Journal of Ecology

Good things take time – diversity effects on tree growth shift from negative to positive during stand development in boreal forests

Journal:	*Journal of Ecology*
Manuscript ID	JEcol-2020-0338.R1
Manuscript Type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Jucker, Tommaso; University of Bristol, School of Biological Sciences Koricheva, Julia; Royal Holloway University of London, School of Biological Sciences Finér, Leena; Natural Resources Institute Finland (Luke), P.O. Box 68, 80101 Joensuu, Finland Bouriaud, Olivier; Stefan cel Mare University of Suceava, Faculty of Forestry; IGN, Laboratoire d'Inventaire Forestier Iacopetti, Giovanni; University of Florence Coomes, David; University of Cambridge
Key-words:	biodiversity–ecosystem functioning, canopy packing, competition for light, non-linear growth models, overyielding, plant–plant interactions, tree diversity experiments, tree rings

Good things take time – diversity effects on tree growth shift from negative to positive during stand development in boreal forests

Tommaso Jucker[1], Julia Koricheva[2], Leena Finér[3], Olivier Bouriaud[4,5], Giovanni Iacopetti[6] and David A. Coomes[7]

Author affiliations

[1] School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK

[2] Department of Biological Sciences, Royal Holloway University of London, Egham, TW20 0EX, UK

[3] Finland Natural Resources Institute, Joensuu, FI-80100, Finland

[4] Faculty of Forestry, Stefan cel Mare University of Suceava, 720229 Suceava, Romania

[5] Laboratoire d'Inventaire Forestier, IGN, Nancy, 54000, France

[6] Department of Agriculture, Food, Environment and Forestry, University of Florence, Florence, Italy

[7] Conservation Research Institute, University of Cambridge, Cambridge, CB2 3EA, UK

Corresponding author: Tommaso Jucker (t.jucker@bristol.ac.uk), School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK

Running title: Diversity–productivity relationships through time

Type of article: Research article

ABSTRACT

1. Long-term grassland biodiversity experiments have shown that diversity effects on productivity tend to strengthen through time, as complementarity among coexisting species increases. But it remains less clear whether this pattern also holds for other ecosystems such as forests, and if so why.
2. Here we explore whether diversity effects on tree growth change predictably during stand development in Finland's boreal forests. Using tree ring records from mature forests, we tested whether diameter growth trajectories of dominant tree species growing in mixture differed from those in monoculture. We then compared these results with data from the world's longest running tree diversity experiment, where the same combinations of species sampled in mature forests were planted in 1999.
3. We found that diversity effects on tree growth strengthened progressively through time, only becoming significantly positive around 20 years after seedling establishment. This shift coincided with the period in which canopy closure occurs in these forests, at which time trees begin to interact and compete aboveground. These temporal trends were remarkably consistent across different tree species sampled in mature forests, and broadly matched growth responses observed in the much younger experimental plots.
4. *Synthesis*. Our results mirror those from grassland ecosystems and suggest that canopy closure is a key phase for promoting niche complementarity in diverse tree communities. They also provide a series of testable hypotheses for the growing number of tree diversity experiments that have been established in recent years.

Key words: biodiversity–ecosystem functioning; canopy packing; competition for light; non-linear growth models; overyielding; plant–plant interactions; tree diversity experiments; tree rings

INTRODUCTION

All things being equal, diverse tree communities generally sequester and store more carbon from the atmosphere than their species-poor counterparts (Morin *et al.* 2011; Vilà *et al.* 2013; Jucker *et al.* 2014a; Fichtner *et al.* 2018). Yet underlying this overall positive relationship between tree diversity and productivity is a considerable degree of spatial and temporal variation in the strength of diversity effects on tree growth (Forrester 2014; Jucker *et al.* 2014b, 2016; Searle & Chen 2020). Recent work has highlighted how differences in climate, soils, canopy structure and species composition account for much of the spatial variation in the strength and direction of these diversity effects (Forrester 2014; Toïgo *et al.* 2015; Jucker *et al.* 2016; Ratcliffe *et al.* 2016; Baeten *et al.* 2019). However, considerably less is known about how and why diversity effects on tree growth change through time during stand development (Zhang, Chen & Reich 2012; Taylor, Gao & Chen 2020).

Long-term grassland biodiversity experiments have shown that diversity effects on productivity tend to strengthen through time (Cardinale *et al.* 2007; Reich *et al.* 2012; Zuppinger-Dingley *et al.* 2014; Guerrero-Ramírez *et al.* 2017). This pattern has been attributed to diverse communities progressively optimizing the use of limiting resources, resulting in stronger complementarity and lower redundancy among coexisting species (Reich *et al.* 2012; Zuppinger-Dingley *et al.* 2014). In forests, numerous mechanisms have been put forward to explain the positive effects of diversity on tree growth, including reduced pest and pathogen loads, trophic interactions, and increased water- and nutrient-use efficiency belowground (Jactel & Brockerhoff 2007; Sapijanskas, Potvin & Loreau 2013; Brassard *et al.* 2013; Ammer 2019). But perhaps the most important of these is that by combining species with contrasting crown architectures and abilities to tolerate shade, trees in mixed-species forests are able to use canopy space more efficiently (Sapijanskas *et al.* 2014; Pretzsch 2014; Jucker, Bouriaud & Coomes 2015; Kunz *et al.* 2019). These crown complementarity effects can alleviate competition for light among neighbouring trees, allowing them to grow faster in mixture (Sapijanskas *et al.* 2014; Williams *et al.* 2017; Kunz *et al.* 2019; Searle & Chen 2020).

However, unlike in grassland ecosystems where community dynamics are relatively fast, in forests the process of canopy filling is a slow one which unfolds over the course of multiple successive growing seasons during which neighbouring trees expand their crowns and begin competing for light. Consequently, overyielding – whereby species in mixture outperform those in monoculture – may take years to manifest in regenerating stands. This may help explain why, in contrast to observational studies conducted in mature forests, most tree diversity experiments established in temperate and boreal forests in the last 5–10 years have so far found little evidence of overyielding (Haase *et al.* 2015; Verheyen *et al.* 2016; Grossman *et al.* 2018; Kambach *et al.* 2019; although see Williams *et al.* 2017). The problem is that testing this hypothesis would require long-term, annually resolved growth records for trees exposed to different levels of diversity, data which are not typically recorded in forests.

Here we overcome this challenge by using tree ring records to reconstruct the growth trajectories of individual trees from stands that span a tree diversity gradient ranging from monocultures to 3-species mixtures. Using this dataset, we explore how diversity effects on tree growth change during the early stages of stand development in regenerating boreal forests in Finland. We hypothesise that diversity effects should become increasingly positive with time and that this shift should coincide with the period of canopy closure – which occurs approximately 20–25 years after a stand-replacing disturbance in these forests (Angelstam &

Kuuluvainen 2004; Shorohova *et al.* 2009). To complement this analysis, we then compare these growth responses with those observed in the Satakunta experiment in Finland – one of the world's longest running tree diversity experiments where the same combinations of species we sampled in closed-canopy forests were planted two decades ago. We expect that temporal trends in the strength of diversity effects on tree growth in these experimental plots should mirror those observed in closed-canopy forests. However, because of the relatively young age of trees in the Satakunta experiment, overyielding will be less evident.

MATERIALS AND METHODS

Overview

To explore how diversity effects on tree growth vary through time, here we take advantage of two complementary research platforms: the FunDivEUROPE plot network, which captures closed-canopy forests characterised by different levels of tree diversity, and the Satakunta tree diversity experiment. Below we provide an overview of these two platforms before detailing the approach we used to model the effects of diversity on tree growth. For a comprehensive description of the FunDivEUROPE project and of the Satakunta experiment see Baeten *et al.* (2013) and Verheyen *et al.* (2016), respectively.

Note that while the FunDivEUROPE network spans multiple sites across Europe, here we focus exclusively on the site in Finland. This is for two main reasons. Firstly, this site lies less than 400 km east of Satakunta (see Appendix S1 in Supporting Information), which is one longest running tree diversity experiments anywhere in the world. The two platforms share the same target tree species – which include *Pinus sylvestris*, *Picea abies* and *Betula pendula* – and replicated plots with all possible combinations of these species are found at both sites

(Table 1). This provides a unique opportunity to compare tree growth responses to diversity in natural and experimental forests in a way that would be hard to do anywhere else. Secondly, the FunDivEUROPE plots in Finland all consist of even-aged stands that have regenerated naturally following clear cutting in the past 40–60 years (Table 1 and Appendix S1). This makes comparing growth trajectories through time and across plots much simpler than would be the case in older, uneven-aged stands.

FunDivEUROPE plot network

As part of the FunDivEUROPE project six study sites were established across Europe, including one in the region of Northern Karelia in eastern Finland. At this site, 28 permanent plots (30 × 30 m in size) with all possible combinations of the three locally dominant tree species – *P. sylvestris*, *P. abies* and *B. pendula* – were established in 2012 in closed-canopy forest stands. This includes seven possible species combinations – three monoculture treatments, three 2-species mixtures and one 3-species mixture – each of which was replicated at least 3 times (Table 1). This full factorial design mimics that of most tree diversity experiment, thus allowing diversity effects to be teased apart from identity and compositional effects. To enable statistically rigorous comparisons across diversity levels, the final list of 28 plots was selected from a wider pool of candidates following a screening procedure that aimed to maximise community evenness while minimising differences in topography, soil properties, climate, stand development stage and management history among plots (for details see Baeten *et al.* 2013 and Jucker *et al.* 2014a). In particular, all plots were established in even-aged stands that regenerated naturally following clear cutting and have not been actively managed. Stand age varied between 40–60 years, resulting in predictable differences in stem density and mean tree size among plots (Table 1). Importantly, however, we found no evidence that these differences in stem density and mean tree size were related to variation in tree diversity among stands when the plots were established (see Appendix S2 for details).

Reconstructing temporal growth trends from tree ring data

Within each FunDivEUROPE plot, all stems ≥ 7.5 cm in diameter were mapped, identified to species and permanently marked (*n* = 2,146 stems). For each stem, we measured diameter at 1.3 m aboveground (*D*, in cm) using diameter tape and tree height (*H*, in m) using a vertex hypsometer (Haglöf AB, Sweden). To reconstruct the growth trajectories of individual trees, in September 2012 we extracted bark-to-pith increment cores from a subset of trees in each plot following a size-stratified random sampling approach (for details see Jucker *et al.* 2014a). Specifically, we cored 12 trees per species in monoculture plots and 8 trees per species in all mixture plots (*n* = 438 cores). This approach ensures that the tree size distribution of each plot is adequately captured by the subsample without needing to core all trees in a plot (Nehrbass-Ahles *et al.* 2014). This is important, as growth trajectories and responses to competition of canopy dominant and suppressed trees can vary considerably (Luo *et al.* 2020).

Wood cores were extracted using a 5.15 mm diameter increment borer (Haglöf AB, Sweden) and stored in polycarbonate sheeting to air dry. Cores were then mounted on wooden boards and sanded with progressively finer grit sizes before being digitally scanned using a high-resolution flatbed scanner (2400 dpi optical resolution). From the scanned images we measured annual radial increments for all cored trees using the software CDendro (Cybis Elektronik & Data, Sweden). Individual chronologies were crossdated against species-level reference curves generated by pooling all samples belonging to a given species to detect any misplaced or missing ring boundaries. From these chronologies we calculated the annual diameter increment of each cored tree (D_{incr}, in cm yr^{-1}), as well as its age. For trees in which cores did not include the pith, we estimated the number of missing rings by first calculating the distance to pith from the innermost visible ring using the pith locator tool in CDendro and then dividing this distance by the mean increment of the five innermost rings (Rozas 2003). Finally, the true age of each tree was adjusted to account for the number of years needed for trees to reach a height of 1.3 m at which cores were extracted. We did this by fitting species-specific height–age functions using data from the Satakunta experiment (see section below and Appendix S3 for details). We chose to use D_{incr} to represent tree growth instead of basal area increments because the former showed a simpler relationship with tree age which we were able to capture using well established non-linear plant growth models (see below and Appendix S4 for details). The disadvantage of D_{incr} is that, compared to basal area increments, it is a poorer surrogate of whole-tree biomass growth. We note, however, that replacing D_{incr} with basal area increments in our analysis did not affect our results (Appendix S4).

