Climatic criteria for successful introduction of Quercus species identified by use of Arboretum data

Corrie Lynne Madsen*, Erik Dahl Kjær and Anders Ræbild

Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958 Frederiksberg C, Denmark

*Corresponding author Tel: +45 35320571; E-mail: clm@ign.ku.dk

Received 1 May 2020

Climate change is projected to have a major influence on forest tree populations and composition. Translocation of species outside their historic range has been suggested to maintain healthy forests and tree species. The introduction of exotic species into botanical gardens and arboreta worldwide demonstrates the ability of many trees to grow outside their natural habitat and may play an important part in avoiding climate driven extinction if grown in a matching climate. However, it remains to be determined which climatic factors are the most important predictors of climatic match. In this study we use information from the arboretum in Hørsholm, Denmark, to analyse differences in performance of translocated Oak (Quercus) and show how data from tree collections can be used to predict success of assisted migration. Our data included archive lists of georeferenced Northern hemisphere introductions of Quercus, and assessments of their survival and growth rates in nursery and the Hørsholm arboretum. Using logistic and linear regression we modelled the importance of different bioclimatic predictor variables for survival and growth rate. Several correlations were identified across the Quercus genus. Survival of Quercus species depended primarily on the temperatures at the origin, whereas growth on the other hand was more dependent on a match in precipitation. The negative correlations indicated that introductions were less successful from sites with higher temperatures and wetter conditions. The study demonstrates an approach to use historical data collected from arboreta and botanical gardens in climate change research. This new approach can provide useful information in relation to assisted migration for an array of poorly investigated species where this may be the only source of information.

Introduction

Over the past century, climate is believed to have changed at a faster rate than terrestrial ecosystems have experienced in the last 65 million years (Diffenbaugh and Field, 2013). With a projected doubling of atmospheric carbon dioxide concentration over the next century (IPCC, 2007), the composition of forests can undergo substantial change. Aitken et al. (2008) projected three possible outcomes for forest tree populations: they can persist through natural migration to suitable ecological niches, adapt to new conditions in current locations or cease to exist. Tree populations have typically undergone adaptation to local growth conditions (Alberto et al., 2013), and they are therefore potentially vulnerable to rapid changes in the climate.

Melillo (1999) found that the ideal range for some North American forest species could shift as much as 480 km to the north over the next 100 years. Pollen-estimated migration rates between 6000 and 5000 years ago show movement of 2-2.5 km/decade for tree species (Davis, 1989), and a study in the US showed that some species were able to spread on average 100–200 m per year (Iverson et al., 2004). A study on oak (Quercus robur L.) in Denmark found that offspring could be observed > 700 m away from the parent trees (Olrik et al., 2012), which may correspond to a slightly slower speed given a generation time of 10–15 years. This is clearly insufficient to stay within the climate range for which they are adapted. In fact, Aitken et al. (2008) found that if trees are to remain within their optimal climatic range, as potential distribution ranges move towards the Poles and to higher elevations, they will be required to move at a rate of > 1000 m per year. Besides, trees which may be optimally adapted to their environment at the time of establishment will most likely not be the best suited individuals for that same environment at maturity (Thomson et al., 2009). Thus, if species are not able to adapt this projected shift in optimal range can lead to local extinction of economically and ecologically important species by the end of the next century. The potential for local adaptation probably depends on the traits examined. Evidence from tree breeding demonstrates that landrace formation can be rapid and that the first generation offspring of newly introduced trees show a considerable adaptation in their phenology (Lundstrømer et al., 2020). This may partly be due to epigenetics regulating phenology (Dia Sow et al., 2018; Yakovlev et al., 2010), which indicates some potential for local adaptation leading to improved
survival after a single generation at a new site. On the other hand, hydraulic traits show limited variation within species, indicating a slow adaptation to drought and a risk if climates become drier (Lamy et al., 2014; Lobo et al., 2018).

One potential strategy to mitigate the inability of trees to adapt or migrate apace with changing climates is to consider assisted migration which, according to Hewitt et al. (2011), involves ‘the intentional translocation or movement of species outside their historic ranges in order to mitigate actual or anticipated biodiversity losses caused by anthropogenic climatic change’. Although many consider this strategy to be too high a risk to be applied at all, or in any but a few exceptional circumstances (Davidson and Simkanin, 2008; Fazey and Fischer, 2009; Huang, 2008; Ricciardi and Simberloff, 2009; Sandler, 2010), human mediated movement of species has a long history in agricultural, medicinal and ornamental practices. In southern Europe and New Zealand plantations of exotic species such as Eucalyptus (Eucalyptus spp.) and Radiata pine (Pinus radiata D. Don.) have been established (Aubin et al., 2011). Numerous timber species native to North America have also become part of European forestry e.g. Douglas Fir (Pseudotsuga menziesii (Mirb.) Franco), Sitka spruce (Picea sitchensis (Bong.) Carr) and Lodgepole pine (Pinus contorta Doug. Ex Loud.; Kjær et al., 2014). These large-scale introductions are based on economically important species used for silviculture/forestry. Albeit on a smaller scale in terms of area, many exotic species have been introduced into Botanical gardens and arboreta worldwide, demonstrating that many trees are able to grow outside their natural habitat (Primack and Miller-Rushing, 2009; Vetaas, 2002). The introduction of a wider array of species to arbores provides knowledge that can help to identify species which in the future may be well suited in new locations, and may play an important part in avoiding climate driven extinction. Rehfeldt et al. (1999) suggested that a major redistribution of tree species and genotypes across the landscape may be needed to maintain forest productivity, health and biodiversity if climate scenarios are realized. The admixture of potentially better adapted tree species will provide the forest with a buffer towards climate change by increasing the pool of potentially adaptive species (Jandl et al., 2019). But which species are highly sensitive to movement to other environments and climates? Here, lessons learned from unsuccessful planting can also improve knowledge about phenotypic plasticity at the species level—how sensitive are species to modification in their climatic growth conditions?

To what extent are we able to understand and predict the success of species moved by assisted migration? Within the major forest tree species, numerous provenance trials have documented genotype by environment interactions. This emphasized the importance of selection of the suitable origins and can guide choice of provenances for commercial plantations (Li et al., 2017; Rehfeldt et al., 1999; Soenz-Romero et al., 2017). Predicting the success of assisted migration of larger numbers of species is likely to require different methods because field trials are expensive and results are only available after decades of testing. Over the years, dendrologists have participated in collection travels and have accumulated vast knowledge about which areas are likely to harbour material that will thrive under specific situations (e.g. Dossmann and Del Tredici, 2003, 2005; Leverenz, 2007). In some cases, survival after introduction has been analyzed to identify climatic patterns at the planting sites, determining their success, underlining matches in temperature and humidity between site of origin and planting site (Widrlechner et al., 1992, 1998). Likewise, Griffith et al. (2008) studied cyclone damage to palms in a tree collection in Florida and showed that damage was associated with cyclone likelihood at the sites of origin. Such examples show that botanical collections can provide information to guide assisted migration.

Here, we propose a new statistical approach to study assisted migration specifically by using empirical data from arboreta. In this paper, we use information from the arboretum in Hørsholm, Denmark, to analyse differences in seed source performance. Oak (Quercus) is used as a model genus since Oaks are considered important forest forming trees in the Northern Hemisphere and have great global ecological, scientific and economic importance (Simeone et al., 2013). Differences in performance are related to climate conditions at provenance origin and thereby interpreted across environmental gradients. Ultimately, our goal is to clarify whether data collected from arboreta can be used for scientific study to identify which climatic variables are most important for predicting growth and survival when translocating species outside their natural distribution.

