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Species-specific, pan-European diameter increment models based on data of 2.3 million trees

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Abstract

Background: Over the last decades, many forest simulators have been developed for the forests of individual European countries. The underlying growth models are usually based on national datasets of varying size, obtained from National Forest Inventories or from long-term research plots. Many of these models include country- and location-specific predictors, such as site quality indices that may aggregate climate, soil properties and topography effects. Consequently, it is not sensible to compare such models among countries, and it is often impossible to apply models outside the region or country they were developed for. However, there is a clear need for more generically applicable but still locally accurate and climate sensitive simulators at the European scale, which requires the development of models that are applicable across the European continent. The purpose of this study is to develop tree diameter increment models that are applicable at the European scale, but still locally accurate. We compiled and used a dataset of diameter increment observations of over 2.3 million trees from 10 National Forest Inventories in Europe and a set of 99 potential explanatory variables covering forest structure, weather, climate, soil and nutrient deposition.

Results: Diameter increment models are presented for 20 species/species groups. Selection of explanatory variables was done using a combination of forward and backward selection methods. The explained variance ranged from 10% to 53% depending on the species. Variables related to forest structure (basal area of the stand and relative size of the tree) contributed most to the explained variance, but environmental variables were important to account for spatial patterns. The type of environmental variables included differed greatly among species.

Conclusions: The presented diameter increment models are the first of their kind that are applicable at the European scale. This is an important step towards the development of a new generation of forest development simulators that can be applied at the European scale, but that are sensitive to variations in growing conditions and applicable to a wider range of management systems than before. This allows European scale but detailed analyses concerning topics like CO_2 sequestration, wood mobilisation, long term impact of management, etc.

Keywords: European forests, Diameter increment model, Climate change, Growth modelling, National forest inventory

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Background

The EU has a vision of sustainable forestry contributing to the economy of its Member States and to the environment—both regionally and globally. In the latter context, the role of forests in biodiversity conservation and climate change mitigation as well as raw material provision has become increasingly important through the United Nations Convention on Biological Diversity (CBD) and the United Nations Framework Convention on Climate Change (UNFCCC). Forests in the EU's 28 Member States stretch over a huge variety from the Atlantic in the west to the Black Sea in the east, and from the Mediterranean in the south to the boreal in the north covering 157 million ha (FOREST EUROPE 2015). Forest management has evolved at a national or subnational level influenced by the quantity and nature of the forest resources available, forecasts on their future development, perceived demand for raw material and services, and local economic and social factors. The management of forest resources has been affected in recent years by substantial shifts in the demands and expectations put on forests, while the forest resource itself is subject to new pressures which are not yet sufficiently taken into account in national or international policies.

These pressures include diseases, invasive species, and the effects of climate change on forests through, e.g. drought, and storms (Lindner et al. 2014). Many forests continue to provide the traditional forest products of timber, pulp, paper, etc., but forested areas are also expected to provide important ecosystem services, including climate change mitigation, conservation of biodiversity, recreation and protection of water and soil (Nabuurs et al. 2006; Verkerk et al. 2011). A key policy issue is how the existing and future forests in the EU, which are limited in size and have a fragmented ownership, should be managed to deliver in a sustainable way an optimal mix of social, environmental (including biodiversity conservation) and economic services. These uncertainties plus a long planning horizon in forestry, require us to predict the long term impacts of management and environmental changes. One avenue is the employment of resource projection models (Barreiro et al. 2017).

Making scenario projections of European forests is a hugely challenging task. Not only do they cover a large range of biotic and abiotic conditions, but they are spread over 46 countries, each with their own (forest) policies, inventory systems (Tomppo et al. 2010) and national forest resource projection systems (Barreiro et al. 2016; Barreiro et al. 2017). National forest inventory systems (NFIs), if existing at all, differ considerably in design, size thresholds, definitions, estimation methods, census interval, and importantly, in data access policy. A few countries have made their raw measurements available on the web (Netherlands, Germany, France, Spain), a few make them available on request (e.g. Norway, Sweden), but still most results are only available in aggregated tables and reports. Even when the data are accessible, standardisation and harmonisation between NFIs remains difficult (Köhl et al. 2000; McRoberts et al. 2009; Dunger et al. 2012). Data collection efforts like FOREST EUROPE (FOREST EUROPE 2015) and the Global Forest Resource Assessments by FAO (FAO 2015) try to improve the harmonisation, but it remains a challenge (COSTE43 2011). National forest resource projection systems show an even larger variety in design, methodologies, processes and update cycles (Barreiro et al. 2016; Barreiro et al. 2017), which makes it almost impossible to compare projections among countries.

Resource projections for Europe show different approaches for handling the harmonisation challenge. For a long time, the European Timber Trend Studies (ETTS) as published by the UNECE/FAO were a collection of nationally executed projections of a set of standardised scenarios (Schelhaas et al. 2017). Nilsson et al. (1992) were the first to use a common, empirical projection tool applied country-wise on aggregated national forest inventory data. Since then, the same age-volume class matrix approach was developed and commonly applied as EFISCEN (European Forest Information Scenario model) in studies down to provincial resolution for the total European scale (Nabuurs et al. 2006; Schelhaas et al. 2015; Verkerk et al. 2016) for carbon balance studies, wood availability and e.g. trade-offs with biodiversity. Also, other models like CBM-CFS3 are being employed for European forest carbon balance assessments (Pilli et al. 2016).

When the first European-scale forest resource models were developed, the approach chosen matched best with the predominant forest management approach in Europe (mostly even-aged management), the data availability (only aggregated data available), the issues to be addressed (large-scale resource availability, Member State level carbon sequestration) and the computing power available. In the meantime, the situation has changed drastically. Forestry is now increasingly incorporating natural processes taking into account effects of climate change on growth (Peng 2000) as well as the fulfilment of forest functions other than wood production (Verkerk 2015). As a consequence, the forests are becoming more heterogeneous in species and structure (Hector and Bagchi 2007; Morin et al. 2011; Zhang et al. 2012), and a larger range of management options need to be considered (Duncker et al. 2012; Hengeveld et al. 2012).

At the same time, the data policies are becoming more open and the computing power has increased dramatically. These developments are reflected in the construction of more complex national projection models, often simulating individual trees, with high geographical detail and usually based on NFI data (Barreiro et al. 2016), sometimes capable of incorporating anticipated future growth changes. These tools are usually not transferable to other countries because they are developed on very specific national conditions and datasets. However, a clear need can be identified for such simulation tools at the European level (Schelhaas et al. 2017). Such a tool should be able to 1) cover a wide range of biotic and abiotic conditions, 2) have growth models sensitive to changing environments, 3) be sensitive to varying forest systems and forest management approaches, and 4) be age-independent and have a high geographical detail. In this paper, we aim to develop a set of empirical individual-tree growth models that could be used in such a model at the European scale.

Methods

National forest inventory data

We collected individual tree measurements from available National Forest Inventories to represent the range in growing conditions in Europe (Fig. 1). We included NFI data from Norway (Tomter et al. 2010), Sweden (Fridman et al. 2014), Netherlands (Schelhaas et al. 2014; Oldenburger and Schoonderwoerd 2016), Germany (Riedel et al. 2016), a part of Ireland (Redmond 2016), Poland (Anonymous 2015), France (Hervé 2016), Switzerland (Lanz et al. 2016), Spain (Alberdi et al. 2016) and the Italian regions Piemonte (Camerano et al. 2008) and Aosta (Camerano et al. 2007). NFI systems differ in terms of inventory cycles, sampling system, plot radius, diameter threshold etc. (Table 1). Germany uses an angle count method (Bitterlich 1952), while other countries use a design with circular plots, either with a variable radius depending on the plot conditions, or with different radii with corresponding diameter thresholds. In total, observations were available for more than 2.3 million trees on over 190,000 plots, from 10 different NFIs. Except for France and the two Italian regions, data consisted of repeated tree diameter observations from permanent sample plots. Tree data included observation of diameter at breast height (DBH, hereafter simply referred to as diameter; all countries use a breast height of 1.3 m) during two consecutive measurements and identification of the tree species, for all trees that were alive both at the first and second observation.

In France, increment was recorded as the width of the last 5 tree rings as measured on a core, for all trees on the plot. In the two Italian regions, increment was available as the 10-year radial increment of the tree closest to the plot centre, as measured on a core. Radial increment from tree core data was converted to diameter increment (France, the two Italian regions). For these countries we considered the measured diameter increment in the past as a prediction of the diameter increment in the years after the observation, i.e. we did not reconstruct the diameter 5 or 10 years ago as starting point for the analysis. We chose this approach because plot basal area is one of the potential explanatory variables, and we didn't have sufficient information to reconstruct plot basal area in the past. Tree circumference as measured in France was converted to diameter. All observations were converted to annual diameter increment by dividing the total diameter increment by the number of years between the measurements, using the YEARFRAC function in Excel. Occasional observations of negative diameter change were assumed to result from unbiased measurement errors, therefore these negative diameter changes were kept to avoid introducing bias.