Satakunta tree diversity experiment

The Satakunta tree diversity experiment was established in the Satakunta region of southwestern Finland in 1999. It forms part of TreeDivNet – a global network of tree diversity experiments – of which it is the longest running study and the only one in the boreal forest biome (Verheyen *et al.* 2016). The experiment includes 114 plots (20 × 20 m in size) in which different combinations of five target tree species were planted in clear-cut areas (Table 1). Diversity treatment include monocultures, 2-, 3- and 5-species mixtures. Plots are grouped into three blocks, with all species compositions replicated twice within each block. The target species include *P. sylvestris*, *P. abies* and *B. pendula*, as well as *Larix sibirica* and

Alnus glutinosa. For the purposes of this study only plots which feature combinations of *P. sylvestris*, *P. abies* and *B. pendula* were analysed (42 plots; 14 × 3 blocks). 169 seedlings were planted in each plot (13 × 13 rows with seedlings 1.5 m apart). Seedlings of *P. abies* were two years old at the time of planting, while those of *P. sylvestris* and *B. pendula* were one. An equal number of seedlings was planted for each species in the mixture treatments, but planting locations inside the plots were assigned randomly.

Tree growth measurements

Tree growth was monitored at four points in time during the experiment. In 2004, 2009 and 2011, D and H were measured for a random subset of 10 trees per species in each plot. Additionally, because only 53% of selected trees had reached a height of 1.3 m by age seven, in 2004 we also recorded the basal stem diameter at 10 cm aboveground (D_{base}, in cm) of each tree. While D_{base} was, on average, 2.3 cm greater than D, the two measures of tree size were closely correlated to one another (Pearson's correlation coefficient = 0.77, $P < 0.0001$). In 2016, an additional census was conducted, during which D was measured for a random subset of 5 trees per species in each plot. However, because half of the Satakunta plots were experimentally thinned in 2013, for the 2016 census we only included growth data from 18 unthinned plots. This included three replicate plots per treatment (one per block) for all species combinations, except for *P. sylvestris* monocultures, *P. sylvestris* + *P. abies* 2-species mixtures and *P. sylvestris* + *B. pendula* 2-species mixtures, for which only two replicate plots were sampled.

Using tree ring data to test how diversity effects on growth vary through time in the FunDivEUROPE plots

Comparing alternative tree growth models

Having reconstructed diameter growth trends from the tree ring records, we then used these data to model the growth trajectory of trees across the FunDivEUROPE plots to determine how diversity effects on tree growth vary through time (Fig. 1). We started by comparing different diameter growth models using the approach outlined in Paine *et al.* (2012). Because diameter growth tends to vary non-linearly with tree age – with initial increases in growth rates followed by a decline and levelling-off phase – we used non-linear regression to model changes in growth rate through time. All models were fit using the *nls* function in R (R Core Development Team 2019). Following a comprehensive comparison of alternative models based on AIC (Appendix S4), we settled on the Ricker function (Bolker 2008) to capture how D_{incr} varies as a function of tree age (A; in years):

$$D_{incr} = \alpha + \beta A e^{-\gamma A} \tag{1}$$

where α, β and γ are parameters to be estimated from the data using a non-linear least squares approach. This flexible function outperformed all other non-linear plant growth models we tested (Appendix S4). Integrating eqn 1 provides a function for modelling cumulative diameter increments through time:

$$D = \alpha A + \frac{\beta(\gamma A + 1)e^{-\gamma A}}{\gamma^2} + \frac{\beta}{\gamma^2} \tag{2}$$

where α, β and γ are the same parameters estimated for eqn (1). Eqn 2 allows the diameter of a tree to be estimated based on its age. This is particularly convenient as it provides a way to directly compare growth trends in the FunDivEUROPE plots to those observed at Satakunta, where tree growth increments were not measured on an annual basis.

Testing the effects of diversity on tree growth through time

Having identified a growth function that captures age-related variation in tree growth for all three study species, we then used this model to quantify how diversity effects on tree growth change through time. To do this, for each species we first fit separate growth models for trees growing in all possible species combinations (i.e., monoculture, the three possible 2-species mixtures and the 3-species mixture). We then used the fitted models to predict D_{incr} and D as a function of tree age for each of these treatments and calculated the differential between tree growth trajectories in monoculture and the mixtures through time (see Fig. 1 for a schematic representation). This allowed us to not only test whether trees in mixture grow faster than those in monoculture, but also determine at what age diversity effects emerge. For the purposes of model fitting we restricted the analysis to include only the first 30 years of growth, as beyond this threshold the number of trees with complete chronologies dropped off sharply (Appendix S1). In order to test whether growth differences between treatments were statistically significant, we used Monte Carlo simulations as implemented by the *predictNLS* function in the *propagate* R package to estimate 95% confidence intervals for each fitted model (Spiess 2018).

Our analysis makes two important assumptions about the FunDivEUROPE data which are worth stating explicitly. The first is that species composition and diversity have remained relatively stable since stand establishment. If true, current-day species composition can be combined with tree ring records to infer how diversity effects on growth have changed through time. While we have no information on the community composition of the plots prior to their establishment in 2012, a second census was conducted in 2017. This shows that in the five years following our initial sampling, the species composition of the plots has remained unchanged (Appendix S2). While these observations do not capture the initial phases of stand development in the FunDivEUROPE plots, a second census of the Satakunta plots in 2011 revealed almost no changes in community composition during the first 12 years of the experiment (Appendix S2). Together, these data suggest that species composition and diversity are likely to have remained relatively constant during the initial stages of stand development in these forests.

The second assumption is that stand structural attributes known to influence tree growth – such as the number and size of trees in a plot (Coomes *et al.* 2014) – vary independently of tree diversity. Note that this does not mean we assume that the number and size of trees in a plot has remained constant through time. Instead, the assumption is that changes in the number and size of trees have been similar among plots, allowing us to directly compare the growth trajectories of trees across the diversity gradient. Supporting this premise, the repeat census data from the FunDivEUROPE plots shows that the number and mean size of trees varies closely with stand age (Appendix S2), following a classic self-thinning pattern (Yoda *et al.* 1963). Crucially, however, at the time of establishing the plots we found no significant differences in mean tree size and density across diversity levels (Appendix S2). A very similar pattern emerged from the Satakunta plots, where rates of stem exclusion during the initial 12 years of the experiment were statistically indistinguishable across the diversity treatments (Appendix S2).

Comparing diversity effects on growth in the FunDivEUROPE and Satakunta plots

To compare diversity effects on tree growth between the FunDivEUROPE plots and the Satakunta experiment, we used mixed-effects models to estimate differences in diameter between trees in monoculture and mixture at each census period of the experiment (2004, 2009, 2011 and 2016). For each species, we modelled stem diameter as a function of census year, species composition and their interaction, with plot and experimental block as nested random effects. Year was treated as a categorical variable in the models, as surveys were too few and infrequent to fit continuous tree size–age functions. The interaction between year and species composition tests whether the effects of species mixing on growth changed during the experiment. Fitted models were used to estimate differences in stem diameters between trees in monoculture and mixture at each census period, which we then compared to those observed in FunDivEUROPE plots.

Models were fit using the *lme4* package in R (Bates *et al.* 2015). Parametric bootstrapping as implemented by the *bootMer* function was used to generate 95% confidence intervals for the predictions. Note that for the 2004 census we used D_{base} instead of D as a measure of tree size, as by age seven only around 50% of surveyed trees had reached a height of 1.3 m. For all other years we modelled differences in D between treatments. The few trees that had not yet reached a height of 1.3 m by 2009 and 2011 were assigned a value of $D = 0$ (15 and 9 trees, respectively).

RESULTS

Diversity effects on growth in the FunDivEUROPE plots

While the shape of the relationship between D_{incr} and age was similar across the three species, clear quantitative differences in their growth trajectories also emerged (Fig. 2). Of the three, *P. sylvestris* was the fastest growing early on (mean D_{incr} before age 15 = 0.81 cm yr^{-1}, compared to 0.69 and 0.72 cm yr^{-1} in *P. abies* and *B. pendula*, respectively). However, *P. sylvestris* also showed the steepest decline in diameter growth rate with age of all three species, and by age 30 growth differences between species had reversed (mean D_{incr} after age 30 = 0.31 cm yr^{-1} in *P. sylvestris* compared to 0.41 and 0.40 cm yr^{-1} in *P. abies* and *B. pendula*, respectively). As a result, by age 30–35 all three species had reached similar diameters on average (Fig. 2). Clear between-species differences were also observed for height growth, although in this case *B. pendula* grew fastest early on, while the two conifers progressively narrowed the height gap with time (Appendix S3).

When we compared the growth trajectories of trees in monoculture and mixture, we found that on average diversity effects on growth tended to shift from mostly negative to overwhelmingly positive during stand development (Fig. 3). This pattern matched our predictions and was remarkably consistent across species and diversity treatments (Fig. 3 and Table 2). By age 35 the average diameter growth rate of a tree in mixture was 25% faster than that of a tree in monoculture (Table 2). This overyielding effect was significantly strongest for trees in the 3-species mixtures (+32%, compared to +22% in the 2-species mixture) and for *B. pendula* (+39% across treatments, compared to +21% and +15% for *P. sylvestris* and *P. abies*, respectively). Moreover, when comparing across species and treatments we found that the average age at which diversity effects on growth shifted to significantly positive was 21 (Table 2). This coincides with the period in which regenerating boreal forests in Finland typically achieve canopy closure.

Comparing diversity effects on growth in the FunDivEUROPE and Satakunta plots

The cumulative diameter growth trajectories of trees in the Satakunta experiment were very similar to those observed in the FunDivEUROPE plots (Fig. 2 a–c), although on average *P. sylvestris* grew quicker at Satakunta (*D* at age 18 = 11.2 cm, compared to 9.9 cm in the FunDivEUROPE plots). When we compared the effects of diversity on diameter growth between the two platforms, we found good or partial agreement for 7 of the 9 possible species combinations (Fig. 4). In particular, *P. abies* showed similar responses to diversity in the FunDivEUROPE and Satakunta plots, particularly when mixed with *P. sylvestris* (Fig. 4 d) and in the 3-species mixture (Fig. 4 f). Equally, for all three species, temporal trends in diversity effects in the 3-species mixtures were broadly consistent with those observed in the FunDivEUROPE plots (Fig. 4 c,f,i).

The clear exception where growth responses to diversity did not match between the two research platforms was the *P. sylvestris* + *B. pendula* mixture. In contrast to what we observed in the FunDivEUROPE plots, *P. sylvestris* trees in this mixture grew significantly slower than their counterparts in monoculture at Satakunta, with no sign of this trend abating by the time of the last census in 2016 (Fig. 4b). As for *B. pendula*, at Satakunta trees in this mixture showed strong signs of overyielding much earlier than in the FunDivEUROPE plots (Fig. 4g). By age 18, the average *B. pendula* tree growing in mixture with *P. sylvestris* at

Satakunta was 3.0 cm larger in diameter than its equivalent in monoculture (+34% increase in size).

DISCUSSION

Across the FunDivEUROPE plots we found a clear pattern whereby diversity effects on tree growth shifted from mostly negative to positive during the first 35 years of stand regeneration following clear cutting. This trends was remarkably consistent across species and mixture types (Fig. 3), and closely matches what has previously been observed in long-term grassland biodiversity experiments (Cardinale *et al.* 2007; Reich *et al.* 2012; Zuppinger-Dingley *et al.* 2014; Guerrero-Ramírez *et al.* 2017). Observational studies conducted across a range of forest ecosystems have revealed a considerable degree of variation in the strength and even the direction of diversity effects on productivity (Paquette & Messier 2011; Vilà *et al.* 2013; Ratcliffe *et al.* 2016). Previous work has shown that this context-dependency can be partially explained by environmental differences among forest types, such as those associated with climate or soils (Forrester 2014; Jucker *et al.* 2014b, 2016; Toïgo *et al.* 2015; Ratcliffe *et al.* 2017). Our study highlights how changes in species interactions during stand development can also play an important role in determining the strength of diversity–productivity relationships in forests (Lasky *et al.* 2014; Taylor *et al.* 2020). It also illustrates the value of focusing on how individual trees respond to species mixing in order to better understand community level responses (Chamagne *et al.* 2017; Fichtner *et al.* 2018).

Canopy packing as a driver of diversity–productivity relationships in forests

On average, overyielding in the FunDivEUROPE plots first became apparent around 20 years after seedling establishment (Fig. 3 and Table 2). This coincides with the period in which boreal forests in norther Europe typically undergo canopy closure and enter the phase of stem exclusion (based on observations in the Satakunta experimental plots; see also: Angelstam & Kuuluvainen 2004; Shorohova *et al.* 2009), lending support to our hypothesis that the process of canopy filling is key to promoting positive diversity–productivity relationships in forests. Growing evidence suggests that by combining tree species with complementary crown architectures, phenologies and abilities to tolerate shade, diverse forests are able to use canopy space more efficiently (Pretzsch 2014; Jucker *et al.* 2015; Williams *et al.* 2017). This in turn alleviates the effects of competition for light among neighbours, allowing trees to grow faster in mixture and pack more densely in space (Sapijanskas *et al.* 2014; Williams *et al.* 2017; Kunz *et al.* 2019; Searle & Chen 2020).

