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Modelling Dominant Tree Heights of *Fagus sylvatica* L. Using Function-on-Scalar Regression Based on Forest Inventory Data

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Abstract: European beech (*Fagus sylvatica* L.) is an important tree species throughout Europe but shifts in its suitable habitats are expected in the future due to climate change. Finding provenances that are still economically viable and ecologically resilient is an ongoing field of research. We modelled the dominant tree heights of European beech as a trait reflecting growth performance dependent on provenance, climate and soil conditions. We derived dominant tree heights from national forest inventory (NFI) data from six European countries spanning over large ecological gradients. We performed function-on-scalar regression using hierarchical generalized additive models (HGAM) to model both the global effects shared among all provenances and the effects specific to a particular provenance. By comparing predictions for a reference period of 1981–2010 and 2071–2100 in a RCP 8.5 scenario, we showed that changes in growth performance can be expected in the future. Dominant tree heights decreased in Southern and Central Europe but increased in Northern Europe by more than 10 m. Changes in growth performance were always accompanied by a change in beech provenances, assuming assisted migration without dispersal limitations. Our results support the concept of assisted migration for the building of resilient future forests and emphasize the use of genetic data for future growth predictions.

Keywords: hierarchical GAMs; functional regression; *Fagus sylvatica*; provenance; assisted migration

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1. Introduction

The choice for a specific tree species is an important management decision when planning future forest composition. European beech (*Fagus sylvatica* L.) has been a widespread and economically important species for European forestry and is considered a viable option for future forests under climate change [1], yet severe growth declines are expected under future climate conditions [2]. Many species distribution models (SDMs) predict shifts in suitable habitats for European beech in the future, assuming that dispersal limitations can be overcome with assisted migration [3,4] Despite the importance of genetic resources as a source of evolutionary potential for climate change adaptation [5], SDMs have been ignoring intraspecific variation [6], phenotypic plasticity and local adaptions [7]. Only recently, the incorporation of genetic and phenotypic information into SDMs has been strongly facilitated with the availability of genetic and species trait data bases, such as GenTree [8], WOODIV [9] or TRY [10], which span over large ecological gradients. For instance, a genetically-informed SDM for *Fagus sylvatica* L. has been found more adequate at identifying suitable habitats [11], and phenotypic plasticity recognized in SDMs leads to overall less-alarming predictions in the future than SDMs without trait information [12].

For European beech, Ref [13] lists more than 400 seed zones in Europe with unique genetic resources accompanied by specific traits and local adaptions. Beech genetic resources are characterized by spatial patterns along environmental gradients [14,15], high intra-population variability [16,17] and high phenotypic plasticity [18] supporting environmental adaptation. Due to these factors, phenotypic traits are strongly influenced by site conditions [19]. For instance, Ref. [20] showed that beech saplings from five provenances developed different physiological and morphological adaptations, such as in their specific root area and leaf water potential, when exposed to different precipitation regimes. Similarly, Ref. [21] reported sclerophyllous leaf structures indicating drought resistance in provenances from Central/Eastern Europe when growing under unfavorable growth conditions at marginal sites. In contrast to such climate adaptations, Ref. [22] shows that the seed origin of beech saplings had a greater effect than adaptation to soil conditions. It appears clear that its high intra-population variability and phenotypic plasticity is an advantage for the European beech, enabling this species to survive in changing climate conditions, which might counteract the large area losses predicted by [23] as a result of dispersal limitations, habitat fragmentation and climate change. It appears that the survival and adaptation of European beech can be supported by identifying suitable provenances and consequent assisted migration. Therefore, we assume that provenances have adaptions to their environment that can be transferred to other sites with similar conditions. Contrary to this, some beech provenances have been reported to show generalist characteristics that can only be revealed with genetic analysis and field trials; for instance, beech from high-altitude sites in Germany showed sclerophyllous leaf structures under warm-dry sites on lower altitudes [24]. However, this study focuses on specialist roles for beech provenances throughout Europe.

In order to distinguish phenotypic adaptivity and provenance effects, common garden experiments are traditionally used [25,26], where survival and performance are quantified under different environmental conditions. However, the number of populations and their associated climatic range is often insufficient for developing reliable climate-growth response functions [27]. Those challenges can be overcome by modeling the growth-environment relationships with intra- and inter-provenance effects, such as with universal response functions [27–29]. The aim to model growth–environment relationships that are shared among provenances (global effects) and provenance-specific effects (local effects) simultaneously can be achieved by implementing a hierarchical model structure, such as with hierarchical generalized additive models (HGAMs) [29]. Generalized additive models [30] are frequently used by ecologists to estimate smooth functional relationships between predictor variables and a response by means of flexible spline functions [31]. GAMs can be made hierarchical by varying the smooth functions over a factor variable (e.g., provenance) [32]. This variation of the response (e.g., tree growth) is a type of functional data [33] that may be explained by scalar predictors through functional regression [34]. The use of a HGAM with tree provenance as factor variable is then a form of function-on-scalar-regression [32]. HGAMs have recently been used in various ecological fields, such as the analysis of species distributions [35–37]

In this study, we use national forest inventory (NFI) data from six European countries and existing phenotypic trait databases, such as Gen-Tree [8], instead of common garden experiments to derive genecological zones (provenances) for the European beech in Europe [38]. These provenances are used as factor-input to our function-on-scalar-regression.

