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The Potential for Future Shifts in Tree Species Distribution Provided by Dispersal and Ecological Niches: A Comparison between Beech and Oak in Europe

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Abstract: (1) Due to global warming, distribution ranges of temperate tree species are shifting northwards and upslope to cooler areas. Shifts in distribution first become visible through changes in regeneration dynamics. However, the future distribution of tree species in the face of rapid climate change depends not only on the climatic suitability of the tree species, but also on its ability to disperse into new habitats. The aim of the study was therefore to examine how the distribution of European beech and European oak shifts and how species can spread from fragmented seed trees. (2) In order to investigate the shift in distribution of beech and oak, the bioclimatic envelopes of the old trees and different size classes of the natural regeneration were compared. Subsequently, a simulation of the potential distribution for the present climate, as well as for the climate for the reference period 2091–2100, for three different representative concentration pathways (RCP) scenarios was determined. In order to determine which of these areas can actually be colonised, a dispersal potential for the species was determined using a quantile regression, taking habitat fragmentation into account. (3) The results of the present study demonstrate range shifts of the tree species regeneration distribution (*B0*, *B1* and *B2*) compared to the overstorey distribution (*OST*). While oak regeneration shows an expansion of its distribution in the cold-wet range, beech regeneration shows a reduction of its distribution in the dry-warm range. As the dispersal potential of oak exceeds that of beech, it is expected that oak will be better able to spread from fragmented seed trees. However, the results also indicate that many areas, despite climatic suitability, cannot be colonised due to too large dispersal distances. (4) For the forest management, this results in an important planning tool for future tree species composition, as climatic suitability, habitat connectivity and dispersal ability are taken into account.

Keywords: bioclimatic envelopes; climate change; dispersal; biogeography; tree migration; habitat fragmentation

1. Introduction

In natural forests, among the most important late-successional deciduous tree species in Europe are: European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.). Both oak species show a wide ecological amplitude in terms of climate. The distribution of the two oak species is sympatric in many parts and extends over large parts of Europe, reaching, in the north, to Norway and Sweden and, in the south, to the northern part of the Iberian peninsula, southern Italy, the Balkans and Turkey [1,2]. The distribution in the north is mainly limited by low temperature, while, in the south, a lack of precipitation limits the distribution [1–3]. Within the regeneration cycle,

temperatures lower than $-6\text{ }^{\circ}\text{C}$ can cause damage when acorns are stored on the forest floor and represent the bottleneck in successful regeneration [4,5].

The natural range of beech coincides with the temperate and warm temperate regions of Europe and extends from southern Sweden to central Italy and northern Portugal to Greece [6,7]. The review by Bolte et al. [8] reveals that it is difficult to attribute the distribution of beech to a specific climatic factor. However, lack of frost resistance of buds, shoots and bark [9,10] and late frost damage to young leaves and flowers [6], as well as drought damage to leaves, are identified as climatic causes for distribution limits of beech [11].

Evidence from pollen studies shows that changing climate during the Holocene had a profound impact on the occurrence and abundance of tree species [12–17]. Favoured by the warming of the climate at the start of the Holocene (10,000 BC) [16], oaks expanded rapidly from the glacial refugia (up to 500 m year^{-1}) [17,18] and characterised the landscape during the Atlantic (from about 5000 BC) [12,19]. The Atlantic period was followed by a cooler and wetter climate, allowing the rapid expansion of beech [13,20,21]. Since the Subatlantic, beech has predominated in the deciduous forests of western and central Europe [7,12,13].

In the course of predicted climate change [22], the distribution of species is expected to change again [23]. Changes in distribution take place through demographic processes such as (a) increased mortality causing a reduction of distribution [24–26] or (b) altered regeneration dynamics favouring the migration of a species [27–29]. Current observations of temperature and drought increases [30,31] indicate that demographic responses to climate change are already taking place. Evidence for a northward expansion [28,32] or expansion to higher altitudes [27,29,33,34], but also a decrease in distribution [28], can be found in various studies. While the presence and density of old trees may reflect past climate in accumulated form, seedlings and saplings show greater sensitivity to current changes in climate variables [27,32,35]. Changes in distribution may, therefore, become apparent due to altered regeneration dynamics.

From large-scale inventory data, bioclimatic envelopes can be created for species distribution based on the mapping of climatic data to geographical coordinates to estimate the realised niche [36]. The realised niche differs from the fundamental niche due to: unsuitable substrate properties, biotic interactions and geographical barriers, as well as human impact [37,38]. The bioclimatic envelope of naturally regenerated seedlings represents the boundary of successful fruiting, dispersal, storage, germination and establishment of seedlings in terms of the abiotic factors studied.

Bioclimatic envelopes can be used to predict the potential distribution of tree species in specific regions under current or future climatic conditions [39,40]. However, bioclimatic envelopes do not consider tree species dispersal [36,41]. Due to migration limitations (Figure 1), the future actual distribution may differ from the prediction of future potential distribution [36,42,43]. Therefore, uncertainty in the prediction of effective dispersal (either under- or over-estimation) is considered the greatest uncertain factor in predicting future species distribution [43–45]. The dispersal potential of a species [46] and the connectivity of the landscape [44] have a decisive influence on the extent to which the new habitat is colonised by a plant that had not previously been present there (on the actual future distribution). Thus, initial approaches have been made to take dispersal into account in distribution models [43,47].

The research by Meier et al. [43] suggests that early-successional tree species can adapt more quickly to climate change through migration than late-successional tree species due to earlier fruiting and greater dispersal distances. Both oaks and beeches are monoecious, wind-pollinated and have irregular masts. Methodologically, however, long-distance dispersal events were not taken into account in this study, although there are references for zoochorous dispersal of late-successional tree species [48–50], as well as evidence for rapid postglacial migration (i.e., Reid's paradox) [15,17,18]. Although primary seed dispersal of beech and both oak species is characterised by barochory of the heavy-seeded acorns and beechnuts [51–53], there is much evidence of secondary seed dispersal by zoochorous

vectors [54–57]. This leads to the need for research on how late-successional tree species can adapt to climate change, considering long-distance dispersal in a fragmented landscape.

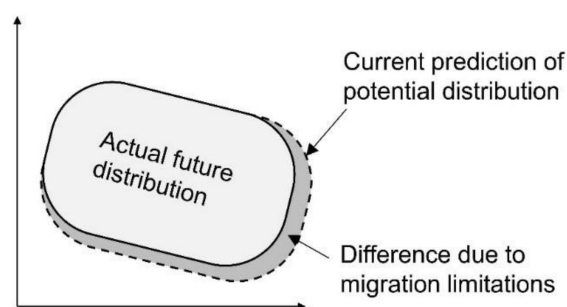


Figure 1. The difference due to dispersal limitation may prevent a species from colonising all potential sites.

We quantified climatic envelopes for the late-successional beech species and both oak species in the overstorey (OST) and three of their regeneration stages to identify differences in the distribution potential of forest tree species as a function of climate. Our overall objective was to determine whether differences in climatic envelopes among regeneration stages indicate a reduction, expansion or shift in the range of species. For this, we compared the area sizes of the climatic envelopes of the different regeneration size classes. By comparing the different size classes, a kind of chronosequence can be represented. This enables the influence of climatic changes on the establishment of regeneration to be derived. For tree species that show distribution changes, the dispersal potential was determined.

The research objectives were to (1) produce a regional model of mean annual temperature and precipitation at which oak and beech regeneration presently occur; (2) develop a regional prediction of beech and oak distribution that may be expected for a range of temperature and precipitation change; and (3) compare current fragmentation of potential seed trees and their ability to migrate in a changing climate.

2. Materials and Methods

2.1. Forest Inventory and Analysis of Data

The study was conducted in the state forest located in Saxony, Germany. The data used in the study were generated in the context of a forest inventory and were provided by Sachsenforst. The data were recorded in a period from 2015 to 2020. The forest inventory surveyed 38,504 permanent sampling plots on a grid square with 200 m side length. Each plot consists of two concentric circles with a 6 and 12 m radius. The overstorey was recorded in the 6 m radius circle for all trees featuring a diameter at breast height (dbh) ≥ 7 cm and <30 cm and in the 12 m radius circle for trees featuring a dbh ≥ 30 cm.

The regeneration was recorded within a 2 m radius subplot (≈ 12.57 m²), located 5 m northbound from the plot centre. Within each subplot, regeneration featuring height ≥ 20 cm and a dbh < 7 cm was measured. The inventory design distinguishes between three size classes for the regeneration. The first size class *B0* includes regeneration featuring a height ≥ 20 cm and <50 cm. The second size class *B1* includes regeneration featuring a height ≥ 50 cm and <130 cm, whereas the third size class *B2* consists of trees featuring a height ≥ 130 cm and a dbh < 7 cm. The number of individuals was recorded separately according to tree species, size class, game damage and game damage protection. Furthermore, a distinction was made between natural and artificial regeneration. The maximum number of regeneration to be recorded was 15, i.e., a theoretical distribution of numbers has to be truncated at 15. The occurrence and density of both oak species and beech natural regeneration was used as a dependent variable for each individual size class, as regeneration of different sizes might have been exposed to different weather conditions due to the different life span of the size classes. The number of pedunculate oak and sessile

oak was analysed collectively as a morphological distinction is difficult and both species also occur sympatrically [2,58,59]. Furthermore, a similar dispersal ecology is expected.

2.2. Baseline Climate and Future Projections

The regional climate of Saxony is characterised by a westerly-moderate climate and is influenced by Mediterranean and continental air masses [60]. The topographical relief can be divided from north to south by lowlands, followed by lower mountainous areas, middle mountainous areas and higher mountainous areas, as well as ridge areas of the Ore mountains.

The data required to assess the actual climate and the climate development in Saxony are provided by the Regional Climate Information System (REKIS) [61]. REKIS, which is recognised as a high-quality spatial climate dataset in central Germany, is an interpolation of meteorological station data from the German Meteorological Service to produce continuous, digital grid estimates of climate parameters, taking into account: location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position and orographic effectiveness of the terrain. The baseline climate values are taken from short-term average climate data (2001–2010) as this period overlaps in time with the establishment of the surveyed regeneration.

By intersecting the coordinates of the sample plots with spatial climate data, the two variables, mean annual average temperature ($^{\circ}\text{C}$), ranging from 3.62 to 10.29, and mean annual total precipitation (mm), ranging from 611 to 1532, were extracted (Figure 2). We used these variables because they are often used for species distribution and thus provide comparability with other studies [8,32]. Whereas temperature is mainly dependent on the altitude, precipitation depends not only on altitude but also on the location within the mountains. Due to the main wind direction from the west, the highest precipitation is measured in the western Ore mountains (Figure 2).

