Climate modulates the effects of tree diversity on forest productivity

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Running headline: Biodiversity and wood production in forests

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 productivity at either end of the latitudinal gradient, where adverse climatic conditions limit productivity and lead to the development of less densely packed stands.

Key-words: above-ground wood production; biodiversity – ecosystem functioning; context dependency; FunDivEUROPE project; plant-climate interactions; stress gradient hypothesis; 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 is that they are not constant in space, but instead shift in importance and intensity along environmental gradients (Brooker *et al.* 2008). This is conceptualized in the stress gradient hypothesis, which predicts that under increasingly stressful environmental conditions competitive interactions weaken and give way to facilitative processes (see Maestre *et al.*, 2009 for a review). Following this reasoning, it has been hypothesized that biodiversity – ecosystem functioning relationships should also vary along environmental gradients (Fig. 1a), becoming progressively stronger as conditions for growth become less favourable (Jucker & Coomes 2012; Gessner & Hines 2012; Wang *et al.* 2013; Forrester 2014). In forests, competitive interactions among neighbouring trees have been shown to vary in strength along environmental gradients (Kunstler *et al.* 2011; He, Bertness & Altieri 2013; Prior & Bowman 2014), and evidence suggests that positive relationships between diversity and productivity are in fact more common where environmental conditions are most limiting (Paquette & Messier 2011; Wu *et al.* 2014; Toïgo *et al.* 2015). A possible explanation for these patterns is that the relationship between diversity and productivity shifts in strength as a result of changes in forest structure which unfold along environmental gradients (Condés, Del Rio & Sterba 2013). For instance, Potter & Woodall (2014) showed that across the USA forest biomass is most strongly related to species richness at sites where unfavourable climatic conditions result in low stem packing densities.

In addition to focusing on spatial environmental gradients, it has also been suggested that interannual variation in climate may influence the strength of the relationship between diversity and productivity (Forrester 2014). In most cases, the expectation seems to be that temporal responses to environmental stress should mirror those observed along spatial 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

STUDY DESIGN

The study was conducted in the FunDivEUROPE permanent forest plot network, the design of which is described in detail in Baeten *et al.* (2013). Here we summarize the key features of the FunDivEUROPE network, which we supplement with a detailed description of the rationale and design of the project in Appendix S1 of Supporting Information. The plot network consists of 209 permanent forest plots (30 × 30 m in size) distributed in six countries across Europe (hereafter referred to as "sites"). Field sites were chosen to represent major European forest types, and include boreal forests in Finland, hemiboreal mixed forests in Poland, beech forests in Germany, mountainous beech forests in Romania, thermophilous deciduous forests in Italy and Mediterranean mixed forests in Spain. At each site, plots contain different combinations of locally dominant tree species, and range in species richness from 1-3 in Finland, 1-4 in Romania, Germany, Italy and Spain, and 1-5 in Poland (see Table S1 for a full species list). Each target tree species is found in monoculture and is represented in all species richness levels, with the majority of species' combinations being replicated at least twice (59 of 91 combinations). This nested design approach was modelled around that of the BIOTREE, ORPHEE and FORBIO tree diversity experiments (see Baeten *et al.*, 2013 and references therein). Plots were selected following a set of strict criteria designed to allow robust comparisons among species richness levels. Specifically, species in mixture share similar relative abundances (i.e., high species evenness; Fig. S3) and the presence of non-target species is minimal (< 5% of the total basal area). In addition, plots were established exclusively in mature forest stands (i.e., those at least in the mid-to-late stages of stem exclusion) with similar management histories. Lastly – and critically for the purposes of this study – great care was taken to ensure that (i) plots within a site share similar environmental conditions and (ii) that stand attributes known to influence productivity (e.g., stem density and stand age; Magnani, Mencuccini & Grace 2000; Kadmon & Benjamini 2006) were not confounded with the species richness gradient (see Appendix S1 and Fig. S4). Consequently, while sites differ markedly from one another in terms of climate and forest structure (e.g., basal area, stem density, maximum height), plots within a site are spatially clustered and have similar elevation, topography and soil type.

ALLOMETRIC DATA

In each plot, all stems ≥7.5 cm in diameter were identified to species and permanently marked (12939 stems in total). We recorded the diameter (measured to the nearest 0.1 cm at a height of 1.3 m off the ground using diameter tape) and height (to the nearest 0.1 m using a vertex hypsometer, Haglöf AB, Sweden) of each stem, and used these measurements to estimate the above-ground biomass of each tree based on published biomass functions (see Jucker *et al.*, 2014a for a complete list of equations used). We also characterized the crown dominance of each tree using the crown illumination index, which consists in scoring trees from 1 (suppressed crown receiving no direct light) to 5 (fully exposed dominant crown) (Clark & Clark 1992). Crown illumination scores are an effective way of gauging the degree to which a tree is shaded by its neighbours (Jennings, Brown & Sheil 1999; Jucker *et al.* 2014b), and were used to model the effects of competition for light on tree growth (see following section).

