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RESEARCH ARTICLE

Tree diversity reduces variability in sapling survival under drought

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Abstract

1. Enhancing tree diversity may be important to fostering resilience to drought-related climate extremes. So far, little attention has been given to whether tree diversity can increase the survival of trees and reduce its variability in young forest plantations.
2. We conducted an analysis of seedling and sapling survival from 34 globally distributed tree diversity experiments (363,167 trees, 168 species, 3744 plots, 7 biomes) to answer two questions: (1) Do drought and tree diversity alter the mean and variability in plot-level tree survival, with higher and less variable survival as diversity increases? and (2) Do species that survive poorly in monocultures survive better in mixtures and do specific functional traits explain monoculture survival?

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3. Tree species richness reduced variability in plot-level survival, while functional diversity (Rao's Q entropy) increased survival and also reduced its variability. Importantly, the reduction in survival variability became stronger as drought severity increased. We found that species with low survival in monocultures survived comparatively better in mixtures when under drought. Species survival in monoculture was positively associated with drought resistance (indicated by hydraulic traits such as turgor loss point), plant height and conservative resource-acquisition traits (e.g. low leaf nitrogen concentration and small leaf size).
4. *Synthesis*. The findings highlight: (1) The effectiveness of tree diversity for decreasing the variability in seedling and sapling survival under drought; and (2) the importance of drought resistance and associated traits to explain altered tree species survival in response to tree diversity and drought. From an ecological perspective, we recommend mixing be considered to stabilize tree survival, particularly when functionally diverse forests with drought-resistant species also promote high survival of drought-sensitive species.

KEYWORDS
climate change adaptation, functional traits, IDENT, relative extractable water (REW), standardized precipitation evapotranspiration index (SPEI), tree mortality, TreeDivNet

1 | INTRODUCTION

Many public actors, such as policymakers, view tree planting as a pathway to offsetting anthropogenic CO_2 emissions (Goffner et al., 2019; Seddon et al., 2021; Verdone & Seidl, 2017). Large-scale monoculture plantations with fast-growing species are often favoured to quickly increase both forested cover and carbon sequestration (Lewis et al., 2019; Seddon et al., 2019). Yet, such monocultures may trade-off short-term productivity against other ecosystem functions (Baeten et al., 2019; Bukoski et al., 2022; van der Plas et al., 2016), potentially at the cost of long-term productivity and resistance to disturbance factors (Bauhus et al., 2017; Felton et al., 2016). Climate change is expected to intensify regional droughts (Chiang et al., 2021; Spinoni et al., 2019; Xu et al., 2019), which should increase tree mortality risk globally (Anderegg et al., 2020; Forzieri et al., 2021; Hammond et al., 2022; Senf et al., 2020). Building on two decades of experimental work, the scientific community and the Tree Diversity Network (TreeDivNet) in particular, have therefore emphasized the need for diversifying planted forests to foster resilience to drought and other disturbances (Grossman et al., 2018; Jactel et al., 2017; Messier et al., 2021; Paquette et al., 2018).

Higher tree diversity could increase the early survival of planted trees and reduce its variability by increasing drought resistance (Aquilué et al., 2020; Ingrisch & Bahn, 2018; Messier et al., 2021; Newton & Cantarello, 2015). In this early stage, planting species mixtures rather than monocultures could reduce survival uncertainty (i.e. variability) as a form of biodiversity insurance to reduce the risk of plantation failure in an uncertain future (Loreau et al., 2021; Van de Peer et al., 2016; Yachi & Loreau, 1999). This approach is based on common economic principles, where diversity in investments is promoted as a risk management strategy to not 'put all one's eggs in one basket' (Figge, 2004; Schindler et al., 2010, 2015). In the context of biodiversity–ecosystem function experiments, a better understanding of survival variability under drought can contribute to an improved notion of ecological stability. If variability in survival remains lower at high tree diversity under drought, then this shows that the drought impact is dampened and the ecosystem shows more resistance to the disturbance than low-diversity communities such as monocultures (Bauhus et al., 2017). Over time, this ability of the ecosystem to resist disturbance impacts from drought may contribute to stability in other ecosystem functions such as biomass production (Van Meerbeek et al., 2021). Despite this importance of understanding variability in community properties, ecologists have generally shown more interest in how mean values of community properties change in response to abiotic and biotic drivers compared to the properties' variability (Holyoak & Wetzel, 2020).

Two main mechanisms could cause a reduced variability in the survival of young trees under drought. First, diversification can lower variability in stand survival by way of a sampling effect (Baeten et al., 2013; Gamfeldt & Källström, 2007), as it is more likely that mixtures will contain a drought-resistant species compared to a given monoculture. Over time, such species with high survival could also become more dominant in the community, which would constitute a selection effect (Loreau & Hector, 2001). Second, complementary use of resources in functionally diverse communities can reduce survival variability as the intensity of intraspecific competition for water in monocultures may be stronger than overall competition between functionally different species in mixtures (Fichtner et al., 2017; Hajek et al., 2022). Alternatively, shade-tolerant species that are vulnerable to drought may benefit from the shade of diverse neighbours (Kothari et al., 2021). Species could thus grow and survive comparatively better in mixture than in monoculture under drought due to complementarity in resource use and/or facilitation effects (Grossiord, 2020). Tree diversity could hence reduce the variability in survival in mixtures compared to monocultures of different species (Van de Peer et al., 2016).

Uncertainties behind the mechanisms driving biodiversity insurance currently limit its application for enhancing resilience in managed forests and ecological restoration projects (Loreau et al., 2021; Zabin et al., 2022). The magnitude by which tree diversity can reduce survival variability may vary with the functional traits of the species used for the mixtures and environmental conditions (Lhomme & Winkel, 2002; Loreau et al., 2021). Hydraulic traits on their own can be predictive of tree mortality during or after drought (Brodribb et al., 2020; Choat et al., 2018; McDowell et al., 2022; Zhu et al., 2018), but they may vary depending on leaf and whole plant economic traits (Greenwood et al., 2017; Guillemot et al., 2022; H. Liu et al., 2019; Sanchez-Martinez et al., 2020). Under non-drought conditions, water availability may have a low impact on tree performance and survival, resulting in overall high survival with low variability in both monocultures and mixtures. However, under severe drought, monocultures of drought-sensitive species may experience higher mortality compared to monocultures of drought-resistant species, thus increasing variability in survival among stands. In mixtures, higher diversity could provide higher drought resistance, which should reduce survival variability at the stand level (Loreau et al., 2021) while also safeguarding forest multi-functionality (van der Plas et al., 2016) and resilience to other disturbances (Messier et al., 2021). Understanding which functional traits drive the drought survival of trees is essential to decide which species mixtures could promote survival and hence foster drought resilience.

