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Effects of tree species identity and mixing on below-ground resources availability and climate-growth relationships. A case study in mixtures of Scots pine and beech across Europe

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"The greatest enemy of knowledge is not the ignorance, it is the illusion of knowledge"

Stephen Hawking, 1942-2018.

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Summary

European forests are confronted to increasing pressure due to large-scale processes such as global change or deteriorating trends in tree foliar nutrition. Increasing stand species diversity is often suggested as a solution to cope with the detrimental consequences of those processes and numerous studies have highlighted significant species-mixing effects on several phenomenon such as productivity or temporal stability of productivity. However, most studies failed to identify the specific mechanisms at the origin of those effects. We therefore investigated to what extent species mixing improves resource availability and/or lowers ecological constraints along gradients of ecological conditions across Europe for a given couple of species. More specifically, we investigated three types of processes that are considered as major determinant of forest growth: water or nutrient related processes and climate-growth relationships.

We explored the variability of the influence of species interaction on these processes along a network of study sites covering a large part of continental Europe and thus, under distinct environmental conditions. Each site was composed of one mixed stand of beech (*Fagus sylvatica* (L.)) and pine (*Pinus sylvestris* (L.)) and the corresponding monocultures, all exposed to similar ecological conditions. We used beech and pine as model species because of their large common distribution range in Europe and because of their strong differences in term of functional traits. Differences in functional traits potentially important for the mechanisms considered include differences in rooting pattern, life form (evergreen *vs.* deciduous), hydraulic strategy (isohydric *vs.* anisohydric), duration of vegetation period, canopy architecture, leaf lifespan or litter decomposition rate.

We first analysed the drivers behind the spatial and temporal variation in species-mixing effects on water-related processes. To do so, we used 22-years time-series of wood carbon isotopic composition (δ^{13}C) from

a subsample of 17 sites from the network. $\delta^{13}C$ is an indicator reflecting the balance between carbon uptake (A) and stomatal conductance (g_s). Under limiting soil water conditions, this indicator is strongly related to g_s. We found strong differences in pine and beech average $\delta^{13}C$ level, suggesting that the two species display distinct patterns of management of the compromise between CO_2 assimilation and H_2O loss. Despite this strong difference in physiological functioning, both species displayed similar spatial and temporal variability of $\delta^{13}C$, indicating that the main environmental drivers are similar for beech and pine. We also found strong spatial variations of species-mixing influence on wood $\delta^{13}C$ that are globally coherent with the existing framework stating that species-mixing effects should increase with increasingly limiting conditions, provided that species interactions improve the limiting growing condition. However, our results also highlighted the importance of taking species characteristics and potential tipping point into account when analysing species-mixing effect along such gradient. Indeed, in benign conditions (sufficient soil water resource), the balance between positive and negative species-mixing effects depended on the traits of the species involved (positive species-mixing effects for beech, negative for pine). Species that tend to prioritize carbon fixation over water regulation seemed to be advantaged while species with tighter water regulation seemed to experience increased competition. In addition, the relationship between species-mixing effects and environmental conditions did not seem to be linear but rather showed tipping point. Indeed, although species-mixing was globally higher under constraining conditions, past a certain threshold, the environmental constraint could be so strong that the species-mixing effects could not express themselves anymore, leading to a hump-shaped curve of the species-mixing effects/resource availability relationship rather than a straight line. Considering temporal variations of species-mixing effects and conformably to the growing body of literature on the subject, we did not find a globally significant difference of trees reaction to extreme drought events between pure and mixed stands across the gradient. Lastly, we did not find any significant difference in temporal constancy of carbon isotopic series between mix-

tures and monocultures at the species level, nor did we find any overall species-mixing effects on tree reaction to extreme drought.

In addition to analysing species-mixing effects on water-related processes, we measured variations in pure and mixed stands foliar nutrient characteristics (nutrients and ratios of nutrients) for pine and beech along a gradient of site nutritional status. We found that species-mixing significantly influenced most foliar characteristics of both species across all sites. In the majority of cases, mixing improved foliar nutrient content. The contrasted foliar characteristics of pine and beech in pure stands alone could not explain this species-mixing effects, which suggests that nutrient input through litterfall is not the sole mechanism driving species-mixing effects on tree nutrition. We also found that the influence of species interactions on tree mineral nutrition did not follow the expected pattern of increasing effects in harsher conditions. Rather, we found that species-mixing effects were stronger on richer sites and we found no or only minor differences in foliar characteristics between mixed stands and monocultures at the lower end of the gradient. Those results call for a better understanding of the influence of species interactions on tree nutrition and for refinement of the existing framework of spatial variation of species-mixing effects along gradient of nutrient availability.

Lastly, we explored how species-mixing influences climate-growth relationships (both average relationships and drought resistance) across a wide range of climatic conditions. We found large regions of homogeneous average climate-growth relationships suggesting that regional climate is the main determinant of tree growth at this spatial scale. On the other hand, there was limited evidence that species-mixing has a strong influence on tree response to climate. We only found coherent species-mixing effects on sites with limited summer water availability. We concluded that species-mixing effects only occur in case of overwhelming climatic constrain, provided that species traits allow for lifting said constraint. In absence of strong climatic limitation or in situations where species traits do not improve the limiting climatic constraint, the result of species-mixing will depend on environmental conditions (*e.g.*

maximum soil water availability). We found no overall species-mixing effects on drought resistance for either species nor did we found any clear geographical pattern. However, pine displayed increased resistance in mixed stands in sites with high fall water balance, suggesting compensatory growth, further favoured by reduced competition in mixed stands due to earlier stop of beech physiological activity.

Globally, this research calls for refinement of the global framework describing the spatial and temporal variations of species-mixing effects. Better characterization of *i)* species-mixing effects dependency on species traits and *ii)* of the shape of the complementarity-growing conditions relationship appeared to be particularly promising focal points for future research. This research also highlights the pertinence of a sampling design based on an observational network and ecophysiological proxies to investigate large-scale spatial and temporal variations of species-mixing effects.

Abbreviations

A	Carbon uptake
AIC	Akaike Information Criterion
APAR	Absorbed Photosynthetically Active Radiation
a.s.l.	Above sea leavel
BA	Basal Area
BCC	Bootstrapped Correlation Coefficients
BIC	Bayesian Information Criterion
EPS	Expressed Population Signal
FD	Functional Diversity
FR	Functional Richness
Fv	Filling value
g_s	Stomatal Conductance
ICP	Inductively Coupled Plasma
ilr	isometric log-ratio
LAI	Leaf Area Index
P	Precipitations
PAR	Photosynthetically Active Radiation
PC	Principal Component
PCA	Principal Component Analysis
PET	Potential Evapotranspiration
RGC	Relative Growth Change

SBP	Sequential Binary Partition
SD	Standard Deviation
SI	Site Index
SPEI	Standardized Precipitation Evapotranspiration Index
SR	Species Richness
SWA	maximum Soil Water Available
T	Temperature
TC	Temporal Constancy
TS	Temporal Stability
VIF	Variance Inflation Factor
WB_{VP}	Water Balance during the Vegetation Period
WUE	Water Use Efficiency
^{13}C	Carbon-13 isotope
δ^{13}C	Carbon isotope composition

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Chapter 1

Introduction

In this chapter, I establish the general context of this research (section 1.1). I then review the main mechanisms driving species-mixing effects on productivity (section 1.2) and stability of productivity (section 1.3). I further address the matters of spatial and temporal variations of species-mixing effects (section 1.4). Those matters are critical for our understanding of mixed-species functioning and are frequently referred to along the present document. Lastly, I sketch up the outline of the thesis document (section 1.5).

1.1 Increasing interest in mixed-species forests in temperate regions

Historically, in numerous regions of Europe, forest practices based on single-species stands were considered to be among the most relevant forest management strategies. The main reason for this orientation of forest management is that principles of modern forestry were founded in Europe around the 18^{th} and 19^{th} centuries [Kelty et al., 2013], at a period where most European forests were in a poor state due to overexploitation. For instance, during this period in Wallonia, Belgium, the steel industry alone (through charcoal production), used at least 1 400 000 steres of wood annually [Hardy and Dufey, 2012b]. When combined with other forest use, this led to the degradation of Walloon forest resources [Goblet d'Aviella, 1927; Hoyois, 1953; Hardy and Dufey, 2012a]. In this context, foresters aimed to create and manage new forests mainly dedicated to timber production and based on single-species stands of species such as spruce or pine. Such preference for monocultures can be found in the work of early foresters like Hartig, forefather of modern forestry, who advised against the use of mixed deciduous-coniferous forests [Pretzsch, 2005]. Despite the fact that other early-age foresters such as von Cotta, Gayer or Möller evoked potential interest of species-mixing, silvicultural theory and practice still mainly focused on monocultures for decades for a number of reasons. Those reasons include the fact that monocultures are comparatively easier to manage; yield is easier to predict; and results showed that productivity of species such as Norway

spruce (*Picea abies* (L.) Karst.) or Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) proved to be higher in monocultures than in mixtures on many sites in temperate and boreal zones [Schwappach, 1912; Wiedemann, 1949; Assmann, 1970; Schober, 1975; Pretzsch, 2005]. In the last decades, however, the interest of both forest scientists and forest managers in mixed-species forests has greatly increased for several reasons. First, there is an increasing concern about stand stability in the face of both abiotic and biotic disturbances [Ammer, 2019; Jactel et al., 2005; Jucker et al., 2014; Morin et al., 2014]. Forest practitioners and forest scientists also realized that mixed-species forests could provide a larger range of ecosystem services [Nadrowski et al., 2010]. In addition, numerous studies have shown that mixed stands are generally preferred over monocultures when it comes to forest recreational value [Filyushkina et al., 2017; Nielsen et al., 2007]. Lastly, scientists and forests managers came to realize that mixed forests have a potential for high productivity [Ammer, 2019; Liang et al., 2016]. Many studies have shown that mixed stands can be significantly more productive than monocultures, although the results may depend on the reference chosen to define productivity. Indeed, even if a species is more productive in mixture compared to the yield expected from its monoculture, the mixed stand as a whole can have lower yield than the most productive monoculture [Kelty, 1992]. Nevertheless, a recent meta-analysis found that in similar site conditions and for similar tree age, the average productivity of mixed-species stands was 24% higher than the mean productivity of the corresponding monocultures [Zhang et al., 2012]. In addition, studies such as the ones from Jucker et al. [2014] and del Río et al. [2017] found that species-mixing increases stability of productivity at the community level.

1.2 Main determinants of species-mixing effects on productivity

In this section, I will first discuss about the effects guiding the relationships between species in mixed forests. I will then consider the processes driving species-mixing influence on productivity (influence on resource

supply, fraction of resource acquired and resource use efficiency). Lastly, I will evoke the importance of considering species functional traits when analyzing potential complementarity effects in mixed stands.

1.2.1 Effects and mechanisms at play in mixed-species forests

Improvement of productivity in more diverse forests results from many processes that belong to two main effects: the complementarity effect and the selection effect. The selection effect refers to the dominance in mixed species stands of a species with particular monoculture traits, usually productivity [Loreau and Hector, 2001].

Selection effect can be positive, negative or neutral depending on whether the dominant species is a very productive or very unproductive one. It arises from stochastic (increased probability for some species to display extreme trait values in more diverse communities) and deterministic processes, such as competitive reduction or facilitative interactions, allowing for those high performing species to have large impact on ecosystem properties [Loreau and Hector, 2001; Fox, 2005; Van de Peer et al., 2018]. In this context, the most competitive species regarding a given resource is the main driver of the resource level and the main determinant of the plot productivity. Recent studies in young tree communities have found that selection effect may be an important driver of positive diversity effects [Tobner et al., 2016; Van de Peer et al., 2018] and that the relative importance of selection and complementarity effects depends on environmental conditions [Mori, 2018]. The complementarity effect is defined as trait variations between the species involved allowing for a permanent association of those species. Those traits differences between co-occurring species enables the community to have a more complete use of the available resources which, in turn, leads to improved collective performances [Ammer, 2019; Loreau, 2000]. Complementarity effect actually refers to a large range of mechanisms that are further grouped into two categories: mechanisms belonging to competitive reduction and those belonging to facilitation [Vandermeer, 1989]. Facilitation indicates situations where a species directly improves

resource availability, biotic or abiotic conditions for another species [Forrester and Bauhus, 2016]. One common example of such process is the association of N_2-fixing species to other species that do not have the ability to use atmospheric nitrogen. Another example of facilitation concerns the association of species allowing for hydraulic redistribution. Hydraulic redistribution designates a situation where a deep-rooted species has access to water in deeper and moister soil layers and redistribute it in more superficial layers where it can benefit shallow-rooted species. Competitive reduction is the process by which differences in species traits allows inter-specific competition in mixtures to be lower than intraspecific competition in monocultures [Scherer-Lorenzen et al., 2005]. A common example of such effect is the association of species with distinct temporal and/or spatial stratification patterns (differences in rooting depths or root vertical distribution, in crown shapes, in growth seasonality). Forest management examples includes stratified mixed-forests of sun-demanding species in the upper stage and shade-tolerant species in the understory. Numerous studies have highlighted these processes both concerning the exploitation of above- [Forrester and Albrecht, 2014; Forrester et al., 2018] and belowground resources [Brassard et al., 2013; Seidel et al., 2013; López-Marcos et al., 2018]. Facilitation and competitive reduction often occur simultaneously and their respective effects are difficult to disentangle, leading authors to refer to it collectively using the term "complementarity" [Forrester, 2014]. Complementarity is often the result of multiple mechanisms depending on one another. For instance, [Binkley et al., 1992a] found that in mixed stands of *Eucalyptus saligna* (Sm.) and *Albizia falcataria* (L.) Fosberg, improvement of nitrogen availability was associated with increased stand-level light interception and light-use efficiency.

Although competitive reduction and facilitation may have a positive effect on limiting factors (improvement of availability, uptake or use efficiency of a limiting resource, reduction of the constraint associated with a non-resource limiting factor), those effects could also have negative implications. Indeed, improved availability of a resource might be associated with increased competition for another one. For instance,

improvement of nutrient availability could lead to increased aboveground biomass according to the balanced-growth hypothesis [Shipley and Meziane, 2002], which, in turn, could induce a higher level of competition for light or increased water transpiration [Forrester et al., 2010]. Therefore, mixing effects result from a balance between positive and negative effects of species interaction.

1.2.2 Species-mixing influence on productivity

The production ecology equation [Monteith et al., 1977] is often used as a framework to describe how species-mixing influences stand productivity by releasing a resource-related constraint:

$$\begin{aligned}\text{Gross primary production} = \text{resource supply x} \\ \text{fraction of resource acquired x} \\ \text{resource use efficiency}\end{aligned} \tag{1.1}$$

This equation is an interesting framework to analyse patterns of woody biomass production ($Mg.ha^{-1}.year^{-1}$) (after subtraction of C allocation to respiration and non-woody tissues in order to get net primary productivity) in relation to supply ($Mg_{resource}.ha^{-1}.year^{-1}$), capture (proportion of available resource taken up) and use of nutrient, light and water ($Mg_{biomass}.Mg_{resource}^{-1}$) [Forrester, 2014; Richards et al., 2010].

Several authors such as Loreau and Hector [2001], Carroll et al. [2011] or Fox [2005] have proposed frameworks to explain the effects of biodiversity on ecosystem functioning. Among those frameworks, the additive partitioning one (AP) from Loreau and Hector [2001] is certainly the one that has been the most widely used. This framework allows to separate species-diversity effects on ecosystem processes into two classes: selection effects and complementarity effects (those effects are presented in section 1.2 of the document). Although the AP framework is certainly useful to interpret results from biodiversity-ecosystem functioning experiments from that perspective [Loreau and Hector, 2001], it does not give

information about the biological processes driving those diversity effects [Loreau et al., 2012; Ammer, 2019]. In addition, both complementarity and selection effects depend on biological processes involving resources, such as competition. As a result, numerous reviews such as the work from Forrester and Bauhus [2016] aiming at analysing the spatial and temporal variations of species-mixing effects depending on environmental conditions, focused on frameworks more directly related to biological mechanisms such as the Monteith Equation (Equation 1.1).

As our objectives were to analyse species-mixing influence on resources along gradients of spatial and temporal conditions and to assess how this could contribute to the higher productivity observed in the mixed stands compared to the monocultures, we selected the Monteith framework, as a reference.

1.2.2.1 Resource Supply

Many studies have highlighted the fact that **nutrient supply** is influenced by species-mixing in many situations through diverse mechanisms. For instance, symbiotic nitrogen fixation is an important N_2 source in some forest ecosystems. In such ecosystems, the increased nutrient availability provided by a N_2-fixing species to one or several other(s) can result in higher stand productivity compared to single-species stands [Binkley et al., 1992b; Forrester et al., 2006b; 2007]. In addition, interspecific differences in canopy structure and leaf characteristics (morphology, phenology and physiology) may lead to increased availability and uptake of gaseous and dissolved elements (NH_4^+, NO_3^-, NO_2^-, NOx, organic N) by leaves [Schwarz et al., 2014]. Increased canopy packing in mixtures can also lead to increased litter production on a surface base [Jucker et al., 2015; Pretzsch, 2014; Scherer-Lorenzen et al., 2007] along with modification of microclimate in the understory (reduced temperature variation, increased soil moisture... - von Arx et al. 2013; Crockatt and Bebber 2015). Such effects can lead to faster litter decomposition and increased nutrient cycling rates [Prescott, 2002; Schwarz et al., 2014; Jucker et al., 2015]. Species diversity can also influence decomposition and mineralization rates by changing the litter quality. For

instance, transfers of nutrients from high quality litters to more recalcitrant ones can stimulate decomposition of the latter. Conversely, decay of litters from co-occurring species can be slowed down by release of decomposition inhibitors (such as phenolics and tanins) [Gartner and Cardon, 2004]. Species-mixing effect on topsoil conditions (pH), detritivores population (such as earthworm) and decomposer community and activity [Hansen and Coleman, 1998] can also alter litter decomposition [Augusto et al., 2002; Gartner and Cardon, 2004; Guckland et al., 2009; Hättenschwiler et al., 2005; Richards et al., 2010; Rothe and Binkley, 2001; Saetre et al., 1999]. Shared mycorrhizal networks between species can also improve the total amount of nutrients (and water) available to the trees [Simard et al., 2012].

Species-mixing has also been shown to influence **water supply** through different mechanisms. For instance, several studies have reported that trees may benefit from the ability of coexisting species to access and redistribute water from deep, moist soil horizons [Brooks et al., 2002; Neumann and Cardon, 2012; Prieto et al., 2012]. Recently, studies conducted on young tree saplings of temperate species showed that hydraulic redistribution may be an important water source for neighboring drought-stressed trees both during intense and moderate drought [Hafner et al., 2017; 2021]. However, contrasted results have been reported in mature temperate forests indicating that even when water is redistributed to upper horizons by individuals from one species, it may not be used by the neighboring trees [Zapater et al., 2011]. Additional research is therefore needed to quantify the relevance of this mechanism for complementarity in temperate mixed forests. Reduced competition for water resources in mixed species stands is also often expected due to spatial and/or temporal stratification. For instance, differences in rooting depth, fine-roots density profile, roots architecture or root density could lead to reduced interspecific competition for water compared to intraspecific competition [Schume et al., 2004; Schwendenmann et al., 2015]. Differences in canopy structure between species influence the proportion of precipitation that is intercepted, which in turn influence the stand water availability [Augusto et al., 2015]. Transpiration, water-use efficiency and drought re-

action (isohydric *vs.* anisohydric species) characteristics of co-occurring species are key factors determining the competition level those species experience in mixed-species stands. For instance, admixing a species with another one displaying less pronounced stomatal control can lead to enhancement of drought stress due to increased competition for water [Gonzalez de Andres et al., 2018]. However, predicting the outcome of species mixing effects on the complementarity/competition balance based on such species characteristics is complex considering that traits are not independent. For instance, species with non-conservative water strategies (late control of water consumption through stomatal resistance during a dry period) are often associated with deep root systems. In such case, the outcome of species mixing will depend not only on the water consumption of the two species but also on differential access to belowground water resources and on root competition (*e.g.* exclusion of one species from deeper horizons) [del Castillo et al., 2016; Grossiord et al., 2014a]. Species-specific differences in litter characteristics have also been shown to impact water storage, evaporation and runoff from the organic horizon [Chen et al., 2018; Ilek et al., 2015].

Species-mixing effects on **Photosynthetically Active Radiation (PAR) availability** and **absorption** are closely related as they both strongly depend on stand structure. PAR availability and absorption can increase in mixed stands compared to pure ones because those stands often present strong differences in canopy structure. Such differences can result, for instance, from the association of a light-demanding species in the upper canopy and a shade-tolerant one underneath, leading to reduced shading and higher Absorbed Photosynthetically Active Radiation (APAR) for the tallest species [Forrester, 2017]. Aside from changes in stand canopy structure, complementary crown shapes of co-occurring species can lead to increased APAR for individual trees through more efficient canopy packing. Temporal changes in canopy structure can also occur if some species of the mixtures lose their leaves when others do not. Although this last effect may be significant in tropical or sub-tropical regions, it is not expected to be highly relevant for temperate or boreal forests considering that, even if some species keep their leaves while

other do not, it happens during periods of the year where their growth is almost null [Forrester, 2017; Sapijanskas et al., 2014]. Species-mixing can also modify crown architecture parameters (crown length and width, leaf area) and lead to increased tree and stand APAR [Forrester, 2017; Forrester et al., 2018; Guisasola et al., 2015; Sapijanskas et al., 2014].

1.2.2.2 Belowground resource uptake

Differences in root characteristics (rooting depth, fine roots density profile...) can induce belowground niche partitioning and reduced competition, improving global nutrient and water uptake [Brassard et al., 2011; 2013; Jacob et al., 2013; Jose et al., 2006; Lang et al., 2014; Richards et al., 2010; Schmid and Kazda, 2002; Valverde-Barrantes et al., 2015]. Indeed, several studies have shown that differences in species rooting characteristics lead to higher vertical and horizontal soil exploration in mixed stands compared to monocultures and therefore, to increased fine root productivity [Brassard et al., 2013; Lei et al., 2012; Sun et al., 2017]. Such increased soil exploration can be caused by vertical root stratification leading coexisting species to occupy distinct soil layers [Laclau et al., 2013; Bolte and Villanueva, 2006; Schmid and Kazda, 2001]. In contrary, Meinen et al. [2009] found no vertical rooting stratification in mixed species stands because the species involved displayed similar rooting patterns, illustrating the importance of trait variations in species interactions.

Total volume of explored soil and shared mycorrhizal networks between species can also improve the total amount of nutrient and water available to the trees [Simard et al., 2012; 2015]. Indeed, studies have shown that fungal diversity can be higher in mixed species stands compared to monocultures [Buée et al., 2011] and that such increased belowground biodiversity can lead to higher aboveground productivity [Wagg et al., 2011]. However, the processes associated with mycorrhizal diversity and their effects on trees performances (nutrition, productivity...) are complex. For instance, other studies such as the one from Lang and Polle [2011] have found that species-mixing effect on nutrient supply through increased mycorrhizal diversity depend on tree species identity. Pena

and Polle [2014] also showed that ectomycorrhizal assemblage improves inorganic N uptake only under environmental constraint such as drought events. In addition, Fruleux et al. [2018] found no significant differences of ectomycorrhizal communities between pure and mixed stands and no fine root vertical segregation between species. Those results led them to conclude that belowground processes do not drive the aboveground overyielding observed in their sampling sites and that aboveground drivers should be considered.

In addition, total resource uptake can increase due to chemical stratification if co-occurring species have different nutritional needs or distinct mycorrhizal associations [Richards et al., 2010]. Differences between species preferences in term of nutrients chemical forms could indeed result in more complete use of soil nutrient resource in mixed stands compared to monocultures. For instance, it is well known that there is a high variability in species preferences for various N chemical forms such as N_2, nitrate or ammonium [McKane et al., 2002; Pfautsch et al., 2009; Richards et al., 2010]. Turner [2008] showed that chemical resource partitioning also exists regarding soil organic phosphorous.

Differences in seasonality of root growth and nutrient requirement can also improve total resource uptake [Brandtberg et al., 2004].

1.2.2.3 Resource use efficiency

Resource use efficiency is generally defined as the aboveground biomass growth per unit of resource taken up. However, **nutrient use efficiency** is more commonly estimated through the aboveground biomass growth per nutrient unit in litterfall [Vitousek, 1982] or in foliage mass [Harrington et al., 1995] which are rough estimates of nutrient uptake. In addition, those estimates are dependent on the total foliar biomass, meaning that non-nutrient related mechanisms impacting the foliar biomass (such as light competition) could influence the nutrient use-efficiency. Those difficulties might explain why few studies have focused on species-mixing effects on nutrient-use efficiency and why they report contrasted results [Binkley et al., 1992b; Richards et al., 2010; Stape et al., 2004]. Because

of those contrasted results, Forrester [2017] suggest that species-mixing effects on nutrient-use efficiency may not follow general trends similar to those observed for light- and water-use efficiency.

Species-mixing effect on **water use efficiency** (WUE) is a complex question and contrasted results have been reported. For instance, Kunert et al. [2012], and Schwendenmann et al. [2015] found lower WUE levels in mixed stands compared to monocultures while Forrester et al. [2010] found the opposite effect. WUE being determined by both photosynthetic activity and stomatal conductance, many mechanisms can influence it, which could explain the contrasted results reported in the literature. Those mechanisms include issues associated with water, nutrients and light. For instance, increased competition for water in mixed stands can induce an increase in WUE through higher stomatal regulation [Farquhar et al., 1989]. The higher growth in mixed stands can also increase the risk of suffering from severe drought [Jacobs et al., 2021]. Increased nutrient availability in mixed stands can improve WUE through increased photosynthetic activity [Hobbie and Colpaert, 2004; Brueck and Senbayram, 2009] or improvement of tree reaction to water limitation [Sardans and Penuelas, 2007]. Light availability can also affect WUE, for instance through reduction of self-shading in mixed stands that result in higher photosynthetic activity [Gonzalez de Andres et al., 2018]. Leaf or wood carbon isotopic composition ($\delta^{13}C$ - the ratio between carbon stable isotopes ^{13}C and ^{12}C in photosynthetates) has been widely used to analyse species-mixing effects on WUE because it represents the balance between photosynthetic rate and stomatal conductance. González de Andrés et al. [2017] used $\delta^{13}C$ to explore the effects of interspecific interaction on iWUE in mixed beech-pine stands. They found contrasted response of iWUE to mixing for both species. Indeed, pine iWUE increased when admixed to beech, an effect they attributed to a reduction of self-shading and an increased in competition for water resources leading to higher photosynthetic rate and lower stomatal conductance, respectively. Conversely, when mixed with pine, beech presented lower iWUE due to a reduction of water stress caused by lower canopy interception and lower transpiration rate

and/or an increased in photosynthetic rate caused by lower competition for light. This indicator has also been widely used to analyse species-mixing effects on tree reaction to drought. In this regard, contrasted results have been reported. For instance, [Grossiord et al., 2015] or [Metz et al., 2016] found that species-mixture influence tree reaction to drought while Bonal et al. [2017], Forrester et al. [2016], Martin-Blangy et al. [2021] or Grossiord et al. [2014c] found no significant generalized effect of species-mixing, although the results from both types of studies often depend on several factors. Two main factors can explain the variability of the reported results: site climatic conditions and functional variability among species [Forrester, 2014; Forrester and Bauhus, 2016; Martin-Blangy et al., 2021]. Functional variability is crucial because species with strongly similar characteristics are not expected to show strong complementarity effects [Ammer, 2019]. Site climatic conditions also modulates the species-mixing effects which is expected to be higher in limiting conditions, provided that the species interactions improve the limiting resource availability, uptake or use-efficiency (see section 1.4 - Forrester and Bauhus 2016). Those studies used either $\delta^{13}C$ alone or $\delta^{13}C$ in combination with other variables such as tree ring width. Using $\delta^{13}C$ instead or in addition to tree ring width is interesting considering that it has been showed to be more closely correlated to drought signal than the latter [Andreu et al., 2008; Mölder et al., 2011]. In addition, combining both variables allows for a better understanding of species-mixing effects on productivity by taking into account the way species-mixing influences water-use efficiency [Metz et al., 2016].

Three mechanism may lead to improvement of **light use efficiency** in mixed stands compared to monocultures: increase in photosynthesis, higher allocation of biomass aboveground, leading to higher level of light captured per unit of net primary production and a closer-to-optimal distribution of nutrients in relation to light availability [Forrester, 2017]. The latter mechanism relates to the "optimality theory" according to which canopy photosynthesis is optimized if leaf mass and leaf nitrogen concentration are maximal at the top of the canopy and decrease in the lower sections of the canopy, following the gradient of light availability.

Such N repartition simultaneously allows for maximal photosynthesis at the top of the canopy (where light availability is the highest) and avoids wasting nitrogen resources in sections where photosynthesis rates are low due to light limitations [Forrester, 2017].

1.2.3 Importance of functional traits

When considering potential complementarity effects between coexisting species, it is crucial to take into consideration their corresponding traits. Indeed, we would not expect for the functioning (*e.g.* productivity) of mixed-species stands composed of species with very similar traits to differ significantly from pure stands functioning. Instead, significant differences in species traits are necessary for complementarity to express itself through reduced inter-specific competition compared to intra-specific competition [Scherer-Lorenzen and Schulze, 2005]. For instance, Brassard et al. [2011] showed that species-specific differences in rooting traits lead to higher soil exploration and increased fine root production in mixed stands while Meinen et al. [2009] did not find any significant belowground complementarity in mixed forests composed of species with comparable root systems. Similarly, differences in hydraulic strategies (isohydric *vs.* anisohydric species) can lead to complementarity for water. Conformably, Bello et al. [2019] found that sessile oak (*Quercus petraea* (Matt) Liebl. - an anisohydric species) is less susceptible to water stress when mixed with Scots pine (*Pinus sylvestris* L. - an isohydric species) than when surrounded by conspecific neighbors. In addition, traits play important roles in the spatial and temporal variability of species-mixing effects. Indeed, the expression of the functional traits are dependent on environmental conditions. One example of this would be that a difference in rooting traits (*e.g.* root distribution) could only express itself in absence of environmental constraint on root development. For instance, soil hypoxia [Kozlowski, 1986] or low bedrock depth [Balneaves and De La Mare, 1989; Fan et al., 2017] could prevent distinction of rooting depth, even in mixed stands involving species with potentially distinct rooting pattern.

1.3 Species-mixing effects on stability of productivity

There has been a long-standing debate concerning the effects of biodiversity on temporal ecosystem stability (the measure of how much a value, such as productivity, fluctuates around its long-term mean between years - Jucker et al. [2014]) [Loreau and de Mazancourt, 2013]. Indeed, the idea that more diverse communities display enhanced ecosystem stability gained force with the work of early ecologists [MacArthur, 1955; Elton, 1958; McCann, 2000] before being challenged by later studies [May, 1973; Yodzis, 1981]. Findings from biodiversity and ecosystem functioning (BEF) experiments provided valuable information to solve this debate [Morin et al., 2014]. Indeed, those studies indicated that diversity tends to have either a neutral (no difference in temporal stability between species growing in conditions of low *vs.* high species diversity) or a destabilizing effect (lower stability at higher diversity conditions) at the species or individual level due to competitive interactions. In contrast, it tends to increase stability of biomass production at the community level [Gross et al., 2014; Morin et al., 2014; del Río et al., 2017; Tilman et al., 2006; Proulx et al., 2010]. However, because of the complexity of the mechanisms involved, large uncertainty remains about our understanding of diversity-stability relationships and their dependency to environmental conditions [Morin et al., 2014; Xu et al., 2015]. It is also important to note that the difference between diversity effects on stability at distinct organizational levels may be particularly important in low diversity communities (such as European temperate mixed forests) as species-specific dynamic might strongly influence ecosystem properties [del Río et al., 2017]. Further research on the difference in temporal stability at the species/individual level between pure and mixed stands and the dependency of this difference on environmental conditions are therefore crucial for our understanding of those communities.

Diversity-stability relationships are most commonly analysed through the use of the ratio between the mean of a productivity indicator (for instance, mean basal area increment) and its standard deviation (SD)

over a given time interval. Temporal stability can thus be improved through *i)* higher productivity (μ) with similar SD, *ii)* lower SD with similar productivity or a combination of the two. As a result, several mechanisms can influence stability of productivity in mixed forests. An increased productivity in mixed stands compared to the weighted average of the corresponding monocultures (overyielding) can increase stability through higher mean productivity with constant SD [Tilman, 1999]. Reduced SD can result from asynchrony of species response to environmental fluctuations [Morin et al., 2014]. More precisely, asynchrony can result from either a differential response to environmental fluctuations between the species involved in the mixture (species respond to different environmental factors) or by a difference in the timing of their response [del Río et al., 2017]. The species differential response to environmental factors can be intrinsic (dependent on species traits; monocultures of the different species respond to different factors) or can be induced by compensatory mechanisms between species [Morin et al., 2014]. Lastly, reduced SD can also be the resultant of temporal shift in species interaction from competition to complementarity between high-growth and low-growth years, respectively [Del Río et al., 2014]. Those mechanisms refer to long-term stability effects, *i.e.* lower average variability of the indicator of interest over an extended period of time. Stability can also be defined with regard to punctual disturbing events. For instance, lower relative growth variation following a drought event (higher resistance *sensu* Lloret et al. [2011]) can also be seen as improved stability.

1.4 Spatial and temporal variations of species-mixing effects

High variability in species-mixing effects on productivity has been reported in the literature, even when similar species pools are being compared. This heterogeneity of species-mixing effects on productivity can be explained by the fact that the net effects of the mechanisms presented above are dynamic and change through time and space [Forrester, 2014]. As a result, the balance between positive and negative effects of species

interaction changes across gradients of environmental conditions [Bertness and Callaway, 1994]. As a general pattern, complementarity is expected to increase along a gradient of decreasing resource availability or increasingly harsh climatic condition. First defined for herbaceous communities, this framework (Stress Gradient hypothesis, SGH) has then been extended to forest ecosystems. The current framework frequently used to interpret the result of studies from forest ecosystems bears three major differences with the classical SGH, as described by Forrester and Bauhus [2016]. First, SGH only takes into account facilitation while the extended framework also considers competitive reduction. Indeed, competitive reduction is crucial for several processes (including light-related ones) that are of major importance in forests ecosystems. Quantification of the effects also differs between strictly SGH studies and forests studies. In the former case, facilitation is generally quantified by comparing the phenomenon of interest (*e.g.* growth, survival...) of plants growing with and without neighbours. In forest studies, absence of neighbours is not common so the comparison is made based on mixed stands and monocultures respectively. As a result, SGH studies tend to confound species identity and density effects. Lastly, in forest, processes driving facilitation and competitive reduction processes often occur simultaneously. As a result, distinction between facilitation and competitive reduction is difficult and they are most commonly referred to, without distinction, as complementarity.

Since its definition, the framework has been proved useful to analyze variations of species-mixing effects along gradients of environmental conditions [Forrester and Bauhus, 2016]. Such relationship, however, is only expected if species interaction improves the availability, uptake or use-efficiency of the limiting resource or improves the limiting non-resource (*e.g.* climate) factor [Fig.1.1a; Forrester and Bauhus [2016]]. It is also interesting to note that different processes are interlocked. For instance, as growing conditions improve, stand aboveground biomass tends to increase, along with certain tree characteristics such as leaf area, leading to increase in competition for light. As a result, complementarity will increase along a gradient of improving growing conditions, provided

that species interaction improves light absorption or light use efficiency [Fig.1.1b, Forrester and Bauhus 2016].

As stated before, improvement of the limiting factor is needed for complementarity to increase with increasingly harsh conditions **if** all the species involved are limited by this factor. However, we could postulate that such species-mixing effect on the limiting factor is not mandatory for complementarity to be significant if only one of the species involved is influenced by this factor. Indeed, the lower performances of the sensitive species at the lower end of the gradient could then lead to reduced competition for the other species.

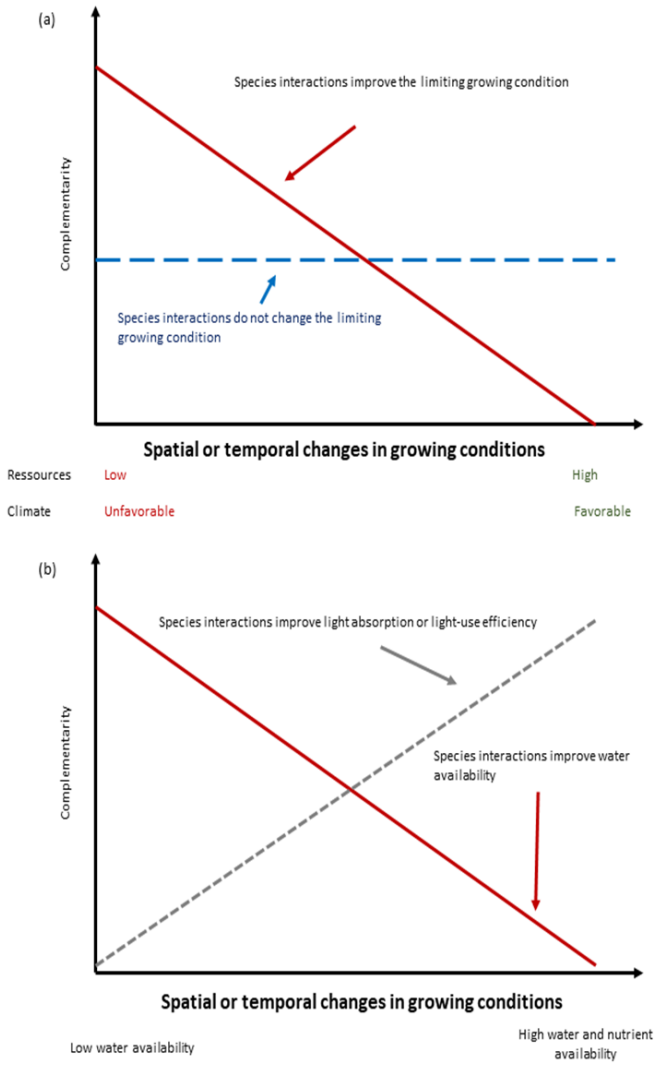


Figure 1.1 – (a) Conceptual framework showing the possible evolution of species-mixing effects for two admixed tree species along spatial or temporal changes of growing conditions in situations where species interactions improve (red) or do not improve (blue) the limiting growing condition. In part (b), the dashed line represent a community for with species mixing improves light absorption or light-use efficiency. In that case, complementarity increases with improving growing conditions because favourable conditions are associated with stand characteristics such as high growth or large leaf areas and thus, with high competition for light. Figure adapted from Forrester and Bauhus [2016].

Although such pattern of spatial and temporal variations of species-mixing effects along gradients of environmental conditions are widely used in interpretation of ecological analyses, several studies have found more complex evolution of species mixing effects with increasingly harsh conditions than linear increase [Tielbörger and Kadmon, 2000]. Recent studies such as Holmgren and Scheffer [2010] or Maestre et al. [2009] suggested that maximal beneficial effect of species- mixing (*e.g.* improved growth) could actually arise under moderately stressful conditions. Indeed, depending on the species characteristics (*e.g.* competitive or stress-tolerant), competition could overrule positive species-mixing effect both under low and very high stress level. In addition, under very high stress level, positive species-mixing effects could be insufficient to significantly improve trees performances (such as growth; Holmgren and Scheffer 2010; Maestre et al. 2009). As a result, the relationship between species-mixing effects and the limiting factor along a gradient of environmental conditions might actually present a more complex structure characterized by threshold points (*e.g.* between positive effects in harsh conditions where species-mixing effects are maximal and neutral effects in drastic conditions where species-mixing effects cannot express themselves anymore).

Species interactions and their results can thus change along a gradient of environmental constraint. In addition, species-mixing effects can also change through time at one specific site due to external (temporal variation of environmental conditions or stand characteristics) or internal (stand development over time) factors. For instance, as stand develops, the competition for the resources increases (*e.g.* increasing light competition as canopy closes) or decreases, inducing changes in net species-mixing effects. Temporal variation of species-mixing effect can also arise from changes in the balance between complementarity and competition at a given site due to a modification of the magnitude and/or nature of the constraint. For instance, at a moist site, complementarity with respect to water-related mechanisms is not expected to play a prominent role; however, a drought event could allow those mechanisms to gain importance. In addition, higher growth due to complementarity in nor-

mal conditions (non-limiting years) can lead to increased competition in harsher conditions such as during drought years [Jacobs et al., 2021].

1.5 PhD Outline and methodology

In the first part of this section, I present the general objectives of this work along with the specific objectives of each section. In a second step, I will address methodological considerations and discuss the relevance of the specific sampling design used in this research.

1.5.1 Objectives

Previous sections demonstrate that decades of ecological research have greatly improved our knowledge of mixed-species forests, their performances and the underlying mechanisms. In particular, great attention has been dedicated to studying the magnitude and variability of species mixing effects on forest growth. However, aside from a few exceptions such as for mixed stands associating N_2 and non-N_2 fixating species, most studies failed to identify the specific mechanisms at play and hinge on hypotheses to explain the observed effects. More specifically, the frameworks used to predict the change in the outcome of species interactions along spatial and temporal gradients of environmental conditions imply that species interactions have specific effects on the limiting factors. However, few studies have actually investigated those effects. Therefore, this research was motivated by the need to analyse to what extent species mixing improves resource availability and/or lowers ecological constraints along gradients of ecological conditions for one single couple of tree species. In this regard, processes associated with water and nutrient availability, uptake or use efficiency as well as with climate-related limitations are particularly relevant as they are major determinants of tree growth [Forrester and Bauhus, 2016; Forrester, 2017; Ammer, 2019]. Difference in sensitivity to such limiting factors are often suggested as promising candidate mechanisms to explain the differences in productivity and stability of productivity between pure and mixed stands [Forrester and Bauhus, 2016; Forrester, 2017; Ammer, 2019].

To achieve my research goals, I investigated the effects of species interactions on resources (water and nutrient) availability and climate-growth relationships using one single couple of model species with a large overlapping natural distribution range (*Fagus sylvatica* L. and *Pinus sylvestris* L.). In this work, I decided to focus on beech and pine because those are the species that have been selected for the EuMIXFOR network covering large gradients of ecological conditions. In addition, the objective is to analyse how potential drivers of complementarity (resource or climate-based interspecific interactions) change along such large gradients of ecological conditions. In that context, analysing diversity effects (through varying levels of species diversity) would strongly increase the complexity of the system, making our sampling network insufficient. In addition, using the same pair of species along the gradients ensures that there is no identity effects involved, which facilitates the interpretation of the variation of species-interactions with environmental conditions.

Aside from sharing a large distribution area in Europe, beech and pine have interesting characteristics for such study. Indeed, they display contrasting traits relevant to water- and nutrients- related processes and/or to climate- growth relationships. For instance, beech and pine display distinct rooting patterns (beech is characterized by a heart-shaped and competitive rooting system while pine root system is more plate-like and superficial - Curt and Prévosto 2003). Beech leaf lower life span and higher nutrient concentration [Mellert and Göttlein, 2012; González de Andrés et al., 2019] suggest a higher nutrient turnover rate. In addition, lower C/N ratio and lower amount of recalcitrant compounds result in beech litter having higher decomposition rate and lower acidifying impacts on soil [Kelty and Cameron, 1995; González de Andrés et al., 2017]. Differences in vegetation period length [Michelot et al., 2012b] or hydraulic strategy (isohydric for pine *vs.* anisohydric for beech - Cochard 1992; Martínez-Vilalta et al. 2004; Schäfer et al. 2017; Pflug et al. 2018) are favourable for the establishment of complex processes such as growth compensation after extreme events or differential timing in stomatal response to drought that can result in complementarity. In

addition, previous empirical results have shown that mixed stands of beech and pine display, on average, increased productivity and higher temporal stability of the productivity at the community level than monocultures across Europe [del Río et al., 2017; Pretzsch et al., 2015] but the mechanisms involved in those effects are not well known.

Considering that we are using one single couple of species (fixed species pool and species identity), this research aims at investigating species-mixing effects rather than diversity effects that would require diversity gradients. This research is based on a network of sampling sites composed of 32 triplets (each one corresponding to one mixed pine-beech stand and two pure stands of the corresponding species, all in similar environmental conditions) established within the frame of the COST EuMIXFOR action. The network was established in 2014 and covers a large part of continental Europe (Fig.1.2). For each site, mostly rectangular stands with size ranging from 0.01 to 1.6 ha were defined. Geographical characteristics (latitude, longitude, altitude, slope and aspect) were recorded for each site/stand. Those geographical characteristics differ between triplets but are similar between stands of a same triplet. Within a stand, for each tree exceeding diameter at breast height of 7 cm, the following variables were recorded: tree species, diameter at breast height, tree height and crown base height. In addition, within each stand 10 to 20 dominant trees were selected as target trees. For each target tree, two cores aiming for the pit (taken at 1.3 m) were sampled in perpendicular directions. Additionally, we realized angle count samples (acs) around the target trees. This set of measurements and sampling was carried out at each stand/site, and represent the basic dataset. More details about data and data collection/processing can be found in Heym et al. [2017]. Additional information have been recorded on distinct subsets of sites depending on the specific research needs. That information is described in the corresponding chapters.

Based on data from the same network, Pretzsch et al. [2015] showed that the productivity was, in average, 12% higher in mixture compared to the weighted mean of the corresponding pure stands. Although the authors proposed several hypotheses potentially explaining those pos-

itive species-mixing effects on productivity, they did not perform any quantitative analyses of the mechanisms at play. Additional research was therefore needed to highlight the dominant mechanisms causing increased productivity in mixed stands. Light related processes such as increased absorption of photosynthetically active radiation (APAR see 1.2.2.1) are good candidates to explain this effect [Forrester and Bauhus, 2016; Forrester et al., 2018; Kelty, 1992]. As a result, several studies have been conducted to investigate the importance of light-related processes and crown architecture on increased productivity observed in the mixed stands of the network.

Although only using a limited number of sites (four sites of distinct productivity), Barbeito et al. [2017] found significant changes in crown characteristics in mixed stands compared to pure ones (higher crown volumes, shifted crown positions) for beech that could improve light absorption. Forrester et al. [2018] also found that predicted annual APAR was in average 14% higher in mixture than the mean of the monocultures. However, this effect was mainly due to higher APAR for Scots pine and light-related interactions could only explain increased growth in mixed stands for pine but not for beech, nor for the whole community. Those results suggest that light-related interactions are not dominant for beech and that water- and nutrient-related interactions should be explored to better understand species-mixing effects on productivity [Forrester et al., 2018]. Consequently, the present research focuses on species-mixing effects on belowground resources and reaction to climate to contribute to a comprehensive analysis of the mechanisms linking species-mixing and improved productivity.

