Universität für Bodenkultur Wien

Department of Forest and Soil Sciences
Institute of Silviculture
Advisor: Ao. Univ. Prof. DI Dr. Manfred J. Lexer

Revealing the intra-specific variation in climate response for adapting forests to climate change: the case of Douglas-fir in Central Europe

Debojyoti Chakraborty

Dissertation for obtaining a doctorate degree (Dr. nat. techn.) at the
University of Natural Resources and Life Sciences (BOKU), Vienna

Vienna, November 2016

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Preface

This thesis is a synthesis of three scientific articles, reprinted in Appendix of this work (sections 7.1 to 7.3) and either published or submitted to a peer reviewed journal. Each article has different structure and citation style conforming to the particular journal.

Whereas a detailed description of experimental design, results, discussion and conclusions can be found in the individual articles, this synthesis aims at providing a comprehensive understanding of the overall study by linking the contributions of the individual articles for a wider audience.

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Acknowledgement

As rightly said by a famous Austrian-British philosopher Ludwig Wittgenstein "Knowledge is in the end based on acknowledgement", for this herculean task of completing my doctoral thesis, I would like to acknowledge the people without whose presence this achievement would have been hard and lackluster.

At the very onset I would like to express my gratitude to my two supervisors Ao. Univ. Prof. DI Dr. Manfred J. Lexer at the University of Natural Resources and Life Sciences (BOKU), Vienna and Dr. Silvio Schüler at the Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), Vienna. Without any doubt, they are both outstanding scientists, yet they are keen to encourage their students to develop into excellent researchers in their own right. I particularly admire their willingness, in spite of their busy schedule, to invest time to relay complex methodologies in an understandable way. I also appreciate their genuine interest in my career, success and overall wellbeing. Here, I would also like to thank Dr. Tongli Wang at University of British Columbia (UBC) for his immense guidance and support during my research stay at the University of British Columbia, Vancouver.

Again, I am particularly indebted to my colleagues and lab mates at BOKU, Vienna and UBC Canada for making me comfortable and extending their selfless support whenever I required it. My particular thanks goes to my amazing colleagues Florian, Dominik, Mathias, Michael, Rupert, Stefan and Werner. I would also like to extend my gratitude to all my colleagues at BFW Vienna, and particularly Thomas Thalmayr for being my SOS, rescuing me from any crisis be it a broken computer or the foreigner's registration office in Vienna. I am thankful to Dr. Monika Konnert at the Bavarian Office of Forest Seedling and planting , Bavaria , Germany and Lambert Weißenbacher of BFW, Vienna for their valuable advice and support with the data.

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I survived… Vielen Dank !

Abstract

Adaptive management aiming at reducing vulnerability and enhancing the resilience of forested ecosystems is a key to preserving the potential of forests to provide multiple ecosystem services under climate change. Adaptive management may include changing the structure and composition of the forests by planting alternative and sometimes non-native tree species adapted to expected future climatic conditions. The North American Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) is one such alternative tree species currently under consideration in Europe because of its excellent growth performance, wood quality and its tolerance of drought. Earlier experiences from planting Douglas-fir in Europe revealed strong intra-specific variations in growth and fitness depending on the geographic origin of the provenance or populations. Therefore, knowledge on suitable provenances/populations is a key issue. The overall aim of this study was to examine the suitability of Douglas-fir populations in central Europe under changing climate conditions focusing on a case study region in Austria and Germany. Multivariate Universal Response Functions (URFs) for dominant height and mean basal area were developed utilizing data from 50 common garden trials across a wide range of climatic conditions in Germany and Austria. The URFs predict growth performance as a function of climate of planting locations (i.e. environmental factors) and provenance/ population origin (i.e. genetic factors). Model comparison with a climate envelope approach revealed that populations origin identified by the URFs are significantly different and have higher growth performance than the populations identified by the climate envelope approach. Model validation against data from across Europe suggested that the URFs perform better in Central and Southeastern Europe compared to maritime Western Europe. Uncertainty in model output due to parameter uncertainty was found to vary not only between different provenance regions of the case study area but also between the analyzed climate change scenarios. Populations identified by the URFs to be optimum for the study area under current climate and climate change scenarios originate from western Cascades and coastal areas of British Columbia, Washington and Oregon. The current seed stands in North America, providing planting materials for Central Europe under the legal framework of the Organization for Economic Cooperation and Development (OECD) were found to have similar growth performance as the optimum populations for future identified by the URFs. This indicates that the seed stands of Douglas-fir currently used for procuring planting material in Europe will also remain suitable in future. Even though calibrated with data from Central Europe, when applied as SDMs, the URFs predicted the observed occurrence of Douglas-fir in its native range in North America with reasonable accuracy compared to contemporary SDMs developed in North America. Overall the study came up with a decision making tool for identifying suitable populations for future conditions.