Despite the low number of tree species present in our study system, differences in their ecological strategies still present numerous opportunities to maximise the use of aboveground space. Firstly, phenological differences between the evergreen conifers and the deciduous *B. pendula* can reduce competition for light among neighbouring trees at the onset and end of the growing season. Secondly, while both *P. sylvestris* and *B. pendula* (in particular) are light-demanding species, *P. abies* is able to persist and grow even in low-light conditions (Niinemets & Valladares 2006). These contrasting abilities to tolerate shade are also reflected in differences in the way the three species invest in vertical growth and crown expansion (Appendix S3), which enables them to vertically and horizontally partition canopy space. Finally, these crown complementarity effects can be further enhanced by the ability of individual trees to plastically adapt the vertical distribution of their branches and leaves to suit that of their neighbours (Sapijanskas *et al.* 2014; Pretzsch 2014; Jucker *et al.* 2015). For example, previous work conducted across the FunDivEUROPE network revealed that trees in mixed-species stands had significantly wider and deeper crowns that their counterparts growing in monoculture (Jucker *et al.* 2015). When scaled up from individual trees to whole stands, these crown complementarity effects allow mixed-species forests to use canopy space more efficiently, thus contributing to overyielding at the community level (Pretzsch 2014; Jucker *et al.* 2015; Williams *et al.* 2017).

While our results are consistent with our hypothesis and match patterns observed in faster-developing ecosystems such as grasslands, the FunDivEUROPE plots in Finland only capture the early-to-mid stages of stand development: canopy closure and the beginning of stem exclusion. Understanding how diversity effects on tree growth are likely to change in the latter stages of stand development – when understorey re-initiation begins and stands become multi-layered and uneven aged – remains a priority. However, because of the timescales involved, very few studies have actually tracked stand development long enough to robustly address this type of question (for rare examples see Pretzsch *et al.* 2014 and Madrigal-González *et al.* 2015).

Tree rings provide one way to address this challenge by allowing the long-term growth trends of individual trees to be accurately reconstructed. However, they tell us nothing about the past composition of a stand. Consequently, attributing growth responses to diversity becomes progressively harder the further back in time one goes. One way around this is to use a space-for-time substitution, where plots at different stages of stand development are compared. Using this approach, Taylor *et al.* (2020) recently showed that in Canada's boreal forests diversity–productivity relationships tended to peak in mid-successional stands. However, the challenge with this type of study is that accounting for differences in management practises is often made challenging by a lack of historical data, particularly for older stands. Moreover, because of recent climate change, conditions under which forests are regenerating today will often be substantially different to those in which currently mature stands developed in the past. To complement these analyses, it can therefore be useful to pair them with simulation models of forest dynamics (Morin *et al.* 2011). In this respect, Holzwarth *et al.* (2015) used the ecosystem model LPJ-GUESS parameterised for temperate forests to show that diversity effects on productivity are likely to be strongest in early-to-mid successional stands. This is consistent with what we know about forest dynamics in European temperate forests, where shade-casting species such as beech tend to outcompete light-demanding ones, leading to lower tree diversity in late successional stands (Pretzsch *et al.* 2015).

While our results are predominantly observational and representative of a single, low-diversity ecosystem, they provide a series of testable hypotheses for the growing number of tree diversity experiments established in recent years. Large-scale syntheses will clarify whether the tendency of diversity effects to strengthen through time is a general one, and if so, help elucidate the mechanisms driving it. Here we focused on one possible explanation for these temporal trends – the slow onset of canopy interactions among neighbouring trees. But other processes are also likely to be at play. For instance, studies in both grasslands and forests have shown that trophic interactions are key to promoting positive biodiversity–ecosystem functioning relationships (Eisenhauer 2012; Ammer 2019), but these interactions take time to establish (Eisenhauer, Reich & Scheu 2012). Similarly, soil nutrients have been shown to influence how quickly diversity effects emerge in grasslands by constraining rates of ecosystem development (Guerrero-Ramírez *et al.* 2017).

Future work leveraging networks of tree diversity experiments will also help clarify whether some of the other trends we observe in our data – such as the tendency of diversity to negatively influence growth in the early stages of stand development – also emerge across different species and forest types (Kambach *et al.* 2019). Contrary to our expectations, which were for diversity effects in the earliest stages of stand development to be mostly neutral, 7 of the 9 species combinations in the FunDivEUROPE plots showed negative effects of diversity on tree growth between ages 5–15 (Fig. 3). This initial negative relationship between diversity and growth likely explains why we found no significant differences in mean tree size across the diversity gradient (Appendix S2), as it would have offset any subsequent increases in growth in mixed-species plots. Early synthesis work from tree diversity experiments outside tropical and subtropical regions has mostly revealed neutral effects of diversity on aboveground productivity at a community level (Grossman *et al.* 2018; Kambach *et al.* 2019). This pattern could emerge even if diversity were to negatively influence the early-stage growth of individual trees, provided that survival rates were higher in mixtures. However, even if this were the case, it still begs the question of what might cause individual trees to grow more slowly at first when in mixture. Aboveground interactions seem an unlikely candidate, as competition for light among neighbouring trees would initially be weak. Trophic interactions, both above and belowground (e.g., slower colonization by mutualistic fungi or increased pest and pathogen loads in mixed-species plots), are possible explanations worth exploring further (Eisenhauer 2012; Ammer 2019).

Bridging the gap between observational studies and tree diversity experiments

The fact that positive diversity effects on tree growth in the FunDivEUROPE plots tended to strengthen with time and only became apparent once stands matured enough to achieve canopy closure may explain why most tree diversity experiments established outside the tropics have so far found little evidence that diverse tree communities are more productive than species-poor ones (Haase *et al.* 2015; Verheyen *et al.* 2016; Grossman *et al.* 2018; Kambach *et al.* 2019). Currently, the average duration of the 26 globally-distributed tree diversity experiments that form TreeDivNet is nine years (range 1–20 years, with Satakunta being the oldest; for details see: http://www.treedivnet.ugent.be and Verheyen *et al.* 2016). Our results from the FunDivEUROPE plots suggest this may simply not be long enough for the aboveground interactions that underpin the positive effects of diversity on tree growth to manifest themselves, particularly in slower-growing boreal and temperate forests.

Exceptions to this pattern are tree diversity experiments established in the tropics and subtropics, where stand regeneration occurs much more rapidly. The two best examples of this are the BEF-China project (Huang *et al.* 2018; Fichtner *et al.* 2018; Kunz *et al.* 2019) and the Sardinilla experiment in Panama (Sapijanskas *et al.* 2014; Schnabel *et al.* 2019), both of which have shown strong effects of diversity on productivity in the first 10 years since planting. What is particularly interesting about these experiments is that both have shown that crown complementarity and canopy filling are key to explaining the positive effects of diversity on productivity (Sapijanskas *et al.* 2014; Kunz *et al.* 2019). Moreover – just as we find in the FunDivEUROPE plots – recent work suggests that in the BEF-China experiment the strength of these diversity effects has been progressively increasing through time (Huang *et al.* 2018).

Outside the tropics, experimental evidence for positive diversity–productivity relationships in the early stages of stand development is much more mixed (for a review see Grossman *et al.* 2018). The one notable exception are studies from the IDENT network (Tobner *et al.* 2014). For instance, Williams *et al.* (2017) found positive effects of diversity on productivity emerging relatively soon after planting in an experiment established in 2009 at the temperate-boreal forest ecotone in Quebec. Crucially, this study also concluded that increased canopy packing in mixed-species plots was driving positive diversity effects on productivity. The fact that these effects emerged so early in the experiment is likely attributable to the study's design, which involved planting seedlings at extremely high densities to speed up their interaction (planting density = 40,000 seedlings ha^{-1}, almost 10 times as high as Satakunta; Tobner *et al.* 2014).

When comparing early-stage tree growth responses to diversity in the Satakunta and FunDivEUROPE plots, we generally found reasonable agreement between the two research platforms (Fig. 4). However, there were a few exceptions, the most notable of which was the behaviour of both *P. sylvestris* and *B. pendula* when grown in combination with one another (Fig. 4b,g). In contrast to what we observed in the FunDivEUROPE plots where both species benefitted from growing in mixture with each other (Fig 3 b,g), at Satakunta only *B. pendula* showed evidence of overyielding when mixed with *P. sylvestris*. By contrast, *P. sylvestris* grew noticeably slower when mixed with *B. pendula*. The fact that we found such marked differences in the behaviour of the same combination of species growing within a few hundred kilometres of each other is less than promising for future efforts to bridge observational and experimental studies of forest dynamics (Kambach *et al.* 2019).

There are several plausible explanations for the mismatch we observed. For instance, spatio-temporal differences in climate and soils can strongly influence species interactions (Forrester 2014; Jucker *et al.* 2014b; Pretzsch *et al.* 2015), and generally speaking diversity effects on tree growth have been shown to be strongest in more stressful and less productive environments (Toïgo *et al.* 2015; Jucker *et al.* 2016). Mean annual temperature at Satakunta is around 3 °C warmer than in Northern Karelia where the FunDivEUROPE plots were established (Table 1) – a difference that would have been further amplified by the fact that Finland has warmed considerably in the decades that separate when the FunDivEUROPE stands established and the Satakunta experiment was planted. These differences in climate may explain why *P. sylvestris* grew faster at Satakunta (Fig. 2) and could have contributed to shifting the competitive balance between the two species.

Another possible explanation for the contrasting responses to diversity in the two platforms is differences in tree density and spatial arrangement (Table 1). As is fairly common practise in tree diversity experiments (e.g., Tobner *et al.* 2014), planting density in the Satakunta plots was higher than what is typically found across managed forests in northern Europe (4,225 ha^{-1}, compared to 1,600–2,000 ha^{-1} in commercially planted stands in Finland). Planting seedlings at high density encourages species interactions to begin sooner, but it may also fundamentally alter their outcome (Ammer 2019). Finally, an additional contributing factor which is worth considering is herbivory. In particular, browsing pressure by moose has been shown to increase in mixed stands of *P. sylvestris* and *B. pendula* relative to monocultures (Milligan & Koricheva 2013; Nevalainen *et al.* 2016). Moreover, work by Muiruri *et al.* (2015) at Satakunta showed that these differences in browsing can actually alter the growth response of *B. pendula* to mixing, shifting it from positive-saturating at low browsing intensities to neutral under high browsing pressure. Given that between the 1980s – when trees in the FunDivEUROPE plots would have been short enough to be susceptible to moose browsing – and the early 2000s damage by moose more than doubled across Finland's forests (Nevalainen *et al.* 2016), it is possible that differences in browsing pressure between the two platforms contributed to the discrepancy in the results.

Conclusions

Using a combination of tree ring records and data from a long-term tree diversity experiment, we find that diversity effects on tree growth change predictably during the early stages of stand development in Finland's boreal forests. In doing so, we take a further step towards reconciling the results of previous studies which suggest that while diversity effects in forests are generally positive, they can also vary substantially through space and time. Our results point to canopy closure as a key phase of stand development during which positive diversity effects on tree growth first emerge. This reinforces the importance of canopy space filling as an ecological mechanism for explaining why diverse forests are, on average, more productive than species-poor ones. It also provides a testable prediction for when positive diversity effects on tree growth should emerge across different forest types. This is critical when it comes to bridging the gap between observational studies – from which most of our understanding of how diversity relates to productivity in forests has traditionally come from – and tree diversity experiments – which have grown rapidly in number and ecological realism in recent years. Overall, our study lends further support to the growing evidence that management and conservation strategies aimed at increasing tree diversity in forests have the potential to enhance carbon sequestration. However, as with most good things, a little patience is needed before we can reap the benefits of what we sow.

ACKNOWLEDGEMENTS

We thank FunDivEUROPE site managers and field technicians for establishing the permanent plots, and are grateful to D. Avăcăriței, I. Bărnoaiea, G. Duduman, I. Dănilă, L. Nichiforel and A. Benneter for assisting with field data collection. The research leading to these results received funding from the European Union Seventh Framework Programme

(FP7/2007-2013) under grant agreement 265171. T. Jucker was supported by a UK NERC Independent Research Fellowship (grant number: NE/S01537X/1).

AUTHOR CONTRIBUTIONS

D.A.C., L.F. and O.B. helped design the FunDivEUROPE research platform, while J.K. runs the Satakunta tree diversity experiment; T.J. designed the study, collected the tree ring data, performed the analyses and wrote the first draft of the manuscript. G.I. and O.B. collected and curated the data from the second census of the FunDivEUROPE plots. All authors contributed substantially to revisions.

DATA AVAILABILITY

The authors confirm that data supporting the results of this manuscript will be archived and made freely available on Figshare and that the corresponding DOI will be included at the end of the article.

REFERENCES

Ammer, C. (2019) Diversity and forest productivity in a changing climate. *New Phytologist*, **221**, 50–66.

Angelstam, P. & Kuuluvainen, T. (2004) Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. *Ecological Bulletins*, **51**, 117–136.