**Methods**

**The Hørsholm arboretum**

The arboretum in Hørsholm (55°52' N, 12°30' E) was established on almost treeless farmland in 1936 (Jensen 1994). The annual mean temperature is 8°C, with an average annual rainfall of 614 mm (DMI—Danish Meteorological Institute). The 25 ha are dominated by moraine clay soils but mixed with sections of more sandy soils and, next to lakes, higher organic content. The collection held in 2017 ∼1400 woody plant taxa, representing 240 genera. This included trees and bushes from most continents based on seed collected from other arboreta, botanical gardens and from expeditions to North and South America, New Zealand, Japan, Korea, China and Taiwan (Leverenz et al., 2005). Plants were propagated in the arboretum nursery and, when reaching an appropriate size, were transplanted to the arboretum. The first 3 years after planting, trees were weeded and watered during drought episodes. This has been the case since the mid-1970s (Head of arboretum, O.R. Byrgesen, pers. comm.) and, as far as we can judge, also in the early life of the collection.

Successful introductions are documented by the living specimens in the arboretum, but the failures are also not forgotten. Information on every seed lot has been collected in hand written registration books from 1951 and onwards, stating seed lot number, collection site, date sown and name of collector. For each seed lot there is information of varying quality regarding collection site, with some having very detailed descriptions of location with coordinates and altitude, whereas others only have location names e.g. town or country.

Index cards were created for each seed lot once sown in the nursery stating accession number (year of collection and seed lot number), species, collection site and name of collector. The date of sowing was noted on the index card, as well as the number of seeds sown and location in the nursery. Each year the number of surviving seedlings was registered, and once the plant reached a...
suitable size the site of translocation was noted (e.g. Hørsholm arboretum or other arboreta and botanical gardens). If several plants from the same accession number were planted, a suffix was added in order to keep track of the individual replicates.

In the 1990s, an electronic database was established, holding all the information from the registration books on all plants, which were planted in the arboretum, along with coordinates for their new location. The database is updated when new individuals are planted or when plants die. Collectively, the data offer a unique opportunity to identify which species have been tested in the arboretum and which origins match the Danish climate in terms of survival and good growth.

The study genus

The genus Quercus comprises 531 accepted species (Govaerts and Frodin, 1998) with a distribution throughout the Northern Hemisphere. Many Quercus species are found from North to South America, where they are distributed from southeastern Canada to the Colombian Andes, and in the forests of East and South-East Asia, including Malaysia, Indonesia and Japan. Oaks are absent in subarctic and arctic Eurasia, and there are relatively few in Europe and in the Mediterranean region (Simeone et al., 2013). The greatest species diversity is found in Mexico (ca. 160 species, of which most are endemic) followed by China with > 100 taxa (Oldfield and Eastwood, 2007). In Europe and the Mediterranean region, Quercus comprises around 30 species (Govaerts and Frodin, 1998; Kubitzki, 1993), whereas Denmark only holds two naturally occurring species, Pedunculate oak (Q. robur L.) and Sessile oak (Quercus petraea Mattuschka Liebl.). The Hørsholm arboretum currently holds 113 (including 18 grafted) species of the genus with representatives of 27 species (three species only as graftings), collected in North America, Europe and Asia.

Arboretum data

Index cards and old versions of the database from 1951, 1977 and 1988 were reviewed and any missing accession numbers were added. The status (live/dead) was added for this analysis and updated for all accession numbers, to gain an overview of the number of tested seed lots and their survival. An accession number was given the status ‘live’ if any replicates were present in the arboretum, irrespective of the number of dead replicates since the number of replicates originally transplanted from the nursery was missing. For each accession number the collection site was identified using atlases, Google Maps as well as various travel descriptions. If not available in the Database, coordinates were given using Google Maps. In a final review, we eliminated all accessions, which could not be identified with a precision of at least a 5 arc-min resolution corresponding to an accuracy of data point within a ca. 9.3 × 9.3 km square at temperate latitudes. Any accessions stemming from vegetative propagation were excluded to avoid an over inflow of tree mortality due to unsuitable grafting material or rootstock damage, and samples not originating from wild collections were excluded.

During fieldwork in July 2014, the presence or absence in the Hørsholm arboretum was noted for each accession number. The height of each tree was measured using either a telescopic height pole or a Haglöf Vertex III V.1.5 and Transponder T3 following manufacturer’s instructions for use and calibration. Trees under the height of 5 m were measured once with the telescopic height pole, and trees taller than 5 m were measured 3 times using the hypsometer. The circumference was measured at 1.3 m height using a tape measure. A health assessment was carried out, identifying symptoms and classifications using (Boa, 2003) resulting in an assessment of the overall tree health being classified as low, normal or high vigor as described in the ISA Basic Tree Risk Assessment Form (Dunster et al., 2013). Data on fruiting were extracted from Knudsen et al. (2011), supplemented with a new registration in the autumn 2020.

For each accession number, the mean diameter and height growth were calculated across all replicates resulting in a single value for each accession number. In order to account for sampling bias, accessions of the same species with multiple collections in the same location (identical source of sampling year, location name and altitude) were pooled together. For each tree, the diameter/age and the height/age were calculated, subsequently referred to as diameter (DGR) and height (HGR) growth rate, respectively.

Climate data

Finding climate data at the sites of origin poses a special problem because many accessions were collected in remote places and before climate stations may have been present in the areas or information from such sources were difficult to access. In addition, we do not know the age of trees from which seeds were collected, making it uncertain to what degree these trees had been exposed to climatic extremes. Here, we base our estimates on two sets of interpolated mean climate data obtained for reasonably recent conditions, because earlier data rely on fewer climate stations and since we expect current conditions to be a fair representation of relative differences between sites. We include data from two different interpolated climate databases to investigate to which degree the choice of database may affect results. The first set was based on interpolations of observed data 1970–2000 from WorldClim Version 2 database –worldclim.org (Hijmans et al., 2005). The second set for the reference period 1961–1990 was downloaded from the Climatic Research Unit, University of East Anglia (UEA; Harris et al., 2020).

Data from WorldClim Version 2 were downloaded using a 5 arc-min resolution as trees have extensive gene flow. Local adaptation therefore is not likely to occur within less than tens or even hundreds of kilometres (Robledo-Arnuncio and Gil, 2005; Savolainen et al., 2007). All 19 bioclimatic variables from WorldClim were downloaded (Table 2), and additionally the altitude raster data were downloaded from WorldClim Version 1 (Hijmans et al., 2005).

The bioclimatic variables represent annual trends, seasonality, extreme or limiting environmental factors (for more details see Hijmans et al., 2005) and are often used in ecological niche modeling. Raster data from WorldClim Version 2 were sampled for individual point locations using QGIS (QGIS_Development_Team, 2015) and RStudio (RStudio_Team, 2015), but altitude data were manually corrected when this information was available in the registration books. In cases where an interval of altitude was stated, the mean altitude was used. Three additional variables

Downloaded from https://academic.oup.com/forestry/advance-article/doi/10.1093/forestry/cpab006/6155838 by guest on 05 May 2021
were previously used to predict Danish plant species sensitivity to climate change (Normand et al., 2007). These were derived based on monthly mean temperature and precipitation (Breckle, 2002; Sykes et al., 1996); water balance (computed as the annual precipitation subtracted the potential evapotranspiration following Holdridge (1967), calculated as the sum of the mean of the monthly biotemperatures multiplied by 58.93 (referred to as bio20)), growing degree days (using a 5°C base temperature following Prentice et al. (1992)) (bio21), and absolute minimum temperature of the coldest month (estimated from mean temperature of the coldest month following Prentice et al. (1992)) (bio22). Biotemperatures were calculated following Lugo et al. (1999) as the mean of the monthly minimum and maximum within 0–30°C. The corresponding set of data was downloaded from UEA, except altitude, which was not available. Grid cell size in the UEA database is 0.5° × 0.5° (latitude and longitude; Harris et al., 2020). The UEA data were used to estimate similar bio climate variables as described previously.