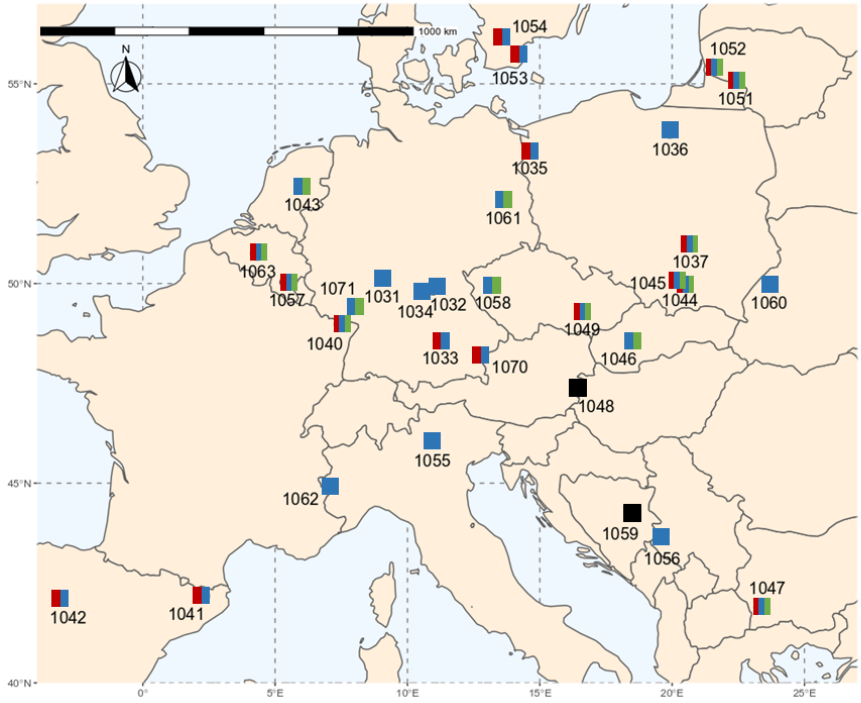


Figure 1.2 – Sites from the EuMIXFOR network. Different colors represent the different subsets of triplets used in the analyses. Red: isotopic analyses (chapter 2); Green: nutrient analyses (chapter 3); Blue: dendrochronological analyses (chapter 4). Black dots represent sites from the EuMIXFOR network that we were unable to use in any of our analyses. Site characteristics are presented in Appendix 1.

This thesis is composed of five chapters: an introduction, three research chapters (chapters 2 to 4) and a general conclusion. The general outline of the thesis is presented in Fig.1.3. Chapters number 2 and 3 look at the influence of species-mixing on resources while chapter 4 focuses on the climate-tree growth relationships in pure and mixed stands.

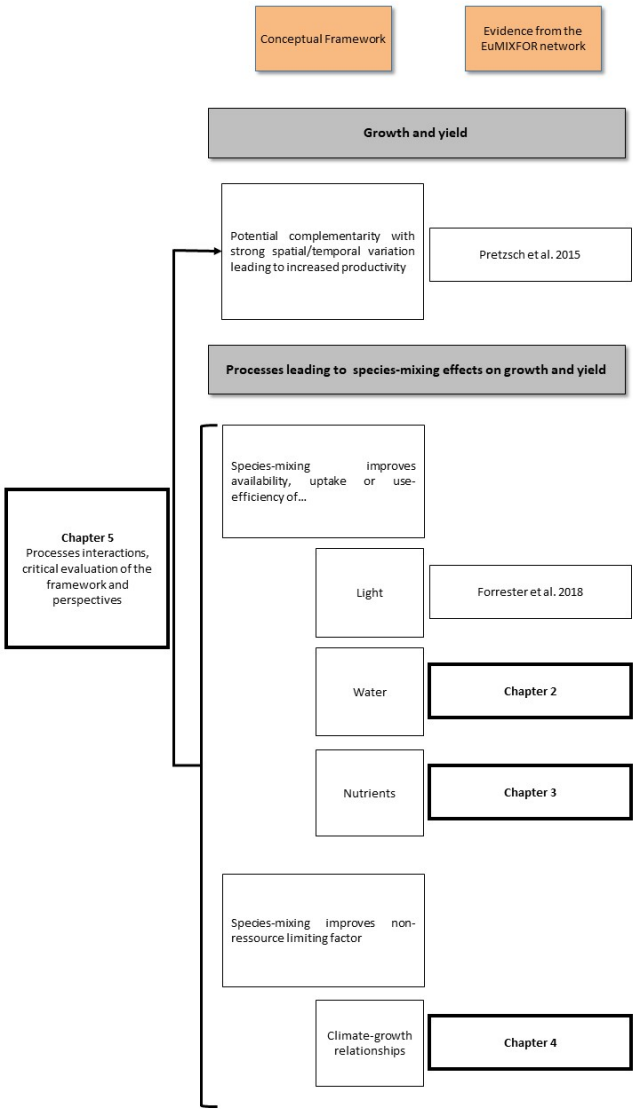


Figure 1.3 – General workflow of the thesis and integration with results from other studies from the EuMIXFOR network. A study conducted on the framework has highlighted species-mixing effects on growth and yield [Pretzsch et al., 2015], as expected from the conceptual framework. Other studies have tested whether such effects are related to certain processes (species-mixing effects on light-, water- or nutrient-related processes or on climate-growth relationships - [Forrester et al., 2018] and studies presented in this document). Chapter 5 consist in a general discussion integrating the results from the analyses, providing critical evaluation of the framework and giving perspective for future research.

Chapter two investigates the differences in water-related mechanisms between pure and mixed stands and their variation through time and space according to average site water availability and interannual variation of water availability. To do so, we analysed the wood isotopic composition (^{12}C and ^{13}C) for 22-year time series (1993 - 2014) of tree-rings originating from wood cores sampled in a subset of 17 sites of the network (Fig.1.2). This chapter aims at testing the following hypotheses: *i)* average wood $\delta^{13}C$ values are influenced by water availability for both species, with higher $\delta^{13}C$ under harsher conditions; *ii)* average wood $\delta^{13}C$ values are lower in mixtures compared to pure stands, with the mixture effect increasing under harsher conditions (drought stress or dry sites) and *iii)* the $\delta^{13}C$ signal is more stable in the mixtures. In **chapter three**, differences in nutrient foliar composition between pure and mixed stands are investigated using both foliar nutrient contents and foliar nutrient balances. Those analyses, conducted on a subset of 15 sites of the network (Fig.1.2), studied the following hypotheses: *i)* differences in foliar nutritional characteristics between species result in significant mixing effects on tree nutrition and *ii)* mixing effects on tree nutrition depend on site nutritional status, with more positive mixing effects in nutrient-limited sites. **Chapter four** is dedicated to the differences in climate-tree growth relationships between pure and mixed stands. This study is conducted using 30 out of the 32 available sites (Fig.1.2) and is based on a dendroecological approach. The objectives of this section are to test the hypotheses that impacts of species-mixing on *i)* average climate-growth relationships and *ii)* resistance to drought events are mostly determined by the regional climate. Ultimately, **chapter 5** summarizes the main findings of the first chapters and points out the need for future research.

Although experimental design is usually optimized in a way that the less common analysis (*e.g.* isotopic analysis) is conducted on a subset of sites used in the most common analysis (climate-growth relationships) leading to a nested design, this approach could not be used here. Instead, while sampling from chapter 3 and 4 are both included in the sampling from chapter 2, they are not nested within each other. Indeed, numerous

practical considerations (need for including as many sites as possible to control the large expected variability of the variables - see section 1.5.2.2, necessity to exclude some sites because of chemical contamination of the cores...) prevented us to follow such guideline. This has strong practical consideration, as it will hinder our ability to analyse the correlations between the different processes considered.

1.5.2 Methodological considerations

1.5.2.1 Types of study design and their characteristics

Numerous methodological approaches have been used to explore the influence of species mixing on stands functioning (*e.g.* stand productivity). A first method relies on data from forest inventory databases and has proved to be a powerful approach to study species diversity effects on productivity at large scales (see for instance Vilà et al. 2007). The strengths of this method lie in the large amount of data usually available, the fact that in numerous situations forest inventory plots have been installed for a long time (leading to a good temporal data coverage) and the representativity of the approach (defined by Nadrowski et al. [2010] as the relevance of the findings for the forest systems as they are found in the landscape). However, the number of variables (*e.g.* tree growth) measured by forest inventories is often limited and cannot easily be modified. In addition, the signal of interest may be difficult to analyse due to the potentially high amount of confounding factors (low orthogonality).

Another approach relies on experimental tree communities (highly controlled plots specifically established to analyse biodiversity effects). Because of the controlled nature of such experimental plots, they are efficient tools to isolate the effects of interest from the noise associated with potential confounding variables [Verheyen et al., 2013]. As they bear high research interests, a large amount of resources are usually allocated to such sites. This leads to intensive instrumentalization and allows to assess simultaneously different ecosystem functions. As a result, it is possible to take into consideration the interactions between

different processes and to conduct ecophysiological studies aiming at studying specific processes (measurements of transpiration or infiltration fluxes...). Despite the fact that this approach is quite robust with respect to the methodological limitations associated with analyses based on forest inventory databases, the highly controlled nature of those experimental plots may lead to low representativity [Baeten et al., 2013].

A third, intermediate approach lies in between the first two. This approach is based on networks of observational plots such as the network used in this research and is often associated with analyses of proxis of ecophysiological or biogeochemical processes. The observational network approach is based on a compromise between careful selection of study sites and stands (to improve orthogonality) and the loss of representativity that it entails. The approach also has a higher flexibility than the forest inventory method in terms of measured variables given that, when working on forest inventory data, we are limited to the information stored in the database while observational networks potentially allow for developing dedicated measurements. This leads to higher comprehensiveness (*i.e.* the spectrum of ecosystem processes and properties quantified in the study - Fig.1.4). In addition, because of its lower resource-intensive nature, the number of sites and the ecological gradient covered is usually higher than for the ecophysiological approach. Those characteristics make of the observational network approach a promising candidate to explore the spatial and temporal variation of mixing effects for a given couple of species on water- or nutrient-based processes or climate-growth relationships over a large gradient of environmental conditions [Baeten et al., 2013].

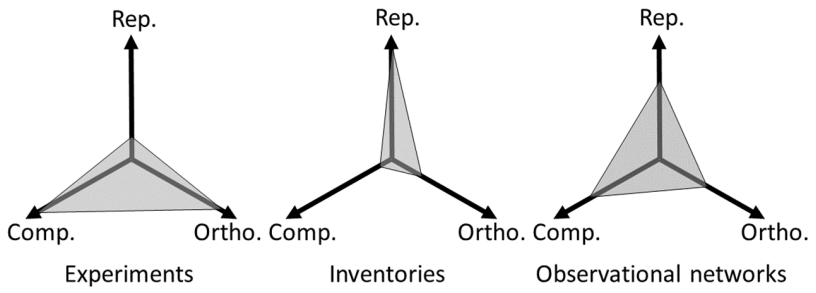


Figure 1.4 – Comparison of Representativeness (Rep.), comprehensiveness (Comp.) and orthogonality (Ortho.) of three methodological approaches (experimental plots, forest inventories and observational networks) used to quantify the effects of biodiversity. Figure from Bauhus et al. [2017].

1.5.2.2 Proxies and their variability along the sampling network

The nature of the proxies used in the present studies can also be seen as intermediate between the nature of the variables used in growth and yield and ecophysiological studies, respectively. Indeed, the approaches that we used allow for exploring specific variables instead of integrative ones such as growth or yield. Such tools could provide valuable information on the processes ultimately underlying species-mixing effects on growth and therefore explaining the variability of those effects depending on environmental conditions. It is important, however, to keep in mind that the analytical methods used here are proxis rather than direct measurements of ecophysiological processes. Indeed, those methods are influenced by several factors (*e.g.* δ^{13}C is related to water-related processes but is also influenced by light availability). Although this implies that the results should be interpreted with caution, such intermediate methods present the great advantage of being fairly easily implemented over large experimental set-ups (which is usually not the case for specific ecophysiological methods that are highly resource-demanding), therefore

complementing the results from growth and yield studies. Measuring ecophysiological proxies also lead to a better understanding of the environmental constraints. For instance, high $\delta^{13}C$ levels in some sites suggest that water availability is probably a highly limiting factor and that processes associated with this resource would probably be determinants of the results of species interactions. As a result, they provide valuable information to provide answers to the research questions.

It is important to note that covering such a large range of environmental conditions necessarily induces a great complexity. This complexity originates from the high number of mechanisms involved, as well as from plant plasticity (individuals from the same species can display distinct characteristics due to the influence of local conditions such as climate factors). Such systems are hardly predictable. In addition, clear identification and quantification of the influence of some factors may be difficult due to the covariation of several factors. For instance, the large gradient of temperature expected over a continental scale might make it difficult to identify a simultaneous effect of solar irradiance on tree growth. In order to deal with such complexity while using a somewhat limited number of sampling sites, several approaches were used. The first approach consists in reducing the complexity as much as possible. This is done, by focusing on indicators that are as specific as possible. For instance, analyses of foliar nutrient contents/balances between pure and mixed stands give valuable information on species-mixing effects on tree mineral nutrition without being significantly influenced by differences in light availability in the two stand types. Additionally, as we aim at analysing how potential drivers of complementarity change with time and/or space, we chose to work on one specific pair of species across the network. Studying species-mixing effects rather than diversity effects reduces complexity (no variability associated with the number or identity of the species involved).

Considering the analyses on climate-growth relationships, the number of variables to take into account is high because we need to consider not only distinct variables (climatic water balance, temperature) but also the seasonality of those variables. In such circumstances, multi-

variate approaches are frequently used to synthesize such large amount of information (see Lebourgeois et al. 2013; Lévesque et al. 2014; Weber et al. 2007). Those approaches allow identifying large patterns of climate-growth relationships (*e.g.* dependency to summer temperature for some sites, to spring precipitations for others...) among a large number of initial variables. In addition, using ecophysiological proxies helps reducing those issues. Indeed, integrative variables (*e.g.* growth) are influenced by a large number of factors. In such case, there is a high risk of one factor displaying a large range of values along the studied gradient to overshadow other important factors with smaller ranges of variation. Focusing on more process-oriented variables (less integrative such as δ^{13}C) reduces this risk. Lastly, sampling design based on a triplet approach along with the care dedicated to ensure homogeneity of environmental conditions between stands from a same site allow to control the number of confounding factors. Controlling the confounding factors allows to reduce complexity and reduces the sampling effort needed to find statistically significant effects.

Chapter 2

Contrasting patterns of tree species mixture effects on wood δ^{13}C along an environmental gradient *

*Adapted from de Streel, G., Collet, C., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Brazaitis, G., Coll, L., Drössler, L., Forrester, D., Heym, M., Löf, M., Pach, M., Pretzsch, H., Ruiz-Peinado, R., Skrzyszewski, J., Stankeviit, J., Svoboda, M., Verheyen, K., Zlatanov, T., Bonal, D., and Ponette, Q. (2020) Contrasting patterns of tree species mixture effects on wood δ^{13}C along an environmental gradient, *European Journal of Forest Research*, 139(2), 229-245.

Abstract

Context Establishing mixed-species stands is frequently proposed as a strategy to adapt forests to the increasing risk of water scarcity, yet contrasted results have been reported regarding mixing effects on tree drought exposure.

Methods To investigate the drivers behind the spatial and temporal variation of water-related mixing effects, we analyzed the δ^{13}C variation in 22-year tree ring chronologies for beech and pine trees sampled from 17 pure and mixed pine-beech stands across a large gradient of environmental conditions throughout Europe.

Results In the pure stands, average δ^{13}C values were lower for beech (-27.9‰ to -22.2‰) than for pine (-26.0‰ to -21.1‰), irrespective of site conditions. Decreasing SPEI values (calculated over June to September) were associated with an increase in δ^{13}C for both species, but their effect was influenced by stand basal area for pine and site water availability for beech. Mixing did not change the temporal constancy of δ^{13}C nor the tree reaction to a drought event, for any of the species. While the mixing effect ($\Delta\delta^{13}\text{C} = \delta^{13}C_{pure\ stands}$ - $\delta^{13}C_{mixed\ stands}$) was on average positive for beech and non-significant for pine across the whole gradient, this effect strongly differed between sites. For both species, mixing was not significant at extremely dry sites and positive at dry sites; on moderately wet sites, mixing was positive for beech and negative for pine; at sites with permanent water supply, no general patterns emerge for any of the species.

Conclusion The pattern of mixing effect along the gradient of water availability was not linear but showed threshold points, highlighting the need to investigate such relation for other combinations of tree species.

2.1 Introduction

Both the frequency and intensity of drought events are expected to increase in the Northern hemisphere in the upcoming decades as a result of climate change [Stocker et al., 2013]. The impacts on tree functioning due to water shortages are an important concern to foresters. Such impact include hydraulic failure leading to tree mortality [McDowell, 2011], carbon starvation due to stomatal closure [McDowell, 2011], increased fine root mortality or changes in fine-root dynamics (increase in fine-root productivity, Meier and Leuschner 2008). In addition, drought-induced stress increases the risk of wildfires and insect attacks that may lead to tree mortality [Schlesinger et al., 2016].

Favouring mixed-species stands has been proposed as a strategy to adapt forests to the increasing risk of water scarcity. However, quite contrasting results have been reported regarding the effects of mixing tree species on soil water availability and drought exposure of the trees. For instance, Lebourgeois et al. [2013], Pretzsch et al. [2013] and Anderegg et al. [2018] found an improved drought response in more diverse plots while Bosela et al. [2018] and Vanhellemont et al. [2019] found the opposite effect. Complementarity, which is a major determinant of mixing effects [Ammer, 2019], is expected to depend both on the pool of species in presence and on the set of environmental conditions [Forrester and Bauhus, 2016]. A prerequisite for synergistic interactions to occur is therefore to admix species with distinct traits in terms of physiology, phenology, or morphology. When water is the resource of interest, difference in rooting pattern [Schume et al., 2004], canopy interception [Augusto et al., 2015], transpiration and water use efficiency [Gebauer et al., 2012] and phenology [Forrester, 2015] between associated species are of special relevance. For a given set of species, the environmental conditions are the other major determinant of tree species-mixture effects. They first influence the expression of species traits. For example, soil constraints such as hypoxia [Kozlowski, 1986], compacity [Greacen and Sands, 1980] or bedrock depth [Balneaves and De La Mare, 1989] are well known to strongly limit the rooting depth of most tree species, leveling off any

potential root stratification. A second way environmental conditions may alter complementarity is through their impact on the level of the target resource over space and time. Complementarity effects are thus expected to increase along a gradient of decreasing resource availability if the species mixture improves the availability, uptake or use efficiency of the limiting resource [Forrester, 2014]. Hence, while mechanisms influencing water availability are of potential relevance for mixing effects in drier sites, we would not expect to find strong species-mixture effects related to water in wet sites. Variations in species-mixture effects can also occur due to temporal changes in environmental conditions [Del Río et al., 2014; Forrester, 2014], for example in the case of an annual drought [Grossiord et al., 2014b; Lebourgeois et al., 2013; Pretzsch et al., 2013]. It is worth noting that temporal and spatial variation of species mixture effects might not be independent of each other. For instance on sites that are moist on average, complementarity with respect to water, while absent in normal years, might operate when water becomes limiting due to a drought event. It is also important to note that, although complementarity in water-related processes would probably be absent on such sites in average conditions, complementarity interactions could be at play for other resources (*e.g.* light). This means there is room to switch between different types of complementary interactions, depending on the temporal fluctuations in environmental conditions. However, the possible trade-offs between those mechanisms as well as their respective temporal dynamics, remain largely unknown.

In this context, this paper aims to investigate the drivers behind the spatial and temporal variation of the water-related mixing effects. For that, we use a well documented network of pure and mixed stands of pine and beech trees distributed over a large gradient of climate conditions in Europe [Pretzsch et al., 2015; del Río et al., 2017; Dirnberger et al., 2017; Heym et al., 2017]. *Fagus sylvatica* (L.) and *Pinus sylvestris* (L.) are two species which present contrasting traits relevant to water-related processes: potential root-system shape (heart-shaped for beech and tap root for pine), shade tolerance (high *vs.* low respectively), stomatal density (around 200 mm^{-2} *vs.* 84 mm^{-2}), and strategies in regard to

drought resistance (anisohydric tendency *vs.* isohydric) [Cochard, 1992; Martínez-Vilalta et al., 2004; Pflug et al., 2018; Schäfer et al., 2017; Yang et al., 2016]. Based on the same network of plots, the mixture with pine and beech at the community level has been shown to have both a higher productivity [Pretzsch et al., 2015] and a higher temporal stability of productivity [del Río et al., 2017] than expected from the corresponding pure stands. Complementarity with respect to water resources has been proposed as a possible mechanism to explain those species mixture effects.

We used the δ^{13}C signal as an indicator of water use efficiency [Farquhar and Richards, 1984] and analysed its variation in 22-year tree ring chronologies from trees of each species sampled in pure and mixed pine-beech stands. We hypothesized that the spatial and temporal patterns in wood δ^{13}C values are influenced by water availability for both species, with higher δ^{13}C under harsher conditions. We further expected to observe lower wood δ^{13}C values in the mixtures compared to the pure stands, with the mixing effect increasing under drought stress or as the sites are dryer. Finally, we anticipated an overall increased stability of the δ^{13}C signal in the mixtures.

2.2 Materials and methods

2.2.1 Study area and site/stand characteristics

The tree data used in this study come from 17 pine-beech triplets established under the COST Action FP1206 EuMIXFOR (European Network on Mixed Forests). This network covers a large gradient of environmental conditions within the overlapping natural ranges of pine and beech (Fig.2.1). For this study, 17 triplets were used. Each triplet consists of pure stands of pine and beech and a mixed stand of both species, all located in similar conditions. The stands are mostly even-aged and mono-layered, and are typical of the (near-)mature development stage. No silvicultural activities had been conducted in the stands during the preceding decade. A standard protocol for tree data collection (diameters, heights of trees and crown bases) and tree coring was applied.

The full measurement protocol was described in details by Heym et al. [2017]. Site characteristics for each stand are presented in Appendix 2.

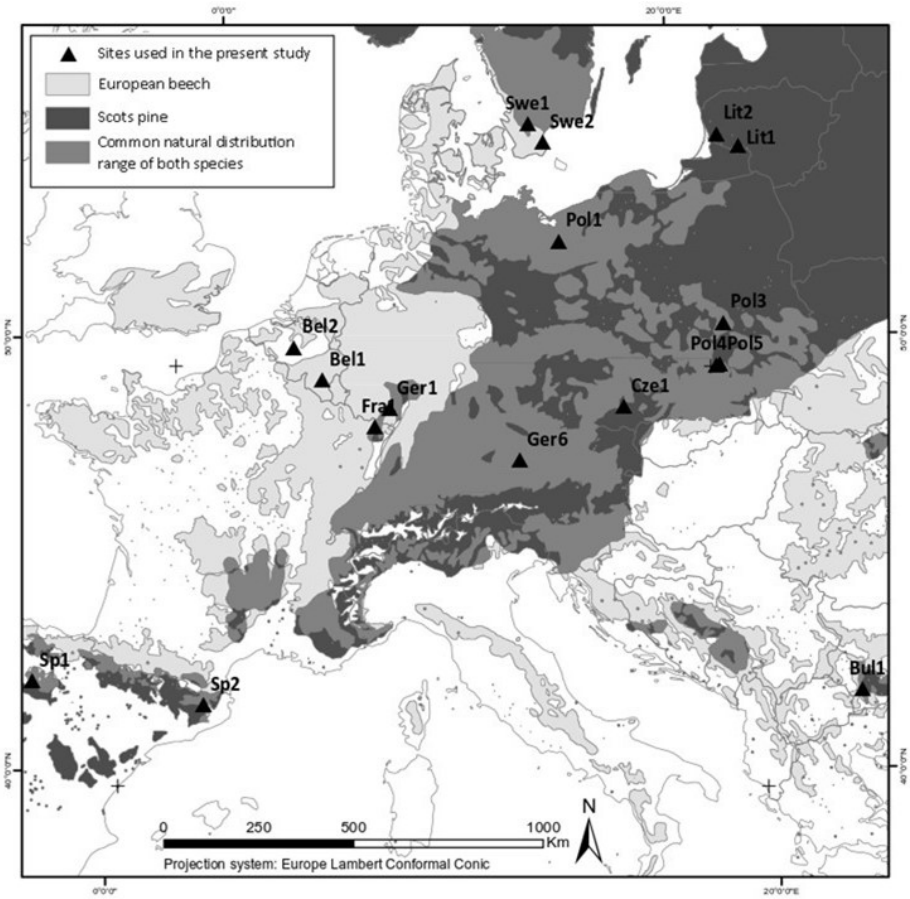


Figure 2.1 – Distribution of the triplets across Europe and natural distribution range of European beech and Scots pine according to EUFORGEN (www.euforgen.org).

The triplets (Fig.2.1) cover a wide range of environmental conditions and stand productivity classes (Table 2, Fig.2.2). Elevations range from 20 to 1339 m; mean annual precipitation (P) from 556 to 1175 mm; mean annual temperature (T) from 6 to 10.5 °C; and the de Martonne index (M = annual precipitation (mm)/mean annual temperature (°C + 10); De Martonne [1926]) from 29 to 67. The Site Index (average height of the 100 largest-diameter trees of that species per hectare in pure stands

at age 50 years; Forrester et al. 2017) ranges from 11.7 to 27.6 m for beech, and from 9.5 to 26.9 m for pine.

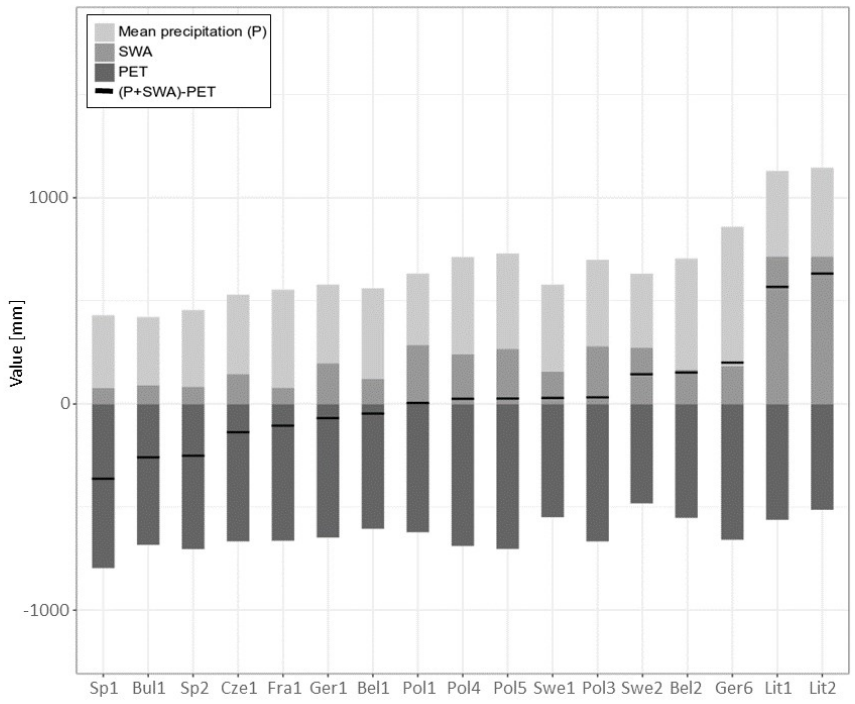


Figure 2.2 – Components of the water balance (Precipitation + maximum Soil Water Available (SWA) - Potential Evapotranspiration (PET)) for each site. Climatic components of the water balance are calculated over the vegetation period (March - September) and averaged over the 1950-2014 period. Sites are ordered by increasing value of mean water resources ((P + SWA) - PET).

Stand age and basal area are provided in Appendix 3. In the mixtures, the percentage of basal area represented by pine ranged from 33% to 74%; total basal area ranged from 30 to 79 $m^2.ha^{-1}$, the total number of trees per hectare from 248 to 2,421 and stand age from 40 to 130 years.

2.2.2 Isotope data

In this study, we used the wood carbon isotopic composition, which reflects the balance between the CO_2 diffusion and carboxylation rates, as it is proportional to the ratio of internal CO_2 to atmospheric CO_2 concentrations [Farquhar et al., 1982]. Various environmental factors

such as light, temperature, and water availability do have an influence on δ^{13}C, and their relative importance depends on environmental conditions. Under limiting soil water conditions, higher δ^{13}C values primarily result from the stronger decrease in stomatal conductance compared to the one in CO_2 assimilation [Farquhar et al., 1989]. Where water is non-limiting, other factors than drought, including light availability, may have an influence on the wood isotopic signature. For instance, change in light competition arising from stand development could have an impact on the wood carbon isotopic composition over the 20-year study period, yet we expect this effect to be limited for such predominantly mature stands.

For each site, five cores from five different trees per species and per stand type were randomly selected from 10 - 20 dominant trees that had been cored per species in each stand. The cores were sampled to the pith at an height of 1.3 m. For each core and for each annual ring within the period 1993 - 2014, we used a scalpel and a stereomicroscope to sample the last third of the ring. We only took the last third of each ring in order to avoid carry-over effects on wood isotopic composition [Michelot et al., 2012a]. While this does not match specifically the latewood, it ensures that the carbon isotope signature we obtained for each year characterized the functioning of the selected trees during the second part of the growing season. The five samples were then pooled per species and stand, resulting in four samples per triplet and year (total number of samples: 4×17 [number of triplets] $\times 22$ [years] = 1,496).

At the INRA Silvatech platform (Nancy, France), the pooled samples were ground to a fine powder in a ball mill (MM400, Retsch).The $^{13}C/^{12}C$ ratio was measured with a mass spectrometer (Isoprime 100 (Isoprime Ltd., Cheadle Hulme, UK) coupled with an elemental analyser (Elementar vario, ISOTOPE cube, Elementar Analysen Systeme GmbH, Hanau, Germany)). The standard deviation for the analysis of standard saccharose was 0.12‰.

The isotopic composition (δ^{13}C) relative to the standard Vienna Pee Dee Belemnite scale was calculated as follows (Equation 2.1)

$$\delta^{13}C_{plant} = [(^{R_{sample}}/_{R_{standard}}) - 1] \times 1000 \quad (2.1)$$

with $R_{standard}$ being the isotopic ratio ($^{13}C/^{12}C$) of a belemnite fossil from the Pee Dee Formation, corresponding to the international standard [Stichler et al., 1995].

Isotopic composition of pooled samples was corrected to take into account the change in the isotopic composition of atmospheric CO_2 due to industrialization, (Equation 2.2; McCarroll and Loader 2004):

$$\delta^{13}C = \delta^{13}C_{plant} - (\delta^{13}C_{atm} + 6.4) \quad (2.2)$$

with $\delta^{13}C_{plant}$ being the isotopic ratio of the plant, $\delta^{13}C_{atm}$ being the isotopic ratio of the atmosphere and -6.4‰ corresponding to a preindustrial standard value.

Isotopic composition was also corrected to reflect rising atmospheric CO_2 concentrations since 1850 (reference period) following the method suggested by McCarroll et al. [2009]. This non-linear method aims to extract low frequency variations in $\delta^{13}C$ series based on a theoretical plants reaction to rising atmospheric CO_2 [Lévesque et al., 2013]. Corrected $\delta^{13}C$ series are hereafter referred to as $\delta^{13}C_{cor}$.

2.2.3 Climate data

We used the 0.25°-gridded E-OBS dataset from EU-FP6 ENSEMBLES project. From this dataset, we obtained series of daily minimum, maximum and mean temperatures, cumulative daily precipitation and daily average sea level pressure for the period 1950 - 2014. Monthly potential evapotranspiration (PET) was derived from these data following the modified Hargreaves equation [Choisnel et al. 1992, Droogers and Allen 2002], which provides estimations that are close to those obtained from the Penman-Monteith equation [Beguería et al., 2014].

We used both long-term (averaged over the 1950 - 2014 period) and short-term (inter-annual) water-balance indices. As a long-term index of water availability, we used a simplified water balance calculated over the vegetation period (March - September), WB_{VP}, defined as: total Precipitation over the vegetation period (P) - total Potential Evapotranspiration over the vegetation period (PET) + Maximum Soil Water Available (SWA). Maximum Soil Water Available (data from Forrester et al. 2017) was calculated from soil depth, soil water holding capacity estimated from soil texture, and the proportion of stones in the soil. To take into account short-term variations in water availability during the period 1993 - 2014, we used the Standardized Precipitation Evapotranspiration Index (SPEI). SPEI [Vicente-Serrano et al., 2010] is a multi-scalar index that can be calculated over different time scales, and which can be used to determine the onset, duration and magnitude of drought conditions with respect to normal conditions. The average SPEI value over 1993-2014 was zero for each site. Positive values indicate above-normal wet conditions, whereas negative values identify dry periods. SPEI values between -0.67 and 0.67 are considered normal, values between -0.67 and -1.28 indicate moderate drought, and values < -1.28 indicate severe drought [Isbell et al., 2015]. SPEI was calculated over the second half of the vegetation period (June-September) which correspond to the part of the tree rings that were sampled. Calculation were made using the SPEI-package in R software [R Development Core Team 2014, Beguería et al. 2014].

2.2.4 Statistical analysis

2.2.4.1 Spatial and temporal patterns of $\delta^{13}C$ in pure stands

Welch's t-tests were used on the annual $\delta^{13}C_{cor}$ values to assess the tree species effect (pine *vs.* beech) within each site. Linear models were then used to test for the effects of site and stand variables (Appendix 5) on the average differences between beech and pine $\delta^{13}C_{cor}$ chronologies per triplet; ln-transformation of the response variable was used to reduce the heteroscedasticity of the residuals. Next, we fitted a linear mixed effect model for each species separately on $\delta^{13}C_{cor}$ time series, considering site

as a random factor in order to identify the major determinants of spatial and temporal variation of $\delta^{13}C_{cor}$ in pure plots for each species:

$$\delta^{13}C_{cor,y} = \boldsymbol{\beta} \times \mathbf{E_y} + s(0, \sigma^2_{site}) + \varepsilon(0, \sigma^2_{\varepsilon}) \tag{2.3}$$

where $\delta^{13}C_{cor,y}$ represents the $\delta^{13}C_{cor}$ of year y, $\boldsymbol{\beta}$ is the vector of the fixed effects parameters, $\mathbf{E_y}$ is the matrix of the predictors of the fixed effects, s the random factor characterized by the inter-site variance σ^2_{site} and ε is the error term. A series of climatic variables, site and stand attributes (see full list in Appendix 5) and their interactions were used as candidate variables for fixed effects. The error term in equation 2.3 originates from inter-annual variability and denotes the error resulting from the constraint associated with the use of a linear model. To avoid missing any key explanatory variable, we first used various selection procedures (Lasso, Elastic Net and stepwise forward selection with Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC)) and retained all variables selected by at least one method. Variance Inflation Factors (VIF) were calculated in order to measure the degree of multi-collinearity of the variables. The low VIF values (< 4) indicate that multi-collinearity was not a problem [Obrien, 2007]. Starting from the model with the full set, the variables with the lower predictive power were then progressively removed based on the likelihood ratio test [Gonzalez de Andres et al. 2018, Zuur et al. 2009].

To investigate whether the two species had a similar temporal response to environmental fluctuations (synchronism), we calculated correlation coefficients between the beech and pine time-series of non-corrected $\delta^{13}C$ per site, following del Río et al. [2017]. Values can range from -1 (complete asynchrony of species response to environmental fluctuations) to $+1$ (complete synchrony).

2.2.4.2 Temporal constancy

Two types of indices were used to analyze the temporal constancy of carbon isotope series: (*i*) the Temporal Stability index (TS Equation 2.4), and (*ii*) sensitivity (Equation 2.5). TS is an indicator of the dis-

persion of corrected $\delta^{13}C$ values with regard to the mean isotopic composition, while sensitivity is an indicator of the year-to-year variability of the time series. Increased TS indicates higher stability due to either a higher mean value or a lower standard deviation. High sensitivity values indicate important year-to-year variation of $\delta^{13}C$ values due to high sensitivity to external (*e.g.* climatic) parameters.

$$TS = |\mu|/\sigma \tag{2.4}$$

$$Sensitivity = \frac{\overline{\sum_{i=1}^{n-1} |S_{i+1}|}}{n-1} \tag{2.5}$$

where μ is the mean of the corrected $\delta^{13}C$ series; σ is its standard deviation; n is the number of year; and $S_{i+1} = (\delta_{i+1} - \delta_i)$ and δ_i are the corrected isotope values [Saurer et al., 1997]. TS and sensitivity are calculated per site, species and stand type (pure *vs.* mixed). We used mixed effects models with site as a random intercept to test the species-mixture effect on these two indices, as follows:

$$TC_j = (a_0 + a_{0j}) + a_1 \times \text{Stand composition} + \varepsilon \tag{2.6}$$

where TC_j is the temporal constancy index (temporal stability or sensitivity) of one species at site j; a_0 and a_1 are the fixed parameters of the model; a_{0j} is the random parameter associated to site; Stand composition is a dummy variable with two levels (pure/mixed); and ε is the error term. Site- and stand-level variables (*e.g.* BA, altitude, WB_{VP}...) that could potentially influence TC were included as additional predictors in the model (Appendix 5).

2.2.4.3 Spatial and temporal patterns of mixing

For each species, the mixing effect was quantified by $\Delta\delta^{13}$C, the difference in δ^{13}C between pure and mixed stands per year and site. For this specific analysis, non-corrected δ^{13}C values were used because computing the difference in δ^{13}C values from a same site cleaned the signal of

long-term trends. For each species, we first tested whether the $\Delta\delta^{13}$C time series significantly deviated from the expected null value under a no mixing effect hypothesis, using one sample t-tests for each site separately as well as across all sites. The possible effects of average site conditions, stand structure and interannual climate variability on the spatial and temporal patterns of the mixing effect were then analysed by fitting linear mixed models on the $\Delta\delta^{13}$C series of each species, following the same procedure as previously explained for the $\delta^{13}C_{cor}$ time-series from the pure stands. We also investigated the effect of species mixture on species asynchrony by analyzing the relationship between correlation coefficients of beech and pine time series in pure and mixed stands.

2.2.4.4 Resilience and resistance to drought in pure and mixed stands

Resistance and resilience were calculated to analyze tree reaction to a drought event [Lloret et al., 2011]. Resistance was calculated as the difference in $\delta^{13}C_{cor}$ values between a reference year *i.e.* without water limitation preceding the drought and a drought year with water shortage ($\delta^{13}C_{ref,before} - \delta^{13}C_{drought}$); resilience was computed as the difference in $\delta^{13}C$ values between two reference years preceding and following the drought year, respectively ($\delta^{13}C_{ref,before} - \delta^{13}C_{ref,after}$). To select the drought years, we first identified the year with the lowest SPEI (June - September) values during the 1994 - 2013 period. In order to avoid carry-over effects, we then checked that the SPEI value for the previous year had been normal or moderately wet/dry (*i.e.* within the interval $[-1.28 - 1.28]$). If this specification was not met, we shifted to the year with the second lowest SPEI value and started over. The reference years were selected as the wettest years preceding and following the corresponding drought year, and the associated SPEI values were further checked to ensure they were > -0.67. Selected years and their associated SPEI and P − PET values are presented in Appendix 6. The resistance index should be negative since $\delta^{13}C_{cor}$ values are expected to rise during drought events; the more negative the resistance index (low resistance), the higher the drought effect (stress). A resilience value not significantly

different from zero indicates that trees have a high capacity to return to pre-drought $\delta^{13}C_{cor}$ levels after being subject to a drought event (high resilience); a negative value indicates low tree resilience. For each index, we tested for species and stand composition effects separately according to the following mixed model:

$$R_j = (a_0 + a_{0j}) + a_1 \times Effect + \varepsilon \tag{2.7}$$

where R_j is either resistance or resilience at site j; a_0 and a_1 are the fixed parameters of the model; a_{0j} is the random parameter associated to site j; and ε is the error term. Effect is a dummy variable with two levels (pine *vs.* beech or pure *vs.* mixed for the species identity and stand composition effects, respectively). Site- and stand-level variables (*e.g.* BA, altitude, WB_{VP}...) that could potentially influence R were also included as additional predictors in the model (Appendix 5).

All statistical analyses were conducted with the R software, version 3.4.1 [R Development Core Team, 2014]. Mixed models were fitted with the package "nlme" [Pinheiro et al., 2017].

2.3 Results

2.3.1 Spatial and temporal patterns of $\delta^{13}C$ in pure stands

In general, pine reached higher (less negative) mean isotope values than beech (Fig.2.3). Average beech and pine $\delta^{13}C_{cor}$ values across all sites were -25.3‰ and -23.7‰ respectively. The range of site average values were [-27.9‰ to -22.2‰] for beech and [-26.0‰ to -21.1‰] for pine. Average $\delta^{13}C_{cor}$ values were always lower for beech than for pine, for all sites. Differences were always statistically significant, with the exception of Pol1 (Appendix 7). The magnitude of the difference between species was site-dependent with values ranging from 0.25‰ (Pol1) to 3.23‰ (Lit2). None of the variables tested in the linear model (Appendix 5) had a significant effect on this difference (data not shown).

There was a global coherence between the beech and pine time-series (Appendix 9) that was confirmed by the high correlation coefficients

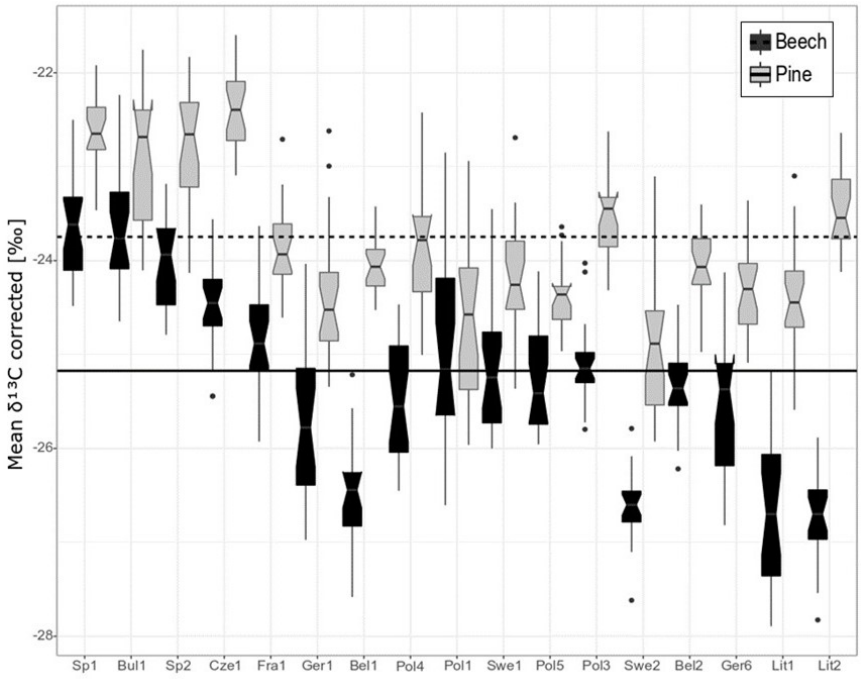


Figure 2.3 – Mean $\delta^{13}C_{cor}$ values for each site and each species in the pure stands. Horizontal bars represent the median; notches in the boxes is a rough proxy for comparing medians. Upper and lower hinges on the boxes indicate the 25^{th} and 75^{th} percentiles; whiskers extend from the hinges to the largest value no further than 1.5×the interquartile range. The horizontal lines (dashed: pine, plain: beech) represent average values per species across all sites. Sites are shown by increasing value of mean water resources (mean over the pure stands).

values observed in most sites (Appendix 8). Sites with a lower level of correlation between the two species time-series were well distributed along the gradient of average water availability (sites with WB_{VP} ranging from 249 to 632 mm, while water availability across the whole gradient ranged from 366 to 632 mm). Linear mixed effect models adjusted on each species $\delta^{13}C_{cor}$ time-series highlighted a significant, negative effect of $SPEI_{June-September}$ on $\delta^{13}C_{cor}$ for both beech and pine (Table 2.1). In pine stands, this SPEI effect depended on basal area only, while in beech stands, it depended on basal area, WB_{VP} and slope (Table 2.1). In pine stands, higher basal area was associated with a more negative slope of the $\delta^{13}C_{cor}$/SPEI relationship. In beech stands, higher basal

area, lower WB_{VP} and less steeper stand slopes were associated with a more negative slope of the $\delta^{13}C_{cor}$/SPEI relationship. Only beech showed a significant influence of WB_{VP} on $\delta^{13}C_{cor}$. This influence followed the expected pattern; *i.e.* higher values of average water resources were related to lower $\delta^{13}C_{cor}$ values.

Table 2.1 – Parameter estimates, p-values and R-squared for the linear mixed models adjusted on the 1993-2014 $\delta^{13}C_{cor}$ series in the pure stands. For both models, we used site as a random intercept. Marginal R-squared (R^2_m) represents the variance explained by fixed factors. Conditional R-squared (R^2_c) represents the variance explained by both fixed and random factors (whole model). WB_{VP} is the average water balance over the vegetation period (precipitation + potential available soil water - potential evapotranspiration) calculated over the period 1950-2014. The intercept indicates the value that the dependent variable (here, $\delta^{13}C_{cor}$) would take if all the explanatory variables were null, except for basal area (BA). Indeed, basal area has been centered as a null value would not be meaningful. The intercept therefore indicates $\delta^{13}C_{cor}$ value for a BA value corresponding to the average of the dataset. Parameters of the main effect variables indicates the change in $\delta^{13}C_{cor}$ values associated with a one-unit increment change of the variable. Significant effects are indicated in bold.

Species	R^2_m	R^2_c	Fixed effects parameters		parameters	p-values
Scots pine	0.2634	0.7043	Intercept		-23.812	**<.01**
			$SPEI_{June-September}$		-0.220	**<.01**
			Basal area		0.023	0.15
			WB_{VP}		-0.001	0.10
			$SPEI_{June-September}$ Basal area	x	-0.005	**0.04**
European beech	0.53	0.7603	Intercept		-25.336	**<.01**
			$SPEI_{June-September}$		-0.371	**<.01**
			Basal area		-0.002	0.91
			Slope		0.017	0.30
			WB_{VP}		-0.003	**<.01**
			$SPEI_{June-September}$ WB_{VP}	x	0.001	**<.01**
			$SPEI_{June-September}$ Basal area	x	-0.009	**0.02**
			$SPEI_{June-September}$ Slope	x	0.016	**<.01**

2.3.2 Temporal constancy

Temporal stability and sensitivity values are shown in Appendix 4. There were no significant difference in temporal stability nor sensitivity between pure and mixed stands for any of the species (Table 2.2). Climatic variables (average WB_{VP} and average temperature over the pe-

riod 1993 - 2014) did not explain the variability of temporal constancy between sites; for Pine, temporal stability increased as stands became older. No climatic or site characteristics was found to impact sensitivity (Table 2.2).