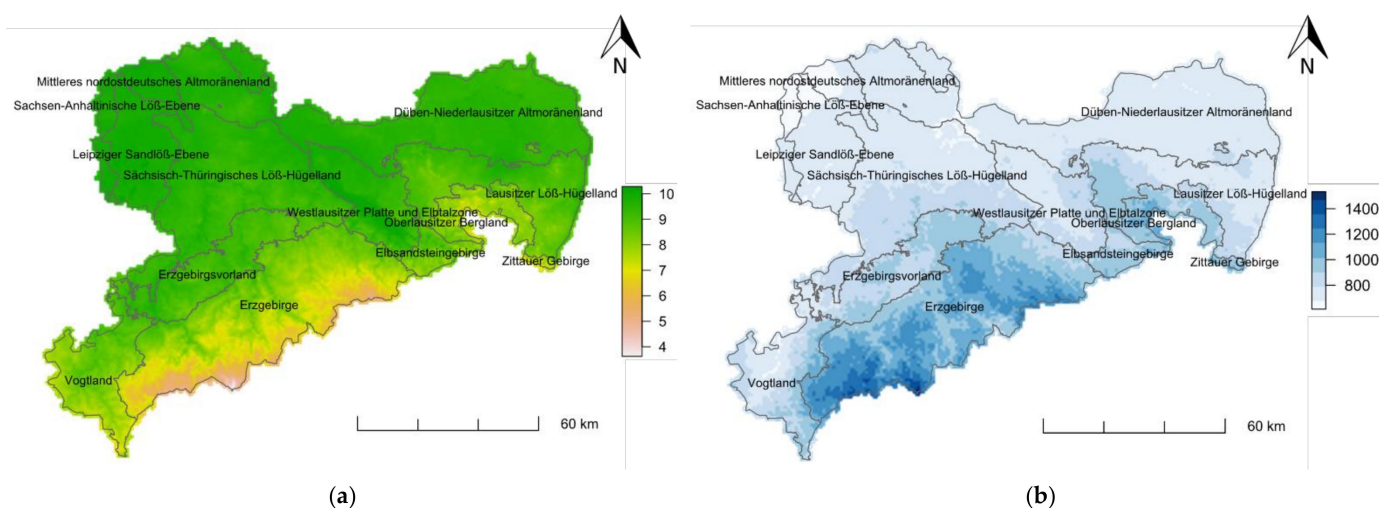


Figure 2. Map of the spatial distribution of mean annual temperature (a) and mean annual precipitation (b) for the reference period (2001–2010).

In addition to the baseline climate, climate projections were used for predictions. For this dataset, which was provided, statistical relationships between large-scale and local climate were determined and applied to a future climate state and its development [61,62]. Three representative concentration pathways (RCP 2.6, RCP 4.5, and RCP 8.5.) that approximately represent the range of possible future emission trajectories were used. The scenarios are defined as radiative forcing values in W/m^2 relative to pre-industrial values [63]. The period 2091–2100 was used as the reference period (Supplementary Material, Figure S1).

2.3. Descriptive Analysis of Bioclimatic Envelopes

Taking exclusively Saxonian data into account, the respective occurrence of oak and beech in the overstorey and regeneration density at the sample plot was plotted against the two climatic variables. The two-dimensional bioclimatic envelopes for beech and oak natural regeneration and trees in the overstorey were calculated as the minimum-area convex polygon containing the set of sample plots containing beech or oak regeneration [64]. Thus, the climatic information from all sample points with natural regeneration and trees in the overstorey of the respective tree species was used to create the polygon. The function `chull` of the R package `grDevices` was applied [65]. The area size of the polygon was calculated to characterise the polygon. It is a dimensionless unit. We compared the areas and polygon locations of the different size classes to detect differences in the patterns.

Based on the climatic envelopes, a prediction for the occurrence of size class *B0* for the two tree species was made using the maps of the spatial distribution of mean annual temperature and mean annual precipitation for the reference period (2001–2010). In addition, predictions for the period 2091–2100 were calculated for the different climate scenarios RCP 2.6, 4.5 and 8.5. A point in polygon query was performed to check whether the respective temperature and precipitation (*x* and *y* values of the point) of the grid cell lie within the polygon characterising the species' range of occurrence. The function `point.in.polygon` of the R package `sp` was applied [66]. By this method, the climatic values were used to check in which parts of the study area the species could potentially occur {0;1}.

2.4. Dispersal Potential

After determining the climatic suitability for the two tree species, the extent to which the species can fill these niches by dispersal was examined. For this purpose, the dispersal potential of the two tree species was determined. The dispersal potential of oaks and beeches was determined by estimating the potential regeneration density as a function of the distance to the nearest seed source.

The location of potential seed trees was provided from remote sensing data from Sachsenforst [67]. Aerial digital orthophotos were used to classify tree species based on RGB pixel values (red-green-blue). The pixel resolution on the surface was 20 cm. The tree species groups beech, oak, birch, spruce, pine and larch were classified on the basis of spectral characteristics of the pixels. Sessile oak and pedunculate oak were recorded together in the category oak. The distance to the nearest seed source was determined as the distance between the spatial polygons with oak or beech stands, determined from the remote sensing data, and the sample points. The `gDistance` function was used to determine the distance [68]. The shortest distance between point and polygon was determined. Overlapping effects were not taken into account.

For the dispersal potential, a quantile regression was used following Axer et al. [69]. The 996th quantile (τ) was used to calculate the maximum regeneration densities as a function of the distance to the nearest seed source. Thus, factors that reduce regeneration density are left out of the analysis. Instead, the long-distance dispersal of tree species can be quantified. Furthermore, the 996th quantile was used in order to exclude outliers. Compared to least-squares regression, the quantile regression minimises the weighted absolute errors. The parameters of the below mentioned non-linear functions were estimated by:

$$\sum_{i=1}^n x_i w_i |y_i - \eta_i|, \quad (1)$$

where $y_1, \dots, y_n$ are the observed regeneration numbers and $x_1, \dots, x_n, \eta_1, \dots, \eta_n$ are defined as above. According to the 996th quantile, an asymmetric error weighting was applied when minimising the sum of the absolute error [70]:

$$w_i = \begin{cases} \tau & \text{if } y_i > \eta_i \\ 0 & \text{if } y_i = \eta_i \\ 1 - \tau & \text{if } y_i < \eta_i \end{cases} \quad (2)$$

The following log-normal model was used to model the predicted oak regeneration density η_i in plot i [69,71]:

$$\eta_i = N \frac{1}{2\pi x_i^2 \sqrt{2\pi\sigma^2}} e^{-\frac{(\log x_i - \log a)^2}{2\sigma^2}} \quad (3)$$

where x_i is the distance to the nearest seed source and N, a, σ are parameters to be estimated. The equation means $\log \eta_i$ is a quadratic function of $\log x_i$ with a maximum at $\log a - 2\sigma^2$.

The Clark2DT function was used to model the predicted beech regeneration density η_i in plot i [72]:

$$\eta_i = N \frac{p}{\pi u (1 + x_i^2/u)^{p+1}}, \quad (4)$$

where x_i is the distance to the nearest seed source and N, p, u are parameters to be estimated.

In order to estimate the area in which both species can potentially disperse, a spatial prediction was made for the entire study area using the parameterised functions described above. For this purpose, the distance to the nearest potential seed source was determined for the entire study area. The fragmentation of seed trees and its consequences for the potential dispersal are thus taken into account.

2.5. Intersection of Climatic Suitability and Potential Dispersal

Subsequently, the map of potential dispersal (D) was intersected with the map of climatic suitability (C) (Figure 3). This reveals areas that could potentially be colonised ($C \cap D$). According to Soberón and Peterson [73], this approach was chosen to identify where both climatic suitability and potential dispersal occur. In this way it was possible to distinguish which of the two factors (climatic suitability and/or dispersal) is limiting.

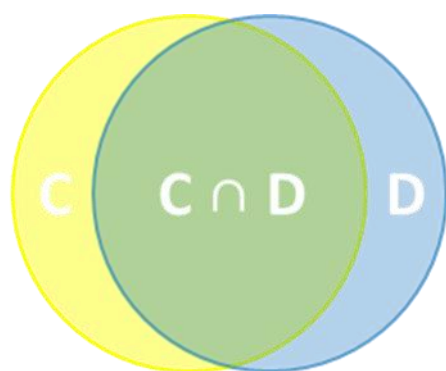


Figure 3. Definition of the intersection of climatic suitability (C) and potential dispersal (D).

3. Results

3.1. Descriptive Analysis of Bioclimatic Suitability

The climatic variables of plots with natural regeneration occurrence and trees in the overstorey were used to create the envelopes (Figure 4). The majority of the entire plots did not contain oak or beech regeneration. However, 3463 plots contained oak regeneration of size class B_0 , while 1204 and 492 plots contained oak regeneration of size classes B_1 and B_2 , respectively. Only 2990 of the plots were located in oak stands. For the beech envelopes, 3032 plots with beech regeneration of size class B_0 were used as the data basis. Beech regeneration of size classes B_1 and B_2 was found on 2482 and 2148 plots, respectively. With 5759 plots, there were more plots located in beech stands than plots with beech regeneration. The observed regeneration density on the plots varied between 1 and 15 seedlings, which corresponded to a density of 795 and 11,936 seedlings per

hectare. Compared to beech regeneration density, most plots with oak regeneration were characterised by a low regeneration density (Figure 4).

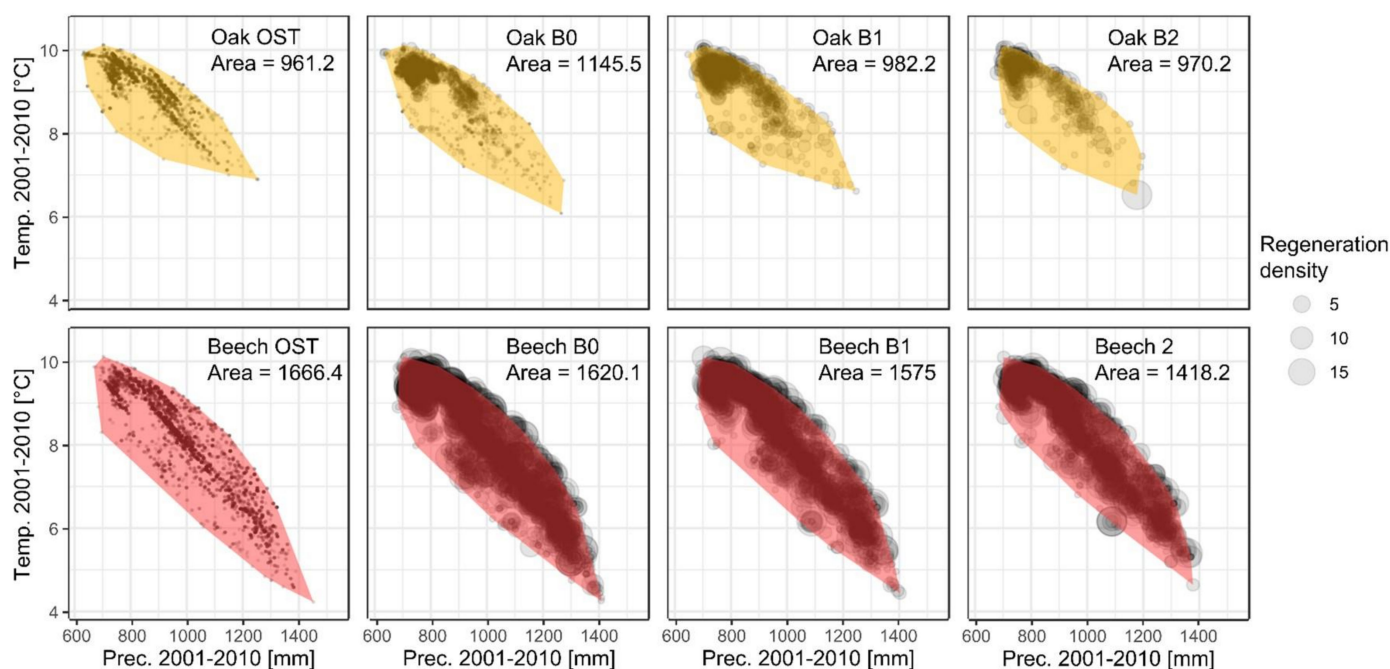


Figure 4. Bioclimatic envelopes for oak and beech in the overstorey (OST) and for the different regeneration size classes (B0, B1, and B2).