Lastly, the Köppen–Geiger climate classification (Kottek et al., 2006) was determined for each accession using RStudio.

**Statistical analyses**

Our analysis consisted of two main components: (1) logistic regression analyses to determine factors affecting survival and (2) linear regression analyses to determine factors important to growth rate. All statistical analyses were conducted using R Studio (RStudio_Team, 2015).

We used logistic regressions to model the impact of all predictor variables (bioclimatic variables) on the binary dependent variable ‘survival’. Two models were used for each predictor variable, one based on the single predictor variable, and the second including the predictor variable and its square value to account for any non-linear effects. The two models were compared using Akaike’s information criteria as a relative measure of the quality of the two models. In order to evaluate the influence of the length of the assessment periods, we conducted the analysis on three datasets corresponding to minima of 10, 20 and 30 years of survival in the arboretum.

We used linear regressions to relate seed source growth rates (diameter and height growth) to climate at seed origin, using the same predictor variables. Again, in each regression we included a variable and its quadratic term in order to accommodate any non-linear tendencies in the data. No quadratic terms were significant and will not be included further. Models were validated by graphical analysis of residuals, which showed that it was necessary to transform the growth data using the Box-Cox transformation found in the MASS library (Venables and Ripley, 2002). The average value of the transformation for each trait value was used, since the values varied between 0.87–0.95 and 1.23–1.47 for diameter and height growth rate, respectively. The model was fitted with the expected value of each of the two measures of growth rate as a linear function of the bioclimatic variables and altitude.

In order to assess the risk of false positive results we applied multiple comparison adjustments using Holm’s sequential Bonferroni correction (Holm, 1979). The adjustments were applied for each dependent variable (survival, diameter and height growth rate), using the number of tests as the basis number (23 for WorldClim data and 22 for UEA data in each case).

Finally, correlations between bioclimatic variables were examined using Pearson’s correlation analysis.

**Results**

Since the establishment in 1936, 27 species of known origin from the genus Quercus, corresponding to 62 accessions from four continents, were tested in the arboretum (Figure 1). Representatives of the subgenera Quercus and Cerris were tested in the arboretum with main focus on the sections Quercus and Lobatae. Of these, 11 species survived < 30 years in the Hørsholm arboretum, whereas red dots represent accessions that have died before reaching 30 years of age.

![Figure 1](https://example.com/figure1.png) Distribution of collection sites in (a) North America, (b) Europe and (c) Asia for *Quercus*. Green squares represent seed collections that have survived a minimum of 30 years in the Hørsholm arboretum, whereas red dots represent accessions that have died before reaching 30 years of age.
The number of surviving accessions decreased with age from about two-thirds surviving after 10 years to less than half after 30 years (Table 1). Regressions between bioclimatic variables and survival depended on the success criteria in terms of length of survival (Table 2). Considering WorldClim estimations, the number of significant regressions increased from only four and five after 10 and 20 years, to 11 after 30 years of testing. For UEA estimations, the numbers of significant bioclimatic variables were higher but revealed a similar tendency of increase with increasing length of survival. We therefore decided to focus on trees that had survived for at least 30 years in our analysis. WorldClim and UEA estimations mostly had similar significances with the exceptions of variables relating to the warmest temperatures and temperature seasonality (bio4, bio5 and bio10) which were significant for UEA and temperature annual range (bio7) only significant for WorldClim.

Variables significant from 10 years age were related to temperature, whereas variables relating to precipitation were significant only after 20 and 30 years of testing. The temperature related variables annual mean temperature (bio1), minimum temperature of the coldest month (bio6), mean temperatures of the driest and coldest quarters (bio9 and bio11), growing degree days (bio21) and absolute minimum temperatures (bio22) were significant for both WorldClim and UEA estimations. In all these variables, the slopes of the regressions were negative, indicating lower survival for accessions coming from areas with higher temperatures (Figure 2a and Table 3). The precipitation related variables significant for both the WorldClim and UEA climatic estimates were precipitation of the driest month and of the driest quarter (bio14 and bio17, respectively), and precipitation seasonality (bio15). Whereas the slopes indicated a positive association between rainfall of the driest month and quarter and survival, the negative slopes for bio15 indicated a lower survival for accessions from areas with high precipitation seasonality. Finally, a negative association was found between altitude (bio23) and survival. Despite high initial significance levels for several bioclimatic variables, according to the Bonferroni correction none of these were significant after 30 years.

According to the Köppen–Geiger classification, 12 classes were present, and the survival was found to be different between classes (Fisher’s exact test, \( P = 0.013 \)). For the five classes represented by more than four accessions, no accessions in the class Csa survived, whereas survival increased in the order Dfb, Cfa, Cfb and especially Dfa (Table 4).

Diameter growth rates varied between 0.15 and 0.95 cm y\(^{-1}\). Some non-native Quercus species were at par with the two native species found in Denmark, Pedunculate oak and Sessile oak (Supplementary Table S2). This included six North American species, white oak (\( Q. \) alba L.), swamp white oak (\( Q. \) bicolor Willd.), Hill’s oak (\( Q. \) ellipsoidalis E.J. Hill), chestnut oak (\( Q. \) montana Willd.), Pin oak (\( Q. \) palustris Münchh.) and black oak (\( Q. \) velutina Lam.), from sections Quercus and Lobatae, and Turkey oak (\( Q. \) cerris L.) native to SE Europe and Turkey from the Quercus section. None of the East Asian origins showed fast growth.

Regression analyses showed a significant impact of 11 variables for WorldClim and UEA estimations on diameter growth rate (Table 3). The only difference between the two climate estimates was significance in growing degree days (bio21) rather than mean diurnal range (bio2) for UEA. Variables having the largest significance (significant after Bonferroni correction) and explaining most of the variation (as expressed by the \( R^2 \) values) were associated with precipitation; notably annual precipitation (bio12, Figure 2d), precipitation of the wettest month (bio13, Supplementary Figure S1a), precipitation of the wettest quarter (bio16 Supplementary Figure S1b) and precipitation of the warmest quarter (bio18, Supplementary Figure S1c). The negative slopes indicated that higher precipitation at the origin was associated with slower growth. Variables associated with temperature were also significant, including maximum temperature of the warmest month (bio5, Supplementary Figure S1d), temperature annual range (bio7, Supplementary Figure S1e) and mean temperature of the warmest quarter (bio10, Supplementary Figure S1f) that were significant both for WorldClim and UEA estimations. Bonferroni correction however removed significance. For these bioclimatic variables, larger values were also associated with slow growth, indicating that origins from warmer climates had poorer performance in Hørsholm.

Height growth rates varied between 10 and 44 cm y\(^{-1}\). Several non-native species had a high mean height growth rate (Supplementary Table S2). These included Scarlet oak (\( Q. \) coccinea Münchh.), Hill’s oak, Pin oak, Shumard’s oak (\( Q. \) shumardii Buckley), Black oak and also Turkey oak.

