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RESEARCH ARTICLE

Tree species identity drives nutrient use efficiency in young mixed-species plantations, at both high and low water availability

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Abstract

1. Previous studies have demonstrated that tree species diversity increases productivity and may enhance nutrient cycling in forests. The effect of mixing tree species on stand-level nutrient use efficiency (NutUE) has seldom been studied, and even less so in the context of climate change. Here we present the first study examining how diversity effects on NutUE may be modified by growing season water availability (low vs. high), and importantly, during periodic drought or on water-limited sites.
2. We tested the interaction of water availability and tree species diversity (i.e. species richness and species identity) on NutUE in two young, experimental plantations located in south-western France (ORPHEE), and northern Ontario, Canada (IDENT-SSM). We calculated stand-level NutUE as above-ground net primary productivity (ANPP) divided by the product of litterfall mass and macronutrient concentrations, of monocultures and mixed tree communities composed of several temperate tree species, with a focus on birch and pine at both sites.
3. We found significant species richness and water availability effects on NutUE, but they were weakly and inconsistently expressed, detected only for specific nutrients, and differed between the two sites. Species identity had much stronger effects on NutUE when examined using the birch–pine plots at both sites. At ORPHEE, nitrogen use efficiency (NUE) and phosphorus use efficiency (PUE) were significantly greater in the birch–pine mixture than in each monoculture. This was due to an increase in ANPP coupled with a decrease in litter nutrient concentrations in the two-species plot that was driven by the dominance of pine in the mixture. In the comparatively younger, denser plots at IDENT-SSM, birch was the dominant species that resulted in positive mixing effects on ANPP and litter nutrient concentrations and a neutral effect of mixing on NUE and PUE in the birch–pine mixture.

Laurent Augusto and Alison D. Munson should be considered joint senior authors.

4. Overall, the effects of mixing did not differ with water availability treatments, suggesting that species composition of mixtures is more important than water availability for stand-level NutUE in these young forest communities.

KEYWORDS
biodiversity, drought, IDENT, litterfall, nutrient cycling, nutrient resorption efficiency, species identity, TreeDivNet

1 | INTRODUCTION

Increasing tree species diversity is a long-term management strategy proposed to increase resistance and resilience of forests to drought (Lebourgeois et al., 2013), due to asynchrony and complementarity of functional traits (e.g. shade tolerance, nutrient content, water use) among species (Jucker et al., 2014; Morin et al., 2014). Tree productivity is often central to biodiversity–ecosystem function research (Morin et al., 2020; Zhang et al., 2012), yet it is tightly linked to nutrient use efficiency (NutUE), that is, the efficiency by which tree species utilize available nutrients to produce biomass (Binkley et al., 2004). Tree NutUE is calculated as above-ground net primary productivity (ANPP) divided by the quantity of nutrients in the litterfall (Vitousek, 1982). Thus, NutUE can be increased by some combination of increased ANPP:litterfall ratio and/or decreased litter nutrient concentrations.

Previous studies have frequently shown a positive effect of species richness on litter mass production (Huang et al., 2017; Scherer-Lorenzen et al., 2007) and above-ground productivity (Toïgo et al., 2015; Zhang et al., 2012). The authors attributed these effects to an increase in structural heterogeneity of tree canopies, or spatio-temporal complementarity in light interception (Pretzsch et al., 2014; Williams et al., 2017). Water availability can also affect the relationship between tree species diversity and productivity (Belluau et al., 2021; Grossiord, 2020). A recent global meta-analysis found that overyielding increased with local precipitation (Jactel et al., 2018). Root stratification, hydraulic redistribution or dominance of species with particular traits may all contribute to the positive effect of species richness on above-ground biomass (Grossiord, 2020). Trees have generally been found to exhibit lower ANPP and litter production during periodic drought (Brando et al., 2008). Because drought has a negative effect on soil diffusive processes and nutrient mobility, one might expect that water-limited conditions may also decrease uptake and modify use of nutrients by trees (Schlesinger et al., 2016).

Tree species diversity and water availability may influence stand NutUE additionally through interactive effects on soil nutrient availability, nutrient resorption efficiency (NutRE) and litterfall nutrient concentrations (Richards et al., 2010). Independent of site moisture conditions, litterfall with higher nutrient concentrations in mixed forests could accelerate litter decomposition, while increasing litter quantity could contribute to higher total input of N and P to the soil (Chapman et al., 2013). Soil moisture deficits can decrease below-ground process rates by reducing microbial activity (Borken & Matzner, 2009), which may decrease soil nutrient availability. Nutrient use efficiency is also influenced by NutRE (Hayes et al., 2014), that is, the ability of trees to efficiently retranslocate foliar nutrients to developing tissues or storage sites prior to leaf abscission (Wright & Westoby, 2003). When soil nutrient availability is high, nutrients are remobilized to a lesser extent from green leaves (Achat et al., 2018; Wright & Westoby, 2003) and this can result in increased litterfall nutrient concentrations and decreased NutUE (Hayes et al., 2014). Studies investigating the direct effect of tree species diversity on litterfall nutrient concentrations have shown variable effects, depending on species identity of mixed-species communities (Ball et al., 2008). Seasonal changes in water availability can influence nutrient uptake, above-ground nutrient cycling and/or retranslocation (Schlesinger et al., 2016). To our knowledge, ours is the first study investigating the interactive effect of tree species diversity and water availability on soil nutrient availability, NutUE and NutRE.

The species identity of a mixture may be as important as species richness in determining diversity effects on ecosystem function (Baeten et al., 2019; Van Der Plas et al., 2016). Positive effects of mixing can depend on whether species interactions reduce competition for a growth-limiting resource (Forrester, 2014), and mixing species with different life-history strategies can lead to positive diversity effects on stand productivity (Grossiord, 2020). For example, evergreen–deciduous mixtures have been found to be more resilient to drought than mixtures of deciduous species (Pardos et al., 2021). This may be due to the resource conservative strategy of evergreen coniferous species that have evolved in nutrient poor and xeric ecosystems, and are characterized by higher NutUE and lower litter nutrient concentrations than deciduous species (Augusto et al., 2014; Chapin et al., 1993). Identifying species with complementary nutrient use strategies for use in plantations on nutrient limited sites is of great interest to improve productivity (Zeugin et al., 2010).

In the present study, we asked how low and high soil water availability may influence the effect of species richness and species identity on NutUE. We hypothesized that (H_1) mixing tree species would decrease NutUE in comparison with monocultures, due to an increase in soil nutrient availability, resulting from faster decomposition of more diverse leaf litter (Chapman et al., 2013). Increased soil nutrient availability should in turn lead to lower retranslocation (Achat et al., 2018; Wright & Westoby, 2003) and thus to an increase in litter nutrient concentrations. Because we expected increases in production in mixed-species plots via isometric growth between ANPP and litterfall (Enquist & Niklas, 2002), the increase in litter nutrient concentration would lead to a decrease in NutUE with mixing. We also hypothesized that (H_2) higher water availability would have a positive effect on NutUE due to faster growth (both ANPP and litterfall mass) per unit of nutrient. Finally, because we expected a strong, positive diversity effect on soil nutrient availability under low water supply (Ratcliffe et al., 2017), we hypothesized that (H_3) the negative effect of mixing on NutUE would be stronger under lower water availability conditions.

2 | MATERIALS AND METHODS

2.1 | Experimental sites

Our study was conducted at two experimental sites located in temperate forest regions in France and in Canada, both of which are part of the world-wide Tree Diversity Network (TreeDivNet) (Figure 1). These two common garden experiments (Table S1) were established to investigate the interaction of tree species diversity (hereafter referred to as SR, for species richness) and water availability (hereafter referred to as H_2O) on ecosystem functions. Both sites have a low and high H_2O treatment created by some combination of rainfall exclusion and/or irrigation. These sites were selected due to their similar experimental designs, temperate forest location and the presence of species of similar genus. Licenses and permits were not needed to carry out fieldwork.

