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Effects of tree mixture on forest productivity: tree species addition versus substitution

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Abstract

The effects of tree mixture on stand productivity are usually examined using a substitutive approach whereby productivity in mixed stands is compared to productivity in monocultures, at comparable tree density. This approach has proved that mixed stands usually perform better than pure stands. The addition of a second tree species to an existing mono-specific stand has received less consideration. Yet, this approach may separate the facilitation effect from the complementarity effect. We compared the effect of tree species substitution *vs*. addition on the productivity of maritime pine and silver birch in a 7-year-old tree diversity experiment in south-western France. Given the very young age of the stands, the 2014 tree volumes were used as a proxy for tree productivity. Substituting pines with birches resulted in a significant increase in tree productivity at the stand level, beyond expectations from the weighted mean of monocultures (i.e. overyielding). In contrast, creating a mixture by adding birches to pine stands had no significant effect on the maritime pine productivity: the transgressive mixture effect was not significant. This absence of an effect was produced by two distinct density-dependence responses at the individual tree level. Our results suggest that the addition of a pioneer species with low demands in soil water and nutrients during young developmental stages can diversify stands and increase the provision of ecosystem services without altering the productivity of the target species.

Keywords *Betula pendula* · *Pinus pinaster* · Biodiversity · Ecosystem functioning · Overyielding · Transgressive overyielding · Forest

Introduction

Challenges and determinants of mixed plantations

Despite ample evidence that mixed stands provide more ecosystem services than monospecific forests under various ecological conditions (Baeten et al. 2019), most planted forests are still managed as monocultures. Moving towards ecologically intensive and sustainable forest management requires

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a sound understanding of the drivers likely to improve or hamper the benefits of mixed forests (Felton et al. 2010; Messier et al. 2021). The positive effects of tree species diversity on tree productivity are well documented (Gamfeldt et al. 2013). Such positive effects are driven by complementarity and selection effects (Loreau & Hector 2001). Complementarity mostly refers to (1) niche partitioning processes whereby mixed stands capture resources better than monospecific stands do (Loreau & Hector 2001), and (2) facilitation, where one species in the mixture benefits to the others, *e.g.* via improved resource quality (N-fixing species), acquisition (water uptake) or protection against herbivores (Caspersen et al. 2018; Kunz et al. 2019). The selection effect refers to situations where a highly productive species recruited in the mixed stand drives positive mixture effects (Fox 2005; Loreau and Hector 2001). However, recent studies have highlighted that the positive diversity–productivity relationship is strongly context dependent. For instance, functional characteristics of species or stand structure can modify the shape and strength of the diversity–productivity

relationship (Amoroso and Turnblom 2006; Brunner 2020; Condés et al. 2013; Forrester 2014; Grossman et al. 2017). Disentangling the drivers of the mixture effect requires an innovative conceptual framework supported by novel experimental approaches based on stand density, a major component of stand structure that can be controlled by thinning operations.

Stand density: a key determinant of the effect of mixture on stand productivity

Stand density influences the degree of canopy closure, which in turn participates in the regulation of light transmittance, the interception of water precipitation, belowground competition for water, and can modify understory microclimate, understory vegetation and soil biodiversity (Baeten et al. 2019; Gaudio et al. 2011; Henneron et al. 2017; Ligot et al. 2014; Perot et al. 2017). Stand density is also a major driver of tree–tree competition, and used to calculate several competition indices in forest (Biging and Dobbertin 1992). Despite the considerable effects of tree density on canopy packing and of abiotic factors in forest stands, only a few studies addressing the effect of tree diversity on productivity in temperate forests have explicitly questioned the importance of stand density (Forrester 2014; Jucker et al. 2016). Yet, species complementarity and intra-specific competition both intensify with stand density. This was documented in mixed stands of late-successional species (Amoroso and Turnblom 2006; Forrester et al. 2013) harbouring slow- and fast-growing tree species (Condés et al. 2013; Garber and Maguire 2004; Maguire and Mainwaring 2021) and species with contrasting shade tolerance (del Rio and Sterba 2009). However, data about how the mixture effect can be modified by stand density are still scarce, especially in young plantations of fast-growing tree species.

Controlling stand density to compare monocultures to mixed stands: overyielding, the classical index based on species substitution

The net biodiversity effect generally simply compares the observed productivity of a mixture with a theoretical mixture assembled with the same proportion of trees drawn from the component monocultures (Loreau 1998; Loreau and Hector 2001). As such, overyielding can be seen as a measure of changes in stand productivity due to the substitution of a species by others. Estimating the effect of species mixture on productivity through overyielding has several advantages. First, it provides a quantitative estimate of the net biodiversity effect on stand productivity (Tobner et al. 2016). Second, because it compares the productivity of the mixture to the weighted productivity of the component monocultures, it makes it possible to determine whether the mixture performs better than the average of monocultures (*overyielding*) or the most productive monoculture (*transgressive overyielding*).