Key words: *adaptation, climate change, Douglas-fir, provenance trials, species distribution models, universal response function, uncertainties*

Kurzfassung

Anpassungsmaßnahmen, die die Vulnerabilität reduzieren und die Resilienz von Waldökosystemen erhöhen sind ein Schlüsselelement, um die Bereitstellung von Ökosystemleistungen im Klimawandel sicherzustellen. Eine mögliche Maßnahme ist das Einbringen von nicht-heimischen Baumarten, die besser an zukünftige Umweltbedingungen angepaßt sind. Die Douglasie (*Pseudotsuga menziesii* [Mirbel] Franco) wird wegen ihrer hohen Produktivität, der guten Holzqualität und ihrer Tolranz gegenüber Trockenheit als eine mögliche alternative Baumart in europäischen Wäldern angesehen. Bisherige Versuche mit Douglasie in Europa zeigten die hohe innerartliche Variabilität des Wachstumsverhaltens in Abhängigkeit der geographischen Herkunft auf. Das Ziel der vorliegenden Arbeit war es daher, die Eignung von Douglasienherkünften in Mitteleuropa (Süddeutschland, Österreich) unter Klimawandelbedingungen zu untersuchen. Universal Response Functions (URFs) für Douglasienpopulationen wurden als multivariate Modelle, die das Wachstumsverhalten in Abhängigkeit von Klimavariablen erklären. Dazu wurden Daten von 50 Versuchsortenin Deutschland und Österreich verwendet. Zielvariablen der URFs waren die Oberhöhe und die Grundfläche im Alter 24. Ein Vergleich der von den URFs ermittelten bestgeeigneten Provenienzen mit den Ergebnissen eines Klimahüllen-Ansatzes zeigte auf, dass sich die Herkünfte der URFs deutlich von denen des Klimahüllen-Ansatzes unterscheiden und ausserdem bessere Wachstumsperformance aufwiesen. Die Validierung der URFs an unabhängigem Datenmaterial brachte bessere Resultate in Zentral- und Südosteuropa im Vergleich zu atlantisch und maritim getönten Regionen in Westeuropa. Die kumulierte Unsicherheit in den URF-Modelloutputs aufgrund der Parameterunsicherheit variierte stark in Abhängigkeit von Herkunftsregionen in Europa und des verwendeten Klimaänderungs-szenarios. Die von den URFs für heutiges Klima als optimal identifizierten Herkünfte stammen aus den Westkaskaden und den

Küstengebieten British Columbias, Washingtons und Oregons. Die derzeit von der OECD für Mitteleuropa empfohlenen Saatgutbestände in Nordamerika wiesen ähnliche Wachstumsperformance auf, wie die von den URFs als zukünftig optimal identifizierten Herkünfte. Dies deutet an, dass die derzeitigen Saatgutbestände auch unter geänderten Klimabedingungen als geeignet angesehen werden können. Werden die URFs als Artenverbreitungsmodell eingesetzt, vermochten sie die beobachtete Verbreitung von Douglasie in Nordamerika mit ausreichender Genauigkeit zu repräsentieren. Es wird gefolgert, dass die entwickelten URFs als Entscheidungs-unterstützung bei der Auswahl geeigneter Herkünfte unter Klimawandelbedingungen geeignet sind.

Schlüsselwörter**:** *Anpassung, Klimawandel, Douglasie, Herkunfstversuche, Artenverbreitungsmodell, universal response function, Unsicherheit*

Contents

1 Introduction

Decades of scientific research have provided convincing evidence of observed and likely impacts of human-induced climate change on natural systems. Today it is undisputed that climate change will require substantial mitigation and adaptation measures (IPCC 2013).Forests, because of their ability to sequester and store carbon, have been recognized by the Kyoto Protocol as a potential means for mitigating climate change (UNFCCC 1998). Forests cover nearly half of the earth's terrestrial surface (Melillo et al. 1993) and besides being an important carbon sink provide numerous ecosystem services and resources for human use. Climate change is projected to have long-lasting effects on forests worldwide because climate is one of the major drivers of forest development (Overpeck et al. 1990; Allen et al. 2010).

In Europe effects of climate change on forests may include changes in forest productivity (Reyer et al. 2014), changes in distribution of tree species and economic value of forests (Hanewinkel et al. 2013), effects of intensifying disturbance regimes (Seidl et al. 2011) and droughts (Allen et al. 2010). A prominentexample of forests which are vulnerable to climate change are the secondary Norway Spruce (*Picea abies* [L.] Karst) dominated forests at low elevations in Central Europe. Such forests are likely to experience drastic decline in productivity and abundance accompanied by higher risk of wind throw and bark beetle attack (Klimo and Hager 2000; Bolte et al. 2009; Lindner et al. 2010; Seidl et al. 2011; Spiecker et al. 2012).

