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RESEARCH ARTICLE

Tree drought–mortality risk depends more on intrinsic species resistance than on stand species diversity

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Abstract

Increasing tree diversity is considered a key management option to adapt forests to climate change. However, the effect of species diversity on a forest's ability to cope with extreme drought remains elusive. In this study, we assessed drought tolerance (xylem vulnerability to cavitation) and water stress (water potential), and combined them into a metric of drought–mortality risk (hydraulic safety margin) during extreme 2021 or 2022 summer droughts in five European tree diversity experiments encompassing different biomes. Overall, we found that drought–mortality risk was primarily driven by species identity (56.7% of the total variability), while tree diversity had a much lower effect (8% of the total variability). This result remained valid at the local scale (i.e within experiment) and across the studied European biomes. Tree diversity effect on drought–mortality risk was mediated by changes in water stress intensity, not by changes in xylem vulnerability to cavitation. Significant diversity effects were observed in all experiments, but those effects often varied from positive to negative across mixtures for a given species. Indeed, we found that the composition of the mixtures (i.e., the identities of the species mixed), but not the species richness of the mixture per se, is a driver of tree drought–mortality risk. This calls for a better understanding of the underlying mechanisms before tree diversity can be considered an operational adaption tool to extreme drought. Forest diversification should be considered jointly with management strategies focussed on favouring drought-tolerant species.

For affiliations refer to page 11.

KEYWORDS
forest adaptation, forest management, hydraulic traits, species interactions, species richness, tree diversity, water stress, xylem embolism

1 | INTRODUCTION

Forest ecosystems around the world are experiencing more frequent and intense droughts as a result of climate change (Trenberth et al., 2014), which is associated with increased tree mortality (Allen et al., 2010; Hammond et al., 2022) and increasingly affects forest functions and services (Anderegg et al., 2013; Hammond et al., 2022). Increasing tree species diversity is advocated as an important management option to adapt forests to climate change (Messier et al., 2022). Indeed, more diverse forests and plantations are thought to better cope with a number of abiotic and biotic disturbances while exhibiting comparable or higher levels of crucial functions and services, such as productivity (Depauw et al., 2023; Jactel et al., 2017). For this reason, promoting species diversity in forests is proposed as a 'no-regret approach' for climate-smart forestry, which can be immediately implemented at large scale (Messier et al., 2022; Muys & Messier, 2023).

However, the effects of tree species diversity on drought resistance remain elusive (Grossiord, 2020). In particular, most of previous studies measured indirect proxies of drought resistance, such as growth increments, wood carbon isotope composition, temporal dynamics of Normalized Difference Vegetation Index (NDVI) or, in some rare cases, sapflow-derived tree transpiration (e.g., Grossiord, 2020; Grossiord et al., 2014; Haberstroh & Werner, 2022; Liu et al., 2022; Pardos et al., 2021; Schnabel et al., 2022). Because these proxies are related to physiological processes that are down-regulated early during the onset of drought, they do not inform about the risk of tree mortality under extreme drought (Torres-Ruiz et al., 2024). Consequently, whether stand species diversity can mitigate the risk of drought-induced tree mortality is largely unknown (but see Hajek et al., 2022; Shovon et al., 2024). To this day, this knowledge gap has blurred the significance of tree diversity as a crucial management leverage for climate-smart forestry, in contrast to other management strategies focussed on favouring the introduction or regeneration of drought-resistant species. Indeed, comparing intrinsic species resistance to the magnitude of diversity effects on tree drought resistance requires experimental designs where these two effects can be quantified and tested, which is often impractical in observational studies because of confounding factors (Baeten et al., 2013). Moreover, measuring drought–mortality risk along diversity gradients requires measuring both the water stress experienced by tree species and the vulnerability of these tree species to water stress, as both are possibly affected by species diversity.

If species interactions affect the amount of water available for trees in mixtures during periods of water deficit, tree diversity could influence tree water stress (commonly measured using water potential; Choat et al., 2018). A variety of ecological mechanisms have been proposed to explain tree diversity effects on resource-use and forest functioning (Barry et al., 2019; Nadrowski et al., 2010), which can be applied to water use and water stress (Grossiord, 2020). Resource partitioning effects can occur if tree species use water differently in space, time and magnitude, thereby alleviating competition for water in mixtures, for example if root systems explore soil at different depths. Facilitation effects happen when one species has a positive effect on the functioning of neighbouring species. Typical examples include the effect of tree diversity on forest microclimate buffering (Zhang et al., 2022), which can alleviate atmospheric drought in understorey tree species (Ma et al., 2023). Finally, selection effects account for increased probability of including drought-resistant species in diverse forests. However, these beneficial effects may be overridden by increased competition for soil water in case of severe drought (Haberstroh & Werner, 2022). Moreover, if tree diversity has a positive effect on growth and crown development in favourable periods, as is frequently observed (Guillemot et al., 2020; Williams et al., 2017), it may worsen the consequences of severe droughts by increasing the mismatch between water demand (driven by leaf area and therefore, tree size) and availability (i.e., 'structural overshoot' sensu Jump et al., 2017).

Tree drought vulnerability is commonly quantified using the xylem resistance to cavitation, typically captured by the water potential causing 50% of hydraulic conductivity loss in the xylem (P_{50}, Anderegg et al., 2016; Choat et al., 2018; Martin-Stpaul et al., 2017). Tree diversity could affect P_{50}, because diversity can substantially affect the growing conditions and therefore xylem features through anatomical plasticity. Although current evidence suggests that traits related to drought vulnerability are less plastic than traits related to water acquisition (Fuchs et al., 2021; Lamy et al., 2014; Lauriks et al., 2021), P_{50} was occasionally shown to respond to changes in light exposure or long-term water deficit (Feng et al., 2023; Lemaire et al., 2021).

Both maximal water stress and vulnerability to water stress are integrated in the hydraulic safety margin (HSM), a direct measure of the risk of hydraulic failure under drought (Choat et al., 2012; Martin-Stpaul et al., 2017; Sanchez-Martinez et al., 2023). HSM has been shown to be a good predictor of drought-induced mortality across several tree species (Anderegg et al., 2016; Nolan et al., 2021). It is defined as the difference between the maximum water stress experienced by a tree (i.e., the minimum measured water potential in the xylem) and its drought vulnerability (measured using P_{50}; Choat et al., 2012). To the best of our knowledge, the effect of species diversity on the two components determining HSM, and therefore drought–mortality risk, was never quantified. However, we note that HSM estimated using P_{50} averaged at the species level and hydrology-derived water stress model (i.e., without any information about species diversity) can successfully predict tree mortality at large scale (Anderegg et al., 2015; Tai et al., 2019). This suggests that the effect of tree species diversity on drought–mortality risk is smaller than the effect of intrinsic species resistance to drought.

