

1 *Special profile:* Forest biodiversity and ecosystem services studies

2

3 *Running head:* Forest diversity promotes tree growth

4 Forest diversity promotes individual tree growth in central European forest stands

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30 Statement of authorship: The authors declare no conflict of interest. JC, AH, RM,

31 CETP, MS and LT conceived and designed the research; JC, AH, RM, CP, MS and

32 DV conducted the research; JC, MT, DF, AH, CDP, CETP, and LAT designed and

33 conducted the analyses and interpretation; JC, AH, and MT led the manuscript writing

34 with substantial contributions from DF, CDP, CETP and LAT and input from all

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36

37 *Total length: 6384 words*

38 *Length Main text: 3409 words*

39 *Abstract length: 136 words*

40 *Number of references: 53*

41 *Tables and Figures: 4*

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

45

46 **Summary**

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

51 2) We used dendrochronology to compare tree radial growth rates of four study
52 species in replicated, spatially mapped stands that differed in tree composition and
53 diversity within a central European managed forest.

54 3) Growth rates differed among species but were largely unaffected by the density of
55 neighbouring trees.

56 4) After controlling for effects of tree density and size, increasing stand diversity
57 enhanced individual growth rates. These increases were statistically indistinguishable
58 among species.

59 5) *Policy implications:* Our results show that levels of tree diversity can be increased
60 without negatively impacting forest productivity, but with the potential for modest
61 increases in tree growth rates.

62

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

65 **Introduction**

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

76

77 Low diversity forestry stands are one of the systems where there have been calls to
78 increase diversity and where we need to know the costs and benefits of doing so.
79 Forest ecosystems support humanity with services that are essential for its survival
80 and well-being (Gamfeldt *et al.* 2013), among which wood production is of special
81 importance. Trees not only provide timber for energy, construction or paper, they also
82 directly mitigate the effects of global warming by transforming atmospheric CO₂ into
83 biomass ('Millennium Ecosystem Assessment' 2005; Naeem *et al.* 2009). If we are to
84 sustain the services that forests provide to humankind it is crucial to understand how
85 tree diversity affects the functioning of these ecosystems.

86

87 Much of the research on the relationship between biodiversity and ecosystem
88 functioning has been conducted in grasslands and other systems that are relatively
89 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 depend 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 more affected by species evenness than by richness (Zhang, Chen & Reich 2012). Tree diversity can 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: observational studies and planted experiments similar to those conducted in grasslands. Both have 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).

Observational studies, on the other hand, provide data on older forests of greater societal and scientific interest (Vilà *et al.* 2003; Paquette & Messier 2011).

Established plots often cover a dilution gradient (Nadrowski, Wirth & Scherer-Lorenzen 2010), however, in which one matrix species is always present (often *Fagus sylvatica* in Europe) and is the only species present in monoculture. Additionally,

environmental heterogeneity is often not accounted for, potentially biasing the inferred effect of diversity on productivity (Healy, Gotelli & Potvin 2008). Finally, growth is calculated on diameter increment measured every five to ten years only, which is not detailed enough to consider effects of tree size on radial growth in these 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 doing this is not straightforward since trees are such large and long-lived organisms. Here, we use tree rings to reconstruct the cumulative growth and estimate growth rates of individual trees in a setting that combines features of both observational and experimental studies (Methods).

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), as was shown by the FunDivEUROPE permanent forest plot network (Baeten *et al.* 2013; Jucker *et al.* 2014a). We took advantage of established stands in the Training Forest Enterprise (TFE), a research and training forest of the Mendel University of Brno, in the Czech Republic, to examine the effects of varying tree diversity on forest ecosystem functioning. The literature on biodiversity and ecosystem functioning has tended to focus on testing whether levels of ecosystem processes including tree growth are significantly greater

in mixtures than in monocultures. However, increasing diversity in forests could conceivably also decrease productivity, especially in temperate to boreal forests, where tree species occupy similar niches and functional characteristics (Pretzsch 2009). 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 net biomass production (tree growth rates).