The ORPHEE site is located in southwestern France (44°44.35′N, 00°47.9′W, 60 m a.s.l.), 40 km southwest of Bordeaux (Table S1). The soil is sandy with low fertility, particularly in phosphorus (Trichet et al., 2009). We selected plots with three levels of SR to examine diversity effects: pure silver birch (*Betula pendula*, Be), pure maritime pine (*Pinus pinaster*, Pp), birch–pine mixture (Be–Pp) and pine–birch–oak mixture (Be–Pp–*Quercus robur*, Qo). Each plot had 100 trees planted in 2008, at 2 m spacing within a 20 m by 20 m area. The plots were separated by 3 m, and randomly located within six blocks: three unirrigated, control blocks (low H_2O), subject to the dry summer climate and three irrigated blocks (high H_2O). Seasonal irrigation treatment began in 2015, to alleviate summer moisture deficits from early May to late October (Figure S1). A 2-m-tall sprinkler installed in the centre of each plot delivered 3 mm every evening during this period.

The IDENT-SSM site is located in Sault Ste. Marie, Ontario, Canada (46°32.47′N, −84°27.20′W, 210 m a.s.l.), and is part of the International Diversity Experiment Network with Trees (IDENT) (Belluau et al., 2021). The soil texture varies from sandy loam to loamy fine sand (Table S1). In each 10.24 m^2 square plots, 49 trees were planted in 2013 at 40 cm spacing. We worked with five monocultures (*Acer saccharum*, As; *Betula papyrifera*, Ba, *Larix laricina*, Ll; *Pinus strobus*, Ps; *Quercus rubra*, Qu), four 2-species mixtures (Ba–Ps, Ba–As, Ba–Ll, Ll–Qu), and two 4-species mixtures (As–Ll–Ps–Qu, As–Ba–Ll–Ps). Each mixture is present in eight blocks, with four blocks exposed to high or low H_2O treatments (started in June 2014). The high H_2O blocks are weekly irrigated with the equivalent of 25 mm of rain over the course of 4 hr from June 1 to August 31. The low H_2O blocks have a rain exclusion system that removes 25% of ambient throughfall precipitation from all plots from early May to late October (see Belluau et al., 2021 for further details).

Both sites have pure birch, pure pine and mixed birch–pine tree communities. Both birch species (Be and Ba) are relatively short-lived, shade intolerant pioneer species that exhibit best growth on mesic to slightly xeric sites and siliceous soils. Similarly, both pine

FIGURE 1 Images of the birch–pine mixtures at the (A) IDENT-SSM (*Betula papyrifera–Pinus strobus*) and (B) ORPHEE (*Betula pendula–Pinus pinaster*) study sites in 2019 (credit: Tania L. Maxwell).

species (Pp and Ps) are calcifuge species, adapted to well-drained, sandy soils. Unlike Pp, which is a fast growing, early successional species, Ps is a mid-successional species that generally grows more slowly than Pp.

2.2 | Ion-exchange resins

Ion-exchange resin (IER) capsules (UNIBEST, PST-1 Capsule) were installed at both sites to estimate annual soil nutrient availability (Binkley & Matson, 1983). The capsules were placed at a depth of 8 cm in the mineral soil for 6 months, retrieved, and replaced at an adjacent location for a second 6-month period. The sum of the two IER samples were used to estimate annual available soil nutrient concentrations. In ORPHEE, four IER capsules were installed in each plot from November 2018 to November 2019. The IERs were extracted by 1 M KCl and the final solution extractant was measured for concentrations of ammonium ([NH_4]), nitrate ([NO_3]) and phosphate ([PO_4]) by colorimetry (SKALAR, San ++). At IDENT-SSM, three capsules were installed per plot from May 2019 to May 2020. The IER were extracted by 1 M KCl and [NH_4], [NO_3] and [NO_2] measured by flow injection analysis (Lachat, FIA Quickchem series 2) and the [PO_4] by spectrometry (Agilent Technologies, ICP-OES 5110). The plots with tree communities that contained Qu (Qu, Ll–Qu, As–Ll–Ps–Qu) were not sampled. Data are presented in μg capsule^{-1} year^{-1} as this unit is most appropriate for these data.

2.3 | Leaf sample collection and analyses

Litterfall was collected several times a year using litter traps. At ORPHEE, traps were a hollow, 10 cm tall plastic cylinder with a mesh covering at the bottom (0.72 m^2 surface area), suspended from wooden stakes 50 cm above-ground. Two traps were placed in the monocultures and two-species mixtures, and three traps were placed in the three-species mixture. Traps were installed prior to the 2019 growing season, and litterfall was collected in May, June, August, October and December of 2019, and February 2020. After collection, samples were dried at 40°C to constant mass, separated by species and weighed. At IDENT-SSM, the litter traps were 14 cm tall rectangular plastic basins (0.09 m^2 surface area), suspended 5 cm above-ground. The bottom of the basins had several 1.2 cm diameter holes and were lined with window screening to prevent litterfall loss. Two traps per plot were installed in May 2019, and the litterfall was collected in August 2019, October 2019 and May 2020. Litter was sorted by species, dried at 60°C for at least 48 hr, and weighed to calculate annual litter mass for each species and plot. Annual litterfall mass was calculated in g/m^2 for each target species and plot. Oven-dried litter from both sites was ground in preparation for nutrient analysis.

Green leaf collection occurred during the seasonal period of peak leaf development at both sites. At ORPHEE, 30 leaves were collected in July 2019 from the upper canopy of four representative trees per species in each plot. Composite leaf samples for each species and plot were dried at 40°C for at least 48 hr. At IDENT-SSM, composite samples were collected in early August 2019 and consisted of 5–10 leaves harvested along a diagonal plot transect from five trees per species in monocultures and two-species mixtures, and three trees per species in the four-species mixtures. Leaves were dried in an oven at 60°C for at least 48 hr, and separated by species and plot. Oven-dried samples from both sites were ground and stored for nutrient analysis.

The N concentration of both litter and green leaf samples from both sites were analysed based on Dynamic Flash Combustion technology (Thermo Flash, EA 1112). A subset of ground leaves from ORPHEE was mineralized in an oven at 370°C for 4 hr (J.P SELECTA, BLOC DIGEST M40). Afterwards, 75 ml of distilled water was added to the ashes, and the solution was analysed for P (SEAL, AutoAnalyzer 3 HR), while potassium (K), calcium (Ca), magnesium (Mg) and manganese (Mn) concentrations were measured by flame atomic absorption spectrophotometry (VARIAN, SpectrAA-20). At IDENT-SSM, subsets of ground leaves were mineralized in an oven at 550°C for 6 hr, after which the ashes were placed in solution with HCl:HNO_3, which was then diluted, filtered and analysed for P, K, Ca, Mg and Mn concentrations (Agilent Technologies, ICP-OES 5110).

2.4 | Above-ground net primary productivity (ANPP)

Annual tree size assessments at both sites were used to estimate ANPP (kg m^{-2} year^{-1}) for the 2019 growing season using allometric equations. At ORPHEE, tree diameter at 1.3 m above-ground for all living trees within the central core area of the plot (i.e. excluding two perimeter rows of trees) and allometric equations for Pp (Shaiek et al., 2011) and Be (Johansson, 1999) were used to calculate plot-level biomass by species. Qo biomass was negligible in the three-species plot due to poor growth of the species, and was not included in the plot-level ANPP and NutUE calculations. At IDENT-SSM, species-specific allometric equations to predict above-ground biomass from basal stem diameter were derived from annual destructive harvest of either potted seedlings or block-level buffer trees (Belluau et al., 2021). Only the central 25 trees were included in plot-level biomass estimation (i.e. excluding one perimeter row of trees). The difference in biomass between 2018 and 2019 was used as an estimate of ANPP for each plot and each species within a plot.