We use the growth performance of beech as response to our model analysis for which we derive dominant tree heights from NFI data. The term dominant height describes the height potential of a tree species at a certain location as the average height of the dominant portion of a forest stand (e.g., 10 percent biggest trees) [39]. This measure is used as input to site-index calculations, which may assume a dominant height for a specified tree age (100 years) (e.g., [40]). The site index is considered more suitable in reflecting site quality effects on tree growth rather than stand density effects [39]. In this study, however, we analyze the relationships between dominant height and environment based on NFI data with partially absent or unreliable tree age information, which questions the use of a site index as growth performance measure Therefore, we derive age-independent relationships between dominant height and the environment instead. The dominant height itself has been used as proxy for site quality when the site index was unavailable (e.g., [41–43])

We explain the variability of dominant tree heights as a function of climate and soil conditions impacted by the provenance as factor variable by means of a hierarchical GAM. The smoothing function on the dominant tree heights varies between the grouping levels (provenances), which can be described as a function-on-scalar regression [29]. This model setting is used to investigate the following questions: (1) Is there a trade-off between survivability and performance for *Fagus sylvatica* in a representative concentration pathway (RCP) 8.5 scenario [44] in Europe? and (2) How does growth performance change under a RCP 8.5 scenario in different geographical areas in Europe?

2. Materials and Methods

We obtained climate and soil data for every plot location extracted from the NFI data. We then derived dominant heights from the variable input space and established our HGAM, which we used to make predictions for Europe in the future. Detailed information is provided in the following.

2.1. Climate Data

We base our analysis on climate data derived from the CHELSA data set version 2.1 [44] on a resolution of 30 arc sec with a reference period from 1981–2010, which is closer to the survey years of the national forest inventories (Table 1). We use average monthly temperatures and monthly precipitation sums to calculate the variables, mean annual temperature (Temp) and the precipitation sum of the warmest quarter (Prec). The choice for these variables was carefully made after following the variable selection procedure according to [45] and after a necessary reduction in concurvity in the hierarchical GAM. We decided to investigate model predictions by applying the strong RCP scenario 8.5. The data for this scenario was derived from MPIESM model and regionalized for Europe by the CLM model to a resolution of 12 km [46]. Reference period for the emission scenario was 2071–2100.

Table 1. Inventory data of *Fagus sylvatica* L. tree heights used from six different EU countries. Recorded heights span a wide range over the associated mean annual air temperature (Temp, °C), precipitation sum of the warmest quarter (Prec, mm), water content at field capacity (FC, cm) and soil nutrient status (SN).

Country	Year	Number of Trees	Temp	Prec	FC	SN
Germany	2012	4886	2.9–11.0	208–1077	8–47	1–8
France	2009–2014	5271	−0.7–16.6	97–839	5–40	1–9
Italy	2005	1023	1.9–13.6	141–954	7–38	1–6
Slovenia	2018	413	3.7–12.3	382–1152	9–30	1–8
Sweden	2020	102	6.0–7.9	213–453	4–67	1–4
Spain	2007	4173	4.2–14.0	141–529	6–36	1–6

2.2. Soil Data

We used nutrient status and the plant-available water capacity of the soil as inputs to our analysis, as dominant tree heights are assumed to increase on soils richer in minerals and plant-available water. The inventory plot locations span over six countries in Europe (Figure 1) with a considerable ecological gradient, which makes harmonized soil data necessary. We, therefore, used the SoilGrids database on a resolution of 250 m [47] for our analysis, which provides soil physical properties in seven soil depths from 0 to 200 cm. We used the volume of coarse fragments, the bulk density, the silt content, the clay content and the absolute soil depth as inputs to calculate the water content at field capacity according to [48] for every soil depth and subsequent integration to the recorded absolute soil depth. The authors of [48] developed water retention curves specifically for forest soils in Europe, which was suited for this investigation. The soil nutrient status was derived from [49], who classified soil mapping units based on the SoilGrids database into nine classes. The amount of available soil nutrients increases from class 1 to 7 from nutrient poor acidic soil (1,2) to carbonatic soils (5,6) to alkali soils (7). Class 8 are hydromorphic soils and class 9 stands from soil covered by glaciers, water or cities. In this classification, we assume dominant tree heights in class 4 with decreasing heights the more acidic or alkaline the soil becomes due to nutrient limitations.

