

GfÖ Ecological Society of Germany,  
Austria and Switzerland

Basic and Applied Ecology xxx (2017) xxx–xxx

Applied Ecology

www.elsevier.com/locate/baae

## Species and structural diversity affect growth of oak, but not pine, in uneven-aged mature forests

Margot Vanhellemont<sup>a,\*</sup>, Rienk-Jan Bijlsma<sup>b</sup>, Luc De Keersmaecker<sup>c</sup>,  
Kris Vandekerckhove<sup>c</sup>, Kris Verheyen<sup>a</sup>

<sup>a</sup>Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium

<sup>b</sup>Wageningen Environmental Research (Alterra), P.O. Box 47, 6700 AA Wageningen, The Netherlands

<sup>c</sup>Research Institute for Nature and Forest (INBO), Gaverstraat 4, B-9500 Geraardsbergen, Belgium

Received 23 August 2017; accepted 25 January 2018

### Abstract

The effects of mixing tree species on tree growth and stand production have been abundantly studied, mostly looking at tree species diversity effects while controlling for stand density and structure. Regarding the shift towards managing forests as complex adaptive systems, we also need insight into the effects of structural diversity. Strict forest reserves, left for spontaneous development, offer unique opportunities for studying the effects of diversity in tree species and stand structure. We used data from repeated inventories in ten forest reserves in the Netherlands and northern Belgium to study the growth of pine and oak. We investigated whether the diversity of a tree's local neighbourhood (i.e., species and structural diversity) is important in explaining its basal area growth. For the subcanopy oak trees, we found a negative effect of the tree species richness of the local neighbours, which – in the studied forests – was closely related to the share of shade-casting tree species in the neighbourhood. The growth of the taller oak trees was positively affected by the height diversity of the neighbour trees. Pine tree growth showed no relation with neighbourhood diversity. Tree growth decreased with neighbourhood density for both species (although no significant relationship was found for the small pines). We found no overall diversity-growth relationship in the studied uneven-aged mature forests; the relationship depended on tree species identity and the aspect of diversity considered (species vs. structural diversity).

© 2018 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

**Keywords:** Biodiversity; Ecosystem functioning; Productivity; *Quercus robur*; *Quercus petraea*; *Pinus sylvestris*; Temperate forest

### Introduction

In the face of global changes, adaptive forest management becomes a key element. Mixing tree species, for instance,

may help in ensuring the future resilience of forests. Yet, forest managers are requesting more detailed knowledge about and insight into the effects of mixing tree species on ecosystem functioning (Carnol et al., 2014; Coll et al., 2017). Generalized conclusions or guidelines on biodiversity-ecosystem functioning (BEF) relationships are, indeed, not sufficient; BEF relationships tend to be context-dependent rather than universal. With regard to tree growth and biomass production, the relationship with tree species richness has been found to be negative (e.g., Firm, Erskine, & Lamb, 2007;

\*Corresponding author.

E-mail addresses: [margot.vanhellemont@ugent.be](mailto:margot.vanhellemont@ugent.be) (M. Vanhellemont), [rienkjan.bijlsma@wur.nl](mailto:rienkjan.bijlsma@wur.nl) (R.-J. Bijlsma), [luc.dekeersmaecker@inbo.be](mailto:luc.dekeersmaecker@inbo.be) (L. De Keersmaecker), [kris.vandekerckhove@inbo.be](mailto:kris.vandekerckhove@inbo.be) (K. Vandekerckhove), [kris.verheyen@ugent.be](mailto:kris.verheyen@ugent.be) (K. Verheyen).

<https://doi.org/10.1016/j.baae.2018.01.003>

1439-1791/© 2018 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Please cite this article in press as: Vanhellemont, M., et al. Species and structural diversity affect growth of oak, but not pine, in uneven-aged mature forests. *Basic and Applied Ecology* (2017), <https://doi.org/10.1016/j.baae.2018.01.003>

Pretzsch et al., 2010), positive (e.g., Jucker et al., 2014; Liang et al., 2016; Pretzsch et al., 2013), or hump-shaped (Gamfeldt et al., 2013). The impact of tree species diversity on tree growth or stand production may be site-specific (Forrester, Kohnle, Albrecht, & Bauhus, 2013; Toïgo et al., 2015) and depend on species identity (Jucker et al., 2014; Piotta, 2008; Toïgo et al., 2018). Different mechanisms related to facilitation and competition can explain the positive or negative effects of mixing on tree growth (see also Forrester, 2014). For instance, the overall resource availability can be higher in mixed stands as mixing may improve litter decomposition and therefore speed up nutrient cycling (Cuchietti, Marcotti, Gurvich, Cingolani, & Pérez Harguindeguy, 2014; but see Jacob, Viedenz, Polle, & Thomas, 2010b), the total soil space filling by fine roots and hence the exploitation of soil nutrients and water may be larger in mixed stands (Brassard, Chen, Bergeron, & Paré, 2011; Brassard et al., 2013), and mixing may promote canopy packing (Jucker, Bouriaud, & Coomes, 2015; Pretzsch et al., 2016) and thus a more optimal use of canopy space and incoming radiation. In addition, damage by host-specific herbivores or pathogens might be lower because hosts are less abundant and less apparent (Castagneyrol, Giffard, Péré, & Jactel, 2013; but see Haase et al., 2015) and enemies of forest pests may be more common (Jäkel & Roth, 2004; Kaitaniemi, Riihimäki, Koricheva, & Vehviläinen, 2007) in mixed stands.

Many of the early tree diversity studies focused on stand-level productivity differences between monocultures and two-species mixtures. Yet, individual plant performance shapes plant communities (Violle et al., 2007) and local neighbourhoods drive tree growth (Potvin & Dutilleul, 2009; Ratcliffe, Holzwarth, Nadrowski, Levick, & Wirth, 2015). In addition, a review on BEF studies in forests (Nadrowski, Wirth, & Scherer-Lorenzen, 2010) pointed out the need for delving into the effects of tree diversity on the performance of individual trees. To enhance the representativeness (*sensu* Nadrowski et al., 2010) of the results of BEF research, studying complex, real-world situations is necessary (Naeem, Duffy, & Zavaleta, 2012). Mixed forests can be structurally more heterogeneous than monocultures (Pretzsch et al., 2016). Variation in, e.g., tree dimensions, can lead to a higher degree of vertical space occupation, which might affect overall light capture and therefore tree and stand growth. Tree density, another aspect of forest structure known to affect tree and stand growth (cf. Forrester, 2014), may vary as well. The effects of this structural diversity have recently begun to gain more attention (see Dănescu, Albrecht, & Bauhus, 2016). Gaining insight in the effects of forest structure on, for instance, tree growth may improve our understanding of mixing effects on forest functioning. In this respect, strict forest reserves, i.e., protected forests left for free development without human interference, may represent an interesting additional platform for forest BEF research that takes into account various aspects of structural diversity. The long-term monitoring areas in these forest reserves enable detailed investigation of various ecosystem processes in semi-natural