Materials and Methods

Study design

The Training Forest Enterprise is located north of the city 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). It is a managed forest, owned by the Mendel University in Brno, in which stands have been planted and managed by the university for a hundred years. 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 TFE) while comprising an ecologically varied set of species in terms of functional and life-history traits. 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. Thus, every level of species richness (except the highest) was replicated with different species combinations and each of the 15 compositions was replicated three times. Sites were selected to be as homogeneous as possible in terms of their soil type and slope (Scherer-Lorenzen *et al.* 2005), so that all sites had Cambisol as a soil type, and the average slope was 7% (standard deviation: 4.9%). Furthermore, they were chosen to maximize evenness, and minimize the abundance of non-target species. At each of the 45 sites, six trees of each focal species were cored, such that six trees were measured in monocultures, and 24 in the full mixtures. In order to have a reasonable record of growth, only trees (≥ 14 cm) were cored. With this constraint, trees to be cored were chosen such that they were separated by at least six meters, and that their sizes spanned the range found at the site. All cored trees of the four study species, together with 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/>) so that all mapped trees defined each site. The stumps of recently felled trees (those estimated to have been cut in the last five years) were also mapped. Each mapped tree was identified to species and its Diameter at Breast Height (DBH) at 1.3 m was recorded. The 45 sites ranged from 0.07 to 0.6 ha in size and covered an area of 11 ha in total. A total of 8,919 trees were measured of which 576 were target trees of the four study species. All mapping and coring data were collected in 2011.

Data collection

Mapping Data

At each site, maps were used to calculate tree diversity and density for each of the target trees neighbourhoods, that is, based on all trees in a 10-m radius around each target. 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; Jost 2006; 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. When all species are equally abundant, $e^{H'}$ approaches SR. In contrast, when species composition is very uneven and approaches a monoculture $e^{H'}$ approaches one (Supporting Information). Some high values of diversity are due to non-target tree species, which represented 2.6% of stem density and 2% of the total basal area. Tree density was defined as the total basal area of canopy trees standardized by area, and ranged from 122 to 425 m² ha⁻¹ at the site level, and from 40 to 398 m² ha⁻¹ at the neighbourhood level (mean: 162 m² ha⁻¹, sd: 52 m² ha⁻¹). Because all the target trees were in the main canopy we used the basal area of all trees as a measure of density, which represents symmetrical competition for nutrients and affects trees of all sizes (Coomes & Allen 2007), whereas asymmetrical competition for light (which can be modelled as the basal area of taller trees) mostly affects the growth of small trees. Both diversity and density were measured as an average over the past ten years. We assessed both diversity and density in 2011, by working on living trees only, to obtain measures that were valid for the last five years. Then, adding the stumps that were

felled in the previous five years, we calculated the density and diversity present in 2006. Averaging both values gave us precise estimates of diversity and density for the last ten years.

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 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 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 calculated basal area (BA) as $\pi(\text{DBH}/2)^2$. To obtain basal area increment (BAI), we subtracted basal area in subsequent years. At the time of sampling, target trees ranged in age from 29 to 155 years, and from 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).

239 *Statistical analysis*

240 Although we have long time series of growth with many trees older than a hundred
241 years, tree diversity and density were measured based on the maps created in 2011.
242 Therefore, we focused on the most recent period of where growth appeared most
243 linear. We log-transformed BAIs as they showed a skewed distribution and averaged
244 them over 10 years per individual. We then modeled tree growth over the studied
245 interval – average log(BAI) - as a function of species identity (a factor with four
246 levels for the study species) and species diversity (the continuous variable of e^H
247 values) in a linear mixed-effect model that also controlled for mean tree size (i.e.
248 average log of the basal area over the last 10 years) and site tree density (Barrufol *et*
249 *al.* 2013). The model included the 15 different species compositions of the four study
250 species as a random effect. In addition to that, site was included as a random factor
251 (with 45 levels) to account for variation in growth due to abiotic features. The site
252 effect was strongly affected by species identity, and we therefore allowed the model
253 to have a different random intercept for each combination of site and species identity
254 (species ID). Models were fitted in R 3.2.2 (R Development Core Team 2011) using
255 the lmer function in the lme4 package (version 1.1-10) following a model-building
256 approach (Pinheiro & Bates 2009). Statistical inference was carried out with
257 likelihood ratio tests. In one case the p-value obtained was close to the significance
258 level. For this variable (i.e. diversity) and for the retained variance components (i.e.
259 site and site:species) confidence intervals were estimated through non-parametric
260 bootstrap. The R formula of the starting model initially fitted to the data (see
261 supporting information) was:
262 $m.logBAI \sim SpeciesID + Diversity.tree + Density.tree + log.size$
263 $+ SpeciesID:Diversity.tree + SpeciesID:Density.tree + SpeciesID:log.size$

$$+ (1|\text{Composition}) + (1 | \text{SiteID}) + (1 | \text{SpeciesID:SiteID})$$

