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## Research Paper

## Climatic conditions, not above- and belowground resource availability and uptake capacity, mediate tree diversity effects on productivity and stability



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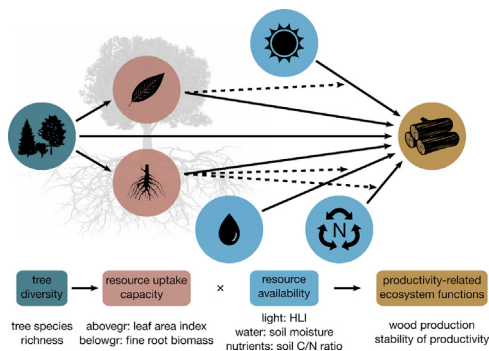
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## HIGHLIGHTS

- We studied tree diversity effects on productivity and stability of European forests.
- Impact of above and belowground resource availability and uptake capacity was small.
- Diversity effects on forest productivity were only observed in arid regions.
- Diversity effects on forest stability were only observed in humid regions.
- Tree diversity effects are largely mediated by differences in climatic conditions.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Tree species diversity promotes multiple ecosystem functions and services. However, little is known about how above- and belowground resource availability (light, nutrients, and water) and resource uptake capacity mediate tree species diversity effects on aboveground wood productivity and temporal stability of productivity in European forests and whether the effects differ between humid and arid regions. We used the data from six major European forest types along a latitudinal gradient to address those two questions. We found that neither leaf area index (a proxy for light uptake capacity), nor fine root biomass (a proxy for soil nutrient and water uptake capacity) was related to tree species richness. Leaf area index did, however, enhance productivity, but negatively affected stability. Productivity was further promoted by soil nutrient availability, while stability was enhanced by fine root biomass. We only found a positive effect of tree species richness on productivity in arid regions and a positive effect on stability in humid regions. This indicates a possible disconnection between productivity and stability regarding tree species richness effects. In other words, the mechanisms that drive the positive effects of tree species richness on productivity do not per se benefit stability simultaneously. Our findings therefore suggest that tree species richness effects are largely mediated by differences in climatic conditions rather than by differences in above- and belowground resource availability and uptake capacity at the regional scales.

## 1. Introduction

Forests cover ~30% of the Earth's land surface, contain ~80% of terrestrial biodiversity (FAO, 2018; WWF, 2020), and deliver a wide range of ecosystem services to humans, such as the production of timber and food (Brockerhoff et al., 2017; Gamfeldt et al., 2013), sequestering carbon (Pan et al., 2011) and contributing to human health and well-being (Rasolofson et al., 2018). Yet, forest ecosystems and their biodiversity are at risk globally because of deforestation, climate change and other global change drivers (Curtis et al., 2018; Malhi et al., 2008). Since biodiversity can directly promote ecosystem functioning (van der Plas, 2019), biodiversity loss may threaten the provision of diverse forest ecosystem functions and services (e.g. Ratcliffe et al., 2017; Schuldt et al., 2018; Trogisch et al., 2017). Therefore, knowing the underlying mechanisms driving biodiversity-ecosystem functioning (BEF) relationships is crucial for better predicting the consequences of biodiversity loss for forest ecosystems (Forrester and Bauhus, 2016; Grossman et al., 2018; Scherer-Lorenzen, 2014).

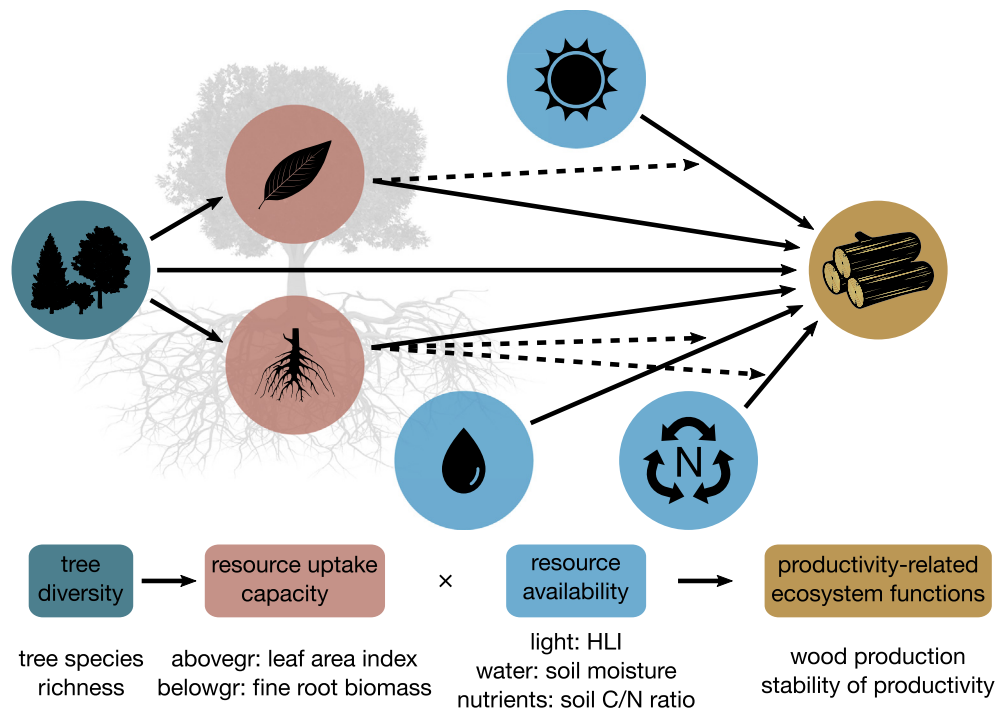
Complementarity is often considered as one of the fundamental mechanisms responsible for the positive effects of tree species diversity on forest primary productivity (a frequently measured component of ecosystem functioning) (Barry et al., 2019; Jing et al., 2021; Scherer-Lorenzen, 2014; Trogisch et al., 2017). For instance, complementarity in resource uptake ensures a higher amount of resources captured and thus a higher productivity (Forrester and Bauhus, 2016). Indeed, mixed-species forest stands generally have complementary crown and root characteristics to efficiently use above- and belowground available resources, including light, water, and nutrients (Morin et al., 2011; Peng et al., 2020; Williams et al., 2017). However, complementarity in root characteristics is much less studied than complementary crown (Forrester and Bauhus, 2016). Moreover, while complementarity in resource uptake has been well described and is likely to be the main determining mechanism driving BEF relationships for a given forest stand, it remains largely unknown how above- and belowground resource availability and resource uptake capacity interactively affect forest productivity and other ecosystem functions.