Limitations linked to species substitution and the related overyielding

The use of overyielding at the stand level estimate also has several shortcomings. First, because it is inherently defined at the stand level, overyielding does not account for species-specific responses to tree diversity. Yet, knowing which species benefits or not from the mixture is of primary importance, particularly when it comes to harvesting species at different times because of differences in growth patterns. The effects of tree diversity may not be symmetrical, *i.e.* the effects of species A on species B are not equal to the effects of species B on species A (del Rio and Sterba 2009). This is a major concern when it comes to understanding the functioning of mixed forests. As a consequence, considering the mixture effect on species productivity and on individual tree productivity is a first step in the understanding of the mechanisms underlying the diversity–productivity relationship (Nadrowski et al. 2010). Moreover, from a practical point of view, the conversion of monocultures to mixed stands through species substitution does not go without management problems. On the one hand, the silviculture of mixed stands, particularly in cases of intimate mixing, is complicated by the different growth rates of the different species and the knowledge gap about the growing space necessary to optimise the productivity and wood quality of each tree species. On the other hand, wood product processing chains are often specialised in a limited number of species and may not be able to offer a market for substitute species.

Species addition as an alternative to species substitution

An alternative to species substitution is the addition of a new species within an existing stand; both methods are traditionally used to measure species interactions (Hamilton 1994). Species addition could be less constraining in terms of management operations than species substitution by making it possible to keep the same harvesting rate for the target tree species, *e.g.* in alternate-row mixing. Therefore, species addition or substitution should be considered to design and manage mixed forests, and dedicated experiments are needed to disentangle their specific effects on productivity.

Objectives and hypotheses

Using a tree diversity experiment, we uncoupled the effect of species addition *vs*. substitution on forest stand productivity; the control of stand and species-specific density provided further insights into the mechanisms underlying the effect

of species addition and substitution. We focused on two-species mixtures of maritime pine (*Pinus pinaster Ait.*) and silver birch (*Betula pendula Roth*) at two stand densities. Although both species are fast-growing species, they are distinct in terms of growth dynamics and tree size. In the case of species substitution, we expected a positive global mixture effect (ME) with positive specific effects for both pines and birches. By contrast, we anticipated a negative transgressive mixture effect (TME) because birch is notably less productive than maritime pine in the local conditions of the experiment. In the case of species addition, we hypothesised opposite response patterns, *i.e*. a negative ME because of increased competition among trees due to higher tree density, but a positive TME due to a tree packing effect and low competition from silver birch in pine stands. Lastly, we expected that all mixture effects would intensify with stand density.

Methods

Maritime pine and silver birch are two light-demanding, fast-growing tree species, and are native to the site. The area of distribution of maritime pine is mainly restricted to Spain, the south-west of France and the north-west of Italy. Maritime pine is a highly drought-tolerant species and a major production species in France grown exclusively in monoculture. Conversely, silver birch is widely distributed across Europe, from the Atlantic Ocean to eastern Siberia. Silver birch is grown in northern and eastern Europe, but despite the interest shown by these countries, it is depreciated along the Atlantic European shoreline, especially in southwestern and western France (Hynynen et al. 2010).

Experimental design

The ORPHEE experiment was carried out 40 km south of Bordeaux (44°440 N, 00° 460 W) and belonged to the world-wide Tree Diversity Network (TreeDivNet). The experimental plantation was established in 2008 on a clear cut of former maritime pine stands on a sandy podzol. Stumps were removed, and the site was ploughed and fertilised with phosphorus and potassium before planting. In total, 25,600 trees of five native species (silver birch (*B. pendula)*; pedunculate oak (*Quercus robur)*; Pyrenean oak (*Quercus pyrenaica)*; holm oak (*Quercus ilex)* and maritime pine (*P. pinaster*)) were planted in a 12-ha area. Eight blocks were established, with 32 plots in each block, corresponding to the 31 possible combinations of one to five species, with an additional replicate of the combination of five species. Each 400-m^2 plot contained 10 rows of 10 trees planted 2 m apart, resulting in 100 trees *per* plot. The total initial stand density was 2500 trees *per* hectare

in each plot. Inside the plots, individual trees from different species were planted in a regular alternate pattern, such that a tree of a given species had at least one neighbour from each of the other species within a 2-m radius. The plots were three meters apart and were randomly distributed within blocks. The entire experimental site was fenced to prevent grazing by mammalian herbivores.