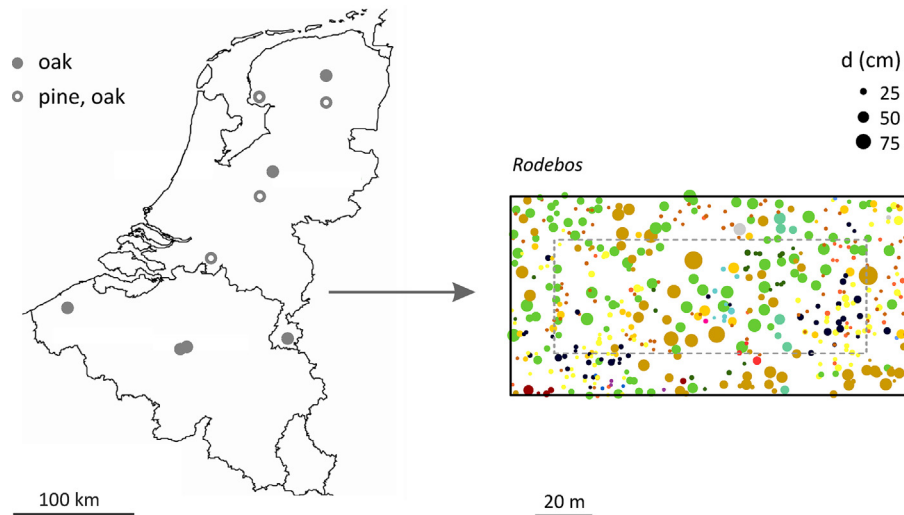
forests (Meyer, 2005; Parviainen, Bücking, Vandekerckhove, Päivinen, & Schuck, 2000). As these long-term monitoring areas are monitored regularly, they can serve as a research platform (a ‘Forest Observational Network’ *sensu* von Gadow et al., 2016) to study forest dynamics and BEF relationships in semi-natural forests diverse in tree ages, sizes, and species. The spatially explicit monitoring data collected in strict forest reserves allow to focus on the performance of individual trees in relation to their local neighbourhood, which may quickly yield a vast amount of information (von Gadow et al., 2016). Moreover, observational studies of spontaneously developing forests complement experimental studies in forest plantation trials and planted biodiversity experiments used to address specific hypotheses (Forrester & Bauhus, 2016). Observational studies are essential for obtaining regionally validated information about insights gathered from experiments.

In the Netherlands and northern Belgium, strict forest reserves have been systematically monitored to study forest dynamics since 1987 and 2000, respectively. We chose ten of these strict forest reserves to study the growth of individual trees in uneven-aged mature forests, thus meeting the need for forest BEF studies that investigate tree-level processes (cf. Nadrowski et al., 2010) in complex forest ecosystems (cf. Naeem et al., 2012). To move beyond the narrow focus on species richness (Balvanera et al., 2006), we looked into the effects of species diversity as well as structural diversity. Our hypotheses were that (1) trees grow better when surrounded by diverse neighbours (i.e., diverse in species or tree dimensions) and (2) tree growth decreases with neighbourhood density. We focused on oak (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) and pine (*Pinus sylvestris* L.) as they are economically important on relatively nutrient-poor soils in Western Europe.

## Materials and methods

### Forest reserve data

The ten forest reserves used in our study (Fig. 1, Table 1) were selected from the strict forest reserves of the Netherlands and northern Belgium, based on the criteria ‘mature forest’, ‘mixed tree layer with oak or pine’, and ‘data of two inventories available’. All ten selected forest reserves contained oak (*Q. robur* L. or *Q. petraea* (Mattuschka) Liebl.); four of them contained pine (*P. sylvestris* L.). Both oak species co-occur in many European regions (Annighöfer, Beckschäfer, Vor, & Ammer, 2015; Jones, 1959) and are often studied together (e.g., Annighöfer et al., 2015; Kuster, Dobbertin, Günthardt-Goerg, Schaub, & Arend, 2014; Saha et al., 2012). From each forest reserve, we used the permanent rectangular 70 m × 140 m ‘core’ plot (Fig. 1). In this plot, spatially explicit individual-tree data are collected every 10 years: position (*x*, *y* coordinates), tree species, diameter at breast height, and status (alive/dead) are recorded for each tree or shrub with a diameter at breast height larger than 5 cm.



**Fig. 1.** The ten strict forest reserves of the study. The tree layer contains either oak or both oak and pine. The map of the rectangular monitoring plot (70 m × 140 m) of forest reserve *Rodebos* shows all trees with diameter at breast height (*d*) larger than 5 cm; different colours represent different species, and the size of the dots indicates the diameter of the trees. The grey dotted lines indicate the zone in which we selected the target trees (15 m buffer from the border of the monitoring plot).

**Table 1.** Characteristics of the ten strict forest reserves used in the study.

Name	Country	Lat	Lon	Soil <sup>a</sup>	Climate <sup>b</sup> AMT, AP	History <sup>c</sup>	Main tree species <sup>d</sup>	Focal species <sup>e</sup>	Inventories
Starnumansbos	NL	52° 53'	5° 33'	Podzol	8.9, 790	Old (1983)	<i>Ps</i> , <i>Qr</i> , <i>Bp</i>	Oak + pine	1986, 1996
Lheebroek	NL	52° 50'	6° 27'	Arenosol	8.8, 786	Young (1983)	<i>Ps</i> , <i>Qr</i>	Oak + pine	1987, 1999
Galgenberg	NL	52° 00'	5° 30'	Cambisol	9.3, 790	Young (1983)	<i>Ps</i> , <i>Qr</i> , <i>Bp</i>	Oak* + pine	1986, 1995
Tussen de Goren	NL	51° 31'	4° 55'	Podzol	9.6, 797	Young (1983)	<i>Ps</i> , <i>Qr</i>	Oak + pine	1987, 1996
Vijlnerbos	NL	50° 46'	5° 58'	Luvisol	9.4, 907	Old (1951)	<i>Qp</i> , <i>Bp</i> , <i>Fs</i>	Oak**	1987, 1996
Pijpebrandje	NL	52° 15'	5° 42'	Cambisol	9.0, 800	Old (1965)	<i>Fs</i> , <i>Qr</i>	Oak	1987, 1999
Norgerholt	NL	53° 03'	6° 27'	Cambisol	8.7, 791	Old (1964)	<i>Qr</i> , <i>Ia</i>	Oak	1982, 1992
Rodebos	BE	50° 46'	4° 37'	Luvisol	10, 802	Old (1988)	<i>Qr</i> , <i>Fs</i>	Oak	2001, 2011
Wijnendalebos	BE	51° 04'	3° 02'	Cambisol	10, 694	Old (1983)	<i>Qr</i> , <i>Ap</i> , <i>Fs</i>	Oak	2003, 2012
Everzwijnbad	BE	50° 48'	4° 41'	Luvisol	9.9, 808	Old (1997)	<i>Qr</i> , <i>Ap</i>	Oak	2003, 2012

