Special profile: Forest biodiversity and ecosystem services studies

Running head: Forest diversity promotes tree growth

Forest diversity promotes individual tree growth in central European forest stands

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Supplementary material: A pdf summarizing the analysis that includes all computer (R language) code necessary to run the analysis and all the output and figures together with text files of the data.

Summary

1) Most of the experimental evidence on the relationship between biodiversity and ecosystem functioning comes from grasslands and other fast growing systems, and while forests provide essential ecological services to humanity they have been less well investigated.

2) We used dendrochronology to compare tree radial growth rates of four study species in replicated, spatially mapped stands that differed in tree composition and diversity within the Mendel University research and training forest.

3) Growth rates differed among species and declined with tree age as expected but were largely unaffected by the range of observed basal area density.

4) Increases in stand diversity enhanced individual growth rates by between 18 and 28% and these increases were statistically indistinguishable between species. Despite the potentially high levels of heterogeneity of the semi-natural stands of the Brno research and training forest there were no residual spatial correlations to confound these results.

5) Policy implications: Our results show that levels of tree diversity could be increased without a cost to forest productivity and even with the potential for modest increases in tree growth rates.

Key-words: Biodiversity, forest productivity, ecosystem functioning, tree growth rates, tree rings

Introduction

One of the greatest environmental changes that our planet endures is the loss of biological diversity, which affects the functioning of ecosystems and has effects comparable to other global change drivers (Rockström *et al.* 2009; Isbell *et al.* 2011; Cardinale *et al.* 2012; Tilman, Isbell & Cowles 2014). The effect of biodiversity loss on a single ecosystem process (most often productivity or surrogates for it) is generally positive but saturating, indicating that the initial effects of species loss are on average weak (unless a dominant species is lost). However this effect is curvilinear or non-linear such that impacts accelerate with the loss of additional species. This relationship also suggests that, from a restoration point of view, diversity should have its strongest impacts on ecosystem processes when increasing levels from monoculture.

Low diversity forestry stands are one of the systems where there have been calls to increase diversity and where we need to know the costs and benefits of doing so. Forest ecosystems support humanity with services that are essential for its survival and well-being (Gamfeldt *et al.* 2013), among which wood production is of special importance. Trees not only provide timber for energy, construction or paper, they also directly mitigate the effects of global warming by transforming atmospheric CO_2 into biomass ('Millennium Ecosystem Assessment' 2005; Naeem *et al.* 2009). If we are to sustain the services that forests provide to humankind it is crucial to understand how tree diversity affects the functioning of these ecosystems.

Much of the research on the relationship between biodiversity and ecosystem functioning has been conducted in grasslands and other systems that are relatively easy to manipulate and quick to respond. Forest ecosystems have been less frequently investigated, and although similar influences of biodiversity have been suggested, the results are far from conclusive (Thompson *et al.* 2009; Nadrowski, Wirth & Scherer-Lorenzen 2010; Cardinale *et al.* 2011). For example, the relationship between species diversity and forest productivity can be dependent on site richness (Belote *et al.* 2011) or forest type (Paquette & Messier 2011; Vilà *et al.* 2013) and enhanced productivity has even been found to be driven more by species evenness than by richness (Zhang, Chen & Reich 2012). Tree diversity has been shown to promote forest stand productivity through an increase in tree density rather than through enhanced individual tree growth (Vilà *et al.* 2013).

Evidence on the effects of tree diversity on forest functioning comes from two types of investigations: planted experiments similar to the grasslands experiments, and inventory data. Both have their strengths and weaknesses (Nadrowski, Wirth & Scherer-Lorenzen 2010). Planted experiments can include a broad gradient of species richness replicated with different species (Scherer-Lorenzen *et al.* 2007; Healy, Gotelli & Potvin 2008; Hector *et al.* 2011), and trees are regularly measured, allowing for precise estimations of their growth rates (Potvin & Dutilleul 2009). These experiments however, are very young and thus do not yet address the functioning of mature forests (Nadrowski, Wirth & Scherer-Lorenzen 2010).

