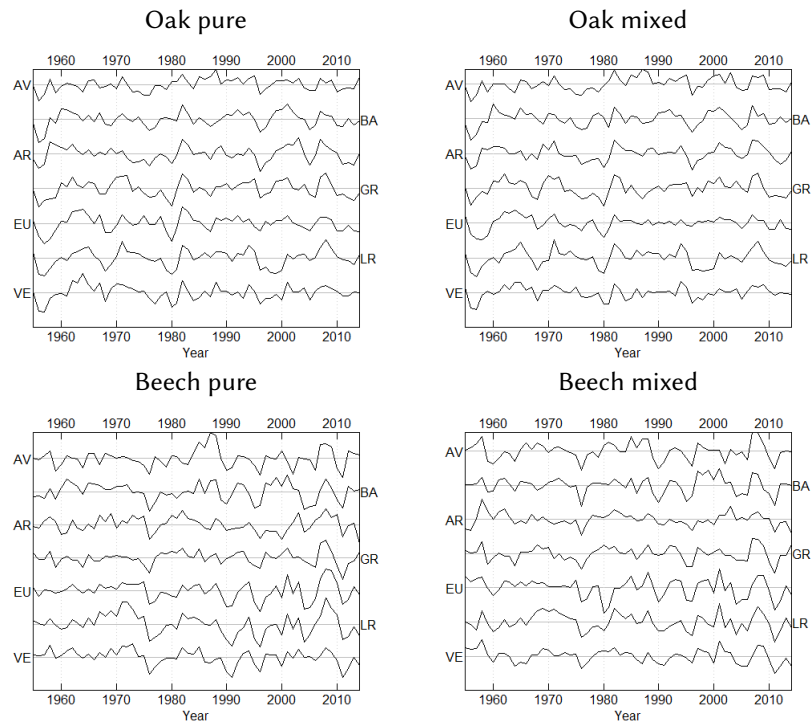


Figure B.4: Master chronologies for all forest stands based on detrended ring widths. Detrending happened using a modified negative exponential followed by smoothing splines Cook and Peters (1981) and Bunn (2008).

B.10 Results of growth models

Table B.7: Model results for the oak and beech growth models. Variables not included were removed based on significance or AIC. Marginal R^2 (R^2_m) and conditional R^2 (R^2_c) represent respectively the variance explained by fixed factors and the variance explained by both fixed and random factors (Nakagawa and Schielzeth, 2013). Significant parameter estimates ($p < 0.05$) are indicated in bold. Response variable: ring width, D: tree diameter at the start of the growing season; mixing: dummy variable that takes 1 for trees in mixed stands and 0 for trees in pure stands; swrank: soil-related variable ranking sites according to water availability (higher values for wetter sites); precipitation: precipitation variable constructed using lasso models.

variable	Oak			Beech		
	Estimate	Std. Error	Pr(> t)	Estimate	Std. Error	Pr(> t)
Intercept	1.431	0.1436	< 0.0001	1.142	0.1575	< 0.0001
<i>year</i> − 1953	-0.00278	0.0007785	0.0004	-0.009614	0.001516	< 0.0001
$(\textit{year} - 1953)^2 / 40$	-0.00362	0.0007787	< 0.0001	-0.007658	0.001359	< 0.0001
D (m)	0.08759	0.04055	0.03	0.8165	0.03751	< 0.0001
$D^2(m^2)$	-0.1512	0.04739	0.001	-1.219	0.04774	< 0.0001
mixing	-0.08978	0.05271	0.09	0.3727	0.0877	< 0.0001
precipitation	0.1521	0.005709	< 0.0001	0.3535	0.01509	< 0.0001
swrank (std)	-0.157	0.109	0.2	-0.2492	0.1204	0.09
mixed x precipitation				0.07246	0.0213	0.0007
precipitation x swrank (std)	-0.07041	0.006037	< 0.0001	-0.07938	0.01197	< 0.0001
mixed x swrank (std)	-0.1153	0.05655	0.044			
	AIC	R^2_m	R^2_c	AIC	R^2_m	R^2_c
	11606	0.1662	0.5271	19900	0.2706	0.5246

