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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, DF, AH, CDP, CETP, LAT and MT designed and
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36

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

45

46 **Summary**

- 47 1) Most of the experimental evidence on the relationship between biodiversity and
48 ecosystem functioning comes from grasslands and other fast growing systems, and
49 while 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 the Mendel University research and training forest.
- 54 3) Growth rates differed among species and declined with tree age as expected but
55 were largely unaffected by the range of observed basal area density.
- 56 4) Increases in stand diversity enhanced individual growth rates by between 18 and
57 28% and these increases were statistically indistinguishable between species. Despite
58 the potentially high levels of heterogeneity of the semi-natural stands of the Brno
59 research and training forest there were no residual spatial correlations to confound
60 these results.
- 61 5) *Policy implications:* Our results show that levels of tree diversity could be
62 increased without a cost to forest productivity and even with the potential for modest
63 increases in tree growth rates.
- 64

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

67 **Introduction**

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

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

89
90 Much of the research on the relationship between biodiversity and ecosystem
91 functioning has been conducted in grasslands and other systems that are relatively
92 easy to manipulate and quick to respond. Forest ecosystems have been less frequently
93 investigated, and although similar influences of biodiversity have been suggested, the
94 results are far from conclusive (Thompson *et al.* 2009; Nadrowski, Wirth & Scherer-
95 Lorenzen 2010; Cardinale *et al.* 2011). For example, the relationship between species
96 diversity and forest productivity can be dependent on site richness (Belote *et al.* 2011)
97 or forest type (Paquette & Messier 2011; Vilà *et al.* 2013) and enhanced productivity
98 has even been found to be driven more by species evenness than by richness (Zhang,
99 Chen & Reich 2012). Tree diversity has been shown to promote forest stand

100 productivity through an increase in tree density rather than through enhanced
101 individual tree growth (Vilà *et al.* 2013).
102
103 Evidence on the effects of tree diversity on forest functioning comes from two types
104 of investigations: planted experiments similar to the grasslands experiments, and
105 inventory data. Both have their strengths and weaknesses (Nadrowski, Wirth &
106 Scherer-Lorenzen 2010). Planted experiments can include a broad gradient of species
107 richness replicated with different species (Scherer-Lorenzen *et al.* 2007; Healy,
108 Gotelli & Potvin 2008; Hector *et al.* 2011), and trees are regularly measured, allowing
109 for precise estimations of their growth rates (Potvin & Dutilleul 2009). These
110 experiments however, are very young and thus do not yet address the functioning of
111 mature forests (Nadrowski, Wirth & Scherer-Lorenzen 2010).
112
113 Inventories on the other hand provide data on older forests that are more suitable for
114 exploring such questions (Vilà *et al.* 2003; Paquette & Messier 2011). But these
115 established plots often cover a dilution gradient (Nadrowski, Wirth & Scherer-
116 Lorenzen 2010), where one matrix species is always present (often *Fagus sylvatica* in
117 Europe) and the only one found in monocultures. Additionally, environmental
118 heterogeneity is often not accounted for potentially biasing the effects of diversity on
119 productivity (Healy, Gotelli & Potvin 2008). Finally growth is calculated on diameter
120 increment measured every five to ten years only, and the necessary data to consider
121 effects of tree age on radial growth are generally not available from large-scale
122 monitoring efforts. In contrast to grasses, trees can be individually examined, and
123 precisely measuring tree growth (ideally at least annually in seasonal systems) is a
124 critical step towards the understanding of what affects it. However it is not
125 straightforward since trees are such large and long-lived organisms. Here, we use tree
126 rings as a record of their past growth to reconstruct their cumulative growth in and
127 estimate growth rates
128
129 In temperate zones, species carry out most of the photosynthesis during the growing
130 season, and they record this cambial growth in annual rings (Speer 2012; Bowman *et*
131 *al.* 2013). Whereas height growth tends to be rapid at first and then slow dramatically,
132 radial growth is more consistent, and can even be considered linear over short periods
133 of time (Bowman *et al.* 2013). Using annual ring width as a proxy for annual growth

