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The Role of Provenance for the Projected Growth of Juvenile European Beech under Climate Change

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Abstract: European beech is one of the most common tree species in Europe and is generally suggested to play even more of a prominent role in forestry in the future. It seems to have the potential to partially replace Norway spruce, as it is less sensitive to expected warmer and drier conditions. It is, however, not well known in which regions these new plantings would be particularly favourable and if specific provenances may be better adapted to the new conditions than others. Therefore, we estimated the potential early height growth under climate conditions in 2040–2060 for 20 beech provenances across a region covering the Czech Republic and Slovakia. This Central European region is expected to experience considerably drier and warmer conditions in the future. For this exercise, we implemented a new neural network model developed from height growth information obtained from the open-access BeechCOSTe52 database. The simulations are driven by past and future climate data obtained from the WorldClim database of historical climate data and future climate projections. Simulations revealed that provenances originating from drier regions performed on average significantly better than those from regions with good water supply. Moreover, provenances originating from drier regions had a particularly large advantage in the relatively arid regions of Central Czechia and Southern Slovakia. We can also confirm that all provenances showed a high phenotypic plasticity of height growth across the whole investigated region.

Keywords: *Fagus sylvatica*; eco distance; phenotypic plasticity; neural network model; common garden; local adaptation

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Citation: Petrík, P.; Grote, R.; Gömöry, D.; Kurjak, D.; Petek-Petrik, A.; Lamarque, L.J.; Sliacka Konôpková, A.; Mukarram, M.; Debta, H.; Fleischer, P., Jr. The Role of Provenance for the Projected Growth of Juvenile European Beech under Climate Change. *Forests* **2023**, *14*, 26. https://doi.org/10.3390/f14010026

Academic Editors: Marcin Klisz and Radosław Puchałka

Received: 22 November 2022
Revised: 19 December 2022
Accepted: 20 December 2022
Published: 23 December 2022

1. Introduction

The global climate change (GCC) affects productivity and resilience of many forest ecosystems across Europe [1–4]. European beech (*Fagus sylvatica* L.) is the most abundant tree species in Central Europe and, therefore, an essential target for investigations that elucidate its growth responses under future climate conditions [5–8]. Generally, adverse effects of decreased precipitation, extreme summer temperature, and an increased frequency of late frosts in spring has been demonstrated [9–11]. Drought impacts can be particularly expressed since a large leaf area of European beech leads to relatively high evaporative demands, and the fine root system is expensive to maintain [12,13]. In addition, extreme heat in spring and summer has been shown to decrease assimilation due to depigmentation of beech leaves [14–16]. In addition, late frost events as well as drought stress can lead to premature defoliation in European beech, which negatively affects growth in the current and the following vegetation season [17,18]. Thus, large uncertainties exist about the future development of beeches in Central Europe, which may be addressed with scenario simulations that consider future environmental conditions [19]. A simulation study indicated a growth decline between 10–16% in Denmark [20]. Moreover, recent scenario analysis by Martinez del Castillo et al. [21] showed that a reduction of biomass production of European beech forests throughout the whole of Europe can be expected, which would also negatively affect carbon sequestration [22,23]. In the Czech Republic and Slovakia, growth of European beech has already declined during the past 20 years, which was attributed to reduced water availability [24–27].

In order to avoid or minimise growth reductions, adaptation strategies are needed to increase the resilience of beech under a warmer and drier climate. This includes the application of 'assisted migration', which means an intentional translocation of individuals within the natural range of a species [28,29]. Assisted migration assumes that a specific population adapts with time to their local site conditions and will express a specific phenotype via natural selection [30]. Indeed, it has been demonstrated that local adaptations show improved performance for the specific environmental limitations under which they have been developed [31,32]. For practical purposes, common gardens, where multiple provenances are grown together at one site, allow to differentiate between the effects of genotype and environment and enable to select specific populations according to their trait performance [33]. The prevailing hypothesis in provenance research is that southern populations from more xeric and warmer environments are better adapted to warmer and drier conditions in the future [34,35]. In other words, we assume that the hot and dry sites today reflect the conditions of mesic sites in the future. The local adaptation of southern provenances to drought can be then reflected in various morpho-physiological and biochemical traits [36]. A better performance of southern populations under marginal environmental conditions has indeed been observed in many studies [32,37–41], while no particular trade-off between drought resistance and growth has been found [42].

Another important component of population resilience is phenotypic plasticity, which is the range of phenotypes expressed under specific environmental conditions [43]. This can be evaluated by investigations at multiple common garden sites using the 'ecodistance' metric introduced by Mátyás [33]. Ecodistance is the difference of an environmental variable between the site of origin and the new location where a provenance has been transferred to. It can be defined with any kind of site characteristic but is typically linked to a climatic variable (e.g., average temperature of the growing season). It has already been successfully used to explain climate-dependent intra-specific growth variability of European beech across Europe [44,45]. Here, we apply several ecodistance-metrics together and link them to the height growth development of provenances using a neural network (NN) approach. The resulting height growth model is then able to project the performance of a specific provenance at any site within the parameterisation space (central Europe here), provided the necessary site information is available.

We hypothesise that beech provenances of southern origin grow better in regions that are expected to experience warmer and drier conditions. In contrast, we expect that provenances from sites that are characterised by a relatively good water supply will suffer most under expected climate change. To evaluate these hypotheses, we use the open-access BeechCOSTe52 database [46], providing information from 39 trial sites and 217 provenances covering the whole distribution of beech in Central Europe to develop the NN-based growth model. The model is then run with a climate scenario running up to 2060, to compare future plasticity and growth of selected provenances, specifically for the regions of the Czech Republic and Slovakia.

