

Environmental drivers interactively affect individual tree growth across temperate European forests

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Abstract

Forecasting the growth of tree species to future environmental changes requires a better understanding of its determinants. Tree growth is known to respond to global-change drivers such as climate change or atmospheric deposition, as well as to local land-use drivers such as forest management. Yet, large geographical scale studies examining interactive growth responses to multiple global-change drivers are relatively scarce and rarely consider management effects. Here, we assessed the interactive effects of three global-change drivers (temperature, precipitation and nitrogen deposition) on individual tree growth of three study species (*Quercus robur/petraea*, *Fagus sylvatica* and *Fraxinus excelsior*). We sampled trees along spatial environmental gradients across Europe and accounted for the effects of management for *Quercus*. We collected increment cores from 267 trees distributed over 151 plots in 19 forest regions and characterized their neighbouring environment to take into account potentially

confounding factors such as tree size, competition, soil conditions and elevation. We demonstrate that growth responds interactively to global-change drivers, with species-specific sensitivities to the combined factors. Simultaneously high levels of precipitation and deposition benefited *Fraxinus*, but negatively affected *Quercus*' growth, highlighting species-specific interactive tree growth responses to combined drivers. For *Fagus*, a stronger growth response to higher temperatures was found when precipitation was also higher, illustrating the potential negative effects of drought stress under warming for this species. Furthermore, we show that past forest management can modulate the effects of changing temperatures on *Quercus*' growth; individuals in plots with a coppicing history showed stronger growth responses to higher temperatures. Overall, our findings highlight how tree growth can be interactively determined by global-change drivers, and how these growth responses might be modulated by past forest management. By showing future growth changes for scenarios of environmental change, we stress the importance of considering multiple drivers, including past management and their interactions, when predicting tree growth.

KEYWORDS

basal area increment, climate change, *Fagus*, *Fraxinus*, historical ecology, nitrogen deposition, *Quercus*, tree-ring analysis

1 | INTRODUCTION

Forests are key providers of numerous ecosystem services such as water protection or carbon uptake, but it remains unclear how forests will respond to future environmental changes (Aber et al., 2001; Doblas-Miranda et al., 2017; Keenan, 2015; Lindner et al., 2014; Reyer, 2015; Schröter et al., 2005; Trumbore, Brando, & Hartmann, 2015). Altered precipitation amounts and distribution, climate warming and increased atmospheric deposition of nitrogen and sulphur causing eutrophication and/or acidification are amongst the most important global-change drivers affecting forests (Laubhann, Sterba, Reinds, & de Vries, 2009). By influencing tree growth, these global-change drivers can alter the future composition and functioning of forests (Aber et al., 2001).

Trees in Europe are also exposed to these environmental changes. In Central and Western European forests, an overall warming trend accompanied by more frequent and intense heat waves and droughts during summer is expected, as well as increases in heavy precipitation events (Christensen et al., 2007; Jacob et al., 2014; Orłowsky & Seneviratne, 2012). At the same time, studies have projected both a decreased as well as increased future nitrogen deposition for Europe throughout the 21st century, while sulphur deposition is expected to remain constant or decrease (EEA, 2007; Engardt, Simpson, Schwikowski, & Granat, 2017; Leip et al., 2011). Diverging effects of global-change drivers on tree growth have been observed among forests in Europe (Laubhann et al., 2009; Ruiz-Benito et al., 2014). For instance, while nitrogen deposition has been identified as the main driver of increased growth in the 20th century (Camarero & Carrer, 2016; de Vries et al., 2009; Fowler et al., 2013;

Magnani et al., 2007), it has also been shown to decrease growth in regions where critical nitrogen loads are exceeded (Aber, 1992; Bobbink et al., 2010; Sutton et al., 2014). Different tree species also show divergent growth responses to global-change drivers due to their different autecological characteristics (e.g., competitive ability, drought sensitivity; Bosela et al., 2016; Charru, Seynave, Hervé, Bertrand, & Bontemps, 2017; Mette et al., 2013). In addition, interactive effects of multiple drivers acting simultaneously upon trees might cause tree growth responses to differ from those in single-factor studies, highlighting the need for multi-factor studies (Braun, Schindler, & Rihm, 2017; Laubhann et al., 2009).

Forests are managed throughout the world, but particularly intensively in Europe over the past few centuries (McGrath et al., 2015). Forest management may have even greater influence on tree growth in Europe than global-change drivers (Altman et al., 2013; De Vries et al., 2007; Foster, Finley, D'Amato, Bradford, & Banerjee, 2016). Forest management can influence tree growth by altering the availability and uptake of resources (e.g., nutrients and light) and conditions (e.g., temperature) to which trees are subjected (Altman et al., 2013). Two widespread historical forest management systems in Europe, that is high forest and coppice(-with-standards), differ strongly in management regime; hence they might differently affect tree growth (McGrath et al., 2015; Sjölund & Jump, 2013; Stojanović et al., 2017). In coppice systems, canopy opening occurs regularly through cutting multi-stemmed individuals on relatively short rotation cycles ("coppicing" occurs typically every 7–30 years) with an undisturbed period in between. This creates a cyclic variation in light and warm temperatures, whereas high forests often show a more

continuous disturbance regime, for example, through continuous removal of thinned trees (Buckley, 1992; Kopecký, Hédli, & Szabó, 2013; Sjölund & Jump, 2013). By altering the resources and conditions available for trees (e.g., temperature, light and nutrient availability), and shaping the present structure and composition of the current forests, past forest management may have influenced their growth and may also modulate growth responses to global-change drivers such as temperature (Stojanović et al., 2017; Vayreda, Martínez-Vilalta, Gracia, & Retana, 2012).

Previous studies have explored how global-change drivers affect tree growth, but mostly on a restricted geographical scale (Bauwe, Jurasinski, Scharnweber, Schröder, & Lennartz, 2016; Braun et al., 2017; Ibáñez, Zak, Burton, & Pregitzer, 2018; Martínez-Vilalta, Lopez, Adell, Badiella, & Ninyerolas, 2008). Tree growth studies covering larger geographical scales and taking into account interactions between global-change drivers at the same time (e.g., Laubhann et al., 2009; Solberg et al., 2009) are relatively scarce. Tree growth studies that additionally also consider the effects of land-use legacies such as forest management (e.g., Stojanović et al., 2017; Vayreda et al., 2012) across large geographical scales are, to our knowledge, even lacking. Yet, in order to make accurate projections of future tree growth responses, we need a better understanding of the growth determinants of trees at large geographical scales (Babst, Poulter, Bodesheim, Mahecha, & Frank, 2017; Bowman, Brienen, Gloor, Phillips, & Prior, 2013; Mäkinen et al., 2003). By evaluating (past) growth responses to large *spatial* gradients in different global-change drivers, and by controlling for confounding factors, we may infer responses to *temporal* changes in these drivers in different regions. Furthermore, seeing the impact that forest management can have on tree growth and the potential of interaction with other global-change drivers (Vayreda et al., 2012), it is key to also take management legacies into account in such large-scale tree growth studies (Mausolf et al., 2018; Noormets et al., 2015).

Our study aims to assess interactive tree growth responses to large spatial gradients in environmental variables, representing the global-change drivers—that is, for the three study species. Furthermore, we want to assess whether plot management histories (i.e., disturbance regimes) influenced tree growth and potentially modulated tree growth responses to global-change drivers—that is, for *Quercus* only. We chose 19 temperate deciduous Central-Western European forest regions in such a way that we maximized differences in global-change drivers (temperature, precipitation and deposition) *between* the regions, reflecting three important global environmental changes (climate warming, changing precipitation and eutrophication/acidification); while maximizing past and current forest management differences *within* regions. We minimized the effects of potentially confounding factors such as tree size, local competition, soil conditions and elevation. In every region, we collected increment cores of three economically and ecologically important European tree species (*Quercus robur/petraea*, *Fagus sylvatica* and *Fraxinus excelsior*) combined with in-situ measurements of the local soil and stand conditions and reconstructed plot management histories.

We expect to find interactive effects between the global-change drivers on tree growth and hypothesize that the type of interaction and magnitude may differ between the study species due to the different ecological characteristics of the species. Furthermore, we hypothesize that *Quercus*' growth response to the global-change drivers might be modulated by the past forest management context of the plots.