In the study area, natural oak regeneration of size class B0 occurs at a temperature range from 6.08 to 10.12 °C and a precipitation range from 633 to 1274 mm. It is obvious that the climatic envelope of size class B0 is larger and covers a wider climatic range than the climatic envelopes of size classes B1 and B2. Especially in the cold-humid areas (e.g., temperature lower than 6.5 °C combined with precipitation higher 1200 mm), several plots with regeneration of size class B0 can be observed, where larger oak regeneration does not occur. The comparison of the climatic envelopes of size classes B0 and B2 also shows a difference in the dry-warm area of Saxony. While B0 even occurs on plots with rainfall from 633 mm, B2 occurs on plots with rainfall above 681 mm. Compared to the regeneration, the bioclimatic envelope of oak in the overstorey shows a smaller envelope. While oak regeneration B0 occurs up to 6.08 °C, oak in the overstorey is only detected up to 6.89 °C.

The climatic envelope of natural beech regeneration is larger than that of oak regeneration. The distribution of B0 covers a temperature range of 4.26 to 10.12 °C and a precipitation range of 685 to 1402 mm. The climatic envelopes of size classes B1 and B2 are smaller than those of B0. In the dry-warm area, all size classes show the same distribution limit. In the humid-cold range, however, the smaller beech regeneration indicates a further distribution. The climatic envelope of beech in the overstorey is larger than the climatic envelope of the beech regeneration. The beech trees in the overstorey also occur in drier areas up to 669 mm.

Based on the climatic values for the study area (Figure 2), it was examined, i.e., simulated, in which parts of the study area the regeneration of beech and oak could potentially occur given the recent climate and no dispersal restrictions. As size class B0 has the largest bioclimatic envelope, this size class was used for the simulation. Figure 5 shows the simulations for the potential distribution of the two tree species. According to the larger bioclimatic envelope, the actual potential distribution area of beech is larger than the actual potential distribution area of oak. In the Ore mountains, there are only small areas where beech would not be able to establish itself under the current climatic

conditions if there were no spreading restrictions. In the case of oak, however, the ridges of the Ore mountains cannot be colonised due to climatic restrictions.

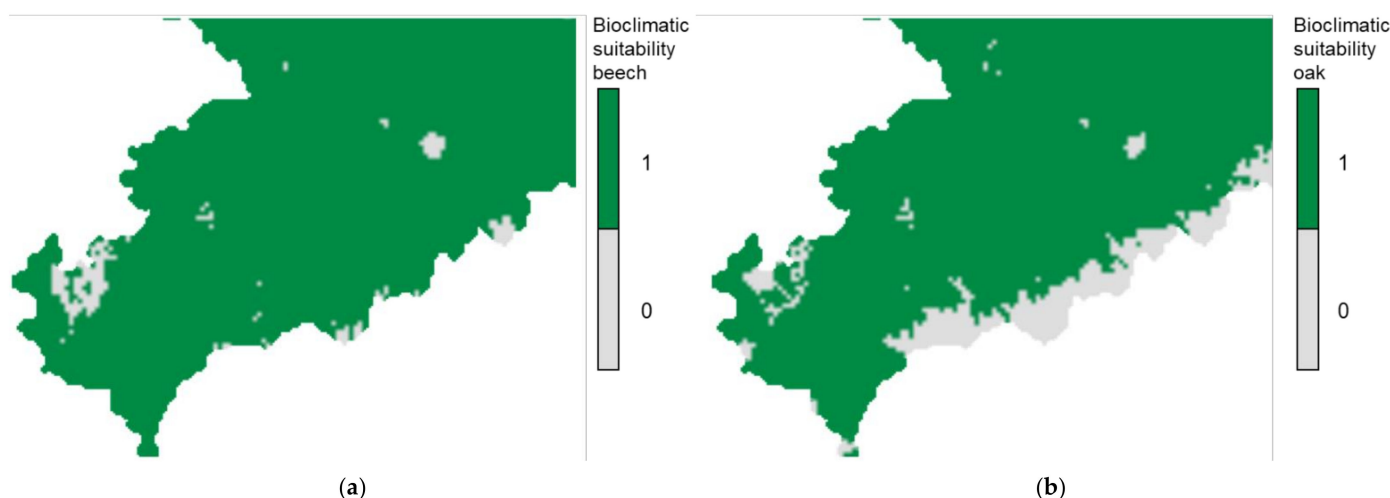


Figure 5. Spatial prediction for the bioclimatic suitability of beech regeneration (a) and oak regeneration (b) of size class B0 for a part of the study area. The value 1 means bioclimatic suitability.

The change in climatic suitability for the two tree species in the future is shown in the Supplementary Material. Since a large part of the future climate in the project area lies outside our previous data range (Supplementary Material, Figure S2 and Table S2), a comparison was made with literature data (Supplementary Material, Figure S3) [74,75]. The climatic suitability for the two tree species changes in the course of projected climate change (Supplementary Material, Figure S4). Depending on the climate projection, oak can even expand its climatically suitable area. In Supplementary Material, Figure S4 shows a decline in the climatically suitable area for beech in the lower altitudes.

3.2. Potential Dispersal of Oak and Beech

As can be seen from Figure 6, the 996th quantile regression demonstrated a clear relationship between the potential natural regeneration density of beech and oak and the distance to the nearest seed source. The potential regeneration density of beech was highest in the immediate vicinity of the seed source and is 12,300 seedlings per ha. At longer distances, the predicted potential regeneration density decreased strongly. At a distance of 500 m, only 2500 beech seedlings per ha were predicted. At 1000 m, the potential regeneration density has dropped to 740 plants per ha. From the figures, it is apparent that, from 2000 m on, no more beech regeneration is predicted.

The maximum potential regeneration density of oak is not predicted in the direct vicinity of seed trees, but at a distance of approximately 120 m from the nearest oak. The potential regeneration density here is 9000 oaks per ha. With increasing distance, the potential regeneration density decreases again. At a distance of 500 m, 6000 oak seedlings per ha were determined. As the distance increases, the potential regeneration density decreases further. At a distance of 1500 m, 1600 oaks per ha are predicted. After that, the regeneration density decreases further.

According to the location of potential seed trees in the study area, predictions on the potential regeneration density can be made using distance calculations for the entire study area. Figure 7 shows the potential regeneration density for both tree species for a part of the study area. Areas can be identified where natural regeneration of beech and oak can potentially establish in a certain density according to the distance to seed trees. Especially in the vicinity of beech and oak trees, a high potential regeneration density is predicted. At the same time, areas can be identified where, due to limited seed availability, no natural regeneration will occur despite suitable environmental conditions.

The dispersal distance of oak is greater than the dispersal distance of beech (Figure 6). From seed trees, oak can disperse in varying densities throughout almost the entire study area (Figure 7). However, at the distribution edge of the oak, in the higher altitudes of the Ore mountains, the distances to seed trees would be very large. In these areas, oak regeneration will not be able to spread because the distances required are too large. Although the dispersal distances of beech are generally smaller, beech can potentially disperse in the higher parts of the Ore mountains. In the Ore mountains are more beech stands, and the distances to potential regeneration places are thus shorter. At the same time, it is evident that there are many areas, particularly in lower elevations, where beech potentially cannot disperse due to too great distances to the nearest seed tree.

Taking into account the predicted data, we can surmise that the impact of seed tree fragmentation is more evident for beech than for oak.

3.3. Difference Due to Migration Restrictions

After examining the potential distribution that would be possible due to climatic conditions without dispersal restrictions (Figure 5), as well as the potential dispersal given the location of seed trees (Figure 7) of the two species, the extent to which the two species may colonise the potential distribution area by migration was examined in a third step (Figure 3).

Figure 8 shows whether there is both current climatic suitability and potential dispersal starting from fragmented seed sources. Compared to the climatic distribution of beech regeneration, the actual possible distribution of the beech regeneration is reduced by the lower dispersal distance and fragmented seed trees (Table S3). There are just a few areas where a climatic limitation of distribution occurs.

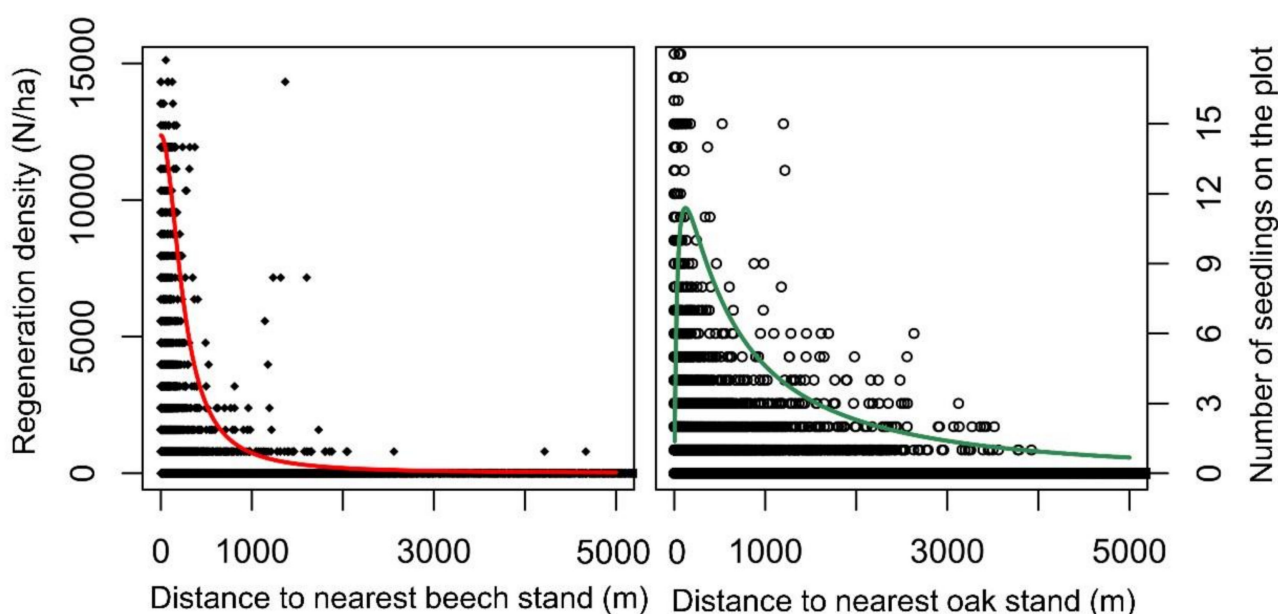


Figure 6. Regeneration density as a function of distance to the nearest seed tree for beech (left) and oak (right). The graphs show the result of the 99th quantile regression.

In the case of oak regeneration, on the other hand, there is a climatic limitation and dispersal limitation on the ridges in the Ore mountains. At the same time, it becomes apparent that there are areas that are climatically suitable, but there are no seed trees in sufficient proximity (Figure 8 and Table S3). Furthermore, there are areas where oak can potentially disperse, but where it is currently too cold. Predictions of potential climatic suitability under climate change scenarios indicate that this will change in the future (Figures S2 and S3). In the lower and middle altitudes of the Ore mountains, oak regeneration can potentially establish almost everywhere, based on climatic factors and distances to seed sources.