Increasing tree species diversity has been also shown to enhance the temporal stability (or constancy (Van Meerbeek et al., 2021)) of productivity (Jucker et al., 2014a; Morin et al., 2014). Temporal stability of productivity involves several mechanisms, including temporal complementarity between species in response to environmental fluctuations and a reduction in competition strength (Loreau and de Mazancourt, 2013). However, we still know little on how above- and belowground resources mediate the relationship between tree species richness and temporal stability of productivity (Grossiord et al., 2014; Merlin et al., 2015). For instance, while competition for light is responsible for the positive effects of tree species diversity on stability, the role of competition for other resources (including

soil water and nutrients) has not been well investigated (Morin et al., 2014). Even though there is evidence that belowground resource availability and resource uptake capacity tend to be important drivers of stability of forest productivity (Grossiord et al., 2014; Scherer-Lorenzen, 2014), more work is needed to pinpoint the concurrent effects of above- and belowground resources driving the relationship between tree species diversity and ecosystem functioning.

It is well known that abiotic context can exert a powerful influence on BEF relationships in forests (e. g. Craven et al., 2020; Fei et al., 2018; Mina et al., 2018; Ratcliffe et al., 2017), and there is evidence that biodiversity effects become stronger and more positive with increasing environmental stress due to decreased competition as well as enhanced facilitation among species (Bertness and Callaway, 1994). This so-called 'Stress-Gradient Hypothesis' is a special case of the 'Complementarity framework', and was extended to BEF context by Forrester and Bauhus (2016) and Barry et al. (2019). The complementarity framework follows the idea that complementarity increases if species interactions enhance the availability, uptake or use efficiency of limiting resources when climate conditions are hostile. Recent studies demonstrate that the effects of tree species richness on forest productivity shift from strongly positive in stressful environments, e.g., in water-limiting regions, to weakly positive, neutral or even negative under more favorable conditions (Fei et al., 2018; Jucker et al., 2016). In addition, some studies have shown that the effects of plant species richness on ecosystem stability are strong at sites where high drought stress prevails (García-Palacios et al., 2018; Grossiord et al., 2014). However, other studies did not find any significant changes in tree species richness-forest productivity relationships or tree species richness-forest stability relationships with contrasting climatic conditions (del Río et al., 2017; Hisano and Chen, 2020; Merlin et al., 2015; Staples et al., 2019). These findings suggest that it remains to be determined whether the mediation of above- and belowground resources on the BEF relationships differs among contrasting climatic conditions as predicted by the complementarity framework.

Here, we investigated the mechanisms underpinning tree species richness effects on aboveground wood productivity and temporal stability of productivity. Hereto, we designed a method based on above- and belowground resource availability and resource uptake capacity at forest stand level using structural equation models (Fig. 1). We applied this method to mature forests along a latitudinal gradient from the European research project, Functional Significance of Forest Biodiversity in Europe (FunDivEUROPE). In addition, we used this latitudinal gradient to study context-dependence of BEF relationships in contrasting climatic conditions, i.e., regions with water-limiting summer conditions (hereafter, arid regions) vs. regions with non-water-limiting summer conditions (hereafter, humid regions) (Fig. S1). Specifically, we addressed the following questions: (i) Do above- and belowground resource availability and resource uptake capacity mediate BEF relationships? (ii) Do the effects of tree species



**Fig. 1.** Conceptual framework illustrating the hypothesized relationships between tree species richness and productivity-related ecosystem functions with measures of above- and belowground resource uptake capacity and resource availability. Solid lines represent direct relationships and dashed arrows represent the interaction between resource availability and uptake capacity. HLI, heat load index.

richness on productivity and stability change with climatic conditions? We hypothesized that (H1) tree species richness positively affects productivity through enhancing above- and belowground resource uptake capacity; (H2) the effects of tree species richness on stability are mainly driven by belowground resource availability and uptake capacity; (H3) the relative importance of above- and belowground resources on productivity and stability changes along with climatic conditions. Specifically, productivity is mainly driven by belowground resource availability and resource uptake capacity in arid regions, and by aboveground resource uptake capacity in humid regions. This is because belowground resource availability and uptake capacity tend to be the limiting factors for plant growth in arid regions, while competition for aboveground resources tend to be more important for plant growth than competition for belowground nutrients and water in humid regions (Forrester and Bauhus, 2016; Grossiord et al., 2014). Stability is mainly driven by belowground resource availability and uptake capacity, with resource-mediated effects being more pronounced in humid regions than in arid regions. This is because tree growth can be stabilized by enhancing belowground resource availability and uptake capacity under environmental fluctuations (Grossiord et al., 2014). Since trees and ecosystems are less adapted to environmental fluctuations (e.g. droughts) in humid regions, the resource-mediated diversity effects on stability may be promoted more in humid regions than in arid regions.

## 2. Methods

### 2.1. FunDivEUROPE exploratory platform

Our data were collected from 209 forest stands of the FunDivEUROPE exploratory platform (<http://www.fundiveurope.eu>) established in 2011–2012 to assess the influence of tree species diversity on ecosystem functions and services in mature European forests. The study regions are located in six European countries (Finland, Poland, Germany, Romania, Italy and Spain) and represent six main European forest types, i.e., boreal (number of plots = 28), hemiboreal (43), temperate deciduous (38), mountainous deciduous (28), thermophilous deciduous (36) and Mediterranean mixed (36) forests. The regions can be divided into two groups by their

summer climatic conditions (Zepner et al., 2020): regions where arid climatic conditions predominate during the summer in the thermophilous deciduous and Mediterranean mixed forests (arid regions), and regions where humid climatic conditions predominate during the summer in boreal, hemiboreal, temperate deciduous and mountainous deciduous forests (humid regions) (Fig. S1). Forest stands were all closed canopy and were carefully selected so that correlations were minimized between tree species richness and species composition, topography, and other potential confounding soil characteristics, including soil type, texture, and depth. Trees in the studied regions were naturally regenerated except for Finland, where trees were planted after a clear-cut. The age of trees ranged from 73 to 173 years in Poland, from 65 to 100 years in Romania, from 30 to 80 years in Italy, and from 39 to 49 years in Finland (no data available in Germany and Spain). In each forest type, between three to five tree species were selected. These target species are regionally common broadleaved (e.g. *Fagus sylvatica*, *Quercus robur*, *Quercus petraea*, *Quercus ilex* and *Betula pendula*) and coniferous (i.e. *Abies alba*, *Picea abies* and *Pinus nigra*) tree species (Table S1) and account for 94% of the individuals and 91% of the basal area in total. Species richness per plot ranged from one (monocultures) to five (mixed stands) tree species. More details about the design of the exploratory platform can be found in Baeten et al. (2013).

