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Xin Jing<sup>1</sup>  | Bart Muys<sup>1</sup>  | Helge Bruelheide<sup>2,3</sup>  | Ellen Desie<sup>1</sup>  |  
Stephan Hättenschwiler<sup>4</sup>  | Hervé Jactel<sup>5</sup>  | Bogdan Jaroszewicz<sup>6</sup>  | Paul Kardol<sup>7</sup>  |  
Sophia Ratcliffe<sup>8</sup>  | Michael Scherer-Lorenzen<sup>9</sup>  | Federico Selvi<sup>10</sup>  |  
Karen Vancampenhout<sup>1</sup>  | Fons van der Plas<sup>11,12</sup>  | Kris Verheyen<sup>13</sup>  |  
Lars Vesterdal<sup>14</sup>  | Juan Zuo<sup>1,15</sup>  | Koenraad Van Meerbeek<sup>1</sup> 

<sup>1</sup>Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium; <sup>2</sup>Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany; <sup>3</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; <sup>4</sup>CEFE, University of Montpellier, CNRS, EPHE, IRD, University of Paul-Valéry Montpellier, Montpellier, France; <sup>5</sup>INRAE, University of Bordeaux, BIOGECO, Cestas, France; <sup>6</sup>Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Białowieża, Poland; <sup>7</sup>Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden; <sup>8</sup>NBN Trust, Nottingham, UK; <sup>9</sup>Geobotany, Faculty of Biology, University of Freiburg, Freiburg, Germany; <sup>10</sup>Department of Agriculture, Food, Environment and Forestry, University of Firenze, Firenze, Italy; <sup>11</sup>Systematic Botany and Functional Biodiversity, Life Science, Leipzig University, Germany; <sup>12</sup>Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, The Netherlands; <sup>13</sup>Forest and Nature Lab, Campus Gontrode, Department of Environment, Ghent University, Melle-Gontrode, Belgium; <sup>14</sup>Department of Geosciences and Natural Resource Management, University of Copenhagen, Frederiksberg C, Denmark and <sup>15</sup>Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, China

## Correspondence

Koenraad Van Meerbeek

Email: koenraad.vanmeerbeek@kuleuven.be

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## Abstract

1. Biodiversity experiments have identified both complementarity and selection as important drivers of the relationship between biodiversity and ecosystem functioning. However, their relative importance in above- and below-ground ecosystem compartments of mature forests remains yet to be explored.
2. We adopted a trait-based approach to partition biodiversity effects in above- and below-ground complementarity and selection. This approach was based on canopy and root traits measured in single- and mixed-species plots in mature forests across a European latitudinal gradient.
3. We assessed the relative importance of above- and below-ground selection and complementarity in driving the relationship between tree species diversity and above-ground wood production. We used the expected values (based on the values measured in monocultures) of leaf area index (LAI) and fine root biomass as proxies for above- and below-ground selection, whereas canopy packing and rooting depth variability were used as proxies for above- and below-ground complementarity.
4. Our results showed that tree species richness–wood production relationships were driven by above- and below-ground complementarity (i.e. canopy packing and rooting depth variability), rather than selection. The proxies for selection

were found to have a positive effect on wood production but were not affected by tree species richness.

5. We concluded that above-ground- but also the largely neglected below-ground complementarity drives biodiversity–productivity relationships in mature forests. Our findings suggest that choosing tree species with complementary above- and below-ground traits should be considered in afforestation and forest management to promote tree diversity and productivity in European forests.

#### KEYWORDS

canopy packing, ecosystem functioning, fine root biomass, FunDivEUROPE, leaf area index, mature forests, rooting depth

## 1 | INTRODUCTION

Biodiversity–ecosystem functioning (BEF) relationships have been extensively studied for nearly three decades (Tilman et al., 2014; van der Plas, 2019). Much of the knowledge has been gained through biodiversity experiments using artificially designed short-lived systems, for example microcosms, mesocosms or synthetic grassland communities (Hooper et al., 2005; Schmid et al., 2002). The extrapolation of their findings to real-world systems with long-lived plant species such as forests remains a major challenge (Baeten et al., 2013; Forrester & Bauhus, 2016; Mori, 2018; Paquette & Messier, 2011). However, much progress has been made during the last decade with the maturation of tree diversity experiments (Grossman et al., 2018; Huang et al., 2018; Verheyen et al., 2016), the development of exploratory platforms in mature forests (Baeten et al., 2013; Liu et al., 2018) and the use of large-scale inventory data (e.g. Fei et al., 2018; Liang et al., 2016; Mori, 2018). The results of these studies underpin the fundamental importance of tree species diversity for many ecosystem functions and services, from the provision of wood products to the resistance and resilience to climatic extremes, and other disturbances (Mensah et al., 2020; Scherer-Lorenzen, 2014; Teben'Kova et al., 2020; Yuan et al., 2020).

