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Modes of functional biodiversity control on tree productivity across the European continent

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Keywords:	climatic gradient, environmental filtering, forest succession, FunDivEUROPE, landscape scale, plant functional traits, tree productivity

Modes of functional biodiversity control on tree productivity across the European continent (Ref. GEB-2015-0039.R1)

We thank the Editor in Chief and the Reviewer for their additional comments on our revised manuscript. We believe that the revised version addresses the Editor and Reviewer's concerns. We provide a point-by-point reply (indented) answering the Editor or Reviewer's comments (italics). The additional text in the revised version of the manuscript is marked in blue for easier identification. We have exceeded the word count limit (5042) with the new text; we hope that this is allowable.

List of major changes:

1. We have used a different line type in Figure 2 and different point shapes in Figure 3 for each variable.
2. We have estimated the proportion of the variance in the data that is explained by the model.
3. The trait data and species pool citation lists have been moved to Appendix 1 and 2, respectively, in the main manuscript.
4. A section has been added to the Results for the control analyses.

Reply to the Editor in Chief

In my comments on the first version of the manuscript, I mentioned the colour publication fees. Since then, it has come to my attention that the number of print copies is very, very small. The standard procedure will be to use colour on-line only, unless authors specifically want to have the figures printed in colour and to pay the colour publication charge.

It still makes sense, however, to have figures that are understandable when they are printed in black and white. For Fig. 2 and perhaps 3, could you not use different line styles as well as different colours?

We thank you for the details of the standard procedure for colour figures. Following your suggestion we have added different line styles to Figure 2 and different point shapes to Figure 3. Both figures should be understandable in black and white. Unfortunately, there is nothing we can do about Figure 3 and we will pay for this figure to be printed in colour.

I confess that my knowledge of Bayesian statistics is very limited. However, I am still bothered that there is no way to indicate whether the effects you describe are large or small relative to the unexplained variation. You added Fig. S4.6, which is useful, but it still only shows relative effects without any indication of how much variance these variables capture. IS it truly impossible to estimate this in Bayesian models? At minimum, the legend of the figure could say something about the odds ratios. No?

Following Korner-Nievergelt *et al.* (2015) we have calculated the R^2 of the model as 1 minus the residual variance divided by the variance in the data. The calculation is averaged over the posterior distribution of the predicted values. The R^2 is 0.684. Not all the variance explained can be attributed to the predictors; some will be explained

Ratcliffe *et al.* Comments for reviewers (GEB-2015-0039.R1)

by the cluster and country effects.

The method for the calculation has been added to Appendix S3 under the Model fitting section, and the caption of Table S3.1 has been updated with the R^2 value.

GEB has had another change of policy. Because the references to the data sources in on-line appendices are not captured by the citation indexing services (e.g., the Web of Science), please now put them in Appendices after the biosketch (e.g. Appendix 1 References for the trait data used in this study.; Appendix 2, References used to estimate species pools". These will be printed in reduced font in the main paper.

We have moved the trait data and regional species pool citations lists to Appendix 1 and 2, respectively, in the main manuscript, and reordered the sections following the author guidelines.

We have removed the text at the end of the main citation list that indicated the additional trait data and species pool citations in the Supplementary Material.

Reply to Referee 1

The authors have done a fantastic job of revising the manuscript and arguing their case. I was impressed by several items.

- (1) The control analysis testing a different dispersion and distance measure.*
- (2) The extended control analysis on the environmental drivers. Given the differences that were found between the MAT-MAP analysis and the first two PCA-axes of 19 variables in the boreal region, I would like to see a short note of this in the results section and/or discussion.*

We have added a Control Analyses section to the end of the Results section (see lines 321 - 326). In addition, we have added a bit more text to the Control Analyses section of Appendix S3 describing the predicted difference in the importance of leaf nitrogen content between the different climate models.

- (3) Choices in the analysis were better justified.*
 - (4) A more refined discussion on functional identity and functional diversity*
- I enjoyed the open-minded and diligent consideration of my comments.
Well done.*

Many thanks for your comments on the revised version of our manuscript.

Reference

Korner-Nievergelt, F., Roth, T., von Felten, S., Guélat, J., Almasi, B., & Korner-Nievergelt, P. (2015). *Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS, and Stan*. Academic Press.

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10 40 **Short running-title:** Functional biodiversity control on tree growth
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13 41 **Keywords:** climatic gradient, environmental filtering, forest succession, FunDivEUROPE,
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16 42 landscape scale, plant functional traits, tree productivity.
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3 48 **ABSTRACT**
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6 49 **Aim**
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9 50 The relative contribution of community functional diversity and composition to ecosystem
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11 51 functioning is a critical question in ecology in order to enable better predictions of how
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13 52 ecosystems may respond to a changing climate. However there is little consensus of which
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15 53 modes of functional biodiversity are most important for tree growth at large spatial scales.
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17 54 Here we assessed the relative importance of climate, functional diversity and functional
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19 55 identity (i.e. the community mean values of four key functional traits) for tree growth across
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21 56 the European continent, spanning the northern boreal to the southern Mediterranean forests.
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25 57 **Location**
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28 58 Finland, Germany, Sweden, Spain and Wallonia (Belgium)
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31 59 **Methods**
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34 60 Using data from five European National Forest Inventories we applied a hierarchical linear
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36 61 model to estimate the sensitivity of tree growth to changes in climate, functional diversity and
37
38 62 functional identity along a latitudinal gradient.
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42 63 **Results**
43
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45 64 Functional diversity was weakly related to tree growth in the temperate and boreal regions
46
47 65 and more strongly in the Mediterranean region. In the temperate region, where climate was
48
49 66 the most important predictor, functional diversity and identity had a similar importance for
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51 67 tree growth. Functional identity was strongest at the latitudinal extremes of the continent,
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53 68 largely driven by strong changes in the importance of maximum height along the latitudinal
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55 69 gradient.
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3 70 **Main conclusions**
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6 71 Functional diversity was an important driver of tree growth in the Mediterranean region,
7
8 72 providing evidence that niche complementarity may be more important for tree growth in
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10 73 water-limited forests. The strong influence of functional identity at the latitudinal extremes
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12 74 indicates the importance of a particular trait composition for tree growth in harsh climates.
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15 75 Furthermore, we speculate that this functional identity signal may reflect a trait-based
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17 76 differentiation of successional stages rather than abiotic filtering due to water or energy
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19 77 limitation.
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79 INTRODUCTION

80 With the increasing threat of climate and land-use change there is deepening concern that
81 continued biodiversity loss may jeopardise key ecosystem services (Cardinale *et al.*, 2012;
82 Thomas *et al.*, 2013). Therefore it is becoming ever more critical to improve our
83 understanding of the interplay between abiotic and biotic controls on ecosystem processes
84 (Díaz *et al.*, 2007; Hillebrand & Matthiessen, 2009), especially at scales relevant to
85 conservation policy makers (Thomas *et al.*, 2013; Violle *et al.*, 2014). The functional
86 structure of a community (i.e. the distribution and relative abundance of plant functional
87 traits) is known to directly influence ecosystem processes (Díaz *et al.*, 2007) and recently
88 there have been several large-scale observational studies in forests with a focus on detecting
89 an influence of diversity on tree productivity (e.g. Paquette & Messier, 2011; Vilà *et al.*,
90 2013; Ruiz-Benito *et al.*, 2014). However, the relative importance of functional diversity and
91 composition for tree growth has received little attention at large spatial scales (Conti & Díaz,
92 2013), despite its importance for understanding how forests may respond to climate change
93 (Violle *et al.*, 2014).

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

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3 104 consistently been found to be a key component through which plant traits control
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5 105 productivity, and is often found to be more important than the functional diversity of the
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7 106 community (Mokany *et al.*, 2008; Conti & Díaz, 2013; but see Valencia *et al.*, 2015).
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11 107 The European continent spans large gradients in climate and resource availability, from the
12
13 108 northern boreal latitudes where productivity is primarily limited by energy (i.e. temperature
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15 109 and radiation; Körner 1998) to southern Mediterranean latitudes where water is the primary
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17 110 limiting resource (Babst *et al.*, 2013). In the temperate mid-latitudes neither energy nor water
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19 111 is strongly limiting, and, as a consequence, productivity peaks there (see Fig. 1). Thus
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21 112 stressful climatic conditions predominate at the southern and northern extremes of the
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23 113 European continent but are exerted by different environmental constraints (i.e. lack of water
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25 114 versus a lack of energy). Along such a climatic gradient competitive interactions and abiotic
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27 115 filtering assembly processes act on community functional structure (Maire *et al.*, 2012) and
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29 116 thus ecosystem functioning (Spasojevic & Suding, 2012).
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33 117 According to Harpole & Tilman (2007) the number of resource-related niche dimensions is
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35 118 greater in stressful environments and more species with a particular specialisation in
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37 119 acquiring resources are needed to maintain productivity. We therefore expect productivity at
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39 120 the extremes of our latitudinal gradient to be most sensitive to functional trait diversity, as a
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41 121 proxy for the potential degree of niche complementarity realised by a community. Recent
42
43 122 observational studies in forests support this view (Paquette & Messier, 2011; Jucker *et al.*,
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45 123 2014a). However, the evidence is equivocal, and other studies have found no difference in the
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47 124 importance of functional diversity for tree growth between regions with different productivity
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49 125 rates (e.g. Zhang *et al.*, 2012; Ruiz-Benito *et al.*, 2014). Environmental filters increase the
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51 126 functional similarity of species through abiotic constraints that select for particular trait
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53 127 expressions generally characterising the locally most productive and best adapted tree species
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55 128 (Wright *et al.*, 2005; Cornwell & Ackerly, 2009). At the same time, competition between
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3 129 species with similar resource acquisition abilities can result in community trait convergence
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5 130 (Mayfield & Levine, 2010; Kraft *et al.*, 2015). Given that abiotic filtering and competition
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7 131 occur in all biomes, we predict functional identity to be important across the entire continent
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10 132 but that the identity of the most influential trait may change, reflecting contrasting climate
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12 133 and successional niches along the latitudinal gradient (Hillebrand & Matthiessen, 2009).

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15 134 Using data from five European National Forest Inventories, we investigated the relative
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17 135 influence of climate, functional diversity and functional identity for tree growth along a
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19 136 multi-biome climate gradient. We tested the following hypotheses: i) climate drives tree
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21 137 productivity across the entire gradient; ii) the relative importance of functional diversity for
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23 138 tree growth increases with resource limitation; and iii) functional identity is important for tree
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25 139 growth along the entire latitudinal gradient but the identity of the most important trait
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27 140 changes. To this end, we map the relative influence of different modes of trait influence on
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29 141 tree growth, elucidating the functional drivers of tree growth at a biogeographical scale
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31 142 (Violle *et al.*, 2014).

32 33 34 35 36 143 **MATERIALS AND METHODS**

37 38 39 144 **Inventory data**

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42 145 We compiled data from the National Forest Inventories (NFIs) of Finland, Germany, Spain,
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44 146 Sweden and Wallonia, Belgium (see a detailed description of each NFI in Appendix S1 in
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46 147 Supporting Information). To select comparable data from the different inventories we only
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48 148 included those trees that had a diameter at breast height (d.b.h) of 10 cm or more and plots
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50 149 with a basal area of 4 m² ha⁻¹ or greater in consecutive surveys. For each tree we compiled the
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52 150 species (nomenclature follows the Atlas Florae Europaea), exotic status (following DAISIE:
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54 151 <http://www.europe-aliens.org>, see Table S1.2 in Appendix S1), d.b.h. and status (ingrowth,
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56 152 survivor, dead due to natural mortality or harvesting). In each plot we calculated the basal
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3 153 area of each species ($\text{m}^2 \text{ha}^{-1}$), mean tree d.b.h. (mm), a single annual growth estimate (as the
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5 154 sum of the basal area increments ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) of all surviving and ingrowth trees) and the
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7 155 annual natural mortality rate ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$). The plots were classified by biome (boreal,
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9 156 temperate or Mediterranean) following Olson *et al.* (2001), see Figs S1.1 and S1.2 in
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11 157 Appendix S1.

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15 158 Plots in which trees had been harvested between surveys were excluded to reduce the
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17 159 influence of recent stand structure changes on growth rates. From the available data we
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19 160 excluded plots that had zero or negative growth (i.e. 154 of 39,604 plots), and selected those
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21 161 with less than the 99.9% upper quantile to remove outliers (Table S1.3).

162 **Climate data**

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27 163 We used the inventory plot coordinates to extract plot-level climatic variables from the
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29 164 WorldClim database (Hijmans *et al.*, 2005). We selected mean annual precipitation (MAP,
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31 165 mm) and mean annual temperature (MAT, °C) to describe the climate gradient. The variables
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33 166 were weakly correlated in our dataset (Spearman rank coefficient: -0.18, $p < 0.001$), had
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35 167 better predictive power than the first two axes of a PCA of 22 climatic variables (see
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37 168 Appendix S2), and are easily interpretable across the large latitudinal gradient of this study.

169 **Community functional composition**

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44 170 We compiled trait data from the TRY initiative (Kattge *et al.* 2011a) and additional published
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46 171 data sources for the 138 species in the final analysis (Table S2.2 in Appendix S2). We
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48 172 selected five key functional traits that are indicative of species' ecological strategies of
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50 173 resource acquisition and growth: maximum tree height (m); leaf nitrogen content (mg g^{-1});
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52 174 maximum tree lifespan (yrs); seed mass (mg); and wood density (g cm^{-3}). Maximum tree
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54 175 height quantifies species' resource acquisition via light capture (Falster & Westoby, 2003).

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3 176 Leaf N is a key trait of the leaf economics spectrum (LES); it characterises species' resource
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5 177 use strategy from acquisitive, fast-growing to conservative and slow-growing (Wright *et al.*,
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7 178 2004). Maximum tree lifespan reflects species' life history strategy and relates to their
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10 179 defensive investment (Wirth & Lichstein, 2009). Seed mass relates to seedling survival rates
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12 180 (Leishman *et al.*, 2000) and species' resource use strategy and successional status. Finally,
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14 181 wood density relates to efficient and safe water transport and allocation to mechanical
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16 182 stability, correlates negatively with growth rates and mortality (Enquist *et al.*, 1999).

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19 183 The functional diversity of each plot was quantified using the functional dispersion index
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21 184 (FDis: Laliberté & Legendre 2010) using the five traits. FDis quantifies how species in a
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23 185 community differ in their distance from the centre of the multi-trait functional space.
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25 186 Functional identity was derived as the community-weighted mean of each trait for each plot
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27 187 (FI_{mh}: maximum tree height; FI_{ln}: leaf N content; FI_{ls}: maximum tree life span; FI_{sm}: seed
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29 188 mass; FI_{wd}: wood density). FI_{sm} and FI_{wd} were highly positively correlated (Spearman rank
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31 189 coefficient: 0.74; $p < 0.001$) thus FI_{sm} was not considered further in the analysis. See
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33 190 Appendix S2 for full details on the functional composition estimation of the plots.
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38 191 Theoretical reasoning suggests that a region with a larger species pool, and thus potential for
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40 192 larger trait ranges, is more likely to contain complementary species and/or species that are
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42 193 well adapted and thus may be more productive. Therefore the regional species pool was
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44 194 determined for each plot location from tree species distribution maps (see Appendix S2).

45 46 47 195 **Statistical methods**

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50 196 We modelled plot-level growth ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) using a linear model including the following
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52 197 predictors: mean annual temperature (MAT, °C, log +7); mean annual precipitation (MAP,
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54 198 mm); functional dispersion (FDis, square root transformed); and the four functional identity
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56 199 measures. MAT value was incremented by 7 before logging to account for negative values.
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3 200 We also included four covariates: basal area (BA, m² ha⁻¹, log); mean d.b.h. (DBH, mm, log);
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5 201 annual mortality rate (MR, m² ha⁻¹ yr⁻¹); and the species pool (SP, log). Basal area and mean
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7 202 tree size were included to account for stand density and developmental stage. The predictors
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10 203 and covariates were transformed, as indicated, to linearise relationships with the response
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12 204 variable. To investigate how the influence of the five biodiversity measures on tree growth
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14 205 varied with climate, first-order interaction terms were included between both MAT and MAP
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16 206 and each biodiversity measure. First-order interaction terms were also fitted between both
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18 207 MAT and MAP and each of the covariates. All explanatory variables were centred on 0 and
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20 208 scaled to 1 standard deviation to aid model interpretation.

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24 209 Sample plots from the Finnish, Swedish and German NFIs are grouped in clusters, thus the
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26 210 nested data structure required three hierarchical levels for data from these three inventories
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28 211 (plot, cluster and NFI). We assumed that growth came from a lognormal distribution, such
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30 212 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
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32 213 basal area increment, m² ha⁻¹ yr⁻¹ of all surviving and ingrowth trees), μ_i is the expected plot
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34 214 growth rate and σ_u is the standard deviation, both on the log scale. μ_i was modelled using the
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36 215 following equation:

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

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51 217 where α_0 is the expected plot growth rate under average conditions, α_r the cluster or NFI
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53 218 intercept, Z_b are each of the biodiversity measures (i.e. FDis and four FI measures), C_k are the
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55 219 four covariates (BA, DBH, MR and SP), β_{MAT} , β_{MAP} , β_b and β_k are the intercepts for MAT,
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57 220 MAP, biodiversity variable b and covariate k , respectively, and γ_b and δ_k indicate interaction
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3 221 terms between climate (MAT and MAP) and biodiversity variable b and covariate k ,
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5 222 respectively. The model was fitted in a Bayesian framework in using the 'rstan' R package
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7 223 (Stan Development Team, 2013). Details of the model fitting and priors are in Appendix S3.
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10 224 All analyses were performed in R version 3.0.2.

11 12 13 225 **Model evaluation**

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16 226 Figs S3.1a, b & c in Appendix S3 map the growth, predicted growth and the model residuals,
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18 227 respectively. There appears to be no strong spatial pattern in the residuals. Partial residual
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20 228 plots for each of the predictor variables show satisfactory linear relationships between the
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22 229 predictors and tree growth (Fig. S3.2). FDis was not strongly correlated with any of the FI
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24 230 measures (largest correlation was with FI_{ln}, Spearman rank coefficient: 0.29; $p < 0.001$).

25 26 27 28 231 **Sensitivity of plot growth to changes in climate and biodiversity**

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30 232 Assumptions that we made in our model (equation 1), namely that the biodiversity measures
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32 233 (and covariates) are dependent on climate and that these dependencies are linear, allow us to
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34 234 explore how the sensitivity of plot growth to changes in each biodiversity measure varies
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36 235 with climate and, conversely, how the sensitivity of plot growth to changes in climate is
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38 236 modified by the biotic conditions in each plot. As such the geographic signal comes from
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40 237 model interaction terms between climate and the biodiversity and covariate variables.