### 2.2. Aboveground wood productivity and temporal stability of productivity

Stand-level productivity and stability (Tables S2-S3) were derived from tree ring data across the six regions of the FunDivEUROPE exploratory platform. We used the approach that was developed in previous papers (Jucker et al., 2016; Jucker et al., 2014a). In brief, a total of 3138 out of 12,939 (24%) trees (diameter at breast height (DBH)  $\geq 7.5$  cm) were originally cored between March and October of 2012. Wood cores were air-dried and scanned using a flatbed scanner (2400 dpi optical resolution) for tree ring measurement. Due to insufficient quality compared to the standard species-level reference curves (derived by taking the average of all tree ring chronologies for a given species at each site), 6% of the tree ring chronologies were discarded including those cored samples that did not cover the 1992–2011 period, resulting in 2926 chronologies. The annual biomass



growth of individual trees was calculated from diameter increments using allometric functions as the difference between the tree biomass of two consecutive years and was expressed in units of carbon (C) ( $\text{kg C yr}^{-1}$ ) based on a proxy of C concentration of  $0.5 \text{ g C g}^{-1}$  dry weight. The biomass allometric equations were species- and site-specific and included tree diameter and height as predictors of biomass. Past diameters were reconstructed from the tree cores, while past tree heights were estimated by fitting empirical height-diameter relationships for each species using data from the FunDivEUROPE plots (Jucker et al., 2014a). The individual tree biomass growth was then modelled using the linear mixed-effects models, in which individual tree biomass growth was treated as response variable, species richness, tree size and crown illumination index (a measure of the amount of light received by each tree determined by its crown position regarding openings in the adjacent canopy) were treated as fixed factors and sampling plot was treated as a random factor. This model was used to estimate the biomass growth of those trees that had not been cored (see Jucker et al. (2014a) for more information on model selection and model robustness assessment). Productivity was calculated between 2007 and 2011 to reflect the short-term tree growth dynamics of the sampling period by taking the sum of the annual biomass growth of all trees in a plot ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ). Stability (unitless) was calculated between 1992 and 2011 to reflect the long-term effects of tree mortality on wood productivity using a function of the inverse coefficient of variation  $\mu/\sigma$ , where  $\mu$  and  $\sigma$  are the temporal mean and standard deviation of productivity at plot level, respectively.

### 2.3. Aboveground and belowground resource availability and uptake capacity

We compiled four stand-level proxies for above- and belowground resource availability and uptake capacity, including heat load index (HLI), leaf area index (LAI), soil carbon (C)/nitrogen (N) ratio (soil C/N ratio), soil moisture and fine root biomass (Tables S2-S3).

Specifically, HLI is defined as the potential annual direct incident radiation received by a certain location and used as a proxy for light availability. It was estimated using eq. 3 of the work of McCune and Keon (2002):

$$HLI = 0.339 + 0.808 \times \cos(L) \times \cos(S) - 0.196 \times \sin(L) \times \sin(S) - 0.482 \times \cos(A) \times \sin(S)$$

where  $L$  represents latitude ranging from  $30^\circ\text{N}$  to  $60^\circ\text{N}$ ,  $S$  represents slope ranging from  $0^\circ$  to  $60^\circ$ , and  $A$  represents a folded aspect on the NE-SW line. The values of stand-level HLI were normalized by the maximum value in each region to reduce the correlation of changes in HLI with latitude (De Wandeler et al., 2018).

LAI is considered as a proxy for light absorption (Binkley et al., 2013) and used as a measure of aboveground resource uptake capacity (Asner et al., 2003; Forrester et al., 2016). Stand-level LAI was measured between June and August in 2012 and 2013 using a plant canopy analyzer LAI-2000 (LI-Cor Inc., Nebraska, USA) (Pollastrini et al. 2016). In brief, five measurements within the plots (light transmission below the canopy) and five measurements outside the forest (a proxy of the light incidence above the canopy) were taken at two time points (shortly before sunrise and shortly after sunset). The total one-side area of leaf tissue per unit ground surface area ( $\text{m}^2 \text{ m}^{-2}$ ) was computed using Li-Cors FV2000 software (LI-Cor Inc., Nebraska, USA). LAI was calculated by taking the mean of the five measurements for a given plot. Note there is one unmeasured source of uncertainty on the measurement of LAI, i.e., annual variation in LAI was not considered, that is known to be  $\sim 15\text{--}20\%$  for deciduous forests.

Since soil total N is not a good measure for soil nutrient availability, and soil available N was not directly measured in the FunDivEUROPE exploratory platform, we considered soil C/N ratio as a proxy for soil nutrient status and used as a measure of belowground nutrient availability (Hedwall et al., 2019; Mayor et al., 2017; Peters et al., 2019). Soil C/N ratio was calculated based on soil C and N stock in forest floor plus 0–10 cm of mineral topsoil. Soil C and N concentration were measured with a Thermo Scientific FLASH 2000 soil CN analyzer. Soil total C and N stock ( $\text{Mg ha}^{-1}$ ) were

calculated based on soil C and N concentrations, bulk density and soil depth in the forest floor and top 10 cm mineral layer (Dawud et al., 2016; Dawud et al., 2017).

As an alternative to a direct measurement of soil water availability, which provides only a snapshot of information in time, the species composition of a site can give valuable information on soil water conditions that may fluctuate strongly in time and space (Anenkhonov et al., 2015). This concept of bioindication has been formalized in ecological indicator values, assigning ordinal values for certain environmental conditions to individual plant species based on their realized optimum along an environmental gradient, see detailed information of species indicator values synthesized by Diekmann (2003). As plant species responses can shift throughout their range, many local ecological indicator systems have been developed in Europe. Here, we used the community weighted mean (CWM) of the ecological indicator values of the understory plant species for soil moisture as a measure of soil water availability. For each region (Table S4), the ecological indicator system was selected with the application region corresponding or closest by that study region (Bita-Nicolae and Sanda, 2011; Ellenberg et al., 1992; Mayor López, 1999; Pignatti, 2005; Zarzycki et al., 2002). Three subplots ( $5 \text{ m} \times 5 \text{ m}$ ) were established for the survey of understory communities in three of the nine quadrants (upper right, central and lower left) (Landuyt et al., 2020). Species cover of all vascular plant species was estimated in each subplot and used to calculate a stand-level weighted average of species indicator values (i.e. soil moisture) as follows:

$$CWM_{moisture} = \frac{\sum_{i=1}^n (r_{ij} * x_i)}{\sum_{i=1}^n r_{ij}}$$

where  $CWM_{moisture}$  is community weighted mean of soil moisture,  $r_{ij}$  is the abundance of species  $i$  in sample plot  $j$ ,  $n$  is the number of species in sample plot  $j$  and  $x_i$  is the indicator value (i.e. soil moisture) of species  $i$ .