Inventories on the other hand provide data on older forests that are more suitable for exploring such questions (Vilà *et al.* 2003; Paquette & Messier 2011). But these established plots often cover a dilution gradient (Nadrowski, Wirth & Scherer-Lorenzen 2010), where one matrix species is always present (often *Fagus sylvatica* in Europe) and the only one found in monocultures. Additionally, environmental heterogeneity is often not accounted for potentially biasing the effects of diversity on productivity (Healy, Gotelli & Potvin 2008). Finally growth is calculated on diameter increment measured every five to ten years only, and the necessary data to consider effects of tree age on radial growth are generally not available from large-scale monitoring efforts. In contrast to grasses, trees can be individually examined, and precisely measuring tree growth (ideally at least annually in seasonal systems) is a critical step towards the understanding of what affects it. However it is not straightforward since trees are such large and long-lived organisms. Here, we use tree rings as a record of their past growth to reconstruct their cumulative growth in and estimate growth rates

In temperate zones, species carry out most of the photosynthesis during the growing season, and they record this cambial growth in annual rings (Speer 2012; Bowman *et al.* 2013). Whereas height growth tends to be rapid at first and then slow dramatically, radial growth is more consistent, and can even be considered linear over short periods of time (Bowman *et al.* 2013). Using annual ring width as a proxy for annual growth appears to be a good way to explore the effects of diversity on individual tree growth (Nadrowski, Wirth & Scherer-Lorenzen 2010). We took advantage of established stands in the research and training forest of the University of Brno in the Czech Republic that contain different tree diversities to examine the effects on forest ecosystem functioning. The academic literature on biodiversity and ecosystem functioning has tended to focus on testing whether levels of ecosystem processes are significantly higher in mixtures than in monocultures. However, increasing diversity in forests could conceivably also decrease productivity. Nevertheless, where there is a conservation motivation to increase levels of diversity, some decrease in productivity may be an acceptable trade off. We therefore take a broader view in investigating the general costs and benefits of increased forest diversity (Chamagne 2014; Chamagne et al. in press) focusing here on productivity (tree growth rates).

Materials and Methods

Experimental design

The Mendel University Training Forest Enterprise (TFE) is located north of the cite of Brno in the Czech Republic (49°3'N and 16°7'E), lying 310 to 560 m above sea level (Fig 1) and covering 10,000 ha. The annual mean temperature is 7.5°C, the average annual precipitation 610 mm, and soils are principally Cambisols (Truhlář 1997). The forest has been managed by the University for the last century for commercial activity and for forestry education and research. The pedology, geology and topography have been mapped and forest type, age, density and volumetric species composition are estimated in each of 4,000 stands every decade (www.mapserver-slp.mendelu.cz/). Norway spruce (*Picea abies*), European larch (*Larix decidua*), Sessile oak (*Quercus petraea*) and European beech (*Fagus sylvatica*) (henceforth referred to by their generic names) were chosen as our study species since they are some of the most economically important species in this region (representing 75% of timber volume in the training forest) while comprising an ecologically varied set of species in terms of their ecology and life history traits. Sites corresponding to the 15 possible combinations of these four focal species were sampled and each of the 15 compositions was replicated three times. In this way, every level of species richness (except the highest) was replicated with different species combinations and all combinations were also replicated to manipulate species composition. Based on the TFE records for the 4,000 stands, we chose a subset planted with all the possible species richness and species combinations (composition) of our four study species. Sites were selected to be as homogeneous as possible in terms of their bedrock, soil type, aspect and slope (Scherer-Lorenzen *et al.* 2005). At each of the 45 sites, six trees of each focal species were targeted, so that six trees were measured in monocultures, and 24 in the full mixtures. In order to have a reasonable record of growth via the tree rings, small trees (<14 cm) were not sampled. With this constraint, target trees were chosen in such that they were separated by at least six meters, and that their sizes spanned the range of sizes found at the site. Target trees of the four study species and neighbouring individuals (>10 cm DBH) of all species within a 10 m radius were mapped with the Field-Map technology (Hédl *et al.* 2009, http://www.fieldmap.cz/). Each mapped tree was identified to species and its Diameter at Breast Height (DBH) at 1.3 m was recorded. The stumps of recently thinned trees were also included in the maps. The 45 sites ranged from 0.07 to 0.6 ha in size and covered an area of 11 ha in all. A total of 8,919 trees were measured of which 576 were target trees of the four study species.

