

1 Modes of functional biodiversity control on tree productivity across the

2 European continent

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ABSTRACT

Aim

The relative contribution of community functional diversity and composition to ecosystem functioning is a critical question in ecology in order to enable better predictions of how ecosystems may respond to a changing climate. However there is little consensus of which modes of functional biodiversity are most important for tree growth at large spatial scales. Here we assessed the relative importance of climate, functional diversity and functional identity (i.e. the community mean values of four key functional traits) for tree growth across the European continent, spanning the northern boreal to the southern Mediterranean forests.

Location

Finland, Germany, Sweden, Spain and Wallonia (Belgium)

Methods

Using data from five European National Forest Inventories we applied a hierarchical linear model to estimate the sensitivity of tree growth to changes in climate, functional diversity and functional identity along a latitudinal gradient.

Results

Functional diversity was weakly related to tree growth in the temperate and boreal regions and more strongly in the Mediterranean region. In the temperate region, where climate was the most important predictor, functional diversity and identity had a similar importance for tree growth. Functional identity was strongest at the latitudinal extremes of the continent, largely driven by strong changes in the importance of maximum height along the latitudinal gradient.

Main conclusions

Functional diversity was an important driver of tree growth in the Mediterranean region, providing evidence that niche complementarity may be more important for tree growth in water-limited forests. The strong influence of functional identity at the latitudinal extremes indicates the importance of a particular trait composition for tree growth in harsh climates. Furthermore, we speculate that this functional identity signal may reflect a trait-based differentiation of successional stages rather than abiotic filtering due to water or energy limitation.

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INTRODUCTION

With the increasing threat of climate and land-use change there is deepening concern that continued biodiversity loss may jeopardise key ecosystem services (Cardinale *et al.*, 2012; Thomas *et al.*, 2013). Therefore it is becoming ever more critical to improve our understanding of the interplay between abiotic and biotic controls on ecosystem processes (Díaz *et al.*, 2007; Hillebrand & Matthiessen, 2009), especially at scales relevant to conservation policy makers (Thomas *et al.*, 2013; Violle *et al.*, 2014). The functional structure of a community (i.e. the distribution and relative abundance of plant functional traits) is known to directly influence ecosystem processes (Díaz *et al.*, 2007) and recently there have been several large-scale observational studies in forests with a focus on detecting an influence of diversity on tree productivity (e.g. Paquette & Messier, 2011; Vilà *et al.*, 2013; Ruiz-Benito *et al.*, 2014). However, the relative importance of functional diversity and composition for tree growth has received little attention at large spatial scales (Conti & Díaz, 2013), despite its importance for understanding how forests may respond to climate change (Violle *et al.*, 2014).

Two central mechanisms underpin how plant functional traits can influence ecosystem processes: the niche complementarity hypothesis (Tilman, 1994) and Grime's mass ratio hypothesis (Grime, 1998). Functional diversity (FD), i.e. the dispersion of trait values in a community (Laliberté & Legendre, 2010), is hypothesised to increase the ways in which species access and utilise resources, allowing a greater resource use and niche packing in more functionally diverse communities. Evidence from natural forests for the niche complementarity hypothesis is mixed, with both positive (Paquette & Messier, 2011; Ruiz-Benito *et al.*, 2014) and negative (Conti & Díaz, 2013) diversity effects found. Congruent with the mass ratio hypothesis, the functional identity (FI), i.e. community mean trait values (Violle *et al.*, 2007), are hypothesised to greatly influence community-level processes. FI has

consistently been found to be a key component through which plant traits control productivity, and is often found to be more important than the functional diversity of the community (Mokany *et al.*, 2008; Conti & Díaz, 2013; but see Valencia *et al.*, 2015).

The European continent spans large gradients in climate and resource availability, from the northern boreal latitudes where productivity is primarily limited by energy (i.e. temperature and radiation; Körner 1998) to southern Mediterranean latitudes where water is the primary limiting resource (Babst *et al.*, 2013). In the temperate mid-latitudes neither energy nor water is strongly limiting, and, as a consequence, productivity peaks there (see Fig. 1). Thus stressful climatic conditions predominate at the southern and northern extremes of the European continent but are exerted by different environmental constraints (i.e. lack of water versus a lack of energy). Along such a climatic gradient competitive interactions and abiotic filtering assembly processes act on community functional structure (Maire *et al.*, 2012) and thus ecosystem functioning (Spasojevic & Suding, 2012).

According to Harpole & Tilman (2007) the number of resource-related niche dimensions is greater in stressful environments and more species with a particular specialisation in acquiring resources are needed to maintain productivity. We therefore expect productivity at the extremes of our latitudinal gradient to be most sensitive to functional trait diversity, as a proxy for the potential degree of niche complementarity realised by a community. Recent observational studies in forests support this view (Paquette & Messier, 2011; Jucker *et al.*, 2014a). However, the evidence is equivocal, and other studies have found no difference in the importance of functional diversity for tree growth between regions with different productivity rates (e.g. Zhang *et al.*, 2012; Ruiz-Benito *et al.*, 2014). Environmental filters increase the functional similarity of species through abiotic constraints that select for particular trait expressions generally characterising the locally most productive and best adapted tree species (Wright *et al.*, 2005; Cornwell & Ackerly, 2009). At the same time, competition between

species with similar resource acquisition abilities can result in community trait convergence (Mayfield & Levine, 2010; Kraft *et al.*, 2015). Given that abiotic filtering and competition occur in all biomes, we predict functional identity to be important across the entire continent but that the identity of the most influential trait may change, reflecting contrasting climate and successional niches along the latitudinal gradient (Hillebrand & Matthiessen, 2009).