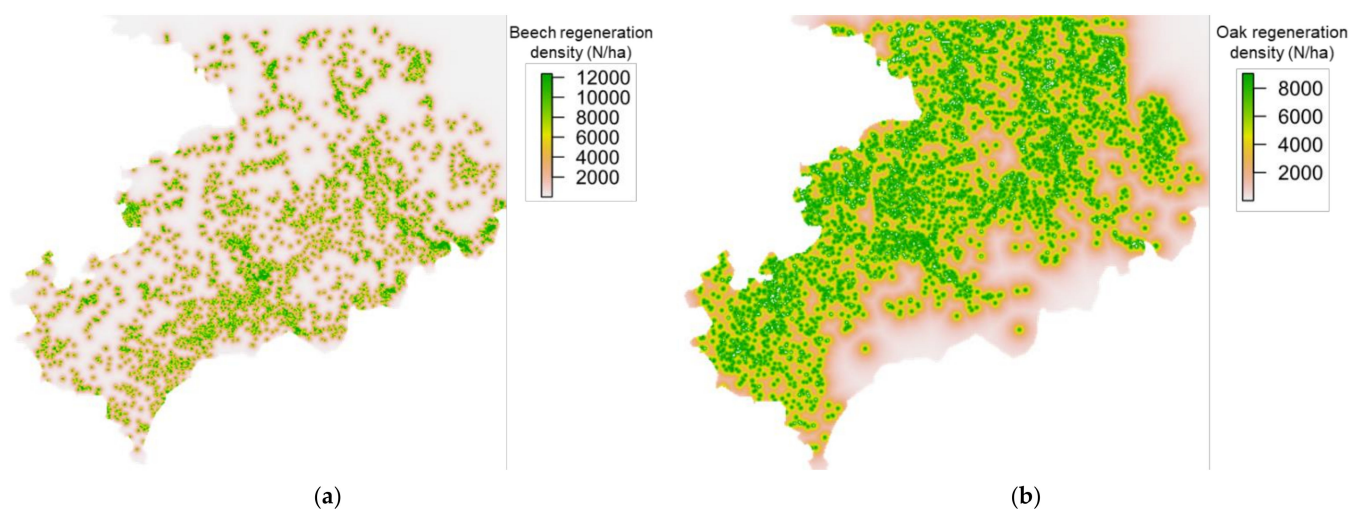


Figure 7. Spatial prediction for the potential regeneration density of beech (a) and oak (b) for a partial section of the study area.

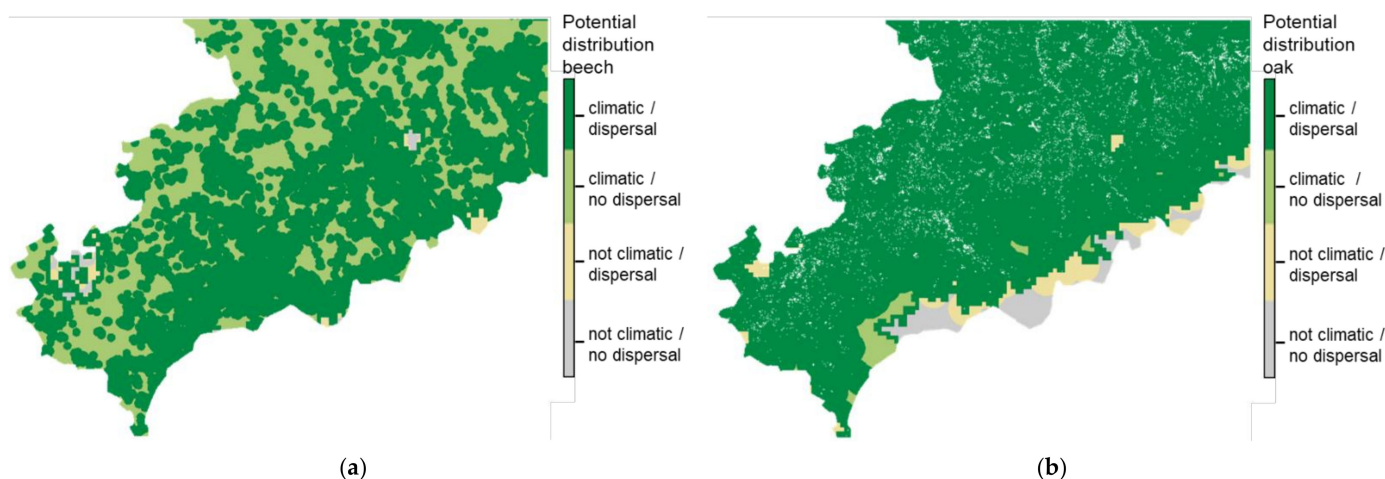


Figure 8. Result of climatic suitability and potential dispersal on the actual potential establishment of natural regeneration size class B0 for beech (a) and oak (b).

4. Discussion

4.1. Methodological Discussion

The study area shows a large variation within precipitation and temperature due to the different altitudes and windward and leeward effects (Figure 2). As highlighted by Dobrowski et al. [76], the process of distribution change can be observed particularly well in the mountains, since a change in abiotic conditions already takes place at small geographical distances. The increase in the predicted mean annual temperature is accompanied by a reduction in annual precipitation, depending on the RCP scenario (Figure S1) and will increase the probability of long and intense summer droughts in the study area. This shifts the climatic conditions in the study area to such an extent that a large part of it lies outside the current data range of the climatic envelopes of both species (Figure S2 and Table S2). As there is no directly comparable research on bioclimatic envelopes of beech and oak regeneration, our own results are compared with results from climatic envelopes of adult trees in Section 4.2.: “The bioclimatic suitability of beech and oak” [2,74,75]. In this way, it was also possible to make a prediction for the areas that were not represented by our data basis for the different scenarios (Figure S3).

The informative value of bioclimatic envelopes has been discussed for years and Pearson and Dawson [36], as well as Araújo and Peterson [77], provide a comprehensive

overview of this methodology. Although it is to be expected that the regeneration envelope is different from the adult envelope [29], the differences we observed in the climatic envelope between life stages suggest that tree populations respond to climatic changes. Furthermore, we assume that seedling establishment is an important stage in the regeneration cycle for the species [78]. The comparison of the bioclimatic envelopes of the different regeneration stages is based on the assumption that regeneration of the smallest size class has established under the most recently prevailing climatic conditions. This procedure thus creates a theoretical time series of different size classes. More accurate results are provided by real time series in the form of a repeated inventory [33]. However, there are also several studies that use different stages for the analysis [27–29,32,79].

Rather than informing where distribution may increase for the tree species, our approach provides geographically referenced matches between suitable climate conditions and potential tree species dispersal (Figures 3 and 8). It is a well-known fact that dispersal and habitat connectivity often limit the distribution of species from reaching some habitable areas [16,17,21,42]. Biotic interactions, including interspecific competition or human impacts, can further prevent establishment in some areas [42,47,77,80–83]. Limited dispersal can cause an imbalance in distribution between climatically suitable and actually accessible areas [38,84]. For example, Svenning et al. [85] found that the distribution ranges of many widespread forest plant species are probably still moderately to strongly limited by postglacial migration lag. A comparison of the European and North American tree species composition shows that the postglacial migration has a decisive influence on today's tree species composition [19]. However, as can be seen from Seaborn et al. [47], few published studies used dispersal data to model species distribution. The lack of studies suggests that dispersal data for the species are lacking, as parameter estimation of long-distance dispersal events is difficult [86]. By using a quantile regression, the potential dispersal of species can be determined by indirect variables, such as the distance to the nearest seed tree on the basis of inventory data [69].

From the previous discussion, it is obvious that changes in distribution can only occur when both climatic suitability and potential dispersal overlap [73,87]. We believe that our study will improve the ecological understanding of these two factors. Since regeneration of the small size classes had larger bioclimatic envelopes and developed in cooler-humid climatic areas, the influence of climate change on the establishment of regeneration might be inferred. There might also be processes that lead to the die-back of the larger regeneration [8,10,11]. From an ecological perspective, this area is repeatedly entered by the tree species. However, it is uncertain whether they will establish to larger size classes under the current climate. Therefore, through the process of dispersal, there is a scanning of the environmental conditions. If climatic conditions change positively for the tree species, regeneration can then be established.

4.2. Bioclimatic Suitability of Beech and Oak

Evidence from numerous studies suggests that the ranges of temperate tree species are strongly constrained by physiological thresholds of cold in winter and heat and drought during the growing season [88–91]. Gómez-Aparicio et al. [92] reported the occurrence of beech in Spain with rainfall of more than 587 mm and mean annual temperatures of up to 13.7 °C. Zimmermann et al. [93] estimated a critical precipitation amount for beech at 600–640 mm. This is in agreement with our observation that beech regeneration only occurs down to 685 mm while oak regeneration occurs down to 633 mm annual precipitation (Figure 4). The examples given above prove that different water storage capacities of the soils are probably the reason for different critical rainfall amounts in the studies, which are partly said to be as low as 550 mm [8,74].

The larger bioclimatic envelopes of beech in the overstorey could be attributed to their establishment when climatic conditions were better for beech (Figure 4) and to human impact. As work by Di Filippo et al. [94] indicates, drought can increase the mortality of old beech trees. In addition, further work shows the sensitivity of summer drought on beech

growth [95–100]. For beech regeneration, the negative influence of drought has also been demonstrated by Silva et al. [78] and Muffler et al. [101]. The smaller envelopes for beech regeneration compared to the overstorey indicate a reduction in the distribution area in the drier region (Figure 4). A decline in the population at the edge of the beech distribution is well supported in some studies [24,95]. Temperatures will rise and precipitation will decrease in these regions (Figure S1), so the behaviour of beech regeneration cannot be accurately derived from our data (Figure S2). In accordance with our results (Table S2), Walentowski et al. [102] was able to demonstrate that beech exceeds its climatic range in 44% of the climate change scenarios. As predicted in Figure S4, Cheaib et al. [103] could also detect a significant decline in the distribution area of beech in future climate projections.

As the current climatic suitability shows, aside from the dry areas previously mentioned, beech regeneration cannot establish in the highest altitudes of the Ore mountains (Figure 5). The now given limiting factor frost will probably be of lower importance in future in the higher altitudes in the Ore mountains due to climate change (Figure S1). Numerous studies prove the late frost sensitivity of beech trees [8,104–106]. Warmer temperatures increase the likelihood of successful fruiting and reduce the likelihood of late frost damage to the leaves within the regeneration cycle. An actual shift in altitude in the occurrence of beech regeneration and old trees has been demonstrated by Peñuelas et al. [34] and Vitasse et al. [27]. Consistent with the findings of Saltré et al. [81] and Machar et al. [107], as well as Pavlović et al. [108], beech will probably also be able to establish in the higher areas of the Ore mountains (Figure S2). Similar to the altitudinal shift, an extension of the distribution northwards was also proven by several studies [43,109,110].