Data collection

Mapping Data

Tree neighbourhood maps were used to calculate tree diversity and density for each of the 45 sites. Tree diversity was calculated as the effective number of canopy tree species - the exponent of the Shannon index ($e^{H'}$) - taking both species richness and evenness into account (Magurran 1988; Beck & Schwanghart 2010). The Shannon index is calculated as:

$$H' = -\sum_{i=1}^{SR} p_i ln p_i,$$

Where, SR is the total species richness, and p_i is the relative abundance of species i. Taking the exponent of H’ provides an estimate of the number of equally abundant species. The H’ index increases with species richness and with equality in relative abundances. When all species are equally abundant, H’ approaches ln(SR), and the effective number of species approaches SR. In contrast, when species composition is very uneven and approaches a monoculture, H’ approaches zero and the effective number of species equals one. Sites were chosen to cover a gradient of species richness going from one to four, and the measured values for $e^{H'}$ ranged from 1 to 3.93 (Table 1). Tree density was defined as the total basal area of canopy trees standardized by area, and ranged from 122 to 425 $m^2\ ha^{-1}$. Both diversity and density were measured as an average over the past ten years. We did this with and without the stumps of trees that were removed with approximately the last five years and took an average value so that the thinned trees contribute to the measure but to a lesser degree than trees present during the whole period.

Tree coring data

Every target tree was cored twice, at right angles at 1 - 1.2 m height on the stem. The cores were kept dry in newspaper and glued on wooden mounts. They were then sanded with progressively finer sandpaper with a bench belt sander, and measured at the Institute for Forest, Snow and Landscape (WSL) in Birmensdorf, Switzerland. Ring width was measured to the nearest 0.01 mm by scanning at high resolution with the software WinDENDRO (Regent Instruments Inc 2009). All cores were then cross-dated by species to assign the correct calendar year to each annual ring. Cross dating was checked using the program COFECHA (Holmes 1983) and any possible errors were identified and corrected. Nineteen of the 576 target trees were omitted from the analysis because they could not be confidently cross-dated. The pith-offset (i.e. number of missing rings and the distance to the pith) was estimated with a graphical method using concentric circles on a transparent sheet when pith was not reached (Villalba & Veblen 1997). With these methods we were able to attribute a year to every annual ring, and thus calculate ages and total diameters (DBH: Diameter at Breast Height). We then extrapolated diameters to BA (Basal Area) by using the following equation:

$$BA = \pi * \left(\frac{DBH}{2}\right)^2.$$

To obtain BAI (Basal Area Increment), we subtracted diameters in subsequent years, so that BAI in year t is equal to: $BAI_t = BA_t - BA_{t-1}$. At the time of sampling, target trees ranged from 29 to 155 years old and 143 to 668 mm in DBH. For every individual, growth curves were obtained as the cumulative sum of ring width over years, averaging measurements from both cores (Fig. 2).