In recent years, there has been an increased interest in understanding the mechanistic basis of biodiversity–productivity relationships (Isbell et al., 2018; Loreau & Hector, 2019). Loreau and Hector (2001) developed the widely used additive partitioning approach, which provides a statistical method to partition net biodiversity effect into selection and complementarity in biodiversity experiments. However, such statistical selection and complementarity could be driven by different biological mechanisms. For example, selection effects can emerge from a stochastic component, that is, with increasing species richness there is an increasing chance of a well-performing species to be included in the community (Huston, 1997), and a functional component, that is, a well-performing species with a particular combination of trait values becomes dominant and thus positively affects productivity, which is defined as the ‘dominance effect’ by Fox (2005) since the functional component reflects the dominance of a mixture by plants with particular traits at the expense of others.

In contrast, complementarity effects can have at least four different causes: (a) niche differentiation, resulting in increased resource use efficiency or an increased proportion of resources captured, (b) herbivore and pathogen dilution with increasing host diversity, which is particularly relevant for specialist species, (c) facilitation and mutualism, with one species being positively affected by the presence of another species and (d) the reduction of interference competition or other negative species interactions (Ammer, 2019; Barry et al., 2019; Halliday et al., 2020; Jactel et al., 2017). Furthermore, these statistical and biological mechanisms do not always correspond to each other. For example, Williams et al. (2017) found that the physical crown complementarity is correlated with statistical selection, rather than statistical complementarity.

To disentangle the biological mechanisms underlying BEF relationships, different variables characterizing the distribution of plant functional traits have been used (Díaz et al., 2007; Funk et al., 2017; Lavorel & Garnier, 2002; Roscher et al., 2012). Specifically, community-weighted means (CWMs) of traits have been proposed to identify the functional component of selection (Ali et al., 2017; Mouillot et al., 2011; Van de Peer et al., 2018) whereby a high weight is given to the trait values of well-performing, and hence dominant species. In this way, CWMs identify the effects of dominant trait values in a community, that is, the functional component of selection. Variation in trait values, on the other hand, captures complementary resource use and can be used as a proxy for the niche differentiation component of complementarity (Ali et al., 2017; Jucker et al., 2015; Morin et al., 2011). One caveat to this approach is that the trait values of species in polycultures used to calculate the CWMs are also affected by species interactions, and thus not only reflect the selection effect. Nevertheless, this trait-based approach has often been applied in forest ecosystems, with both complementarity and selection identified as driving components of diversity effects on ecosystem functioning (Ali et al., 2017; Huang et al., 2018; Morin et al., 2011; Ratcliffe et al., 2016; Ruiz-Benito et al., 2014; Tobner et al., 2016).





The majority of these studies have focused on above-ground plant traits, such as tissue chemistry (e.g. leaf nitrogen and phosphorus content), morphology (e.g. SLA) and physiological traits

(e.g. tolerance to shade; Ali et al., 2017; Mensah et al., 2018; Toïgo et al., 2018). Less understood is the role of below-ground plant traits in driving forest biodiversity–productivity relationships (but see, Bu et al., 2017; Li et al., 2019; Sun et al., 2017). This is partially because of the difficulty of measuring below-ground plant traits (Jacob et al., 2013). However, there is increased evidence that below-ground plant traits influence many below-ground processes (Bardgett, 2017). For example, variation in below-ground plant traits (e.g. rooting depth) can lead to a complementary colonization of below-ground space, and thus complementary use of resources, and eventually increases total resource uptake (Fahey et al., 2016; Jones et al., 2005; Nepstad et al., 1994). As a result, spatial resource partitioning, for example complementarity in rooting depth among species may enhance primary productivity (Barry et al., 2019), as has been observed in grassland biodiversity experiments (Verheyen et al., 2008; Yanai et al., 2008). In addition, although high fine root biomass could increase productivity through enhancing nutrient and water uptake (Hertel et al., 2013; Jackson et al., 1997), it is unknown whether this is driven by below-ground selection or complementarity. The knowledge gaps in our understanding of the functioning of the below-ground subsystem hinder our ability to fully comprehend and predict BEF relationships (Barry et al., 2019).