To test how tree diversity and functional traits affect plot-level mean and variability in survival under varying environmental conditions, we used data collected within the Tree Diversity Network (TreeDivNet; Figure 1). We first tested the hypothesis that *tree diversity reduces mortality under drought*, with less variability in survival as tree diversity increases. In addition to using species richness as a predictor of survival, we also looked at the role of functional diversity. Expectations suggest that communities characterized by higher functional dissimilarity in key traits, which define distinct ecological strategies, will demonstrate enhanced survival and diminished variability. This stands in contrast to communities possessing an equivalent species count (i.e. independent of a sampling effect) but exhibiting a lower degree of functional dissimilarity. Next, we tested the hypothesis that *species that survive poorly in monocultures survive better in mixtures*. Species with poor survival in monocultures have identifiable functional traits related to strategies in drought tolerance, resource acquisition, reproduction and whole plant economics that explain their vulnerability to drought.

2 | MATERIALS AND METHODS

2.1 | TreeDivNet

TreeDivNet is a global network of tree diversity experiments that collectively covers 857 ha and over a million trees (www.treedivnet.ugent.be; Paquette et al., 2018; Verheyen et al., 2016). We gathered data on sapling survival from TreeDivNet for over 350,000 trees

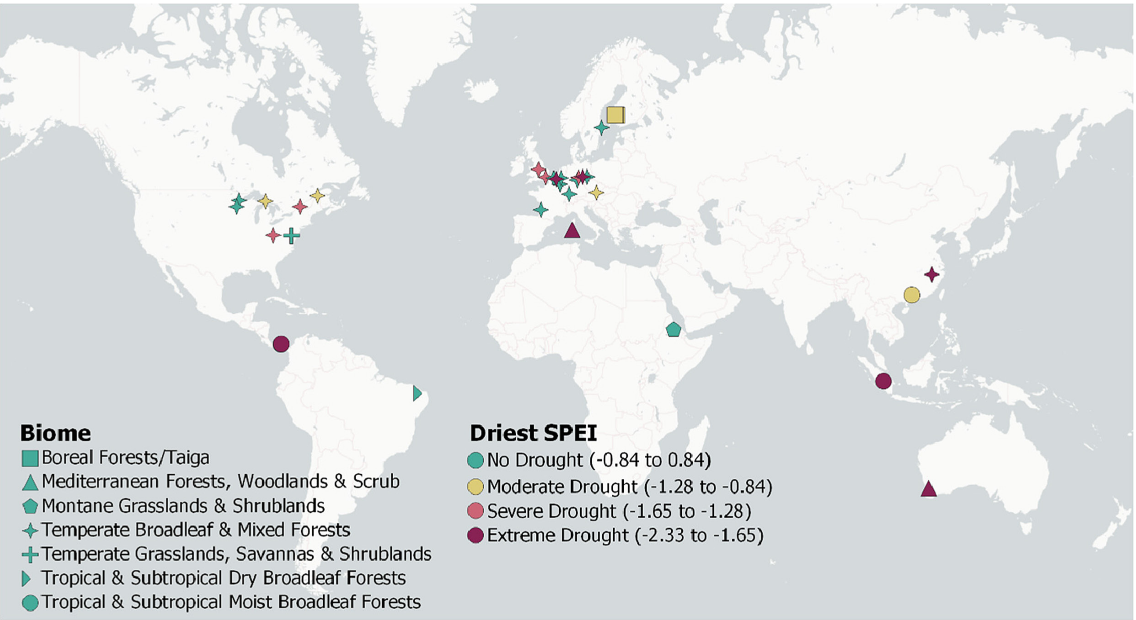

FIGURE 1 Experiment location and comparative drought severity of 34 sites in TreeDivNet. The drought severity of the driest growing season between planting and survival sampling is shown here using the standardized precipitation evapotranspiration index.

from 34 sites located in boreal, temperate, Mediterranean and tropical biomes. In these experiments, trees were planted in various plot-based designs, but always included monocultures and mixtures of two or more species. The species pools for each experiment varied and generally consisted of native species adapted to local growing conditions (Supplementary Metadata M1). For this analysis, we compiled survival data from all diversity levels within experiments at an early stage of development and excluded plots with treatments other than diversity (e.g. water addition, fertilization etc.) to avoid confounding between experiments.

2.2 | Tree survival data

We attempted to include survival data from each site around year three after planting, to provide a balance between data availability and comparability among sites. As not all sites provided data for year three, we used survival data of saplings and seedlings for between two (i.e. after two entire growing seasons) and 5 years after planting (Supplementary Metadata M2). This allowed us to capture the effects of site-specific drought events within multiple growing seasons. The first growing season was not included in the analysis to minimize any nursery and management effects on initial establishment. The upper end of the sampling period was set at 5 years after planting to avoid the potential effects of crown closure and light limitation on tree performance and survival. While crown interactions may generally be limited (given the age of the saplings), whether significant root interactions are present will depend on the planting density in the site, growth rates of the included species and the climate system (Sinacore et al., 2017; Van de Peer et al., 2018). Each experimental site provided survival data for a single year (median: year three), yielding data from 363,167 saplings representing 167 tree species collected from 3744 plots, 34 sites and seven biomes (Figure 1, Supplementary Metadata M1).

2.3 | Climate and drought indices

A meteorological drought is commonly defined as any prolonged period with a meteorological water deficit, relative to the long-term local climatic conditions (Slette et al., 2019). Drought periods can be identified in this way via the standardized precipitation evapotranspiration index (SPEI). SPEI is calculated from the local monthly climatic water balance (precipitation minus potential evapotranspiration) over a selected time window of interest, with its deviation from the long-term mean expressed as a standardized Gaussian variable with a mean of zero and a standard deviation of one (Beguería et al., 2014; Vicente-Serrano et al., 2010). As such, drought severity quantified via SPEI disregards soil moisture or inherent climatic aridity. Instead, SPEI can identify dry periods with an abnormal climatic precipitation deficit for a given location and climate system (Slette et al., 2019) that can be discretely categorized into four drought classes related to drought severity (Agnew, 2000; Figure 1).