2.5 | Calculations

Above-ground NutUE of all six elements for each species in each plot was calculated using the following equation (Binkley et al., 2004):

$$\text{NutUE} = \frac{\text{ANPP}}{\text{litterfall mass} \times \text{litter nutrient concentration}} / 1{,}000 \qquad (1)$$

where, ANPP is measured in kg m^{-2} year^{-1}, litterfall mass in g m^{-2} year^{-1} and litter nutrient concentrations in mg/g, which is divided by 1,000 to give NutUE values in g mg^{-1} nutrient. For mixed-species plots (i.e. a plot of species A and B), the NutUE calculation for each nutrient was the following:

$$\mathrm{NutUE} = \frac{\mathrm{ANPP_A} + \mathrm{ANPP_B}}{\left[\text{litterfall mass}_\mathrm{A} \times \text{litter nutrient}_\mathrm{A}\right] + \left[\text{litterfall mass}_\mathrm{B} \times \text{litter nutrient}_\mathrm{B}\right]} \tag{2}$$

We calculated the nutrient resorption efficiency (NutRE) for each species, plot and element with the following equation (Augusto et al., 2017; Vergutz et al., 2012),

$$\mathrm{NutRE} = \frac{\left([\mathrm{Nut}]_\mathrm{green} - \left([\mathrm{Nut}]_\mathrm{senescent} \times \mathrm{MLCF}\right)\right)}{[\mathrm{Nut}]_\mathrm{green}} \tag{3}$$

where, $[\mathrm{Nut}]_\mathrm{green}$ and $[\mathrm{Nut}]_\mathrm{senescent}$ are nutrient concentration values in green and senescent (litter) foliage, respectively, and MLCF is the mass leaf correction factor used to account for the decrease in leaf mass during senescence (Vergutz et al., 2012). To calculate MLCF at IDENT-SSM, a subsample ($n = 40$–100) of equal numbers of oven-dried green and senescent foliage for a given species and plot, were weighed to estimate average MLCF for each species, as the ratio of senescent to green leaf dry mass (pine = 0.761, birch = 0.582, larch = 0.732, maple = 0.519, oak = 0.548). At ORPHEE, where trees are comparatively older and taller than at IDENT-SSM, leaf mass varied widely with vertical position in the canopy and prevented calculation of site-level MLCF values. Instead, values reported in the literature (pine = 0.775, birch = 0.719) were used (Vergutz et al., 2012). Comparatively low NutRE values imply decreased nutrient resorption and are reflective of low site nutritional limitation (Augusto et al., 2017).

To estimate plot-level litterfall nutrient concentrations ([Nut]) and NutRE for mixed-species plots, we first calculated the proportional contribution (Prop) of each species to the total litter mass. For example, in a two-species mixture with species A and B:

$$\begin{aligned} \mathrm{Prop}_{\mathrm{A\ in\ A+B}} &= \frac{\text{Litterfall mass}_{\mathrm{A\ in\ A+B}}}{\text{Litterfall mass}_{\mathrm{A+B}}} \\ \mathrm{Prop}_{\mathrm{B\ in\ A+B}} &= \frac{\text{Litterfall mass}_{\mathrm{B\ in\ A+B}}}{\text{Litterfall mass}_{\mathrm{A+B}}} \end{aligned} \tag{4}$$

The plot-level [Nut] for a plot with species A and B can be calculated by adding the product of each species [Nut] and litter mass proportion in the mixture:

$$[\mathrm{Nut}]_{\mathrm{A+B}} = [\mathrm{Nut}]_\mathrm{A} \times \mathrm{Prop}_{\mathrm{A\ in\ A+B}} + [\mathrm{Nut}]_\mathrm{B} \times \mathrm{Prop}_{\mathrm{B\ in\ A+B}} \tag{5}$$

This same equation was used to calculate plot-level NutRE for species mixtures by substituting NutRE for [Nut].

2.6 | Statistical analyses

All statistical analyses were performed using R software (version 4.1.0). Prior to formal analysis, extreme values were removed from the dataset following the outlier labelling rule with a conservative tuning parameter of $g = 2.2$ (Hoaglin & Iglewicz, 1987). On average, from 0% (ANPP, litter mass, NutUE) to 4% (litter and soil nutrient concentrations) of data were removed. Linear mixed effect models were used to quantify the effect of the following fixed effect factors: SR, H_2O treatment, and their interaction on soil nutrient availability, ANPP, litter mass, litter [Nut], NutRE and NutUE values separately for each site. Pairs of low and high H_2O blocks (i.e. one 'Superblock') were included as a random factor to account for the spatial structure of our experimental design, with H_2O treatment nested into 'Superblock'. The models were coded using the 'NLME' package (Pinheiro & Bates, 2020) with $\alpha = 0.05$ as the significance level. Most variables were log-transformed to improve the normality of residuals (except for ANPP, litter mass). When significant fixed factor effects were found, a Tukey's HSD post-hoc test was used for treatment mean comparisons using the 'MULTCOMP' package (Hothorn et al., 2020). The same models were used to examine the species identity effects at each site, by replacing SR with species composition (pine, birch and pine–birch mixture).

Linear correlations between soil N and P availability and NUE and PUE values were quantified using Pearson's product–moment correlation coefficients. Significant differences between the expected and observed values for each species in the mixed-species plots in both H_2O treatments were determined with Welch two sample *t*-tests. These tests were also used to quantify significant differences in green leaf [Nut] between species and between H_2O treatments for each species. Graphs were generated with the 'GGPLOT2' package (Wickham, 2016). All data and associated code are openly available (Maxwell et al., 2022).

3 | RESULTS

3.1 | Soil and leaf nutrient concentrations

At both sites, available soil $[NH_4]$, $[NO_3]$ and $[PO_4]$ did not differ with SR, H_2O treatment or their interaction (Table 1, Table S2). There was no significant linear correlation between total available soil mineral [N] and NUE, or between soil $[PO_4]$ and PUE (Figure S2). Birch foliage had a higher green [N] than pine ($p < 0.001$), with average values ranging between 22.9 ± 0.8 mg N g^{-1} in Be at ORPHEE and 24.8 ± 0.6 mg N g^{-1} in Ba at IDENT-, compared with 9.1 ± 0.3 mg N g^{-1} in Pp and 19.3 ± 0.5 mg N g^{-1} in Ps respectively (Table S3).

3.2 | Effect of species richness and water availability on NutUE

At IDENT-SSM, SR had a statistically significant positive effect on ANPP, litterfall mass, litter [N], [P] and [Mg], but not on NutUE of these three elements (Table S2, Figure 2, Figure S3). Post-hoc tests indicate that positive SR effects differed between H_2O treatments (Figure 2). Mean ANPP was significantly higher in the two- and four-species mixtures than monocultures in the high H_2O treatment but did not differ within the low H_2O treatment (Figure 2). Litter [N] and [Mg] was significantly ($p < 0.001$) higher in the two-species mixture than the monoculture in both H_2O treatments (Figure 2, Figure S3). Litter [P] was significantly higher ($p = 0.029$) in the two-species mixture than the monoculture in the low H_2O treatment, while the two- and four-species mixtures had significantly higher litter [P] than the monocultures in the high H_2O treatment. Litter concentration and NutUE of other macronutrients were independent of SR (Table S2, Figure S3). Water availability treatment had no effect on ANPP, litterfall mass, litter [Nut] or NutUE, except for litter [Mg] and [Mn] (Table S2, Figure S3). MgUE was significantly higher in the low H_2O treatment (Table S2, Figure S3). Above-ground productivity, litterfall mass, litter [Nut] and NutUE were independent of SR × H_2O effects (Table S2).