Plot selection

We analysed growth data collected by the end of 2014 on 7-year-old trees at the centre of the plots to avoid edge effects (number of measured planting locations = 36). At this time of plot development, oak trees were on average 112 cm high and had a negligible growth in diameter (most of them did not reach breast height), whereas pines and birches were on average five times taller than oaks (563 and 510 cm high, respectively). As a consequence, oak trees were confounded with the understory vegetation. By considering oak seedlings as part of the understory vegetation, we solely focused on birch and pine growth. However, belowground interactions most probably occurred, as the understory can represent a large part of the fine root biomass in maritime pine stands (Bakker et al. 2006). The three oak species represented only a few individuals among the 25 species found in the understory (the most common ones were *Molinia caerulae*, *Ulex minor* and *Pteridium aquilinum* (Corcket et al. 2020)). Therefore, we assumed that the impact of these relatively few oak individuals on the productivity of pine and birch at these developmental stages was negligible. We tested the effect of species addition and substitution on tree and stand volume by selecting plots at three levels of pine and birch tree density: the "high-density plots" (2500 t/ha) had 100 pines or 100 birches in monocultures or a mixture of 50 pines and 50 birches. The "medium-density plots" (1250 t/ha) had 50 pines or 50 birches in monocultures (in the plots where birches or pines were associated with one oak species), or a mixture of 25 pines and 25 birches (in the plots where birches and pines were associated with two oak species). We completed the sampling by selecting "low-density plots" as monocultures (625 t/ha) with 25 pines or 25 birches (in the plots where birches or pines were associated with three oak species) (Fig. 1). To avoid biases when comparing the volumes in the mixed stands and the monocultures, we selected plots with less than 15% of dead trees as an optimal balance between the number of plots *per* treatment and the number of trees *per* plot (Supplementary Table 1).

Dendrometric data

We measured the height of the 36 innermost planted trees at the centre of each plot using a graduated pole each year from 2008 to 2014. We measured 36, 18 or 9 pines or birches
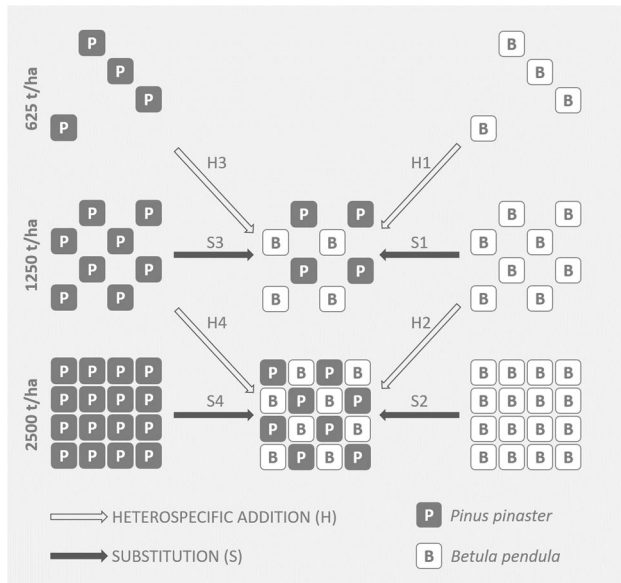
Fig. 1 Schematic representation of the experimental treatments consisting in three levels of stand density (low, 625t/ha; medium, 1250t/ha; high 2500t/ha) and composition. From left to right: *P. pinaster* in monocultures, mixed *B. pendula–P. pinaster* stands (50% of each species) and monocultures of *B. pendula*. Arrows indicate the pairwise comparisons of treatments. Solid arrows, heterospecific addition; black-outlined arrows, species substitution. Arrows are numbered according to the different experimental treatments compared in the Results section

in the high-, medium- and low-density plots, respectively. We also measured circumferences at 1.30 m from 2012 to 2014 on 7 randomly chosen pines and 7 randomly chosen birches *per* plot, irrespective of plot composition. We used height–circumference relationships to estimate the circumferences of trees that had not been measured in 2014 (Supplementary Fig. 1), and then, we estimated tree volume following the generic model developed by Deleuze et al. (2014). We assigned a minimum volume of 0.000144 m^3 to the few trees below 1.30 m in height (corresponding to the minimum volume found in the dataset). Finally, we estimated the dimensions of missing trees (dead trees) by averaging the diameter, height and volume of the trees in the plot. Given the very young age of the stands, the 2014 tree volumes were used as a proxy for tree productivity. Stand dendrometric characteristics are summarised in Table 1.

Transgressive mixture effects and mixture effects for species substitution and addition

We calculated two integrated indices of mixture effects for heterospecific addition and substitution of birches and pines, *i.e.* the mixture effect (ME) and the transgressive mixture effect (TME). Transgressive overyielding and overyielding are two standardised indices of mixture effect on stand productivity calculated by comparing monocultures with mixed stands at similar stand density (Jolliffe 2000; Pretzsch and Schütze 2009; Steckel et al. 2019; Toigo et al. 2015, *i.e.* in species substitution). The major difference between species substitution and species addition is that total stand density increases from monocultures to mixed stands in an additive design, while it is kept constant in a substitutive design. It follows that the reference monoculture used to calculate ME and TME differs between additive and substitutive designs. We calculated TME in the same way for species substitution