Using data from five European National Forest Inventories, we investigated the relative influence of climate, functional diversity and functional identity for tree growth along a multi-biome climate gradient. We tested the following hypotheses: i) climate drives tree productivity across the entire gradient; ii) the relative importance of functional diversity for tree growth increases with resource limitation; and iii) functional identity is important for tree growth along the entire latitudinal gradient but the identity of the most important trait changes. To this end, we map the relative influence of different modes of trait influence on tree growth, elucidating the functional drivers of tree growth at a biogeographical scale (Violle *et al.*, 2014).

MATERIALS AND METHODS

Inventory data

We compiled data from the National Forest Inventories (NFIs) of Finland, Germany, Spain, Sweden and Wallonia, Belgium (see a detailed description of each NFI in Appendix S1 in Supporting Information). To select comparable data from the different inventories we only included those trees that had a diameter at breast height (d.b.h) of 10 cm or more and plots with a basal area of 4 m² ha⁻¹ or greater in consecutive surveys. For each tree we compiled the species (nomenclature follows the Atlas Florae Europaea), exotic status (following DAISIE: <http://www.europe-aliens.org>, see Table S1.2 in Appendix S1), d.b.h. and status (ingrowth, survivor, dead due to natural mortality or harvesting). In each plot we calculated the basal

area of each species ($\text{m}^2 \text{ha}^{-1}$), mean tree d.b.h. (mm), a single annual growth estimate (as the sum of the basal area increments ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) of all surviving and ingrowth trees) and the annual natural mortality rate ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$). The plots were classified by biome (boreal, temperate or Mediterranean) following Olson *et al.* (2001), see Figs S1.1 and S1.2 in Appendix S1.

Plots in which trees had been harvested between surveys were excluded to reduce the influence of recent stand structure changes on growth rates. From the available data we excluded plots that had zero or negative growth (i.e. 154 of 39,604 plots), and selected those with less than the 99.9% upper quantile to remove outliers (Table S1.3).

Climate data

We used the inventory plot coordinates to extract plot-level climatic variables from the WorldClim database (Hijmans *et al.*, 2005). We selected mean annual precipitation (MAP, mm) and mean annual temperature (MAT, $^{\circ}\text{C}$) to describe the climate gradient. The variables were weakly correlated in our dataset (Spearman rank coefficient: -0.18, $p < 0.001$), had better predictive power than the first two axes of a PCA of 22 climatic variables (see Appendix S2), and are easily interpretable across the large latitudinal gradient of this study.

Community functional composition

We compiled trait data from the TRY initiative (Kattge *et al.* 2011a) and additional published data sources for the 138 species in the final analysis (Table S2.2 in Appendix S2). We selected five key functional traits that are indicative of species' ecological strategies of resource acquisition and growth: maximum tree height (m); leaf nitrogen content (mg g^{-1}); maximum tree lifespan (yrs); seed mass (mg); and wood density (g cm^{-3}). Maximum tree height quantifies species' resource acquisition via light capture (Falster & Westoby, 2003).

Leaf N is a key trait of the leaf economics spectrum (LES); it characterises species' resource use strategy from acquisitive, fast-growing to conservative and slow-growing (Wright *et al.*, 2004). Maximum tree lifespan reflects species' life history strategy and relates to their defensive investment (Wirth & Lichstein, 2009). Seed mass relates to seedling survival rates (Leishman *et al.*, 2000) and species' resource use strategy and successional status. Finally, wood density relates to efficient and safe water transport and allocation to mechanical stability, correlates negatively with growth rates and mortality (Enquist *et al.*, 1999).

The functional diversity of each plot was quantified using the functional dispersion index (FDis: Laliberté & Legendre 2010) using the five traits. FDis quantifies how species in a community differ in their distance from the centre of the multi-trait functional space. Functional identity was derived as the community-weighted mean of each trait for each plot (FI_{mh}: maximum tree height; FI_{ln}: leaf N content; FI_{ls}: maximum tree life span; FI_{sm}: seed mass; FI_{wd}: wood density). FI_{sm} and FI_{wd} were highly positively correlated (Spearman rank coefficient: 0.74; $p < 0.001$) thus FI_{sm} was not considered further in the analysis. See Appendix S2 for full details on the functional composition estimation of the plots.

Theoretical reasoning suggests that a region with a larger species pool, and thus potential for larger trait ranges, is more likely to contain complementary species and/or species that are well adapted and thus may be more productive. Therefore the regional species pool was determined for each plot location from tree species distribution maps (see Appendix S2).

Statistical methods

We modelled plot-level growth ($\text{m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$) using a linear model including the following predictors: mean annual temperature (MAT, °C, log +7); mean annual precipitation (MAP, mm); functional dispersion (FDis, square root transformed); and the four functional identity measures. MAT value was incremented by 7 before logging to account for negative values.

We also included four covariates: basal area (BA, m² ha⁻¹, log); mean d.b.h. (DBH, mm, log); annual mortality rate (MR, m² ha⁻¹ yr⁻¹); and the species pool (SP, log). Basal area and mean tree size were included to account for stand density and developmental stage. The predictors and covariates were transformed, as indicated, to linearise relationships with the response variable. To investigate how the influence of the five biodiversity measures on tree growth varied with climate, first-order interaction terms were included between both MAT and MAP and each biodiversity measure. First-order interaction terms were also fitted between both MAT and MAP and each of the covariates. All explanatory variables were centred on 0 and scaled to 1 standard deviation to aid model interpretation.