At ORPHEE, SR tended to positively affect ANPP ($p = 0.064$), but had no effect on litterfall mass (Table S2, Figure S4). The higher SR levels had statistically significantly lower litter [P] ($p = 0.034$) and [K] ($p = 0.038$), but SR did not affect litter concentrations of other elements (Table S2, Figures S4 and S5). The combined influence of SR on ANPP, litterfall mass and litter [Nut] was associated with a significant positive effect of SR on NUE, PUE, KUE, MgUE and MnUE (Table S2). Under low H_2O, both NUE and PUE were higher in the two- and three-species mixtures than the monocultures (Figure S4). Similar positive effects of SR were observed for KUE, MgUE and MnUE (Table S2, Figure S5). Water availability did not affect ANPP, litterfall mass or NutUE (Table S2, Figure S5). There was no significant SR × H_2O effect on most NutUE (Table S2).

3.3 | Species identity and water availability effects on nutrient relations of mixed-species communities

At ORPHEE, mean ANPP and litter mass were significantly higher in Pp and Be–Pp than Be in both H_2O treatments, with both measures of productivity being higher in the high H_2O treatment (Figure 3). Species identity had a significant effect on litter [Nut] of all elements, which were significantly lower in Pp and Be–Pp compared with Be plots (Figure 3, Figure S6). Species identity also had a significant effect on NutUE of all elements, but NutUE was independent of H_2O treatment (Table S4, Figure 3, Figure S6). In most cases, NutUE was significantly higher in Pp and Be–Pp than Be communities in both H_2O treatments (Figure 3, Figure S6). Species identity and H_2O treatment had comparatively little effect on NutRE (Table S4, Figure 5).

At IDENT-SSM, species identity had a largely similar effect on ANPP and litter mass to that observed at ORPHEE, with both measures of productivity in most cases being higher in the Ps and Ba–Ps communities than the Ba monoculture (Table S4, Figure 4). Species identity had significant effects on all litter [Nut] except Mn (Table S4). Litter [Nut] were higher in Ba and Ba–Ps than Ps and did not differ with H_2O treatment, except for litter [Mg] that was significantly higher in the high H_2O treatment (Figure 4, Figure S7). There was also a significant species identity × H_2O treatment interaction, such that differences among communities in litter [N] and [P] were diminished in the high H_2O treatment (Table S4, Figure 4). Similar species identity and H_2O treatment effects were observed for NutUE. Nutrient use efficiency of Ps was higher than in Ba communities in both H_2O treatments, with the exception of CaUE where

TABLE 1 Mean (± *SE*) soil N-NH_4^+, N-NO_3^- and P-PO_4^{3-} concentrations and sample size (*n*) for species richness (SR) and water availability (H_2O) treatments at the ORPHEE and IDENT-SSM sites. Means for H_2O treatments across SR levels at a given site are presented in bold.

			N-NH_4^+		N-NO_3^-		P-PO_4^{3-}	
Site	**H_2O**	**SR**	***n***	**(µg capsule $year^{-1}$)**	***n***	**(µg capsule $year^{-1}$)**	***n***	**(µg capsule $year^{-1}$)**
IDENT-SSM	Low	1	46	77.4 ± 12.0	46	9.4 ± 2.0	46	9.1 ± 1.7
	Low	2	35	93.7 ± 14.4	35	9.4 ± 1.9	35	11.1 ± 2.0
	Low	4	12	101.3 ± 28.3	12	12.5 ± 3.3	12	20.7 ± 7.0
			93	**86.6 ± 8.8**	**93**	**9.8 ± 1.3**	**93**	**11.4 ± 1.5**
	High	1	46	108.4 ± 14.5	48	15.2 ± 2.5	45	11.9 ± 1.8
	High	2	35	88.6 ± 15.1	36	14.4 ± 2.5	35	15.7 ± 2.5
	High	4	12	116.2 ± 23.4	12	11.7 ± 2.1	12	14.0 ± 3.0
			93	**102.0 ± 9.6**	**96**	**14.5 ± 1.6**	**92**	**13.6 ± 1.4**
ORPHEE	Low	1	20	99.5 ± 35.2	22	242.0 ± 53.3	24	37.3 ± 6.5
	Low	2	12	89.1 ± 27.1	12	207.2 ± 50.7	12	30.1 ± 7.0
	Low	3	9	129.9 ± 59.0	9	177.5 ± 74.3	9	21.0 ± 8.3
			41	**103.2 ± 22.5**	**43**	**218.8 ± 33.9**	**45**	**32.1 ± 4.3**
	High	1	18	3.4 ± 0.6	18	110.2 ± 28.2	18	10.0 ± 1.3
	High	2	10	2.3 ± 0.5	10	35.4 ± 7.9	10	12.9 ± 9.2
	High	3	9	26.5 ± 19.4	9	100.7 ± 23.9	9	13.0 ± 7.4
			37	**8.7 ± 4.8**	**37**	**87.7 ± 15.7**	**37**	**11.5 ± 3.0**