Where m.logBAI is the average log basal area increase over the studied ten years, SpeciesID is the individual species identity (a factor with four level for the study species), Diversity.tree is the neighbouring diversity, Density.tree is the neighboring density (continuous variable of total BA of neighbors), log.size is the mean tree size, Composition is the chosen site composition (a factor with 15 levels), and SiteID is the site identity (a factor with 45 levels). Model assumptions were checked with classical graphical diagnostics. Finally, spatial autocorrelation was inspected graphically and using variograms from the geoR package (version 1.7-5.1). Spatial correlation was estimated to be negligible (see supporting information). R-code and data are provided for full reproducibility of the analysis. The entire analysis is documented in a supplementary dynamic document (generated using the knitr package) that includes integrated R input and output (including figures).

Results

In relation to the variables of main interest, individual tree growth was affected by both target tree species identity (Fig. 3) and the diversity of the surrounding neighbors (Fig. 4) without any detectible statistical interaction between the two (Likelihood Ratio Test: 0.72, DF = 3, P = 0.87; Supporting Information). Individual growth rates varied among species with *Fagus* having the fastest growth rate, followed by *Quercus*, *Picea* and *Larix* (Fig 3). Radial growth rate (log-transformed) increased linearly with species diversity (Fig 4). The analysis controlled for the effects of covariates expected a priori to have potential effects. Of these, tree density had a negligible effect on growth rate, going from slightly negative for *Quercus* to slightly positive for *Fagus*, *Larix*, and *Picea* (Supporting Information). However, radial

growth (log-transformed) increased strongly with tree size, with differing magnitude depending on species identity (Supporting Information).

Discussion

Modern plantation forestry has traditionally focused on growing trees in monoculture (Evans 2009; Richards *et al.* 2010). In recent years, however, there have been calls to consider increasing tree diversity in forestry (Knoke *et al.* 2008; Felton *et al.* 2010; Verheyen *et al.* 2015). These calls have been spurred in part because trees grown in monocultures can be more vulnerable to threats, including fire and windstorms, but especially host-specific and density-dependent pests and pathogens. Increasing plantation diversity is also seen as a way to increase landscape-level species diversity. However, many forest owners are motivated primarily by economic considerations rather than by ecological reasons and they often favour monocultures over mixed forests, assuming the former to be more profitable (Knoke *et al.* 2008). There is a belief among foresters that a greater diversity of trees can not only increase costs of silviculture, harvesting and processing, but 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 diversity, instead showing modest increases of the growth rates. The increases in growth rates were statistically indistinguishable among species, despite the clear differences in growth rates among them. In other words, there was no interaction between the identity of the focal tree and the diversity of its neighbourhood on its growth. 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 size. We found no consistent effect of density on tree growth, presumably due to the limited

range of densities in our sample of stands, but a strong and positive effect of size on growth rates. Bowman et al. (2013) found that basal area absolute growth rates increase until trees reach about 50 years, and then it starts reducing slowly.

The effects of species identity were largely as expected. *Fagus* was the fastest grower, followed by *Quercus*, *Picea* and *Larix*. *Fagus* 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). Among common European broadleaved species, beech is the most successful in both aboveground (due to its high shade-tolerance) and belowground competition (Rewald & Leuschner 2009); therefore it is not surprising to see that beech grew the fastest at the studied location. Our study site is located at rather low altitudes with warmer climate, so a faster growth of sessile oak than Norway spruce could be expected. Oak is a drought-resistant species with well-developed deep rooting system, while spruce is susceptible to heat and drought, due to its shallow root system (Kutschera & Lichtenegger 2002). The native altitudinal range of *Picea abies* lies higher than most of the site but it has been widely planted for decades because of high demand for its timber. The lower growth rate of larch may be somewhat surprising, considering its well-developed heart root system and its ability to grow fast under many conditions. However, larch is more of a pioneer than late-successional species, therefore its mature growth rate may slow earlier than in other species.