CLIMATE DATA

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, Saltsjöbaden, Sweden). Finally, radial increments for each year between 1997 and 2011 were converted to annual biomass growth (kg C yr^{-1}) using the biomass functions described above. Biomass growth was expressed in units of carbon by applying the standard conversion of 0.5 g C per gram of biomass.

Modelling individual tree biomass growth

For each year between 1997 and 2011, we used linear mixed-effects models coded in R (3.0.1; R Core Development Team, 2013) to model the biomass growth (*G*) of each target species as a function of tree size, competition for light, species richness and a random plot effect:

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

where D_i and CI_i are, respectively, the stem diameter and crown illumination index of tree *i* growing in plot *j* (as measured in 2011); SR_j is the species richness of plot *j*; $\beta_{0_{j[i]}}$ is a species' intrinsic growth rate for a tree growing in plot *j* (*sensu* Rüger *et al.*, 2012); $\beta_{1\text{-}3}$ are, respectively, a species' growth response to size, light availability and species richness; and ε_i is the residual error. Equation 1 effectively captured variation in biomass growth within and among species [average R^2 across species = 0.80; for further information see Jucker *et al.* (2014a)].

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

Equation 1 was used to estimate the annual biomass growth of all trees that had not been cored for each year between 1997 and 2011. The annual AWP of each plot was then quantified by summing the biomass growth of all trees within a plot. This step was repeated for each year between 1997 and 2011 to generate a 15-year time series of AWP for all 209 plots. This approach to estimating AWP was chosen after having ruled out potential biases associated with temporal autocorrelation in the AWP time series (see Appendix S2). Similarly to previous diversity – productivity studies in forests (e.g., Paquette & Messier 2011; Vilà *et al.* 2013), estimates of AWP are based exclusively on the growth of trees present in 2011, with the implicit assumption that mortality rates are unrelated to tree species diversity (Liang *et al.* 2007).

RELATING VARIATION IN AWP ACROSS AND WITHIN SITES TO CLIMATE

We combined data on AWP and climate to identify which climatic predictors best explain variation in wood production across sites (i.e., spatial variation in AWP) and within them (i.e., interannual variation in AWP). To understand how differences in climate among sites shape geographic patterns of wood production, we calculated mean annual values of T, P, R, AET, PET and P/PET for each study site and related these to mean annual AWP using univariate regressions (Appendix S3). Following the same approach, we also tested the ability of climatic predictors to explain interannual variation in AWP within sites. For each site, we aggregated daily climate values to obtain both yearly and seasonal (spring = March, April, May; summer = June, July, August; autumn = September, October, November) estimates of T, P, R, AET, PET and P/PET for each year between 1997 and 2011. We then fitted univariate regressions relating interannual variation in AWP within sites to each climatic predictor in turn (Appendix S3).

STATISTICAL MODELLING OF AWP – DIVERSITY RELATIONSHIPS

We devised a two-step approach to test whether AWP – diversity relationships change predictably (i) across sites and (ii) among years within a site (Fig. 1). We first used a linear regression model to estimate the effects of species richness on AWP (i.e., the slope of the AWP – species richness relationship) for (i) each site and (ii) for every year within a site. We then related the slope estimates obtained from the model to (i) differences in climate and packing density among sites, and (ii) interannual variation in climate within sites (e.g., Reich *et al.*, 2012; Wu *et al.*, 2014). We favoured this approach over one in which climatic effects on AWP were modelled directly, as it allows the strength of the species richness effect on AWP to be intuitively compared both among and within sites (Nakagawa & Cuthill, 2007).

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

We modelled AWP as a function of (i) species richness, (ii) plot basal area (to account for the effects of stem packing density on productivity), (iii) site (i.e., accounting for variation in AWP among study sites), (iv) year nested within site (i.e., allowing AWP to vary among years within each site), (v) an interaction term between species richness and site (testing whether species richness effects on AWP vary among sites), and (vi) an interaction term between species richness and year nested within site (to determine whether species richness effects on AWP vary among years within sites):

$$\log(AWP_{ijk}) = \beta_0 + \beta_1\log\left(BA_{ij}\right) + \beta_2\log\left(SR_{ij}\right) + \beta_3\text{Site}_j + \beta_4\text{Year}_{jk} + \beta_5\left[\log\left(SR_{ij}\right) \times \text{Site}_j\right] + \beta_6\left[\log\left(SR_{ij}\right) \times \text{Year}_{jk}\right] + \varepsilon_{ijk} \qquad \text{(eqn 2)}$$

where AWP_{ijk} is the above-ground wood production of plot i in site j in year k; SR_{ij} and BA_{ij} are, respectively, the species richness and basal area of plot i in site j; $Site_j$ and $Year_{jk}$ are categorical grouping variables which capture how AWP varies among the j sites and among the k years within each of the j sites, respectively; $\beta_0 - \beta_6$ are parameters to be estimated from the data (i.e., intercept and slope coefficients); and ε_{ijk} is the residual error.