Here, we aimed to unravel the biological mechanisms rather than the statistical partitioning, in order to better understanding BEF relationships in forest ecosystems. Specifically, we focused on the physical selection and complementarity (i.e. the functional component of selection and niche partitioning; Table 1), but not the

statistical selection and complementarity effects (sensu Loreau and Hector (2001)). Hereafter, we use the terms selection and complementarity to refer to the studied biological mechanisms. We adapted the trait-based approach to partition observed species richness effects on forest productivity, whereby the assessment of above- and below-ground selection in polycultures relies on the values of traits measured in the monocultures of the constituent species. Hereto, we used ecosystem traits, that is community-level organismal traits expressed as the intensity (or density) normalized per unit land area (He et al., 2019), because they match the scale on which productivity is measured. We applied this approach to data generated by the FunDivEUROPE exploratory platform to study how above- and below-ground complementarity and selection drive above-ground wood production (AWP) in mature forests across Europe. We used the response variable AWP because it is a key forest ecosystem function, underpinning many ecosystem services (Gamfeldt et al., 2013), and because it is positively associated with tree species richness in this dataset (Jucker et al., 2014, 2016). We additionally studied how simultaneous consideration of selection and complementarity in above- and below-ground ecosystem compartments adds to the understanding of forest ecosystem functioning compared to studies that have followed a narrower focus. We expect that in particular complementarity is a key driver of positive diversity–productivity relationships, and that complementarity is especially important for the acquisition of above- and below-ground resources because of the complementary resource use of different tree species in polycultures (Barry et al., 2019).

**TABLE 1** Tree structural variables to study above- and below-ground selection and complementarity on productivity

Community characteristics	Targeted mechanism	General description	Relevance in forests
 <p>Expected value of leaf area index</p>	Functional component of selection	Species-rich communities are more likely to include a species with above-ground traits that have disproportionately large effects on productivity (Forrester & Bausch, 2016)	Leaf area index is positively related to tree productivity (Arias et al., 2007; Bolstad et al., 2001; Jose & Gillespie, 1997; Morin et al., 2011)
 <p>Canopy packing</p>	Niche complementarity	Species-rich communities include species with complementary above-ground traits	Crown complementarity enhances above-ground resource partitioning (Jucker et al., 2015; Sapjanskas et al., 2014)
 <p>Expected value of fine root biomass</p>	Functional component of selection	Species-rich communities are more likely to include species with below-ground traits that have disproportionately large effects on productivity (Chanteloup & Bonis, 2013)	More fine root biomass increases nutrient and water uptake (Hertel et al., 2013; Jackson et al., 1997)
 <p>Rooting depth variability</p>	Niche complementarity	Species-rich communities include species with complementary below-ground traits (Oram et al., 2018)	Complementarity in rooting depth enhances below-ground resource partitioning (Brassard et al., 2011, 2013; Fahey et al., 2016; Forrester & Bausch, 2016; Jones et al., 2005)

## 2 | MATERIALS AND METHODS

### 2.1 | FunDivEUROPE exploratory platform

This study was conducted in the FunDivEUROPE exploratory platform (<http://www.fundiveurope.eu>), extending over six regions in Europe, where the main vegetation types are boreal (Finland), hemiboreal (Poland), temperate deciduous (Germany), mountainous deciduous (Romania), thermophilous deciduous (Italy) and Mediterranean mixed (Spain) forests. The study regions host many regionally common and economically important European broad-leaved and coniferous tree species. Large climatic gradients are covered with a mean annual temperature ranging from 2.1°C in Finland to 13°C in Italy and a mean annual precipitation from 499 mm in Spain to 850 mm in Italy.

In 2011, a total of 209 plots (30 m × 30 m) with a total of 15 tree species (i.e. *Acer pseudoplatanus*, *Betula pendula/pubescens*, *Carpinus betulus*, *Castanea sativa*, *Fagus sylvatica*, *Fraxinus excelsior*, *Ostrya carpinifolia*, *Quercus cerris*, *Quercus faginea*, *Quercus ilex*, *Quercus robur/petraea*, *Abies alba*, *Picea abies*, *Pinus nigra* and *Pinus sylvestris*) were selected across the six regions (number of plots: 28 in Finland and Romania, 43 in Poland, 38 in Germany and 36 in Italy and Spain). Plots were carefully selected to minimize the correlations between tree species richness and topography, and other confounding soil variables such as bedrock type, soil type, texture and depth (Baeten et al., 2013). In addition, the study design allowed age distribution to covary with the gradient of species richness to some degree (e.g. more uneven-aged and multi-layered plots at the higher species richness levels). Trees in Finland were planted after a clear-cut, while all other sites were naturally regenerated forest stands. The age of trees in Finland was 39–49 years, 73–193 years in Poland, 65–100 years in Romania and 30–80 years in Italy (no age data available for Germany and Spain). More detailed information about the FunDivEUROPE exploratory platform can be found in the study by Baeten et al. (2013).