134 appears to be a good way to explore the effects of diversity on individual tree growth
135 (Nadrowski, Wirth & Scherer-Lorenzen 2010). We took advantage of established
136 stands in the research and training forest of the University of Brno in the Czech
137 Republic that contain different tree diversities to examine the effects on forest
138 ecosystem functioning. The academic literature on biodiversity and ecosystem
139 functioning has tended to focus on testing whether levels of ecosystem processes are
140 significantly higher in mixtures than in monocultures. However, increasing diversity
141 in forests could conceivably also decrease productivity. Nevertheless, where there is a
142 conservation motivation to increase levels of diversity, some decrease in productivity
143 may be an acceptable trade off. We therefore take a broader view in investigating the
144 general costs and benefits of increased forest diversity (Chamagne 2014; Chamagne et
145 al. in press) focusing here on productivity (tree growth rates).

146

147 **Materials and Methods**

148 *Experimental design*

149 The Mendel University Training Forest Enterprise (TFE) is located north of the cite of
150 Brno in the Czech Republic (49°3'N and 16°7'E), lying 310 to 560 m above sea level
151 (Fig 1) and covering 10,000 ha. The annual mean temperature is 7.5°C, the average
152 annual precipitation 610 mm, and soils are principally Cambisols (Truhlář 1997). The
153 forest has been managed by the University for the last century for commercial activity
154 and for forestry education and research. The pedology, geology and topography have
155 been mapped and forest type, age, density and volumetric species composition are
156 estimated in each of 4,000 stands every decade (www.mapserver-slp.mendelu.cz/).
157 Norway spruce (*Picea abies*), European larch (*Larix decidua*), Sessile oak (*Quercus*
158 *petraea*) and European beech (*Fagus sylvatica*) (henceforth referred to by their
159 generic names) were chosen as our study species since they are some of the most
160 economically important species in this region (representing 75% of timber volume in
161 the training forest) while comprising an ecologically varied set of species in terms of
162 their ecology and life history traits. Sites corresponding to the 15 possible
163 combinations of these four focal species were sampled and each of the 15
164 compositions was replicated three times. In this way, every level of species richness
165 (except the highest) was replicated with different species combinations and all
166 combinations were also replicated to manipulate species composition. Based on the
167 TFE records for the 4,000 stands, we chose a subset planted with all the possible

168 species richness and species combinations (composition) of our four study species.
169 Sites were selected to be as homogeneous as possible in terms of their bedrock, soil
170 type, aspect and slope (Scherer-Lorenzen *et al.* 2005). At each of the 45 sites, six trees
171 of each focal species were targeted, so that six trees were measured in monocultures,
172 and 24 in the full mixtures. In order to have a reasonable record of growth via the tree
173 rings, small trees (<14 cm) were not sampled. With this constraint, target trees were
174 chosen in such that they were separated by at least six meters, and that their sizes
175 spanned the range of sizes found at the site. Target trees of the four study species and
176 neighbouring individuals (>10 cm DBH) of all species within a 10 m radius were
177 mapped with the Field-Map technology (Hédli *et al.* 2009, <http://www.fieldmap.cz/>).
178 Each mapped tree was identified to species and its Diameter at Breast Height (DBH)
179 at 1.3 m was recorded. The stumps of recently thinned trees were also included in the
180 maps. The 45 sites ranged from 0.07 to 0.6 ha in size and covered an area of 11 ha in
181 all. A total of 8,919 trees were measured of which 576 were target trees of the four
182 study species.

183

184 ***Data collection***

185 *Mapping Data*

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

191

$$192 H' = -\sum_{i=1}^{SR} p_i \ln p_i,$$

193

194 Where, SR is the total species richness, and p_i is the relative abundance of species i .
195 Taking the exponent of H' provides an estimate of the number of equally abundant
196 species. The H' index increases with species richness and with equality in relative
197 abundances. When all species are equally abundant, H' approaches $\ln(SR)$, and the
198 effective number of species approaches SR. In contrast, when species composition is
199 very uneven and approaches a monoculture, H' approaches zero and the effective
200 number of species equals one. Sites were chosen to cover a gradient of species

201 richness going from one to four, and the measured values for e^H ranged from 1 to 3.93
202 (Table 1). Tree density was defined as the total basal area of canopy trees
203 standardized by area, and ranged from 122 to 425 $m^2 ha^{-1}$. Both diversity and density
204 were measured as an average over the past ten years. We did this with and without the
205 stumps of trees that were removed with approximately the last five years and took an
206 average value so that the thinned trees contribute to the measure but to a lesser degree
207 than trees present during the whole period.