In equation 2, both “Site” and “Year” were modelled as fixed effects so that we could estimate uncertainties for all parameters. To verify the robustness of the parameter estimates obtained from equation 2 (particularly β_5 and β_6, which define how the effect of tree diversity on AWP varies across and within sites), we first compared them with those estimated using a mixed-effects modelling approach. In addition to this, we also fitted an additional model in which we accounted for a number of potentially confounding factors which could conceivably alter the relationship between tree diversity and AWP (elevation, terrain slope, soil depth, rock cover and stand age). As all three approaches yielded almost identical results (see Appendix S4), here we focus on the parameter estimates obtained through equation 2. Note that support for the interaction terms in equation 2 was assessed through comparison with simpler models lacking interacting effects.

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

From equation 2 we obtained the slope of the AWP – species richness relationship for (i) each site (i.e., β_5) and (ii) for all years within a site (i.e., β_6). We then used Pearson’s correlation coefficients (r) to explore whether (i) variation in the strength of the species richness effect among sites is related to differences in macroclimate and/or basal area (a measure of tree packing density which captures both the mean size and number of trees within a plot) (Curtis & Marshall 2000), and (ii) whether the influence of species richness on AWP changes over time within a site depending on how suitable climatic conditions are in a given year.

Results

INFLUENCE OF CLIMATE AND PACKING DENSITY ON AWP

AWP varied considerably among sites (M2 vs M1 in Table 1), differing almost fivefold between Spain (0.65 Mg C ha^{-1} yr^{-1}) – the least productive site – and Romania (3.11 Mg C ha^{-1} yr^{-1}), where AWP rates were highest. Geographic variation in AWP was strongly related to differences in evapotranspiration among sites (Fig. 2a; see Appendix S3 for comparison with other climatic drivers). Sites where annual AET was low – either because of insufficient rainfall (e.g., Spain) or low temperatures (e.g., Finland) – had much slower rates of AWP than those where AET was high (e.g., Germany and Romania). However, AET was only a weak predictor of interannual variation in AWP within sites (see Table S2 and following paragraph). Instead, we found that increased annual AET was associated with the development of forests with greater basal areas (Fig. S7). This in turn resulted in markedly faster rates of AWP – as basal area was a key driver of AWP across the plot network (Fig. 2b and Table 1) – suggesting that at least in part the link between evapotranspiration and productivity is mediated through changes in stand packing density.

In addition to varying across sites, AWP also fluctuated strongly among years within each site (M3 vs M2 in Table 1). Climate explained much of this interannual variation in productivity (Fig. 3), with a clear distinction emerging between Finland – where AWP was co-limited by temperature and solar radiation – and all other sites – where annual growth was instead primarily water-limited (Table 2). In Finland, the single best climatic predictor of annual AWP was spring PET (Fig. 3b and Table 2), with productivity peaking in years characterized by high solar radiation and mild spring temperatures which together contributed to high PET rates (Table S2). For all other sites, fluctuations in annual AWP was best captured by P/PET (Table 2), with productivity declining sharply in years when evaporative demands (i.e., PET) were not met by precipitation (Fig. 3a,c-f). The timing of drought proved equally important in explaining AWP patterns. For both Mediterranean sites, low P/PET values during spring months were associated with strong reductions in AWP (Fig. 3a,c), while summer drought had a much less pronounced influence on productivity (Table S2). In contrast, for Germany and Poland the best predictor of AWP was P/PET integrated over the entire year (Fig. 3d-f), while in Romania AWP was influenced by autumn P/PET (Fig. 3e). Note that for all sites, AWP – climate relationships were best captured by linear functions (see Table 2 for estimated regression coefficients).

AWP – DIVERSITY RELATIONSHIPS ACROSS SITES

We found strong support for the inclusion of the interaction term between species richness and “site” in equation 2 (M4 vs M3 in Table 1), indicating that the effect of species richness on AWP varies substantially across sites. In accordance with the stress gradient hypothesis (Fig. 1a), the slope of the AWP – species richness relationship decreased progressively along the AET climatic productivity gradient (r = -0.88, P = 0.020, n = 6; Fig. 2c), ranging from strongly positive in Spain (0.24 ± 0.06) – where evapotranspiration and productivity were low – to weakly negative in Romania (-0.05 ± 0.07) – where AET and AWP were greatest. This shift in the strength of the diversity effect on productivity was equally well captured by accounting for differences in basal area across sites (r = -0.90, P = 0.013, n = 6), with diversity effects being strongest at sites where environmental conditions led to the development of less densely packed stands (Fig. 2d and Fig. S7).