In our study, the effect of diversity on growth was positive, even when controlling for density. 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, considered only stand-level productivity, meaning that diversity increased productivity via an increased number of trees, and not via enhanced individual growth. Here, in contrast, the growth of individual trees responds directly from higher species diversity. A similar pattern was observed in a young tree plantation in Panama (Potvin & Gotelli 2008). Our results are supported by (Jucker *et al.* 2014b) who also used tree rings to measure tree growth in European forests. They found that mixed stands were more productive than monocultures due to complementarity for light. *Pinus* showed increased growth when planted in mixture with *Quercus* due to reduced intraspecific competition, while the growth of the *Quercus* remained similar whether planted in mixture with the pine or in monoculture (except in drought years when *Quercus* became water stressed and the beneficial effect of mixture disappeared). In Germany, inventory data showed mixtures of *Fagus* and *Picea* to be more productive than their respective monocultures (Pretzsch & Schütze 2008). This effect was explained by facilitation for *Picea*, and by a reduction in competition for *Fagus*. The effects of diversity on forest biomass can therefore occur through a variety of proximate effects (via increased density or individual tree size) and biological mechanisms (Pretzsch & Schütze 2015). Intraspecific competition is usually stronger than interspecific competition, leading to a more efficient use of resources in mixtures. For example, it was shown that canopy packing is more efficient in mixtures, because crowns are significantly larger (Morin *et al.* 2011; Jucker, Bouriaud & Coomes 2015). Our study showed that radial growth of individual trees of all species was enhanced by increased stand diversity, even when combining ecologically very different species such as shallow (*Picea*), medium (*Fagus*) and deep rooting (*Quercus* and *Larix*), or light

demanding (*Quercus* and *Larix*) and shade tolerant (*Fagus* and *Picea*) species. Indeed, niche differentiation and better use of resources due to a high variability of ecology and life history traits of four study species is likely the reason for observed enhanced growth in mixtures.

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. TreeDivNet, 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 (Baeten *et al.* 2013; Verheyen *et al.* 2015). 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 Training Forest Enterprise 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. This particular setup allowed us to infer effects of neighbourhood diversity on mature tree growth, without having to plant different levels of tree diversity. The effects of species identity and species diversity on tree growth in our study were robust to variation in tree density and tree size.

CONCLUSIONS AND IMPLICATIONS FOR FOREST MANAGEMENT

Our study of long-established central European forest stands revealed a modest but consistently positive effect of forest diversity on the growth of adult individuals of the

dominant tree species of Central Europe. These results suggest that, in addition to the biodiversity and risk mitigation benefits associated with shifting practices away from monoculture management, increased carbon sequestration and yields in mature forests are likely to be realized. 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) and there may be also difficulties in finding markets for timber of less demanded species. 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, our results suggest that it is possible to increase forest diversity with little or no costs to production and even with the potential for modest increases in tree growth rates.

Acknowledgements

We thank Philippe Saner and Libor Jankovský for their help in establishing this collaboration and Peter McCullagh for discussion of the statistical analysis. This work was supported by a UZH Forschungsstiftung award, by the EU Seventh Framework Program grant 265171 (FunDivEUROPE) and by SNSF grant 121967 (to AH).

