1 **Climate modulates the effects of tree diversity on forest productivity**

2 Tommaso Jucker[1*], Daniel Avăcăriței[2], Ionuț Bărnoaiea[2], Gabriel Duduman[2], Olivier

3 Bouriaud[2] and David A. Coomes[1]

4 [1]Forest Ecology and Conservation, Department of Plant Sciences, University of Cambridge,

5 Downing Street, Cambridge, CB2 3EA, UK.

6 [2]Forestry Faculty, University Stefan cel Mare of Suceava, 13 Strada Universității, 720229,

7 Suceava, Romania.

8 [*]**Correspondence author**. E-mail: tj272@cam.ac.uk

9 **Running headline**: Biodiversity and wood production in forests

10

Summary

1. Despite growing evidence that, on average, diverse forests tend to be more productive than species poor ones, individual studies often report strongly contrasting relationships between tree species richness and above-ground wood production (AWP). In the attempt to reconcile these apparently inconsistent results, we explored whether the strength and shape of AWP – diversity relationships shifts along spatial and temporal environmental gradients in forests across Europe.

2. We used tree ring data from a network of permanent forest plots distributed at six sites across Europe to estimate annual AWP over a 15 year period (1997–2011). We then tested whether the relationship between tree species richness and AWP changes (i) across sites as a function of large-scale gradients in climatic productivity and tree packing density, and (ii) among years within each sites as a result of fluctuating climatic conditions.

3. AWP – species richness relationships varied markedly among sites. As predicted by theory, the relationship shifted from strongly positive at sites where climate imposed a strong limitation on wood production and tree packing densities were low, to weakly negative at sites where climatic conditions for growth were most suitable. In contrast, we found no consistent effect of interannual fluctuations in climate on the strength of AWP – species richness relationships within sites.

4. *Synthesis*. Our results indicate that the shape and strength of the relationship between tree diversity and forest productivity depends critically on environmental context. Across Europe, tree diversity shows the greatest potential to positively influence forest

33   productivity at either end of the latitudinal gradient, where adverse climatic conditions

34   limit productivity and lead to the development of less densely packed stands.

35   **Key-words**: above-ground wood production; biodiversity – ecosystem functioning; context

36   dependency; FunDivEUROPE project; plant-climate interactions; stress gradient hypothesis;

37   tree packing density; tree ring data

Introduction

As evidence that biodiversity promotes key ecosystem functions and services continues to amass (Cardinale *et al.* 2012), the argument for conserving biodiversity is increasingly being framed in terms of developing natural capital (Naeem, Duffy & Zavaleta 2012). In the context of forests, the consensus is that diverse stands are generally more productive than species-poor ones (Paquette & Messier 2011; Morin *et al.* 2011; Vilà *et al.* 2013; Jucker *et al.* 2014a). Consequently, promoting tree diversity is seen as a promising strategy for increasing timber yields and carbon sequestration rates across forest landscapes, while also ensuring a host of additional ecological co-benefits (Scherer-Lorenzen 2014). Yet despite synthesis work showing that the overall relationship between diversity and forest productivity is positive, both the strength and shape of this relationship vary considerably among individual studies (Zhang, Chen & Reich 2012). Recent work has helped resolve some of these context dependencies, highlighting how the effects of diversity on productivity are scale-dependent (Chisholm *et al.* 2013) and can change during stand development (Cavard *et al.* 2011; Lasky *et al.* 2014). A critical next step is to understand how environmental conditions influence the relationship between species richness and above-ground wood production (AWP) in forests, so that we may identify where and when tree diversity has the greatest potential to positively influence forest productivity (Paquette & Messier 2011; Jucker *et al.* 2014a).

Predicting how the relationship between AWP and diversity is likely to change along spatial environmental gradients requires an understanding of how species interactions are influenced by environmental conditions. Species interactions are central to explaining positive biodiversity – ecosystem functioning relationships in plant communities, as they underpin the role of niche complementarity (Loreau & Hector 2001). A key feature of species interactions

[4]

61   is that they are not constant in space, but instead shift in importance and intensity along

62   environmental gradients (Brooker *et al.* 2008). This is conceptualized in the stress gradient

63   hypothesis, which predicts that under increasingly stressful environmental conditions

64   competitive interactions weaken and give way to facilitative processes (see Maestre *et al.*,

65   2009 for a review). Following this reasoning, it has been hypothesized that biodiversity –

66   ecosystem functioning relationships should also vary along environmental gradients (Fig. 1a),

67   becoming progressively stronger as conditions for growth become less favourable (Jucker &

68   Coomes 2012; Gessner & Hines 2012; Wang *et al.* 2013; Forrester 2014). In forests,

69   competitive interactions among neighbouring trees have been shown to vary in strength along

70   environmental gradients (Kunstler *et al.* 2011; He, Bertness & Altieri 2013; Prior & Bowman

71   2014), and evidence suggests that positive relationships between diversity and productivity

72   are in fact more common where environmental conditions are most limiting (Paquette &

73   Messier 2011; Wu *et al.* 2014; Toïgo *et al.* 2015). A possible explanation for these patterns is

74   that the relationship between diversity and productivity shifts in strength as a result of

75   changes in forest structure which unfold along environmental gradients (Condés, Del Rio &

76   Sterba 2013). For instance, Potter & Woodall (2014) showed that across the USA forest

77   biomass is most strongly related to species richness at sites where unfavourable climatic

78   conditions result in low stem packing densities.

79   In addition to focusing on spatial environmental gradients, it has also been suggested that

80   interannual variation in climate may influence the strength of the relationship between

81   diversity and productivity (Forrester 2014). In most cases, the expectation seems to be that

82   temporal responses to environmental stress should mirror those observed along spatial

83   environmental gradients. Specifically, years characterized by unfavourable climatic

conditions are predicted to exhibit stronger relationships between diversity and AWP (Fig.

1b). However, evidence that the relationship between diversity and forest productivity shifts

consistently between years as a function of climate is far from clear cut, as studies have

reported both stronger and weaker diversity effects in stressful years (del Río, Schütze &

Pretzsch 2013; Jucker *et al.* 2014b; Grossiord *et al.* 2014). Part of the problem is that most

studies so far have only compared the response of two contrasting years (e.g., normal vs

drought year). Consequently, it is hard to know whether underlying patterns are going

unnoticed because of the incomplete temporal resolution of most studies (i.e., comparisons

made exclusively for a select number of years, usually two), or if instead the effects of tree

diversity on productivity simply do not vary systematically in response to interannual

fluctuations in climate.

Here we take advantage of the FunDivEUROPE permanent plot network – a novel research

platform designed specifically to quantify the functional significance of biodiversity in

mature forests (Baeten *et al.* 2013) – to test how the effects of tree diversity on productivity

change along both spatial and temporal environmental gradients. We use tree ring data

collected at six sites across Europe to estimate the annual AWP of 209 forest plots over a 15

year period (1997 – 2011). In a first step, we relate trends in productivity to climate data with

the aim of identifying the primary climatic drivers of AWP both across sites (i.e., spatial

patterns) and within them (i.e., temporal patterns). We then test whether the relationship

between tree species richness and productivity changes (i) across sites as a function of large-

scale gradients in climatic productivity and tree packing density (Fig. 1a), and (ii) among

years within each site as a result of fluctuating climatic conditions (Fig. 1b).