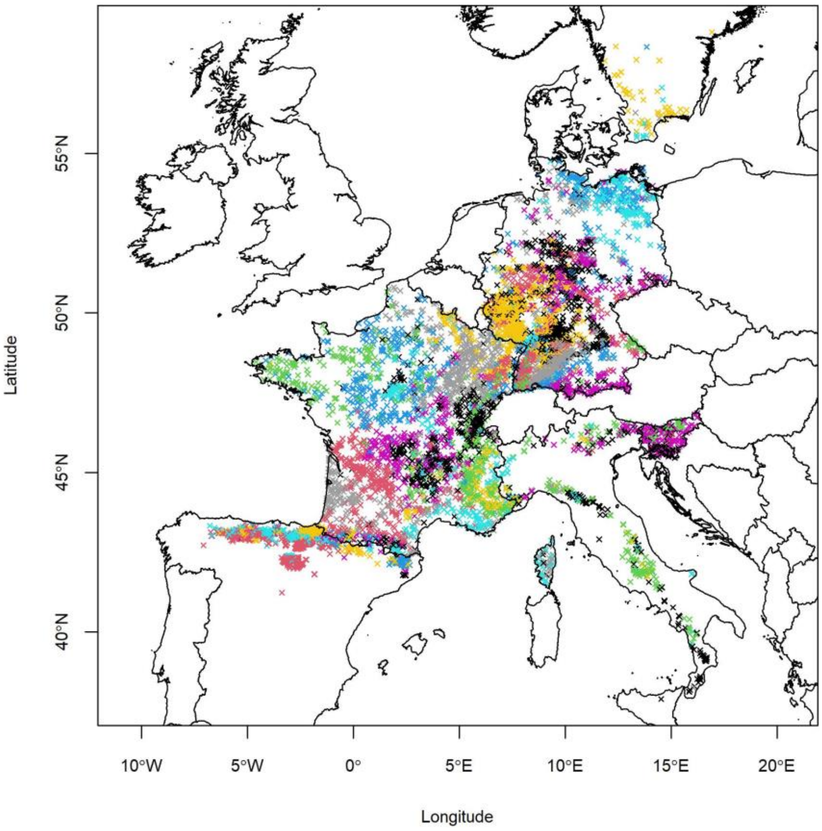

Figure 1. Distribution of inventory plots of six national forest inventories. The colors reflect the provenance cluster of the plots.

2.3. Tree Data

We used individual tree data from national forest inventories of six European countries as input to our analysis, of which four (Germany, France, Italy, Spain) are publicly available (Table 1).

In case of the French forest inventory, we used the inventory years from 2009–2014, as this inventory system does not revisit the same inventory plots located in grid cells within a 5-year cycle. The inventory plot locations span over wide ecological gradients, although Eastern Europe and the British Isles are not covered (Figure 1).

For all national forest inventories, the exact geolocations of plot centers were unavailable for this study. Instead, plot center coordinates were rounded on the nearest inspire grid cell 1 km × 1 km. For every plot location (Figure 1), we obtained the associated mean annual temperature, the precipitation sum of the warmest quarter, the water content at field capacity and the soil nutrient status. As the inventory data are made up of trees in every age class and social position, there is no clear relationship of the considered variables with the recorded tree height (Figure 2).

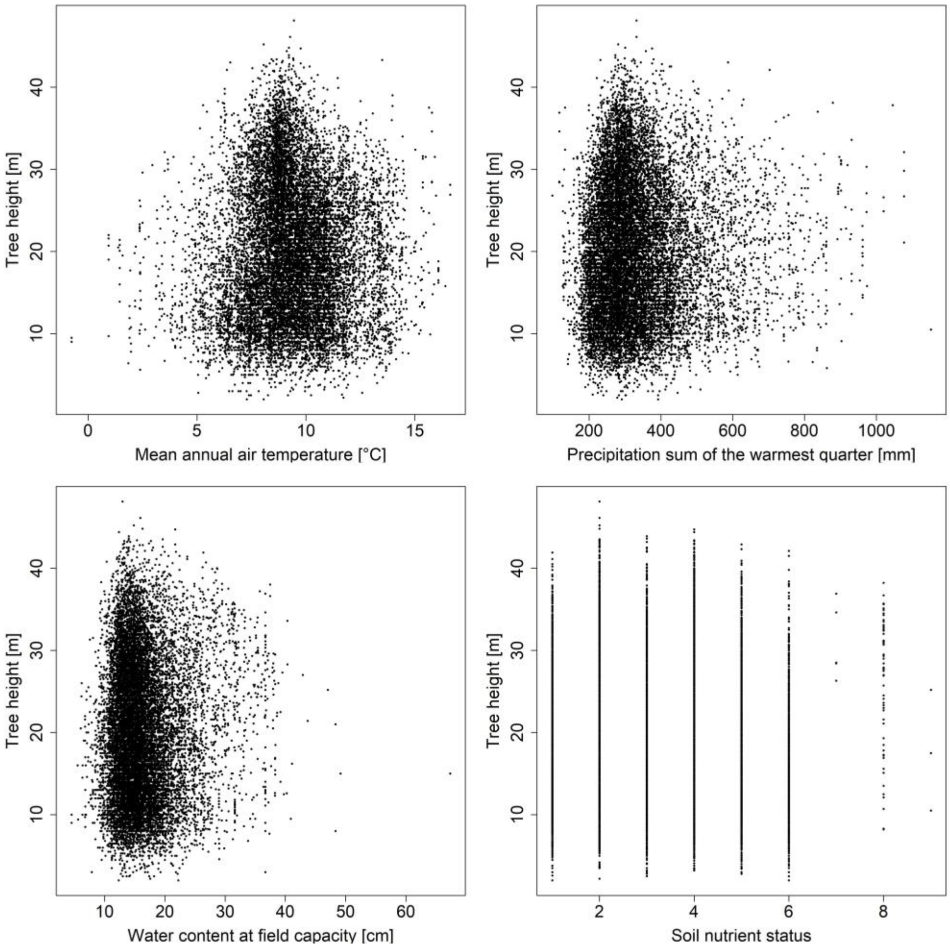

Figure 2. Recorded tree heights of *Fagus sylvatica* L. over the associated mean annual temperature (**top-left**), the precipitation sum of the warmest quarter (**top-right**), the water content at field capacity (**bottom-left**) and the soil nutrient status (**bottom-right**).