### 2.2 | Tree species richness and above-ground wood production

The study plots varied in species richness, ranging from one (monoculture) to five (polyculture) tree species within regions. Above-ground wood production was obtained from tree ring data covering a 5-year period between 2007 and 2011 (van der Plas, Manning, Soliveres, et al., 2016). Between March and October of 2012, a total of 3,138 wood cores (5 mm in diameter) were collected (Jucker et al., 2014). The number of cored trees was 12 per plot in monocultures and six per species in polycultures except for Poland, where five cores per plot were taken. Air-dried wood cores were scanned by a flatbed scanner with 2,400 dpi optical resolution. AWP data were then estimated as described by Jucker et al. (2014) and Jucker et al. (2016). In brief, radial growth increments (mm/year) were measured from each scanned wood core. In this step, 188 cores were

excluded due to poor quality compared to the standard species-level reference curves, and 2,950 tree ring chronologies were included. From this, annual diameter increments were calculated as the difference between the diameter of two consecutive years. The annual biomass growth was calculated from the diameter increments and was expressed in units of carbon (C) through dividing the above-ground biomass data by 2 (kg C year<sup>-1</sup>). The individual tree biomass growth was modelled by linear mixed-effects models considering tree size, competition for light, species richness and a random plot term (Jucker et al., 2014, 2016). The fitted linear mixed-effects models were used to estimate the biomass growth for all trees that had not been cored. Finally, the annual biomass growth of all trees (stem ≥7.5 cm in diameter) in a plot was summed to get the plot-level AWP (Mg C ha<sup>-1</sup> year<sup>-1</sup>).

### 2.3 | Quantifying above- and below-ground selection and complementarity

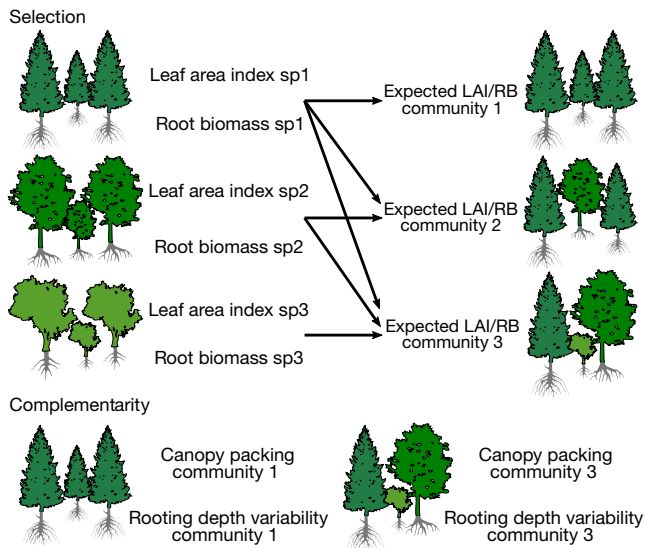
We compiled data on the following ecosystem traits: leaf area index (LAI), canopy packing, fine root biomass and rooting depth variability (Table S1). Data were selected based on their relevance to forest productivity (Table 1) and their availability. Apart from rooting depth, LAI, canopy packing and fine root biomass were obtained from in situ measurements. Details of the measurements of these traits can be found in Appendix S1.

To assess above- and below-ground selection on forest productivity, we used two ecosystem traits (He et al., 2019), that is, LAI and fine root biomass respectively (Table 1; Figure 1). To be able to isolate the functional component of selection from other effects (i.e. complementarity), we did not use the observed trait values in polycultures, as the observed values of the individual species are likely to be influenced by interspecific interactions. Instead, we calculated the expected values based on the values measured in the monocultures of the constituent species. Because the expected trait values reflect the dominance of a mixture by plants with particular traits at the expense of others (the ‘dominance effect’ as described by Fox (2005) and remove any influence of complementarity), they could be used to identify the functional component of selection (van der Plas, Manning, Allan, et al., 2016). We first calculated the mean trait values of all monoculture plots of a species within a region. Then, the proportional basal area for a given species was used to weight the monoculture trait values and calculate the expected value of every polyculture plot  $j$  of a region as follows (Enquist et al., 2015):

$$\text{Expected value}_j = \sum_{k=1}^{n_j} A_{k,j} \times z_k, \quad (1)$$

where  $n_j$  represents the number of species in plot  $j$ ;  $A_{k,j}$  represents the relative basal area of species  $k$  in plot  $j$ ; and  $z_k$  represents the mean trait values of species  $k$  that is calculated from the monocultures.

To quantify the complementarity in below-ground resource use, rooting depth variability was used (Table 1; Figure 1) and calculated



**FIGURE 1** Conceptual framework illustrating the estimation of above- and below-ground selection and complementarity. The positive effects of species richness on productivity can be explained by both complementarity and selection. That is, species richness can increase productivity by enhancing above- and below-ground niche complementarity or by influencing mean trait values in a community. The framework aims at unravelling the relative importance of these two effects on observed positive biodiversity–productivity relationships in forests. Specifically, selection in polycultures is calculated by using the weighted mean values of leaf area index (LAI) and fine root biomass (RB) in monocultures of the constituent species using the relative abundance of the species as weighting factor. Above-ground complementarity is directly estimated by the observed canopy packing in a community, while below-ground complementarity is estimated by rooting depth variability, calculated as the variance of rooting depth weighted by the relative abundance of species in a community

as the basal area-weighted squared differences from the mean of rooting depth in a plot. It can be written as follows (Enquist et al., 2015):

$$\text{Rooting depth variability}_j = \sum_{k=1}^{n_j} A_{kj} \times (z_k - \text{CWM}_j)^2. \quad (2)$$

In addition, we used the observed canopy packing to represent the complementarity in above-ground resource use (Jucker et al., 2015).