While beech recently showed a reduction of the climatic envelope in Saxony, the climatic envelope of oak regeneration increased compared to the overstorey's envelope (Figure 4). This shape of the graph could indicate climatic conditions that are becoming more favourable for the oak regeneration today. Compared to beech regeneration, oak regeneration shows more tolerance in dry areas (Figure 4). Previous studies reveal that oak can occur beyond our covered data range of 633 mm, even with annual precipitation of 450 or 461 mm [74,92]. Märkel and Doloss [111] also showed the highest probability of occurrence at warm temperatures and low-to-medium annual precipitation. Furthermore, dendroecological studies have found a high drought tolerance for oak compared to beech [93,112–115].

While beech regeneration was also detected in areas of 4.26 °C annual mean temperature, oak regeneration only reaches areas with 6.08 °C. This is in agreement with Gómez-Aparicio et al. [92], who detected pedunculate oak occurrence at a range of 6.4 to 14.7 °C. Since oak is not yet able to establish in the higher altitudes of the Ore mountains due to harsh conditions (Figure 5), it will be able to significantly extend its distribution in the course of climate change (Figure S2 and Table S2) due to its very good spreading ability. At the same time, oak will not exceed its distribution limit on many lowland sites [102]. For the central European oak species, Zimmermann et al. [41] and Machar et al. [107] were able to determine a clear expansion of distribution in their study area in the course of climate change, as in this study. Furthermore, Dyderski et al. [116] was able to predict range shifts of the oak for central Europe.

From the aforementioned discussion, it is evident how the potential distributions of beech and oak are shifting (Figure S3). If both species occur in the same area, there is also interspecific competition between them. According to Mette et al. [117], the dominance of beech declines in favour of oak at mean annual temperatures between 11 and 12 °C and precipitation totals between 500 and 530 mm. For the management, this results in decisive findings for the tree species selection. Based on the sensitivity that regeneration shows to climatic variables, the future tree species composition can be better estimated. The extent to which natural regeneration of beech and oak is possible in climatically suitable areas or whether assisted migration in the form of artificial regeneration must be applied will be discussed below.

4.3. Potential Dispersal and Consideration of Seed Tree Fragmentation

While climate has long been considered the main driver of species distribution, several studies indicate that the role of dispersal may have been underestimated [38,42,85]. As discussed in the previous section, there is evidence in the data to suggest range shifts of regeneration compared to the overstorey. Given the rapidity of climatic changes (Figure S1), the dispersal potential of the species is crucial for adaptation [118] since the dispersal of species initiates important ecological and evolutionary processes [119].

It is clearly visible in Figure 6 that the dispersal potential of oak exceeds the dispersal potential of beech. Although the distances to the nearest oaks are greater than for beech, these areas can potentially be colonised due to the large dispersal potential (Figure 7). Several previous studies on the dispersal and especially the long-distance dispersal of the two species confirm our finding [55,56,69,120–124]. Foraging behaviour and habitat use are decisive for long-distance dispersal [125]. While mice transport beechnuts and acorns only a maximum of 30–130 m [50,126,127], larger transport distances have been shown for birds [48,54]. For the dispersal of beechnuts, the marsh tit (*Parus palustris* L.), the nuthatch (*Sitta europaea* L.) and the European jay (*Garrulus glandarius* L.) are possible zoochorous vectors [48,128–130]. In the case of acorn dispersal, the jay is probably the main vector [131], although other vectors were detected [57,132,133]. The greater dispersal distances of oak regeneration result from the jay's preference for acorns over beechnuts [48,134]. In any case, seed dispersal behaviour of the zoochorous vector is strongly dependent on the habitat [54–56]. Evidence from tropical forests shows that fragmentation reduces the movement of seed-bearing animals that are associated to specific habitats [135].

For the management, the dispersal potential and the fragmented seed trees indicate the need for landscape corridors and assisted migration [136,137]. Due to the limited seed dispersal potential and fragmentation of the seed trees, there are some areas that cannot be colonised by beech as well as by oak (Figure 7), although they are partly climatically suitable (Figure 8 and Table S3). Human-influenced landscapes have artificial barriers through habitat fragmentation that act as a barrier to species dispersal [138,139]. As the landscape is fragmented, it contains fewer individuals that produce seeds [43]. At the same time, this greatly increases the distance to the seed trees.

As a result, the expansion of beech in particular is reduced [140,141]. Our findings are partially in line with Meier et al. [43] and Saltré et al. [84] that, due to the low dispersal potential and slow demography of beech, the recolonisation rate of newly climatically suitable habitats turns out to be very low. The discrepancy between the palaeontological migration rates of beech and oak [13,17,18,20,21] and Meier et al.'s [43] results suggest an underestimation of the potential dispersal of the species due to a lack of methodological consideration of long-distance dispersal. However, rare long-distance dispersal events recorded by our methodology are very important for reaching patches with favourable habitats [15]. For oak species, García-Valdés et al. [82] were able to show that dispersal was the most important predictor of colonisation.

Studies of long-distance gene flow (i.e., consisting of pollen and seed dispersal) confirm that genes can move within a generation over spatial scales larger than the habitat shifts predicted under climate change [142]. Further, genetic studies demonstrate dispersal leading to considerable distances [53,123]. However, genetic studies also show that populations differ from each other due to fragmentation [118,143]. As a result of isolation, the risk of pollination taking place between local partners or through self-pollination increases [144].

In addition to the areas that cannot be reached so far due to the distance to seed trees, there are areas, especially in the higher altitudes of the mountains, where the species can potentially disperse, but which are climatically insufficient up to now (Table S3). In the course of climate changes, it is appropriate to scientifically accompany a distribution shift in these areas. An actual observed upward shift for beech has been observed by Peñuelas et al. [34]. They were able to prove up to 100 m for the distance between the tree line and the outpost trees. Vitasse et al. [27] was able to demonstrate a dispersal of seedlings at higher altitudes compared to old trees in the case of beech and oak up to 200 m height difference.

The previous discussion reveals that the limited dispersal of beech and oak are crucial for their potential distribution. At the landscape level, seed trees should therefore be maintained as regeneration initials in order to be able to deliver the best possible adaptation to climate change. A sufficient number and distribution of seed trees as regeneration initials are therefore important at the landscape level to enable the best adaptation to climate change. Due to the greater dispersal potential of oak, a faster colonisation of climatically suitable habitats can be expected. Only a few areas can potentially not be reached by dispersal.

5. Conclusions

Our study serves as a window to understand the process of climate change on the potential distribution of oak and beech natural regeneration. The integration of a greater understanding of climatic factors on the occurrence of natural regeneration and dispersal potential increases the sustainability of management. We developed an approach to consider climatic suitability and habitat connectivity, as well as dispersal of species in distribution.

Based on distance determinations to potential seed trees and climatic suitability, spatial predictions can be made for the forest management for areas where natural regeneration can potentially establish. At the same time, areas can be determined where artificial regeneration will be necessary. Assisted migration can be planned and carried out through planting of valuable tree provenances.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/su132313067/s1>. Figure S1: Map of the spatial distribution of mean annual temperature and mean annual precipitation for the reference period (2091–2100) for the RCP scenario 2.6, the RCP 4.5 scenario and the RCP 8.5 scenario. Figure S2: Spatial prediction for the bioclimatic suitability of beech regeneration (above) and oak regeneration (down) of size class *B0* for a part of the study area. The prediction is based on mean annual temperature and mean annual precipitation for the reference period (2091–2100) for the RCP scenario 2.6, the RCP 4.5 scenario and the RCP 8.5 scenario. Figure S3: Spatial prediction for the bioclimatic suitability of beech regeneration (above) and oak regeneration (down) of size class *B0* for the study area. The prediction is based on mean annual temperature and mean annual precipitation for the reference period (2091–2100) for the RCP scenario 2.6, the RCP 4.5 scenario, the RCP 8.5 scenario and for the bioclimatic envelope of Kölling [74] and Ammer et al. [75]. Figure S4: Percentage of climatically suitable habitat of oaks and beeches projected on 1 km raster cells currently and under three future climate scenarios for the reference period 2091–2100 according to the bioclimatic envelope of Kölling [74] and Ammer et al. [75]. Table S1: Regression coefficients of the non-linear quantile regressions for beech and oak. Table S2: Current state and prediction of the bioclimatic suitability of beech regeneration and oak regeneration of size class *B0* for the study area. The prediction is based on mean annual temperature and mean annual precipitation for the reference period (2091–2100) for the RCP scenario 2.6, the RCP 4.5 scenario and the RCP 8.5 scenario. Table S3: Current state of climatic suitability and potential dispersal on the actual potential establishment of natural regeneration size class *B0* for beech and oak.

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References

1. Jones, E.W. *Quercus L.* *J. Ecol.* **1959**, *47*, 169–222. [\[CrossRef\]](#)
2. Eaton, E.; Caudullo, G.; Oliveira, S.; de Rigo, D. *Quercus robur* and *Quercus petraea* in Europe: Distribution, habitat, usage and threats. In *European Atlas of Forest Tree Species*; The Publications Office of the European Union: Luxembourg, 2016; pp. 160–163.
3. Thomson, J.D.; Weiblen, G.; Thomson, B.A.; Alfaro, S.; Legendre, P. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. *Ecology* **1996**, *77*, 1698–1715. [\[CrossRef\]](#)
4. Guthke, J.; Spethmann, W. Physiological and pathological aspects of long-term storage of acorns. *Ann. For. Sci.* **1993**, *50*, 384–387. [\[CrossRef\]](#)
5. Savill, P.S. *The Silviculture of Trees Used in British Forestry*, 3rd ed.; CABI: Wallingford, UK, 2019; Available online: http://slubdd.de/katalog?TN_libero_mab2 (accessed on 18 August 2021).
6. Peters, R. *Beech Forests*; Kluwer: Dordrecht, The Netherlands, 1997; ISBN 0169-3174.
7. Ellenberg, H.; Leuschner, C. *Vegetation Mitteleuropas Mit Den Alpen in Ökologischer, Dynamischer und Historischer SICHT*; UTB: Stuttgart, Germany, 2010; ISBN 3825281043.
8. Bolte, A.; Czajkowski, T.; Kompa, T. The north-eastern distribution range of European beech—A review. *Forestry* **2007**, *80*, 413–429. [\[CrossRef\]](#)
9. Jönsson, A.M. Soil treatment effects on bark lesions and frost sensitivity of beech (*Fagus sylvatica*) in southern Sweden. *For. Ecol. Manag.* **2000**, *129*, 167–175. [\[CrossRef\]](#)
10. Visjic, C.; Dohrenbusch, A. Frostresistenz und phänologie europäischer Buchenprovenienzen (*Fagus sylvatica* L.). *Allg. Forst-Und Jagdztg.* **2004**, *175*, 101–108.
11. Bolte, A.; Czajkowski, T.; Coccozza, C.; Tognetti, R.; de Miguel, M.; Pšidová, E.; Ditmarová, L.; Dinca, L.; Delzon, S.; Cochard, H.; et al. Desiccation and mortality dynamics in seedlings of different European beech (*Fagus sylvatica* L.) populations under extreme drought conditions. *Front. Plant Sci.* **2016**, *7*, 751. [\[CrossRef\]](#)
12. Firbas, F. *Spät- und Nacheiszeitliche Waldgeschichte Mitteleuropas Nördlich der Alpen Zweiter Band Waldgeschichte der Einzelnen Landschaften*; Fischer: Jena, Germany, 1952.
13. Huntley, B.; Bartlein, P.J.; Prentice, I.C. Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. *J. Biogeogr.* **1989**, *16*, 551–560. [\[CrossRef\]](#)
14. Penalba, M.C. The history of the Holocene vegetation in northern Spain from pollen analysis. *J. Ecol.* **1994**, *82*, 815–832. [\[CrossRef\]](#)
15. Clark, J.S.; Fastie, C.; Hurtt, G.; Jackson, S.T.; Johnson, C.; King, G.A.; Lewis, M.; Lynch, J.; Pacala, S.; Prentice, C.; et al. Reid's paradox of rapid plant migration: Dispersal theory and interpretation of paleoecological records. *Bioscience* **1998**, *48*, 13–24. [\[CrossRef\]](#)
16. Brewer, S.; Cheddadi, R.; de Beaulieu, J.L.; Reille, M. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *For. Ecol. Manag.* **2002**, *156*, 27–48. [\[CrossRef\]](#)
17. Lowe, A.; Unsworth, C.; Gerber, S.; Davies, S.; Munro, R.; Kelleher, C.; King, A.; Brewer, S.; White, A.; Cottrell, J. Route, speed and mode of oak postglacial colonisation across the British Isles: Integrating molecular ecology, palaeoecology and modelling approaches. *Bot. J. Scotl.* **2005**, *57*, 59–81. [\[CrossRef\]](#)
18. Le Corre, V.; Machon, N.; Petit, R.J.; Kremer, A. Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: A simulation study. *Genet. Res.* **1997**, *69*, 117–125. [\[CrossRef\]](#)
19. Leuschner, C.; Ellenberg, H. *Ecology of Central European Forests*; Revised and Extended Version of the 6th German edition; Springer International Publishing AG: Cham, Switzerland, 2017; ISBN 9783319430409.
20. Björkman, L. The establishment of *Fagus sylvatica* at the stand-scale in southern Sweden. *Holocene* **1999**, *9*, 237–245. [\[CrossRef\]](#)
21. López-Merino, L.; López-Sáez, J.A.; Zapata, M.R.; García, M.G. Reconstructing the history of beech (*Fagus sylvatica* L.) in the north-western Iberian Range (Spain): From Late-Glacial refugia to the Holocene anthropic-induced forests. *Rev. Palaeobot. Palynol.* **2008**, *152*, 58–65. [\[CrossRef\]](#)
22. IPCC. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the INTERGOVERNMENTAL Panel on Climate Change*; IPCC: Geneva, Switzerland, 2014; ISBN 978-92-9169-143-2.
23. Takolander, A.; Hickler, T.; Meller, L.; Cabeza, M. Comparing future shifts in tree species distributions across Europe projected by statistical and dynamic process-based models. *Reg. Environ. Chang.* **2018**, *19*, 251–266. [\[CrossRef\]](#)
24. Allen, C.D.; Macalady, A.K.; Chenchouni, H.; Bachelet, D.; McDowell, N.; Vennetier, M.; Kitzberger, T.; Rigling, A.; Breshears, D.D.; Hogg, E.T.; et al. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* **2010**, *259*, 660–684. [\[CrossRef\]](#)