2. Materials and Methods

2.1. Phenotypic Data

The data for feeding the NN approach are derived from the open-access BeechCOSTe52 database (version 3.0), which originated from the COST Action E52 [46] available at https://zenodo.org/record/1040664 (accessed on 19 December 2022). The dataset contains phenotypic information of two sets of provenances transferred to common garden sites across Europe. The database includes the longitude and latitude of each provenance's origin and those of the common gardens they were planted into (Figure 1). The first set of provenances was planted in 1995, and the second set in 1998. In both cases, the height of the trees was measured seven years after the translocation to the new environment. For this analysis, we merged the two provenance sets (1995–2002 and 1998–2005) so that in total, information of 46289 individuals from 227 provenances planted at 13 common gardens sites was derived. IDs of provenances and common gardens are kept identical as given in the BeechCOSTe52 database, available at https://zenodo.org/record/1040664 (accessed on 19 December 2022). The specific height development, seven years after translocation, is presented for all provenances in the Supplementary Data file and visualised in Supplementary Figure S1.

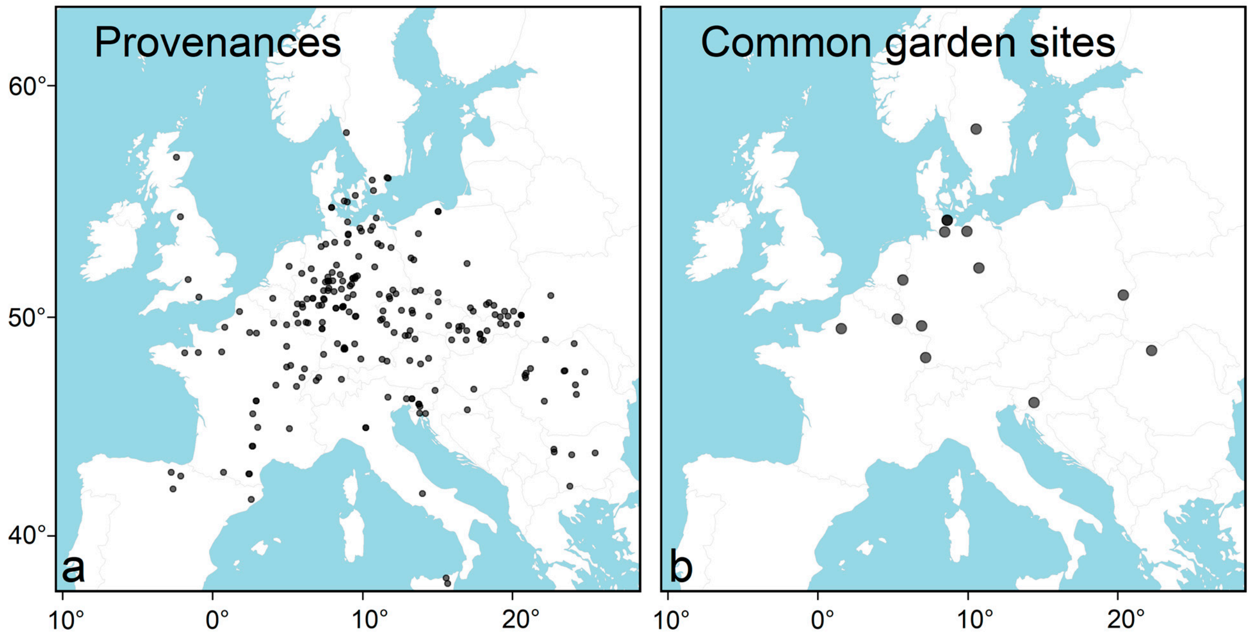

Figure 1. Geographical locations of European beech provenances (**a**) and common garden sites (**b**) used in this study.

2.2. Climatic Data

The climate information at the specific locations of provenance origin, as well as for the common garden sites were downloaded from the WorldClim v2.1 database [47], available at https://www.worldclim.org/data/worldclim21.html (accessed on 19 December 2022). Since the earliest historical weather records in this database are from 1960, we derived the climate for the sites of provenance origin from the period 1961–1990. Use the climate period immediately before seed collection is assumed to deliver the best available estimates for characterising the conditions under which the genotypes developed before being transferred to common garden sites [45]. The environmental conditions that characterise the test sites at which the provenances were growing after the transfer were calculated as mean values for the period from planting (1995/1998) to measurement (2002/2005). The temperature and precipitation distribution at the sites of provenance origin, as well as at the common garden sites, is presented in Figure 2. The ecodistances for all climatic parameters were then calculated as the difference between the respective metric at the provenance origin and that at the common garden site [33]. Historical climate data and ecodistances for all sites and provenances are given in the in Supplementary Materials.