Table 2.2 – Parameter estimates, p-values and R-squared for the linear mixed models adjusted for temporal stability and sensitivity values. Site is used as the random intercept. Marginal R-squared (R^2_m) represents the variance explained by fixed factors. Conditional R-squared (R^2_c) represents the variance explained by both fixed and random factors (whole model). The intercept indicates the value that the dependent variable would take if all the explanatory variables were null. Parameters of the main effect variables indicate the change in the dependent variable values associated with a one-unit increment change of the variable. Significant effects are indicated in bold.

	R^2_m	R^2_c	Species	Fixed effects	parameters	p-values
Temporal stability	0.046	0.272	Beech	Intercept	45.275	**0.00**
				Stand composition (mixed)	-3.931	0.36
	0.342	0.446	Pine	Intercept	26.248	**0.00**
				Age	0.313	**0.00**
				Stand composition (mixed)	4.048	0.31
Sensitivity	0.006	0.163	Beech	Intercept	0.665	**0.00**
				Stand composition (mixed)	-0.067	0.65
	0.0389	0.592	Pine	Intercept	0.625	**0.00**
				Stand composition (mixed)	-0.175	0.10

2.3.3 Spatial and temporal patterns of species-mixture effects

For beech, seven sites showed no significant species-mixture effect on $\delta^{13}C$, while two showed a negative effect and eight showed a significant positive effect (lower $\delta^{13}C$ values in mixed stands compared to pure ones) (Fig.2.4). The mean $\Delta\delta^{13}$C across all sites was significantly positive (value = 0.318, p-value = $< .001$). For pine, eight sites showed a significant negative effect of species mixture, five showed a significant positive effect and four showed no significant effect (Fig.2.4). The mean $\Delta\delta^{13}$C across all sites was significantly different from zero (value = -0.108, p-value = .01). Four sites showed a positive species-mixture effect for both species and two showed a negative effect for both species. When species-mixture effect was positive for pine, it was either also positive for beech (four sites) or neutral (no significant species-mixture effect;

one site), but never negative. On the other hand, when species-mixture effect was positive for beech, it was positive (four sites), negative (three sites) or neutral (one site) for pine. Three sites also displayed a negative species-mixture effect for pine but no significant effect for beech, and three sites displayed no significant species-mixture effect for either species (Appendix 10).

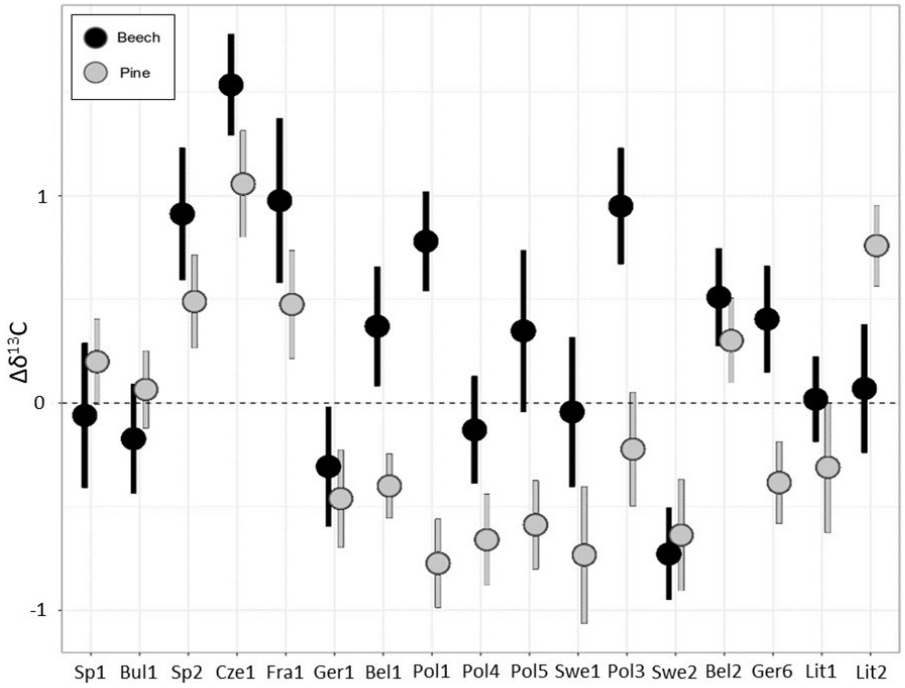


Figure 2.4 – Mean difference between $\delta^{13}C$ in pure and mixed stands ($\Delta\delta^{13}$C = $\delta^{13}C_{pure\ stands}$ - $\delta^{13}C_{mixed\ stands}$), for beech (black bullet) and pine (grey bullet). Vertical bars represent 95% confidence intervals around the mean. The dashed line indicates zero. Absence of intersection between this line and the confidence interval bars gives strong indication of a mean which is significantly different from zero. Sites are shown in increasing order of average WB_{VP} calculated aver the 1950 - 2014 period (mean over pure and mixed stands).

Looking at the drivers behind the temporal and spatial patterns of mixture effects (Table 2.3), we found that beech $\Delta\delta^{13}$C was not influenced by any of the site or stand characterization variables, but that SPEI had a significant positive effect. Between-site variability of pine $\Delta\delta^{13}$C was linked to WB_{VP} and to mean age of the stand (the $\Delta\delta^{13}$C/ WB_{VP} re-

lationship becoming less negative as age increased). No annual climatic variable successfully explained the species-mixture effect on pine (Table 2.3).

Table 2.3 – Parameter estimates, p-values and R-squared for the linear mixed models adjusted on the 1993-2014 series of $\delta^{13}C_{pure\ stands}$ - $\delta^{13}C_{mixed\ stands}$. For both models, we used site as the random intercept. Marginal R-squared (R^2_m) represents the variance explained by fixed factors. Conditional R-squared (R^2_c) represents the variance explained by both fixed and random factors (whole model). WB_{VP} is the average water balance over the vegetation period (precipitation + potential available soil water potential evapotranspiration) calculated over the period 1950-2014. The intercept indicates the value that the dependent variable would take if all the explanatory variables were null. Parameters of the main effect variables indicates the change in the dependent variable values associated with a one-unit increment change of the variable. Significant effects are indicated in bold.

Species	R^2_m	R^2_c	Fixed effects	parameters	p-values
Scots pine	0.237	0.543	Intercept	-0.532	0.16
			WB_{VP}	-0.006	**<.01**
			Age	0.003	0.56
			$SPEI_{June-September}$	-0.026	0.37
			Age x WB_{VP}	0.0001	**<.01**
European beech	0.029	0.4381	Intercept	0.347	**0.01**
			WB_{VP}	-0.001	0.36
			$SPEI_{June-September}$	0.082	**0.02**

There was no significant difference in correlation coefficients between the $\delta^{13}C$ time series for beech and pine in pure and mixed stands (Appendix 11), thus indicating that species mixture did not change the synchrony of the two species reactions to environmental fluctuations.

2.3.4 Resilience and resistance to a drought event in pure and mixed stands

In pure stands, Pine displayed a negative index for resistance to drought (p-value = .03). This effect was not significant for beech (p-value = .07). The resilience index was not significantly different from 0 for pine but was significantly positive for beech (Table 2.4 and Fig.2.5). No effects of site or of stand characterization variables were found except for the beech resilience index, which was significantly influenced by stand age (estimate = −0.022; p-value = .00) and site WB_{VP} (estimate = 0.002; p-

value = .01) (data not shown). There was no significant mixture effect on either resistance or resilience, for either of the species (Table 2.4, Fig.2.5).

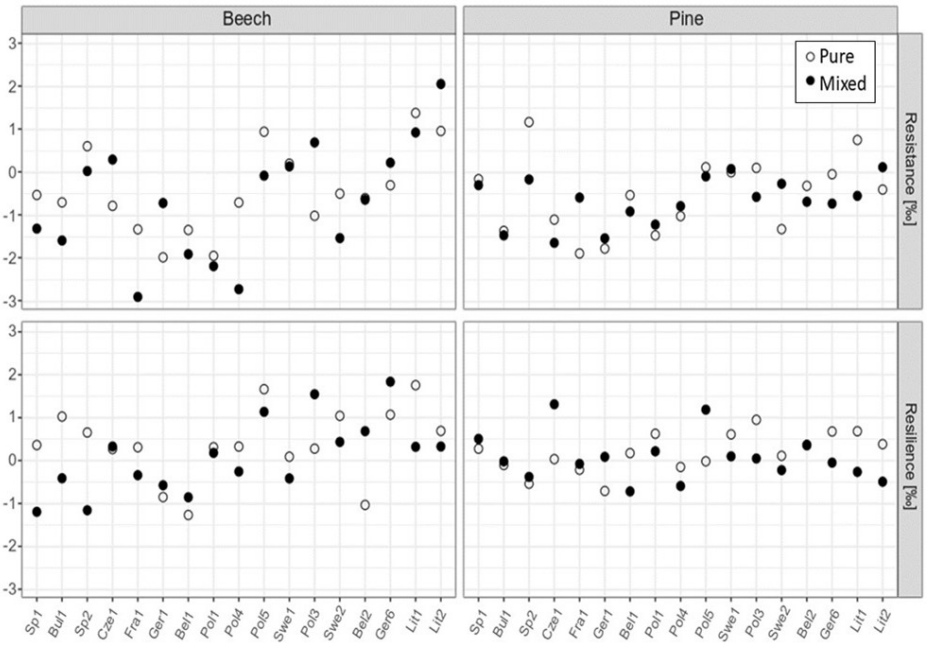


Figure 2.5 – Resilience component indices (Resistance: upper panel, Resilience: lower panel) for pure (empty dots) and mixed (black dots) stands of both species (Beech: left panel, Pine: right panel). Study sites are shown in increasing order of average water resources (WB_{VP}) over the 1950-2014 period (mean over pure and mixed stands). Statistical significance of the effects across all sites are given in Table 2.4.

2.4 Discussion

2.4.1 Spatial and temporal variation of $\delta^{13}C$ in pure stands

Carbon isotope composition in tree rings was systematically higher in pine than in beech (Fig.2.3), pointing to greater intrinsic water use efficiency for pine compared to beech; this is consistent with previous studies [Daux et al., 2018; Hemming et al., 1998; Szczepanek et al., 2006].

Table 2.4 – Parameter estimate, standard error and p-values for the models testing for species identity and species-mixture effects on resilience component indices. For species identity effect, "beech" is the value estimated for pure beech, "pine - beech" is the difference between pure pine and pure beech stands and "pine" is the value estimated for pure pine stands. For species-mixture effect, "pure" is the value estimated for pure stands, "mixed" for the species in mixed stand and "mixed - pure" is the difference between mixed and pure stands. Significant effects are indicated in bold.

	Resilience components	Species	Stand	Estimate	Std. err.	p-value
Species identity effect	Resistance index	-	beech	-0.441	0.226	0.07
			pine - beech	-0.096	0.163	0.56
			pine	-0.537	0.226	**0.03**
	Resilience	-	beech	0.397	0.164	**0.03**
			pine - beech	-0.208	0.214	0.34
			pine	0.189	0.164	0.27
Species mixture effect	Resistance index	Beech	pure	-0.441	0.29	0.15
			mixed - pure	-0.211	0.253	0.42
			mixed	-0.652	0.290	**0.04**
		Pine	pure	-0.537	0.177	**0.01**
			mixed - pure	-0.122	0.172	0.49
			mixed	-0.659	0.177	**0.00**
	Resilience index	Beech	pure	0.397	0.208	0.07
			mixed - pure	-0.300	0.239	0.23
			mixed	0.097	0.208	0.65
		Pine	pure	0.189	0.122	0.14
			mixed - pure	-0.126	0.172	0.48
			mixed	0.063	0.122	0.61

Several explanations for these differences are possible. Firstly, because of differences in physiological or morphological characteristics (such as higher light availability associated with lower light interception in pine stands due to a less dense canopy), the carbon uptake (A) is higher in pine which results in lower leaf internal CO_2 concentrations, thus leading to increased $\delta^{13}C$, all other things being equal. Daux et al. [2018] recently discarded this explanation as a cause for the observed difference in isotopic composition between beech and pine because conifers usually have lower A than broadleaved trees. However, Medlyn et al. [1999] reported a higher potential electron rate and maximum rate of Rubisco activity for pine compared to beech, suggesting that this general rule of lower A for conifers than for broadleaves might not hold true for pine and beech. The difference in $\delta^{13}C$ levels between the two species could also be explained by lower stomatal conductance (g_s) in pine. Lower g_s could originate either as a direct effect of morphological characteristics (*e.g.* lower stomatal density, smaller stomata), or as an indirect effect of ecological functioning. Indirect effects include (*i*) lower leaf area index in closed stands for pine compared to beech leading to higher evapotranspiration from the soil and the understory [Daux et al., 2018]; and (*ii*) lower access to belowground water reserves due to shallower rooting [Daux et al., 2018]. These indirect effects tend to reduce water availability in pine stands. However, if indirect effects do indeed prevail, we would expect the difference in $\delta^{13}C$ between species to be lower or, even, to disappear when water availability is higher. We did not observe any such pattern leading us to think that the difference in $\delta^{13}C$ between species is probably rather due to an effect either of light interception or a difference in stomatal characteristics of beech and pine.

As hypothesized, pine and beech $\delta^{13}C_{cor}$ values were significantly influenced by water availability during the last part of the vegetation period (Table 2.1). These results are consistent with previous studies and with physiological models of the response of isotopic discrimination and water use efficiency during carbon assimilation under soil drought conditions [Farquhar et al., 1989]. Saurer et al. [2008] found that $\delta^{13}C$ chronologies of pine and beech were negatively correlated with precipitation on

non water-limited sites, while Gonzalez de Andres et al. [2018] found a negative influence of water balance (P − PET over the summer) on $\delta^{13}C_{cor}$ for climatically contrasted sites. A few sites (Sp1, Sp2, Swe1, Lit1 and Lit2) did however not respond to SPEI, even when additional starting time and aggregation periods were considered (Appendix 12); in addition, none of the site, stand or climate characterisation variables were able to explain the variability in the $\delta^{13}C_{cor}$/SPEI relationship for this limited subset of sites. Regarding the spatial variations in $\delta^{13}C$, we expected to find a negative relationship between carbon isotopic composition in tree rings and average water availability for both species [Saurer et al., 1995]. While $\delta^{13}C_{cor}$ was negatively related to WB_{VP} for beech, confirming the hypothesis of higher $\delta^{13}C_{cor}$ levels in drier sites for that species, this was not the case for Pine (Table 2.1). We hypothesize that this is due to the non-linear pattern of variation in average $\delta^{13}C_{cor}$ along the water availability gradient (Fig.2.3), where dry sites clearly displayed higher $\delta^{13}C_{cor}$ values.

It is important to note that spatial and temporal variations of carbon isotope composition are not independent of each other. Indeed, we found that for beech, due to the SPEI/WB_{VP} interaction, the WB_{VP} effect on $\delta^{13}C_{cor}$ disappeared during extremely wet years (SPEI > 3), but held in other situations. Saurer et al. [1995] found a similar increase in $\delta^{13}C_{cor}$ values for pine and beech on drier sites in Switzerland. The absence of any significant influence of the interaction term $SPEI_{June-September}$ x WB_{VP} on pine $\delta^{13}C_{cor}$ suggests the existence of local adaptation mechanisms as well as long-term genetic divergence within species; this means ecotypes vary in functional traits, as previously proposed by Weigt et al. [2015] and Härdtle et al. [2013]. We also found that the inter-annual variation in $\delta^{13}C_{cor}$ was influenced by stand variables (basal area for pine, and basal area and slope for beech). Basal area in both pine and beech stands (and lower WB_{VP} in beech stands), could have been aggravating factors as they induce a higher sensitivity of $\delta^{13}C_{cor}$ to annual water balance (more negative $\delta^{13}C_{cor}$/SPEI slope). The aggravating effect of basal area can probably be linked to increased competition among trees for soil water, and low WB_{VP} is likely to be correlated to higher sensitiv-

ity to annual variations in the water balance. Surprisingly, stand slope did not have such an aggravating effect on the $\delta^{13}C_{cor}$/SPEI relationship in the pure beech stands, probably because this effect was confounded with that of slope aspect.

The $\delta^{13}C_{cor}$ time-series for both species were quite coherent within a site (Appendix 9 and 8), which is a further indication that beech and pine trees tend to respond in a comparable way when facing similar temporal fluctuations of environmental conditions (Table 2.1). There were, however, a few exceptions. In most cases, those exceptions were linked to the long-term trend in the $\delta^{13}C_{cor}$ time-series of one of the two species, thus decoupling pine and beech $\delta^{13}C_{cor}$ values. For instance, such an effect can be seen in the decreasing trend in beech $\delta^{13}C_{cor}$ series at Bel2 or in the drop in beech $\delta^{13}C_{cor}$ values around 1995 - 2003 at Bel1 (Appendix 9). The considerable length of those trends suggest that they are not of climatic origin but are probably rather due to changes in stand characteristics (*e.g.* changes in access to light, management effect), long-term changes in global circulation models [González de Andrés et al., 2019; Rozas et al., 2015; Sardans et al., 2017] or to tree weakening (dieback), which could have influenced the physiological functioning of the trees.

Looking now at the tree reaction to a drought event (Table 2.4, Fig.2.5), a significant increase in $\delta^{13}C_{cor}$ was observed for pine; surprisingly, this effect was non-significant for beech, but by a very slight margin. Inspection of Fig.2.5 suggests that beech response was related to site water availability, the drought effect being generally dampened on wetter sites. Such a difference in drought reaction between dry and wet sites was not observed for pine. We attribute this to the fact that pine is a drought-avoiding species. Such species close their stomata quickly during water shortages to avoid damage to the conductive system [Cochard, 1992; Martínez-Vilalta et al., 2004]. This drought avoidance strategy is common in conifers (especially *Pinus* species), which tend to have lower embolism resistance than angiosperms [Martínez-Vilalta et al., 2004; Choat et al., 2012]. In addition, LAI reduction through leaf shedding under drought stress has been shown to be a strategy which buffers water loss in pine trees, resulting in the formation of tree-rings with increased in-

trinsic Water Use Efficiency (iWUE) [González de Andrés et al., 2019]. Beech, on the other hand, is more anisohydric [Pflug et al., 2018; Schäfer et al., 2017]. However, there was no overall significant difference between pine and beech resistance. This could indicate that, while pine reacts more promptly than beech to drought, both species end up being affected in a similar way during extreme events. Between-site variability in resistance to drought event could also be partially explained by other variables not considered in this study, such as nutrient availability. Potassium and phosphorus are known to be particularly important, as they are involved in various water-related mechanisms [Newton et al., 1986]. For instance, potassium influences stomatal function, osmosis and hydraulic conductance [González de Andrés et al., 2019; Khosravifar, 2008; Wang et al., 2013]. On another hand, we did not find any lasting effect of drought on tree functioning as trees of both species were able to return to pre-drought levels of carbon isotope composition (pine) or even show lower $\delta^{13}C_{cor}$ values (beech) after the extreme event.

2.4.2 Temporal constancy

A species-mixture effect on temporal stability or sensitivity could be caused either by a differential response (sensitivity to different parameters or differential temporality of the response) of each species to environmental changes [Loreau and de Mazancourt, 2008; Hector et al., 2010], or by reduced competition in mixed stands compared to pure ones [Tilman, 1999]. The lack of any mixing effect in our case (Table 2.2) is therefore in agreement with the tight correlation we observed in pure stands between the $\delta^{13}C$ time-series of beech and pine trees growing in a same site (Appendix 8); in addition, as there was no significant difference in the correlation between the two species in mixed and pure stands, species mixture did not induce a decoupling of the species reaction to environmental fluctuations (Appendix 11). Contrasting results have been reported with respect to diversity-stability relationship, from the total absence of a stabilizing effect in single-trophic communities [Jiang and Pu, 2009] to higher stability in mixed forests [Jucker et al., 2014]. It is currently becoming more and more accepted that diversity improves

stability at the community level but decreases stability, or does not affect it, at the species level. del Río et al. [2017] recently highlighted this stabilizing/destabilizing pattern for productivity in mixed pine/beech stands across Europe. Although water is often considered a main factor of resource-driven effects, we found no clear stabilizing/destabilizing species-mixture effect on water-related processes at the species level.

2.4.2.1 Species-mixture effects on $\delta^{13}C$

While the mixing effect ($\Delta\delta^{13}$C) was on average positive for beech and non-significant for pine across the whole gradient, the major result or our study is that this effect strongly differed between sites, depending on the average water availability (Figure 2.4). On *wet* sites (*i.e.* sites with permanent available belowground water resources), the species-mixture effect on δ^{13}C should be close to zero on average, that is if the species-mixture effect is indeed mainly due to water-related processes. If the species-mixture effect differs from zero, then other processes should be considered. A key mechanism influencing δ^{13}C values, and therefore $\Delta\delta^{13}$C, is the access to light [Ehleringer et al., 1986; Farquhar et al., 1989]. Our results showed a high variability of $\Delta\delta^{13}$C in wet sites (Bel2, Swe2, Ger6 and Lit2), which could be due to a species-mixture effect on light availability. Indeed, Forrester et al. [2016] and Barbeito et al. [2017] have shown that higher stand diversity is associated with increased crown size, which could lead to increased light absorption. In addition, Barbeito et al. [2017] showed that this effect is dependent of site conditions, the difference between pure and mixed stands being higher in more productive sites. We used delta height (the difference between the height of the cored target-species trees in mixed stands and the mean height of the mixed stand) to investigate the potential effect of light interception on $\Delta\delta^{13}$C. However, light interception did not fully explain $\Delta\delta^{13}$C deviation from zero on very humid sites. Indeed, some sites for which access to light did not differ between pure and mixed stands still displayed significant $\Delta\delta^{13}$C deviation from zero and vice versa (we found differences in access to light but no significant $\Delta\delta^{13}$C deviation from zero). On *moderately wet sites* (average WB_{VP} close to zero), the

same consideration should hold (species mixture effect close to zero), on the condition that the addition of a second species does not influence water availability (increased belowground competition in mixed stands compared to pure ones). If this is the case, species-mixture effect could be negative for one or both species, depending on their ecophysiological characteristics. On this type of site, we found a high variability in beech $\Delta\delta^{13}$C, suggesting the influence of non-water-related processes as stated earlier. For pine however, $\Delta\delta^{13}$C was consistently negative. We could thus conclude that in moderately wet sites (theoretically non-stress sites), adding beech would induce a stress on pine, which is consistent with previous findings [Gonzalez de Andres et al., 2018]. This would also be consistent with the difference in the compromise strategies of the two species between carbon uptake and water loss highlighted above for pure stands. On *dry sites*, the species mixture effect is expected to be positive (see Forrester and Bauhus 2016) (*i*) if species mixture has a positive influence on water availability, (*ii*) if this influence is large enough to affect carbon isotope composition, and (*iii*) if potential negative species-mixture effects (competition) are lower than the positive effects. We found that species-mixture effect tends to be positive for both species on dry sites (Sp2, Cze1, Fra1) but, as we move towards *extremely dry sites* (Sp1, Bul1), this positive effect seems to disappear. This is probably indicative of the fact that the positive species-mixture effect on water availability is not strong enough to compensate for the increasing environmental constraint. While this result questions the linear relation between complementarity and resource availability along a gradient of environmental conditions hypothesized by Forrester and Bauhus [2016], a possible decrease in the positive effects of species mixture in extremely harsh situations is not a new idea [Maestre and Cortina, 2004; Tielbörger and Kadmon, 2000]. The species-mixture effects presented in this study may therefore be indicative of a more complex structure with threshold points (Figure 2.4). These threshold points could correspond to the level of average site water availability where beech starts to regulate its water consumption (Figure 2.3), thus reducing competition and inducing a switch from negative to positive species-mixture effects

in pine. Additional sites would however be needed to fully test this hypothesis. The complex relationship between species mixing effects and average site water availability could also arise from interactions with other drivers of water availability, in particular those related to nutrient availability [Sardans and Penuelas, 2007].

Our models for pine confirmed the role average site water balance plays on the species-mixture effects, in contrast to the lack of any effects related to interannual variations in SPEI (Table 2.3). The average site water balance effect further depended on the mean age of pine stands since, in older stands, the slope of the $\Delta\delta^{13}C/WB_{VP}$ relationship was less negative. We should eliminate two unlikely causes of the age effect in mature stands such as the ones used in this study: (*i*) vegetation growing close to the forest floor using air with increased $^{12}C/^{13}C$ ratio due to respiration [McCarroll and Loader, 2004], and (*ii*) variation of bark refixation of respired CO_2 as bark is usually too thick in mature stands for bark refixation to play a major role [McCarroll and Loader, 2004]. Ontogenic changes in rooting patterns [Claus and George, 2005; Finér et al., 2007; Yuan and Chen, 2010] could possibly be involved, but testing this hypothesis would need thorough field root investigation we did not performed. It is possible, however, that this age effect was confounded with the effect of height, considering that using mean stand height instead of age as a variable only slightly decreases the performance of the model. By contrast to Pine, difference in WB_{VP} was unable to explain the variability in mixing effects for beech. The beech model rather highlighted an annual water balance (SPEI) effect on beech $\Delta\delta^{13}C$, with increased complementarity effects during wet years. Altogether, those findings are in agreement with the beech more intense competitive strategy [Gonzalez de Andres et al., 2018]. Beech high competitive strategy is well known and has been reported to originate from its ability for intense environment foraging through root and crown development, its high resource use and high growth intensity [Curt and Prévosto, 2003; Dieler and Pretzsch, 2013; Gonzalez de Andres et al., 2018; Martinez del Castillo et al., 2018; Schume et al., 2004].

While mixing affected the $\delta^{13}C$ signal for both species in a complex way related to site water availability (Fig.2.4, Table 2.3; see above), it did not influence the tree response to a drought event (Table 2.4, Fig.2.5). Considering the whole gradient, pure plots displayed higher $\delta^{13}C$ levels under more intense water-limiting conditions, and mixed stands had a similar behavior. Such a result is consistent with the growing body of literature on the subject, which reports that species mixture does not always improve reaction to drought [Bonal et al., 2017; Forrester et al., 2016; Grossiord et al., 2014b], although this may indeed be the case in certain situations [Grossiord et al., 2015; Lebourgeois et al., 2013; Pretzsch et al., 2013].

2.5 Conclusion

We conclude from the present study that pine and beech present different levels of average $\delta^{13}C$ values indicative of the compromise between CO_2 assimilation and H_2O loss, but that the spatial and temporal variations in their $\delta^{13}C$ values are similar.

We did not find any species-mixture effects on trees reaction to drought events, in accordance with the growing body of literature on this topic. However, analyses of spatial and long-term temporal variations in species-mixture effects showed that mixing species leads to contrasting effects on beech and pine carbon isotope composition (a slightly positive effect for beech and no significant effect for pine) when the whole gradient of water availability is taken into account. The global pattern of species-mixture effect along this gradient is consistent with some theories [Forrester and Bauhus, 2016]: an increasingly positive species-mixture effect on drier sites until the drought constraint becomes too strong for the species-mixture effect to compensate. Our study demonstrates the importance of considering the non-linear relationships of species-mixture effects on wood isotopic composition and that species-mixture effects appear at certain threshold points. Intrinsic species characteristics concerning water-related processes play a critical role in species-mixture effects, especially at moderately wet sites. A combination of the

difference in the two species CO_2/H_2O compromise and average environmental conditions in terms of water availability therefore determines the balance between competition and complementarity in mixed stands.

Chapter 3

Mixing has limited impacts on the foliar nutrition of European beech and Scots pine trees across Europe *

*Adapted from de Streel, G., Ammer, C., Annighöfer, P., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Brazaitis, G., Buraczyk, W., Collet, C., Hurt, V., Kurylyak, V., den Ouden, J., Pach, M., Pretzsch, H., Skrzyszewski, J., Sramek, V., Stankeviit, J., Strelcova, K., Svoboda, M., Verheyen, K., Zlatanov, T., Ponette, Q. (2021) Mixing has limited impacts on the foliar nutrition of European beech and Scots pine trees across Europe, *Forest Ecology and Management*, 479, 118551.

Abstract

Context Tree species-mixing has been suggested as one option to counteract the adverse effects of global change on tree mineral nutrition, yet the effect of mixing on nutrient availability remains poorly documented.

Methods We therefore analysed the current foliar nutrient (N, P, K, Ca, Mg) quantities and *ilr* balances (isometric log-transformed ratios between elements or groups of elements) for 261 European beech and 248 Scots pine trees from 15 sites, each consisting of one beech-pine mixed stand and the respective monocultures, across a gradient of environmental conditions in Europe. We hypothesized an overall positive effect of mixing on tree foliar nutrient content, and that this mixing effect would be stronger on nutrient-poor sites. Using linear mixed models and multivariate linear regression models, we first tested for the effects of species (beech/pine) and composition (pure/mixed) across all sites; we then investigated whether species-mixing effects were related to site fertility.

Results The nutrient composition of beech leaves and pine needles differed significantly for all *ilr* balances. For both species, significant mixing effects were detected for some nutrients and *ilr* balances; those effects, however, could not be consistently related to contrasted nutrient composition between species. For most nutrients and *ilr* balances, the mixing effect was influenced by the site nutritional status, but the pattern differed from expectation: absence or minor differences between monocultures and mixtures at the lower end of the chemical fertility gradient, and maximum differences in rich soils.

Conclusion The contrasting foliar nutrient composition of pine and beech trees and the site nutrient status only partly explained the mixing effects on tree mineral nutrition. Our results claim for a better understanding of nutrient-related mechanisms associated with complementarity and points towards the need to further expand the existing frameworks to account for the multivariate nature of tree nutrition.

3.1 Introduction

Many recent studies underline that tree mineral nutrition is deteriorating in Europe under global environmental changes [Jonard et al., 2015; Peñuelas et al., 2013]. For instance, negative trends in foliar P concentration were found for *Fagus sylvatica* (L.) and *Pinus sylvestris* (L.) along with negative Ca and Mg trends in the case of the first species and negative S trend for the latter one [Jonard et al., 2015]. While concentrations of some elements are declining, N foliar concentrations tend to increase for several species [Jonard et al., 2015]. Such opposite trends induce foliar imbalances which, in turn, may impact the ability of forests to provide ecosystem services such as biomass production [Oren and Schulze, 1989]. In that context, species-mixing could be an efficient management tool to improve stand nutrition through the potential positive effects of interspecies interactions on the availability, uptake or use efficiency of nutrients [Ammer, 2019; Forrester and Bauhus, 2016; Nickmans et al., 2015; Rothe and Binkley, 2001].

Nutrient availability is influenced by many mechanisms. Richards et al. [2010] reported several ways by which tree species mixture may improve nutrient supply, including enhanced mineralisation, reduced loss of nutrient through leaching and erosion, increased rate of N_2 fixation or weathering, and increased quality, quantity and decomposition rates of the leaf litter. Species-mixing effects on nutrient *uptake* are often associated with differences in physiological, morphological or phenological characteristics between the tree species involved in the mixture [Forrester and Bauhus, 2016]. An example is fine root overyielding in tree mixtures resulting from belowground niche differentiation for species with contrasting rooting traits [Leuschner et al., 2001]. Through improvement of soil resources, species-mixing could also induce a reallocation of carbon to aboveground biomass, resulting in a higher *nutrient use efficiency* compared to pure stands [Epron et al., 2013; Forrester et al., 2006a]. All the mechanisms listed above have to be seen in the light of the biogeochemical niche hypothesis [Urbina et al., 2017]. The hypothesis states that, because of differences in growth and nutrient

use strategies, co-occuring species use mineral elements in different proportions, which leads to species specific stoichiometry and associated stoichiometric flexibility. Such differences in biogeochemical niches between coexisting species allows for reduced competition and nutrient use optimization at the community level [Urbina et al., 2017].

It is frequently thought that admixing tree species has beneficial impacts on tree nutrition. In temperate forests, those effects have mostly been studied for mixed stands of coniferous and broadleaved trees [Brown, 1992; Rothe and Binkley, 2001; Thelin et al., 2002]. Such expected impacts result from differences in biogeochemical cycle, nutrient demand and nutrient use between conifers and broadleaves. For instance, nitrogen mineralization and nitrification fluxes are generally lower in coniferous than in broadleaves stands, an effect commonly attributed to more acidic conditions, higher C:N ratio of organic matter, and higher amounts of inhibiting and/or recalcitrant compounds under conifers [Augusto et al., 2015]. The same mechanisms could also hold true for other nutrients such as P and Ca because their availability is partly related to organic matter mineralization. Additional mechanisms involve distinct impacts of coniferous *vs.* broadleaved trees on atmospheric deposition and mineral weathering [Augusto et al., 2015]. Differences in nutrient demand and nutrient use between coniferous and broadleaves species also leave room for beneficial impacts of admixing these species. Such differences include a generally higher nutrient concentration in litter and fine roots for broadleaves, and longer nutrient residence time for conifers [Augusto et al., 2015].

The impact of admixing coniferous and broadleaf species on tree nutrition has been highlighted in previous studies. For instance, Brandtberg [2001] found that admixing birch species (*Betula pendula* Roth and *Betula pubescens* Ehrh.) and Norway spruce (*Picea abies* (L.) Karst) increased P and K concentrations of spruce needles (but did not influence N, Ca, Mg or Mn concentrations). Thelin et al. [2002] reported higher P and K concentration in Norway spruce needles when mixed with beech, birch or oak (*Quercus robur* (L.) and *Quercus petraea* (Matt.) Liebl.). Brown [1992] found that interspecific differences in tissue concentration

of N and possibly P, were key factors responsible for contrasting types of mixture effects (positive, compensatory and negative) on Norway spruce when mixed with Scots pine, black alder and sessile oak, respectively. However, other studies failed to find any significant differences in foliar nutrient concentrations between pure and mixed stands of conifers and broadleaved species [Heinsdorf, 1997; Magh et al., 2018; Neft and Stangl, 1985; Rothe et al., 2003]. An explanation for those inconsistent results is the dependency of species-mixing effects to environmental conditions [Ratcliffe et al., 2017]. Building on the framework developed by Forrester and Bauhus [2016], effects of mixing on nutrition are expected to increase along a gradient of decreasing nutrient availability provided that species interactions improve the availability, uptake or resource use efficiency of limiting nutrients. In accordance with this pattern, Magh et al. [2018] found that in the absence of any water limitation, there was a facilitative effect of silver-fir on N nutrition of beech in N-limited sites, but an antagonistic effect in N-rich soils. However such a simple framework might not be sufficient to explain the full range of patterns for nutrient related mixing effects along environmental gradients. First, it does not account for nonlinearity of the relationship between resource availability and mixing effects. For instance, while their focus was on the mixing effect on drought exposure, de Streel et al. [2020] highlighted tipping points along a nearly similar environmental gradient. Second, the above framework does not take into account simultaneous limiting factors. Sardans and Penuelas [2007], however, showed that species-mixing effects on foliar nutrition could be influenced by site water status through its impact on nutrient uptake.

The assessment of tree nutrition is largely based on analyzing single foliar nutrient concentrations or contents (*i.e.* amount of a nutrient in a given number of leaves/needles), as well as ratios between pairs of elements (*e.g.* Jonard et al. 2015). This approach yields valuable information about mineral elements that are essential to plant functioning and to their metabolism, and the reported values can easily be compared with thresholds [Mellert and Göttlein, 2012]. More recently, a complementary method, where nutrients are subjected to isometric logratio (*ilr*)

transformation (see Materials and methods below), has been proposed to better account for the interactions between nutrients while limiting biases related to using raw compositional data [Egozcue, 2003]. Since its development, this method was successfully applied in different contexts. For instance, Parent et al. [2013a] used it to analyse the mineral plasticity of cloudberry and Parent [2013], Modesto et al. [2014] and Hájek et al. [2014] used it to study the nutrition of Mango trees, maize or mosses, respectively. Recently, Collin et al. [2016] used the *ilr* method to study the nutritional characteristics of Sugar Maple (*Acer saccharum* Marsh.) and Red Maple (*Acer rubrum* (L.)) under varying proportions of conifers, while Nowaki et al. [2017] used this approach to assess the response of irrigated tomato crops to P fertilization. Although the relationship between foliar nutrient ratios and tree growth remains unclear [Binkley and Fisher, 2019], critical ratios have been shown to influence a number of important processes such as masting [Fernandez-Martínez et al., 2019] or herbivory [Lind and Barbosa, 2012], and are often related to forest dieback [Hevia et al., 2019].

The objective of this paper was to assess the impact of mixing broadleaves and conifers on tree nutrition. Focusing on the widespread European beech - Scots pine mixture, we sampled the foliage of 261 beech (*Fagus sylvatica* (L.)) and 248 pine (*Pinus sylvestris* (L.)) trees at 15 sites distributed over Europe, each of which contained a triplet of stands including a mixture and the monocultures of each species. We used the *ilr* approach to obtain a synthetic and non-redundant characterization of the overall nutritional signature, in complement to the classical nutrient content/concentration approach. We hypothesized that differences in foliar nutritional characteristics between species would result in significant mixing effects on tree nutrition. We further hypothesized that mixing effects would be dependent on site nutritional status.

3.2 Materials and methods

3.2.1 Study area and site/stand characteristics

This study is based on data from 15 sites each consisting of pure stands of pine and beech and a mixed stand of both species (Fig.3.1), with all three of them located in similar conditions. The sites have been established under the COST Action FP1206 EuMIXFOR (European Network on Mixed Forests). This network covers a large gradient of environmental conditions and site nutrient status (Fig.3.1; Appendix 14 and 15) within the overlapping natural ranges of pine and beech. Elevations varies between 20 and 1190 m a.s.l; mean annual precipitation sum (P) ranges from 520 to 1175 mm and mean annual temperature (T) from 6 to 10.5°C. The stands are mostly even-aged and mono-layered. A summary of stand characteristics is provided in Appendix 16. In the mixtures, the percentage of basal area represented by scots pine ranged from 25% to 69%; total basal area ranged from 16 to 79 $m^2.ha^{-1}$ and stand age from 45 to 130 years. Stand size ranged from 0.025 to 0.73 ha for pure beech stands, from 0.025 to 1.55 ha for pure pine stands and from 0.045 to 0.462 ha for mixed stands (Appendix 16). No silvicultural activities had been conducted in the stands during the preceding decade. A standard protocol for tree data collection (diameters, heights of trees and crown bases) and tree coring was applied. The full measurement protocol was described in details by Heym et al. [2017].

3.2.2 Leaf collection, pretreatment and analysis

Across the 15 sites-network, 509 trees (261 European beech and 248 Scots pine) were sampled. In each site and stand (pure beech, pure pine, mixed beech-pine), 5 - 10 trees were sampled per species (*i.e.* beech or pine in the pure stands, beech and pine in the mixed stand) among the dominant trees during the summer 2016 (second part of the vegetation period, before autumnal colouring) for a total of 24 - 40 sampled trees per site. Current year leaves/needles were collected from several branches located in the upper third of the crown, resulting in one sample per tree. Leaves/needles were dried at 40°C until constant weight was

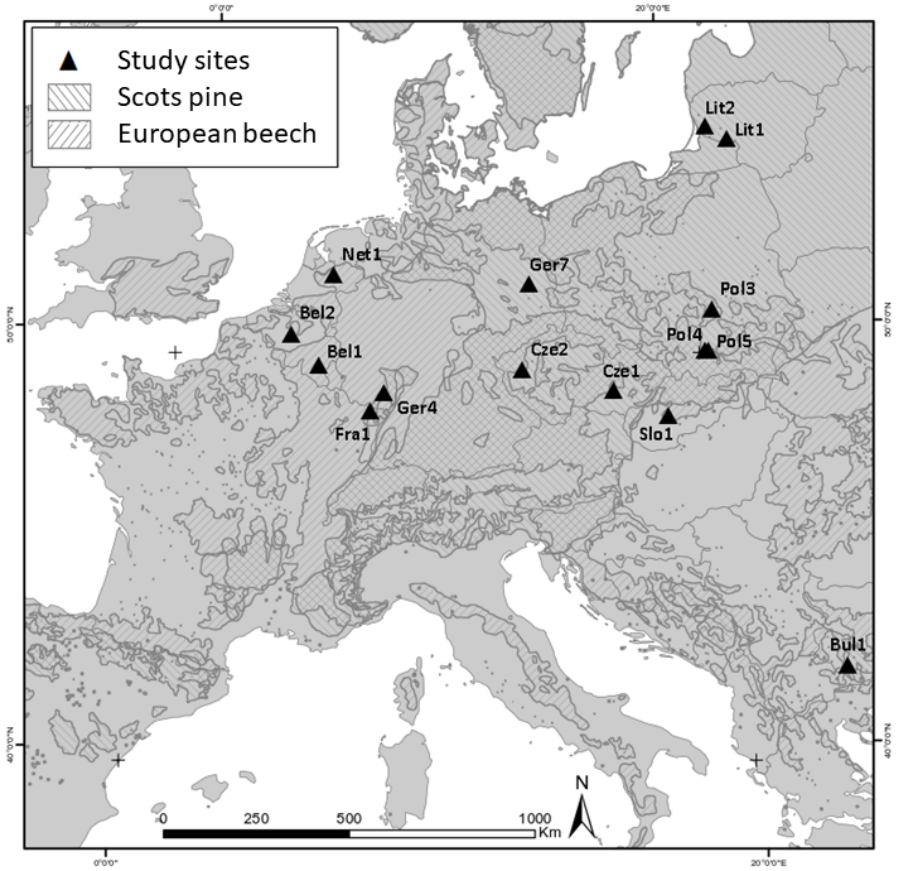


Figure 3.1 – Distribution of the 15 EuMIXFOR beech-pine triplets used in the present study and distribution of European beech and Scots pine according to EUFORGEN (www.euforgen.org).

achieved for the nutrient analysis. To determine the dry mass, a subsample was additionally oven-dried at 70°C (50 leaves/500 needles). Foliar N concentrations were measured using the dry combustion method with a Flash Analyzer (Thermo Finnigan Flash EA 1112 elemental analyser) and the other elements (P, K, Ca and Mg) were determined by ICP spectrometry (Varian 720 E-S) after digestion with HNO_3 in a microwave oven (Milestone UltraWAVE, Germany). All analyses were done on a per tree basis.

3.2.3 Tree nutrition assessment

For each tree, the foliar nutrient composition was characterized by single nutrient (N, P, K, Ca, Mg) concentrations and contents, as well as by isometric log transformed ratios (*ilr*) between elements or groups of elements (Table 3.1).

Table 3.1 – Sequential Binary Partition (SBP) of foliar nutrients of beech and pine trees based on prior knowledge of nutrient interaction in higher plants and number of components in the (+) et (-) groups (n^+ and n^-, respectively).

Balance	**SBP parts**						$\mathbf{n^+}$	$\mathbf{n^-}$
[-1 subset| +1 subset]	**N**	**P**	**K**	**Ca**	**Mg**	**Fv**		
$[Fv\|N, P, K, Ca, Mg]$	1	1	1	1	1	-1	5	1
$[Mg, Ca\|K, P, N]$	1	1	1	-1	-1	0	3	2
$[K\|P, N]$	1	1	-1	0	0	0	2	1
$[P\|N]$	1	-1	0	0	0	0	1	1
$[Mg\|Ca]$	0	0	0	1	-1	0	1	1

Nutrient concentrations and contents. Nutrient concentrations in current-year foliage were first used to rank each site by comparison to species-specific reference thresholds [Mellert and Göttlein, 2012]. Though such thresholds do not account for nutrient interactions (*e.g.* Marschner and Marschner 2012), they are useful as baseline values to assess the nutrient status (*e.g.* Jonard et al. [2015]). For all subsequent analyses, we used nutrient contents instead of nutrient concentrations to account for differences in leaf/needle dry mass resulting from contrasting growing conditions which would impact foliar nutrient concentrations through concentration/dilution effects [Binkley and Fisher, 2013; Jarrell and Beverly, 1981]. The content of each individual nutrient in 50 leaves or 500 needles was calculated by multiplying its concentration by the corresponding leaf or needle dry mass.

Isometric log transformed ratios (*ilr*). The chemical composition of a plant tissue is a closed system in that all constituting nutrients are constrained to sum to 100%. Data corresponding to quantitative descriptions of the parts of a closed system are defined as compositional data

[Collin et al., 2016]. Among others, the components of such system are not independent. Indeed, if the value of one component increases, the value of at least one other component has to decrease in order to keep the sum constant. Therefore, specific compositional data analyses techniques such as the isometric log-ratio techniques have been developped. Despite its limited use for the assessment of tree foliar nutrition, the *ilr* transformation technique has been proved useful for analysing plant nutrient composition [Hájek et al., 2014; Modesto et al., 2014; Parent et al., 2013a; Parent, 2013]. In addition to constraining the system to 100%, it also accounts for the physiological interactions between nutrients [Collin et al., 2016; Nowaki et al., 2017]. The *ilr* transformation technique gives information about the relative amounts of elements or groups of elements, allowing D-1 orthogonal (geometrically independent) balances to be produced for a D part composition. D is the number of measured elements plus a filling value (Fv). The filling value corresponds to the difference between the unit or scale of measurement (*e.g.* 100%) and the sum of all measured elements [Parent et al., 2013b]. In this context, a balance, hereafter referred to as *ilr* balance, is defined as the relationship between groups composed of one or several nutrients [Egozcue and Pawlowsky-Glahn, 2005]. A closure operation is applied to the resulting matrix of compositional data [Aitchison, 1986], which computes the constant sum of components as follows [Egozcue and Pawlowsky-Glahn, 2005]:

$$S^D = C(c_1, c_2, ..., c_D) = [{}^{c_1 k}/_{\sum_{i=1}^{D} c_i}, {}^{c_2 k}/_{\sum_{i=1}^{D} c_i}, ..., {}^{c_D k}/_{\sum_{i=1}^{D} c_i}] \quad (3.1)$$

Where S^D is a vector of D components adding up to a constant k (*e.g.* 100%), C is the closure operator, c_i is the i_{th} part of a composition of D components.