Baeten, L., Bruelheide, H., van der Plas, F., Kambach, S., Ratcliffe, S., Jucker, T., Allan, E., Ampoorter, E., Barbaro, L., Bastias, C.C., Bauhus, J., Benavides, R., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Chećko, E., Coomes, D.A., Dahlgren, J., Dawud, S.M., De Wandeler, H., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Koricheva, J., Lehtonen, A., Müller, S., Muys, B., Nguyen, D., Pollastrini, M., Radoglou, K., Raulund-Rasmussen, K., Ruiz-Benito, P., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Verheyen, K., Wirth, C., Zavala, M.A. & Scherer-Lorenzen, M. (2019) Identifying the tree species compositions that maximize ecosystem functioning in European forests. *Journal of Applied Ecology*, **56**, 733–744.

Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., Jaroszewicz, B., Selvi, F., Valladares, F., Allan, E., Ampoorter, E., Auge, H., Avăcăriei, D., Barbaro, L., Bărnoaiea, I., Bastias, C.C., Bauhus, J., Beinhoff, C., Benavides, R., Benneter, A., Berger, S., Berthold, F., Boberg, J., Bonal, D., Brüggemann, W., Carnol, M., Castagneyrol, B., Charbonnier, Y., Chećko, E., Coomes, D.A., Coppi, A., Dalmaris, E., Dănilă, G., Dawud, S.M., de Vries, W., De Wandeler, H., Deconchat, M., Domisch, T., Duduman, G., Fischer, M., Fotelli, M., Gessler, A., Gimeno, T.E., Granier, A., Grossiord, C., Guyot, V., Hantsch, L., Hättenschwiler, S., Hector, A., Hermy, M., Holland, V., Jactel, H., Joly, F.-X., Jucker, T., Kolb, S., Koricheva, J., Lexer, M.J., Liebergesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nichiforel, L., Pollastrini, M., Proulx, R., Rabasa, S., Radoglou, K., Ratcliffe, S., Raulund-Rasmussen, K., Seiferling, I., Stenlid, J., Vesterdal, L., von Wilpert, K., Zavala, M.A., Zielinski, D. & Scherer-Lorenzen, M. (2013) A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics*, **15**, 281–291.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.

Bolker, B.M. (2008) Deterministic functions for ecological modeling. *Ecological Models and Data in R*, pp. 72–102. Princeton University Press.

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

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M. & Weis, J.J. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, **104**, 18123–18128.

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

Coomes, D.A., Flores, O., Holdaway, R., Jucker, T., Lines, E.R. & Vanderwel, M.C. (2014) Wood production response to climate change will depend critically on forest composition and structure. *Global Change Biology*, **20**, 3632–3645.

Eisenhauer, N. (2012) Aboveground-belowground interactions as a source of complementarity effects in biodiversity experiments. *Plant and Soil*, **351**, 1–22.

Eisenhauer, N., Reich, P.B. & Scheu, S. (2012) Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants. *Basic and Applied Ecology*, **13**, 571–578.

Fichtner, A., Härdtle, W., Bruelheide, H., Kunz, M., Li, Y. & Von Oheimb, G. (2018) Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nature Communications*, **9**, 1144.

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.

Grossman, J.J., Vanhellemont, M., Barsoum, N., Bauhus, J., Bruelheide, H., Castagneyrol, B., Cavender-Bares, J., Eisenhauer, N., Ferlian, O., Gravel, D., Hector, A., Jactel, H., Kreft, H., Mereu, S., Messier, C., Muys, B., Nock, C., Paquette, A., Parker, J., Perring, M.P., Ponette, Q., Reich, P.B., Schuldt, A., Staab, M., Weih, M., Zemp, D.C., Scherer-Lorenzen, M. & Verheyen, K. (2018) 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*, **152**, 68–89.

Guerrero-Ramírez, N.R., Craven, D., Reich, P.B., Ewel, J.J., Isbell, F., Koricheva, J., Parrotta, J.A., Auge, H., Erickson, H.E., Forrester, D.I., Potvin, C., Roscher, C., Ruijven, J. Van, Tilman, D., Wilsey, B. & Eisenhauer, N. (2017) Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nature Ecology & Evolution*, **1**, 1639–1642.

Haase, J., Castagneyrol, B., Cornelissen, J.H.C., Ghazoul, J., Kattge, J., Koricheva, J., Scherer-Lorenzen, M., Morath, S. & Jactel, H. (2015) Contrasting effects of tree diversity on young tree growth and resistance to insect herbivores across three biodiversity experiments. *Oikos*, **124**, 1674–1685.

Holzwarth, F., Rüger, N. & Wirth, C. (2015) Taking a closer look: disentangling effects of functional diversity on ecosystem functions with a trait-based model across hierarchy and time. *Royal Society Open Science*, **2**, 140541.

Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., Li, Y., Härdtle, W., Von Oheimb, G., Yang, X., Liu, X., Pei, K., Both, S., Yang, B., Eichenberg, D., Assmann, T., Bauhus, J., Behrens, T., Buscot, F., Chen, X.Y., Chesters, D., Ding, B.Y., Durka, W., Erfmeier, A., Fang, J., Fischer, M., Guo, L.D., Guo, D., Gutknecht, J.L.M., He, J.S., He, C.L., Hector, A., Hönig, L., Hu, R.Y., Klein, A.M., Kühn, P., Liang, Y., Li, S., Michalski, S., Scherer-Lorenzen, M., Schmidt, K., Scholten, T., Schuldt, A., Shi, X., Tan, M.Z., Tang, Z., Trogisch, S., Wang, Z., Welk, E., Wirth, C., Wubet, T., Xiang, W., Yu, M., Yu, X.D., Zhang, J., Zhang, S., Zhang, N., Zhou, H.Z., Zhu, C.D., Zhu, L., Bruelheide, H., Ma, K., Niklaus, P.A. & Schmid, B. (2018) Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science*, **362**, 80–83.

Jactel, H. & Brockerhoff, E.G. (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters*, **10**, 835–848.

Jucker, T., Avăcăriței, D., Bărnoaiea, I., Duduman, G., Bouriaud, O. & Coomes, D.A. (2016) Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology*, **104**, 388–398.

Jucker, T., Bouriaud, O., Avăcăriei, D. & Coomes, D.A. (2014a) Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. *Ecology Letters*, **17**, 1560–1569.

Jucker, T., Bouriaud, O., Avăcăriei, D., Dănilă, I., Duduman, G., Valladares, F. & Coomes, D.A. (2014b) 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.

Kambach, S., Allan, E., Bilodeau-Gauthier, S., Coomes, D.A., Haase, J., Jucker, T., Kunstler, G., Müller, S., Nock, C., Paquette, A., Plas, F., Ratcliffe, S., Roger, F., Ruiz-Benito, P., Scherer-Lorenzen, M., Auge, H., Bouriaud, O., Castagneyrol, B., Dahlgren, J., Gamfeldt, L., Jactel, H., Kändler, G., Koricheva, J., Lehtonen, A., Muys, B., Ponette, Q., Setiawan, N., Van de Peer, T., Verheyen, K., Zavala, M.A. & Bruelheide, H. (2019) How do trees respond to species mixing in experimental compared to observational studies? *Ecology and Evolution*, **9**, 11254–11265.

Kunz, M., Fichtner, A., Härdtle, W., Raumonen, P., Bruelheide, H. & von Oheimb, G. (2019) Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. *Ecology Letters*, **22**, 2130–2140.

Lasky, J.R., Uriarte, M., Boukili, V.K., Erickson, D.L., Kress, W.J. & Chazdon, R.L. (2014) The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters*, **17**, 1158–1167.

Luo, Y., McIntire, E.J.B., Boisvenue, C., Nikiema, P.P. & Chen, H.Y.H. (2020) Climatic change only stimulated growth for trees under weak competition in central boreal forests (ed P Bellingham). *Journal of Ecology*, **108**, 36–46.

Madrigal-González, J., Hantson, S., Yue, C., Poulter, B., Ciais, P. & Zavala, M.A. (2015) Long-term wood production in water-limited forests: evaluating potential CO2 fertilization along with historical confounding factors. *Ecosystems*, **18**, 1043–1055.

Milligan, H.T. & Koricheva, J. (2013) Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. *Journal of Animal Ecology*, **82**, 739–748.

Morin, X., Fahse, L., Scherer-Lorenzen, M. & Bugmann, H. (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, **14**, 1211–1219.

Muiruri, E.W., Milligan, H.T., Morath, S. & Koricheva, J. (2015) Moose browsing alters tree diversity effects on birch growth and insect herbivory. *Functional Ecology*, **29**, 724–735.

Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., Dobbertin, M. & Frank, D. (2014) The influence of sampling design on tree-ring based quantification of forest growth. *Global Change Biology*, **20**, 2867–2885.

Nevalainen, S., Matala, J., Korhonen, K.T., Ihalainen, A. & Nikula, A. (2016) Moose damage in national forest inventories (1986– 2008) in finland. *Silva Fennica*, **50**, 1–23.

Niinemets, Ü. & Valladares, F. (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs*, **76**, 521–547.

Paine, C.E.T., Marthews, T.R., Vogt, D.R., Purves, D., Rees, M., Hector, A. & Turnbull, L.A. (2012) How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods in Ecology and Evolution*, **3**, 245–256.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: From temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.

Pretzsch, H. (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management*, **327**, 251–264.

Pretzsch, H., Biber, P., Schütze, G., Uhl, E. & Rötzer, T. (2014) Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Communications*, **5**, 4967.

Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T. & Bravo-Oviedo, A. (2015) Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient through Europe. *European Journal* *of Forest Research*, **134**, 927–947.

R Core Development Team. (2019) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ratcliffe, S., Liebergesell, M., Ruiz-Benito, P., Madrigal González, J., Muñoz Castañeda, J.M., Kändler, G., Lehtonen, A., Dahlgren, J., Kattge, J., Peñuelas, J., Zavala, M.A. & Wirth, C. (2016) Modes of functional biodiversity control on tree productivity across the European continent. *Global Ecology and Biogeography*, **25**, 251–262.

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C.C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Chećko, E., Dawud, S.M., Wandeler, H.D., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Kambach, S., Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Ruiz-Benito, P., Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Vesterdal, L. & Baeten, L. (2017) Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, **20**, 1414–1426.

Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B. & Eisenhauer, N. (2012) Impacts of biodiversity loss escalate through time as redundancy fades. *Science*, **336**, 589–92.

Rozas, V. (2003) Tree age estimates in Fagus sylvatica and Quercus robur: testing previous and improved methods. *Plant Ecology*, **167**, 193–212.

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N. & Loreau, M. (2014) Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology*, **95**, 2479–2492.

Sapijanskas, J., Potvin, C. & Loreau, M. (2013) Beyond shading: litter production by neighbours contributes to overyielding in tropical trees. *Ecology*, **94**, 941–952.

Schnabel, F., Schwarz, J.A., Dănescu, A., Fichtner, A., Nock, C.A., Bauhus, J. & Potvin, C. (2019) Drivers of productivity and its temporal stability in a tropical tree diversity experiment. *Global Change Biology*, **25**, 4257–4272.

Searle, E.B. & Chen, H.Y.H. (2020) Complementarity effects are strengthened by competition intensity and global environmental change in the central boreal forests of Canada. *Ecology Letters*, **23**, 79–87.

Shorohova, E., Kuuluvainen, T., Kangur, A. & Jõgiste, K. (2009) Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. *Annals of Forest Science*, **66**, 201.

Spiess, A.-N. (2018) *Propagate: Propagation of Uncertainty*. R package version 1.0-6. https://CRAN.R-project.org/package=propagate.

Taylor, A.R., Gao, B. & Chen, H.Y.H. (2020) The effect of species diversity on tree growth varies during forest succession in the boreal forest of central Canada. *Forest Ecology and Management*, **455**, 117641.

Tobner, C.M., Paquette, A., Reich, P.B., Gravel, D. & Messier, C. (2014) Advancing biodiversity-ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia*, **174**, 609–621.

Toïgo, M., Vallet, P., Perot, T., Bontemps, J., Piedallu, C. & Courbaud, B. (2015) Overyielding in mixed forests decreases with site productivity. *Journal of Ecology*, **103**, 502–512.

Verheyen, K., Vanhellemont, M., Auge, H., Baeten, L., Baraloto, C., Barsoum, N., Bilodeau-Gauthier, S., Bruelheide, H., Castagneyrol, B., Godbold, D., Haase, J., Hector, A., Jactel, H., Koricheva, J., Loreau, M., Mereu, S., Messier, C., Muys, B., Nolet, P., Paquette, A., Parker, J., Perring, M., Ponette, Q., Potvin, C., Reich, P., Smith, A., Weih, M. & Scherer-Lorenzen, M. (2016) Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio*, **45**, 29–41.

Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G., Schelhaas, M. & Trasobares, A. (2013) Disentangling biodiversity and climatic determinants of wood production. *PLoS ONE*, **8**, e53530.

Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C. & Reich, P.B. (2017) Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nature Ecology & Evolution*, **1**, 0063.

Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology*, **14**, 107–129.

Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *Journal of Ecology*, **100**, 742–749.

Zuppinger-Dingley, D., Schmid, B., Petermann, J.S., Yadav, V., De Deyn, G.B. & Flynn, D.F.B. (2014) Selection for niche differentiation in plant communities increases biodiversity effects. *Nature*, **515**, 108–111.

TABLES

Table 1: Summary of the FunDivEUROPE plot network and the Satakunta tree diversity experiment.

	FunDivEUROPE network	Satakunta experiment
Location	29°04' – 30°22'E, 62°08' – 63°01'N	21°42' – 22°09'E, 61°39' – 61°42'N
Climate[a]	MAT = 2.1 °C ; MAP = 632 mm	MAT = 5.3 °C ; MAP = 586 mm
Species pool (target species in bold)	***Pinus sylvestris*, *Picea abies*, *Betula pendula***, *Betula pubescens*	***Pinus sylvestris*, *Picea abies*, *Betula pendula***, *Larix sibirica, Alnus glutinosa*
No. of plots	28 plots	42 plots arranged in 3 blocks[b]
Plot size	30 × 30 m	20 × 20 m
Stem density[c]	852 stems ha^{-1} (range = 444–1911)	4225 stems ha^{-1}
Quadratic mean stem diameter[d]	19.0 cm (range = 12.5–23.1)	
Stand age	42 years (range = 32–49)	19 years
Study design[e]	3–4 × monocultures 4–5 × 2-species mixtures 3 × 3-species mixtures	6 × monocultures 6 × 2-species mixtures 6 × 3-species mixtures
Sampling design	12 trees cored in monoculture plots 8 trees cored per species in all mixtures	10 trees per species per plot in 2004–11 5 trees per species per plot in 2016
No. of growth measurements	438 individual trees cored 14970 annual growth measurements	852 individual trees measured 2103 diameter measurements[f]

[a] Mean annual temperature (MAT) and mean annual precipitation (MAP) between 1981–2010.

[b] The Satakunta experiment includes a total of 114 plots (38 plots × 3 blocks). Only plots which feature combinations of *P. sylvestris, P. abies* and *B. pendula* were used for this study (42 plots; 14 × 3 blocks).

[c] For the FunDivEUROPE plots stem densities include all trees with $D \geq 7.5$ cm in the plot. For the Satakunta experiment 169 trees were initially planted in each plot (13 × 13 rows with seedlings 1.5 m apart).

[d] Calculated as $\sqrt{\Sigma D^2/n}$, where n is the number of stems with $D \geq 7.5$ cm in the plot. See Appendix S2 for the relationship between stem density, quadratic mean stem diameter and stand age in the FunDivEUROPE plots.

[e] In the FunDivEUROPE network *B. pendula* monocultures were replicated 3 times and the 2–species mixture of *B. pendula* and *P. sylvestris* was replicated 4 times.

[f] Tree diameters in the Satakunta plots were measured in 2004, 2009, 2011 and 2016.

Table 2: Summary statistics of diversity effects on tree growth for the three study species in the FunDivEUROPE plots (PINSYL: *Pinus sylvestris*; PICABI: *Picea abies*; BETPEN: *Betula pendula*). The age at which diameter growth in mixture first becomes significantly greater than that in monoculture was determined by comparing the 95% confidence intervals of the diameter growth model predictions.

Species combination	Difference in diameter growth relative to monoculture at age 35			Age at which diameter growth in mixture exceeds that in monoculture		
	PINSYL	PICABI	BETPEN	PINSYL	PICABI	BETPEN
PINSYL + PICABI	+16%	+17%		22	23	
PINSYL + BETPEN	+18%		+35%	26		20
PICABI + BETPEN		+10%	+35%		12	22
PINSYL + PICABI + BETPEN	+29%	+19%	+47%	25	27	16

FIGURES

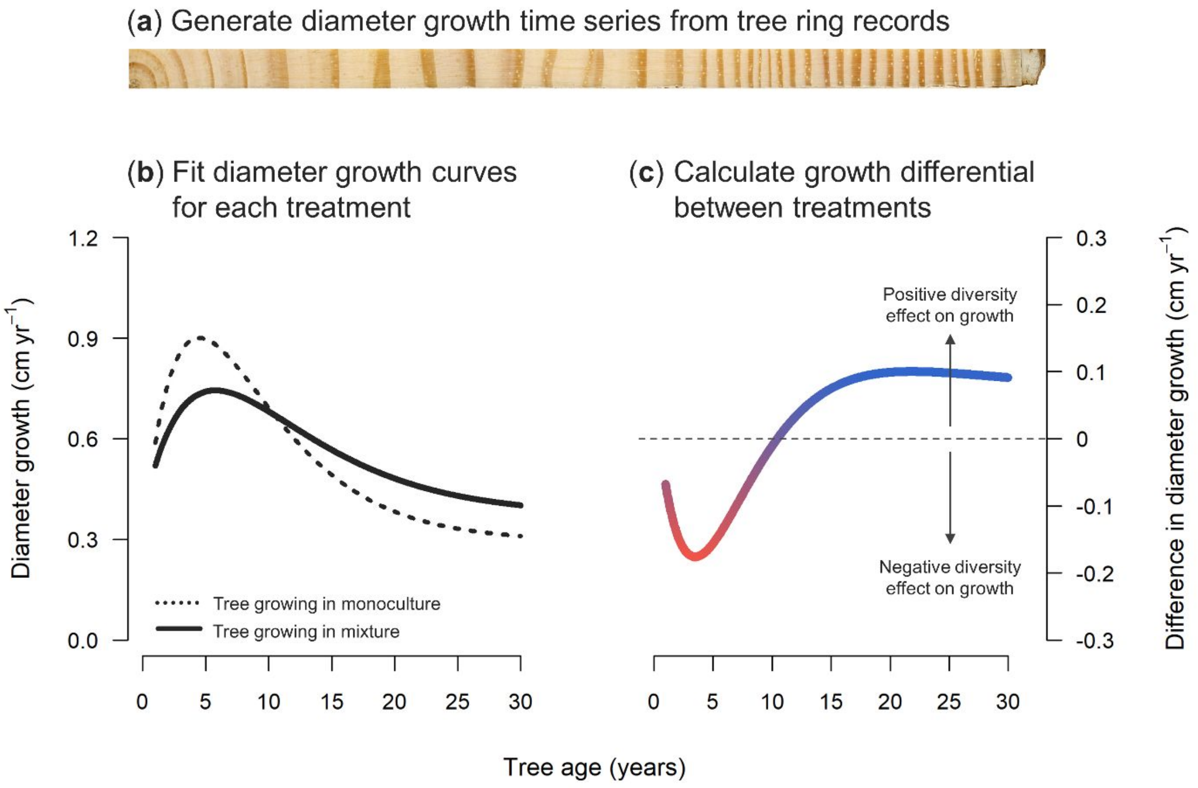

Fig. 1: Schematic diagram illustrating how tree ring data from the FunDivEUROPE plots were used to test how diversity effects on tree growth vary through time. (**a**) Radial increments measured from tree cores were used to generate diameter growth time series for each sampled tree. (**b**) Non-linear growth models were used to fit diameter growth curves for trees growing in monoculture (dashed line) and in mixture with other species (solid line). (**c**) By calculating the difference between the two growth trajectories we can identify periods when growth was faster in monoculture (in red below the dashed line) or in mixture (in blue above the dashed line).

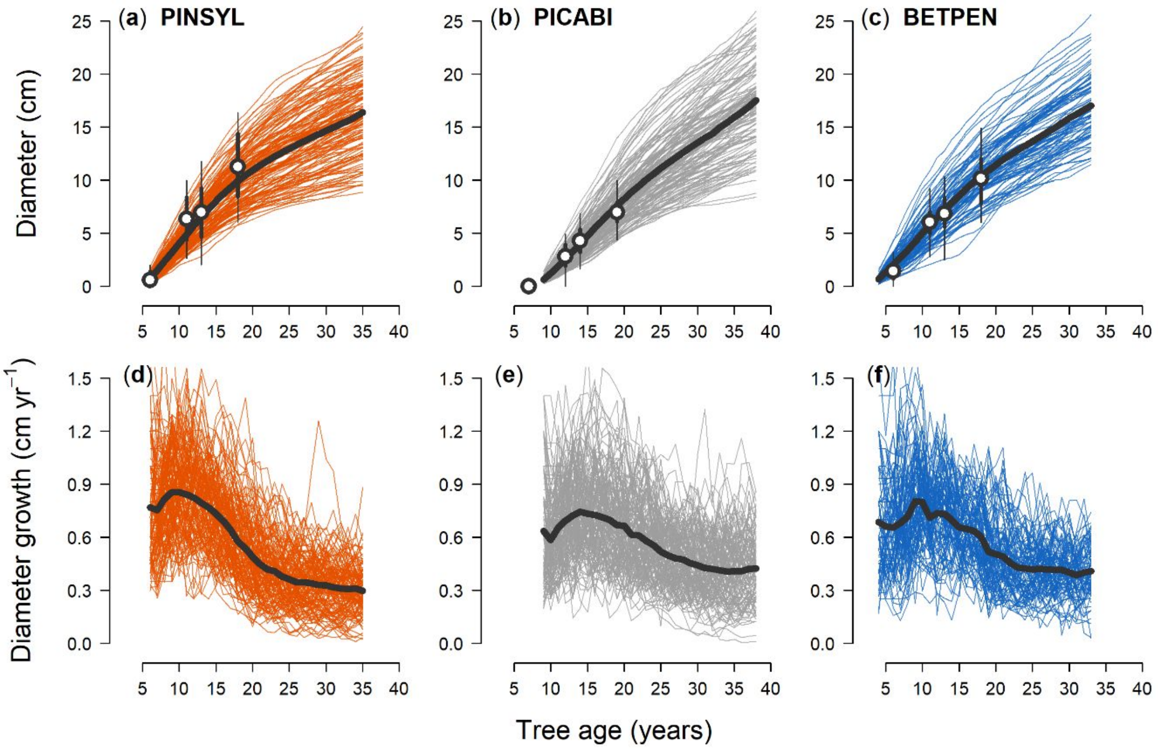

Fig. 2: Cumulative diameter increment (**a**–**c**) and annual diameter growth rate (**d**–**f**) through time for each study species in the FunDivEUROPE plots (PINSYL: *Pinus sylvestris*; PICABI: *Picea abies*; BETPEN: *Betula pendula*). Thin coloured lines show the growth trajectory of individual trees, whereas thick black lines correspond to mean values across all sampled trees. For comparison, empty circles in panels (**a**–**c**) show the mean diameter value of trees in the Satakunta experiment at the four time periods in which they were measured. Error bars show the interquartile range (thick lines) and 95% range (thin lines) of the diameter values of the Satakunta trees. Note that a correction was applied to the age of trees in the FunDivEUROPE plots to account for the fact that tree cores were sampled at a height of 1.3 m above-ground (see main text and Appendix S3 for details).