41 42 43 44 45 238 *Biodiversity*

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48 239 For a fixed MAT-MAP combination in plot i the predicted sensitivity of plot growth (S_{bi}) to
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50 240 changes in biodiversity measure b can be estimated as $\beta_b + \gamma_b^{(MAT)}.MAT_i + \gamma_b^{(MAP)}.MAP_i$,
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52 241 where β_b , $\gamma_b^{(MAT)}$ and $\gamma_b^{(MAP)}$ are the mean of the posterior distribution of the coefficients of b ,
53
54 242 the interaction coefficient of b with MAT and the interaction coefficient of b with MAP,
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56 243 respectively. MAT_i and MAP_i are the plot-level MAT and MAP values. Thus, S_{bi} is the
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3 244 predicted sensitivity of the growth of plot i to changes in biodiversity measure b , modulated
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5 245 by the plot-level climate conditions.
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8 246 *Climate*
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11 247 For each plot the predicted sensitivity of plot growth to changes in MAT (S_{MAT}) and MAP
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13 248 (S_{MAP}) can be estimated as, for MAT:
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$$S_{MATi} = \beta_{MAT} + \sum_{b=1}^5 (\gamma_b^{(MAT)} \cdot Z_{bi}) + \sum_{k=1}^4 (\delta_k^{(MAT)} \cdot C_{ki})$$

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22 249 (2)
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24
25 250 where the parameters are the same as in the full model (equation 1). Equation 2 can be used
26
27 251 to estimate S_{MAP} by replacing MAT with MAP. This gave us the predicted sensitivity of plot
28
29 252 growth to both climate variables, modified by the covariates and biodiversity measures.
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31

32 253 **Relative importance calculation**
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34
35 254 *Climate and biodiversity*
36

37
38 255 For each plot, the relative importance of MAT, MAP, FI and FDis were calculated from their
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40 256 predicted sensitivities as, for example with MAT: $|S_{MATi}| / \max(|S_{MATi}|, |S_{MAPi}|, |S_{FDisi}|, |S_{Fii}|)$,
41
42 257 where S_{MATi} , S_{MAPi} and S_{FDisi} are the sensitivities of growth to MAT, MAP and FDis in plot i ,
43
44 258 respectively, and S_{Fii} is the mean of the absolute sensitivities of the four FI measures in plot i .
45
46 259 The variable with the greatest influence on growth in a plot had a relative importance of 1.
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48

49
50 260 *Biodiversity*
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52
53 261 In a similar vein, for each plot the relative importance of the five biodiversity measures (FDis
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55 262 and the four FI measures) were calculated as the ratio of the absolute value of the biodiversity
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57 263 sensitivity ($|S_b|$) and the maximum biodiversity sensitivity in the plot: $|S_b| / \max(\{$
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1
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3 264 $|S_m|_{m=1,\dots,5}$). In contrast to the analysis above, where the four FI measures are treated in
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5 265 aggregate, here we treat each FI measure separately to quantify their relative importance. In
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7 266 both cases, however, the relative importance estimates are calculated from the coefficients of
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9
10 267 the same model (Table S3.1 in Appendix S3).

11 12 13 268 **Control analyses**

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15
16 269 We performed three control analyses to test the robustness of the model predictions and
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18 270 inferences made thereof (see Appendix S3). Specifically, we tested for: (i) the influence of
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20 271 climate variable selection; (ii) possible problems arising from collinearity between FI
21
22 272 measures; and (iii) the influence of exotic tree species, which are often more productive than
23
24 273 native species (Kawaletz *et al.*, 2013).

25 26 27 274 **RESULTS**

28 29 30 275 **Tree growth, climate and functional composition along the latitudinal gradient**

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33 276 Mean plot-level tree growth rates ranged from 0.35 and 0.37 m² ha⁻¹ yr⁻¹ in the Mediterranean
34
35 277 and boreal regions, respectively, to 0.68 m² ha⁻¹ yr⁻¹ in the temperate mid-latitudes (Fig. 1,
36
37 278 Fig. S3a). Average mean annual temperature (MAT) ranged from 12 °C in the Mediterranean
38
39 279 to 2 °C in the boreal region, whilst mean annual precipitation (MAP) ranged from 596 mm in
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41 280 the Mediterranean to 874 mm in the temperate zone.

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45 281 Mean FDis was greatest across the temperate and southern boreal regions (Fig. S4.1a in
46
47 282 Appendix S4), despite a pronounced decline in the species pool with latitude and greater
48
49 283 maximum FDis in the Mediterranean. Mean FI values varied across the continent except FI_{ls},
50
51 284 which showed no clear pattern (Fig. S4.4a). FI_{mh} was highest in temperate and lowest in
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53 285 Mediterranean (Fig. S4.2a). FI_{ln} was highest in temperate regions and low in both the
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55 286 Mediterranean and boreal regions (Fig. S4.3a). The highest values of FI_{wd} were in the low to
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3 287 mid-latitudes and levelled off at a mean of 0.55 g cm^{-3} in the northern temperate and boreal
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5 288 regions (Fig. S4.5a).
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8 289 **Effects of stand structure, climate and functional composition on tree growth**

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10
11 290 Stand structure (BA and mean DBH) had a greater influence on growth than climate (MAT
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13 291 and MAP) or any of the biodiversity measures (see Table S3.1 in Appendix 3 for the mean
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15 292 and 95% credible intervals of the model parameters). Of the two climate variables, MAT had
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17 293 the strongest influence on tree growth, exceeding those of the biodiversity measures. Across
18
19 294 the continent, tree growth was related to all of the biodiversity measures, with FI_{wd} and FI_{ls}
20
21 295 having the largest effect and FI_{ln} and $FDis$ the smallest (Fig. S4.6 in Appendix 4). However a
22
23 296 change in either MAT or MAP altered the relationship between growth and all of the
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25 297 biodiversity measures.
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29 300 **Relative importance of climate and functional composition for tree growth**

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32
33 299 We compared the relative importance of the mean sensitivity of the FI measures, $FDis$, MAT
34
35 300 and MAP across the latitudinal gradient (Fig. 2). The relative importance of FI was greatest at
36
37 301 low and high latitudes; in the Mediterranean region the average sensitivity of the FI measures
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39 302 was more important than either MAT or MAP (0.78 compared with 0.71 and 0.59 for MAT
40
41 303 and MAP) and in the northern boreal region it was as important as MAT (Fig. 2). The
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43 304 importance of $FDis$ was highest in the Mediterranean region (0.49) and this importance
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45 305 rapidly declined with increasing latitude, to a very low importance in the highest latitudes
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47 306 (0.08).
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51 307 **Relative importance of each biodiversity component for tree growth**

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54 308 The relative importance of each FI measure varied across the continent and none of the
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56 309 measures was the most important across the entire latitudinal gradient (Figs 3 & 4). The
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3 310 relative importance of FDis was constant across the Mediterranean and temperate regions
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5 311 (0.38 and 0.36, respectively), becoming much less important in the boreal region (0.08). FI_{wd}
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7 312 and FI_{ls} showed similar patterns of importance; both were very important in the lower and
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9 313 especially mid latitudes and had a very low importance in the northern boreal region.
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11 314 Increasing FI_{wd} and FI_{ls} had a negative effect on tree growth across the entire continent. At
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13 315 either end of the latitudinal gradient FI_{mh} was the most important functional trait for tree
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15 316 growth, however the influence of FI_{mh} on tree growth changed from positive in the lower and
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17 317 mid-latitudes to negative in the boreal latitudes. FI_{ln} had the weakest effect on growth of all
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19 318 the FI measures; its relative importance was very low across the entire continent until the
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21 319 boreal latitudes where its importance exceeded that of FI_{wd} and FI_{ls} .

22 23 24 25 26 320 **Control Analyses**

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29 321 The control analyses were consistent with the results and interpretation from the main
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31 322 analysis (see Appendix S3, Figs S3.3 – 6). However, the model with alternative climate
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33 323 variables predicted a reduced importance of FI_{mh} , and no large increase in the importance of
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35 324 FI_{ln} in the boreal region (Fig. S3.3). Nevertheless, the general patterns of trait influence on
36
37 325 tree growth were robust between the different climate models.

38 39 40 41 326 **DISCUSSION**

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43
44 327 We found that community functional composition was a relevant driver of tree growth across
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46 328 the entire European continent. Functional diversity was more important in the Mediterranean
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48 329 region, whilst functional identity effects were strongest at the latitudinal extremes of the
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50 330 continent (Fig. 4).

51 52 53 54 331 **Relative importance of functional diversity and functional identity for tree growth**

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3 332 We found a strong climatic control on tree productivity, as evidenced by high relative
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5 333 importance values of mean annual temperature and mean annual precipitation in the boreal
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7 334 and Mediterranean biome, respectively (Fig. 2). The relative importance of functional
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9 335 diversity was comparable with climate in the Mediterranean region, consistent with Ruiz-
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11 336 Benito *et al.* (2014). However we did not find an increase in the importance of functional
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13 337 diversity with increasing climatic constraints in the boreal region, in contrast to other studies
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15 338 (Paquette & Messier, 2011); the importance of functional diversity declined across the
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17 339 temperate region from south to north and was relatively unimportant for tree growth in the
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19 340 boreal region (Figs 2 & 3). The concept that abiotic stress may increase the number of
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21 341 available resource-related niche dimensions may not be true for all sorts of adversities
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23 342 (Harpole & Tilman, 2007), and in this real-world scenario water stress seems to be very
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25 343 relevant. This is consistent with recent pan-European study that found that tree diversity
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27 344 promotes water use efficiency, an indication of how species compete for water belowground,
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29 345 only in drought prone environments (Grossiord *et al.*, 2014).

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35 346 Comparing just the relative importance of the individual biodiversity components (Figs 3 &
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37 347 4), we found a similar importance of functional diversity in the Mediterranean and temperate
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39 348 regions (Fig. 3). The traits in our functional diversity measure (leaf N content, maximum
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41 349 height, maximum tree life span, seed mass and wood density) reflect species' life history,
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43 350 strategies of resource capture and growth (Falster & Westoby, 2003; Wright *et al.*, 2004;
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45 351 Chave *et al.*, 2009). We found that dissimilarity in life history and resource capture of
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47 352 coexisting trees can promote tree growth, adding to the growing evidence that
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49 353 complementarity effects through niche differentiation promotes productivity in certain forests
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51 354 (Paquette & Messier, 2011; Ruiz-Benito *et al.*, 2014). In our study we are unable to establish
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53 355 the mechanisms driving the potential complementarity effect; however, complementary light
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55 356 use strategies (Morin *et al.*, 2011; Jucker *et al.*, 2014b) and root architectures (Brassard *et al.*,

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2
3 357 2013) have been linked with positive diversity effects in forests. In addition, more diverse
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5 358 forests have been found to have greater stability in wood production over time (Jucker *et al.*,
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7 359 2014a).

9
10 360 Consistent with other studies, we found functional identity to have a greater influence on
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12 361 productivity than functional diversity (Mokany *et al.*, 2008; Ruiz-Benito *et al.*, 2014).
13
14 362 However, this relationship was not constant over the entire continent; the relative importance
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16
17 363 of functional identity was greater at the latitudinal extremes of the continent (Fig. 2),
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19 364 indicating the importance of trait identity for plant growth in harsh climates (Wright *et al.*,
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21 365 2005; Spasojevic & Suding, 2012).
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24 366 **Identity effects point to the relevance of successional differentiation**

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27 367 Not only were identity effects stronger at the extreme ends of the gradient, but also the
28
29 368 relative importance of the traits underlying the identity control changed. What are the
30
31 369 biological underpinnings of this pattern?
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34
35 370 In the Mediterranean biome, functional identity had a stronger influence on tree growth than
36
37 371 climate (Fig. 2) and was primarily controlled by maximum height and wood density (relative
38
39 372 importance *c.* 1) and maximum life span (relative importance *c.* 0.75, see Fig. 3). All else
40
41 373 being equal, Mediterranean forests composed of species with low wood densities, large
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43 374 maximum heights and short maximum life spans exhibited the highest productivity. Low
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45 375 wood density and short maximum life span are features typical of early successional species
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47 376 (Bazzaz, 1979), who maximise resource acquisition and growth at the expense of chemical
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49 377 and structural tissue protection and longevity (Wirth & Lichstein, 2009). Succession in the
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51 378 Iberian Peninsula is leading to changes in the dominance of forests from gymnosperms to
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53 379 angiosperms (Carnicer *et al.*, 2014). The strong influence of maximum height may also point
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55 380 to a successional signature because some slow-growing, late-successional species in the
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3 381 Mediterranean tend to be small statured (e.g. *Quercus ilex* or *Quercus suber*; maximum
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5 382 height of *c.* 18 m), whilst early-successional pines are taller in stature (e.g. *Pinus halepensis*,
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7 383 *Pinus pinaster* or *Pinus pinea*; maximum height of *c.* 26 m).
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10 384 The situation in the temperate biome appears to follow a similar pattern to that in the
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12 385 Mediterranean; forests dominated by species with low wood density and short maximum life
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14 386 spans, i.e. pioneer species, tend to exhibit the highest growth rates. The relative influence of
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16 387 maximum height decreased from south to north in temperate forests, perhaps reflecting that
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18 388 fast growing pioneers such as *Salix caprea* and *Betula pendula* reach shorter maximum
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20 389 heights than typical late successional forest species (e.g. *Fagus sylvatica* or *Quercus robur*).
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22

23 390 A sharp change in trait control occurred towards the boreal biome; wood density and
24
25 391 maximum life span were no longer influential and maximum height resumed a strong
26
27 392 importance but its effect changed sign. Thus, forests with short statured species appear to
28
29 393 have higher growth rates in the boreal region than species with greater maximum heights.
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32 394 Again, we postulate that this may be a successional signature because in the boreal region fast
33
34 395 growing pioneer species (e.g. *Betula pendula*, *Betula pubescens* and *Populus tremula*) reach
35
36 396 shorter maximum heights (*c.* 30 m) than the late successional, slower growing, conifers *Pinus*
37
38 397 *sylvestris* and *Picea abies* (*c.* 40 m). Succession in boreal regions usually progresses from
39
40 398 deciduous to coniferous species (Bergeron & Dansereau, 1993), thus from species with
41
42 399 intermediate and high wood densities to those with low wood density, in contrast to
43
44 400 succession in temperate and Mediterranean regions. The weakened negative effect of wood
45
46 401 density in the boreal region is likely to be due to the narrow range of wood density values
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48 402 compared to the other regions (Fig. S4.7a). We found leaf nitrogen content to be relatively
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50 403 unimportant for tree growth in Mediterranean and temperate regions but to be one of the
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52 404 more important traits in the northern temperate and boreal regions (Fig. 3). There was a
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54 405 transition from a positive influence of leaf nitrogen content on growth in the Mediterranean
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3 406 biome to a negative effect elsewhere. This finding is unexpected, but in line with recent
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5 407 studies, which have not found consistent trends in the shifts of leaf nitrogen content (and
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7 408 other leaf traits) with succession (Douma *et al.*, 2012; Wilfahrt *et al.*, 2014).
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10 409 In summary, the functional identity signal may reflect a trait-based differentiation of
11
12 410 successional stages (Huston & Smith, 1987; Wirth & Lichstein, 2009; Lasky *et al.*, 2014)
13
14 411 rather than an environmental filter reflecting drought or energy limitation at the southern and
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16 412 northern climate extremes, respectively. In different regions late-successional communities
17
18 413 may have a lower or higher growth rate depending on the particular traits of the species,
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20 414 driven in this study, one may speculate, by the dominant role of gymnosperms in the
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22 415 Mediterranean and boreal biomes. It is important to note that this analysis controls, along the
23
24 416 entire gradient, for the structural effects of climate and forest succession with respect to basal
25
26 417 area and tree size, thereby isolating the successional identity effects. Nevertheless, our results
27
28 418 suggest that the successional transition from gymnosperms to angiosperms in the
29
30 419 Mediterranean and from angiosperms to gymnosperms in the boreal regions control the
31
32 420 functional identity effects on tree growth in these latitudes.
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38 421 **Limitations**

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41 422 Due to the different NFI sampling methods, we used a 10 cm d.b.h. threshold for including
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43 423 trees in the study. This restriction is likely to have reduced the diversity of the plots,
44
45 424 especially in the Mediterranean region where much of the diversity is in the tall shrub layer.
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47 425 In addition, plot size could not be standardised across the different inventories, and although
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49 426 we allowed for random variation between inventories, this may have led to an
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51 427 underrepresentation of the diversity of the boreal plots.
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55 428 As with other large-scale trait analyses we were limited by the trait data available (Paquette
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57 429 & Messier, 2011; Ruiz-Benito *et al.*, 2014). We selected five key traits that reflect plant life
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3 430 history strategies, however including other traits, especially root traits or traits unrelated to
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5 431 successional status, may provide additional insight. Our analysis ignored intraspecific trait
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7 432 variation and applied the same trait value to individuals of the same species across the
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9 433 continent. These factors are likely to have resulted in a conservative estimate of the relevance
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11 434 of biodiversity. Due to limited data availability, we were not able to account for other
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13 435 confounding factors that are known to influence tree growth, such as nutrient availability or
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15 436 local hydrology (Pretzsch *et al.*, 2013) or to incorporate an estimate of the successional stage
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17 437 of the plots (Lasky *et al.*, 2014).

20
21 438 This analysis was undertaken on a continent with a large and long-standing impact of forest
22
23 439 management (Bengtsson *et al.*, 2000), which is likely to leave a signature in our results.

24
25 440 Whilst the direct influence of recent management was accounted for, indirect and long-term
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27 441 management effects are likely to persist. The tree species and functional composition of
28
29 442 managed forests may differ from natural assemblies due to planting and promoting of tree
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31 443 species outside of their ecological niche, which could change the causal nature of species
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33 444 identity on tree growth.

34 35 36 37 38 445 **CONCLUSIONS**

39
40 446 Our study contributes to the emerging field of functional biogeography (Violle *et al.*, 2014),
41
42 447 which explores the mechanisms underlying biogeographical patterns of biodiversity and
43
44 448 ecosystem functioning relationships. Functional diversity was an important driver of tree
45
46 449 growth in the Mediterranean region, providing evidence that niche complementarity may be
47
48 450 particularly important in water-limited forests. Across the temperate region the influence of
49
50 451 functional diversity and identity were comparable in magnitude, but were much less
51
52 452 important than climate. The strong influence of functional identity at the latitudinal extremes
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54 453 of the continent indicates the importance of a particular trait composition for tree growth in
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3 454 harsh climates. We have shown how different modes of trait influence vary in their
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5 455 importance for tree growth along a large latitudinal gradient, contributing to a better
6
7 456 understanding of the functional drivers of ecosystem functioning across the forests of Europe.
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10 457

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3 479 **SUPPORTING INFORMATION**

4
5 480 Appendix S1 National Forest Inventory Details

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7 481 Appendix S2 Supplementary Information on Climate, Functional Composition and Species
8 482 Pool Variables

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10 483 Appendix S3 Supplementary Statistical Methods

11
12 484 Appendix S4 Supplementary Figures

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14 485

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17 486 **BIOSKETCH**

18
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21 489 ecosystem functioning, and functional biogeography. This research is part of the
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24
25 491 Author contributions: SR and PRB compiled the inventory data, ML and JK compiled the
26 492 trait data, SR, JMC and CW designed the analysis, SR analysed the data, and SR and CW
27 493 wrote the first draft of the manuscript, with comments from all authors.

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667 APPENDICES

668 Appendix 1 References for the trait data used in this study

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3 957 **FIGURE LEGENDS**

4
5 958 Figure 1. Climate gradients of mean annual temperature (MAT, °C) and mean annual
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7 959 precipitation (MAP, mm) across the latitudinal gradient covered by the National Forest
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9 960 Inventory plots. Mean plot basal area growth (Growth, m² ha⁻¹ yr⁻¹). Dotted lines indicate
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11 961 95% confidence intervals. The white section depicts missing data. Values were calculated at a
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13 962 2° latitude spatial resolution.

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17 963 Figure 2. Predicted relative importance of mean annual precipitation, mean annual
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19 964 temperature, functional identity (aggregated effect of the community mean value of the four
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21 965 functional traits selected) and functional dispersion for tree growth. The sensitivity of plot
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23 966 growth to changes in each variable was estimated from the hierarchical linear model; the
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25 967 variable with the greatest influence in the plot has a relative importance of 1 and the other
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27 968 variables are scaled accordingly. Values are aggregated at 0.5° latitude thus the average
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29 969 relative importance of each predictor is shown. White section depicts missing data. A version
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31 970 with confidence bands is given in Appendix 4, Fig. S4.7.