Sample plots from the Finnish, Swedish and German NFIs are grouped in clusters, thus the nested data structure required three hierarchical levels for data from these three inventories (plot, cluster and NFI). We assumed that growth came from a lognormal distribution, such that $G_i \sim \text{Lognormal}(\mu_i, \sigma_u)$, where i is an individual plot, G_i is the plot growth (sum of the basal area increment, m² ha⁻¹ yr⁻¹ of all surviving and ingrowth trees), μ_i is the expected plot growth rate and σ_u is the standard deviation, both on the log scale. μ_i was modelled using the following equation:

$$\begin{aligned} \mu_i = & \alpha_0 + \alpha_r + \beta_{MAT} \cdot MAT_i + \beta_{MAP} \cdot MAP_i \\ & + \sum_{b=1}^5 (\beta_b^{(z)} + \gamma_b^{(MAT)} \cdot MAT_i + \gamma_b^{(MAP)} \cdot MAP_i) Z_{bi} \\ & + \sum_{k=1}^4 (\beta_k^{(c)} + \delta_k^{(MAT)} \cdot MAT_i + \delta_k^{(MAP)} \cdot MAP_i) C_{ki} \end{aligned} \quad (1)$$

where α_0 is the expected plot growth rate under average conditions, α_r the cluster or NFI intercept, Z_b are each of the biodiversity measures (i.e. FDis and four FI measures), C_k are the four covariates (BA, DBH, MR and SP), β_{MAT} , β_{MAP} , β_b and β_k are the intercepts for MAT, MAP, biodiversity variable b and covariate k , respectively, and γ_b and δ_k indicate interaction

terms between climate (MAT and MAP) and biodiversity variable b and covariate k , respectively. The model was fitted in a Bayesian framework in using the ‘rstan’ R package (Stan Development Team, 2013). Details of the model fitting and priors are in Appendix S3. All analyses were performed in R version 3.0.2.

Model evaluation

Figs S3.1a, b & c in Appendix S3 map the growth, predicted growth and the model residuals, respectively. There appears to be no strong spatial pattern in the residuals. Partial residual plots for each of the predictor variables show satisfactory linear relationships between the predictors and tree growth (Fig. S3.2). FDis was not strongly correlated with any of the FI measures (largest correlation was with FI_{ln}, Spearman rank coefficient: 0.29; $p < 0.001$).

Sensitivity of plot growth to changes in climate and biodiversity

Assumptions that we made in our model (equation 1), namely that the biodiversity measures (and covariates) are dependent on climate and that these dependencies are linear, allow us to explore how the sensitivity of plot growth to changes in each biodiversity measure varies with climate and, conversely, how the sensitivity of plot growth to changes in climate is modified by the biotic conditions in each plot. As such the geographic signal comes from model interaction terms between climate and the biodiversity and covariate variables.

Biodiversity

For a fixed MAT-MAP combination in plot i the predicted sensitivity of plot growth (S_{bi}) to changes in biodiversity measure b can be estimated as $\beta_b + \gamma_b^{(MAT)}.MAT_i + \gamma_b^{(MAP)}.MAP_i$, where β_b , $\gamma_b^{(MAT)}$ and $\gamma_b^{(MAP)}$ are the mean of the posterior distribution of the coefficients of b , the interaction coefficient of b with MAT and the interaction coefficient of b with MAP, respectively. MAT_i and MAP_i are the plot-level MAT and MAP values. Thus, S_{bi} is the

predicted sensitivity of the growth of plot i to changes in biodiversity measure b , modulated by the plot-level climate conditions.

Climate

For each plot the predicted sensitivity of plot growth to changes in MAT (S_{MAT}) and MAP (S_{MAP}) can be estimated as, for MAT:

$$S_{MATi} = \beta_{MAT} + \sum_{b=1}^5 (\gamma_b^{(MAT)} \cdot Z_{bi}) + \sum_{k=1}^4 (\delta_k^{(MAT)} \cdot C_{ki})$$

(2)

where the parameters are the same as in the full model (equation 1). Equation 2 can be used to estimate S_{MAP} by replacing MAT with MAP. This gave us the predicted sensitivity of plot growth to both climate variables, modified by the covariates and biodiversity measures.

Relative importance calculation

Climate and biodiversity

For each plot, the relative importance of MAT, MAP, FI and FDis were calculated from their predicted sensitivities as, for example with MAT: $|S_{MATi}| / \max(|S_{MATi}|, |S_{MAPi}|, |S_{FDisi}|, |S_{FIi}|)$, where S_{MATi} , S_{MAPi} and S_{FDisi} are the sensitivities of growth to MAT, MAP and FDis in plot i , respectively, and S_{FIi} is the mean of the absolute sensitivities of the four FI measures in plot i . The variable with the greatest influence on growth in a plot had a relative importance of 1.

Biodiversity

In a similar vein, for each plot the relative importance of the five biodiversity measures (FDis and the four FI measures) were calculated as the ratio of the absolute value of the biodiversity sensitivity ($|S_b|$) and the maximum biodiversity sensitivity in the plot: $|S_b| / \max\{$

$|S_m|\}_{m=1,\dots,5}$). In contrast to the analysis above, where the four FI measures are treated in aggregate, here we treat each FI measure separately to quantify their relative importance. In both cases, however, the relative importance estimates are calculated from the coefficients of the same model (Table S3.1 in Appendix S3).

Control analyses

We performed three control analyses to test the robustness of the model predictions and inferences made thereof (see Appendix S3). Specifically, we tested for: (i) the influence of climate variable selection; (ii) possible problems arising from collinearity between FI measures; and (iii) the influence of exotic tree species, which are often more productive than native species (Kawaletz *et al.*, 2013).