Table 1 Mean (minimum–maximum) values of tree height, tree circumference and plot basal area of maritime pine (*Ppin*) and silver birch (*Bpen*) in monocultures (*mo*) and mixed stands (*mx*) at three stand densities: low (625 t/ha), medium (1250 t/ha) and high (2500 t/ha)

		Stand density				
		Low	Medium		High	
		Mo	Mo	Mx	Mo	Mx
Plot basal area (m²/ha)	*Bpen*	1.41	2.39		3.55	
		0.84–2.25	0.80–4.62		1.71–5.10	
	Ppin	7.22	11.4		17.2	
		6.17–8.30	4.69–14.7		11.3–21.3	
	Bpen + Ppin			7.42		11.2
				4.54–9.10		8.24–14.7
Tree height (cm)	*Bpen*	526	537	513	517	508
		85–764	120–900	106–795	95–791	148–729
	Ppin	570	575	581	571	567
		232–706	133–801	250–780	200–810	161–795
Tree circumference at breast height (cm)	*Bpen*	16.6	14.9	13.3	13.0	12.0
		2.4–26.7	1.52–28.2	1.5–28.5	2.3–24.2	1.1–22.5
	Ppin	37.6	33.4	36.1	29.1	30.6
		9.5–51	0.7–50.2	10.1–49.9	5.3–45.2	2.6–47

and species addition at medium and high stand densities by comparing the mean total stand volume (SV) of the mixed stands (*mx*) and monocultures (*mo*) of the most productive species, *i.e.* maritime pine (Fig. 2). Given the very young age of the stands, the 2014 tree volumes were used as a proxy for tree productivity. We averaged the productivity values within each block because the mixed stands and the monocultures were not paired:

$$TME = \left(SV_{mx} - SV_{mo.pine}\right) / SV_{mo.pine} \tag{1}$$

where SV_{mx} is the stand volume, averaged *per* block, and SVI_{mo} is the stand volume in monocultures of birch or pine, averaged *per* block.

The mixture effect (ME) was calculated for each block separately at the medium and high levels of stand density, as:

$$ME = \left(SV_{mx} - SV_{exp}\right)/SV_{exp} \tag{2}$$

where SI_{mx} is the observed volume of mixed pine–birch stands and SV_{exp} is the expected volume of these same mixed stands. SV_{mx} was the same for both species substitution and species addition, but SV_{exp} differed between the additive and substitutive scenarios.

For species substitution, $SV_{exp.sub}$ was calculated as follows:

$$SV_{exp.sub} = 0.5 \times SV_{mo.pine} + 0.5 \times SV_{mo.birch} \tag{3}$$

where $SV_{mo.pine}$ and $SV_{mo.birch}$ are the stand volumes of the pine and birch monocultures averaged *per* block, and 0.5 corresponds to the species proportion.

For species addition, we compared SV_{mx} with $SV_{exp.add}$ based on an equal number of trees *per* species. Thus, for a SV_{mx} at a density of n trees, we derived $SV_{exp.add}$ by summing the volumes in monocultures of n/2 trees (see Fig. 2):

$$SVI_{exp.add.n} = SVI_{mo}.pine.n/2 + SVI_{mo}.birch.n/2 \tag{4}$$

Statistical analyses

All analyses were performed with R 4.0.2 and the functions gam, lme and glht in the packages mgcv, nlme and multcomp.

We conducted separate analyses at the stand and tree levels by fitting a set of linear mixed-effect models. We analysed four response variables at the plot level: (i) the total stand volume (SV) estimated by summing the tree volumes at the plot level, (ii) the mixture effects (MEs) resulting from species substitution (ME_{sub}) and species addition (ME_{add}) and (iii) the transgressive mixture effects (TMEs) resulting from species substitution (TME_{sub}) and species addition (TME_{add}). We completed the analyses at the plot level by also considering the tree volume (TV) of individual maritime pine and silver birch trees in monocultures and mixed plots.

SV and TV models included the effects of stand density (low, medium and high) and tree mixture (monoculture *vs.* two-species mixture) as fixed-effect factors. ME and TME models included the effects of stand density (high and medium) and mixture scenario (substitution *vs.* addition) as fixed-effect factors. We added block as a random effect estimating between-block variability, except for the analyses conducted at the level of individual trees where we nested plot within block to account for the non-independence of multiple trees sampled within the same plots and blocks.

To consider residual heteroscedasticity, SV and TV analyses were carried out by introducing a variance model into the linear mixed models to allow for unequal variance among experimental treatments (Pinheiro & Bates, 2006).