<sup>a</sup>Soil type based on the nomenclature of FAO (2006) and using Den Ouden, Mohren, De Waal, and De Schrijver (2010).

<sup>b</sup>AMT – annual mean temperature (°C), AP – annual precipitation (mm) data from WorldClim (<http://worldclim.org>).

<sup>c</sup>Old – forested since at least 1775; young – afforestation end 19th century, early 20th century; between brackets: year of last management interventions.

<sup>d</sup>The main tree species (based on basal area and stem density) in the plot; *Ap* – *Acer pseudoplatanus* L., *Bp* – *Betula pendula* Roth, *Fs* – *Fagus sylvatica* L., *Ia* – *Ilex aquifolium* L., *Ps* – *Pinus sylvestris* L., *Qp* – *Quercus petraea* (Mattuschka) Liebl., *Qr* – *Quercus robur* L.

<sup>e</sup>Oak – *Quercus robur*, oak\* – *Q. petraea* + *Q. robur*, oak\*\* – *Q. petraea*, pine – *Pinus sylvestris*.

In the Dutch monitoring protocol, tree height and crown projection are also measured for every tree. In the Flemish forest reserves, tree height is measured for a subset of the trees. We used this subset to parameterize allometric height-diameter relationships (see Appendix A: Table 1) and then estimated tree height for all the trees in the plot.

### Neighbourhood approach

The **target trees** were all the oak and pine trees in the central area of the permanent monitoring plots (edge buffer = 15 m, see Fig. 1). For each target tree, we calculated the annual basal area increment ( $\text{cm}^2 \text{yr}^{-1}$ ) as the difference

in basal area between the two inventories, divided by the time interval between the inventories. We used basal area increment, a two-dimensional variable, as it represents overall tree growth better than a one-dimensional variable such as diameter increment (cf. Biondi & Qeadan, 2008). We only considered trees that survived both inventories; dead trees and recruits were ignored. In addition, we only included trees with positive basal area increment; negative and zero basal area increments over the 10-year inventory period were considered the result of measurement errors. We looked at the full dataset of target trees and at subsets of small trees (i.e., subcanopy trees) and tall trees (i.e., canopy trees) of each tree species, as the canopy layer of the studied forest reserves

was rather poor in tree species, compared to the subcanopy (see Appendix A: Fig. 1). In addition, the relative impact of neighbourhood diversity and density on growth may differ depending on tree size (cf. Jucker et al., 2014). Based on the density plots (see Appendix A: Fig. 1) and the mean and median height of the target trees of each species, we set the height threshold between small and tall trees at 16 m. The target tree dataset consisted of 374 oaks (160 small oaks, 214 tall oaks) and 421 pines (268 small, 153 tall pines).

For each target tree, all the trees within a certain radius around the tree were considered its **neighbour trees**. We considered neighbourhoods with a radius of 7.5, 10, 12.5, and 15 m. This range covered the ‘zone of influence’ (cf. Ratcliffe et al., 2015) of the oak and pine trees in the Dutch forest reserves, based on the crown projection data available for these forest reserves. For each local neighbourhood size around each target tree, we quantified seven measures of density and four measures of diversity using the data of the living trees from the first inventory.

To characterize local stand density, we calculated stem density and basal area of the local neighbourhood, the quadratic mean diameter of the neighbour trees, the summed basal area of neighbour trees with a larger diameter than the target tree, and a neighbourhood competition index (*NCI*) based on the diameter of the neighbour trees ( $d_j$ ) and the distances between the target tree  $i$  and its neighbours ( $distance_{ij}$ ):

$$NCI_i = \sum_{j=1}^n \frac{d_j}{distance_{ij}} \quad (1)$$

Close neighbours with a large diameter will exert more competition than slender neighbours growing further from the target tree. This *NCI* competition index has been used as a proxy for tree competition in forests before (Canham, LePage, & Coates, 2004; Ratcliffe et al., 2015). Finally, we also partitioned the neighbourhood competition index (*NCI*) into competition by light-demanding neighbours (*NCIL*) and competition by shade-tolerant neighbours (*NCIS*), with light-demanding species generally casting less shade than shade-tolerant species. For oak and pine, both intolerant to shade, the competitive effect of neighbour trees might depend on the shade-casting ability of these neighbour trees. The ordinal shade-casting ability index (*SCA*) describes the shade-casting ability of individual tree and shrub species, from low (1) to high (6, cf. Van Calster et al., 2008). We classified all neighbours of a species with intermediate to high shade-casting ability (*SCA* 4–6) as shade tolerant, all neighbours with an extremely low to low shade-casting ability (*SCA* 1–3) as light demanding.

As a simple measure of diversity, we used the species richness, i.e., the number of species, of the neighbour trees. Then, we calculated the species diversity of the neighbour trees as the Shannon index (Shannon, 1948), i.e.,

$$H_s = - \sum_{i=1}^{n_s} \frac{N_i}{N_{tot}} \ln \frac{N_i}{N_{tot}} \quad (2)$$

with  $N_i$  the number of neighbour trees of species  $i$  and  $N_{tot}$  the overall number of neighbour trees. We used the number of neighbour trees rather than their basal area to avoid (partially) including a structural diversity in this measure of species diversity. The Shannon index has been successfully used before to quantify the tree species diversity of forests (Liang, Buongiorno, Monserud, Kruger, & Zhou, 2007; Ratcliffe et al., 2015). For the size diversity of the local neighbourhoods, we looked at both the diversity in tree diameter and tree height. We first grouped all trees into discrete 5 cm diameter classes or 2 m height classes and then calculated the Shannon index using these size classes, e.g., for the diameter class diversity:

$$H_d = - \sum_{j=1}^{n_d} \frac{N_j}{N_{tot}} \ln \frac{N_j}{N_{tot}} \quad (3)$$

with  $N_j$  the number of neighbour trees of diameter class  $j$  and  $N_{tot}$  the overall number of neighbour trees. Such measures of size diversity have been successfully linked to forest growth before (Lei, Wang, & Peng, 2009; Liang et al., 2007).