For height growth rate, only four bioclimatic variables were significant for both climate estimations, all related to precipitation: precipitation of the wettest month (bio13, Supplementary Figure S2a), precipitation seasonality (bio15, Supplementary Figure S2b), precipitation of the wettest quarter (bio16, Supplementary Figure S2c) and precipitation of the warmest quarter (bio18, Supplementary Figure S2d), thus to some extent matching the precipitation dependence of diameter (Supplementary Table S3 and Table 3). Significance levels were not as high, meaning that after the correction for multiple comparisons, none of the variables were significant at the \( P < 0.05 \) level. Again, slopes were negative, indicating that trees from origins with higher precipitation had a slower height growth rate.

Only one bioclimatic variable, bio15 (precipitation seasonality), was significant across all dependant variables affecting both survival and growth rates negatively. High precipitation seasonality was associated with lower chance of survival and growth rates.

The correlation analyses showed that the bioclimatic variables were highly correlated, with more than half of the correlations being significant (Supplementary Figure S3). Correlations were more frequently significant within the group of temperature dependent bioclimatic variables (bio1–bio11) and within the group of precipitation dependent variables (bio12–bio19) than

| Table 1 Overview of number of known accessions alive or dead 10, 20 or 30 years after planting in the Hørsholm arboretum |
| --- |
| **Minimum years of survival** |
| **10 years** | **20 years** | **30 years** |
| Alive | 10 | 20 | 30 |
| Dead | 20 | 20 | 20 |
Table 2 Overview of bioclimatic variables significance after definition of survival based on 10, 20 or 30 years in the Hørsholm arboretum, using climate estimates from WorldClim or UEA

| Climate variable                                      | WorldClim          | UEA             |
|-------------------------------------------------------|--------------------|-----------------|
|                                                       | 10 years | 20 years | 30 years | 10 years | 20 years | 30 years |
| Bio1: annual mean temperature                         | 0.08      | 0.044     | 0.0123   | 0.010    | 0.0079   | 0.0055   |
| Bio2: mean diurnal range (Mean of monthly (max temp-min temp)) | 0.08      | 0.31      | 0.176    | 0.016    | 0.14     | 0.11     |
| Bio3: isothermality                                    | 0.037     | 0.078     | 0.0567   | 0.026    | 0.054    | 0.030    |
| Bio4: temperature seasonality (standard deviation *100) | 0.17      | 0.13      | 0.134    | 0.121    | 0.0696   | 0.068    |
| Bio5: max temperature of the warmest month            | 0.42      | 0.51      | 0.204    | 0.011    | 0.024    | 0.020    |
| Bio6: min temperature of the coldest month             | 0.18      | 0.077     | 0.0443   | 0.054    | 0.016    | 0.015    |
| Bio7: temperature annual range                         | 0.54      | 0.31      | 0.0375   | 0.73     | 0.30     | 0.30     |
| Bio8: mean temperature of the wettest quarter          | 0.79      | 0.8       | 0.425    | 0.70     | 0.55     | 0.15     |
| Bio9: mean temperature of the driest quarter           | 0.13      | 0.053     | 0.0469   | 0.019    | 0.0073   | 0.0089   |
| Bio10: mean temperature of the warmest quarter         | 0.66      | 0.49      | 0.2      | 0.010    | 0.016    | 0.0084   |
| Bio11: mean temperature of the coldest quarter         | 0.073     | 0.039     | 0.0204   | 0.032    | 0.017    | 0.012    |
| Bio12: annual precipitation                            | 0.76      | 0.17      | 0.342    | 0.76     | 0.19     | 0.41     |
| Bio13: precipitation of the wettest month              | 0.98      | 0.59      | 0.658    | 0.90     | 0.39     | 0.38     |
| Bio14: precipitation of the driest month               | 0.33      | 0.068     | 0.0316   | 0.30     | 0.010    | 0.041    |
| Bio15: precipitation seasonality (coefficient of variation) | 0.44  | 0.195     | 0.0249   | 0.3520   | 0.155    | 0.0148   |
| Bio16: precipitation of the wettest quarter            | 0.97      | 0.539     | 0.797    | 0.99     | 0.41     | 0.89     |
| Bio17: precipitation of the driest quarter             | 0.28      | 0.0571    | 0.0258   | 0.28     | 0.073    | 0.034    |
| Bio18: precipitation of the warmest quarter            | 0.81      | 0.258     | 0.603    | 0.23     | 0.079    | 0.40     |
| Bio19: precipitation of the coldest quarter            | 0.53      | 0.732     | 0.853    | 0.99     | 0.93     | 0.70     |
| Bio20: water balance                                   | 0.35      | 0.0583    | 0.0787   | 0.15     | 0.022    | 0.046    |
| Bio21: growing degree days                             | 0.0047    | 0.00175*  | 0.00565  | 0.0079   | 0.0073   | 0.0047   |
| Bio22: absolute minimum temperature                    | 0.0076    | 0.00518   | 0.0182   | 0.021    | 0.011    | 0.0091   |
| Bio23: altitude                                        | 0.0056    | 0.0135    | 0.0373   | n.a.     | n.a.     | n.a.     |
| Number of significant bioclimatic variables            | 4         | 5         | 11       | 9        | 9        | 13       |

* Indicates significance after Holms’ sequential Bonferroni test; n.a.: not available.

between the two groups. Still, a large fraction of the correlations between variables of the two groups was significant.

Finally, with respect to fruiting, seven of the surviving species so far were observed to bear fruits (Supplementary Table S2).

Discussion

Data from the Hørsholm arboretum (and other arboreta) are seen from a traditional experimental point of view marred by lack of repetitions, imbalances in the data, variations in microclimate across the site and sometimes incomplete information about the origin. We assume that horticultural practices have been fairly constant but cannot rule out certain inconsistencies. Climatic extremes occurring at a critical stage in the life of seedlings may also have removed species able to survive as a tree, and conversely, watering of young plants during the establishment phase may have given them an unnatural advantage. Limitations are illustrated by the mortality of some Danish accessions (Figure 1). Assessing individual species based on a single introduction is therefore questionable. In an assessment of the role of botanical gardens in research on climate change, Primack and Miller-Rushing (2009) emphasized the advantageous features and resources available at botanical gardens in climate change research as being primarily due to controlled growing conditions and living collections with broad taxonomic representation. Yet, the aggregated data presented here demonstrates that even with a relatively restricted data set, interesting patterns of adaptation can be extracted. The analysis applied a meta-type approach, where focus is not on the individual tree or species, but rather on the performance of the whole assembly of introductions. Although our analyses can give probabilities for performance of individual species or origins, the major advantages of the approach seem to be identification of areas with potential homologous climates for trees, and help in identifying the underlying climatic factors. A related approach of combining data from many species was applied by Iturbide et al. (2015) to improve distribution models in European Quercus. An alternative strategy was used to study the success in the introduction of plants from two collection travels (to the Balkans and to Japan, respectively) in a range of tree collections in Northeast US (Widrlechner et al. 1992, 1998). Since accessions were introduced to a range of sites, it was possible to correlate survival to temperature and humidity index at the sites, suggesting which sites may be more favourable for the introductions from the area in question.