Materials and Methods

Materials and Methods

107 STUDY DESIGN

108 The study was conducted in the FunDivEUROPE permanent forest plot network, the design

109 of which is described in detail in Baeten *et al.* (2013). Here we summarize the key features of

110 the FunDivEUROPE network, which we supplement with a detailed description of the

111 rationale and design of the project in Appendix S1 of Supporting Information. The plot

112 network consists of 209 permanent forest plots (30 × 30 m in size) distributed in six countries

113 across Europe (hereafter referred to as "sites"). Field sites were chosen to represent major

114 European forest types, and include boreal forests in Finland, hemiboreal mixed forests in

115 Poland, beech forests in Germany, mountainous beech forests in Romania, thermophilous

116 deciduous forests in Italy and Mediterranean mixed forests in Spain. At each site, plots

117 contain different combinations of locally dominant tree species, and range in species richness

118 from 1-3 in Finland, 1-4 in Romania, Germany, Italy and Spain, and 1-5 in Poland (see Table

119 S1 for a full species list). Each target tree species is found in monoculture and is represented

120 in all species richness levels, with the majority of species' combinations being replicated at

121 least twice (59 of 91 combinations). This nested design approach was modelled around that

122 of the BIOTREE, ORPHEE and FORBIO tree diversity experiments (see Baeten *et al.*, 2013

123 and references therein). Plots were selected following a set of strict criteria designed to allow

124 robust comparisons among species richness levels. Specifically, species in mixture share

125 similar relative abundances (i.e., high species evenness; Fig. S3) and the presence of non-

126 target species is minimal (< 5% of the total basal area). In addition, plots were established

127 exclusively in mature forest stands (i.e., those at least in the mid-to-late stages of stem

128 exclusion) with similar management histories. Lastly – and critically for the purposes of this

129 study – great care was taken to ensure that (i) plots within a site share similar environmental

130 conditions and (ii) that stand attributes known to influence productivity (e.g., stem density

131 and stand age; Magnani, Mencuccini & Grace 2000; Kadmon & Benjamini 2006) were not

132 confounded with the species richness gradient (see Appendix S1 and Fig. S4). Consequently,

133 while sites differ markedly from one another in terms of climate and forest structure (e.g.,

134 basal area, stem density, maximum height), plots within a site are spatially clustered and have

135 similar elevation, topography and soil type.

136 ALLOMETRIC DATA

137 In each plot, all stems ≥7.5 cm in diameter were identified to species and permanently

138 marked (12939 stems in total). We recorded the diameter (measured to the nearest 0.1 cm at a

139 height of 1.3 m off the ground using diameter tape) and height (to the nearest 0.1 m using a

140 vertex hypsometer, Haglöf AB, Sweden) of each stem, and used these measurements to

141 estimate the above-ground biomass of each tree based on published biomass functions (see

142 Jucker *et al.*, 2014a for a complete list of equations used). We also characterized the crown

143 dominance of each tree using the crown illumination index, which consists in scoring trees

144 from 1 (suppressed crown receiving no direct light) to 5 (fully exposed dominant crown)

145 (Clark & Clark 1992). Crown illumination scores are an effective way of gauging the degree

146 to which a tree is shaded by its neighbours (Jennings, Brown & Sheil 1999; Jucker *et al.*

147 2014b), and were used to model the effects of competition for light on tree growth (see

148 following section).

We obtained data on air temperature (T; °C), precipitation (P; mm), solar radiation (R; J cm^{-2}), actual evapotranspiration (AET; mm), potential evapotranspiration (PET; mm) and the ratio between precipitation and potential evapotranspiration (P/PET; a measure of water availability) in the form of daily values covering the period between 1997 and 2011 for each of the six study sites. With the exception of AET, which was derived from the water balance model BILJOU (Granier *et al.* 1999; https://appgeodb.nancy.inra.fr/biljou/), all climatic data were obtained directly from the CGMS database of interpolated meteorological data (AGRI4CAST; http://mars.jrc.ec.europa.eu/mars). The AGRI4CAST system combines meteorological observations, remote sensing imagery and agro-meteorological modelling to generate climate surfaces for Europe (25×25 km resolution).

ESTIMATING ANNUAL ABOVE-GROUND WOOD PRODUCTION FROM TREE RING DATA

We used tree ring data to obtain a time series of annual above-ground wood production (AWP; Mg C ha^{-1} yr^{-1}) for all 209 plots covering the 15 year period between 1997 and 2011. The approach used to estimate AWP from tree ring data is outlined in detail in Jucker *et al.*, (2014a). Here we summarize the main analytical steps of this workflow.

Measuring individual tree growth from wood cores

We used 5.15 mm diameter increment borers (Haglöf AB, Sweden) to extract wood cores from 2950 trees across the plot network following a size-stratified random sampling approach (Nehrbass-Ahles *et al.* 2014). Once mounted and sanded, wood cores were scanned using a high resolution flatbed scanner (2400 dpi). From the scanned images we measured annual radial growth increments for all cored trees using CDendro (Cybis Elektronik & Data,

[9]

171   Saltsjöbaden, Sweden). Finally, radial increments for each year between 1997 and 2011 were

172   converted to annual biomass growth (kg C yr^{-1}) using the biomass functions described above.

173   Biomass growth was expressed in units of carbon by applying the standard conversion of 0.5

174   g C per gram of biomass.

175   *Modelling individual tree biomass growth*

176   For each year between 1997 and 2011, we used linear mixed-effects models coded in R

177   (3.0.1; R Core Development Team, 2013) to model the biomass growth (*G*) of each target

178   species as a function of tree size, competition for light, species richness and a random plot

179   effect:

180
$$\log(G_i) = \beta_{0_{j[i]}} + \beta_1 \log(D_i) + \beta_2 CI_i + \beta_3 SR_j + \varepsilon_i \qquad \text{(eqn 1)}$$

181   where D_i and CI_i are, respectively, the stem diameter and crown illumination index of tree *i*

182   growing in plot *j* (as measured in 2011); SR_j is the species richness of plot *j*; $\beta_{0_{j[i]}}$ is a

183   species' intrinsic growth rate for a tree growing in plot *j* (*sensu* Rüger *et al.*, 2012); $\beta_{1\text{-}3}$ are,

184   respectively, a species' growth response to size, light availability and species richness; and ε_i

185   is the residual error. Equation 1 effectively captured variation in biomass growth within and

186   among species [average R^2 across species = 0.80; for further information see Jucker *et al.*

187   (2014a)].

188   *Scaling up from tree-level biomass growth to plot-level AWP*

189   Equation 1 was used to estimate the annual biomass growth of all trees that had not been

190   cored for each year between 1997 and 2011. The annual AWP of each plot was then

191   quantified by summing the biomass growth of all trees within a plot. This step was repeated

192   for each year between 1997 and 2011 to generate a 15-year time series of AWP for all 209

[10]

193   plots. This approach to estimating AWP was chosen after having ruled out potential biases

194   associated with temporal autocorrelation in the AWP time series (see Appendix S2).

195   Similarly to previous diversity – productivity studies in forests (e.g., Paquette & Messier

196   2011; Vilà *et al.* 2013), estimates of AWP are based exclusively on the growth of trees

197   present in 2011, with the implicit assumption that mortality rates are unrelated to tree species

198   diversity (Liang *et al.* 2007).

199   RELATING VARIATION IN AWP ACROSS AND WITHIN SITES TO CLIMATE

200   We combined data on AWP and climate to identify which climatic predictors best explain

201   variation in wood production across sites (i.e., spatial variation in AWP) and within them

202   (i.e., interannual variation in AWP). To understand how differences in climate among sites

203   shape geographic patterns of wood production, we calculated mean annual values of T, P, R,

204   AET, PET and P/PET for each study site and related these to mean annual AWP using

205   univariate regressions (Appendix S3). Following the same approach, we also tested the ability

206   of climatic predictors to explain interannual variation in AWP within sites. For each site, we

207   aggregated daily climate values to obtain both yearly and seasonal (spring = March, April,

208   May; summer = June, July, August; autumn = September, October, November) estimates of

209   T, P, R, AET, PET and P/PET for each year between 1997 and 2011. We then fitted

210   univariate regressions relating interannual variation in AWP within sites to each climatic

211   predictor in turn (Appendix S3).