208

209 *Tree coring data*

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

$$226 \quad BA = \pi * \left(\frac{DBH}{2}\right)^2.$$

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

232

233 *Statistical analysis*

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

262

263 **Results**

264 Individual tree growth was significantly affected by both target tree species identity
265 (Fig. 3) and the diversity of the surrounding neighbours (Fig. 4) without any detectible
266 statistical interaction between the two (supplement). Individual growth rates varied
267 between species with *Fagus* having the fastest growth rate, followed by *Picea*,

268 *Quercus* and *Larix* (Fig 3). Radial growth rate increased with species diversity (Fig 4).
269 Increasing species diversity from one to four species enhanced individual tree growth
270 by 18 to 28%.

271

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

277

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

282

283 **Discussion**

284 Modern plantation forestry has traditionally focused on growing species in
285 monoculture. However, in recent years there have been calls to consider increasing
286 tree diversity in forestry (Verheyen et al. 2015). This is partly because growing trees
287 in monoculture can make them more vulnerable to some threats (particularly specialist
288 pests and diseases that thrive in high densities of their host species but also potentially
289 fire and high winds) and partly as a way to increase levels of diversity in the
290 landscape. However, a greater diversity of trees can pose practical problems during
291 harvesting and processing and could also come at a cost in reduced productivity due
292 to slower growth rates. Our analysis of the growth rates of four common timber
293 species showed no cost in productivity of increasing forest stand diversity, instead
294 showing modest increases of the growth rates. Increasing species diversity from one
295 to four species enhanced the individual growth rate of our four species by 18 to 28%
296 on average. The increases in growth rates were statistically indistinguishable between
297 species despite the clear differences in growth rates among them (that is there was no
298 interaction between the identity of the focal tree and the diversity of its
299 neighbourhood). These effects of species identity and species diversity on growth
300 rates were robust to differences in observed levels of tree (basal area) density and
301 individual tree age. We found no effect of density (presumably due to the limited

302 range of densities in our sample of stands) and while there were statistically
303 significant negative effects of age they were small. Radial growth naturally decreases
304 with size, because a constant diameter increment corresponds to an increasing
305 biomass increment as trees become larger (Pallardy 2010; Speer 2012; Bowman *et al.*
306 2013).

307

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

317

318 In our study, the positive effect of diversity on growth was independent of density
319 effects. In contrast, several studies found that the positive effect of tree diversity on
320 forest productivity was mediated through increased tree density (Paquette & Messier
321 2011; Barrufol *et al.* 2013; Vilà *et al.* 2013). These studies however, consider only
322 stand-level productivity, so that diversity increases productivity via an increased
323 number of trees, and not via enhanced individual growth. Here we show that the
324 growth of individual trees benefits directly from higher species diversity, as was also
325 found by Potvin & Gotelli (2008), in a young tree plantation in Panama. Our results
326 are also supported by Jucker *et al.* (2014) who also used tree rings to measure past
327 growth in Spanish forests. They found that mixed stands of Iberian pine and oak were
328 more productive than monocultures due to complementarity for light. The Iberian pine
329 showed increased growth when planted in mixture with oak due to reduced
330 intraspecific competition while the growth of the oak remained similar whether
331 planted in mixture with the pine or in monoculture (except in drought years when the
332 oak becomes water stressed and the beneficial effect of mixture disappears). The
333 effects of diversity on forest biomass can therefore come about through a variety of
334 proximate effects (via increased density or individual tree size) and biological
335 mechanisms.