Since fine roots are an key pathway for plant water and nutrient uptake (Carmona et al., 2021; Jackson et al., 1997), the biomass of fine roots (diameter  $< 2 \text{ mm}$ ) was used as a proxy for belowground resource uptake capacity (Barry et al., 2020; Brassard et al., 2013). Fine root biomass was collected from the forest floor (litter layer + humus layer) and mineral soil horizons of nine quadrants per plot between May and October 2012 (Finér et al., 2017). The forest floor was sampled using a wooden frame ( $25 \text{ cm} \times 25 \text{ cm}$ ). The mineral soil horizons were sampled using soil cores ( $36 \text{ mm}$  in diameter) to a depth of  $40 \text{ cm}$  in Poland,  $10 \text{ cm}$  in Spain, and  $20 \text{ cm}$  in the remaining study regions (Finér et al., 2017). Samples were divided into  $10 \text{ cm}$  sections. Living fine roots were extracted from the forest floor and mineral soil layers and were pooled into one sample per  $10 \text{ cm}$  section. The fine roots were dried in the lab at  $40^\circ\text{C}$  until constant mass and weighed. Stoniness of the mineral soil was accounted for in the calculation of fine root biomass ( $\text{g m}^{-2}$ ) following Tamminen and Starr (1994). We used the total biomass of living fine roots in forest floor and mineral soil horizons for further data analysis. The within-region standardization of the variables in the SEM analysis (see statistical analyses) allowed to use all data based on different sampling depths.

### 2.4. Statistical analyses

To link tree species richness, above- and belowground resource availability and uptake capacity to productivity and stability at the stand level, we conducted structural equation models (SEMs) based on the conceptual framework shown in Fig. 1. Basal area (based on DBH of all individuals within a plot  $\geq 7.5 \text{ cm}$ ) was included as a covariate to account for its effects on resource uptake capacity proxies (LAI and fine root biomass), productivity and stability that were beyond the direct effects of tree species richness (Forrester et al., 2016). We included interactions between proxies for resource availability and proxies for resource uptake capacity for light, soil water and soil nutrients (Fig. 1). We first used general linear models to regress all the variables described above (also shown in Tables S2 and S3)

against region (factor variable with six levels) and extracted the residuals of each model to account for the influence of region on each variable. HLI was corrected for cloudiness through regressing LAI against region and mean annual cloud cover. Mean annual cloud cover was compiled from the global 1-km cloud cover project (Wilson and Jetz, 2016). The standardized residuals were then used in the SEM analyses (Desie et al., 2020; García-Palacios et al., 2018; Jing et al., 2021). In addition, plant species responses to environmental changes can shift throughout their range, and many regional ecological indicator value systems have been developed in Europe, each with a different ordinal scale, spanning different environmental gradients and their own region of application (Diekmann, 2003). Standardizing the CWMs of the ecological indicator values of soil moisture within each region therefore allowed us to use ecological indicator values from different regional systems.

SEMs that included all plots across the six study regions were fit to productivity and stability separately. We also fit the SEMs to data from the arid regions and humid regions separately (Fig. S1). Finally, we explored complex SEMs considering both productivity and stability in one model to analyze their correlation (Wang et al., 2021). Although the results (Figs. S2-S3) were similar compared to the main SEM analyses, complex SEMs - relative to the number of observations - may result in unreliable significance testing of individual paths and the evaluation of the goodness of model fit (Grace, 2020). Thus, we only reported the results of separate SEMs for productivity and stability. Being ecosystem engineers, trees have a strong influence on soil water, soil nutrient, and light availability in a forest stand. However, we expected that trees indirectly influence above- and belowground resource availability through changes in resource capture capacity, which is indicated by the dashed arrows (Fig. 1). Therefore, the direct pathways from tree species richness to above- and belowground resource availability are not considered in the SEMs. The goodness of fit was determined using the Chi-square test ( $P$ -value  $> 0.05$ ), comparative fit index (CFI  $> 0.90$ ), root mean square error approximation (RMSEA  $< 0.10$ ), and standardized root mean square residual (SRMR  $< 0.10$ ). Productivity, stability and basal area were log-transformed to meet the assumptions of homogenous variances and normal distributions. All SEMs were conducted with the lavaan package (Rosseel, 2012) in R version 3.6.1 (R Development Core Team, 2019).

### 3. Results

#### 3.1. Effects of tree species richness and basal area on resource uptake capacity

Tree species richness was not significantly associated with LAI and fine root biomass ( $P > 0.10$ ; Figs. 2-4). However, basal area was marginally positively associated with LAI (standardized path coefficient [hereafter  $\beta_{\text{std}}$ ] = 0.12,  $P = 0.079$ ), and was positively associated with fine root biomass ( $\beta_{\text{std}} = 0.18$ ,  $P = 0.010$ ) across all six regions (Fig. 2; Tables S5-S6). These positive associations with basal area tended to be stronger for LAI ( $\beta_{\text{std}} = 0.35$ ,  $P = 0.002$ ) and fine root biomass ( $\beta_{\text{std}} = 0.32$ ,  $P = 0.005$ ) in arid regions than in humid regions ( $\beta_{\text{std}} = 0.03$ ,  $P = 0.977$ , LAI;  $\beta_{\text{std}} = 0.09$ ,  $P = 0.314$ , fine root biomass) (Figs. 3-4; Tables S5-S6).