We calculated SPEI over a 30-year climate period (1991–2021) for each study site to ascertain whether any dry growing seasons occurred within the year of planting and the year of the survival survey. We downloaded the ERA5-Land monthly averaged data (1990–2021) for total precipitation and potential evaporation at 0.1°×0.1° or 9 km horizontal resolution for each grid cell that contained a focal site, as well as air temperature measured at 2 m height. To estimate the site-specific length of the growing season, we obtained data on the total leaf area index (LAI) from ERA5Land (Figure S1). We calculated the start and end of the growing season as the first and last month, respectively, with total LAI greater than the annual mean (Supplementary Metadata M1 and Supplementary Information 1.1). For tropical systems with year-round biomass production, this growing season period can be interpreted as the period of peak biomass production. The SPEI of each site was calculated with the *spi* function in R (Beguería & Vicente-Serrano, 2017) over the site-specific growing season, that is accounting only for drought in the growing season. To estimate drought intensity at each site, we used the minimum SPEI observed between the year of planting and the survival survey. We used the Ecoregions2017 dataset of Dinerstein et al. (2017) to classify each site into one of 846 global ecoregions and one of 14 terrestrial biomes (see Supplementary Metadata M1) based on its point coordinate.

To characterize the drought intensity in terms of drought stress experienced by the trees, we also calculated the relative extractable water (REW) in the soil of each site for the period January 1990 to December 2022 (see Supplementary Information Section 1.1.2). To calculate REW, we used the process-based model SurEau (Ruffault et al., 2022). SurEau is dedicated to the computation of extreme drought stress impacts on vegetation using plant hydraulic theory, but includes all the functions to compute forest stand water balance (Granier et al., 1999; Ruffault et al., 2013). The model is driven by hourly climatic data aggregated per day, soil parameters (e.g. soil water retention curves, soil depth), plant parameters describing stomatal regulation and resistance to drought-induced cavitation as well as LAI. The model estimates the stand water balance and the water potential of the trees at an hourly time step. The REW is computed from soil water content as follows:

$$\mathrm{REW} = \frac{\theta - \theta_{\wp}}{\theta_{fc} - \theta_{\wp}}$$

where θ is the actual soil water content, θ_{fc} is the soil water content at field capacity and $\theta_{\wp}$ is the soil water content at the wilting point (i.e. at −1.5 MPa). The REW equals 1 when soil water is at field capacity, 0 when soil water content reaches the wilting point and can have negative values in SurEau at soil water content below the permanent wilting point. The latter can occur due to delayed stomatal closure or residual transpiration. The model was applied at each site using vegetation parameters specific to one species representative of the biome and the local species pool of each experiment (see Supplementary Metadata M3). The trait data were gathered from global databases (see Section 2.4). The soil parameters were extracted from the SoilGrids database (Poggio et al., 2021). The input LAI data for the SurEau model were obtained from the high resolution (333 m) Copernicus database (Baret et al., 2013; Lacaze et al., 2015). The climate data for each study was obtained from ERA5-Land hourly data (Muñoz-Sabater et al., 2021). The minimum monthly REW during the growing season was calculated as a measure of drought intensity. The drought stress threshold is considered as being at a REW value below 0.4 (Granier et al., 1999).

2.4 | Functional traits

We collected species-level hydraulic, leaf and whole plant economic traits from various sources to test the relationship of traits with species survival. Not only did we include hydraulic traits that may indicate a plant's drought strategy, we also considered traits related to reproductive strategy, resource-acquisition strategy and whole plant economics to provide a holistic understanding of which traits can influence species' responses to drought in this multi-site study (see Supplementary Metadata M4 for an overview of the traits and the strategies they represent). The hydraulic traits were water potential at which 50% of xylem cavitates (P50, unit: MPa), minimum water potential (Ψmin, unit: MPa) and turgor loss point (TLP, unit: MPa), all collected from multiple sources (Bartlett et al., 2012; Choat et al., 2018; Guillemot et al., 2022; Kunert & Tomaskova, 2020; Larter et al., 2017; Lens et al., 2016; Liu et al., 2019; Lobo et al., 2018; Maitner, 2022; Martin-StPaul et al., 2017; Sjöman et al., 2015; Skelton et al., 2021; Song et al., 2022; Ziegler et al., 2019). Leaf traits and whole plant economic traits were collected from the TRY database (Kattge et al., 2011) and the BIOMASS database (Réjou-Méchain et al., 2017). The included leaf traits were leaf mass per area (LMA, unit: $mg\,mm^{-2}$), leaf nitrogen (N) concentration (unit: $mg\,g^{-1}$), leaf phosphorus (P) concentration (unit: $mg\,g^{-1}$) and leaf size (unit: cm^2). The whole plant economic traits were wood density (unit: $g\,cm^{-3}$) and maximum height (unit: m). We also included seed mass (unit: g) as a trait related to reproduction and contributing to a plant's ecological strategy (Díaz et al., 2016; Westoby, 1998). Trait data availability was variable among species, with only 24 of the 168 species having values for the complete set of traits, but widely collected traits (e.g. seed mass, LMA, height, …) were much more available than measurement-intensive traits such as the hydraulic ones (see Supplementary Metadata M4 for the data availability between traits and species). We chose not to impute trait values and instead constrained the analysis to those species with available trait values from databases. Furthermore, trait values found in databases mostly originated from adult trees and not saplings. Hence, we did not interpret any trait values as stand-alone findings or used them to estimate ecosystem functions or processes from our experimental plots. We rather applied the trait-based approach to get an integrated indication of the ecological strategy of the species included.

We calculated plot-level functional diversity using Rao's quadratic entropy (Rao's Q). Rao's *Q* is the abundance-weighted variance of trait dissimilarities between all species pairs and hence a measure of functional divergence (Schleuter et al., 2010). It was calculated using the *fundiversity* package in R (Villéger et al., 2008), on a trait dissimilarity matrix using the Gower distance, and as such, it was able to handle the missing trait values in our dataset. Given the constraining trait data availability between plots, we did not compute any community weighted means (CWM) and performed an analysis of species-level survival instead.

2.5 | Analysis of plot-level survival

We tested whether the change in between-plot variability (i.e. variance) in survival along the species diversity gradient was dependent on drought intensity. Survival data were scored as a binary tree-level condition (0 = dead, 1 = alive). We aggregated data to the plot level, calculating the percent survival in each plot by dividing the number of living trees by the total number of planted trees, regardless of species. Plot-level survival was used as the response variable in a hierarchical beta regression modelled within a Bayesian framework.