RESULTS

Tree growth, climate and functional composition along the latitudinal gradient

Mean plot-level tree growth rates ranged from 0.35 and 0.37 m² ha⁻¹ yr⁻¹ in the Mediterranean and boreal regions, respectively, to 0.68 m² ha⁻¹ yr⁻¹ in the temperate mid-latitudes (Fig. 1, Fig. S3a). Average mean annual temperature (MAT) ranged from 12 °C in the Mediterranean to 2 °C in the boreal region, whilst mean annual precipitation (MAP) ranged from 596 mm in the Mediterranean to 874 mm in the temperate zone.

Mean FDis was greatest across the temperate and southern boreal regions (Fig. S4.1a in Appendix S4), despite a pronounced decline in the species pool with latitude and greater maximum FDis in the Mediterranean. Mean FI values varied across the continent except FI_{ls}, which showed no clear pattern (Fig. S4.4a). FI_{mh} was highest in temperate and lowest in Mediterranean (Fig. S4.2a). FI_{ln} was highest in temperate regions and low in both the Mediterranean and boreal regions (Fig. S4.3a). The highest values of FI_{wd} were in the low to

mid-latitudes and levelled off at a mean of 0.55 g cm^{-3} in the northern temperate and boreal regions (Fig. S4.5a).

Effects of stand structure, climate and functional composition on tree growth

Stand structure (BA and mean DBH) had a greater influence on growth than climate (MAT and MAP) or any of the biodiversity measures (see Table S3.1 in Appendix 3 for the mean and 95% credible intervals of the model parameters). Of the two climate variables, MAT had the strongest influence on tree growth, exceeding those of the biodiversity measures. Across the continent, tree growth was related to all of the biodiversity measures, with FI_{wd} and FI_{ls} having the largest effect and FI_{ln} and $FDis$ the smallest (Fig. S4.6 in Appendix 4). However a change in either MAT or MAP altered the relationship between growth and all of the biodiversity measures.

Relative importance of climate and functional composition for tree growth

We compared the relative importance of the mean sensitivity of the FI measures, $FDis$, MAT and MAP across the latitudinal gradient (Fig. 2). The relative importance of FI was greatest at low and high latitudes; in the Mediterranean region the average sensitivity of the FI measures was more important than either MAT or MAP (0.78 compared with 0.71 and 0.59 for MAT and MAP) and in the northern boreal region it was as important as MAT (Fig. 2). The importance of $FDis$ was highest in the Mediterranean region (0.49) and this importance rapidly declined with increasing latitude, to a very low importance in the highest latitudes (0.08).

Relative importance of each biodiversity component for tree growth

The relative importance of each FI measure varied across the continent and none of the measures was the most important across the entire latitudinal gradient (Figs 3 & 4). The

relative importance of FDis was constant across the Mediterranean and temperate regions (0.38 and 0.36, respectively), becoming much less important in the boreal region (0.08). FI_{wd} and FI_{ls} showed similar patterns of importance; both were very important in the lower and especially mid latitudes and had a very low importance in the northern boreal region. Increasing FI_{wd} and FI_{ls} had a negative effect on tree growth across the entire continent. At either end of the latitudinal gradient FI_{mh} was the most important functional trait for tree growth, however the influence of FI_{mh} on tree growth changed from positive in the lower and mid-latitudes to negative in the boreal latitudes. FI_{ln} had the weakest effect on growth of all the FI measures; its relative importance was very low across the entire continent until the boreal latitudes where its importance exceeded that of FI_{wd} and FI_{ls} .

Control Analyses

The control analyses were consistent with the results and interpretation from the main analysis (see Appendix S3, Figs S3.3 – 6). However, the model with alternative climate variables predicted a reduced importance of FI_{mh} , and no large increase in the importance of FI, in the boreal region (Fig. S3.3). Nevertheless, the general patterns of trait influence on tree growth were robust between the different climate models.

DISCUSSION

We found that community functional composition was a relevant driver of tree growth across the entire European continent. Functional diversity was more important in the Mediterranean region, whilst functional identity effects were strongest at the latitudinal extremes of the continent (Fig. 4).

Relative importance of functional diversity and functional identity for tree growth

We found a strong climatic control on tree productivity, as evidenced by high relative importance values of mean annual temperature and mean annual precipitation in the boreal and Mediterranean biome, respectively (Fig. 2). The relative importance of functional diversity was comparable with climate in the Mediterranean region, consistent with Ruiz-Benito *et al.* (2014). However we did not find an increase in the importance of functional diversity with increasing climatic constraints in the boreal region, in contrast to other studies (Paquette & Messier, 2011); the importance of functional diversity declined across the temperate region from south to north and was relatively unimportant for tree growth in the boreal region (Figs 2 & 3). The concept that abiotic stress may increase the number of available resource-related niche dimensions may not be true for all sorts of adversities (Harpole & Tilman, 2007), and in this real-world scenario water stress seems to be very relevant. This is consistent with recent pan-European study that found that tree diversity promotes water use efficiency, an indication of how species compete for water belowground, only in drought prone environments (Grossiord *et al.*, 2014).

Comparing just the relative importance of the individual biodiversity components (Figs 3 & 4), we found a similar importance of functional diversity in the Mediterranean and temperate regions (Fig. 3). The traits in our functional diversity measure (leaf N content, maximum height, maximum tree life span, seed mass and wood density) reflect species' life history, strategies of resource capture and growth (Falster & Westoby, 2003; Wright *et al.*, 2004; Chave *et al.*, 2009). We found that dissimilarity in life history and resource capture of coexisting trees can promote tree growth, adding to the growing evidence that complementarity effects through niche differentiation promotes productivity in certain forests (Paquette & Messier, 2011; Ruiz-Benito *et al.*, 2014). In our study we are unable to establish the mechanisms driving the potential complementarity effect; however, complementary light use strategies (Morin *et al.*, 2011; Jucker *et al.*, 2014b) and root architectures (Brassard *et al.*,

2013) have been linked with positive diversity effects in forests. In addition, more diverse forests have been found to have greater stability in wood production over time (Jucker *et al.*, 2014a).