The *ilr* transformation is then applied to the closed data. This system of lineary independent ratios is called Sequental Binary Partition (SBP) and describes the D-1 orthogonal balances between nutrients or groups of nutrients [Parent et al., 2013b]. The SBP of a D-elements composition is a (D-1) $\times$ D matrix where columns correspond to the parts of the

composition and rows to the *ilr* balances. In the SBP, elements labelled +1 correspond to balances numerators, elements labelled -1 correspond to balance denominators and elements labelled 0 are not part of the balance in question. This SBP is defined a priori, for instance, based on user knowledge. In our case, the SBP (Table 3.1) is based on prior knowledge of plant nutrition [Collin et al., 2016; Marschner and Marschner, 2012; Parent et al., 2013b]. The first partition contrasts all measured elements (N, P, K, Ca, Mg) to the filling value (Fv). The second partition contrasts Mg and Ca to K, P and N ($[Mg, Ca|K, P, N]$). The sub-compositions are then divided into $[K|P, N]$, $[P|N]$ and $[Mg|Ca]$. $[P|N]$ is representative of the Redfield ratio which is an indicator of the balance between processes associated with the synthesis of N-rich proteins and the synthesis of P rich r-ARN respectively [Agren, 2004; Loladze and Elser, 2011]. $[Mg|Ca]$ is an indicator of the geographical position and soil mineralogy [Walworth and Sumner, 1988]. Once the SBP was defined, we used the following equation to calculate the *ilr* balances [Egozcue and Pawlowsky-Glahn, 2005]:

$$ilr_j = \sqrt{\frac{n_j^+ n_j^-}{n_j^+ + n_j^-}} \ln \frac{g(c_j^+)}{g(c_j^-)} \tag{3.2}$$

ilr_j corresponds to the j^{th} isometric log-ratio, n_j^+ and n_j^- are the number of components in the (+) et (-) groups, $g(c_j^+)$ and $g(c_j^-)$ are the geometric means of groups (+) and (-). $\sqrt{\frac{n_j^+ n_j^-}{n_j^+ + n_j^-}}$ corresponds to the orthogonal coefficient of the j^{th} balance defined in the SBP. *Ilr* balances are conventionally presented in the form [components in denominator|components in numerator] because log ratios become more negative as the denominator increases and hence, the balance leans to the left as in algebra where negative numbers are located on the left side of the zero [Nowaki et al., 2017; Parent et al., 2013a]. Thus, an increase in *ilr* balance can be attributed to either a decrease in the left part of the balance or an increase in the right part of the balance. For instance, the $[P|N]$ balance is defined by $\sqrt{\frac{1}{2}} \ln \frac{N}{P}$. As a consequence, an increase in N or a decrease

in P concentration will lead to increased *ilr* balance value and the $[P|N]$ partition leans to the right [Collin et al., 2016; Parent et al., 2013a].

3.2.4 Statistical analyses

To test the differences in foliar *ilr* balances, foliar nutrient concentrations and foliar nutrient contents between species, we conducted Student's t-tests. By informing about the biogeochemical niche of the studied species, those analyses are used to interprete the species-mixing effects. In order to test whether stand composition (pure *vs.* mixed), species identity (beech *vs.* pine) and their interaction influenced the current *ilr* balance or the foliar nutrient content, we fitted linear mixed models on each *ilr* balance or nutrient content, considering site and stand nested within site as random factors

$$Y_{hijs} = \boldsymbol{\beta} \times \mathbf{E_{hjs}} + a_s(0, \sigma_s^2) + a_{j|s}(0, \sigma_j^2) + \varepsilon(0, \sigma_\varepsilon^2) \tag{3.3}$$

Y_{hijs} represents the *ilr* balance/content of interest for the i^{th} individual (tree) in the j^{th} stand (pure or mixed) and the s^{th} site for species h (pine or beech), $\boldsymbol{\beta}$ is the vector of the fixed effect parameters (species identity, stand composition and their interaction), $\mathbf{E}$ is the matrix of the predictors of the fixed effects, a_s is the random factor characterized by the inter-site variance σ_s^2 , $a_{j|s}$ is the random factor characterized by the inter-stand variance within a same site σ_j^2 and ε is the error term of variance σ^2. In addition, linear mixed effect models using site as random factor were used to test the significance of the difference between pure and mixed stands within each species for each *ilr* balance or nutrient content.

We then investigated the relationship between species-mixing effects on tree nutrition, and site nutritional status. To do so, we computed the difference between the *ilr* balances/nutrient contents per tree and the corresponding average value per site, for each species separately, and used this index as the response variable. Stand composition (pure *vs.* mixed), site nutritional status and their interaction were used as explanatory variables in multivariate linear regression models (Equation

3.4)):

$$Y_{ijs} - \overline{Y_s} = \alpha + \boldsymbol{\beta} \times \mathbf{E_{js}} + \varepsilon(0, \sigma^2_{\varepsilon}) \tag{3.4}$$

Y_{ijs} represents the *ilr* balance/content of interest for the i^{th} individual (tree) in the j^{th} stand (pure or mixed) and the s^{th} site for each species separately, and $\overline{Y_s}$ is the average value of the *ilr* balance content of either beech or pine trees across the pure and mixed stands in site s. α is the intercept, $\boldsymbol{\beta}$ is the vector of the parameters, $\mathbf{E}$ is the predictor matrix (stand composition, site nutritional status and their interaction) and ε is the error term of variance σ^2_{ε}. Considering that the *ilr* balance $[Fv|Mg, Ca, K, P, N]$ contrasts five mineral elements of major importance for tree growth and functioning against all other elements, we used its average value per site and species as an index of site nutritional status for all *ilr* balance models. For the foliar nutrient content models, we used the average value of the corresponding nutrient content per site and species as the index of site nutritional status. In all cases, the variables used as indicators of site nutritional status were centered. The contrasting average values of either *ilr* balance or nutrient contents between sites resulted in empirical gradients of nutritional status. Dependent variables of the mixed and multivariate linear models were normally distributed with the exception of the nutrient contents used in the mixed models which were therefore ln-transformed. All statistical analyses were conducted using the R software, version 3.4.1 [R Development Core Team, 2014]. Compositional data analyses were conducted using the "composition" package [Van den Boogaart et al., 2019]. The closure operation was conducted using the "acomp" function while the *ilr* transformation operation was done on the closed data space with the "ilr" function. Mixed models were fitted with the package "nlme" [Pinheiro et al., 2017].

3.3 Results

3.3.1 Site nutrient status

The ranges of foliar nutrient concentrations within and among sites for beech and pine, along with the corresponding optimum range [Mellert and Göttlein, 2012], are presented in Fig.3.2. For both species and most combinations of sites and nutrients, there was a high variability in foliar concentrations. Also, the studied sites spanned a large range of tree nutrient status (Appendix 14 and 15). With the exception of K for pine, all nutrients were found to be deficient for at least one combination of site and species (Appendix 15). While nutrition appeared to be non limiting for neither beech nor pine in two sites (Bul1, Cze1), some sites showed deficiencies for more than one nutrient. For beech, Bel1 and Fra1 were deficient for the same three nutrients (P, Ca, Mg); for pine, two different nutrient deficiencies were observed in Fra1 (P, Mg), Lit2 (N, Ca) and Pol3 (N, P). At some sites, the same nutrients appeared to be limiting for both beech and pine (Ca in Bel1; P and Mg in Fra1). Two sites (Ger7 and Lit1) displayed no deficiencies for beech while deficiencies were observed for pine (P and N limitation in Ger7; N limitation in Lit1).

3.3.2 Foliar nutrient composition of beech and pine

As shown in Table 3.2, beech leaves and current year pine needles differed significantly for all investigated *ilr* balances. The $[Fv|Mg, Ca, K, P, N]$, $[K|P, N]$, $[P|N]$ and $[Mg|Ca]$ balances were higher in beech leaves, while the $[Mg, Ca|K, P, N]$ was higher in current year pine needles. While P concentrations were similar for both species, the concentrations of all other nutrients were higher in beech leaves compared to current pine needles; the relative difference between species was most pronounced for Ca, followed by Mg and N concentrations, and then K (Table 3.2).

3.3.3 Stand composition effect on *ilr* balances and nutrient content

Species identity had a significant effect on all *ilr* balances (Fig.3.3). For all investigated *ilr* balances, at least one species displayed a sig-

Table 3.2 – Summary of the foliar nutrient composition of beech and current year pine needles. Mean *ilr* balances (1) and nutrient concentrations ($mg.g^{-1}$) (2) across all stands and sites (standard errors in parentheses). For each foliar variable (*ilr* balances or nutrient concentrations) means within a column that are followed by the same letter do not differ at $P < 0.05$ (Students t-Tests).

(1)	[Fv|Mg, Ca, K, P, N]		[Mg, Ca|K, P, N]		[K|P, N]		[P|N]		[Mg|Ca]	
Beech	-4.83a	(±0.01)	0.77a	(±0.03)	-0.36a	(±0.02)	1.94a	(±0.01)	1.22a	(±0.02)
Pine	-5.17b	(±0.01)	1.34b	(±0.02)	-0.44b	(±0.01)	1.66b	(±0.01)	0.66b	(±0.01)

(2)	N		P		K		Ca		Mg	
Beech	21.9a	(±0.2)	1.4a	(±0.0)	9.0a	(±0.2)	8.1a	(±0.2)	1.5a	(±0.0)
Pine	15.1b	(±0.2)	1.4a	(±0.0)	8.1b	(±0.1)	2.7b	(±0.1)	1.0b	(±0.0)

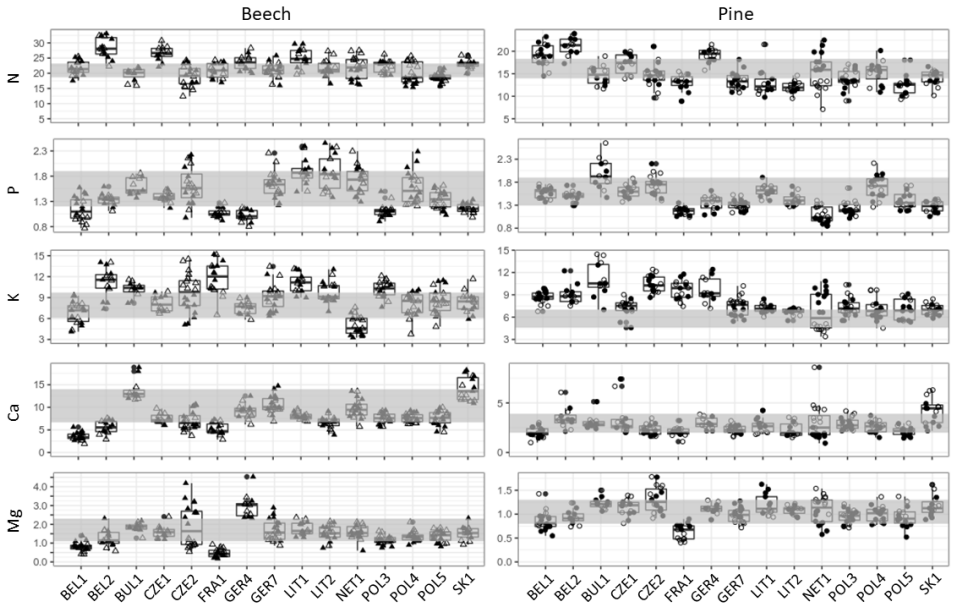
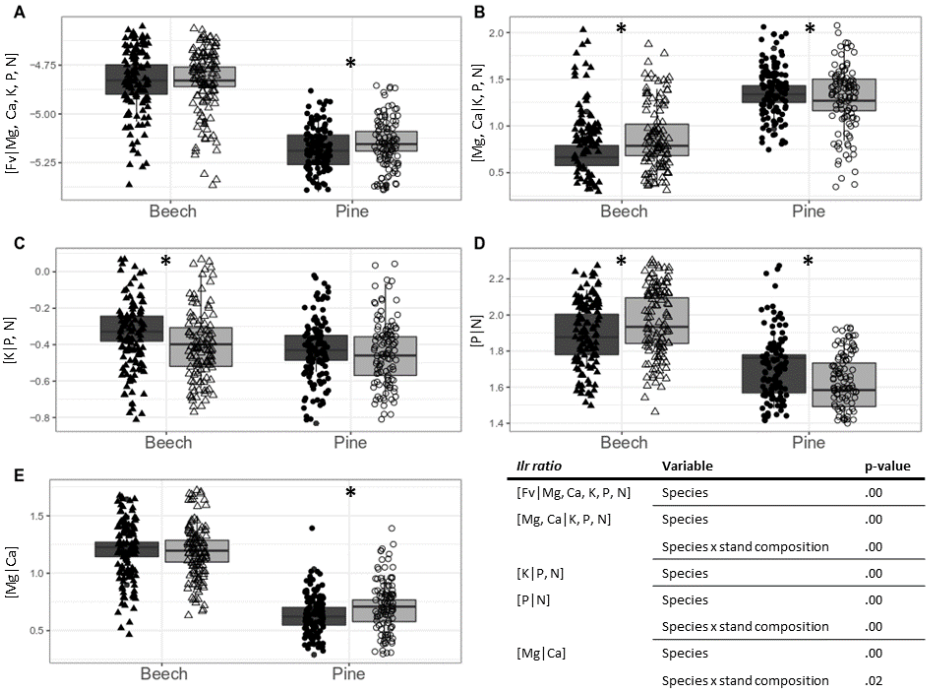


Figure 3.2 – Foliar nutrient concentration ($mg.g^{-1}$) of N, P, K, Ca and Mg in beech leaves (left) and current-year pine needles (right) in the different sites. For each combination of site and species, boxplots are used for concentrations across stands (pure, mixed). Individual tree nutrient concentrations are represented by triangles (beech) or dots (pine); filled and open symbols denote pure and mixed stands, respectively. The grey banner indicates the optimum range of foliar nutrient concentrations as defined by Mellert and Göttlein [2012]. Y axis may differ between species.

nificant species-mixing effect (Fig.3.3). For beech, $[Mg, Ca|K, P, N]$ and $[P|N]$ balances were higher in mixed stands than in monocultures while the opposite was true for $[K|P, N]$. For pine, mixed stands displayed higher $[Fv|Mg, Ca, K, P, N]$ and $[Mg|Ca]$ balances and lower $[Mg, Ca|K, P, N]$ and $[P|N]$ balances than monocultures. For three *ilr* balances ($[Mg, Ca|K, P, N]$, $[Mg|Ca]$ and $[P|N]$), the effect of stand composition differed between species (Fig.3.3; significant species $\times$ stand composition interaction), with two *ilr* balances showing opposite effects of mixing: compared to monocultures the $[Mg, Ca|K, P, N]$ and $[P|N]$ balances in mixed stands were higher for beech and lower for pine. Looking at nutrient contents (Fig.3.4), mixing increased P contents in pine and K contents in beech; compared to the monocultures, Ca contents of the mixed stands were lower in beech and higher in pine.

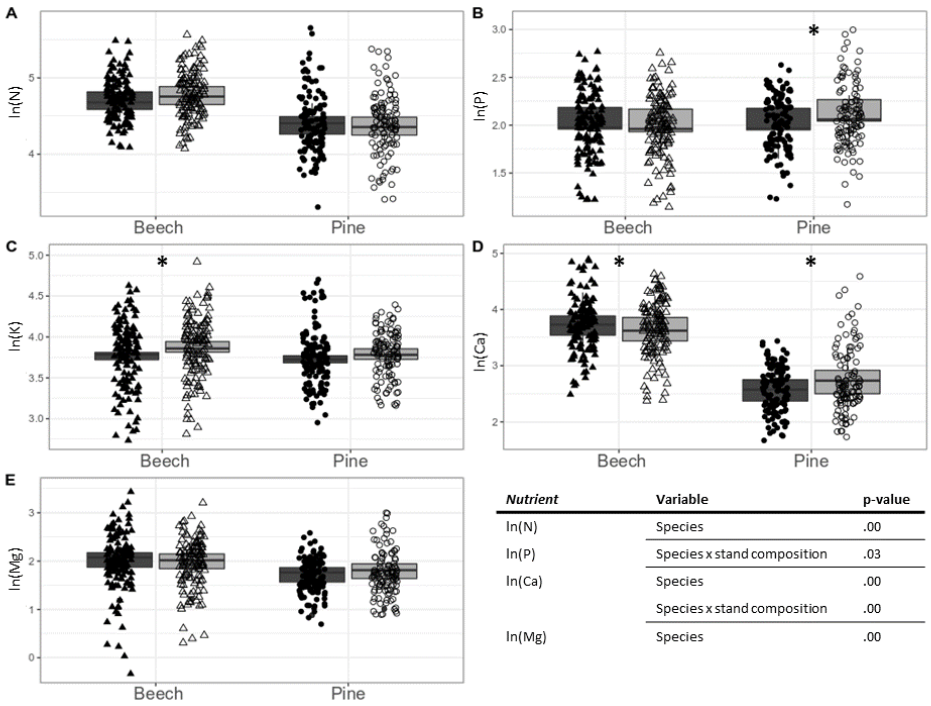


Ilr ratio	Variable	p-value
[Fv|Mg, Ca, K, P, N]	Species	.00
[Mg, Ca|K, P, N]	Species	.00
	Species x stand composition	.00
[K|P, N]	Species	.00
[P|N]	Species	.00
	Species x stand composition	.00
[Mg|Ca]	Species	.00
	Species x stand composition	.02

Figure 3.3 – Beech and pine foliar *ilr* balances (boxplots and individual (tree) observations) as a function of species identity (beech/pine - current-year needles) and stand composition (pure/mixed) across all sites. The individual tree observations are depicted by black filled triangles (beech) or dots (pine); filled and open symbols denote pure and mixed stands, respectively. Black stars indicate significant differences between pure and mixed stands of a same species at $P < 0.05$ from linear mixed models adjusted on each species and each *ilr* balance separately. The statistical significant effects of the mixed models (Equation 3.3) are shown in the enclosed table, while the detailed statistics for all *ilr* balance models are given in Appendix 17.

3.3.4 Impact of site nutrient status on species mixing effects

The influence of species-mixing effects on *ilr* balances along the gradient of site nutritional status for beech and pine are displayed in Figs.3.5 and 3.6, respectively. For beech, the $[Mg|Ca]$ and $[P|N]$ balances were significantly affected by the site nutrient level, the stand composition, and their interaction. For both *ilr* balances, the difference between pure and mixed stands was highest at the lower end of the gradient where mixed stands were associated with higher $[P|N]$ and lower $[Mg|Ca]$ bal-



Nutrient	Variable	p-value
ln(N)	Species	.00
ln(P)	Species x stand composition	.03
ln(Ca)	Species	.00
	Species x stand composition	.00
ln(Mg)	Species	.00

Figure 3.4 – Beech and pine foliar nutrient contents (boxplots and individual observations as a function of species identity (beech/pine - current-year needles) and stand composition (pure/mixed) across all sites. The individual tree observations are depicted by triangles (beech) or dots (pine); filled and open symbols denote pure and mixed stands, respectively. Black stars indicate significant differences between pure and mixed stands of a same species at $P < 0.05$ from linear mixed models adjusted on each species and each nutrient content separately. The statistically significant effects of the mixed models (Equation 3.3) are shown in the enclosed table, while the detailed statistics for all models are given in Appendix 18.

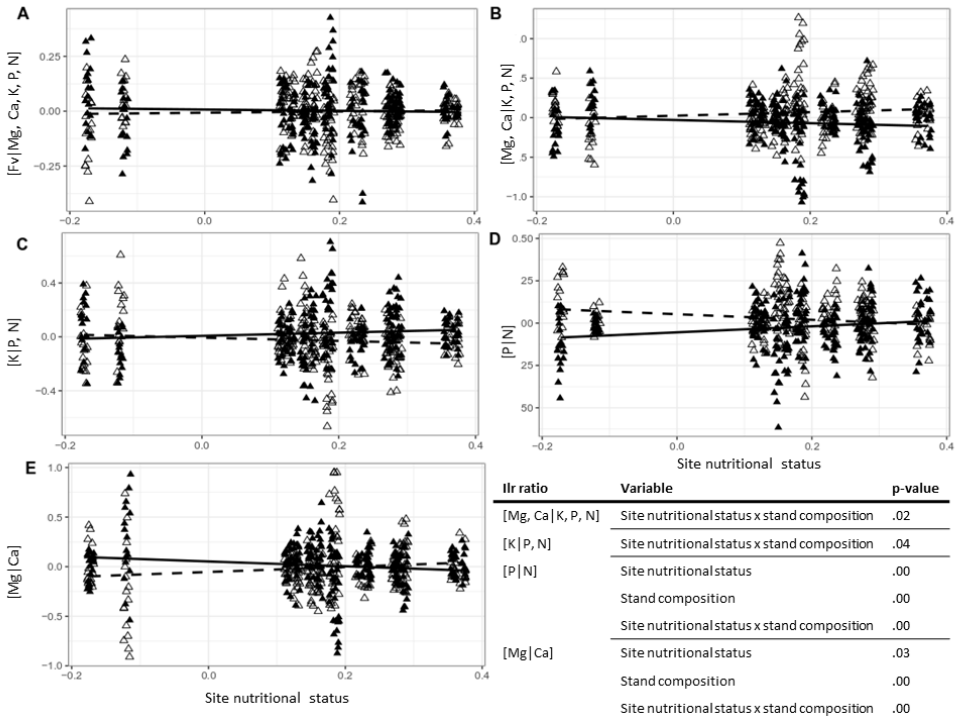
ances, compared to pure stands. For the $[Mg, Ca|K, P, N]$ and $[K|P, N]$ balances, only the interaction of site and stand was significant, indicating that the site nutrient status had a different impact in pure and in mixed stands. No significant effect was detected for the $[Fv|elements]$ balance. For pine, the $[Fv|elements]$ balance was significantly higher in mixed than in pure stands, and the effect was constant along the soil fertility gradient. The interaction of site and stand was significant for the $[K|P, N]$ and $[Mg|Ca]$ balances, showing significantly different responses to site nutrient status of pure and mixed stands. Looking at

the nutrient contents of beech leaves (Fig.3.7), stand composition had a significant effect on both K and Ca. The foliar K contents were higher in the mixed stands irrespective of site fertility; by contrast, the effect of stand composition on Ca differed along the gradient, with lower Ca contents in mixtures on nutrient-rich sites and almost similar contents for both stand types at the lower end of the gradient. For N and Mg, the effect of site differed between pure and mixed stands, with the strongest difference among stand types observed at the richer sites. There was no main stand composition effect, yet the associated p-value was quite close to 0.05 (Appendix 20). P contents did not respond to either site nutrient status nor stand composition. For pine nutrient contents (Fig.3.8), P and Mg showed a similar pattern. There was an overall significant site and stand composition effect, yet the effect of an increased site fertility was negative in the pure stands and positive in the mixtures. For K and Ca, the effect of site also differed between pure and mixed stands. For K, the interaction was associated with a significant site effect and to opposite effects of stand composition at both extremities of the gradient (higher K content in mixed stand at the lower end of the gradient and lower K content in mixed stand at the higher end of the gradient). The Ca contents of pine needles were on average significantly higher in the mixed stands, yet the stand composition effect was more pronounced as soil fertility increased. N contents in pine needles did not change significantly with either stand composition nor site fertility.

3.4 Discussion

3.4.1 Foliar *ilr* balances and individual nutrient concentrations in beech and pine

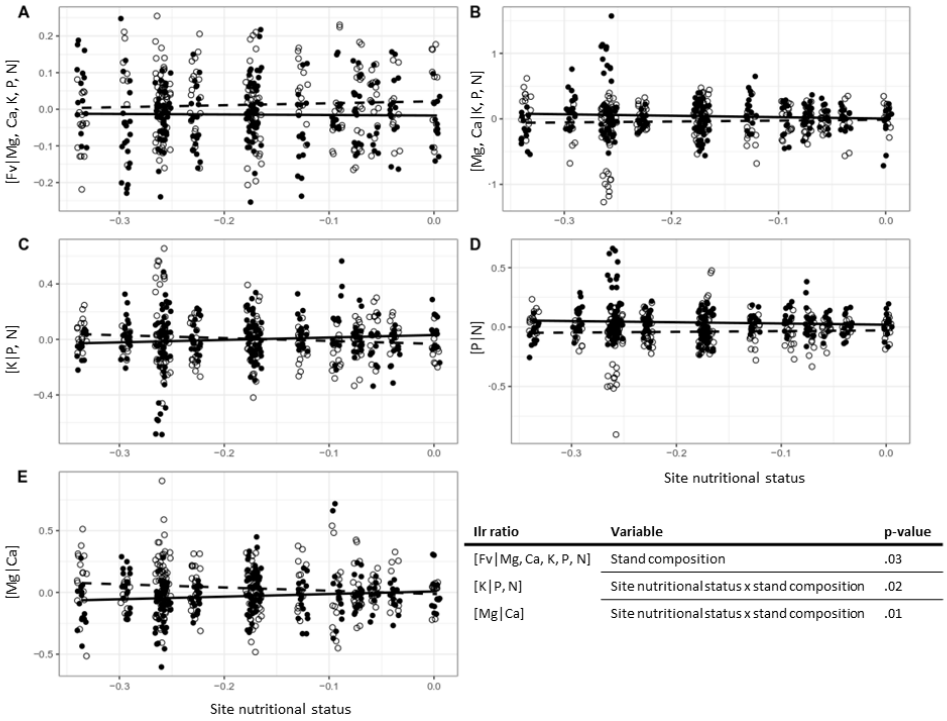
Our results showed that beech leaves and current year pine needles have distinct foliar nutrient signatures. To start with, it is essential to remember that as a result of the computation procedure and notation (Equation 3.2), the *ilr* balances behave differently than traditional raw elemental ratios. An increase in *ilr* balance means that either the left part (the balance denominator) has decreased, and/or the right part (the



Ilr ratio	Variable	p-value
[Mg, Ca|K, P, N]	Site nutritional status x stand composition	.02
[K|P, N]	Site nutritional status x stand composition	.04
[P|N]	Site nutritional status	.00
	Stand composition	.00
	Site nutritional status x stand composition	.00
[Mg|Ca]	Site nutritional status	.03
	Stand composition	.00
	Site nutritional status x stand composition	.00

Figure 3.5 – Difference between individual *ilr* balances of beech trees and the corresponding average value per site as a function of site nutritional status and stand composition. The *ilr* balance differences are represented by filled (pure stands) or open triangles (mixed stands). The lines represent the predictions for the pure (solid line) and mixed stands (dashed line), using Equation 3.4. For all *ilr* balances, the site nutritional status is quantified by the site-average species-specific $[Fv|Mg, Ca, K, P, N]$ *ilr* balances. Significant effects of the linear models (Equation 3.4) are shown in the enclosed table, while the detailed statistics for all *ilr* balance models are given in Appendix 19. In the table, default value for stand composition is "pure".

balance numerator) has increased. In this respect, the higher $[P|N]$ and $[Mg|Ca]$ balances in beech leaves compared to pine needles are consistent with the corresponding average nutrient concentrations (Table 3.2). The increased $[K|P, N]$ in beech leaves can mainly be attributed to the much higher N concentrations in beech leaves compared to pine needles, given the limited difference in K concentrations and the similarity of P concentrations. The significantly higher $[Mg, Ca|K, P, N]$ balance in pine needles can primarily be attributed to the strongly reduced Ca concentrations of pine needles compared to beech leaves, and to a lesser

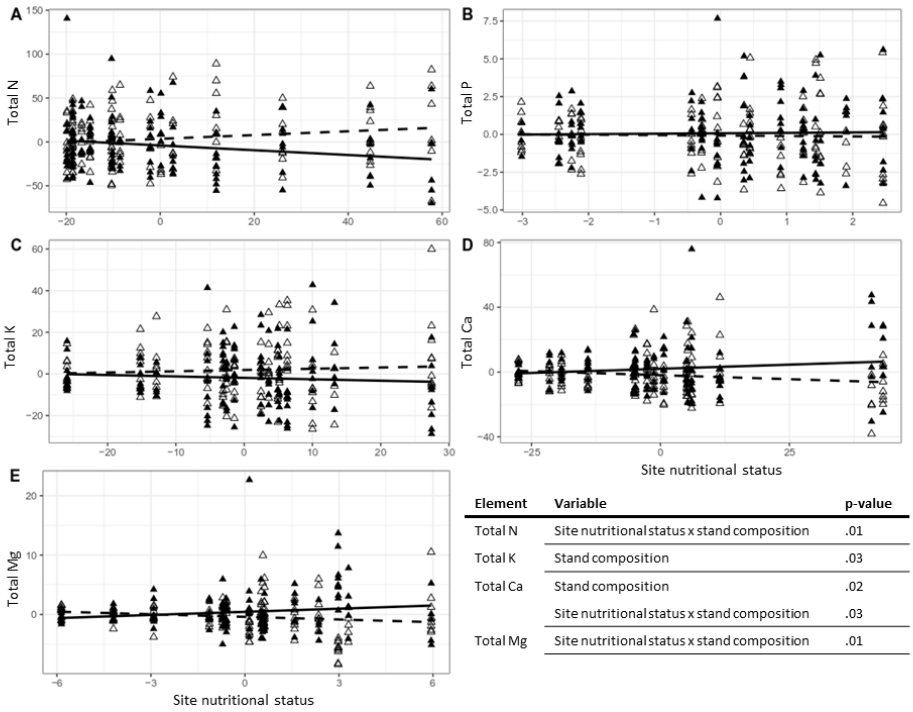


Ilr ratio	Variable	p-value
[Fv|Mg, Ca, K, P, N]	Stand composition	.03
[K|P, N]	Site nutritional status x stand composition	.02
[Mg|Ca]	Site nutritional status x stand composition	.01

Figure 3.6 – Difference between individual *ilr* balances of pine trees and the corresponding average value per site as a function of site nutritional status and stand composition. The *ilr* balance differences are represented by filled (pure stands) or open dots (mixed stands). The lines represent the predictions for the pure (solid line) and mixed stands (dashed line), using Equation 3.4. For all *ilr* balances, the site nutritional status is quantified by the site-average species-specific $[Fv|Mg, Ca, K, P, N]$ *ilr* balance. Significant effects of the linear models (Equation 3.4) are shown in the enclosed table, while the detailed statistics for all *ilr* balance models are given in Appendix 19. In the enclosed table, default value for stand composition is "pure".

extent, to the lower Mg concentrations of pine needles. Finally, the higher $[Fv|Mg, Ca, K, P, N]$ value in beech leaves is consistent with the higher concentrations of most measured nutrients in beech leaves (Table 3.2), and their significantly lower Fv value (data not shown); the latter is composed of unmeasured macro- and micro-elements. We are not able to point out those elements, which are involved in this difference.

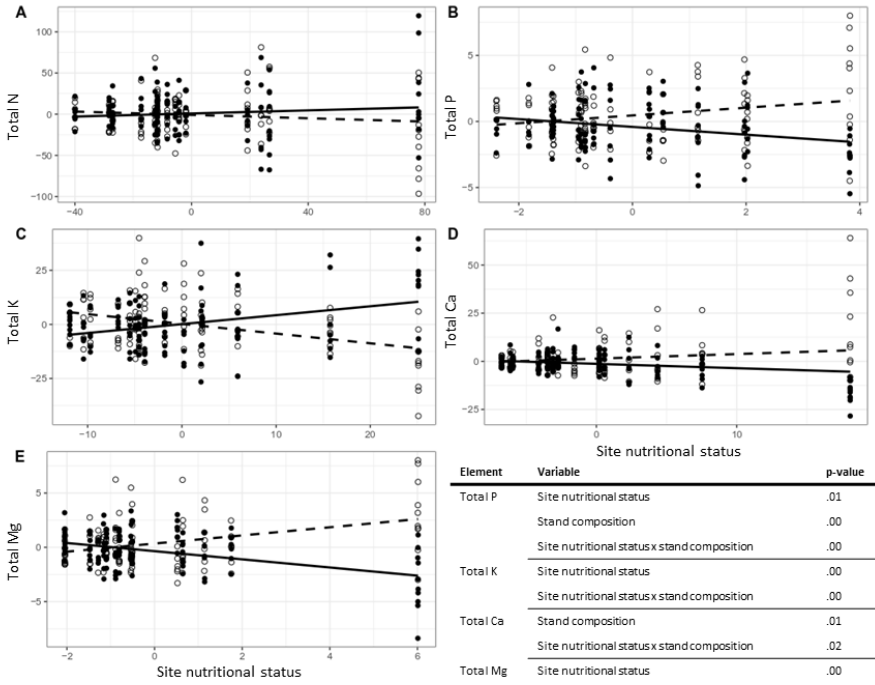
Previous studies, conducted on both litterfall and fresh leaves, have found similar differences in foliar nutrient concentrations between beech and pine [González de Andrés et al., 2019; Mellert and Göttlein, 2012],



Element	Variable	p-value
Total N	Site nutritional status x stand composition	.01
Total K	Stand composition	.03
Total Ca	Stand composition	.02
	Site nutritional status x stand composition	.03
Total Mg	Site nutritional status x stand composition	.01

Figure 3.7 – Difference between individual foliar content (mg in 50 leaves) of beech trees and the corresponding average value per site as a function of site nutritional status and stand composition. The nutrient content differences are represented by filled (pure stands) or open triangles (mixed stands). The lines represent the predictions for the pure (solid line) and mixed stands (dashed line), using Equation 3.4. For all elements, the site nutritional status is quantified by the site-average species-specific nutrient content. Significant effects of the linear models (Equation 3.4) are shown in the enclosed table, while the detailed statistics for all nutrient content models are given in Appendix 20. In the enclosed table, default value for stand composition is "pure".

confirming the distinctly higher N, Ca and Mg concentrations in beech leaves compared to current year pine needles [Liu et al., 2006; Sardans et al., 2015]. According to Sardans et al. [2015] such distinct foliar signatures probably result from long-term differentiation of metabolic and physiological functions and morphology leading to species-specific optimal elemental composition according to the biogeochemical niche hypothesis.



Element	Variable	p-value
Total P	Site nutritional status	.01
	Stand composition	.00
	Site nutritional status x stand composition	.00
Total K	Site nutritional status	.00
	Site nutritional status x stand composition	.00
Total Ca	Stand composition	.01
	Site nutritional status x stand composition	.02
Total Mg	Site nutritional status	.00
	Stand composition	.00
	Site nutritional status x stand composition	.00

Figure 3.8 – Difference between individual foliar content (mg in 500 needles) of pine trees and the corresponding average value per site as a function of site nutritional status and stand composition. The nutrient content differences are represented by filled (pure stands) or open dots (mixed stands). The lines represent the predictions for the pure (solid line) and mixed stands (dashed line), using Equation 3.4. For all elements, the site nutritional status is quantified by the site-average species-specific nutrient content. Significant effects of the linear models (Equation 3.4) are shown in the enclosed table, while the detailed statistics for all nutrient content models are given in Appendix 20. In the enclosed table, default value for stand composition is "pure".

The contrasted elemental composition and stoichiometries thus indicates differences in nutritional characteristics between species. Because distinct characteristics between co-occurring species are necessary to entail complementarity, such differences could lead to reduced competition [Sardans et al., 2015] and improved nutrition in mixed stands.

3.4.2 Overall mixing effects on *ilr* balances and nutrient content

When significant, the stand composition effect resulted in increased nutrient contents in the mixed stands compared to the monocultures in all (P and Ca in pine, K in beech) but one case (Ca in beech) (Figs.3.3 and 3.4). The positive effect of beech on pine Ca and the corresponding negative effect of pine on beech Ca could be related to the strong difference in foliar Ca concentration between beech leaves and pine needles (Table 3.2), resulting in changed nutrient inputs through litterfall. Differences in litterfall between species have been shown to influence soil nutrient availability [Fassnacht and Gowerr, 1999; Polyakova and Billor, 2007; Vesterdal, 1998]. However, such a difference in nutrient composition between leaves and needles could not explain the other synergistic effects. Indeed, pine P content and beech K content increased in mixed stands compared to pure stands even though foliar P concentrations are similar for both species and K foliar concentrations are lower in pine than in beech. In addition, no stand composition effect could be detected for some nutrients, *e.g.* for nitrogen contents in pine needles, despite the much higher N concentrations in beech leaves compared to pine. Previous studies have found contrasting results on the impact of species mixing on tree foliar nutrition depending on the element considered. Some studies are consistent with our results. For instance, Brandtberg [2001] and Thelin et al. [2002] found P and K concentrations in foliage of conifers to increase if broadleaves were present. Berger et al. [2009] found a tendency to higher Ca concentrations in mixed stands compared to pure stands for coniferous species and lower concentrations for beech stands. On the other hand, our findings differed from some other studies. For instance, Magh et al. [2018] hypothesized broadleaves N acquisition to be lower in mixed stands due to a negative impact of the more recalcitrant conifer litter on the mineralization rates of organic matter. However, we did not find lower amounts of N in beech foliage in mixed stands compared to pure stands. One possible explanation is that soil N availability is also strongly influenced by other environmental drivers than litter quality [Anderson and Domsch, 1993; Brown, 1992].

Such simultaneous influence of several factors and their interaction on species-mixing effects on foliar are not well studied yet.

Altogether, our results suggest that differences in foliar nutrient concentrations between associated species and the corresponding change in nutrient inputs, are not strong enough to be used as predictors of overall species-mixing effects. Obviously, additional factors should be considered to explain the large variability in species-mixing effects between sites. This is in line with the results from Rothe et al. [2003]. In their study, foliar nutrient pools were not always good predictors of nutrient availability. Several other mechanisms such as the effect of species mixing on litter production through increased canopy packing [Barbeito et al., 2017; Jucker et al., 2015; Pretzsch, 2014; Scherer-Lorenzen et al., 2007] or species mixing effects on rates of litter decomposition [Joly et al., 2016; Jonard et al., 2008] can be expected to also come into play although we were not able to properly assess their relevance for and contribution to our findings. More specifically, beech is expected to have a positive impact on pine nutrition through improvement of the humus layer, the upper mineral soil and exploitation of nutrients from deeper soil horizons [Chodzicki, 1934; Pretzsch et al., 2015]. The higher nutrient content, lower C:N ratio and lower amount of recalcitrant compound in beech litter compared to pine [Rumberger et al., 2004; Zhong and Makeschin, 2004] could lead to reduced soil acidity and richer humus which will in turn improve nutrient availability in mixed stands compared to pure pine stands [Collin et al., 2016; González de Andrés et al., 2017]. In addition, the distinct potential rooting pattern of both species (heart-shaped fine root profile for beech *vs.* peak of fine root biomass in the most superficial soil layers for pine; Prévosto and Curt 2004) can lead to higher combined root occupancy in mixture and thus, more complete belowground exploitation at least in some sites [González de Andrés et al., 2017].

In addition to the observed effects on selected nutrient contents, mixing beech and pine also changed nutrient balances. Two *ilr* balances significantly differed between pure and mixed stands for both pine and beech trees: [Mg,Ca|K,P,N], [P|N], yet in an opposite direction (Fig.3.3). The

three other *ilr* balances were also affected by stand composition, but only for one species. To our knowledge, few studies analyzed the influence of species mixing on tree foliar nutrition using elements balances. Thelin et al. [2002] found the classical ratio $P : N$ to be higher in Norway spruce needles when mixed with deciduous species (beech, birch or oak), which is coherent with our findings. The absence of species mixing effect on beech $[Mg|Ca]$ is coherent with the findings of Collin et al. [2016] who used isometric log-ratios to study the nutritional characteristics of sugar maple and red maple in different contexts (pure stands *vs.* mixed with conifers; increasing soil acidity levels). They explained the absence of effects by a simultaneous decrease in Mg and Ca with increased conifer proportions. In contrast to our results, however, Collin et al. [2016] also found a decrease in the $[Fv|Mg, Ca, K, P, N]$ balance with increasing proportions of conifers, which they attributed to the effect of increased soil acidity on Al and Mn availability (higher ionic activity in more acidic conditions); as those elements were not measured in the leaves, they were expected to increase correspondingly the Fv value. The dependency of those mechanisms on local factors, like the forest management strategy, the acidifying potential of the species involved or the initial soil acidity could explain contrasting results between studies. Importantly, the change in *ilr* balance suggests that mixing can modify tree nutrition by altering some key nutrient balances, well beyond changing specific individual nutrients. This suspected complementarity with regard to mineral nutrition could be, at least in part, the cause of the increased productivity highlighted on the same network of pine and beech by Pretzsch et al. [2015] as proposed by Burkhart and Tham [1992], Frivold and Kolström [1999], and Kelty [1992]. However, our data set does not allow to properly explore the relationships between tree/stand productivity and nutrition, due to the limited number of sites compared to the potentially high number of processes involved (*cf. e.g.* Forrester and Bauhus [2016] for a comprehensive review on those processes).

3.4.3 Mixing effects as a function of site nutrient status

Regarding the impacts of mixing on nutrient contents, there was a close agreement between the results of the overall analysis (Equation 3.3) and the analysis where the nutrient gradient was explicitly accounted for (Equation 3.4); the only exception to this agreement was Mg under pine for which the stand composition effect was not significant in the overall analyses (p-value = 0.13). By contrast, we found more discrepancies between the two approaches for the *ilr* balances. A possible explanation could be related to the index we used to characterize the gradient of nutrient availability for the latter approach ($[Fv|Mg, Ca, K, P, N]$ for all *ilr* balances). We deliberatively selected $[Fv|Mg, Ca, K, P, N]$ over the traditional site index (SI) in our case as the latter integrates all site factors, and not only nutrients [Brandl et al., 2014]. The use of other indicators such as foliar nutrient remobilization [Achat et al., 2018], soil pH or soil exchangeable cation pools in future studies should help improve our understanding of the dependency of species-mixing effects on site chemical fertility. It is also important to note that, for beech, the sites were not homogeneously distributed along the $[Fv|Mg, Ca, K, P, N]$ gradient (Fig.3.5); the two sites at the lower end of the gradient could have had a strong influence on the slope for some models (see the $[P|N]$ balance for instance). One way to cope with this would be to select alternative indicators of soil fertility (see above), and/or to increase the sampling to fill-in the current gaps along the gradient.

Focusing on the contents, we expected for mixing effects to increase with a decrease in nutrient availability according to the framework proposed by Forrester and Bauhus [2016]. However, in all cases where we found a significant overall stand composition effect (K and Ca for beech, Fig.3.7; P, Ca, Mg for pine, Fig.3.8), we actually observed the opposite, with only minor or no difference between monocultures and mixtures on the poorest sites, and maximum differences on richer sites.

The limited stand composition effects or even the lack of any significant mixing effects in low-nutrient sites could first be explained by the co-occurrence of several nutrient limiting factors. Indeed, the uptake

of a nutrient is not only determined by its availability but also by the availability of other nutrients and their interactions, and by environmental conditions such as soil pH or water availability [Marschner and Marschner, 2012; Wilkinson, 2000]. Simultaneous limitations of distinct nutrients have been observed for both beech and pine stands at several locations (for instance, site Fra1 displayed P and Mg deficiencies for both species and Bel1 displayed Ca deficiency for both species and Mg deficiency for beech) and could originate from the coexistence of several factors limiting nutrient availability. It might be advocated that even in the case where the availability of one limiting nutrient has increased as a result of mixing, this would not translate into an increased foliar content as far as another constraint limiting nutrient availability (*e.g.* limited water availability) would still be present.

A second hypothesis to explain our results is related to all those situations where species interactions may not improve the availability of the limiting nutrient. This could be due to the intrinsic pool of traits present, where inter-specific differences in physiology, phenology or morphology do not improve nutrient availability. Indeed, traits of the species involved in the mixture are of primary importance to determine whether this mixture benefits from improvement of resources availability, uptake or use-efficiency [Ammer, 2019]. We expected from an association of species with such distinct foliar traits as beech and pine (for instance in term of leaf life span), to induce differences in foliar nutrient composition compared to monocultures. However, such differences in traits may not systematically influence the availability, uptake or resource-use efficiency of nutrients and thus, the foliar nutrient composition. Another possible explanation is the existence of factors limiting the expression of any potential complementarity interaction. Jucker et al. [2014] highlighted such a mechanism in Mediterranean mixed forests. They found that species mixing improved stand growth through complementary light use but that this effect was severely reduced if water resources became limiting. Considering the interspecific differences in rooting patterns between beech and pine [Prévosto and Curt, 2004] as a candidate mechanism to increase nutrient availability in mixed species stands compared to mono-

cultures [Forrester and Bauhus, 2016], any constraint that would limit the potential development of the rooting system (*e.g.* anoxic conditions; Kozlowski 1986) would alter this potential spatial stratification.

The largest differences in foliar nutrient contents between monocultures and mixed-species stands were observed on the richer sites, with synergistic effects in all cases except for Ca in beech (see previous section). The improved tree nutrient composition of the mixtures at the higher end of the fertility gradient was unexpected, as those situations reflect normal ranges or even a surplus of the nutrient in question. However, an adequate supply of one given nutrient does not exclude potential limitations of others, whereas their availability could in turn limit the uptake of the target nutrient. If mixing removes this constraint, this could explain why a synergistic effect of mixture occurred. An additional explanation is an increased competition in pure stands on the nutrient rich sites due to increased growth, not compensated for by the higher nutrient availability. Bravo-Oviedo et al. [2006] for instance, found that faster tree growth in richer sites lead to increased competition and higher individual tree mortality. In this context, species-mixing could reduce resource competition, leading to increased species-mixing effects on richer sites.

3.5 Conclusion

Considering the impact of mixing on single nutrient contents, we mostly found either no effect or synergies, with only one case where nutrient contents were lower in mixed stands (antagonism for Ca in beech). Our results showed that the contrasting foliar nutrient compositions of pine and beech trees alone were unable to explain the mixing effects on tree nutrition, which suggests that other mechanisms than a simple change of nutrient inputs through litterfall are at play. Far beyond changing the foliar contents of single individual nutrients, mixing was found to significantly alter key nutrient balances in both beech leaves and current year pine needles.

Our analysis also revealed unexpected patterns of complementarity as a function of nutrient availability, with only minor or no differences

between monocultures and mixtures at the lower end of the nutritional gradient, and maximum differences on nutrient rich soils. This clearly points to further expanding the existing frameworks to account for the multivariate nature of tree nutrition. In this paper, we made a first attempt in that direction by working on both contents and *ilr* balances. Further work is needed to disentangle the underlying processes, using a combination of field work and modelling approaches. This claims for the establishment of controlled standardized experiments across Europe to test for specific mechanisms.

Chapter 4

Regional climate moderately influences species-mixing effect on tree growth-climate relationship and drought resistance for beech and pine across Europe

Abstract

Increasing species diversity is considered a promising strategy to mitigate the negative impacts of global change on forests. However, the way regional climate conditions shape the patterns of species-mixing effects on climate-growth relationships and drought resistance remains poorly documented. In this context, resistance refers to the ability of the trees to limit growth reduction during such episode.