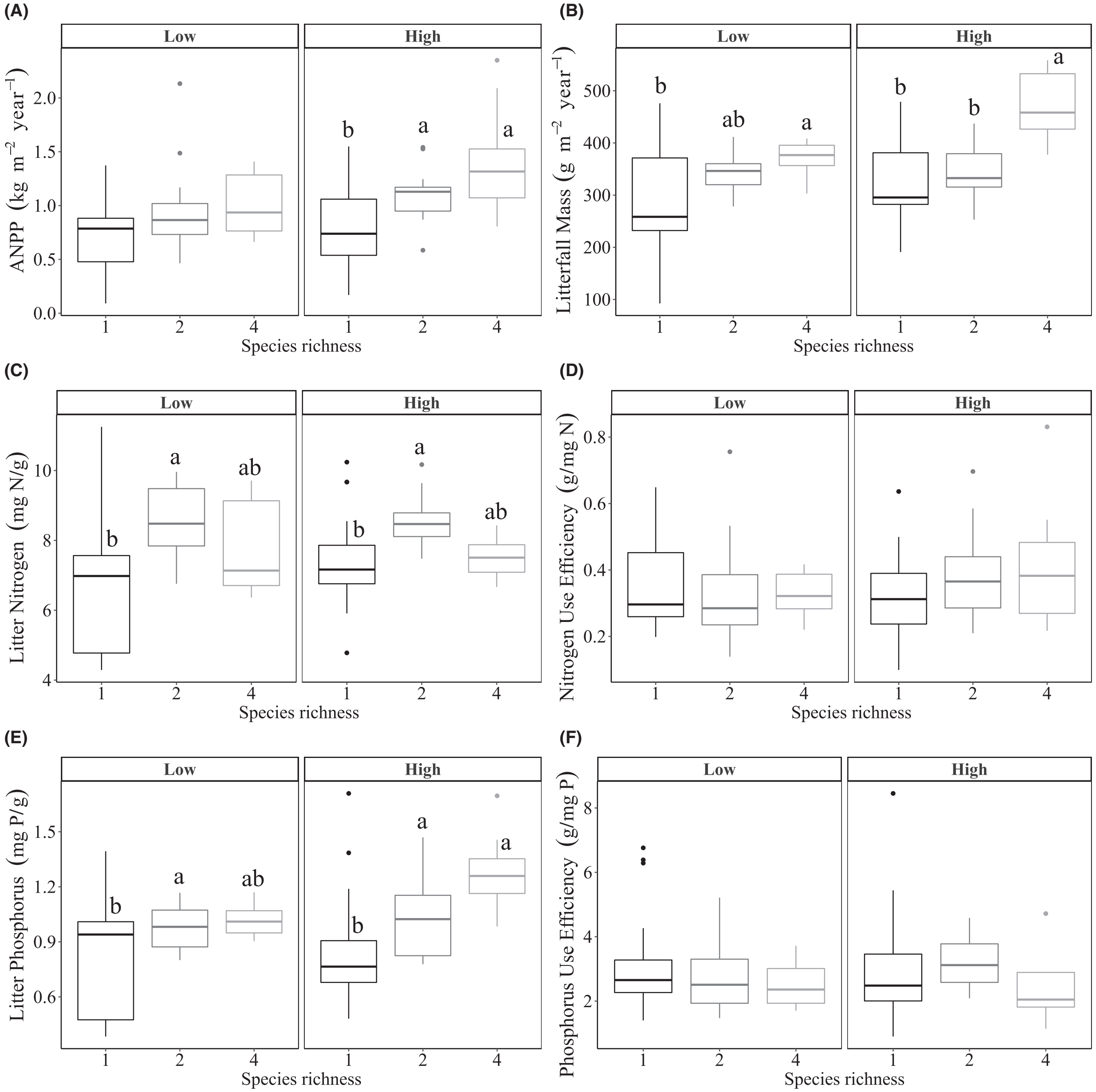


FIGURE 2 Stem and box plots showing the effect of tree species richness (1, 2 or 4 species) and water availability treatment (low or high H_2O) on (A) above-ground net primary productivity (ANPP), (B) litterfall biomass, (C) litter nitrogen (N) concentration, (D) nitrogen use efficiency (NUE), (E) litter phosphorus (P) concentration, and (F) phosphorus use efficiency (PUE) at the IDENT-SSM site. Pairs of graphs lacking letters indicate no significant treatment effect (Table S2). SR means that share the same lowercase letters within an H_2O treatment are not significantly different ($p < 0.05$, Tukey's HSD test).

this species identity effect was only noted in the high H_2O treatment (Figure 4, Figure S7). Nutrient resorption efficiency differed with species identity for P, Ca, Mg and Mn. The Ps plots exhibited lower NRE than the Ba and Ba–Ps communities, only in the high H_2O treatment due to a significant species identity × H_2O interaction (Table S4, Figure 5).

The effect of mixing birch and pine is summarized in Figure 6. At ORPHEE, Pp exhibited statistically significantly greater ANPP in both H_2O treatments, and higher litterfall mass in the high H_2O treatment when grown in mixture with Be. Mixing also significantly increased both NUE and PUE of Pp in the low H_2O treatment. Be derived no apparent benefit from being grown in mixture with Pp in either H_2O treatment. At IDENT, Bp exhibited significantly higher productivity (ANPP, litterfall mass) in both the low and high water treatments when grown in mixture with Ps, while Ps exhibited the opposite effect of mixing with Ba.

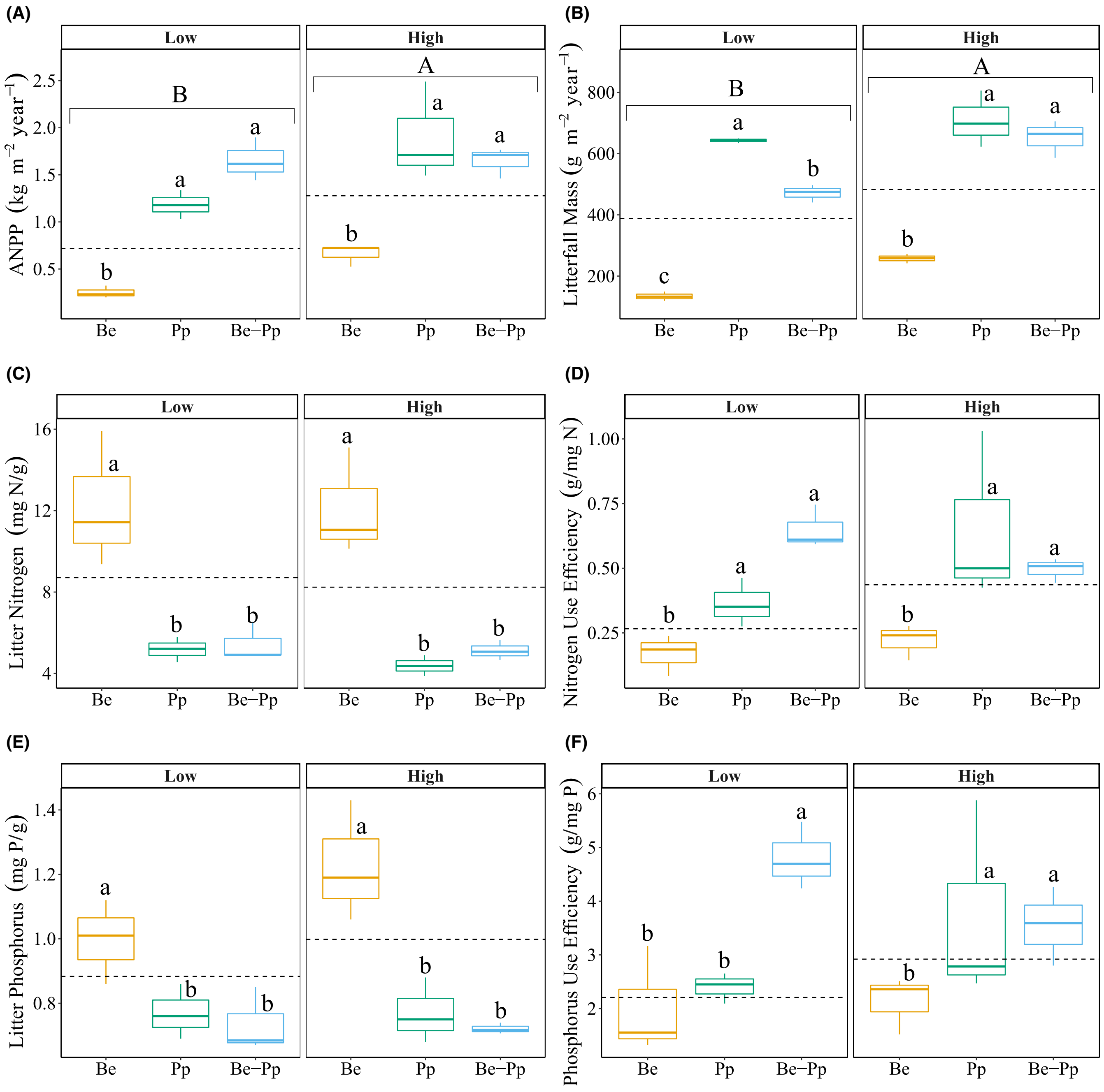


FIGURE 3 Box and stem plots showing the effects of species identity and water availability treatment (low or high H_2O) on (A) above-ground net primary productivity (ANPP), (B) litterfall biomass (C) litter nitrogen (N) concentration, (D) nitrogen use efficiency (NUE), (E) litter phosphorus (P) concentration, and (F) phosphorus use efficiency (PUE) for *Betula pendula* (Be), *Pinus pinaster* (Pp), and Be–Pp mixtures at the ORPHEE site. The horizontal dashed line represents the expected value for a 50% Be–Pp mixture value. Pairs of graphs lacking letters indicate no significant treatment effect (Table S4). SR means that share the same lowercase letters within an H_2O treatment are not significantly different ($p < 0.05$, Tukey's HSD test). Significant overall H_2O treatments are indicated by uppercase letters ($p < 0.05$).