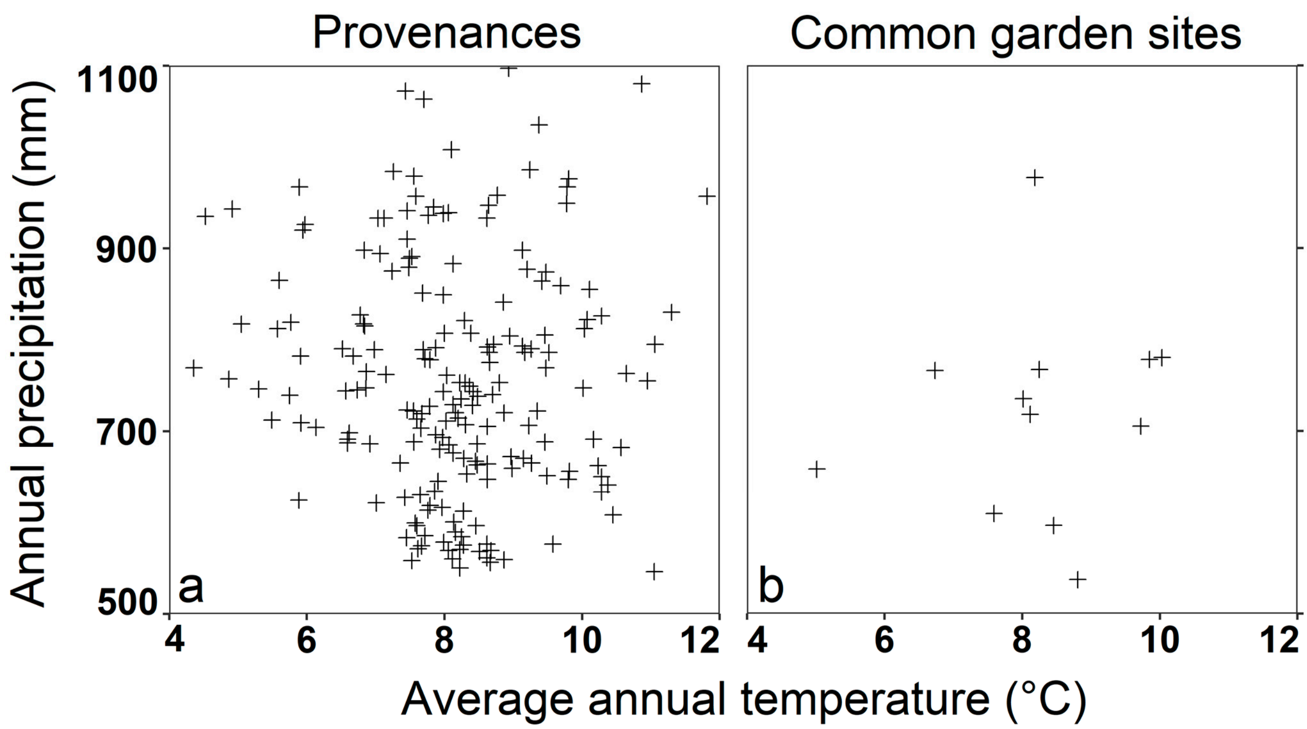

Figure 2. Average annual precipitation and average annual temperature at the sites of provenance origin (1961–1990, (**a**)) and at the common garden sites (1995–2002/1998–2005, (**b**)).

For the scenario calculations (2041–2060), we used the results from the ACCESS-ESM1–5 CMIP6 [48] ensemble simulation (mild Shared Socio-economic Pathways, SSP245, RCP4.5) also available from the WorldClim v2.1 database [47]. The data were then filtered at 15 min spatial resolution for an area within the Czech Republic and Slovakia. For the scenario simulation, the same set of ecodistances as before was calculated as difference between the respective climate metric at the site of provenance origin (1961–1990) and the climate at each grid point within the target region (2040–2060).

2.3. Model Development

To integrate various ecodistance values into a generally applicable site-dependent growth model, we used an artificial neural network (feed-forward back propagation, FFBPNN) approach. Neural networks are extremely useful for solving problems involving multiple influences and complex interactions, such as those given by the interplay of various climate conditions and provenances [49,50]. NNs are based on a general approximation theorem [51] and consist of so-called layers, which are collections of processing nodes (neurons) fully connected with the nodes in other layers but not within their own layer. These layers can be differentiated into input, output, and one or more hidden layers in between. It has been shown that systems with only one hidden layer can already approximate any continuous function, but usually, more than one is used. The reason is that with any additional interaction, a single hidden layer increases exponentially and thus becomes very large when capturing complex relationships. If datasets are small, simple networks with only a few layers and neurons often perform best [52].

Therefore, we used a NN model with three hidden layers consisting of 36, 18, and 9 neurons in each layer (Figure S2). The input layer initially considers 47 variables (climatic characteristics, ecodistance, longitude, latitude, altitude) described in Supplementary Table S1. All climatic influences were centred and normalised to ensure that every influence was equally weighted. In order to reduce the number of variables used in the base line model, we defined so-called hyper parameters that needed to be determined before the training of the final neural network. These hyper parameters determinate the overall structure of the neural network. The selection of hyper parameters values directly affects the performance and generalisation capability of a network. For optimum hyper parameter selection, grid and manual search are the most commonly applied strategies, which both were used here. First, the NN was run with the following setting: activation function was set to rectified linear unit (RELU) and Kernel initialiser was set to normal, learning rate was set to 0.01, number of epochs was set to 500, and batch size was set to 200. Then, the package Dalex, freely available in Phyton libraries, was used to assess the variable importance of investigated variables as predictors. Therefore, a script in Python was developed, combining a 10-fold cross-validation with a hyper parameter search. The best performance was achieved when seven predictors were used according to coefficient of determination (R^2), mean square error (MSE), root mean square error (RMSE), and mean absolute deviation (MAD). After identifying and optimising the number of predictors fed into the input layer, the selected hyper parameters were tuned (grid searched). Because the grid search was computationally demanding, an optimisation was carried out per part by considering a combination of grids of two, and three hyper parameters. The batch size was set to 10, 20, 30, 60, 120, and 200, with the number of epochs: 50, 100, 200, 300, 500; drop-out rate was tested with the values: 1, 0.9, 0.8, 0.7, 0.6; learning rate with 0.001, 0.01, 0.05, 0.1; number of hidden layers: 1, 2, 3, 4; number of neurons in a hidden layer: 4, 8, 16, 32, 6. The applied activation functions were: RELU, exponential linear unit (ELU), softmax, sigmoid, linear and tanh; and the kernel initialisation: uniform, normal, and zero. Finally, the RELU function showed the best performance, according to mean absolute error, which was determined by stochastic gradient descent.