The analysis of survival indicates that longer testing increase probabilities of revealing significant patterns of variation. The number of significant bioclimatic variables increased with
| Climate variable                          | Tree survival (TS) | Diameter growth rate (DGR) |
|------------------------------------------|--------------------|---------------------------|
|                                          | Logistic regression| Linear regression         |
| WorldClim                                | P-value            | P-value                    |
| UEA                                      |                    |                           |
| Bio1: annual mean temp.                   | Bio2: mean dbh     | Bio10: temp. of the warmest quarter |
| $\ell = 2.71 - 0.29Bi01$                 | $\ell = 1.87 - 0.15Bi02$ | $\ell = 2.26 - 0.12Bi10$ |
| P-value 0.012                            | P-value 0.11       | P-value 0.038              |
| Bio3: isothermality                       | Bio4: temp. seasonality | Bio13: precip. seasonality |
| $\ell = 2.81 - 0.097Bi03$                | $\ell = -1.63 + 0.0018Bi04$ | $\ell = -0.65 - 0.027Bi16$ |
| P-value 0.057                            | P-value 0.13       | P-value 0.037              |
| Bio5: max temp. of the warmest month     | Bio6: min temp. of the coldest month | Bio17: precip. of the driest quarter |
| $\ell = 2.06 - 0.087Bi05$                | $\ell = -0.83 - 0.108Bi06$ | $\ell = -1.18 + 0.0076Bi17$ |
| P-value 0.20                             | P-value 0.044      | P-value 0.025              |
| Bio7: temp. annual range                 | Bio8: mean temp. of the wettest quarter | Bio18: precip. of the warmest quarter |
| $\ell = -1.15 + 0.032Bi07$              | $\ell = 0.44 - 0.0378Bi08$ | $\ell = -0.32 + 0.0006Bi18$ |
| P-value 0.38                             | P-value 0.43       | P-value 0.60               |
| Bio9: mean temp. of the driest quarter   | Bio11: temp. of the coldest quarter | Bio19: precip. of the coldest quarter |
| $\ell = 0.045 - 0.064Bi09$              | $\ell = -0.19 - 0.148Bi11$ | $\ell = -0.23 + 0.0006Bi19$ |
| P-value 0.047                            | P-value 0.020      | P-value 0.85               |
| Bio10: temp. of the warmest quarter      | Bio12: annual precip. | Bio20: water balance      |
| $\ell = 2.26 - 0.12Bi10$                 | $\ell = 0.81 + 0.00073Bi12$ | $\ell = -0.51 + 0.0013Bi20$ |
| P-value 0.0084                           | P-value 0.34       | P-value 0.079              |
| Bio13: precip. of the wettest month      | Bio14: precip. of the driest month | Bio21: growing degree days |
| $\ell = 0.055 - 0.0014Bi13$              | $\ell = -1.07 + 0.023Bi14$ | $\ell = 2.52 - 0.0010Bi21$ |
| P-value 0.658                            | P-value 0.0373     | P-value 0.0057             |
| Bio15: precip. the wettest quarter       | Bio16: precip. of the wettest quarter | Bio22: absolute minimum temp. |
| $\ell = 0.66 - 0.0218Bi15$              | $\ell = -0.011 - 0.00034Bi16$ | $\ell = -2.43 - 0.108Bi22$ |
| P-value 0.025                            | P-value 0.80       | P-value 0.018              |
| Bio17: precip. of the driest quarter     | Bio18: precip. of the warmest quarter | Bio23: altitude |
| $\ell = -1.18 + 0.0076Bi17$              | $\ell = -0.32 + 0.0006Bi18$ | $\ell = 0.37 - 0.0012Bi23$ |
| P-value 0.025                            | P-value 0.60       | P-value 0.037              |
| Bio19: precip. of the coldest quarter    | Bio20: water balance |                  |
| $\ell = -0.23 + 0.00061Bi19$            | $\ell = -0.51 + 0.0013Bi20$ |                  |
| P-value 0.85                            | P-value 0.079      |                  |
| Bio21: growing degree days               | Bio22: absolute minimum temp. |                  |
| $\ell = -0.65 - 0.027Bi16$              | $\ell = -0.50 - 0.148Bi22$ |                  |
| P-value 0.037                            | P-value 0.0091     |                  |
| Bio23: altitude                          | Bio24: absolute maximum temp. |                  |
| $\ell = -0.37 - 0.0012Bi23$             | $\ell = 0.54 - 0.0028Bi22$ |                  |
| P-value n.a.                            | P-value 0.043      |                  |

* Indicates significance after Holm's sequential Bonferroni test; n.a.: not available.
Logistic (a and c) and linear regression (b and d) for Annual mean temperature (°C) (bio1) and Annual precipitation (mm) (Bio 12). Only d was significant after Holms’ sequential Bonferroni test with P values of 0.0008 and 0.002 for respectively WorldClim and UEA. Blue crosshairs and line represent results based on climate estimates from WorldClim, whereas red crosshairs and line represent results based on climate estimates from UEA. Vertical dotted lines denotes the values of the bioclimatic value at Hørsholm arboretum according to the two climate estimators (blue for WorldClim, red for UEA and black for a value shared by both climate estimates). Shaded areas show the 95% confidence intervals around the estimated lines.

Table 4: Overview of number of known accessions alive or dead 30 years after planting divided by their Köppen–Geiger climate classification according to Kottek et al. (2006)

| Köppen classification and description | Alive | Dead |
|--------------------------------------|-------|------|
| BSk—cold semi-arid                   | 0     | 1    |
| Cfa—warm temperate humid hot summer  | 3     | 2    |
| Cfb—warm temperate humid warm summer | 8     | 5    |
| Csa—warm temperate dry hot summer    | 0     | 7    |
| Csb—warm temperate dry warm summer   | 0     | 1    |
| Cwa—warm temperate dry winter hot summer | 1    | 1    |
| Cwb—warm temperate dry winter warm summer | 0  | 3    |
| Dfa—snow climate humid hot summer   | 7     | 1    |
| Dfb—snow climate humid warm summer   | 6     | 9    |
| Dfc—snow climate humid cool summer cold winter | 1  | 0    |
| Dwa—snow climate dry winter hot summer | 1  | 2    |
| Dwb—snow climate dry winter warm summer | 2  | 1    |

Climate at the Hørsholm testing site is Cfb.

In our analysis, we were limited to evaluate the survival at an accession level. We could not analyse survival of individual trees because it was often not known how many seedlings were planted originally and because the causes of death were not known. With more detailed registrations (absent from the early databases used) it would have been possible to include analyses of probabilities for survival for each accession, supposedly increasing the precision of our estimates.

Global climate datasets such as WorldClim, despite being available in relatively high resolution, suffer from inaccuracies compared with detailed, downscaled models. Precipitation estimates are especially uncertain in mountainous areas (Bedia et al., 2013), which may lead to errors in correlations with climate. We compared WorldClim bioclimatic variables with the same variables obtained by another global database (UEA) and found only small differences e.g. data from UEA often showed displacement to a higher range of values compared with WorldClim. Errors stemming from the bioclimatic variables would be incorporated in the residual errors and may be one of the causes of the large scatter around the estimated lines in e.g. Figure 2. Unfortunately, given that downscaled climate models are not available throughout our sampling area, there is currently no good alternative to the approach used here.
Compatible climates