336

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

352

353 CONCLUSIONS AND IMPLICATIONS FOR FOREST MANAGEMENT

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

366

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372

373 **Data accessibility**

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

375

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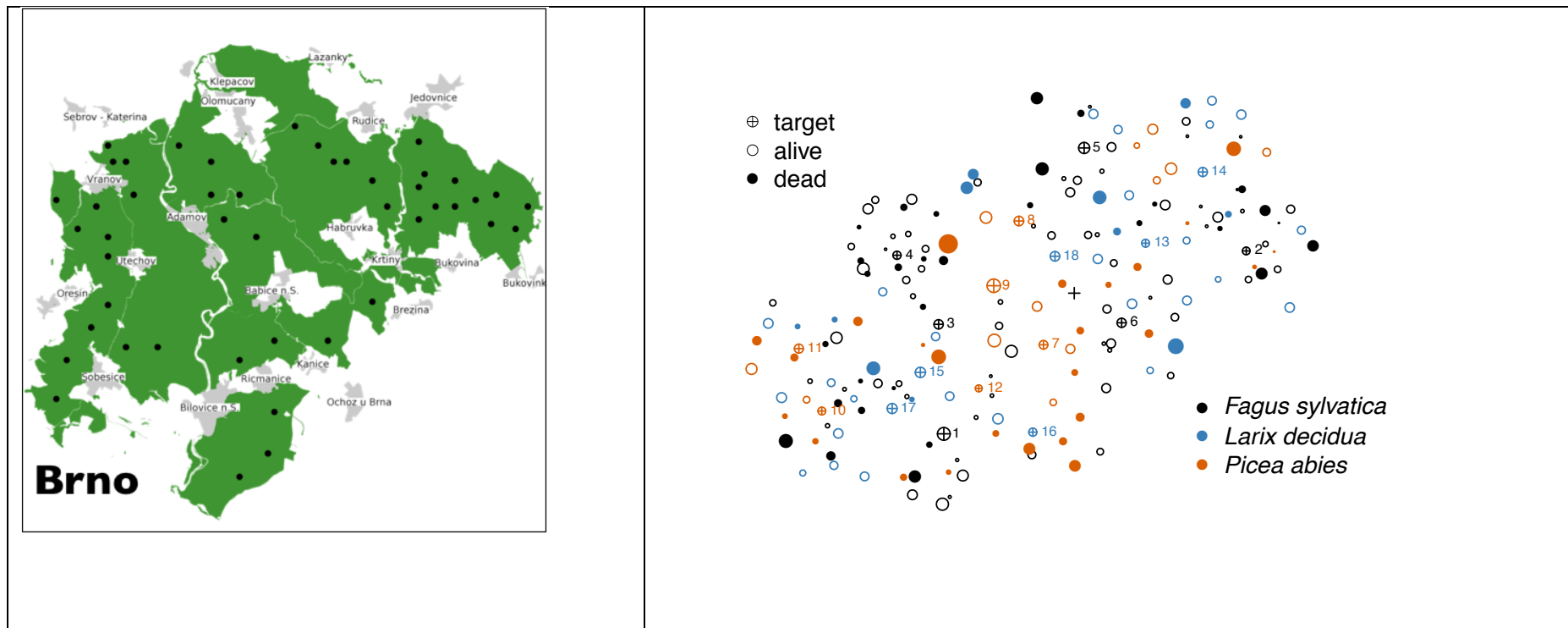