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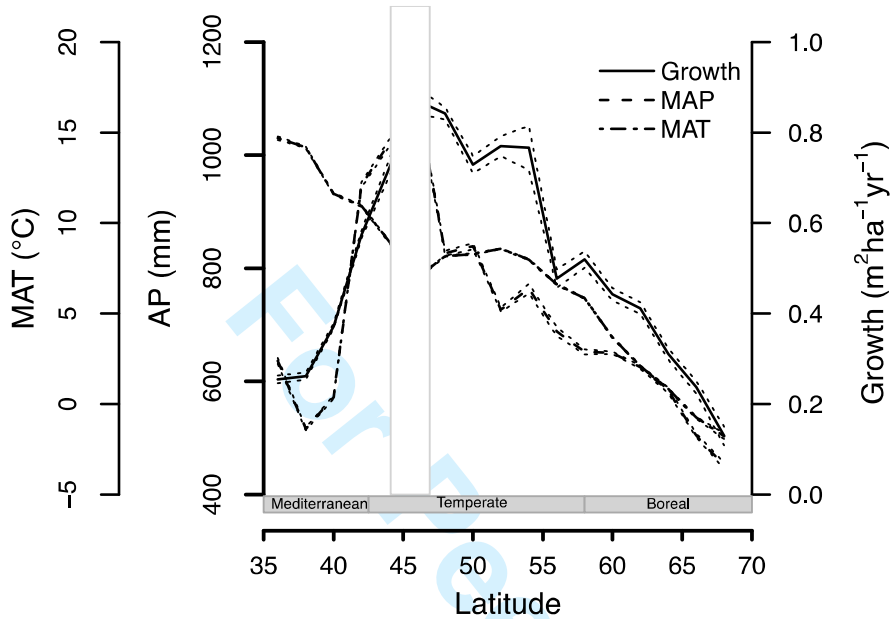
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39 972 Figure 3. Predicted relative importance of five components of functional biodiversity
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41 973 (functional dispersion and the community weighted mean of four functional traits) for tree
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43 974 growth. The sensitivity of plot growth to changes in each component was estimated from the
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45 975 hierarchical linear model; the biodiversity component with the greatest influence in the plot
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47 976 has a relative importance of 1 and the other measures are scaled accordingly. Values are
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49 977 aggregated at 0.5° latitude thus the average relative importance of each predictor is shown.
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51 978 Solid lines indicate a positive influence of the biodiversity measure on plot growth, whilst
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53 979 dashed lines indicate a negative influence. White section depicts missing data. A version with
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55 980 confidence bands is given in Appendix 4, Fig. S4.8.

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3 981 Figure 4. Predicted relative importance of a) FDis (functional diversity; red), FI_{ln}
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5 982 (community-weighted mean (CWM) leaf N mass ($mg^{-1} g$); green) and FI_{wd} (CWM wood
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7 983 density ($g cm^{-3}$); blue); b) FI_{mh} (CWM maximum height (m); red), FI_{ln} (CWM leaf N mass
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9 984 ($mg g^{-1}$); green) and FI_{wd} (CWM wood density ($g cm^{-3}$); blue), for tree growth. The sensitivity
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11 985 of plot growth to changes in each biodiversity component was estimated from a hierarchical
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13 986 linear model using spatial maps of mean annual temperature and mean annual precipitation at
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15 987 spatial resolution of $1 km^2$; the biodiversity measure with the largest effect size in the grid has
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17 988 a relative importance of 1 and the other two measures are scaled accordingly. The RGB cube
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19 989 illustrates how the colour gradient reflects the changes in relative importance of the
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21 990 biodiversity component, such that areas of white indicate an equal importance of all three
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23 991 measures. The arrows indicate an increasing relative importance.
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993 FIGURES

994 Figure 1.



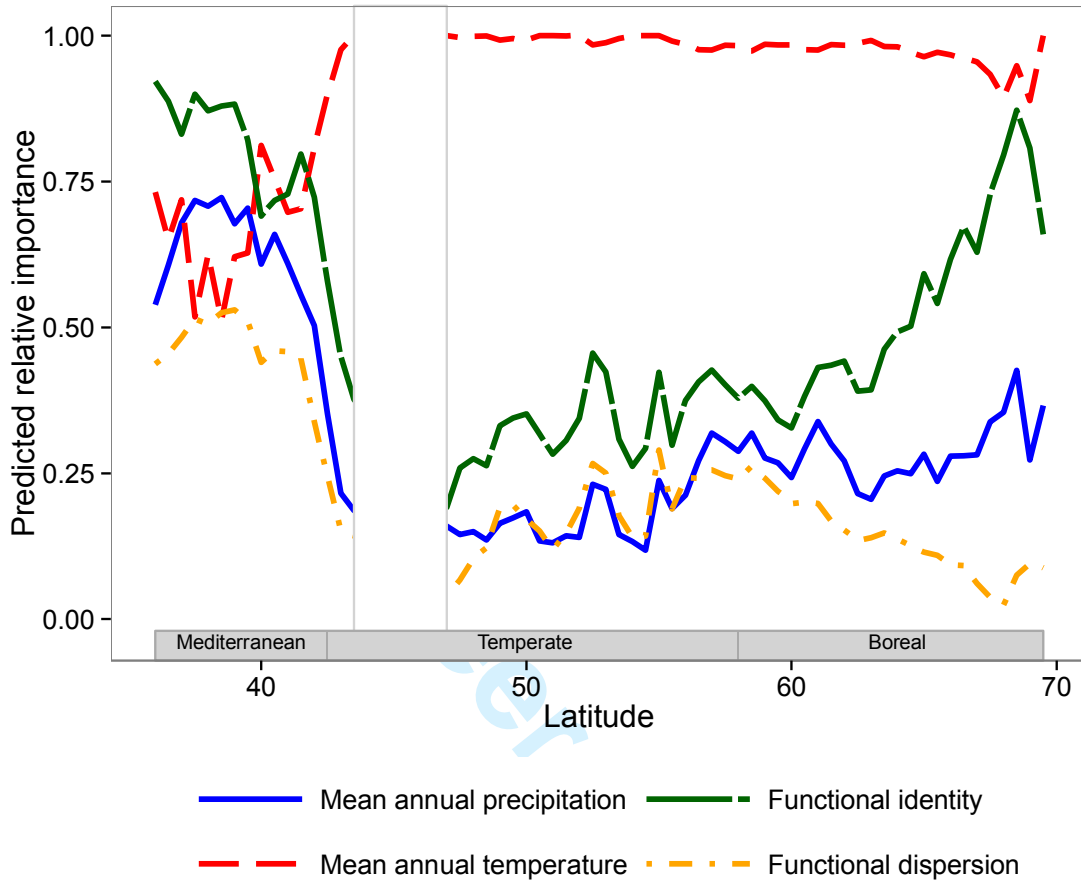
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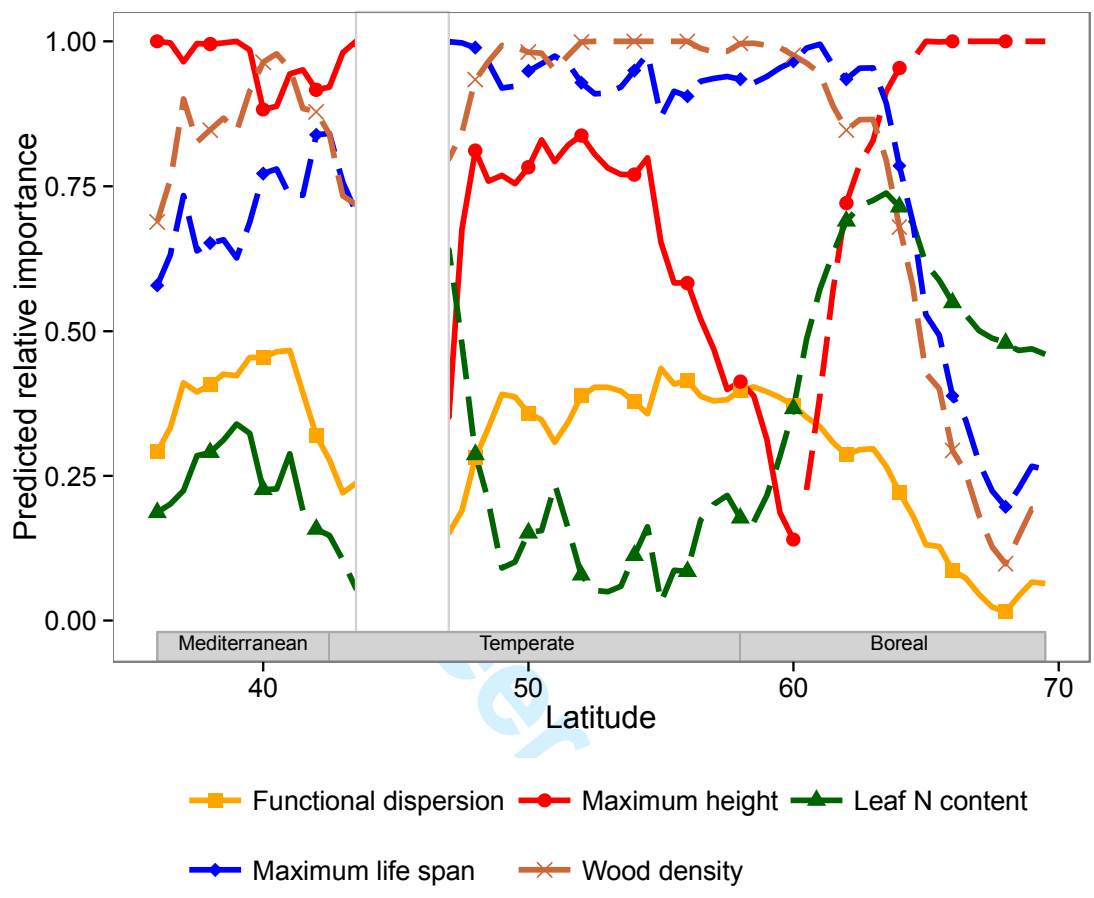


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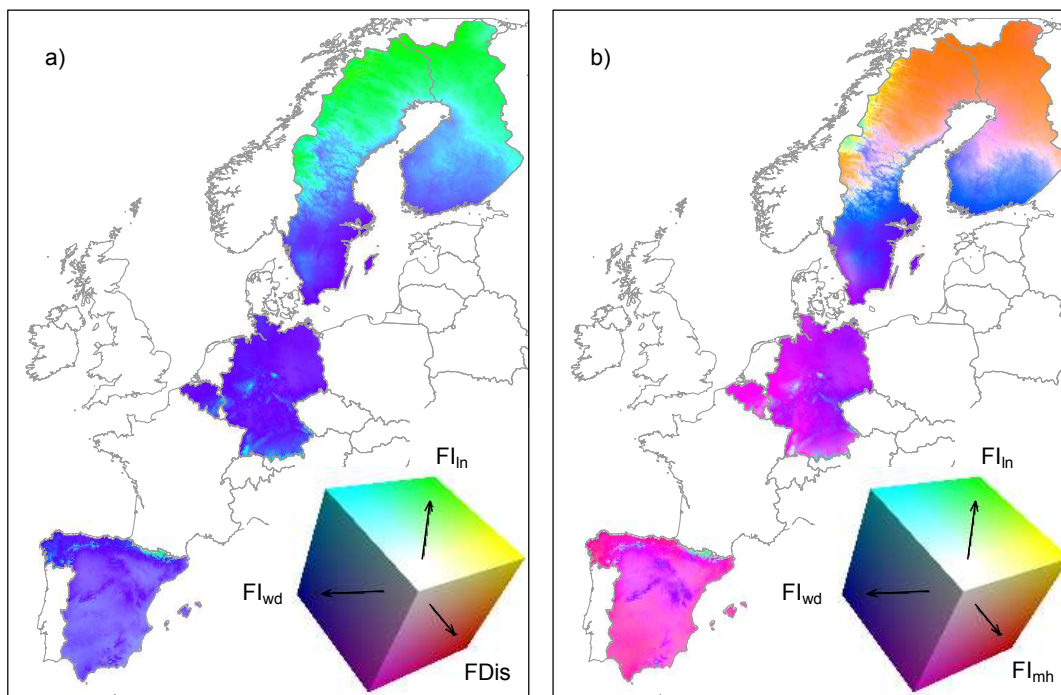
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1002 Figure 3.



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Supporting Information Appendix S1

National Forest Inventory Details

We compiled data from the National Forest Inventories (NFIs) of Finland, Germany, Spain, Sweden and Wallonia, Belgium. Table S1.1 provides a summary of each NFI sampling design. 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. This resulted in 39554 plots with 138 species.

Table S1.1. Summary of the individual National Forest Inventory sampling designs

	Finland	Germany	Spain	Sweden	Wallonia
Survey dates	Subset of NFI 8: 1985-1986 and 1995	BWI 1 (1986-1990) and BWI 2 (2001-2002)	SFI 2 (1986-1996) and SFI 3 (1997-2007)	Inventories 2005-2007 and 2008-2010	Inventories 1994-2003 and 2008-2011
Sample plot design	Cluster design, number and grid size depend on location, see text for details	Cluster design, 4 subplots. Grid size depends on region. Standard grid size is 4 by 4 km	1 km by 1 km grid of single sample plots	Cluster design, number and grid size depend on region. Tract size is between 300-1800 m in length.	1km by 0.5 km grid of single sample plots
Sample tree survey design	Variable radius	Angle-count	Variable radius	Variable radius	Variable radius
Plot size (m ²)	100, 300	BAF 4 m ² ha ⁻¹	79, 315, 707, 1964	38, 314	63, 254, 1017
Minimum tree DBH (cm)	1	10 BWI1 7 BWI2	7.5	4	6.4

Finland

The Finnish data is from a subset of NFI8 from a network of permanent sample plots established to follow changes in forest vegetation. We were given data from two surveys: 1985 to 1986 and 1995. The sample plots are in a systematic grid across the country (Mäkipää & Heikkinen, 2003; Tomppo & Tuimainen, 2010), are located on forest land and form a regular network of clusters. The size of the grid and the number of plots within each cluster depends on the location. In Southern Finland the grid is 16 by 16 km square and there are four plots in each cluster, at 400 m intervals. In Northern Finland the grid is a 24 by 32 km rectangle with three plots per cluster, at 600 m intervals.

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3 The plot size depends on the diameter at breast height (d.b.h.) of the sample trees; trees <
4 10.5 cm d.b.h. the plot size is 100 m², >10.5 cm d.b.h. the plot size is 300 m². The plots are in
5 intensively managed forests, where suppressed trees are thinned.
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8 9 **Germany**

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11 We received data from the first two German NFIs. The first inventory (BW11) was surveyed
12 between 1986 and 1990 (undertaken in West Germany only) and the second (BW12) between
13 2001 and 2002. The mean survey period was 12 years.
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17 The German NFI is based on a systematic rectangular grid, the dimensions of which are
18 determined by the Federal State; the standard size is 4 by 4 km and it is intensified in some
19 States to either 2.83 by 2.83 km or 2 by 2 km (Polley *et al.*, 2010). In each grid square is a
20 quadratic tract of 150 m in length. Each corner of the tract has a sample plot and the tracts are
21 surveyed if at least one of the corners is in forest.
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26 Trees with a minimum d.b.h. of 10 cm, in BW11, and 7 cm, in BW12, were surveyed based on
27 callipered angle count sampling using a basal area factor (BAF) of 4 m² ha⁻¹.
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30 31 **Spain**

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33 We used data from the permanent sample plots of the second (NF12) and third (NF13)
34 Spanish NFIs. NF12 was surveyed between 1986 and 1996 and NF13 between 1997 and 2007,
35 with a mean survey period of 10 years. The sample plots of the Spanish NFI are on a
36 systematic 1 km² grid in forested areas of the country, and are not grouped in tracts but
37 simply one plot in each grid square (Villaescusa & Diaz, 1998; Villanueva, 2005).
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42 The Spanish NFI used a variable radius plot size depending on the d.b.h. of the sample trees;
43 each plot has four nested subplots of 5, 10, 15 and 25 m radius and the minimum d.b.h. for a
44 tree to be recorded within a subplot is 7.5 cm, 12.5 cm, 22.5 cm and 42.4 cm, respectively.
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48 49 **Sweden**

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51 We received data from the permanent sample tracts of the Swedish NFI. The inventory uses a
52 randomly planned regular sampling grid and includes about 4,500 permanent tracts, each
53 surveyed every five years (Axelsson *et al.* 2010). Plots in the first census were surveyed
54 between 2003 and 2005 and plots in the second census were surveyed between 2008 and
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2010. The tracts are rectangular and have different dimensions depending on the location within the country. Each tract has between 4 and 8 circular sample plots.

Trees greater than 1.3 m high are sampled in two different plot sizes depending on the d.b.h. of the tree: 40-99 mm d.b.h.: 3.5 m radius; and greater than 100 mm d.b.h.: 10 m radius.

Wallonia

The Walloon NFI follows a systematic non-stratified sampling methodology on a 1 km by 0.5 km grid (Rondeux *et al.* 2010). One circular sampling plot is located within each grid intersection. Areas are sampled if the area of land is greater than 0.1 ha and has at least 10% covered by a forest canopy (trees must be able to reach a minimum of 5 m). Plots in the first census were surveyed between 1994 and 2003 and plots in the second census were surveyed between 2008 and 2011.

The inventory employs a variable plot size depending on the circumference of the tree: Trees with a circumference between 20-69 cm: 4.5 m radius; 70-119 cm: 9 m radius; and greater than 120 cm: 18 m radius.

Figure S1.1. Biome classification of the selected inventory plots, following Olson *et al.* (2001). Blue: boreal; green: temperate; red: Mediterranean.

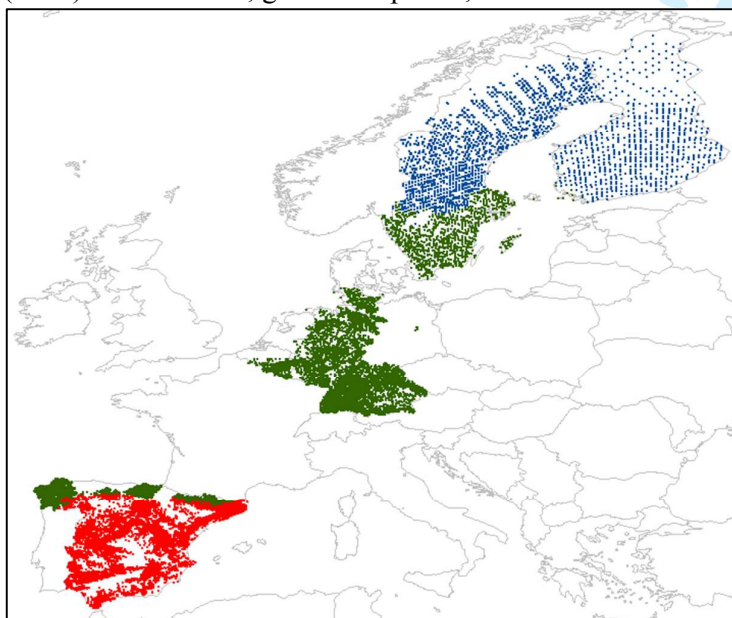
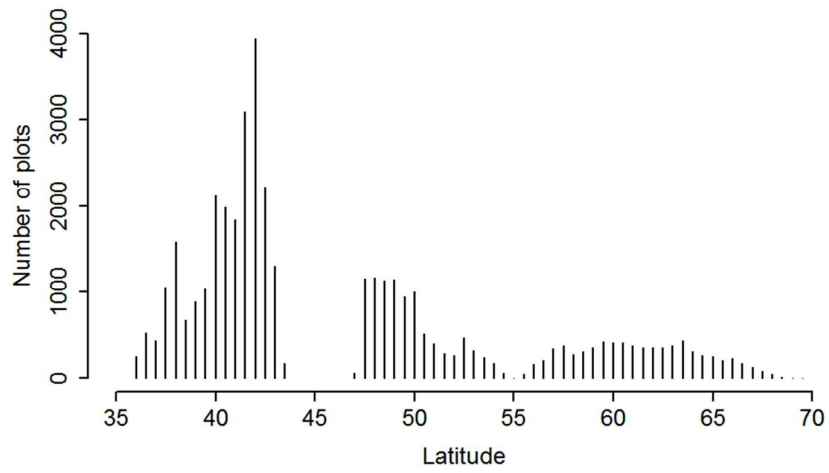


Figure S1.2. Latitudinal distribution of the selected National Forest Inventory plots across the continent.