Our study site is placed at the dry and cool end of the tested origins (Figure 2), which may explain that we in general found linear relationship with these climatic parameters. Bonferroni corrections removed significance from the survival data, but since annual mean temperature (bio1) and several other bioclimatic variables point in the same direction (Figure 2 and Table 3) we interpret data to mean that an overall picture emerges. Survival of Quercus species increased with decreasing temperatures at the origin, i.e. origins from warmer climate have poorer survival when moved to Hørsholm. This interpretation is supported by findings that Quercus species are limited by cold temperatures (Askeyev et al., 2005; Kaku and Iwaya, 1979; Repo et al., 2008) and it seems likely that origins from warmer climates may be less tolerant to cold Danish winters. Because many of the bioclimatic variables co-vary (Supplementary Figure S3), it is difficult to say exactly which parameters that are decisive. For example, annual mean temperatures (bio1) co-vary positively with isothermality (bio3), maximum and minimum temperatures as well as with growing degree days (bio21), while co-varying negatively with temperature seasonality (bio4). Continentality, as implied by the temperature annual range (bio7) was not significant, suggesting that this is not decisive for adaptation to Danish conditions. On the other hand, when comparing the Köppen-Geiger classification of seedlots, it is interesting to note that the class Dfa with cold winters and hot humid summers appear to have high chances of survival compared with other classes (Table 4), including Cfb which include Danish climate. Low survival in class Csa with warm temperate climate and hot dry summers is supported by the correlations, indicating that a more even distribution of rainfall—as reflected in precipitation seasonality (bio15) and higher precipitation during the driest months (bio14)—increased survival.

With respect to diameter growth, variables related to both temperature and precipitation were significant after the correction for multiple comparisons, adding confidence to the results. Continentality as implied by large temperature variations (bio7) seems to give slow growth, and introductions from humid origins tended to be slower growing than drier origins. Variables relating to total precipitation (bio12) and precipitation in the wettest (bio16) and warmest (bio18) quarters were significant, suggesting that summer precipitation is important for adaptation. High rainfall in the growing season correlates positively with diameter increment in Quercus (Pilcher and Gray, 1982; Sanders et al., 2013), and some distribution models show correlations between occurrence of Quercus species and precipitation (e.g. Li et al., 2012; Vessella et al., 2015). Saenz-Romero et al. (2017) compared growth of Sessile oak origins in common garden trials across Europe and Turkey. Here, the climatic transfer distance, defined as the difference between climate at the planting site and climate at the origin of the seedlots, was found to affect success. In particular, survival was affected by the annual dryness transfer distance, whereas growth was affected by the growing season dryness transfer index. Our data confirm these tendencies and suggest that they are valid across a larger group of Quercus species.

Hence, it seems that temperature and precipitation at the origin define limits for a climatic match for Quercus species in Hørsholm. The importance of precipitation cause concerns for Quercus trees in Denmark with future climate predictions indicating lower levels of precipitation during summer (Olesen et al., 2014). By analogy with Saenz-Romero et al. (2017) climate change means that the location of the arboretum site (denoted by red and blue vertical lines in Figure 2) will shift along the response curves, thus modifying the climatic transfer distances of introduced seeds and plants. Similar studies in arboreta under different conditions will help to predict success under such changed conditions. A highly useful tool could be developed through establishment of common databases spanning across many collections (Dosmann, 2006), such metacollections could for example be established in the context of the Global Biodiversity Information Facility (GBIF) or the Botanical Gardens Conservation International.

Species and sections of Quercus

The Hørsholm arboretum has tested approximately one tenth of the ca. 530 recognized species (Nixon, 1993), with representatives from both subgenera and all sections except sections Cyclobalanopsis and Protobalanus. The sections Quercus, Lobatae and Cerris all had species surviving > 30 years in the arboretum, whereas section Illex, tested by one species, survived < 30 years. However, due to the limited phylogenetic representation it would be premature to draw any conclusions. Species showing fast growth were distributed across sections and across the North American and Eurasian continents, with the native Pendunculate oak and Sessile oak performing at par with species such as swamp white oak, Hill’s oak pin oak and Turkey oak. There are few comparisons of performance of broader ranges of Quercus species, but Sanders et al. (2013) found that three exotic species marginally outperformed the native Pendunculate oak and Sessile oak in England. The only geographical signals in our study was the failure of southern introductions (Mexico and Morocco) and the slow growth of Asian introductions.

On the other hand, Figure 1 reveals a poor sampling of several regions, and much more remains to be learnt about patterns of adaptation in Quercus. The Hørsholm arboretum has only tested three ‘age and location known’ accessions from Mexico, one from Western US and none from China. Surprisingly, Europe is poorly sampled with few introductions that are sufficiently well documented to be included in this analysis. As the Mediterranean climate is expected to become dryer (Beckman et al., 2019), a closer sampling of Europe would be a natural follow-up and also to help protecting the genetic diversity of the European species.

Modelling of climate effects on species mainly focusses on range contraction or expansion within the natural distribution area. Although long-distance assisted migration is considered controversial, it seems reasonable to identify potential successful long-distance translocations to counteract the expected speed of climate changes (Aitken et al., 2008). Arboreta and botanical gardens have already started this line of research with detailed records of species collected from other countries and continents (Primack and Miller-Rushing, 2009), which could be expanded to show the potential for survival and growth, such as this pilot study has demonstrated. If our data for Quercus can be extrapolated it suggests that transfers can be made to warmer climates,
but that trees from the genus will be poorly adapted when transferred to areas with lesser rainfall.

**Inputs to distribution modelling**

A basic assumption in species distribution modelling is that climate is the main limiting factor for species distributions, and species distribution models are usually based on presence or presence/absence data (e.g. Dyderski et al. 2018). To the extent that species distribution is limited by dispersal or competition, and not by climatic extremes, this may result in bias when the potential natural distributions are mapped. Recently it has even been questioned whether species distribution models ignore important bioclimatic variables (Gardner et al. 2019). In that respect, tree collections and arboreta provide experimental evidence of the climatic suitability outside the natural range (Booth, 2015), and hence may verify variables used in distribution modelling.

Sykes et al. (1996), based on physiological models, suggested that water balance (bio20), growing degree days (bio21) and absolute minimum temperature (bio22) were important parameters determining tree distributions. Our models for Quercus support this choice of variables, as both bio21 and bio22 were significant for survival and bio20 was significant for diameter growth. These variables have been used to predict future distribution of a range of Northern European species (Normand et al., 2007), and the current study seems to confirm their relevance.

In general, there is a need to better understand of relations between climate, survival and growth. For example, Nechita et al. (2017) showed that growth in oak trees in Northern Romania was driven by different climatic factors even on different sides of the Carpathian Mountains. This is not surprising considering local adaptation to site-specific conditions, but general implementation of such results on a larger scale is often problematic. Likewise, Dyderski et al.'s (2018) analysis of papers relevant for species distribution models showed a tendency for performing site or species specific studies and highlighted general flaws in this kind of studies. The solution of this paradox could be to include more experimental data when performing distribution modelling, be it from stress trials, common garden trials or arboreta. It is our opinion that data from tree collections have so far been underutilized and we suggest that they possess a wide range of information needed to understand tree performance under future climates. The inclusion of arboretum data may reduce the effect of non-climatic constraints and offer tested and proven data for identifying climatic matches. Including additional factors such as production of fertile seed and possibilities for natural regeneration would be an additional asset to further improve models of potential distributions of forest species.

**Conclusion**

We find that arboretum data contain biogeographic information that may help interpret factors involved in climatic adaptation, and assist in selecting suitable source areas for assisted migration. The full potentials can only be realized, however, if data from several arboreta are combined. Here we determined criteria for successful migration under current conditions, but what will they be under future conditions? Establishing a network of collections (‘metacollections’ as coined by Dosmann 2006) across Europe or the world would make it possible to expand the scope of analyses considerably by verifying whether the same parameters are decisive for success under different conditions, and by allowing more detailed studies of individual species or genera. This could potentially lead to a new understanding of assisted migration under climate change.