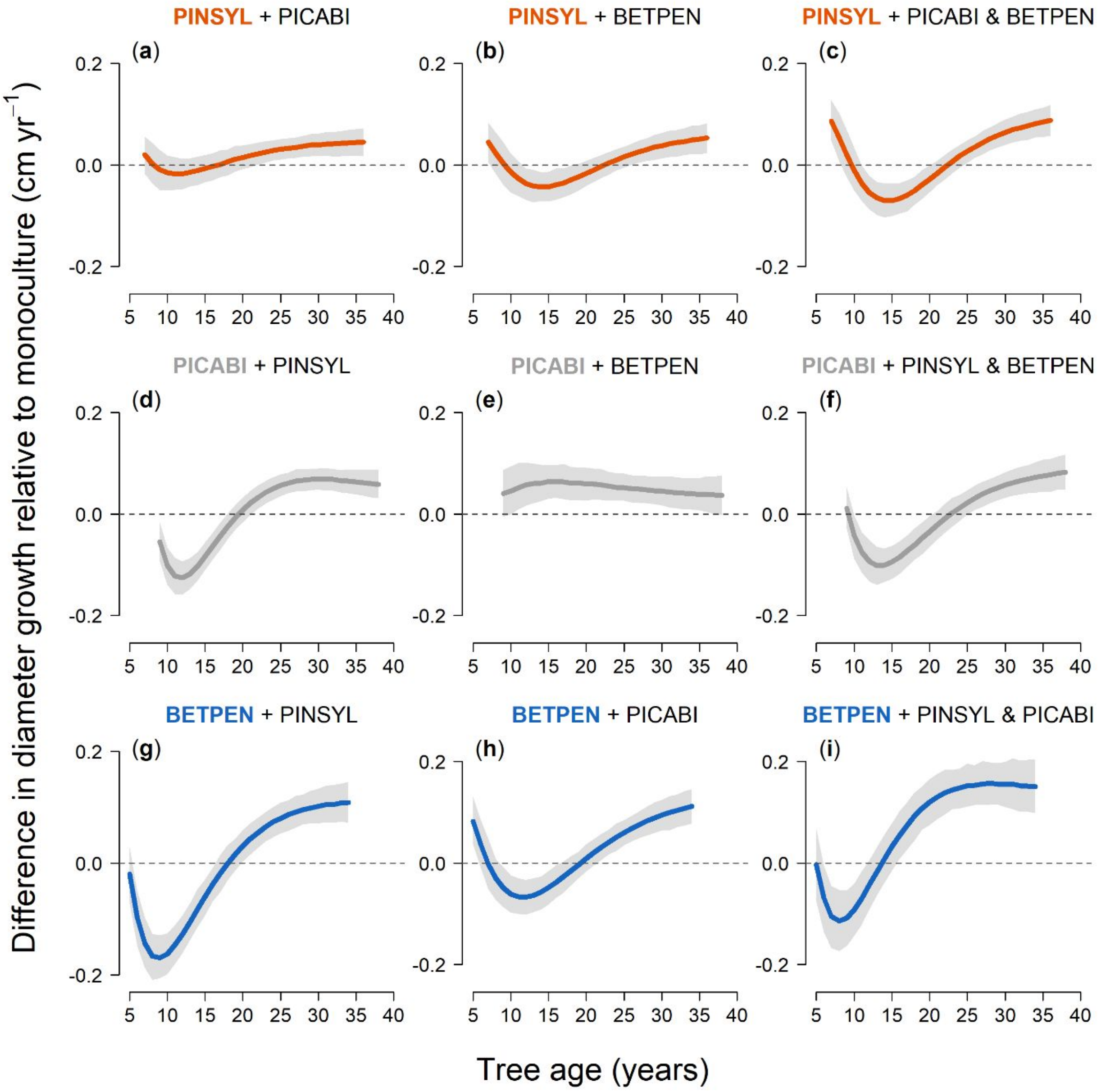

Fig. 3: Difference in diameter growth between trees in monoculture and those in mixture as a function of tree age for (**a**–**c**) *Pinus sylvestris* (PINSYL), (**d**–**f**) *Picea abies* (PICABI) and (**g**–**i**) *Betula pendula* (BETPEN) in the FunDivEUROPE plots. Shaded regions in grey correspond to the 95% confidence intervals of the curves. See Fig. 1 for a schematic interpretation of the results.

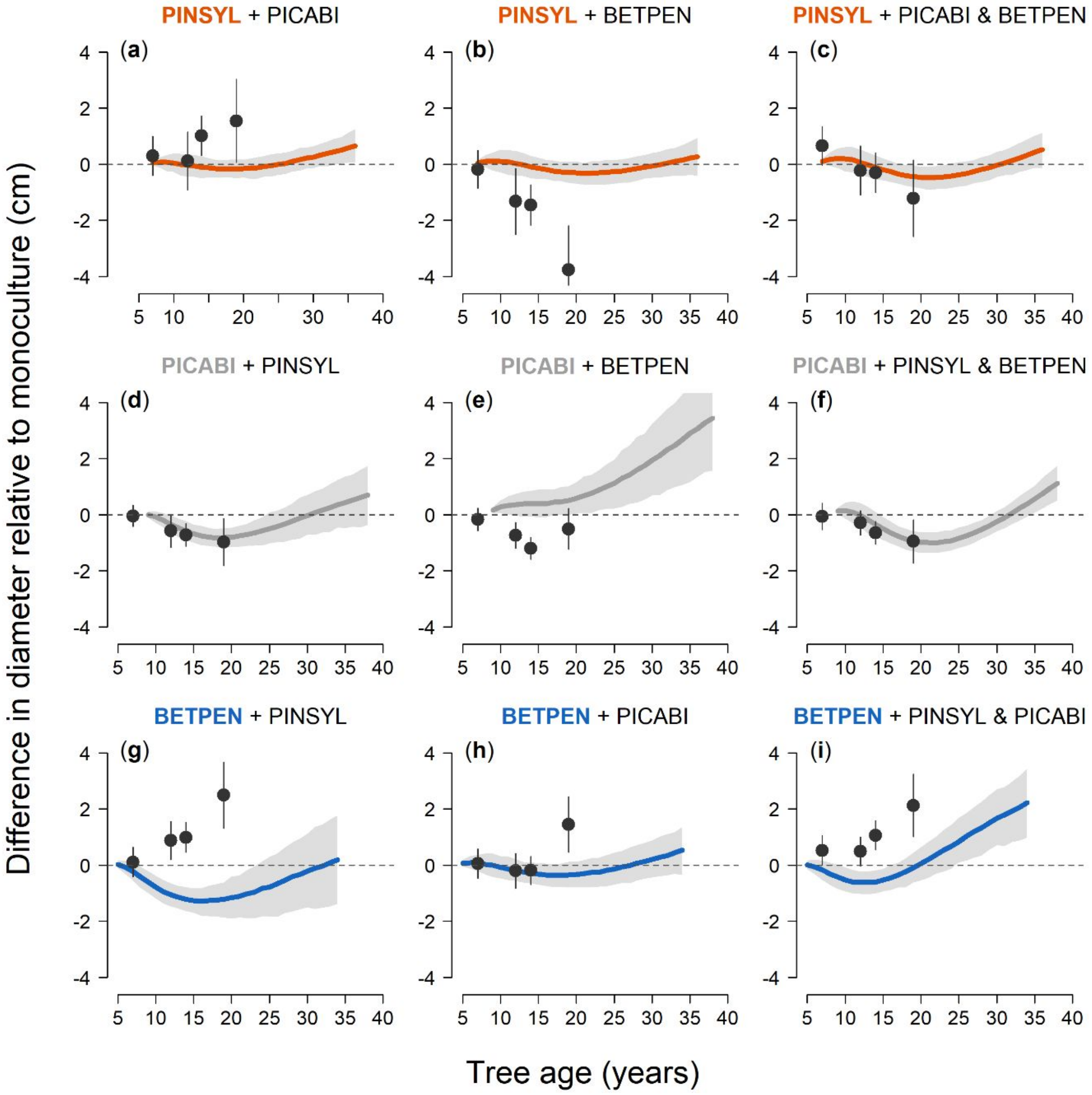

Fig. 4: Difference in diameter between trees in monoculture and those in mixture as a function of tree age for (**a**–**c**) *Pinus sylvestris* (PINSYL), (**d**–**f**) *Picea abies* (PICABI) and (**g**–**i**) *Betula pendula* (BETPEN) in the FunDivEUROPE plots. Shaded regions in grey correspond to the 95% confidence intervals of the curves. For comparison, the results of the same analysis conducted on trees from the Satakunta experiment are shown as filled circles (mean difference in diameter between monoculture and mixture ± 95% confidence intervals).

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1: FunDivEUROPE plot network and tree ring data

Appendix S2: Changes in species composition and stand density through time in the FunDivEUROPE and Satakunta plots

Appendix S3: Tree height–age curves

Appendix S4: Comparing alternative tree growth models

Supporting information

Appendix S1 | FunDivEUROPE plot network and tree ring data

Plot locations

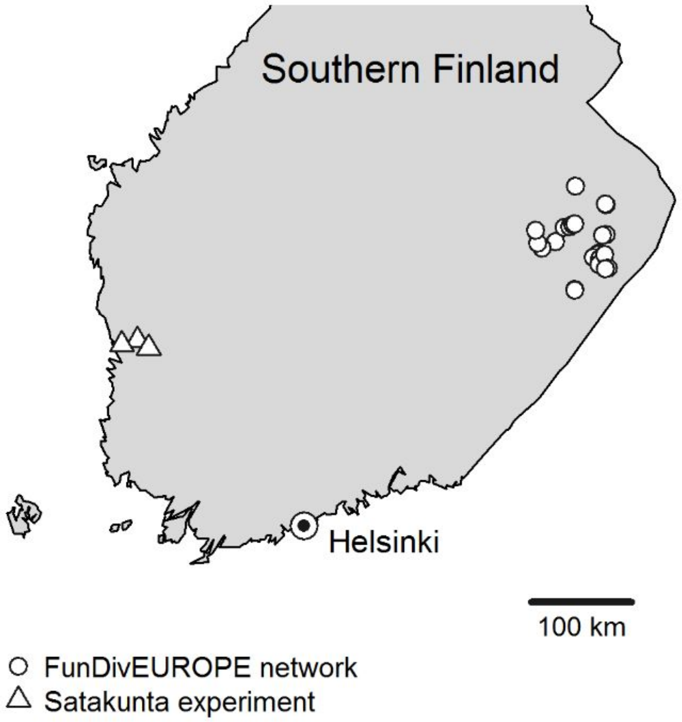

Fig. S1 | Map of southern Finland showing the location of the FunDivEUROPE plots (circles) relative to the three sites of the Satakunta tree diversity experiment (triangles).

Tree age variation within and among FunDivEUROPE plots

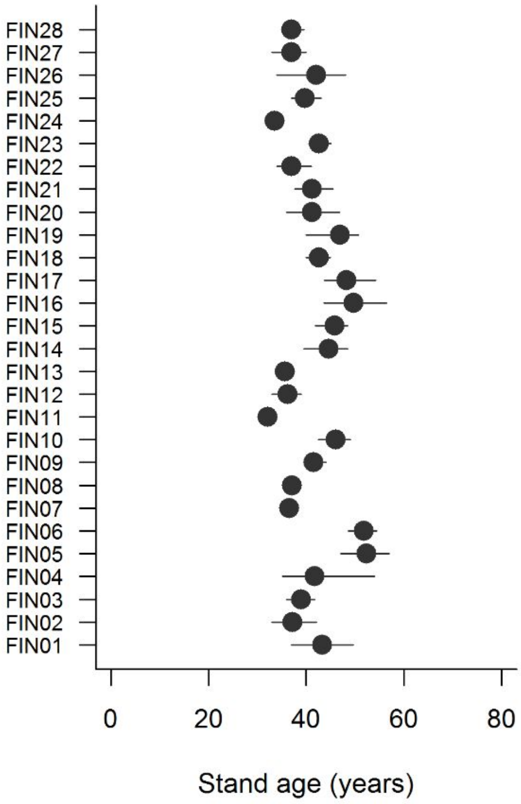

Fig. S2 | Tree age (mean and range) across the 28 FunDivEUROPE plots based on tree ring records.

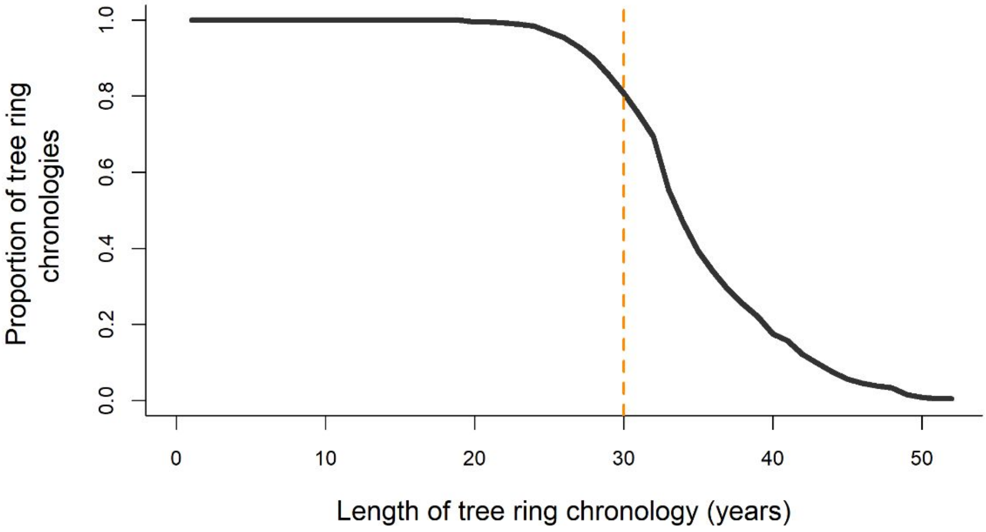

Fig. S3 | Proportion of the 438 tree ring samples that exceed a specific length.