Here, we build upon TreedivNet, a global network of field tree experiments specifically designed to quantify and test species diversity effects (Verheyen et al., 2016) to explore whether stand species diversity can mitigate the risk of drought-induced tree mortality. We measured drought–mortality risk (i.e., HSM) during the extreme 2021 or 2022 summer droughts in five European experiments, encompassing Mediterranean, continental and oceanic climate. We specifically tested two hypotheses: (1) Species diversity alters both determinants of drought–mortality risk, that is the level of tree water stress and the vulnerability of the tree vascular system to drought (i.e., P_{50}); (2) the risk of drought-induced tree mortality depends more on intrinsic species resistance to drought than on stand species diversity.

2 | MATERIALS AND METHODS

2.1 | Experimental design

This study was conducted at five tree diversity experiments located in contrasting climate and soil conditions throughout western and southern Europe (Figure 1) as part of the TreeDivNet network (Verheyen et al., 2016). All experiments include tree species grown in both monoculture and mixture in a replicated randomised design that allows for the effect of tree diversity to be tested. The studied experiments included ORPHEE in France, IDENT-Freiburg in Germany, FORBIO-Gedinne in Belgium, IDENT-Macomer in Italy and B-Tree in Austria (Table 1). The tree species grown in the experiments are adapted to local climate and soil conditions.

Tree planting density ranged from 2500 (ORPHEE) to 62,500 (IDENT-Macomer) trees per hectare. A comprehensive description of the experiments can be found in Supporting information S1. In each experiment, we selected plots along a species richness gradient (1–6 species mixtures). We aimed at sampling mixtures exhibiting contrasting functional diversity (i.e., species mixtures with comparable growth rates and similar leaf habits versus mixtures with contrasted growth rates and containing both broadleaf and conifer species). All the studied species were sampled in both mixtures and monocultures. A total of 21 different species, 43 different species compositions (21 monoculture and 22 mixtures) and 116 'species × species richness' levels were studied (all of them were measured for water stress, but only a subset of species was measured for drought vulnerability, see dedicated sections). Tree ages at the time of sampling varied among experiments, ranging from 8 (IDENT-Macomer) to 14 years (ORPHEE). Sampled trees had dominant or codominant status, with only living neighbours. Sampled trees of a given plot and species had comparable sizes. Average tree height varied largely between species and experiments, ranging from 0.7 m (*Phillyrea latifolia* at IDENT-Macomer) to 11.8 m (*Pinus pinaster* at ORPHEE and *Larix x eurolepsis* at FORBIO-Gedinne, Tables S2). Trees were sampled in the inner part of the plots, and we avoided sampling trees grown in the same vicinity.

2.2 | Physiological traits

2.2.1 | Xylem vulnerability to drought

A subset of species and experiments were measured for xylem vulnerability to drought. Long-vessel species (i.e., *Quercus* species in our dataset) were not measured because of the documented risk of artefact measurements associated with Cavitron for these species (Sergent et al., 2020; Torres-Ruiz et al., 2014, 2015). The IDENT-Macomer experiment were not measured for P_{50} due to logistical constraints. In total, 11 species were measured for xylem vulnerability to cavitation across diversity gradients. The sample collection took place in 2022, except for *Betula pendula* and *Pinus pinaster* in the ORPHEE experiment that were measured in 2020. Measurements were conducted in the morning, in May and June 2022, that is after the growing season to ensure mature xylem structures, but before the severe drought summer period to avoid native embolism. Five trees were sampled per species in all studied plots, and two blocks were sampled in each experiment (totalling $n=10$ measurements for each species in each diversity level). We sampled fully grown branches of 100 to 120 cm length located at the top of the trees, exposed to sunlight and aged 2 to 3 years. Vulnerability to cavitation was measured using the 'Cavitron' flow-centrifuge method following standard protocols for short-vessel coniferous and diffuse-porous species (Cochard et al., 2005). Sampled branches immediately recut under water in the field. Lateral branches and leaves were immediately cut underwater, wrapped in humid paper towels and sealed in plastic to avoid drying during shipment to the laboratory (Torres-Ruiz et al., 2015). Measurements were carried out within 2 weeks after sampling (Platform INRAE PHENOBOIS at UMR BIOGECO Bordeaux and UMR PIAF Clermont Ferrand). In the laboratory, samples were stored between 4 and 6°C. A few minutes before the Cavitron measurement, samples were re-cut underwater to 28 cm length. The principle of the cavitron is to assess the loss of hydraulic conductance of the branch segment while progressively increasing the xylem tension (equivalent water potential) until most hydraulic conductance loss has been reached. The different water potential steps are reached through the centrifugal force, which generates an increasing negative xylem pressure. Finally, we expressed the percent loss of hydraulic conductance (PLC) as a function of xylem pressure (ψ) to build the vulnerability curves using a sigmoidal function (Pammenter & Van Der Willigen, 1998), as follows:

$$\mathrm{PLC} = \frac{1}{1 + e^{sl/25*(\Psi - \mathrm{P}_{50})}}$$

where P_{50} is the pressure causing 50% loss of conductivity and *sl* the slope value at this point. A total of 628 xylem vulnerability curves were analysed in this study.