Data accessibility

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

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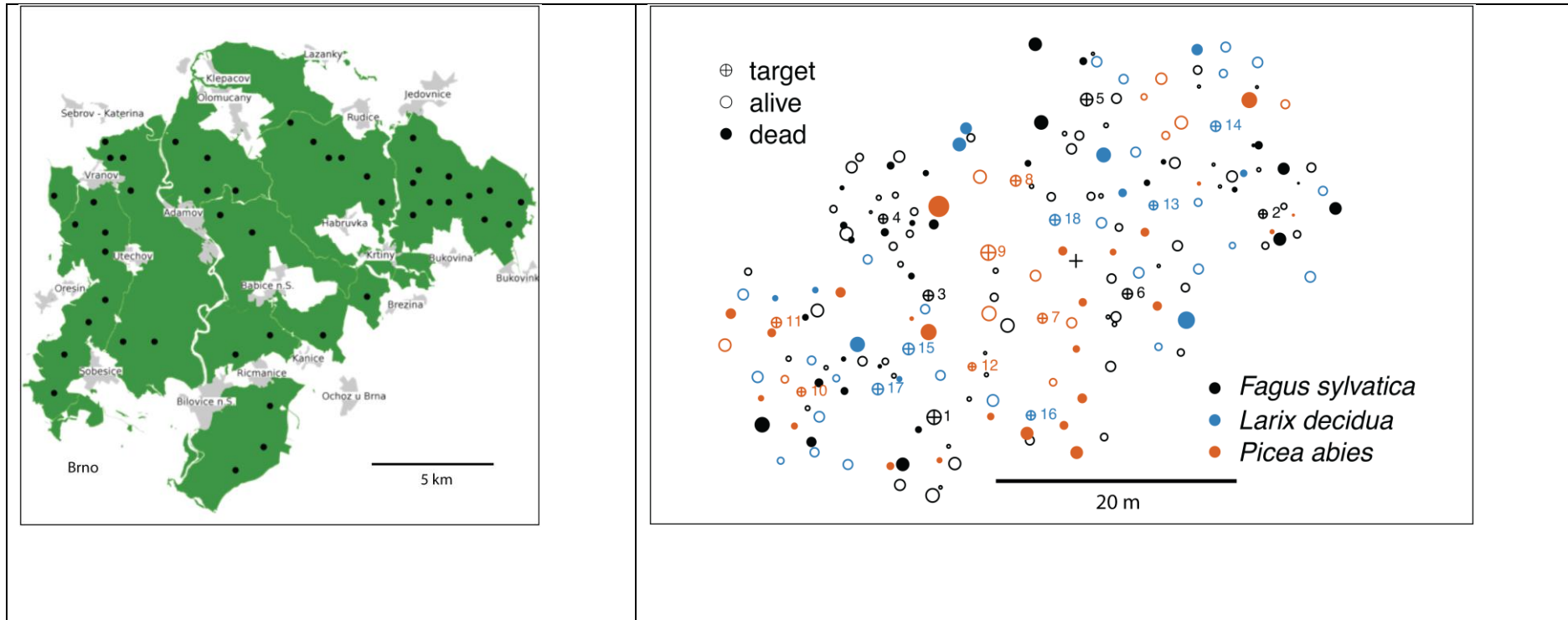