Statistical analysis

Although we have long time series of growth with many trees older than a hundred years, tree diversity and density were measured only once in 2011 and so we focused on the most recent period of growth. Growth, measured in relative terms, also tends to slow with age raising the complexity of curvilinear or non-linear patterns over the whole time series. We thus considered only the last 10 years after 2001 where growth appeared most linear, and chose individual basal area increment (BAI) as our measure of growth. We log-transformed BAIs as they showed a skewed distribution, averaged them over 10 years per individual, and then analysed these in relation to the effects of species identity (a factor with four levels for the study species) and species diversity (the continuous variable of $e^{H'}$ values) in a linear mixed-effect model that also controlled for mean age (i.e. average tree's age during the last 10 years) and site density where necessary (Barrufol *et al.* 2013). Our design includes all the different species compositions of the four study species. Unfortunately, we were unable to simultaneously include effects of species diversity and species composition. These terms are not all orthogonal but are unavoidably (biologically) confounded and the model would not be identifiable (i.e. some parameters cannot be estimated and additional constrains are needed to carry out the estimation process). Instead, we graphically inspected the effects of species composition in a separate post-hoc analysis. In the main analysis, site was included as a random factor (with 45 levels) to account for variation in growth due to abiotic features. The Site effect was strongly affected by species identity, and we therefore allowed the model to have a different random intercept for each combination site species ID. Models were fitted in R 3.2.0 (R Development Core Team 2011) using the lmer function in the lme4 package (version 1.1-8) following a model-building approach (Pinheiro & Bates 2009). Finally we inspected the residuals of the model to make sure that there was no spatial correlation using the variogramm from the geoR package. Reproducible research documents generated using the knitr package that include integrated R input and output (including figures) are provided as supplementary material.

Results

Individual tree growth was significantly affected by both target tree species identity (Fig. 3) and the diversity of the surrounding neighbours (Fig. 4) without any detectible statistical interaction between the two (supplement). Individual growth rates varied between species with *Fagus* having the fastest growth rate, followed by *Picea,* *Quercus* and *Larix* (Fig 3). Radial growth rate increased with species diversity (Fig 4). Increasing species diversity from one to four species enhanced individual tree growth by 18 to 28%.

Growth rates in the subset of recent years included in our analyses appeared to be approximately linear over time. However, growth rates generally decline with age so based on this *a priori* expectation we added a covariate to estimate any effect. Growth rate did decrease with age but the covariate was not significant and its effect was weak (supplement).

We could not include species composition in the model because diversity and composition are intimately connected - the diversity term is a subset of the composition term. Since diversity has a clear effect, composition has one too, as can be seen from our post-hoc graphical investigation (supplement).

Discussion

Modern plantation forestry has traditionally focused on growing species in monoculture. However, in recent years there have been calls to consider increasing tree diversity in forestry (Verheyen et al. 2015). This is partly because growing trees in monoculture can make them more vulnerable to some threats (particularly specialist pests and diseases that thrive in high densities of their host species but also potentially fire and high winds) and partly as a way to increase levels of diversity in the landscape. However, a greater diversity of trees can pose practical problems during harvesting and processing and could also come at a cost in reduced productivity due to slower growth rates. Our analysis of the growth rates of four common timber species showed no cost in productivity of increasing forest stand diversity, instead showing modest increases of the growth rates. Increasing species diversity from one to four species enhanced the individual growth rate of our four species by 18 to 28% on average. The increases in growth rates were statistically indistinguishable between species despite the clear differences in growth rates among them (that is there was no interaction between the identity of the focal tree and the diversity of its neighbourhood). These effects of species identity and species diversity on growth rates were robust to differences in observed levels of tree (basal area) density and individual tree age. We found no effect of density (presumably due to the limited range of densities in our sample of stands) and while there were statistically significant negative effects of age they were small. Radial growth naturally decreases with size, because a constant diameter increment corresponds to an increasing biomass increment as trees become larger (Pallardy 2010; Speer 2012; Bowman *et al.* 2013).

The effects of species identity were largely as expected. Beech was the fastest grower, followed by pine, oak and larch. Beech is the most abundant broad-leaved species in Europe where it grows in a wide range of abiotic conditions and is often found to be the matrix species (i.e. the species always present but with variable relative abundance, Dittmar, Zech & Elling 2003). Therefore it is not surprising to see that beech grew the fastest at the studied location. The native range of *Picea abies* does not include the study site but it has been widely planted for decades because it is also usually a fast-growing species that quickly reaches harvestable dimensions. *Larch* and oak were both slower and had similar average growth rates.