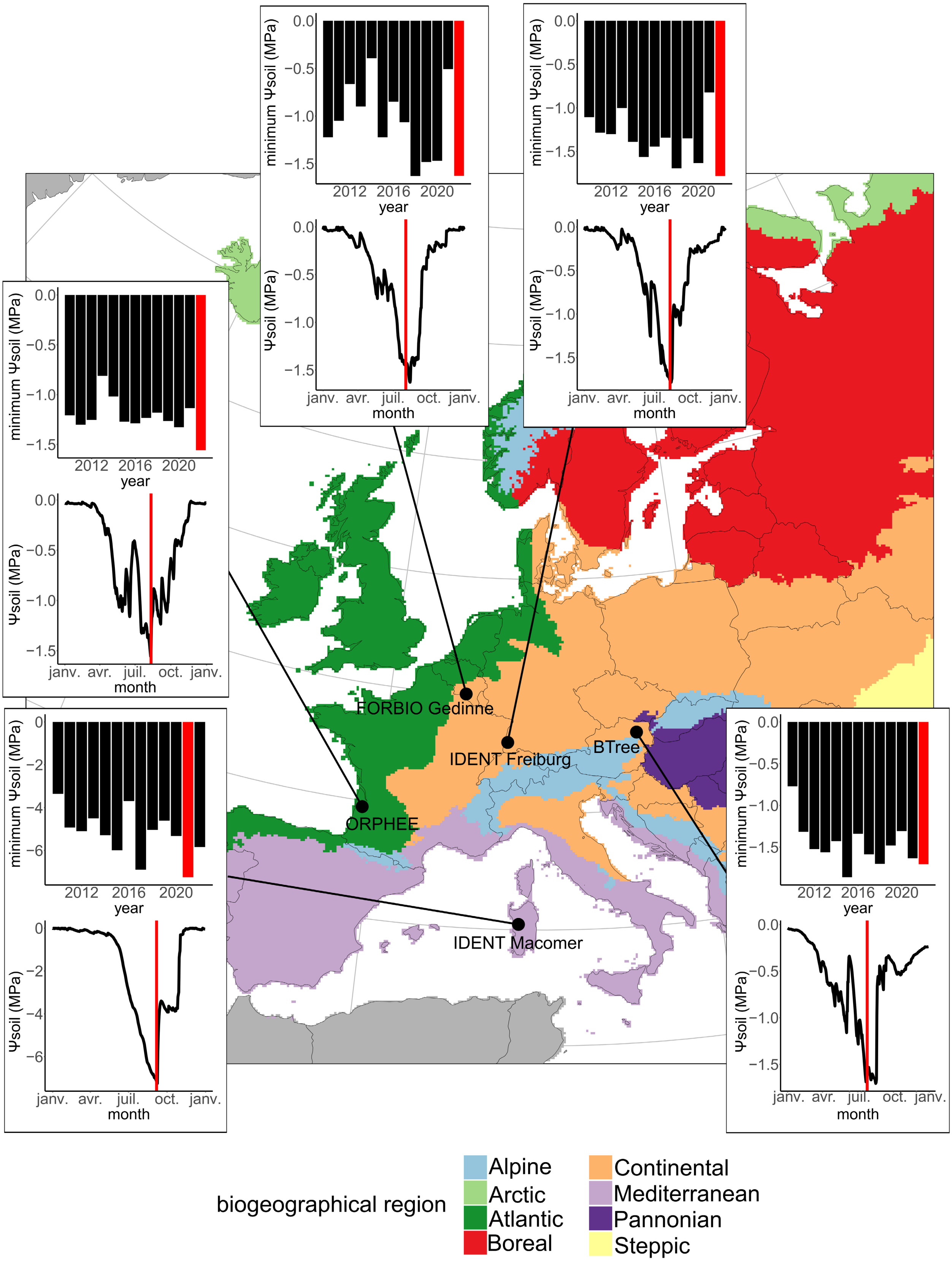

FIGURE 1 Location of the five studied experiments and drought intensity at the time of water stress measurement. Drought intensity is characterised using simulation of soil water potential (ψ_{soil}) from the SurEau model (Ruffault et al., 2022; Supporting information S2). For each experiment, the upper plot shows the annual minimum of ψ_{soil} and the bottom plot shows the daily dynamics of ψ_{soil} during the year of sampling. Red colour indicates year and date of sampling. The biogeographical region layer is based on Cervellini et al. (2020). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

TABLE 1 Description of the tree diversity experiments.

Experiment name	B-TREE	FORBIO Gedinne	IDENT Freiburg	ORPHEE	IDENT Macomer
GPS position	48°19′3.62″ N; 16°4′0.81″ E	49°59′N; 4°59′ E	48°01′10″ N; 7°49′37″ E	44°44′23.27″ N; 0°47′46.68″ W	40°14′N; 8°42′ E
Altitude	200 m	367–426 m	278 m	60 m	615 m
Plot size	variable	42 m × 42 m	3.6 m × 3.6 m	20 m × 20 m	3.2 m × 3.2 m
Plot density	9166 trees/ha	4444 trees/ha	37,692 trees/ha	2500 trees/ha	62,500 trees/ha
Planting date	2013	2010	2013	2008	2014
Studied sp. Richness levels	1, 2, 4	1, 2, 4	1, 2, 6	1, 2, 3	1, 2
Studied species pool	*Acer platanoides, Carpinus betulus, Quercus robur, Tilia cordata*	*Acer pseudoplatanus, Fagus sylvatica, Larix x eurolepis, Pseudotsuga menziesii, Quercus petraea*	*Acer platanoides, Acer saccharum, Betula papyrifera, Betula pendula, Quercus robur, Quercus rubra*	*Betula pendula,Quercus ilex, Pinus pinaster*	*Acer monspessulanum, Arbutus unedo, Fraxinus ornus, Phillyrea latifolia, Pinus halepensis, Pinus pinaster, Quercus pubescens*

Note: Table of the Material and methods section synthetising experimental sites global informations.

2.2.2 | Water stress

We aimed at measuring water stress during extreme drought conditions in the different experiments. To achieve this, we conducted measurements during exceptionally dry years in the different experiments: in summer 2021 for the IDENT-Macomer experiment, summer 2022 otherwise. In addition, we aimed at sampling each experiment at the seasonal peak of drought intensity. The date of sampling was planned 1 or 2 days ahead of the measurements, based on weather forecasts, aiming to conduct the sampling at the end of a long dry period and just before the beginning of autumn rainfall events. The extreme drought intensity of the year and day of measurement was subsequently confirmed using simulations of soil water potential from the trait-based plant hydraulics model SurEau (Ruffault et al., 2022; Figure 1; Supporting information S2). In each experiment, measurements were conducted within two to three consecutive sunny days to ensure comparable weather conditions.

Leaves or shoots from the tree canopy were sampled using pole pruners. Ψ_{pd} was measured in a 2 h slot before sunrise and Ψ_{md} was measured in a 2 h slot around solar midday on the same trees. Samples collected were south-oriented and on top of the tree crown. Four trees were sampled for both Ψ_{pd} and Ψ_{md} per species and plot, and two blocks were sampled (totalling $n = 8$ measurements for each species in each diversity level) in all experiments except for the IDENT-Macomer, where three trees were sampled for Ψ_{pd} per species in all studied plots (i.e., no Ψ_{md} measurements were conducted), and three blocks were sampled (totalling $n = 9$ measurements for each species in each diversity level). Samples were immediately sealed in plastic Ziplock bags after blowing in it to saturate it with humidity. The samples were then placed in a portable cooler (avoiding contact with ice) in the dark before being measured with the Scholander pressure bomb directly in the field (i.e., less than half an hour after sampling, Rodriguez-Dominguez et al., 2022). A total of 621 measurements of Ψ_{pd} and 468 of Ψ_{md} were analysed in this study.