We grouped the tree species in 20 species groups (Table 2). Minor species or species groups were iteratively merged until sufficiently large groups remained. Species or species groups were retained if they covered at least 5% of the total dataset over all countries, or if they were considered as an important species in a certain region of Europe, either in terms of production (like poplar plantations) or in coverage (like *Quercus ilex* (L.) and *Quercus suber* (L.) in the Mediterranean region). The group '*Populus* plantations' includes only *Populus* species and hybrids that are commonly used in commercial plantations while other *Populus* species are included in the category 'shortlived broadleaves'. For completeness in view of intended model application, 'rest' groups were created for broadleaves and conifers. For broadleaves the rest category was split into shortlived and longlived species based on authors' judgement.

Explanatory variables

We constructed a set of potential explanatory variables, covering information on the forest structure (F), soil (S), climate (C), weather (W) and nutrient deposition (D). Forest structure was represented by stand basal area at the time of first measurement as delivered by the different NFIs, and the variable F-rDiffDq, a proxy for the social position of each tree within the stand defined as:

$$\mathrm{F-rDiffDq} = DBH/DBH\mathrm{q}{-}1 \quad (1)$$

with *DBH* the diameter of the tree and *DBH*q the quadratic mean diameter of all trees on the plot at the first observation. Values smaller than zero indicate that the tree is relatively small and more likely to be suppressed, while values larger than zero indicate that the tree is more likely to be dominant.

Soil, climate, weather and nutrient deposition variables were derived from data sets with full European coverage, using the plot coordinates. To derive soil characteristics, we used the 1 km resolution SoilGrids dataset (Hengel et al. 2014). This dataset covers soil pH, sand/silt/clay

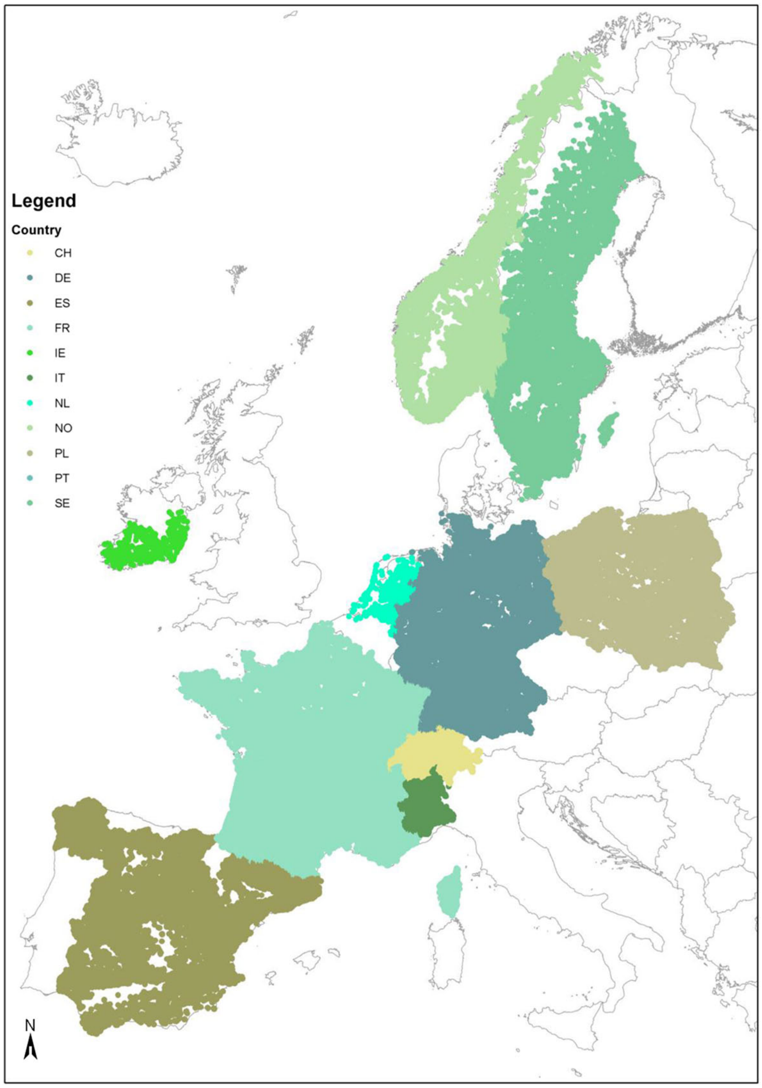

Fig. 1 NFI plot locations

fraction, depth to bedrock, bulk density, cation exchange capacity (CEC), soil organic fraction and fraction of coarse fragments. The dataset consists of estimates of the respective properties at 7 depths ranging from 0 to 200 cm. We only used the third depth (15 cm), since the values at different depths were highly correlated. We also included a map with natural soil susceptibility to compaction from the European Soil Data Centre (Panagos et al. 2012).

To derive climate characteristics, we used the WorldClim (Hijmans et al. 2005) and the GEnS (Metzger et al. 2013, based on the WorldClim (Hijmans et al. 2005) and CGIAR-CSI data (Trabucco et al. 2008; Zomer et al. 2008)) datasets. Both datasets cover a range of climatic variables and indices (like monthly and annual means and extremes for temperature and precipitation, temperature and precipitation in coldest/warmest/wettest driest quarter or summer/winter, several aridity and humidity indices, etc.), averaged for the period 1950–2000, at 1 km resolution. The datasets partly overlap but each set has some unique variables. Altitude correlates with weather and climate variables and is often included as predictor in similar studies. However, the inclusion of altitude makes it impossible to include climate change effects directly in the model and thus we excluded it from the predictor set. For the same reason, latitude was not included either.

For nutrient deposition we used the EMEP data, containing deposition of oxidised and reduced nitrogen and oxidised sulphur at the 50 km grid (www.emep.int). Average nutrient deposition values were calculated for the period 1990–2010.

For weather, we obtained data from Agri4Cast (http://agri4cast.jrc.ec.europa.eu/), at 25 km resolution for the period 1975–2015. We used this dataset to calculate a

Table 1 Overview of the NFI datasets used and their most important features

Country/Region	Inventory cycle	Inventory dates	Mean census interval (years)	Number of plots	Plot radius (m)	Diameter threshold (cm)	Comment	NTrees
France	NFI5–6	2005–2012	5 (core of all trees on the plot)	50,404	15	7.5		474,588
Germany	NFI1/NFI2	1986 – 1989/ 2000–2002	14.3	10,344	angle count method			137,425
Germany	NFI2/NFI3	2002–2012	10.2	17,604	angle count method			272,034
Italy - Piemonte		1999–2004	10 (core from 1 tree per plot)	13,192	variable (8-15 m)	7.5	DBH rounded to cm	13,192
Italy - Aosta		1992–1994	10 (core from 1 tree per plot)	1691	variable (8-15 m)	7.5	DBH rounded to cm	1691
Ireland	NFI1/NFI2	2004–2006/ 2009–2012	6.1	577	3/7/12.62	7/12/20		8859
Netherlands	NFI5/NFI6	2001–2005/ 2012–2013	9.5	1235	variable (5–20 m)	5		18,348
Norway	NFI9/NFI10	2004–2008/ 2009–2013	5	9243	8.92	5		201,484
Poland	NFI1/NFI2	2005–2009/ 2010–2014	5	17,488	variable (7.98, 11.28 or 12.62)	7		350,487
Spain	NFI2/NFI3	1986–1995/ 1996–2008	11.2	50,957	5/10/15/25	7.5/12.5/22.5/42.5		557,848
Sweden	NFI7–8/ NFI8–9	2005–2009/ 2010–2014	5	14,833	3.5/10	4/10		246,852
Switzerland	NFI2/NFI3	1993–1996/ 2004–2006	10.9	5217	8/12.6 (in flat terrain)	12/36	DBH rounded down to cm	49,192
Total		1986–2014		192,785				2,332,000

Multiple diameter thresholds indicate a design with plots consisting of concentric circles with their radii and the corresponding thresholds

range of weather indices (similar to the climate indices) for the actual observation period of each tree in our dataset. See Appendix 1 for more information on weather indices and calculation procedures. In total we included 99 abiotic explanatory variables (for a full list see Appendix 2).

To avoid simultaneous use of explanatory variables with large correlations in the models, we made a selection among variables with correlations greater than 0.8 or smaller than – 0.8. This selection was based on scores that preferred simpler variables over more complicated ones (like average temperature over degree days above a certain threshold), weather variables over climate and easily available ones over those that are usually more difficult to obtain. The full list of variables and their priority in the data preparation is given in Appendix 2. Exclusion of correlated variables was done for each species group separately, since the spatial occurrence pattern of the species influences the observation range of the explanatory variables. Incomplete cases in the remaining dataset were removed.

Diameter increment model

Here, we restrict ourselves to modelling the diameter increment. Of all variables measured in the NFIs across Europe, diameter is probably the most harmonised one, available for the largest number of trees, available as repeated observations on the same tree, and directly measured without further interpretation.