Consistent with other studies, we found functional identity to have a greater influence on productivity than functional diversity (Mokany *et al.*, 2008; Ruiz-Benito *et al.*, 2014). However, this relationship was not constant over the entire continent; the relative importance of functional identity was greater at the latitudinal extremes of the continent (Fig. 2), indicating the importance of trait identity for plant growth in harsh climates (Wright *et al.*, 2005; Spasojevic & Suding, 2012).

Identity effects point to the relevance of successional differentiation

Not only were identity effects stronger at the extreme ends of the gradient, but also the relative importance of the traits underlying the identity control changed. What are the biological underpinnings of this pattern?

In the Mediterranean biome, functional identity had a stronger influence on tree growth than climate (Fig. 2) and was primarily controlled by maximum height and wood density (relative importance *c.* 1) and maximum life span (relative importance *c.* 0.75, see Fig. 3). All else being equal, Mediterranean forests composed of species with low wood densities, large maximum heights and short maximum life spans exhibited the highest productivity. Low wood density and short maximum life span are features typical of early successional species (Bazzaz, 1979), who maximise resource acquisition and growth at the expense of chemical and structural tissue protection and longevity (Wirth & Lichstein, 2009). Succession in the Iberian Peninsula is leading to changes in the dominance of forests from gymnosperms to angiosperms (Carnicer *et al.*, 2014). The strong influence of maximum height may also point to a successional signature because some slow-growing, late-successional species in the

Mediterranean tend to be small statured (e.g. *Quercus ilex* or *Quercus suber*; maximum height of c. 18 m), whilst early-successional pines are taller in stature (e.g. *Pinus halepensis*, *Pinus pinaster* or *Pinus pinea*; maximum height of c. 26 m).

The situation in the temperate biome appears to follow a similar pattern to that in the Mediterranean; forests dominated by species with low wood density and short maximum life spans, i.e. pioneer species, tend to exhibit the highest growth rates. The relative influence of maximum height decreased from south to north in temperate forests, perhaps reflecting that fast growing pioneers such as *Salix caprea* and *Betula pendula* reach shorter maximum heights than typical late successional forest species (e.g. *Fagus sylvatica* or *Quercus robur*).

A sharp change in trait control occurred towards the boreal biome; wood density and maximum life span were no longer influential and maximum height resumed a strong importance but its effect changed sign. Thus, forests with short statured species appear to have higher growth rates in the boreal region than species with greater maximum heights. Again, we postulate that this may be a successional signature because in the boreal region fast growing pioneer species (e.g. *Betula pendula*, *Betula pubescens* and *Populus tremula*) reach shorter maximum heights (c. 30 m) than the late successional, slower growing, conifers *Pinus sylvestris* and *Picea abies* (c. 40 m). Succession in boreal regions usually progresses from deciduous to coniferous species (Bergeron & Dansereau, 1993), thus from species with intermediate and high wood densities to those with low wood density, in contrast to succession in temperate and Mediterranean regions. The weakened negative effect of wood density in the boreal region is likely to be due to the narrow range of wood density values compared to the other regions (Fig. S4.7a). We found leaf nitrogen content to be relatively unimportant for tree growth in Mediterranean and temperate regions but to be one of the more important traits in the northern temperate and boreal regions (Fig. 3). There was a transition from a positive influence of leaf nitrogen content on growth in the Mediterranean

biome to a negative effect elsewhere. This finding is unexpected, but in line with recent studies, which have not found consistent trends in the shifts of leaf nitrogen content (and other leaf traits) with succession (Douma *et al.*, 2012; Wilfahrt *et al.*, 2014).

In summary, the functional identity signal may reflect a trait-based differentiation of successional stages (Huston & Smith, 1987; Wirth & Lichstein, 2009; Lasky *et al.*, 2014) rather than an environmental filter reflecting drought or energy limitation at the southern and northern climate extremes, respectively. In different regions late-successional communities may have a lower or higher growth rate depending on the particular traits of the species, driven in this study, one may speculate, by the dominant role of gymnosperms in the Mediterranean and boreal biomes. It is important to note that this analysis controls, along the entire gradient, for the structural effects of climate and forest succession with respect to basal area and tree size, thereby isolating the successional identity effects. Nevertheless, our results suggest that the successional transition from gymnosperms to angiosperms in the Mediterranean and from angiosperms to gymnosperms in the boreal regions control the functional identity effects on tree growth in these latitudes.

Limitations

Due to the different NFI sampling methods, we used a 10 cm d.b.h. threshold for including trees in the study. This restriction is likely to have reduced the diversity of the plots, especially in the Mediterranean region where much of the diversity is in the tall shrub layer. In addition, plot size could not be standardised across the different inventories, and although we allowed for random variation between inventories, this may have led to an underrepresentation of the diversity of the boreal plots.

As with other large-scale trait analyses we were limited by the trait data available (Paquette & Messier, 2011; Ruiz-Benito *et al.*, 2014). We selected five key traits that reflect plant life

history strategies, however including other traits, especially root traits or traits unrelated to successional status, may provide additional insight. Our analysis ignored intraspecific trait variation and applied the same trait value to individuals of the same species across the continent. These factors are likely to have resulted in a conservative estimate of the relevance of biodiversity. Due to limited data availability, we were not able to account for other confounding factors that are known to influence tree growth, such as nutrient availability or local hydrology (Pretzsch *et al.*, 2013) or to incorporate an estimate of the successional stage of the plots (Lasky *et al.*, 2014).