2.2.3 | Hydraulic safety margins

Xylem vulnerability to drought and water stress measurements were used to calculate hydraulic safety margins (HSM). Average P_{50} values of species that were not measured in this study were obtained from the literature (Martin-StPaul et al., 2017). To ensure consistency among species, P_{50} data obtained in this study were averaged at the species level to calculate HSM. This was possible because we did not find any overall significant diversity effect on P_{50} (Figure 2b). In addition, when tested at the species level, no species exhibited a significant effect of species richness (Figure 2a). Yet, one species out of 21 showed a significant mixture effect (i.e., monoculture versus mixture, see next section) on P_{50}. However, the amplitude of the effect was small. Therefore, we confirmed on the 11 species measured for both P_{50} and water stress that averaging P_{50} at species level did not affect our estimates of HSM across species and diversity gradients ($R^2 = 1$; Supporting information S3).

Two different definitions of HSM were used in this study: $\Psi_{md} - P_{50}$ (HSM_{md}, corresponding to the original definition of Choat et al., 2012) and $\Psi_{pd} - P_{50}$ (HSM_{pd}). Although using Ψ_{md} to calculate HSM is the most commonly used definition, we argue that Ψ_{pd} is a more reliable measurement of the aggregated effects of local conditions (in our case neighbouring tree diversity) on water stress over time. Indeed, Ψ_{pd} is related to the water content of the soil volume explored by tree roots, which integrates tree water use over the whole drought sequence. By contrast, Ψ_{md} also integrates the effects of the fluctuating environmental midday conditions. Consequently, Ψ_{md} measurement is more challenging because values can strongly vary from day to day, depending on weather, but also from leaf to leaf, as, for example radiation interception or wind exposure can vary, even among sunlit leaves of a given tree, and affect Ψ_{md} (Martínez-Vilalta et al., 2021). However, Ψ_{pd} and Ψ_{md} and, therefore, HSM_{pd} and HSM_{md} rank comparably under drought, as tree water loss is low (due to low stomatal conductance) under these stressful conditions, which was confirmed in our dataset (the R^2 of the linear relationship between HSM_{md} and HSM_{pd} was 0.91, Supporting information S4). In the following, when the generic term 'HSM' only to refer to the general concept of drought-mortality risk, and used HSM_{pd} and HSM_{md} otherwise.

2.2.4 | Tree species diversity

We explored the effects of three facets of tree diversity on xylem vulnerability to drought (P_{50}), water stress (ψ) and drought–mortality risk (HSM): (1) the 'mixture effect', a binary variable that contrasts a species grown in monoculture from the same species grown in any type of mixture. It allows testing the overall effect of mixing species, regardless of the mixture's characteristics. (2) The 'species richness effect', where species richness is included in models as a categorical variable with six levels, because species richness in our dataset ranges from 1 to 6. It allows testing the effect of species richness, regardless of the identities of the species in the mixtures. (3) The 'species composition effect', where species composition is included in models as a categorical variable with 43 levels. It allows testing the effect of species composition, that is how the identities of the species in mixture drive diversity effects.

For HSM_{pd}, we additionally quantified diversity effect in each mixture composition, as follows:

$$\text{“Diversity effect on HSM”}_{s,c} = \left(\overline{\mathrm{HSM}_{\mathrm{pd}\,\mathrm{mixture}_{s,c}}} - \overline{\mathrm{HSM}_{\mathrm{pd}\,\mathrm{monoculture}_{s}}}\right) \tag{1}$$

where s is the species and c is the mixture composition.

We then evaluated the maximum diversity effect exhibited by each species in each experiment.

2.3 | Statistical analyses

We used linear models (ANOVA type II, 'car' R package, Fox et al., 2012) to quantify the variance explained by species identity and tree diversity in our P_{50}, water stress and HSM dataset. The effects of the three facets of diversity (mixture effect, species richness effect and composition effect, see the 'Tree diversity' section) were explored in separate models to avoid collinearity problems. Specifically, the models tested were as follows:

$$Y_{t,s,d} = ID_s + DIV_d + ID_s \times DIV_d + \varepsilon_{t,s,d} \tag{2}$$

where Y is the dependent variable (P_{50}, Ψ or HSM), *ID* is the species identity, *DIV* is the tree diversity variable, ε is the error term. Indices are as follows: t is tree, s is species and d is diversity level (depends on the *DIV* variable tested, i.e., mixture effect, species richness effect and composition effect, see the 'Tree diversity' section). For all dependent variables, model residuals were visually checked for normality (Supporting information S5). Because all studied species but, two in P50 and consequently HSM dataset, and four in Ψ dataset, were grown in only one experiment, the species and experiment effects were confounded. Therefore, we did not include the experiment as an independent variable in the models, but rather considered species grown in two experiments as distinct species in the analyses. We tested the significance of the diversity effect in each species using one-way ANOVA and Tukey's post hoc tests ('car' R package, Fox et al., 2012).

In addition, we aimed at evaluating how neighbouring basal area and tree size mediate tree diversity effects on P_{50}, water stress and HSM (Fichtner et al., 2020; Prendin et al., 2018). Therefore, we performed models including these variables, as follows:

$$Y_{t,p,s,d} = ID_s + DIV_d + ID_s \times DIV_d + BA_{p,s} + SIZE_{p,s} + \varepsilon_{t,p,s,d} \tag{3}$$

where Y is the dependent variable (P_{50}, Ψ, or HSM), ID is the species identity, DIV is the tree diversity variable, BA is the average neighbouring basal area of a species in a plot ($m^2\,ha^{-1}$), SIZE is the height of the trees of a species in a plot (m), ε is the error term. Indices are as follows: t is tree, p is plot, s is species and d is diversity level (depends on the DIV variable tested, that is mixture effect, species richness effect and composition effect, see the 'Tree diversity' section).

Although our data set exhibits a nested structure, with trees nested within plots, plots nested within blocks and blocks nested with experiments, random effect accounting for this structure yielded singular matrix estimates. It was only possible to include an 'experiment' random effect in models when including diversity metric either as 'mixture' or 'species richness'. For this reason, we explored our data sets using linear models. Yet, we aimed at quantifying the effects of tree diversity and species identity on drought risk at both European scale (i.e., considering variation among and within experiments) and local scale (i.e., only considering within-experiment variation). To this aim, we performed the models described in Equation 2 and Equation 3 using raw data, and data standardized within experiment (i.e., each continuous variable was scaled ($\frac{X-\overline{X}}{\sigma_X}$) per experiment). When this comparison was possible, we verified that analyses conducted using ANOVAs with the standardized dataset yielded results qualitatively similar to a mixed model with a random 'experiment' effect on raw data (Supporting information S5).