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Table S1.2. List of species names and families following, where possible, the nomenclature of *Atlas Florae Europaea*. NFI indicates which inventory the species was present in and the exotic status of the species is given where the species was found in the particular NFI (DE: Germany; ES: Spain; FI: Finland; SW: Sweden; and WA: Wallonia).

Name	Family	NFI	Exotic
<i>Abies alba</i> Mill.	<i>Pinaceae</i>	DE, ES, WA	
<i>Abies grandis</i> (D.Don) Lindl.	<i>Pinaceae</i>	DE, WA	DE, WA
<i>Abies pinsapo</i> Boiss.	<i>Pinaceae</i>	ES	
<i>Abies procera</i> Rehder	<i>Pinaceae</i>	DE	DE
<i>Abies</i> spp.	<i>Pinaceae</i>	DE, SW	
<i>Acacia dealbata</i> Link	<i>Leguminosae</i>	ES	ES
<i>Acacia melanoxylon</i> R.Br.	<i>Leguminosae</i>	ES	ES
<i>Acacia</i> spp.	<i>Leguminosae</i>	ES	ES
<i>Acer campestre</i> L.	<i>Aceraceae</i>	DE, ES, WA	
<i>Acer monspessulanum</i> L.	<i>Aceraceae</i>	DE, ES	
<i>Acer negundo</i> L.	<i>Aceraceae</i>	DE, ES	DE, ES
<i>Acer opalus</i> Mill.	<i>Aceraceae</i>	ES	
<i>Acer platanoides</i> L.	<i>Aceraceae</i>	DE, ES, SW, WA	ES
<i>Acer pseudoplatanus</i> L.	<i>Aceraceae</i>	DE, ES, SW, WA	
<i>Aesculus hippocastanum</i> L.	<i>Hippocastanaceae</i>	DE, WA	DE, WA
<i>Ailanthus altissima</i> (Mill.) Swingle	<i>Simaroubaceae</i>	ES	ES
<i>Alnus glutinosa</i> (L.) Gaertn.	<i>Betulaceae</i>	DE, ES, SW, WA	
<i>Alnus incana</i> (L.) Moench	<i>Betulaceae</i>	DE, FI, SW, WA	
<i>Alnus</i> spp.	<i>Betulaceae</i>	FI	
<i>Alnus viridis</i> (Chaix) DC.	<i>Betulaceae</i>	DE	
<i>Arbutus unedo</i> L.	<i>Ericaceae</i>	ES	
<i>Betula pendula</i> Roth	<i>Betulaceae</i>	DE, ES, FI, SW	
<i>Betula pubescens</i> Ehrh.	<i>Betulaceae</i>	DE, FI, SW	
<i>Betula</i> spp.	<i>Betulaceae</i>	ES, SW, WA	
<i>Buxus sempervirens</i> L.	<i>Buxaceae</i>	ES	
<i>Carpinus betulus</i> L.	<i>Betulaceae</i>	DE, ES, SW, WA	
<i>Castanea sativa</i> Mill.	<i>Fagaceae</i>	DE, ES, WA	
<i>Cedrus atlantica</i> (Endl.) Carrière	<i>Pinaceae</i>	ES	ES
<i>Cedrus deodara</i> (D.Don) G.Don	<i>Pinaceae</i>	ES	ES
<i>Cedrus libani</i> A.Rich.	<i>Pinaceae</i>	ES	ES
<i>Celtis australis</i> L.	<i>Ulmaceae</i>	ES	
<i>Ceratonia siliqua</i> L.	<i>Leguminosae</i>	ES	
<i>Chamaecyparis lawsoniana</i> (A.Murray bis) Parl.	<i>Cupressaceae</i>	DE, ES	DE, ES
<i>Corylus avellana</i> L.	<i>Betulaceae</i>	ES	
<i>Crataegus laciniata</i> Ucria	<i>Rosaceae</i>	ES	
<i>Crataegus monogyna</i> Jacq.	<i>Rosaceae</i>	ES	
<i>Crataegus</i> spp.	<i>Rosaceae</i>	ES, WA	
<i>Cupressus arizonica</i> Greene	<i>Cupressaceae</i>	ES	ES
<i>Cupressus lusitanica</i> Mill.	<i>Cupressaceae</i>	ES	ES
<i>Cupressus macrocarpa</i> Hartw.	<i>Cupressaceae</i>	ES	ES
<i>Cupressus sempervirens</i> L.	<i>Cupressaceae</i>	ES	ES

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Name	Family	NFI	Exotic
<i>Eucalyptus camaldulensis</i> Dehnh.	Myrtaceae	ES	ES
<i>Eucalyptus globulus</i> Labill.	Myrtaceae	ES	ES
<i>Eucalyptus gomphocephalus</i> DC.	Myrtaceae	ES	ES
<i>Eucalyptus nitens</i> (H.Deane & Maiden) Maiden	Myrtaceae	ES	ES
<i>Eucalyptus viminalis</i> Labill.	Myrtaceae	ES	ES
<i>Euonymus europaeus</i> L.	Celastraceae	ES	
<i>Fagus sylvatica</i> L.	Fagaceae	DE, ES, SW, WA	
<i>Frangula alnus</i> Mill.	Rhamnaceae	DE, ES	
<i>Fraxinus americana</i> L.	Oleaceae	DE	
<i>Fraxinus angustifolia</i> Vahl	Oleaceae	ES	
<i>Fraxinus excelsior</i> L.	Oleaceae	DE, ES, SW, WA	
<i>Fraxinus ornus</i> L.	Oleaceae	ES	
<i>Ilex aquifolium</i> L.	Aquifoliaceae	DE, ES	
<i>Juglans regia</i> L.	Juglandaceae	DE, ES, WA	DE, ES, WA
<i>Juniperus communis</i> L.	Cupressaceae	ES	
<i>Juniperus oxycedrus</i> L.	Cupressaceae	ES	
<i>Juniperus phoenicea</i> L.	Cupressaceae	ES	
<i>Juniperus</i> spp.	Cupressaceae	DE, FI	
<i>Juniperus thurifera</i> L.	Cupressaceae	ES	
<i>Larix decidua</i> Mill.	Pinaceae	DE, ES	ES
<i>Larix kaempferi</i> (Lamb.) Carrière sec. Franco	Pinaceae	DE, ES	DE, ES
<i>Larix</i> spp.	Pinaceae	DE, ES, SW, WA	
<i>Laurus nobilis</i> L.	Lauraceae	ES	
<i>Malus sylvestris</i> Mill.	Rosaceae	DE, ES	
<i>Morus alba</i> L.	Moraceae	DE, ES	
<i>Olea europaea</i> L.	Oleaceae	ES	
<i>Phillyrea latifolia</i> L.	Oleaceae	ES	
<i>Picea abies</i> (L.) H.Karst.	Pinaceae	DE, ES, FI, SW, WA	ES
<i>Picea omorika</i> (Panc\$Kic\$A) Purk.	Pinaceae	DE	
<i>Picea pungens</i> Engelm.	Pinaceae	DE	DE
<i>Picea sitchensis</i> (Bong.) Carrière	Pinaceae	DE, WA	DE, WA
<i>Picea</i> spp.	Pinaceae	DE, SW	
<i>Pinus canariensis</i> Sweet ex Spreng.	Pinaceae	ES	
<i>Pinus contorta</i> Douglas ex Loudon	Pinaceae	DE, SW	DE, SW
<i>Pinus halepensis</i> Mill.	Pinaceae	DE	
<i>Pinus mugo</i> Turra	Pinaceae	DE, SW	
<i>Pinus nigra</i> J.F.Arnold	Pinaceae	DE, ES	
<i>Pinus pinaster</i> Aiton	Pinaceae	ES	
<i>Pinus pinea</i> L.	Pinaceae	ES	
<i>Pinus ponderosa</i> Douglas ex P.Lawson & C.Lawson	Pinaceae	DE	DE
<i>Pinus radiata</i> D.Don	Pinaceae	ES	ES
<i>Pinus</i> spp.	Pinaceae	DE, SW	
<i>Pinus strobus</i> L.	Pinaceae	DE	DE

Name	Family	NFI	Exotic
<i>Pinus sylvestris</i> L.	Pinaceae	DE, ES, FI, SW, WA	
<i>Pinus uncinata</i> Mill. ex Mirb.	Pinaceae	ES	
<i>Pistacia terebinthus</i> L.	Anacardiaceae	ES	
<i>Platanus hispanica</i> Ten.	Platanaceae	ES	
<i>Populus alba</i> L.	Salicaceae	DE, ES	
<i>Populus balsamifera</i> Brayshaw	Salicaceae	DE	DE
<i>Populus nigra</i> L.	Salicaceae	DE, ES	
<i>Populus</i> spp.	Salicaceae	DE, WA	
<i>Populus tremula</i> L.	Salicaceae	DE, ES, FI, SW, WA	
<i>Populus x canadensis</i> Moench	Salicaceae	DE, ES	DE, ES
<i>Prunus avium</i> L.	Rosaceae	DE, ES, SW, WA	
<i>Prunus lusitana</i> L.	Rosaceae	ES	
<i>Prunus padus</i> L.	Rosaceae	DE, ES	
<i>Prunus serotina</i> Ehrh.	Rosaceae	DE	DE
<i>Prunus spinosa</i> L.	Rosaceae	ES	
<i>Prunus</i> spp.	Rosaceae	ES, WA	
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Pinaceae	DE, ES, WA	DE, ES, WA
<i>Pyrus</i> spp.	Rosaceae	DE, ES	
<i>Quercus canariensis</i> Willd.	Fagaceae	DE	
<i>Quercus faginea</i> Lam.	Fagaceae	DE	
<i>Quercus ilex</i> L.	Fagaceae	DE	
<i>Quercus palustris</i> Münchh.	Fagaceae	DE	DE
<i>Quercus petraea</i> (Matt.) Liebl.	Fagaceae	DE, ES	
<i>Quercus pubescens</i> Willd. (Q. Humilis)	Fagaceae	DE	
<i>Quercus pyrenaica</i> Willd.	Fagaceae	DE	
<i>Quercus robur</i> L.	Fagaceae	DE, ES	
<i>Quercus rubra</i> L.	Fagaceae	DE, ES, WA	DE, ES, WA
<i>Quercus</i> spp.	Fagaceae	DE, ES, SW, WA	
<i>Quercus suber</i> L.	Fagaceae	ES	
<i>Rhamnus alaternus</i> L.	Rhamnaceae	ES	
<i>Robinia pseudacacia</i> L.	Leguminosae	DE, ES, WA	DE, ES, WA
<i>Salix alba</i> L.	Salicaceae	ES	
<i>Salix atrocinerea</i> Brot.	Salicaceae	ES	
<i>Salix caprea</i> L.	Salicaceae	DE, ES, SW, WA	
<i>Salix elaeagnos</i> Scop.	Salicaceae	ES	
<i>Salix fragilis</i> L.	Salicaceae	ES	
<i>Salix</i> spp.	Salicaceae	DE, ES, FI, WA	
<i>Sambucus nigra</i> L.	Caprifoliaceae	ES	
<i>Sambucus racemosa</i> L.	Caprifoliaceae	ES	
<i>Sorbus aria</i> (L.) Crantz	Rosaceae	DE, ES	
<i>Sorbus aucuparia</i> L.	Rosaceae	DE, ES, SW, WA	
<i>Sorbus domestica</i> L.	Rosaceae	DE, ES	
<i>Sorbus intermedia</i> (Ehrh.) Pers.	Rosaceae	SW	

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Name	Family	NFI	Exotic
<i>Sorbus</i> spp.	<i>Rosaceae</i>	DE, ES, FI	
<i>Sorbus torminalis</i> (L.) Crantz	<i>Rosaceae</i>	DE, ES	
<i>Taxus baccata</i> L.	<i>Taxaceae</i>	DE, ES	
<i>Thuja</i> spp.	<i>Cupressaceae</i>	DE, ES	DE, ES
<i>Tilia cordata</i> Mill.	<i>Tiliaceae</i>	ES	
<i>Tilia platyphyllos</i> Scop.	<i>Tiliaceae</i>	ES	
<i>Tilia</i> spp.	<i>Tiliaceae</i>	DE, ES, SW, WA	
<i>Tsuga</i> spp.	<i>Pinaceae</i>	DE, WA	DE, WA
<i>Ulmus glabra</i> Huds.	<i>Ulmaceae</i>	ES	
<i>Ulmus minor</i> Mill.	<i>Ulmaceae</i>	ES	
<i>Ulmus</i> spp.	<i>Ulmaceae</i>	DE, SW, WA	

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Table S1.3. Summary statistics of the selected plots from each National Forest Inventory. BA: mean basal area ($\text{m}^2 \text{ha}^{-1}$); DBH: mean d.b.h. (mm); MR: annual natural mortality rate ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$); SP: species pool; FDis: functional dispersion; FI_{mh} : CWM maximum height (m); FI_{ln} : CWM leaf N mass (mg g^{-1}); FI_{ls} : CWM maximum tree life span (yr); FI_{wd} : CWM wood density (g cm^{-3}).

	Spain	Germany	Sweden	Finland	Wallonia (Belgium)
Number of plots	22989	8821	6083	1174	488
Growth ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$)	0.41 (0.04 – 1.30)	0.82 (0.18 – 1.99)	0.42 (0.05 – 1.18)	0.43 (0.06 – 0.99)	0.52 (0.15 – 1.51)
BA ($\text{m}^2 \text{ha}^{-1}$)	15.52 (4.85 – 39.07)	30.54 (8.00 – 62.71)	17.60 (4.95 – 41.02)	16.41 (5.60 – 34.08)	23.04 (8.63 – 52.24)
DBH (mm)	290.07 (146 – 618.43)	327.94 (146 – 618.7)	198.33 (130.3 – 351.6)	192.84 (133.7 – 306.4)	405.03 (158.3 – 638)
MR ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$)	1.37 (0.0 – 11.81)	0.33 (0.0 – 3.44)	0.33 (0.0 – 3.00)	0.16 (0.0 – 1.68)	0.22 (0.0 – 2.49)
SP	62.25 (4 – 108)	71.22 (8 – 101)	33.32 (8 – 53)	28.68 (8 – 41)	71.37 (52 – 94)
Monocultures (%)	52.2	32.0	19.5	26.5	28.7
FDis	0.03 (0.0 – 0.27)	0.05 (0.0 – 0.19)	0.05 (0.0 – 0.21)	0.05 (0.0 – 0.14)	0.06 (0.0 – 0.19)
FI_{mh} (m)	30.08 (18.67 – 40.25)	40.48 (25.00 – 56.54)	35.32 (22.76 – 50)	35.32 (20.07 – 50)	32.02 (21.51 – 50)
FI_{ln} (mg g^{-1})	13.54 (10.04 – 23.1)	17.57 (12.44 – 26.92)	14.80 (12.44 – 24.25)	14.67 (12.44 – 23.87)	19.35 (12.44 – 25.0)
FI_{ls} (yr)	473.39 (2 – 1000)	479.79 (120 – 800)	430.97 (126 – 600)	437.61 (155 – 600)	428.84 (138 – 581)
FI_{wd} (g cm^{-3})	0.65 (0.48 – 0.9)	0.55 (0.44 – 0.72)	0.51 (0.44 – 0.60)	0.51 (0.44 – 0.56)	0.69 (0.44 – 0.86)

For species pool (SP) and functional diversity (FDis) the mean and range (maximum and minimum) are given. For all the other variables the mean and 2.5 and 97.5 percentiles are presented.

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Supporting Information Appendix S2 Climate, Functional Composition and Species Pool Variables

Climate variable selection

We used the inventory plot coordinates to extract plot-level climatic variables from the WorldClim database (Hijmans *et al.*, 2005) and potential evapotranspiration (PET; mm yr⁻¹) and an aridity index (MAP / PET, where MAP is mean annual precipitation) from CGIAR-CSI (Trabucco & Zomer, 2009). WorldClim database includes 19 climatic variables based on temperature and precipitation over the period 1950-2000, including seasonal variability indices. In addition, we calculated a water availability index (WAI) as the proportion of water available with respect to water climate demand (i.e. $WAI = (MAP - PET) / PET$).

Rather than perform a length model selection process testing each climate variable, we performed a dimension reduction using a principal component analysis (PCA) on all 22 climate variables, to determine which variables best represent the climate data cloud. The first axis accounted for 52.25% of the variation in the climate data and the second axis 26.53%. PET and WAI both loaded strongly to the first axis (0.97 and 0.93, respectively) and temperature seasonality (standard deviation of yearly MAT values) loaded strongly on the second axis (0.91). MAT and MAP also loaded strongly to the two PCA axes (0.85 and 0.73, respectively).

The model (equation 1 in the manuscript) was refitted replacing MAT and MAP in the equation with:

1. the scores of the first two PCA axes;
2. PET and temperature seasonality;
3. WAI and temperature seasonality.

The deviance information criterion (DIC) values for each model are listed in Table S2.1, where the model with the smallest DIC is considered a better model fit, based on the number of parameters in the model and the model fit (Spiegelhalter *et al.*, 2002). We included the WAI and temperature seasonality model because PET and temperature seasonality were moderately correlated (Spearman rank coefficient = -0.35), which is not ideal, and WAI and TS were not correlated (Spearman rank coefficient = -0.004). MAT and MAP were weakly correlated (Spearman rank coefficient: -0.18, $p < 0.001$).

Table S2.1. Comparison of growth models based on DIC parameterised using different climate variables. Climate variables are MAT (mean annual temperature; °C), MAP (mean annual precipitation; mm), PCA1 (first axis of the PCA), PCA2 (second axis of the PCA), PET (potential evapotranspiration; mm), and temperature seasonality (standard deviation of yearly MAT values). Deviance Information Criterion (DIC) and Δ DIC are shown.

Climate variables	DIC	Δ DIC
MAT and MAP	-29361.72	0.00
PCA1 and PCA2	-29316.62	45.10
PET and temperature seasonality	-28980.64	381.08
WAI and temperature seasonality	-28890.31	471.41

MAT and MAP were selected as the climate variables due to their better predictive power (by DIC comparison) and parsimony over the first two PCA axes of the 22 climate variables.