## Statistical analysis

We investigated whether local neighbourhood diversity explains additional variation in the growth of individual oak and pine trees when added to a growth model containing standard drivers of tree growth such as tree size, site conditions, and stand density. As tree *size* variables, we considered diameter, height, and the height over diameter ratio based on the data from the first inventory; the *site* conditions were characterized by using the mean annual temperature and mean annual precipitation for the period between the two inventories (cf. Dănescu et al., 2016; data from the closest weather station: [www.kmi.be](http://www.kmi.be) and [www.knmi.nl](http://www.knmi.nl)) as well as the factor soil type. For neighbourhood *density* and *diversity*, we considered the eleven variables described in the part on neighbourhood approach above. For both oak and pine, we thus modelled the natural logarithm of the basal area increment of a tree ( $bai_i$ ) as a function of neighbourhood diversity ( $div$ ), whilst accounting for tree *size*, *site* conditions, and neighbourhood density ( $dens$ ):

$$\ln(bai_i) = \beta_0 + \beta_{size}size + \beta_{site}site + \beta_{nc}dens + \beta_{div}div \quad (4)$$

There was considerable correlation between several of the explanatory variables (see Appendix A: Fig. 2). Hence, for each set of variables, i.e., tree size, site, neighbourhood density (for the different neighbourhood sizes), and neighbourhood diversity (for the different neighbourhood sizes), we first constructed separate univariate models for the basal area increment and each explanatory variable. For each category, we then retained the explanatory variable that gave the lowest AIC (cf. Castagneyrol et al., 2013).



We fitted a null model ( $M_0$ : *size + site + dens*) and a model that additionally included neighbourhood diversity ( $M_{div}$ : *size + site + dens + div*) and followed the protocol described in Zuur, Ieno, Walker, Saveliev, and Smith (2009) to find the ideal random and fixed structure for our growth models. The models were fitted with *lme* (linear mixed effects) or *gls* (generalized least squares) of the *nlme* package in R (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2016) or with a simple *lm* (linear model). The fit of the models ( $M_0$ ,  $M_{div}$ ) was compared by AIC and the log likelihood ratio test for each dataset. In the mixed models, we used *forest reserve* as a random factor to control for similarities in growth data among trees from the same forest reserve and differences between forest reserves not accounted for by the *site* variables (soil and climate) included in the model. To account for heterogeneity, we included a variance structure in the generalized least squares models for the variance covariates *diameter* and *forest reserve* allowing for an increase in residual variance with diameter (*VarExp*) and a different spread per forest reserve (*VarIdent*). Before the analysis, all continuous explanatory variables were standardized. All analyses were done in R version 3.4.2 (R Core Team 2017); graphs were made with the R library ggplot2 (Wickham, 2009).

## Results

The overall mean basal area increment between the two inventories for trees in the studied forest reserves was  $13.8 \text{ cm}^2 \text{ yr}^{-1}$  for oak and  $12.6 \text{ cm}^2 \text{ yr}^{-1}$  for pine (Table 2),

but the mean basal area increment per tree differed strongly between forest reserves, with oak showing a mean increment of minimum 3.0 and maximum  $42.9 \text{ cm}^2 \text{ yr}^{-1}$  (in *Starnumansbos* and *Wijnendalebos*) and pine 9.7 and  $18.4 \text{ cm}^2 \text{ yr}^{-1}$  (*Tussen de Goren*, *Galgenberg*).

The growth models explained more variation for the oak trees ( $R^2 = 0.38\text{--}0.79$ ) than for the pine trees ( $R^2 = 0.17\text{--}0.29$ ). The basal area increment of the target trees increased with tree size (Table 3), with different tree size variables included in the different growth models: height (full oak dataset), diameter (small and tall oaks, full pine dataset, small pines), height over diameter ratio (tall pines). The site conditions were an important predictor in the growth models for the small pines and the full pine dataset. Pine basal area increment differed between the soil types, with a better growth in the Cambisol forest reserve, compared to the Arenosol forest reserve and the two forest reserves on Podzols. For the small oaks and the overall oak dataset, part of the variation in basal area increment could also be attributed to the overall effect of *forest reserve*, included as a random effect in the models (see the difference between the conditional and marginal  $R^2$  in Table 3).

The local neighbourhood effects differed among the datasets. Local density generally had a negative effect on growth. The basal area of the larger neighbour trees was negatively related to basal area increment for oak and for the full pine dataset; the neighbourhood competition index was negatively related to growth for the tall pine trees. The local neighbourhood diversity was only included in the models for oak. Species richness had a negative effect (for the small oaks,

**Table 2.** The variables used to characterize the target trees and their local neighbourhoods. The mean and range (minimum, maximum) are given for the 374 oaks and 421 pines.

Variable	Description	Oak	Pine
<i>Target tree</i>			
<i>bai</i>	Mean basal area increment ( $\text{cm}^2 \text{ yr}^{-1}$ ) <sup>a</sup>	13.8 (0.5, 82.2)	12.6 (1.9, 54.5)
<i>d</i>	Diameter at breast height (cm)	28.7 (5, 114)	27.2 (14, 51)
<i>h</i>	Tree height (m)	16.0 (3, 35)	15.7 (8, 23)
<i>h/d</i>	Height over diameter ratio (m/m)	66 (24, 140)	59 (33, 86)
<i>Neighbourhood</i> <sup>b</sup>			
<i>N</i>	Stem density ( $\text{ha}^{-1}$ )	658 (212, 2009)	593 (240, 1797)
<i>BA</i>	Basal area ( $\text{m}^2 \text{ ha}^{-1}$ )	25.6 (10.5, 45.5)	22.5 (12.2, 45.1)
<i>BAL</i>	Basal area larger neighbours ( $\text{m}^2 \text{ ha}^{-1}$ )	17.1 (0, 37.5)	11.6 (0, 33.5)
<i>Dq</i>	Quadratic mean diameter	23.4 (11.3, 42.2)	22.9 (11.4, 29.9)
<i>NCI</i>	Neighbourhood competition index	1.0 (0.5, 2.1)	1.0 (0.5, 1.9)
<i>NCIL</i>	<i>NCI</i> based on the light-demanding neighbours	0.8 (0.0, 2.1)	1.0 (0.5, 1.9)
<i>NCIS</i>	<i>NCI</i> based on the shade-tolerant neighbours	0.2 (0.0, 1.0)	0.0 (0.0, 0.2)
<i>SR</i>	Species richness, number of tree species	4.8 (1, 12)	3.1 (1, 6)
<i>H<sub>s</sub></i>	Tree species diversity <sup>c</sup>	3.4 (1.0, 9.6)	2.1 (1.0, 4.3)
<i>H<sub>d</sub></i>	Tree diameter diversity	6.1 (2.0, 11.2)	5.0 (2.8, 8.2)
<i>H<sub>h</sub></i>	Tree height diversity	7.0 (2.7, 11.9)	4.8 (2.3, 9.4)