#### 3.2. Effects of tree species richness on productivity and stability

Across all regions, tree species richness, proxies for above- and belowground resource availability and uptake capacity explained 33% of the variation in productivity (Fig. 2a). Productivity was positively associated with tree species richness ( $\beta_{\text{std}} = 0.18$ ,  $P = 0.002$ ), basal area ( $\beta_{\text{std}} = 0.44$ ,  $P < 0.001$ ) and LAI ( $\beta_{\text{std}} = 0.13$ ,  $P = 0.024$ ) (Fig. 2a; Table S5). Productivity was negatively associated with soil C/N ratio ( $\beta_{\text{std}} = -0.16$ ,  $P = 0.009$ ) (Fig. 2a; Table S5). There were no direct associations between productivity and fine root biomass, soil moisture and interaction terms ( $P > 0.10$ ). In addition, tree species richness, above- and belowground resource availability and uptake capacity explained 10% of the variation in stability (Fig. 2b). Stability was positively associated with tree species richness ( $\beta_{\text{std}} = 0.20$ ,

$P = 0.004$ ) and fine root biomass ( $\beta_{\text{std}} = 0.12$ ,  $P = 0.083$ ), but was negatively associated with LAI ( $\beta_{\text{std}} = -0.18$ ,  $P = 0.006$ ) (Fig. 2b; Table S6).

#### 3.3. Differences in tree species richness effects on aboveground wood productivity between arid and humid regions

In arid regions, tree species richness and basal area explained 45% of the variation in productivity (Fig. 3a). Specifically, productivity was only found strongly associated with tree species richness ( $\beta_{\text{std}} = 0.34$ ,  $P < 0.001$ ) and basal area ( $\beta_{\text{std}} = 0.45$ ,  $P < 0.001$ ) (Fig. 3a, Table S5). In humid regions, the model accounted for 32% of the variation in productivity (Fig. 3b). Productivity was positively associated with basal area ( $\beta_{\text{std}} = 0.39$ ,  $P < 0.001$ ), fine root biomass ( $\beta_{\text{std}} = 0.13$ ,  $P = 0.066$ ) and interactions between fine root biomass and soil moisture ( $\beta_{\text{std}} = 0.13$ ,  $P = 0.075$ ), but was negatively associated with soil C/N ratio ( $\beta_{\text{std}} = -0.23$ ,  $P = 0.002$ ) (Fig. 3b; Table S5). There were no direct relationships between productivity and tree species richness, fine root biomass and soil moisture (Fig. 3b).

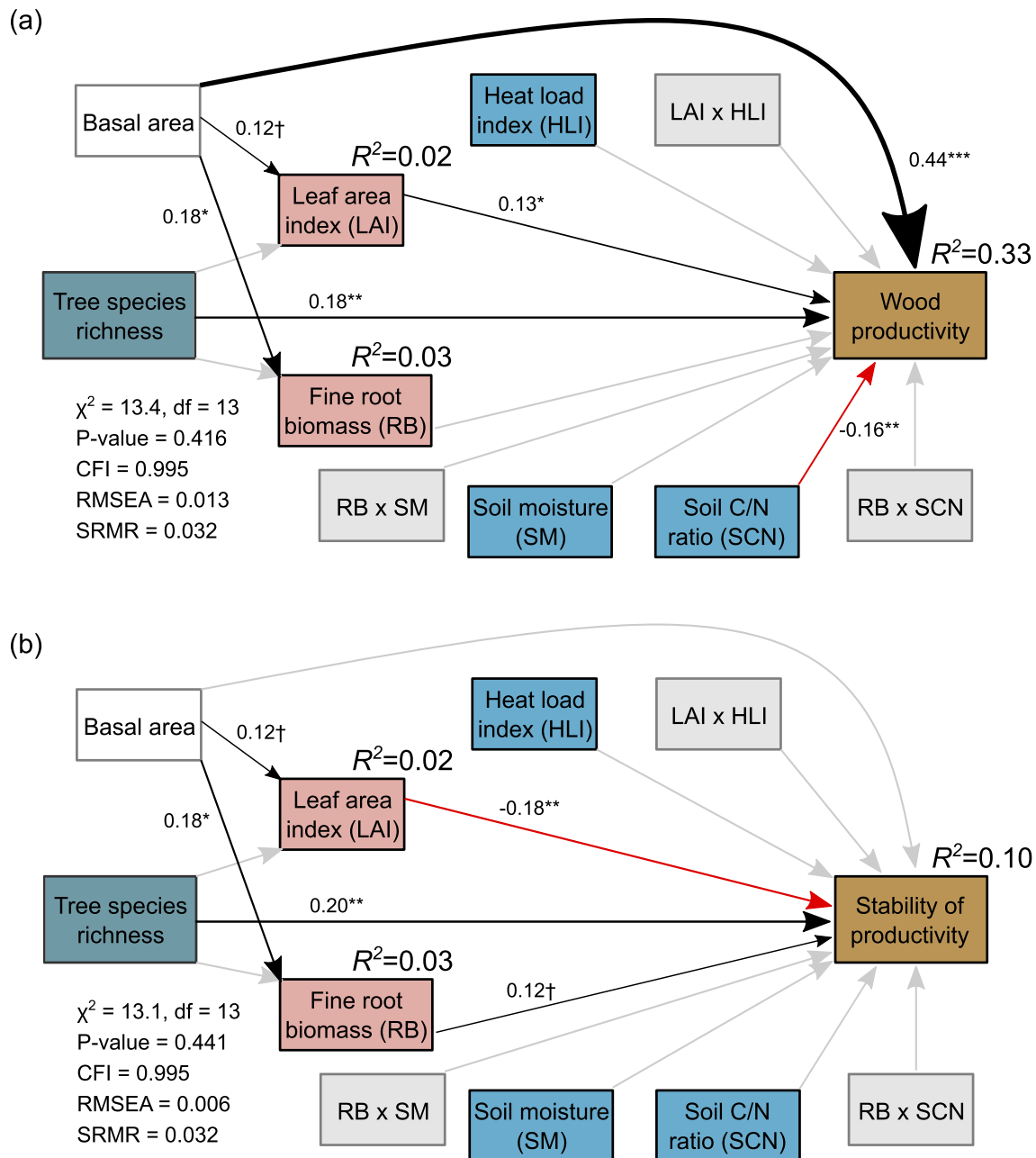
#### 3.4. Differences in tree species richness effects on stability between arid and humid regions

In arid regions, the model accounted for 10% of the variation in stability (Fig. 4a). There were no significant direct relationships between stability and any of the predictive variables examined (Fig. 4a). In humid regions, the model of tree species richness and stability accounted for 20% of the variation in stability (Fig. 4b). Stability was positively associated with tree species richness ( $\beta_{\text{std}} = 0.22$ ,  $P = 0.006$ ), basal area ( $\beta_{\text{std}} = 0.24$ ,  $P = 0.003$ ) and root biomass ( $\beta_{\text{std}} = 0.16$ ,  $P = 0.045$ ) (Fig. 4a; Table S6). Stability was negatively associated with LAI ( $\beta_{\text{std}} = -0.17$ ,  $P = 0.033$ ).