In our study, the positive effect of diversity on growth was independent of density effects. In contrast, several studies found that the positive effect of tree diversity on forest productivity was mediated through increased tree density (Paquette & Messier 2011; Barrufol *et al.* 2013; Vilà *et al.* 2013). These studies however, consider only stand-level productivity, so that diversity increases productivity via an increased number of trees, and not via enhanced individual growth. Here we show that the growth of individual trees benefits directly from higher species diversity, as was also found by Potvin & Gotelli (2008), in a young tree plantation in Panama. Our results are also supported by Jucker *et al.* (2014) who also used tree rings to measure past growth in Spanish forests. They found that mixed stands of Iberian pine and oak were more productive than monocultures due to complementarity for light. The Iberian pine showed increased growth when planted in mixture with oak due to reduced intraspecific competition while the growth of the oak remained similar whether planted in mixture with the pine or in monoculture (except in drought years when the oak becomes water stressed and the beneficial effect of mixture disappears). The effects of diversity on forest biomass can therefore come about through a variety of proximate effects (via increased density or individual tree size) and biological mechanisms.

The first generation of research on the effects of biodiversity on ecosystem functioning used grasslands and other systems that are relatively easily manipulated and quick to respond. A global network of tree diversity experiments has been established but long-term results are limited by the decadal time scale of forestry management and harvest cycles. By using dendrochronology to estimate past growth and spatial mapping technology to characterise tree neighbourhoods we were able to study the relationship between tree diversity and forest ecosystem functioning (Chamagne *et al.* in press; Chamagne 2014). While the Brno Training Forest provides an invaluable research platform and has a well-documented history of management (Truhlář 1997) research conducted there lies somewhere between observational studies and manipulative experiments such that uncontrolled variables could confound results. The effects of species identity and species diversity on tree growth in our study were robust to variation in tree density and tree age and, perhaps surprisingly given the semi-natural setting, we found no residual spatial effects in our analysis to confound our results.

CONCLUSIONS AND IMPLICATIONS FOR FOREST MANAGEMENT

Our study of long-established central European forest stands revealed a modest but consistent positive effect of forest diversity on the growth of target individuals of the four study species. Our analyses estimate that stands with 4 species have growth rates increased by approximately 18 – 28 percent relative to monocultures. However, wood quality (not just quantity) can also be an issue and there are often logistical constraints to increasing tree diversity in forestry such as saw mill machinery only being able to handle certain species, types or sizes of trees (Spiecker 2003). Further research that combines these socio-economic aspects together with the ecological issues addressed here will be needed to assess the full costs and benefits of increased forest diversity. Nevertheless, the results of our research suggest that it may well be possible to increase forest diversity with little or no costs to production and even with the potential for modest increases in tree growth rates.

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Data accessibility

[Files of the data can be published as supplements to the article]