Fig. 2 Schematic representation of the calculations of the transgressive mixture effect (TME) and mixture effect (ME) of the stand volume (SV) for species substitution and species addition, based on observed (obs.) and expected (exp.) values
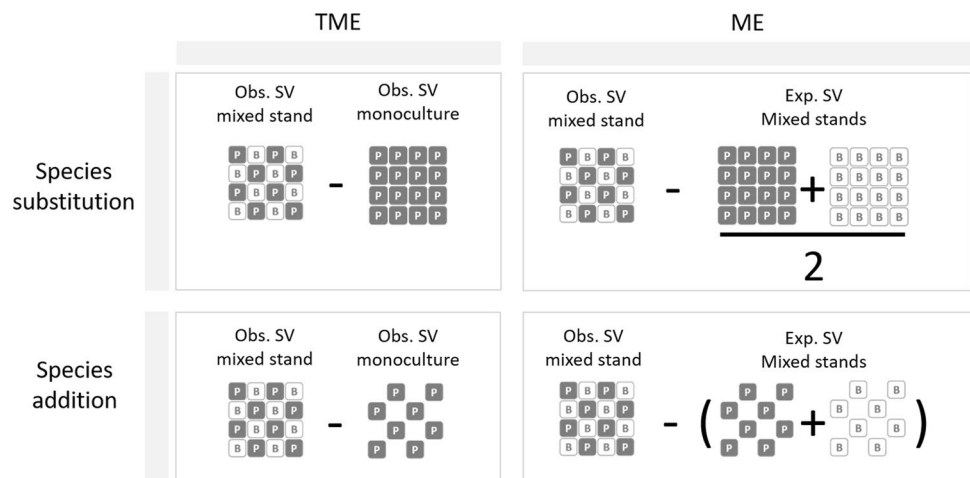
Results

Tree species substitution

Substitution of silver birch with maritime pine significantly multiplied the SV 3.6-fold at medium stand density (Fig. 3, 38.8 ± 5.67 m^3/ha, $n = 18$; S1 in Fig. 1) and at high stand density (Fig. 3, 56.6 ± 10.6 m^3/ha, n = 8; S2 in Fig. 1). Conversely, substitution of maritime pine with silver birch significantly decreased the SV by 35% (Fig. 3, S3 in Fig. 1, Supplementary table 2) and 36% (Fig. 3, S4 in Fig. 1, Supplementary table 2) at medium and high stand densities, respectively.

The birch–pine mixtures obtained through substitution were significantly less productive than the most productive-pine-monoculture (TME$_{sub}$ < 0, Fig. 4) at both medium (-0.35 ± 0.08, $n = 8$) and high (-0.35 ± 1.45, $n = 8$) species densities. The mixture effect (ME$_{sub}$, Fig. 4) indicated that pine-birch mixtures were marginally significantly more productive (overyielding) than their monoculture counterparts at medium (0.10 ± 0.14, $n = 8$) and high (0.10 ± 0.20, $n = 8$, Fig. 4) stand densities.

Species substitution had opposite effects on the TV of the two species at medium stand density: substitution of maritime pine with silver birch caused a significant 15% increase of the pine TV (Fig. 5), but also a significant 23% reduction
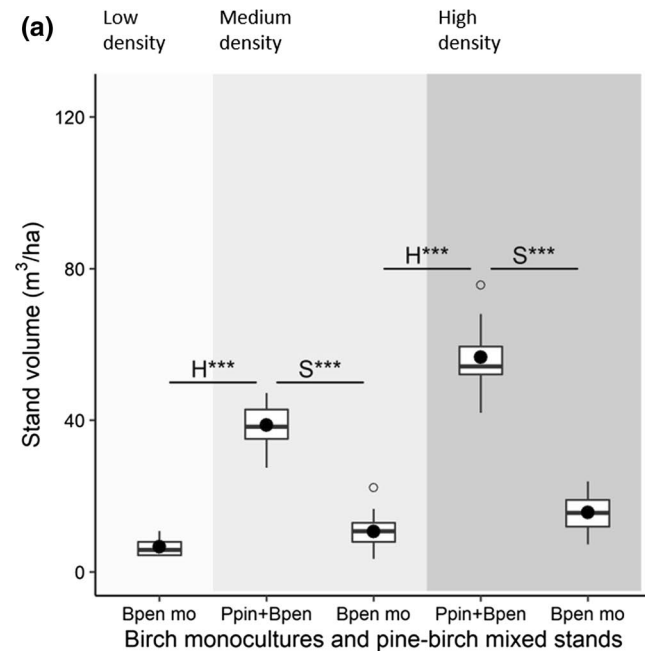
Fig. 4 Transgressive mixture effect (TME) and mixture effect (ME) at the stand level for species substitution and species addition at medium and high stand densities. Black dots, mean effects. Stars, 5% significance levels: (.) $0.1 > p$-values > 0.05; *$0.05 > p$-values > 0.01; **$0.01 > p$-values > 0.001; ***p-values > 0.001; ns, no significant effect