Following (Stoffel et al., 2021), we considered that the proportion of variance (i.e., partial R^2) that is assigned to an explanatory variable (i.e., diversity or species identity) is the sum of the proportion of variance that is explained by main effect, together with the variance jointly explained with its interaction to the other main effect (*Option C* in Stoffel et al., 2021). A significant p-value threshold was set at .05. All analyses and figures were produced using the R software (v. 4.3.1, R core team, 2021).

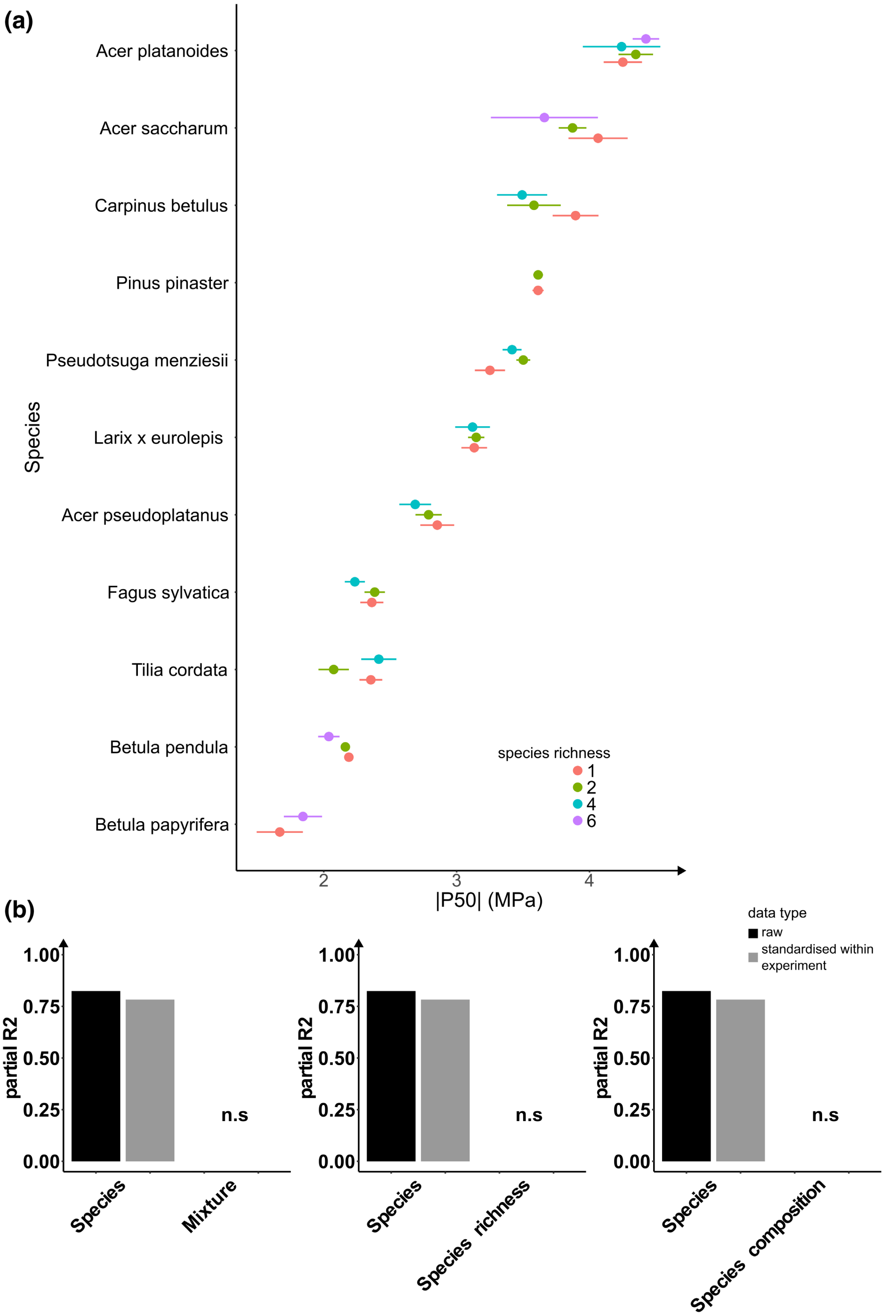

FIGURE 2 (a) Effect of tree species diversity on xylem vulnerability to cavitation (P_{50}). Points are observed mean, and error bars are standard errors. We did not report any significant effect of species richness on P_{50} when tested at species level ($p > .07$). (b) Partitioning of variance in the P_{50} dataset. Bars indicate the proportion of variance (partial R^2) explained by the variables. The effects of three facets of diversity (mixture effect, species richness effect and composition effect) were explored in separate models to avoid collinearity problems (see main text). n.s. means that the variable had no significant effect in Equation 2.

3 | RESULTS

3.1 | Tree species diversity effect on xylem vulnerability to cavitation

There was no evidence of overall effect of mixture, species richness or species composition on P_{50} (Figure 2). This result remains valid whether using raw data or standardized data within experiment. In addition, we did not report a significant effect of neighbouring basal area and tree size on P_{50} (Supporting information S7). When tested at species level, diversity effect was found to be significant only in *Pseudotsuga menziesii* (FORBIO-Gedinne experiment), in which we identified a significant mixture effect ($p = .032$, $R^2 = .1$) on P_{50}. Post hoc tests performed for *Pseudotsuga menziesii* showed that vulnerability to cavitation was lower when grown in association with *Larix x eurolepsis* (Δ0.33 MPa, $p = .042$, Supporting information S8). Because we did not find any significant experiment effect in the two species found in two different experiments (*Betula pendula* and *Acer platanoides*, $p > .29$), data were pooled at the species level for those two species for visualization (Figure 2) and HSM calculation.

3.2 | Tree species diversity effects on water stress and drought–mortality risk

Water stress (leaf water potential) and drought–mortality risk (HSM) measured in tree species grown in mixtures were well-predicted by measurements in the same species grown in monocultures, following

