Tree neighbourhood matters – Tree species composition drives diversity–productivity patterns in a near-natural beech forest

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ABSTRACT

European beech forest with a variable admixture is one of the most important forest types in Central Europe. Growing evidence has demonstrated the positive effect of increased biodiversity on vital forest ecosystem functions and services such as productivity and nutrient cycling. Both complementarity in resource use and species identity are known to influence tree productivity but they have received relatively little attention in observational studies. Using a large dataset of repeat inventory trees in a near-natural deciduous forest in Central Germany we test whether tree diversity enhances tree productivity at the tree and the stand level, whilst accounting for tree size, tree vitality, local topography and the potentially confounding effects of spatial autocorrelation and negative growth estimates. Beech and hornbeam individual tree growth was sensitive to their neighbourhood diversity and composition whilst ash trees were only sensitive to the neighbourhood tree density. Neighbourhood complementarity effects were driven by differences in species' competitive strengths, whilst at the stand level productivity gains were primarily attributable to the density of ash and diversity effects were less prominent. We conclude that small-scale admixture with patches of different species promotes tree growth in European beech forest; congruent with current management plans for beech and hardwood forests.

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1. Introduction

Forests provide us with a wealth of products and services. There is concern that the loss of biodiversity within forests is jeopardising these services (Aerts and Honnay, 2011). Growing empirical evidence demonstrates that biodiversity loss can affect major ecosystem properties such as primary productivity and nutrient cycling (Cardinale et al., 2012; Isbell et al., 2011). Unlike in grassland ecosystems, where clear productivity–diversity relationships have been identified (Balvanera et al., 2006; Hooper et al., 2005), the relationship between tree species diversity and tree productivity in forest ecosystems, and its underlying mechanisms, are less well understood (Nadrowski et al., 2010; Vilà et al., 2003).

Both the diversity and the identity of species are known to influence ecosystem processes; complementarity (Tilman, 1988) and selection effects (Loreau, 2000) are the key mechanisms underpinning these relationships. In theory, diverse forest stands have a higher productivity due to species-specific differences in, for example, phenology or root architecture, so that interspecific competition is less intense than intraspecific (Kelty, 1992; Pretzsch and Schütze, 2009), or due to facilitation where positive interspecific interactions promote species' performance (Cardinale et al., 2002). Diverse forests are also more likely to contain highly productive tree species that come to dominate, and most influence, community-level processes (selection effect: Loreau, 2000). A fundamental aspect of the selection effect is that it is the identity of the dominant species that most drives community-level processes. The extent to which complementarity and species identity control tree productivity has received relatively little attention in studies in natural and near-natural forests, and is a focus of this study.

Current knowledge on biodiversity–productivity relationships in forest ecosystems stem from three approaches (classic forestry trials, experiments and observational studies), each with their own advantages and disadvantages with respect to resolving mechanisms and stand level representation (Baeten et al., 2013). Classic forestry trials explore the productivity of planted mixtures (Pretzsch, 2005). Their plot sizes are typically at a scale relevant for management but the focus is on a few selected merchantable tree

species and diversity gradients are short (rarely more than 2 species). More recent biodiversity-ecosystem functioning experiments maximise the diversity gradient and avoid species identity effects by randomly selecting species from a large pool (Bruelheide et al., 2014; Scherer-Lorenzen et al., 2007). However, the plots are typically small (~0.2 ha) and the trees are still young (<15 years), which limits scaling-up their results to mature forests at scales relevant for forest management (Chisholm et al., 2013). Observational studies, often using data from National Forest Inventories (NFI), are based on plots in existing forest, representing all age-classes and forest types (Gamfeldt et al., 2013; Paquette and Messier, 2011; Ruiz-Benito et al., 2014). However, individual plots are particularly small (<0.05 ha) and so suffer from strong edge effects when defining neighbourhood diversity and are often confounded by environmental heterogeneity (Baeten et al., 2013; Vilà et al., 2005). The focus of many tree productivity diversity studies has been at small spatial scales and there is a need for studies that are not constrained by the size of the plot.

Overall, the results of observational studies on the relationship between tree species diversity and productivity have been inconclusive; positive (Erskine et al., 2006; Gamfeldt et al., 2013; Paquette and Messier, 2011; Ruiz-Benito et al., 2014; Vilà et al., 2013, 2007), negative (Firn et al., 2007; Jacob et al., 2010; Szwagrzyk and Gazda, 2007) and no relationships (Nguyen et al., 2012; Vilà et al., 2003) have been found. The identification and magnitude of diversity effects on tree productivity depend, in part, on the scale (spatial, temporal and extent) of the study (Chase and Knight, 2013; Chisholm et al., 2013; Potvin and Dutilleul, 2009; Scherer-Lorenzen, 2005), the stand developmental stage (Vilà et al., 2007), and site conditions such as water and nutrient availability (Healy et al., 2008; Kelty, 1992; Pretzsch and Schütze, 2005; Pretzsch, 2003; Pretzsch et al., 2013). The lack of consistent support for a general tree diversity–productivity relationship is likely to be largely due to these confounding influences; the existence and likelihood of detection of diversity–productivity relations is inherently more context-dependent in forests than in grasslands.