2 | MATERIALS AND METHODS

To assess tree growth response, we calculated basal area increment (BAI) from tree cores in plots situated across temperate Europe along environmental (all study species) and management (*Quercus* only) gradients. Sampling trees “across” spatial gradients of environmental variables allows to disentangle the interactions among the global-change drivers through an orthogonal design, and for *Quercus*, to assess whether the effects of global-change drivers depends upon past forest management (Verheyen et al., 2017). We collected cores from 267 trees located in 151 20 × 20 m plots across 19 regions, where we characterized region-scale global-change drivers, plot-scale management variables and potential plot- and tree-level confounding factors.

2.1 | Study regions

To maximize differences in global-change drivers across our study regions, we selected 19 regions along a spatial environmental gradient of atmospheric deposition and climatic conditions (temperature and precipitation) within the European temperate forest biome (Figure 1a, Supporting Information Table S1). Mean annual temperature (MAT), total annual precipitation (TAP) and nitrogen deposition (Ndep) at the study regions ranged from 6.9 to 12.9°C, from 472 to 1,852 mm/year and from 7 to 30 kg/ha year, respectively (Figure 1b, Supporting Information Table S1, values for the year 2000). At the same time, we tried to maximize differences in past and current forest management between plots (i.e., within regions, Supporting Information Table S2), while minimizing differences in site conditions such as soil texture or elevation between plots and between regions. All forest regions comprised closed-canopy forests with a diverse tree and shrub layer composition in which forest management had occurred at some point between 1940 and 2015 (except for the Moricsala nature reserve, which had never been managed).

2.2 | Study species

We cored three tree species across the study regions, representing ecologically and economically important tree species in temperate Europe, that is, the diffuse-porous *Fagus sylvatica* (73 trees, 50 plots, 10 regions) and the ring-porous *Fraxinus excelsior* (49 trees, 39 plots, 10 regions) and *Quercus robur/petraea* (145 trees, 87 plots, 15 regions) (Figure 1a, Supporting Information Table S1). Since the sample sizes depended on which species were present in the plots, they each cover slightly different environmental gradients (Figure 1b).

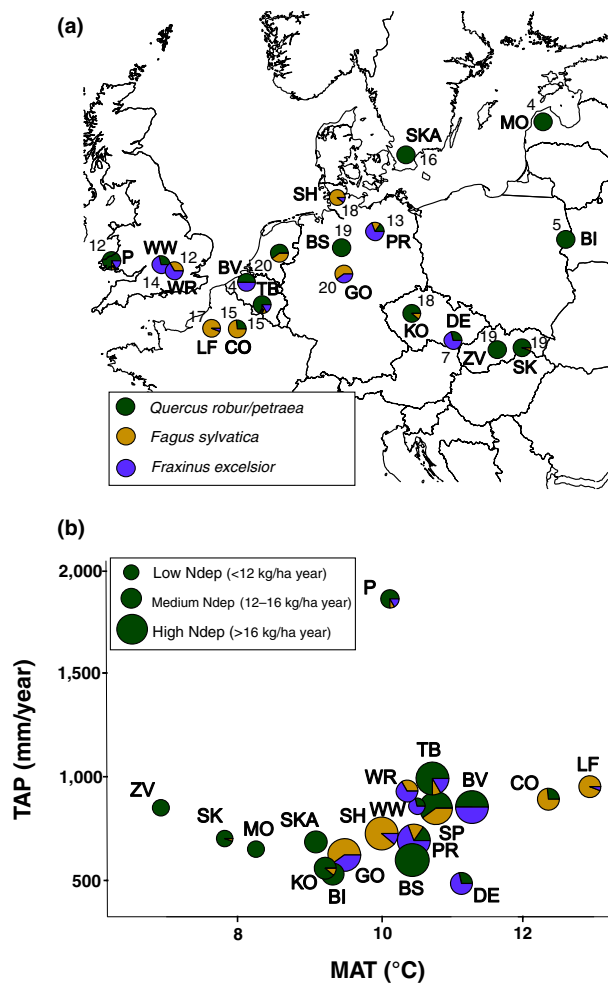


FIGURE 1 (a) The 19 forest regions with the distribution of the cored tree species from each region. Each pie chart visualizes the proportion of cored trees of the three study species per region, with *Quercus*, *Fagus* and *Fraxinus* respectively displayed in green, orange and purple. The total number of cored trees per region and the Region code is given next to the pie charts. (b) Environmental gradients covered by the study species: total annual precipitation (TAP – mm/year) versus mean annual temperature (MAT – °C) is plotted, with a pie chart representing the distribution of the cored tree species in each region, and the pie chart size reflecting the nitrogen deposition load in that region (Ndep – kg/ha year). Environmental values from the year 2000 were used. Region codes, and country codes between brackets, are as follows: BI = Białowieża Forest (PL), BS = Braunschweig (GE), BV = Binnen-Vlaanderen (BE), CO = Compiègne (FR), DE = Devin Wood (CZ), GO = Göttingen (GE), KO = Koda Wood (CZ), LF = Lyons-la-Forêt (FR), MO = Moricsala (LTV), P = Pembrokeshire (UK), PR = Prignitz (GE), SH = Schleswig-Holstein (GE), SKA = Skåne (SW), SK = Slovak Karst (SLK), SP = Speulderbos (NL), TB = Tournibus (BE), WR = Warburg Reserve (UK), WW = Wytham Woods (UK), and ZV = Zvolen (SLK). Details on these regions can be found in Supporting Information Table S1 [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

Since we often could not distinguish *Q. robur* from *Q. petraea* in the field due to hybridization of the two subspecies, they were merged for the analyses and we further denote them as one species

“*Quercus robur/petraea*”. *Quercus robur* and *petraea* are thermophilous, light-demanding species that are rather indifferent to nutrient availability and quite drought-tolerant (Ellenberg & Leuschner, 2010). *Fagus sylvatica* is a drought-sensitive, shade-tolerant species, indifferent to nutrient availability, whereas *Fraxinus* is a moderate light-demanding species with high nutrient requirements preferably growing on quite wet, rich soils (Ellenberg & Leuschner, 2010; Scharnweber et al., 2011). We chose these species because they are typically (co-)dominant in temperate broadleaved European forests (Bohn et al., 2003; Leuschner & Ellenberg, 2017), and they show different growth sensitivities to global-change drivers due to the different autecological characteristics (e.g., Laubhann et al., 2009; Mette et al., 2013). Furthermore, they have been commonly used in dendrochronological studies (e.g., Latte, Lebourgeois, & Claessens, 2015; Mette et al., 2013; Rieger, Kowarik, Cherubini, & Cierjacks, 2017).

2.3 | Data collection

In each 400 m² plot, we recorded the coordinates and elevation (metres) at the centre of the plot with a GPS GARMIN *e-TREX 10*, sampled the soil and forest floor (organic litter and organic fragmentation/humus layer), made a description of the soil profile, measured diameters of all trees with a diameter at breast height (DBH) larger than 7.5 cm (i.e., basal area measurements) and measured for each cored tree the diameters of all trees (with DBH > 7.5 cm) within a radius of 9 m around that tree as well as the distances to that tree (i.e., neighbourhood measurements). For details on our sampling protocol, see Supporting Information Table S3.