In this study, we investigated the patterns of species-mixing effects over a large gradient of environmental conditions throughout Europe for European beech (*Fagus sylvatica* (L.)) and Scots pine (*Pinus sylvestris* (L.)), two species with contrasted functional traits. We hypothesized that the effects of mixing on tree response to climate would be mostly affected by the regional climate. We used tree ring chronologies derived from 1143 beech and 1164 pine trees sampled in 30 study sites, each composed of one mixed stand of beech and pine and of the two corresponding pure stands. For each site and stand, we used Bootstrapped Correlation Coefficients (BCCs) on standardized chronologies and growth reduction during drought years on raw chronologies to analyse the species-mixing effects on average climate-tree growth relationships and resistance to drought, respectively.

We found consistent large-scale spatial patterns of average climate-growth relationships reflecting similar regional climate effects on beech and pine. With the exception of the driest climate zone where mixing consistently reduced the correlation with the main climatic drivers for beech, the mixing effects on the BCCs were highly variable within all other climate regions, resulting in the lack of a coherent response to mixing. No consistent species-mixing effect on drought resistance was found within and across climate zones. On average, mixing had no significant effect on drought resistance for neither species, yet it increased pine resistance in sites with higher climatic water balance in autumn. Also, beech and pine most often differed in the timing of their drought response within similar sites, irrespective of the regional climate, which

might increase the temporal stability of growth in mixed compared to pure stands.

Our results showed that the regional climate only partly determined the impact of mixing on tree response to climate, indicating the interacting influences of species identity, stand characteristics, drought events characteristics as well as local site conditions.

4.1 Introduction

The effects of global change on forest functioning are a major concern for both forest scientists and forest managers. With respect to climate, changes in local average precipitations and temperatures as well as in the frequency and intensity of extreme events such as drought, are expected to impact the provision of many forest ecosystem services, including wood production [Albrich et al., 2018], in terms of both average performance and temporal stability [Boisvenue and Running, 2006; Allen et al., 2010]. Indeed, numerous studies reported that the increased frequency and intensity of drought events significantly reduced growth and increased mortality risks [Allen et al., 2010; Lévesque et al., 2014; Meir et al., 2015]. As a result, great research effort is devoted to finding ways to adapt forests and forest management to cope with those adverse effects of climate change [Seynave et al., 2018; Bowditch et al., 2020]. In addition to selecting tree species or provenances adapted to expected future climate conditions [Bolte et al., 2009; Frischbier et al., 2019; Bert et al., 2020], increasing stand species diversity has also been proposed to cope with detrimental effects of global change on forests [Ammer, 2019; Vilà-Cabrera et al., 2018]. Several studies reported a significant influence of species-mixing on climate-growth relationships, including higher resistance to extreme events such as drought; yet those effects were found to be affected by environmental conditions such as site water availability or identity of the species involved [Lebourgeois et al., 2013; Pretzsch et al., 2013; Gazol and Camarero, 2016; Thurm et al., 2016; Bosela et al., 2018; Pretzsch et al., 2020; Steckel et al., 2020b]. As demonstrated by Babst et al. [2013] tree growth response to climate across Europe showed consistent biogeographic patterns in relation with distinct climatic constraints, from zones where tree growth was mainly driven by precipitations (*e.g.* Southern Europe or low elevation regions of Central Europe) to others where temperature was the main driver (*e.g.* high elevation and high latitude regions). Species-mixing effects, which are known to be dependent on environmental constraints, are therefore likely to differ between such regions. Indeed, Grossiord et al. [2014c] have shown that higher species diversity improved resistance to drought events in certain

forest types (temperate beech and thermophilous deciduous forests, *i.e.* drought-prone environments) while no significant effects were found in hemi-boreal, mountainous beech and Mediterranean forests. In addition to those large-scale patterns, local site conditions can also shape the mixing effects, resulting in the lack of any significant relationship between species diversity and drought resistance in selected regions [Grossiord et al., 2014b; Ratcliffe et al., 2017]. Overall, there is a growing body of literature pointing towards the fact that species-mixing does not always improve trees reaction to drought [Grossiord et al., 2014c; Bonal et al., 2017; Pardos et al., 2021]. Competitive interaction could, indeed, result in negative-species mixing effects in drought-prone environments [Gonzalez de Andres et al., 2018] unless complementarity interactions (belowground niche partitioning of facilitation) improves water availability, uptake or use-efficiency [Grossiord et al., 2014b]. In addition, tree acclimation to drought conditions might limit growth reaction to drought events, thus reducing the potential amplitude of species-mixing effects on growth during such extreme events [Lévesque et al., 2013; Steckel et al., 2020a]. Additional research is therefore crucial for understanding spatial and temporal variability of species-mixing effects on tree drought reaction, which is of major interest for forest management.

Complementarity is considered as a major determinant of species-mixing effects [Ammer, 2019], and encompasses several types of interspecific interactions leading to competitive reduction and facilitation [Vandermeer, 1989]. Facilitation refers to mechanisms through which one species improves the resource supply as well as biotic or abiotic conditions for another species [Forrester and Bauhus, 2016]. Competitive reduction is the process by which inter-species traits variation leads to lower inter-specific competition compared to intra-specific competition [Scherer-Lorenzen et al., 2005], and results from either spatial (*e.g.* difference in rooting depth) or temporal (*e.g.* difference in growing period) niche complementarity.

Because those mechanisms rely largely on inter-specific differences between associated tree species as well as on intra-specific differences resulting from interspecific interactions, trait diversity and trait plasticity

are critical determinants for the outcome of mixing [Jactel and Brockerhoff, 2007; Dawud et al., 2017]. Numerous traits can influence tree growth response to climate, and thus determine the species-mixing effects. For instance, by their longer vegetation period, coniferous species could have more opportunity for compensatory growth [Seidel et al., 2019] during climatically favourable periods following a drought event than broadleaves [D'Andrea et al., 2020]. If conifer compensatory growth happens after the end of the admixed broadleaves vegetation period, conifer could additionally benefit from lower interspecific competition in mixed stands compared to pure stands. Traits associated with tree hydraulic and physiological characteristics are also major determinants of tree growth reaction to climatic variations. Numerous traits are involved in tree reaction to drought through different mechanisms defining avoidance, resistance and recovery strategies [Aubin et al., 2016]. Key traits determining drought avoidance strategy include rooting depth and distribution, water supply-to-demand ratio, stomatal characteristics (density and control), water use efficiency, leaf morphology (*e.g.* leaf mass area), xylem conductance or leaf area control (*e.g.* leaf shedding). Species resistance to drought is mainly driven by xylem resistance to cavitation while the main determinant of recovery is the capacity to resume conductivity of embolised tissues and capacity of carbohydrate storage [Aubin et al., 2016]. As a result, high drought tolerance is often found in species with deep root system, intense stomatal control and/or high xylem resistance to cavitation [Chaves et al., 2002; Allen et al., 2010; Choat et al., 2012]. Association of species displaying variations in those traits could lead to improved drought response in mixture compared to monocultures. Differences in rooting traits (rooting depth, root vertical distribution...) are also paramount to competitive reduction through their impact on belowground niche partitioning [Filella and Penuelas, 2003; del Castillo et al., 2016].

Species-mixing effects depend not only on the combination of traits of the species in presence but also on their interaction with environmental conditions. First, the environmental conditions can influence the expression of the traits for the species in presence. As an example, con-

straints such as temporary soil waterlogging [Kozlowski, 1986] or limited depth to bedrock [Balneaves and De La Mare, 1989] could prevent any belowground niche partitioning through their negative effects on root development, resulting in a lack of mixing effects on drought response even for species with otherwise potentially different rooting patterns. Second, spatial and temporal variations of environmental conditions influence species-mixing effects through their impacts on both resources and modulators. According to Forrester and Bauhus [2016], mixing effects are predicted to increase along temporal or spatial gradients of increasing environmental limitation as far as species interactions reduce the constraint. Based on this framework, we might expect contrasting impacts of mixing on the response to both average climate-growth relationships and reaction to drought events, depending on regional climate as well as on local site characteristics such as microclimate or soil water availability.

The main objective of this study is to investigate how mixing affects the growth response (measured by tree-ring width of dominant trees) to average climate and drought along an unprecedented gradient of environmental conditions across Europe, for European beech and Scots pine. Those two species are of high relevance in this context as they display strong differences in a series of traits potentially involved in growth response to climate variation. More specifically, they differ in the distribution of root biomass along the soil profile (heart-shape rooting pattern for beech *vs.* peak in most superficial soil layers for pine, higher competitivity of beech root system - Curt and Prévosto 2003; Prévosto and Curt 2004), in the length of the vegetation period (longer growing season of pine compared to beech) and in their hydraulic strategies (isohydric for pine *vs.* anisohydric for beech - Cochard 1992; Martínez-Vilalta et al. 2004; Schäfer et al. 2017; Pflug et al. 2018). Because the functional traits of the two species are so contrasted, complementarity effects are expected to occur. Using the same dataset from the EuMIXFOR COST action [Heym et al., 2017] as the one used in the present study, Pretzsch et al. [2015] and del Río et al. [2017] showed that both productivity and temporal stability of productivity, respectively, were on average higher

in mixed pine/beech stands than expected from pure stands. They also found a high between-site variability of species-mixing effects on productivity and temporal stability.

For both species, we hypothesized for the impact of mixing on the response to climate and drought events to be mostly determined by the regional climate, resulting in consistent regional patterns across Europe. To test this hypothesis, we conducted dendroecological analyses. First, we analysed the average climate-tree growth relationships of both species in pure and mixed stands, using Bootstrapped Correlation Coefficients (BCCs). We then tested the difference in resistance to drought event between pure and mixed stands, and investigated its relationship with regional climate.

4.2 Materials and methods

4.2.1 Study area and site/stand characteristics

The tree data used in this study came from 30 sites established under the COST Action FP1206 EuMIXFOR (European Network on Mixed Forests). Each site consisted of three stands with similar ecological conditions but varied composition: pure stands of pine and beech and a mixed stand of both species, according to a triplet-transect approach [Pretzsch et al., 2015]. This network covered a large environmental gradient within the overlapping natural ranges of pine and beech (Fig.4.1). Elevation varied between 20 and 1475 m a.s.l; mean annual precipitation sum (P) ranged from 520 to 1175 mm and mean annual temperature (T) from 6 to 10.5°C. In the mixtures, the percentage of basal area represented by Scots pine ranged from 25 % to 74 %; total basal area ranged from 16 to 80 $m^2.ha^{-1}$ and stand age from 40 to 130 years. The stands were mostly even-aged and mono-layered. No silvicultural activities had been conducted in the stands during the preceding decade. A standard protocol for tree data collection (diameters, heights of trees and crown bases) and tree coring was applied. The full measurement protocol was described in details by Heym et al. [2017]. Selected site and stand characteristics for each site are presented in Appendix 21.

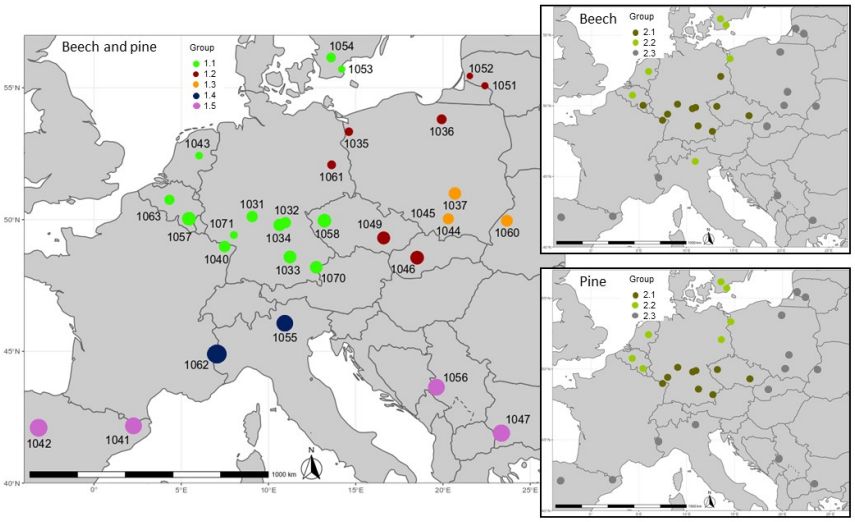


Figure 4.1 – Distribution of the 30 study sites across Europe. Numbers are the site-ID (Appendix 21). The size of the points is proportional to the site altitude (20 - 1475 m). The colors refer to groups of sites showing similar climate-growth relationships. Those groups are based on a clustering analysis performed on the first (main map common for the two species, groups 1.1 to 1.5) and second (smaller maps, groups 2.1 to 2.3; beech: above, pine: below) compositional planes of a PCA performed on Bootstrapped Correlation Coefficients. Group 1.5 was obtained by merging clusters 1.5 and 1.6 (see section 4.3.2 for details).

4.2.2 Climate data

We used the 0.25°- gridded E-OBS dataset from the EU-FP6 ENSEMBLES project. From this dataset, we obtained series of daily minimum and maximum temperatures and cumulative daily precipitations for the 1979 - 2013 period (*i.e.* the length of the dendrochronological series). Climate variables were used to analyse the influence of climate on tree growth. Mean monthly temperature and monthly Standardized Precipitations Evapotranspiration Index (SPEI) were used. SPEI is a multi-scalar index that can be used to determine the onset, duration and magnitude of drought conditions with respect to normal conditions [Vicente-Serrano et al., 2010]. Positive values indicate above-normal wet conditions, whereas negative values identify dry periods. SPEI val-

ues between -0.67 and 0.67 are considered normal, values between -0.67 and -1.28 indicate moderate drought, and values <-1.28 indicate severe drought [Isbell et al., 2015]. The potential evapotranspiration (PET) necessary to calculate SPEI was determined using the modified Hargreaves equation [Choisnel et al., 1992; Droogers and Allen, 2002], which provides estimations that are close to those obtained from the Penman-Monteith equation [Beguería et al., 2014]. Calculations were made using the SPEI-package in R software [Beguería et al., 2014; R Development Core Team, 2014]. Climatic parameters were considered from June of the previous year to October of the current year. Climate variables were standardized to remove long-term variability using a smoothing spline with 50% frequency cut-off at a wavelength of two-third of the length of each series [Cook and Peters, 1981]. Standardized climate variables were calculated by taking the difference between climatic values and the spline [Bert et al., 2020].

4.2.3 Dendrochronological methods

4.2.3.1 Sampled trees and master chronologies

At each site and stand, a minimum of 10 dominant or co-dominant trees per species (*i.e.* beech or pine in the pure stands, beech and pine in the mixed stand) were cored at breast height in 2013 or 2014 (two cores per tree; northern and eastern directions; last complete tree-ring in 2013). Individual tree-ring series were crossdated and series with unresolvable crossdating problems were dropped [Heym et al., 2017]. For each tree, measurements from the two cores were averaged to obtain one individual series. In a limited number of cases (15% of total number of trees), however, only one core per tree could be used for the analyses. In total, 1143 beech trees (592 from pure stands; 551 from mixed stands) and 1164 pine trees (597 from pure stands; 567 from mixed stands) were used for dendrochronological analyses. To remove long- and medium-term growth trends and to focus on high-frequency growth variation, individual tree-ring series were detrended using a smoothing spline with 50% frequency cut-off at a wavelength of two-third of the length of each series [Cook and Peters, 1981]. Master chronologies were

calculated using biweighted robust mean [Cook and Kairiukstis, 2013] on the maximum period common to all sites (1979 - 2013). A master chronology was established for each stratum (stratum = site x species x stand composition; total number of strata = 120). Detrending was conducted using the DENDRO script [Mérian, 2012] within the R software [R Development Core Team, 2014]. Expressed Population Signal (EPS) was calculated to assess the suitability of the dataset for dendroecological analyses. The high EPS values indicated that the chronologies can be used for the analyses (mean and standard deviation = 0.90 ± 0.07 and 0.90 ± 0.05 for pure and mixed beech respectively; 0.92 ± 0.07 and 0.90 ± 0.05 for pure and mixed pine respectively).

4.2.3.2 Identification of drought events

To analyze tree growth response to drought events, we selected site specific drought events that had a negative effect on tree growth. First, we identified negative pointer years for each species using the Relative Event Year definition of Schweingruber et al. [1990], *i.e.* at least 75% of the trees displayed a reduction of raw growth superior to 15% compared to the average raw growth of the previous 4-year period (Relative Growth Change (RGC) method - Becker 1989; Schweingruber et al. 1990; Jetschke et al. 2019). Due to this 4-year window, dry years were selected within the period 1983 - 2013. In order to ensure that growth limitation was related to a drought event, we then only kept the negative pointer years associated with monthly SPEI values lower than -1.28 [Isbell et al., 2015] for at least one month during the growing period (March - August) of either the current year or the previous year. Taking into account the previous-year drought allowed to account for possible carry-over effects. As a result of the selection process, several drought years could be selected for each combination of site and species, and those years could vary between species within a site (see Appendix 27).

4.2.4 Statistical analyses

4.2.4.1 Climate-growth relationships

Bootstrapped Correlation Coefficients (BCC; Blasing et al. 1984; Guiot 1991) were used to analyze the tree climate-growth relationships. Master chronologies per strata were used as dependent variable. Correlation functions were calculated using 34 climate regressors: 17 Tmean and 17 monthly SPEI values from June of the previous growing season to October of the current growing year. Climatic regressors were written in the form: Variable_{Month}; months written in full caps indicate variables from the current year while months written in lower case letters indicate climatic variables from the previous year. Sample size-related bias between strata was corrected by dividing BCC values by the square root of the Expressed Population Signal (EPS) as proposed by Mérian et al. [2013].

We first used Principal Component Analysis (PCA) followed by hierarchical ascending clustering according to Ward D2 method to identify the different patterns in climate-growth relationships over the strata [Richman, 1986; Lebourgeois et al., 2014]. The number of groups defined by the clustering algorithm was based on the elbow method and the Calinski-Harabasz index. Clustering allowed us to identify groups of sites displaying similar climate-growth relationships. Clustering dendrograms are presented in Appendices 22 to 25. Stand and climatic characteristics for the groups of sites resulting from the clustering are presented in Table 4.1 and Fig.4.3.

Thereafter, to better highlight the influence of mixing on climate-tree growth relationships for each species independently, we calculated the distance between the pure and the mixed stands of a given site along the principal components, using the following equation:

$$D_{ij} = |P_{ij}| - |M_{ij}| \tag{4.1}$$

Where D_{ij} corresponds to the displacement from the projection of each species in pure stand to the projection of each species in mixed stand for

site i along PC_j. P_{ij} is the correlation of the projection of the pure stand from site i with principal component j; similarly, M_{ij} is the correlation of the projection of the mixed stand from site i with principal component j. As a result, inward displacement (*i.e.* displacement in the direction of the origin of the principal component) is positive while negative values are associated with outward displacement. Inward displacement can indicate a decrease in correlation with all variables associated with the corresponding PC. Within each group previously defined by the clustering algorithm, we calculated the displacement of each site along the PCs to which the group was the most strongly associated. As a result, along the first PC, we tested the average displacement of group 1.5 (4 sites), 1.4 (2 sites), 1.3 (4 sites), 1.2 (7 sites) and 1.1 (13 sites); along the second one, we tested the displacement of groups 1.4, 1.3, 1.2 and 1.1; along the third PC, we tested the displacement of groups 1.5 and 2.1 (11 sites for beech, 9 for pine); lastly, along the fourth PC, we tested displacement for group 1.5 and 2.2 (6 sites for beech, 7 for pine). In some cases, the low number of sites prevented us to properly assess the displacement direction and amplitude. One-sample t-tests were then used to assess whether the average displacements within groups along a PC were significantly different from zero.

4.2.4.2 Response to extreme drought

To assess how the growth response to drought differed between pure and mixed chronologies, we calculated the relative growth change per stand type × site × drought event for each species separately, using the corresponding species-related drought years. In a first analysis, a PCA was performed on RGC values to explore to which extent growth response to drought differed between stand types and sites. The displacements of projection from pure to mixed stands were also calculated, and average displacements within groups were tested as described above. In a second step, we used mixed effect models for each species separately, considering year nested within site as random factor, to test for the significance of stand composition (pure *vs.* mixed), average site climatic parameters (average temperature and difference between precipitation

and potential evapotranspiration for the following periods: Mar-May, Jun-Aug, Sep-Nov, Dec-Feb in each site), site geographic characteristics (altitude and latitude) and stand characteristics (age and basal area) on growth reduction (RGC) during drought events, according to:

$$RGC_{sty} = \boldsymbol{\beta} \times E_{st} + a_s(0, \sigma_s^2) + a_{y|s}(0, \sigma_y^2) + \varepsilon(0, \sigma_\varepsilon^2) \tag{4.2}$$

Where RGC_{sty} represents the stand average relative growth change for site s, stand composition t and year y, $\boldsymbol{\beta}$ is the vector of fixed effect parameters, $\mathbf{E}$ is the matrix of the predictors of the fixed effects, a_s is the random factor characterized by the inter-site variance σ_s^2, $a_{y|s}$ is the random factor characterized by the interannual variance within a site σ_y^2 and ε is the error term of variance σ_ε^2. In addition to the above-mentioned fixed factors, we also tested for the interaction between stand composition and all other variables. Starting from the model with the full set of parameters, the variables with the lowest predictive power were then progressively removed based on the Akaike Information Criterion (AIC). In addition, simpler models using similar structure but including only stand composition, identity of the climatically homogeneous groups (based on the first two PCs) to which the site belongs (Gr.1.1-1.5; see 4.3.1) and their interaction as fixed effects were used to test for differences in species-mixing effects on growth reduction during drought between those groups; inclusion of "site within group" as an additional random effect did not improve the model based on a likelihood ratio test.

All calculations were made using the R software [R Development Core Team, 2014]. All analyses and their relationships are summarized in Fig.4.2.

Table 4.1 – Range (minimum/maximum) of selected site and stand characteristics for groups of sites showing comparable climate-growth relationships. The groups are based on a clustering analysis performed on the first (groups 1.1 to 1.5) and second (groups 2.1 to 2.3) compositional planes of a PCA performed on Bootstrapped Correlation Coefficients. Because clustering analysis performed on the second compositional planes yielded slightly different groups between the two species, characteristics are given separately for beech and pine for groups 2.1, 2.2 and 2.3. Spring: Mar-May, Summer: Jun-Aug, Fall: Sep-Nov, Winter: Dec-Feb. Tmean, mean air temperature (°C); WB, climatic water balance (mm): precipitation minus potential evapotranspiration; Stand type, with BE for beech, PI for pine; BA, basal area ($m^2.ha^{-1}$). Climate data are averages over 1979 - 2013. Age in mixed stands is indicated as follows: beech age range (min-max)/pine age range.

Group	**Latitude range** [°]	**Altitude range** [m]	**Tmean**$_{spring}$ [°C]	**Tmean**$_{summer}$ [°C]	**Tmean**$_{fall}$ [°C]	**Tmean**$_{winter}$ [°C]	**WB**$_{spring}$ [mm]	**WB**$_{summer}$ [mm]	**WB**$_{fall}$ [mm]	**WB**$_{winter}$ [mm]	**Stand type**	**Composition**	**BA range** [$m^2.ha^{-1}$]	**Age range** [years]
1.1	48.2/56.2	27/547	6.2/10.1	15.5/18.1	7.3/11.2	-1.4/3.7	-106.5/40.9	-192.1/-10.4	1.3/165.2	58.4/244.2	Pure	BE	23/54	46/150
												PI	11/59	45/150
											Mixed	BE/PI	30/52	45-115/45-130
1.2	48.6/55.5	20/533	6.6/9.0	16.7/17.9	7.5 /9.3	-2.6/0.6	-119.6/-54.4	-221.9/-38.9	0.4/185.7	53.3/159.3	Pure	BE	21/45	45/102
												PI	24/45	45/102
											Mixed	BE/PI	16/63	45-102/45-102
1.3	50.0/51.0	209/383	7.6/8.6	17.1/17.9	7.8/8.7	-2.3/-1.3	-91.7/-80.5	-151.8/-136.3	11.1/23.6	59.7/82.3	Pure	BE	18/53	55/105
												PI	30/64	55/105
											Mixed	BE/PI	33/47	55-105/55-105
1.4	44.9/46.1	1038/1475	4.7/5.2	14.2/14.7	6.9/6.9	-2.6/-1.2	-10.0/166.9	-109.9/-103.8	101.1/232.7	35.2/240.6	Pure	BE	23/41	40/55
												PI	47/52	40/55
											Mixed	BE/PI	22/41	40-55/40-55
1.5	41.9/43.6	1080/1292	5.7/10.2	16.0/19.6	7.3/12.8	-2.6/5.1	-54.4/-7.7	-387.8/-168.0	-51.6/90.4	80.0/157.0	Pure	BE	20/52	40/75
												PI	33/55	40/75
											Mixed	BE/PI	27/80	40-75/40-75

Table 4.2 - Continued

Group	Latitude range [°]	Altitude range [m]	$Tmean_{spring}$ [°C]	$Tmean_{summer}$ [°C]	$Tmean_{fall}$ [°C]	$Tmean_{winter}$ [°C]	WB_{spring} [mm]	WB_{summer} [mm]	WB_{fall} [mm]	WB_{winter} [mm]	Stand type Composition		BA range [$m2.ha^{-1}$]	Age range [years]
2.1 - Beech	48.2/52.1	40/547	7.5/9.8	15.9/18.1	7.3/10.0	-1.4/2.0	-119.6/40.9	-221.9/-10.4	0.4/147.9	53.3/244.2	Pure	BE	21/54	45/150
											Mixed	BE/PI	16/52	45-100/45-130
2.1 - Pine	48.2/50.1	40/540	7.5/9.8	16.4/18.1	7.3/10.0	-1.4/2.0	-106.5/2.4	-192.1/-10.4	0.4/100.8	53.3/177.5	Pure	PI	25/59	45/73
											Mixed	BE/PI	32/52	45-70/45-70
2.2 - Beech	46.1/56.2	27/1038	5.2/10.1	14.7/17.6	6.9/11.1	-2.6/3.7	-96.9/-10.0	-163.6/-93.2	30.5/165.2	35.2/205.6	Pure	BE	23/52	40/115
											Mixed	BE/PI	16/46	40-115/40-115
2.2 - Pine	40.0/56.2	27/547	6.2/10.1	15.1/17.6	7.7/11.1	-0.7/3.7	-119.6/40.9	-221.9/-56.5	7.1/165.2	90.8/244.2	Pure	PI	11/48	48/150
											Mixed	BE/PI	16/46	46-115/46-130
2.3 - Beech	41.9/55.5	20/1475	4.7/10.2	14.2/19.6	6.9/12.8	-2.6/5.1	-91.7/166.9	-387.8/-38.9	-51.6/232.7	59.7/240.6	Pure	BE	18/53	40/105
											Mixed	BE/PI	22/80	40-105/40-105
2.3 - Pine	41.9/55.5	20/1475	4.7/10.2	14.2/19.6	6.9/12.8	-2.6/5.1	-91.7/166.9	-387.8/-38.9	-51.6/232.7	35.2/240.6	Pure	PI	30/64	40/105
											Mixed	BE/PI	22/80	40-105/40-105

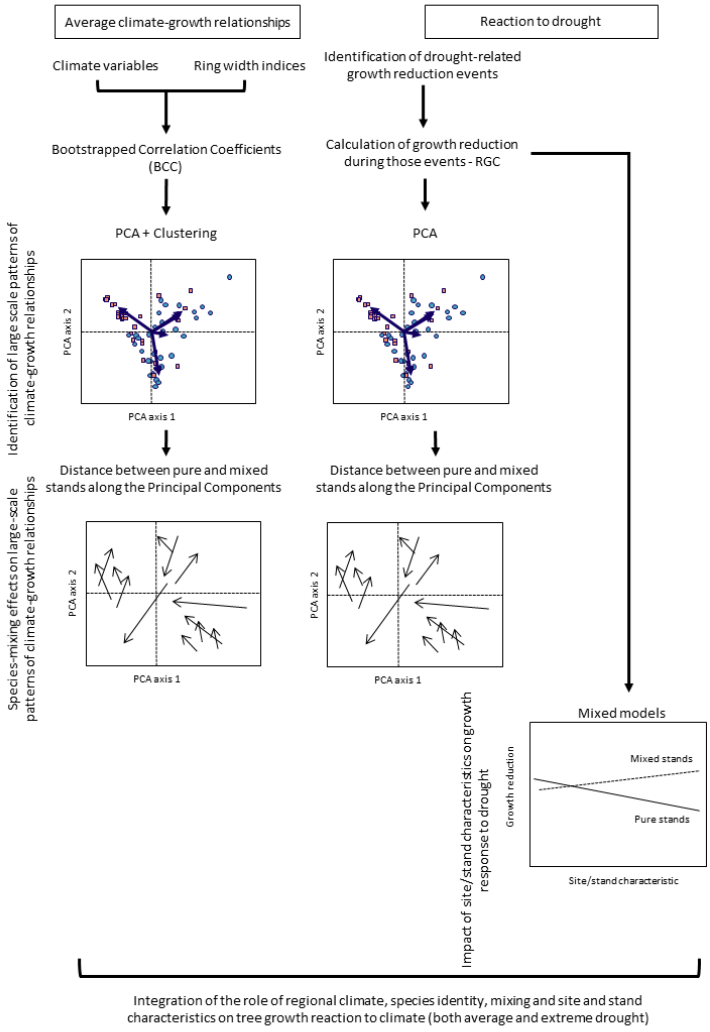


Figure 4.2 – Workflow of analyses from chapter 4.

4.3 Results

4.3.1 Major climatic drivers of radial growth

The first principal component accounted for 24% of the total variance for both species (Fig.4.4, A and C). Both species presented similar pattern with a major role of summer and fall temperatures. For beech, PC1 revealed an opposition between the current average temperature in September ($Tmean_{SEP}$) and the average temperature of previous September and July ($Tmean_{Sep}$/$Tmean_{Jul}$) while for pine $Tmean_{Sep}$/$Tmean_{Jul}$ *vs.* $Tmean_{SEP}$/$SPEI_{Jun}$ were determinant. The second principal component accounted for 17% of the total variance. As for PC1, both species showed a rather similar response yet with a more important role of summer drought: PC2 was positively associated with $SPEI_{AUG}$ (for beech) and $SPEI_{Aug}$ (for pine) and negatively associated with $Tmean_{JUL}$ (beech) and $Tmean_{AUG}$ (beech and pine). PC3, which held 11% of total variance for both species, was determined by $SPEI_{APR}$ and $SPEI_{Sep}$. Lastly, PC4 (10% of total variance) was negatively correlated with June temperature of the current year.

4.3.2 Geographic pattern of major climatic drivers of radial growth

Clustering made on PC1/2 (clusters 1.1. to 1.6.) and PC3/4 (clusters 2.1. to 2.3.) (Appendix 22) revealed a clear geographic pattern of climate-tree growth relationships across Europe (Fig.4.1) and highlighted several groups of sites displaying similar climate-growth relationships (Fig.4.4).

On the first compositional plane, the Spanish sites (1041, 1042; cluster 1.5) displayed distinct climate sensitivity, mainly due to a strong positive correlation with $Tmean_{SEP}$ (and $SPEI_{Jun}$ for pine) and a negative correlation with $Tmean_{Sep}$ and $Tmean_{Jul}$. The sites from the southeastern part of the network (1056 and 1047; cluster 1.6) were also strongly associated with PC1 but through a negative correlation. Although the sign of the climate-growth relationship differed between these two clus-

ters, their high sensitivity to the same climatic factors led us to merge them into one single group (Gr1.5) for subsequent analyses. Gr1.4 (corresponding to cluster 1.4.) was composed of the two Italian sites (1062 and 1055) and was positively associated with PC1 and, to a lower extent, with PC2. Gr1.3 (cluster 1.3.) was equally associated with PC1 and PC2 as was Gr1.2 (cluster 1.2.), although the correlation with climatic variables was much lower for the latter. Lastly, the clustering algorithm grouped all the sites with low correlation with any of the first two PCs into one large group: Gr1.1 (cluster 1.1.).

On the second compositional plane, clustering defined three groups. Two of them displayed strong and coherent correlation with PC3 and PC4: Gr2.1 (cluster 2.1.) and 2.2 (cluster 2.2.), respectively. The vast majority of sites associated with groups Gr2.1 and 2.2 on the second compositional plane belonged to group Gr1.1 on the first plane. Gr2.1 corresponded to sites from Central Europe (South of Germany, Czech Republic, Slovakia), while Gr.2.2 brought together sites from the Northwestern part of Europe (Figs.4.1 and 4.4).

Groups differed both in geographic (altitude, latitude) and climatic characteristics (Table 4.1 and Fig.4.3). Indeed, Gr1.4 and Gr1.5 were both low latitude/high altitude groups (Fig.4.1). Gr1.5 was characterized by very dry summer, while Gr1.4 showed cold and humid conditions throughout the year (Fig.4.3). Gr1.1, 1.2 and 1.3 were all mid-range latitude and low altitude groups. Gr1.3 displayed characteristically low P - PET values during the non-growing period (fall, winter); there was a clear pattern of decreasing P - PET level during the non-growing period when moving from Gr1.1 to Gr1.3.

The patterns highlighted by the PCA were almost similar for both species, indicating growth was affected by similar climatic drivers irrespective of species identity.

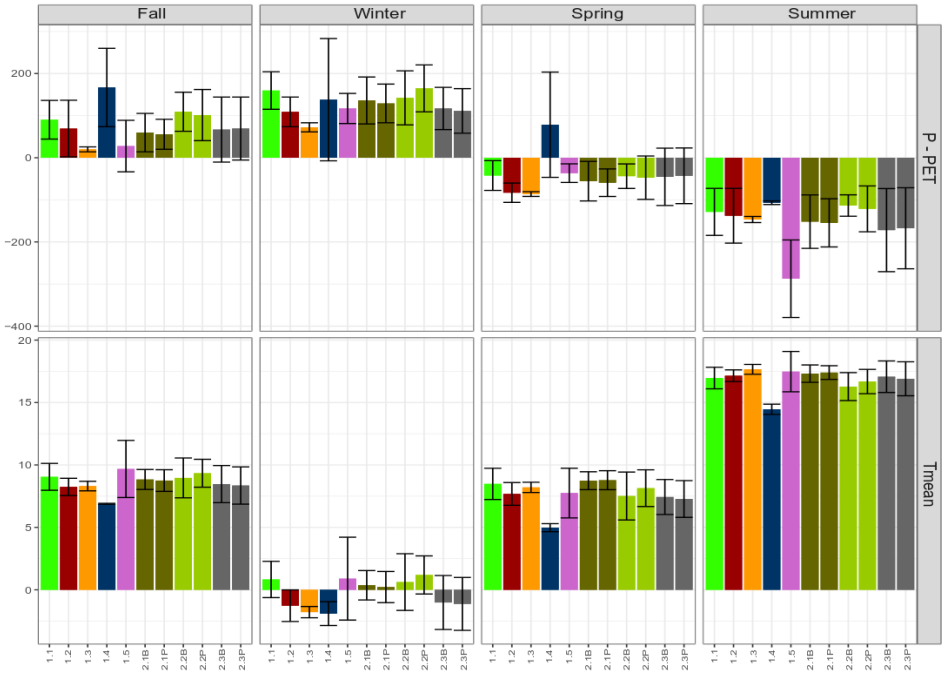


Figure 4.3 – Climate characteristics (P-PET [mm] and Tmean [°C]) of the groups of sites defined according to their similar tree climate-growth relationships. Whiskers represent standard deviations around the means. Groups resulting from clustering performed on the second compositional plane (groups 2.1, 2.2 and 2.3) noted B and P refer to beech and pine, respectively.

4.3.3 Species-mixing effects on climate-growth relationships

The amplitude and direction of change (displacement along the PCs) of loadings values from pure to mixed chronologies on each PC were highly dependent on site identity for both species, and no global pattern could be found (Fig.4.4). For pine, none of the groups displayed significant displacement in any direction. For beech, we found a significant displacement for sites included in Gr1.5 along the first (inward displacement - p-value = .01) and third (displacement to the right (not shown) - p-value = .01) PCs (Fig.4.4). Those displacements mainly implied a reduced correlation with the climatic variables associated with the corresponding PCs, although a slightly higher correlation with pre-

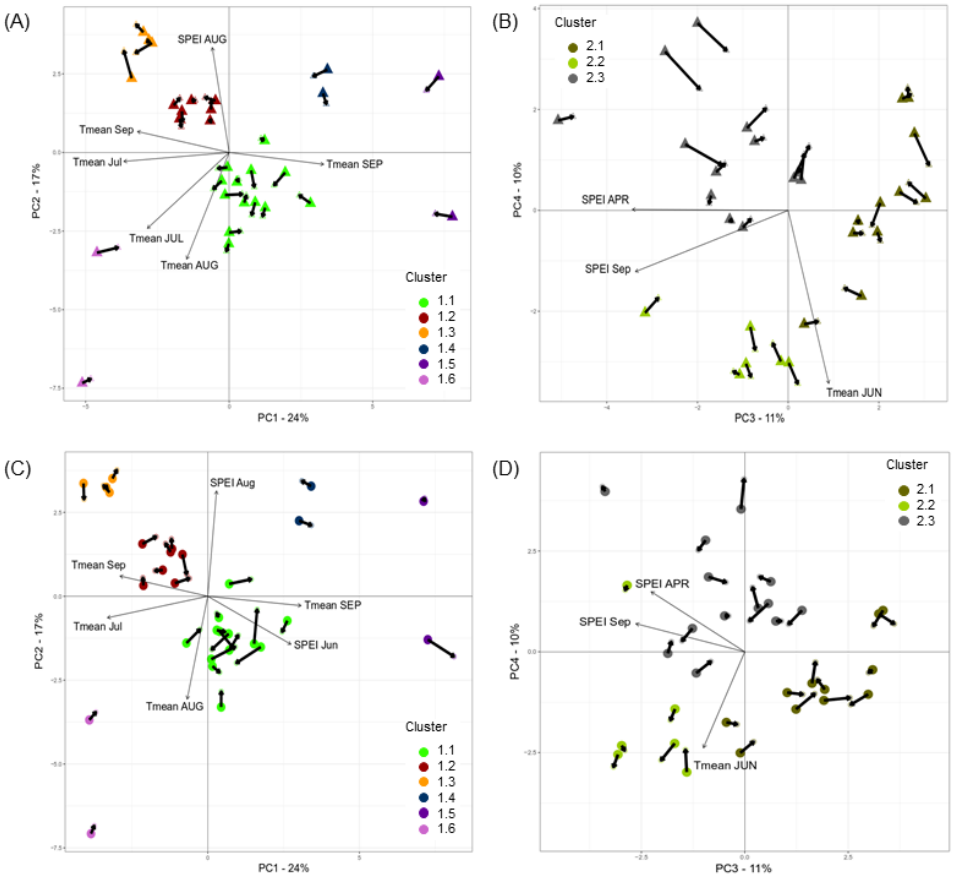


Figure 4.4 – Principal Component Analysis of the Bootstrapped Correlation Coeficients for beech (A and B) and pine (C and D) between standardized tree-ring width of each strata (site x species x stand) and climatic variables (monthly Tmean and SPEI values from June of the previous year to November of the current year). Strata corresponding to pure and mixed chronologies are depicted by big filled and small open symbols, respectively. Only variables with $\cos^2 > 0.5$ are drawn. Arrows indicate the displacement from the pure to the mixed chronologies within each site. Strata and climatic vectors pointing in the same direction indicates positive correlation, whereas the opposite indicates negative correlation. For climatic variables, months in full caps refer to the current year (previous year otherwise). Colors indicate sites grouped together by the clustering algorithm, based on the first (clusters 1.1 to 1.6) and second (clusters 2.1 to 2.3) compositional planes (Appendix 22). Clusters 2.1 and 2.2 are mostly composed of sites belonging to cluster 1.1.

vious September temperature was found for the mixed stands compared to the monocultures for the Spanish sites (data not shown).

4.3.4 Response to extreme drought

The average number of drought years across the period 1983-2013 (Appendix 27) was similar for beech and pine (mean ± standard deviation = 1.4 ± 1.3 and 2.2 ± 1.4 for beech and pine respectively). However, the number of drought years strongly differed between specific combinations of site and species, ranging from 0 to 6 for beech and from 0 to 7 for pine. The number of drought years that cleared the Relative Event Year criteria was similar between pure and mixed stands of a same species (3.4 ± 1.6 *vs.* 3.0 ± 2.2 in pure and mixed beech, respectively; 3.5 ± 2.1 *vs.* 3.6 ± 2.0 in pure and mixed pine, respectively).

In most cases (63% of cases for beech, 60% for pine), strata-level drought years corresponded to Relative event years for both pure and mixed stands. When only one of the two plots displayed a relative event year, the response was almost equally shared between pure (56%) and mixed (44%) stands for beech; for pine, pure plots responded more frequently (73% of cases). Beech and pine also tended to react to different years as, out of the total of 93 drought events identified for at least one of the two species at a same site, only 15 were common to both species; out of the 78 remaining events, 50 were associated with pine. Beech displayed high apparent variability in species-mixing effects on growth reduction during drought years. Indeed, out of the 19 sites displaying at least one drought year, 11 sites displayed situations of both positive (lower growth reduction in mixed stands) and negative species mixing effects, depending on the year (Appendix 27); the 8 remaining sites displayed systematically negative (4 sites) or positive (4 sites) species-mixing effects. Species-mixing effects on drought response appeared to be more coherent for pine as out of the 26 sites displaying at least one drought year, 18 sites displayed systematically negative (5 sites) or systematically positive (13 sites) species mixing effects. For both species, sites displaying such consistent positive or negative species-mixing effects across years were found in all groups of sites showing comparable climate-growth relationships.

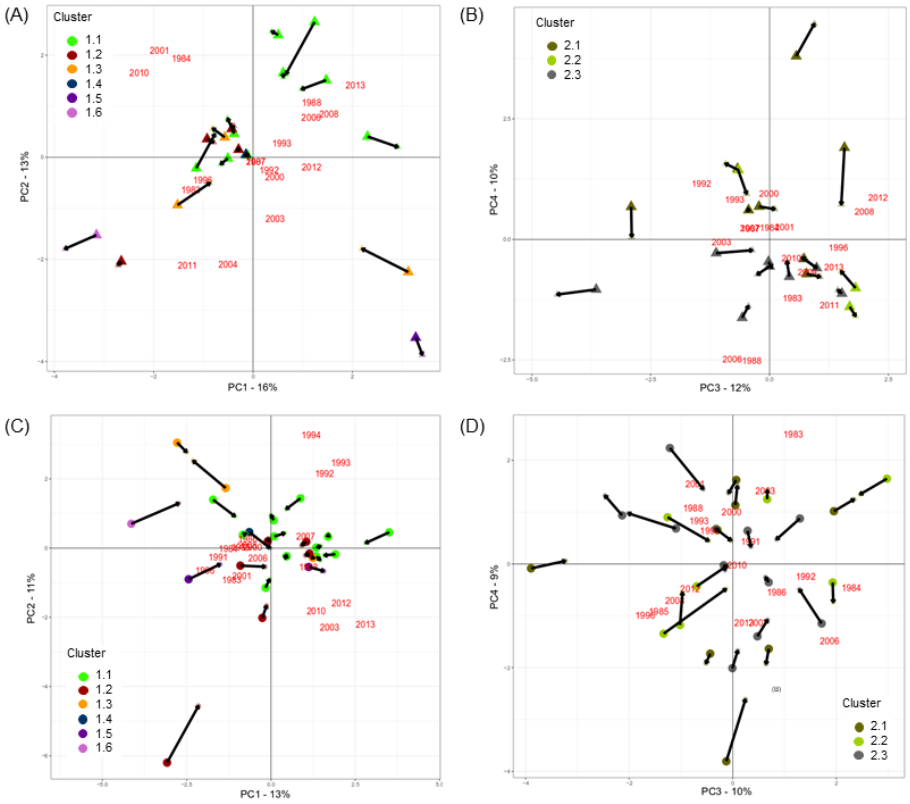


Figure 4.5 – Principal Component Analysis performed on the Relative Growth Variation during drought years for beech (A and B) and pine (C and D). Pure and mixed chronologies are depicted by filled and open symbols, respectively. Arrows indicate the displacement from the pure to the mixed chronologies within each site. Colors represent the clusters delimited based on the main climate-growth relationships patterns found in the PCA conducted on Boostrapped Correlation Coefficients (see Fig.4.4). Red numbers indicate drought years. A total of 11 sites and 4 sites for beech and pine, respectively, were found to be non responsive to drought (Appendix 27).

For beech, the first four axes of the PCA conducted on the drought events accounted for 16, 13, 12 and 10% of total variance respectively. For pine, they accounted for 13, 11, 10 and 9% (Fig.4.5). In strong contrast to the PCA conducted on BCC, no clear grouping of sites could be detected when considering the relative growth variation during drought events (Fig.4.5). No coherent drought response could be found within the groups of BCC similar sites, indicating those sites had no or only

limited drought years in common. In addition, non-responsive sites (11 for beech, 4 for pine; Appendix 27) were found in all groups.

There was no globally coherent difference in the response to drought between pure and mixed chronologies (Fig.4.5). Despite large differences in the position of pure and mixed stands along the PCA planes for some sites, the displacement of chronologies projections from pure to mixed stands did not show any consistent pattern for beech (Fig.4.5). For pine, the displacements along the first and fourth PC were significantly positive when all sites were considered together (p-values of 0.03 in both cases); in addition, all sites from group 2.2. showed a significantly positive displacement along the third PC (p-value = 0.04).

According to the linear mixed effect model fitted on beech RGC, pure and mixed stands did not display any significant difference in growth reduction during drought years. For pine, there was no main effect of stand composition, but a significant interaction between stand composition and P - PET during fall as illustrated in Fig.4.6. The growth reduction was less pronounced in mixed than in pure stands only for sites with high P - PET_{fall}. The simpler models confirmed there was no significant difference in species-mixing effects between groups of climatically homogeneous sites for either species.