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Table S2.2. References for the trait data used in the study

The trait matrix, for the 138 species in the final analysis, was 87% complete. We increased this to 94% by computing genus-level means. Genus-level trait values were taken as the average values of the available species. Plots with species groups such as ‘other conifers’ were excluded. [The reference list is given in Appendix 1 of the main manuscript.](#)

Reference	Accessed from TRY	Leaf N	Maximum height	Maximum tree life span	Seed mass	Wood density
Aas 1999				X		
Atkin <i>et al.</i> 1999	Yes	X				
Bahn 1999	Yes	X				
Briemle <i>et al.</i> 2002	Yes				X	
Campbell <i>et al.</i> 2007	Yes	X				
Castro-Diez <i>et al.</i> 1998	Yes	X	X		X	X
Castro-Diez <i>et al.</i> 2000	Yes	X	X		X	X
Chave <i>et al.</i> 2009	Yes					X
Cornelissen 1996	Yes	X	X		X	X
Cornelissen <i>et al.</i> 1996	Yes	X	X		X	X
Cornelissen <i>et al.</i> 1999	Yes	X	X		X	X
Cornelissen <i>et al.</i> 2001	Yes	X	X		X	X
Cornelissen <i>et al.</i> 2003	Yes	X	X		X	X
Cornelissen <i>et al.</i> 2004	Yes	X	X		X	X
Cornwell <i>et al.</i> 2006	Yes	X	X		X	X
Cornwell <i>et al.</i> 2008	Yes	X	X		X	X
Craine <i>et al.</i> 2009	Yes	X				
Dabernig 1996				X		
Diaz <i>et al.</i> 2004	Yes	X	X		X	X
Durka 2002	Yes				X	
Fischer <i>et al.</i> 2008				X		
Fitschen 2007			X	X		
Fonseca <i>et al.</i> 2000	Yes	X	X			
Freschet <i>et al.</i> 2010a	Yes	X				
Freschet <i>et al.</i> 2010b	Yes	X				
Garnier <i>et al.</i> 2007	Yes	X			X	
Godet 2006						X
Green 2009	Yes				X	
Han <i>et al.</i> 2005	Yes	X				
He <i>et al.</i> 2006	Yes	X				
Hecker 2012				X		
Jordano 2007					X	
Kattge <i>et al.</i> 2009	Yes	X				
Kattge <i>et al.</i> 2011a	Yes	X	X		X	
Kattge <i>et al.</i> 2011b			X	X	X	X
Kerkhoff <i>et al.</i> 2006	Yes	X				
Kirkup <i>et al.</i> 2005	Yes		X			
Kleyer <i>et al.</i> 2008	Yes		X		X	X
Klotz <i>et al.</i> 2002	Yes				X	
Krumbiegel 2002	Yes				X	
Kühn <i>et al.</i> 2004	Yes				X	
Laughlin <i>et al.</i> 2010	Yes	X	X		X	
Loveys <i>et al.</i> 2003	Yes	X				
McDonald <i>et al.</i> 2003	Yes	X	X			
Medlyn <i>et al.</i> 1999	Yes	X				
Moles <i>et al.</i> 2004	Yes		X	X	X	
Niinemets 2001	Yes	X				
Ogaya & Peñuelas 2003	Yes	X	X			X
Ogaya & Peñuelas 2006	Yes	X	X			X
Ordoñez <i>et al.</i> 2010a	Yes	X	X			X

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3	Ordoñez <i>et al.</i> 2010b	Yes	X	X			X
4	Otto 2002	Yes			X		
5	Pakeman <i>et al.</i> 2008	Yes	X		X		
6	Paula <i>et al.</i> 2009	Yes		X	X		
7	Paula & Pausas 2008	Yes			X		
8	Peñuelas <i>et al.</i> 2010a	Yes	X	X			X
9	Peñuelas <i>et al.</i> 2010b	Yes	X	X			X
10	Preston <i>et al.</i> 2006	Yes	X	X	X		X
11	Quested <i>et al.</i> 2003	Yes	X	X	X		X
12	Reich <i>et al.</i> 2008	Yes	X				X
13	Reich <i>et al.</i> 2009	Yes	X				X
14	Roloff <i>et al.</i> 1994				X		X
15	Royal Botanical Gardens Kew 2008	Yes			X		
16	Schütt <i>et al.</i> 2002			X	X		
17	Seifert 1971				X		
18	USDA, NRCS 2011			X			
19	van Bodegom <i>et al.</i> 2005	Yes	X				
20	van Bodegom <i>et al.</i> 2008	Yes	X				
21	Vorreiter 1949						X
22	Wächtershäuser & Trageser 2011				X		
23							
24	Wagenführ & Scheiber 1985				X		
25	Willis <i>et al.</i> 2010	Yes	X				X
26	Wirth & Lichstein 2009	Yes		X	X		
27	Wohlfahrt <i>et al.</i> 1999	Yes	X				
28	Wright <i>et al.</i> 2004	Yes	X	X			
29	Wright <i>et al.</i> 2006	Yes	X	X			
30	Zanne <i>et al.</i> 2009						X

Functional Composition Estimation

The functional diversity of each plot was quantified using the functional dispersion index (FDis) of Laliberté & Legendre (2010) using the five traits selected and weighted by their relative abundance: maximum tree height (m); leaf nitrogen content (mg g^{-1}); maximum tree lifespan (yrs); seed mass (mg); and wood density (g cm^{-3}).

Due to the very low species richness of the plots we were limited in the choice of functional diversity indices available to use. The FDis can be calculated for communities with two or more singular species, i.e. species that differ in one or more traits. It is also possible with Rao's quadratic entropy (Botta-Dukát, 2005). Other functional diversity indices such as functional divergence (Mason *et al.*, 2005) and functional evenness were not possible to calculate for a large number of the plots in our dataset, where the number of traits exceeded the number of species in the plot. Both FDis and Rao's Q include elements of evenness and divergence (Mason *et al.*, 2013), which together have been shown to be important for estimating complementarity in communities.

We used the Gower distance matrix, rather than a Euclidean matrix, even though the traits are all continuous, because the Gower distance matrix is more stable against missing values (Pavoine *et al.*, 2009) of which there were 6% in the trait matrix. The trait variables were transformed (either log or square root) following Botta-Dukát (2005) and Pavoine *et al.* (2009), to ensure that where the distribution of traits is highly skewed extreme values do not exert a greater effect.

The 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). FDis and FI were calculated using the 'FD' package in R (Laliberté & Shipley, 2011). 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.

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Species Pool Estimation

The species pool was estimated from tree species distribution maps. The distribution maps were provided by Martin Freiberg from the Botanical Gardens, Leipzig and Erik Welk from the Botanical Gardens, Halle, and compiled for the FunDivEUROPE project (<http://www.fundiveurope.eu>) by Mario Liebergesell at 5 arc minute resolution. Nomenclature follows the *Atlas Florae Europaea*.

The reference list for the tree species distribution maps is given in Appendix 2 in the main manuscript.

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Supporting Information Appendix S3 Supplementary Statistical Methods

Model fitting and prior information

For data from Finland, Sweden and Germany the random intercepts (α_r) were cluster-level intercepts ($\alpha_{cluster}$) modelled from a normal distribution, such that

$$\alpha_{cluster} \sim Normal(\alpha_{nfi}, \sigma_{cluster})$$

where α_{nfi} is the NFI-level mean growth and $\sigma_{cluster}$ the cluster-level s.d.. For the data from Spain and Wallonia the random intercepts (α_r) were NFI-level intercepts (α_{nfi}). The NFI-level intercepts (α_{nfi}), from all five inventories, were modelled such that:

$$\alpha_{nfi} \sim Normal(0, \sigma_{nfi})$$

where σ_{nfi} is the standard deviation.

We tested for model convergence by running three chains with different starting values and checked the Rhat statistic, where a value of <1.1 indicates convergence (Gelman *et al.*, 2004).

The following priors were used:

$$\alpha_0, \alpha_{cluster}, \alpha_{nfi}, \beta_{1-29} \sim Normal(0, 10)$$

$$\sigma_{\mu}, \sigma_{cluster}, \sigma_{nfi} \sim Uniform(0, 1)$$

Convergence took between 250 and 500 iterations; we ran the model for 500 iterations of warm up and an additional 10,000 iterations for sampling. Samples were taken every 10 iterations. The Deviance information criterion (DIC) was calculated as the model fit statistic following (Spiegelhalter *et al.*, 2002). A simple model was tested that only included an nfi-level random intercept (no cluster-level) but the DIC comparison indicated that the more complex model was justified ($\Delta DIC > 1000$). A more complicated model was also tested allowing a different $\sigma_{cluster}$ for Finland, Germany and Sweden but $\sigma_{cluster}$ parameters did not converge.

The proportion of the variance in plot-level growth explained by the final model was estimated as 1 minus the residual variance divided by the variance in the data. The calculation was averaged over the posterior distribution of the predicted values (Korner-Nievergelt *et al.*, 2015).

References

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Model Evaluation

Table S3.1. Mean and 95% credible intervals of the posterior distribution of the model parameters. The model predicts plot-level growth rate ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) depending on structural, climatic and biodiversity variables. Predictor variables were centred on 0 and scaled to 1 standard deviation. The proportion of the variance in plot-level growth explained by the final model was 0.684. Not all of the variance explained can be attributed to the predictors; some will be explained by the cluster and country effects. *

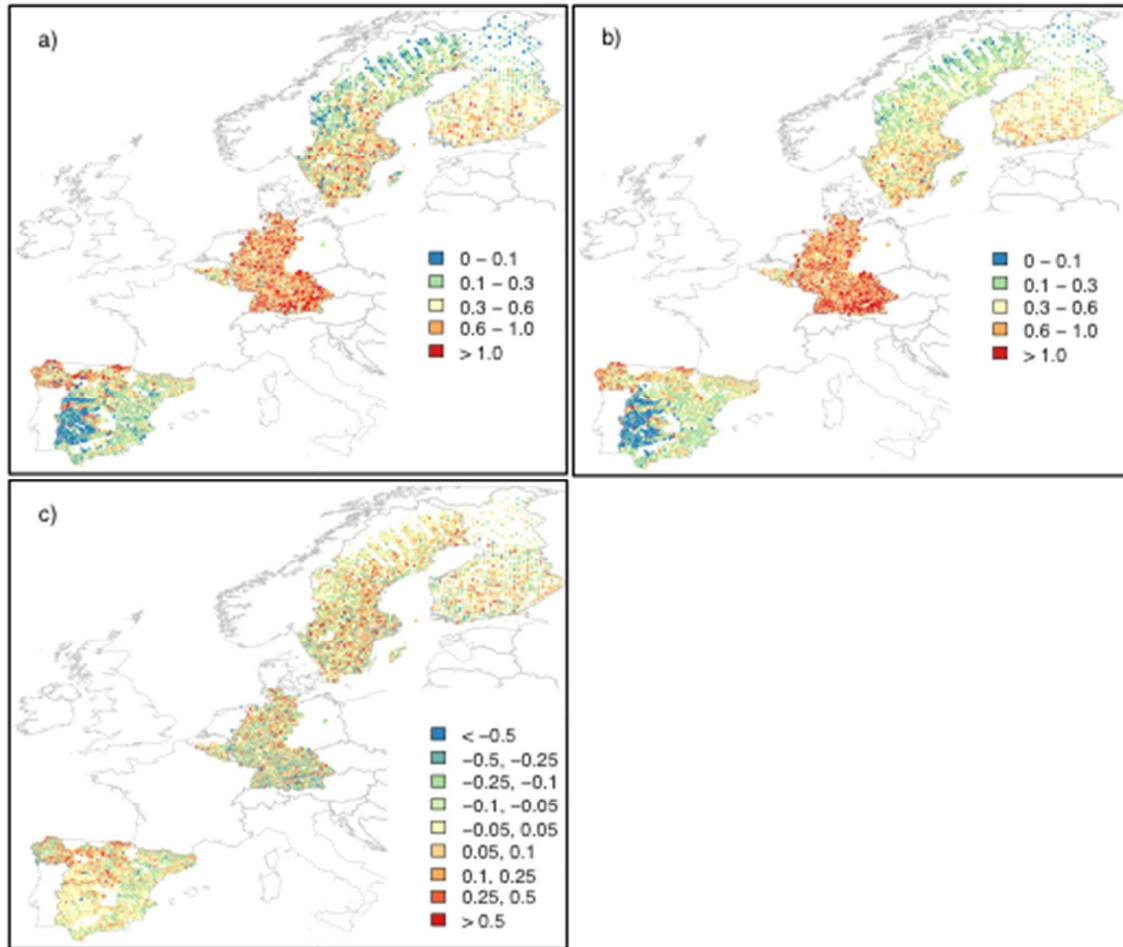
Variable	Model			
	coefficient	Mean	2.5 %	97.5 %
	α_0	-0.911	-1.07	-0.802
MAT	β_{MAT}	0.205	0.191	0.217
MAP	β_{AP}	0.067	0.060	0.074
BA	$\beta_1^{(c)}$	0.490	0.484	0.496
DBH	$\beta_2^{(c)}$	-0.314	-0.320	-0.308
MR	$\beta_3^{(c)}$	-0.074	-0.082	-0.066
SP	$\beta_4^{(c)}$	0.064	0.054	0.074
FDis	$\beta_1^{(z)}$	0.054	0.049	0.060
FI _{wd}	$\beta_2^{(z)}$	-0.134	-0.145	-0.123
FI _{mh}	$\beta_3^{(z)}$	0.113	0.106	0.120
FI _{ls}	$\beta_4^{(z)}$	-0.120	-0.130	-0.111
FI _{ln}	$\beta_5^{(z)}$	-0.001	-0.007	0.008
BA x MAT	$\delta_1^{(\text{MAT})}$	0.014	0.007	0.020
DBH x MAT	$\delta_2^{(\text{MAT})}$	0.048	0.041	0.056
MR x MAT	$\delta_3^{(\text{MAT})}$	0.028	0.018	0.036
SP x MAT	$\delta_4^{(\text{MAT})}$	-0.010	-0.016	-0.004
BA x MAP	$\delta_1^{(\text{AP})}$	-0.037	-0.043	-0.031
DBH x MAP	$\delta_2^{(\text{AP})}$	0.010	0.004	0.015
MR x MAP	$\delta_3^{(\text{AP})}$	-0.014	-0.017	-0.010
SP x AP	$\delta_4^{(\text{AP})}$	0.013	0.004	0.022
FDis x MAT	$\gamma_1^{(\text{MAT})}$	0.017	0.010	0.023
FDis x MAP	$\gamma_1^{(\text{AP})}$	-0.013	-0.018	-0.008
FI _{wd} x MAT	$\gamma_2^{(\text{MAT})}$	-0.028	-0.042	-0.015
FI _{wd} x MAP	$\gamma_2^{(\text{AP})}$	0.007	0.0002	0.015
FI _{mh} x MAT	$\gamma_3^{(\text{MAT})}$	0.096	0.087	0.103
FI _{mh} x MAP	$\gamma_3^{(\text{AP})}$	0.011	0.005	0.017
FI _{ls} x MAT	$\gamma_4^{(\text{MAT})}$	-0.014	-0.025	-0.002
FI _{ls} x MAP	$\gamma_4^{(\text{AP})}$	-0.008	-0.015	-0.001
FI _{ln} x MAT	$\gamma_5^{(\text{MAT})}$	0.040	0.031	0.050
FI _{ln} x MAP	$\gamma_5^{(\text{AP})}$	-0.024	-0.031	-0.018
	σ_μ	0.451	0.447	0.454
	σ_{cluster}	0.223	0.212	0.233
	σ_{nfi}	0.171	0.089	0.277

* MAT: mean annual temperature ($^{\circ}\text{C}$, log+7); MAP: mean annual precipitation (mm); BA: mean basal area ($\text{m}^2 \text{ha}^{-1}$, log); DBH: mean d.b.h. (mm, log); MR: annual natural mortality rate ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$);

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3 SP: regional species pool (log); FDis: functional dispersion (sqrt); FI_{wd} : CWM wood density ($g^{-1} cm^3$);
4 FI_{mh} : CWM maximum height (m); FI_{ls} : CWM maximum tree life span (yr); FI_{ln} : CWM leaf N mass
5 ($mg^{-1} g$); α_0 : expected plot growth rate under average conditions (log scale); σ_{μ} : residual standard
6 deviation (log scale); $\sigma_{cluster}$: cluster-level standard deviation (log scale); σ_{nfi} : inventory-level standard
7 deviation (log scale). α_r has not been included in the table for brevity as there are 8493 cluster values
8 estimated in the model.
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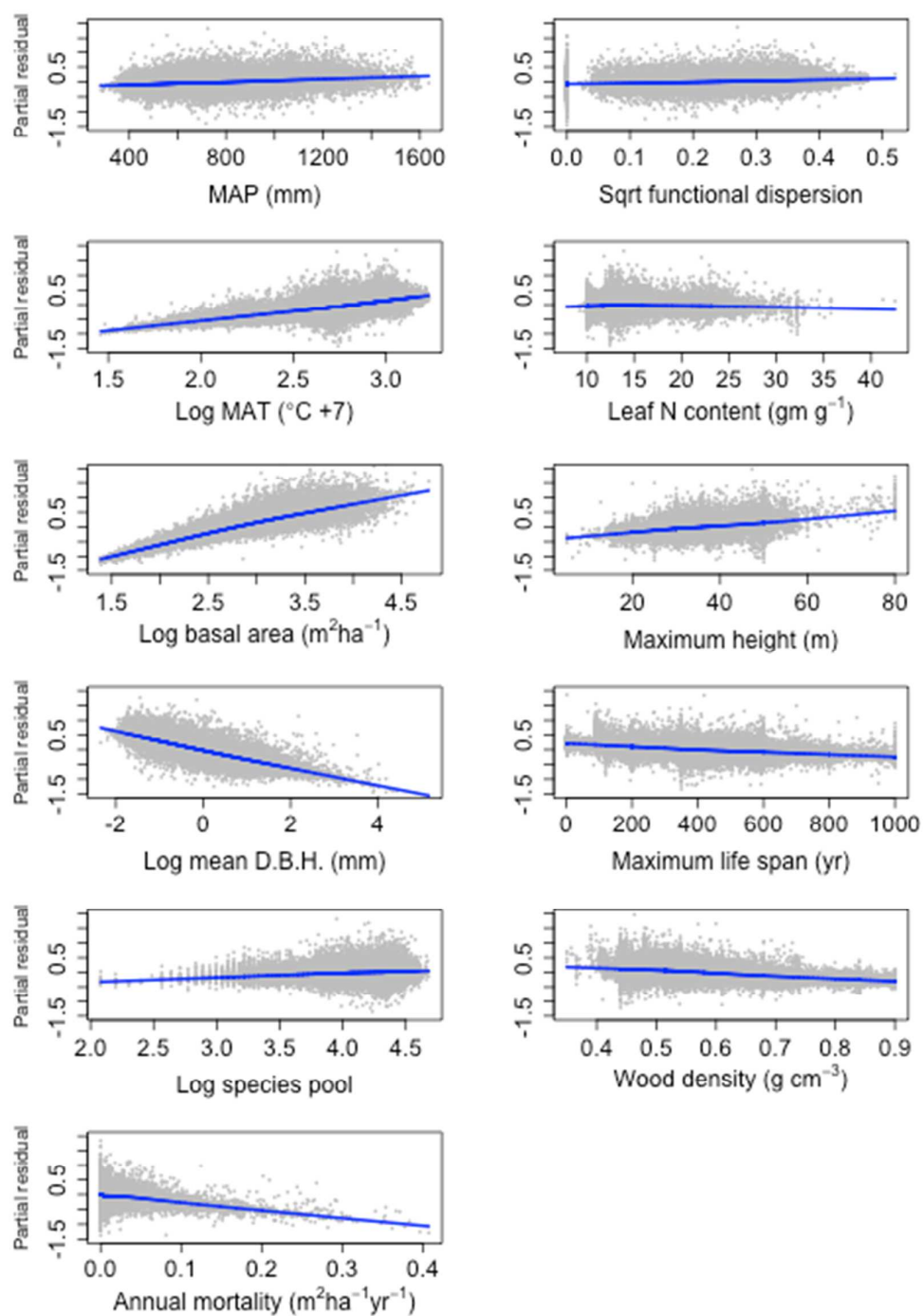
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Figure S3.1. Growth ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) (a); predicted growth ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) (b); and the model residuals ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) (c) in each inventory plot.



view

Figure S3.2. Partial residual plots for each predictor in the full model. The partial residual was calculated in each plot (i) as $residual_i + \beta_i X_i$, where $residual_i$ is the residual for plot i , β_i is the mean of the posterior distribution of predictor X and X_i is the value of predictor X in plot i . The blue line is the lowest smoothing line. The plots illustrate the relationship between each of the predictor variables and tree growth once all the other predictors have been accounted for in the model and they are useful to identify non-linear relationships. In each case, after appropriate transformations, no large deviations from linear relationships were observed and the linear approximations justified.