We cored dominant trees of the study species to maximize our chances of extracting the longest possible tree-ring series for each species and minimize competition effects from the last few decades. In each plot, we generally sampled the two most dominant trees (max 14.1 m apart, up to three trees were sampled if more than one of the species was dominant (cfr. *Classic sampling design* sensu Nehr-bass-Ahles et al. (2014)). From each tree, we took two perpendicular cores at breast height (Buchanan & Hart, 2011; Woodall, 2008). We checked for signs of ash dieback (Vasitis et al., 2017), only coring healthy individuals of *Fraxinus excelsior* to avoid confounding effects of dieback on the tree growth response. After drying the samples (24 hr at 103°C) to obtain correct wood density estimates, they were scanned with the X-ray Computed Tomography scanner (XCT, 110 µm resolution) (Dierick et al., 2014; Mil, Vannoppen, Beeckman, Acker, & Bulcke, 2016; Van den Bulcke et al., 2014). Ring widths were measured with the MATLAB-program *DHXCT* (De Mil et al., 2016). We used the automatic detection procedure based on wood density and visually inspected for missing and/or falsely indicated rings. We additionally measured badly visible ring sections with a Lintab™ 6 (RINNTECH, Germany, 10 µm resolution) after planing the samples with a Core Microtome (Gärtner & Nievergelt, 2010). To ensure correctly dated tree-ring series, we crossdated the two cores per tree, all cores of the same species per plot, and ultimately all cores of the same species per region. For details on the crossdating

procedure and results see Maes et al. (2017) section 2.5 and Supporting Information Table S4. After crossdating, the mean ring-width series (i.e., the average of the two crossdated cores) of each individual dominant tree was used to calculate its basal area increment (BAI, cm²/year) series. Furthermore, we calculated a time series of the previous-year diameter (Dprev, cm) based on the measured diameters and the tree-ring series to take into account tree size, a commonly used proxy for developmental stage (e.g., Kint et al., 2012; Martin-benito, Kint, Muys, & Cañellas, 2011; Rozas, 2014).

2.4 | Data analysis

2.4.1 | Response variable

We used basal area increment as a measure for tree growth. Three very large and two very young trees were excluded from the analyses because of their outlier behaviour, and the sampling years (2014, 2015 or 2016—region-specific: Supporting Information Table S1) were excluded because of unfinished growth for those years. We only investigated the time period of 1940–2015 (or 2013/2014—region-specific) to avoid including juvenile growth (i.e., <30 years: cf. cambial age limit Aertsen et al., 2014) as well as to minimize the influence of off-pith coring.

2.4.2 | Predictor variables

We used time series of two climatic and two atmospheric deposition variables, estimated at the regional scale, to quantify potential tree growth drivers: (a) mean annual temperature (MAT, °C), (b) total annual precipitation (TAP, mm/year), (c) atmospheric nitrogen deposition (Ndep, kg/ha year) and (d) acidification rate (AcidRate, keq/ha year) (Table 1, Supporting Information Figure S4). We used nitrogen deposition as a measure of potential eutrophication and acidification rate as a measure of potential acidification. For the climatic time series, we extracted monthly climate data from the gridded CRU TS3.24 data set (Climate Research Unit, 0.1° resolution: Harris, Jones, Osborn, & Lister, 2014). Time series of total nitrogen deposition (NH₃ + NO_x) and sulphur deposition (SO_x) were created by using data for the year 2000 from the European Monitoring and Evaluation Programme (EMEP) combined with annual correction factors from Duprè et al. (2010) to calculate deposition values for all other years between 1940 and 2015 (Supporting Information Figure S4). Annual acidification rate (AcidRate) was calculated based on annual nitrogen (N_{dep}) and sulphur deposition (S_{dep}) as (cf. Verheyen et al., 2012):

$$\text{AcidRate} = \frac{N_{\text{dep}}}{14} + 2 * \frac{S_{\text{dep}}}{32.06}$$

Assuming homogeneous environmental conditions within a region, we extracted all time series on a plot level and then calculated the mean of the plot-level time series for each region. For the climatic variables, we used the time series of mean annual temperature and total annual precipitation as well as the time series of spring (April–June) and summer (July–September) temperature and precipitation. Seasonal

TABLE 1 Variables used to model the basal area increment of individual trees, reflecting the global-change drivers, forest management history and potentially confounding factors (local soil and stand conditions + tree size)

Spatial scale	Predictor	Variable (unit)	Description
Region	Temperature	MAT (°C)	Annual average (+spring, summer— Supporting Information (Appendix S1))
	Precipitation	TAP (mm)	Annual total (+spring, summer— Supporting Information (Appendix S1))
	N Deposition	Ndep (kg/ha)	Annual total (NO _x , NH ₃)
	Acidification Rate	AcidRate (keq/ha)	Annual total (NO _x , NH ₃ , SO _x)
Plot	Elevation	Elev (m)	Elevation of the plot
	Soil depth	Soil Depth (cm)	Depth of the bedrock
	Soil conditions	PC1, PC2 (dimensionless)	1st and 2nd axis of PCA on chemical soil variables (see Supporting Information Figure S1)
	Past forest management	CoppHist	Categorical (0 or 1): coppicing between 1940 and 2015?
		ManHist	Categorical ("C(WS) to HF" or "HF"): management history between 1940 and 2015?
Tree	Tree size	Dprev (cm) Dprev ² (cm ²)	Previous-year diameter (see Supporting Information Figure S2)
	Competition	NCI (dimensionless)	Neighbourhood competition index

Note. All variables were continuous except for the categorical variables of past forest management. Variables in bold represent the variables of interest (global-change drivers and past forest management); Italic variables were included as time series. C(WS) and HF represent the coppice-(with-standards) and high forest management type. Past forest management was only included in the *Quercus* models.

climate effects on tree growth have been demonstrated before, with spring conditions especially important for ring-porous species such as *Quercus* and *Fraxinus* and summer conditions mainly important for diffuse-porous species such as *Fagus* (e.g., Latte, Lebourgeois, & Claessens, 2016). Because seasonal values were strongly correlated with annual values allowing the inclusion of only one term in each model (see Supporting Information Figure S5), we kept the focus in the main text on the annual results and present the seasonal results in Supporting Information Table S10. We chose annual values because they capture potential drivers from all seasons, reflecting the temporal scale of "annual" ring measurements, as well as they allowed us to create similar models for the three study species.

For each plot, the management history between 1940 and 2015 was reconstructed based on a combination of expert knowledge of

our local contact person in each region, a thorough search of site-specific maps and literature (e.g., management plans) and oral interviews. The plots were classified as belonging to one of seven management histories between 1940 and 2015: Coppice or Coppice-With-Standards (C(WS)) throughout, High Forest (HF) throughout, Zero management (ZM) throughout, C(WS) to HF, C(WS) to ZM, HF to ZM and C(WS) to HF to ZM (Details: Supporting Information Table S2) (McGrath et al., 2015). We derived two categorical variables (Table 1) from the management information (Supporting Information Tables S2 and S4). Coppice History (*CoppHist*) reflects whether the studied plot had been managed as coppice or coppice-with-standards between 1940 and 2015 (yes or no, for all 87 *Quercus* plots: Supporting Information Table S5). Management History (*ManHist*) reflects whether a plot had been continuously managed as high forest between 1940 and 2015 or had been converted from coppice or coppice-with-standards to high forest within this period (for a subset of 47 plots: Supporting Information Table S5). We could only analyse the effects of forest management for *Quercus*, because for *Fagus* or *Fraxinus*, the different categories of past forest management were not well represented across their environmental gradients.

The local growing conditions (elevation and soil) competition with neighbouring trees as well as tree size may confound the response of tree growth to the global-change drivers and past management. Hence, we used several variables related to these potentially confounding factors: elevation, soil depth, soil conditions (two variables) at the plot level, and neighbourhood competition and tree size at the tree level (Table 1).

We inferred soil depth (cm), representative of the root growing space for the trees from our soil profile descriptions (0–50 cm deep) per plot. If we reached the bedrock before a depth of 50 cm, the bedrock depth (e.g., 20 cm) was used as soil depth. In all other cases, soil depth was assumed 50 cm. We included information on the soil physical-chemical conditions by performing a principal correspondence analysis (PCA) on the following soil variables: pH_{KCl} , soil texture, base saturation, total and Olsen Phosphorus, Carbon/Nitrogen ratio, inorganic Carbon content, dry weight of forest floor layer and bulk density (for sampling and chemical analysis details see Supporting Information Table S3). The scores from the first two PCA axes were used as two predictors of soil conditions. These axes explained 60% of the variance (PC1: 48%, PC2: 12%), allowing us to reduce the number of potential explanatory variables related to soil conditions in the model and avoid multicollinearity. See Supporting Information Figure S1 for details on the PCA. Overall, the plots comprised quite rich (mesic) soil conditions—that is, mean pH_{KCl} of 4.4, mean base saturation of 0.8 (Weil & Brady, 2017) and mean C/N ratio of 13.9.