This analysis was undertaken on a continent with a large and long-standing impact of forest management (Bengtsson *et al.*, 2000), which is likely to leave a signature in our results. Whilst the direct influence of recent management was accounted for, indirect and long-term management effects are likely to persist. The tree species and functional composition of managed forests may differ from natural assemblies due to planting and promoting of tree species outside of their ecological niche, which could change the causal nature of species identity on tree growth.

CONCLUSIONS

Our study contributes to the emerging field of functional biogeography (Violle *et al.*, 2014), which explores the mechanisms underlying biogeographical patterns of biodiversity and ecosystem functioning relationships. Functional diversity was an important driver of tree growth in the Mediterranean region, providing evidence that niche complementarity may be particularly important in water-limited forests. Across the temperate region the influence of functional diversity and identity were comparable in magnitude, but were much less important than climate. The strong influence of functional identity at the latitudinal extremes of the continent indicates the importance of a particular trait composition for tree growth in

harsh climates. We have shown how different modes of trait influence vary in their importance for tree growth along a large latitudinal gradient, contributing to a better understanding of the functional drivers of ecosystem functioning across the forests of Europe.

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SUPPORTING INFORMATION

Appendix S1 National Forest Inventory Details

Appendix S2 Supplementary Information on Climate, Functional Composition and Species Pool Variables

Appendix S3 Supplementary Statistical Methods

Appendix S4 Supplementary Figures

BIOSKETCH

Sophia Ratcliffe is a postdoctoral researcher based at Leipzig University in Germany. She is interested in large-scale patterns in ecology, particularly in relation to biodiversity and ecosystem functioning, and functional biogeography. This research is part of the FunDivEUROPE project (<http://www.fundiveurope.eu>).

Author contributions: SR and PRB compiled the inventory data, ML and JK compiled the trait data, SR, JMC and CW designed the analysis, SR analysed the data, and SR and CW wrote the first draft of the manuscript, with comments from all authors.

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APPENDICES

Appendix 1 References for the trait data used in this study

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899 **Appendix 2 References used to estimate regional species pools**

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956

FIGURE LEGENDS

Figure 1. Climate gradients of mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) across the latitudinal gradient covered by the National Forest Inventory plots. Mean plot basal area growth (Growth, $\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$). Dotted lines indicate 95% confidence intervals. The white section depicts missing data. Values were calculated at a 2° latitude spatial resolution.

Figure 2. Predicted relative importance of mean annual precipitation, mean annual temperature, functional identity (aggregated effect of the community mean value of the four functional traits selected) and functional dispersion for tree growth. The sensitivity of plot growth to changes in each variable was estimated from the hierarchical linear model; the variable with the greatest influence in the plot has a relative importance of 1 and the other variables are scaled accordingly. Values are aggregated at 0.5° latitude thus the average relative importance of each predictor is shown. White section depicts missing data. A version with confidence bands is given in Appendix 4, Fig. S4.7.

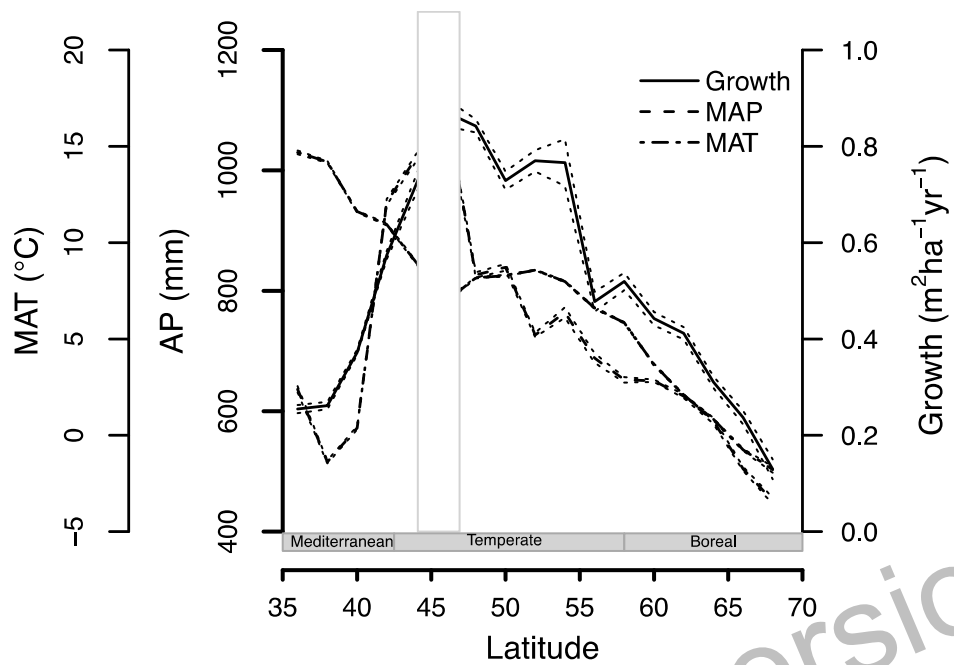
Figure 3. Predicted relative importance of five components of functional biodiversity (functional dispersion and the community weighted mean of four functional traits) for tree growth. The sensitivity of plot growth to changes in each component was estimated from the hierarchical linear model; the biodiversity component with the greatest influence in the plot has a relative importance of 1 and the other measures are scaled accordingly. Values are aggregated at 0.5° latitude thus the average relative importance of each predictor is shown. Solid lines indicate a positive influence of the biodiversity measure on plot growth, whilst dashed lines indicate a negative influence. White section depicts missing data. A version with confidence bands is given in Appendix 4, Fig. S4.8.