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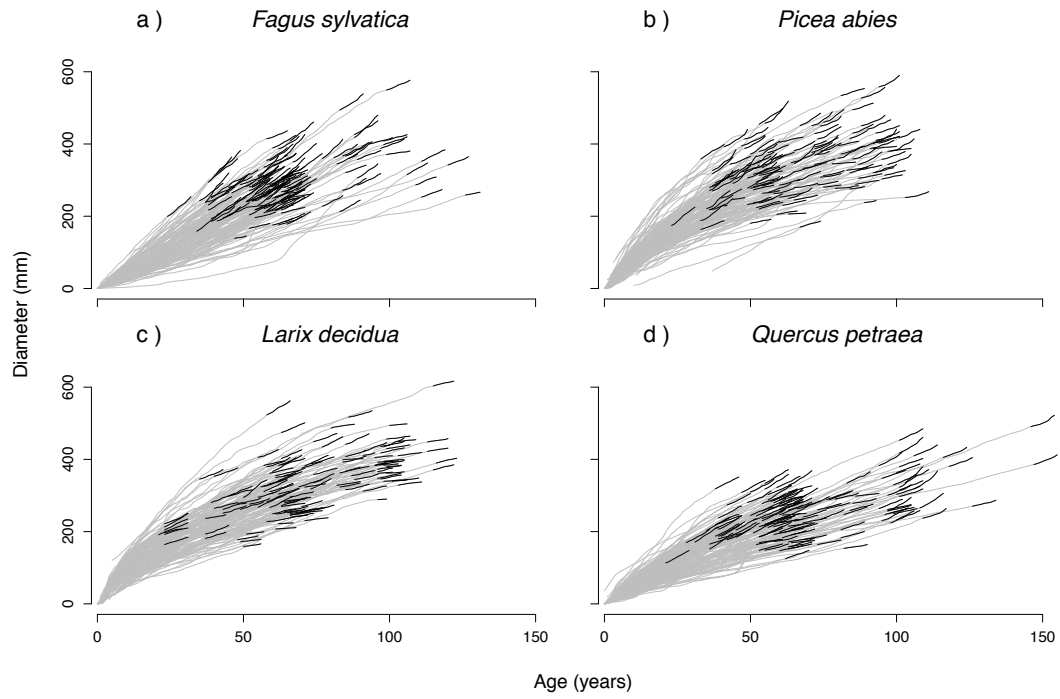
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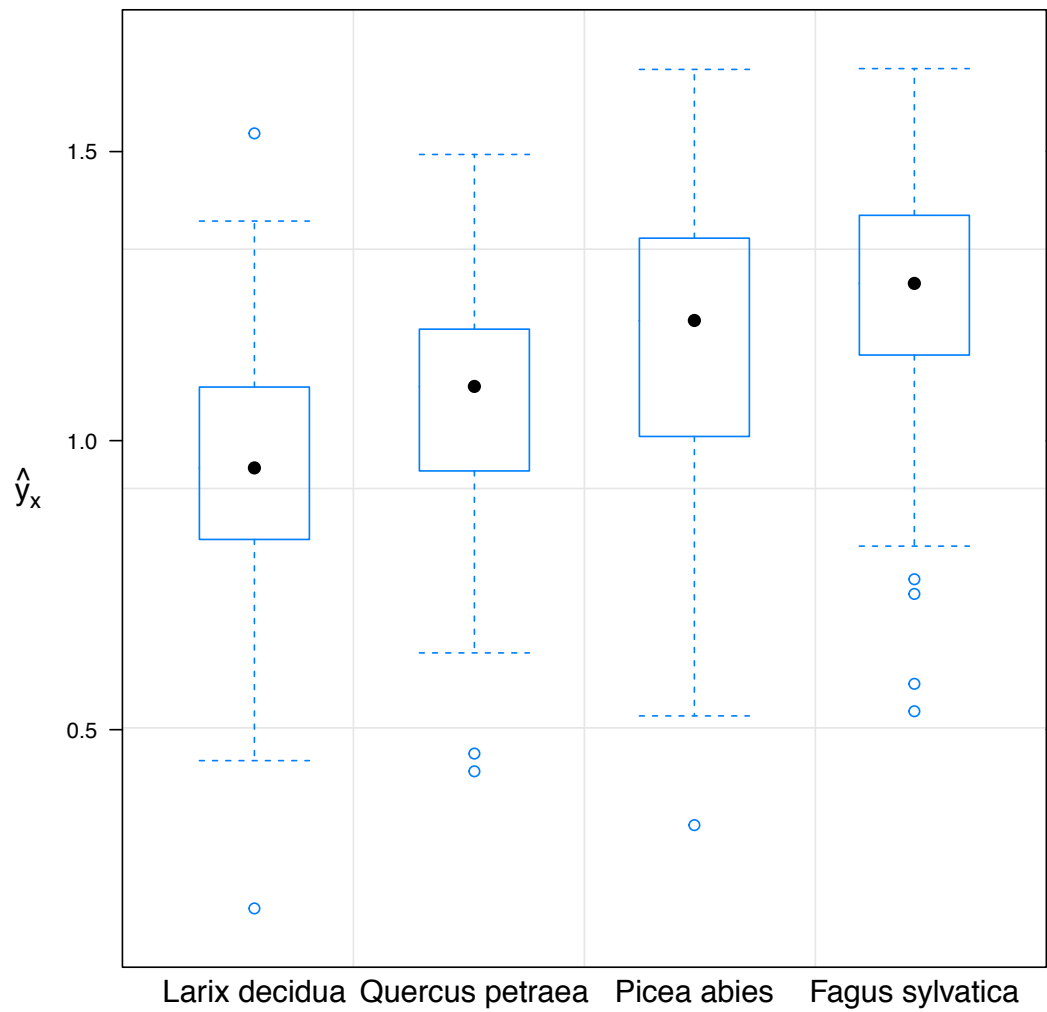
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500 **Fig. 1.** (A) The Mendel University of Brno Training Forest (green) showing the sampled stands (black dots). (B) An example spatial map of one
 501 of the sampled stands showing 18 target trees (dots with a cross in it and a number besides) and their live and dead (stumps) neighbours.