25. Ruiz-Benito, P.; Ratcliffe, S.; Zavala, M.A.; Martinez-Vilalta, J.; Vilà-Cabrera, A.; Lloret, F.; Madrigal-González, J.; Wirth, C.; Greenwood, S.; Kändler, G.; et al. Climate-and successional-related changes in functional composition of European forests are strongly driven by tree mortality. *Glob. Chang. Biol.* **2017**, *23*, 4162–4176. [\[CrossRef\]](#)
26. Anderegg, W.R.L.; Anderegg, L.D.L.; Kerr, K.L.; Trugman, A.T. Widespread drought-induced tree mortality at dry range edges indicates that climate stress exceeds species' compensating mechanisms. *Glob. Chang. Biol.* **2019**, *25*, 3793–3802. [\[CrossRef\]](#) [\[PubMed\]](#)
27. Vitasse, Y.; Hoch, G.; Randin, C.F.; Lenz, A.; Kollas, C.; Körner, C. Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. *J. Biogeogr.* **2012**, *39*, 1439–1449. [\[CrossRef\]](#)
28. Zhu, K.; Woodall, C.W.; Clark, J.S. Failure to migrate: Lack of tree range expansion in response to climate change. *Glob. Chang. Biol.* **2012**, *18*, 1042–1052. [\[CrossRef\]](#)
29. Bell, D.M.; Bradford, J.B.; Lauenroth, W.K. Early indicators of change: Divergent climate envelopes between tree life stages imply range shifts in the western United States. *Glob. Ecol. Biogeogr.* **2014**, *23*, 168–180. [\[CrossRef\]](#)
30. Buras, A.; Rammig, A.; Zang, C.S. Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. *Biogeosciences* **2020**, *17*, 1655–1672. [\[CrossRef\]](#)
31. Büntgen, U.; Urban, O.; Krusic, P.J.; Rybníček, M.; Kolář, T.; Kyncl, T.; Trnka, M. Recent European drought extremes beyond Common Era background variability. *Nat. Geosci.* **2021**, *14*, 190–196. [\[CrossRef\]](#)
32. Zhu, K.; Woodall, C.W.; Ghosh, S.; Gelfand, A.E.; Clark, J.S. Dual impacts of climate change: Forest migration and turnover through life history. *Glob. Chang. Biol.* **2014**, *20*, 251–264. [\[CrossRef\]](#) [\[PubMed\]](#)
33. Rigling, A.; Bigler, C.; Eilmann, B.; Feldmeyer-Christe, E.; Gimmi, U.; Ginzler, C.; Graf, U.; Mayer, P.; Vacchiano, G.; Weber, P.; et al. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Glob. Chang. Biol.* **2013**, *19*, 229–240. [\[CrossRef\]](#)
34. Peñuelas, J.; Ogaya, R.; Boada, M.; Jump, A.S. Migration, invasion and decline: Changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* **2007**, *30*, 829–837. [\[CrossRef\]](#)
35. Niinemets, Ü. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *For. Ecol. Manag.* **2010**, *260*, 1623–1639. [\[CrossRef\]](#)
36. Pearson, R.G.; Dawson, T.P. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **2003**, *12*, 361–371. [\[CrossRef\]](#)
37. Meier, E.S.; Edwards Jr, T.C.; Kienast, F.; Dobbervin, M.; Zimmermann, N.E. Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *J. Biogeogr.* **2011**, *38*, 371–382. [\[CrossRef\]](#)
38. Saltré, F.; Saint-Amant, R.; Gritti, E.S.; Brewer, S.; Gaucherel, C.; Davis, B.A.S.; Chuine, I. Climate or migration: What limited European beech post-glacial colonization? *Glob. Ecol. Biogeogr.* **2013**, *22*, 1217–1227. [\[CrossRef\]](#)
39. Mellert, K.H.; Fensterer, V.; Küchenhoff, H.; Reger, B.; Kölling, C.; Klemmt, H.-J.; Ewald, J. Hypothesis-driven species distribution models for tree species in the Bavarian Alps. *J. Veg. Sci.* **2011**, *22*, 635–646. [\[CrossRef\]](#)
40. Gray, L.K.; Hamann, A. Tracking suitable habitat for tree populations under climate change in western North America. *Clim. Chang.* **2013**, *117*, 289–303. [\[CrossRef\]](#)
41. Zimmermann, N.E.; Jandl, R.; Hanewinkel, M.; Kunstler, G.; Kölling, C.; Gasparini, P.; Breznikar, A.; Meier, E.S.; Normand, S.; Ulmer, U.; et al. Potential future ranges of tree species in the Alps. In *Management Strategies to Adapt Alpine Space Forests to Climate Change Risks*; IntechOpen: London, UK, 2013; pp. 37–48. ISBN 9789535142409.
42. Svenning, J.-C.; Skov, F. Limited filling of the potential range in European tree species. *Ecol. Lett.* **2004**, *7*, 565–573. [\[CrossRef\]](#)
43. Meier, E.S.; Lischke, H.; Schmatz, D.R.; Zimmermann, N.E. Climate, competition and connectivity affect future migration and ranges of European trees. *Glob. Ecol. Biogeogr.* **2012**, *21*, 164–178. [\[CrossRef\]](#)
44. Neilson, R.P.; Pitelka, L.F.; Solomon, A.M.; Nathan, R.A.; Midgley, G.F.; Fragoso, J.M.V.; Lischke, H.; Thompson, K.E. Forecasting regional to global plant migration in response to climate change. *Bioscience* **2005**, *55*, 749–759. [\[CrossRef\]](#)
45. Araujo, M.B.; Guisan, A. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* **2006**, *33*, 1677–1688. [\[CrossRef\]](#)
46. Clark, C.J.; Poulsen, J.R.; Levey, D.J.; Osenberg, C.W. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *Am. Nat.* **2007**, *170*, 128–142. [\[CrossRef\]](#) [\[PubMed\]](#)
47. Seaborn, T.J.; Goldberg, C.S.; Crespi, E.J. Integration of dispersal data into distribution modeling: What have we done and what have we learned? *Front. Biogeogr.* **2020**, *12*, 1–14. [\[CrossRef\]](#)
48. Nilsson, S.G. Ecological and evolutionary interactions between reproduction of beech *Fagus sylvatica* and seed eating animals. *Oikos* **1985**, *44*, 157–164. [\[CrossRef\]](#)
49. Kollmann, J.; Schill, H.-P. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. *Vegetatio* **1996**, *125*, 193–205. [\[CrossRef\]](#)
50. Den Ouden, J.; Jansen, P.A.; Smit, R. Jays, mice and oaks: Predation and dispersal of *Quercus robur* and *Q. petraea* in North-western Europe. *Seed Fate Predation Dispersal Seedl. Establ.* **2005**, 223–240. [\[CrossRef\]](#)
51. Sagnard, F.; Pichot, C.; Dreyfus, P.; Jordano, P.; Fady, B. Modelling seed dispersal to predict seedling recruitment: Recolonization dynamics in a plantation forest. *Ecol. Model.* **2007**, *203*, 464–474. [\[CrossRef\]](#)
52. Wagner, S.; Collet, C.; Madsen, P.; Nakashizuka, T.; Nyland, R.D.; Sagheb-Talebi, K. Beech regeneration research: From ecological to silvicultural aspects. *For. Ecol. Manag.* **2010**, *259*, 2172–2182. [\[CrossRef\]](#)