Figure 4. Predicted relative importance of a) FDis (functional diversity; red), FI_{ln} (community-weighted mean (CWM) leaf N mass (mg⁻¹ g); green) and FI_{wd} (CWM wood density (g cm⁻³); blue); b) FI_{mh} (CWM maximum height (m); red), FI_{ln} (CWM leaf N mass (mg g⁻¹); green) and FI_{wd} (CWM wood density (g cm⁻³); blue), for tree growth. The sensitivity of plot growth to changes in each biodiversity component was estimated from a hierarchical linear model using spatial maps of mean annual temperature and mean annual precipitation at spatial resolution of 1 km²; the biodiversity measure with the largest effect size in the grid has a relative importance of 1 and the other two measures are scaled accordingly. The RGB cube illustrates how the colour gradient reflects the changes in relative importance of the biodiversity component, such that areas of white indicate an equal importance of all three measures. The arrows indicate an increasing relative importance.

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993 **FIGURES**

994 Figure 1.



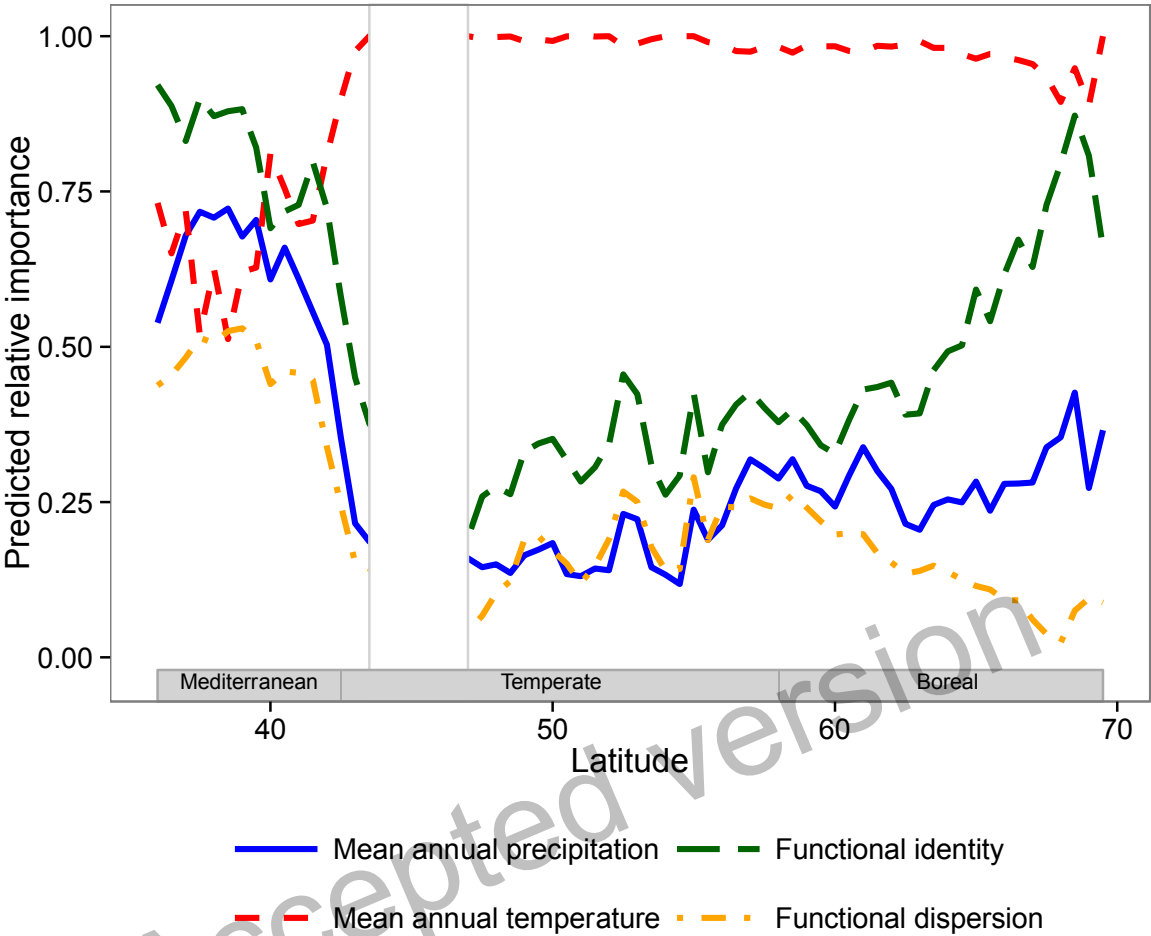
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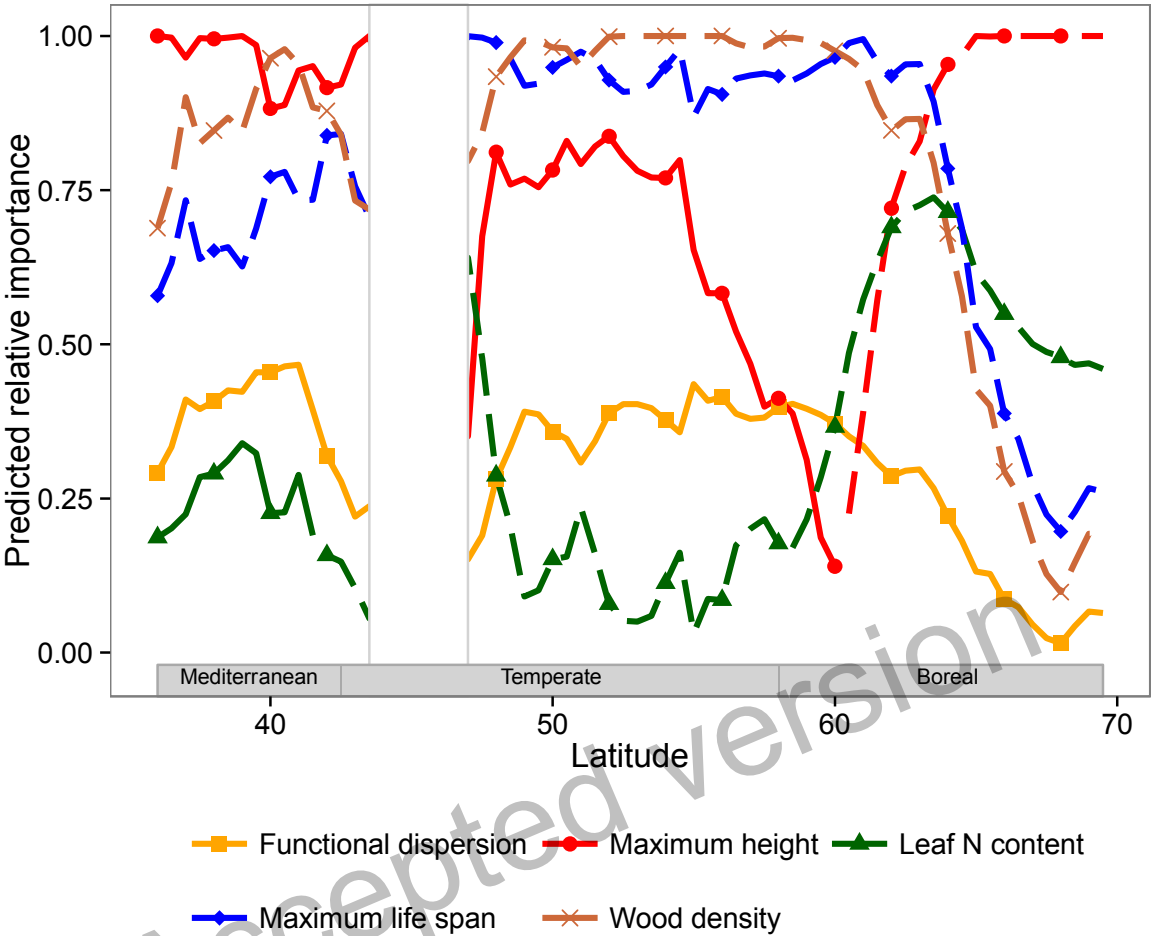
999 Figure 2.