For calibration and evaluation, all data were divided into two subsets. The model was trained with 66% of the provenance–ecodistance relationships, while the performance was tested with the remaining subset of data (34% of the total). The analysis was run in Python (3.10, Python Software Foundation, Wilmington, Delaware, USA), using the libraries Pandas 1.51, NumPy 1.23.0 scikit-learn 1.1.3, Keras 2.11.0 and TensorFlow 2.11.0. The final model was run in R (Version 4.2.1, Vienna, Austria) and passed to Dalex 2.4.2 package to assess the ultimate variable importance of the seven predictors and partial dependence plots.

2.4. Statistical Analysis

All statistical analyses were conducted in R 4.2.1 software (R Core Team, Vienna, Austria). ANOVA assumptions of normal distribution of height growth were tested by the Shapiro–Wilk test, and homoscedasticity between months was tested by the Bartlett's test. Afterwards, the statistical differences in historical seedlings' height between provenances and common garden sites were tested by two-way ANOVA (initial dataset). The comparison of provenance height simulation values of specific climatic groups was analysed by Tukey's HSD post-hoc test (future growth data).

3. Results

3.1. Climatic Variable Importance in Model

The European beech provenances showed high intraspecific variability of height growth among the common garden sites (Figure S1). Height differences were significant between the provenances within a common garden site, as well as for the same provenance at the different sites (Table 1). The final NN model showed the R^2 of 77% and mean absolute error of 71.25 cm for tree height prediction among the provenances and sites (Figure 3). The sensitivity analysis revealed that out of all the best explanatory values (Figure 4), three were climatic variables from the sites of growth: mean temperature of wettest quarter of the year (Bio8), precipitation of driest month (Bio14), and precipitation of warmest quarter of the year (Bio18). The other four variables describe a particular ecodistance between the site of origin and the site of growth: mean temperature of wettest quarter of the year (Bio8 ED), annual precipitation sum (Bio12ED), precipitation of the wettest month (Bio13ED), and precipitation of warmest quarter of the year (Bio18ED).

Table 1. Results of two-way ANOVA for height variability among provenance populations and common garden sites.

Factor	Df	SumSq	MeanSq	F	*p*
Provenance	130	71,289,815	548,383	109.66	<0.001
Site	13	188,718,150	14,516,781	2902.8	<0.001
Provenance × Site	409	22,573,979	55,193	11.04	<0.001
Residuals	45,735	228,715,682	5001		

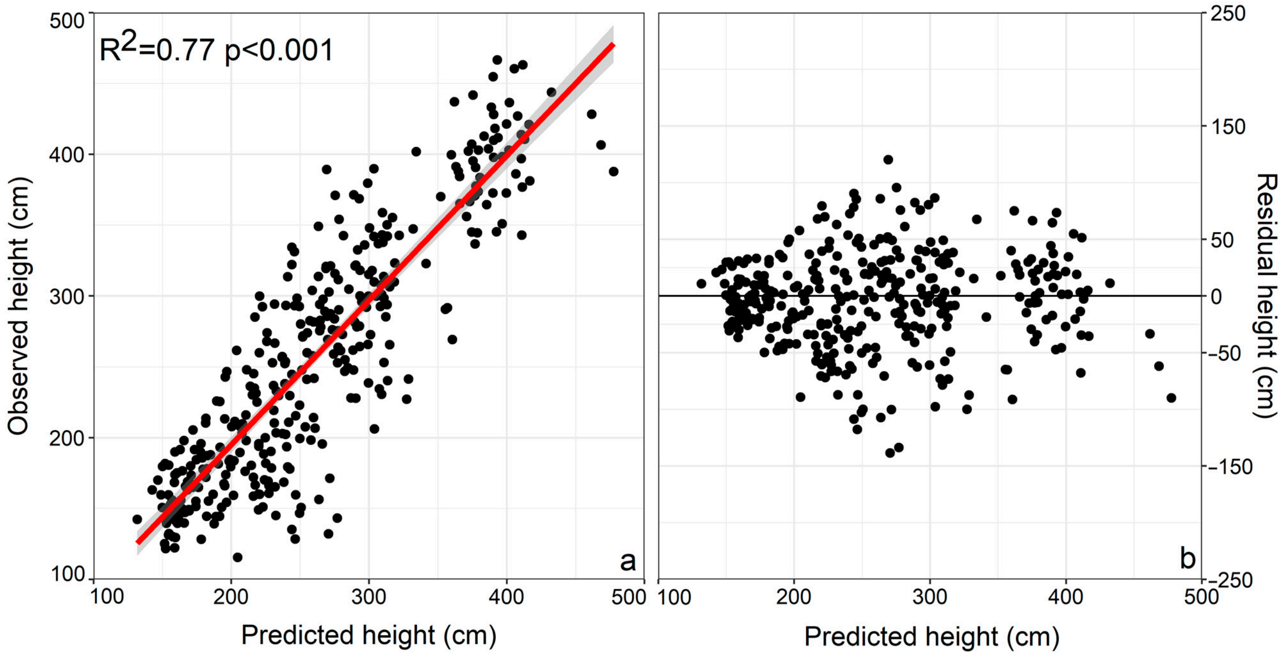

Figure 3. The comparison of observed and predicted values by the neural network model (**a**) and residual scatter plot (**b**).

The height growth responses in relation to these seven variables, which are used as independent determinants, are shown in Figure 4. They suggest that provenances performed better at warmer environments (Bio8) and sites with higher precipitation during the driest month (Bio14). In addition, provenances showed better height growth at sites warmer than the locations of origin (Bio8ED), or had higher annual precipitation (Bio12ED). Interestingly, translocation to sites with more unevenly distributed rainfall, as expressed by the precipitation during the wettest month of the year (Bio13ED), as well as during the warmest quarter of the year (Bio18ED), had a negative impact. The ecodistance parameters had generally greater importance in the model than the climatic parameters of the original provenance sites.