Some authors prefer to use basal area increment models over diameter increment models (Wykoff 1990; Quicke et al. 1994; Monserud and Sterba 1996; Schröder et al. 2002,) but Vanclay (1994) argues that both approaches are essentially the same, since one can be derived from the other. Tree diameter generally develops according to an asymmetric sigmoidal function through time, with a slow, but rapidly increasing growth at establishment, almost constant growth during the mature phase followed by a slow decline in growth during senescence (Tomé et al. 2006). Because creating new tree rings is essential for water transport, diameter increment will theoretically never reach zero, although the rings can be very small at old age.

Although age is known to be one of the best predictors of growth (Pukkala 1989; MacFarlane et al. 2002; Zhao et al. 2006; Tomé et al. 2006), we explicitly aim to exclude it as a predictor since it is not directly measured for all trees in the NFIs and forest situations in Europe. Instead, we selected diameter, which is directly measured, as the predictor.

Table 2 Summary of observed characteristics of the species after removing incomplete records

	Reason for inclusion	Number of trees	Mean dbh (mm)	99th percentile DBH (mm)	Mean increment ($mm{\cdot}yr^{-1}$)	Mean basal area ($m^2{\cdot}ha^{-1}$)	Mean mat (mean annual temperature) (degrees c)	Mat standard deviation	Mean tap (total annual precipitation) ($mm{\cdot}yr^{-1}$)	Tap standard deviation
Abies spp.	A	54,974	340	799	4.8	38.4	9.7	1.5	855	202
Larix spp.	A	24,508	332	700	3.9	31.5	8.9	2.5	871	287
other conifers	D	31,063	271	613	5.4	22.5	11.3	4.0	817	368
Picea abies	A	373,235	248	635	3.6	34.5	7.1	2.8	836	273
Picea sitchensis	B	8074	253	554	7.0	39.1	10.5	0.9	983	220
Pinus nigra + mugo	C	66,237	239	579	2.9	21.7	12.1	1.7	500	189
Other indigenous pines	C	204,443	268	580	4.0	20.5	13.6	2.4	563	305
Pinus sylvestris	A	529,184	237	531	2.9	28.7	8.5	2.8	641	152
Pseudotsuga menziesii	B	23,070	333	736	7.2	34.8	10.8	1.1	794	146
Betula spp.	A	149,484	145	414	1.8	21.4	5.9	3.6	752	220
longlived broadleaves	D	199,048	223	673	2.9	25.3	11.3	2.0	726	201
shortlived broadleaves	D	109,732	189	589	3.1	27.2	9.6	3.1	763	215
Castanea sativa	C	34,812	287	1114	3.9	31.5	12.4	1.6	832	227
Eucalyptus spp.	B	6770	273	678	7.9	18.7	15.2	1.3	1014	421
Fagus sylvatica	A	163,123	331	807	3.6	33.0	10.1	1.5	791	176
Populus plantations	B	2513	392	925	9.3	26.5	11.3	1.5	690	155
Quercus ilex	C	68,173	237	764	1.8	12.2	14.3	2.1	536	156
Quercus robur + petraea	A	179,861	335	827	3.3	28.7	10.9	1.6	778	204
Quercus suber	C	20,616	319	796	2.3	16.6	16.3	1.4	640	161
Robinia pseudoacacia	B	10,154	212	551	4.2	26.3	11.7	1.7	783	176

Reason for inclusion of species group: A = more than 5% of total data coverage; B = important commercial species; C = important for regional coverage; D = rest group

Modelling of sigmoidal relationships is usually achieved with so-called theoretical growth curves, such as the Lundqvist (Korf 1939; Stage 1963), Gompertz (Winsor 1932) and Chapman-Richards (Richards 1959) functions. Here, we choose the Gompertz function, because it has the following properties:

1. The function is right-skewed, with a maximum growth at 1/e times the asymptotic diameter.
2. The derivative of the function with respect to time (e.g. growth) can be written in a form only dependent on diameter.

Thus, for estimating diameter increment the derivative of the Gompertz equation is used:

$$\frac{dDBH}{dt} = \beta_1 DBH + \beta_2 DBH \ln DBH + \varepsilon \quad (2)$$

with $dDBH/dt$ the diameter increment (in mm), DBH the diameter (in mm), β_1 and β_2 parameters and ε is the error term with an assumed distribution $N\sim(0, \sigma)$. These parameters are a function of a set of independent variables X_i expressed as:

$$\beta_1 = c_1 + \sum_{i=1}^{p} \theta_{i,1} X_i \quad (3)$$

$$\beta_2 = c_2 + \sum_{i=1}^{p} \theta_{i,2} X_i \quad (4)$$

For both β_1 and β_2 the variables X_i used to estimate the parameter vectors are the same. The procedure for the selection of the p variables that best explain the diameter increment is described later. Values for c and θ are estimated using ordinary least squares (OLS) by substituting Eqs. 3 and 4 in Eq. 2.

The diameter when maximum growth occurs is defined by:

$$DBH_{opt} = e^{-\left(\frac{\beta_1}{\beta_2}+1\right)} \quad (5)$$

with a maximum growth equal to:

$$\frac{dDBH}{dt}_{max} = -\beta_2 DBH_{opt} \quad (6)$$

The census interval in the datasets is overall either around 5 or 10 years depending on the country. To relate the total diameter increment in this varying period to the diameter using a non-linear model, we use the average between the two measured diameters as a proxy for the diameter.

Figure 2 illustrates the shape of the growth model. A simultaneous increase of β_1 and β_2 by the same percentage increases the maximum diameter increment that can be reached, but leaves the diameter with maximum diameter increment and the maximum diameter unchanged. A small relative decrease of β_1, or the same relative increase in β_2, lowers the curve as a whole, resulting in smaller maximum diameter increment, a smaller diameter of maximum diameter increment and a smaller maximum diameter that can be reached.

Variable selection and model fitting

The selection of variables to be included in the model was performed in two phases for each species independently. First, a forward selection procedure was used. Given the large number of data points, the dataset was split in a selection-dataset (75%) and an acceptance-dataset (25%). Variables were added one-at-a-time. First, using the selection-dataset the additional variables were ranked based on the Akaike information criterion (AIC, Akaike 1974). Because the large number of observations bias the AIC towards ever decreasing values with increasing numbers of variables, acceptance of the best ranking variable was subsequently based on an F-test performed on the predicted values for the acceptance-dataset (Zar 1996). The variables selected for 10 independent data-splits were combined to obtain a list of candidate variables. Secondly, these candidate variables were used in a backward selection procedure on the full dataset for the final selection of explanatory variables. In this procedure the variable to be excluded was again selected based on AIC and it was actually excluded based on an F-test. The selected variables were used to estimate the full set of coefficients of the final model. The full models (substituting Eqs. 3 and 4 in Eq. 2) were fitted using OLS in the lm function in R (R:stats) (R core team 2014). For all F-tests a conservative α-value of 0.0001 was used to avoid overfitting the data. The average observed diameter increment was used as reference for calculation of F-tests and R^{2^*}, rather than a reference value of 0 as is default when no intercept is included in the model. Model residuals showed some heteroscedasticity at small diameters (Additional file 1), but seemed homoscedastic over a large range of observations. We did not transform our data, which would introduce bias due to the need to exclude negative observations. In view of the intended model application we also calculated the R^{2^*} of the total predicted basal area increment at plot-level for all available plots, including all species.

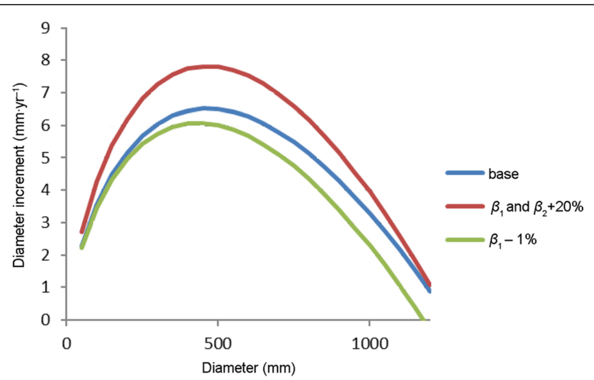

Fig. 2 Shape of the growth model with $\beta_1 = 0.1$ and $\beta_2 = -0.014$ (base), if β_1 and β_2 are increased by 20% and if β_1 is decreased by 1%

Results

The number of explanatory variables included in the final diameter increment models ranged between 2 and 25 for all species/species groups (Tables 3 and 4). Variables of forest structure were always included (Table 4), weather and climate were included for 18 species, while soil and nutrient deposition were included for 16 and 13 species, respectively. R^{2^*} ranged from 0.10 for *Quercus ilex* to 0.53 for other conifers (Table 4). The R^{2^*} for total basal area increment at the plot level was 0.85. Conifers generally had greater R^{2^*} than broadleaves (conifers 0.32 on average over all species and broadleaves 0.22). There was no clear relationship between the number of variables or variable groups selected and the explained variance. We tested the contribution to the explained variance of each group of variables by fitting the full model again, excluding the variables from that group, and recorded the decrease in R^{2^*}. If forest structural variables were left out from the model, the explained variance decreased by 43.9%, on average over all species groups. If weather variables were left out, the explained variance decreased by 8.7% and for climate by 3.8%. Soil and nutrient deposition accounted for respectively 2.2% and 1.4% of the explained variance. The weather variables most often selected were generally related to annual temperature (W-MaT), temperature variations (annual temperature range W-aTR, mean diurnal range W-MaDR) or radiation (W-TaR), while less frequently selected variables tended to include indices and minima and maxima