The beta distribution is a flexible exponential distribution well suited to modelling ecological phenomena measured using proportional data ranging between 0 and 1 (Damgaard & Irvine, 2019; Douma & Weedon, 2019). The beta distribution is defined by an expected value μ (logit link function) and a precision parameter φ (log link function) that can be moderated separately (Damgaard & Irvine, 2019). The expected value μ can be intuitively interpreted as plot-level mean survival, so the model quantifies how mean survival changes with tree species diversity and drought. The precision parameter φ is the inverse of a dispersion parameter; as for fixed μ, the larger the φ value, the smaller the variance in the response variable. The φ parameter thus allows the modelling of heteroscedasticity, in this case, between-plot variability in percent survival. A higher value of φ will thus result in a lower variability in the distribution.

Each model included an interaction term between species diversity and drought, which quantified how changes in variance in survival along the diversity gradient are moderated by drought. Four versions of the model were fitted (see Supplementary Information Section 1.2.1), one for each combination of the diversity metrics (species richness and functional diversity) and the drought index (SPEI and REW). Inter-tree planting distance (median: 1.36 m) was included as a covariate in the model to control for density effects. The hierarchical structure of the data was accounted for by including group-level (random) effects for biome and site within biome. Plot size was not included in the models as it did not explain any residual variation (see Supplementary information Section 1.2.1). This multilevel model was fitted using the R package *brms* function (Bürkner, 2017) in R version 4.2.1 (R Core Team, 2021). Predictions from this model were performed on a new dataset containing a gradient of 1–6 species (a common gradient in TreeDivNet experiments, Supplementary Metadata M1) and the boundary values of the four SPEI classes (see colour codes on Figure 1) or four REW values (0.6 = no drought stress, 0.4 = drought stress threshold, 0.2 = drought stress, 0 = permanent wilting point) as input data. For the predictions of functional diversity effects, we used the observed gradient in Rao's Q (between 0 and 0.2). Variability in survival is presented on a 90% prediction interval to avoid sampling instability in the presented tails of the posterior distribution (Kruschke, 2014; McElreath, 2020). For further details on model specifications, see Supplementary Information Section 1.2.

2.6 | Analysis of species-level survival

To test for differences in species-level drought survival between monocultures and mixtures, the average survival of a species at a given richness level was subtracted from the average survival in monocultures of that species (Δsurvival). We expected that increases in survival in mixtures would be more pronounced under drought and in those species that survived more poorly in monoculture. The Δsurvival value was fitted as the response variable to the survival of that species in monoculture (see also King et al., 2023), in interaction with SPEI and REW using a Gaussian distribution and the *brms* package (Bürkner, 2017). See Supplementary Information, Section 1.2.2, for further details.

To quantify the relationship between functional traits and species survival, we examined the effect of the 10 different functional traits on species survival in monoculture. Rather than imputing missing trait data, we fitted separate models for each functional trait to account for differences in data coverage between traits. Each trait was modelled separately to estimate its effect on species survival in monoculture. The hierarchical structure of the data was accounted for by including group-level (random) effects for biome and site within biome. This multilevel model was fitted using the R package *brms* (Bürkner, 2017) in R version 4.2.1 (R Core Team, 2021). The effects are presented on a 90% credible interval (CI). For further details, see Supplementary Information, Section 1.2.2.

We constructed a correlation plot to display the pairwise correlations between traits and support the interpretation of the results. In addition, we used principal component analysis (PCA) to graphically depict the multi-dimensional correlation structure of all functional traits using the function *bpca* of the R package (Faria et al., 2023). The PCA only included the 24 species with complete records for all 10 traits.

3 | RESULTS

3.1 | Analysis of plot-level survival

Mean plot-level survival was not sensitive to tree species richness and drought conditions, as indicated by SPEI and REW. In contrast, variability in survival was sensitive to richness and drought (Figure 2). Predictions from the posterior distributions using a 1–6 species richness gradient as input values showed that mean survival ranged from 88% under non-drought conditions (SPEI = 0) to 85% under extreme drought (SPEI = −1.65) (Figure 2a), with a near equal pattern emerging with REW as the predictor variable (Figure 2b). This means that plot-level survival was not increased by tree species richness under any drought intensity. Variability in survival decreased with increasing species richness and increased with drought intensity, but with an interactive effect on the slope of the precision parameter φ. The effect on the precision parameter φ showed that richness reduced variability more with increasing drought intensity (Supplementary Information Figure S11). Under non-drought conditions (SPEI = 0 and similarly for REW = 0.6), the model estimated that the 90th percentile of survival ranged from 65% to 100% for monocultures but from 70% to 100% for six-species mixtures. Under extreme drought conditions (SPEI = −1.65, REW = 0), each additional species increased survival rate precision by 2 percentage points. This means that the 5% poorest surviving monocultures (falling outside the low-end of the 90th percentile range) had a predicted maximum survival of ca. 50% that increased to ca. 60% for six-species mixtures. The density covariate was negative in value, indicating higher survival in plots with a lower inter-tree planting distance. For site-specific model outcomes, see Supplementary Information 2.1.2.

Mean survival marginally increased in response to functional diversity (Rao's Q entropy) and the drought indicators SPEI (Figure 3a) and REW (Figure 3b). This effect was evident on a 90% CI (Figure S12), with an added 2%–5% points over the observed functional diversity gradient depending on the drought indicator (Figure 3). Variability in survival consistently decreased in response to functional diversity, albeit more strongly when using SPEI as the drought indicator compared to REW. SPEI and functional diversity had an interactive effect on the precision parameter φ and hence the variance (Figure S13), indicating that variability in survival decreases faster in response to functional diversity with increasingly negative SPEI (Figure 3a). The slope of this interactive effect was different when using REW as the indicator, showing a smaller decrease in variability with increasing functional diversity as REW approached zero (Figure 3b).

3.2 | Analysis of species-level survival

Species with low survival in monoculture survived comparatively better in mixture, but this effect varied between drought indicators. This effect was only marginal for SPEI, showing a consistent negative slope for the relationship of monoculture survival with Δsurvival (Figure 4a). At high monoculture survival, the regression line shows a slight negative response, but with considerable variability in observed differences. However, a clear interaction with REW was exhibited, showing that once the drought stress threshold (REW = 0.4) was surpassed, the slope of the linear relationship was more negative, leading to a larger difference (Δsurvival) for species with low survival in monoculture (Figure 4b, Supplementary Information Section 2.2.1).