We calculated the distance-dependent neighbourhood competition index (NCI) from the neighbourhood measurements for each cored tree as:

$$NCI_i = \sum_{j=1}^n \frac{DBH_j}{Dist_{ij}}$$

where NCI_i is the current competition index for the subject tree, DBH_j is the diameter of the j -th competitor, $Dist_{ij}$ is the distance

TABLE 2 Minimum-maximum ranges for several tree characteristics of the cored trees across the 19 forest regions

	BAI (cm ² /year)	DBH (cm)	NCI
<i>Quercus robur/petraea</i>	0–114.32	26.5–107	0–2.65
<i>Fagus sylvatica</i>	0–112.32	27–100	0–1.36
<i>Fraxinus excelsior</i>	0.03–130.4	22–89.25	0.06–3.24

Note. BAI represents the basal area increment, DBH the diameter at breast height and NCI the neighbourhood competition index.

from subject tree i to the j -th competitor and n the number of competitors within a radius of 9 m of the subject tree (Hegyí, 1974). We included tree size as a time series of the previous-year diameter (D_{prev}). Several characteristics of the cored tree species (basal area increment, diameters, heights and competition index) across the study regions are shown in Table 2 (details per region: Supporting Information Tables S6–S8).

2.4.3 | Modelling

We built species-specific models to study the effects of the global-change drivers on the growth of each of the three study species. Then, we tested whether past forest management additionally affected the growth of *Quercus*. Linear mixed-effect models were built in two stages (similar methodologies as Aertsen et al., 2014; Kint et al., 2012; Martinez-Vilalta et al., 2008).

First, we built a *base model* (M_b) for each species, with predictors that might have influenced tree growth in our study, but are not part of our research questions:

$$M_b : \log(BAI_t + 1) = \beta_0 + \beta_{size}SIZE + \beta_{comp}COMP + \beta_{site}SITE$$

where *SIZE* includes the tree size variables (D_{prev} , D_{prev}^2), *COMP* tree competition (NCI) and *SITE* the plot-level site conditions (Elevation, PC1, PC2, Soil depth). All models assumed a quadratic relation between basal area increment and D_{prev} since a size-mediated effect (related to a tree age effect) is well known to increase tree growth until a certain maximum is reached, after which growth starts to decline (Gower, McMurtrie, & Murty, 1996; Wykoff, 1990).

Then, to assess the main and interactive effects of the global-change drivers, we built an *environment model* (M_e) for each species. Here, the environmental factors representative of the global-change drivers (ENV) and the three two-way interactions between these factors (ENV:ENV) were added to the base model.

$$M_e : \log(BAI_t + 1) = M_b + \beta_{env}ENV + \beta_{env_i-env_j}ENV_i : ENV_j$$

where $i, j = MAT, TAP, Ndep$ or $AcidRate$.

Because we expected that the effect of precipitation or deposition on tree growth might be quadratic rather than linear, we additionally tested for significant quadratic effects of mean annual precipitation and nitrogen deposition in the environment model.

Finally, to test whether past forest management additionally affected tree growth of *Quercus*, and interacted with the

environmental drivers, we built a *forest management model* (M_{fm}) for *Quercus* as:

$$M_{fm} : \log(\text{BAI}_t + 1) = M_e + \beta_{fm} \text{FM} + \beta_{fm-env_i} \text{FM} : \text{ENV}_i$$

where FM = CoppHist or ManHist and i = MAT, TAP, Ndep or AcidRate. Separate models were built for each of the two forest management variables.

Several variables required a transformation prior to analysis to achieve normality of their distribution. We log+1 transformed the distribution of basal area increment to remove its right skewness and to avoid negative values of the transformed variable (cfr. Martin-benito et al., 2011). We also transformed the following predictor variables: mean annual precipitation (log-transformed, only for *Quercus* and *Fraxinus*), elevation (square-root transformed), NCI (log $(x + 1)$ transformed) and soil depth ($1/\log(x)$). We checked for potential confounding and collinearity issues between the predictor variables by means of boxplots and correlograms. We did not find any confounding or multicollinearity issues between the predictors, except for nitrogen deposition and acidification rate, which were highly correlated (Pearson $\rho > 0.7$) (Supporting Information Figure S3). Therefore, we built separate models using either Ndep or AcidRate. Finally, all continuous predictors were standardized (scaled and centred) prior to analysis to enable comparison of their effect sizes.

To take into account the hierarchical structure of our data (trees within plots within regions), a nested random intercept "Region\Plot\Tree" was included in the models. To take into account the temporal autocorrelation present in tree-ring series, we added a second-order autoregressive covariance structure (ARMA(2,0)) to the models. The model procedure of Zuur, Ieno, Walker, Saveliev, and Smith (2009) was used to determine the optimal random and fixed effect structure for all models. Significance of fixed effects was tested by performing likelihood ratio tests on nested models and by comparing Akaike Information Criteria (AIC) between the models by means of the function "stepAIC" in R (backward selection procedure). Only for the forest management model of *Quercus*, we did not use stepAIC, but performed the likelihood ratio tests manually to test for significant improvements of the environment model when adding one of the two forest management variables as a main effect or as an interaction with each of the environmental drivers (Supporting Information Table S9). We fitted final models with restricted maximum likelihood (REML) and evaluated their performance graphically by looking at plots of the residuals versus fitted values and of the fitted versus observed values (i.e., "goodness of fit"). We also calculated the marginal and conditional R^2 (proportion of variance explained by fixed factors— R_m^2 , and by both fixed and random factors— R_f^2) following Nakagawa and Schielzeth (2013), as well as the relative root mean squared error (RMSE, %) between predicted and observed values of BAI. Given the large sample sizes of our data set ($n = 10,498, 5,157, 3,182$ for *Quercus*, *Fagus* and *Fraxinus*), we used a significance threshold of 0.001 in our interpretation of effects, but a threshold of 0.05 when comparing between models. All statistical analyses were performed in R (version 3.3.3: R Core & Team, 2017) with the packages

"dplR," "MASS," "nlme" and "ggplot2" (Bunn, 2008; Pinheiro, Bates, DebRoy, & Sarkar, 2016; Venables & Ripley, 2002; Wickham, 2009).

2.4.4 | Future growth scenarios

In order to better understand the implications of our findings in terms of future tree growth response across European forests, we calculated changes in basal area increment (compared to an average scenario, i.e., all continuous predictors set at the observed mean) for different scenarios of future environmental change. Since temperatures will likely rise, but future changes in nitrogen deposition and precipitation are more uncertain and depend on location (Christensen et al., 2007; Engardt et al., 2017; Simpson et al., 2014), we chose four scenarios. All scenarios assume an increase in mean annual temperature of 3°C. The "dry" and "wet" scenarios, respectively, assume a decrease and increase in total annual precipitation of 100 mm/year. The "−N" and "+N" scenario, respectively, assume a decrease and increase in nitrogen deposition of 10 kg/ha year. A detailed explanation of the chosen scenarios can be found in the Supporting Information (Appendix S1). We calculated 95% confidence intervals following an informal Bayesian approach (Gelman & Hill, 2007). For each prediction, we drew 1,000 random samples from a normal distribution for the mean and standard error of each model parameter for the different scenarios. For each of these samples, we then calculated the percentage basal area increment change compared to the average scenario and computed the confidence intervals around the predictions. We used the environment models for the three study species, and for *Quercus*, we additionally used the forest management model with "Coppice History" as management variable, to compare predictions in the two management categories. Our aim with Figure 4 is to demonstrate the implication of our findings in terms of future growth predictions.

3 | RESULTS

3.1 | Interactive effects of global-change drivers

The models including the global-change drivers showed good predictions (high R_f^2 and R_m^2 and low RMSE) (Table 3). For *Quercus*, the three global-change drivers (mean annual temperature, total annual precipitation and nitrogen deposition) significantly increased tree growth (Table 3, Supporting Information Figure S6), while only precipitation significantly affected tree growth in *Fagus* and *Fraxinus*. For *Fraxinus*, the effect of nitrogen deposition on basal area increment was quadratic instead of linear (Table 3). The magnitude of the effects in *Quercus* (parameter estimates or effect sizes in Table 3) suggests weaker effects of deposition than of precipitation and temperature. Acidification rate was not retained as a fixed effect in any of the models, so we subsequently present and discuss only effects due to nitrogen deposition. When including seasonal (spring and summer) temperature and precipitation instead of annual values, spring conditions seemed more important for *Fagus* tree growth than summer conditions (Supporting Information Table S10).