Table 3 Selected variables and parameter estimates per species group. For abbreviations of variables see Appendix 2

		Abies spp.			*Larix* spp.			*Picea abies*			*Picea sitchensis*	
		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$
c		6.65E–01	−1.13E–01		3.58E–01	−5.34E–02		− 1.80E + 00	2.94E–01		5.13E–01	−7.59E–02
X1	F-lnBA	−6.10E–02	9.12E–03	F-BA	9.60E–04	−1.59E–04	F-lnBA	−5.07E–02	7.70E–03	F-BA	− 1.79E–03	2.88E–04
X2	F-rDiffDq	1.36E–02	−2.07E–03	F-lnBA	−8.61E–02	1.37E–02	F-rDiffDq	5.90E–03	−9.13E–04	F-lnBA	−3.90E–02	5.65E–03
X3	W-MaT	3.35E–03	−4.90E–04	W–MaT	3.77E–03	−5.82E–04	W-MaT	6.34E–04	−5.79E–05	F-rDiffDq	6.23E–02	−9.29E–03
X4	W-TaR	1.15E–06	−8.65E–07	W-TaR	−3.61E–05	5.11E–06	W-TaP	1.87E–06	−6.67E–08	W-aTR	−1.10E–02	1.67E–03
X5	W-aTR	−2.83E–03	4.20E–04	W-SDmR	2.85E–04	−3.92E–05	W-aTR	3.06E–04	−6.98E–05	W-MweqR	2.21E–04	−3.50E–05
X6	W-SDmR	2.33E–05	3.22E–06	W-MweqR	4.46E–05	−7.37E–06	W-MweqT	8.21E–04	−1.26E–04	C-TwaqP	−5.48E–04	8.90E–05
X7	W-MwaqP	3.56E–04	−5.39E–05	C-TaAET	1.12E–04	−1.74E–05	C-TaP	3.30E–05	−5.56E–06			
X8	C-MaT	−1.62E–04	2.97E–05	C-seaP	2.76E–04	−3.87E–05	C-ISO	1.52E–03	− 1.58E–04			
X9	C-TaP	−9.37E–05	1.31E–05	S-PHIHOX	−4.41E–04	5.31E–05	C-MaDR	−7.93E–04	9.44E–05			
X10	C-TaAET	1.29E–04	−2.03E–05	D-DepRedN	−2.30E–05	3.89E–06	C-seaPET	−5.91E–06	1.50E–06			
X11	C-MaDR	−8.56E–05	2.38E–05	D-DepOxN	−2.65E–05	3.80E–06	C-Ari	−1.43E–06	2.26E–07			
X12	C-seaP	−9.66E–04	1.34E–04				C-MwamT	6.73E–04	−1.10E–04			
X13	C-MwemP	2.15E–04	−2.19E–05				C-MweqT	−5.30E–05	7.78E–06			
X14	C-MweqT	−8.95E–05	1.21E–05				S-BLD	6.77E–05	−1.06E–05			
X15	S-BLD	1.46E–05	−1.69E–06				S-BDRICM	9.98E–05	−1.25E–05			
X16	S-CRFVOL	−4.75E–04	6.38E–05									
X17	S-BDRICM	3.34E–04	−4.84E–05									
X18	D-DepOxN	−1.63E–05	1.84E–06									
X19	D-DepOxS	2.41E–06	−2.49E–07									

		Pseudotsuga menziesii			*Pinus nigra + mugo*			Other indigenous pines			*Pinus sylvestris*	
		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$
c		2.44E + 00	−3.70E–01		5.86E–01	−9.12E–02		5.36E–01	−8.42E–02		2.45E + 00	−3.76E–01
X1	F-lnBA	−8.26E–02	1.23E–02	F-BA	−1.90E–04	2.24E–05	F-BA	−9.62E–04	1.60E–04	F-BA	−1.34E–04	1.75E–05
X2	F-rDiffDq	6.35E–02	−9.66E–03	F-lnBA	−3.09E–02	5.06E–03	F-lnBA	−2.10E–02	3.05E–03	F-lnBA	−4.77E–02	7.73E–03
X3	C-MaT	−7.39E–04	1.13E–04	W-TaP	−1.49E–05	3.03E–06	F-rDiffDq	−5.77E–03	1.17E–03	F-rDiffDq	1.62E–02	−2.39E–03
X4	C-TaAET	4.11E–05	−5.45E–06	W-aTR	−4.02E–03	5.98E–04	W-MaT	6.00E–03	−8.98E–04	W-MaT	−1.21E–03	2.18E–04
X5	S-CRFVOL	7.72E–04	−1.19E–04	W-MINmPET	−2.45E–03	3.83E–04	W-TaR	3.82E–06	−1.02E–06	W-TaP	−1.44E–05	2.94E–06
X6				W-MdrqT	1.51E–03	−2.18E–04	W-aTR	−3.38E–03	5.52E–04	W-aTR	−3.17E–04	4.57E–06
X7				W-MweqR	−1.56E–04	2.43E–05	W-MINmPET	−1.76E–03	2.60E–04	W-ARi	−1.32E–03	−3.32E–04
X8				C-seaT	−2.33E–05	3.56E–06	W-MweqT	−4.60E–03	7.38E–04	W-SDmP	4.43E–04	−6.87E–05
X9				C-ISO	9.18E–04	−1.28E–04	W-MweqR	−4.05E–06	−8.03E–07	W-MINmP	−5.34E–04	8.22E–05
X10				C-MweqT	−1.30E–04	2.08E–05	C-TaPET	4.84E–05	−6.69E–06	W-McoqP	7.19E–05	−8.80E–06
X11				S-PHIHOX	−1.47E–03	2.23E–04	C-seaP	−8.93E–04	1.62E–04	C-TaAET	1.57E–04	−2.47E–05
X12				S-ORCDRC	−4.82E–04	7.43E–05	C-MweqT	−3.15E–04	5.12E–05	C-MaDR	−5.63E–04	6.90E–05
X13				D-DepRedN	−1.87E–05	3.11E–06	S-SLTPPT	−5.94E–04	1.32E–04	C-seaP	−3.60E–04	6.77E–05
X14							S-CEC	1.40E–03	−2.57E–04	C-seaPET	2.81E–05	−3.97E–06
X15							S-PHIHOX	−4.49E–03	7.25E–04	C-ThARi	1.61E–03	−2.61E–04
X16							S-ORCDRC	−7.32E–04	1.23E–04	C-MwamT	−8.09E–04	1.25E–04
X17							S-CRFVOL	−8.61E–04	1.34E–04	C-MweqT	7.75E–05	−1.22E–05
X18							D-DepOxN	5.93E–05	−9.84E–06	C-TwaqP	2.14E–05	−5.36E–06
X19							D-DepOxS	−1.20E–05	2.21E–06	S-CLYPPT	1.18E–03	−2.04E–04
X20										S-CEC	−7.36E–04	1.25E–04
X21										S-PHIHOX	−1.88E–03	2.98E–04
X22										S-ORCDRC	3.11E–05	−1.09E–05

Table 3 Selected variables and parameter estimates per species group. For abbreviations of variables see Appendix 2 *(Continued)*

X23										S-BDRICM	0.000117916	−1.93E−05
X24										D-DepRedN	8.31E−07	−5.66E−08
X25										D-DepOxN	7.32E−06	−1.28E−06