212   STATISTICAL MODELLING OF AWP – DIVERSITY RELATIONSHIPS

213   We devised a two-step approach to test whether AWP – diversity relationships change

214   predictably (i) across sites and (ii) among years within a site (Fig. 1). We first used a linear

215 regression model to estimate the effects of species richness on AWP (i.e., the slope of the

216 AWP – species richness relationship) for (i) each site and (ii) for every year within a site. We

217 then related the slope estimates obtained from the model to (i) differences in climate and

218 packing density among sites, and (ii) interannual variation in climate within sites (e.g., Reich

219 *et al.*, 2012; Wu *et al.*, 2014). We favoured this approach over one in which climatic effects

220 on AWP were modelled directly, as it allows the strength of the species richness effect on

221 AWP to be intuitively compared both among and within sites (Nakagawa & Cuthill, 2007).

222 *Step 1: Estimate AWP – species richness slopes across and within sites*

223 We modelled AWP as a function of (i) species richness, (ii) plot basal area (to account for the

224 effects of stem packing density on productivity), (iii) site (i.e., accounting for variation in

225 AWP among study sites), (iv) year nested within site (i.e., allowing AWP to vary among

226 years within each site), (v) an interaction term between species richness and site (testing

227 whether species richness effects on AWP vary among sites), and (vi) an interaction term

228 between species richness and year nested within site (to determine whether species richness

229 effects on AWP vary among years within sites):

230 $$\log(AWP_{ijk}) = \beta_0 + \beta_1 \log(BA_{ij}) + \beta_2 \log(SR_{ij}) + \beta_3 \text{Site}_j + \beta_4 \text{Year}_{jk} +$$

231 $$\beta_5 [\log(SR_{ij}) \times \text{Site}_j] + \beta_6 [\log(SR_{ij}) \times \text{Year}_{jk}] + \varepsilon_{ijk} \qquad \text{(eqn 2)}$$

232 where AWP_{ijk} is the above-ground wood production of plot i in site j in year k; SR_{ij} and BA_{ij}

233 are, respectively, the species richness and basal area of plot i in site j; $Site_j$ and $Year_{jk}$ are

234 categorical grouping variables which capture how AWP varies among the j sites and among

235 the k years within each of the j sites, respectively; $\beta_0 - \beta_6$ are parameters to be estimated from

236 the data (i.e., intercept and slope coefficients); and ε_{ijk} is the residual error.

[12]

237   In equation 2, both "Site" and "Year" were modelled as fixed effects so that we could

238   estimate uncertainties for all parameters. To verify the robustness of the parameter estimates

239   obtained from equation 2 (particularly β_5 and β_6, which define how the effect of tree diversity

240   on AWP varies across and within sites), we first compared them with those estimated using a

241   mixed-effects modelling approach. In addition to this, we also fitted an additional model in

242   which we accounted for a number of potentially confounding factors which could

243   conceivably alter the relationship between tree diversity and AWP (elevation, terrain slope,

244   soil depth, rock cover and stand age). As all three approaches yielded almost identical results

245   (see Appendix S4), here we focus on the parameter estimates obtained through equation 2.

246   Note that support for the interaction terms in equation 2 was assessed through comparison

247   with simpler models lacking interacting effects.

248   *Step 2: Relate variation in slopes to climate and packing density*

249   From equation 2 we obtained the slope of the AWP – species richness relationship for (i)

250   each site (i.e., β_5) and (ii) for all years within a site (i.e., β_6). We then used Pearson's

251   correlation coefficients (*r*) to explore whether (i) variation in the strength of the species

252   richness effect among sites is related to differences in macroclimate and/or basal area (a

253   measure of tree packing density which captures both the mean size and number of trees

254   within a plot) (Curtis & Marshall 2000), and (ii) whether the influence of species richness on

255   AWP changes over time within a site depending on how suitable climatic conditions are in a

256   given year.

[13]

257 **Results**

259 AWP varied considerably among sites (M2 vs M1 in Table 1), differing almost fivefold

260 between Spain (0.65 Mg C ha^{-1} yr^{-1}) – the least productive site – and Romania (3.11 Mg C ha^{-}

261 ^{1} yr^{-1}), where AWP rates were highest. Geographic variation in AWP was strongly related to

262 differences in evapotranspiration among sites (Fig. 2a; see Appendix S3 for comparison with

263 other climatic drivers). Sites where annual AET was low – either because of insufficient

264 rainfall (e.g., Spain) or low temperatures (e.g., Finland) – had much slower rates of AWP

265 than those where AET was high (e.g., Germany and Romania). However, AET was only a

266 weak predictor of interannual variation in AWP within sites (see Table S2 and following

267 paragraph). Instead, we found that increased annual AET was associated with the

268 development of forests with greater basal areas (Fig. S7). This in turn resulted in markedly

269 faster rates of AWP – as basal area was a key driver of AWP across the plot network (Fig. 2b

270 and Table 1) – suggesting that at least in part the link between evapotranspiration and

271 productivity is mediated through changes in stand packing density.

272 In addition to varying across sites, AWP also fluctuated strongly among years within each

273 site (M3 vs M2 in Table 1). Climate explained much of this interannual variation in

274 productivity (Fig. 3), with a clear distinction emerging between Finland – where AWP was

275 co-limited by temperature and solar radiation – and all other sites – where annual growth was

276 instead primarily water-limited (Table 2). In Finland, the single best climatic predictor of

277 annual AWP was spring PET (Fig. 3b and Table 2), with productivity peaking in years

278 characterized by high solar radiation and mild spring temperatures which together contributed

[14]

279 to high PET rates (Table S2). For all other sites, fluctuations in annual AWP was best

280 captured by P/PET (Table 2), with productivity declining sharply in years when evaporative

281 demands (i.e., PET) were not met by precipitation (Fig. 3a,c-f). The timing of drought proved

282 equally important in explaining AWP patterns. For both Mediterranean sites, low P/PET

283 values during spring months were associated with strong reductions in AWP (Fig. 3a,c),

284 while summer drought had a much less pronounced influence on productivity (Table S2). In

285 contrast, for Germany and Poland the best predictor of AWP was P/PET integrated over the

286 entire year (Fig. 3d-f), while in Romania AWP was influenced by autumn P/PET (Fig. 3e).

287 Note that for all sites, AWP – climate relationships were best captured by linear functions

288 (see Table 2 for estimated regression coefficients).

289 AWP – DIVERSITY RELATIONSHIPS ACROSS SITES

290 We found strong support for the inclusion of the interaction term between species richness

291 and "site" in equation 2 (M4 vs M3 in Table 1), indicating that the effect of species richness

292 on AWP varies substantially across sites. In accordance with the stress gradient hypothesis

293 (Fig. 1a), the slope of the AWP – species richness relationship decreased progressively along

294 the AET climatic productivity gradient ($r = $ -0.88, $P = 0.020$, $n = 6$; Fig. 2c), ranging from

295 strongly positive in Spain (0.24 ± 0.06) – where evapotranspiration and productivity were

296 low – to weakly negative in Romania (-0.05 ± 0.07) – where AET and AWP were greatest.