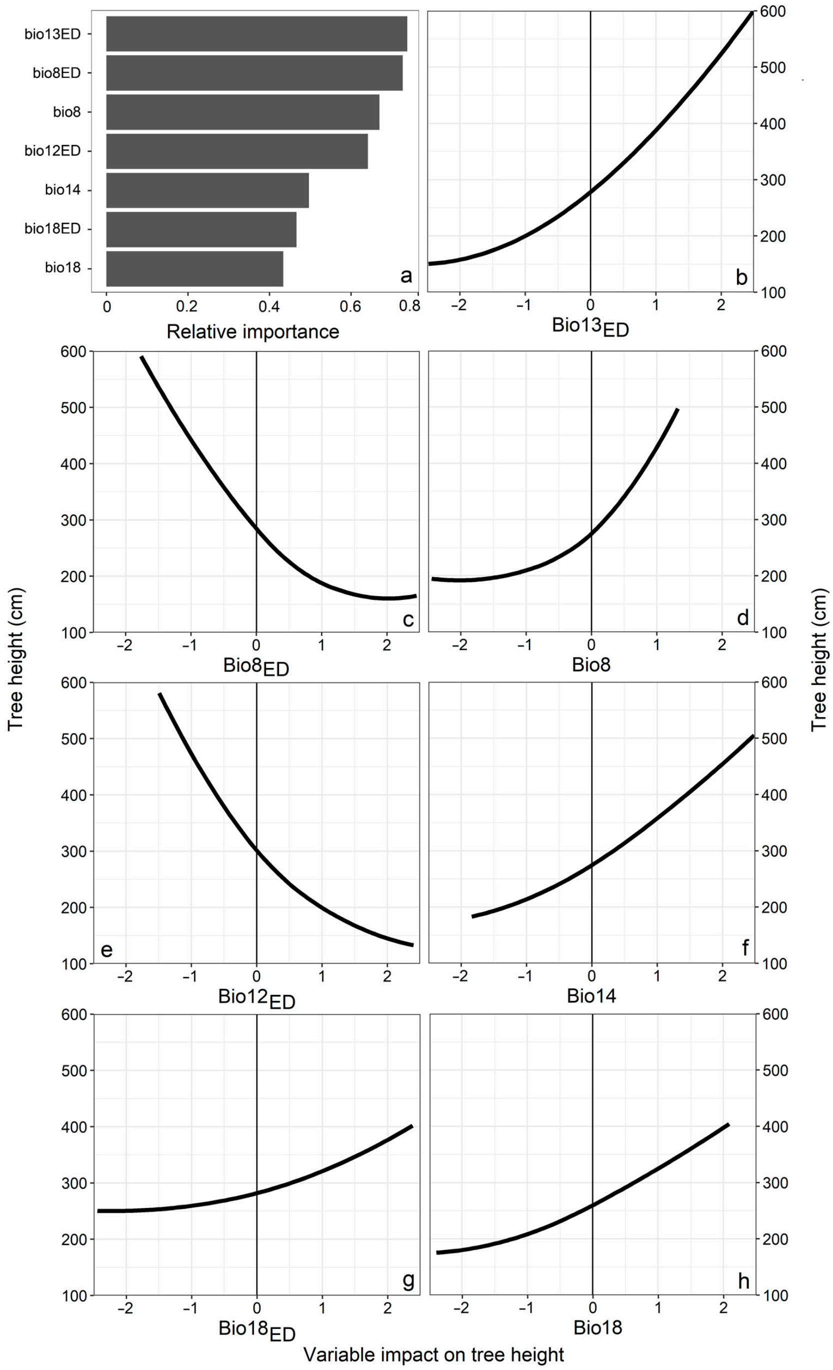

Figure 4. Sensitivity analysis of standardised variables within the neural network model (**a**), Bio13 = precipitation of wettest month (**b**), Bio8 = mean temperature of wettest quarter (**c**,**d**), Bio12 = annual precipitation (**e**), Bio14 = precipitation of driest month (**f**), Bio18 = precipitation of warmest quarter (**g**,**h**). Bio variables with ED subscript represent the ecodistance, which is the difference between the climate at the site of origin and the climate of new sites.

3.2. Model Climatic Limits and Provenance Grouping

The potential responses of the provenances to future climate conditions were analysed based on the SSP245/RCP4.5 scenario, simulating the height growth for 2041–2060 throughout the Czech Republic and Slovakia at 15 min spatial distribution. Other SSP (higher temperature) scenarios and later time periods exceeded the climatic boundary conditions in which the model has been developed (see Table 2) and were thus not used for the analysis. For simplicity reasons, we grouped all provenances according to their climate of origin into hot and wet, cold and wet, hot and dry, and cold and dry. The threshold for dry vs. wet characterisation was annual precipitation of 800 mm, and the threshold for hot vs. cold characterisation was annual mean temperature of 7 °C. Then we randomly selected five provenances out of each group and simulated their height response for each of the grids within the geographical constraints of the Czecho–Slovak region (Figure 5). The climatic characteristics of the 20 chosen provenances are presented in Table 3.

Table 2. Climatic boundary conditions of the neural network model based on minimal and maximal values from the original dataset used for development of the model.