TABLE 3 Parameter estimates and model evaluation of the final environment M_e models for the basal area increment of the three study species

Fixed effects	<i>Quercus robur/petraea</i> [n = 10,498]			<i>Fagus sylvatica</i> [n = 5157]			<i>Fraxinus excelsior</i> [n = 3,182]		
	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value
(Intercept)	2.7580	0.0555	<0.0001**	3.1955	0.0461	<0.0001**	2.8357	0.0628	<0.0001**
Dprev	0.6304	0.02070	<0.0001**	0.0564	0.0267	<0.0001**	0.7760	0.0453	<0.0001**
Dprev ²	-0.1715	0.0103	<0.0001**	-0.2329	0.0164	<0.0001**	-0.3258	0.0294	<0.0001**
Soil shallowness	–	–	–	-0.1225	0.0410	0.0049 ns	–	–	–
MAT	0.0538	0.0062	<0.0001**	-0.0047	0.0091	0.6060 ns	–	–	–
TAP	0.0480	0.0040	<0.0001**	0.0182	0.0047	0.0001**	0.0308	0.0058	<0.0001**
Ndep	0.0370	0.0109	0.0003 [†]	0.0324	0.0172	0.0600 ns	0.0300	0.0181	0.0970 ns
Ndep ²	–	–	–	–	–	–	-0.0336	0.0086	0.0001**
MAT:TAP	–	–	–	0.0214	0.0050	<0.0001**	–	–	–
MAT:Ndep	–	–	–	-0.0182	0.0092	0.0482 ns	–	–	–
TAP:Ndep	-0.0182	0.0039	0.0007 [†]	–	–	–	0.0229	0.0059	0.0001**
Model evaluation	R_f^2	R_m^2	RMSE	R_f^2	R_m^2	RMSE	R_f^2	R_m^2	RMSE
	0.76	0.48	1.27%	0.64	0.49	1.58%	0.63	0.55	10.70%

Notes. The sample size for each model is given by n (number of rings). Dprev, MAT, TAP, Ndep respectively refer to previous-year-diameter ("tree size"), mean annual temperature, total annual precipitation and nitrogen deposition. R_f^2 : conditional R^2 or proportion explained by fixed and random factors; R_m^2 : marginal R^2 or proportion of variance explained by fixed factors; RMSE: root mean squared error between predicted and observed values of basal area increment. p-value: ns: $p > 0.001$; * $p \leq 0.001$; ** $p \leq 0.0001$. Significant p-values are in bold.

Crucially, the impact of a given main effect on growth depends on the levels of other drivers, on the European scale. Namely, *Quercus* showed an antagonistic linear interaction between nitrogen deposition and precipitation (Table 3, Figure 2a). The positive growth response to increased deposition declined with increasing precipitation levels (Figure 2a). For *Fagus*, we saw a synergistic interaction between temperature and precipitation, with stronger positive growth effects to increased temperatures when precipitation levels were higher (Figure 2b). When using seasonal (spring and summer) temperature and precipitation instead of annual values, this interaction only appeared with spring conditions (seasonal analyses: Supporting Information Table S10). In contrast, for *Fraxinus*, a synergistic quadratic interaction between deposition and precipitation was observed, with weaker growth responses to increased deposition when precipitation was also lower, whereas precipitation levels did not seem to matter so much at lower deposition values (Figure 2c).

3.2 | Forest management effects

For both forest management variables used (i.e., *Coppice history* and *Management history*), a significant interaction between mean annual temperature and the management variable was found for *Quercus* (Table 4). The positive growth response to temperature was stronger in plots that had been managed as coppice or coppice-with-standards (CWS) at some point between 1940 and 2015 versus plots that were not managed as coppice or CWS during that time period (Table 4, Figure 3a). When comparing only those plots managed as high forest between 1940 and 2015 with those that had been converted from coppice or CWS to high forest, the model similarly showed a stronger growth response to temperature in the plots that

had been converted than in the continuously high forested plots (Table 4, Figure 3b).

3.3 | Future growth scenarios

When examining changes in basal area increment under four scenarios of environmental change, we clearly see species-specific growth differences, as well as interactive effects (Figure 4). For instance, at the mean observed level of deposition, *Quercus* would show growth increases from an increase in deposition, and especially when precipitation also increases; whereas *Fraxinus* shows more chances of decreased growth at the mean deposition level, except for a potential growth increase when both deposition and precipitation increase. The observed interaction between forest management and environmental drivers for *Quercus* also results in future growth changes (Figure 4). Namely, when forest management is not taken into account, tree growth is expected to decrease or increase slightly with reduced deposition and increase with greater deposition, regardless of precipitation change. However, if we consider the management history, growth increases in all environmental change scenarios when *Quercus* grows in plots that have a history of coppicing. Without a history of coppicing, there is a tendency for growth to decline, regardless of the environmental change scenario, although there is a lower reliability for this scenario.

4 | DISCUSSION

In this study, the patterns of basal area increment along several environmental gradients of deposition and climate provide evidence for species-specific, main and interactive effects of environmental