AWP – DIVERSITY RELATIONSHIPS WITHIN SITES

In contrast to patterns across sites, we found little evidence to suggest that species richness effects on AWP varied strongly among years within sites (M5 vs M4 in Table 1). Furthermore, we found no consistent relationship between the strength of the species richness effect on AWP and climatic conditions within a given year when looking across the six sites (Fig. 4). The only site to show a relationship between the magnitude of the species richness slope and climate was Finland (Fig. 4b), where species richness effects weakened in years when spring PET was high and climatic conditions for growth were favourable (r = -0.73, P < 0.01, n = 15). A similar response was found for Romania, although the pattern between diversity effects and climate (autumn P/PET) was weaker (r = -0.44, P = 0.10, n = 15; Fig. 4f). Instead, in the case of Poland (Fig. 4d), and to a much lesser extent Spain (Fig. 4a), we observed the opposite trend, with diversity effects strengthening during non-drought years (r = 0.49, P = 0.06 and r = 0.21, P = 0.45, respectively; n = 15). These observations do not support the predictions of the stress gradient hypothesis (Fig. 1b). Lastly, in the case of Italy (Fig. 4c) and Germany (Fig. 4e) we found no discernible pattern linking diversity effects and climatic conditions across years (r = 0.03, P = 0.93 and r = 0.05, P = 0.87, respectively; n = 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 variation in productivity within sites (Tables S2), sites with higher mean annual AET also had greater basal areas, which in turn drove faster rates of wood production (Fig. 2b).

The strength of the species richness effect on productivity also shifted along the evapotranspiration gradient, and was strongest at sites where AET was low – either as a result of low annual rainfall (e.g., Spain) or because of low temperatures (e.g. Finland) – and conditions for growth were poor (Fig. 2c). Conversely, at sites where conditions for growth were more favourable, we saw a drastic reduction in the importance of diversity as a driver of wood production. These results are broadly consistent with the predictions of the stress gradient hypothesis (Fig. 1a), as well as the findings of a number of recent papers (Paquette & Messier 2011; Jucker & Coomes 2012; Wu *et al.* 2014; Toïgo *et al.* 2015). For instance, using forest inventory data from France, Toïgo *et al.* (2015) showed that overyielding was more frequent at low productivity sites. Similarly, Wu *et al.* (2014) found that the strength of the relationship between tree diversity and biomass weakened when transitioning from boreal, to temperate and subtropical forests in China.

In addition to the stress gradient hypothesis, a number of alternative frameworks have also been proposed to explain how environmental conditions shape the relationship between diversity and productivity. For instance, Forrester (2014) noted that the outcome of species interactions will depend on the type of limiting resource or resources (e.g., water, light, nutrients), and whether – on average – interactions among neighbouring trees improve the availability of those resources (also see Pretzsch *et al.* 2015). What our results suggest is that the net outcome of species interactions shifts along environmental gradients and that – on balance – competition tends to decrease in importance in more stressful environments allowing greater room for complementarity (Kunstler *et al.* 2011; Prior & Bowman 2014).

Climate can influence interactions among neighbouring trees directly by modulating the relative performance and strategy of species within a community (Brooker *et al.* 2008; Maestre *et al.* 2009). In addition to this, climate can influence interactions among neighbouring trees indirectly through its effect on forest structure. Climate plays an important role in determining local species pools through environmental filtering (e.g., Stahl *et al.*, 2014), as well as shaping species demographic rates (Lines, Coomes & Purves 2010; Vanderwel, Lyutsarev & Purves 2013; Coomes *et al.* 2014) and influencing how trees allocate carbon above and below-ground (Lines *et al.* 2012; Reich *et al.* 2014), all of which interact to determine forest structure. As our results suggest that positive AWP – diversity relationships are much more likely in forests with low packing densities (Fig. 2d), the effect of climate on forest structure appears to be particularly important in modulating the effects of diversity on productivity (Condés *et al.* 2013; Potter & Woodall 2014). This may explain why in Mediterranean forests, where drought impedes the development of densely packed stands, the effects of diversity on productivity tend to be strongly positive (Vilà *et al.* 2007; Ruiz-Benito *et al.* 2014; Jucker *et al.* 2014b).

INTERANNUAL FLUCTUATIONS IN CLIMATE HAVE WEAK AND IDIOSYNCRATIC EFFECTS ON AWP –DIVERSITY RELATIONSHIPS WITHIN SITES

AWP responses to interannual fluctuations in climate within sites closely matched expectations based on published reports, with most forest types in Europe being primarily limited by water availability, while productivity in boreal forests depends strongly on temperature and solar radiation (Boisvenue & Running 2006; Babst *et al.* 2013). In terms of AWP – diversity relationships, we generally found that variation within sites was considerably weaker than variation among them (Table 1). Moreover, we found no evidence of consistent pattern linking variation in diversity effects across years to climate (Fig. 4). Certain functional responses match expectations, such as the decreased strength of diversity effects during warmer years in Finland (Fig. 4b). In boreal systems, warmer springs are associated with earlier leaf-out dates (Polgar & Primack 2011). While this positively influences productivity by increasing the length of the growing season (Chen *et al.* 1999; Polgar & Primack 2011), it is also likely to reduce the degree of phenological mismatch (i.e., temporal complementarity) between evergreen conifers and deciduous broadleaf species (Sapijanskas *et al.* 2014). In contrast, we found no consistent effect of drought on the strength of diversity effects across forest types (Grossiord *et al.* 2014). For Spain, our results generally confirm those of a previous study comparing responses in two years with contrasting climate (a drought year and a wet year), which showed that drought tends to exacerbate competition among neighbouring trees (Jucker *et al.* 2014b). However, in the case of Poland, Germany and Romania we find strongly contrasting patterns despite the fact that these sites share similar species compositions and have broadly similar climates.