297 This shift in the strength of the diversity effect on productivity was equally well captured by

298 accounting for differences in basal area across sites ($r = $ -0.90, $P = 0.013$, $n = 6$), with

299 diversity effects being strongest at sites where environmental conditions led to the

300 development of less densely packed stands (Fig. 2d and Fig. S7).

[15]

302   In contrast to patterns across sites, we found little evidence to suggest that species richness

303   effects on AWP varied strongly among years within sites (M5 vs M4 in Table 1).

304   Furthermore, we found no consistent relationship between the strength of the species richness

305   effect on AWP and climatic conditions within a given year when looking across the six sites

306   (Fig. 4). The only site to show a relationship between the magnitude of the species richness

307   slope and climate was Finland (Fig. 4b), where species richness effects weakened in years

308   when spring PET was high and climatic conditions for growth were favourable ($r = -0.73$, P

309   < 0.01, $n = 15$). A similar response was found for Romania, although the pattern between

310   diversity effects and climate (autumn P/PET) was weaker ($r = -0.44$, $P = 0.10$, $n = 15$; Fig.

311   4f). Instead, in the case of Poland (Fig. 4d), and to a much lesser extent Spain (Fig. 4a), we

312   observed the opposite trend, with diversity effects strengthening during non-drought years (r

313    $= 0.49$, $P = 0.06$ and $r = 0.21$, $P = 0.45$, respectively; $n = 15$). These observations do not

314   support the predictions of the stress gradient hypothesis (Fig. 1b). Lastly, in the case of Italy

315   (Fig. 4c) and Germany (Fig. 4e) we found no discernible pattern linking diversity effects and

316   climatic conditions across years ($r = 0.03$, $P = 0.93$ and $r = 0.05$, $P = 0.87$, respectively; $n = $

317   15).

Discussion

In line with a number of recent studies, we found a generally positive relationship between tree diversity and forest productivity across Europe (Morin *et al.* 2011; Vilà *et al.* 2013; Pretzsch *et al.* 2015). Importantly, however, our results also highlighted that the effects of species richness on productivity are strongly context dependent, varying in space and – to a lesser extent – time. Specifically, AWP – species richness relationships shifted predictably in strength across sites, becoming progressively stronger under harsher environmental conditions (Fig. 2). In contrast, we found that interannual variation in the strength of species richness effects within sites was rather weak and could not be consistently explained by year-to-year fluctuations in climate (Fig. 4).

AWP – DIVERSITY RELATIONSHIPS ARE STRONGEST IN STRESSFUL ENVIRONMENTS

Macro-scale patterns in wood production were best captured by differences in evapotranspiration among sites (Fig. 2a), confirming what has previously been reported in the literature (Stephenson 1998; Oberle, Grace & Chase 2009). Evapotranspiration integrates the effects of water availability and temperature on plant growth (Stephenson 1998; Boisvenue & Running 2006): in order for trees to grow, temperatures need to be sufficient to initiate photosynthesis and allow the microbially driven mobilization of soil nutrients, and at the same time enough water needs to be available to meet evaporative demands. Our results also suggest that the link between evapotranspiration and productivity is largely mediated through changes in stand basal area which unfold across AET gradients (Fig. S7), as opposed to a direct influence of AET on AWP (Stephenson 1998; Coomes *et al.* 2014; Michaletz *et al.* 2014). While interannual fluctuations in AET were not a particularly strong predictor of

[17]

340   variation in productivity within sites (Tables S2), sites with higher mean annual AET also

341   had greater basal areas, which in turn drove faster rates of wood production (Fig. 2b).

342   The strength of the species richness effect on productivity also shifted along the

343   evapotranspiration gradient, and was strongest at sites where AET was low – either as a result

344   of low annual rainfall (e.g., Spain) or because of low temperatures (e.g. Finland) – and

345   conditions for growth were poor (Fig. 2c). Conversely, at sites where conditions for growth

346   were more favourable, we saw a drastic reduction in the importance of diversity as a driver of

347   wood production. These results are broadly consistent with the predictions of the stress

348   gradient hypothesis (Fig. 1a), as well as the findings of a number of recent papers (Paquette

349   & Messier 2011; Jucker & Coomes 2012; Wu *et al.* 2014; Toïgo *et al.* 2015). For instance,

350   using forest inventory data from France, Toïgo *et al.* (2015) showed that overyielding was

351   more frequent at low productivity sites. Similarly, Wu *et al.* (2014) found that the strength of

352   the relationship between tree diversity and biomass weakened when transitioning from

353   boreal, to temperate and subtropical forests in China.

354   In addition to the stress gradient hypothesis, a number of alternative frameworks have also

355   been proposed to explain how environmental conditions shape the relationship between

356   diversity and productivity. For instance, Forrester (2014) noted that the outcome of species

357   interactions will depend on the type of limiting resource or resources (e.g., water, light,

358   nutrients), and whether – on average – interactions among neighbouring trees improve the

359   availability of those resources (also see Pretzsch *et al.* 2015). What our results suggest is that

360   the net outcome of species interactions shifts along environmental gradients and that – on

361   balance – competition tends to decrease in importance in more stressful environments

362   allowing greater room for complementarity (Kunstler *et al.* 2011; Prior & Bowman 2014).

[18]

363   Climate can influence interactions among neighbouring trees directly by modulating the

364   relative performance and strategy of species within a community (Brooker *et al.* 2008;

365   Maestre *et al.* 2009). In addition to this, climate can influence interactions among

366   neighbouring trees indirectly through its effect on forest structure. Climate plays an important

367   role in determining local species pools through environmental filtering (e.g., Stahl *et al.*,

368   2014), as well as shaping species demographic rates (Lines, Coomes & Purves 2010;

369   Vanderwel, Lyutsarev & Purves 2013; Coomes *et al.* 2014) and influencing how trees

370   allocate carbon above and below-ground (Lines *et al.* 2012; Reich *et al.* 2014), all of which

371   interact to determine forest structure. As our results suggest that positive AWP – diversity

372   relationships are much more likely in forests with low packing densities (Fig. 2d), the effect

373   of climate on forest structure appears to be particularly important in modulating the effects of

374   diversity on productivity (Condés *et al.* 2013; Potter & Woodall 2014). This may explain why

375   in Mediterranean forests, where drought impedes the development of densely packed stands,

376   the effects of diversity on productivity tend to be strongly positive (Vilà *et al.* 2007; Ruiz-

377   Benito *et al.* 2014; Jucker *et al.* 2014b).

378   INTERANNUAL FLUCTUATIONS IN CLIMATE HAVE WEAK AND IDIOSYNCRATIC EFFECTS ON AWP

379   –DIVERSITY RELATIONSHIPS WITHIN SITES

380   AWP responses to interannual fluctuations in climate within sites closely matched

381   expectations based on published reports, with most forest types in Europe being primarily

382   limited by water availability, while productivity in boreal forests depends strongly on

383   temperature and solar radiation (Boisvenue & Running 2006; Babst *et al.* 2013). In terms of

384   AWP – diversity relationships, we generally found that variation within sites was

385   considerably weaker than variation among them (Table 1). Moreover, we found no evidence

386   of consistent pattern linking variation in diversity effects across years to climate (Fig. 4).