However, maximum recorded tree heights obviously describe sharp gradients over the variables except for the nutrient status, where only slight changes occur. In case of the soil nutrient status, the maximum recorded tree heights are found in class 2 (moderate acidic soil).

2.4. Dominant Tree Heights

To obtain the dominant tree heights under given environmental conditions, we performed a grid-based approach. We first divided the variable space of the mean annual temperature, the precipitation sum of the warmest quarter, the water content at eld capacity and the soil nutrient status into equally spaced subdivisions, and then obtained dominant tree heights for every subdivision. To avoid bias by measurement errors and outliers, we calculated the mean recorded tree height of the 10 percent tallest trees for every subdivision of the variable space. This procedure provided 7754 dominant tree heights as input for the subsequent model analysis.

2.5. Provenance Clusters

We used the tree provenance as a factor variable in the hierarchical GAM setting, and used the GenTree database [8] and the BeechCOSte52 database [50] to obtain distinct populations of *Fagus sylvatica* L. The 22 and 39 populations obtained from the GenTree and BeechCOSTe52 databases cover a great ecological gradient over Europe but are far less than the over 400 seed zones reported in [13]. We then performed cluster analysis on the variable space and the longitude–latitude coordinates using the populations of the GenTree and BeechCOSte52 databases as the initial cluster centers. The cluster analysis was implemented with kmeans clustering using the R-package Cluster, R version 4.0.5 [51]. For an optimal number of cluster centers present in the data space, we used the R-function Nbclust in the R-package NbClust [52] with 30 different indices and Manhattan distance metric. In accordance with the majority of indices, we chose the optimal number of 40 provenance clusters or genecological zones [38]. We assume that trees in those clusters have undergone a distinct migration and selection history. Although the genotypic differentiation between the provenance clusters essentially remains unknown, we expect to find differences in environmentally related traits [53]. The resulting clusters are provided in Figure 1.

For the future climate scenario RCP 8.5 2071–2100 [54], it has to be considered that the temperature change between the recent climate (1981–2010) and the climate scenario RCP 8.5 (2071–2100) exceeds the present temperature range in most of the provenance clusters. We obtained future provenance distributions by performing kmeans clustering of 1 km × 1 km grid locations throughout Europe with their associated climate and soil information. Where climate was outside the range of the present beech distribution, no dominant tree heights were predicted, e.g., for the lower elevations in southern France, Spain and Italy.

2.6. Hierarchical GAM

We use the R-package mgcv [55] to set up the hierarchical GAM, according to [32]. Out of the many possible architectures for a hierarchical GAM, we decided it may be more meaningful to model both the global (entire population) and local (intrapopulation) effects. The rationale behind this is that trees may share certain growth-environment relationships but exhibit local adaptions to them. In this study, we focus on the dominant height as the trait and dependent variable, which is modelled as a smooth function varying over the group factor, i.e., the 40 clusters we devised earlier. For the global effects, we use thin-plate-regression splines [31]. The local effects are modelled as factor-smooth-interaction splines between the variable (e.g., the annual mean temperature) and the cluster as factor [31,32]. With this setting, every provenance has an individual functional response that is penalized for deviations far from the average. We made an additional constraint on the wigglines of the smooth functions by setting the parameter k to 3 for all splines [55]. The best model-fit was obtained with a Gaussian distribution family and identity-link formulation [31,55]. The general model formula can be described as follows:

$$E(Y) = g\left(\beta_0 + \sum_{j=1}^{j} f(x_j, p_j)\right) \tag{1}$$

where $E\ (Y)$ is the expected value of the response Y (dominant height), g denotes the link function, β_0 is the intercept and f denotes the jth smooth function of the covariate x and the factor p (provenance). In our hierarchical GAM setting, we include two smooth functions for every covariate, the global effect denoted by f and its group (local) effect denoted by f_{prov}:

$$\begin{gathered} Height_i = f(Temp_i) + f(Prec_i) + f(FC_i) + f(SN_i) + f_{prov}(Temp_i) \\ + f_{prov}(Prec_i) + f_{prov}(FC_i) + f_{prov}(SN_i) \end{gathered} \tag{2}$$

where i is the plot location at which the dominant height ($Height$) is estimated, $Temp.$ is the mean annual temperature, $Prec_i$ is the precipitation sum of the warmest quarter, FC_i is the soil water content at field capacity and SN_i is the soil nutrient status. Each smooth function (f) consists of a number of (k) fixed basis functions (b) multiplied by a set of coefficients (β) that are estimated:

$$f_j(x_j) = \sum_{k=1}^{K} \beta_{j,k} b_{j,k}(x_j) \tag{3}$$

In case of factor-interaction smooths, a smooth curve is estimated for every group factor (provenance) providing the smooth deviations from the global effect *f*.