Differences between responses across sites – which strongly matched theoretical predictions – and those within sites – which instead exhibited weak and contrasting patterns – suggest that in addition to climate itself, a key factor in shaping the strength of diversity effects on productivity is how densely trees pack in space. If the relationship between diversity and productivity was directly influenced by climate, diversity effects would be expected to shift consistently both across and within sites. Instead, under the assumption that packing density is what ultimately determines the strength of the relationship between diversity and productivity (Condés *et al.* 2013; Potter & Woodall 2014), temporal patterns would be unlikely to match spatial trends. The reason for this is that although basal area varies strongly among sites (Fig. 2b), changes in packing density are decoupled from interannual variation in climate in forest ecosystems (i.e., basal area does not increase or decrease markedly from one year to next based on climatic suitability). Recent work in coastal dunes plant communities has shown that shifts from competition to facilitation among years depend critically on differences in vegetation cover: during years characterized by harsh environmental conditions vegetation cover decreases, resulting in an increase in facilitation, while in more favourable years increased vegetation cover exacerbates competition (Doxford, Ooi & Freckleton 2013). However, because trees are long-lived and do not regenerate the bulk of their above-ground biomass each year, a similar response in terms of basal area cannot be observed in forests (Stephenson & Mantgem 2005). As a result, the way in which diversity effects change among years may simply be more context dependent in the case of forests [e.g., highly dependent on species' traits or on the type of limiting resource; Forrester (2014)].

IMPLICATIONS FOR FOREST CONSERVATION AND MANAGEMENT

Identifying where and when tree diversity has the greatest potential to positively influence forest productivity has important implications for forest management and conservation practises, as well as efforts to mitigate climate change (Zhang *et al.* 2012; Cardinale *et al.* 2012; Scherer-Lorenzen 2014). We found that in terms of maximising rates of wood production, the benefits of maintaining diverse forests are most pronounced in systems where environmental conditions strongly limit productivity. While our study provides a useful framework for predicting under which conditions tree diversity is likely to matter most, there are however several reasons why practises aimed at maintaining diverse forests should not necessarily be limited to specific ecological contexts or geographic regions. For instance, in addition to promoting forest productivity, tree diversity has also been shown to help stabilize wood production over time across a range of forest types, highlighting the fact that mixed-species forests are able to remain productive under a wider range of environmental conditions than monocultures (Jucker *et al.* 2014a; Morin *et al.* 2014). Secondly, although we detected clear differences in the importance of tree diversity as a driver of productivity among forest types, only one site showed any indication of a negative association between diversity and productivity. Consequently, even though gains in productivity may be negligible for certain forest types, maintaining diverse forests is unlikely to adversely affect wood production and has the advantage of delivering a number of added ecological and economic co-benefits (e.g., reduced risk of pest and pathogen outbreaks, increased associated biodiversity, greater soil carbon storage; Scherer-lorenzen, 2014).

In addition to highlighting under which circumstance tree diversity is currently most important for forest productivity, our study also provides a number of clues as to how climate change is likely to influence AWP – diversity relationships in future forests. By the end of this century Mediterranean forests in Europe are expected to suffer more frequent and prolonged periods of drought, while boreal systems are predicted to warm considerably and experience longer growing seasons (Jacob *et al.* 2014). As a result, diversity effects may weaken in strength, particularly in the case of boreal forests where spring warming is expected to reduce the degree of phenological mismatch among coexisting tree species (Polgar & Primack 2011). More importantly, however, our results suggest that longer-term responses of forests to climate change – such as changes in species composition and forest structure – are what will ultimately determine how the relationship between tree diversity and forest productivity will look like in the future.

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Data Accessibility

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

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Supporting information

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

Appendix S1: FunDivEUROPE project

Appendix S2: Temporal autocorrelation in AWP

Appendix S3: Relating variation in AWP to climate

Appendix S4: Estimating diversity effects across and within sites

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

Tables

Table 1: Model comparison statistics for a set of candidate models testing whether diversity effects on above-ground wood production (AWP) vary across and within sites. In the baseline model (M1), AWP is expressed as a function of plot basal area (BA) and species richness (SR). “Site” indicates a model which accounts for variation in AWP among sites, while “Year” tests whether AWP varies among years within each site. Model M4 tests whether the effects of SR on AWP varies among sites (i.e., interaction between SR and Site), while model M5 further allows species richness effects to vary among years within a site (i.e., interaction between SR and Year) and corresponds to equation 2 in the text. Models of increasing complexity were compared to simpler ones (e.g., M5 vs M4) using F-tests to determine whether the reduction in the residual sum of squares between models was statistically significant ($\alpha = 0.05$). In addition to this we also report the R^2 and AIC of each model. Note 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

Table 2: Best climatic predictors of interannual variation in above-ground wood production (AWP) for each study site. Regression equations (with 95% confidence intervals for parameter estimates in brackets) correspond to fitted relationships illustrated in Fig. 3. To facilitate the interpretation of regression coefficients, climatic predictors were cantered prior to model fitting (i.e., for each site, intercepts indicate the mean AWP across years). PET = potential evapotranspiration; P/PET = precipitation/PET.