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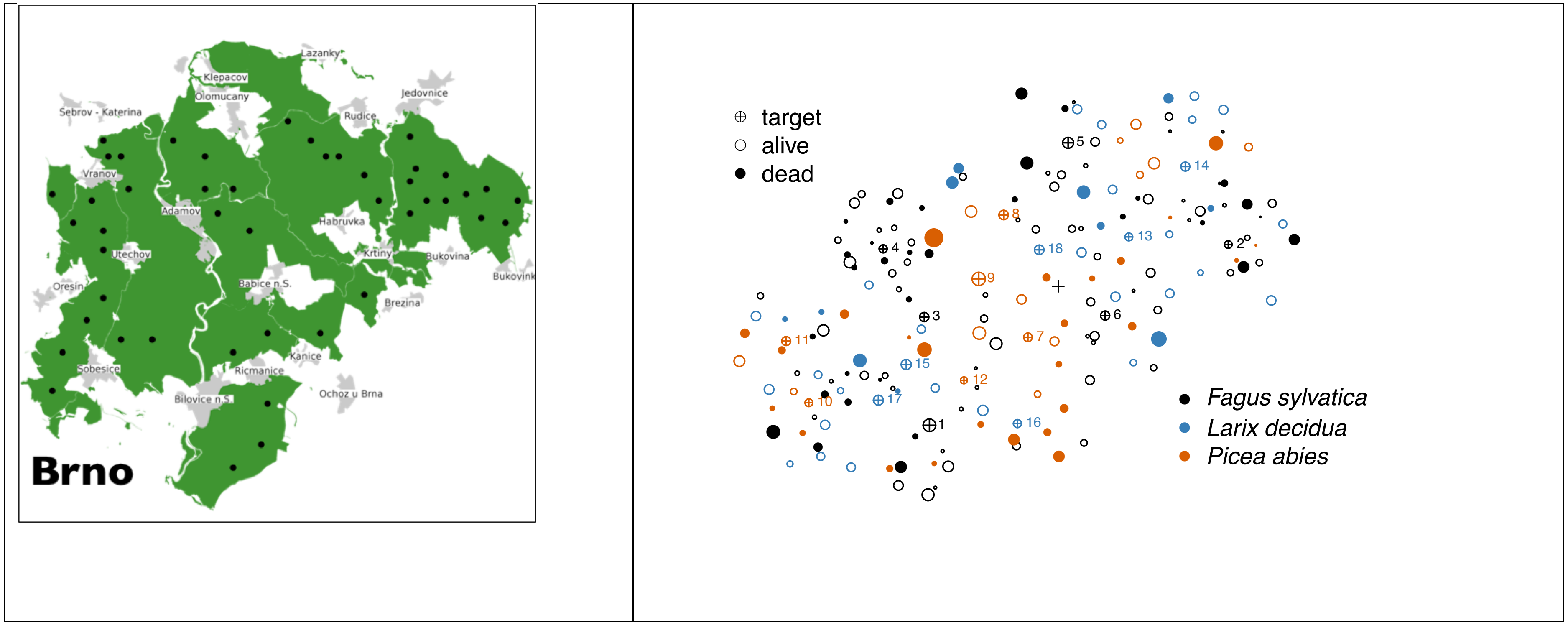

Fig. 1. (A) The Mendel University of Brno Training Forest (green) showing the sampled stands (black dots). (B) An example spatial map of one of the sampled stands showing 18 target trees (dots with a cross in it and a number besides) and their live and dead (stumps) neighbours.

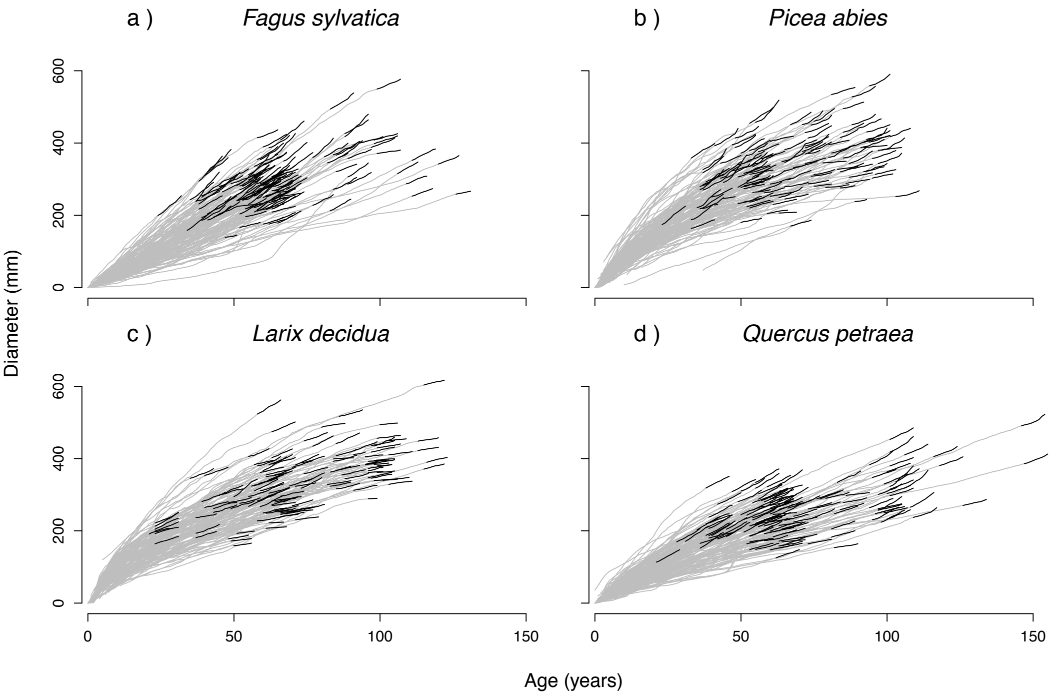

Fig 2. Individual growth trajectories for each of the four study species with the last 10 years of growth shown in black. Diameter increment was derived from cumulated tree ring width.