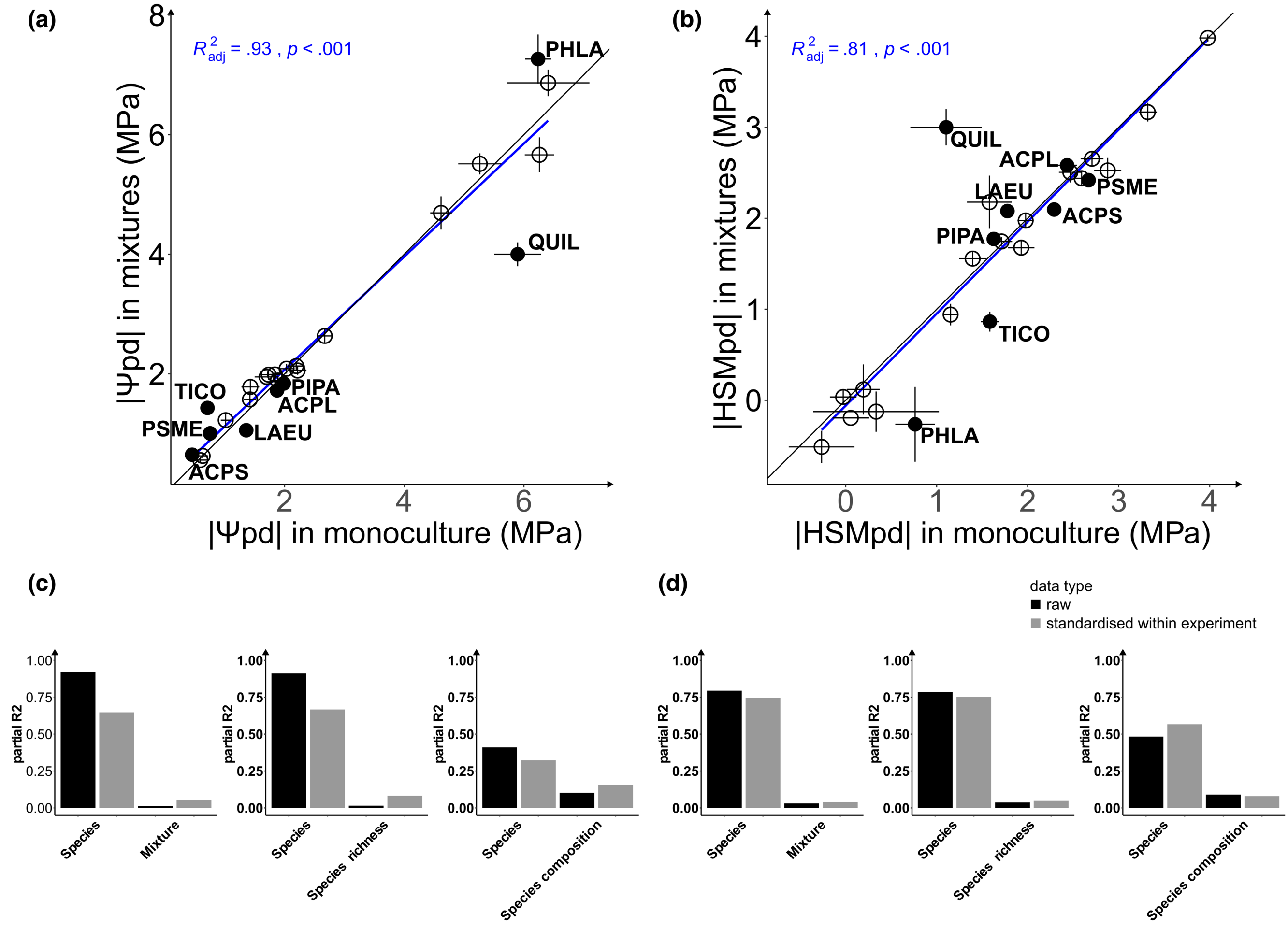

FIGURE 3 (a, b) Effect of tree species diversity on predawn water potential (Ψ_{pd}, a) and hydraulic safety margin (HSM_{pd}, b). Filled points indicate that HSM of the species in at least one studied composition differs from monoculture. Blue line is the linear relation between monocultures and mixtures, black line is the 1:1 line. Only the identity of species exhibiting a significant diversity effect is shown: ACPL is *Acer platanoides*, ACPS is *Acer pseudoplatanus*, QUIL is *Quercus ilex*, LAEU is *Larix x eurolepis*, PIPA is *Pinus pinaster*, PHLA is *Pinus halepensis*, PSME is *Pseudotsuga menziesii*, TICO is *Tilia cordata*. (c, d) Partitioning of variance in the Ψ_{pd} (c) and HSM_{pd} (d) datasets. Bars indicate the proportion of variance (partial R^2) explained by the variables. The effects of three facets of diversity (mixture effect, species richness effect and composition effect) were explored in separate models to avoid collinearity problems (see main text). All the bars shown in (c, d) correspond to significant effect in Equation 2.

a linear relationship. This result remains valid for both ψ_{pd} ($R^2 = .93$, $p < .001$) and ψ_{md} ($R^2 = .89$, $p < .001$), HSM_{pd} ($R^2 = .76$, $p < .001$) and HSM_{md} ($R^2 = .74$, $p < .001$) (Figure 3 and Supporting information S9). Because results were qualitatively similar for predawn and midday measurements but predawn measurements are available for more species, only predawn measurement are presented in the following (see Supporting information S7–S9 for midday results). The slopes of the monoculture versus mixture relationships were not significantly different from one and the intercept slope was not significantly different from zero, which indicate no overall effect of mixture on water potential (i.e., water stress) and HSM. This was confirmed by variance partitioning (Equation 2), which showed little effect of mixture and species richness on ψ_{pd} or HSM_{pd}. Species composition (i.e., the identities of all the species in the mixture) had a greater effect on ψ_{pd} and HSM_{pd} ($p < .001$), although it explained only a moderate proportion of variance (10.2% and 9% for raw data, 15.4% and 8% for data standardized within experiment). Results were qualitatively similar when analysing raw data or standardized data within experiment (Figure 3; Supporting information S7). Neighbouring basal area and tree size had significant effect on water stress and HSM in some of the explored models but explained only a small proportion of variance (Supporting information S7). When they had a significant effect, higher neighbouring basal area and greater tree size were associated with reduced water stress and higher HSM.

When evaluated at species level, a significant composition effect on ψ_{pd} and HSM_{pd} was found in eight species out of 21 (Figure 3). Yet, the principal variable explaining ψ_{pd} or HSM_{pd} variance (41.1% and 48.4% for raw data, 32.3% and 56.7% for data standardized within experiment) was species identity. Among the 22 studied mixtures, nine contained no species exhibiting a tree diversity effect on HSM, and only one contained only species exhibiting a positive effect (Supporting information S10). In most of