2.7. Provenance Groups

We grouped provenance clusters according to the 0.25 and 0.75 quantile of the annual mean temperature (Temp) and summer precipitation sum (Prec) to analyze if a particular provenance can be located in the warm-dry or cool-moist edge distribution or if it is in the center of the distribution range. Provenances with a Temp greater than the 0.75 quantile (11 °C) and Prec smaller than the 0.25 quantile (248 mm) are considered as warm-dry. Provenances with a Temp smaller than the 0.25 quantile (4.3 °C) and Prec greater than the 0.75 quantile (370 mm) are considered cool-moist. Any other provenance is considered central to the distribution range of *Fagus sylvatica* L. These provenance groups help to analyze and highlight the changes in productivity and provenance in Europe, as we cannot associate our 40 provenance clusters with their respective genetical data and trait variation. We instead rely on the assumption that marginal provenances exhibit niche adaptations and genetic differences from provenances central to the distribution range. Marginal provenances for *Fagus sylvatica* L., such as warm-dry or cool-moist, have been similarly defined using different indices derived from the temperature and precipitation data for the purpose of identifying more resilient and resistant provenances [4,24,25]

3. Results

The explained deviance for the resulting hierarchical GAM is 78.7%. All model terms are significant (p-value < 0.001), except for the smooths $f\,(FC_i)$ and $f\,(SN_i)$ (Table 2), which are almost flat (Figure 3).

Table 2. Model summary statistics for the hierarchical GAM with the approximate significance of smooth terms [31]. K denotes the number of basis dimensions used for smooth construction, edf denotes the estimated degrees of freedom (reflect smooth complexity), F denotes the F-statistic and p-values denotes the approximate p-value. The smooth types are thin-plate-regression (TPR) and factor-smooth-interaction (FSI) with 40 group levels (provenances).

Term	Smooth Type	k	Edf	F	p-Value
f (Temp)	TPR	3	1.978	32.956	<0.0001
f (Prec)	TPR	3	1.984	71.936	<0.0001
f (FC)	TPR	3	1.001	0.147	0.703
f (SN)	TPR	3	1.001	0.031	0.861
f_{prov} (Temp)	FSI	3 (40 levels)	86.246	25.791	<0.0001
f_{prov} (Prec)	FSI	3 (40 levels)	56.451	13.210	<0.0001
f_{prov} (FC)	FSI	3 (40 levels)	17.623	0.297	0.0005
f_{prov} (SN)	FSI	3 (40 levels)	28.898	0.601	<0.0001

Most of the variance is explained by the factor-interaction smooths that capture the provenance effects (Figure 4). Absolute deviations between predicted and dominant heights from the NFI data show no trend over the plot locations (Figure 5). Largest deviations reach 15 m, while 90% of deviations are smaller than 3.6 m. Absolute deviations slightly increase with decreasing dominant heights (Figure 5).

Predicted dominant tree heights for Europe for the reference periods 1981–2010 and 2071–2100 are provided in Figure 6. Predicted dominant tree heights decrease significantly in Southern and Central Europe, while a strong increase is observable in Northern Europe. Further, higher dominant tree heights are predicted at higher altitudes in mountain areas, such as the Alps or the Carpathian Mountains.

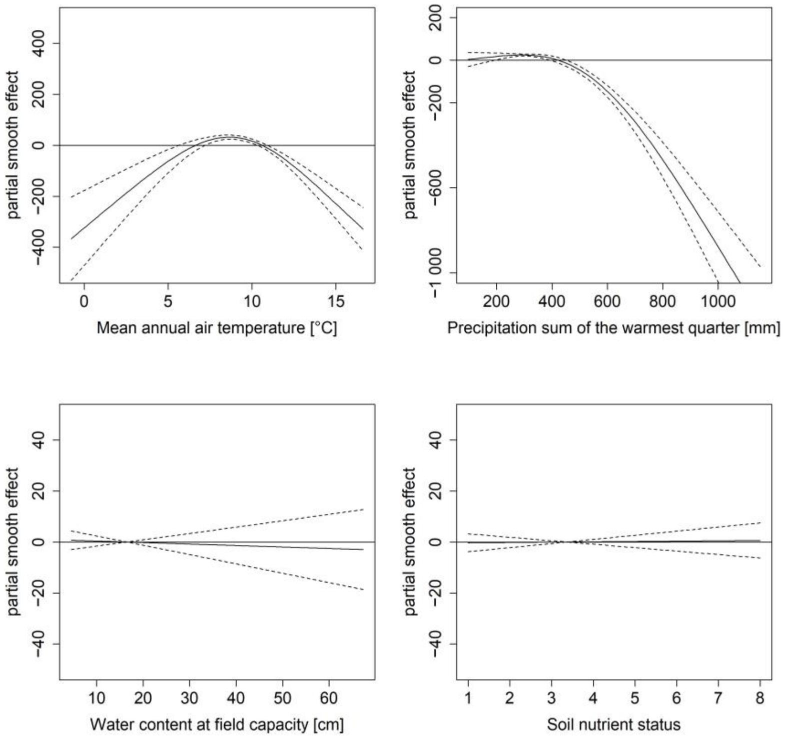

Figure 3. Partial effect plots for the global effects of the mean annual temperature, the precipitation sum of the warmest quarter, the water content at field capacity and the soil nutrient status.