**Supplementary data**

Supplementary data are available at Forestry online.

**Acknowledgements**

We thank 15. Juni Fonden and G.B. Hartmann’s Familiefond for financial support. Thank you to the two anonymous reviewers for valuable comments and to Jon Kehlet Hansen for support with climate data.

**Conflict of interest statement**

None declared.

**Funding**

This work was supported by 15. Juni Fonden [Grant no. 2012-A-77A]; and the G.B. Hartmann’s Familiefond.

**Data policy**

Data is available at the University of Copenhagen Electronic Research Data Archive at https://erda.ku.dk/public/archives/f346dcca034482e09527f9d15c3b54e2/published-archive.html.

**References**

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. and Curtis-McLane, S. 2008 Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolut. Appi. 1, 95–111.

Alberto, F.J., Aitken, S.N., Alia, R., Gonzalez-Martinez, S.C., Hanninnen, H., Kremer, A. et al. 2013 Potential for evolutionary responses to climate change evidence from tree populations. Glob. Chang. Biol. 19, 1645–1661.

Askeyev, O.V., Tischin, D., Sparks, T.H. and Askeyev, I.V. 2005 The effect of climate on the phenology, acorn crop and radial increment of pedunculate oak (Quercus robur) in the middle Volga region, Tatarstan, Russia. Int. J. Biometeorol. 49, 262–266.

Aubin, I., Garbe, C.M., Colombo, S., Drevet, C.R., Mckennon, D.W., Messier, C. et al. 2011 Why we disagree about assisted migration: Ethical implications of a key debate regarding the future of Canada’s forests. For. Chron. 87, 755–765.

Beckman, E., Meyer, A., Denvir, A., Gill, D., Man, G., Pivorunas, D. et al. 2019 Conservation Gap Analysis of Native U.S. The Morton Arboretum, Oaks, Lisle, IL.

Bedia, J., Herrera, S. and Gutierrez, J.M. 2013 Dangers of using global bioclimatic datasets for ecological niche modeling. Limitations for future climate projections. Global Planet. Change 107, 1–12.
Boa, E. 2003 An Illustrated Guide to the State of Health of Trees – Recognition and Interpretation of Symptoms and Damage. Food and Agriculture Organization of the United Nations, Rome.

Booth, T.H. 2015 Using a global botanic gardens database to help assess the capabilities of rare eucalypt species to cope with climate change. Int. For. Rev. 17, 259–268.

Breckle, S.W. 2002 Walter’s vegetation of the Earth. Springer, Berlin, Germany.

Davidson, I. and Simkanin, C. 2008 Skeptical of assisted colonization. Science 322, 1048–1049.

Davis, M.B. 1989 Legs in vegetation response to greenhouse warming. Clim. Change 15, 75–82.

Dia Sow, M., Allona, I., Ambroise, C., Conde, D., Fichat, R., Gribkova, S. et al. 2018 Chapter Twelve-Epigenetics in Forest Trees: State of the Art and Potential Implications for Breeding and Management in a Context of Climate Change. In Plant Epigenetics Coming of Age for Breeding Applications. Jacquot, J.-P. (ed.) Academic Press.

Diffenbaugh, N.S. and Field, C.B. 2013 Changes in ecologically critical terrestrial climate conditions. Science 341, 486–492.

Dosmann, M. and Del Tredici, P. 2003 Plant introduction, distribution, and survival: a case study of the 1980 Sino-American botanical expedition. Bioscience 53, 588–597.

Dosmann, M.S. 2006 Research in the garden: averting the collections crisis. Bot. Rev. 72, 259–268.

Dosmann, M.S. and Del Tredici, P. 2005 The Sino-American botanical expedition of 1980: a retrospective analysis of success. Hortscience 40, 302–303.

Dunster, J., Smiley, E.T., Matheny, N. and Liley, S. 2013 Tree Risk Assessment – Manual. International Society of Arboriculture, Champaign, IL.

Dyderski, M.K., Paz, S., Frelich, L.E. and Jagodzinski, A.M. 2018 How much does climate change threaten European forest tree species distributions? Glob. Chang. Biol. 24, 1150–1163.

Fazey, I. and Fischer, J. 2009 Assisted colonization is a techno-fix. Trends Ecol. Evol. 24, 475–475.

Gardner, A.S., Maclean, I.M.D. and Gaston, K.J. 2019 Climatic predictors of species distributions neglect biophysically meaningful variables. Diversity and Distributions 25, 1318–1333.

Govaerts, R. and Frodin, D.G. 1998 World Checklist and Bibliography of Families and Genera of Vascular Plants. Royal Botanic Gardens. Kew, Great Britain.

Griffith, M.P., Noblick, L.R., Dowe, J.L., Husby, C.E. and Colarulie, M.A. 2008 Cyclone tolerance in New World Arecaceae: biogeographic variation and abiotic natural selection. Ann. Bot. 102, 591–598.

Harris, I., Osborn, T.J., Jones, P. and Lister, D. 2020 Version 4 of the CRU TS monthly high-resolution gridded multimarine climate dataset. Scientific Data 7, 1–18.

Hewitt, N., Klenk, N., Smith, A.L., Bazely, D.R., Yan, N., Wood, S. et al. 2011 Taking stock of the assisted migration debate. Biol. Conserv. 144, 2560–2572.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. 2005 Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Holdridge, L.R. 1967 Life zone ecology Tropical Science Center. San Jose, Costa Rica.

Holt, S. 1979 A simple sequentially rejective multiple test procedure. Scand. J. Stat. 6, 65–70.

Huang, D. 2008 Assisted colonization won’t help rare species. Science 322, 1049–1049.

IPCC, I. P. O. C. C 2007 Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Iturbide, M., Bedía, J., Herrera, S., del Hierro, O., Pinto, M. and Gutiérrez, J.M. 2015 A framework for species distribution modelling with improved pseudo-absence generation. Ecological Modelling 312, 166–174.

Iversen, L.R., Schwartz, M.W. and Prasad, A.M. 2004 How fast and far might tree species migrate in the eastern United States due to climate change? Glob. Ecol. Biogeogr. 13, 209–219.

Jandl, R., Spathelf, P., Bolte, A. and Prescott, C.E. 2019 Forest adaptation to climate changeis non-management an option? Ann. For. Sci. 76, 48.

Jensen, N. 1994 Guide til Arboretet i Hørsholm (Guide to the Arboretum in Hørsholm, Denmark). Dansk Dendrologisk Årsskrift XII, 1–237.

Kaku, S. and Iwawa, M. 1979 Deep Supercooling in xylems and ecological distribution in the genera illex, viburnum and Quercus in Japan. Oikos 33, 402–411.

Kjær, E.D., Lobo, A. and Myking, T. 2014 The role of exotic tree species in biodiversity management. Scand. J. For. Res. 29, 323–332.

Knudsen, M.A., Kjær, E.D., Ræbild, A. and Leverenz, J.W. 2011 Timing and abundance of flowering and fruiting of woody plants in Harsholm Arboretum: results from three years survey. Vol. 57. Forest & Landscape, University of Copenhagen. Working Papers / Forest & Landscape.

Kottek, M., Grieser, J., Beck, C., Rudolf, B. and Rubel, F. 2006 World map of the Köppen-Geiger climate classification updated. Meteorol. Z. 15, 259–263.