	Bio8	Bio14	Bio18	$Bio8_{ED}$	$Bio12_{ED}$	$Bio13_{ED}$	$Bio18_{ED}$
Min	0.1	12	78	−16.4	−928	−122	−342
Max	19.9	88	533	17	1261	138	319
Unit	°C	mm	mm	°C	mm	mm	Mm

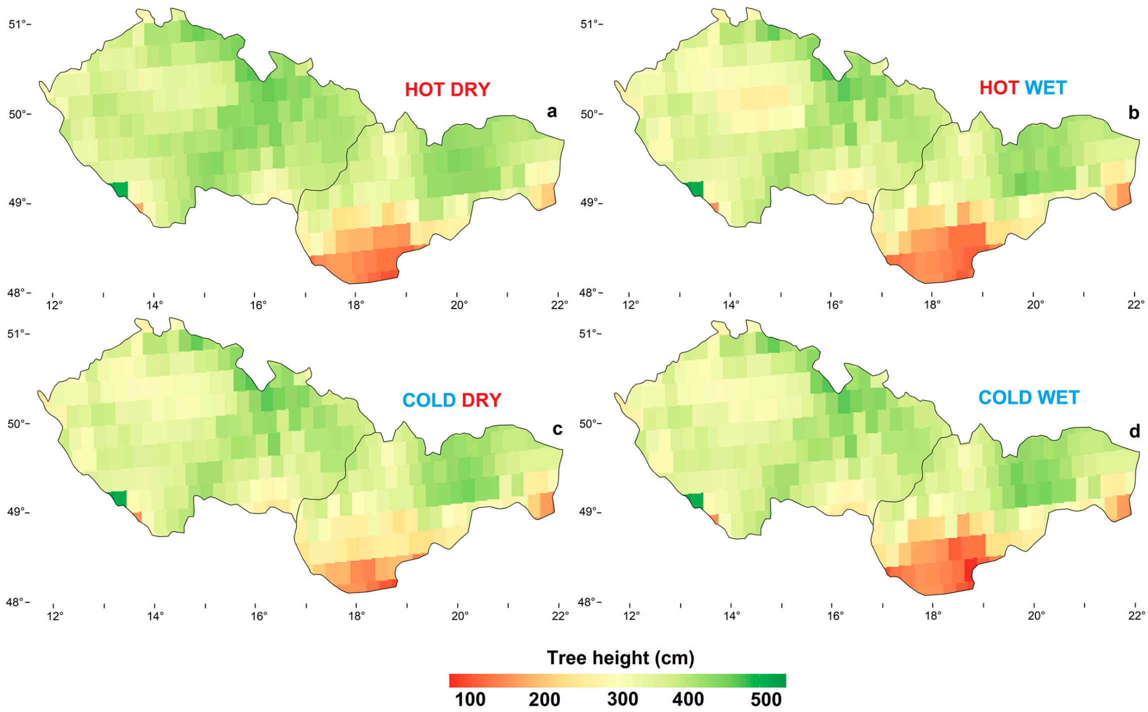

Figure 5. Maps of simulated height growth for four contrasting provenance groups during seven years under 2040–2060 climate derived from the SSP245/RCP4.5 climate scenario (**a**—hotdry origin, **b**—hotwet origin, **c**—colddry origin, **d**—coldwet origin). The height is simulated for trees that are approximately 10 years old at the end of the simulation. The state on the left side is the Czech Republic, and the state on the right side is Slovakia.

Table 3. Annual mean temperature (T) and annual precipitation sum (P) for original location of provenance groups used for simulation of growth, divided into contrasting climate groups. Full names of provenances are listed in Supplementary Table S2.

PV	T (°C)	P (mm)	PV	T (°C)	P (mm)
	Hot–Dry			Hot–Wet	
FR02	10.6	682	ESP02	9.8	967
ESP05	10.5	633	FR23	9.8	975
GER47	8.8	556	IT37	12.3	1251
IT78	13.8	595	IT108	10.9	1080
IT80	8.2	762	CR139	14.4	1271

Table 3. *Cont.*

PV	T (°C)	P (mm)	PV	T (°C)	P (mm)
Cold–Dry			Cold–Wet		
PL38	5.9	624	AU35	2.4	1524
CZ48	4.4	769	AU36	4	1184
GER85	5.1	709	CZ51	4.6	1124
PL117	4.9	757	AU39	3.8	1067
RO155	6.5	583	UA141	4.9	943

3.3. Spatial Height Growth Predictions

According to the model, all groups of provenances show a high phenotypic plasticity within the analysed region. The best growth is predicted to occur in the mountainous regions of Central and North Slovakia and the Jeseníky Mountains of Czech Republic. The least height growth has been simulated for southern Slovakia, in the area of the Hungarian border and Central Czechia (Figure 5). The average height within each group of origin (given with standard errors) was 421 $\pm$ 2.1 cm for the hot–dry group, 368 $\pm$ 4.82 cm for the hot–wet group, 384 $\pm$ 1.74 cm for the cold–dry group, and 379 $\pm$ 2.92 cm for the cold–wet group (Figure 6). Overall, the provenances from the hot–dry environment show the highest height growth across the whole Czecho–Slovak region. The Austrian provenance AU35 from a high altitude, cold and wet location showed worst height growth performance across provenances overall. Moreover, provenances from the cold–dry environment showed the smallest variability and the ones from the hot–wet environment showed the greatest variability (Figure 6).