B.11 Results of mixing index models

Table B.8: Model results for the mixing index in oak and beech including (a) detrended growth $(M + P)_{det}$ averaged over both species and (b) the constructed climate variable (precipitation) and (a and b) the site ranking according to soil water availability (swrank) in oak. Marginal R^2 (R^2_m) and conditional R^2 (R^2_c) represent respectively the variance explained by fixed factors and the variance explained by both fixed and random factors (Nakagawa and Schielzeth, 2013). Significant parameter estimates ($p < 0.05$) are indicated in bold.

	Oak			Beech		
variable	Estimate	Std. Error	Pr(> t)	Estimate	Std. Error	Pr(> t)
a) using detrended growth						
Intercept	-0.04711	0.009761	0.005	0.1085	2.495	0.047
$(M_{det} + P_{det})$	-0.0136	0.006149	0.027	-0.04731	-4.237	< 0.0001
swrank	-0.05222	0.01054	0.004			
	AIC	R^2_m	R^2_c	AIC	R^2_m	R^2_c
	-1326	0.3508	0.6921	-826	0.01247	0.7087
b) using precipitation						
Intercept	-0.04665	0.009676	0.005	0.1076	0.04346	0.048
precipitation	-0.00193	0.002596	0.5	-0.006011	0.005236	0.3
swrank	-0.05182	0.01043	0.004			
	AIC	R^2_m	R^2_c	AIC	R^2_m	R^2_c
	-1296	0.3462	0.682	-791	0.0009936	0.6924

Appendix C

Appendices to chapter 4

C.1 Proof that τ_ρ , τ_μ and τ_σ form a multiplicative partitioning of τ_T

We prove two equalities: (a) $\tau_T = \tau_\rho \cdot \tau_\mu \cdot \tau_\sigma$ and (b) $\tau_{\mu,\sigma} = \tau_\mu \cdot \tau_\sigma$.

(a) We can easily see that $\tau_T = \tau_\rho \cdot \tau_\mu \cdot \tau_\sigma$ by writing out the definitions of the variables

$$\frac{TS_O}{TS_{ref}} = \frac{TS_O}{\left(\frac{\sum \mu_{Y_O,i}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_O,i} \sigma_{Y_O,j}}} \right)} \cdot \frac{\left(\frac{\sum \mu_{Y_O,i}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_E,i} \sigma_{Y_E,j}}} \right)}{TS_{ref}} \cdot \frac{\left(\frac{\sum \mu_{Y_E,i}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_O,i} \sigma_{Y_O,j}}} \right)}{TS_{ref}}$$

If we then replace one of the instances of TS_{ref} at the right hand side by its definition we obtain the following equality

$$\frac{TS_O}{TS_{ref}} = \frac{TS_O}{\left(\frac{\sum \mu_{Y_O,i}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_O,i} \sigma_{Y_O,j}}} \right)} \cdot \frac{\left(\frac{\sum \mu_{Y_O,i}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_E,i} \sigma_{Y_E,j}}} \right)}{TS_{ref}} \cdot \frac{\left(\frac{\sum \mu_{Y_E,i}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_O,i} \sigma_{Y_O,j}}} \right)}{\left(\frac{\sum \mu_{Y_E,i}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_E,i} \sigma_{Y_E,j}}} \right)}$$

which is obviously true.