## 4. Discussion

#### 4.1. Do above- and belowground resource uptake capacity mediate BEF relationships across six European forest types?

We studied the mechanisms driving biodiversity-ecosystem functioning relationships by considering the role of above- and belowground resource uptake capacity and availability. Contrary to our first hypothesis (H1), tree species richness was not significantly associated with LAI or fine root biomass, which were considered as proxies for resource uptake capacity. These results contradict previous studies that reported positive associations between tree species richness and LAI (Peng et al., 2017; Unger et al., 2013) or between tree species richness and root biomass (Brassard et al., 2013; Zeng et al., 2020; Zeng et al., 2021) in both planted experiments and natural forests. The positive association between tree species richness and LAI can be driven by increased photosynthetic efficiency or reduced clumping of the leaf area at higher species richness, thereby enhancing the interception and/or use efficiency of incoming radiation at a given LAI (Hardiman et al., 2011; Hardiman et al., 2013). However, no or negative relationships between species richness and LAI have also been documented (Castro-Izaguirre et al., 2016; Liu et al., 2021). The fact that we did not include small trees (DBH  $< 7.5$  cm) could have contributed to our results because species richness of the larger trees is reported to have less influence on the LAI (Liu et al., 2021). In addition, we observed a very weak relationship between LAI and basal area (as well as LAI and productivity) (Fig. 2), which is out of our expectation based on allometric scaling, given that leaf area should scale closely with tree size/basal area (and in turn, productivity should scale closely with leaf area). One possible explanation is that the LAI estimates obtained using the LAI-2000 Plant Canopy Analyzer often saturate quickly after canopy closure (Fig. S4), which would limit our ability to detect any increases in LAI in forests where tree density is already high as a baseline, e.g., in the non-water limiting regions (Fig. 3b). However, the reasons for the lack of tree species richness effects on fine root biomass are less understood (Finér et al., 2017) and appear to be region-specific, since a positive effect of species richness was reported for subsoil root biomass in the

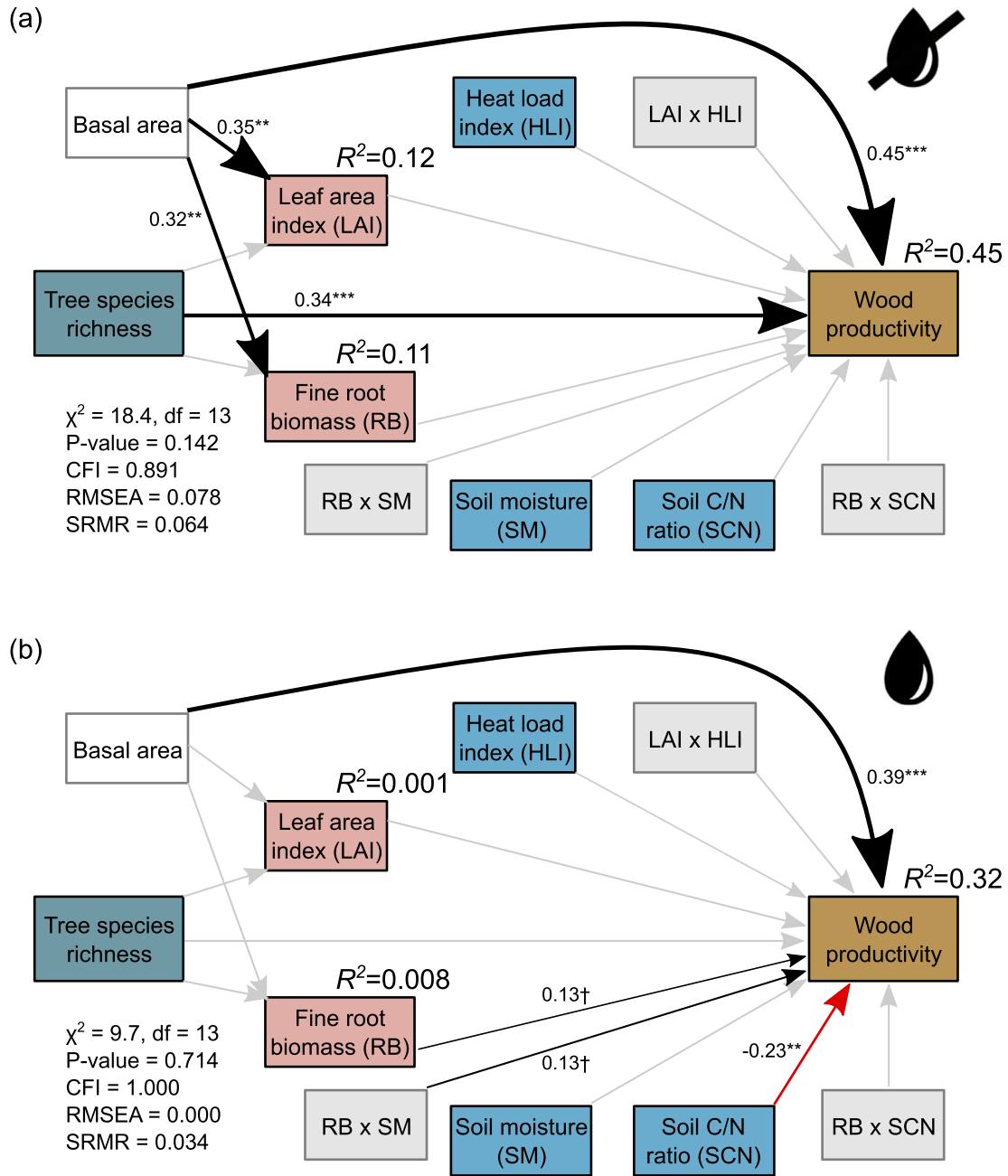


**Fig. 2.** Effects of tree species richness on (a) aboveground wood productivity and (b) temporal stability of productivity across the six European forests. Standardized path coefficients ( $P < 0.10$ ,  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ), the explained variation ( $R^2$ ) and fit measures of SEM are shown. Black, grey and red lines indicate significantly positive, non-significant and significantly negative effects, respectively. Abbreviations are LAI, leaf area index; HLI, heat load index; RB, fine root biomass; SM, soil moisture; SCN, soil C/N ratio; LAI  $\times$  HLI, LAI and HLI interaction; RB  $\times$  SM, fine root biomass and soil moisture interaction; RB  $\times$  SCN, fine root biomass and soil C/N ratio interaction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Polish study region of FunDivEUROPE (Dawud et al., 2016). Although species interactions can result in overyielding through niche partitioning and facilitation, commonly referred to as complementarity (Loreau and Hector, 2001), our results suggest that complementarity through changes in the studied components of above- and belowground resource capture capacity played a minor role in mediating the relationships between tree species richness and productivity, and between tree species richness and stability.