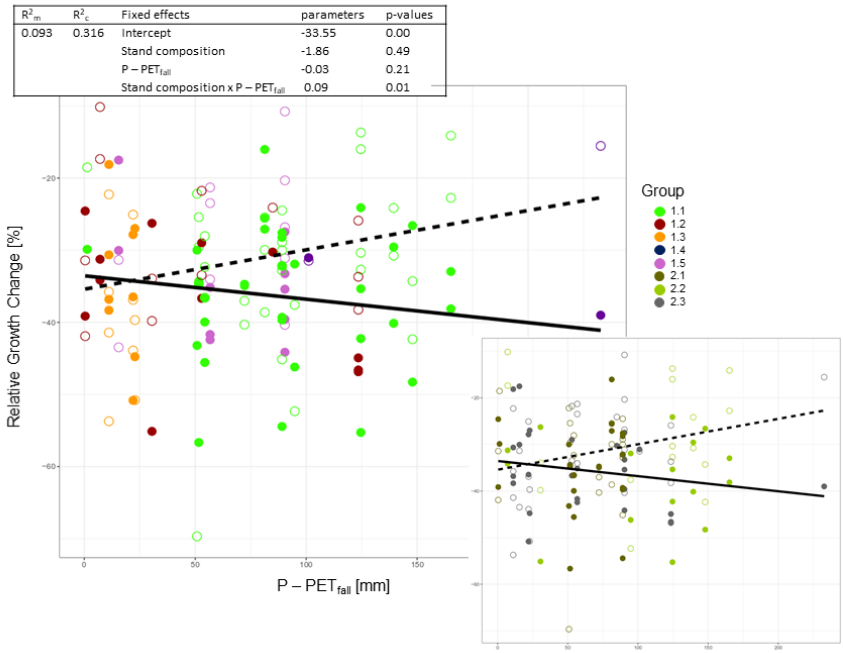


Figure 4.6 – Predicted (lines) and observed (dots) RGC values for pine as a function of P - PET$_{fall}$ in pure and mixed stands. Parameter estimates, p-values and R-squared for the linear mixed models adjusted on pine RGC values are presented in the enclosed table. Marginal R-squared (R^2_m) represents the variance explained by fixed factors; conditional R-squared (R^2_c) represents the variance explained by both fixed and random factors (full model). Reference level for stand composition is pure. The intercept indicates the value that the dependent variable would take if all the explanatory variables were null. Parameters of the main effect variables indicates the change in the dependent variable values associated with a one-unit increment change of the main effect. Open symbols and dashed line represent mixed stands; filled symbols and continuous line represent pure stands. The colors refer to groups of sites showing similar climate-growth relationships; those groups are based on a clustering analysis performed on the first (main figure, groups 1.1 to 1.5) and second (smaller figure, groups 2.1 to 2.3) compositional planes of a PCA performed on Bootstrapped Correlation Coefficients.

4.4 Discussion

4.4.1 Geographical pattern of climate-growth relationships

Our results clearly showed that the response of tree growth to climate at the European scale was primarily driven by the regional climate conditions, for both tree species (pine/beech) and all stand composition (pure/mixed). According to our results, summer/fall temperatures (July/September - Fig.4.4 and Appendix 26) of both current and previous years were the main climatic drivers of tree growth at the European scale. This is consistent with previous studies that have shown summer temperatures to be the most influential climatic parameters of tree-ring growth when analysed over large geographical scale [Briffa et al., 2002; Wettstein et al., 2011]. Such results should however call for cautious interpretation. Indeed, the very large gradient of temperature values across such a large spatial network might hide the effects of other variables (*e.g.* radiation) that display smaller range of realized values. The clusters resulting from the PCA performed on the BCC (Fig.4.4) agreed with biogeographical patterns of climate-tree growth response in Europe such as the one highlighted by Babst et al. [2013]. Those authors showed that tree growth sensitivity to either temperature or precipitations was highly dependent on both latitude and altitude. They showed that high latitude sites were strongly associated with a temperature signal. When moving towards lower latitude sites, tree growth switched to a higher sensitivity to precipitations with a transition zone in-between where tree growth was sensitive to both climatic parameters. In addition, they showed that the boundary between temperature-driven and precipitation-driven growth sensitivity was altitude-dependent. Indeed, at lower latitude, the boundary was located at higher altitude.

Our results are coherent with this pattern. Growth in cold and high altitude sites from Gr1.4 (Table 4.1) was mainly driven by temperature parameters, confirming temperature as the main determinant of tree growth in cold regions [Babst et al., 2013]. For lower altitude sites such as Gr2.1 and Gr2.2, latitudinal differences could explain the difference in

growth response to climate between groups of sites, with Gr2.2 mainly associated with temperature and Gr2.1 with SPEI. Sites from Gr1.5 were located at a similar elevation range than Gr1.4 sites but at a much lower latitude (Table 4.1); in this case, the summer temperature dependency of growth could not be explained by lower annual temperature, but rather by the characteristically low summer P - PET, shifting tree growth to the end of the vegetation period.

In contrast to previous studies conducted at local scales (*e.g.* Gonzalez de Andres et al. 2018), species identity had a minor impact on climate-growth relationships in our dataset (Fig.4.4). At European scale, the site geographical and climatic characteristics were stronger determinants of climate-growth relationships than species identity.

4.4.2 Species-mixing effects on climate-growth relationships

We found a coherent response to species-mixing for beech in Gr1.5, while we were unable to detect any such effect for beech in the other groups, or for pine in any groups.

We hypothesize that the changes in growth-climate correlations observed for beech when moving from pure to mixed stands in Gr1.5 are related to a beneficial effect of pine admixture on growth constraints imposed by limited water availability in summer. This hypothesis stems from inspection of the summer water deficits, which are more negative for Gr1.5 compared to the other groups (Fig.4.3), suggesting an important growth constraint during this period. Due to its highly efficient use of growing space and competitive root system [Curt and Prévosto, 2003; Dieler and Pretzsch, 2013], beech could experience reduced competition for the limiting resource in mixtures, particularly when admixed with pine, compared to a monoculture [Milios, 2004; Condés et al., 2013; Metz et al., 2016]. Indeed, beech could benefit from pine traits and associated impacts on water availability: lower transpiration rates [González de Andrés et al., 2017], smaller and lighter crowns that intercept less water [van der Salm et al., 2007] or lower fine root biomass in all soil depth

[Curt and Prévosto, 2003]. Beech could also benefit from the reduced growth of pine resulting from the isohydric behavior of the latter [del Castillo et al., 2016]. The lack of any mixing effect for pine in such constraining conditions is also in agreement with its isohydric behavior, which would lead to an early stop of growth irrespective of stand composition. In the long-term, changes in average climate-growth relationships between pure and mixed stands may explain the higher stand density often observed in mixed stands [Pretzsch and Biber, 2016].

By contrast to Gr1.5, Gr1.4 did not display such coherent displacement from pure to mixed stands, yet this group is also made of high-elevation sites. In this case however, the summer climatic water deficit was much reduced while average temperatures were consistently lower across the year, indicating no major constraint that could be removed by mixing. Groups 2.1, 2.2, 1.2 and 1.3, which are all mid-range latitude and low to mid-elevation sites, show limited differences in either average temperature or average water balance, over the season. Those groups are mainly characterized by their distinct water balance during non-growth period (winter/fall - Fig.4.3) and are not associated with major climatic constraint during the vegetation period. Altogether, those findings suggest that for a coherent response to be observed within one group, there is a need to have some overwhelming common constraint, which could then be alleviated by the complementary between associated species, depending on their specific traits. This would fit within the general framework proposed by Forrester and Bauhus [2016] stating that complementarity increases when environmental conditions become harsher, provided that species-mixing has an impact on the limiting factor. In agreement with this pattern, Lebourgeois et al. [2013] found that the shift in the response of silver fir (*Abies alba* Mill.) to climate induced by mixing was restricted to the driest sites. In the absence of any major climatic constraint, the response to mixing would be mainly driven by local site conditions, whose diversity within a region would explain the lack of any coherent response (see next section).

While admixing pine in beech stands was shown to reduce the constraint on beech trees in water-limited conditions [González de Andrés et al.,

2017], the general climate might also impose limitations which could be more difficult to alleviate through mixing. An example of such potential limiting environmental factors are the consistently low temperatures observed throughout the year in Gr1.4. Change in microclimate conditions resulting from difference in canopy structure, phenology or modifications in the length of the growing period, have been reported for some mixtures with respect to their monocultures (*e.g.* Lebourgeois et al. 2013; Ehbrecht et al. 2017), yet the extent to which this affects growth still remains to be documented. Therefore, the absence of coherent species-mixing effect in Gr1.4. despite the significantly lower temperature observed in sites from this group implies either that those low temperatures are actually not strongly limiting or that species-mixing cannot release such low temperature related constraint [Forrester and Bauhus, 2016].

4.4.3 Response to a drought event

In contrast to our findings on average growth-climate relationships, we were unable to detect any geographical pattern of tree resistance to drought for any of the species (Fig.4.5). We expected sites experiencing similar average climatic conditions to display some consistent response to climatically extreme events such as drought but such trend was not visible in the PCA. In addition, we found limited evidence that species-mixing effects on drought resistance were driven by average regional climate conditions. In most cases the average displacement from pure to mixed stands was not significant, irrespective of the BCC group (Fig.4.5). Similarly, the results of the mixed models showed no principal effect of stand composition for neither species, nor did they show any significant effect of average regional climate conditions. Only the sites from Gr.2.2. showed a coherent species-mixing effect on drought resistance, yet limited to pine (Fig.4.5D). This group brings together low-elevation sites from the Northwestern part of Europe (Fig.4.1), characterized by highly positive water balance during fall/winter and limited average (P - PET) deficits in summer (Fig.4.3). As shown in Fig.4.6, many sites from Gr2.2. displayed high P - PET_{fall} values and lower growth reduction during drought events in mixed stands than in monoculture. Such favor-

able climatic conditions at the end of the vegetation period would allow pine to take advantage of its longer vegetation period to compensate for any drought limitation experienced during spring and/or summer; during this late growing period, pine growth could be further favored by the earlier stop of beech physiological activity.

Altogether, the contrasting response to drought and mixing between sites and species (Appendix 27) might be explained by a combination of different sources of variability occurring simultaneously at various scales.

The regional climate is expected to shape the response to a drought event, as well as the mixing effect on that response, through different ways. First, individual trees of a given species might be less vulnerable to a similar drought event when growing under dry compared to humid climatic conditions due to long-term adaptation mechanisms [Martín-Benito et al., 2010; Martínez-Vilalta et al., 2012; Trouvé et al., 2017; Stojni et al., 2018]. Such intra-specific traits variations associated with adaptation to dry environments include differences in rooting depth, root to shoot ratio, leaf/sapwood area ratio, wood anatomy (thickness of xylem walls, tracheid diameters) or changes in leaf anatomic features such as leaf area [Linton et al., 1998; Lloret et al., 1999; Grill et al., 2004; Martínez-Vilalta et al., 2009; Pritzkow et al., 2020]. Under similar drought intensities, the constraint experienced by the trees would thus differ depending on the average regional climate. On the other hand, it is also possible that the additional constraint resulting from a drought event in such inherently water limited sites cannot be alleviated by species-mixing as suggested by de Streel et al. [2020]. Average regional climate could further influence species-mixing effects on drought reaction by allowing for possible compensatory growth. As suggested above for pine in Gr2.2, favorable climate conditions at the end of the vegetation period could allow species with long growing period such as conifers to compensate for growth loss during an extreme event [Lassoie and Salo, 1981; Lévesque et al., 2014; Seidel et al., 2019]. Lastly, average climatic characteristics could also influence species-mixing effect on drought reaction by changing the relative competitivity between species. For instance, beech is known for his intense competitive behav-

ior [Goisser et al., 2016] that can induce negative effects on pine [Primicia et al., 2013; 2016; de Streel et al., 2020]; as a result, any climatic conditions that would negatively impact beech to a greater extent than pine could lead to significantly lower inter-specific competition for the latter. For example, beech is considered to have a high sensitivity to late frost [Pretzsch et al., 2015; D'Andrea et al., 2020] and such frost damage can strongly affect beech functioning during the growing season that follows [Rubio-Cuadrado et al., 2020; D'Andrea et al., 2020], possibly leading to reduced competition for pine.

The regional climate impact may however be offset by factors varying at the site level, such as difference in the characteristics of triggering years (*e.g.* differences in droughts timing - D'Orangeville et al. 2018) or in local conditions of soil water availability [Carrière et al., 2020]. Although we were not able to consistently assess the impact of potential available soil water on drought response due to a lack of soil data in many sites, the information available at some sites shows it ranged between 28 and 715 mm [de Streel et al., 2020]; such a large range is expected to greatly impact tree response to drought [Lévesque et al., 2013].

Lastly, the interannual variation of drought response and of its modulation by mixing within a given site suggests that the timing, duration and intensity of the drought events is important. For instance, Bhuyan et al. [2017] recently showed that beech was sensitive to both short- and long-term drought although this sensitivity to drought length was dependent on site climate and altitude. Several studies have also shown that drought timing and intensity were major determinants of tree growth response. Tree growth proved to be more severely affected by more intense drought [D'Orangeville et al., 2018] and drought with different timing affect distinct species differently, depending on specific characteristics such as phenology [Vanhellemont et al., 2019].

Our results also showed contrasting patterns between beech and pine, in terms of both response to drought and mixing effects. Regarding the reaction to drought, the number of non-responsive sites was much higher for beech compared to pine. In addition, pine and beech most

often differed in the timing of their drought response within similar sites, reflecting contrasting sensitivity to drought and suggesting a large decoupling in possible mixing effects between those two species. As previously stated, while no main effect of mixing could be detected for neither species, pine showed a positive mixing effect in sites with high P - PET in the late growing period.

We suggest that the differences in drought response and mixing effects between the two species result from the interaction between the isohydric *vs.* anisohydric behavior of the species and the characteristics (timing, duration, intensity) of the drought event, under the control of regional climate and local site conditions. For instance, because pine is considered an isohydric species, a moderate drought could have strong negative effects on pine growth, while the anisohydric beech species could keep its stomata open longer and thus maintain growth for a longer period. In mixed stands, this interspecific difference could lead to a positive effect on beech as the early stop of pine growth could reduce interspecific competition experienced by beech. Bello et al. [2019] reported similar complementarity between iso- and anisohydric species in oak-pine stands in France. On the other hand, pine could benefit from an improved water availability at the end of the vegetation period following an early and extreme drought. In such situation, both species would see their growth reduced during the drought event. However, pine could take advantage of its longer vegetation period [Michelot et al., 2012b] to perform compensatory growth when conditions improve, while beech might not have this possibility [Lassoie and Salo, 1981; Lévesque et al., 2014; Seidel et al., 2019]. During this period of compensatory growth, pine in mixed stand might experience lower competition level than in pure stand due to the early stop of beech growth.

Because beech and pine were found to respond to distinct drought events, we might expect temporal stability to be higher in mixed stand compared to the monocultures. This would be coherent with the results from del Río et al. [2017] using the same triplet network who found an increased in temporal stability of productivity at the community level in mixed stands.

4.5 Conclusion

We assessed the large-scale spatial variability of species-mixing effects on average climate-growth relationships and resistance to drought events for European beech and Scots pine across Europe. We found limited support to our initial hypothesis that the impact of mixing on the response to climate and drought events would be mostly driven by the regional climate, resulting in a coherent response of both climate-tree growth relationships and drought resistance to mixing within climatic groups.

Our analyses conclude that an overwhelming climatic constraint is needed to observe a coherent species mixing effect, provided that the traits of the species allow for raising the constraint. If there is no major climatic constraint or if species-mixing does not alleviate it, the relative sensitivity of tree climate-growth relationships to climatic and edaphic conditions will lead to positive, neutral or negative species-mixing effects, depending on local factors. Regarding the resistance to drought, we were unable to detect any significant mixing effect for neither of the species, and no clear geographical pattern emerged. Interestingly however, regional climate was found to impact pine resistance, through a positive effect of higher climatic water balance in autumn, suggesting compensatory growth. These results suggest that species-mixing effects on tree drought resistance are site-dependent (*e.g.* influenced by site maximal water availability). Such observation is coherent with the growing body of literature showing that higher diversity can improve forest drought resistance but that this effect can hardly be generalized.

Our results showed that the regional climate only partly determined the impact of mixing on the tree response to climate, and highlight the interacting influences of species identity, stand characteristics, drought events characteristics as well as local site conditions. Integrating all those factors into mechanistic models of tree growth such as HETEROFOR [Jonard et al., 2020] is the next step to quantify the relative contribution of each, and to be able to make reliable context-dependent predictions.

Chapter 5

General discussion

The objectives of this thesis were to investigate the influence of species-mixing on several key components of forest ecosystem functioning and to improve our understanding on how those mixing effects change through time and space depending on environmental conditions. I focused on three types of processes that are often considered as key determinants of forest productivity and stability of productivity: *i)* water-related processes, *ii)* nutrient-related processes and *iii)* climate-growth relationships. In this section, I present the main findings of the thesis, including suggestions to improve the existing framework describing variations of species-mixing effects along gradients of environmental conditions. I also present the potential interest of this work for forest management and make suggestions for possible future research.

5.1 Key findings

5.1.1 Resource-related processes

Our first objective was to investigate the spatial and temporal patterns of species-mixing effects on **water-related processes** through the use of $\delta^{13}\mathbf{C}$, an indicator of water-use efficiency. Our results showed that pine and beech displayed distinct average levels of δ^{13}C, suggesting that both species have distinct characteristics in terms of water-related processes (and thus, in term of compromise between CO_2 assimilation and H_2O loss). The difference in wood isotopic composition between the two species probably originates from differences in species traits (*e.g.* lower stomatal conductance in pine) and we could therefore hypothesize that it could result in possible mixing effects. As expected, we then found that species-mixing influenced average δ^{13}C levels for both species and that this effect was different for pine and beech in moderately wet sites (positive species-mixing effect for beech *i.e.* lower δ^{13}C values in mixed stands compared to pure ones; negative for pine). This suggests that the balance between positive and negative mixing effects on δ^{13}C is determined by species-specific traits. Indeed, difference in δ^{13}C level between species could indicate a difference in the strategy of management of the CO_2 uptake/water loss balance between beech and pine (less parsimo-

nious water use by beech). However, the species-mixing effect on $\delta^{13}C$ was also dependent on environmental conditions (the difference in $\delta^{13}C$ between pure and mixed stands varies strongly along a gradient of water availability) and our results showed that this effect was non-linear. Indeed, as stated above, we found that for intermediate water availability levels, species-mixing effects were mainly determined by species identity (and thus, characteristic trait), resulting in negative effects for pine and positive for beech. However, when moving towards dryer conditions, beech probably started to exert a stronger stomatal regulation, which reduced its competitiveness, leading to a switch towards positive species-mixing effects for both species. Then, on extremely dry sites, the intensity of the constraint was too high and positive species-mixing effects could not express themselves anymore, leading to similar $\delta^{13}C$ values in pure and mixed stands for both species.

In chapter 3, we investigated the influence of species mixing on **tree nutrition**, using foliar nutrient composition as an indicator. More specifically, we looked at the foliar nutrient contents and at the ratios between nutrient or groups of nutrients. It is well known that pine and beech display distinct foliar nutrient characteristics. We thus hypothesized that admixing both species would lead to significant changes in the foliar nutrient composition of each component species, and that those changes would depend on the site nutritional status. We first confirmed the significant differences in foliar composition between species and found that, conformably to what we expected, species mixing significantly affected several single nutrient contents. Assuming higher nutrient inputs through foliar litterfall in mixed-species stands to be a possible complementarity mechanism (hypothesis 1 - HYP1), we could expect the nutrient contents of a target species to increase when mixed with a species with higher foliar nutrient contents. Our results do not confirm this hypothesis. Indeed, only two cases were in agreement with this hypothesis and they only applied to the nutrient for which the difference between both species was the greatest (Ca). Instead, in the majority of cases (N, K and Mg for pine; N and Mg for beech), we observed a difference in elemental foliar composition between species (higher nutri-

ent contents in beech leaves) but no significant difference between pure and mixed stands. Resorption effects, which were not taken into account, could partly explain our results. Indeed, it is well known that some species recycle elements before leaf shedding [Eckstein et al., 1999; Achat et al., 2018]. In such case, foliar nutrient composition does not reflect appropriately nutrient input through litterfall. Another possible explanation is that differences in species-specific foliar composition are not major determinants of species mixing effects on tree nutritional status. Many other mechanisms have been suggested to explain potential differences in tree foliar composition between pure and mixed stands (HYP2). For instance, higher soil carbon content in mixed stands can lead to increased amount of exchangeable cations because soil ability to retain nutrients is correlated to soil carbon content and decomposition of organic material releases nutrients [López-Marcos et al., 2018]. The implication of other mechanisms than nutrient return though litterfall would, for instance, explain the observed difference in pine phosphorous content between pure and mixed stands despite the absence of significant difference in P foliar content between the two species. Considering that results confirming HYP1 [Nickmans et al., 2019] and HYP2 [Chapman et al., 1988; Gartner and Cardon, 2004] are reported in the literature, it is probable that in reality there is a continuum of situations ranging from HYP1 being dominant (for instance for low-mobility elements and/or elements displaying a large difference in contents between both species) to situations where nutrient return through litterfall is overshadowed by other mechanisms (HYP2). In addition, other mechanisms such as nutrient remobilization and leaf biomass production could influence the relationship between individual species nutrient foliar contents and species-mixing effects on nutrition. For instance, the species with the lowest nutrient contents could produce more leaves, resulting in a similar nutrient input through litterfall in mixed stands. The absence of species-mixing effect for some elements displaying contrasted levels in both species could also be explained by a relatively large abundance of those elements in most sites. Indeed, we would not expect species-mixing to significantly improve the availability of a non-limiting

resource. Lastly, this absence of species-mixing effect on selected foliar nutrient content could also be explained by the co-occurrence of several limiting factors (deficiency in other nutrients, low water availability).

Our results also highlight the fact that species mixing does not only affect the foliar contents of isolated elements but also key balances between elements or groups of elements. Such result is in line with the increasing scientific interest for understanding how key balances of elements influence plant functioning. Indeed, critical ratios have been shown to be associated with a number of important processes such as forest decline, drought response or herbivory (see for instance González de Andrés et al. 2019; Lind and Barbosa 2012; Schulze 1989; Sardans et al. 2013). Those considerations are especially important for mixed-species forests considering that more diverse forests are frequently suggested as potential management options to address those rising issues.

When analysing the species-mixing effects on foliar composition along the gradients of environmental conditions we surprisingly found that species-mixing effects were stronger in milder conditions than in harsher ones, which is the opposite of what we expected based on the framework of Forrester and Bauhus [2016]. We hypothesize that the absence/lower species-mixing effects on sites at the lower end of the nutritional gradients could be caused by the co-occurrence of other factors limiting tree foliar nutrition (for instance lower water availability is associated with lower nutrient mobility in the soil - Marschner and Marschner 2012). Therefore, even if the co-occurrence of different species could influence the availability of one specific element, it is possible that this effect could not express itself due to the existence of some other limiting factor. Another possible explanation is that species mixing does not influence the availability, uptake or use-efficiency of the considered element. This could originate either from the fact that the respective traits of the admixed species do not influence those mechanisms or that other environmental factors limit the expression of the relevant traits. Several hypotheses can explain the strong species-mixing effects on tree nutrition on sites at the richest end of the gradients. First, gradients are defined based on foliar characteristics, which are integrative indicators

as they are influenced not only by soil nutrient availability but also by other mechanisms such as translocation. As a result, soil nutrient content might not be well reflected by foliar nutrient composition [Netzer et al., 2017]. Another possible explanation is that in our study, gradients are defined considering one foliar characteristic at a time, meaning that even at the richer end of the gradient, there could still be a limitation due to another factor. In case of such co-limitation, release of one constraint through species mixing can then lead to improvement of the other foliar characteristic in mixed stands compared to monoculture, even in rich sites. Indeed, although studies of nutrient co-limitation in forest ecosystems largely focused on the main limiting elements (namely, N and P - Goswami et al. 2018; Hedwall et al. 2017; Wu et al. 2020), several studies suggest that co-limitation can exist for other association of elements, such as N and K [Sayer et al., 2012; Wright et al., 2011]. Lastly, richer sites are often associated with increased growth level. This could lead to increased competition, which could prevent the trees to reach the maximal nutritional status possible in those sites. Species mixing could then reduce the competition level resulting in positive effects on foliar nutrient contents. Our dataset does not allow us to identify the most probable mechanism. Indeed, the low number of sites available at the richer end of the gradient makes it difficult to discriminate between the possibility of a stochastic effect (due to random sampling, richer sites are, by chance, co-limited) or a deterministic (positives species-mixing effects in rich sites are caused by competition release that systematically happen in such potentially high growth sites) effect. See section 5.4.2 for discussion of sampling issues.

In addition to the effects on belowground resources, **light-related mixing effects** are often considered good candidates to explain the generally higher productivity in mixed stands. Using the same network of plots, [Forrester et al., 2018] tested the hypothesis that species-mixing effects on growth were caused by light-related interactions. They hypothesized that these interactions are caused by a wide range of mechanisms such as changes in vertical canopy structure or changes in tree size or stand density between pure and mixed stands and that the relative impor-

tance of those mechanisms changes with site characteristics. They found that annual absorbed PAR was 14% higher in mixtures than the mean of the monocultures. They also found contrasting patterns depending on the organizational level. Indeed, at the whole community level the complementarity with regard to light absorption increased with site productivity but the species-mixing effects on light absorption occurred on different sites for beech and pine. In addition, the species-mixing effects on light absorption could only be related to species-mixing effects on growth for pine, not for beech nor the whole community. This suggests that while species-mixing effects on pine growth is driven by light-related interactions, other types of interactions (*e.g.* for water or nutrients) are driving beech and whole community growth.

5.1.2 Climate-related processes

In chapter 4, we explore the **relationship between tree growth and climate variations**, including drought events, and tested the influence of species mixing on those relationships. We found a strong geographical pattern defined by regional climate characteristics in the average tree growth-climate relationships. This pattern allows for defining groups of sites for which growth was mainly determined by similar climatic variables. Although we hypothesized that species-mixing effects on climate-growth relationships would be dependent on the regional climatic conditions, we found little evidence to support this assumption. Indeed, in most of the groups of sites displaying similar climate-growth relationships, no coherent changes in those relationships between pure and mixed stands could be found. Those groups of sites did not seem to present any clear climatic constraint to tree growth. Conversely, the group associated with the lowest water balance during the vegetation period was the only one displaying a coherent species-mixing effect, which corresponded to a lowering of the climate-growth correlation, probably explained by lower climatic constraint during the vegetation period in mixed stands. However, this coherent species-mixing effect on dry sites is only found for beech and not for pine. We hypothesize that this difference between the two species originates from their difference of growth

strategy. Indeed, pine tend to display an extensive growth strategy (long duration of cambial activity but low growth rate - Cuny et al. 2012) while beech is characterized by an intensive growth strategy (shorter xylogenesis duration and higher xylem production rate - Martinez del Castillo et al. 2018). As a result, while temporary unfavourable growing conditions can significantly affect beech annual growth, pine might be able to compensate for this loss by maintaining growth during more favourable periods (*e.g.* late summer/ early fall - Lassoie and Salo 1981; Lévesque et al. 2014; Seidel et al. 2019). Another possibility would be that, due to its highly competitive nature [Curt and Prévosto, 2003; Dieler and Pretzsch, 2013], beech could experience reduced competition when admixed with pine [Milios, 2004; Condés et al., 2013; Metz et al., 2016]. In addition, in such water-limited conditions, beech could benefit from the reduced growth of pine resulting from the isohydric behaviour of the latter [del Castillo et al., 2016]. Pine isohydric behaviour could lead to early growth stop in pure and mixed stands alike, leading to a lack of species-mixing effects for this species in water-limited conditions.

Contrarily to what we found for the average growth-climate relationships, no spatial pattern of tree growth reaction to drought events could be found. We hypothesize that this lack of coherent response from sites displaying similar average climatic conditions is caused by a strong dependency on local conditions (influence of soil water holding capacity, presence of shallow water table...). We found little evidence of increased resistance to drought in mixed stands compared to monocultures. Notable species-mixing effects on drought response (higher resistance in mixed stands compared to monocultures) were limited to pine on sites displaying high water availability at the end of the growing season. Those favorable climatic conditions could allow pine to take advantage of its longer growing season to compensate for growth reduction experienced during spring and/or summer drought. During this late growing period, pine growth could be further favored by the earlier stop of beech physiological activity.

5.1.3 Result integration and management implications

The results presented in sections 5.1.1 and 5.1.2 strongly suggest that the framework describing the expected change in complementarity along a gradient of environmental conditions as a linear increase with increasingly harsher environmental conditions if species-mixing improves the limiting factor [Forrester and Bauhus, 2016] is an oversimplification. Indeed, the patterns that we observed for water and nutrient related interactions both differ from this framework (see section 5.3 for critical discussion of the framework).

Interestingly, such deviation from the framework seems to depend on the level of the response variable under study. Indeed, analyses using proxies of physiological processes such as water use efficiency or of foliar nutrition differ more strongly from the framework than analyses conducted using integrative response variables (*e.g.* growth). I hypothesize that this difference in pattern of spatial variation of species-mixing effects between variables of different integration level is at least partly caused by issues associated with definition of site quality. Indeed, one of the main hypothesis to explain high species-mixing effects on one specific variable in rich sites is the existence of a co-limiting factor. For instance, a nutrient-rich site could be water-limited which could prevent trees foliar nutrient contents to reach their full potential. Releasing the co-limiting factor could therefore allow for the expression of species-mixing effects on tree foliar nutrients. On the other hand, for a site to be considered favourable when focusing on integrative variables, it has to be exempt of any strong limiting effect. As a result, we would not expect species-mixing effects on such variables to increase with more favourable conditions.

The combination of the results from chapter 2 to 4 also points to another important observation: it is highly unlikely that one single process can fully explain the significant large-scale species-mixing effects on productivity that have been previously highlighted [Pretzsch et al., 2015; Pretzsch and Biber, 2016; Zhang et al., 2012]. Indeed, analyses presented in chapters 2 to 4 highlighted some influence of species mixing on water

and nutrient-related mechanisms and on climate-growth relationships at site and regional scales and even sometimes along gradients of environmental conditions. However, because of the large variability of species mixing influence on those mechanisms it is unlikely that one of them alone could be responsible of a productivity increase as large as 12% as found by Pretzsch et al. [2015] on the same network. For instance, mixing has positive impact on water-related processes only in dry conditions or in moderate wet conditions for beech (chapter 2). Analyses from chapter 3 also showed that strong species-mixing influence on tree nutrition only happens on a limited number of sites corresponding to the richest conditions. Lastly, in chapter 4 we saw that growth-climate relationships were coherently modified by mixing only in sites with high water constraint during summer. All those results point to the fact that the observed average increase in productivity and stability of productivity in mixed stands is probably an "emergent property", taking advantage of the higher trait diversity in mixed stands to improve specific mechanisms according to local limiting conditions.

Those observations bear strong practical interest for forest management as they highlight the interest of forest tree species diversification. Indeed, although the complex spatial patterns of species-mixing effects observed in chapter 2 to 4 pinpoint the difficulty of relying on species diversity to deal with one specific limitation (*e.g.* drought), overall it appears that counting on more diverse stands allows for optimizing chances of having the right traits to cope with any local constraints.

Although it is difficult to rely on species-mixing to address one specific limiting conditions, chapter 2 highlights a notable exception. Indeed, mixing two species with distinct traits in regard to water-related processes led to positive or, at worse, neutral effects in dry or very dry sites, making it a safe choice for forest management. In addition, by showing that the increase of $\delta^{13}C$ values with decreasing water availability is exacerbated by basal area, our results show that forest management in pure stands is an important tool to adapt the forests to the expected change in water regime.

Another important management consideration resulting from our results is that, when considering water- or climate-related interactions, the more competitive species (beech in this case) is highly favoured. Indeed, no negative species-mixing effect has been found for the most competitive species while pine, a less competitive and more stress-tolerant species, frequently suffered from beech admixture. This is an important consideration for management strategies focusing on a limited number of individuals such as tree-oriented forestry. Indeed, such approach aim at focusing the management actions on a limited number of high potential individuals, giving them the right conditions to produce high quality products (highly qualitative wood) at a high rate. It addition, concentrating the actions on a limited number of trees allows for minimizing labour costs and improving stand profitability. In mixed-species stands, selecting objective trees from the most competitive species could therefore optimize productivity as they are the most susceptible to gain from inter-specific interactions.

In addition to concentrating the management actions on the most competitive species (objective species), forest management could be further optimized by selecting a companion species with distinct growth dynamics than the objective one. For instance, selecting a companion species with a longer growing period could allow it to compensate for the relative loss caused by the competing from the main species and therefore keep a productive value.

It is important to note however that we ought to be cautious when considering the practical implications of our results as statistically significant results does not necessarily imply strong ecological effects. For the results presented in Figs.3.5 to 3.8 for instance, the high number of individual measurements leads to a great statistical power. As a result, small differences between pure and mixed stands can be detected and considered significant. However, the figures show that the between-site variation is small compared to the inter-individual variability. Therefore, the statistically significant species-mixing effects found in those analyses probably refer to an effect whose magnitude is actually too small to be of ecological relevance.

5.2 Interaction between processes

In chapter 4, we found that four sites (Sp2: 1041, Sp1: 1042, Bul1: 1047 and Ser1: 1056) from a specific group showed coherent species-mixing effects on tree-growth relationships for beech. Three of those four sites (Sp1, Sp1 and Bul1) were available for isotopic analyses and they corresponded to the sites with the highest δ^{13}C and lowest water availability. Because those sites were characterized by low summer P-PET, we hypothesized that the coherent species-mixing effects on tree-growth relationships was due to reduced growth constraint in regard to this limiting factor (water availability) in beech mixed stands caused by lower inter- than intraspecific competition. As a result, we might expect a lowering of drought exposure (and thus, a positive $\Delta\delta^{13}$C) in beech mixed stands on those sites. However, only site Sp2 displayed positive $\Delta\delta^{13}$C values. No difference in wood isotopic composition were found between pure and mixed stands for sites Sp1 and Bul1.

Overall, there was no clear correlation between species-mixing effects on wood isotopic composition and on climate-growth relationships (Fig.5.1). Indeed, even though some sites (*e.g.* site 1041 = Sp2) displayed significant species-mixing effects both on wood isotopic composition and on climate-growth relationships, most sites did not fit this expectation. For instance, site 1049 (Cze1) displayed low water balance (Fig.2.2, Chapter 2), strong influence of SPEI_{APR} and SPEI_{Sep} on growth (PC3 - Chapter 4) but no species-mixing effects on climate-growth relationships despite the significantly lower δ^{13}C level in mixed stands compared to monocultures. One possible explanation for this lack of correlation between species-mixing effects on climate-growth relationships and wood isotopic composition is that the latter effect would not originate from a reduced drought exposure in mixed stands but rather from an effect on light availability. However, this hypothesis is not highly probable given the site low water balance. A second, more probable, hypothesis would be that species mixing does reduce drought exposure but not enough to remove the main climatic constraint, thus only slightly impacting the climate-growth relationships (see section 5.3).

Conversely, several dry sites (1042 = Sp1 and 1047 = Bul1) displayed strong species-mixing effects on climate-growth relationships but no difference in wood isotopic composition between pure and mixed stands. This raises questions about the processes causing the changes in climate-growth relationships. Again, several hypotheses could explain this effect. One of them would be that water constraint is not the main growth-limiting factor and that another factor, such as temperature, plays a prominent role. This hypothesis, however, is doubtful given that temperature control over tree growth is supposed to be lower than precipitation control and its effects should be located mainly at the beginning and the end of the growing period [Lebourgeois et al., 2010; 2013]. In addition, Fig.4.3 from chapter 4, Fig.2.2 from chapter 2 and the site average $\delta^{13}C$ values from Fig.5.1 all point towards a strong water constraint in those sites.

When analysing species-mixing effects on forest functioning, we should also take into consideration the interaction between nutrient- and water-related processes. For instance, it is well known that potassium has a strong influence on drought resistance through its effects on osmosis, stomatal control and hydraulic conductance [Babita et al., 2010; Khosravifar, 2008; Oddo et al., 2011]. As a result, released water constraint in water-limited sites could originate either from improvement of water availability, uptake or use-efficiency or from similar effects on K resources. Alternatively, trees growing in sites with sufficient water resources could still display symptoms of water deficiency if K levels are highly limiting [Arquero et al., 2006], yet this effect is still debated and contrasted results have been reported [Wang et al., 2013]. Unfortunately, our dataset did not allow us to test formally such interaction. For instance, very few sites displayed strong foliar K limitations (Net1 and, to a much lesser extent, Bel1 for beech; no sites for pine - Fig.3.2), and only Bel1 was available for isotopic analysis.

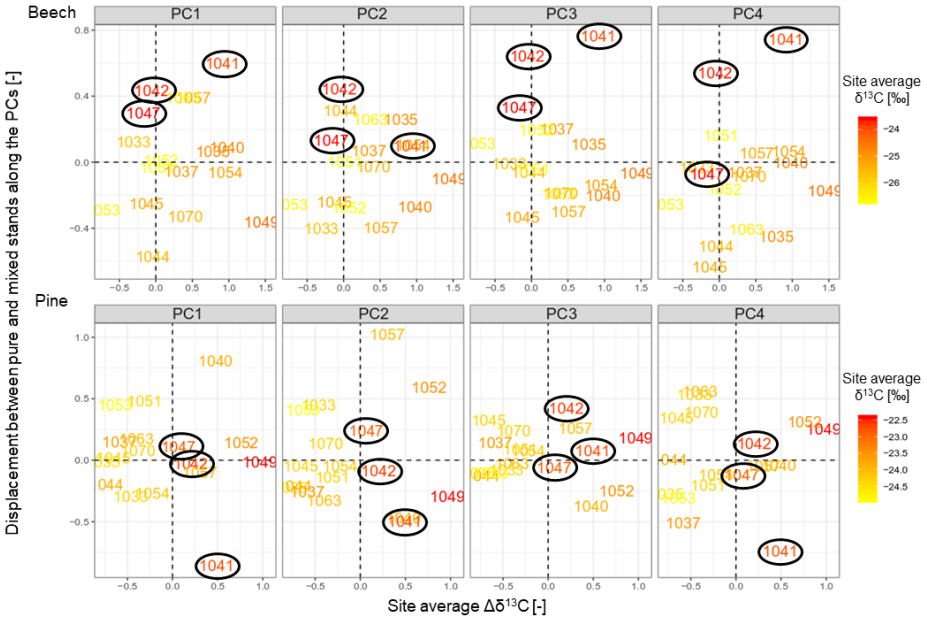


Figure 5.1 – Relationships between site average species-mixing effects on wood isotopic composition ($\Delta\delta^{13}C = \delta^{13}C_{pure}$ - $\delta^{13}C_{mixed}$) and species-mixing effects on climate-growth relationships (displacement from pure to mixed stands along the PC). Positive $\Delta\delta^{13}C$ values indicate more negative $\delta^{13}C$ values (and thus higher isotopic discrimination) in mixed stands. Sites from Gr1.5 (the only group of sites that displayed a coherent and significant species-mixing effect on climate-growth relationships) are circled in black.

5.3 General framework of variation of species-mixing effects depending on growing conditions

The general framework proposed by Forrester and Bauhus [2016] has been widely used to interpret the spatial and temporal variations of species-mixing effects. It suggests that those effects are stronger under harsher environmental conditions, provided that species interactions have a positive effect on the limiting factor. Results from our analysis of species-mixing effects on climate-growth relationships are globally in accordance with this framework. Indeed, species-mixing effects were mostly found for beech in sites with strong water limitations during

summer. However, this framework might not be generalized. Indeed, when analyzing the influence of species interactions on foliar nutrition, we found the opposite pattern: increasing species-mixing effects with improving site nutritional status. Interestingly, Forrester et al. [2018] also suggested that complementarity for light might increase with improving growing conditions. They argued that higher growth in more favorable conditions could lead to increased competition for light. Forrester et al. [2018] further highlighted such increased importance of species-mixing influence on light-related processes in richer sites leading to increased growth for *Pinus sylvestris* when admixed with beech. The importance of interaction improving light interception or light-use efficiency thus increases with improving growing conditions. Our results suggest that such effect might not only be true for light-related processes but also for other growth limiting factors. In addition, when analyzing the spatial variation of species-mixing effects on carbon isotope composition, we found complex effects such as strong influence of species traits and existence of thresholds, notably between positive and neutral species-mixing effects toward the most limiting end of the gradient. These results suggest a non-linear relationship between species-mixing effects and growing conditions.

As a result, spatial variation of species-mixing effects for a given couple of species might follow a more complex pattern, such as the one presented in Fig.5.2. In this framework, the species involved are considered to have distinct characteristic traits such that their interactions influence the processes associated with the limiting factor. In such case, species-mixing effects under harsh conditions are expected to be positive (conformably to Forrester and Bauhus 2016 - (a) in Fig.5.2). However, when moving towards extremely harsh environmental conditions (sites located at the left hand of the X axis of the figure - (b) on Fig.5.2), species interactions may not be strong enough to express themselves anymore, leading to a neutral species-mixing effect. In situations of such intense environmental constraint, we do not expect for species traits to have a major influence on the results of species interactions, leading to similar effects for both species (*e.g.* differences in traits associated with

hydraulic strategy such as iso- *vs.* anisohydric character might not be of paramount importance if water availability is so low that both species exert high stomatal control). However, under mild environmental conditions (Fig.5.2c), specific traits might strongly influence the outcome of species interactions. For instance, an anisohydric species could be favored by the admixing of an isohydric species under those conditions while the latter would experience neutral or even negative species-mixing effects. In rich sites, several scenarios are possible. For instance, the high growth level in pure stands could lead to competition that can be released by species interactions, resulting in positive species-mixing effects (Fig.5.2d). On the other hand, species mixing has been shown to improve growth, including in rich sites. This higher growth could lead to increased competition compared to the pure stands (Fig.5.2e). However, we would not expect this last effect to be very strong. Indeed, if it were the case, it would reduce growth and, consequently, competition (feedback effect).

Results of species mixing also depend on temporal variations of growing conditions. For instance, in a site with sufficient water availability where species-mixing effects strongly depends on species traits, a drought event could induce a switch towards complementarity for both species. In this respect, the drought event acts as if it moves the site towards the left of the gradient (Fig.5.2f). On the other hand, mixed stands in rich sites that display high growth level could be more sensitive to a drought event, leading to negative species-mixing effects during this period (Fig.5.2g). Temporal and spatial gradients could, however, be of different nature (distinct limiting resource). For instance, on a site with high water availability but that is strongly limited by another resource (*e.g.* nutrient availability), any observed complementarity would be explained by species-mixing effects on the latter. However, a drought could then lead to a shift in the nature of the constraint. As a result, complementarity would then be dependent on species-mixing effects on water-related processes. In the absence of such effects, the temporal variations of growing conditions could lead to the loss of complementarity.

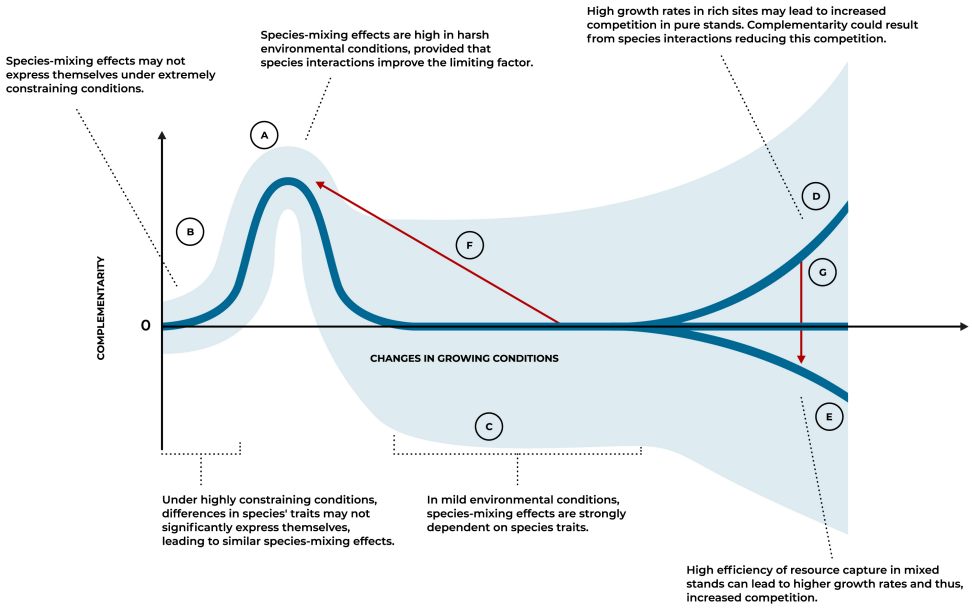


Figure 5.2 – Conceptual framework showing the possible evolution of species-mixing effects for two admixed tree species along spatial or temporal gradients of growing conditions. The associated tree species are hypothesized to have traits such that their interactions influence the processes associated with the limiting factor. The solid blue lines show the expected evolution of species-mixing effects along the gradient while the shaded area indicates the possible range of species-mixing effects depending on species specific traits. Red arrows indicate how temporal variations of growing conditions such as drought events can influence the results of species interactions.

5.4 Suggestion for future research

5.4.1 Increased focus on soil properties and belowground processes

It is well known that soil is a critical compartment of forest ecosystems. Among other important roles, it is a major determinant of nutrient- and water-related processes. For instance, López-Marcos et al. [2018] found that mixing species, even displaying similar traits (species from the same genus), strongly affect several soil characteristics such as C stock and therefore, soil exchangeable cations. However, acquisition of information on soil properties and belowground processes is often diffi-

cult, time-consuming and is not a systematic practice of forest scientists and practitioners.

Due to those difficulties, most measurement campaigns conducted over large spatial area (large-scale datasets) tend to focus on other determinants of forest functioning such as local climate or dendrometric measurements (basal area, aboveground growth). As a result, interpretation of ecological processes over large-scale datasets can be challenging.