	Other conifers			*Betula* spp.			Broadleaves longlived			Broadleaves shortlived		
		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$
c		4.28E−01	−6.48E−02		−2.87E−01	4.87E−02		2.71E−01	−4.01E−02		1.13E−01	−2.10E−02
X1	F-BA	−3.18E−03	4.79E−04	F-BA	−1.09E−03	2.00E−04	F-lnBA	−2.66E−02	4.05E−03	F-lnBA	−3.18E−02	4.67E−03
X2	F-rDiffDq	1.85E−02	−2.77E−03	F-lnBA	−1.04E−02	9.42E−04	W-MaT	2.07E−03	−2.77E−04	W-aTR	3.23E−03	−6.25E−04
X3	W-MaT	−3.23E−03	1.03E−03	F-rDiffDq	5.70E−03	−6.83E−04	W-TaR	−1.67E−05	2.41E−06	W-SDmPET	−1.93E−03	3.08E−04
X4	W-TaR	−2.88E−05	2.75E−06	W-MaT	2.28E−03	−3.14E−04	W-aTR	−4.52E−03	6.69E−04	W-SDmR	2.28E−04	−3.25E−05
X5	W-MaDR	7.36E−03	−1.12E−03	W-aTR	2.75E−03	−4.86E−04	W-ISO	−6.38E−02	8.32E−03	C-TaP	9.83E−05	−1.79E−05
X6	W-ThHUi	1.21E−04	−1.29E−05	W-MaDR	1.65E−03	−2.93E−04	C-aTR	3.11E−04	−5.04E−05	C-TaAET	−2.38E−05	6.85E−06
X7	W-SDmR	−1.82E−03	3.01E−04	W-ARi	−5.58E−03	7.71E−04	C-seaPET	−9.14E−06	1.63E−06	C-ARi	−5.32E−06	9.86E−07
X8	W-MweqT	8.80E−03	−1.67E−03	W-SDmPET	−6.57E−04	8.35E−05	C-MweqT	−7.00E−05	1.12E−05	C-MaDR	1.83E−04	−4.53E−05
X9	W-MweqR	−2.44E−04	4.53E−05	W-SDmR	2.19E−04	−2.80E−05	S-CLYPPT	−1.31E−03	2.04E−04	C-seaP	−5.17E−04	7.30E−05
X10	C-MaDR	8.02E−04	−1.36E−04	C-seaP	−6.96E−04	1.18E−04	S-SLTPPT	9.24E−04	−1.37E−04	C-seaPET	−1.17E−05	2.87E−06
X11	C-seaP	2.54E−03	−3.87E−04	C-ThARi	2.16E−03	−3.50E−04	S-CEC	−6.14E−04	9.11E−05	C-ThARi	5.40E−04	−8.44E−05
X12	C-MweqT	−3.90E−04	5.05E−05	C-Tmm0P	8.94E−05	−1.52E−05	S-CRFVOL	−7.39E−04	1.16E−04	S-CEC	−9.07E−04	1.40E−04
X13	D-DepOxN	1.54E−04	−2.29E−05	C-TwaqP	2.64E−04	−3.95E−05	S-BDRICM	4.46E−05	−6.12E−06	S-PHIHOX	−1.59E−04	5.27E−05
X14				S-SLTPPT	3.34E−04	−5.11E−05	D-DepRedN	1.79E−05	−2.57E−06	S-BLD	2.72E−05	−4.41E−06
X15				S-BLD	1.08E−04	−1.75E−05				S-CRFVOL	−3.40E−04	3.71E−05
X16										S-BDRICM	1.87E−04	−2.29E−05
X17										D-DepRedN	8.21E−06	−1.15E−06
X18										D-DepOxN	−2.70E−05	4.28E−06

	Castanea sativa			*Eucalyptus* spp.			*Fagus sylvatica*			*Populus* plantations		
		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$
c		9.71E−01	−1.12E−01		−7.62E−01	4.22E−02		−4.53E−01	4.85E−02		5.08E−01	−7.29E−02
X1	F-BA	7.11E−04	−1.11E−04	F-BA	−1.67E−03	2.46E−04	F-BA	6.27E−04	−9.59E−05	F-lnBA	−6.96E−02	1.03E−02
X2	F-lnBA	−6.26E−02	9.43E−03	F-lnBA	−3.55E−02	5.21E−03	F-lnBA	−5.56E−02	8.38E−03	W-aTR	−9.81E−03	1.43E−03
X3	F-rDiffDq	−1.09E−02	1.50E−03	F-rDiffDq	−1.23E−02	8.33E−04	W-TaR	−1.10E−05	1.70E−06			
X4	W-ISO	−7.33E−02	1.14E−02	W-MaT	1.53E−02	−2.88E−03	W-ISO	−1.23E−01	1.78E−02			
X5	W-MINmP	5.37E−04	−9.91E−05	W-TaP	5.78E−05	−9.31E−06	W-MaDR	4.24E−03	−5.96E−04			
X6	C-MwamT	−2.61E−04	2.78E−05	W-TaR	−7.71E−05	1.18E−05	W-ThHUi	6.90E−06	8.34E−08			
X7	C-TcoqP	1.04E−04	−1.45E−05	C-Ti	1.26E−04	−9.33E−06	W-ThARi	2.69E−04	−4.46E−05			
X8	S-BLD	3.53E−05	−5.17E−06	S-SLTPPT	−3.43E−04	1.38E−04	W-SDmPET	−4.54E−04	5.58E−05			
X9	S-CRFVOL	−6.68E−04	9.19E−05				W-MweqT	9.60E−04	−1.40E−04			
X10	D-DepRedN	2.63E−05	−3.67E−06				W-MdrqT	−3.73E−04	5.33E−05			
X11							C-MaT	−2.74E−05	1.04E−05			
X12							C-ISO	1.82E−03	−2.89E−04			
X13							C-MINwamT	2.56E−04	−3.76E−05			
X14							S-CLYPPT	−6.78E−04	1.05E−04			
X15							S-SLTPPT	−5.87E−04	9.68E−05			
X16							S-BLD	3.47E−05	−5.01E−06			
X17							S-BDRICM	6.87E−05	−9.11E−06			
X18							D-DepRedN	5.09E−06	−7.16E−07			
X19							D-DepOxS	−3.39E−06	4.97E−07			

Table 3 Selected variables and parameter estimates per species group. For abbreviations of variables see Appendix 2 *(Continued)*

		Quercus ilex			*Quercus robur + petraea*			*Quercus suber*			*Robinia pseudoacacia*	
		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$		$\theta_{i,1}$	$\theta_{i,2}$
c		1.72E−01	−2.68E−02		2.05E−01	−3.61E−02		1.09E + 00	−1.88E−01		2.24E−01	−3.30E−02
X1	F-lnBA	−8.96E−03	1.30E−03	F-BA	1.05E−03	−1.58E−04	F-lnBA	−1.39E−02	2.02E−03	F-lnBA	−4.99E−02	7.51E−03
X2	F-rDiffDq	−2.11E−02	3.10E−03	F-lnBA	−5.93E−02	8.93E−03	F-rDiffDq	−2.70E−02	3.89E−03	W-SDmP	3.35E−04	−4.12E−05
X3	W-MaDR	−2.12E−03	3.51E−04	F-rDiffDq	1.01E−03	−1.20E−05	C-MaT	−3.61E−04	6.31E−05			
X4	W-MINmPET	−4.56E−04	6.33E−05	W-TaR	−7.46E−06	8.98E−07	S-comp	7.19E−03	−1.11E−03			
X5	C-ISO	−1.60E−03	2.72E−04	W-MINmPET	1.18E−04	−8.25E−06	D-DepOxS	3.67E−06	−4.94E−07			
X6	C-TaP	−6.10E−06	1.25E−06	C-TaPET	5.44E−05	−8.34E−06						
X7	S-PHIHOX	−3.17E−04	4.18E−05	C-seaP	4.16E−04	−6.10E−05						
X8	D-DepOxN	−1.33E−05	3.20E−06	C-MwamT	−3.02E−05	7.03E−06						
X9				S-CEC	−8.33E−04	1.17E−04						
X10				S-BLD	2.80E−05	−4.04E−06						
X11				S-CRFVOL	−4.36E−04	5.94E−05						
X12				S-BDRICM	2.34E−04	−3.72E−05						
X13				D-DepOxN	4.34E−06	−5.10E−07						

Table 4 First column: Number of variables selected per species group and R^{2*} for the full model. Following columns: Number of variables selected per variable group in the final model, and the relative decrease in R^{2*} if this variable group is omitted from the model and fitted again

	Total		Forest structure		Weather		Climate		Soil		Deposition	
	N	R^2*	*N*	R^2* relative decrease	*N*	R^2* relative decrease	*N*	R^2* relative decrease	*N*	R^2* relative decrease	*N*	R^2* relative decrease
Abies spp.	19	0.29	2	32.3%	5	6.2%	7	3.3%	3	2.8%	2	0.7%
Larix spp.	11	0.28	2	60.7%	4	29.9%	2	2.0%	1	1.2%	2	3.3%
Picea abies	15	0.29	2	37.4%	4	0.6%	7	3.4%	2	0.9%	0	0.0%
Picea sitchensis	6	0.32	3	46.4%	2	13.0%	1	2.2%	0	0.0%	0	0.0%
Pseudotsuga menziesii	5	0.37	2	65.7%	0	0.0%	2	1.2%	1	0.2%	0	0.0%
Pinus nigra + mugo	13	0.33	2	28.3%	5	15.9%	3	3.7%	2	1.4%	1	0.3%
Other indigenous pines	19	0.26	3	32.2%	6	12.5%	3	3.5%	5	6.2%	2	1.1%
Pinus sylvestris	25	0.17	3	73.3%	7	3.7%	8	13.8%	5	4.0%	2	0.1%
Other conifers	13	0.53	2	16.5%	7	12.2%	3	3.9%	0	0.0%	1	3.0%
Betula spp.	15	0.27	3	27.1%	6	1.9%	4	2.8%	2	2.0%	0	0.0%
Broadleaves longlived	14	0.2	1	28.0%	4	13.1%	3	1.3%	5	4.1%	1	2.8%
Broadleaves shortlived	18	0.25	1	25.1%	3	1.7%	7	5.8%	5	3.3%	2	0.5%
Castanea sativa	10	0.13	3	76.5%	2	5.2%	2	16.1%	2	5.1%	1	6.7%
Eucalyptus spp.	8	0.51	3	17.4%	3	23.5%	1	1.2%	1	0.9%	0	0.0%
Fagus sylvatica	19	0.25	2	27.9%	8	6.0%	3	3.1%	4	2.4%	2	0.3%
Populus plantations	2	0.2	1	73.5%	1	14.3%	0	0.0%	0	0.0%	0	0.0%
Quercus ilex	8	0.1	2	47.4%	2	8.0%	2	3.6%	1	1.3%	1	6.3%
Quercus robur + petraea	13	0.17	3	51.2%	2	1.8%	3	2.6%	4	5.4%	1	0.4%
Quercus suber	5	0.1	2	42.5%	0	0.0%	1	2.7%	1	2.5%	1	1.6%
Robinia pseudoacacia	2	0.21	1	68.6%	1	4.9%	0	0.0%	0	0.0%	0	0.0%

for specific 3-month periods (quarters), related to precipitation and potential evapotranspiration (PET). For the climate variables no clear pattern could be distinguished, but also here annual variables were more often selected than indices and values for specific quarters.