<sup>a</sup>The basal area increment is the mean annual increment for the period between the two inventories; the tree and neighbourhood characteristics are based on the data of the first inventory.

<sup>b</sup>The neighbourhood data are for the neighbourhood with 15 m radius; see Appendix A: Table 2 for the other neighbourhood sizes.

<sup>c</sup>The diversity measures are expressed as the exponent of the Shannon index.

**Table 3.** The final basal area increment models for oak and pine. Models were fit for the full dataset as well as for the small trees (<16 m tall) and the tall trees (height > 16 m). We used linear mixed models with a random term (1|site), simple linear models, and generalized least squares models with a variance term ( $\text{var I + E} = \text{varIdent}(\text{site}) + \text{varExp}(1/d)$ ).

Species	Data	N	Model	Var <sub>radius</sub> <sup>a</sup>	Coef	p	Fit <sup>b</sup>	
Oak	Full	374	lme (1 site)	Size	<i>h</i>	1.00	<0.001	$R_m^2 = 0.68$
				Dens	<i>BAL</i> <sub>15</sub>	-0.22	<0.001	$R_c^2 = 0.79$
	Small	160	lme (1 site)	Size	<i>d</i>	0.63	<0.001	$R_m^2 = 0.48$
				Dens	<i>BAL</i> <sub>15</sub>	-0.13	0.020	$R_c^2 = 0.75$
				Div	<i>SR</i> <sub>15</sub>	-0.25	0.003	
	Tall	214	lm	Size	<i>d</i>	0.36	<0.001	$R_{adj}^2 = 0.38$
				Dens	<i>BAL</i> <sub>15</sub>	-0.17	0.001	
				Div	<i>H</i> <sub>h15</sub>	0.12	0.007	
	Pine	Full	421	gls (var I + E)	Size	<i>d</i>	0.13	<0.001
Dens					<i>BAL</i> <sub>15</sub>	-0.12	<0.001	
Site					Cambisol	0.33	<0.001	
					Podzol	-0.21	0.001	
Small		268	lm	Size	<i>d</i>	0.25	0.000	$R_{adj}^2 = 0.17$
				Site	Cambisol	1.12	0.007	
Tall		153	lm	Size	<i>h/d</i>	-0.12	0.002	$R_{adj}^2 = 0.29$
				Dens	<i>NCI</i> <sub>10</sub>	-0.29	<0.001	

<sup>a</sup>The variables included in the models. For the neighbourhood variables, the radius (in m) of the neighbourhood used to calculate the variable is indicated in subscript.

- size variables: *h* tree height, *d* diameter at breast height, *h/d* height over diameter ratio.

- density variables: *BAL* summed basal area of neighbours with a larger diameter than the target tree, *NCI* neighbourhood competition index.

- diversity variables: *SR* species richness, *H<sub>h</sub>* tree height diversity.

- site variables: soil types *Cambisol* and *Podzol*, compared to *Arenosol*.

<sup>b</sup>For the mixed models, marginal ( $R_m^2$ ) and conditional ( $R_c^2$ ) values are given.

Fig. 2A), while height diversity had a positive effect (for the tall oaks) (Table 3). In the neighbourhood of the small oaks, the species richness was positively correlated with the share of shade-casting species in the neighbourhood (Fig. 2B). A comparison of the different neighbourhood sizes suggested that the best predictive power for the basal area increment was provided by a neighbourhood of a 15 m radius for the oaks and 10 m for the pines.

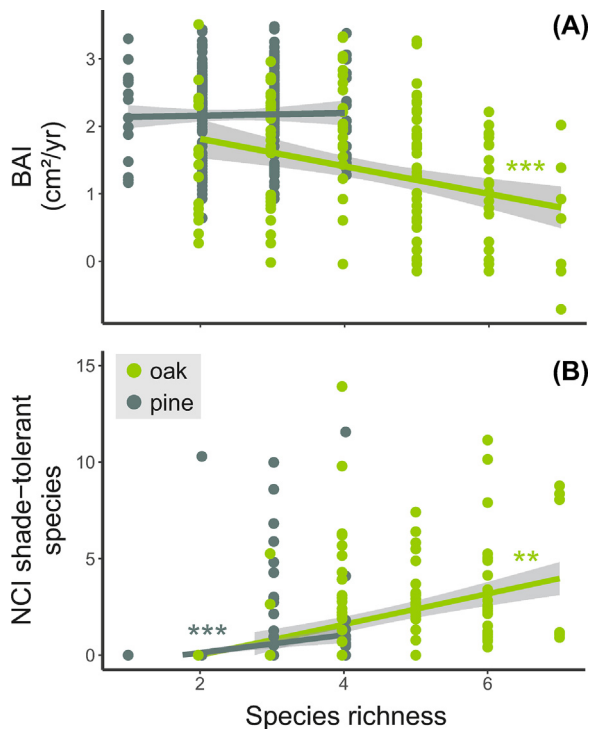
## Discussion

In the forest reserves of our study, we found only clear effects of neighbourhood diversity for the growth of small oaks (species richness) and tall oaks (tree height diversity); for the pines, no diversity variable was included in the final growth models. The absence of an overall diversity effect is not unprecedented. No or only weak effects of compositional diversity on tree growth have been reported before for mature forests (del Río, Schütze, & Pretzsch, 2014; Jacob, Leuschner, & Thomas, 2010a; Ratcliffe et al., 2015) as well as young plantations (Grossman et al., in press).