Appendix S2 | Changes in species composition and stand density through time in the FunDivEUROPE and Satakunta plots

FunDivEUROPE plots

In addition to the initial 2012 census, the FunDivEUROPE plots were re-surveyed a second time in 2017. During this second census, the diameter (*D*, in cm) of all previously tagged stems was measured again and any trees that died or recruited between census periods were recorded. Using these data, we can test the extent to which the species composition of the FunDivEUROPE plots changed over a 5-year period. To do this, for each plot we calculated the exponential of the Shannon diversity index in both 2012 and 2017, which Jost (2006) defines as a measure of the 'effective number of species' of a community:

$$\text{Effective no. species} = \exp\left(-\sum_{i=1}^{S}\frac{BA_i}{BA}\ln\left(\frac{BA_i}{BA}\right)\right) \tag{S1}$$

where S is the number of unique species within a plot, BA_i is the basal area of species i and BA is the total basal area of the plot. This provides a measure of diversity that directly account for species' relative abundances (i.e., evenness), while also being easily interpretable and directly relatable to species richness (as when species' relative abundances in a plot are equal, species richness = effective number of species; Jost 2006). By comparing the effective number of species recorded in 2012 and 2017 across the FunDivEUROPE plots, we found that species composition remained almost identical over this 5-year period (Fig. S4).

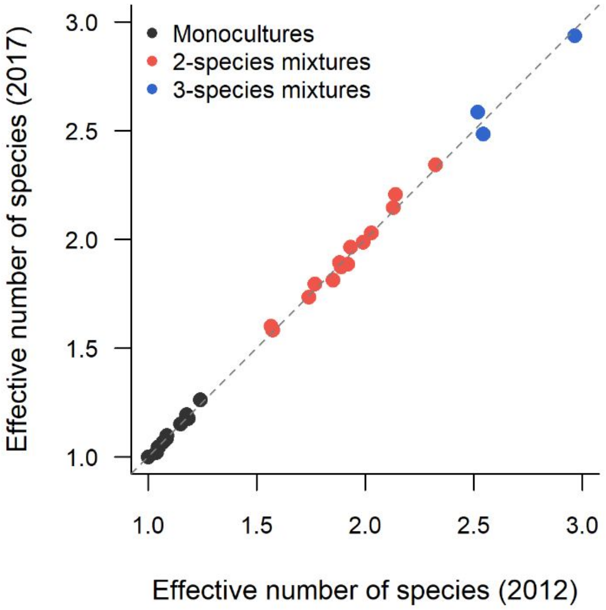

Fig. S4 | Relationship between the effective number of species recorded in the FunDivEUROPE plots in 2017 and 2012. A 1:1 line is shown in grey. Plots categorised as monocultures, 2-species mixtures and 3-species mixtures are shown in black, red and blue, respectively. Note that because some of the monoculture plots contain a small number of non-target trees (≤5% of the plot basal area in all cases), their effective number of species is >1. See Baeten *et al.* (2013) for details on the criteria used to select the FunDivEUROPE plots, including thresholds for non-target species.

The repeat-census data from the FunDivEUROPE plots also provide an opportunity to explore how stand density has changed through time and how this varies among plots at different stages of stand development and in relation to tree diversity. In particular, it allowed us to test one of the key assumptions of our analysis: that differences in stand density among the FunDivEUROPE plots simply reflect differences in development stage (i.e., stand age) and not ones in species composition or diversity. To do this, we first used the census data from both 2012 and 2017 to calculate two measures of stand density which together capture information on both the number and size of trees in a plot: stem density (N, in stems ha^{-1}) and the quadratic mean stem diameter (QMD, in cm), which is calculated as $\sqrt{\sum D^2/N}$. Combined together, QMD and N determine the basal area of a forest stand (Curtis & Marshall 2000; Jucker *et al.* 2016) and the relationship between QMD and N captures key information on stand development and self-thinning (Yoda *et al.* 1963; Westoby 1984). We then used linear models to explore whether the relationship between (i) N and stand age (as estimated from the tree ring data), (ii) QMD and stand age and (iii) QMD and N are modulated by the species richness of the plot (tested by including an interaction term between species richness and the explanatory variable). N, QMD and stand age were all log-transformed prior to model fitting to normalise the residuals.

This analysis revealed clear changes in N and QMD during stand development, with N declining sharply and QMD increasing steadily with stand age (Fig. S5a–b). This resulted in older stands being characterised by fewer, larger stems – a pattern consistent with self-thinning (Fig. S5c). However, we found no significant difference in the shape of these relationships for plots characterised by different levels of tree diversity (i.e., interaction terms between tree species richness and the explanatory variable were not statistically significant in all three models). These results support our assumption that differences in stand density among the FunDivEUROPE plots reflect differences in stand development stage, and not ones in tree diversity or species composition.

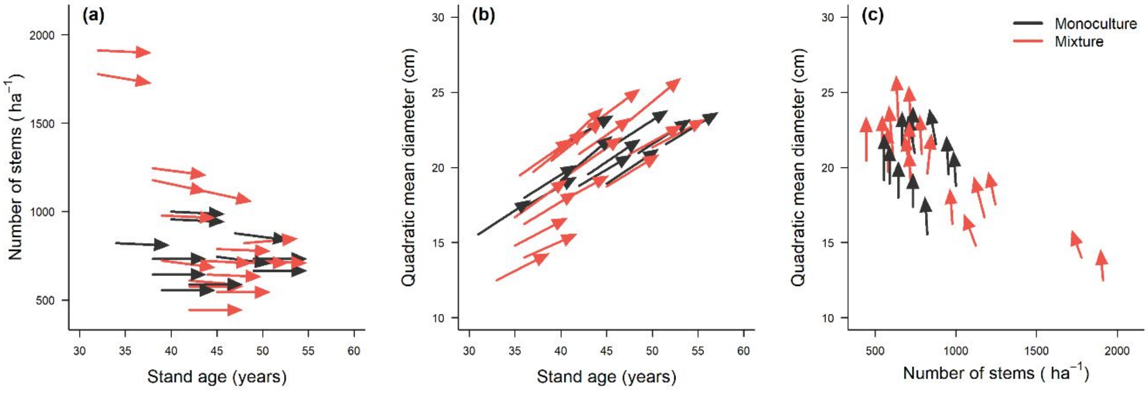

Fig. S5 | Relationship between (**a**) stem density (*N*) and stand age, (**b**) quadratic mean diameter (*QMD*) and stand age and (**c**) *QMD* and *N* across the FunDivEUROPE plots. Arrows depict temporal changes in *QMD* and *N* that occurred between the 2012 (starting point of the arrow) and 2017 census (tip of the arrow). Monoculture plots are shown in black, while mixed-species plots are in red.

Satakunta plots

In 2011 a complete second census of the Satakunta plots was conducted, at which time any trees that had died since planting in 1999 were recorded. These data provide an opportunity to determine how species composition and tree density changed during the early stages of stand development at Satakunta. To explore how species composition may have changed since the experiment was first established, we used the 2011 census data to calculate the effective number of species in each plot based on the relative abundance of live stems (as described above for the FunDivEUROPE plots). When we compared these values to those of the initial tree species richness at the time of planting in 1999, we found that species composition in the Satakunta plots had remained very consistent during the first 12 years of stand development (Fig. S6a).

In terms of tree density, by 2011 the number of live stems per plot had declined to 123 ± 20 (mean ± 1 standard deviation) from the initial 169 that were planted in 1999. However, an ANOVA conducted on the 2011 data revealed no significant differences in tree density across the diversity gradient (Fig. S6b) or among the various species composition treatments. So despite changes in stem density consistent with the initial phases of self-thinning, mortality rates were found to be similar across the tree diversity gradient during the early stages of stand development.

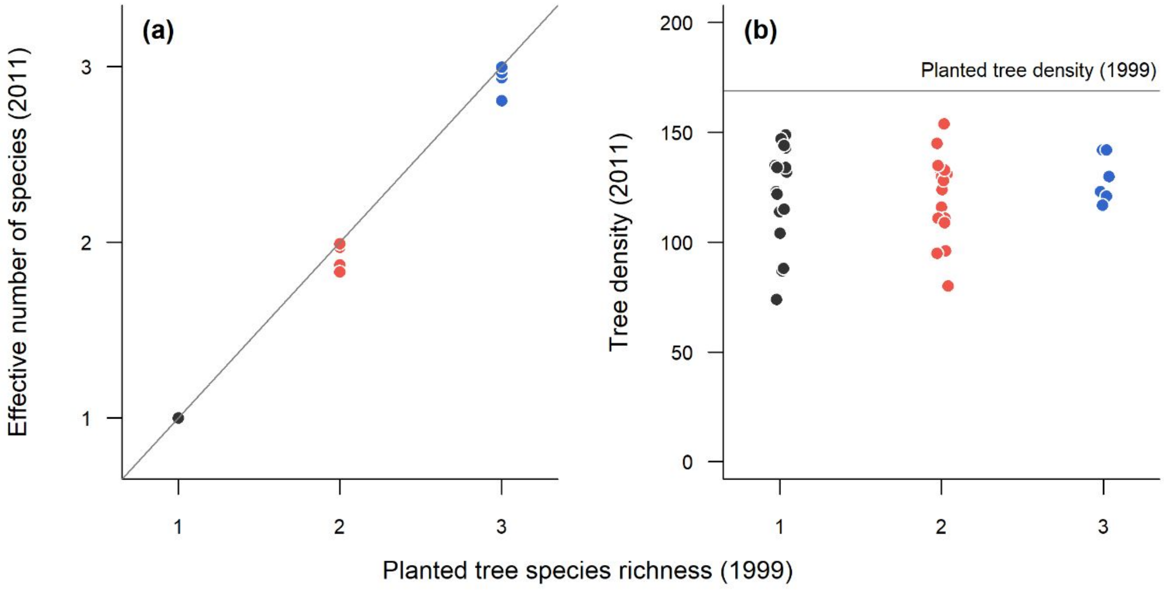

Fig. S6 | Relationship between planted tree species richness in 1999 and (**a**) effective number of species in 2011 and (**b**) tree density in 2011 across the Satakunta plots. In (**b**) we applied a jitter to the x-axis so that overlapping points could be more easily distinguished.

Appendix S3 | Tree height–age curves

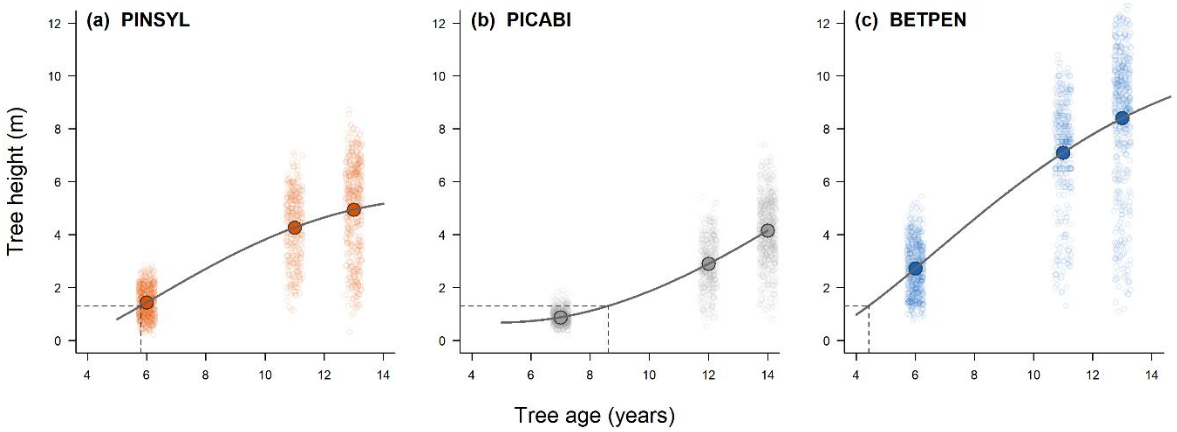

Fig. S7 | Height–age curves for trees in the Satakunta biodiversity experiment (PINSYL: *Pinus sylvestris*; PICABI: *Picea abies*; BETPEN: *Betula pendula*). Tree height was measured during three census periods (age 7, 12 ad 14). Small empty circles are individual trees, while large filled circles are mean height values for each census year. The following height (H, in m) – age (T, in years) function was used to estimate the age at which the average tree reaches a height of 1.3 m for each study species: $H = \alpha + \beta T e^{-\gamma T}$ (see where dashed lines intercept the height – age curves).

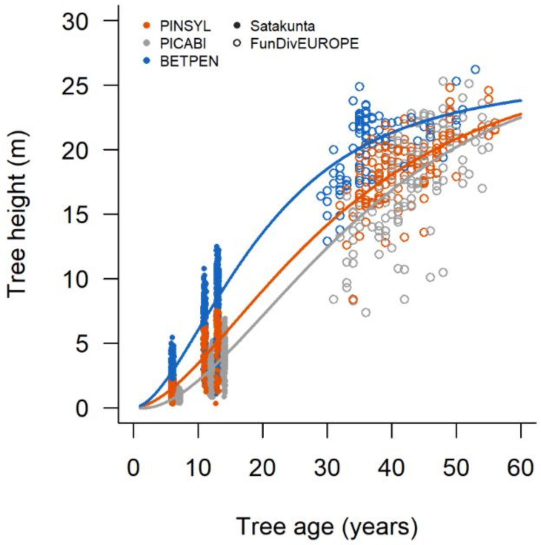

Fig. S8 | Tree height as a function of tree age for each study species (PINSYL: *Pinus sylvestris*; PICABI: *Picea abies*; BETPEN: *Betula pendula*) in the FunDivEUROPE plots (open circles) and the Satakunta biodiversity experiment (filled circles). Height – age curves for each species were fit using the function described in Fig. S7 using data from both the FunDivEurope and Satakunta plots.