To get an impression of the spatial variability in predicted diameter increment, we calculated the growth of a tree for all locations where a tree of that species was present in our dataset. We assumed the tree had a diameter equal to the average diameter of the species in the full dataset (Table 2), an F-rDiffDq of 0 (i.e. the social position of the tree was neutral) and that it was growing in a stand with a basal area equal to the average basal area listed in Table 2. We used the weather conditions of the period 2000–2014. Species groups show distinctively different spatial growth patterns (Fig. 3; Additional file 2). Some species, like *Fagus sylvatica* and *Abies* spp., have slow growth at their southern distribution limit and show good growth towards their northern limit, while other species like *Picea abies* show the opposite pattern. Many species (*Picea abies*, *P. sitchensis*, *Populus plantations*) show an east-west gradient with better growth along the coast and less growth going east, but *Pseudotsuga menziesii* and *Quercus robur* + *petraea* show the opposite tendency. Only few groups (*Pinus sylvestris*, *Betula* spp.) show an optimum in their mid-range and decreased growth towards their distribution limits.

To illustrate the sensitivity of the final models we show the predicted diameter increment for a range of conditions (Fig. 4; Additional file 3). The main curve depicts the median diameter increment as predicted for all sites assuming the median F-BA and a neutral social position (F-rDiffDq = 0). Ranges depict deviations from this median growth for 5th and 95th percentile of increment predicted for all locations, 5th and 95th percentile of F-BA observed in all locations and 5th and 95th percentile of F-rDiffDq observed in all locations. Additional file 4 shows the distribution of the underlying data and the moving average curves of both data and predictions.

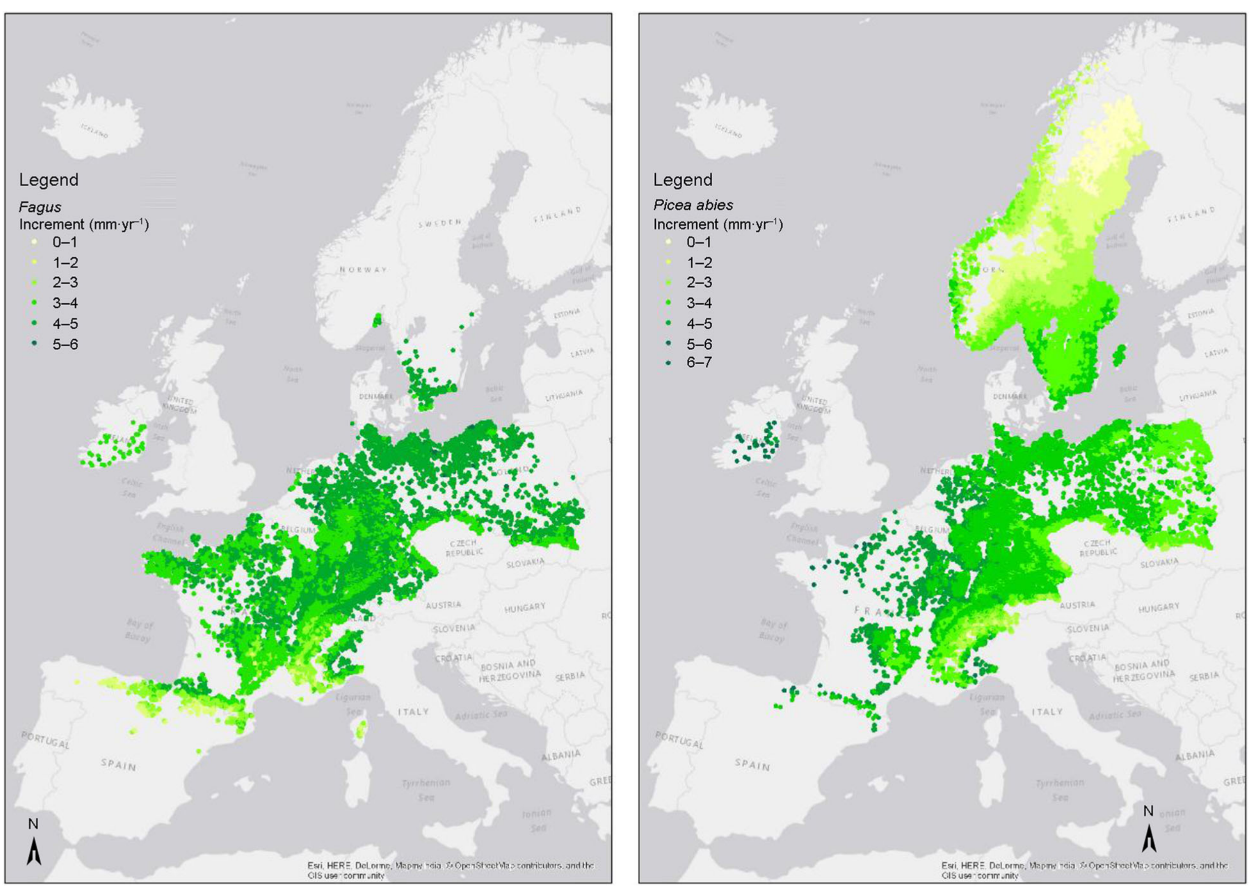

Fig. 3 Predicted diameter increment (mm/yr) of *Fagus sylvatica* and *Picea abies* at all sites where it is present, assuming average diameter and basal area (Table 2) and a neutral social position (F-rDiffDq = 0), with weather conditions for the period 2000–2014. Please note that the scale is different between the species. For all maps see Additional file 2

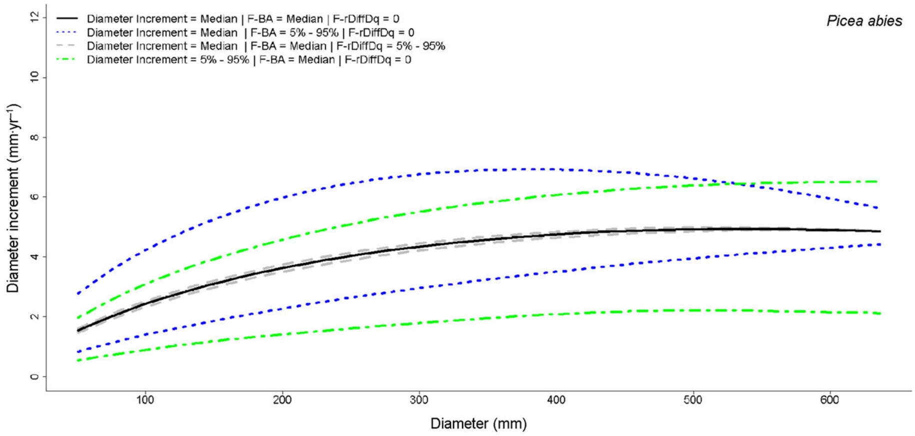

Fig. 4 Sensitivity of predicted diameter increment in relation to diameter for *Picea abies* for a range of site and stand conditions. The maximum value at the x-axis corresponds to the 99th percentile of diameter observed per species (Table 2)

Discussion

Growth of trees is governed by physical processes, plant physiological processes and ecological processes (Muys et al. 2010; Sterck et al. 2010). We have established a general description of the predicted diameter increment of European tree species as a function of the diameter and the biotic and abiotic environment of the tree. Even with the rather crude estimates of weather, climate, soil and nutrient deposition that were used, the strict shape of the growth curve, and the exclusion of the known good predictors age, latitude and altitude, we were able to explain between 10% and 53% of the variation in diameter growth of individual trees of the main European tree species and species groups. This level of explained variation is in line with the values reported by other studies based on country-scale forest inventory datasets (e.g. Andreassen and Tomter 2003; Laubhann et al. 2009; Cienciala et al. 2016; Charru et al. 2017). Much of the unexplained variance seems to be attributable to within-stand variation, given the high R^{2^*} value for total basal area increment at the plot level given in the results section. Further application of the models should give insight in the predictive value at larger scales. Other studies (e.g. Laubhann et al. 2009) already applied regression models on individual-tree measurements for multiple European countries, but these studies were aimed at estimating effect sizes, rather than for predictive purposes. To our knowledge our study is the first to present tree diameter increment models with a European-wide validity.