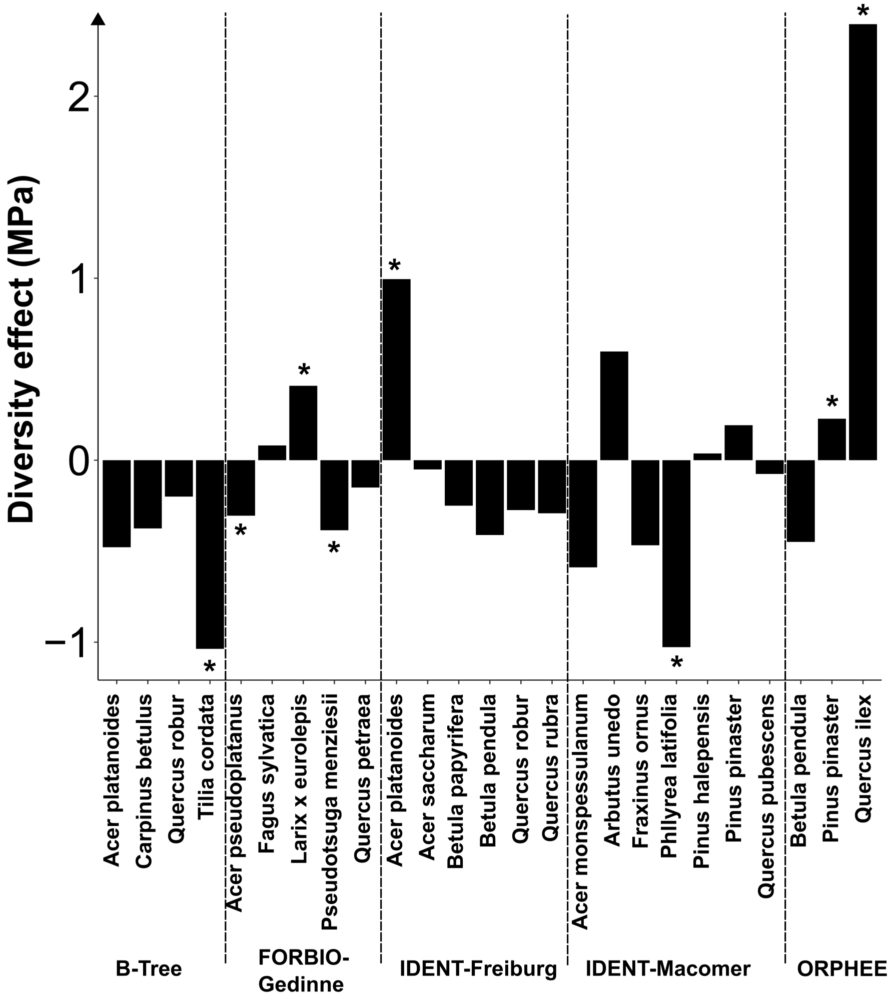

FIGURE 4 Maximum diversity effect (MPa) on HSM_{pd} (i.e., only the diversity effect observed in the mixture exhibiting the greatest difference with monoculture for drought-mortality risk is shown). Stars indicate a significant diversity effect.

the mixtures, only a subset of species exhibited a significant diversity effect (five mixture out of 22 contained species with either positive or no effects, six out of 22 contained species with either negative or no effects).

3.3 | Maximum diversity effect on HSM

The maximum diversity effect on HSM (i.e., the diversity effect observed in the mixture exhibiting the greatest difference with monoculture) was small in most of the studied species (Figure 4). However, at least one species per experiment exhibited a substantial (ΔHSM_{pd}>0.4) diversity effect in at least one mixture composition. The greatest diversity effect was reported for *Quercus ilex* (ORPHEE experiment), which exhibited a 2.4 greater HSM_{pd} in mixture than monoculture in the most favourable composition, that is in mixture with *Pinus pinaster* and *Betula pendula*, (Supporting information S8). *Quercus ilex* was also the only studied species that exhibited a significant diversity effect in all of the studied mixture compositions where it was found (Supporting information S8). Conversely, the greatest negative effect of tree diversity ($\Delta HSM_{pd}=-1.04$) was reported for *Tilia Cordata* (Btree experiment) when grown in mixture with *Acer platanoides*, *Carpinus betulus* and *Quercus robur*.

4 | DISCUSSION

4.1 | Tree species diversity effect on xylem vulnerability to cavitation

Overall, xylem vulnerability to cavitation (P_{50}) was unaffected by tree diversity, which contradicts our first hypothesis. P_{50} has been recognized as a key trait structuring drought tolerance between species (Choat et al., 2018; Martin-StPaul et al., 2017). However, plasticity of the P_{50} has been much less studied than interspecific differences, although a few previous reports showed that changes in light exposition or water deficit could increase P_{50} in some tree species (e.g. Herbette et al., 2010; Schoonmaker et al., 2010; Schuldt et al., 2016). Two mechanisms could explain the overall lack of plasticity of P_{50} in our data: (1) P_{50} of the studied species is a conserved trait that do not vary with local growing conditions (Lamy et al., 2014) (2) the environmental drivers affecting P_{50} (e.g., light exposition or water deficit) did not exhibit substantial changes along the studied diversity gradients in the few years before sampling. Most of the studied mixtures includes species with contrasting growth rates, which results in high tree size heterogeneity compared to monocultures (Supporting information S8). Moreover, leaf area index (LAI, estimated at plot level) strongly varies across diversity gradient (> Δ1 m^2/m^2) in all experiments (Supporting information S11). Together, these data suggest that at least some of the studied species experienced very contrasted light exposition across diversity gradients. Moreover, all experiments experienced at least one drought year in the 5 years before measurement (Figure 1). For these reasons, we posit that our results are primarily explained by the low environmental plasticity of hydraulic safety traits in trees (e.g. Lamy et al., 2014). Therefore, our findings add to a growing body of evidence suggesting that intra-species variability of P_{50}, in particular its environmental plasticity, is limited compared to its inter-species variability (Fuchs et al., 2021; Martínez-Vilalta et al., 2009). This lack of directional change in xylem embolism resistance also corroborates the premise of P_{50} as an evolutionary canalised trait (Guillemot et al., 2022; Lamy et al., 2011; Sanchez-Martinez et al., 2020). At species level, we only reported a small but significant tree diversity effect towards an increase in xylem embolism resistance in *Pseudotsuga menziesii*. Previous studies provide contrasting evidence regarding the intraspecific variability of P_{50} for this species (Chauvin et al., 2019; Condo & Reinhardt, 2019; Stout & Sala, 2003). *Pseudotsuga menziesii* at the FORBIO experiment was affected at the time of sampling by an insect outbreak that resulted in a partial defoliation. If the intensity of the biotic attack varied across diversity gradients, this could have contributed to the tree diversity effect that we report here.