Fig. 3 Stand volume (SV) for different plot compositions: in monocultures (mo), the SV is the sum of the tree volumes of the target species; in mixed plots (Ppin + Bpen), the SV cumulates the tree volumes of silver birch (Bpen) and maritime pine (Ppin) (H, see solid arrows in Fig. 1) and species substitution (S, see black-outlined arrows in Fig. 1) on the stand volume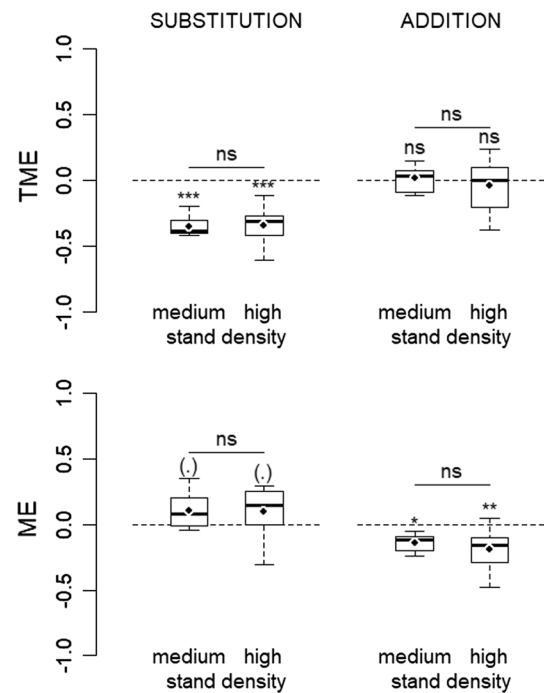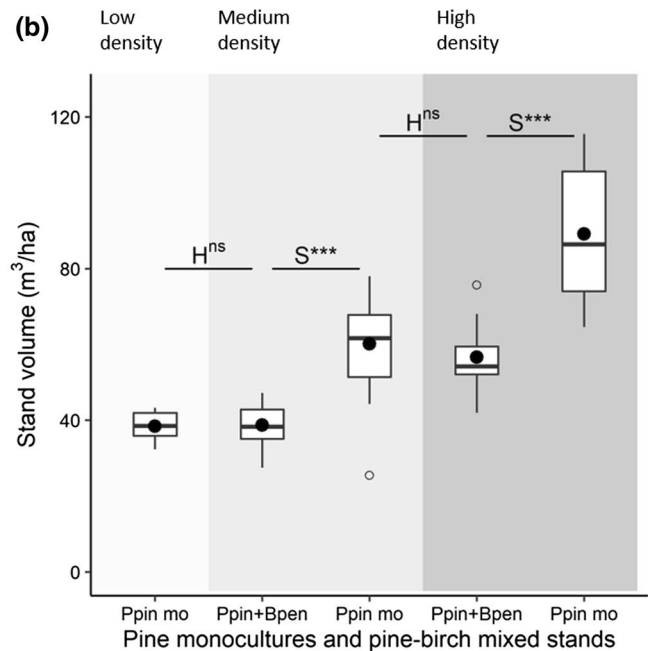s (SVs) of silver birch (a) and maritime pine (b) at low, medium and high stand densities. Black dots indicate mean values. Stars, 5% significance levels: (.) $0.1 > p$-values > 0.05; *$0.05 > p$-values > 0.01; **$0.01 > p$-values > 0.001; ***p-values > 0.001; ns, no significant effect. Please note that the SVI$_{Ppin + Bpen}$ of the medium- and high-density mixed stands are the same in (a) and (b)

of the birch TV (Fig. 5). At high stand density, species substitution did not have any significant effect on the TVs of silver birch or maritime pine (Fig. 5).

Heterospecific tree addition

Heterospecific species addition of maritime pine in silver birch stands significantly multiplied the SV 5.8-fold at medium stand density (Fig. 3, H1 in Fig. 1) and 5.2-fold at high stand density (H3 in Fig. 1). Heterospecific species addition of silver birch in maritime pine stands did not have any significant effect on the SV, whether at medium stand density (Fig. 3, H3 in Fig. 1) or at high stand density (H4 in Fig. 1).

ME$_{add}$ indicated that pine–birch mixtures were significantly less productive (underyielding) than their monoculture counterparts at intermediate (-0.14 ± 0.07, $n = 8$) and high (-0.19 ± 0.16, $n = 8$, Fig. 4) stand densities. TME$_{add}$ at medium (0.01 ± 0.10, $n = 6$) and high (-0.05 ± 0.20, $n = 8$) stand densities was not significantly different from zero, indicating that the SV of mixed stands did not differ from the SV of pine in monoculture, *i.e.* no transgressive overyielding (Fig. 4).

Heterospecific addition of silver birch in maritime pine stands did not cause any significant change in the TV of maritime pine at medium stand density (Fig. 5), but a significant 17% reduction (Fig. 5) at high stand density. Heterospecific

addition of maritime pine in silver birch stands caused significant reductions of 42% (Fig. 5) and 36% (Fig. 5) of the TVs of silver birch at medium and high stand densities, respectively. Effect of heterospecific addition.