(b) In a similar fashion $\tau_{\mu,\sigma} = \tau_\mu \cdot \tau_\sigma$ we replace the variables by their definition

$$\frac{\left(\frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}} \right)}{TS_{ref}} = \frac{\left(\frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}} \right)}{TS_{ref}} \cdot \frac{\left(\frac{\sum \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}} \right)}{TS_{ref}}$$

Again, we replace one of the instances of TS_{ref} at the right hand side by its definition in order to obtain an obvious equality

$$\frac{\left(\frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}} \right)}{TS_{ref}} = \frac{\left(\frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}} \right)}{TS_{ref}} \cdot \frac{\left(\frac{\sum \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}} \right)}{\left(\frac{\sum \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}} \right)}$$

C.2 Correction of upscaled population-level σ

We calculate $Y_{O,i}$ (or equivalently $Y_{E,i}$) using about 10 trees per population. While a reasonable estimate of $\mu_{Y_{O,i}}$ can be made based on a limited number of trees, $\sigma_{Y_{O,i}}$ will likely be overestimated. Due to asynchrony among individual trees, the standard deviation (σ) tend to decrease when more trees are used in the calculation. Ideally, population level calculations should be based on a number of trees (n) high enough so that the calculation of σ has stabilised, thus, so that increasing n_i will no longer affect σ in a meaningful way. Any n larger than this, including $n_i = \infty$ is appropriate. We remove the bias by estimating σ for $n_i = \infty$.

We are able separate the contribution of each cored tree k in population i to $Y_{O,i}$ as $Y_{O,i} = \sum_k \text{contr}_{i,k}$ where $\text{contr}_{i,k} = p_i \cdot \frac{1}{n_i} \cdot \frac{1}{\pi \cdot 18^2 \cdot 10^{-4} \text{ha} \cdot \text{share}_k} \cdot \text{BAI}_{i,k}$ (or equivalent for $Y_{E,i}$). We calculate $\sigma_{Y_{O,i}}$ in function of mean variances and covariances of this contribution.

$$\begin{aligned} \sigma_{Y_{O,i}} &= \sqrt{\sum_k \sigma^2(\text{contr}_{i,k}) + \sum_k \sum_{l \neq k} \text{cov}(\text{contr}_{i,k}, \text{contr}_{i,l})} \\ &= \sqrt{n_i \cdot \mu_{\sigma^2}(\text{contr}_{i,k}) + n_i \cdot (n_i - 1) \cdot \mu_{\text{cov}}(\text{contr}_{i,k}, \text{contr}_{i,l})} \\ &= \sqrt{n_i \cdot \mu_{\sigma^2}(\text{contr}_{i,k}) + n_i \cdot (n_i - 1) \cdot \mu_{\rho}(\text{contr}_{i,k}, \text{contr}_{i,l}) \cdot \sigma(\text{contr}_{i,k}) \cdot \sigma(\text{contr}_{i,l})} \end{aligned}$$

where $\mu_{\text{cov}}(\text{contr}_{i,k}, \text{contr}_{i,l})$ represents the mean covariance between the per-hectare-level tree BAI series of tree i and tree k , and $\text{cor}(i, k)$ the analogous correlation.

If we increase the number of trees in the sample by replacing n_i by $q \cdot n_i$, this will scale $\text{contr}_{i,k}$ and its standard deviation by $1/q$.

We further assume that the standard deviations and correlations among tree BAI series in the sample are representative for the population as a whole.

We then calculate $\sigma_{Y_{O,i}}$ for infinite sample sizes.

$$\begin{aligned}
& \lim_{q \rightarrow \infty} \sqrt{qn_i \cdot \mu_{\sigma^2(contr_{i,k}/q)} + qn_i \cdot (qn_i - 1) \cdot \mu_{cor(contr_{i,k}, contr_{i,l}) \cdot \frac{\sigma(contr_{i,k})}{q} \cdot \frac{\sigma(contr_{i,l})}{q}}} \\
&= \lim_{q \rightarrow \infty} \sqrt{\frac{qn_i}{q^2} \cdot \mu_{\sigma^2(contr_{i,k})} + \frac{qn_i \cdot (qn_i - 1)}{q^2} \cdot \mu_{cor(contr_{i,k}, contr_{i,l}) \cdot \sigma(contr_{i,k}) \cdot \sigma(contr_{i,l})}} \\
&= \lim_{q \rightarrow \infty} \sqrt{qn_i \cdot \frac{\mu_{\sigma^2(BAI_i)}}{q^2} + \frac{qn_i \cdot (qn_i - 1)}{q^2} \cdot \mu_{cov(contr_{i,k}, contr_{i,l})}} \\
&= \sqrt{n_i^2 \mu_{cov(contr_{i,k}, contr_{i,l})}}
\end{aligned}$$

considering that $\mu_{cov(i,k)}$ and $\mu_{cor(i,k)}$ are calculated over the situations $k \neq l$. $\sigma_{Y_{E,i}}$ is calculated analogously.