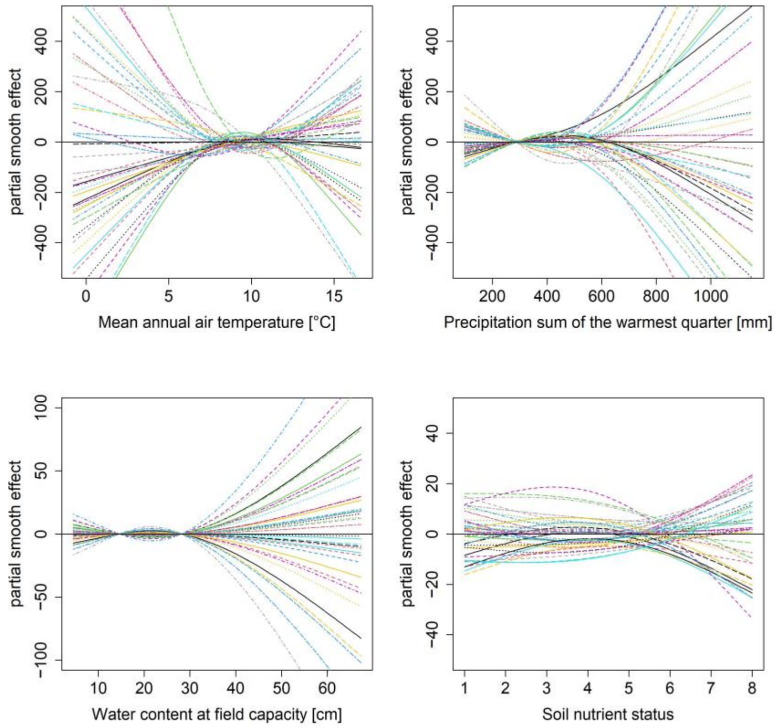

Figure 4. Partial effect plots for the provenance effects of the mean annual temperature, the precipitation sum of the warmest quarter, the water content at field capacity and the soil nutrient status. Every curve shows the partial effect for a specific provenance (factor) as a result of factor-smooth interaction.

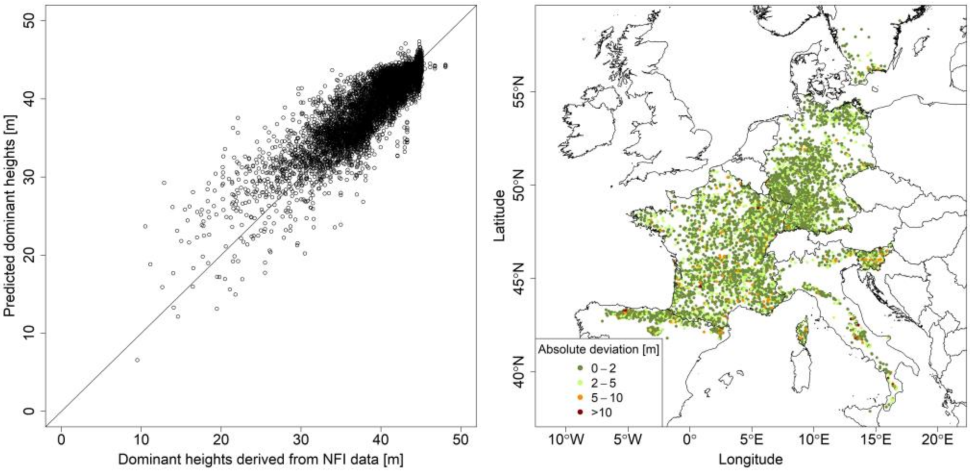

Figure 5. Predicted dominant heights over dominant heights derived from the NFI data (**left**). Absolute deviation in m between dominant heights derived from the NFI data and predicted dominant heights over the plot locations (**right**).

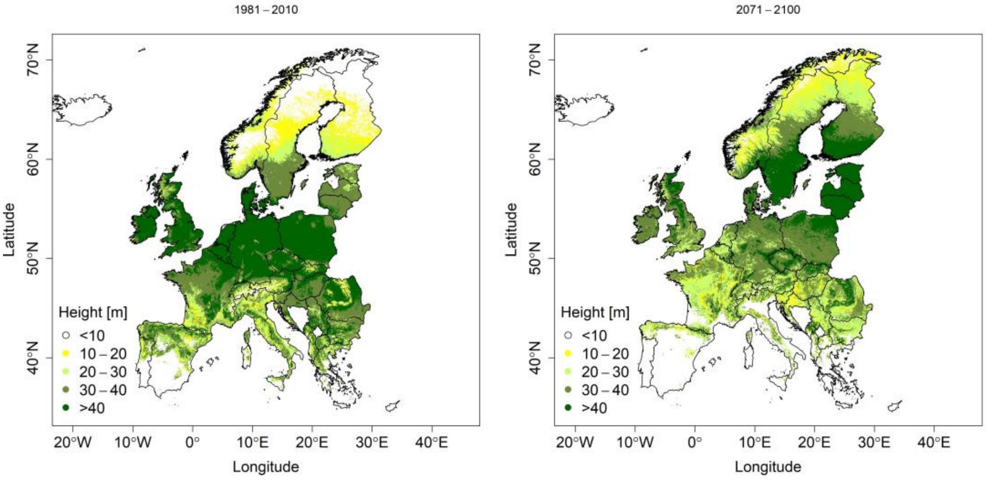

Figure 6. Predicted dominant heights [m] for the periods 1981–2010 (**left**) and 2071–2100 (**right**).