Maximum height, water potential at the turgor loss point (Ψtlp), leaf N concentration, leaf size and leaf P concentration showed

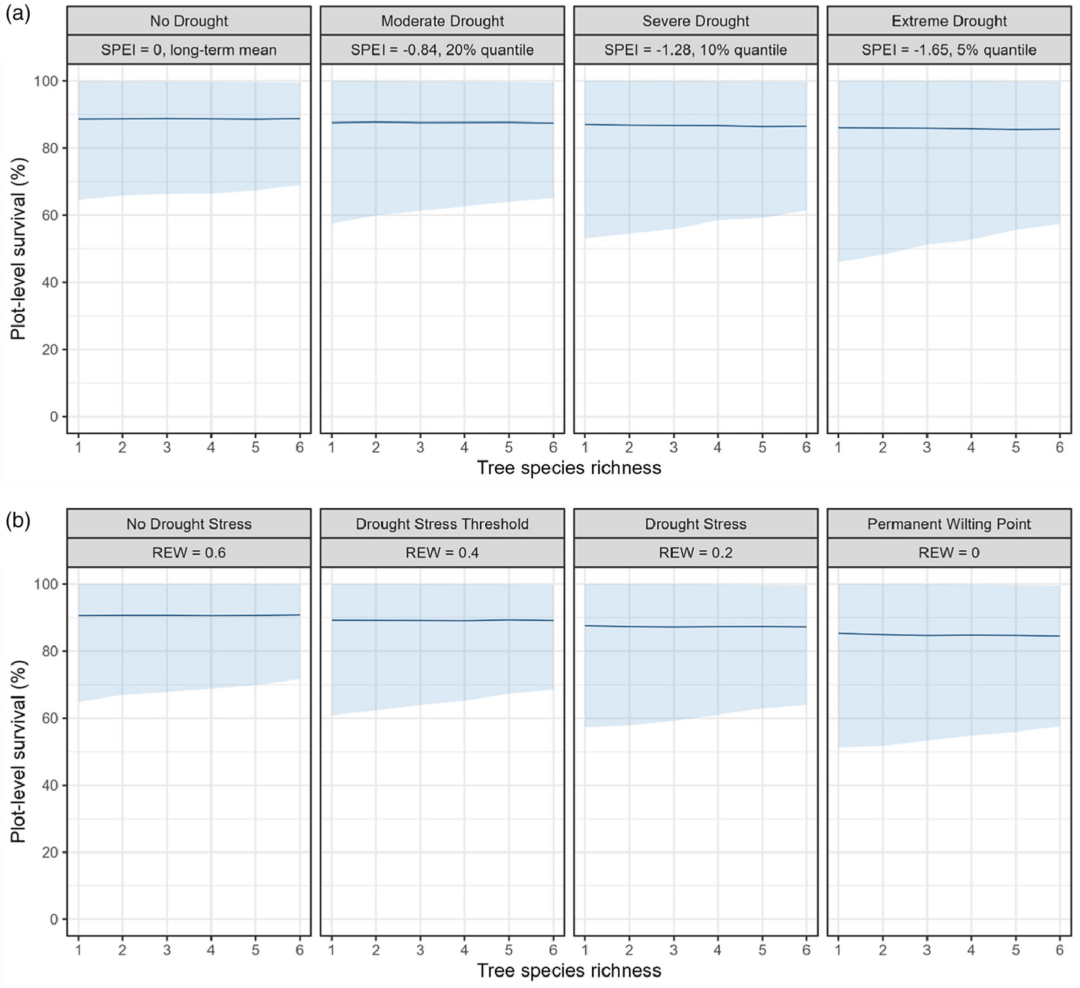

FIGURE 2 Changes in plot-level percent survival with increasing species richness at four levels of growing season drought are indicated by SPEI (panel a) and REW (panel b). Predicted mean survival (blue line) and its variability (90% percentile, light blue shaded area) are presented for an input dataset with a species richness ranging from 1 to 6 species.

significant (90%) effects on species survival in monoculture (Figure 5). With increasing maximum height and leaf P, survival in monoculture increased. Ψtlp showed a negative effect, meaning that species with less negative Ψtlp (i.e. lower leaf drought resistance and/or water-saving strategy) showed a lower survival in monoculture. The other hydraulic traits (ΨP50 and Ψmin) showed similar effect sizes but with larger variability, so that the effects cannot be reported as significant on a 90% CI. Species with high leaf N concentration and large leaf size had lower survival in monoculture. The pairwise correlation matrix using Spearman's rank correlations showed that the hydraulic traits (Ψtlp, ΨP50 and Ψmin) are highly correlated between themselves ($p<0.001$) and with wood density ($p<0.001$). The leaf traits (leaf N, leaf P, LMA, leaf size), seed mass and maximum height showed varying pairwise correlations (Supplementary Information Section 2.2.2). The first axis of the PCA alone explained 30.29% of the multi-dimensional functional space variation; it was dominated by characteristics of hydraulic resistance to drought (lower ΨP50, Ψtlp and Ψmin). This first axis was to a lesser extent associated with small leaves and low leaf N and P concentrations, a large seed mass and a high wood density, but only in a limited manner with height (Supplementary Information Section 2.2.3).

4 | DISCUSSION

Our analysis of sapling survival showed that higher tree species richness and functional diversity reduced variability in survival. This effect became stronger as drought severity increased. Using a species-based approach, we found that species with low survival in monocultures survived comparatively better in mixtures when under drought (as indicated by REW and independent of SPEI). A higher species survival in monoculture was associated with drought resistance (characterized by hydraulic traits), greater maximum height and conservative resource-acquisition traits (e.g. low leaf size and low leaf N concentration). These results highlight: (1) the importance of tree diversity as a form of insurance to increase sapling survival during drought; and (2) the importance of drought resistance and associated traits to explain altered tree species survival in response to