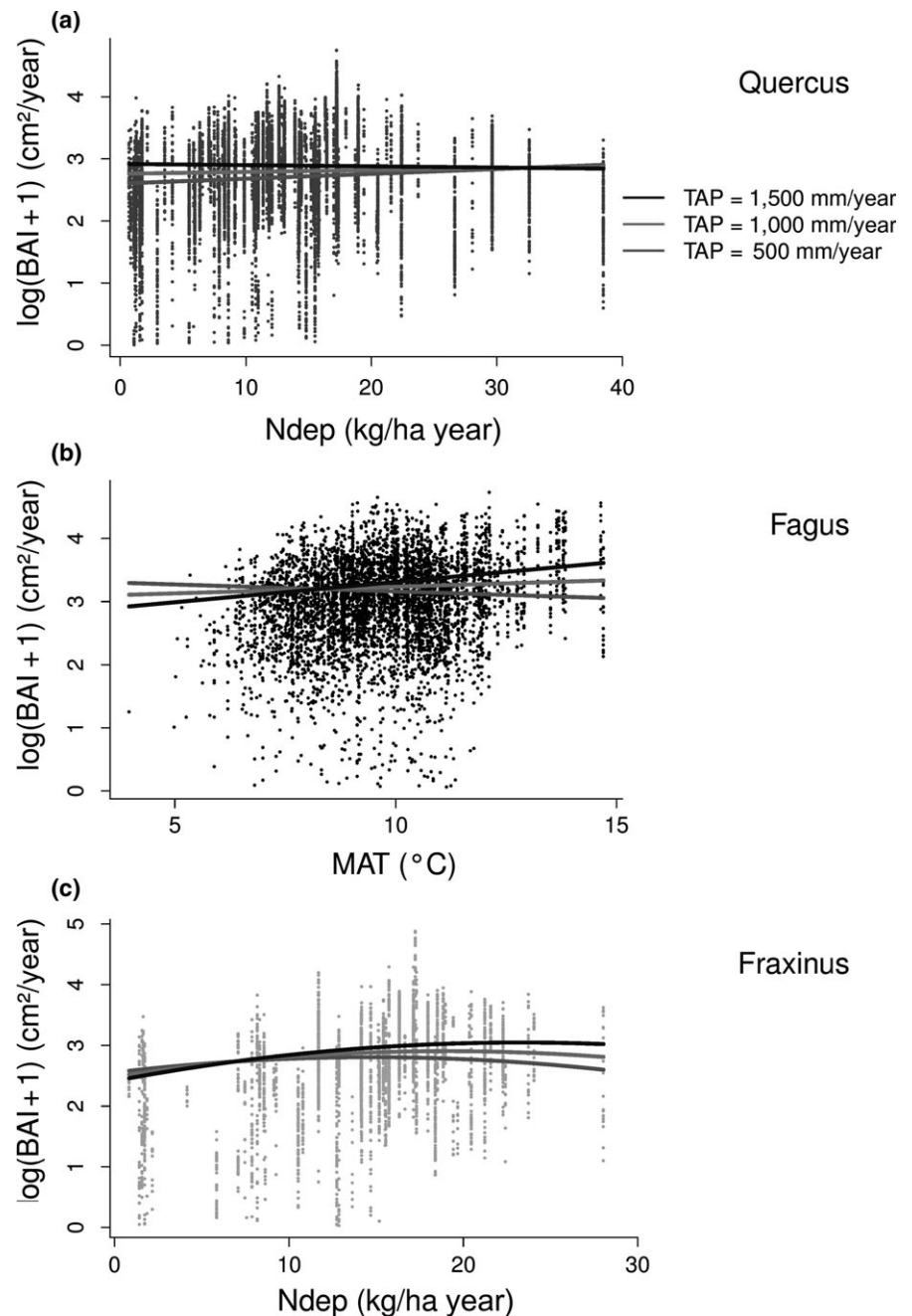


FIGURE 2 The interaction between (a) nitrogen deposition and total annual precipitation (TAP) on basal area increment (BAI) for *Quercus robur/petraea* ($n = 10,498$), (b) mean annual temperature (MAT) and total annual precipitation for *Fagus sylvatica* ($n = 5,157$) and (c) nitrogen deposition and total annual precipitation for *Fraxinus excelsior* ($n = 3,182$). Actual data points (dots) and model estimates of the effects (full lines), in which the values of the other continuous variables were set at their observed mean, are shown

drivers (i.e., global-change drivers (for the three study species) and past forest management (for *Quercus* only)) on growth of three European tree species at a sub-continental scale. Importantly, the observed interactions along spatial environmental gradients suggest that in relatively nutrient-rich, mesic forests, tree growth responses to environmental change should not be estimated from effects of single drivers alone, nor should drivers be assumed to affect all species equally. Instead, the impact of a given driver depends on the levels of at least one other driver and the species considered. Furthermore, when translating responses over spatial gradients to scenarios of change in a given location for *Quercus*, our results demonstrate that accounting for prior management can alter not only the magnitude, but also the direction, of likely growth response to probable future environmental changes. Here, we present

particularly pertinent interactions, discuss potential mechanisms behind the responses observed and suggest that our results have implications for the management of forests to mediate the influence of global-change drivers and for the estimation of forests as carbon sources/sinks under future conditions.

4.1 | Species-specific drivers of tree growth across Europe

The global-change drivers had a positive overall effect on basal area increment. The growth of *Quercus* increased with temperature; all tree species showed increased growth with increasing precipitation; and both *Quercus* and *Fraxinus* growth increased with nitrogen deposition (Table 3; Supporting Information Figure S6). This positive

TABLE 4 Parameter estimates and model evaluation of the final forest management (M_{fm}) models for the basal area increment of *Quercus robur/petraea*

Fixed effects	Coppice history [n = 10,498]			Management history [n = 5,450]		
	Estimate	SE	p-value	Estimate	SE	p-value
(Intercept)	2.8760	0.0718	<0.0001**	3.0019	0.1184	<0.0001**
Dprev	0.6306	0.0207	<0.0001**	0.5882	0.0277	<0.0001**
Dprev ²	-0.1702	0.0103	<0.0001**	-0.2648	0.0173	<0.0001**
MAT	0.0780	0.0094	<0.0001**	0.1316	0.0142	<0.0001**
TAP	0.0477	0.0040	<0.0001**	0.0568	0.0057	<0.0001**
Ndep	0.0366	0.0108	0.0007*	0.0419	0.0138	0.0025 ns
TAP:Ndep	-0.0182	0.0039	<0.0001**	-0.0174	0.0049	0.0003*
CoppHist=0	-0.1952	0.0822	0.0203 ns	-	-	-
MAT:CoppHist	-0.0420	0.0122	0.0006*	-	-	-
ManHist=HF	-	-	-	-0.0818	0.0989	0.4142 ns
MAT:ManHist	-	-	-	-0.1129	0.0178	<0.0001**
Model evaluation	R_f^2	R_m^2	RMSE	R_f^2	R_m^2	RMSE
	0.76	0.49	1.30%	0.77	0.53	1.21%

Notes. The forest management models included information on the Coppice history (left) and on the Management history (right) in the plot. The sample size for each model is given by n (number of rings). *Dprev*, *MAT*, *TAP*, *Ndep*, *CoppHist* ("0" or "1") and *ManHist* ("C(WS) to HF" or "HF") respectively refer to previous-year-diameter ("tree size"), mean annual temperature, total annual precipitation, nitrogen deposition, coppice history and management history. R_f^2 : conditional R^2 or proportion explained by fixed and random factors; R_m^2 : marginal R^2 or proportion of variance explained by fixed factors; RMSE: root mean squared error between predicted and observed values of basal area increment; All fixed effects were standardized (scaled and centred) prior to analysis. p -value: ns: $p > 0.001$; * $p \leq 0.001$; ** $p \leq 0.0001$. Significant p -values are in bold.

response concurs with other studies investigating global change effects on tree growth (Laubhann et al., 2009; Lindner et al., 2014). Indeed, to a certain extent, and as long as other factors do not become limiting (Martinez-Vilalta et al., 2008), warming may increase growth because of increases in metabolic rates, or longer growing seasons (Way & Oren, 2010). *Quercus* responded more strongly to temperature than to precipitation or deposition (Table 3). Other researchers have also suggested that *Quercus* may benefit from a warmer future to a certain extent, as opposed to *Fagus*, which is already showing growth declines (Jump, Hunt, & Penuelas, 2006; Kint et al., 2012; Latte et al., 2015; Piovesan et al., 2008). *Quercus*, *Fagus* and *Fraxinus* all responded more strongly to precipitation than to nitrogen deposition (Table 3). Yet, many other studies have identified deposition as the main driver of tree and forest growth in Europe (Aertsens et al., 2014; Augustaitis et al., 2016; Kahle et al., 2008; Laubhann et al., 2009; Magnani et al., 2007). The relatively low importance of nitrogen deposition in our study may be explained by the rich, mesic soils of our study regions (mean pH_{KCl} 4.4, mean base saturation 0.8, mean C/N 13.9). In richer soils, the effect of additional nitrogen from atmospheric deposition may be smaller than in studies such as Laubhann et al. (2009). In addition, the higher pH and cation exchange capacity of rich soils also represent a buffer against acidification (Kauppi, Kämäri, Posch, Kauppi, & Matzner, 1986), which may explain why we did not find acidification effects on tree growth. The growth of *Fraxinus*, however, did decline again at high deposition levels, that is, when deposition exceeded the critical load (ca. 18 kg/ha year for trees: Bobbink, Ashmore, Braun, Flückiger, & Van den Wyngaert, 2017; Table 3, Supporting Information Figure S6). Careful interpretation of the results for ash is warranted

though, since ash dieback has affected the growth of a large number of *Fraxinus* trees across Europe since 1990s and may have had an effect on the studied ash trees as well (Vasitis et al., 2017).

4.2 | Tree growth responds interactively to global-change drivers

Importantly, we show that only considering simple effects overlooks interactions among drivers. In other words, tree growth response to a certain global-change drivers can depend on the level of another driver, as was observed in our study species (Figure 2). First, for *Quercus*, at low levels of nitrogen deposition, higher precipitation led to higher growth rates, whereas precipitation levels did not influence growth rates at higher deposition levels (Figure 2a). Second, for *Fraxinus*, the opposite interaction was found at lower levels of nitrogen deposition, precipitation did not strongly affect tree growth, whereas higher precipitation led to higher growth rates at higher deposition levels (Figure 2c). Third, *Fagus* showed a much stronger growth response to higher temperatures when precipitation was also higher (Figure 2b), which is consistent with the high sensitivity of *Fagus* to soil water availability. Furthermore, tree growth response to a certain global-change drivers can also be modulated by the past forest management (Figure 3). The *Quercus* trees growing in forests with a history of coppice, even when converted to high forest, showed stronger positive growth responses to increased temperatures across the study regions (Table 4, Figure 3). Although very few studies investigating tree growth response to environmental factors have taken into account the past forest management, some studies did evaluate potential interactions between environment and