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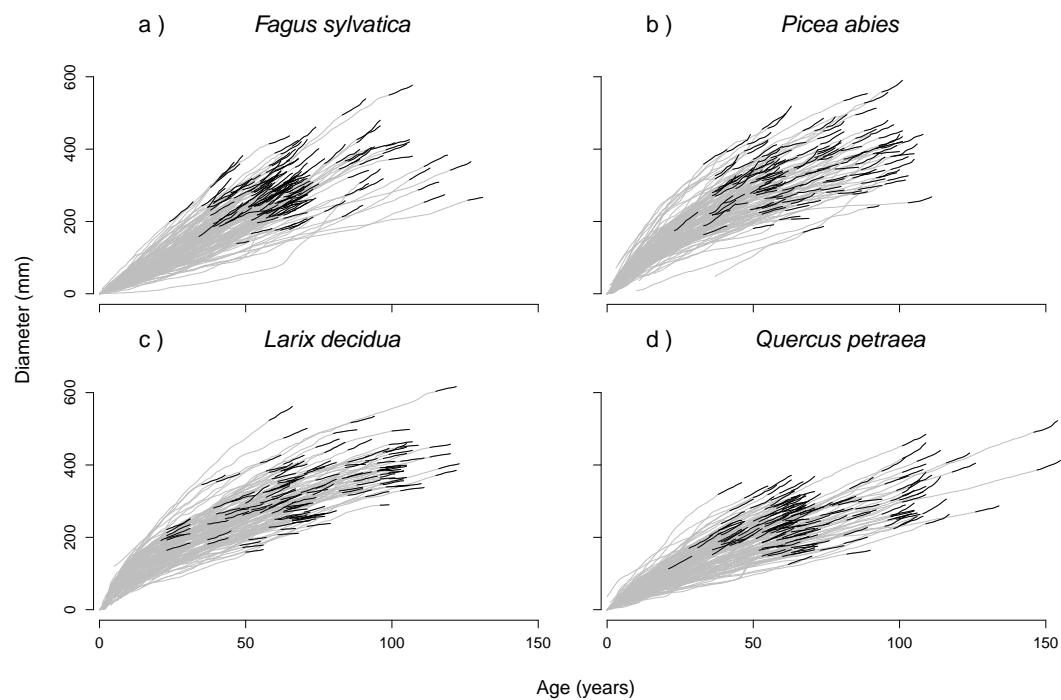
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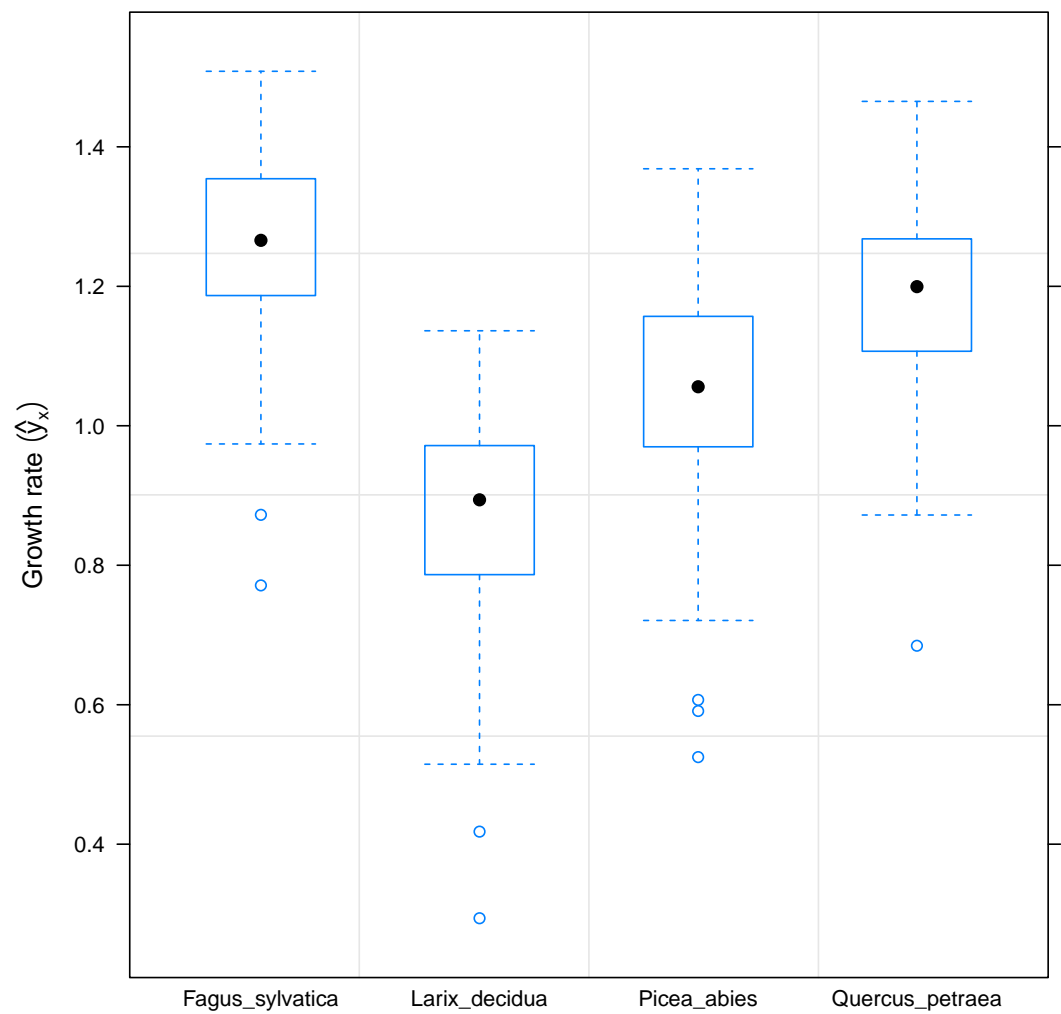