Apart from the regular measurement errors within an NFI (McRoberts et al. 1994), our dataset may contain extra variability by mixing different NFIs with different designs, measurement methods, protocols and thresholds (Table 1). On first screening of the data, we could not find indications for systematic differences between data from different NFIs, probably because we used the original diameter measurements without any further processing or interpretation. Additional noise is caused by the inclusion of explanatory variables of varying resolution (1–25 km), making it impossible to detect small-scale variation as present for example in mountainous terrain. However, the presented models are designed to be applied on a broad scale for large sets of plots, which will result in averaging out such errors. For studies on smaller scales, local or national diameter increment models might be better suited.

The largest part of the explained variance in the final models is attributed to parameters related to the forest structure, where basal area of the stand seems to be more important than the relative size of the tree (Fig. 4; Additional file 3). This is in line with many other studies that found stand density (Cienciala et al. 2016) or basal area (Hökkä et al. 1997) to be important variables. Despite the relatively low contribution of other variable groups to the explained variance, they are important to explain spatial patterns of diameter increment over Europe (Fig. 3; Additional file 2). The spatial patterns of diameter increment as presented in Additional file 2 seem plausible. *Picea abies* and *Picea sitchensis* are known to grow well under wet conditions and moderate temperatures. At higher latitudes and altitudes, growth of *Picea abies* is limited by a short growing season and low average temperatures, as indicated by declining diameter increment. For *Picea abies* a similar gradual decline is not visible on the southern edge. This is probably because trees are killed by attacks of bark beetles after drought or heat waves (Seidl et al. 2007). The opposite pattern is found in *Fagus sylvatica*. At the southern edge, increment slows down as temperatures rise, while there is an abrupt halt at the northern edge. This may be caused by mortality due to cold winters, or because *Fagus* is still expanding its range northwards (Kramer et al. 2010). *Pinus sylvestris* is known for its wide ability to survive in a wide range of environmental conditions. This is reflected in the spatial growth pattern with a large distribution over Europe, a moderate to good growth over a large range and declining growth only in harsh environments, such as dry inland Spain and under boreal conditions. Application of the models under climate change scenarios should give more information on the sensitivity of these patterns to climate change.

The diameter increment models presented allow for more detailed and consistent modelling of tree-growth at the European scale. With these models such modelling can take into account differences and changes in weather, climate and soil conditions across the continent and over time. As shown in Additional file 3, the models give realistic predictions over a large range of conditions. We recommend to use the models not further than the 99th percentile of diameter, as indicated in Table 2. Beyond these values the data support is very sparse, and the models may give unreasonable results. Similarly, the user should be aware that the models may predict small negative diameter increments for some species for specific combinations of poor locations, small diameters and high basal areas. The development of diameter increment models is a first step towards a full simulation model of forest development at the European scale. Such a growth model should include a way to estimate individual-tree volume from diameter, either directly (Zianis et al. 2005), via height/diameter ratio models (Mehtätalo 2005), or by inclusion of a height growth model (Ritchie and Hann 1986; Hasenauer and Monserud 1997), preferably climate-dependent. Furthermore, modules are needed to cover other important processes, like establishment of new trees, mortality and forest management.

Conclusions

The presented diameter increment models are the first of their kind that are applicable at the European scale. They are based on a unique dataset that covers the full range of growing conditions in Europe, and are sensitive to forest structure and environmental conditions, showing realistic patterns over their application range. This is an important step towards the development of a new generation of forest development simulators that can be applied at the European scale, but being sensitive to variations in growing conditions and applicable to a wider range of management systems than before.

Appendix 1

Calculation of weather indices

Data were downloaded from the Agri4Cast website (http://agri4cast.jrc.ec.europa.eu/). It contains daily data for the period 1975–current, at 25 km resolution. We extracted monthly values for mean temperature, total precipitation, total potential evapotranspiration and total radiation, for the period 1990–2015. For all four variables we then computed for each year the annual total (or mean in the case of temperature), the standard deviation and the maximum and the minimum. For every year, the warmest, the coldest, the wettest and the driest quarter of the year was identified. A quarter was defined as a successive period of 3 months, where the value for the months January–March was assigned to January, February–April to February, etc. For the quarters starting in November and December, the months of the next year were used. For every warmest, coldest, wettest and driest quarter, the mean monthly value of all four variables was computed. The resulting explanatory variables where labelled according to their operator (denoted by M for mean, SD for standard deviation, MAX for maximum and MIN for minimum), their aggregation period (a for annual, m for month, waq for warmest quarter, coq for coldest quarter, weq for wettest quarter and drq for driest quarter) and their variable (T for temperature, P for precipitation, PET for potential evapotranspiration and R for radiation), 32 in total.

In addition we calculated the following indices, all on an annual basis:

- Mean diurnal range (labelled as MaDR) from the difference between the monthly averages of the daily maximum and the daily minimum temperature
- Annual temperature range (aTR) as the difference between MAXmT and MINmT
- Isothermality (ISO) as the ratio between MaDR and aTR
- Annual degree days with thresholds 0, 5 and 10 (labelled respectively as DD0, DD5 and DD10)
- Aridity index (ARi) as TaP/TaPET
- Thornthwaite 1948 humidity index (ThHUi), being the accumulated precipitation surplus divided by PET in those months
- Thornthwaite 1948 aridity index (ThARi), being the accumulated precipitation deficit divided by PET in those months

For every observation of individual tree growth, we calculated the average of each variable for the period of observation, including both full years when the tree was measured. Please note that the order of calculation for some variables may lead to different values as presented in the BIOCLIM dataset. For computational efficiency we first aggregated to annual values before averaging over the years.

Appendix 2
Full list of potential explanatory variables and their scoring

Table 5 List of potential explanatory variables included. When two variables are correlated, the one with the highest score is discarded

Type	Source / time span / resolution	Variable name	Explanation	Unit	Preference score
Forest structure	NFI / at first year of inventory	F-BA	basal area of the plot	m2/ha	
		F-lnBA	Ln(F-BA)	–	
		F-rDiffDq	proxy for tree social position	–	
Weather	Agri4Cast / during observed growth period / 25 km	W-MaT	mean annual temperature	°C	111,111
		W-SDmT	standard deviation of monthly mean temperature	°C	122,111
		W-MAXmT	maximum monthly temperature	°C	123,111
		W-MINmT	minimum monthly temperature	°C	123,121
		W-MaDR	mean diurnal range	°C	112,141
		W-aTR	annual temperature range	°C	112,121
		W-ISO	isothermality	index	112,131
		W-DD0	degree days above 0 degrees Celsius	°C	111,511
		W-DD5	degree days above 5 degrees Celsius	°C	111,521
		W-DD10	degree days above 10 degrees Celsius	°C	111,531
		W-TaP	total annual precipitation	mm	111,211
		W-SDmP	standard deviation of monthly precipitation	mm	122,211
		W-MAXmP	maximum monthly precipitation	mm	123,211
		W-MINmP	minimum monthly precipitation	mm	123,221
		W-TaPET	total annual potential evapotranspiration	mm	111,411
		W-SDmPET	standard deviation of monthly PET	mm	122,411
		W-MAXmPET	maximum monthly PET	mm	123,411
		W-MINmPET	minimum monthly PET	mm	123,421
		W-TaR	total annual radiation	$GJ{\cdot}m^{-2}$	111,311
		W-SDmR	standard deviation of monthly radiation	$GJ{\cdot}m^{-2}$	122,311
		W-MAXmR	maximum monthly radiation	$GJ{\cdot}m^{-2}$	123,311
		W-MINmR	minimum monthly radiation	$GJ{\cdot}m^{-2}$	123,321
		W-MwaqT	mean warmest quarter temperature	°C	131,111
		W-McoqT	mean coldest quarter temperature	°C	131,131
		W-MweqT	mean wettest quarter temperature	°C	131,121
		W-MdrqT	mean driest quarter temperature	°C	131,141
		W-MwaqP	mean warmest quarter precipitation	mm	131,211
		W-McoqP	mean coldest quarter precipitation	mm	131,231
		W-MweqP	mean wettest quarter precipitation	mm	131,221
		W-MdrqP	mean driest quarter precipitation	mm	131,241
		W-MwaqR	mean warmest quarter radiation	$GJ{\cdot}m^{-2}$	131,311
		W-McoqR	mean coldest quarter radiation	$GJ{\cdot}m^{-2}$	131,331
		W-MweqR	mean wettest quarter radiation	$GJ{\cdot}m^{-2}$	131,321
		W-MdrqR	mean driest quarter radiation	$GJ{\cdot}m^{-2}$	131,341
		W-MwaqPET	mean warmest quarter PET	mm	131,411
		W-McoqPET	mean coldest quarter PET	mm	131,431
		W-MweqPET	mean wettest quarter PET	mm	131,421