Our findings suggest that the phenotypic expression of xylem embolism resistance is largely independent from stand species diversity. To the best of our knowledge, this conservatism of P_{50} has been assumed in biodiversity-ecosystem functioning studies (Hajek et al., 2022; Mas et al., 2024), but had never been tested. It has important implications for the process-based modelling of tree diversity effects on forest drought-induced mortality, as these models commonly overlook intra-species variability in hydraulic safety traits (Ruffault et al., 2022; Venturas et al., 2021). It also implies that the tree diversity effect on drought-mortality risk (i.e., HSM) is mostly driven by tree diversity effect on tree water stress and not on tree vulnerability to drought. Tree water stress being determined by the soil properties and the control of water acquisition and losses at tree to stand level, a better understanding of the biological determinants of these process in diverse forests is crucial for the prediction of drought-induced tree mortality under climate change.

4.2 | Tree species diversity effects on water stress and drought-mortality risk

We did not find a consistent effect of stand species richness on tree water stress (i.e., water potential, Ψ), which ranged from positive, to neutral, to negative across species, plots and experiments. By contrast, species composition (i.e., the identity of the species in mixture) had a significant, but moderate in most cases, effects on tree water stress for a given species, in line with our first hypothesis. This, in turn, affected drought-mortality risk (i.e., hydraulic safety margins, HSM), which was also influenced by species composition. These findings corroborate previous knowledge gained using indirect proxies of water stress such as growth, sap-flow-derived transpiration and carbon isotope composition (Grossiord, 2020). Altogether, they support the view that local species interactions can mediate the effects of tree diversity on drought responses along the entire drought sequence, including physiological processes that are down-regulated early during drought (e.g., growth and transpiration) and processes governing tree responses under extreme drought (i.e., measured by HSM). Our results contrast with a recent global study reporting a consistent positive effect of species richness on drought resilience estimated using eddy-covariance fluxes (Anderegg et al., 2018) or estimated using satellite-derived NDVI (Liu et al., 2022). Better understanding the extent to which phenological patterns captured by NDVI quantify actual water stress or species strategies to avoid drought may allow explaining this apparent discrepancy (Oliveira et al., 2021).

Our results partly contradict the recent proposition from Haberstroh and Werner (2022) that negative interactions among species are prominent under extreme droughts because of increased competition for soil water. Indeed, our data, acquired in extreme drought conditions, do not show any particular trend towards negative interactions in mixtures. By contrast, in the ORPHEE experiment, drought-mortality risk was significantly reduced in mixture for two species (*Quercus ilex* and *Pinus pinaster*). This discrepancy likely results from the fact that the different processes driving tree water stress can be affected by tree diversity. In particular, both soil water content and microclimate conditions (i.e., local temperature, radiation, vapour pressure deficit), that is, both soil and atmospheric drought, can be influenced by tree diversity (Ma et al., 2023; Martin-Guay et al., 2022; Zhang et al., 2022). Even if complementarity in soil water use is overridden by increased competition intensity for soil water during extreme drought, the beneficial effect of microclimate buffering for shade-tolerant species growing in the understory of diverse stands can still reduce their drought–mortality risk. This is supported by the fact that in the ORPHEE experiment, *Quercus ilex* is largely dominated by *Pinus pinaster* (Supporting information S8). Consequently, *Quercus ilex* experiences very contrasted microclimatic conditions in monoculture and mixtures, as suggested by an increase >30% in leaf area index in mixture (Supporting information S11). This likely translates into an important alleviation of atmospheric drought experienced by *Quercus ilex* and may explain the strongly positive diversity effect shown in Figure 4. Moreover, a recent diversity experiment conducted in greenhouse with *Quercus ilex* and *Pinus halepensis* showed that their complementarity in hydraulic strategies (in terms of stomatal regulation and hydraulic connection to the soil and the atmosphere) benefit both species in mixture (Moreno et al., 2021). In addition to the reduction of water competition intensity for *Pinus pinaster* in mixtures (as *Quercus ilex* exhibited much slower growth), this mechanism may contribute to explain the positive diversity effect on *Pinus pinaster* observed in the ORPHEE experiment.

More generally, our results suggest that higher neighbouring basal area is associated with reduced water stress and greater HSM in our data set. Although this effect is small and likely varies with species and composition, this indicates that facilitation mechanisms such as microclimate buffering are important drivers of diversity outcome in the studied experiment (Ma et al., 2023; Zhang et al., 2022). In addition, we report that in some cases, taller trees of a given species exhibited reduced water stress and greater HSM. This may be due to a better soil exploration by the roots of taller trees (Bolte et al., 2004), and indicates that diversity effects on forest productivity and growth may indirectly affect the drought resistance of mixed forests.

4.3 | Broad perspectives for forest management

In line with our second hypothesis, we found that drought-mortality risk in relatively young (8- to 14-year-old) plantations depends more on intrinsic species resistance than on stand species diversity. Therefore, tree vulnerability and water stress under extreme drought exhibit much greater interspecific variability than diversity-driven intraspecific variability. This implies that the species favoured by forest managers, either through natural regeneration or tree planting, will strongly condition the drought resistance of young stands, even in diverse forests. Interestingly, our results were comparable when analysing the raw data (i.e., including both the variability within and among experiments) and the data standardized within experiment (i.e., focussing on species identity and diversity effects within each experiment). This means that in practice, the preponderant importance of species selection over diversification holds true regardless of whether the selection involves only local species or includes species from different biomes through assisted migration.

Tree diversity effect was not significant in many species and its effect magnitude on drought-mortality risk was commonly (but not always) small. Given the ongoing increase in intensity and frequency of extreme drought, it is likely the tree diversity effects documented in this study will not substantially change the way most species cope with future conditions. Overall, our results suggest that tree diversity has inconsistent effects on drought–mortality risk in young trees. This calls for a better understanding of the underlying mechanisms before tree diversity can be considered an operational adaption tool to extreme drought. Moreover, forest diversification should be considered jointly with management strategies focussed on favouring drought-tolerant species. It should also be noted that all but one of the studied mixtures did not exhibit positive effects in all species. This means that forest managers will in most cases need to identify target species, which will benefit from the mixture and exhibit increased drought resistance, and companion species, which will be used to optimize the growth and survival of the target species without benefiting from the mixture.

Importantly, our study was conducted in young plantations (<14 years), where ecological interactions among species may substantially change along stand development (Jucker et al., 2020). Further study in mature stands will be necessary to draw general forest guidelines for drought adaptation. Nonetheless, our study was based on five experiments with very different soil and climate conditions, and contrasting management (especially initial planting density). This suggests that our main results are generalisable to a large variety of young forests and plantations. More generally, it will be crucial to integrate this new knowledge of tree diversity effects on extreme drought resistance with the other constraints and objectives of forest management. In particular, potential diversity-mediated trade-off between drought risk and growth should be identified to allow designing adaptive silviculture guidelines in production forests and plantations.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from Recherche Data Gouv at https://doi.org/10.57745/F4QITZ.

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