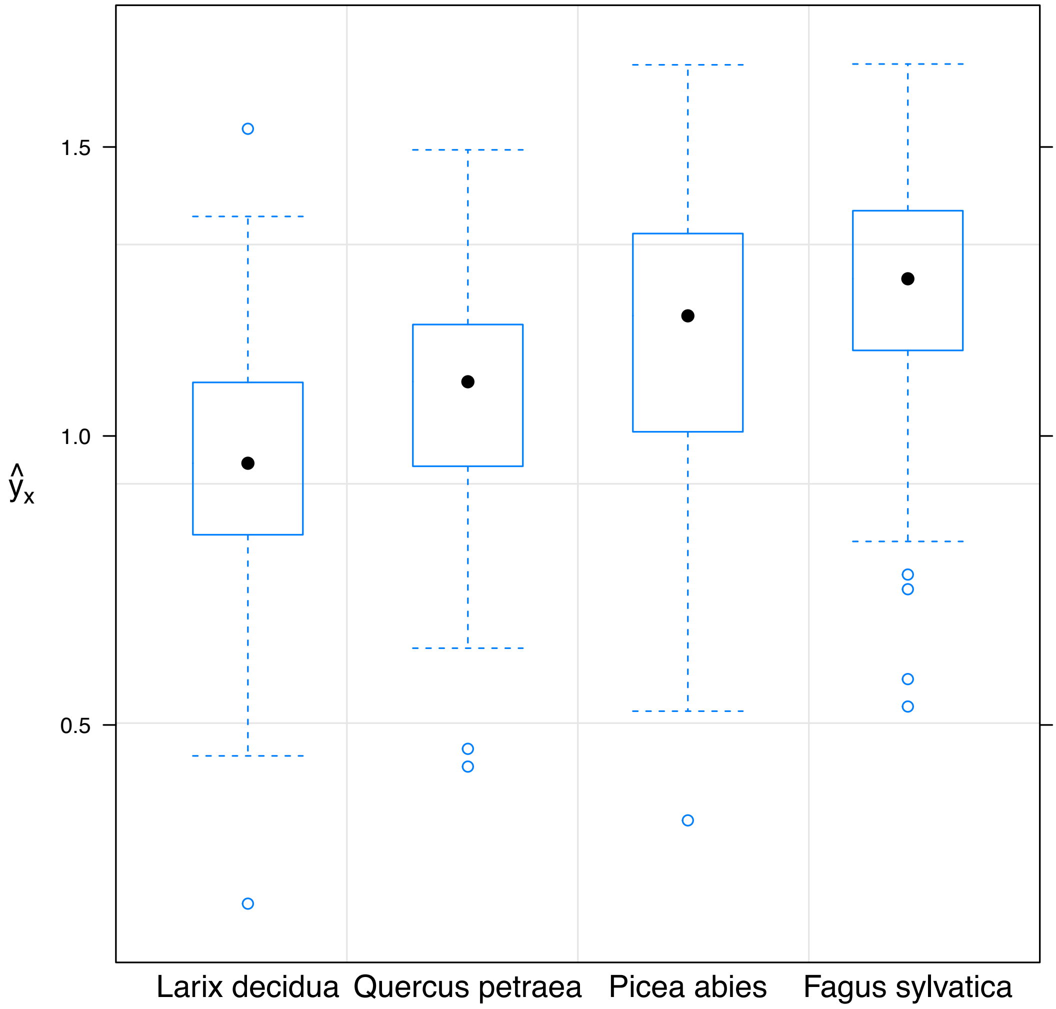

Fig 3. Effects of the species identity of the four study species on growth rate. The box plot shows the partial estimates of annual growth rates (i.e. keeping other main effects constant) derived from a linear mixed effect model.