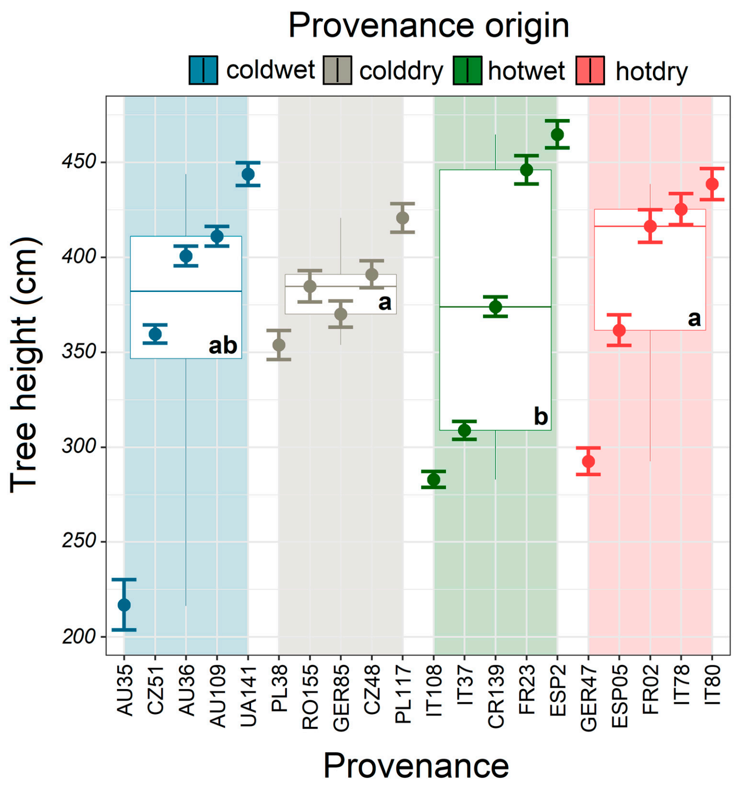

Figure 6. Mean and 95% confidence intervals of simulated height growth (2040–2060), for 20 provenances, from 4 provenance groups with contrasting original climate. Boxplots on provenance group level with lowercase letters showing results of Tukey HSD post-hoc test. AU—Austria, CR—Croatia, CZ—Czech Republic, ESP—Spain, FR—France, GER—Germany, IT—Italy, PL—Poland, RO—Romania, UA—Ukraine.

4. Discussion

The scenario simulations showed that the mild SSP245/RCP4.5 climate change scenario particularly favours the growth of beech provenances from hot–dry and cold–dry environments. Provenances from more humid environments performed significantly worse than provenances originating from drier regions. The growth for all groups seems to be retarded around southern Slovakia, likely due to the relatively low rainfall and, thus, greater drought risk in this region. Best height growth was predicted for high altitude locations for all provenances. The historical increase in European beech growth at higher altitudes can be attributed to the extended growing season [53]. The spatial distribution of height growth from our simulation generally corresponds to the BAI estimates for beech under a mild scenario for the same period, reported recently by Martinez del Castillo et al. [21]. Moreover, locations with the reduced height growth match with the climate change hot-spots identified by Hlásny et al. [54].

4.1. Ecodistance as a Predictor of Provenance Response

Ecodistance captures the climatic difference between the region of provenance and the new location to which it is transferred. The term was coined by Mátyás [33] and has been widely used in provenance research. Ecodistance variables that indicate the aridity of a site already showed great explanatory power for the interpretation of intra-specific variability of vitality [55], mortality [56], and growth [57] of European beech provenances.

This is in accordance with findings that also investigated beech provenances and demonstrated impacts of both drought and temperature ecodistances on stomatal and leaf morphology [58] and of a drought-related ecodistance on the antioxidant system efficiency [59]. In addition, aridity-related ecodistance also showed great explanatory power regarding the intra-specific variability of root growth dynamics [60]. The results indicate that European beech can acclimate (water uptake and retention) to different climatic conditions as induced by geographic transfer (which can be seen as analogy to climate change). Similar results have also been achieved for other tree species such as oak [61], Norway spruce [62,63] and Scots pine [45].

The application of ecodistance metrics has been used before to explain the intra-specific variability of European beech growth within common garden sites [44,45,64]. However, it is the first time here that it is used for scenario analysis where the ecodistance metrics are calculated from a regionally differentiated future climate. Using a NN model is also a new approach, which elaborates the methodology of Mátyás et al. [55], who conducted mono-dimensional extrapolations of beech height growth based on the ecodistance of Forest Aridity. The relatively weak relationship they found inspired the development of a more complex multi-factorial neural network. The resulting model based on four normalised ecodistance indices and additional three site climate variables is now able to explain 77% of total height variability across provenances and common garden sites. The combination of climate-related ecodistance values can thus certainly be viewed as a powerful tool for the explanation of provenance phenotypic transfer responses.

4.2. Limitations of the Study

It should be noted that the model does not account for soil conditions, which are difficult to define for a region (of origin) and often not available for a target site (at least for regionally distributed simulations). Given the dependence of root systems on soil depth and of potential water uptake from soil texture, including such factors will likely have an additional explanatory impact on provenance development [65]. Additionally, growth limitation due to nutrition constraints can have a significant impact on the accuracy of the presented results [66], although nutrition and water availability are also related to a certain degree [67]. Another influencing factor that we miss is the difference in past and future atmospheric CO_2 concentration, which may decrease the impact of aridity and thus mitigate future impacts of drought and high temperatures [68,69]. This is an effect difficult to include in models that are based on statistical performance of the past because future

CO_2 concentrations have never been experienced before. As another influencing factor, the topography of the locations was not accounted for, since slope and elevation can influence water and nutrient availability beyond what can be estimated from soil texture and depth. However, topography is generally closely related to site climate conditions. It is also not possible to consider the impacts of topography if averaged over a 27.75 km grid which was the spatial resolution in our simulations.

We admit that even though various aspects of tree growth were included, a NN model does not account for any physiological processes or process knowledge. It rather represents a black box that produces output from input based on the statistical relationships of the past. Therefore, it should not be applied outside the range of observations that have been used to calibrate and evaluate the model, which is the reason why we selected a climate scenario that does not reach far into the future, as well as a very specific area, which is close to the region the model has been developed for. Within this domain of climatic constraints, however, we can assume that the model provides reasonable and meaningful results.