4 | DISCUSSION

4.1 | Species richness increases productivity, but not NutUE

Tree species diversity effects on productivity and other ecosystem functions result from complementary species interactions and the presence of fast-growing, competitive species that tend to dominate tree communities. We found an overall positive effect of SR on ANPP and litterfall mass at both sites. The comparatively high above-ground productivity of shade intolerant birch and larch tended to be stable or increase in mixtures at IDENT-SSM, but that of more shade tolerant pine, maple and oak decreased in mixtures (Belluau et al., 2021). At ORPHEE, the positive effect of SR on ANPP was due to the competitive dominance of pine over birch, as previously measured 7 years after plantation establishment (Morin et al., 2020).

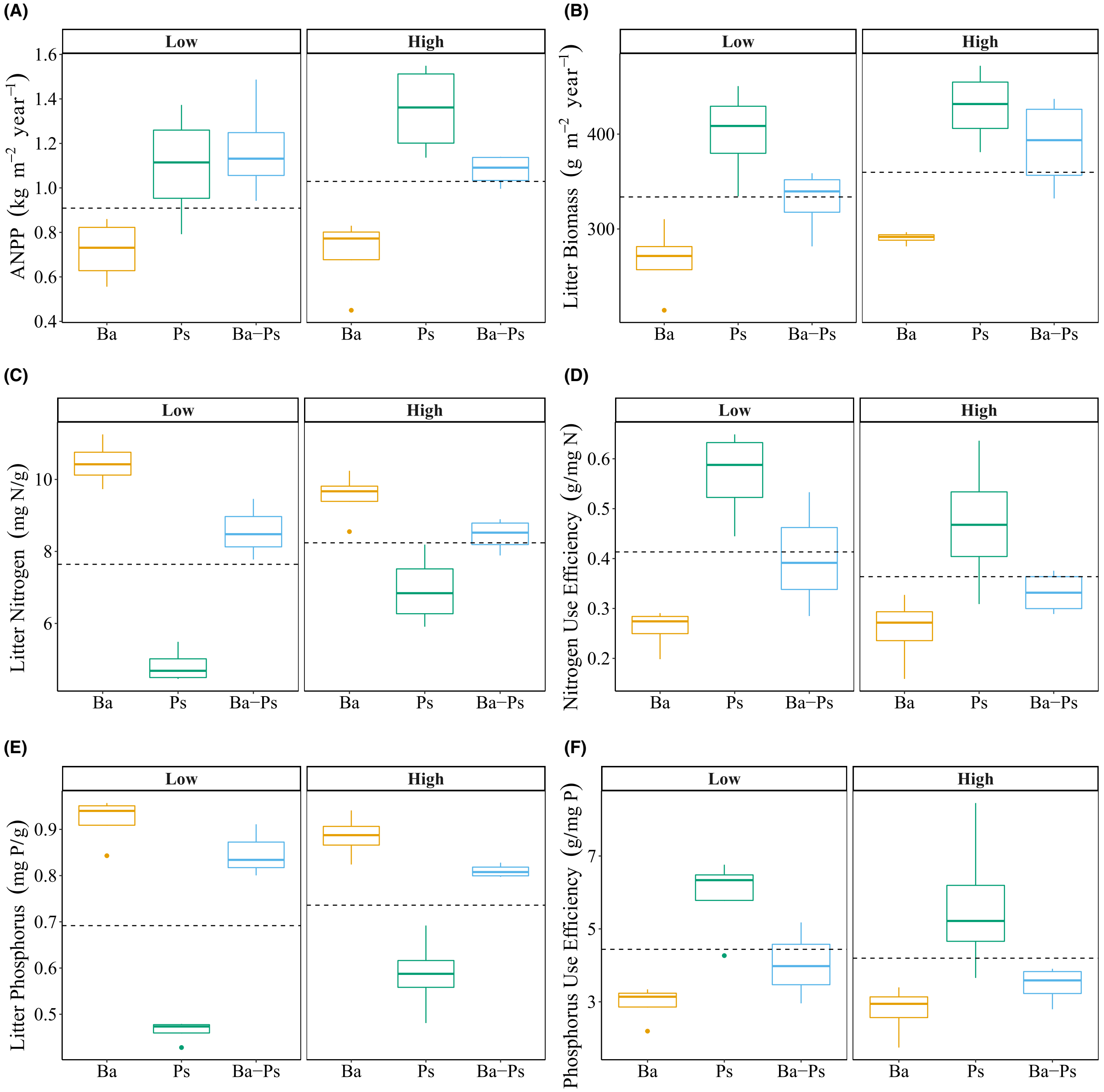


FIGURE 4 Box and stem plots showing the effects of species identity and water availability treatment (low or high H_2O) on (A) above-ground net primary productivity (ANPP), (B) litterfall biomass (C) litter nitrogen (N) concentration, (D) nitrogen use efficiency (NUE), (E) litter phosphorus (P) concentration, and (F) phosphorus use efficiency (PUE) for *Betula papyrifera* (Ba), *Pinus strobus* (Ps), and Ba–Ps mixtures at the IDENT-SSM site. The horizontal dashed line represents the expected value for a 50% Ba–Ps mixture value. Pairs of graphs lacking letters indicate no significant treatment effect (Table S4). SR means that share the same lowercase letters within an H_2O treatment are not significantly different ($p < 0.05$, Tukey's HSD test).

Species combinations that favour increased community-level light interception often drive positive diversity–productivity relationships in forests (Jucker et al., 2014), due to complementarity among species with different shade tolerance, growth rate and crown architecture (Cordonnier et al., 2018). At IDENT-SSM, birch was dominant in all mixtures where it is present and produced between 50% and 75% of the litterfall mass collected in the four- and two-species mixtures respectively. This resource acquisitive species grew more rapidly and dominated the comparatively small plot canopy space at IDENT-SSM 6 years after establishment (Belluau et al., 2021). At ORPHEE, birch also exhibited greater height growth than pine in the first 4 years of growth (Morin et al., 2020), after which pine grew taller than birch. Pine then dominated the canopy space in mixtures (Martin-Blangy et al., submitted) and produced around 90% of the total litterfall mass.