We did not find any strong significant interactions between proxies for resource capture capacity and proxies for resource availability. This does not mean resource capture capacity and resource availability are not important for forest productivity and stability. Indeed, we found that soil nutrient availability (inversely related to soil C/N ratio) and light uptake capacity

(LAI) were all positively correlated with productivity across the six major European forest types (Fig. 2a). In contrast, LAI had a significantly negative effect on stability (Fig. 2b), which could be explained by the higher susceptibility to droughts because of a high transpiration capacity (Jucker et al., 2014b) induced by the high LAI. In addition, fine root biomass had a weak positive effect on stability, possibly because of its mitigating effect on the impact of droughts. These results, therefore, provide weak support for our second hypothesis (H2) that the belowground forest compartment is an important driver of stability. Interestingly, these results provide evidence that investments in above- and belowground tissue differently affect stability. Previous studies reported that the relative investments in above- and belowground tissue (i.e. the root-shoot ratio) could be mediated by nutrient availability, e.g., a higher N availability in soils leads to higher



**Fig. 3.** Effects of tree species richness on aboveground wood productivity depending on climatic conditions. (a) arid region; (b) humid regions. Standardized path coefficients ( $\dagger P < 0.10$ ,  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ), the explained variation ( $R^2$ ) and fit measures of SEM are shown. Black, grey and red lines indicate significantly positive, non-significant and significantly negative effects, respectively. Abbreviations are provided in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

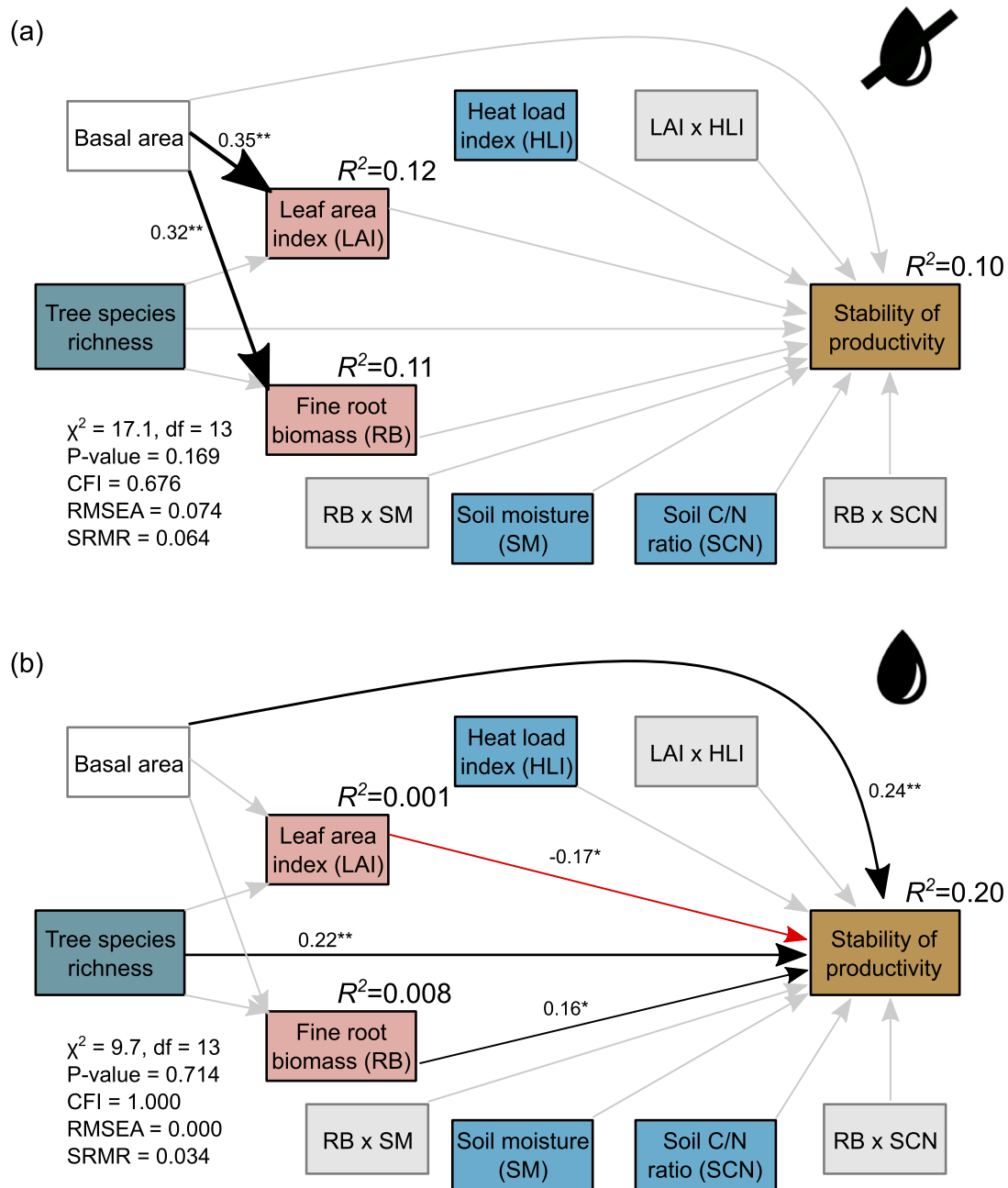
investment in aboveground tissue compared to belowground tissue in several tree species (Binkley and Fisher, 2019). However, we did not find evidence for interactions between LAI to fine root biomass ratio (a proxy for above- to belowground biomass fraction) and soil C/N ratio in the model of productivity, nor for stability (Fig. S5).