387   Certain functional responses match expectations, such as the decreased strength of diversity

388   effects during warmer years in Finland (Fig. 4b). In boreal systems, warmer springs are

389   associated with earlier leaf-out dates (Polgar & Primack 2011). While this positively

390   influences productivity by increasing the length of the growing season (Chen *et al.* 1999;

391   Polgar & Primack 2011), it is also likely to reduce the degree of phenological mismatch (i.e.,

392   temporal complementarity) between evergreen conifers and deciduous broadleaf species

393   (Sapijanskas *et al.* 2014). In contrast, we found no consistent effect of drought on the strength

394   of diversity effects across forest types (Grossiord *et al.* 2014). For Spain, our results generally

395   confirm those of a previous study comparing responses in two years with contrasting climate

396   (a drought year and a wet year), which showed that drought tends to exacerbate competition

397   among neighbouring trees (Jucker *et al.* 2014b). However, in the case of Poland, Germany

398   and Romania we find strongly contrasting patterns despite the fact that these sites share

399   similar species compositions and have broadly similar climates.

400   Differences between responses across sites − which strongly matched theoretical predictions

401   − and those within sites − which instead exhibited weak and contrasting patterns − suggest

402   that in addition to climate itself, a key factor in shaping the strength of diversity effects on

403   productivity is how densely trees pack in space. If the relationship between diversity and

404   productivity was directly influenced by climate, diversity effects would be expected to shift

405   consistently both across and within sites. Instead, under the assumption that packing density

406   is what ultimately determines the strength of the relationship between diversity and

407   productivity (Condés *et al.* 2013; Potter & Woodall 2014), temporal patterns would be

408   unlikely to match spatial trends. The reason for this is that although basal area varies strongly

[20]

409   among sites (Fig. 2b), changes in packing density are decoupled from interannual variation in

410   climate in forest ecosystems (i.e., basal area does not increase or decrease markedly from one

411   year to next based on climatic suitability). Recent work in coastal dunes plant communities

412   has shown that shifts from competition to facilitation among years depend critically on

413   differences in vegetation cover: during years characterized by harsh environmental conditions

414   vegetation cover decreases, resulting in an increase in facilitation, while in more favourable

415   years increased vegetation cover exacerbates competition (Doxford, Ooi & Freckleton 2013).

416   However, because trees are long-lived and do not regenerate the bulk of their above-ground

417   biomass each year, a similar response in terms of basal area cannot be observed in forests

418   (Stephenson & Mantgem 2005). As a result, the way in which diversity effects change among

419   years may simply be more context dependent in the case of forests [e.g., highly dependent on

420   species' traits or on the type of limiting resource; Forrester (2014)].

421   IMPLICATIONS FOR FOREST CONSERVATION AND MANAGEMENT

422   Identifying where and when tree diversity has the greatest potential to positively influence

423   forest productivity has important implications for forest management and conservation

424   practises, as well as efforts to mitigate climate change (Zhang *et al.* 2012; Cardinale *et al.*

425   2012; Scherer-Lorenzen 2014). We found that in terms of maximising rates of wood

426   production, the benefits of maintaining diverse forests are most pronounced in systems where

427   environmental conditions strongly limit productivity. While our study provides a useful

428   framework for predicting under which conditions tree diversity is likely to matter most, there

429   are however several reasons why practises aimed at maintaining diverse forests should not

430   necessarily be limited to specific ecological contexts or geographic regions. For instance, in

431   addition to promoting forest productivity, tree diversity has also been shown to help stabilize

[21]

432 wood production over time across a range of forest types, highlighting the fact that mixed-

433 species forests are able to remain productive under a wider range of environmental conditions

434 than monocultures (Jucker *et al.* 2014a; Morin *et al.* 2014). Secondly, although we detected

435 clear differences in the importance of tree diversity as a driver of productivity among forest

436 types, only one site showed any indication of a negative association between diversity and

437 productivity. Consequently, even though gains in productivity may be negligible for certain

438 forest types, maintaining diverse forests is unlikely to adversely affect wood production and

439 has the advantage of delivering a number of added ecological and economic co-benefits (e.g.,

440 reduced risk of pest and pathogen outbreaks, increased associated biodiversity, greater soil

441 carbon storage; Scherer-lorenzen, 2014).

442 In addition to highlighting under which circumstance tree diversity is currently most

443 important for forest productivity, our study also provides a number of clues as to how climate

444 change is likely to influence AWP – diversity relationships in future forests. By the end of

445 this century Mediterranean forests in Europe are expected to suffer more frequent and

446 prolonged periods of drought, while boreal systems are predicted to warm considerably and

447 experience longer growing seasons (Jacob *et al.* 2014). As a result, diversity effects may

448 weaken in strength, particularly in the case of boreal forests where spring warming is

449 expected to reduce the degree of phenological mismatch among coexisting tree species

450 (Polgar & Primack 2011). More importantly, however, our results suggest that longer-term

451 responses of forests to climate change – such as changes in species composition and forest

452 structure – are what will ultimately determine how the relationship between tree diversity and

453 forest productivity will look like in the future.

[22]

461   **Data Accessibility**

462   Above-ground wood production (AWP) data: uploaded as online supporting information

References

Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M., Tegel, W., Levanic, T., Panayotov, M., Urbinati, C., Bouriaud, O., Ciais, P. & Frank, D. (2013) Site- and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography*, **22**, 706–717.

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.

Boisvenue, C. & Running, S.W. (2006) Impacts of climate change on natural forest productivity - evidence since the middle of the 20th century. *Global Change Biology*, **12**, 862–882.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B. & Michalet, R. (2008) Facilitation in plant communities: The past, the present, and the future. *Journal of Ecology*, **96**, 18–34.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., Laganière, J. & Brassard, B.W. (2011) Competition and facilitation between tree species change with stand development. *Oikos*, **120**, 1683–1695.

[24]

Chen, W.J., Black, T.A., Yang, P.C., Barr, A.G., Neumann, H.H., Nesic, Z., Blanken, P.D., Novak, M.D., Eley, J., Ketler, R.J. & Cuenca, R. (1999) Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. *Global Change Biology*, **5**, 41–53.

Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebber, D.P., Bin, Y., Bohlman, S.A., Bourg, N.A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L.-W., Chiang, J.-M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S.J., Duque, A., Fletcher, C., Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.-F., Hubbell, S.P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma, K., Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Mohd. Razman, S., Morecroft, M.D., Nytch, C.J., Oliveira, A., Parker, G.G., Pulla, S., Punchi-Manage, R., Romero-Saltos, H., Sang, W., Schurman, J., Su, S.-H., Sukumar, R., Sun, I.-F., Suresh, H.S., Tan, S., Thomas, D., Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z. & Zimmerman, J.K. (2013) Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology*, **101**, 1214–1224.

Clark, D.A. & Clark, D.B. (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs*, **62**, 315–344.

Condés, S., Del Rio, M. & Sterba, H. (2013) Mixing effect on volume growth of Fagus sylvatica and Pinus sylvestris is modulated by stand density. *Forest Ecology and Management*, **292**, 86–95.

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.

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

Doxford, S.W., Ooi, M.K.J. & Freckleton, R.P. (2013) Spatial and temporal variability in positive and negative plant-bryophyte interactions along a latitudinal gradient. *Journal of Ecology*, **101**, 465–474.

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.

Gessner, M.O. & Hines, J. (2012) Stress as a modifier of biodiversity effects on ecosystem processes? *Journal of Animal Ecology*, **81**, 1143–5.

Granier, A., Bréda, N., Biron, P. & Villette, S. (1999) A lumped water balance model to

534   evaluate duration and intensity of drought constraints in forest stands. *Ecological*
535   *Modelling*, **116**, 269–283.

536   Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Chećko, E., Forrester,
537   D.I., Dawud, S.M., Finér, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F.,
538   Bonal, D. & Gessler, A. (2014) Tree diversity does not always improve resistance of
539   forest ecosystems to drought. *Proceedings of the National Academy of Sciences*, **111**,
540   14812–14815.