Species-mixing effects on wood isotopic composition and climate growth relationships may be largely affected by water-related processes. In this regard, the climatic water balance (precipitation minus potential evapotranspiration) calculated over variable time steps provide valuable information about the constraint experienced by the trees. However, maximum available soil water can strongly modulate this constraint. As a result, knowledge of soil water availability, in particular the maximum available water capacity of the soil, is crucial to analyse such mechanisms of species-mixing effects, as demonstrated by the analyses from chapter 2. In addition, chapter 4 shows that despite a large-scale geographical pattern of average climate-growth relationships, no coherent pattern of tree response to drought events could be found across Europe. This suggests that factors varying at the site level influence tree response to drought, thus dampening any potential large-scale climatic pattern. Differences in soil water availability, which are not known in the case of this specific study but are expected to be quite large, are good candidate to explain such site-level component of variability in tree drought response. Additional information such as the presence/absence of temporary or permanent water table or of indurated horizon would also be critical to accurately estimate the water reserve available to the trees. Such information would allow for a better characterization of the gradient of water availability and could therefore improve our understanding of the spatial variation of species-mixing effects on water-related processes. In addition, despite the fact that recent studies confirmed the high belowground competitivity of beech in mixed beech-pine stands [Yeste et al., 2021], the effects of species-mixing on pine and beech actual rooting distribution is still not well known. Better characterization of

those effects is crucial to understand the relative importance of positive and negative belowground interactions in mixed stands and therefore deserve additional research. On the other hand, direct measurements of soil nutrient availability might help shedding light on the patterns of spatial variability of species-mixing effects on foliar nutrition observed in Chapter 3 by reducing the influence of other processes such as nutrient translocation. However, measuring the amount of available nutrient in the soil is not an easy task. For instance, most traditional soil sampling methods only provide information on a specific point in time and space even though soil nutrient content is dynamic due to nutrient release and transport. Ion-exchange resins integrating measurements over a longer period of time (*e.g.* the growing season) have thus been proposed to address this issue and have been successfully used in the field [Nickmans et al., 2019]. Contrarily to foliar nutrient content which is an integrative indicator that can reflect influence of non-nutrient related processes (for instance, tree mineral nutrition has been shown to be significantly influenced by both drought and excess of water - Kreuzwieser and Gessler 2010), such methods can provide direct information about the amount of nutrients available in the soil and thus can be more directly representative of site nutritional status. While this method allows for temporal integration of the measurements, spatial integration (both horizontally and vertically) remains challenging.

5.4.2 Methodological sampling considerations and expansion of the dataset

One of the main originalities of this research lies in its methodology. Indeed, most large scale studies of species-mixing effects on forest processes focus on widely integrative indicators (*e.g.* growth - see for instance Pretzsch et al. 2015 or Morin et al. 2011), making the identification of the mechanisms at play difficult. On the other end of the spectrum, ecophysiological studies are often used to gain detailed insight on specific mechanisms but are often local and therefore do not cover wide ranges of ecological conditions (see for instance Forrester 2015). The methodological approach used here is based on an intermediate approach that

consists in analysing proxies of specific processes on sites from an observational triplet network covering a large gradient of environmental conditions.

In the introduction, we discussed about the fact that observational networks such as the one used in the present research are potentially powerful tools to study the effects of species-mixing on several ecosystem processes (such as resource availability) and their spatial and temporal variability depending on environmental conditions. However, the suitability of the approach regarding those objectives cannot be analysed independently of sampling considerations. In our case, despite the great care dedicated to controlling the complexity of the dataset, statistical results were frequently non- or barely significant, which could indicate that the signal-to-noise ratio of the dataset is not favourable for detecting the potential effects due to the large number of variables involved.

Specifically, the network of sites used in analyses of chapter 2 covers well the right hand of the soil water availability gradient (moderately wet and wet sites). However, dry and very dry sites are not as well represented and additional sampling would be needed to better assess the different thresholds. Indeed, in order to improve our understanding of the spatial variation of species-mixing effects on water-related processes, we need a better characterization of the situations leading to a switch from a situation where species-mixing effects are positive for one species and negative for the other depending on their specific traits and a situation where species-mixing effects becomes positive for both species. Similarly, characterization of the tipping point defining the switch between positive and neutral species-mixing effects is critical for forest management given the importance currently given by forests policies and practitioners to mixed-species stands for mitigation of climate-change effects on forest ecosystems functioning.

Future research should also focus on producing a more balanced sampling all along the nutrient gradient (chapter 3). Indeed, in our dataset, a few sites were located far from the others on the gradient and thus, had a strong influence on the measured effects. More balanced sampling

should provide more confidence on the pattern of spatial variation of species-mixing effects on foliar nutrient composition. More specifically, the unexpected larger species-mixing effects on foliar nutrient contents observed in richer sites is actually driven by a few sites at the extreme end of the gradient. Considering that the mechanisms leading to those effects are not clearly established, increased sampling in those conditions would be crucial to confirm or infirm the pattern. Indeed, increased species-mixing effects in richer sites could originate from co-limitation by another element or another factor such as water availability (see section 5.4.3). In such conditions, the effects could be site-dependent (increased species-mixing effects in richer sites would depend on the existence of an other limiting factor in those sites). Increased sampling could therefore reveal that the species-mixing pattern is actually not generalized. On the other hand, if increased growth in richer sites leading to increased competition is at the origin of the higher species-mixing effects in more favourable conditions, increased sampling could confirm the pattern. In addition, a major constraint on the analysis of spatial variability of species-mixing effects on tree nutrition was the amount of available information on nutrient availability. Because of its integrative nature, we used foliar characteristics as indicator of site nutrient richness. However, foliar nutrient composition is not influenced solely by soil nutrient availability. For instance, drought can influence tree nutrition through impacts on nutrient mobility, fine roots dynamics or root uptake capacities, while excess water availability affects tree nutritional status through impact on the physiology of mycorhizal tree roots, alteration of soil redox status or loss of elements through leaching [Johnson et al., 2002; Kreuzwieser and Gessler, 2010]. As a result, depending on local conditions, foliar nutrient composition might not adequately express site nutrient richness and further research using other indicators of site nutrient availability could improve our understanding of the spatial variability of species-mixing effects on tree nutrition. In this regard, methods such as ion-exchange resins have proved useful [Nickmans et al., 2019]. Indeed, such resins allows for determining the nutrient concentrations in the soil. Additionally, that method has the advantage of integrating the

measurement over time, rather than providing a punctual information, which would not allow for accounting for nutrient release or transport in the soil [Abrams and Jarrell, 1992; Curtin et al., 1987; Nickmans et al., 2019].

Concerning the climatic analyses (chapter 4), all groups of sites with climatically similar tree growth-climate relationships could benefit from increased sampling. Indeed, although the tree growth-climate relationships were fairly homogenous within the different groups, there was a large variability in the species-mixing effects. Increased sampling could allow for exploring this variability (*e.g.* dependency on stand characteristics such as basal area, on site characteristics such as soil maximal water availability). However, the greatest research efforts should be allocated to the group displaying coherent species mixing effects (group characterized by dry summer conditions). Indeed, although the species-mixing effects were coherent in this group, it only counted 4 sites and still displayed some variability. Additional research effort should allow for better understanding of species-mixing effects under such environmental conditions and its dependency on non-climatic parameters (basal area). In addition, in our dataset, the sites displaying coherent species-mixing effects on growth-climate relationships were characterized by both low summer water availability and high altitude. Increased sampling could thus help disentangle the importance of climate and altitude on the observed species-mixing effects. Lastly, our results showed that pine tended to have a higher resistance to drought events in mixed stands, provided that fall water availability was high. Although this effect was found to be significant, it was strongly influenced by a limited number of values corresponding to sites with high fall water balance. Increased sampling in those specific conditions could improve the estimation of the shape and strength of the relationship.

Therefore, this work provides valuable information about the environmental conditions where particular sampling efforts should be conducted in order to improve our understanding of the effects of species mixing and their spatial/temporal variations. For instance, sites with strong expected effects (dry sites when considering growth-climate relationships)

or where our observed effects are unexpected in the light of the current ecological theories (extremely dry sites when considering the effects on water availability, rich sites when considering the effects on mineral nutrition) deserve special attention.

In addition to sampling consideration, the approach used in this research suffers from two main drawbacks. First, such observational plots often lack historical data. Indeed, information about past management activities, density or specific composition is seldom available which can make challenging the analyses of long chronological series. Second, despite the care dedicated to find stands with similar growing conditions, comparison between stands might be difficult because perfect control of confounding factors cannot be achieved. It is all the more problematic in the case of a triplet approach where there is only one stand of each type and therefore, where there is no replication within similar ecological conditions.

Despite the difficulties associated with the approach, observational networks appear promising. Indeed, they allow analysing specific processes over large spatial or temporal scales using experimental setups that are representative to forests as they are found in the landscape. Although highly interesting, this approach shows its limits when considering several processes simultaneously. Indeed, such consideration should imply that sampling is conducted simultaneously along two (or more) ecological gradients (*e.g.* sites with water limitation but no nutrient limitations, sites with nutrient limitations but no water shortage, sites with no limitation whatsoever...). In practice, finding sites that fit such ecological considerations while being free of any major confounding factors (no major differences in topography or climate, in stand age or density...) seems difficult. Controlled environmental designs seem therefore more suited to provide answer to such questions.

Another specificity of this work has been to explicitly measure resource level in the different sites. This allowed for specific characterization of spatial gradients in regard to the processes considered rather than relying on indicators such as Site Index that integrate several factors (tem-

perature regime, water supply, soil nutrients... - Brandl et al. 2014). Such direct characterization of site resource level should result in better representation of species-mixing effects variation along gradients of limiting resources. This approach is therefore particularly suited to compare observational data to conceptual frameworks such as the one proposed by Forrester and Bauhus [2016].

In this research, several analytical methods have been used. Although analysis of wood stable isotopic composition or dendrochronological series for climate-growth relationships are well-known and widely used methods (see for instance González de Andrés et al. [2017] for isotopic analyses and Pretzsch et al. [2015] or Lebourgeois et al. [2013] for dendrochronological analyses), foliar nutrient analyses based on foliar nutrient ratios (*ilr* ratios) are not. The method based on *ilr* ratios suffers from one major drawback: its complexity that makes interpretation difficult. The use of the *ilr* method in the framework of forest nutrition is particularly challenging because balances are harder to understand in forest than in crops where they can be associated with well-known fertilization effects, liming effects, deficiencies... However, the relevance of using an integrative method such as the nutrient balance concept to study plant nutrition is gaining wider acceptance in the scientific community. Indeed, far from only providing a solution on potential numerical biases associated with more classical approaches of foliar nutrient analyses, this method puts the focus on the importance of the relative abundance of different elements/groups of elements. Such balances between elements/groups of elements have been shown to be critical in numeral processes such as masting [Fernandez-Martínez et al., 2019], herbivory [Lind and Barbosa, 2012] or forest dieback [Hevia et al., 2019]. Such an integrated approach of mineral nutrition is all the more important that recent studies have highlighted the existence of long-term trends in tree foliar nutrient composition that may differ between elements (augmentation *vs.* diminution), thus changing the ratios between such elements and possibly leading to unbalances [Jonard et al., 2015]. In this research, the combination of both methods (*ilr* method and analyses of foliar nutrient quantities) is intended as a way to highlight the impor-

tance of considering the ionome in an integrative way while providing interpretability of the *ilr* results.

5.4.3 Considering interaction between processes

The analyses presented in this thesis have the specificity of being conducted at a large geographical scale, thus covering a wide range of ecological conditions. Over such a large gradient based on an observational network, we expect the relative importance of ecological factors to vary depending on local conditions. For instance, water-related processes should be of paramount importance in dry sites while they may not strongly influence tree functioning under moister conditions. In those cases, other ecological factors (*e.g.* light-related processes) could play a more important role. Interaction between ecological factors could also play an important role in shaping the response to mixing within the network. For instance, it is well known that water availability and tree mineral nutrition are not independent of each other. As a result, while nutrient availability is not expected to be a major ecological determinant of tree functioning on nutrient-rich sites, chronic low water availability could have detrimental effects on tree nutrition (through reduced microbial activity, lower ion mobility... - Kreuzwieser and Gessler 2010), thus increasing the relative ecological importance of nutrient availability. In addition, large-scale species-mixing effects on productivity are emerging properties of species interactions resulting from the fact that more diverse stands have more opportunities to present a combination of traits allowing to cope with a large range of limiting factors, depending on local conditions (see section 5.1.3). As a result, mechanistic analyses of mixed-species forests functioning should not consider one limiting factor at a time but should allow for the analysis of potential cross-limitations and for the analysis of the effects of several simultaneous processes.

Despite analysing species mixing effects processes using datasets of unprecedented scale, the amount of available information proved to be insufficient to properly address the interactions between the different processes. In our case, different subsets of sites from the network were used for the various analyses (isotopes, foliar nutrients, climate-growth

relationships). As a result, the number of sites for which information on multiple processes is known is somewhat limited. Our ability to test formally such interaction effects are also limited by the way our sampling sites are distributed along the corresponding gradients of resource availability. For instance, it is well known that some elements, such as potassium have strong influence on drought resistance. In consequence, it would be interesting to compare carbon isotopic composition between pure and mixed stands in sites with and without *i.)* limitations in term of water availability and *ii.)* limitations in term of K availability. Such analysis would require cautious experimental planning that could hardly be met in a network of observational plots. Given the current state of knowledge on such processes, it is my belief that experimental designs optimizing orthogonality (ability to detect and quantify diversity effects from a background of confounding variables) and comprehensiveness (representation of the spectrum of ecosystem functions and services), such as synthetic community approach [Nadrowski et al., 2010; Verheyen et al., 2013] would be powerful tools to identify and quantify the major determinant of those processes. Indeed, use of an experimental framework would allow for a better control of confounding factors (such as stand density for instance) in addition to rigorously and systematically assess the interactions between limiting factors.

5.4.4 Modelling approach

Our results showed that the context-dependency of species-mixing effects differed between beech and pine. For instance, species mixing had a positive effect on beech $\delta^{13}C$ values on moderately wet sites while it tended to have a deterrent effect on pine in the same environmental conditions (chapter 2). Results from chapter 4 suggest that species mixing tend to reduce the environmental constraint experienced by beech but does not affect pine on dry sites. During drought events, pine tended to display higher resistance in mixed stands compared to monocultures if water availability at the end of the vegetation period was sufficient while beech did not. Those differences highlight the fact that species-mixing effects not only depend on environmental conditions but are also

strongly dependent on species functional traits. Traits should consequently be taken into account when trying to understand and predict species-mixing effects on forest functioning. However, establishing a link between traits and net complementarity-competition effects in mixed forests is not straightforward. A promising approach to take into account simultaneously the interaction between limiting factors, the influence of species traits and the impact of spatial and temporal variations of the associated processes is to use process-based models. Although the large number of variables involved make the use of such models difficult, previous studies proved them to be useful to disentangle the processes involved in mixed-stands productivity along with identifying and quantifying the key processes involved in species-mixing effects in a given condition [Forrester et al., 2017; Gupta and Sharma, 2019].

However, the use of such mechanistic modelling approach to explore species-mixing effects on specific processes (*e.g.* water or nutrient availability) and their spatial/temporal variability would require a strong characterization of the growing environment and particularly, of belowground resources and processes (soil availability, mineral weathering, atmospheric deposition...). In a first step, such models should therefore be developed on highly instrumented sites such as stands from experimental networks (see section 1.5.2.1).

In addition to such deterministic approaches, it is also possible to use empirical models to compare the observed and predicted values of certain processes. Trouvé et al. [2017] used such an approach to investigate the effects of several factors (such as site water status, stand density and tree social status) on growth resistance and resilience to extreme drought events. One main advantage of this approach is that, in contrast to an approach where tree reaction is analysed by comparing growth during drought and growth during a period preceding the event, modelling takes explicitly into account the dendrometric and climatic variables that may affect growth independently of the drought during the year of interest [Fritts, 1976; Preztsch, 2009; Trouvé et al., 2017]. Such approach proved to be useful to analyze the reaction to extreme events as demonstrated by Trouvé et al. [2017] and in the case of such strong determinants of

tree functioning (*e.g.* drought), it could probably be used to explore the effects on other processes such as water-related ones (through $\delta^{13}C$ for instance). Being able to remove the influence of non-drought related variability of the studied processes during drought events could help to detect and accurately quantify tenuous effects such as the influence of species interactions. Although such approach may be useful to analyse species-mixing effects during specific events (such as drought), using it to analyse long-term trends might be challenging considering that model precision decreases rapidly when moving away from its calibration range. It is even more the case for less integrative processes or processes analysed at a lower scale (*e.g.* foliar rather than total biomass production), notably because of their higher variability [Forrester et al., 2017].

5.5 General conclusion

On average, increasing tree species diversity in forest stands results in higher productivity and stability of productivity, as well as in a larger range of ecosystem services; however, those effects are strongly context-dependent. In my PhD, I therefore explored some processes possibly involved in species-mixing effects and looked at their dependency to spatial and temporal variations of environmental conditions. More specifically, I analysed species-mixing effects on proxies of water and nutrient use, and on climate-growth relationships for Scots pine and European beech growing in pure and mixed-species stands (triplets) using a network of sites covering a large ecological gradient across Europe. This work was conducted along three axes. The first one aimed at analysing the effects of species interactions on water related processes using wood carbon isotopic composition as an indicator of tree water use efficiency. I found that complementarity displayed a humped-shaped curve with maximal (positive) values for dry sites and close-to-zero values for extremely dry ones. In addition, species-mixing effects on non- or moderately constrained sites were strongly dependent on water- and possibly light-related species traits. No coherent species-mixing effects on drought resistance along the gradient was found for either species. The

second axis aimed at analysing pine and beech foliar nutrient composition in pure and mixed stands along a gradient of sites nutritional richness. Significant species-mixing effects on both foliar nutrient concentrations and stoichiometry were found. Interestingly, those effects tended to be higher on richer sites. Lastly, I analysed the large-scale variability of species-mixing effects on average climate-growth relationships and drought resistance for pine and beech across Europe. The results highlighted the strong influence of regional climate on climate-growth relationships but coherent species-mixing effects were only found in case of overwhelming climatic constraint. While no species-mixing effects on drought response was found for beech, a significant effect was highlighted for pine, yet limited to situations where local climatic conditions allowed for compensatory growth to happen during the last part of the vegetation period.

Building on our results, I was able to suggest improvements to an existing framework describing variations of species-mixing effects along gradient of environmental conditions, in particular by considering non-linear relationships. The results of this thesis also highlighted the importance of considering the interactions between processes, rather than considering them independently of each other. In addition to those important ecological considerations, this work bears high relevance for forest management and forest policies. Indeed, it shows that species-mixing effects on forest performances (*e.g.* growth) over large geographical scales are emerging phenomenon. Therefore, mixed-species forests appear to be of high practical importance despite the difficulty of attributing those effects to one dominant process. In addition, results from this thesis show that the most competitive species are the most susceptible to gain from inter-specific interactions. In tree-oriented forestry, concentrating management actions on individuals from the most competitive species could therefore optimize productivity.

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Appendices

Appendix 1 – Selected site characteristics. Explanation of variables: slope: range of stands slope within sites (min - max), mean annual temperature, T [°C], total annual precipitation, P [mm]; de Martonne Index (1926), M.

Country	Triplet name	Triplet code	Longitude	Latitude	Elevation [m]	Slope [degrees]	T [°C]	P [mm]	M
Austria	Aus1	1048	16°23′ 20″	47°22′ 34″	525	18 - 19	8.5	750	41
Belgium	Bel1	1057	5°27′00″	50°01′48.00″	545	0 - 8	7.5	1175	57
Belgium	Bel2	1063	04°19′29.60″	50°45′06.10″	160	0	10.5	852	49
Bosnia and Herzegovina	BHe1	1059	18°29′56″	44°13′35″	697	25	9.5	939	48
Bulgaria	Bul1	1047	23°21′03″	41°53′43″	1187	15 - 20	6	750	47
Czech Republic	Cze1	1049	16°36′08.78″	49°18′14.40″	440	5 - 10	7.5	620	35
Czech Republic	Cze2	1058	13°12′46″	49°58′03″	545	6 - 13	7.1	656	38
France	Fra1	1040	07°29′13.60″	48°58′41.80″	275	28 - 38	9.7	948	48
Germany	Ger1	1033	11°14′12.49″	48°34′57.95″	430	1	8.5	700	38
Germany	Ger2	1031	09°03′54″	50°06′49″	250	0	9	720	38
Germany	Ger3	1032	10°58′13″	49°53′12″	250	2	8	650	36

Appendix 1 - Continued

Country	Triplet name	Triplet code	Longitude	Latitude	Elevation [m]	Slope [degrees]	T [°C]	P [mm]	M
Germany	Ger4	1071	08°01′04″	49°24′58″	40	1	9	675	36
Germany	Ger5	1034	10°38′06.37″	49°47′50.45″	370	3	10	675	34
Germany	Ger6	1070	12°44′08.30″	48°11′12.47″	400	0	8	560	31
Germany	Ger7	1061	13°37′06″	52°04′46″	74	0	8.6	520	28
Italy	Ita1	1055	10°56′11″	46°04′03″	1037	0 - 15	7.8	1050	59
Italy	Ita2	1062	07°03′53″	44°54′12″	1475	25	7.9	938	52
Lithuania	Lit1	1051	22°24′24.01″	55°04′47.30″	25	0	6.5	750	45
Lithuania	Lit2	1052	21°32′23.44″	55°27′02.80″	20	0	6.5	800	48
Netherlands	Net1	1043	06°01′20″	52°25′41″	34	2.3 - 3.4	9.7	825	42
Poland	Pol1	1035	14°36′17.51″	53°20′07.40″	60	0	9.2	556	37
Poland	Pol2	1036	19°54′42.27″	53°48′19.15″	136	0	7.9	666	29

Appendix 1 - Continued

Country	Triplet name	Triplet code	Longitude	Latitude	Elevation [m]	Slope [degrees]	T [°C]	P [mm]	M
Poland	Pol3	1037	20°41′08.90″	50°59′27.96″	383	2	7.8	662	37
Poland	Pol4	1044	20°13′45.84″	50°01′27.60″	209	0 - 4	8.2	650	36
Poland	Pol5	1045	20°19′37.26″	50°01′36.00″	215	0	8.2	650	36
Serbia	Ser1	1056	19°37′30″	43°42′17″	1080	20 - 22	7.7	1020	58
Slovakia	Slo1	1046	18°31′11″	48°33′09″	530	14 - 16	6.9	730	43
Spain	Sp1	1042	03°10′19.00″ W	42°05′57.00″	1293	43 - 53	8.9	860	46
Spain	Sp2	1041	02°15′44.23″	42°10′18.09″	1106	24.4 - 39.8	8	1100	61
Sweden	Swe1	1054	13°35′35.00″	56°09′12.00″	118	10 - 17	8	700	39
Sweden	Swe2	1053	14°11′46.00″	55°42′33.00″	26	4 - 15	7	800	47
Ukraine	Ukr1	1060	23°39′44″	49°57′05″	315	0	7.6	673	38

Appendix 2 – Selected site characteristics. PB: pure beech stand, PP: pure pine stand, M: mixed stand. Explanation of variables: mean temperature calculated over the vegetation period (March-September), T_{VP} [°C]; de Martonne Index (1926), M; mean precipitation calculated over the vegetation period, P_{VP} [mm]; potential available soil water, SWA [mm]; water balance over the vegetation period, WB_{VP}. Sites are ranked according to their average water balance over the vegetation period (mean over pure and mixed stands). Site index is the height [m] of the 100 largest-diameter trees per ha at age 50 years in pure plots and is an indicator of site productivity for each species (Forrester et al. 2017); it is provided first for pine, then for beech. M (de Martonne) = annual precipitation [mm]/mean annual temperature [°C + 10]. WB_{VP} (water balance over the vegetation period (VP)) [mm] = total precipitation over the vegetation period (March - September) + potential available soil water (SWA [mm]) − total potential evapotranspiration over the VP.

Country	Triplet name	Stand	Longitude	Latitude	Elevation [m]	Slope [°]	T_{VP}	M	P_{VP}	SWA	WB_{VP}	Site index
Spain	Sp1	PB PP M	03°10′19.00”W	42°05′57.00”	1293	43 - 53	13.9	46	351	98 30 108	-347 -415 -337	20.9 - 24.8
Bulgaria	Bul1	PB PP M	23°2103	41°5343	1187	15 - 20	12.3	47	331	90 90 90	-262.3 -262.3 -262.3	25.1 - 25.9
Spain	Sp2	PB PP M	02°15′44.23”	42°10′18.09”	1106	24.4 39.8	16.9	61	371	84 84 84	-248.8 -248.8 -248.8	9.5 - 24.3
Czech Republic	Cze1	PB PP M	16°3608.78	49°1814.40	440	5 - 10	13.1	35	384	146 146 146	-136.5 -136.5 -136.5	23 - 23.8
France	Fra1	PB PP M	07°2913.60	48°5841.80	275	28 - 38	14.6	48	474	82 65 91	-107 -124 -94	22.2 - 23
Germany	Ger1	PB PP M	11°1412.49	48°3457.95	430	1	14.5	38	382	273 158 158	7.5 -107.5 -107.5	22.7 - 27.6
Belgium	Bel1	PB PP M	5°2700	50°0148.00	545	0 - 8	13.1	57	439	172 172 151	-44.8 -44.8 44.8	13.2 - 17.3

Appendix 2 - Continued

Country	Triplet name	Stand	Longitude	Latitude	Elevation [m]	Slope [°]	T_{VP}	M	P_{VP}	SWA	WB_{VP}	Site index
Poland	Pol1	PB PP M	14°3617.51	53°2007.40	60	0	13.7	37	347	280 280 280	5.1 5.1 5.1	26.9 - 27.3
Poland	Pol4	PB PP M	20°1345.84	50°0127.60	209	0 - 4	13.2	36	471	215 229 286	-3.1 10.9 67.9	21.3 - 15.8
Poland	Pol5	PB PP M	20°1937.26	50°0136.00	215	0	13.4	36	463	286 229 286	45.6 -11.4 45.6	25.8 - 24.5
Sweden	Swe1	PB PP M	13°35′35.00”	56°09′12.00”	118	10 - 17	12.1	39	421	135 143 194	6.9 14.9 65.9	21 - 13.3
Poland	Pol3	PB PP M	20°4108.90	50°5927.96	383	2	12.7	37	419	280 280 280	32.2 32.2 32.2	20.5 - 22.6
Sweden	Swe2	PB PP M	14°1146.00	55°4233.00	26	4 - 15	12.9	47	359	272 272 272	149.3 149.3 149.3	22
Belgium	Bel2	PB PP M	04°1929.60	50°4506.10	160	0	15	49	540	122 122 122	159.6 159.6 138.6	10.9 - 12
Germany	Ger6	PB PP M	12°4408.30	48°1112.47	400	0	13.6	31	675.00	184 184 184	200.5 200.5 200.5	12.8 - 15.8
Lithuania	Lit1	PB PP M	22°24′24.01”	55°04′47.30”	25	0	12.5	45	415	715 715 715	567.8 567.8 567.8	19.5 - 22.3
Lithuania	Lit2	PB PP M	21°32′23.44”	55°27′02.80”	20	0	12.8	48	431	715 715 715	632.4 632.4 632.4	13.6 - 22.9

Appendix 3 – Selected stand characteristics at each site (for mixed stands, the characteristics are given per component species). Sites are ranked according to the average water balance calculated over the vegetation period (March-September WB_{VP}) (mean over pure and mixed stands).

Site ID	Site name	Species	Stand type	Age [$years$]	Basal area [$m^2.ha^{-1}$]
1042	Sp1	Beech	Pure	40	33
		Beech	Mixed	40	14
		Pine	Pure	40	55
		Pine	Mixed	40	39
1047	Bul1	Beech	Pure	65	41
		Beech	Mixed	65	37
		Pine	Pure	65	54
		Pine	Mixed	65	42
1041	Sp2	Beech	Pure	50	52
		Beech	Mixed	50	21
		Pine	Pure	50	40
		Pine	Mixed	50	11
1049	Cze1	Beech	Pure	45	36
		Beech	Mixed	45	13
		Pine	Pure	45	43
		Pine	Mixed	45	26
1040	Fra1	Beech	Pure	60	26
		Beech	Mixed	60	15
		Pine	Pure	60	41
		Pine	Mixed	60	17
1033	Ger1	Beech	Pure	53	23
		Beech	Mixed	50	16
		Pine	Pure	65	25
		Pine	Mixed	50	17
1057	Bel1	Beech	Pure	150	27
		Beech	Mixed	100	20
		Pine	Pure	150	11
		Pine	Mixed	130	10
1035	Pol1	Beech	Pure	54	38
		Beech	Mixed	54	12
		Pine	Pure	54	42
		Pine	Mixed	54	26

Appendix 3 - Continued

Site ID	Site name	Species	Stand type	Age [years]	Basal area [$m^2.ha^{-1}$]
1044	Pol4	Beech	Pure	57	18
		Beech	Mixed	57	23
		Pine	Pure	57	30
		Pine	Mixed	57	13
1045	Pol5	Beech	Pure	55	25
		Beech	Mixed	55	16
		Pine	Pure	55	34
		Pine	Mixed	55	16
1054	Swe1	Beech	Pure	84	33
		Beech	Mixed	106	20
		Pine	Pure	56	32
		Pine	Mixed	106	20
1037	Pol3	Beech	Pure	69	31
		Beech	Mixed	72	24
		Pine	Pure	80	41
		Pine	Mixed	72	19
1053	Swe2	Beech	Pure	65	52
		Beech	Mixed	65	17
		Pine	Pure	65	48
		Pine	Mixed	65	29
1063	Bel2	Beech	Pure	115	28
		Beech	Mixed	115	17
		Pine	Pure	115	40
		Pine	Mixed	115	29
1070	Ger6	Beech	Pure	64	23
		Beech	Mixed	60	11
		Pine	Pure	73	34
		Pine	Mixed	60	28
1051	Lit1	Beech	Pure	90	26
		Beech	Mixed	90	20
		Pine	Pure	90	35
		Pine	Mixed	90	43
1052	Lit2	Beech	Pure	102	43
		Beech	Mixed	102	18
		Pine	Pure	102	41
		Pine	Mixed	102	41

Appendix 4 – Characteristics of the cored trees. Sites are ranked according to the average water balance over the vegetation period (mean over pure and mixed stands).

Site name	Species	Stand type	Mean height [m]	Mean diameter [cm]	δ^{13}C [‰]		Temporal stability	Sensitivity [‰]
					Mean	Sd		
Sp1	Beech	Pure	18.1	17	-23.7	0.5	45.54	0.07
	Beech	Mixed	16.4	13.1	-23.7	0.6	36.91	0.19
	Pine	Pure	17	22.7	-22.6	0.5	60.98	0.13
	Pine	Mixed	18.1	24.6	-22.7	0.5	44.87	0.13
Bul1	Beech	Pure	25.5	22.1	-23.5	0.6	36.55	1.74
	Beech	Mixed	28.3	22.4	-23.6	0.6	40.91	1.68
	Pine	Pure	27.8	30.5	-22.9	0.7	32.55	1.74
	Pine	Mixed	28.3	33.9	-22.9	0.7	32.12	1.16
Sp2	Beech	Pure	22.6	30	-24	0.5	51.41	0.45
	Beech	Mixed	15.8	25.6	-25.1	0.5	52.49	0.2
	Pine	Pure	10.1	24.4	-22.7	0.6	35.62	0.48
	Pine	Mixed	14.4	26.8	-23.3	0.5	46.01	0.37
Cze1	Beech	Pure	20.8	20.7	-25.2	0.8	49.53	0.48
	Beech	Mixed	21	26.7	-24.5	0.5	79.67	0.43
	Pine	Pure	21.3	24.8	-22.8	0.8	53.76	0.83
	Pine	Mixed	21.1	23.9	-22.4	0.4	27.53	1.28
Fra1	Beech	Pure	21.7	24.8	-25.2	0.5	41	0.64
	Beech	Mixed	25.1	21.1	-24.8	0.6	23.88	0.38
	Pine	Pure	23.4	30.8	-24.1	0.5	53.49	0.92
	Pine	Mixed	25.4	27.1	-23.9	0.4	44.67	0.68
Ger1	Beech	Pure	22.5	22.6	-25.6	0.7	31.68	1.19
	Beech	Mixed	25.5	23.5	-25.7	0.8	46.47	0.15
	Pine	Pure	22.6	32.6	-24.2	0.6	34.8	0.61
	Pine	Mixed	25.8	25.6	-24.4	0.7	48.45	0.16

Appendix 4 - Continued

Site name	Species	Stand type	Mean height [m]	Mean diameter [cm]	δ^{13}C [‰]		Temporal stability	Sensitivity [‰]
					Mean	Sd		
Bel1	Beech	Pure	28	44.7	-26.8	0.7	48.71	0.75
	Beech	Mixed	29.2	44.6	-26.5	0.5	41.11	0.37
	Pine	Pure	33.3	48.3	-24	0.3	80.21	0.24
	Pine	Mixed	28.4	61.8	-24.1	0.3	85.85	0.48
Pol1	Beech	Pure	24.1	29.7	-25.3	1.1	24.83	0.46
	Beech	Mixed	27.2	22.7	-24.9	1	24.28	1.11
	Pine	Pure	26.1	27.4	-23	0.6	29.53	0.11
	Pine	Mixed	27.3	27.6	-24.6	0.8	37.02	0.06
Pol4	Beech	Pure	26.9	24.9	-25.5	0.9	40.76	0.57
	Beech	Mixed	18.3	30.3	-25.5	0.6	22.05	0.48
	Pine	Pure	26.9	33.9	-23.4	0.7	38.44	0.76
	Pine	Mixed	23.1	32.9	-23.9	0.6	52.38	0.29
Pol5	Beech	Pure	24.2	29.7	-25.2	0.5	48.67	0.03
	Beech	Mixed	27	32.4	-25.3	0.5	45.26	1.4
	Pine	Pure	25.2	33.9	-24	0.6	63.04	0.09
	Pine	Mixed	25.9	32	-24.4	0.4	41.76	0.65
Swe1	Beech	Pure	23.3	45.9	-25.2	0.6	39.62	1.08
	Beech	Mixed	20.9	36.8	-26.2	0.4	64.1	0.15
	Pine	Pure	22.3	31.4	-24.2	0.6	40.89	0.62
	Pine	Mixed	23.1	42.1	-23.8	0.4	66.31	0.53
Pol3	Beech	Pure	27.4	30.9	-25.3	0.7	58.24	0.21
	Beech	Mixed	28.4	29	-25.1	0.4	28.57	0.42
	Pine	Pure	27	32.7	-23.4	0.4	54.34	1.21
	Pine	Mixed	26.2	30.4	-23.6	0.4	67.62	0.55

Appendix 4 - Continued

Site name	Species	Stand type	Mean height [m]	Mean diameter [cm]	δ^{13}C [‰]		Temporal stability	Sensitivity [‰]
					Mean	Sd		
Swe2	Beech	Pure	25.3	42.3	-26.6	0.4	73.44	0.13
	Beech	Mixed	27.1	37.2	-25.9	0.6	42.83	0.7
	Pine	Pure	24.7	35.4	-24.9	0.7	37.8	0.64
	Pine	Mixed	25.6	57.9	-24.2	0.3	73.72	0.42
Bel2	Beech	Pure	22.7	31	-25.6	0.5	54.94	0.67
	Beech	Mixed	27.4	32.2	-25.3	0.5	52.37	0.69
	Pine	Pure	22.2	40.3	-24.1	0.4	59.17	0
	Pine	Mixed	19.5	38.3	-24.1	0.4	64.24	0.03
Ger6	Beech	Pure	19.4	25.6	-25.7	0.9	33.3	1.04
	Beech	Mixed	20.5	18.8	-25.5	0.8	27.18	0.25
	Pine	Pure	21.6	20.9	-24	0.5	59.52	0.64
	Pine	Mixed	17.5	22.2	-24.3	0.4	65.14	0.3
Lit1	Beech	Pure	32.3	28.3	-26.7	0.8	35.31	1.13
	Beech	Mixed	29.8	28.2	-26.7	0.7	40.75	0.91
	Pine	Pure	26.5	36.6	-24.4	0.6	38.37	1.54
	Pine	Mixed	33.2	42.6	-24.3	0.5	48.66	0.46
Lit2	Beech	Pure	25.9	30.6	-26.7	0.5	56.15	0.65
	Beech	Mixed	27.7	26.6	-26.6	0.8	34.04	0.68
	Pine	Pure	34.3	44.6	-23.5	0.5	56.53	0.07
	Pine	Mixed	31.1	39.4	-26.6	0.8	49.62	0.1

Appendix 5 – Parameters tested in the different analyses of chapter 2. Age is the mean age of the pure stand or of the target species in mixed stands. BA is the mean basal area of the stand. Mean height is the average height of trees in the pure stand. Height ratio is the ratio of the mean height of the target species in mixed stands to the mean height of the mixed stand. BA ratio is the ratio of the difference between target species BA in pure and mixed stands to the average BA of the target species in pure and mixed stands. WB_{VP} is the water balance calculated over the vegetation period (total precipitation over the vegetation period (March - September) + potential available soil water total potential evapotranspiration over the vegetation period). T_{annual} temperature is the mean of the temperature during the vegetation period calculated for 1950−2014. $T_{1993-2014}$ is the annual June - September Temperature averaged for 1993-2014 [°C]

	Time series of $\delta^{13}C_{cor}$ for each species in the pure stands	**Difference in average $\delta^{13}C_{cor}$ values between species in the pure stands**	**Species response to a drought event**	**Species mixture effects**	**Temporal constancy**
Elevation [m]	X	X	X	X	X
Slope [degrees]	X	X		X	X
Age [year]	X	X	X	X	X
BA [m^2 .ha^{-1}]	X	X	X		X
Mean height [m]	X	X	X		X
Height ratio (Height target species in mixed stand/Mean height mixed stand) [-]				X	
BA ratio [(BA pure stand BA mixed stand)/Mean BA pure/mixed stands] [-]				X	
WB_{VP} [mm]	X	X	X	X	X
$SPEI_{June-September}$ [-]	X			X	
Annual June - September Temperature [°C]	X			X	
$T_{1993-2014}$ [°C]		X	X		X
Species					X
Stand composition (pure/mixed)			X		

Appendix 6 – Selected characteristic years and associated SPEI and P - PET values. Values for all three types of year (driest year, wettest year preceding the driest one and wettest year following the driest one) are presented. SPEI and P - PET indicate respectively the relative and absolute values of the climatic water balance of the year in question, and $(P - PET)_{mean}$ is the average P - PET value (calculated over the 1993 - 2014 period) for the site. Sites are ranked according to their average water balance over the vegetation period (mean over pure and mixed stands).

Site	Type of year	Year	SPEI	P - PET	$(P - PET)_{mean}$
Sp1	Preceding	1997	2.13	-205.98	-457.12
	Dry	2005	-2.26	-608.77	
	Following	2014	0.22	-410.09	
Bul1	Preceding	1995	0.8	-231.39	-316.58
	Dry	2000	-2.12	-522.33	
	Following	2014	2.03	-67.75	
Sp2	Preceeding	1997	0.67	-230.99	-368.83
	Dry	2009	-2.25	-551.86	
	Following	2011	-0.28	-335.71	
Cze1	Preceeding	2001	1.48	-64.97	-194.58
	Dry	2003	-2.07	-386.8	
	Following	2010	1.64	-49.97	
Fra1	Preceeding	2000	1	-55.19	-171.86
	Dry	2003	-2.2	-404.01	
	Following	2007	0.99	-56.39	
Ger1	Preceeding	1995	1.38	-78.82	-213.04
	Dry	2003	-2.38	-459.44	
	Following	2007	0.96	-114.84	
Bel1	Preceeding	2001	1.74	27.16	-97.23
	Dry	2003	-1.61	-293.56	
	Following	2004	1.71	25.08	
Pol1	Preceeding	1993	1.28	-70.83	-164.71
	Dry	1994	-1.59	-329.64	
	Following	2007	2.34	49.27	

Appendix 6 - Continued

Site	Type of year	Year	SPEI	P - PET	(P - PET)$_{mean}$
Pol4	Preceeding	2001	1.88	91.03	-142.59
	Dry	2006	-1.69	-313.69	
	Following	2010	1.64	50.04	
Pol5	Preceeding	1993	-0.28	-187.09	-147.32
	Dry	1994	-1.8	-338.78	
	Following	2010	1.86	80.22	
Swe1	Preceeding	1993	1.6	94.35	-58.2
	Dry	1997	-1.86	-272.61	
	Following	2007	2.3	218.12	
Pol3	Preceeding	1993	0.4	-124.97	-151.92
	Dry	1994	-1.41	-322.03	
	Following	2001	2.15	119.17	
Swe2	Preceeding	1993	1.46	42.43	-84.26
	Dry	2003	-1.68	-235.02	
	Following	2007	2.2	144.76	
Bel2	Preceeding	2000	1.35	104.76	-39.3
	Dry	2003	-1.83	-224.48	
	Following	2004	1.62	141.72	
Ger6	Preceeding	1993	1.34	158.18	-16.61
	Dry	2003	-2.48	-324.01	
	Following	2010	0.37	56.26	
Lit1	Preceeding	1993	0.91	22.77	-92.92
	Dry	1994	-1.47	-258.96	
	Following	2007	1.73	140.62	
Lit2	Preceeding	1998	1.29	146.06	-39.92
	Dry	2006	-1.55	-233.73	
	Following	2007	1.34	153.8	

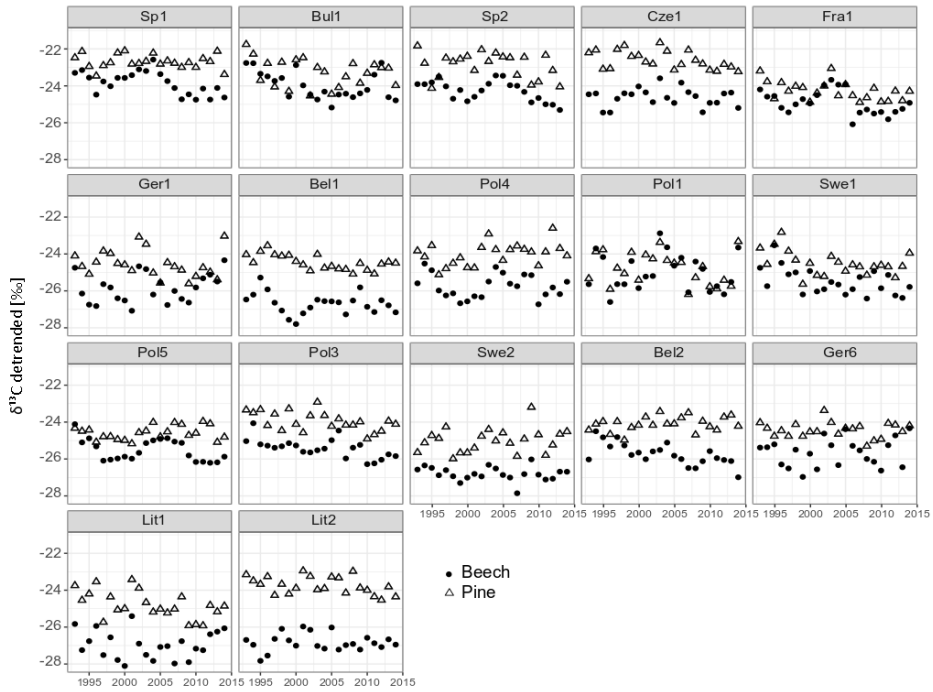
Appendix 7 – Results of paired t-tests for the significance of the difference between average δ^{13}C values for pure stands of each species within each site. p-values indicate the significance of the deviation from zero (mean $\delta^{13}C_{beech}$ - mean $\delta^{13}C_{pine}$). Sites are shown by increasing value of mean water resources in pure stands (WB_{VP} calculated on the approximate vegetation period (March-September) and averaged over the 1950 - 2014 period).

Site	**Mean $\delta^{13}C_{beech}$ - Mean $\delta^{13}C_{pine}$**	**p-values**
Sp1	-1.0897	<.001
Bul1	-0.6833	0.002
Sp2	-1.243	<.001
Cze1	-2.0693	<.001
Fra1	-0.8837	<.001
Ger1	-1.3444	<.001
Bel1	-2.4247	<.001
Pol4	-1.6442	<.001
Pol1	-0.2462	0.381
Swe1	-0.9799	<.001
Pol5	-0.9064	<.001
Pol3	-1.5122	<.001
Swe2	-1.6868	<.001
Bel2	-1.2829	<.001
Ger6	-1.1803	<.001
Lit1	-2.3095	<.001
Lit2	-3.2289	<.001

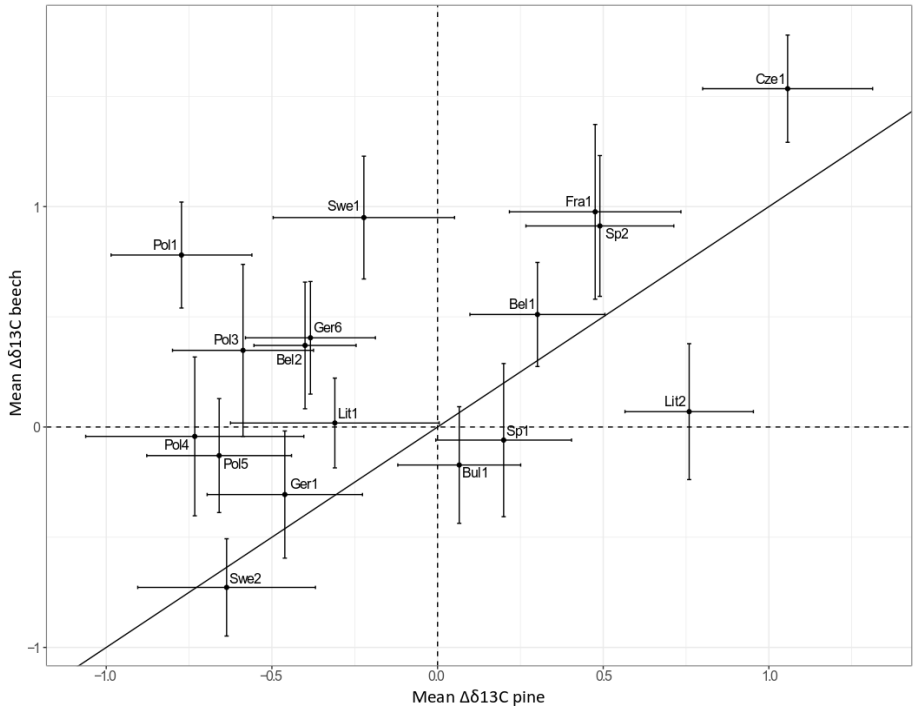
Appendix 8 – Correlation coefficients between $\delta^{13}C_{cor}$ time series of beech and pine in the pure stands for each site. Sites are shown by increasing value of mean water resources in pure stands (WB_{VP} calculated on the approximate vegetation period (March-September) and averaged over the 1950-2014 period).