C.3 Relationship between τ_ρ and φ

Loreau and de Mazancourt (2008) defined a measure of asynchrony in a mixed community as $\varphi = \frac{\sigma_{Y_O}^2}{(\sum_i \sigma_{Y_{O,i}})^2}$.

We can expand this formula as $\varphi = \frac{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \cdot \sigma_{Y_{O,i}} \cdot \sigma_{Y_{O,j}}}{\sum_i \sum_j \sigma_{Y_{O,i}} \cdot \sigma_{Y_{O,j}}}$. This bears resemblance to τ_ρ when we rewrite it as

$$\begin{aligned}
\tau_\rho &= \frac{\left(\frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \cdot \sigma_{Y_{O,i}} \cdot \sigma_{Y_{O,j}}}} \right)}{\left(\frac{\sum \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \cdot \sigma_{Y_{O,j}}}} \right)} \\
&= \sqrt{\frac{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \cdot \sigma_{Y_{O,j}}}{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \cdot \sigma_{Y_{O,i}} \cdot \sigma_{Y_{O,j}}}}
\end{aligned}$$

In fact, $\tau_\rho = \sqrt{1/\varphi}$.

C.4 Results

Table C.1: Calculated indices representing aspects of stability at three levels.

site	AR	AV	BA	EU	GR	LR	VE	mean	P ($\neq 1$)
$TS_{reference}$	3.65	4.33	3.25	4.41	4.06	3.27	5.84	4.12	
TS_{mixed}	5.52	4.90	3.82	5.09	4.45	4.54	6.02	4.91	
τ_T	1.52	1.13	1.17	1.15	1.10	1.39	1.03	1.21	0.0183
τ_ρ	1.06	1.13	1.04	1.10	1.14	1.17	1.08	1.1	
$\tau'_{\rho_{mono}}$	1.12	1.14	1.05	1.06	1.07	1.14	1.03	1.09	
τ'_ρ	1.06	1.12	1.04	1.14	1.17	1.18	1.11	1.12	
$\tau'_\rho - \tau'_{\rho_{mono}}$	-0.06	-0.02	-0.01	0.08	0.10	0.04	0.08	0.03	
τ_μ	1.41	1.03	1.03	1.31	1.08	1.52	1.39	1.25	
τ_σ	1.02	0.97	1.10	0.80	0.89	0.78	0.69	0.89	
$\tau_{\mu,\sigma}$	1.43	1.00	1.13	1.04	0.97	1.18	0.96	1.1	
Population level									
$TS_{E,Oak}$	3.94	6.20	4.67	6.42	4.39	3.87	7.05	5.22	
$TS_{O,Oak}$	4.42	5.20	5.16	8.98	4.57	4.04	7.30	5.67	
$TS_{O,Oak}/TS_{E,Oak}$	1.12	0.84	1.11	1.40	1.04	1.04	1.03	1.08	0.238
$\mu_{Y_{O,Oak}}/\mu_{Y_{E,Oak}}$	1.20	1.01	0.96	1.00	0.81	1.04	0.83	0.98	
$TS_{E,Beech}$	3.51	3.41	2.89	2.79	3.84	2.68	4.97	3.44	
$TS_{O,Beech}$	5.62	3.81	3.31	3.12	3.67	3.77	5.07	4.05	
$TS_{O,Beech}/TS_{E,Beech}$	1.60	1.12	1.15	1.12	0.96	1.41	1.02	1.2	0.0613
$\mu_{Y_{O,Beech}}/\mu_{Y_{E,Beech}}$	1.51	1.05	1.06	1.89	1.29	2.22	1.96	1.57	
Tree level									
$TS_{tree,E,oak}$	3.40	5.09	3.83	4.83	3.47	3.57	4.64	4.12	
$TS_{tree,O,oak}$	3.63	4.26	4.02	5.77	3.45	3.87	4.99	4.28	
$TS_{tree,O,oak}/TS_{tree,E,oak}$	1.07	0.84	1.05	1.19	0.99	1.08	1.08	1.04	0.332
$TS_{tree,E,beech}$	2.59	2.65	2.52	2.14	2.96	2.26	2.65	2.54	
$TS_{tree,O,beech}$	3.50	3.14	2.83	2.44	3.11	2.71	2.90	2.95	
$TS_{tree,O,beech}/TS_{tree,E,beech}$	1.35	1.18	1.12	1.14	1.05	1.20	1.09	1.16	0.00467