541   He, Q., Bertness, M.D. & Altieri, A.H. (2013) Global shifts towards positive species
542   interactions with increasing environmental stress. *Ecology Letters*, **16**, 695–706.

543   Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O.B., Bouwer, L.M., Braun, A.,
544   Colette, A., Déqué, M., Georgievski, G., Georgopoulou, E., Gobiet, A., Menut, L.,
545   Nikulin, G., Haensler, A., Hempelmann, N., Jones, C., Keuler, K., Kovats, S., Kröner,
546   N., Kotlarski, S., Kriegsmann, A., Martin, E., Meijgaard, E., Moseley, C., Pfeifer, S.,
547   Preuschmann, S., Radermacher, C., Radtke, K., Rechid, D., Rounsevell, M.,
548   Samuelsson, P., Somot, S., Soussana, J.-F., Teichmann, C., Valentini, R., Vautard, R.,
549   Weber, B. & Yiou, P. (2014) EURO-CORDEX: New high-resolution climate change
550   projections for European impact research. *Regional Environmental Change*, **14**, 563–
551   578.

552   Jennings, S.B., Brown, N.D. & Sheil, D. (1999) Assessing forest canopies and understorey
553   illumination: canopy closure, canopy cover and other measures. *Forestry*, **72**, 59–73.

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

557   Jucker, T., Bouriaud, O., Avăcăriei, D., Dănilă, I., Duduman, G., Valladares, F. & Coomes,
558   D.A. (2014b) Competition for light and water play contrasting roles in driving diversity-
559   productivity relationships in Iberian forests. *Journal of Ecology*, **102**, 1202–1213.

560   Jucker, T. & Coomes, D.A. (2012) Comment on "Plant species richness and ecosystem
561   multifunctionality in global drylands". *Science*, **337**, 155.

562   Kadmon, R. & Benjamini, Y. (2006) Effects of productivity and disturbance on species
563   richness: a neutral model. *The American Naturalist*, **167**, 939–946.

564   Kunstler, G., Albert, C.H., Courbaud, B., Lavergne, S., Thuiller, W., Vieilledent, G.,
565   Zimmermann, N.E. & Coomes, D.A. (2011) Effects of competition on tree radial-growth
566   vary in importance but not in intensity along climatic gradients. *Journal of Ecology*, **99**,
567   300–312.

568   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**, 1158–67.

Liang, J., Buongiorno, J., Monserud, R.A., Kruger, E.L. & Zhou, M. (2007) Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *Forest Ecology and Management*, **243**, 116–127.

Lines, E.R., Coomes, D.A. & Purves, D.W. (2010) Influences of forest structure, climate and species composition on tree mortality across the eastern US. *PLoS ONE*, **5**, e13212.

Lines, E.R., Zavala, M.A., Purves, D.W. & Coomes, D.A. (2012) Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. *Global Ecology and Biogeography*, **21**, 1017–1028.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.

Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.

Magnani, F., Mencuccini, M. & Grace, J. (2000) Age-related decline in stand productivity: The role of structural acclimation under hydraulic constraints. *Plant, Cell and Environment*, **23**, 251–263.

Michaletz, S.T., Cheng, D., Kerkhoff, A.J. & Enquist, B.J. (2014) Convergence of terrestrial plant production across global climate gradients. *Nature*, **512**, 39–43.

Morin, X., Fahse, L., de Mazancourt, C., Scherer-Lorenzen, M. & Bugmann, H. (2014) Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. *Ecology Letters*, **17**, 1526–35.

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.

Naeem, S., Duffy, J.E. & Zavaleta, E. (2012) The functions of biological diversity in an age of extinction. *Science*, **336**, 1401–1407.

Nakagawa, S. & Cuthill, I.C. (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, **82**, 591–605.

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.

[27]

Oberle, B., Grace, J.B. & Chase, J.M. (2009) Beneath the veil: Plant growth form influences the strength of species richness-productivity relationships in forests. *Global Ecology and Biogeography*, **18**, 416–425.

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

Polgar, C.A. & Primack, R.B. (2011) Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist*, **191**, 926–941.

Potter, K.M. & Woodall, C.W. (2014) Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across U.S. forests. *Forest Ecology and Management*, **321**, 117–129.

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.

Prior, L.D. & Bowman, D.M.J.S. (2014) Across a macro-ecological gradient forest competition is strongest at the most productive sites. *Frontiers in Plant Science*, **5**, 1–12.

R Core Development Team. (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P.B., Luo, Y., Bradford, J.B., Poorter, H., Perry, C.H. & Oleksyn, J. (2014) Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the National Academy of Sciences*, **111**, 13721–13726.

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.

del Río, M., Schütze, G. & Pretzsch, H. (2013) Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biology*, **16**, 166–176.

Rüger, N., Wirth, C., Wright, S.J. & Condit, R. (2012) Functional traits explain light and size response of growth rates in tropical tree species. *Ecology*, **93**, 2626–2636.

Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J. & Zavala, M.A.

636   (2014) Diversity increases carbon storage and tree productivity in Spanish forests.
637   *Global Ecology and Biogeography*, **23**, 311–322.

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

641   Scherer-Lorenzen, M. (2014) The functional role of biodiversity in the context of global
642   change. *Forests and Global Change* (eds D.A. Coomes),, D.F.R.P. Burslem), & W.D.
643   Simonson), pp. 195–238. Cambridge University Press, Cambridge.

644   Stahl, U., Reu, B. & Wirth, C. (2014) Predicting species' range limits from functional traits
645   for the tree flora of North America. *Proceedings of the National Academy of Sciences*,
646   **111**, 13739–13744.

647   Stephenson, N.L. (1998) Actual evapotranspiration and deficit: Biologically meaningful
648   correlates of vegetation distribution across spatial scales. *Journal of Biogeography*, **25**,
649   855–870.

650   Stephenson, N.L. & Mantgem, P.J. (2005) Forest turnover rates follow global and regional
651   patterns of productivity. *Ecology Letters*, **8**, 524–31.

652   Toïgo, M., Vallet, P., Perot, T., Bontemps, J., Piedallu, C. & Courbaud, B. (2015)
653   Overyielding in mixed forests decreases with site productivity. *Journal of Ecology*, **103**,
654   502–512.

655   Vanderwel, M.C., Lyutsarev, V.S. & Purves, D.W. (2013) Climate-related variation in
656   mortality and recruitment determine regional forest-type distributions. *Global Ecology*
657   *and Biogeography*, **22**, 1192–1203.

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

661   Vilà, M., Vayreda, J., Comas, L., Ibáñez, J.J., Mata, T. & Obón, B. (2007) Species richness
662   and wood production: A positive association in Mediterranean forests. *Ecology Letters*,
663   **10**, 241–50.

664   Wang, J., Zhang, C.B., Chen, T. & Li, W.H. (2013) From selection to complementarity: the
665   shift along the abiotic stress gradient in a controlled biodiversity experiment. *Oecologia*,
666   **171**, 227–35.

667   Wu, X., Wang, X., Tang, Z., Shen, Z., Zheng, C., Xia, X. & Fang, J. (2014) The relationship
668   between species richness and biomass changes from boreal to subtropical forests in
669   China. *Ecography*, **38**, 602–613.

670   Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness,
671   species richness and trait variation: A global meta-analysis. *Journal of Ecology*, **100**,
672   742–749.