**4.2. Do the effects of tree species richness on productivity and stability change with climatic conditions?**

Our work provides evidence that the effects of tree species richness on productivity and stability change with climatic conditions. That is, tree species richness promotes productivity or stability in regions with arid or humid climatic conditions, respectively, but does not promote productivity

and stability simultaneously. These results are not consistent with patterns observed in grassland experiments (e.g. Isbell et al., 2015; Tilman and Downing, 1994), where productivity and stability are simultaneously promoted by species richness. We found a shift in the effects of tree species richness under contrasting climatic conditions, which provides partial support for the framework that if species interactions enhance the availability, uptake or use efficiency of the limiting resources under resource limiting environments, diversity effects through complementarity are predicted to increase (Forrester and Bauhus, 2016). Specifically, we found strong effects of tree species richness on productivity in arid regions, whereas these effects were absent in humid regions. In arid regions, however, above- and belowground resource uptake capacity and resource availability are not able to explain the positive BEF relationships, indicated by the remaining





**Fig. 4.** Effects of tree species richness on temporal stability of productivity depending on climatic conditions. (a) arid regions; (b) humid regions. Standardized path coefficients ( $\dagger P < 0.10$ ,  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ), the explained variation ( $R^2$ ) and fit measures of SEM are shown. Black, grey and red lines indicate significantly positive, non-significant and significantly negative effects, respectively. Abbreviations are provided in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

strong direct effects of tree species richness on tree productivity, even though the effects of basal area were accounted for. In humid regions, we found positive effects of soil nutrient availability and fine root biomass on productivity. These results suggest that when water availability is not limited, soil nutrients become important. Our findings do, however, not support our third hypothesis that productivity is mainly driven by belowground resource availability and uptake capacity in arid regions and by aboveground resource uptake capacity in humid regions (H3).

Regarding stability, we found no significant tree species richness effects in arid climatic conditions, while a positive effect of tree species richness was uncovered in humid regions. Our findings are not consistent with a recent study showing that plant species richness can be associated with higher ecosystem stability in very arid, rather than in semi-arid conditions in global drylands (García-Palacios et al., 2018). One reason could be that

some of the tree species (e.g. *Fagus sylvatica*, *Picea abies/alba* and *Pinus sylvestris*) from the studied humid regions may be less adapted to droughts (Buras et al., 2020; Schuldt et al., 2020). As a result, to mitigate drought impacts, high species richness may promote stability through complementarity and perhaps, facilitation (e.g. hydraulic lift) (Anderegg et al., 2018; Pretzsch et al., 2013). Furthermore, fine root biomass was positively correlated with stability, and LAI was negatively correlated with stability in humid regions, while none of the resource-related variables showed a significant relationship with stability in arid regions. These results partially support our third hypothesis (H3) that the relative importance of above- and belowground resources on the stability of productivity depends on climatic conditions, while the lack of resource-mediated effects does not support our prediction that resource-mediated effects in humid regions are more pronounced than in arid regions. Our findings indicate that in regions

with supposedly low water stress (i.e. humid regions), higher LAI values makes them more vulnerable to droughts. This is confirmed by the negative correlation between wood productivity and stability in humid regions (Fig. S3). The positive effects of fine root biomass on stability did not vary with soil moisture or nutrient availability, as we did not find significant interactions between fine root biomass and soil moisture, nor between fine root biomass and soil nitrogen. Our findings suggest that differences in climatic conditions may override the impact of differences in above- and belowground resource availability and uptake capacity on productivity and stability.

The stability of productivity in the arid regions was not well explained by the models. One reason could be that there are unexplored variables, such as climatic variation/seasonality that may drive annual variation in productivity. For example, in the cold climates, the length of the growing season must affect aboveground wood productivity (Jucker et al., 2016; Ratcliffe et al., 2017). In addition, at the regional scale, it has been recognized that many abiotic factors (climate and soil characteristics), biotic factors (tree species composition, stem density and stand age), socio-economic factors and management regimes may jointly affect the relationship between tree species richness and productivity as well as stability (Bravo-Oviedo et al., 2021; Ouyang et al., 2020; Ouyang et al., 2019). Considering restrictions on model complexity imposed by sample size, including more variables would entail an even larger sample size than available in this study. However, considering the large variability in climatic conditions over time, it would be interesting to apply the framework presented in this study to future studies through comparing the effects of above- and belowground resources on productivity in wet vs. drought years within a study region (e.g. Grossiord et al., 2014). Moreover, we only examined a subset of proxies for above- and belowground resource uptake capacity. Future studies could differentiate the capacity of fine root biomass in nutrient partitioning using isotope techniques across time and space. In addition, there could be additional proxies for belowground resource uptake capacity, such as total root length, root surface area per ground area and mycorrhizal surface area. However, these proxies for belowground resource uptake capacity are more difficult to measure with high costs in practice. Finally, LAI and fine root biomass were measured at stand level, it would be helpful to measure leaf mass fractions and root mass fractions at the individual tree level to further compare above- and belowground tissue investment in different climatic conditions.

## 5. Summary

We explored the potential underlying mechanisms of biodiversity-ecosystem functioning relationships by focusing on the mediating effects of above- and belowground resources under contrasting climatic conditions. Our work therefore differs from classical BEF studies that regularly investigate the direct links between diversity and ecosystem functions. We found that the effects of tree species richness on aboveground wood productivity and temporal stability of productivity are overall positive across six major European forest types, but these effects were not well mediated by above- and belowground resource availability and uptake capacity. Zooming in on the contrasting climatic conditions, we found that in arid regions, tree species richness only enhances productivity, leaving stability unaffected, while in humid regions, tree species richness promotes stability, but not productivity. These findings indicate the possible disconnection between productivity and stability, i.e., the mechanisms that drive positive diversity effects on wood productivity are not per se beneficial for temporal stability of productivity: Investments in leaf biomass to compete for light could negatively affect temporal stability in the face of climate change. Taken together, our work suggests contrasting mechanisms at play in regions with different climatic conditions. Altered precipitation regimes with increased drought stress intensity and frequency driven by climate change may override the effects of differences in above- and belowground resources and eventually affect tree species diversity effects on ecosystem functions and services related to European forests.

## Authors' contributions

BJ, FV, FS and HB are site managers and MP co-site manager of FunDivEUROPE. BM, JZ, ED, SH, MSL, KVM, KV and LV participated in the FunDivEurope soil synthesis workshop at KU Leuven (August 2017), where the aim and system boundaries of this study were identified. XJ and KVM performed the analyses and wrote the first draft of the manuscript. All authors contributed substantially to the revisions.

## Data accessibility

Data are available from the FunDivEUROPE online data portal, accessed through URL: <https://data.botanik.uni-halle.de/fundiveurope/> (Data access IDs are provided in Table S2).

## Declaration of Competing Interest

We declare we have no competing interests.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.152560>.

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