Europe has a long tradition of sustainable forest management which in recent years has undergone a shift in focus from predominantly timber production to provision of multiple ecosystem services. This change in management focus has made adaptation to and mitigation of climate change even more challenging (Hanewinkel et al. 2013; Lindner et al. 2014).Even though European forest managers have experience in dealing with biotic and abiotic risks, these experiences might not be adequate to deal with the projected climate change (Bolte et al. 2009). Therefore, current forest management needs to incorporate adaptive management strategies aiming at reducing vulnerability and enhancing resistance and resilience of forested ecosystems (Spittlehouse and Stewart 2003; Millar et al. 2007; Bolte et al. 2009).

A portfolio of different adaptive management strategies ranging from passive strategies like conserving forest structures to active strategies such as changing structure and composition through silviculture have been discussed (Spittlehouse and Stewart 2003; Millar et al. 2007; Bolte et al. 2009). Other adaptive measures which have received intense debate and attention in recent years include *assisted migration* (McLachlan et al. 2007; Marris 2008) and *assisted gene flow* (Aitken and Whitlock 2013). While assisted migration aims at facilitating the colonization of forest tree species in new habitats with suitable climate, assisted gene flow aims at the managed translocation of individuals within the current species range to facilitate rapid adaptation to climate change and improve the long-term prospects of trees and its related communities.

Adaptive management options such as changing the structure and composition are particularly suitable in case of forests with low tolerance of climate change and higher risk of disturbances such as bark beetles and wind throw (Bolte et al. 2009). Changing species composition might also involve planting non-native tree species adapted to expected climate conditions in the future (Klimo and Hager 2000; Bolte et al. 2009; Lindner et al. 2010; Temperli et al. 2012).

The North American Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco)and Red oak (*Quercus rubra*) are two such non-native species which are adapted to climatic conditions expected in the future in Central Europe (Klimo and Hager 2000; Roloff and Grundmann 2006). Douglas-fir is particularly attractive to forest owners because of its superior growth performance, high quality wood, tolerance of drought, and stability against wind disturbance (Hermann and Lavender 1999; Kölling 2008). Because of these characteristics Douglas-fir was planted worldwide including Europe starting in the early 1900s (Hermann and Lavender 1999). However, there are some concerns over planting Douglas-fir in Europe due to fungal pathogens such as *Rhabdocline pseudotsugae* (Morgenstern et al. 2013), invasiveness (Richardson and Rejmánek 2011) and related negative impacts on biodiversity (Schmid et al. 2014), and societal attitude towards non-native species in general.

The success of such adaptation strategies involving planting of alternative or non-native tree species would heavily depend on our knowledge of the intra-specific variations or provenances within the species which are adapted to climatic conditions expected in the future (Matyas 1996; Wang et al. 2006; Bolte et al. 2009). Common garden experiments or provenance trials (Matyas 1996) are excellent data sources for studying the response of populations of a species to environmental gradients. In provenance trials, several populations of a species are planted in a particular climate or along an appropriate climatic gradient with the primary objective of identifying populations with desired growth characteristics and fitness. Due to the increasing interest in climate change, such trials were revisited to understand the relation between growth performance, fitness and climate, and to recommend suitable populations for future conditions (Carter 1996; Matyas 1996; Rehfeldt et al. 1999; Rehfeldt et al. 2001; Rehfeldt et al. 2002; Rehfeldt et al. 2014a; Rehfeldt et al. 2014b).

Predicting suitable habitats under climate change is another important criterion on which the success of adaptive management options involving non native trees and the overall success of assisted migration programs would depend. Application of traditional species distribution models (SDMs) for this purpose have been criticized because such SDMs focus only on where a species currently occurs, whereas in order to predict species distribution under climate change the SDMs should identify where a species could possibly occur (Aitken et al. 2008; Wiens et al. 2009). Moreover, most SDMs consider species as a homogenous entity whereas populations within a species are known to inhabit a wide range of habitats. Therefore SDMs based on the *fundamental niche* approach and integration of intra-specific variations are two major improvements needed for applying SDMs for predicting species distribution under climate change (Oney et al. 2013; Stahl et al. 2014).The *climate envelope models* (Hamann et al. 2010; Isaac-Renton et al. 2014) and the *response function* approach (Wang et al. 2006; Wang et al. 2010; Leites et al. 2012a; Kapeller et al. 2012) are two major conceptual approaches of modeling response of populations to climate. These approaches have their own strengths and limitations (see Appendix 7.1).