The changes in cluster groups are shown in Figure 7. For the period of 1981–2010, marginal provenances from the cool-moist distribution edge are frequent in high-altitude mountain areas, such as the Alps, in Scandinavia, and in the Scottish Highlands. In contrast, marginal provenances from the warm-dry distribution range are frequent in Spain, south France, Italy, and Southeast Europe. Under a RCP 8.5 scenario, large parts of the original distribution edge become uninhabitable (shown in white color). Provenances from the warm-dry edge in Eastern and Western Europe are relocated to the north towards Central Europe and higher altitude areas. Provenances from the cool-moist edge are shifted to the north and west of Scandinavia and towards higher altitudes if available. The average dominant heights in the provenance groups are 25 and 26.6 m for the warm-dry and cool-moist edge group, respectively, and 33.5 m for the central group with an absolute maximum of 48.1 m.

In most countries, predicted dominant tree heights decrease with provenances from the warm-dry distribution edge now growing in areas formerly central to the distribution range (Figure 7). Countries at high latitudes, such as Norway, Sweden, Finland and Latvia observe higher predicted dominant tree heights with the migration of provenances from central distribution range migrating to those areas. For sites above 1000 m elevation and latitudes greater than 45°, 90% of sites experience positive changes in productivity, some of them very large with up to 40 m potential height difference (Figure 8).

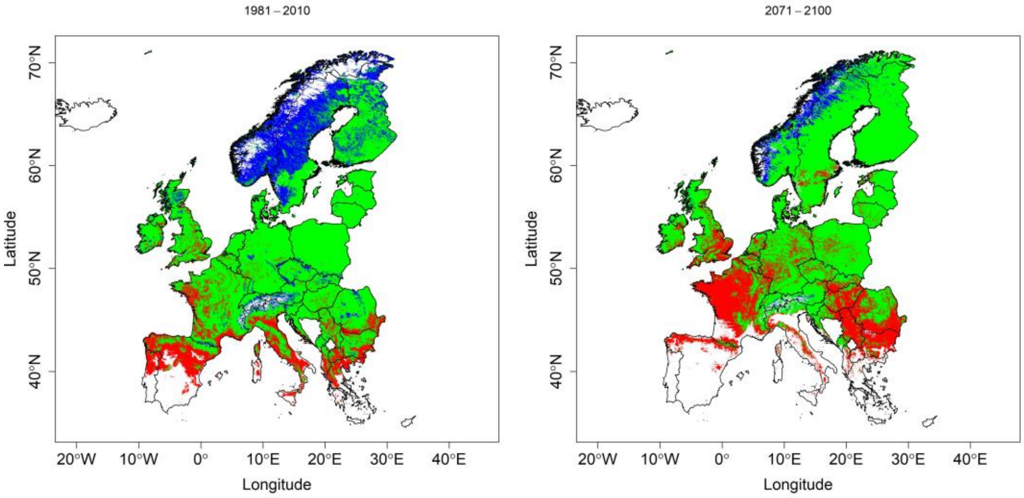

Figure 7. Predicted provenance groups for the periods 1981–2010 (**left**) and 2071–2100 (**right**). Red shows the provenance group from the warm-dry distribution edge, blue from the cool-moist edge and green those provenances from the central distribution range. White areas are considered uninhabitable for European beech.

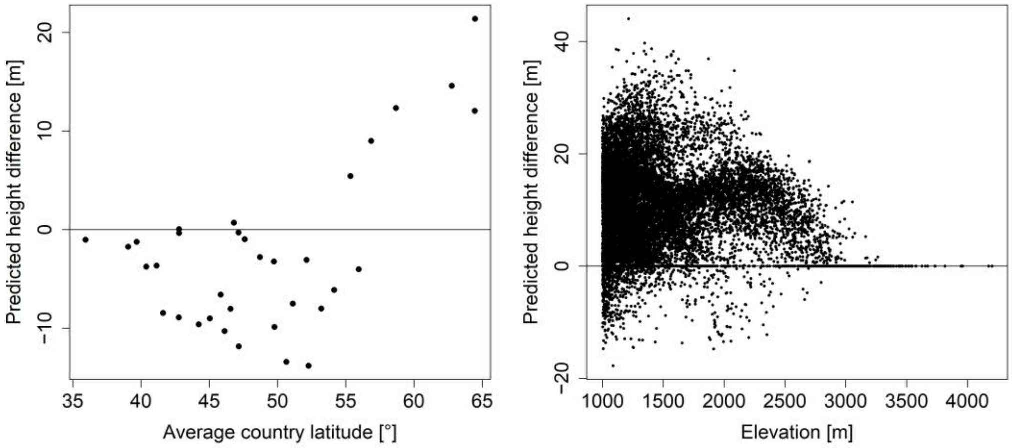

Figure 8. Predicted height difference [m] between the periods 2071–2100 and 1981–2010 over the average EU-country latitude (**left**) and for elevations greater than 1000 m and latitudes greater than 45° (**right**).