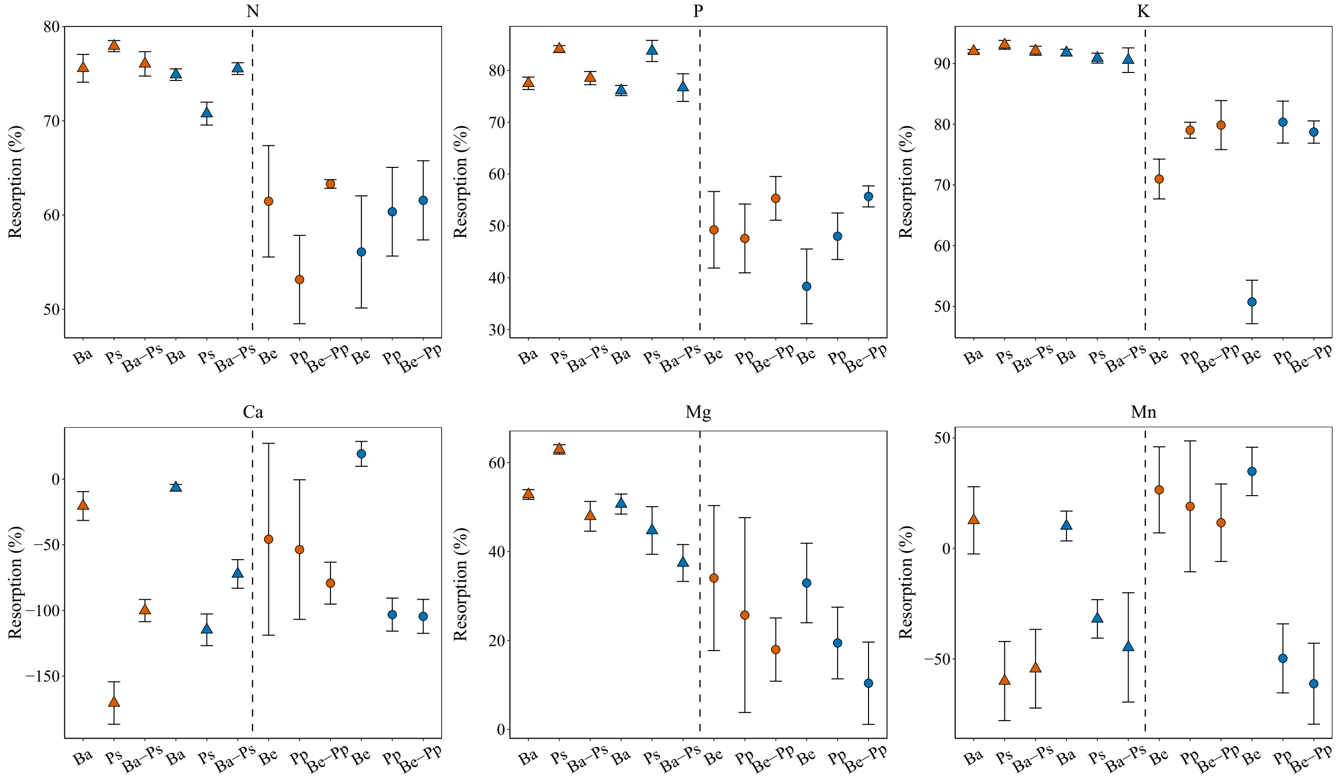


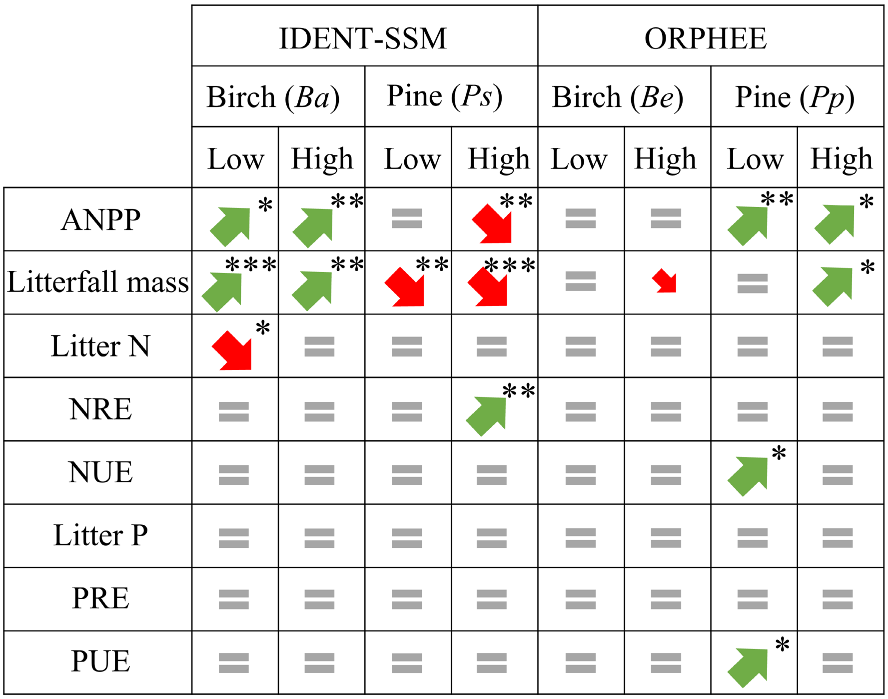
FIGURE 5 Mean (±*SE*) nutrient resorption efficiency (%) for N, P, K, Ca, Mg, Mn for birch, pine, and birch–pine mixtures at the IDENT-SSM (triangles) and ORPHEE (circles) sites, in the low (red symbols) and high (blue symbols) water availability treatments. Results for IDENT-SSM appear to the left of the vertical dashed line in each figure. Species abbreviations: *Betula papyrifera* (Ba), *Pinus strobus* (Ps), *Betula pendula* (Be), and *Pinus pinaster* (Pp).

Species richness strongly influenced litterfall nutrient dynamics, but differently at each sites. At IDENT-SSM, litter [N] and [P] were statistically significantly higher in the two-species mixtures than the monocultures in both H_2O treatments, without any changes in NutRE. At ORPHEE, SR had a negative effect on litter [Nut], likely due to both the larger comparative mass of nutrient-poor pine litter and increased NutRE with mixing. Differences in plot density and age may be associated with site differences in leaf nutrient dynamics. In the comparatively dense IDENT-SSM plots, litterfall mass was dominated by nutrient-rich species, whose relatively rapid decomposition may have led to an increase in soil nutrient availability (Gartner & Cardon, 2004) and increased plot-level leaf nutrient concentrations. These relatively young communities showed no further increase in their comparatively high NutRE values to potential increases in plot-level soil nutrient concentrations, that are adaptive during the period of early growth (Colin-Belgrand et al., 1996). At ORPHEE, the strong contribution of nutrient-poor pine litter to litterfall mass decreased the plot-level litter nutrient concentrations. This was accompanied by an increase in NutRE in both birch and pine in the mixture, which may be due to higher nutrient demand in the mixtures where tree growth was enhanced. However, this pattern was not observed in the soil nutrients extracted from the ion-exchange resins. We found no significant relationship between soil [N] and [P] and the NutUE of either element (Figure S2). These results are consistent with those of Knops et al. (1997), who found no relationship between NutUE and site fertility. However, ion-exchange methods can underestimate soil nutrient availability if nutrients released by forest floor decomposition are rapidly taken up by fine roots. While the resins were placed at 8 cm depth, fine root density in temperate forests have been found to be high in the forest floor organic layer and first 5–10 cm of mineral soil (Altinalmazis-Kondylis et al., 2020).

The combination of increased ANPP and litterfall [Nut] in mixtures was associated with no effect of SR on NutUE at IDENT-SSM. At ORPHEE, the increase in ANPP and litterfall mass in the mixtures was accompanied by a decrease in litterfall [Nut] and an increase in plot-level NutUE with SR. The trends leading to contradiction or support for first hypothesis (H_1) at each site were driven by species composition, and likely also varied due to the different plot ages and densities. Our results agree with that reported in tropical forest ecosystems, in which species identity had a much stronger effect on ecosystem NutUE than SR (Hiremath & Ewel, 2001; Tang et al., 2010). More specifically, the interaction between birch, a resource acquisitive species and a resource conservative pine species was more important than SR itself at each of our sites that differed in age and density.