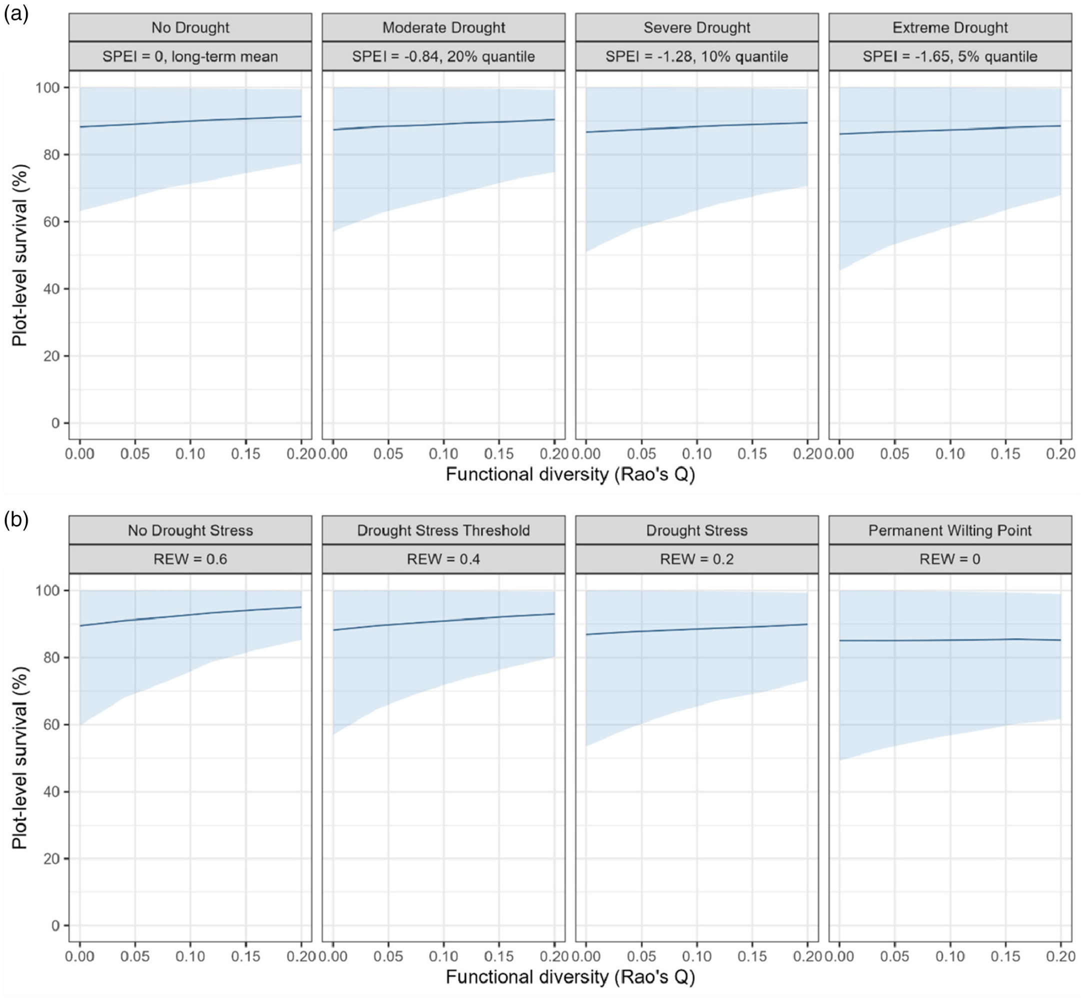

FIGURE 3 Changes in plot-level percent survival with increasing functional diversity at four levels of growing season drought are indicated by SPEI (panel a) and REW (panel b). Predicted mean survival (blue line) and variability in survival (90% percentile, light blue shaded area) are presented.

tree diversity and drought, showing that drought-sensitive species survive comparatively better in mixtures compared to monocultures.

4.1 | Tree diversity reduces variability in survival

Tree species richness did not affect the mean survival of trees but decreased its variability, which is in line with a sampling effect. Mean survival across tree diversity levels was stable at around 85%, which is higher than the 50% survival commonly reported for managed plantations (Banin et al., 2023). In mature forests of Northern America, a clear link between higher tree diversity (Searle et al., 2022) and density (Bradford et al., 2022) on the one hand and lower mean survival on the other was recently reported, but with unclear effects on variability. In contrast, the experimental sites within TreeDivNet are generally young, small in scale (a few ha) and are designed to maximize scientific output (Grossman et al., 2018). Because of this, experimental site managers may invest more in management (e.g. replanting or weed and pest control in the first year) and careful species selection, which could boost mean survival rates compared to commercial plantation forests. In addition, densities in the experiments range from high to hasten interactions between trees (Tobner et al., 2014) to intermediately dense to reflect local silvicultural practice (Verheyen et al., 2013), which may explain the negative density effect that we found in our statistical analysis. Nonetheless, such experiments are needed to accurately quantify the effects of tree diversity and drought on variability in survival with pools of functionally dissimilar species (Baeten et al., 2013; Nock et al., 2017).

While tree species richness effects on mean survival were not observed, we found evidence that functional diversity increased plot-level survival, suggesting that complementary resource uptake and/or facilitation occurred under drought at an early age (Fichtner et al., 2017; Sinacore et al., 2017). Indeed, Urgoiti et al. (2023) too have shown that the mixing of species with contrasting resource-use strategies can decrease rates of mortality (i.e. self-thinning) in a tree diversity experiment. We found that variability in survival was consistently reduced at higher tree species richness and with functional

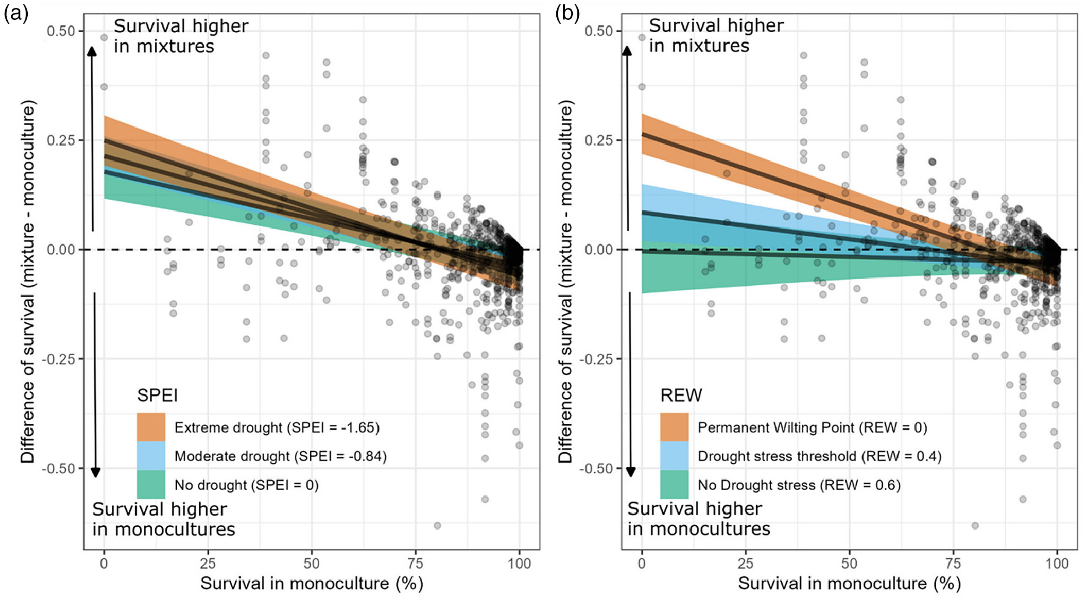

FIGURE 4 Difference in species survival percentage (Δsurvival) in response to the survival of that species in monoculture, varying by SPEI (panel a) and REW (panel b).