Kubitzki, K. 1993 Fagaceae. In The Families and Genera of Vascular Plants. K., Kubitzki, J.G., Rahwer, V., Bittrich (eds.). Vol. 2. Springer, Berlin, pp. 301–309.

Lamy, J.B., Delzon, S., Bouche, P.S., Alia, R., Vendramin, G.G., Cochard, H. et al. 2014 Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. New Phytol. 201, 874–886.

Leverenz, J.W. 2007 The NAU collecting expeditions to Korea and Japan in 1976. Plant introduction, distribution and survival. Dansk Dendrologisk Årsskrift 25, 5–102.

Leverenz, J.W., Nielsen, K.H. and Jacobsen, B. 2005 Timing and abundance of flowering and fruiting in the Harsholm arboretum from September 2003 to October 2004. Center for Skov, Landskab og Planlægning/Københavns Universitet, Working Papers / Forest & Landscape.

Li, G.Q., Liu, C.C., Liu, Y.G., Yang, J., Zhang, X.S. and Guo, K. 2012 Effects of climate, disturbance and soil factors on the potential distribution of Liao tantal oak (Quercus wutaishanica Mayr) in China. Ecol. Res. 27, 427–436.

Li, Y.J., Suontama, M., Burdon, R.D. and Dungey, H.S. 2017 Genotype by environment interactions in forest tree breeding: review of methodology and perspectives on research and application. Tree Genet. Genomes 13, 60.

Lobo, A., Torres-Ruiz, J., Burlett, R., Lemaire, C., Parise, C., Francioni, C. et al. 2018 Assessing inter- and intraspecific variability of xylem vulnerability to embolism in oaks. For. Ecol. Manage. 424, 53–61.

Lugo, A.E., Brown, S.L., Dodson, R., Smith, T.S. and Shugart, H.H. 1999 The Holdridge life zones of the conterminous United States in relation to ecosystem mapping. J. Biogeogr. 26, 1025–1038.

Lundstrømer, J., Karlsson, B. and Berlin, M. 2020 Strategies for deploy-ment of reproductive material under supply limitations – a case study of Norway spruce seed sources in Sweden. Scand. J. For. Res. 35, 495–505.

Melillo, J.M. 1999 Perspectives: Climate change - warm, warm on the range. Science 283, 183–184.
Nechita, C., Popa, I. and Eggertsson, O. 2017 Climate response of oak (Quercus spp.), an evidence of a bioclimatic boundary induced by the Carpathians. Sci. Total Environ. 599, 1598–1607.

Nixon, K.C. 1993 Infrageneric classification of Quercus (Fagaceae) and typification of sectional names. Ann. For. Sci. 50, 25–34.

Normand, S., Svenning, J.C. and Skov, F. 2007 National and European perspectives on climate change sensitivity of the habitats directive characteristic plant species. J. Nat. Conserv. 15, 41–53.

Oldfield, S. and Eastwood, A. 2007 The Red List of Oaks. Fauna and Flora International, Cambridge, UK.

Olesen, M., Madsen, K.S., Ludwigsen, C.A., Boberg, F., Christensen, T., Capellen, J. et al. 2014 Fremtidige klimaforandringer i Danmark. Danmarks Klimacenter rapport. Danmarks Meteorologiske Institut.

Olrik, D.C., Hauser, T.P. and Kjær, E.D. 2012 Natural colonisation of an open area by Quercus robur L. – From where did the vectors disperse the seed? Scand. J. For. Res. 27, 350–360.

Pilcher, J.R. and Gray, B. 1982 The relationships between oak tree growth and climate in Britain. J. Ecol. 70, 297–304.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. and Solomon, A.M. 1992 A global biome model based on plant physiology and dominance, soil properties and climate. J. Biogeogr. 19, 117.

Primack, R.B. and Miller-Rushing, A.J. 2009 The role of botanical gardens in climate change research. New Phytol. 182, 303–313.

QGIS_Development_Team 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

Reinfeldt, G.E., Ying, C.C., Spittlehouse, D.L. and Hamilton, D.A. 1999 Genetic responses to climate in Pinus contorta: Niche breadth, climate change, and reforestation. Ecol. Monogr. 69, 375–407.

Repo, T., Mononen, K., Alivio, L., Pakkanen, T.T. and Hanninen, H. 2008 Cold acclimation of pedunculate oak (Quercus robur L.) at its northernmost distribution range. Environ. Exp. Bot. 63, 59–70.

Ricciodi, A. and Simberloff, D. 2009 Assisted colonization: good intentions and dubious risk assessment. Trends Ecol. Evol. 24, 476–477.

Robledo-Arnuncio, J.J. and Gil, L. 2005 Patterns of pollen dispersal in a small population of Pinus sylvestris L. revealed by total-exclusion paternity analysis. Heredity 94, 13–22.

RStudio_Team 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. URL http://www.rstudio.com/.

Saenz-Romero, C., Lamy, J.B., Ducousso, A., Musch, B., Ehrenmann, F., Delzon, S. et al. 2017 Adaptive and plastic responses of Quercus petraea populations to climate across Europe. Glob. Chang. Biol. 23, 2831–2847.

Sanders, T.G.M., Pitman, R. and Broadway, M.S.J. 2013 Species-specific climate response of oaks (Quercus spp.) under identical environmental conditions. Iforest-Biogeosci. For. 7, 61–69.

Sandler, R. 2010 The value of species and the ethical foundations of assisted colonization. Conserv. Biol. 24, 424–431.

Saolainen, O., Pyhøjärvi, T. and Knurr, T. 2007 Gene flow and local adaptation in trees. Annu. Rev. Ecol. Evol. Syst. 38, 595–619.

Simeone, M.C., Piredda, R., Papini, A., Vessella, F. and Schirone, B. 2013 Application of plastid and nuclear markers to DNA barcoding of euro-Mediterranean oaks (Quercus, Fagaceae): problems, prospects and phylogenetic implications. Bot. J. Linnean Soc. 172, 478–499.

Sykes, M.T., Prentice, I.C. and Cramer, W. 1996 A bioclimatic model for the potential distributions of north European tree species under present and future climates. J. Biogeogr. 23, 203–233.

Thomson, A.M., Riddell, C.L. and Parker, W.H. 2009 Boreal forest provenance tests used to predict optimal growth and response to climate change: 2. Black spruce. Can. J. For. Res.-Revue Canadienne De Recherche Forestiere 39, 143–153.

Venables, W.N. and Ripley, B.D. 2002 Modern Applied Statistics with S. Fourth edn. Springer, New York.

Vessella, F., Simeone, M.C. and Schirone, B. 2015 Quercus suber range dynamics by ecological niche modelling: from the last interglacial to present time. Quat. Sci. Rev. 119, 85–93.

Vetaas, O.R. 2002 Realized and potential climate niches: a comparison of four rhododendron tree species. J. Biogeogr. 29, 545–554.

Widllechner, M., Hasselkus, E., Herman, D., Iles, J., Pair, J., Paparozzi, E. et al. 1992 Performance of landscape plants from Yugoslavia in the North Central United States. J. Environ. Hortic. 10, 192–198.

Widllechner, M., Hebel, J., Herman, D., Iles, J., Kring, G., Ovrom, A. et al. 1998 Performance of landscape plants from Northern Japan in the North Central United States. J. Environ. Hortic. 16, 27–32.

Yakovlev, I.A., Fossdal, C.G. and Johnsen, O. 2010 MicroRNAs, the epigenetic memory and climatic adaptation in Norway spruce. New Phytol. 187, 1154–1169.