Control Analyses

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

Influence of climate variable selection

As a further sensitivity study we repeated the analysis where the climate variables (mean annual temperature and mean annual precipitation) were replaced by the scores of the first two axes of a PCA analysis of 22 climate variables (see Appendix S2). The patterns are **robust** in the Mediterranean and temperate regions (Fig S3.3a & b); however the PCA model does not predict a **large** increase in the importance of functional identity in the boreal region (Fig S3.3b). The reason is because the PCA model does not predict such a drastic increase in the relative importance of FI_{mh} in the boreal region as the MAT-MAP model (Figs S3.3b and S3.4). **In addition, the PCA model does not predict an increase in the importance of FI_m in the boreal region.** With this in mind, we treat our findings in the boreal region with caution.

Figure S3.3. a) Predicted relative importance of climate, represented by two PCA axes (PCA 1 and PCA 2) of 22 climate variables, functional identity (aggregated effect of the community mean value of four functional traits) and functional dispersion for tree growth. b) Predicted relative importance of five components of functional biodiversity (functional dispersion and the community weighted mean of four functional traits) for tree growth.

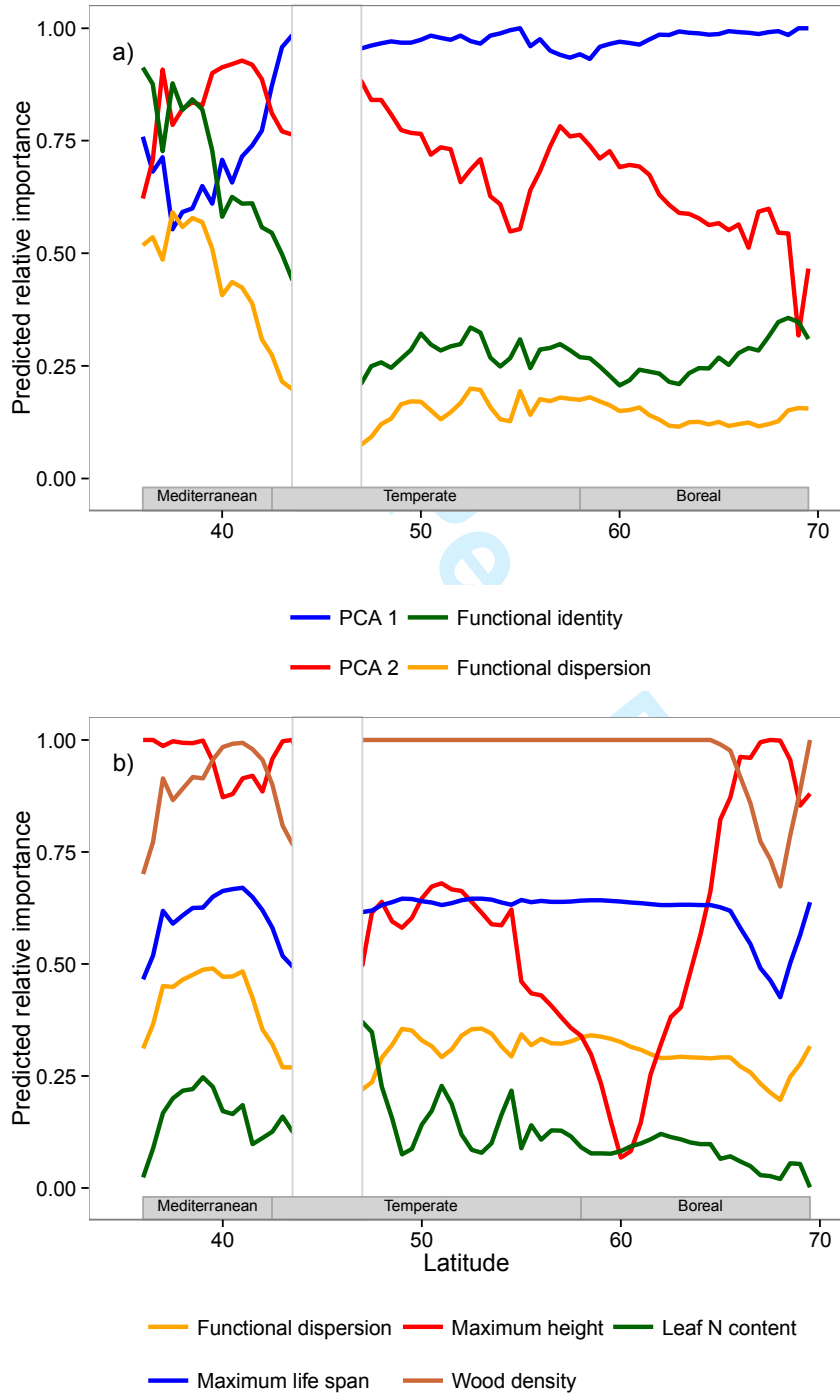
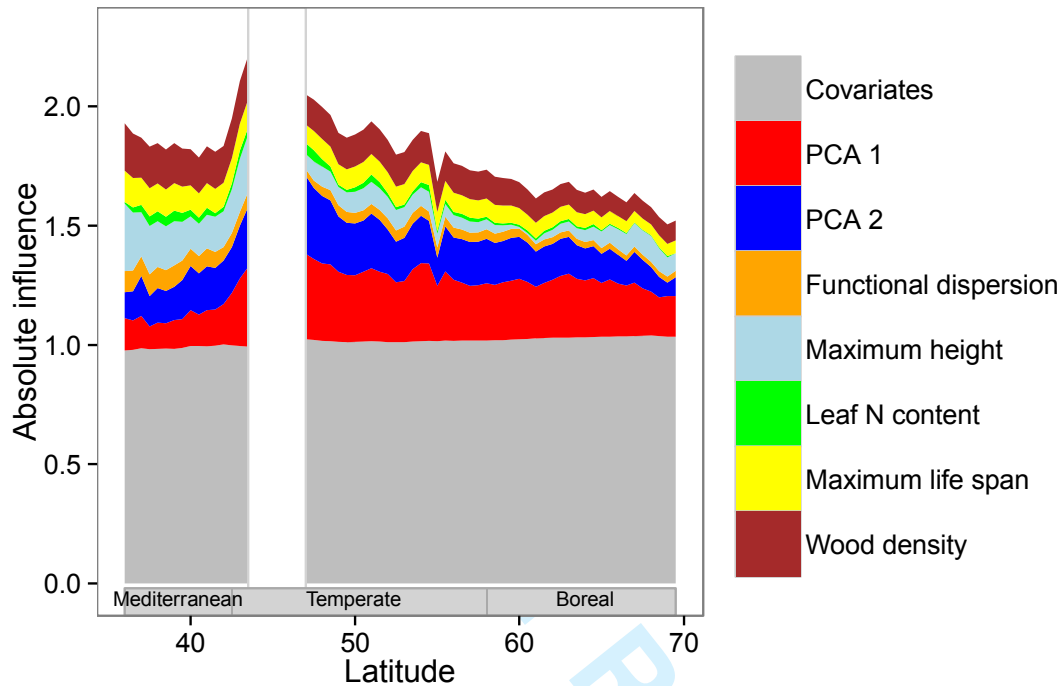


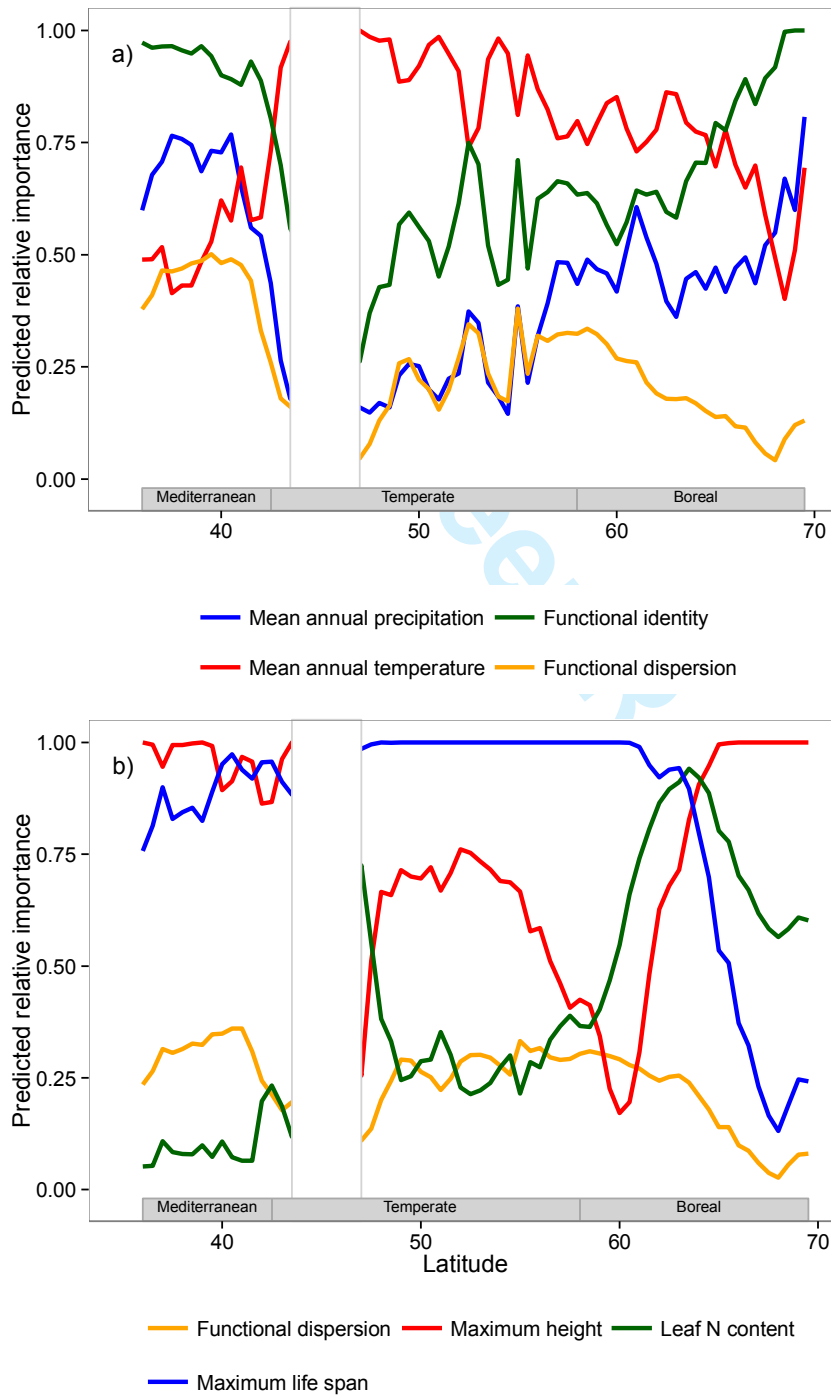
Figure S3.4. The absolute influence of each predictor on plot-level tree growth ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) across the continent. The predictors are: the first PCA axis (PCA 1); second PCA axis (PCA 2); functional dispersion; community-weighted mean (CWM) maximum height; CWM leaf N content; CWM maximum life span; and CWM wood density. The covariates (plot basal area ($\text{m}^2 \text{ha}^{-1}$), mean tree size (mm), species pool and natural mortality rate ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$)) have been group together in grey and labeled covariates.



Influence of multicollinearity

We found that the importance of FI_{wd} and FI_{ls} for tree growth changed in concert across the continent (Fig. 3). Given that their FI values were moderately correlated (Spearman rank coefficient = 0.5; $p < 0.001$) and in order to separate their individual influences, the analysis was repeated excluding FI_{wd} from the model. The general patterns of importance of the predictors left in the model remained the same across the continent (Fig S3.5a & b).

Figure S3.5. a) Predicted relative importance of mean annual temperature, mean annual precipitation, functional identity variables (aggregated effect of the community mean value of three functional traits) and functional dispersion for tree growth; b) Predicted relative importance of four biodiversity measures (functional dispersion and the community weighted mean of three functional traits). The community weighted mean of wood density was excluded from the model.

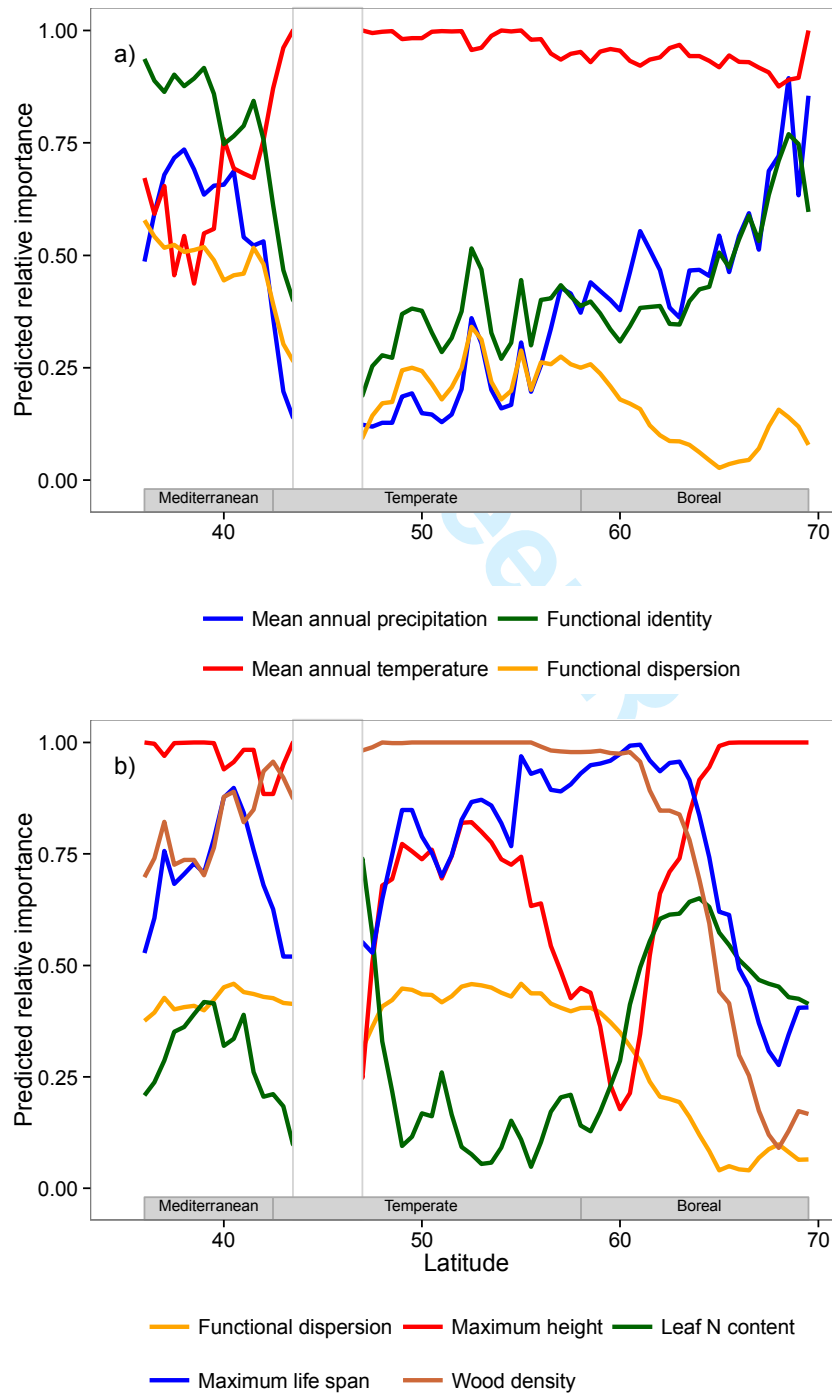


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3 *Influence of exotic tree species*
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5 Exotic tree species are often more productive than native species (Kawaletz *et al.*, 2013). To
6 ensure that dominance of exotic species did not influence the results, we repeated the analysis
7 excluding plots with greater than 80% basal area of non-native species. The general patterns
8 of importance across the continent remained the same (Fig S3.6a & b).
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Figure S3.6. a) Predicted relative importance of mean annual precipitation, mean annual temperature, functional identity (aggregated effect of the community mean value of four functional traits) and functional dispersion; b) Predicted relative importance of five components of functional biodiversity (functional dispersion and the community weighted mean of four functional traits). Plots with greater than 80% basal area of non-native tree species were excluded from the analysis.



References

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Supporting Information Appendix S4 Supplementary Figures

Figure S4.1. Mean and range of functional dispersion (FDIs) across the continent at 2° resolution (a); the predicted effect size (b); and the relative importance (c) of functional dispersion for tree growth; and the predicted growth ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) by functional dispersion in the three biomes (d). When calculating the predicted growth, predictor variables were kept at their mean values for each biome (blue: boreal; green: temperate; red: Mediterranean).