## 2.4 | Statistical analyses

All statistical analyses were conducted in R version 3.6.1 (R Development Core Team, 2019). Data were inspected for distributional properties. Above-ground wood production, tree species richness, expected LAI, expected fine root biomass and rooting depth variability were log-transformed because of this evaluation. Canopy packing was logit-transformed (Jucker et al., 2015).

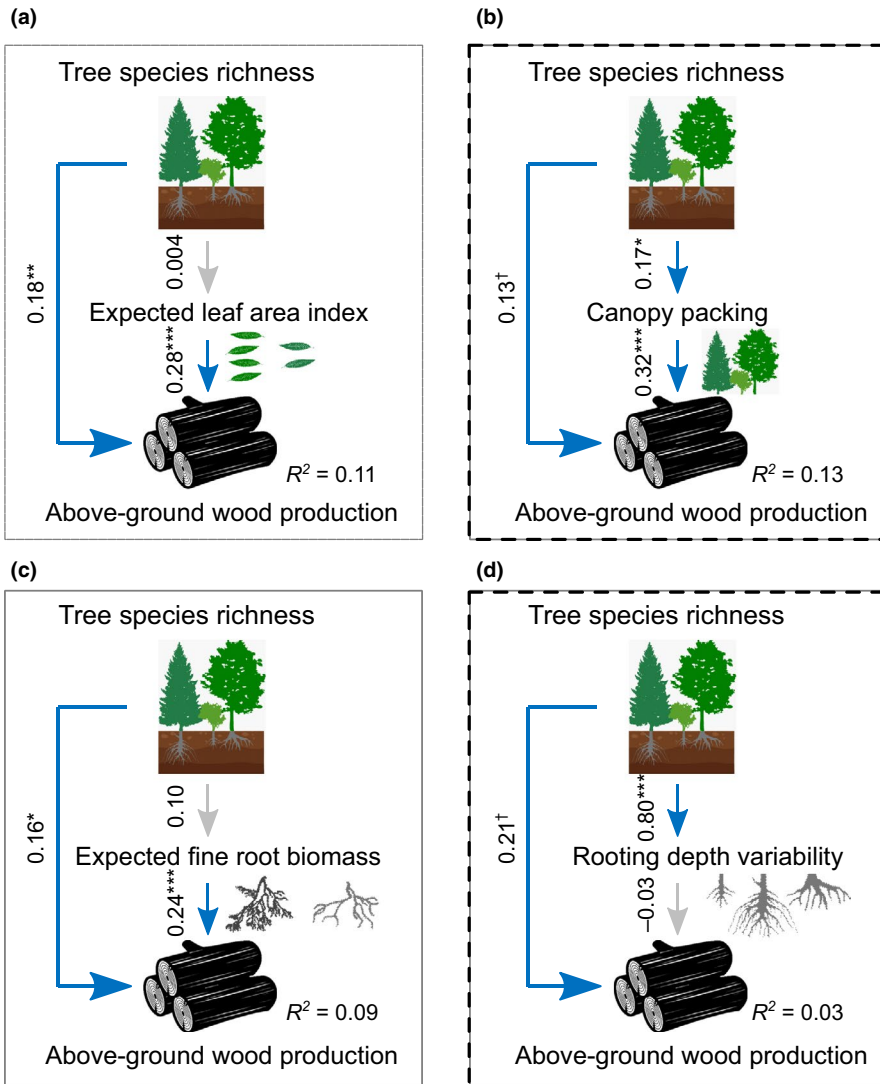
To determine the effects of tree species richness through above- and below-ground selection and complementarity on above-ground wood production, we conducted path analysis (a special case of structural equation models with latent variables) using the LAVAAN package (Rosseel, 2012). It is a multivariate statistical analysis technique that can be used to analyse the covariances between observed variables. It is a powerful tool to integrate different models to uncover the underlying mechanisms between biodiversity and ecosystem functioning (Grace et al., 2007, 2016). Because the number of groups was too low for a multilevel path analysis, and the number of plots too low for a multigroup path analysis, the hierarchical structure of the data (i.e. plots within six study regions) was removed by regressing wood production and the predictor variables on the identity of study regions (variable ~ study region; Desie et al., 2020). We used the residuals of the regression models as input data in the following analyses. Note that the use of residuals of the regression models serves to remove the influences of the confounding factors at the region level (between region/site variation; Desie et al., 2020), for example, climate and water availability (Jucker et al., 2016; Ratcliffe et al., 2017).