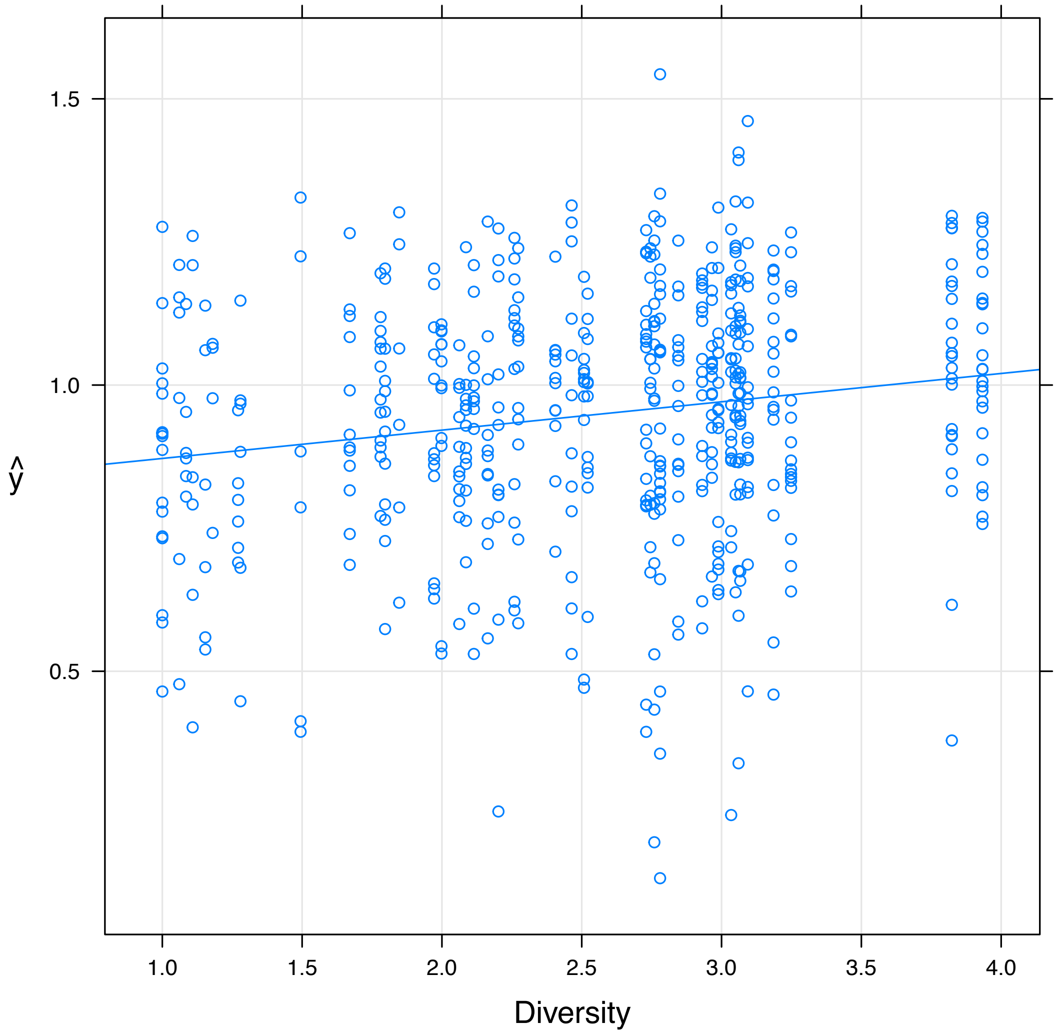

Fig. 4. Effects of species diversity on growth rate. The line shows the partial estimate (i.e. keeping other main effects constant) of the effects on diversity annual growth rate derived from a linear mixed effect model for individual trees in neighbourhoods of varying effective species richness.