4. Discussion

We showed that dominant tree heights of European beech can be modelled with a hierarchical GAM using the clustered variable input space as a grouping factor (provenance). We found changes in performance are accompanied by alterations in provenances associated with a particular area in a RCP8.5 scenario, where only marginal provenances from the warm-dry distribution edge might survive in warmer climate conditions in Southern and Central Europe, but provenances with a higher dominant tree height (higher performance) ideally migrated to Northern Europe and higher altitude areas. Similar effects of a northward migration of species are also reported by [56]. Shifts to higher altitude areas are reported by [57–59]. We showed that most countries in Southern and Central Europe experience a decrease in performance with new marginal provenances from the warm-dry edge distribution as a possible substitute. Climate change in Northern Europe leads to an increase in performance with provenances from the central distribution range of European beech ideally migrated to this area. Those changes in performance and provenance have also been reported by [25]. However, marginal provenances might also exhibit increased tree height due to their local environmental adaptation, not because of their provenance [60].

Increases in dominant heights for sites above 1000 m elevation with up to 40 m difference are questionable, as soil conditions can be expected to not be as favorable (soil depth, content of coarse fragments) as for more developed soils. For those sites, climate change is much faster than changes in soil development, which hinders tree dispersal and establishment [56] and our model overestimates the positive changes.

Our results support the assisted migration of specific provenances of *Fagus sylvatica* L., because of the rapid climate change in a RCP 8.5 scenario that would outpace any natural dispersal by the species itself [61]. However, the assisted migration as adaptive strategy is more complicated due to uncertainties in future climate conditions, risks of species transfer outside their distribution range and risks with current policies [62–64]. The results of this study, under this assumption, must therefore be treated with caution.

The calculation of dominant tree heights prior to our model analysis focuses solely on height–environment relationships, assuming taller trees on favorable sites [65,66]. However, the spatial distribution of the European beech is not only a result of climate and soil, but also affected by forest management that changes species mixing and competition regimes in a forest stand [66–68]. We did not take species mixing and forest management practices, such as thinning, as additional factors into our hierarchical modelling setting so far, but they should be incorporated in future analysis. Furthermore, our NFI data used for this study contains both managed and unmanaged forests of all stand structural types and with all tree ages, which leads to uncertainties regarding the “true” potential dominant height–environment relationships. Beech tree heights and their crown structures have been shown to vary with management practices [69–71]. Further research might elicit these management effects on dominant tree heights at a continental scale.

Our initial assumption of traits transferable to other site conditions than the tree origin is supported by various investigations [60,72–74], yet microevolutionary processes on a smaller scale interrupt this pattern [75]. Functional traits are differently affected by climate change, leading to possible disruptions of current trait-environment relationships [76]. Beech trees transferred to other climate and site conditions acclimate to their new environment [77–79]. Trees with higher phenotypic plasticity may be found in higher altitude regions, not necessarily in warm-dry conditions [80]. Beech trees from marginal sites may be better adapted to warmer and drier conditions [81], supporting the aim of assisted migration, but this adaptation might change due to acclimation, change in morphology and physiology and genetic drift in a new environment. The authors of [75] argue that due to the long life span of trees of up to 500 years [82–84], the transfer of better adapted marginal provenances to other sites might be practical because of the rapid pace of changing climate conditions that alters habitat conditions for the European beech, such as in Serbia [85]. Yet from a long-term perspective, provenances with a high amount of phenotypic plasticity might be more preferable [80].

We did not use genetic data for all trees as input for our analysis, using clusters of climate and site conditions as proxies for genetically similar trees, which is reasonable, because the provenance itself is linked to climate and site conditions [86]. However, we cannot draw conclusions beyond this assumption. We showed that with the assumption of an ideal assisted migration that always finds the best suited provenance for specific climate and soil conditions, large parts of Europe may experience a loss in performance for the European beech, which is a considerable economic factor. Northern Europe, in contrast, benefits from climate change with increased performance.

We chose to set up our hierarchical GAM according to [32] using the R-package mgcv, yet other model architectures, including Bayesian hierarchical models [87,88], might have been better at recognizing data uncertainties that might influence the model output, such as forest management activities. Further research using functional regression [34] or Bayesian models with additional genetic and functional trait data might deepen our understanding of the processes behind tree growth performance under climate change.

5. Conclusions

We successfully implemented a hierarchical GAM to model dominant heights for European beech (*Fagus sylvatica* L.) based on the national forest inventory data of six European countries. Southern and Central Europe may experience a decrease in performance, whereas Northern European countries and growing sites on higher altitudes, such as the Alps, can expect an increase in a RCP 8.5 scenario, given that performance changes are accompanied by a shift in beech provenances. Our results support the idea of assisted migration to rapidly transfer better adapted provenances to sites undergoing fast climate change. However, this study lacks consistent genetic data for the entire inventory set used, which should be incorporated in future studies.

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