We firstly tested the different above- and below-ground effects separately by fitting separate path models for each biodiversity effect, corresponding to one of the tree structural variables (i.e. expected LAI, canopy packing, expected fine root biomass and rooting depth variability). Secondly, we analysed how above- and below-ground complementarity and selection jointly affect the relationship between tree species richness and AWP by including all pathways in the path models. We also added a direct effect of species richness on productivity to assess whether there is a remaining part of the species richness effect that could not be explained by the considered effects (i.e. selection and/or complementarity in the above- and/or below-ground ecosystem compartment). Importantly, only when both the effect of tree species richness on the ecosystem trait and the effect of that ecosystem trait on AWP are found to be significant, we can conclude that there is a significant complementarity or selection effect (see Table 1 and Table S2 for more details on the justification of existing theory and evidence). The goodness-of-fit values of the models were evaluated using chi-squared tests and comparative fit indices (CFI). A  $p$ -value of the chi-squared test  $>0.05$  indicated a good fit of a model. For all the models, we scaled the path coefficients by the standard deviation of each variable to make them comparable. We additionally explored bivariate correlations between tree species richness and ecosystem traits, and their associations with AWP. The results of bivariate correlations (Figures S1 and S2; Tables S3 and S4) were in line with the results of path models (Figures 2 and 3) and thus not reported.

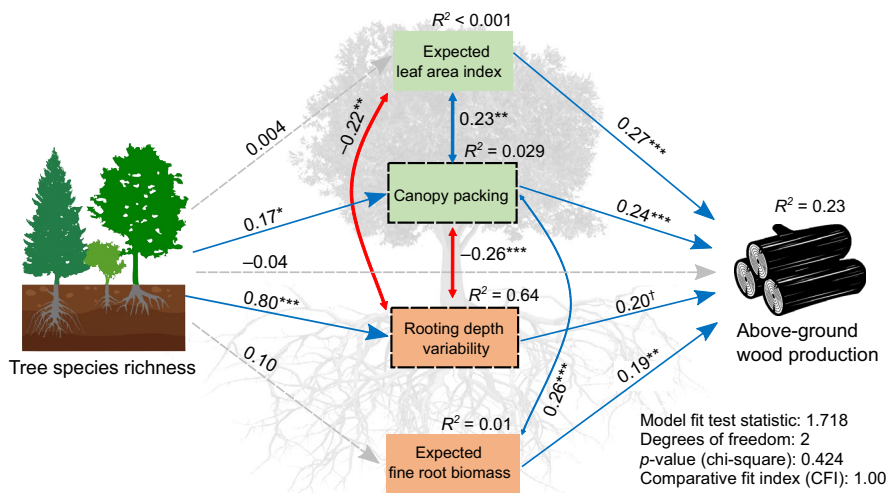
## 3 | RESULTS

In the separate models of above- and below-ground complementarity and selection, we found that tree species richness was always positively associated with AWP (Figure 2). The direct effects of





**FIGURE 2** Individual path models of above- and below-ground complementarity and selection. (a) Expected leaf area index (LAI), (b) canopy packing, (c) expected fine root biomass and (d) rooting depth variability. Solid-line rectangles indicate selection (a and c) and the dashed-line rectangles indicate complementarity (b and d). Standardized path coefficients are shown next to each arrow. Blue and grey arrows indicate significantly positive and non-significant path coefficients respectively. Because these path models are saturated models, the goodness-of-fit cannot be given.  $R^2$  indicates the total variance in above-ground wood production that is explained by tree species richness and plant traits. \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , † $p < 0.10$



**FIGURE 3** Mediation of above- and below-ground ecosystem traits on the relationship between tree species richness and above-ground wood production. Dashed-line rectangles indicate complementarity and the other rectangles indicate selection. Standardized path coefficients are shown next to each arrow. Blue, red and grey arrows indicate significantly positive, significantly negative and non-significant path coefficients respectively; doubled arrows indicate residual correlations.  $R^2$  indicates the total variance of a dependent variable that is explained by predictor variables. \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , † $p < 0.10$

tree species richness on AWP ranged from 0.13 to 0.21 (standardized path coefficient, hereafter  $\beta_{\text{std}}$ ; Figure 2; Table S5). In addition, canopy packing (i.e. above-ground complementarity;  $\beta_{\text{std}} = 0.32$ ) had a greater impact on AWP than expected LAI ( $\beta_{\text{std}} = 0.28$ ), expected fine root biomass ( $\beta_{\text{std}} = 0.24$ ) and rooting depth variability ( $\beta_{\text{std}} = -0.03$ ; Figure 2; Table S5). Canopy packing accounted for 13% of the variance in AWP in combination with tree species richness (Figure 2b), which was greater than other tree structural variables (Figure 2a,c and d). We found that tree species richness was positively associated with canopy packing ( $\beta_{\text{std}} = 0.17$ ) and rooting depth variability ( $\beta_{\text{std}} = 0.80$ ; Figure 2b,d). We did not find significant associations between tree species richness and expected LAI, between tree species richness and expected fine root biomass and between rooting depth variability and AWP (Figure 2a,c and d).