4.3. High Phenotypic Plasticity of European Beech

Populations with higher phenotypic plasticity are generally viewed positively as they can adapt to higher environmental variability and thus can minimise the risk of mortality [70]. The distribution of height growth among provenance groups in our study shows great variability (100 to 500 cm growth within a 7-year period), but similar average growth, which is around 388 cm. These results suggest that European beech is a highly plastic species, especially as these groups originated from contrasting environments. Indeed, this is supported by various studies. For example, Müller et al. [71] showed a high height growth plasticity for European beech across common garden sites all over Germany. Similarly, a study concentrating on climate conditions of Western and Central Europe also investigating trees at common gardens confirms this highly plastic growth responses [45], which is furthermore corroborated by various other provenance observations [33,72,73]. A high intra-specific variability of European beech provenances has been observed not only for growth but also for phenology [74,75], stomatal and leaf morphology [57,76–78], root architecture [59], xylem embolism resistance [79–81], xylem hydraulic conductivity [82], gas-exchange [41], photochemistry [83], $\delta^{13}C$ partitioning [84,85], and establishment success [86]. Overall, the broad range of intra-specific variability of European beech across the traits suggests a great adaptation potential under global climate change.

4.4. Drought and Temperature Limited Growth

Despite its high plasticity, the susceptibility of European beech to more extreme heat and drought events or generally drier conditions is highly disputed. A recent meta-analysis by Leuschner et al. [12] concluded that European beech already shows significant growth reductions in large parts of its distribution range. From a regional perspective, it seems that, in particular, the populations at low altitudes are suffering from decreased precipitation, especially during spring [87]. In fact, beech growth in Slovakia has been declining since the year 2000 [26,27], and a similar trend has also been observed in the Czech Republic [24,25]. The dependency of growth on water availability is also supported for close-by regions such as Hungary [44]. The observed growth reductions in European beech have been attributed to recent increases in summer temperatures [88], decreases in summer precipitation [89], or decreases in relative air humidity [90]. In combination, these findings indicate that the reason for growth decline is an increase in overall aridity [91]. However, at sites where aridity is not increasing or water supply is at least still sufficiently available, beech trees are showing increasing growth trends. This is also confirmed for the target region in this study [92,93].

The simulations reflect these observations well. The retarded growth has been simulated particularly in southern Slovakia, closely related to the greater aridity that emerges during the 2040–2060 period from lower precipitation and greater evaporation demand. In contrast, the highest predicted growth occurred in mountainous areas of the Czech

Republic and Slovakia, which are expected to be relatively well water supplied in the upcoming years. This increase is likely linked to the consideration of the temperature of the wettest time of the year in model, which is usually the spring period. Growth increases originating from higher spring temperatures are caused by the relation to bud burst, which happens sooner each year, elongating the growing period [94,95]. The spring temperature has been observed as a main explanatory factor for the growth variability of European beech in Central Europe [25]. However, this elongation can also increase the sensitivity to late frosts [17,96], particularly at high elevations. If there are more frequent frosts after bud burst, it can cause retardation of growth since the lost foliage has to be replaced with carbon not available anymore for stem growth [97]. The mixed effects of increasing temperature and aridity can have complex effects on tree growth, as viewed in the sensitivity analysis of our NN model.

Overall, the inclusion of various indices enabled not only the responses at specific sites to be described with higher precision but also coverage of the spatial variability that originates from different dominating influences at different sites. In addition, the regional analysis also enabled to highlight differences in growth responses between provenances, i.e., the better performance of plants originating from drier regions, which are better adapted to the expected future conditions.

5. Conclusions

Our results indicate that growth of young European beech trees will be retarded at drier locations of Southern Slovakia and Central Czechia within 2040–2060 period. Overall, the use of provenances originating from Mediterranean regions, and thus generally better adapted to warmer and drier conditions, will be probably advantageous. The exception is in mountainous areas where drought impacts will not be as pronounced. Our model suggests that precipitation and spring temperatures will be prominent drivers of European beech growth in the future in Central Europe, indicating an increasing significance of drought.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14010026/s1, Figure S1: Variability of height among provenance populations at the 13 common garden sites used for NN development; Figure S2: Final architecture of the neural network model. Input layer has seven neurons (climate variables and ecodistances), which are connected to three hidden layers (36, 18, and 9 neurons) and lead to output height. Each line represents a linear or non-linear function between the two connected neurons; Table S1: Initial explanatory variables used for construction of neural network model; Table S2: Full country name of provenance abbreviations used in Table 3.

Author Contributions: P.P. and P.F.J. conceived the research idea and hypotheses. D.G. contributed his data from two Slovak sites to the original BeechCOSTe52 database. D.K. and A.S.K. were in charge of the data acquisition and management. P.P. and P.F.J. conducted the data analysis, simulation and interpreted the results. A.P.-P., M.M., L.J.L., H.D. and P.P. wrote the first draft, which was elaborated by R.G. and D.G., and modified by all co-authors. All authors have read and agreed to the published version of the manuscript.

Funding: This article is based on work from the COST Action CA19128—Pan-European Network for Climate Adaptive Forest Restoration and Reforestation (PEN-CAFoRR), supported by COST (European Cooperation in Science and Technology). The provenance experiment has been established by the European Network for the Evaluation of the Genetic Resources of Beech for Appropriate Use in Sustainable Forestry Management (AIR3-CT94-2091) under the coordination of H.-J. Muhs and G. von Wühlisch. Collection of phenotypic data was accomplished within the COST Action E52: Evaluation of Beech Genetic Resources for Sustainable Forestry. P.P. was supported by the Ministry of Education, Youth and Sports of Czech Republic within the CzeCOS program, grant number LM2018123. D.K., A.S.K. and D.G. were supported by a grant of the Slovak Research and Development Agency no. APVV-21-0270. M.M., A.S.K. and D.K. were supported by the Slovak Grant Agency for Science—grant no. VEGA 1/0535/20.

Data Availability Statement: All data used within this study were open access and are available at respective repositories stated within the article. Climate and ecodistance data used for this study are included in the attached data file in in Supplementary Materials.

Conflicts of Interest: The authors declare no conflict of interest.

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