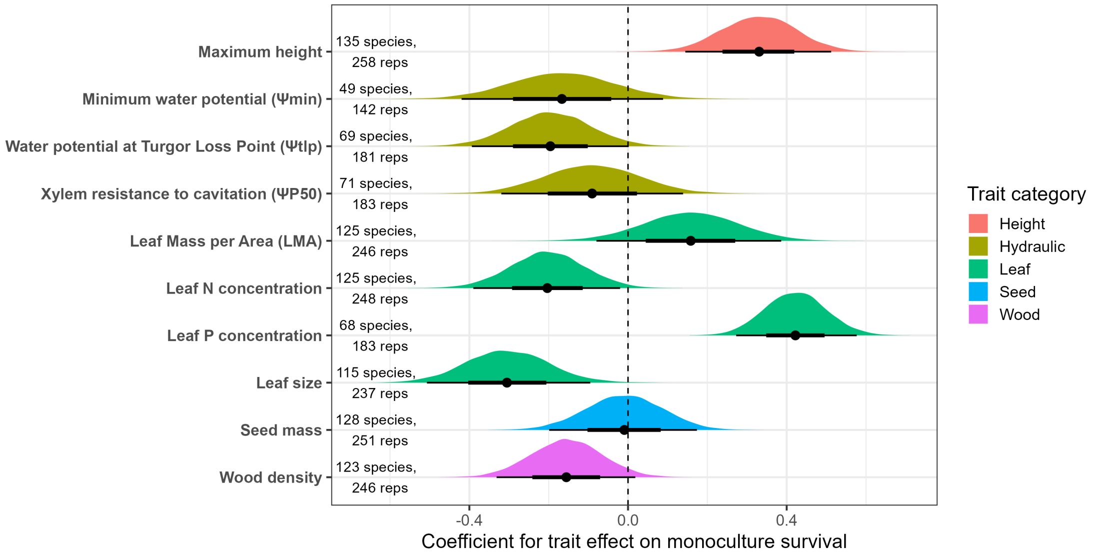

FIGURE 5 Effects of functional traits on mean species survival in monoculture. The posterior distribution of the coefficients for the expected value parameter (μ, logit link function) is displayed for each trait. The effects are displayed per unit increase of the trait value (i.e. one standard deviation). The number of species with trait values and the number of monocultures are listed for each trait. Credible intervals (CI) presented here are on 50% (bold line) and 90% CI (thin line). Estimates with CI's not crossing the zero line are significantly different at 90% CI.

diversity too, which is consistent with a sampling effect (Baeten et al., 2013; Gamfeldt & Källström, 2007; Loreau & Hector, 2001). Simply put, it is more likely to have species that survive well under drought in a mixture than in a monoculture (that is, when species are not chosen specifically for their drought resistance). However, mean survival in mixtures cannot exceed the survival of monocultures of the most drought-resistant species when drought is the major driver of mortality. Tree diversity simply reduced survival variability in more functionally diverse communities, and perhaps due to other site-specific biotic and abiotic disturbances in addition to drought (Messier et al., 2021).

Tree diversity effects on early survival may have important implications for post-drought development and long-term forest functioning (Bauhus et al., 2017; Hisano et al., 2019; Serra-Maluquer et al., 2020). Reducing the risk of tree mortality is crucial during the sapling stage to ensure growth recovery and the development of plantation forests that perform multiple ecosystem functions well (Gessler et al., 2020). Of course, survival in the sapling stage does not necessarily imply long-term survival or sustained growth. After the sapling stage, young trees remain vulnerable to drought (Bretfeld et al., 2018), but diversity can reduce drought impact by, for example, promoting growth recovery via complementarity in resource use (Fichtner et al., 2020; Schnabel et al., 2021; Sinacore et al., 2019).

4.2 | Functional traits influence species' drought response in mixtures and monocultures

Under drought stress, species that survived poorly in monoculture survived comparatively better in mixture. This finding suggests that tree-to-tree interactions can already occur in young mixtures and can influence survival when an acute water limitation occurs. This likely resulted from stronger intraspecific competition in monocultures compared to mixtures (Fichtner et al., 2017; Hajek et al., 2022; King et al., 2023). Alternatively, or in addition, shade-tolerant species that are vulnerable to drought stress may have benefitted from the shade of diverse neighbours (Kothari et al., 2021). Here, we found that species survival in monoculture was strongly associated with leaf drought resistance (lower Ψtlp) and maximum height. The survival of drought-sensitive species was thus improved when they were planted in mixtures. These findings strongly suggest that mixing of drought-sensitive and drought-resistant species can increase total plot or plantation level survival (Ammer, 2019; Forrester, 2015; Su et al., 2022).

The finding of increased survival under drought resistance was associated with functional traits representative of a conservative resource-use strategy. We found that low leaf size and low leaf N concentration were associated with higher species survival in monoculture (Díaz et al., 2016; Reich, 2014; Wright et al., 2004). Surprisingly, leaf P concentration showed an opposite trend, indicating higher survival in species with a higher leaf P concentration. This result may be due to the fact that species with leaf P trait data were mostly from temperate biomes (Supplementary Metadata M4). Another surprising finding at first glance is the positive effect of maximum height and the negative effect of wood density on monoculture survival. High wood density and low maximum plant height are known to promote survival in arid biomes and hence a viable ecological strategy there is to be small in stature with high wood density (Guillemot et al., 2022; Liu et al., 2019). However, tree survival together with plant height is usually lower in stressful arid biomes as opposed to the survival of comparatively larger tree with lower wood density in temperate biomes (Liu et al., 2019). This comparison of within-environmental context findings from literature versus the across-context synthesis in our work may be the cause of our counter-intuitive observed positive effect of maximum plant height and negative effect of wood density on survival. We also found strong positive pairwise correlations between the ΨP50, Ψtlp and Ψmin and wood density. Furthermore, the PCA on the subset of complete trait data showed that functional traits indicative of a conservative resource-use strategy (Díaz et al., 2016; Reich, 2014; Wright et al., 2004) correlated with a negative P50 and TLP along the first axis of variation (30% of variance explained). These results indicate that drought resistance strategies are coordinated with other ecological strategies that may promote survival (Kröber et al., 2014; Liu et al., 2019). Predicting species mortality solely from hydraulic traits can be uncertain given their correlation with other functional traits, but hydraulic characteristics can still be used to rank or define species drought resistance and their capacity to survive climate extremes (Trugman et al., 2021).