In the full model, tree species richness and the four tree structural variables accounted for 23% of variance in AWP (Figure 3). We found that tree species richness was not significantly associated with AWP ( $\beta_{\text{std}} = -0.04$ ), expected LAI ( $\beta_{\text{std}} = 0.004$ ) and expected fine root biomass ( $\beta_{\text{std}} = 0.10$ ; Figure 3; Table S6). In addition, AWP was significantly positively correlated with expected LAI, canopy packing and expected fine root biomass and marginally significantly with rooting depth variability ( $p < 0.10$ ; Figure 3; Table S6). We found significantly negative correlations between rooting depth variability and canopy packing ( $r = -0.26$ ), and between rooting depth variability and expected LAI ( $r = -0.20$ ) and a positive correlation between canopy packing and expected fine root biomass ( $r = 0.27$ ; Figure 3).

## 4 | DISCUSSION

Our results provide insight into the processes that drive biodiversity–productivity relationships in mature forests. When considering tree structural variables individually, we found a consistent direct effect of tree species richness on AWP and evidence for above-ground complementarity via canopy packing. However, in the full model with all pathways considered, the direct effect of tree species richness disappeared. In addition, a second significant effect, that is below-ground complementarity via rooting depth variability emerged in the full model, indicating that it is important to take into account both the above- and below-ground aspects of selection and complementarity to fully understand the mechanisms that underlie how tree diversity promotes forest productivity.

In the full model (Figure 3), below-ground complementarity in rooting depth was found to be the main driver of positive biodiversity–productivity relationships. Despite we did not measure rooting depth in the field, several studies confirmed that interspecific differences in rooting depth and fine root biomass promote below-ground niche differentiation and result in an increased proportion of below-ground resources captured by extracting water and nutrients from different depths (Barry et al., 2019; Bu et al., 2017; Fahey et al., 2016; Forrester & Bausch, 2016; Jones et al., 2005; Sun et al., 2017). An earlier study on the same plots, Ratcliffe et al. (2017), used volumetric stone content in the upper

30 cm of mineral soil layer as a physical proxy for available rooting space and found minor effects of volumetric stone content on multiple ecosystem functions including AWP. Interestingly, we found a negative correlation between below-ground complementarity and above-ground components (Figure 3), suggesting that complementarity in resource use in polycultures manifests itself in either the below- or the above-ground compartment.

We further found evidence for species richness effects on AWP via above-ground complementarity. Specifically, we found significant effects of tree species richness on canopy packing, and significant effects of canopy packing on AWP. Higher canopy packing in polycultures can result from complementary vertical distributions of leaf area, different crown shapes between species or intraspecific variability in crown morphology (i.e. crown plasticity). The positive effect of tree species richness on canopy packing in the FunDivEUROPE sites was largely driven by crown plasticity (Jucker et al., 2015). This allows trees to adjust the shape and size of their crown morphology to surrounding trees (Kunz et al., 2019; Pretzsch, 2014; Pretzsch & Dieler, 2012). For example, a 38% increase in crown volumes has been observed in the mixed-species forest stands of the FunDivEUROPE exploratory platform because of longer lateral branches and deeper crowns (Jucker et al., 2015). Increased canopy packing can promote light interception and thereby AWP (Binkley et al., 2013; Morin et al., 2011; Pretzsch, 2014). Indeed, we found that canopy packing was positively associated with expected LAI, a light interception-related variable (Jonckheere et al., 2004). Moreover, a positive effect of expected LAI on AWP was also observed (Figures 2 and 3). Kunz et al. (2019) showed that these tree diversity effects on AWP via canopy packing increased with time. Our results are consistent with those of forest succession models (Morin et al., 2011) and studies of forest inventories (Mori, 2018), which found that biodiversity effects on productivity were mainly driven by complementary forest stand structure and light interception. Increased canopy packing in diverse plots can, however, have a negative impact on the resistance to droughts by increasing the rainwater interception capacity of the canopy and thus decreasing the water availability in the soil (André et al., 2008; Grossiord et al., 2014).