4.2 | Minimal effect of water availability on NutUE

Contrary to our second hypothesis (H_2), we found no effect of H_2O treatment on NutUE at either site. Generally, higher water



	IDENT-SSM				ORPHEE			
	Birch (*Ba*)		Pine (*Ps*)		Birch (*Be*)		Pine (*Pp*)	
	Low	High	Low	High	Low	High	Low	High
ANPP	↗ *	↗ **	=	↘ **	=	=	↗ **	↗ *
Litterfall mass	↗ ***	↗ **	↘ **	↘ ***	=	↘	=	↗ *
Litter N	↘ *	=	=	=	=	=	=	=
NRE	=	=	=	↗ **	=	=	=	=
NUE	=	=	=	=	=	=	↗ *	=
Litter P	=	=	=	=	=	=	=	=
PRE	=	=	=	=	=	=	=	=
PUE	=	=	=	=	=	=	↗ *	=

FIGURE 6 Response of productivity and nutrient relations of birch (Ba, Be) and pine (Ps, Pp) when grown in mixture under low and high water availability at the ORPHEE (Be, Pp) and IDENT-SSM (Ba, Ps) sites. Arrows represent the direction (positive, negative) of birch and pine in mixture, compared with monocultures for above-ground net primary productivity (ANPP), litterfall mass, litter [N], nitrogen resorption efficiency (NRE), nitrogen use efficiency (NUE), litter [P], phosphorus resorption efficiency (PRE), and phosphorus use efficiency (PUE). Neutral effects are represented by =. Small arrows without asterisks represent trends ($p < 0.1$), and large arrows with asterisks represent significant differences from Welch two sample *t*-tests between the expected and observed values for the mixed-species community ($p < 0.05$*, $p < 0.01$**, $p < 0.001$***). Mean values for monocultures and mixtures can be found in Table S5.

availability has been found to increase tree productivity (Mayor & Rodà, 1994). At ORPHEE, however, ANPP and litterfall mass tended to increase in the high H_2O treatment, primarily in the monocultures. The fact that ANPP increased with SR, coupled with no effect of H_2O treatment in mixtures, suggests that water was not the main limiting growth resource at these two sites. This suggests that nutrients were the primary limiting factor (Albaugh et al., 2016). Nutrient limitation was likely higher in the infertile sandy soils of the ORPHEE site, located in a region where a widespread and severe limitation in P has been found (Trichet et al., 2009). This was consistent with the fact that green leaf [Nut] were near the threshold of adequate foliar [N] and [P] for these two species (Reuter & Robinson, 1997; van den Burg, 1985). In contrast, species at IDENT-SSM exhibited green leaf nutrient concentrations within their optimum nutrition ranges, further supporting our conclusion that nutrient limitation was stronger at ORPHEE. More severe water shortage at our sites might lead to more significant effects of water availability on NutUE.

There was no effect of H_2O treatment on litter [N] or [P] at either site, which also suggests that our two study sites were more limited by nutrients than water, although competition for light also may influence ANPP and nutrient dynamics in these young, dense stands (Martin-Blangy et al., submitted; Williams et al., 2017). However, we did find significantly higher litter [Mg] at IDENT-SSM, and litter [Ca] and [Mn] at ORPHEE, in the high compared to the low H_2O treatments. Both Ca and Mg can accumulate in the foliage (Augusto et al., 2011) via the tree transpiration stream through channel uptake, and accumulate in the xylem and foliage. The transporters for Mn are relatively aspecific, which may make it possible to use leaf [Mn] as a proxy for carboxylates in the rhizosphere (Pang et al., 2018). However, we speculate that tree species in our study intercepted Mn rather than mobilized it through the production of carboxylates (Lambers et al., 2015). Improved water supply should increase transpiration, leading to an increase in [Ca] and [Mg] in the leaf litter (Achat et al., 2018). Consequently, the increase in litter [Nut] of these cations was associated with lower MgUE in the high H_2O treatment at IDENT-SSM, and slightly lower MnUE and CaUE in the high H_2O treatment at ORPHEE.

Our results do not support our third hypothesis (H_3), that SR and water availability would have a significant interactive effect on NutUE. At IDENT-SSM, we did note positive trends of SR on ANPP and litterfall mass under high H_2O, consistent with previous observations at this site (Belluau et al., 2021). However, an interactive effect on NutUE was not observed at this site, nor at ORPHEE.

4.3 | Birch–pine dynamics drive species interactions at both levels of water availability

Species richness is a comparatively poor metric of diversity, with functional diversity and species identity of mixtures often being the operative factors driving diversity–ecosystem function relationships. To better understand SR relationships, we examined the interactions between species identity and water availability, focusing on birch and pine, two genera present at both sites. Interestingly, pine had higher NutUE than birch at both sites. This observation agrees with Vitousek (1982), who found that the efficiency of litterfall production per N and P was higher in temperate coniferous compared to deciduous forests. Evergreen coniferous species typically employ a resource conservative ecological strategy and are often characterized by higher NutUE and lower quality litter than deciduous angiosperm species (Augusto et al., 2014; Chapin et al., 1993). Combining these two strategies in plantations is thus of interest to explore the effect of mixing species on NutUE. Trends in nutrient dynamics in the birch–pine mixtures at each site were influenced by the combination of two different resource acquisition strategies, species within each genus, as well as tree density and stand age.

In the first years of growth, birch grew more rapidly at both sites. At IDENT-SSM, growth of *P. strobus* and did not keep pace with *B. papyrifera* because of the latter's lower shade tolerance and faster initial growth compared to pine (Niinemets & Tamm, 2005). Birch thus gained a size advantage over pine and dominated the available canopy space, leading to productivity overyielding with mixing. Increase in ANPP was associated with an increase in leaf litterfall [Nut], due to the synergistic non-additive presence of nutrient-rich birch litter. This led to an additive effect of mixing birch and pine on NUE and PUE at IDENT-SSM. In the older and less dense plots at ORPHEE, *P. pinaster* eventually overtopped the initially fast growing *B. pendula* canopy (Morin et al., 2020), and had more canopy space to grow than pines in the monocultures, leading to overyielding at that site. The strong effect of pine on total mixture litterfall production decreased litterfall [Nut], thereby increasing NUE and PUE in the mixed birch–pine plots at ORPHEE. Thus, mixing a resource acquisitive species and a resource conservative species will initially favour the former, which will dominate the available canopy space (Williams et al., 2017) and may improve both plot-level productivity and leaf [Nut] in the first few years of growth. However, growing these two species in lower density plots allows the resource conservative species to 'catch up' with age, and may thus improve plot-level NutUE in the longer term.

Mixing was a strong driver of NutUE, and after 4 years of the H_2O treatment, plot-level NUE and PUE of mixtures increased more in the low H_2O treatment at ORPHEE. Indeed, mixing birch and pine, rather than SR itself, had a larger, positive effect on NutUE when water availability was low. Stronger biodiversity–ecosystem functioning relationships have been previously observed in drier areas with more functionally diverse tree species (Ratcliffe et al., 2017) where growth is reduced by lower water availability. We did not, however, find this same trend at IDENT-SSM where the effect of mixing birch and pine was additive under both H_2O treatments. Despite a small interactive effect at ORPHEE, species composition of the mixtures appeared to have a larger effect on NutUE than H_2O treatment.

Our study is the first to test the interactive effect of tree stand diversity (i.e. species richness and species identity) and water availability on nutrient use efficiency (NutUE) of stands. By using two of the few existing experimental sites that manipulate both of these factors, we found that species identity rather than species richness was an important driver of productivity responses, litterfall nutrient dynamics and ultimately NutUE. Depending on the species, birch–pine mixtures may increase stand-level nutrient use efficiency compared to pine monocultures. Overall, we conclude that, regardless of water availability, mixing tree species with certain traits and competitive interactions may be a viable way to improve stand-level NutUE of plantations, once the mechanisms behind species interactions on different sites are fully understood.

AUTHORS' CONTRIBUTIONS

T.L.M., N.F., L.A. and A.D.M. conceived the ideas and designed the methodology; W.C.P. and C.M. designed field setup and collected the data; T.L.M., N.F., L.A., A.D.M., A.B. and M.R.B. collected the data; T.L.M. analysed the data; T.L.M. wrote the first draft of the manuscript in close consultation with L.A. and A.D.M. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Data Portail INRAE at https://doi.org/10.15454/FWC5LP.

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SUPPORTING INFORMATION

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