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

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### 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).

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### 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;

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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.

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