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

Figures

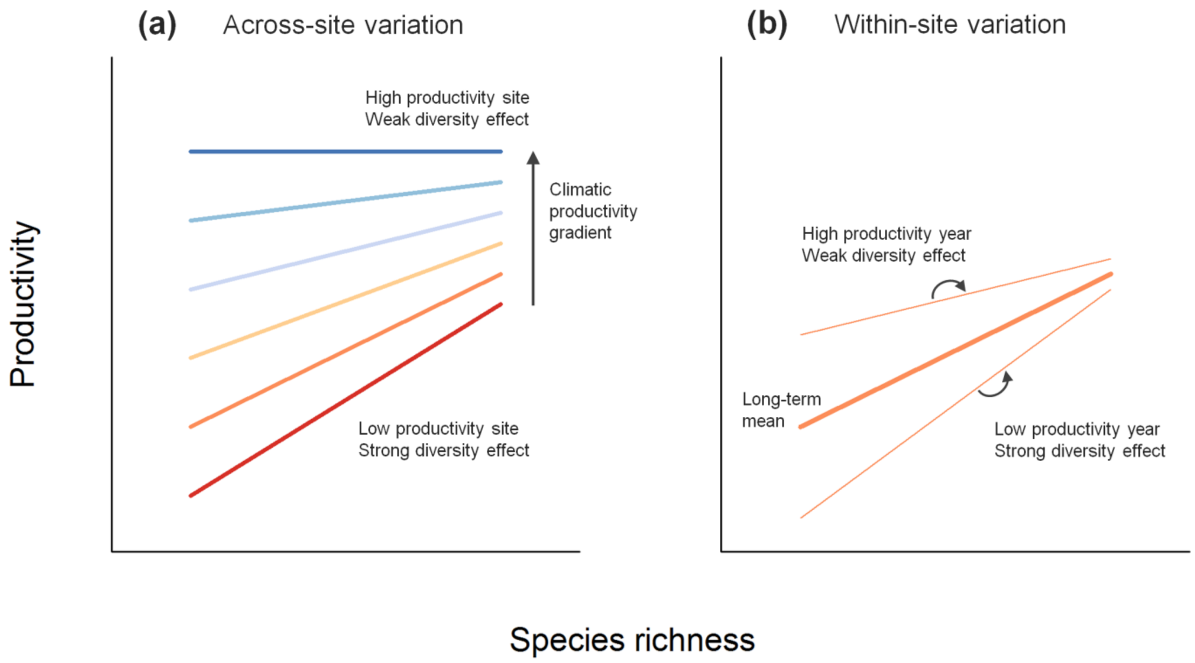

Fig. 1: Schematic diagram illustrating how the relationship between productivity and diversity is expected to change (a) across sites along an environmental gradient and (b) among years within a site. Panel (a) depicts different sites along an environmental gradient. Sites where productivity is low (e.g., as a result of strong environmental limitations on growth) exhibit strong positive effects of diversity on productivity, while sites where growing conditions are more favourable show little or no benefit from species mixing. Panel (b) illustrates how the effects of diversity on productivity vary among years within a given site. The expectation is that the slope of the diversity – productivity relationship will be steeper than average in low productivity years, weakening instead when conditions for growth improve.