673

674 **Supporting information**

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

676 **Appendix S1**: FunDivEUROPE project

677 **Appendix S2**: Temporal autocorrelation in AWP

678 **Appendix S3**: Relating variation in AWP to climate

679 **Appendix S4**: Estimating diversity effects across and within sites

680 **Appendix S5**: Above-ground wood production (AWP) data archive

681

682   **Tables**

683   **Table 1**: Model comparison statistics for a set of candidate models testing whether diversity

684   effects on above-ground wood production (AWP) vary across and within sites. In the baseline

685   model (M1), AWP is expressed as a function of plot basal area (BA) and species richness

686   (SR). "Site" indicates a model which accounts for variation in AWP among sites, while

687   "Year" tests whether AWP varies among years within each site. Model M4 tests whether the

688   effects of SR on AWP varies among sites (i.e., interaction between SR and Site), while model

689   M5 further allows species richness effects to vary among years within a site (i.e., interaction

690   between SR and Year) and corresponds to equation 2 in the text. Models of increasing

691   complexity were compared to simpler ones (e.g., M5 vs M4) using F-tests to determine

692   whether the reduction in the residual sum of squares between models was statistically

693   significant ($\alpha = 0.05$). In addition to this we also report the R^2 and AIC of each model. Note

694   that AWP, SR and BA were log-transformed prior to model fitting.

Model	Model structure	P (>F)	R^2	AIC
M0	AWP ~ BA	–	0.40	4306
M1	AWP ~ BA + SR	<0.0001	0.42	4276
M2	AWP ~ BA + SR + Site	<0.0001	0.74	1738
M3	AWP ~ BA + SR + Site + Year	<0.0001	0.78	1291
M4	AWP ~ BA + SR + Site + Year + SR×Site	<0.0001	0.79	1248
M5	AWP ~ BA + SR + Site + Year + SR×Site + SR×Year	n.s.	0.79	1384

695

[32]

696   **Table 2**: Best climatic predictors of interannual variation in above-ground wood production

697   (AWP) for each study site. Regression equations (with 95% confidence intervals for

698   parameter estimates in brackets) correspond to fitted relationships illustrated in Fig. 3. To

699   facilitate the interpretation of regression coefficients, climatic predictors were cantered prior

700   to model fitting (i.e., for each site, intercepts indicate the mean AWP across years). PET =

701   potential evapotranspiration; P/PET = precipitation/PET.

Site	Climatic predictor	Regression equation
Finland	Spring PET	AWP = 1.85 (0.06) + 0.012 (0.003) $\times$ PET
Poland	Annual P/PET	AWP = 1.81 (0.04) + 0.87 (0.23) $\times$ (P/PET)
Germany	Annual P/PET	AWP = 2.78 (0.07) + 1.11 (0.44) $\times$ (P/PET)
Romania	Autumn P/PET	AWP = 3.11 (0.11) + 0.40 (0.14) $\times$ (P/PET)
Italy	Spring P/PET	AWP = 1.88 (0.05) + 0.48 (0.24) $\times$ (P/PET)
Spain	Spring P/PET	AWP = 0.65 (0.02) + 0.28 (0.09) $\times$ (P/PET)

702

703 **Figures**

(a) Across-site variation **(b)** Within-site variation

Species richness

704

705 **Fig. 1**: Schematic diagram illustrating how the relationship between productivity and

706 diversity is expected to change (a) across sites along an environmental gradient and (b)

707 among years within a site. Panel (a) depicts different sites along an environmental gradient.

708 Sites where productivity is low (e.g., as a result of strong environmental limitations on

709 growth) exhibit strong positive effects of diversity on productivity, while sites where growing

710 conditions are more favourable show little or no benefit from species mixing. Panel (b)

711 illustrates how the effects of diversity on productivity vary among years within a given site.

712 The expectation is that the slope of the diversity – productivity relationship will be steeper

713 than average in low productivity years, weakening instead when conditions for growth

714 improve.
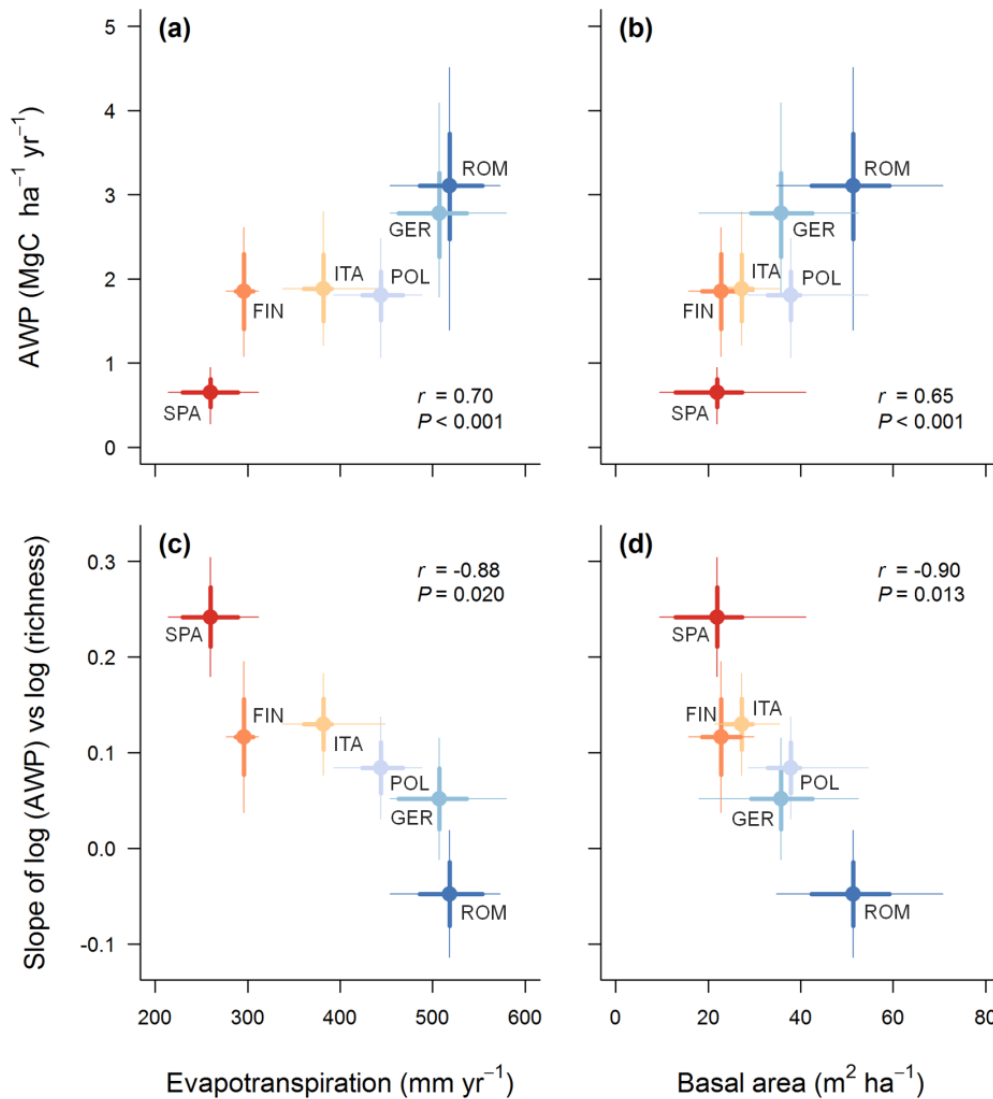
Fig. 2: Variation in (a–b) above-ground wood production (AWP) and (c–d) the slope of the AWP – species richness relationship among sites. Panels on the left show how evapotranspiration (AET) influences (a) AWP and (c) the strength of the AWP – species richness relationship, while right-hand panels (b and d) illustrate variation in response to plot basal area. For AWP and basal area, points represent mean values across all plots within a site, while AET is the long-term mean annual evapotranspiration registered at each site (between 1997 and 2011). Error bars delimit the interquartile range (thick lines) and 95% limits (thin lines) of the data. Slopes of log (AWP) vs log (species richness) were obtained

[35]

724   from equation 2 in the main text (thick lines: ±1 SE; thin lines: ±2 SE). Points are labelled

725   using the first three letters of each site. Pearson's correlation coefficients (*r*) and

726   corresponding *P*-values reported in the top panels (a–b) were calculated for $n = 209$

727   (corresponding to the number of FunDivEUROPE forest plot), while for the bottom panels

728   (c–d) $n = 6$ (corresponding to the number of FunDivEUROPE sites).