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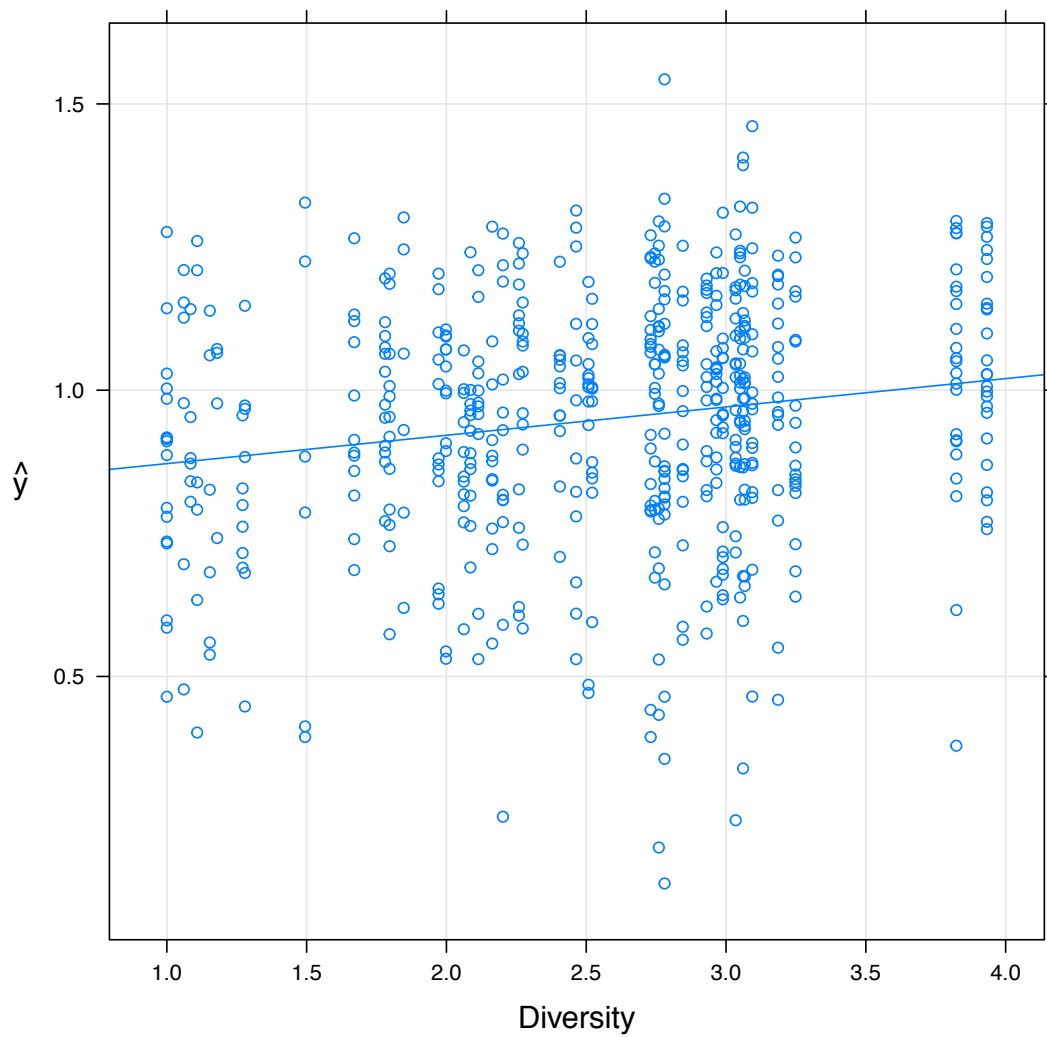
504 **Fig 2.** Individual growth trajectories for each of the four study species with the last 10
505 years of growth shown in black. Diameter increment was derived from cumulated tree
506 ring width.



508

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

512



513

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