C.5 Interpreting τ_μ as measure for overyielding

τ_μ can be used as a measure for overyielding as

$$\tau_\mu = \frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}} / TS_{ref}$$

$$\frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}} / \frac{\sum_i \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}}$$

which simplifies to $\tau_\mu = \sum \mu_{Y_{O,i}} / \sum \mu_{Y_{E,i}}$

C.6 Mixing effects on unevenness in population-level σ

τ_ρ and τ'_ρ both represent the stabilisation through asynchrony under different assumptions regarding the biodiversity effects at the population level. τ_ρ is defined assuming mixing affects population stability (through both μ and σ), whereas τ'_ρ is defined under the assumption that mixing does not. We show that the gap between τ_ρ and τ'_ρ depends only on changes in unevenness among σ of different populations. The assumption that mixing does not affect population-level μ nor σ can be replaced by the assumption that mixing does not affect unevenness in σ among populations.

We calculate the effects of asynchrony (assumption 3 versus 3') in the presence of diversity effects at the population level (assumptions 1' and 2') with the constraint that mixing does not alter the unevenness in population-level σ , that is, σ at population-level is scaled with the same scaling factor p for each population ($\sigma_{Y_{O,i}} = p \cdot \sigma_{Y_{E,i}}$).

We use the definition of τ_ρ (equations 4.6, 4.1)

$$\tau_\rho = \frac{\frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}}}{\frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{O,i}} \sigma_{Y_{O,j}}}}}$$

but we define $\sigma_{Y_{O,i}}$ as $p \cdot \sigma_{Y_{E,i}}$. This allows mixing effects on population-level σ , but not on unevenness. We obtain

$$\begin{aligned}
\tau_\rho &= \frac{\frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \cdot p \cdot \sigma_{Y_{E,i}} \cdot p \cdot \sigma_{Y_{E,j}}}}}{\frac{\sum_i \mu_{Y_{O,i}}}{\sqrt{\sum_i \sum_j 1 \cdot p \cdot \sigma_{Y_{E,i}} \cdot p \cdot \sigma_{Y_{E,j}}}}} \\
&= \frac{\frac{\sum_i \mu_{Y_{O,i}}}{p \cdot \sqrt{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \cdot \sigma_{Y_{E,i}} \cdot \sigma_{Y_{E,j}}}}}{\frac{\sum_i \mu_{Y_{O,i}}}{p \cdot \sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \cdot \sigma_{Y_{E,j}}}}} \\
&= \frac{1}{\sqrt{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \cdot \sigma_{Y_{E,i}} \cdot \sigma_{Y_{E,j}}}} \\
&= \frac{1}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \cdot \sigma_{Y_{E,j}}}} \\
&= \frac{\frac{\sum_i \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j \rho(Y_{O,i}, Y_{O,j}) \sigma_{E,i} \sigma_{E,j}}}}{\frac{\sum_i \mu_{Y_{E,i}}}{\sqrt{\sum_i \sum_j 1 \cdot \sigma_{Y_{E,i}} \sigma_{Y_{E,j}}}}} \\
&= \tau'_\rho
\end{aligned}$$