729
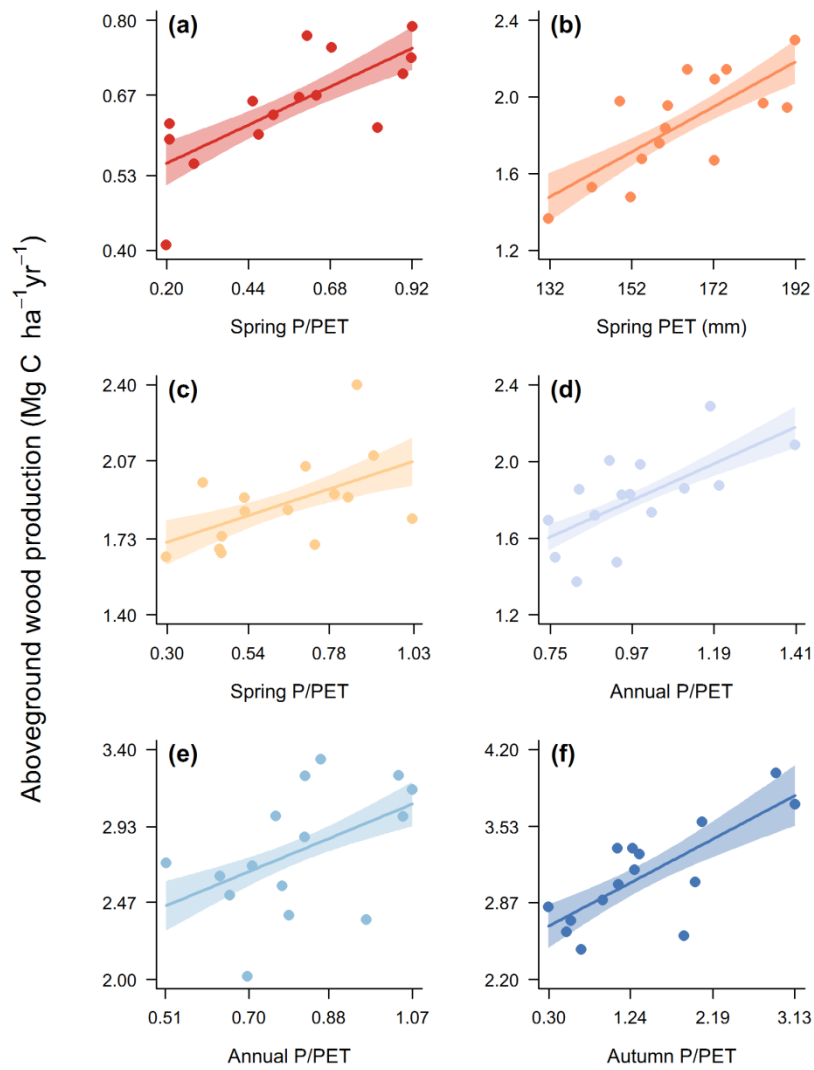
Fig. 3: Variation in annual above-ground wood production (AWP) as a function of climate for (a) Spain, (b) Finland, (c) Italy, (d) Poland, (e) Germany and (f) Romania. Points correspond to the mean AWP of each year (1997 to 2011; calculated across all plots within a site). Fitted relationships from linear regression models (with shaded 95% confidence intervals) are shown for each panel (see Table 2 for regression equations). PET = potential evapotranspiration; P/PET = precipitation / PET.
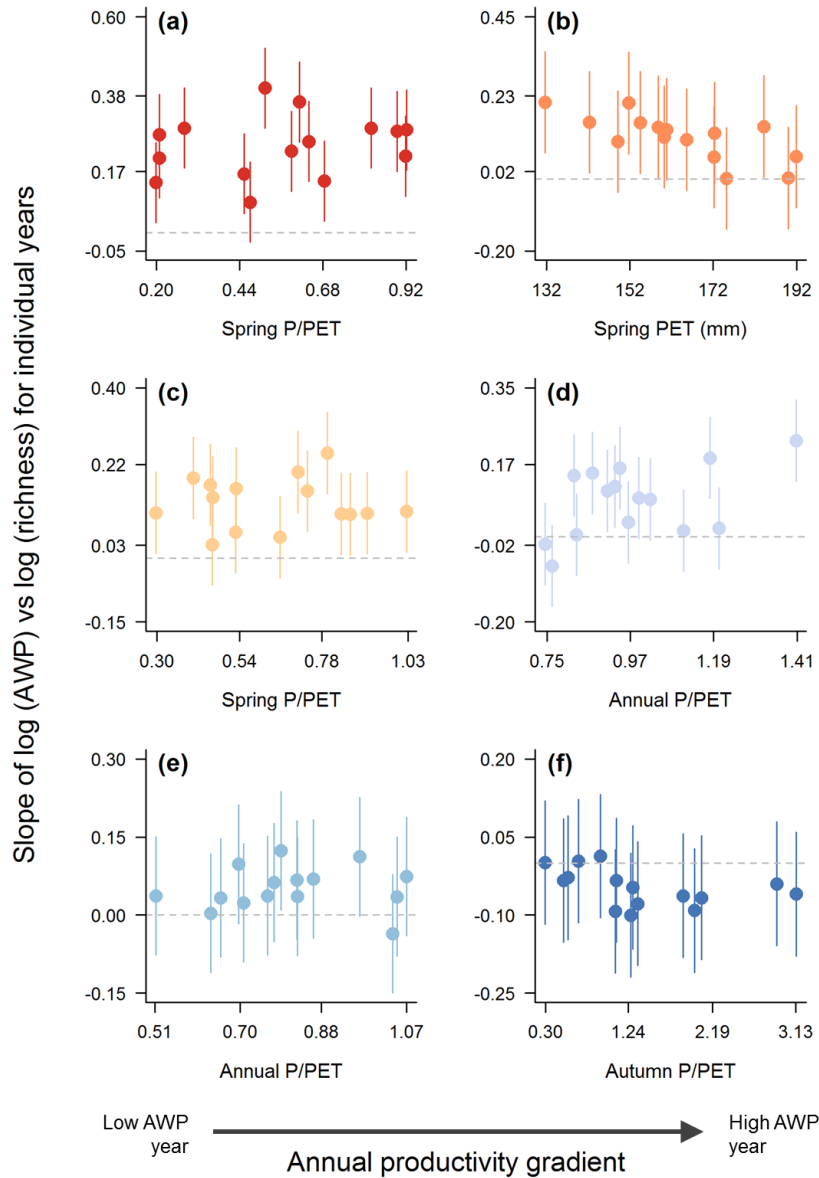
[37]

Fig. 4: Interannual variation in the slope of the AWP – species richness relationship as a function of climate in (a) Spain, (b) Finland, (c) Italy, (d) Poland, (e) Germany and (f) Romania. Slopes (±1 SE) of log (AWP) vs log (species richness) for each year between 1997 and 2011 are estimates from a linear regression model (equation 2 in the main text). Dashed grey lines mark a slope of zero. PET = potential evapotranspiration; P/PET = precipitation / PET.

[38]