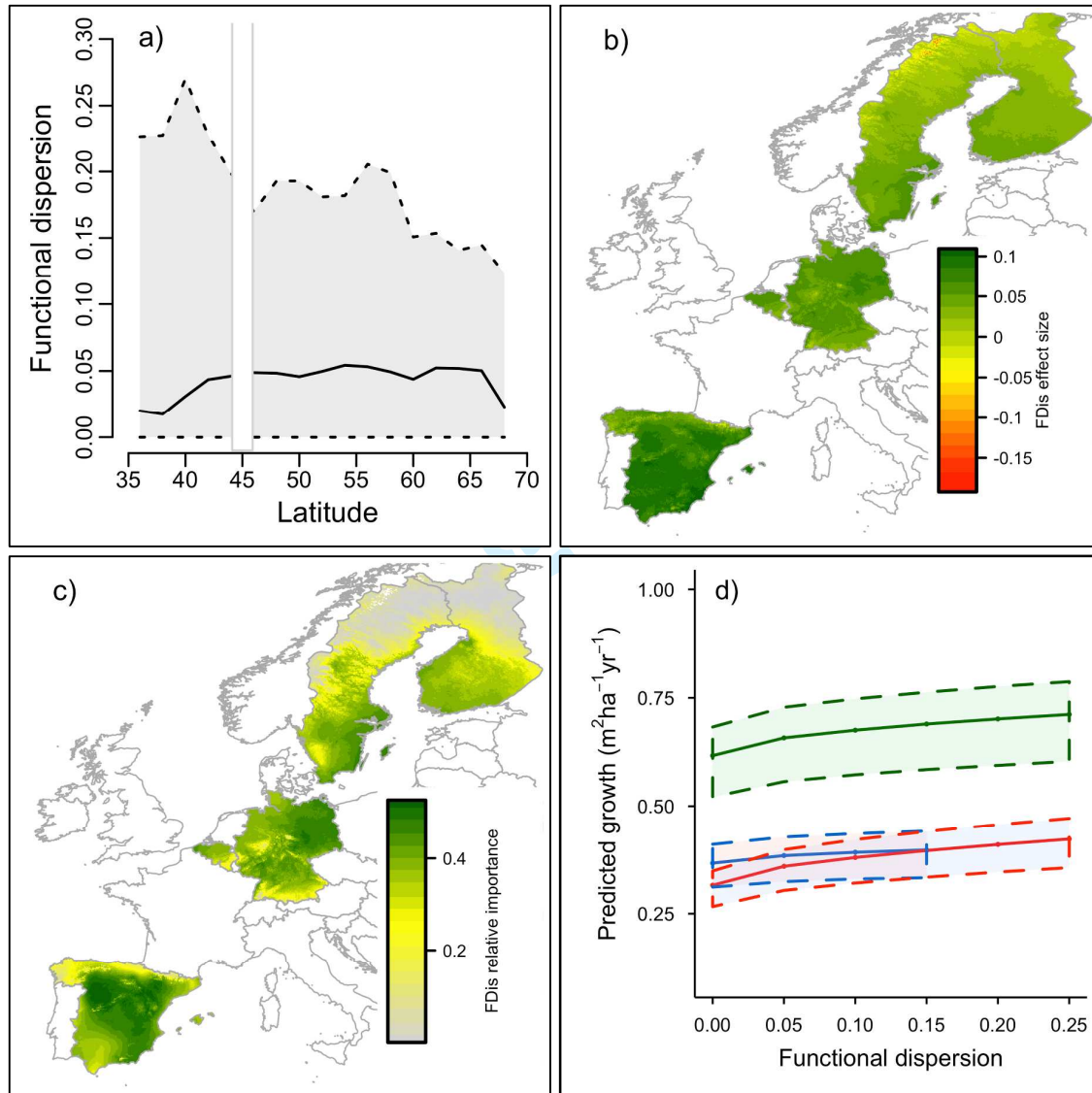


Figure S4.2. Mean and range of community weighted mean of maximum height (FI_{mh}) across the continent at 2° resolution (a); the predicted effect size (b); and the predicted relative importance (c) of FI_{mh} for tree growth; and the predicted growth ($m^2 ha^{-1} yr^{-1}$) by FI_{mh} in the three biomes (d). When calculating the predicted growth all predictor variables were kept at their mean value for each biome (blue: boreal; green: temperate; red: Mediterranean).

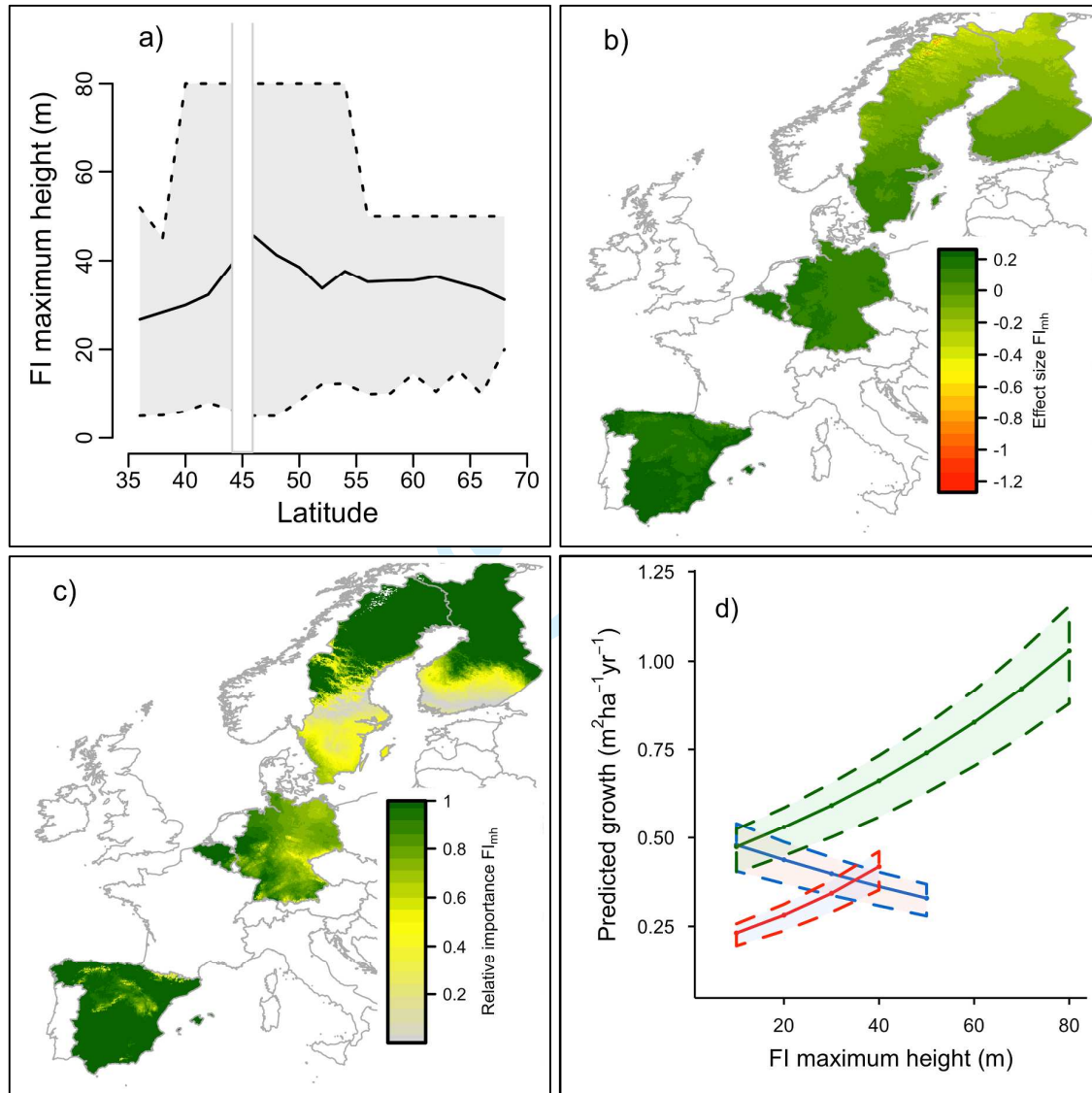


Figure S4.3. Mean and range of community weighted mean leaf N (FI_{ln}) across the continent at 2° resolution (a); the predicted effect size (b); and the predicted relative importance (c) of FI_{ln} for tree growth; and the predicted growth ($m^2 ha^{-1} yr^{-1}$) by FI_{ln} in the three biomes (d). When calculating the predicted growth all predictor variables were kept at their mean value for each biome (blue: boreal; green: temperate; red: Mediterranean).

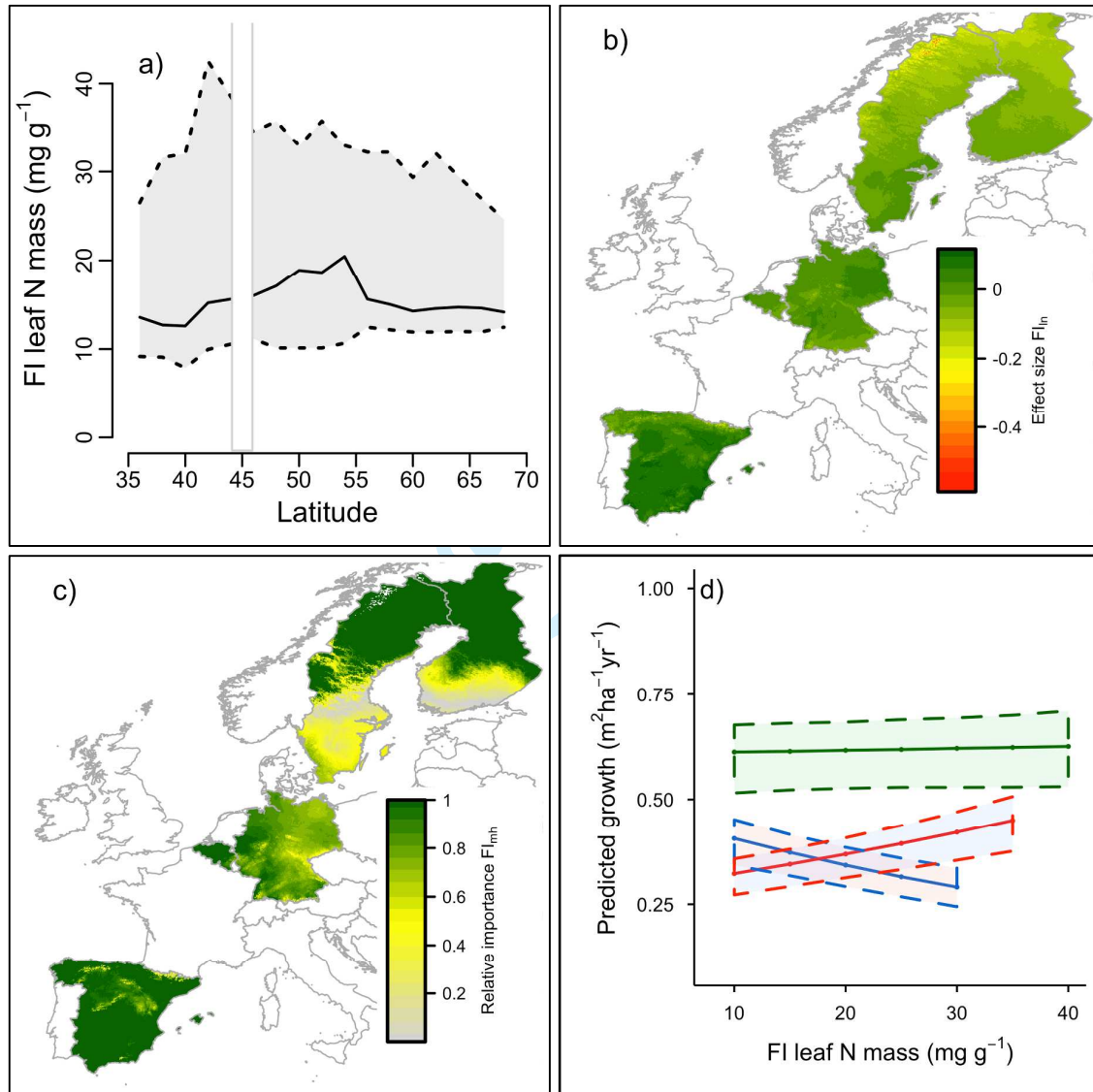


Figure S4.4. Mean and range of community weighted mean maximum life span (FI_{ls}) across the continent at 2° resolution (a) and the predicted relative importance (b) of FI_{ls} for tree growth; and the predicted growth ($m^2 ha^{-1} yr^{-1}$) by FI_{ls} in the three biomes (c). When calculating the predicted growth all predictor variables were kept at their mean values for each biome (blue: boreal; green: temperate; red: Mediterranean).

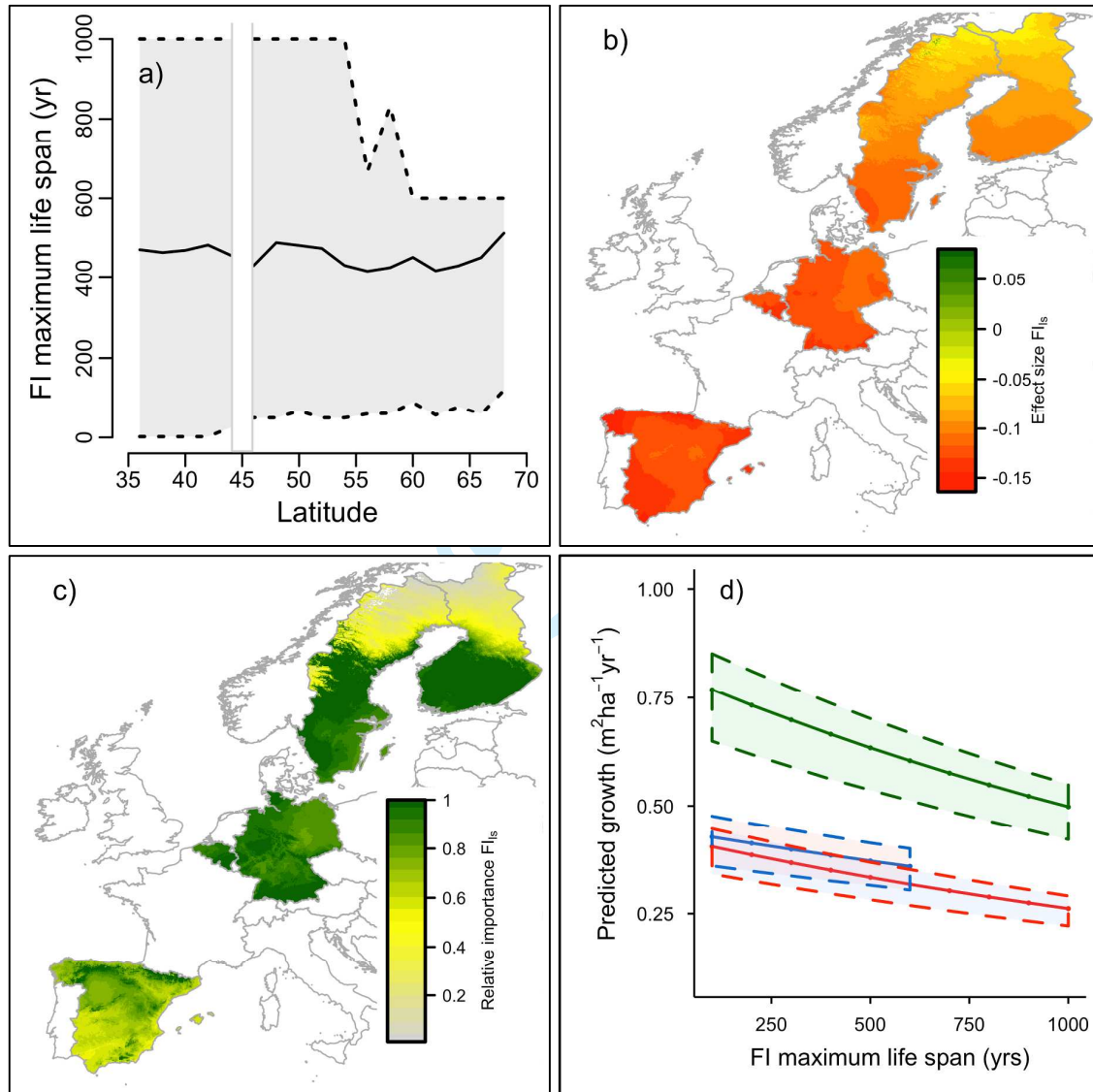


Figure S4.5. Mean and range of community weighted mean wood density (FI_{wd}) across the continent at 2° resolution (a); the predicted effect size (b); and the relative importance (c) of FI_{wd} for tree growth; and the predicted growth ($m^2 ha^{-1} yr^{-1}$) by FI_{wd} in the three biomes (d). When calculating the predicted growth all predictor variables were kept at their mean value for each biome (blue: boreal; green: temperate; red: Mediterranean).

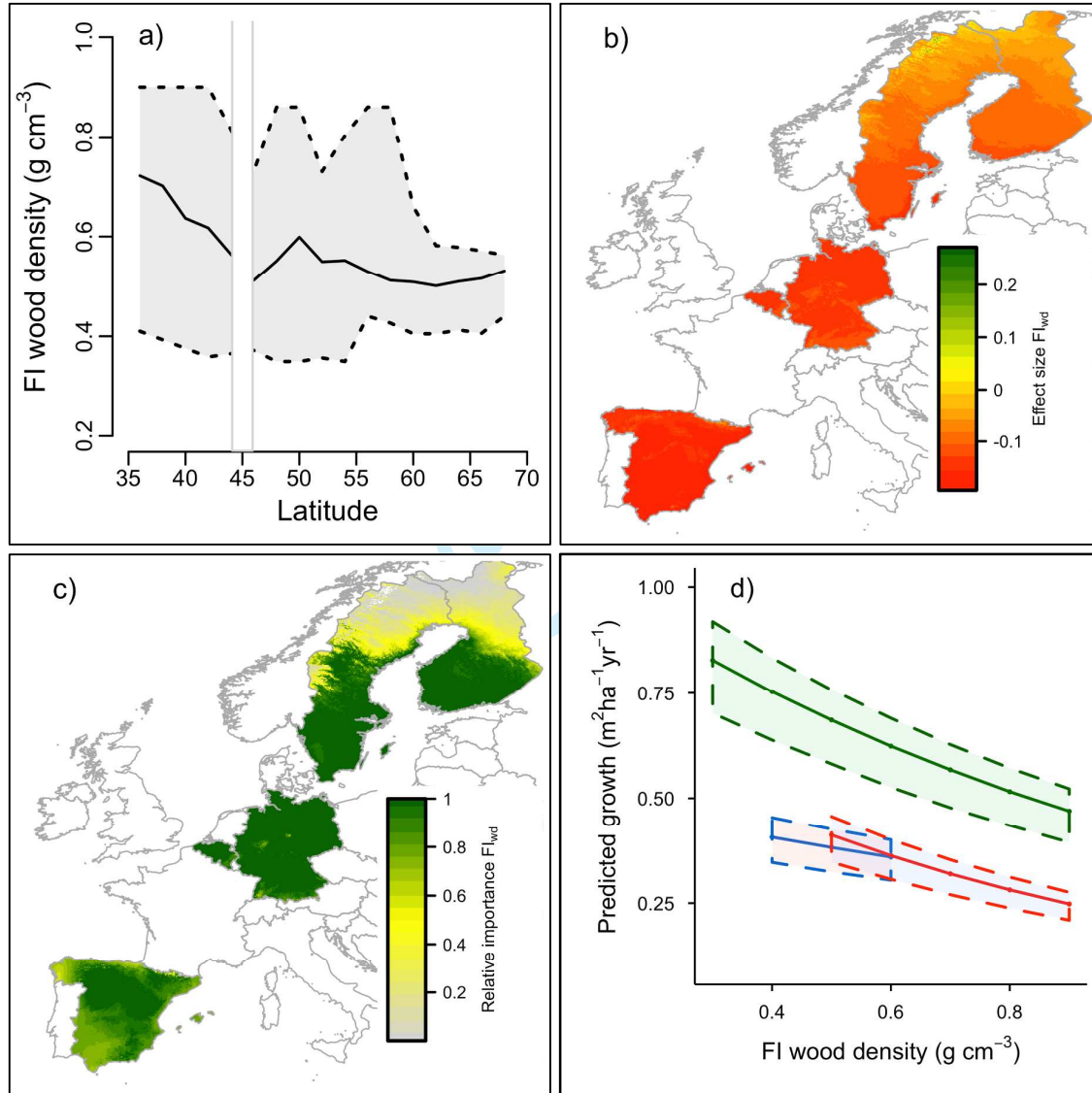


Figure S4.6. The absolute influence of each predictor on plot-level tree growth ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) across the continent. The predictors are: annual mean temperature; mean annual precipitation; functional dispersion; community-weighted mean (CWM) maximum height; CWM leaf N content; CWM maximum life span; and CWM wood density. The covariates (plot basal area ($\text{m}^2 \text{ha}^{-1}$), mean tree size (mm), species pool and natural mortality rate ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$)) have been group together in grey and labeled covariates. The white panel indicates missing values. The data is aggregated at 1° latitude.