Table 5 List of potential explanatory variables included. When two variables are correlated, the one with the highest score is discarded *(Continued)*

Type	Source / time span / resolution	Variable name	Explanation	Unit	Preference score
		W-MdrqPET	mean driest quarter PET	mm	131,441
		W-ARi	aridity index	index	114,411
		W-ThHUi	thorntwaite 1948 humidity index	index	114,421
		W-ThARi	thorntwaite 1948 aridity index	index	114,431
Deposition	EMEP / average 1990–2010 / 50 km	D-DepOxN	deposition of oxidised nitrogen	mg(N)·m^{-2}	411,411
		D-DepOxS	deposition of oxidised sulphur	mg(S)·m^{-2}	412,411
		D-DepRedN	deposition of reduced nitrogen	mg(N)·m^{-2}	411,421
Soil	SoilGrids / NA / 1 km	S-BDRICM	depth to bedrock (R horizon) up to maximum 240 cm	cm	311,411
		S-BLD	bulk density of the fine earth fraction	kg·m^{-3}	311,321
		S-CEC	cation exchange capacity	cmol·kg^{-1}	311,211
		S-CLYPPT	clay content mass fraction	%	311,111
		S-CRFVOL	coarse fragments (> 2 mm fraction) volumetric	%	311,331
		S-ORCDRC	soil organic carbon	%	311,311
		S-PHIHOX	pH in $H_2O \times 10$		311,221
		S-SLTPPT	silt content mass fraction	%	311,121
		S-SNDPPT	sand content mass fraction	%	311,131
	European Soil Data Centre	S-comp	natural susceptibility to soil compaction	6 categories	311,341
	GENS / average 1950–2000 / 1 km	C-wemP (bio13)	precipitation of wettest month	mm	221,223
		C-drmP (bio14)	precipitation of driest month	mm	221,243
		C-MaT (var1)	annual mean temperature	K	211,112
		C-MaDR (var2)	mean diurnal range	K	212,142
		C-ISO (var3)	isothermality	K	212,132
		C-seaT (var4)	temperature seasonality	K	212,112
		C-MAXwamT (var5)	maximum temperature of the warmest month	K	223,113
		C-MINcomT (var6)	minimum temperature of the coldest month	K	223,133
		C-aTR (var7)	annual temperature range	K	212,123
		C-MweqT (var8)	mean temperature of wettest quarter	K	231,123
		C-MdrqT (var9)	mean temperature of driest quarter	K	231,143
		C-MwaqT (var10)	mean temperature of warmest quarter	K	231,112
		C-McoqT (var11)	mean temperature of coldest quarter	K	231,132
		C-DD0 (var12)	degree days above 0 degrees Celsius	°C	211,512
		C-DD5 (var13)	degree days above 5 degrees Celsius	°C	211,522
		C-McomT (var14)	mean temperature of the coldest month	K	221,132
		C-MwamT (var15)	mean temperature of the warmest month	K	221,112
		C-MAXcomT (var16)	maximum temperature of the coldest month	K	223,112
		C-MINwamT (var17)	minimum temperature of the warmest month	K	223,122
		C-NM10 (var18)	number of months with mean temperature > 10		221,512

Table 5 List of potential explanatory variables included. When two variables are correlated, the one with the highest score is discarded *(Continued)*

Type	Source / time span / resolution	Variable name	Explanation	Unit	Preference score
		C-Ti (var19)	thermicity index		214,112
		C-TaP (var20)	total annual precipitation	mm	211,212
		C-MwemP (var21)	precipitation of the wettest month	mm	221,222
		C-MdrmP (var22)	precipitation of the driest month	mm	221,242
		C-seaP (var23)	precipitation seasonality	mm	212,212
		C-TweqP (var24)	precipitation of the wettest quarter	mm	231,222
		C-TdrqP (var25)	precipitation of the driest quarter	mm	231,242
		C-TwaqP (var26)	precipitation of the warmest quarter	mm	231,212
		C-TcoqP (var27)	precipitation of the coldest quarter	mm	231,232
		C-MINjjaP (var28)	minimum June July August precipitation	mm	233,221
		C-MAXjjaP (var29)	maximum June July August precipitation	mm	233,211
		C-MINdjbP (var30)	min Dec Jan Feb precipitation	mm	233,222
		C-MAXdjfP (var31)	max Dec Jan Feb precipitation	mm	233,212
		C-Tmm0P (var32)	total precipitation for months with mean monthly temperature above 0	mm	211,612
		C-TaAET (var33)	annual actual evapotranspiration	mm	211,442
		C-TaPET (var34)	annual potential evapotranspiration	mm	211,432
		C-coefmoist (var35)	coefficient of annual moisture availability		214,442
		C-Ari (var36)	aridity index		214,412
		C-seaPET (var37)	PET seasonality		212,412
		C-ThHUi (var38)	thorntwaite 1948 humidity index		214,422
		C-ThARi (var39)	thorntwaite 1948 aridity index		214,432
		C-EmPQ (var40)	embergers pluviothermic quotient		214,452
		C-TaR (var41)	total annual radiation		211,312

Each explanatory variable X_i was given a score on six different levels (S_AX_i–S_FX_i). The final score S was calculated as:
$SX_i = S_AX_i \times 100000 + S_BX_i \times 10000 + S_CX_i \times 1000 + S_DX_i \times 100 + S_EX_i \times 10 + S_FX_i$
where S_1 is the score at level A, relating to the variable group (weather, climate, soil, nutrient deposition), S_2 the score at level B, relating to the aggregation level of weather-and climate related variables, etc. Scores per level are listed in Table 6 and final score per variable is included in Table 5

Table 6 Scores for elements of explanatory variables

Level											
A	weather:1, climate:2						soil:3				deposition:4
B	annual:1, quarterly:2, monthly:3						all:1				all:1
C	total:1, spread:2, extreme:3, index:4						all:1				N:1, S:2
D	temperature:1, precipitation:2, radiation:3, potential evapotranspiration:4, degree days:5, precipitation days:6						texture:1, chemical:2, structural:3, depth:4				all:1
E	(ranges)	(PET indices)	(degree day indices)	(extremes)	(monthly/ quarterly)	(other cases)	(texture)	(chemical)	(structural)	(depth)	
	seasonal:1, annual:2, ISO:3, daily:4	aridity:1, ThHUi:2, ThARi:3, MA:4, PQ:5	threshold = 0:1, threshold = 5:2, threshold = 10:3	max:1, min:2	warmest:1, wettest:2, coldest:3, driest:4	not defined:1	clay:1, silt:2, sand:3	CEC:1, pH:2	bulk density:1, coarse fragments:2, organic matter content:3, soilcompaction:4	depth to bedrock:1	reduced:1, oxidised:2
F	summer:1, winter:2, BIOCLIM dataset:3, GEnS dataset:4						all:1				all:1

Additional files

Additional file 1: Residual analysis per species. (ZIP 354 kb)

Additional file 2: Maps of predicted diameter increment. (ZIP 3004 kb)

Additional file 3: Sensitivity of predicted diameter increment per species. (ZIP 364 kb)

Additional file 4: Data and fitted values per species. (ZIP 807 kb)

Abbreviations

AIC: Akaike's information criterion; C-: Explanatory variables related to climate; CBD: United Nations Convention on Biological Diversity (CBD); CBM-CFS3: Carbon Budget Model of the Canadian Forest Sector; CEC: Cation exchange capacity; CGIAR-CSI: Consultative Group for International Agricultural Research - Consortium for Spatial Information; D-: Explanatory variables related to deposition; EFISCEN: European Forest Information Scenario model; EMEP: European Monitoring and Evaluation Programme; ETTS: European Timber Trend Studies; F-: Explanatory variables related to forest structure; FAO: Food and Agricultural Organisation; GEnS: Global environmental stratification dataset; NFI: National Forest Inventory; PET: Potential evapotranspiration; S-: Explanatory variables related to soil; UNECE: United Nations Economic Commission for Europe; UNFCCC: United Nations Framework Convention on Climate Change; W-: Explanatory variables related to weather

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Availability of data and materials

Explanatory variables are available via internet at the locations specified. A package of NetCDF files containing all variables is available on request from the authors. Tree data are obtained from NFIs with different data policies and can be made available only with consent of the respective data owners. Data requests can be sent to the corresponding author.

Authors' contributions

The idea for this article came from GJN. GJN and MJS contacted potential data contributors. ET and BR prepared the Swiss data, GV the Italian data, JV the Spanish data, JR the Irish data, JS the Polish data, JF the Swedish data, ST the Norwegian data, MJS the Dutch data. RS and HP assisted with preparing the German data. MJS and GMH processed the input data and collected the set of explanatory variables. AHH prepared the explanatory variables in a standardised format and produced the output maps. MJS, GMH, SB and GV designed the statistical procedures, implemented by GMH. Graphs were created by MJS. Everyone assisted in interpretation of the results and writing the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare that they have no competing interests.

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