In our study, tree species richness showed a negative relationship with the basal area increment of the small oak trees; the small oak trees grew better in a less diverse neighbourhood. Negative effects of species diversity have been found before for stand productivity (Firn et al., 2007; Vilà et al.,

2013), but positive effects of species diversity on tree growth and stand productivity have been reported more often, for mature forests (e.g., Chamagne, Tanadini, Frank, Matula, & Paine, 2017; Condés, Del Rio, & Sterba, 2013; Vilà et al., 2013) and young plantations (Grossman et al., in press). For the small oaks in the studied forests, a diverse neighbourhood meant more competition by shade-tolerant (and hence shade-casting) tree species (see Fig. 2B), which may have negatively affected the growth of the light-demanding oaks (cf. Manso, Morneau, Ningre, & Fortin, 2015). For the (also light-demanding) small pine trees, we did not find an effect of neighbourhood species diversity (see Fig. 2A). Jucker et al. (2014), on the other hand, saw that subcanopy pine trees in Iberian oak-pine forests benefited from tree species mixing; these small pine trees experienced a higher light availability in the mixtures. In our study, the forest structure and species composition experienced by the small pines probably differed too much among the four forest reserves included in our rather small dataset (see Appendix A: Table 1) to lead to a common, overall diversity effect.

Structural diversity showed a positive relationship with the growth of the tall oak trees in our study. The tall oak trees grew better in a neighbourhood with high tree height inequality, which might be related with the high crown plasticity of oaks (Longuetaud, Piboule, Wernsdörfer, & Collet, 2013). Surrounded by neighbours of different heights, they were able to fill the available canopy space around them and



**Fig. 2.** Basal area increment of the small oaks and pines in relation to the species richness of the local neighbourhood (A) and the relation between the competition by shade-tolerant species and the species richness in the local neighbourhood of these small trees (B). Data are shown for a neighbourhood with a 15 m radius, and the BAI axis represents the natural logarithm of the basal area increment. The asterisks indicate the  $p$ -values of the slopes of the linear regressions between the two variables (\*\*\* $p < 0.001$ , \*\* $p < 0.01$ ); the grey shadings show the 95% confidence intervals.

hence capture more light. Dănescu et al. (2016) also showed positive, asymmetric effects of structural diversity; they saw that large trees showed the highest increase in productivity in structurally diverse stands. Zhang and Chen (2015) showed that tree size inequality was the mechanism behind the positive species diversity effects on stand productivity in natural forests. Liang et al. (2007), on the other hand, found a negative relationship between structural diversity and stand productivity, because of lower recruitment or higher mortality in diverse stands. Here, we did not look at the recruits or trees that died between the two inventories.

Kunstler et al. (2016) showed that the total abundance of neighbours, irrespective of their traits, was the strongest driver of individual tree growth in forest across all biomes. In our study as well, neighbourhood density was included in all the growth models, except for the model for the small pines. Similarly, Ratcliffe et al. (2015) showed for a temperate mixed beech (*Fagus sylvatica* L.) forest in Germany that the diversity of the local neighbourhood was relevant for the growth of beech and hornbeam (*Carpinus betulus* L.), but not for ash (*Fraxinus excelsior* L.), whereas local stand density affected the growth of all three study species. For a subtrop-

ical mixed forest, von Oheimb et al. (2011) did also show no effects of local species richness and a prominent effect of neighbourhood competition on tree growth.

Some methodological issues may be raised in relation to our results, such as the high variability associated with large re-inventory datasets, the differences in forest and site characteristics among the studied forest reserves, the choice of the diversity and competition measures, and the definition of the local neighbourhood.

Data from repeated inventories may contain frequent errors, which may lead to a high variability or unlikely values, also in derived measures such as tree growth. Hence, growth models fitted to inventory data may explain only a limited amount of the variation (cf. Condés et al. 2013; del Río & Sterba, 2009). Yet, with  $R^2$ s of 0.17 to 0.79, our models do quite well in this respect.

The differences in site conditions and tree species composition of the studied forest reserves (see Table 1) probably prevented finding an overall diversity–growth relationship. The soil type was included in the models for small pines and the full pine dataset, and the random effect (accounting for differences between the sites, i.e., forest reserves) in the mixed models for oak explained 27% of the variation in growth for the small oaks and 11% for the full oak dataset. The negative effect of tree species richness for the small oaks seemed to be driven by the species composition of the forests (i.e., the share of shade-tolerant species, see Fig. 2). In a study on different forest types with differing site conditions in Europe, the shape of the diversity–productivity relationship was indeed not consistent among the forest types (Vilà et al., 2013). In acidophilous oak forest, for instance, wood production decreased from monocultures to mixed plots while the other ten forest types showed higher production in mixtures.

Tree diversity has been calculated in various ways in former studies on the diversity–growth relationship in forests. The size, number, and identity of a tree’s neighbours all affected tree growth in a young tropical plantation (Potvin & Dutilleul, 2009). Tree species richness (Vilà et al., 2013), tree species diversity (Jucker et al., 2016), tree size diversity (Dănescu et al., 2016; Liang et al., 2007; Zhang & Chen, 2015), and an integrated species–size diversity measure (Lei et al., 2009) have all been successfully correlated with tree growth or stand productivity. Functional diversity (Haase et al., 2015), genetic diversity (Hahn et al., 2017), and species composition (Salisbury & Potvin, 2015) did not show clear links with tree growth. According to Dănescu et al. (2016), the – often subjective – choice of diversity index in studies may account for some of the inconsistent results on the diversity–productivity relationship in literature, and they recommend testing and reporting multiple diversity indices. In our study, both species richness (for small oaks) and tree height diversity (for tall oaks) were included in the final growth models.

The choice of the neighbourhood size in a study on neighbourhood effects may affect its outcome and conclusions, especially in forests in which the spatial distribution of trees

of different ages, sizes, and species is non-regular. In addition, the relevant neighbourhood size will also depend on the size of the target tree (D'Amato & Puettmann, 2004). Following, e.g., Puettmann, D'Amato, Kohnle, and Bauhus (2009) and von Oheimb et al. (2011), we compared different neighbourhood sizes and found that a 10 m radius provided the best predictive power for the tall pine trees, while a 15 m radius provided the best fits for the oaks. This corresponds to the generally larger crown radius for the oak trees compared to the pines in the studied Dutch forest reserves.

## Conclusion

The oak and pine trees growing in the temperate mixed forest stands of our study did show no overall diversity-growth relationship. The growth of the subcanopy oaks (height < 16 m) was negatively related to species richness, and the growth of the tall oaks (height > 16 m) was positively related to structural diversity. For the pines, neighbourhood diversity was not included in the growth models. Target tree size, local density (except for the small pines), and soil type (for the small pines and the full pine dataset) also explained part of the variation in tree growth. Our study on tree growth in uneven-aged mature forests confirms that biodiversity-productivity relationships are context-dependent. The effect of diversity may differ between species (e.g., oak and pine in our study) and depend on the aspect of diversity that is studied (e.g., species diversity vs. structural diversity).