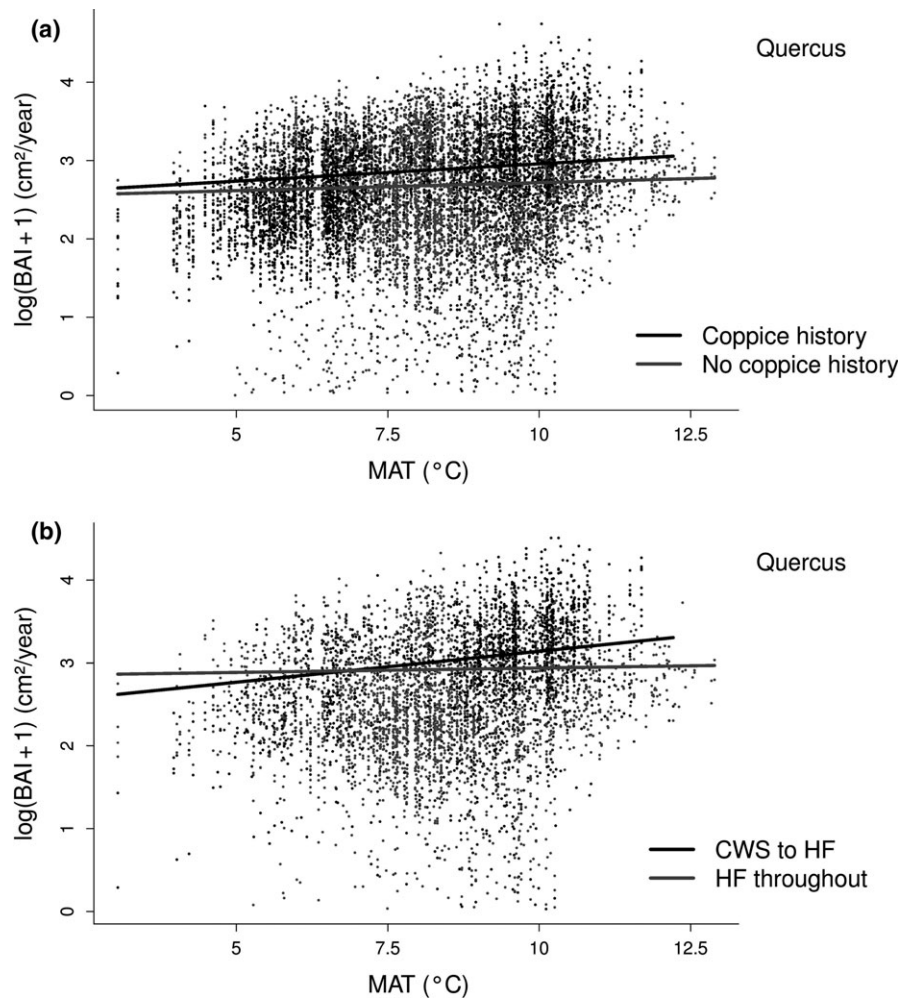


FIGURE 3 The interaction between (a) mean annual temperature (MAT) and coppice history (“yes” or “no”, $n = 10,498$) and (b) mean annual temperature and management history (“coppice/coppice-with-standards (CWS) to high forest (HF)” or “HF throughout”, $n = 5,450$), on basal area increment for *Quercus robur/petraea*. Actual data points (dots) and model estimate of the effects (full lines), in which the values of the other continuous variables were set at their observed mean, are shown

management on tree growth (Latte et al., 2015; Stojanović et al., 2017; Vayreda et al., 2012). Stojanović et al., (2017) also found different climate–growth relationships for *Quercus* trees in past coppiced versus in high forest stands in the Czech Republic. They also show that future climatic changes could differently affect the two origins (coppice vs. high forest), confirming the modulating effect that past forest management can have on current and future tree growth rates. Vayreda et al. (2012) also suggested the potential role of forest management within the context of climate change mitigation (e.g., by enhancing tree growth), based on a reduced carbon sink capacity with warming in unmanaged versus in managed forests in Spain. Interestingly, the potential role of forest management is in contrast with the progressive abandonment of management in many temperate broadleaf European forests over the last decades (Kopecký et al., 2013; Scolastrì, Cancellieri, Iocchi, & Cutini, 2017).

4.3 | Potential mechanisms underlying interactive effects

Although it is not possible to demonstrate mechanisms behind the interactive effects in this observational study, we provide plausible reasons for what we observe. First, species-specific sensitivities to environmental drivers could lie behind some of the observed

interactions. For instance, the contrasting responses in *Quercus* versus *Fraxinus* to precipitation and nitrogen deposition could be due to their colonization of different site conditions, that is, *Fraxinus* grows on wetter and richer soils than *Quercus*. Thus, the joint effect of high deposition as well as precipitation might be positive for *Fraxinus*, whereas negative for *Quercus*. On the other hand, *Quercus* might have a competitive advantage over nutrient-demanding species such as *Fraxinus* under conditions of drought and low nitrogen availability, which has also been described by other researchers (Lévesque, Walthert, & Weber, 2016). In *Fagus*, the antagonistic interaction between precipitation and temperature could be explained by the strong sensitivity of this species to low water availability or drought (Ellenberg & Leuschner, 2010; Vanoni, Bugmann, Nötzli, & Bigler, 2016). Higher temperatures resulting in a higher evapotranspiration might lead to increased drought stress and reduce tree growth of *Fagus* (Aber et al., 2001; Ciais et al., 2005; Scherrer, Bader, & Körner, 2011). Similar interactive effects have been reported by other researchers (Bauwe et al., 2016; Latte et al., 2015; Martínez-Vilalta et al., 2008; Mette et al., 2013). This sensitivity is supported by the fact that only precipitation, and not temperature or deposition, affected tree growth of *Fagus* across all study regions, and by the significant effect of “annual aridity” on the growth of *Fagus* (additional analysis: see Supporting Information Table S11). The

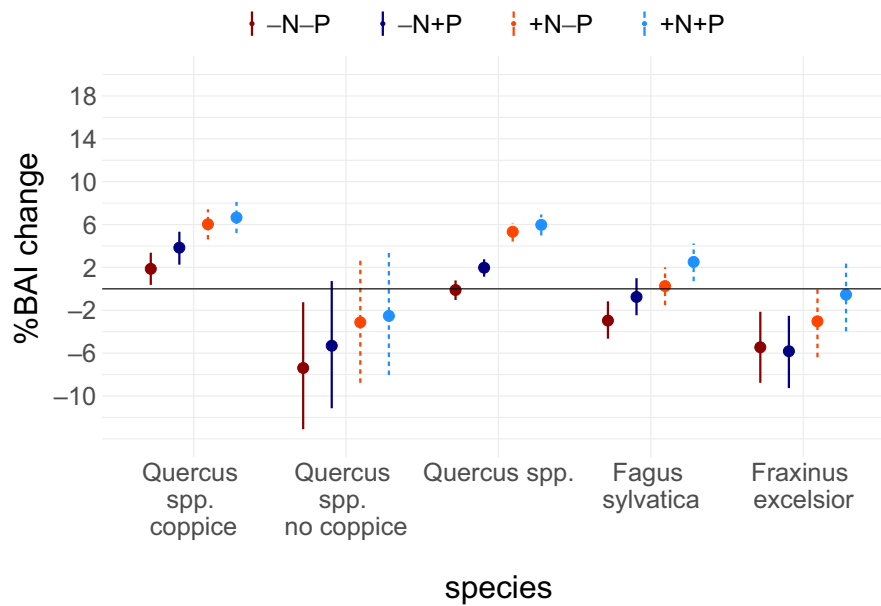


FIGURE 4 Percentage basal area increment change for four scenarios of future environmental change based on final model predictions for the three study species (*Quercus* spp. refers to *Quercus robur/petraea* here). All scenarios assume an increase in mean annual temperature of 3°C compared to the observed mean. The “dry” (red colours) and “wet” (blue colours) scenarios, respectively, assume a decrease and increase in total annual precipitation of 100 mm/year. The “-N” (full lines) and “+N” (dashed lines) scenarios, respectively, assume a decrease and increase in nitrogen deposition of 10 kg/ha year compared to the observed mean. The percentage basal area increment change, compared to an average scenario in which all continuous predictors are set at their observed mean, is calculated according to an informal Bayesian approach. The dots represent the median of 1,000 random samples from a normal distribution for the mean and standard error of each model parameter, whereas the lines represent 95% confidence intervals

antagonistic interaction between temperature and precipitation was not detected for the summer data, but did also occur for the spring data, which suggests that the drought sensitivity of *Fagus* might be associated with spring rather than summer conditions, that is, when the trees' growing season starts (Supporting Information Table S10). Latte et al. (2016) similarly found that intra-annual variation in *Fagus* growth was driven by current-year spring drought in several Belgian sites. The observed interaction between temperature and precipitation could have serious consequences for the future growth of *Fagus*, with the increasing temperatures and more frequent and extreme heat waves expected in Europe (Christensen et al., 2007).