Discussion

Our study assessed the role of tree species addition and substitution on mixture effects in stands at an early age. We highlighted that when controlling stand density, overyielding in young silver birch–maritime pine stands was due to relaxation of intra-individual competition of pine trees. Conversely, addition of silver birch (the least productive species) in a maritime pine stand (the most productive species) did not have a negative impact on stand productivity, which implies a non-significant transgressive mixture effect. Finally, stand density had little impact on the mixture effects and rather contributed to the species responses at an individual scale.

Species substitution induced overyielding in mixtures of two pioneer species

The respective growth rates of tree species are crucial for interactions among species in the early stages of the development of mixed forests; our results confirm that positive effects of biodiversity on productivity are mainly due to the
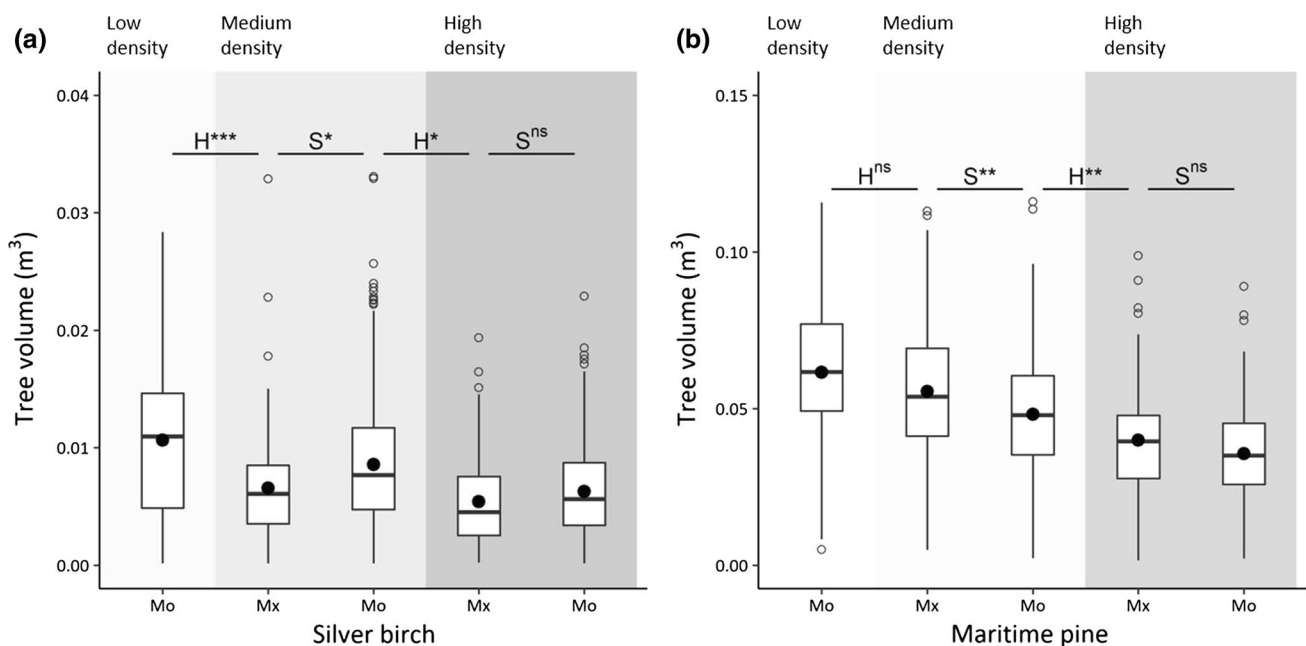

Fig. 5 Effect of heterospecific species addition (H) and species substitution (S) on the tree volumes (TVs) of silver birch (*B. pendula*) (a) and maritime pine (*P. pinaster*) (b) at low, medium and high stand densities and in monocultures (Mo) or mixed (Mx) plots. Black dots, mean values. Stars, 5% significance levels: (.) $0.1 > p$-values > 0.05; *$0.05 > p$-values > 0.01; **$0.01 > p$-values > 0.001; ***p-values > 0.001; ns, no significant effect. Please note that the scales of the two figures (m^3) are different

selection effect (Tobner et al. 2016), *i.e.* a fast-growing and productive species drives ecosystem functioning. Competitive advantage is common in young forests, and positive diversity–productivity relationships at this stage are often attributed to complementarity to a lesser extent, particularly in harsher conditions (Van de Peer et al. 2018). Such positive effects are commonly attributed to differences in shade tolerance: fast-growing species benefit from a relaxation of intraspecific competition, which may or may not be accompanied by niche separation favouring shade-tolerant species rapidly overtopped due to their lower height growth rate (Boyden et al. 2009; Tobner et al. 2016). However, we evidenced that overyielding can be induced by species similarities in their shade tolerance. The mixture effect was not conditioned by different light acquisition strategies, but more probably by their unequal drought tolerance. The experimental plantation was on sandy heathlands that experience intense drought episodes in summer. Water availability is an important limiting factor for tree growth, especially in silver birch, which had the lowest drought tolerance in our experiment. Maritime pine can maintain its stem growth over a longer period and even resume height growth in autumn because it is a fast-growing evergreen species (Heuret et al. 2006). Silver birch remains sensitive to interspecific competition at a young age, even in Nordic countries where temperature is a more limiting factor than water for growth (Jucker et al. 2020); it is likely that dry conditions further accentuate its competitive disadvantage.