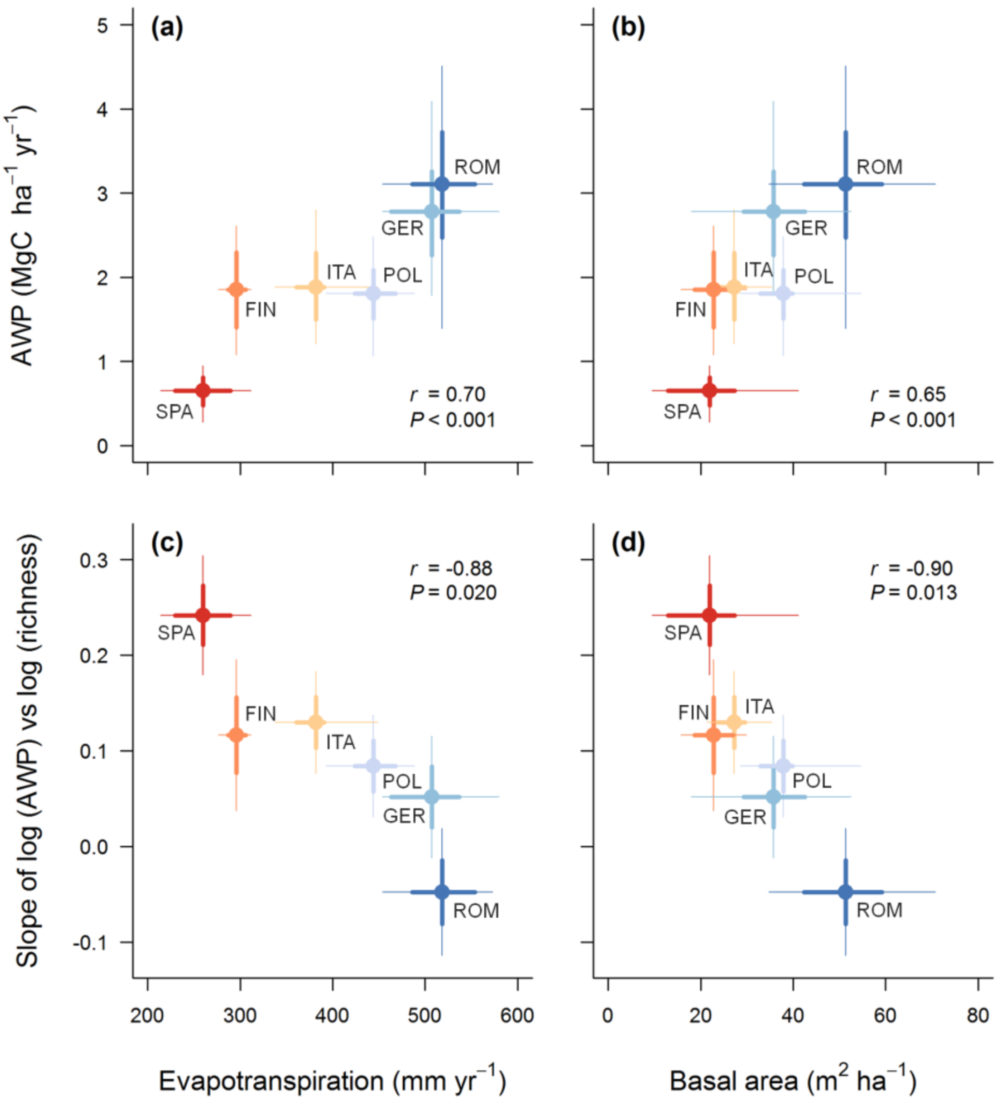

Fig. 2: Variation in (a–b) above-ground wood production (AWP) and (c–d) the slope of the AWP – species richness relationship among sites. Panels on the left show how evapotranspiration (AET) influences (a) AWP and (c) the strength of the AWP – species richness relationship, while right-hand panels (b 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

from equation 2 in the main text (thick lines: ±1 SE; thin lines: ±2 SE). Points are labelled using the first three letters of each site. Pearson's correlation coefficients (*r*) and corresponding *P*-values reported in the top panels (a–b) were calculated for *n* = 209 (corresponding to the number of FunDivEUROPE forest plot), while for the bottom panels (c–d) *n* = 6 (corresponding to the number of FunDivEUROPE sites).