It has been shown that the effects of species diversity on tree growth vary during forest succession (Taylor et al., 2020) with biodiversity effects on productivity strengthening from young to middle-aged forests (Huang et al., 2018; Jucker et al., 2020; Zhang et al., 2012). Time is needed for plant species assemblages in diverse communities to realize the potential niche differentiation in order to optimize the use of limiting resources (Reich et al., 2012; Zuppinger-Dingley et al., 2014). In young forest plantations, the complementarity between species may not have reached its full potential. In ageing forests, gap phase dynamics increase the availability of light and soil resources, reducing the importance of complementarity again (Hume et al., 2016; Kumar et al., 2018).

In contrast to studies in young plantation forests (de Peer et al., 2018; Van Chen et al., 2020), we found no evidence for tree species richness effects on AWP through effects of selection. One explanation for the lack of effects of selection could be that the

forest plots of the FunDivEUROPE exploratory platform were selected to maximize the evenness of stand composition (at least 60% of maximum evenness, see Baeten et al., 2013), minimizing the influence of the functional components of selection on AWP. Further, by having all species at all levels of species richness, as is the case in this study, there is less chance of selection effects because the most (or least) productive species will occur at all levels of species richness (Forrester & Bauhus, 2016). However, it should be noted that the expected values of ecosystem traits only represent the functional component of selection, and do not account for the stochastic component. Nevertheless, strong species identity effects have been found in the same forest plots for other ecosystem functions (Baeten et al., 2019; Ratcliffe et al., 2017). Species traits other than those studied here could also be important for plant growth (e.g. SLA, horizontal root segregation; Ali et al., 2017; von Felten & Schmid, 2008), and hence account for additional variation in biodiversity–ecosystem functioning relationships (Cadotte et al., 2011; Flynn et al., 2011; Fotis et al., 2018; Lavorel & Garnier, 2002).

## 5 | CONCLUSIONS

We proposed a trait-based framework to partition the diversity effects into the physical/functional components of selection and complementarity in both the above- and below-ground compartment of the ecosystem. Applying this framework to data from the FunDivEUROPE exploratory platform, we found that complementarity in above- and below-ground resource use is more important than selection in explaining diversity effects on productivity in European mature forests. Complementarity is expressed by high canopy packing and large variation in interspecific rooting depth. Therefore, maintaining variation in both above- and below-ground tree characteristics is crucial to promote AWP in mature forests. We further show that a comprehensive study of both above- and below-ground processes is necessary to fully disentangle the mechanisms underlying tree diversity–productivity relationships in forest.

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## AUTHORS' CONTRIBUTIONS

B.J., F.S. and H.B. are the site managers of FunDivEUROPE; B.M., J.Z., E.D., S.H., M.S.-L., K.V.M., K.V. and L.V. participated in the FunDivEUROPE soil synthesis workshop at KU Leuven (August 2017), where the aim and system boundaries of this study were identified; K.V.M., X.J., S.R. and F.v.d.P. further designed the study and analyses; X.J. and K.V.M. performed the analyses and wrote the

first draft of the manuscript. All the authors contributed substantially to the revisions.

## DATA AVAILABILITY STATEMENT

All the data are freely available from the TRY plant trait database (<https://www.try-db.org/>) and from the FunDivEUROPE online data portal (<https://data.botanik.uni-halle.de/fundiveurope/>). The reference lists of source datasets are presented in Table S1.

## ORCID

Xin Jing  <https://orcid.org/0000-0002-7146-7180>  
 Bart Muys  <https://orcid.org/0000-0001-9421-527X>  
 Helge Bruelheide  <https://orcid.org/0000-0003-3135-0356>  
 Ellen Desie  <https://orcid.org/0000-0002-5947-9517>  
 Stephan Hättenschwiler  <https://orcid.org/0000-0001-8148-960X>  
 Hervé Jactel  <https://orcid.org/0000-0002-8106-5310>  
 Bogdan Jaroszewicz  <https://orcid.org/0000-0002-2042-8245>  
 Paul Kardol  <https://orcid.org/0000-0001-7065-3435>  
 Sophia Ratcliffe  <https://orcid.org/0000-0001-9284-7900>  
 Michael Scherer-Lorenzen  <https://orcid.org/0000-0001-9566-590X>  
 Federico Selvi  <https://orcid.org/0000-0002-3820-125X>  
 Karen Vancampenhout  <https://orcid.org/0000-0002-9159-7011>  
 Fons van der Plas  <https://orcid.org/0000-0003-4680-543X>  
 Kris Verheyen  <https://orcid.org/0000-0002-2067-9108>  
 Lars Vesterdal  <https://orcid.org/0000-0003-0309-3735>  
 Juan Zuo  <https://orcid.org/0000-0001-6670-392X>  
 Koenraad Van Meerbeek  <https://orcid.org/0000-0002-9260-3815>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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