Site	**Correlation**
Sp1	0.7
Bul1	0.72
Sp2	0.45
Cze1	0.7
Fra1	0.69
Ger1	0.58
Bel1	0.52
Pol4	0.36
Pol1	0.85
Swe1	0.81
Pol5	0.54
Pol3	0.68
Swe2	0.66
Bel2	0.21
Ger6	0.63
Lit1	0.72
Lit2	0.42

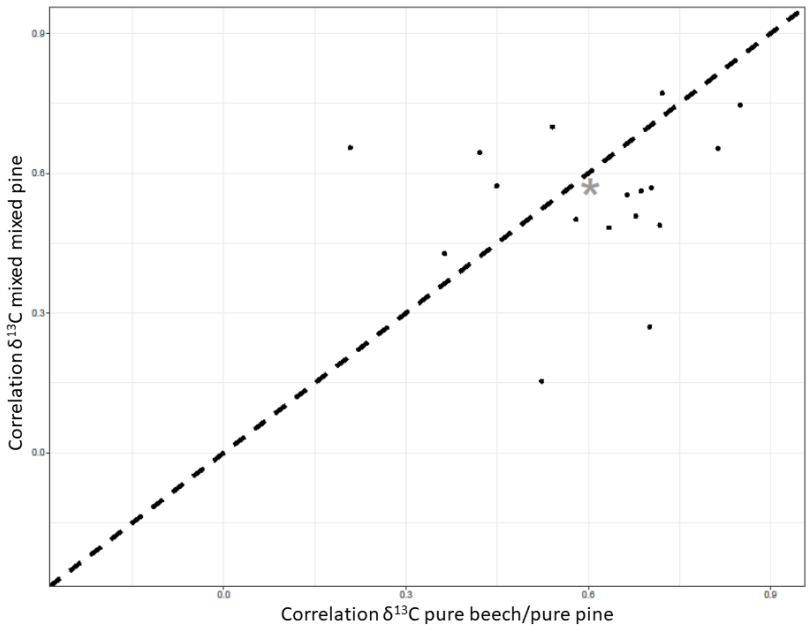
Appendix 9 – Time series of carbon isotopic ratios for both species and every study site in the pure stands. Study sites are ordered by increasing value of mean water resources (mean over pure stands).



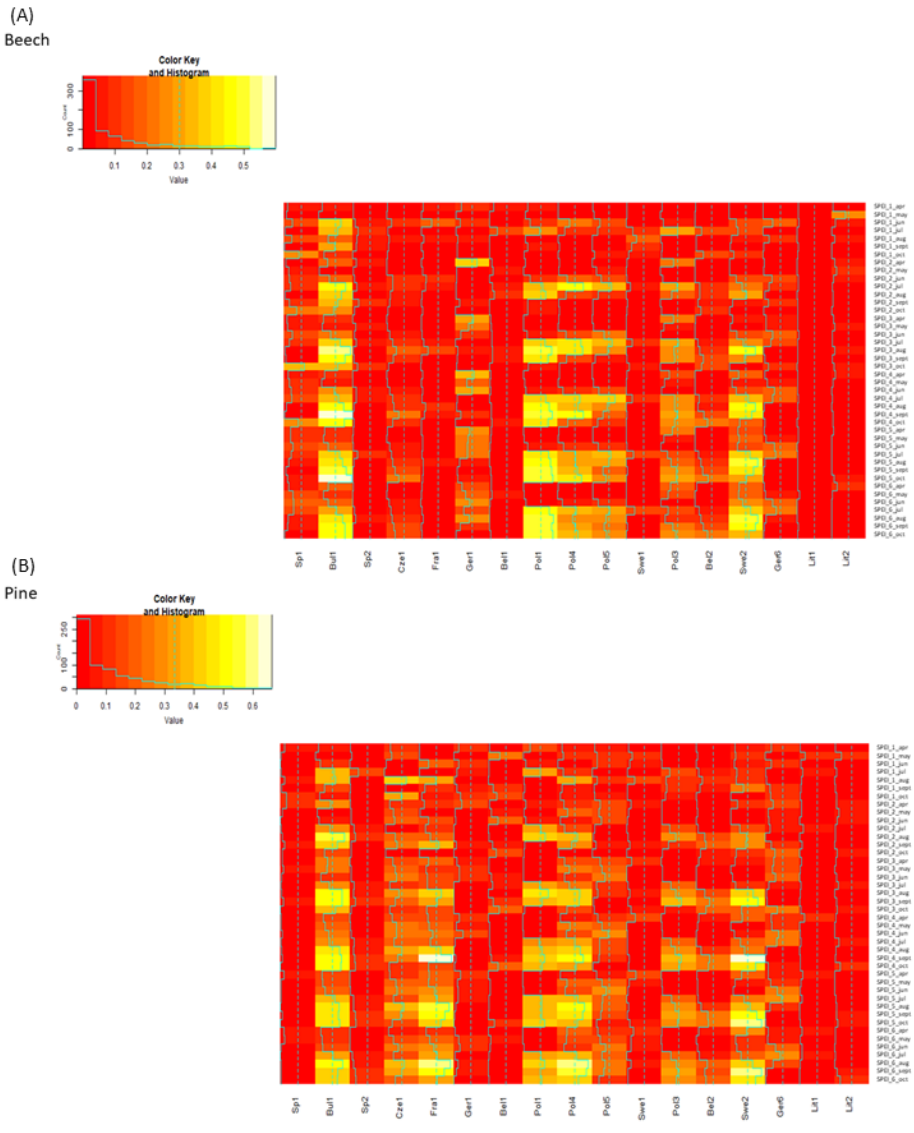
Appendix 10 – Relationship between the mean differences in δ^{13}C between pure and mixed stands ($\delta^{13}C_{pure}$ - $\delta^{13}C_{mixed}$) for beech (Y axis) and pine (X axis). Vertical and horizontal bars represent 95% confidence intervals. Horizontal and vertical dashed lines indicate zero and the solid line indicates the 1:1 relationship.



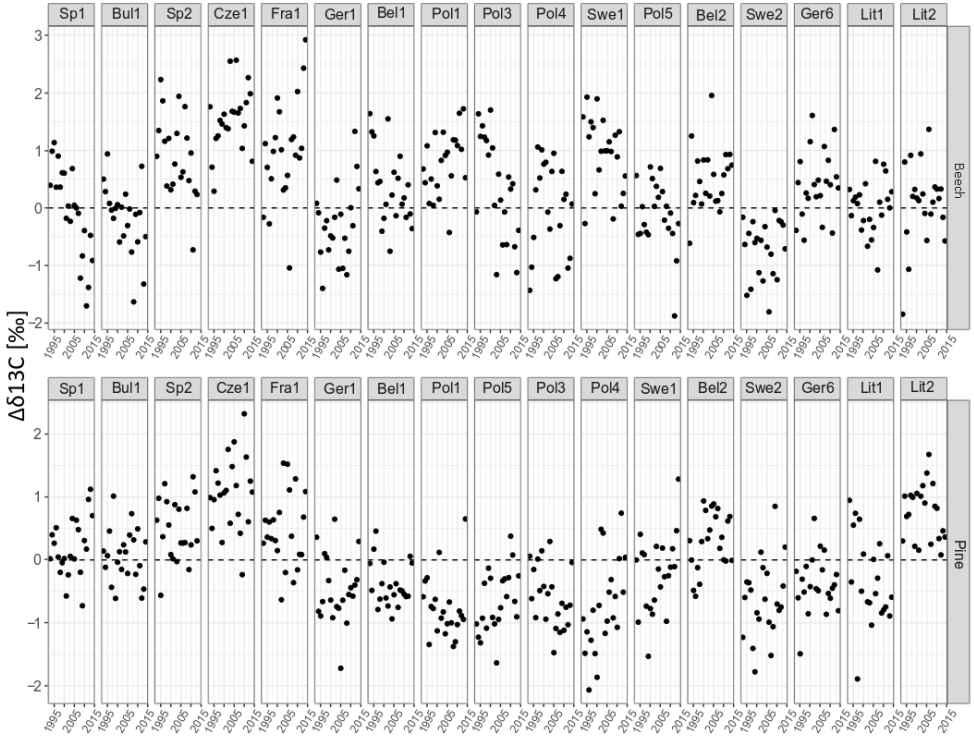
Appendix 11 – Relationship between correlation coefficients of the species δ^{13}C series in pure and mixed stands. The large grey star indicates the mean value.



Appendix 12 – Heatmaps showing the intensity of the linear relationship (R^2 of the models) between δ^{13}C and SPEI at each site, for beech (A) and pine (B) in pure stands. SPEI was calculated for periods of one to six months, ending between March and October. The insert in the top left corner of each panel indicates the level of the R^2 values.



Appendix 13 – Series of $\delta^{13}C_{pure}$ - $\delta^{13}C_{mixed}$ ($\Delta\delta^{13}$C) for both species. Positive values indicated lower (more negative) $\delta^{13}C$ values in mixed stands. Horizontal dashed lines indicate zero. Sites are ranked in increasing order of average WB_{VP} (calculated aver the 1950-2014 period; mean over pure and mixed stands by species).



Appendix 14 – Minima and maxima of the median of foliar nutrient concentrations (N, P, K, Ca and Mg; $[mg.g^{-1}]$) per site for beech and pine (current-year-needles) along the gradient of 15 sites. The lower and upper value correspond to the limits of the normal range of foliar nutrient concentration as defined in Mellert and Göttlein (2012). Values below the lower limit of the normal range correspond to nutrient deficiency while values higher than the upper limit correspond to nutrient surplus.

Element	**Observed range**		**Normal range**	
	Minimum	**Maximum**	**Lower value**	**Upper value**
Beech				
N	18.5	28.1	18.7	23.2
P	1	1.9	1.2	1.9
K	4.6	12	6.1	9.7
Ca	3.3	13.6	6.7	14
Mg	0.4	3	1.1	2.3
Pine				
N	11.9	21.3	14	18.3
P	1	1.9	1.3	1.9
K	5.9	10.5	4.6	7
Ca	2	4.5	2	3.9
Mg	0.7	1.3	0.8	1.3

Appendix 15 – Position of each site with respect to the nutrients deficiency and surplus thresholds defined by Mellert and Göttlein (2012) for beech (B) and pine (P). < indicates that the site median is below the lower limit of optimal nutrient concentration range (deficiency). > indicates that the site median is higher than the upper threshold of optimal nutrient concentration range (surplus). >< indicates that the median is situated within the optimum concentration range.

	BEL1		BEL2		BUL1		CZE1		CZE2		FRA1		GER4		GER7	
	B	P	B	P	B	P	B	P	B	P	B	P	B	P	B	P
N	><	>	>	>	><	><	>	><	><	><	><	<	>	>	><	<
P	<	><	><	><	><	>	><	><	><	><	<	<	<	><	><	><
K	><	>	>	>	>	>	><	>	>	>	>	>	><	>	><	>
Ca	<	<	<	><	><	><	><	><	<	><	<	><	><	><	><	><
Mg	<	><	><	><	><	><	><	><	><	><	<	<	>	><	><	><

	LIT1		LIT2		NET1		POL3		POL4		POL5		Slo1	
	B	P	B	P	B	P	B	P	B	P	B	P	B	P
N	>	<	><	<	><	><	><	<	<	><	<	<	><	><
P	><	><	><	><	><	<	<	<	><	><	><	><	<	<
K	>	>	><	><	<	><	>	>	><	><	><	><	><	><
Ca	><	><	><	<	><	><	><	><	><	><	><	><	><	>
Mg	><	><	><	><	><	><	><	><	><	><	><	><	><	><

Appendix 16 – Site and stand characteristics of the 15 sites. Age and basal area data in mixed stands are provided first for beech, then for pine.

Site	Species	Stand composition	Site/stand characteristics					
			Altitude [m]	Mean annual temperature [°C]	Total annual precipitation [$mm.year^{-1}$]	Age [Years]	Basal area [$m^2.ha^{-1}$]	Size [ha]
Bel1	Beech	Pure	550	7.5	1175	150	27	0.065
	Pine	Pure				150	11	0.068
	Beech/Pine	Mixed				100/130	20/10	0.101
Bel2	Beech	Pure	160	10.5	852	115	28	0.73
	Pine	Pure				115	40	1.55
	Beech/Pine	Mixed				115/115	17/29	0.08
Bul1	Beech	Pure	1187	6	750	65	41	0.03
	Pine	Pure				65	54	0.03
	Beech/Pine	Mixed				65/65	37/42	0.045
Cze1	Beech	Pure	440	7.5	620	45	36	0.077
	Pine	Pure				45	43	0.11
	Beech/Pine	Mixed				45/45	13/26	0.114
Cze2	Beech	Pure	545	7.1	656	55	38	0.025
	Pine	Pure				55	40	0.025
	Beech/Pine	Mixed				55/55	13/22	0.045

Appendix 16 - Continued

Site	Species	Stand composition	Site/stand characteristics					
			Altitude [m]	Mean annual temperature [°C]	Total annual precipitation [$mm.year^{-1}$]	Age [Years]	Basal area [$m^2.ha^{-1}$]	Size [ha]
Fra1	Beech	Pure	275	9.7	948	60	26	0.09
	Pine	Pure				60	41	0.18
	Beech/Pine	Mixed				60/60	15/17	0.16
Ger4	Beech	Pure	400	9	675	60	54	0.032
	Pine	Pure				70	59	0.027
	Beech/Pine	Mixed				70/70	28/24	0.05
Ger7	Beech	Pure	74	8.6	520	80	21	0.473
	Pine	Pure				80	24	0.148
	Beech/Pine	Mixed				80/80	12 - 4	0.462
Lit1	Beech	Pure	25	6.5	750	90	26	0.054
	Pine	Pure				90	35	0.065
	Beech/Pine	Mixed				90/90	20/43	0.07
Lit2	Beech	Pure	20	6.5	800	102	43	0.041
	Pine	Pure				102	41	0.1
	Beech/Pine	Mixed				102/102	18/41	0.07

Appendix 16 - Continued

Site	Species	Stand composition	Site/stand characteristics					
			Altitude [m]	Mean annual temperature [°C]	Total annual precipitation $[mm.year^{-1}]$	Age [Years]	Basal area $[m^2.ha^{-1}]$	Size $[ha]$
Net1	Beech	Pure	34	9.7	825	46	38	0.032
	Pine	Pure				46	39	0.05
	Beech/Pine	Mixed				48/46	19/27	0.056
Pol3	Beech	Pure	383	7.8	662	80	31	0.072
	Pine	Pure				81	41	0.05
	Beech/Pine	Mixed				83/83	24/20	0.086
Pol4	Beech	Pure	209	8.2	650	57	18	0.09
	Pine	Pure				57	30	0.05
	Beech/Pine	Mixed				57/57	23/13	0.086
Pol5	Beech	Pure	215	8.2	650	55	25	0.08
	Pine	Pure				55	34	0.075
	Beech/Pine	Mixed				55/55	16/16	0.18
Slo1	Beech	Pure	530	6.9	730	55	45	0.025
	Pine	Pure				55	45	0.025
	Beech/Pine	Mixed				55/55	13/27	0.15

Appendix 17 – Impact of stand composition, species identity and their interaction on foliar *ilr* balances, using site and stand nested within site as random factors (Equation 3.3). The reference level for stand composition is pure and the reference for species is beech. Those models are illustrated in Fig.3.3. Marginal R-squared (R^2_m) represents the variance explained by the fixed factors. Conditional R-squared (R^2_c) represents the variance explained by both the fixed and random factors (whole model).

***Ilr* balance**	R^2_m	R^2_c	**Fixed effect**	**Value**	**Standard error**	**p-value**
$[Fv\|Mg, Ca, K, P, N]$	0.532	0.747	Intercept	-4.817	0.03	**0.00**
			Stand composition	-0.008	0.02	0.68
			Species	-0.36	0.015	**0.00**
			Stand composition x species	0.03	0.022	0.17
$[Mg, Ca\|K, P, N]$	0.354	0.707	Intercept	0.7	0.08	**0.00**
			Stand composition	0.118	0.06	0.07
			Species	0.675	0.034	**0.00**
			Stand composition x species	-0.193	0.049	**0.00**
$[K\|P, N]$	0.034	0.467	Intercept	-0.341	0.042	**0.00**
			Stand composition	-0.053	0.035	0.15
			Species	-0.105	0.022	**0.00**
			Stand composition x species	0.055	0.031	0.08
$[Mg\|Ca]$	0.51	0.697	Intercept	1.242	0.049	**0.00**
			Stand composition	-0.035	0.039	0.38
			Species	-0.61	0.028	**0.00**
			Stand composition x species	0.091	0.04	**0.02**
$[P\|N]$	0.338	0.718	Intercept	1.916	0.042	**0.00**
			Stand composition	0.055	0.028	0.07
			Species	-0.224	0.017	**0.00**
			Stand composition x species	-0.126	0.025	**0.00**

Appendix 18 – Impact of stand composition, species identity and their interaction on the nutrient content of current foliage, using site and stand nested within site as random factors (Equation 3.3). The reference level for stand composition is pure and the reference for species is beech. Those models are illustrated in Fig.3.4. Marginal R-squared (R^2_m) represents the variance explained by the fixed factors. Conditional R-squared (R^2_c) represents the variance explained by both the fixed and random factors (whole model).

Element	R^2_m	R^2_c	**Fixed effect**	**Value**	**Standard error**	**p-value**
ln(N)	0.203	0.359	Intercept	4.721	0.051	**0.00**
			Stand composition	0.064	0.042	0.15
			Species	-0.324	0.041	**0.00**
			Stand composition x Species	-0.076	0.059	0.20
ln(P)	0.014	0.28	Intercept	2.012	0.051	**0.00**
			Stand composition	-0.015	0.036	0.69
			Species	-0.009	0.036	0.80
			Stand composition x Species	0.109	0.051	**0.03**
ln(K)	0.017	0.113	Intercept	3.782	0.043	**0.00**
			Stand composition	0.09	0.052	0.11
			Species	-0.038	0.044	0.40
			Stand composition x Species	-0.05	0.064	0.43
ln(Ca)	0.534	0.685	Intercept	3.742	0.082	**0.00**
			Stand composition	-0.081	0.056	0.17
			Species	-1.172	0.052	**0.00**
			Stand composition x Species	0.233	0.075	**0.00**
ln(Mg)	0.063	0.406	Intercept	1.986	0.087	**0.00**
			Stand composition	-0.036	0.071	0.62
			Species	-0.307	0.051	**0.00**
			Stand composition x Species	0.103	0.074	0.16

Appendix 19 – Impact of stand composition, site nutritional status and their interaction, on foliar *ilr* balances of current foliage (Equation 3.4). For each species, *ilr* balances are standardized by subtracting the species site-specific average from each individual value. For all balances, the site nutritional status is quantified by the site-average species-specific $[Fv|Mg, Ca, K, P, N]$ *ilr* balance. Default value for stand composition is pure. Those models are illustrated in Fig.3.5 (beech) and Fig.3.6 (pine).

***Ilr* balance**	R^2	**Fixed effect**	**Value**	**Standard error**	**p-value**
Beech					
$[Fv\|Ca, Mg, K, P, N]$	0.002	Intercept	0.008	0.011	0.50
		Site level	-0.029	0.051	0.57
		Stand composition	-0.015	0.016	0.36
		Site level x Stand composition	0.059	0.073	0.42
$[Mg, Ca\|K, P, N]$	0.056	Intercept	-0.029	0.028	0.30
		Site level	-0.206	0.126	0.10
		Stand composition	0.053	0.04	0.18
		Site level x Stand composition	0.433	0.18	**0.02**
$[K\|P, N]$	0.029	Intercept	0.007	0.018	0.68
		Site level	0.119	0.081	0.14
		Stand composition	-0.013	0.025	0.60
		Site level x Stand composition	-0.239	0.115	**0.04**
$[P\|N]$	0.061	Intercept	-0.054	0.013	**0.00**
		Site level	0.178	0.061	**0.00**
		Stand composition	0.107	0.019	**0.00**
		Site level x Stand composition	-0.342	0.086	**0.00**
$[Mg\|Ca]$	0.022	Intercept	0.053	0.024	**0.03**
		Site level	-0.242	0.11	**0.03**
		Stand composition	-0.106	0.034	**0.00**
		Site level x Stand composition	0.495	0.156	**0.00**
Pine					
$[Fv\|Ca, Mg, K, P, N]$	0.022	Intercept	-0.017	0.013	0.18
		Site level	-0.014	0.063	0.82
		Stand composition	0.039	0.018	**0.03**
		Site level x Stand composition	0.067	0.09	0.46
$[Mg, Ca\|K, P, N]$	0.02	Intercept	0.004	0.042	0.93
		Site level	-0.218	0.207	0.29
		Stand composition	-0.017	0.06	0.78
		Site level x Stand composition	0.357	0.296	0.23
$[K\|P, N]$	0.011	Intercept	0.031	0.024	0.19
		Site level	0.175	0.118	0.14
		Stand composition	-0.063	0.034	0.07
		Site level x Stand composition	-0.381	0.168	**0.02**
$[P\|N]$	0.066	Intercept	0.02	0.02	0.33
		Site level	-0.102	0.101	0.32
		Stand composition	-0.048	0.029	0.10
		Site level x Stand composition	0.163	0.145	0.26
$[Mg\|Ca]$	0.041	Intercept	0.008	0.026	0.75
		Site level	0.211	0.129	0.10
		Stand composition	-0.021	0.037	0.58
		Site level x Stand composition	-0.474	0.185	**0.01**

Appendix 20 – Impact of stand composition, site nutritional status and their interaction, on the nutrient content of current foliage (Equation 3.4). For each species, the nutrient contents are standardized by subtracting the species site-specific average from each individual value. For each nutrient, the site nutritional status is quantified by the corresponding site-average species-specific nutrient content. Default value for stand composition is pure. Those models are illustrated in Fig.3.7 (beech) and Fig.3.8 (pine).

Element	R^2	**Fixed effect**	**Value**	**Standard error**	**p-value**
Beech					
Total N	0.043	Intercept	-4.042	2.795	0.15
		Site level	-0.272	0.131	0.06
		Stand composition	7.542	3.952	0.06
		Site level x Stand composition	0.486	0.178	**0.01**
Total P	0.002	Intercept	0.075	0.178	0.68
		Site level	0.028	0.112	0.80
		Stand composition	-0.152	0.252	0.55
		Site level x Stand composition	-0.058	0.156	0.71
Total K	0.021	Intercept	-1.896	1.256	0.13
		Site level	-0.068	0.102	0.50
		Stand composition	3.769	1.776	**0.03**
		Site level x Stand composition	0.129	0.142	0.37
Total Ca	0.039	Intercept	2.019	1.207	0.10
		Site level	0.102	0.066	0.12
		Stand composition	-3.952	1.706	**0.02**
		Site level x Stand composition	-0.201	0.094	**0.03**
Total Mg	0.027	Intercept	0.391	0.323	0.23
		Site level	0.135	0.084	0.13
		Stand composition	-0.775	0.401	0.05
		Site level x Stand composition	-0.266	0.103	**0.01**
Pine					
Total N	0.012	Intercept	0.844	2.449	0.73
		Site level	0.094	0.083	0.26
		Stand composition	-1.719	3.556	0.63
		Site level x Stand composition	-0.196	0.12	0.10
Total P	0.097	Intercept	-0.411	0.183	**0.03**
		Site level	-0.294	0.112	**0.01**
		Stand composition	0.867	0.266	**0.00**
		Site level x Stand composition	0.588	0.158	**0.00**
Total K	0.123	Intercept	0.131	1.069	0.90
		Site level	0.412	0.105	**0.00**
		Stand composition	0.114	1.552	0.94
		Site level x Stand composition	-0.861	0.152	**0.00**
Total Ca	0.146	Intercept	-1.31	0.554	**0.02**
		Site level	-0.226	0.116	0.07
		Stand composition	2.701	0.959	**0.01**
		Site level x Stand composition	0.463	0.202	**0.02**
Total Mg	0.184	Intercept	-0.353	0.166	**0.03**
		Site level	-0.376	0.081	**0.00**
		Stand composition	0.702	0.241	**0.00**
		Site level x Stand composition	0.751	0.115	**0.00**

Appendix 21 – Selected site and stand characteristics of the 30 sites. P: Mean annual precipitation sum [mm], T: Mean annual temperature [°C]. Age and basal area data in mixed stands are provided first for beech, then for pine.

Site name	**Site number**	**Altitude [m]**	**P [mm]**	**T [°C]**	**Stand composition**	**Age [Years]**	**Basal area [$m^2.ha^{-1}$]**
Bel1	1057	545	1175	7.5	Beech Pine Beech/Pine	150 150 100/130	27 11 20/10
Bel2	1063	160	852	10.5	Beech Pine Beech/Pine	115 115 115/115	28 40 17/29
Bul1	1047	1187	750	6	Beech Pine Beech/Pine	65 65 65/65	41 54 37/42
Cze1	1049	440	620	7.5	Beech Pine Beech/Pine	45 45 45/45	36 43 13/26
Cze2	1058	545	656	7.1	Beech Pine Beech/Pine	55 55 55/55	38 40 13/22

Appendix 21 - Continued

Site name	Site number	Altitude [m]	P [mm]	T [°C]	Stand composition	Age [Years]	Basal area [$m^2.ha^{-1}$]
Cze2	1058	545	656	7.1	Beech Pine Beech/Pine	55 55 55/55	38 40 13/22
Fra1	1040	275	948	9.7	Beech Pine Beech/Pine	60 60 60/60	26 41 15/17
Ger1	1033	430	700	8.5	Beech Pine Beech/Pine	53 65 50/50	23 25 16/17
Ger2	1031	250	720	9	Beech Pine Beech/Pine	55 55 55/55	44 53 53/27
Ger3	1032	250	650	8	Beech Pine Beech/Pine	50 45 45/45	34 43 13/31
Ger4	1071	40	675	9	Beech Pine Beech/Pine	60 70 70/70	54 59 28/24

Appendix 21 - Continued

Site name	Site number	Altitude [m]	P [mm]	T [°C]	Stand composition	Age [Years]	Basal area [$m^2.ha^{-1}$]
Ger5	1034	370	675	10	Beech Pine Beech/Pine	58 51 64/64	40 55 17/22
Ger6	1070	400	560	8	Beech Pine Beech/Pine	64 73 60/60	23 34 11/28
Ger7	1061	74	520	8.6	Beech Pine Beech/Pine	80 80 80/80	21 24 12/4
Ita1	1055	1037	1050	7.8	Beech Pine Beech/Pine	40 40 40/40	23 52 10/12
Ita2	1062	1475	938	7.9	Beech Pine Beech/Pine	55 55 55/55	41 47 20/21
Lit1	1051	25	750	6.5	Beech Pine Beech/Pine	90 90 90/90	26 35 20/43

Appendix 21 - Continued

Site name	Site number	Altitude [m]	P [mm]	T [°C]	Stand composition	Age [Years]	Basal area [$m^2.ha^{-1}$]
Lit2	1052	20	800	6.5	Beech Pine Beech/Pine	102 102 102/102	43 41 18/41
Net1	1043	34	825	9.7	Beech Pine Beech/Pine	46 48 46/46	38 39 19/27
Pol2	1036	136	666	7.9	Beech Pine Beech/Pine	84 74 84/84	37 36 18/21
Pol1	1035	60	556	9.2	Beech Pine Beech/Pine	54 54 54/54	38 42 10/26
Pol3	1037	383	662	7.8	Beech Pine Beech/Pine	80 81 83/83	31 41 24/20
Pol4	1044	209	650	8.2	Beech Pine Beech/Pine	57 57 57/57	18 30 23/13

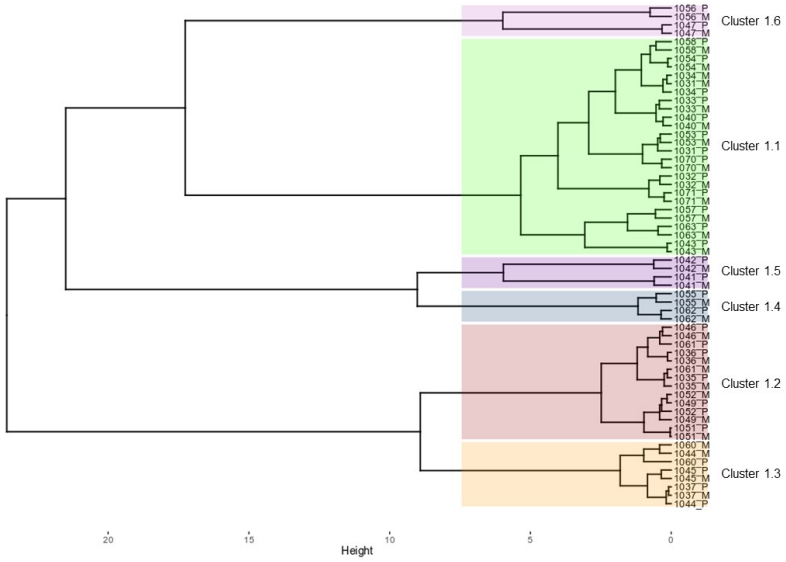
Appendix 21 - Continued

Site name	**Site number**	**Altitude [m]**	**P [mm]**	**T [°C]**	**Stand composition**	**Age [Years]**	**Basal area [$m^2.ha^{-1}$]**
Pol5	1045	215	650	8.2	Beech Pine Beech/Pine	55 55 55/55	25 34 16/16
Ser1	1056	1080	1020	7.7	Beech Pine Beech/Pine	75 75 75/75	20 33 10/17
Slo1	1046	530	730	6.9	Beech Pine Beech/Pine	55 55 55/55	45 45 13/27
Sp1	1042	1293	860	8.9	Beech Pine Beech/Pine	40 40 40/40	33 55 14/39
Sp2	1041	1106	1100	8	Beech Pine Beech/Pine	50 50 50/50	52 40 21/11

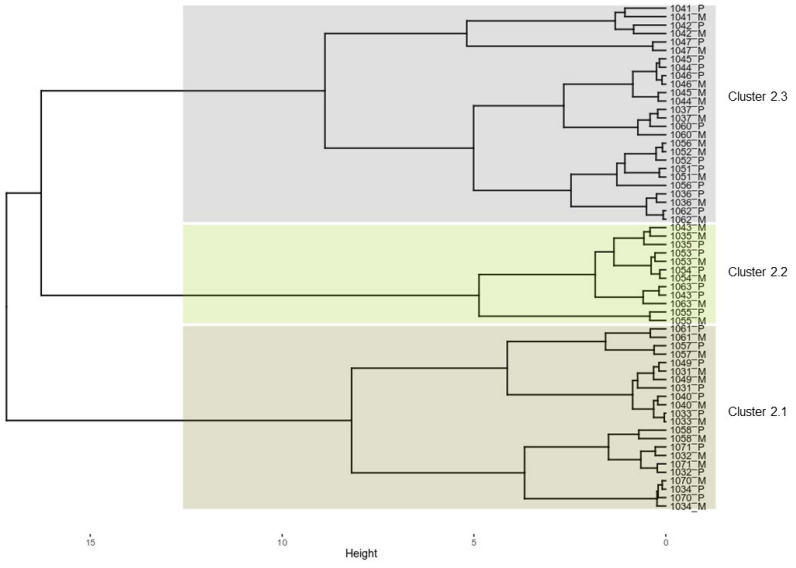
Appendix 21 - Continued

Site name	Site number	Altitude [m]	P [mm]	T [°C]	Stand composition	Age [Years]	Basal area [$m^2.ha^{-1}$]
Swe1	1054	118	700	8	Beech	84	29
					Pine	56	32
					Beech/Pine	106/106	20/20
Swe2	1053	26	800	7	Beech	65	29
					Pine	65	32
					Beech/Pine	65/65	20/20
Ukr1	1060	315	673	7.6	Beech	105	53
					Pine	105	64
					Beech/Pine	105/105	22/25

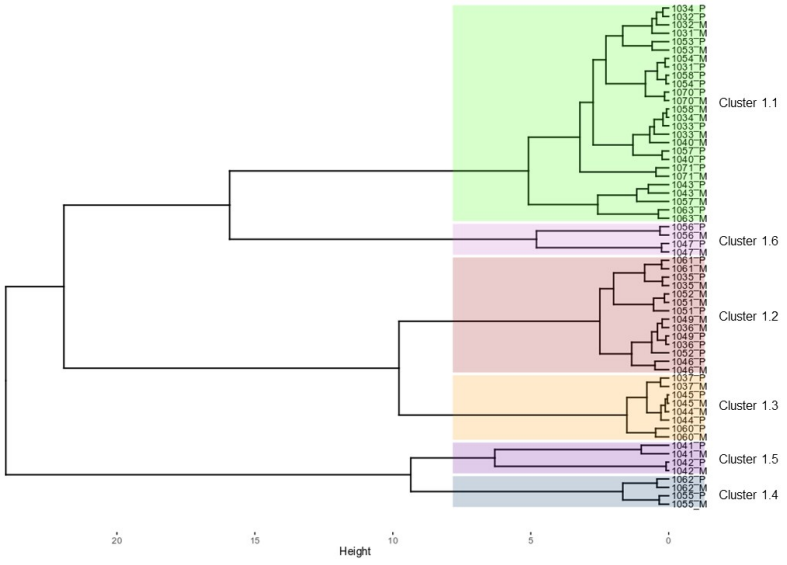
Appendix 22 – Dendrograms of the ward D2 clustering performed on the first two principal components of the PCA of the Bootstrapped Correlation Coefficients for beech between standardized tree-ring width of each strata (site x species x stand) and climatic variables. Numbers are the site id (Table 21); P and M, refer to pure and mixed stands, respectively.



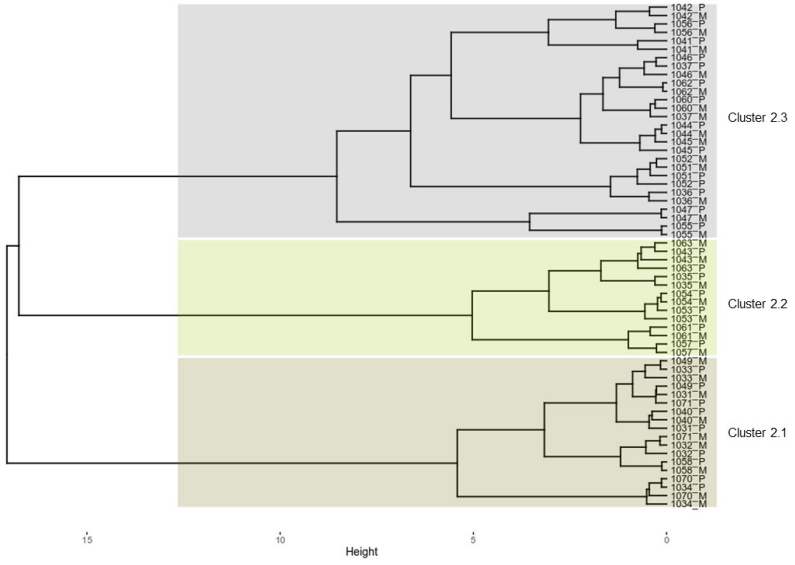
Appendix 23 – Dendrograms of the ward D2 clustering performed on the third and four principal components of the PCA of the Bootstrapped Correlation Coefficients for beech between standardized tree-ring width of each strata (site x species x stand) and climatic variables. Numbers are the site id (Table 21); P and M, refer to pure and mixed stands, respectively.



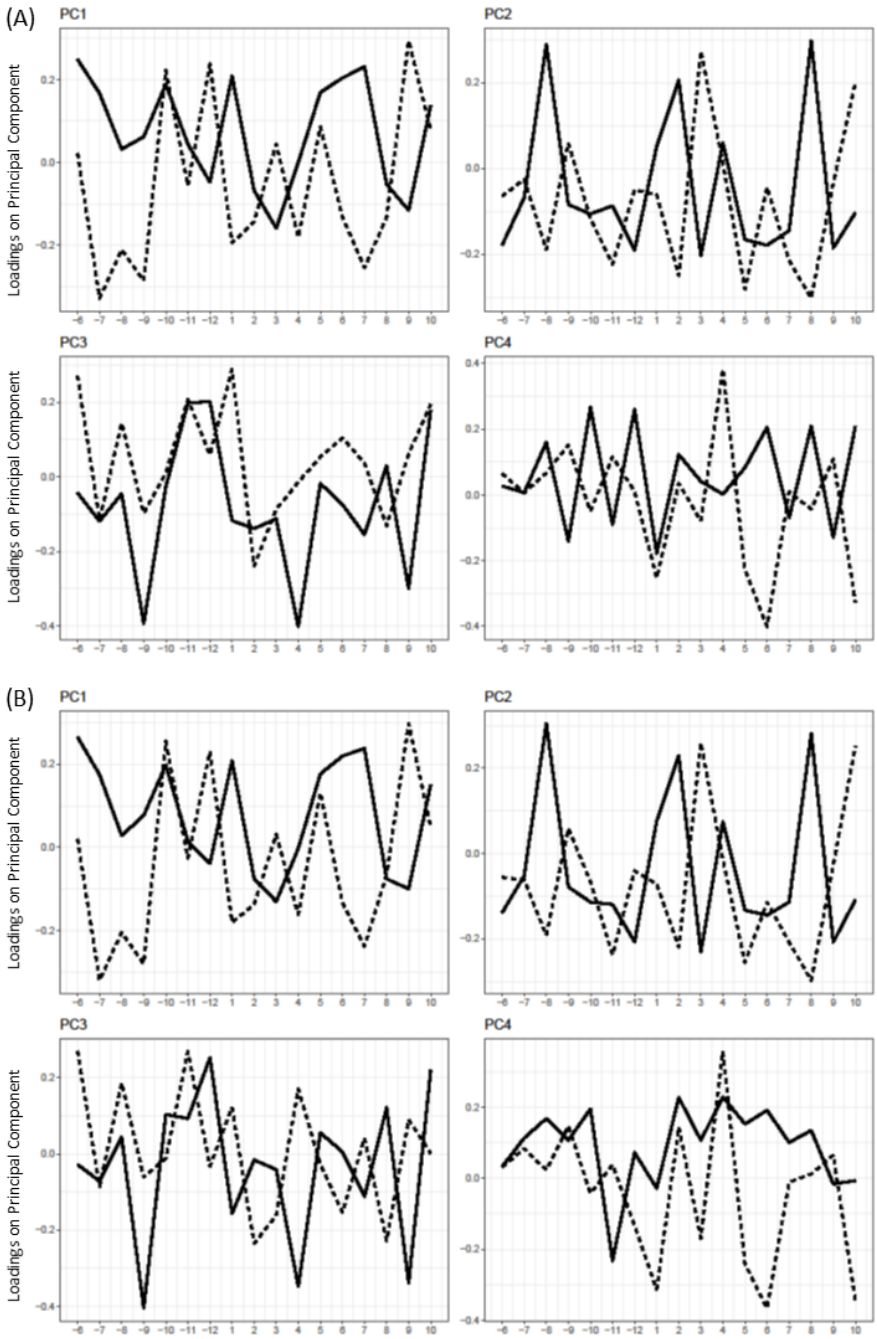
Appendix 24 – Dendrograms of the ward D2 clustering performed on the first two principal components of the PCA of the Bootstrapped Correlation Coefficients for pine between standardized tree-ring width of each strata (site x species x stand) and climatic variables. Numbers are the site id (Table 21); P and M, refer to pure and mixed stands, respectively.



Appendix 25 – Dendrograms of the ward D2 clustering performed on the third and four principal components of the PCA of the Bootstrapped Correlation Coefficients for pine between standardized tree-ring width of each strata (site x species x stand) and climatic variables. Numbers are the site id (Table 21); P and M, refer to pure and mixed stands, respectively.



Appendix 26 – SPEI (plain lines) and Tmean (dashed lines) loading values on each of the 4 first principal components of the Principal Component Analysis performed on the Bootstrapped Correlation Coefficients between standardized tree-ring width of each stratum for beech (A) and pine (B). Months -6 to -12 correspond to June December of the previous year.



Appendix 27 – Radial Growth Variation during dry negative pointer years of Gr1.1. Values in red indicate negative pointer years for which the drought happened the previous year. For brevity, only years with at least one dry pointer year are listed. Cells highlighted in yellow indicates year that are characteristic at the plot level.

Triplet	Plot	Species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1031	mixed	beech														-38	-51					-33		
1031	pure	beech														-22	-61					-31		
1031	mixed	pine											-30					-39						-25
1031	pure	pine											-16					-27						-26
1032	mixed	beech	-11																			-62		
1032	pure	beech	-31																			-59		
1032	mixed	pine	-37													-40								
1032	pure	pine	-35													-35								
1033	mixed	beech																						
1033	pure	beech																						
1033	mixed	pine											-22							-70				
1033	pure	pine											-30							-43				
1034	mixed	beech												-28		-36								
1034	pure	beech												-25		-18								
1034	mixed	pine	-25												-30	-35								
1034	pure	pine	-57												-34	-35								
1040	mixed	beech																						
1040	pure	beech																						
1040	mixed	pine																						
1040	pure	pine																						
1043	mixed	beech	-28																		-50	-53		
1043	pure	beech	-34																		-31	-37		
1043	mixed	pine	-16	-14					-30				-33											
1043	pure	pine	-55	-35					-24				-42											
1053	mixed	beech																						
1053	pure	beech																						
1053	mixed	pine			-24								-31											
1053	pure	pine			-30								-40											

Appendix 27 - Continued. Radial Growth Variation during dry negative pointer years of Gr1.1.

Triplet	Plot	Species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1054	mixed	beech								-35	-31													
1054	pure	beech								-40	-19													
1054	mixed	pine								-23								-14						
1054	pure	pine								-33								-38						
1057	mixed	beech											-34				-15					-49	-41	
1057	pure	beech											-36				-54					-55	-25	
1057	mixed	pine											-42		-34									
1057	pure	pine											-48		-27									
1058	mixed	beech																	-36					
1058	pure	beech																	-17					
1058	mixed	pine																-19						
1058	pure	pine																-30						
1063	mixed	beech																						
1063	pure	beech																						
1063	mixed	pine											-52					-38						
1063	pure	pine											-46					-32						
1070	mixed	beech														-44		-14						
1070	pure	beech														-25		-31						
1070	mixed	pine	-30	-24						-32						-29		-45						-33
1070	pure	pine	-32	-28						-40						-39		-54						-28
1071	mixed	beech															-32					-43		
1071	pure	beech															-38					-39		
1071	mixed	pine																-37					-32	-28
1071	pure	pine																-37					-46	-40

Appendix 27 - Continued. Radial Growth Variation during dry negative pointer years of Gr1.2.

Triplet	Plot	Species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1035	mixed	beech								-24						-32								
1035	pure	beech								-44						-26								
1035	mixed	pine	-40															-34						
1035	pure	pine	-55															-26						
1036	mixed	beech								-46														
1036	pure	beech								-51														
1036	mixed	pine										-24												
1036	pure	pine										-30												
1046	mixed	beech												-40									-27	
1046	pure	beech												-50									-31	
1046	mixed	pine	-22											-33										
1046	pure	pine	-29											-37										
1049	mixed	beech						-40										-29						-34
1049	pure	beech						-36										-22						-45
1049	mixed	pine	-31					-42																
1049	pure	pine	-25					-39																
1051	mixed	beech																						
1051	pure	beech																						
1051	mixed	pine								-26	-38	-34												
1051	pure	pine								-45	-47	-47												
1052	mixed	beech																						
1052	pure	beech																						
1052	mixed	pine																						
1052	pure	pine																						
1061	mixed	beech																						
1061	pure	beech																						
1061	mixed	pine								-17						-10								
1061	pure	pine								-34						-31								

Appendix 27 - Continued. Radial Growth Variation during dry negative pointer years of Gr1.3.

Triplet	Plot	Species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1037	mixed	beech																						
1037	pure	beech																						
1037	mixed	pine		-40														-51						
1037	pure	pine		-45														-27						
1044	mixed	beech									-16													-26
1044	pure	beech									-34													-44
1044	mixed	pine														-37					-25			-44
1044	pure	pine														-36					-28			-51
1045	mixed	beech														-29							-35	
1045	pure	beech														-20							-23	
1045	mixed	pine											-22			-41							-38	-54
1045	pure	pine											-31			-18							-37	-38
1060	mixed	beech											-12		-31						-33			
1060	pure	beech											-32		-48						-32			
1060	mixed	pine																						
1060	pure	pine																						

Appendix 27 - Continued. Radial Growth Variation during dry negative pointer years of Gr1.4.

Triplet	Plot	Species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1055	mixed	beech																						
1055	pure	beech																						
1055	mixed	pine																-31						
1055	pure	pine																-31						
1062	mixed	beech					-19																	
1062	pure	beech					-45																	
1062	mixed	pine																					-16	
1062	pure	pine																					-39	

Appendix 27 - Continued. Radial Growth Variation during dry negative pointer years of Gr1.5.

Triplet	Plot	Species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1041	mixed	beech																						
1041	pure	beech																						
1041	mixed	pine								-21									-23					
1041	pure	pine								-35									-42					-34 -42
1042	mixed	beech		-43											-30						-35			
1042	pure	beech		-30											-33						-42			
1042	mixed	pine		-31		-43																		
1042	pure	pine		-18		-30																		
1047	mixed	beech																						
1047	pure	beech																						
1047	mixed	pine																						
1047	pure	pine																						
1056	mixed	beech																		-32			-51	-73
1056	pure	beech																		-31			-37	-55
1056	mixed	pine						-27			-11					-20							-40	-31
1056	pure	pine						-33			-35					-27							-44	-40

CURRICULUM VITAE

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Publications

Peer-reviewed journal articles

de Streel, G., Collet, C., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Brazaitis, G., Coll, L., Drössler, L., Forrester, D., Heym, M., Löf, M., Pach, M., Pretzsch, H., Ruiz-Peinado, R., Skrzyszewski, J., Stankevičiūtė, J., Svoboda, M., Verheyen, K., Zlatanov, T., Bonal, D., Ponette, Q. Contrasting patterns of tree species mixture effects on wood δ^{13}C along an environmental gradient. European Journal of Forest Research, Vol 139, no.2, p. 229-245 (2020).

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de Streel, G., Henin, J., Bogaert, P., Mercier, E., Rabelo, E., Vincke, C., Jourez, B. Modelling the mortality of *Hylotrupes bajulus* (L.)larvae exposed to anoxic treatment for disinfestation of wooden art objects. In: Wood Science and Technology : journal of the international academy of wood science, Vol. 50, no. 5, p. 1015-1035 (2016).

Submitted peer-reviewed journal articles

Conference presentations

Oral presentations

de Streel, G., Henin, J., Bogaert, P., Mercier, E., Rabelo, E., Vincke, C., Jourez, B. Modelling the mortality of *Hylotrupes bajulus* (L.) larvae exposed to anoxic treatment for disinfestation of wooden art objects (conference IPM). Conference on International Pest Management (IPM) in Museums, Archives, Libraries and Historic Buildings, Paris (France), 13-15 September 2016.