## Acknowledgements

We thank all field workers and data processors involved in the monitoring of the forest reserves in northern Belgium and the Netherlands, at the Research Institute for Nature and Forest, i.e., Peter Van de Kerckhove, Marc Esprit, Stefaan Goessens, Bart Christiaens, and Anja Leyman, and at Wageningen Environmental Research (Alterra). We thank the reviewers for their constructive comments on the manuscript. Margot Vanhellefont was funded as a postdoctoral fellow of FWO-Vlaanderen.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.baae.2018.01.003>.

## References

Annighöfer, P., Beckschäfer, P., Vor, T., & Ammer, C. (2015). Regeneration patterns of European oak species (*Quercus petraea*

(Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. *PLoS ONE*, *10*(8), e0134935.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., et al. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, *9*, 1146–1156.

Biondi, F., & Qeadan, F. (2008). A theory-driven approach to tree-ring standardization: Defining the biological trend from expected basal area increment. *Tree-Ring Research*, *64*, 81–96.

Brassard, B. W., Chen, H. Y. H., Bergeron, Y., & Paré, D. (2011). Differences in fine root productivity between mixed- and single-species stands. *Functional Ecology*, *25*, 238–246.

Brassard, B. W., Chen, H. Y. H., Cavard, X., Laganière, J., Reich, P. B., Bergeron, Y., et al. (2013). Tree species diversity increases fine root productivity through increased soil volume filling. *Journal of Ecology*, *101*, 210–219.

Canham, C., LePage, P. T., & Coates, K. D. (2004). A neighborhood analysis of canopy tree competition: Effects of shading versus crowding. *Canadian Journal of Forest Research*, *34*, 778–787.

Carnol, M., Baeten, L., Branquart, E., Gregoire, J.-C., Heughebaert, A., Muys, B., et al. (2014). Ecosystem services of mixed species forest stands and monocultures: Comparing practitioners' and scientists' perceptions with formal scientific knowledge. *Forestry*, *87*, 639–653.

Castagneyrol, B., Giffard, B., Péré, C., & Jactel, H. (2013). Plant apparency, an overlooked driver of associational resistance to insect herbivory. *Journal of Ecology*, *101*, 418–429.

Chamagne, J., Tanadini, M., Frank, D., Matula, R., Paine, C. E. T., Philipson, C. D., et al. (2017). Forest diversity promotes individual tree growth in central European forest stands. *Journal of Applied Ecology*, *54*, 71–79.

Coll, L., Ameztegui, A., Collet, C., Löf, M., Mason, B., Pach, M., et al. (2017). Knowledge gaps about mixed forests: What do European forest managers want to know and what answers can science provide? *Forest Ecology and Management*, *407*, 106–115.

Condés, S., Del Rio, M., & Sterba, H. (2013). Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. *Forest Ecology and Management*, *292*, 86–95.

Cuchietti, A., Marcotti, E., Gurvich, D. E., Cingolani, A. M., & Pérez Harguindeguy, N. (2014). Leaf litter mixtures and neighbour effects: Low-nitrogen and high-lignin species increase decomposition rate of high-nitrogen and low-lignin neighbours. *Applied Soil Ecology*, *82*, 44–51.

D'Amato, A. W., & Puettmann, K. J. (2004). The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra*/*Pseudotsuga menziesii* stands. *Journal of Ecology*, *92*, 450–463.

Dănescu, A., Albrecht, A. T., & Bauhus, J. (2016). Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. *Oecologia*, *182*, 319–333.

del Río, M., & Sterba, H. (2009). Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*. *Annals of Forest Science*, *66*, 502.

del Río, M., Schütze, G., & Pretzsch, H. (2014). Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biology*, *16*, 166–176.

Den Ouden, J., Mohren, F., De Waal, R., & De Schrijver, A. (2010). Groeiplaats en bodem. In J. Den Ouden, B. Muys, F. Mohren, &