53. Chybicki, I.J.; Burczyk, J. Realized gene flow within mixed stands of *Quercus robur* L. and *Q. petraea* (Matt.) L. revealed at the stage of naturally established seedling. *Mol. Ecol.* **2010**, *19*, 2137–2151. [CrossRef] [PubMed]
54. Gómez, J.M. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* **2003**, *26*, 573–584. [CrossRef]
55. Kunstler, G.; Thuiller, W.; Curt, T.; Bouchaud, M.; Jouvie, R.; Deruette, F.; Lepart, J. *Fagus sylvatica* L. recruitment across a fragmented Mediterranean Landscape, importance of long distance effective dispersal, abiotic conditions and biotic interactions. *Divers. Distrib.* **2007**, *13*, 799–807. [CrossRef]
56. Kurek, P.; Dobrowolska, D.; Wiatrowska, B. Dispersal distance and burial mode of acorns in Eurasian Jays *Garrulus glandarius* in European temperate forests. *Acta Ornithol.* **2019**, *53*, 155–162. [CrossRef]
57. Martínez-Baroja, L.; Pérez-Camacho, L.; Villar-Salvador, P.; Rebollo, S.; Quiles, P.; Gómez-Sánchez, D.; Molina-Morales, M.; Leverkus, A.B. Massive and effective acorn dispersal into agroforestry systems by an overlooked vector, the Eurasian magpie (*Pica pica*). *Ecosphere* **2019**, *10*, e02989. [CrossRef]
58. Kleinschmit, J.R.G.; Bacilieri, R.; Kremer, A.; Roloff, A. Comparison of morphological and genetic traits of pedunculate oak (*Q. robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.). *Silvae Genet.* **1995**, *44*, 256–268.
59. Hertel, H.; Degen, B. Unterscheidung von Stiel- und Traubeneichen (*Quercus robur* L. und *Q. petraea* [Mattuschka] Liebl.) mit Hilfe von genetischen und morphologischen Merkmalen. *For. Snow Landsc. Res. Birmensdorf* **2000**, *75*, 169–183.
60. Schaller, A.S.; Franke, J.; Bernhofer, C. Climate dynamics: Temporal development of the occurrence frequency of heavy precipitation in Saxony, Germany. *Meteorol. Z.* **2020**, *29*, 335–348. [CrossRef]
61. Spekat, A.; Enke, W.; Franke, J. *Regionale Klimaprojektionen für Sachsen WMSax2.0*; Sächsische Landesbibliothek—Staats- und Universitätsbibliothek Dresden: Dresden, Germany, 2020.
62. Enke, W.; Spekat, A.; Kreienkamp, F. Classification by multiple regression—a new approach towards the classification of extremes. *Meteorol. Hydrol. Water Manag. Res. Oper. Appl.* **2016**, *4*, 25–39.
63. Van Vuuren, D.P.; Edmonds, J.; Kainuma, M.; Riahi, K.; Thomson, A.; Hibbard, K.; Hurtt, G.C.; Kram, T.; Krey, V.; Lamarque, J.-F.; et al. The representative concentration pathways: An overview. *Clim. Chang.* **2011**, *109*, 5–31. [CrossRef]
64. Eddy, W.F. A new convex hull algorithm for planar sets. *ACM Trans. Math. Softw. TOMS* **1977**, *3*, 398–403. [CrossRef]
65. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2021. Available online: <https://www.R-project.org/> (accessed on 1 July 2021).
66. Bivand, R.S.; Pebesma, E.; Gomez-Rubio, V. *Applied Spatial Data Analysis with R*, 2nd ed.; Springer: New York, NY, USA, 2013.
67. Hoffmann, K.; Coenradie, B.; Haag, L.; Nitzsche, V. Sachsenforst setzt auf Fernerkundung: Sachsens forstliche Praxis nutzt mit großem Erfolg Daten aus der Fernerkundung. *LWF Aktuell* **2017**, *4*, 26–29.
68. Bivand, R.; Rundel, C. rgeos: Interface to Geometry Engine—Open Source (‘GEOS’). 2019. Available online: <https://CRAN.R-project.org/package=rgeos> (accessed on 1 October 2021).
69. Axer, M.; Schlicht, R.; Wagner, S. Modelling potential density of natural regeneration of European oak species (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) depending on the distance to the potential seed source: Methodological approach for modelling dispersal from inventory data at forest enterprise level. *For. Ecol. Manag.* **2021**, *482*, 118802. [CrossRef]
70. Fahrmeir, L.; Kneib, T.; Lang, S.; Marx, B. *Regression Models, Methods and Applications*; Springer: Berlin/Heidelberg, Germany, 2013; ISBN 3642343333.
71. Stoyan, D.; Wagner, S. Estimating the fruit dispersion of anemochorous forest trees. *Ecol. Model.* **2001**, *145*, 35–47. [CrossRef]
72. Clark, J.S.; Silman, M.; Kern, R.; Macklin, E.; HilleRisLambers, J. Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* **1999**, *80*, 1475–1494. [CrossRef]
73. Soberón, J.; Peterson, A.T. Interpretation of models of fundamental ecological niches and species’ distributional areas. *Biodivers. Inform.* **2005**, *2*, 1–10. [CrossRef]
74. Kölling, C. Klimahüllen für 27 Waldbaumarten. *AFZ-DerWald* **2007**, *23*, 1242–1245.
75. Ammer, C.; Bickel, E.; Kölling, C. Converting Norway spruce stands with beech—a review of arguments and techniques. *Austrian J. For. Sci.* **2008**, *125*, 3–26. [CrossRef]
76. Dobrowski, S.Z.; Abatzoglou, J.; Swanson, A.K.; Greenberg, J.A.; Mynsberge, A.R.; Holden, Z.A.; Schwartz, M.K. The climate velocity of the contiguous United States during the 20th century. *Glob. Chang. Biol.* **2013**, *19*, 241–251. [CrossRef]
77. Araújo, M.B.; Peterson, A.T. Uses and misuses of bioclimatic envelope modeling. *Ecology* **2012**, *93*, 1527–1539. [CrossRef]
78. Silva, D.; Rezende Mazzella, P.; Legay, M.; Corcket, E.; Dupouey, J.L. Does natural regeneration determine the limit of European beech distribution under climatic stress? *For. Ecol. Manag.* **2012**, *266*, 263–272. [CrossRef]
79. Woodall, C.W.; Zhu, K.; Westfall, J.A.; Oswalt, C.M.; D’amato, A.W.; Walters, B.F.; Lintz, H.E. Assessing the stability of tree ranges and influence of disturbance in eastern US forests. *For. Ecol. Manag.* **2013**, *291*, 172–180. [CrossRef]
80. Monsimet, J.; Devineau, O.; Petillon, J.; Lafage, D. Explicit integration of dispersal-related metrics improves predictions of SDM in predatory arthropods. *Sci. Rep.* **2020**, *10*, 16668. [CrossRef] [PubMed]
81. Muñoz Sobrino, C.; Ramil-Rego, P.; Gómez-Orellana, L.; Da Ferreira Costa, J.; Díaz Varela, R.A. Climatic and human effects on the post-glacial dynamics of *Fagus sylvatica* L. in NW Iberia. *Plant Ecol.* **2009**, *203*, 317–340. [CrossRef]
82. GARCÍA-VALDÉS, R.; Gotelli, N.J.; Zavala, M.A.; Purves, D.W.; Araújo, M.B. Effects of climate, species interactions, and dispersal on decadal colonization and extinction rates of Iberian tree species. *Ecol. Model.* **2015**, *309–310*, 118–127. [CrossRef]

83. Liang, Y.; Duveneck, M.J.; Gustafson, E.J.; Serra-Diaz, J.M.; Thompson, J.R. How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. *Glob. Chang. Biol.* **2018**, *24*, e335–e351. [\[CrossRef\]](#)
84. Saltré, F.; Duputié, A.; Gaucherel, C.; Chuine, I. How climate, migration ability and habitat fragmentation affect the projected future distribution of European beech. *Glob. Chang. Biol.* **2015**, *21*, 897–910. [\[CrossRef\]](#)
85. Svenning, J.-C.; Normand, S.; Skov, F. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography* **2008**, *31*, 316–326. [\[CrossRef\]](#)
86. Nathan, R. Long-distance dispersal of plants. *Science* **2006**, *313*, 786–788. [\[CrossRef\]](#)
87. Peterson, A.T.; Soberón, J.; Pearson, R.G.; Anderson, R.P.; Martínez-Meyer, E.; Nakamura, M.; Araújo, M.B. Ecological Niches and Geographic Distributions. Princeton University Press: New Jersey, NJ, USA, 2011; Volume 49. [\[CrossRef\]](#)
88. Woodward, F.I.; Woodward, F.I. *Climate and Plant Distribution*; Cambridge University Press: Cambridge, UK, 1987.
89. Tranquillini, W.; Plank, A. Ecophysiological investigations on beech at various altitudes in northern and southern Tyrol. *Centralblatt für das Gesamte Forstwesen* **1989**, *106*, 225–246.
90. Sykes, M.T.; Prentice, I.C.; Cramer, W. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J. Biogeogr.* **1996**, *23*, 203–233.
91. Chuine, I.; Beaubien, E.G. Phenology is a major determinant of tree species range. *Ecol. Lett.* **2001**, *4*, 500–510. [\[CrossRef\]](#)
92. Gómez-Aparicio, L.; García-Valdés, R.; Ruiz-Benito, P.A.; Zavala, M. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. *Glob. Chang. Biol.* **2011**, *17*, 2400–2414. [\[CrossRef\]](#)
93. Zimmermann, J.; Hauck, M.; Dulamsuren, C.; Leuschner, C. Climate Warming-Related Growth Decline Affects *Fagus sylvatica*, But Not Other Broad-Leaved Tree Species in Central European Mixed Forests. *Ecosystems* **2015**, *18*, 560–572. [\[CrossRef\]](#)
94. Di Filippo, A.; Biondi, F.; Maugeri, M.; Schirone, B.; Piovesan, G. Bioclimate and growth history affect beech lifespan in the Italian Alps and Apennines. *Glob. Chang. Biol.* **2012**, *18*, 960–972. [\[CrossRef\]](#)
95. Jump, A.S.; Hunt, J.M.; Penuelas, J. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Chang. Biol.* **2006**, *12*, 2163–2174. [\[CrossRef\]](#)
96. Geßler, A.; Keitel, C.; Kreuzwieser, J.; Matyssek, R.; Seiler, W.; Rennenberg, H. Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees* **2006**, *21*, 35303. [\[CrossRef\]](#)
97. van der Maaten, E. Climate sensitivity of radial growth in European beech (*Fagus sylvatica* L.) at different aspects in southwestern Germany. *Trees* **2012**, *26*, 777–788. [\[CrossRef\]](#)
98. Müller-Haubold, H.; Hertel, D.; Seidel, D.; Knutzen, F.; Leuschner, C. Climate Responses of Aboveground Productivity and Allocation in *Fagus sylvatica*: A Transect Study in Mature Forests. *Ecosystems* **2013**, *16*, 1498–1516. [\[CrossRef\]](#)
99. Scharnweber, T.; Manthey, M.; Criegee, C.; Bauwe, A.; Schröder, C.; Wilmking, M. Drought matters—Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *For. Ecol. Manag.* **2011**, *262*, 947–961. [\[CrossRef\]](#)
100. Kunz, J.; Löffler, G.; Bauhus, J. Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. *For. Ecol. Manag.* **2018**, *414*, 15–27. [\[CrossRef\]](#)
101. Muffler, L.; Schmeddes, J.; Weigel, R.; Barbata, A.; Beil, I.; Bolte, A.; Buhk, C.; Holm, S.; Klein, G.; Klisz, M.; et al. High plasticity in germination and establishment success in the dominant forest tree *Fagus sylvatica* across Europe. *Glob. Ecol. Biogeogr.* **2021**, *30*, 1583–1596. [\[CrossRef\]](#)
102. Walentowski, H.; Falk, W.; Mette, T.; Kunz, J.; Bräuning, A.; Meinardus, C.; Zang, C.; Sutcliffe, L.M.; Leuschner, C. Assessing future suitability of tree species under climate change by multiple methods: A case study in southern Germany. *Ann. For. Res.* **2017**, *60*, 101–126. [\[CrossRef\]](#)
103. Cheaib, A.; Badeau, V.; Boe, J.; Chuine, I.; Delire, C.; Dufrêne, E.; François, C.; Gritti, E.S.; Legay, M.; Pagé, C.; et al. Climate change impacts on tree ranges: Model intercomparison facilitates understanding and quantification of uncertainty. *Ecol. Lett.* **2012**, *15*, 533–544. [\[CrossRef\]](#)
104. Dittmar, C.; Elling, W. Phenological phases of common beech (*Fagus sylvatica* L.) and their dependence on region and altitude in Southern Germany. *Eur. J. For. Res.* **2006**, *125*, 181–188. [\[CrossRef\]](#)
105. Dittmar, C.; Fricke, W.; Elling, W. Impact of late frost events on radial growth of common beech (*Fagus sylvatica* L.) in Southern Germany. *Eur. J. For. Res.* **2006**, *125*, 249–259. [\[CrossRef\]](#)
106. Kreyling, J.; Thiel, D.; Nagy, L.; Jentsch, A.; Huber, G.; Konnert, M.; Beierkuhnlein, C. Late frost sensitivity of juvenile *Fagus sylvatica* L. differs between southern Germany and Bulgaria and depends on preceding air temperature. *Eur. J. For. Res.* **2012**, *131*, 717–725. [\[CrossRef\]](#)
107. Machar, I.; Vlckova, V.; Bucek, A.; Vozenilek, V.; Salek, L.; Jerabkova, L. Modelling of Climate Conditions in Forest Vegetation Zones as a Support Tool for Forest Management Strategy in European Beech Dominated Forests. *Forests* **2017**, *8*, 82. [\[CrossRef\]](#)
108. Pavlović, L.; Stojanović, D.; Mladenović, E.; Lakićević, M.; Orlović, S. Potential Elevation Shift of the European Beech Stands (*Fagus sylvatica* L.) in Serbia. *Front. Plant Sci.* **2019**, *10*, 849. [\[CrossRef\]](#)
109. Kramer, K.; Degen, B.; Buschbom, J.; Hickler, T.; Thuiller, W.; Sykes, M.T.; de Winter, W. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change—Range, abundance, genetic diversity and adaptive response. *For. Ecol. Manag.* **2010**, *259*, 2213–2222. [\[CrossRef\]](#)