Appendix S4 | Comparing alternative tree growth models

Modelling diameter growth

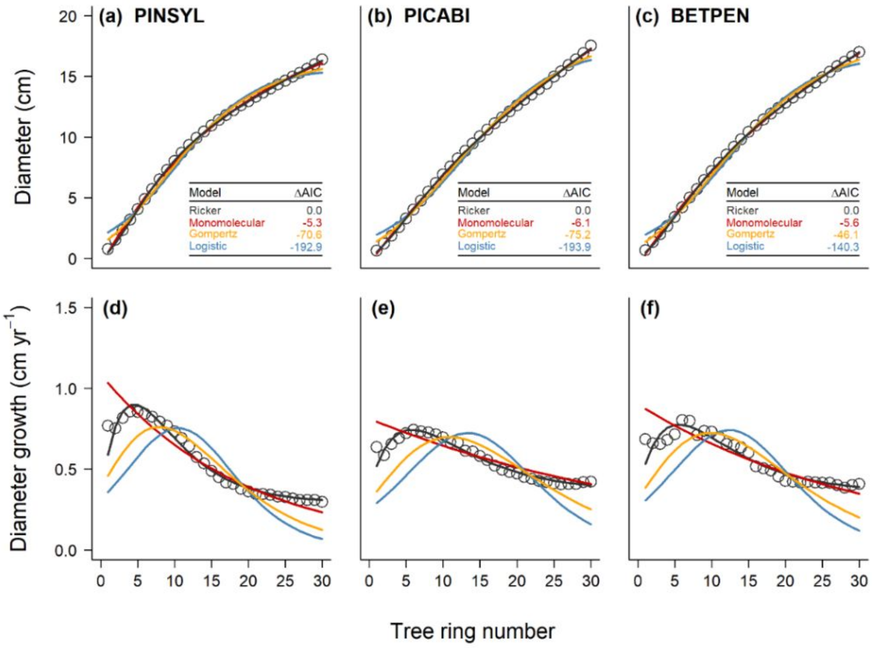

Fig. S9 | Comparison of alternative non-linear models of tree growth for each target species (PINSYL: *Pinus sylvestris*; PICABI: *Picea abies*; BETPEN: *Betula pendula*). Lines show to the fit of four different growth models (Ricker, monomolecular, Gompertz, and a four-parameter logistic), while open circles correspond to observed mean growth values for each year. For both cumulative diameter increments (top row) and annual diameter growth rate (bottom row), the Ricker function outperformed other growth models. A monomolecular function showed a reasonable fit to the cumulative diameter increments (top row), with ΔAIC values within 10 points of those obtained with the Ricker function. However, when the monomolecular function is expressed in terms of annual diameter growth rates (bottom row), the limitations of this function for modelling ontogenetic trends in tree diameter growth become apparent: the monomolecular function fails to capture both the initial inflection point in diameter growth (years 0 – 10) as well as the levelling-off of diameter increment with age. Diagnostic plots of the residuals of the Ricker models are shown in Fig. S10.

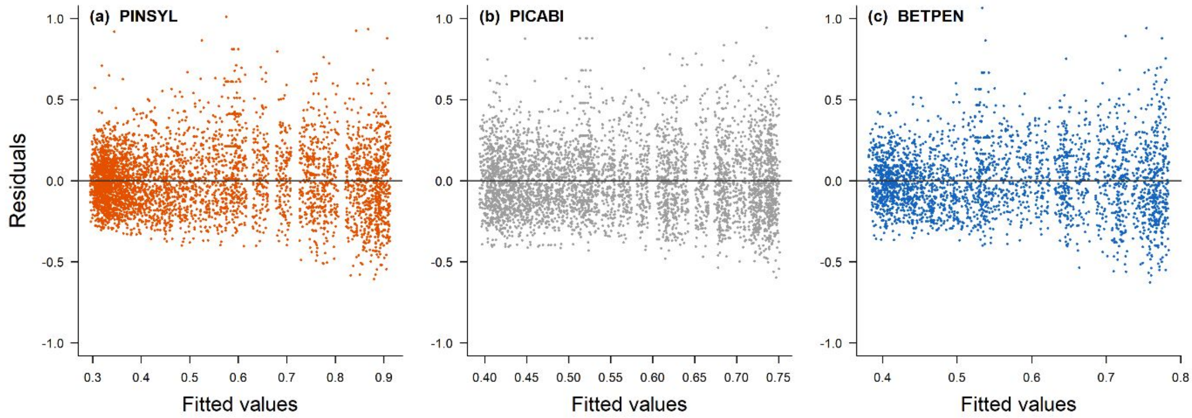

Fig. S10 | Diagnostic plots showing the relationship between residuals and fitted values of the Ricker diameter growth models for each study species.

Modelling basal area growth

Compared to dimeter growth (Fig. S9d–f), basal area growth (BA_{incr}, in cm^2 yr^{-1}) trajectories exhibited much more complex oscillating non-linear temporal trends (Fig. S11). We compared the ability of several non-linear growth models to capture the BA_{incr} trends through time and found the best fitting model to be a four-parameter Weibull implemented using the *SSweibull* function in R:

$$BA_{incr} = \alpha - \beta \times \exp\left(-\exp(\gamma) \times A^{\delta}\right) \qquad \text{(S2)}$$

where A is the age of a tree in years and α, β, γ and δ are the four parameters to be estimated from the data. While this function recreates the early phase of BA_{incr} trends well for all three study species, it does not capture the second phase in which BA_{incr} slows before gradually increasing again (dashed black curves in Fig. S11). In fact, we found that we were able to better capture this complex pattern by simply converting predicted dimeter growth increments obtained using the Ricker growth model [eqn (1) in the main text; black curves in Fig. S9d–f] into basal area increments (red curves in Fig. S11).

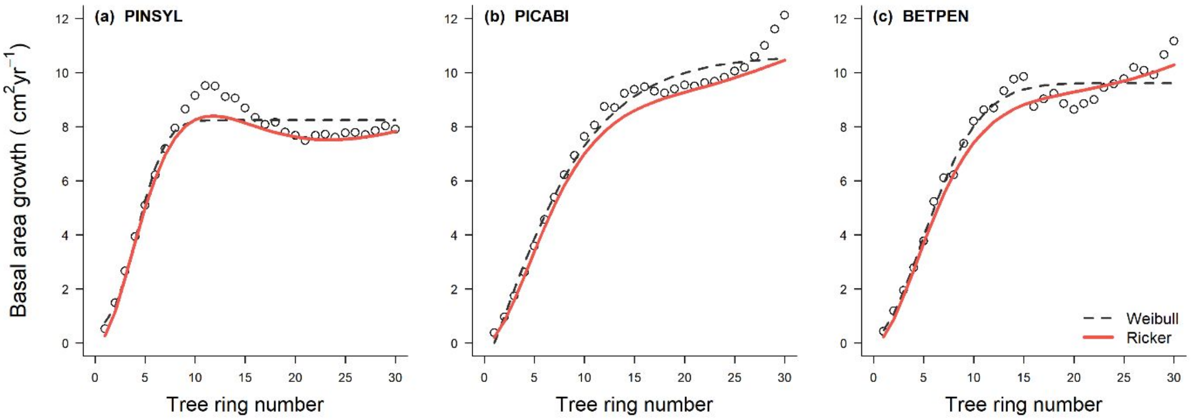

Fig. S11 | Comparison of two different non-linear models of basal area growth for each target species (PINSYL: *Pinus sylvestris*; PICABI: *Picea abies*; BETPEN: *Betula pendula*). Dashed black curves show the fit of the four-parameter Weibull function presented in eqn (S2). Red curves were generated by converting diameter growth increments predicted from the Ricker growth model presented in eqn (1) in the main text into units of basal area growth.

Based on this we chose to use the Ricker function to model differences in basal area growth trajectories of trees in monoculture and mixture. This revealed very similar temporal trends to those highlighted for diameter growth in the main text. In particular, the effects of species mixing on basal area growth tended to strengthen with time in all three study species and across all different possible species combinations (Fig. S12).

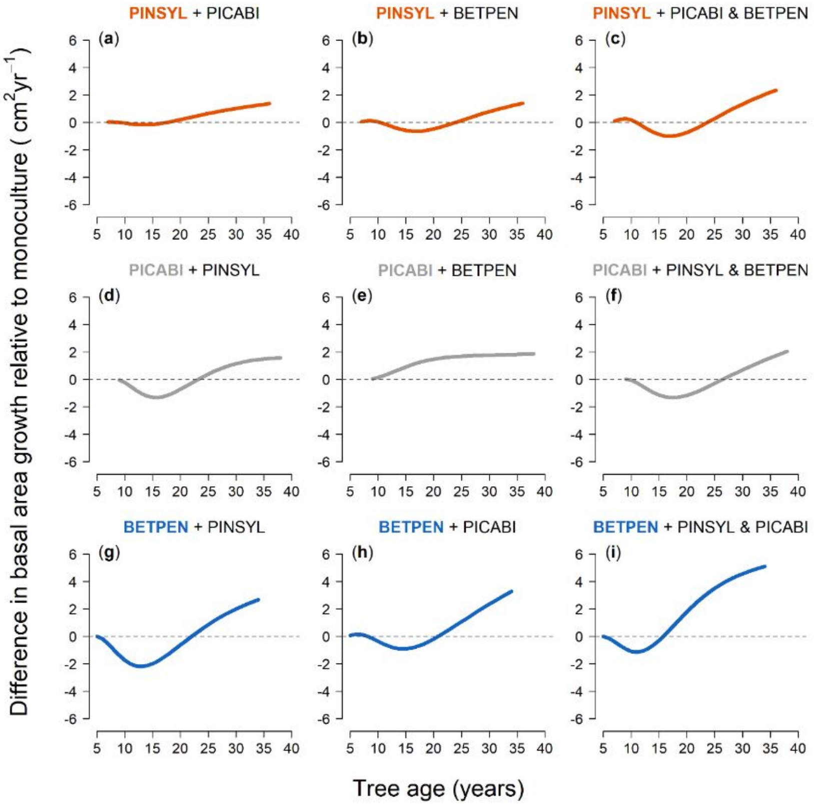

Fig. S12 | Difference in basal area growth between trees in monoculture and those in mixture as a function of tree age for (a–c) *Pinus sylvestris* (PINSYL), (d–f) *Picea abies* (PICABI) and (g–i) *Betula pendula* (BETPEN) as a function of tree age in the FunDivEUROPE plots. The interpretation of the figure is analogous to that of Fig. 3 in the main text.

References

Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., Jaroszewicz, B., Selvi, F., Valladares, F., Allan, E., Ampoorter, E., Auge, H., Avăcăriei, D., Barbaro, L., Bărnoaiea, I., Bastias, C.C., Bauhus, J., Beinhoff, C., Benavides, R., Benneter, A., Berger, S., Berthold, F., Boberg, J., Bonal, D., Brüggemann, W., Carnol, M., Castagneyrol, B., Charbonnier, Y., Chećko, E., Coomes, D.A., Coppi, A., Dalmaris, E., Dănilă, G., Dawud, S.M., de Vries, W., De Wandeler, H., Deconchat, M., Domisch, T., Duduman, G., Fischer, M., Fotelli, M., Gessler, A., Gimeno, T.E., Granier, A., Grossiord, C., Guyot, V., Hantsch, L., Hättenschwiler, S., Hector, A., Hermy, M., Holland, V., Jactel, H., Joly, F.-X., Jucker, T., Kolb, S., Koricheva, J., Lexer, M.J., Liebergesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nichiforel, L., Pollastrini, M., Proulx, R., Rabasa, S., Radoglou, K., Ratcliffe, S., Raulund-Rasmussen, K., Seiferling, I., Stenlid, J., Vesterdal, L., von Wilpert, K., Zavala, M.A., Zielinski, D. & Scherer-Lorenzen, M. (2013) A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics*, **15**, 281–291.

Curtis, R.P. & Marshall, D.D. (2000) Why quadratic mean diameter? *Western Journal of Applied Forestry*, **15**, 137–139.

Jost, L. (2006) Entropy and diversity. *Oikos*, **113**, 363–375.

Jucker, T., Sanchez, A.C., 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.

Westoby, M. (1984) The self-thinning rule. *Advances in Ecological Research*, **14**, 167–225.

Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology*, **14**, 107–129.