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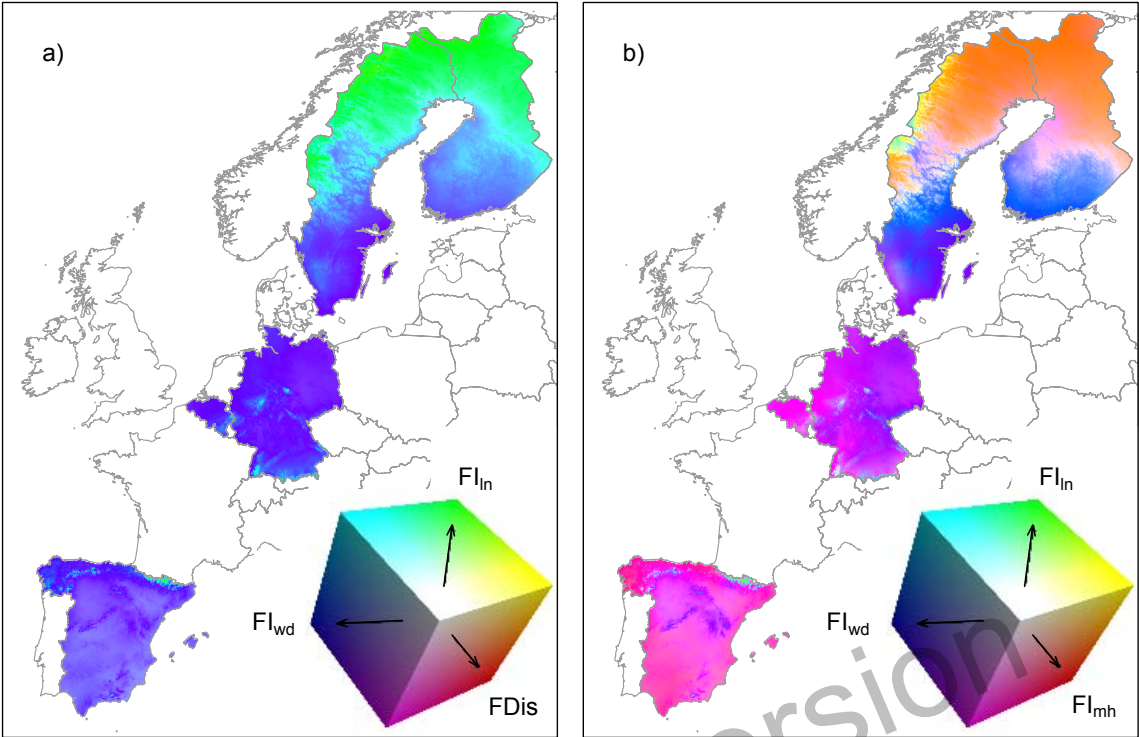
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1002 Figure 3.



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1004 Figure 4.



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