110. Thurm, E.A.; Hernandez, L.; Baltensweiler, A.; Ayan, S.; Rasztoivits, E.; Bielak, K.; Zlatanov, T.M.; Hladnik, D.; Balic, B.; Freudenschuss, A.; et al. Alternative tree species under climate warming in managed European forests. *For. Ecol. Manag.* **2018**, *430*, 485–497. [\[CrossRef\]](#)
111. Märkel, U.; Dolos, K. Tree Species Site Suitability as a Combination of Occurrence Probability and Growth and Derivation of Priority Regions for Climate Change Adaptation. *Forests* **2017**, *8*, 181. [\[CrossRef\]](#)
112. Friedrichs, D.A.; Trouet, V.; Büntgen, U.; Frank, D.C.; Esper, J.; Neuwirth, B.; Löffler, J. Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees* **2009**, *23*, 729–739. [\[CrossRef\]](#)
113. Michelot, A.; Bréda, N.; Damesin, C.; Dufrêne, E. Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *For. Ecol. Manag.* **2012**, *265*, 161–171. [\[CrossRef\]](#)
114. Nechita, C.; Popa, I.; Eggertsson, Ó. Climate response of oak (*Quercus* spp.), an evidence of a bioclimatic boundary induced by the Carpathians. *Sci. Total Environ.* **2017**, 599–600, 1598–1607. [\[CrossRef\]](#)
115. Árvai, M.; Morgós, A.; Kern, Z. Growth-climate relations and the enhancement of drought signals in pedunculate oak (*Quercus robur* L.) tree-ring chronology in Eastern Hungary. *IFor. Biogeosci. For.* **2018**, *11*, 267–274. [\[CrossRef\]](#)
116. Dyderski, M.K.; Paž, S.; Frelich, L.E.; Jagodziński, A.M. How much does climate change threaten European forest tree species distributions? *Glob. Chang. Biol.* **2018**, *24*, 1150–1163. [\[CrossRef\]](#) [\[PubMed\]](#)
117. Mette, T.; Dolos, K.; Meinardus, C.; Bräuning, A.; Reineking, B.; Blaschke, M.; Pretzsch, H.; Beierkuhnlein, C.; Gohlke, A.; Wellstein, C. Climatic turning point for beech and oak under climate change in Central Europe. *Ecosphere* **2013**, *4*, 1–19. [\[CrossRef\]](#)
118. Sork, V.L.; Davis, F.W.; Westfall, R.; Flint, A.; Ikegami, M.; Wang, H.; Grivet, D. Gene movement and genetic association with regional climate gradients in California valley oak (*Quercus lobata* Née) in the face of climate change. *Mol. Ecol.* **2010**, *19*, 3806–3823. [\[CrossRef\]](#) [\[PubMed\]](#)
119. García, C.; Klein, E.K.; Jordano, P. Dispersal processes driving plant movement: Challenges for understanding and predicting range shifts in a changing world. *J. Ecol.* **2017**, *105*, 1–5. [\[CrossRef\]](#)
120. Oddou-Muratorio, S.; Bontemps, A.; Klein, E.K.; Chybicki, I.; Vendramin, G.G.; Suyama, Y. Comparison of direct and indirect genetic methods for estimating seed and pollen dispersal in *Fagus sylvatica* and *Fagus crenata*. *For. Ecol. Manag.* **2010**, *259*, 2151–2159. [\[CrossRef\]](#)
121. Dobrovolny, L.; Tesář, V. Extent and distribution of beech (*Fagus sylvatica* L.) regeneration by adult trees individually dispersed over a spruce monoculture. *J. For. Sci.* **2010**, *56*, 589–599. [\[CrossRef\]](#)
122. Millerón, M.; Lopez de Heredia, U.; Lorenzo, Z.; Alonso, J.; Dounavi, A.; Gil, L.; Nanos, N. Assessment of spatial discordance of primary and effective seed dispersal of European beech (*Fagus sylvatica* L.) by ecological and genetic methods. *Mol. Ecol.* **2013**, *22*, 1531–1545. [\[CrossRef\]](#) [\[PubMed\]](#)
123. Gerber, S.; Chadeuf, J.; Gugerli, F.; Lascoux, M.; Buiteveld, J.; Cottrell, J.; Dounavi, A.; Fineschi, S.; Forrest, L.L.; Fogelqvist, J.; et al. High rates of gene flow by pollen and seed in oak populations across Europe. *PLoS ONE* **2014**, *9*, e85130. [\[CrossRef\]](#)
124. Gerzabek, G.; Oddou-Muratorio, S.; Hampe, A. Recruitment of a genotyped *Quercus robur* L. seedling cohort in an expanding oak forest stand: Diversity, dispersal, and performance across habitats. *Ann. For. Sci.* **2020**, *77*, 78. [\[CrossRef\]](#)
125. Löf, M.; Ammer, C.; Coll, L.; Drössler, L.; Huth, F.; Madsen, P.; Wagner, S. Regeneration Patterns in Mixed-Species Stands. In *Dynamics, Silviculture and Management of Mixed Forests*; Springer: Berlin, Germany, 2018; pp. 103–130.
126. Jensen, T.S. Seed-seed predator interactions of European beech, *Fagus sylvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos* **1985**, *44*, 149–156. [\[CrossRef\]](#)
127. Perea, R.; Miguel, A.S.; Gil, L. Acorn dispersal by rodents: The importance of re-dispersal and distance to shelter. *Basic Appl. Ecol.* **2011**, *12*, 432–439. [\[CrossRef\]](#)
128. Turcek, F.J. *Ökologische Beziehungen der Vögel und Gehölze*; Verlag der Slowakischen Akademie der Wissenschaften: Bratislava, Slovakia, 1961.
129. Moreno, J.; Lundberg, A.; Carlson, A. Hoarding of individual nuthatches *Sitta europaea* and march tits *Parus palustris*. *Ecography* **1981**, *4*, 263–269. [\[CrossRef\]](#)
130. Amann, F. Balzfüttern, Nahrung und Samenverstecken bei der Sumpfmehse *Parus palustris*. *Der Ornithol. Beob.* **2007**, *104*, 91–100.
131. Bossema, I. Jays and oaks: An eco-ethological study of a symbiosis. *Behaviour* **1979**, *70*, 1–116. [\[CrossRef\]](#)
132. Mellanby, K. The effects of some mammals and birds on regeneration of oak. *J. Appl. Ecol.* **1968**, *5*, 359–366. [\[CrossRef\]](#)
133. Pesendorfer, M.B.; Sillett, T.S.; Koenig, W.D.; Morrison, S.A. Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. *Condor Ornithol. Appl.* **2016**, *118*, 215–237. [\[CrossRef\]](#)
134. Perea, R.; San Miguel, A.; Gil, L. Flying vs. climbing: Factors controlling arboreal seed removal in oak-beech forests. *For. Ecol. Manag.* **2011**, *262*, 1251–1257. [\[CrossRef\]](#)
135. Cramer, J.M.; Mesquita, R.C.; Bruce Williamson, G. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biol. Conserv.* **2007**, *137*, 415–423. [\[CrossRef\]](#)
136. Krosby, M.; Tewksbury, J.; Haddad, N.M.; Hoekstra, J. Ecological connectivity for a changing climate. *Conserv. Biol.* **2010**, *24*, 1686–1689. [\[CrossRef\]](#)
137. Vitt, P.; Havens, K.; Kramer, A.T.; Sollenberger, D.; Yates, E. Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biol. Conserv.* **2010**, *143*, 18–27. [\[CrossRef\]](#)

-
138. Malanson, G.P.; Armstrong, M.P. Dispersal probability and forest diversity in a fragmented landscape. *Ecol. Model.* **1996**, *87*, 91–102. [[CrossRef](#)]
 139. Collingham, Y.C.; Huntley, B. Impacts of habitat fragmentation and patch size upon migration rates. *Ecol. Appl.* **2000**, *10*, 131–144. [[CrossRef](#)]
 140. Pitelka, L.F. Plant migration and climate change: A more realistic portrait of plant migration is essential to predicting biological responses to global warming in a world drastically altered by human activity. Plant Migration Workshop Group. *Am. Sci.* **1997**, *85*, 464–473.
 141. Feurdean, A.; Bhagwat, S.A.; Willis, K.J.; Birks, H.J.B.; Lischke, H.; Hickler, T. Tree Migration-Rates: Narrowing the Gap between Inferred Post-Glacial Rates and Projected Rates. *PLoS ONE* **2013**, *8*, e71797. [[CrossRef](#)]
 142. Kremer, A.; Ronce, O.; Robledo-Arnuncio, J.J.; Guillaume, F.; Bohrer, G.; Nathan, R.; Bridle, J.R.; Gomulkiewicz, R.; Klein, E.; Ritland, K.; et al. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecol. Lett.* **2012**, *15*, 378–392. [[CrossRef](#)]
 143. Leonardi, S.; Menozzi, P. Genetic variability of *Fagus sylvatica* L. in Italy: The role of postglacial recolonization. *Heredity* **1995**, *75*, 35–44. [[CrossRef](#)]
 144. Moracho, E.; Moreno, G.; Jordano, P.; Hampe, A. Unusually limited pollen dispersal and connectivity of Pedunculate oak (*Quercus robur*) refugial populations at the species' southern range margin. *Mol. Ecol.* **2016**, *25*, 3319–3331. [[CrossRef](#)]