4.3 | Application of tree diversity to reduce variability in survival

Theoretically, reducing survival uncertainty by increasing tree diversity does not require that trees are planted in mixtures, as planting monocultures of several species could also improve survival at the landscape scale (Loreau et al., 2021). However, from a functional perspective, we found that mixtures of drought-resistant and drought-sensitive species respond differently to the drought disturbance compared with monocultures. First, we found that the survival of drought-sensitive species is enhanced when growing in mixtures. Hence, planting monocultures of different (drought-sensitive) species in a landscape puts the plantations more at risk of dramatic planting failure in the case of increasingly likely intensive droughts. Such a planting failure would result in a significant loss of tree cover, with potential disproportional effects on associated biodiversity, microclimate, soil development and erosion and evapotranspiration (Allen, 2007; Batllori et al., 2020; De Frenne et al., 2019; Senf et al., 2018). Hence, a landscape consisting of large-scaled monocultures from a varied species palette would not be equally functioning under a future climate as a landscape with mixtures from that same varied species palette (Messier et al., 2021) or an already present diverse ecosystem (Fleischman et al., 2020). The risk-spreading role of tree diversity in the sapling stage may be pivotal as a climate change adaptation measure in forest landscapes, in order to safeguard functions such as productivity or carbon storage in the long term (Doak et al., 1998; Lehman & Tilman, 2000; Tilman, 1999).

Even so, trade-offs in the resource-use strategy of tree species should be considered when selecting tree species for planting, so as to balance the outcomes on ecosystem functions and services (Baeten et al., 2019). Drought resistance is correlated to some degree with a conservative resource-use strategy, and such a strategy invokes a trade-off of lower growth rates and short-term carbon uptake against longevity (Díaz et al., 2016; Guillemot et al., 2022). On the other end, resource-acquisitive species are characterized by fast growth and a short life-span of plant tissues, but may boost carbon uptake and ecosystem productivity in the short term (Díaz et al., 2016; Reich, 2014) instead of the long term (Büntgen et al., 2019). Especially in arid environments, the combination of shade-casting fast-growing pioneering species with slow-growing late-successional species is known to benefit the survival and spontaneous recovery of other vegetation as well (Aerts et al., 2007; Elliott et al., 2023; Grossiord, 2020; Poorter et al., 2019). Our findings support that drought-sensitive species are better suited to combat drought effects when in mixture compared to monoculture, and can hence still contribute to the multifunctionality of forests (Baeten et al., 2019; Gillerot et al., 2020; Grossiord et al., 2014; Liu et al., 2022; van der Plas et al., 2016; Zhu et al., 2018).

In conclusion, our findings are relevant to the adaptation of forest management strategies in an era of rapid global environmental change and increasing anthropogenic disturbances. First, more functionally diverse young plantations exhibited lower variability in survival, which can reduce the uncertainty in achieving successful forest development. Second, tree species mixtures of drought-resistant and drought-sensitive species could improve survival and enhance resilience. The application of these findings can contribute to forest management by stabilizing survival of young plantations where climate change and other disturbances are anticipated to increase mortality. Even if managers increase tree diversity to focus on other ecosystem functions (e.g. productivity and nutrient retention), this approach will not decrease the benefits arising from reduced variability in early survival. From an ecological perspective, we recommend consideration of planting intimate tree mixtures to stabilize tree survival and create functionally diverse, drought-adapted, managed forests.

AUTHOR CONTRIBUTIONS

Haben Blondeel: Lead author. Performed data analysis and lead manuscript writing. Joannès Guillemot, Nicolas Martin-StPaul and Arsène Druel: Auxiliary data analysis and writing. Simon Bilodeau-Gauthier, Andrew Hector, Christian Messier and Bart Muys: Conceived an initial version of the manuscript. Commented on later version. Jürgen Bauhus, Charlotte Grossiord and Hervé Jactel: Conceived ideas for the manuscript. Commented on later version. Joel Jensen and Hernán Serrano-León: Aided in data synthesis. Commented on later version. Harald Auge, Nadia Barsoum, Emiru Birhane, Helge Bruelheide, Jeannine Cavender-Bares, Chengjin Chu, Jonathan R. Cumming, Abebe Damtew, Nico Eisenhauer, Olga Ferlian, Sebastian Fiedler, Gislene Ganade, Douglas L. Godbold, Dominique Gravel, Jefferson S. Hall, Dirk Hölscher, Kristin B. Hulvey, Julia Koricheva, Holger Kreft, Cathleen Lapadat, Jingjing Liang, Xiaojuan Liu, Céline Meredieu, Simone Mereu, Rebecca Montgomery, Lourdes Morillas, Charles Nock, Alain Paquette, John D. Parker, William C. Parker, Gustavo B. Paterno, Michael P. Perring, Quentin Ponette, Catherine Potvin, Peter B. Reich, James Rentch, Boris Rewald, Hans Sandén, Katherine Sinacore, Rachel J. Standish, Artur Stefanski, Patrick C. Tobin, Michiel van Breugel, Marina Vergara Fagundes, Martin Weih, Laura J. Williams and Mo Zhou: Contributed with data from unique experiment. Commented on later version. Michael Scherer-Lorenzen and Kris Verheyen: Coordinates TreeDivNet. Contributed with data from unique experiment. Commented on later version. Lander Baeten: Conceived ideas for manuscript, aided in data analysis and lead Principal Investigator for study. Commented on later version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. Andrew Hector, Chengjin Chu and Xiaojuan Liu are on the Editorial Board of Journal of Ecology, but took no part in the peer review or decision-making processes for this manuscript.

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DATA AVAILABILITY STATEMENT

Data are accessible on figshare: https://doi.org/10.6084/m9.figshare.25359751 (Blondeel, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Supplementary text, figures and tables.

Supplementary Metadata M1. Site information on experimental design and environmental variables.

Supplementary Metadata M2. Available tree survival surveys by experimental site, for the years 1999–2020.

Supplementary Metadata M3. Input variables for running the SurEau water balance model.

Supplementary Metadata M4. Functional trait values for each species in the synthesis dataset.

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