Second, whether or not “critical loads” had been exceeded in a region might also explain the contrasting responses in *Quercus* versus *Fraxinus* to precipitation and nitrogen deposition. Smaller or negative effects of nitrogen deposition on tree growth might only occur when deposition levels have exceeded a certain threshold or “critical load” (ca. 18 kg/ha year for trees: see Bobbink et al., 2017; Eugster & Haeni, 2013; Jones et al., 2014), which is more probable within the observed deposition range of *Quercus* (0.7–38.5 kg/ha year) than of *Fraxinus* (0.8–28 kg/ha year and mostly 10–20 kg/ha year). At the highest deposition levels in *Quercus*, precipitation levels might not influence growth from higher deposition anymore, whereas in *Fraxinus*, it might still facilitate additional nitrogen uptake for growth.

Third, the mycorrhizal dynamics may mediate tree growth responses to environmental changes. The different mycorrhizal communities associated with *Quercus* versus *Fraxinus*, that is, respectively ectomycorrhizae (ECM) versus arbuscular mycorrhizae (AM), might

explain their contrasting responses to deposition and precipitation (Lang, Seven, & Polle, 2011; Mohan et al., 2014; Thomas, Canham, Weathers, & Goodale, 2010). Unlike ECM fungi, AM fungi are unable to produce enzymes that breakdown soil organic nitrogen, so they may benefit more from increased deposition or thus increased inorganic nitrogen availability, the latter being their sole source of nitrogen (Thomas et al., 2010).

Finally, the stronger response of trees in plots that have a history of coppicing might be explained by the fact that “standard trees” in *Quercus* coppice-with-standard systems may have better developed (“bigger”) crowns than in continuous high forest, where tree crowns generally overlap more at similar heights. Thus, their bigger crowns create a larger photosynthetic area, which may increase production with increasing temperatures. Another potential explanation might be related to the vigorous growth of surviving trees after a coppice cut, when the trees can profit from plentiful resources and low competition rates (Altman et al., 2013; Deforce & Haneca, 2015; Stojanović et al., 2017). *Quercus* trees growing in plots with a history of coppicing might thus be phenotypically adapted to utilize sudden and strong temperature increases to boost their growth during the phases with high light availability (Thom, Rammer, & Seidl, 2017; Trouvé, Bontemps, Collet, Seynave, & Lebourgeois, 2017).

4.4 | Implications for future tree growth

Here, we evaluated growth responses to *spatial* environmental gradients. Translating these spatial responses into the response of trees

to scenarios of *temporal* changes in these environmental drivers in a given place allows to assess the implications for future tree growth (Figure 4). Our results demonstrate that future growth predictions in global-change studies are influenced by the study species, as well as by interactive effects of the global-change drivers. They also demonstrate that for *Quercus*, growth predictions depend on whether or not past management was accounted for (Figure 4). Accounting for prior management can alter not only the magnitude, but also the direction, of likely growth responses to probable future environmental changes for this species. In the scenario of increased precipitation and deposition (+100 mm/year and 10 kg/ha year) for instance, *Quercus* growth is predicted to increase with 3.9% when coppice history was not taken into account, whereas an increase of 6.7% (i.e., 2.8% more), versus a decrease of -2.5% (i.e., 6.4% less) is expected when we distinguish between plots with a history of coppicing versus no coppicing respectively. It should be noted that we examined annual climatic variables here, and that predictions using seasonal climatic variables may differ, depending on the seasonal climate-growth sensitivity. With more frequent and extreme heat waves expected throughout Europe, a drought-sensitive species such as *Fagus* may be considerably impaired in its growth during and after such events (Latte et al., 2015; Tognetti, Lombardi, Lasserre, Cherubini, & Marchetti, 2014).

Our aim with Figure 4 was to demonstrate the implication of our findings (i.e., species-specificity and interactive effects) in terms of future growth predictions, rather than provide accurate growth predictions. Thus, the actual values should be interpreted with caution, since they are based on the assumption that growth responses to the different global-change drivers do not change over time (nor between 1940 and 2015, nor in the future), which is not necessarily the case (see additional analysis: Supporting Information Table S12). Although investigating temporal changes in the relationship between the global-change drivers and tree growth over time would be an intriguing line of further research, this is beyond the scope of the present paper. Also, accurate prediction of forest growth will not only require taking into account (species-specific) interactive effects, but likely also consideration of (a) stand dynamics (vs. individual growth), (b) site-specific scenario values (e.g., some regions might show stronger vs. weaker temperature increases than +3°C), (c) temporal changes in the relationships between growth and the predictors, (d) legitimacy of the space-for-time approach and (e) consideration of seasonal growth predictors.

Neither tree competition, elevation, soil chemistry or soil depth were retained for our study species in the models, suggesting that we achieved a satisfactory sampling strategy, minimizing the effects of confounding factors in this study. A potentially confounding factor that we did not account for here though was the occurrence of biotic disturbances (i.e., pests and diseases) such as the ash dieback fungus (*Hymenoscyphus fraxineus*) for *Fraxinus excelsior* or the oak processionary moth (*Thaumetopoea processionea*) or Winter Moth (*Operophtera brumata*) for *Quercus robur/petraea*. Although we tried to core healthy trees, biotic disturbances may have affected the growth of our cored trees in the past, without visible signs at the time of coring.

Additional research is needed on the interaction between biotic disturbances and other growth factors, especially with the anticipated increases in pest impacts on trees and forests with global environmental changes (Ramsfield, Bentz, Faccoli, Jactel, & Brockerhoff, 2016). Regarding the choice of climatic variables in the analyses, we acknowledge that the use of climate data of the current year might obscure lagged effects of previous-year conditions. Masting events could also have affected tree growth and climate-growth relationships (e.g., Hackett-Pain, Friend, Lageard, & Thomas, 2015), but unfortunately we did not have data on masting in our plots. Furthermore, we stress that our results concern the growth of individual (co-)dominant trees and acknowledge that environmental or management effects on suppressed trees may be different (Coomes & Allen, 2007; Ford et al., 2017; Meyer & Bräker, 2017). A drawback of our study is that we could only consider management history for *Quercus* here, hence the potential role of forest management for the other study species' tree growth remains unknown. Finally, as we did not cover the whole distribution area of the study species, we stress that our results should not be extrapolated to trees growing, for example, in more southern forest regions without additional research.

Although we cored a considerable number of trees across the whole study area, and the total sample size is large because one tree provides data from many growth years (e.g., environment models: $N = 10,498$ [*Quercus*], 5,157 [*Fagus*], 3,182 [*Fraxinus*]), the small number of trees per plot (mostly 2, maximum 3) could be considered as a limitation which might have affected our findings. To evaluate whether the sample size might have impacted our main results (interactive effects) and the values in Figure 4, we performed several additional analyses testing the robustness of our results and report these in Supporting Information (environment models: Supporting Information Table S13 and Figure S7, forest management models: Supporting Information Table S14 and Figure S8, Figure 4: Supporting Information Table S15). From this, it did not seem like the sample size affected our results.

To conclude, in this study we showed that simultaneously considering multiple global-change drivers as well as the management history might be crucial for solid predictions of tree growth in the face of global environmental change. Tree growth in closed-canopy forests is determined by a complex interaction of factors (e.g., environment, management, soil and stand conditions and tree age/size). Here, we have shown that sampling trees on a larger geographical scale, and across gradients of specific factors of interest (e.g., global-change drivers and forest management), can help in disentangling the effects of these factors. Several species-specific main and interactive effects of the global-change drivers were detected, but additional studies that (a) evaluate management effects for other tree species, (b) cover other study areas and (c) investigate temporal growth responses as well, are needed to validate our findings more generally.

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CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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