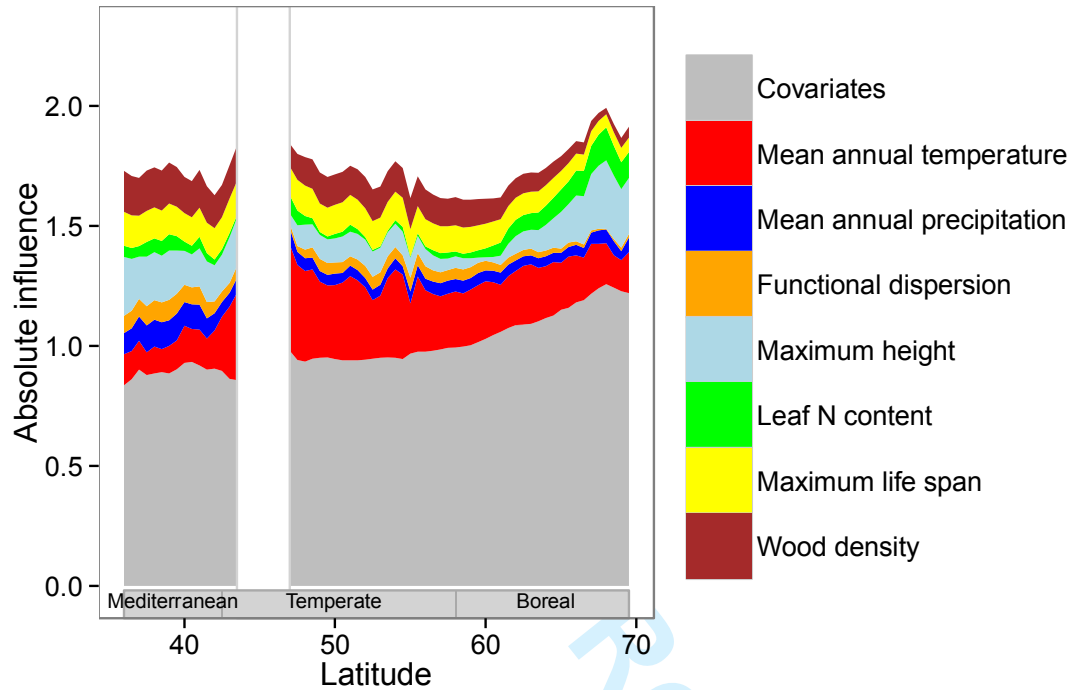


Figure S4.7. Predicted mean relative importance (solid lines) and 95% confidence intervals (dotted lines) of mean annual precipitation, mean annual temperature, functional identity (aggregated effect of the community mean value of the four functional traits selected) and functional dispersion for tree 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. The white section depicts missing data.

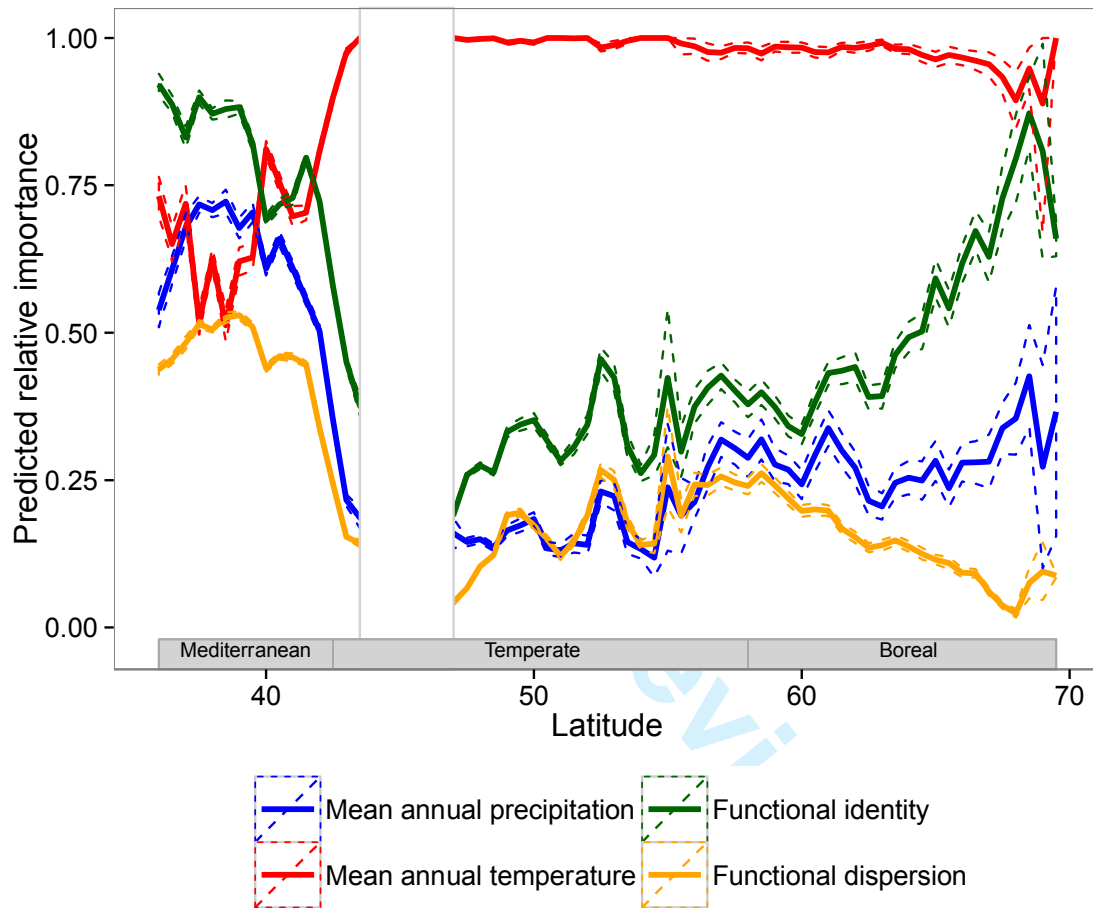
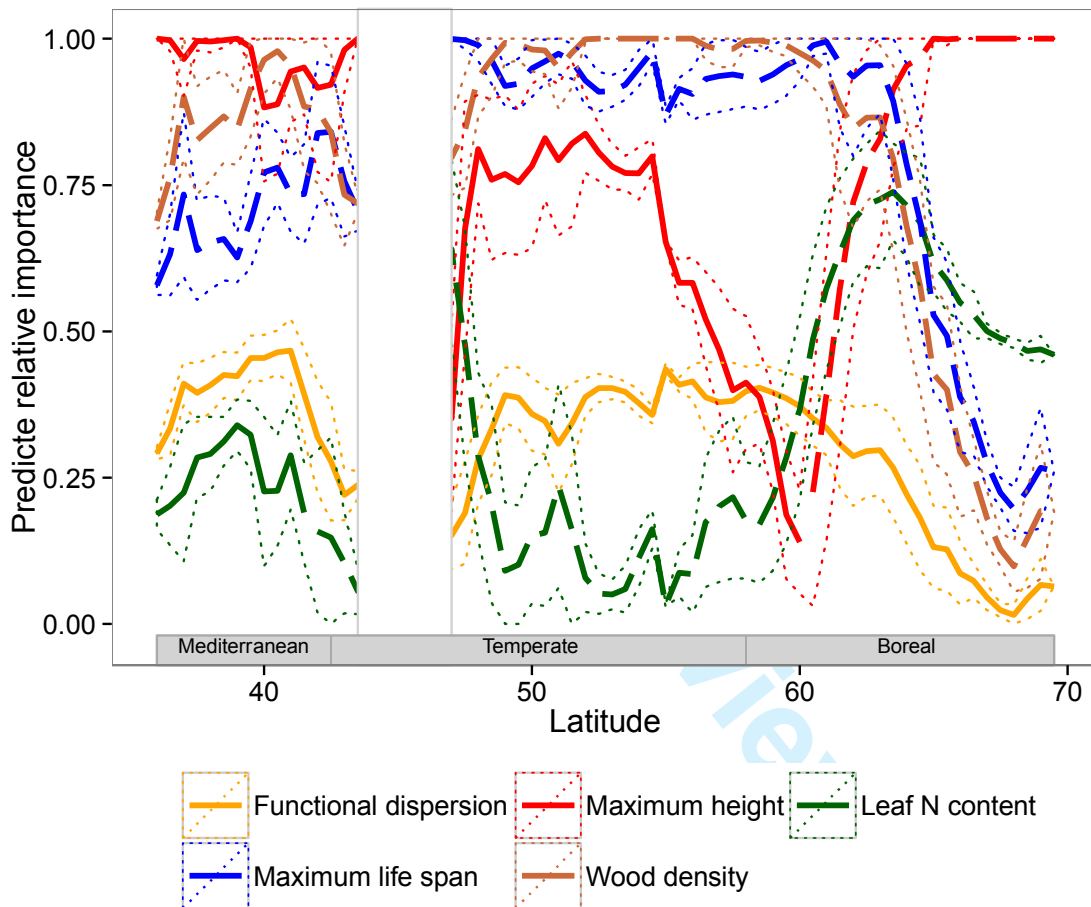
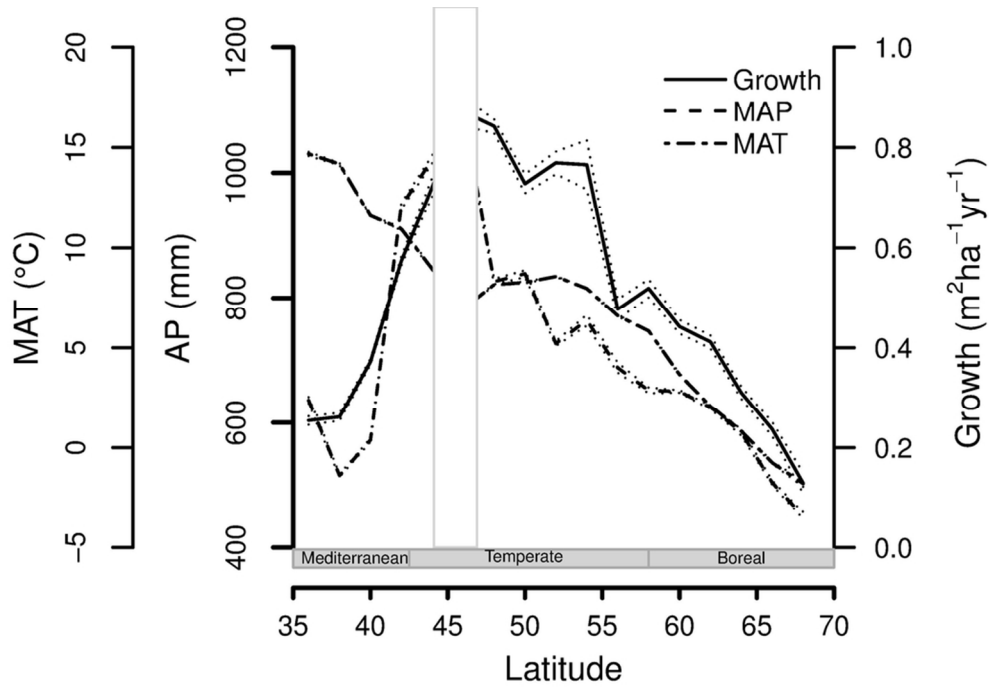


Figure S4.8. Mean predicted relative importance (solid and dashed lines) and 95% confidence intervals (dotted lines) of five components of functional biodiversity (functional dispersion and the community weighted mean of four functional traits) for tree growth. The sensitivity of plot growth to changes in each variable was estimated from a hierarchical linear model; the biodiversity measure 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. The white section depicts missing data.



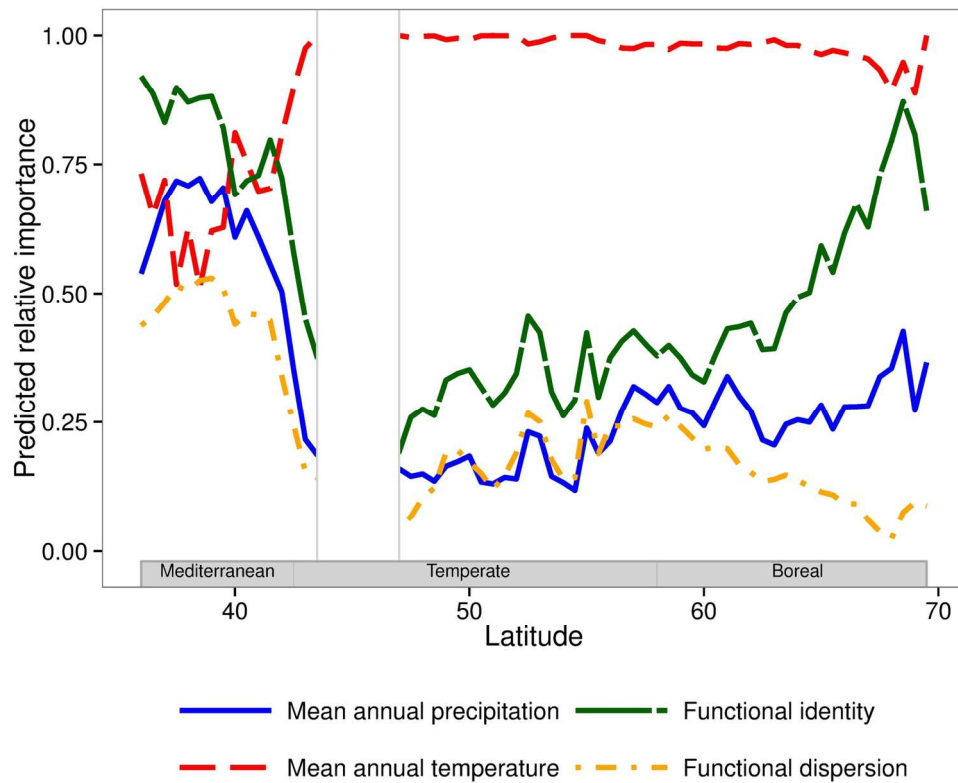


Climate gradients of mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) across the latitudinal gradient covered by the National Forest Inventory plots. Mean plot basal area growth (Growth, m² ha⁻¹ yr⁻¹). Dotted lines indicate 95% confidence intervals. The white section depicts missing data. Values were calculated at a 2° latitude spatial resolution.

88x62mm (300 x 300 DPI)

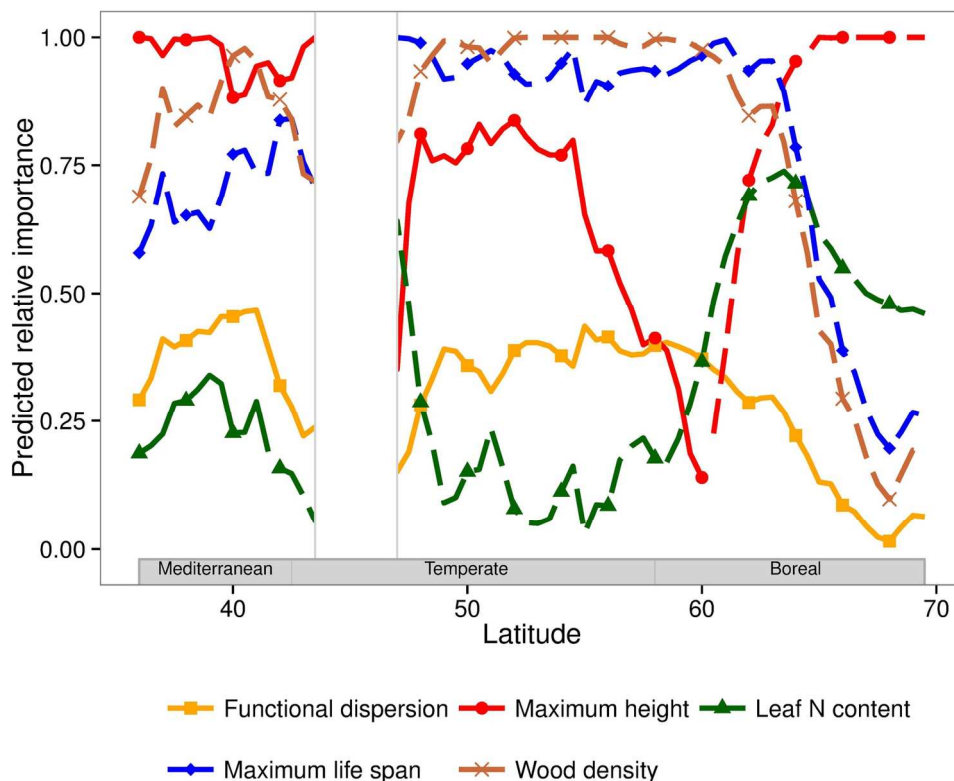
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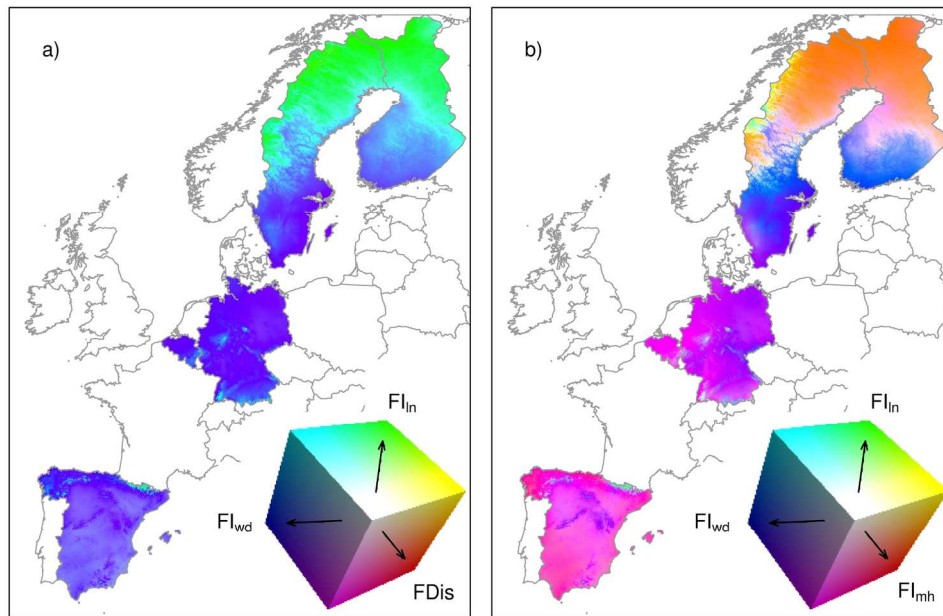


Predicted relative importance of mean annual precipitation, mean annual temperature, functional identity (aggregated effect of the community mean value of the four functional traits selected) and functional dispersion for tree growth. The sensitivity of plot growth to changes in each variable was estimated 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.

152x130mm (300 x 300 DPI)



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.
152x130mm (300 x 300 DPI)



Predicted relative importance of a) FDis (functional diversity; red), FIln (community-weighted mean (CWM) leaf N mass ($\text{mg} \cdot \text{g}^{-1}$); green) and FIwd (CWM wood density ($\text{g} \cdot \text{cm}^{-3}$); blue); b) FI mh (CWM maximum height (m); red), FIln (CWM leaf N mass ($\text{mg} \cdot \text{g}^{-1}$); green) and FIwd (CWM wood density ($\text{g} \cdot \text{cm}^{-3}$); 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 km^2 ; 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.

177x113mm (300 x 300 DPI)