- K. Verheyen (Eds.), *Bosecologie en bosbeheer* (pp. 133–150). Leuven: Acco.
- FAO. (2006). *World reference base for soil resources 2006. A framework for international classification, correlation and communication*. pp. 103. Rome: World Soil Resources Reports.
- Firn, J., Erskine, P. D., & Lamb, D. (2007). Woody species diversity influences productivity and soil nutrient availability in tropical plantations. *Oecologia*, *154*, 521–533.
- Forrester, D. I. (2014). The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *Forest Ecology and Management*, *312*, 282–292.
- Forrester, D. I., & Bauhus, J. (2016). A review of processes behind diversity–Productivity relationships in forests. *Current Forestry Reports*, *2*, 45–61.
- Forrester, D. I., Kohnle, U., Albrecht, A. T., & Bauhus, J. (2013). Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. *Forest Ecology and Management*, *304*, 233–242.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., et al. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, *4*, 1340.
- Grossman, J. J., Vanhellefont, M., Barsoum, N., Bauhus, J., Bruelheide, H., & Castagnyrol, B., et al. Synthesis and future research directions linking tree diversity to growth, survival, and damage in a global network of tree diversity experiments. *Environmental and Experimental Botany*, (in press).
- Haase, J., Castagnyrol, B., Cornelissen, J. H. C., Ghazoul, J., Kattge, J., Koricheva, J., et al. (2015). Contrasting effects of tree diversity on young tree growth and resistance to insect herbivores across three biodiversity experiments. *Oikos*, *124*, 1674–1685.
- Hahn, C. Z., Niklaus, P. A., Bruelheide, H., Michalski, S. G., Shi, M., Yang, X., et al. (2017). Opposing intraspecific vs. interspecific diversity effects on herbivory and growth in subtropical experimental tree assemblages. *Journal of Plant Ecology*, *10*, 242–251.
- Jacob, M., Leuschner, C., & Thomas, F. M. (2010). Productivity of temperate broad-leaved forest stands differing in tree species diversity. *Annals of Forest Science*, *67*, 503.
- Jacob, M., Viedenz, K., Polle, A., & Thomas, F. M. (2010). Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (*Fagus sylvatica*). *Oecologia*, *164*, 1083–1094.
- Jäkel, A., & Roth, M. (2004). Conversion of single-layered Scots pine monocultures into close-to-nature mixed hardwood forests: Effects on parasitoid wasps as pest antagonists. *European Journal of Forest Research*, *123*, 203–212.
- Jones, E. W. (1959). *Quercus L.* *Journal of Ecology*, *47*, 169–222.
- Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., et al. (2014). Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests. *Journal of Ecology*, *102*, 1202–1213.
- Jucker, T., Bouriaud, O., & Coomes, D. A. (2015). Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Functional Ecology*, *29*, 1078–1086.
- Jucker, T., Cuni Sanchez, A., Lindsell, J. A., Allen, H. D., Amable, G. S., & Coomes, D. A. (2016). Drivers of aboveground wood production in a lowland tropical forest of West Africa: Teasing apart the roles of tree density, tree diversity, soil phosphorus, and historical logging. *Ecology and Evolution*, *6*, 4004–4017.
- Kaitaniemi, P., Riihimäki, J., Koricheva, J., & Vehviläinen, H. (2007). Experimental evidence for associational resistance against the European pine sawfly in mixed tree stands. *Silva Fennica*, *41*, 259–268.
- Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., et al. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, *529*, 204–207.
- Kuster, T. M., Dobbertin, M., Günthardt-Goerg, M. S., Schaub, M., & Arend, M. (2014). A phenological timetable of oak growth under experimental drought and air warming. *PLoS ONE*, *9*(2), e89724.
- Lei, X., Wang, W., & Peng, C. (2009). Relationships between stand growth and structural diversity in spruce-dominated forests in New Brunswick, Canada. *Canadian Journal of Forest Research*, *39*, 1347–1835.
- Liang, J., Buongiorno, J., Monserud, R. A., Kruger, E. L., & Zhou, M. (2007). Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *Forest Ecology and Management*, *243*, 116–127.
- Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., et al. (2016). Positive biodiversity–productivity relationship predominant in global forests. *Science*, *354*(6309), aaf8957.
- Longuetaud, F., Piboule, A., Wernsdörfer, H., & Collet, C. (2013). Crown plasticity reduces inter-tree competition in a mixed broadleaved forest. *European Journal of Forest Research*, *132*, 621–634.
- Manso, R., Morneau, F., Ningre, F., & Fortin, M. (2015). Effect of climate and intra- and inter-specific competition on diameter increment in beech and oak stands. *Forestry*, *88*, 540–551.
- Meyer, P. (2005). Network of Strict Forest Reserves as reference system for close to nature forestry in Lower Saxony, Germany. *Forest Snow and Landscape Research*, *79*, 33–44.
- Nadrowski, K., Wirth, C., & Scherer-Lorenzen, M. (2010). Is forest diversity driving ecosystem function and service? *Current Opinion in Environmental Sustainability*, *2*, 75–79.
- Naeem, S., Duffy, J. E., & Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science*, *336*, 1401.
- Parviainen, J., Bücking, W., Vandekerckhove, K., Päivinen, R., & Schuck, A. (2000). Strict forest reserves in Europe: Efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-action E4). *Forestry*, *73*, 107–118.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2016). *nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-127*. Available from: <http://CRAN.R-project.org/package=nlme>
- Piotto, D. (2008). A meta-analysis comparing tree growth in monocultures and mixed plantations. *Forest Ecology and Management*, *255*, 781–786.
- Potvin, C., & Dutilleul, P. (2009). Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. *Ecology*, *90*, 321–327.
- Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., et al. (2013). Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *European Journal of Forest Research*, *132*, 263–280.
- Pretzsch, H., Block, J., Dieler, J., Dong, P. H., Kohnle, U., Nagel, J., et al. (2010). Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Annals of Forest Science*, *67*, 712.

- Pretzsch, H., del Río, M., Schütze, G., Ammer, C., Annighöfer, P., Avdagic, A., et al. (2016). Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with water availability. *Forest Ecology and Management*, 373, 149–166.
- Puettmann, K. J., D'Amato, A. W., Kohnle, U., & Bauhus, J. (2009). Individual-tree growth dynamics of mature *Abies alba* during repeated irregular group shelterwood (Femelschlag) cuttings. *Canadian Journal of Forest Research*, 39, 2437–2449.
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from: <https://www.R-project.org>
- Ratcliffe, S., Holzwarth, F., Nadrowski, K., Levick, S., & Wirth, C. (2015). Tree neighbourhood matters – Tree species composition drives diversity–productivity patterns in a near-natural beech forest. *Forest Ecology and Management*, 335, 225–234.
- Saha, S., Kuehne, C., Kohnle, U., Brang, P., Ehring, A., Geisel, J., et al. (2012). Growth and quality of young oaks (*Quercus robur* and *Quercus petraea*) grown in cluster plantings in central Europe: A weighted meta-analysis. *Forest Ecology and Management*, 283, 106–118.
- Salisbury, C. L., & Potvin, C. (2015). Does tree species composition affect productivity in a tropical planted forest? *Biotropica*, 47, 559–568.
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27, 379–423.
- Toïgo, M., Vallet, P., Perot, T., Bontemps, J. D., Piedallu, C., & Courbaud, B. (2015). Overyielding in mixed forests decreases with site productivity. *Journal of Ecology*, 103, 502–512.
- Toïgo, M., Perot, T., Courbaud, B., Castagneyrol, B., Gégout, J.-C., Longuetaud, F., et al. (2018). Difference in shade tolerance drives the mixture effect on oak productivity. *Journal of Ecology*, <http://dx.doi.org/10.1111/1365-2745.12811> (in press)
- Van Calster, H., Baeten, L., Verheyen, K., De Keersmaecker, L., Dekeyser, S., Rogister, J. E., et al. (2008). Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. *Forest Ecology and Management*, 256, 519–528.
- Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., et al. (2013). Disentangling biodiversity and climatic determinants of wood production. *PLOS ONE*, 8(2), e53530.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., et al. (2007). Let the concept of trait be functional!. *Oikos*, 116, 882–892.
- von Gadow, K., Zhao, X. H., Tewari, V. P., Zhang, C. Y., Kumar, A., Rivas, J., et al. (2016). Forest observational studies: An alternative to designed experiments. *European Journal of Forest Research*, 135, 417–431.
- von Oheimb, G., Lang, A. C., Bruelheide, H., Forrester, D. I., Wäsche, I., Yu, M., et al. (2011). Individual-tree radial growth in a subtropical broad-leaved forest: The role of local neighbourhood competition. *Forest Ecology and Management*, 261, 499–507.
- Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York: Springer.
- Zhang, Y., & Chen, Y. H. (2015). Individual size inequality links forest diversity and above-ground biomass. *Journal of Ecology*, 103, 1245–1252.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer-Verlag.

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

**ScienceDirect**