The effects observed 7 years after planting will change very quickly: the growing gap in height between maritime pine and silver birch is detrimental to birch under current climatic conditions, and tree mortality will intensify (Morin et al. 2020). Long-term simulations of pine and birch stands showed lasting overyielding due to the relaxation of intraspecific competition of pine trees over time (Morin et al. 2020). Oak species, with slower growth rates and varying drought and shade tolerances, will gradually establish in the stands, leading to stratification possibly suitable for mixed stands.

The transgressive mixture effect was not significantly different from zero in the addition scenario

We did not find any significant transgressive mixture effect in the mixed birch–pine stand created by addition of the two species. These results are consistent in mixtures of fast-growing, light-demanding species, as in mixed plantations of *Acacia mangium* and *Eucalyptus grandis* in a tropical context (Bouillet et al. 2013; Laclau et al. 2008). Conversely, the substitutive approach caused a loss of mixed stand productivity compared to pine monocultures due to the substitution of a high productive species (maritime pine) by a low productive one (silver birch). These findings mirror results

from colder, more humid sites for the same species (Frivold and Frank 2002), more generally in mixed forest (Jactel et al. 2018) and in plant communities where positive transgressive overyielding has rarely been reported (Cardinale et al. 2007).

At a medium stand density in the additive scenario, the absence of any competition effect of silver birch on maritime pine can be explained by two mechanisms: (1) a purely neutral effect of the addition of the least productive species due to lower proximity of the stems, or (2) a facilitating effect of birch on the soil resource that compensated for a weak competitive constraint due to species addition. Silver birch leaves have a higher decomposition rate than the needles of *Pinus* species (Palviainen et al. 2004). Moreover, depending on the stand structure, nutrient cycling can be higher in birch regeneration than in pine regeneration (De Schrijver et al. 2009). In the studied site, carbon and nitrogen at an intermediate soil depth were found higher in mixed stands than in monospecific stands (Maxwell et al. 2020), even though there was no evidence of belowground complementarity of fine roots (Altinalmazis-Kondylis et al. 2020).

These findings are also of great ecological relevance because they demonstrate that pine monocultures can be diversified by adding birch at an early age and benefit from ecosystem services like protection from pests (Damien et al. 2016; Jactel et al. 2019) and increased diversity of predatory insects (Jouveau et al. 2020) without compromising the wood production of the target species. Long-term simulations of pine and birch growth on the study sites support our results (Morin et al. 2020), and show that the ecosystem services associated with the diversification of pine monocultures can persist as the stand ages.

Mixture effects and transgressive mixture effects do not change with stand density, but tree productivity does

In young stands, high stand densities usually speed up mixture effects (Tobner et al. 2016; Van de Peer et al. 2018). Yet, we did not observe any intensification of the mixture effect or of the transgressive mixture effect with stand density. However, intensified interactions with stand density were observed at the tree level: at medium density, heterospecific addition did not affect maritime pine trees (the most productive species) but affected silver birch trees (the least productive species). At high density, the intensification of interspecific competition reduced the productivity of both species. Regarding species substitution, at medium density maritime pine benefited from the mixture effect at the expense of silver birch. Changing tree density has an impact on the understory, in particular a higher proportion of birch was associated with a less diverse but a taller understory vegetation in the ORPHEE experiment (Corcket et al. 2020). This may have increased competition

for water and nutrients at higher birch density and might explain the absence of any effect of species substitution. This illustrates that similar response patterns in terms of mixture effect can result from different mechanisms at the individual level. These results are consistent with intensified competitive interactions observed at young and dynamic stages (Boyden et al. 2009) or at least decreased overyielding with density (Kweon and Comeau 2019). Finally, these results contrast with the intensification of the positive diversity–productivity relationship observed as forest stands become older (Huang et al. 2018), particularly when shade-tolerant and shade-intolerant species are mixed (Brunner and Forrester 2020; del Rio and Sterba 2009).

Conclusion

By controlling stand density and species identity, we showed that the selection effect was the main driver of the positive mixture effect on productivity in the early stages of mixed forests. This calls for a careful choice of tree species to be associated when designing plantations of mixed species, especially as regards fast-growing species. Our results also showed that the addition of a pioneer species with low demands in soil water and nutrients during young developmental stages to a monoculture of a high productive species in its young developmental stages offered the opportunity to benefit from ecosystem services associated to mixed stands without affecting the productivity of the target species. The addition of tree species is a promising way to promote multifunctionality in mixed plantations and preserve the harvest of a particular species for timber production, and it circumvents two major obstacles in the implementation of mixed-species forestry.

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