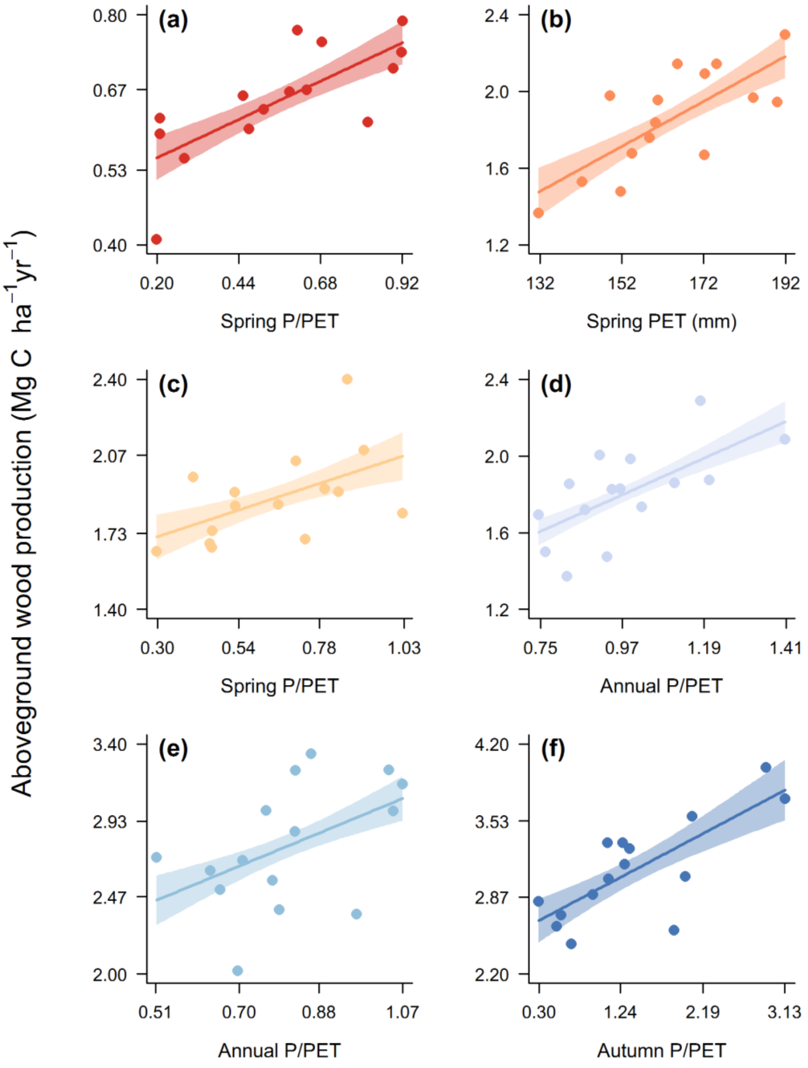

Fig. 3: Variation in annual above-ground wood production (AWP) as a function of climate for (a) Spain, (b) Finland, (c) Italy, (d) Poland, (e) Germany and (f) Romania. Points correspond to the mean AWP of each year (1997 to 2011; calculated across all plots within a site). Fitted relationships from linear 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.

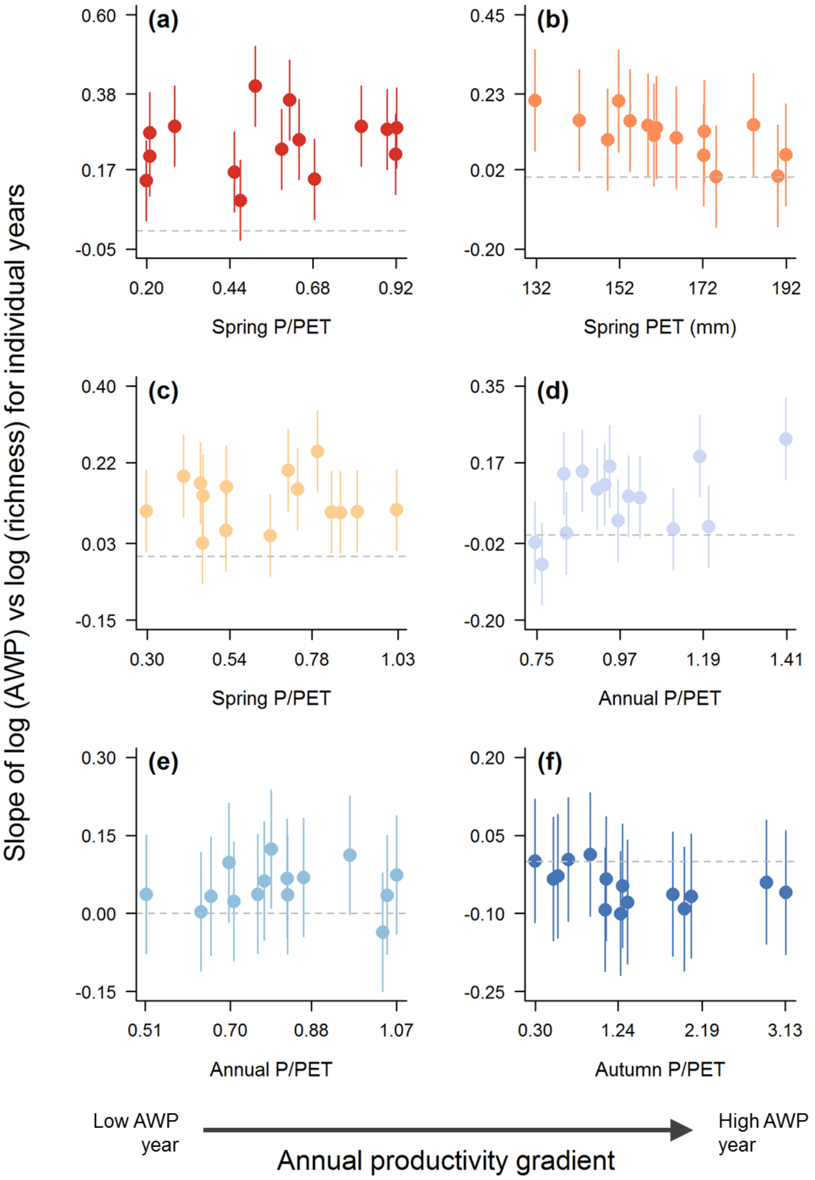

Fig. 4: Interannual variation in the slope of the AWP – species richness relationship as a function of climate in (a) Spain, (b) Finland, (c) Italy, (d) Poland, (e) Germany and (f) Romania. Slopes (±1 SE) of log (AWP) vs log (species richness) for each year between 1997 and 2011 are estimates from a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