585 **Fig. 1.** (A) The Mendel University of Brno Training Forest (green) showing the sampled stands (black dots). (B) An example spatial map of a
 586 sampled three-species stand, showing 18 cored trees (dots with a cross in it and a number besides) and their live and dead (stumps) neighbours.



588 **Fig 2.** Individual growth trajectories (grey) with the last 10 years of growth, which
 589 were analysed in this study highlighted (black). Diameter increment was derived from
 590 cumulated tree ring width.

591



592

593 **Fig 3.** Partial residual plot showing effects of the identity of the four study species on
594 growth rate (average annual basal area increment (log-transformed)). The box plot
595 shows the estimates of annual growth rates (with other main effects held constant)
596 derived from the linear mixed-effect model.

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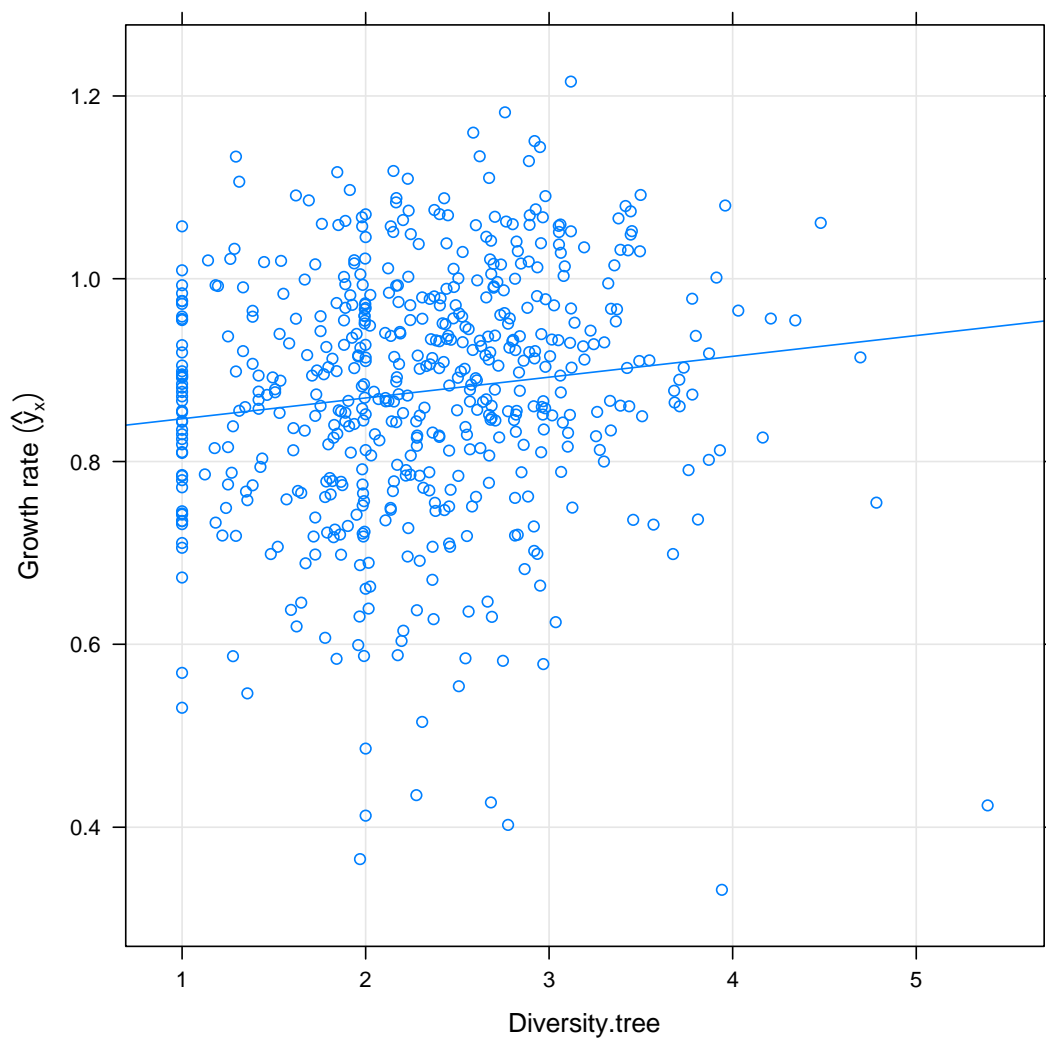


Fig. 4. Effects of neighbourhood species diversity (e^{H^*}) on growth rate (partial residual plot). The line is a regression estimating effect of diversity on annual growth rate, derived from a linear mixed-effect model for individual trees in neighbourhoods of varying effective species richness (with other main effects held constant at the mean value; see Supporting Information). For clarity, only the relationship for *Larix* is shown (the other species show parallel relationships).