Alongside climate and local abiotic conditions, ontogeny (i.e. tree size) and competition (local neighbourhood interactions) are recognised as key factors influencing tree growth (Sanchez-Gomez et al., 2008). Competition, a key mechanism underlying diversity–productivity relationships, occurs between individuals (Potvin and Dutilleul, 2009; Scherer-Lorenzen et al., 2007). Hence a neighbourhood approach may be used to quantify local interactions and infer whether any observed individual tree growth enhancement is driven by altered interactions due to local changes in relative abundance of neighbours (Kirwan et al., 2007; Potvin and Dutilleul, 2009). Potvin and Dutilleul (2009) hypothesised that if a biodiversity effect can be reduced to a neighbourhood scale, then the response to biodiversity at the stand level should be the aggregate effect of local neighbourhoods. Few forest studies have traced community level diversity effects to the individual tree level (but see Pretzsch and Schütze, 2009) and doing so allows us to understand how tree species respond to increased diversity and how this is reflected at the community level.

European beech forest, with a variable admixture, is one of the most important forest types in Central Europe. Using a large dataset (~13,000 trees in a 28 ha stand) of fully inventoried trees in a near-natural deciduous forest in Central Germany we test whether tree diversity enhances tree productivity at the individual tree and the stand level, whilst accounting for tree size, tree vitality and local topography. The benefit of a stand-level inventory is that we can use a neighbourhood approach to estimate the scale over which the trees interact and are not restricted by fixed plot sizes. We also consider the potentially confounding effects of spatial autocorrelation and negative growth estimates by including estimates of the measurement and spatial error.

The aim of this study is to test whether: (1) a greater diversity of neighbourhood tree species enhances individual tree growth; (2) any observed diversity effect is driven by differences in competitive interaction strengths; and (3) determine how individual tree level diversity–productivity relationships are reflected at the stand level.

2. Materials and methods

This study was conducted on a dataset from a 28.5 ha plot of mature deciduous forest in the Hainich National Park (51°06′ N, 10°31′ E), Thuringia, Germany. See Holzwarth et al. (2013) for a detailed site description. The site has been permanently forested for over 200 years and has remained free of harvesting or thinning for over 40 years. The site is dominated by beech (*Fagus sylvatica* L.; 68% of the basal area), with an admixture of ash (*Fraxinus excelsior* L.), hornbeam (*Carpinus betulus* L.) and sycamore (*Acer pseudoplatanus* L.). Additional species, in small numbers, include Wych elm (*Ulmus glabra* Huds.), field maple (*Acer campestre* L.) and Norway maple (*Acer platanoides* L.). The forest stand is unfenced and subject to deer browsing.

All trees with a diameter at breast height (d.b.h.; 130 cm) of 1 cm or more were surveyed in the summers of 1999 and 2007. The diameter at breast height, a Kraft (canopy) dominance rating (Kraft, 1884) and vitality information were recorded. High resolution LiDAR data was available for the whole study area from which we constructed a digital terrain model (DTM) at 0.5 m spatial resolution to derive topographic variables.

Annual diameter growth was calculated for each tree as the difference in d.b.h. between the two inventories, divided by the time interval (8 years). There were only sufficient numbers of ash, beech and hornbeam for the individual analysis. Table 1 includes the mean d.b.h. and diameter growth the three study species. The study site is in continuous forest. However, due to tracks on the southern and northern edges, where there were no trees, buffers of 10 m and 3 m, respectively, were imposed on the data. We only considered those individuals who survived both inventories, thus dead trees and recruits were ignored.

Table 1
Mean and range (minimum, maximum) of diameter at breast height (d.b.h.) and annual diameter growth and neighbourhood level variables for each study species. TWI is the topographic wetness index (unitless) and BA neighbours is the basal area of all trees within the neighbourhood radius.

	Ash	Beech	Hornbeam
No. trees	420	9880	312
d.b.h. (cm)	61.51 (7.1, 126.5)	18.75 (0.8, 105.5)	37.89 (8.7, 70.0)
Growth (cm yr^{-1})	0.459 (−0.2, 1.775)	0.116 (−0.312, 1.325)	0.099 (−0.175, 0.525)
Neighbourhood radius (m)	20	15	15
Species richness (tree layer)	4.038 (2, 6)	2.965 (1, 6)	3.564 (2, 6)
Shannon index (tree layer)	0.948 (0.114, 1.544)	0.696 (0, 1.7)	0.943 (0.085, 1.615)
BA neighbours (m^2 ha^{-1})	35.073 (17.431, 58.788)	34.994 (5.309, 70.330)	32.61 (7.448, 60.309)
TWI	7.447 (6.666, 8.855)	7.357 (6.423, 8.887)	7.240 (6.657, 8.781)
Elevation (m)	438 (404, 455)	438 (402, 457)	434 (404, 455)