However, model outputs have uncertainties arising from model assumptions, parameter estimation, and future climate scenarios which should be considered when using them to develop guidance for managers and policy makers. Model evaluation with independent data, use of multiple climate scenarios and test of model sensitivity and uncertainty are approaches to evaluate models and build confidence in them (Lindner et al. 2014) (see Appendix 7.2).

2 Objectives

The overall aim of this study was to examine the suitability of Douglas-fir in Central Europe under changing climatic conditions.

The specific objectives of the thesis were:

i. Development of Universal Response Functions for Douglas-fir populations

   The first objective of the study was to identify climatic factors that drive genetic and environmental variation in growth performance of Douglas-fir populations in order to develop Universal Response Functions (URFs)(Wang et al. 2010) by integrating both environmental and genetic factors of growth (see paper I in Appendix 7.1 for details).

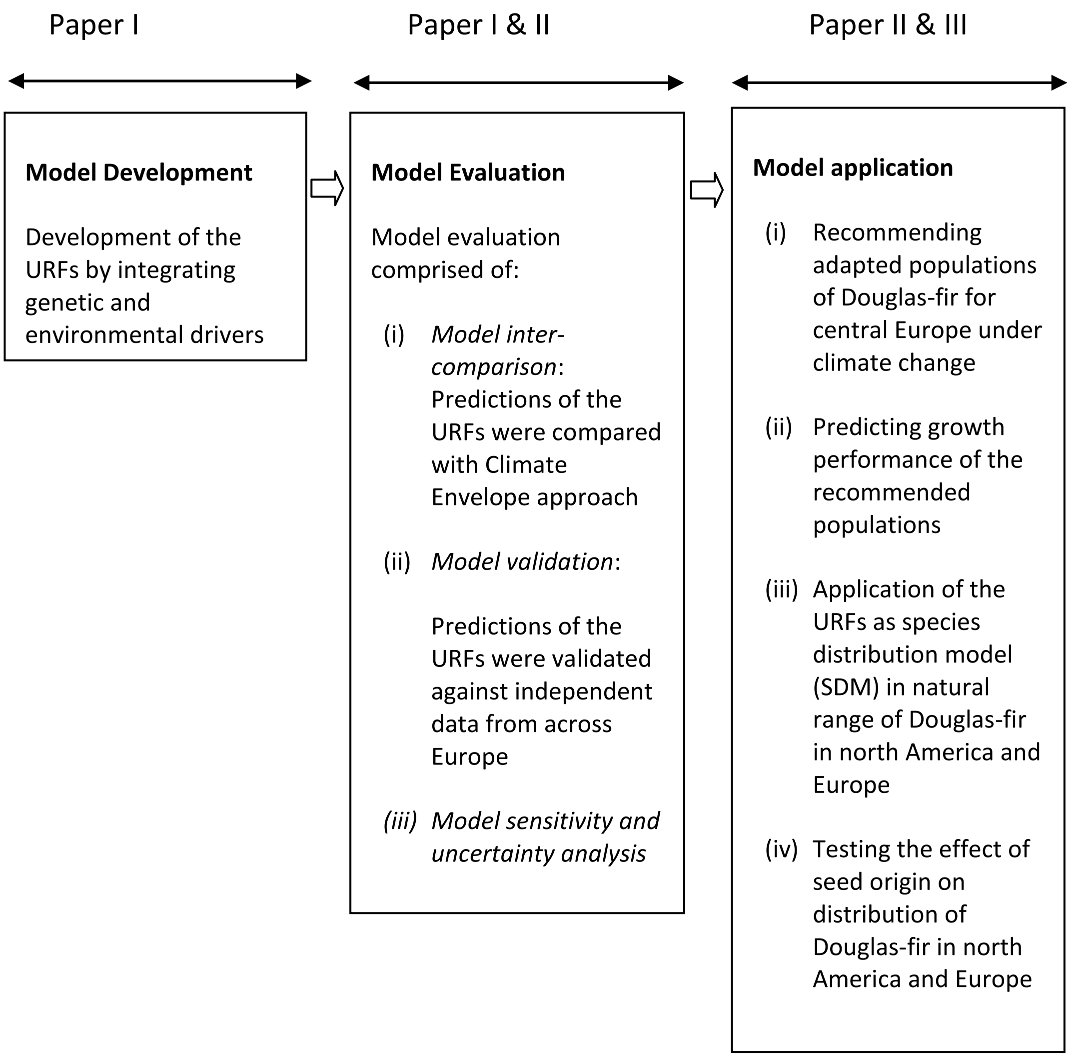
ii. Model evaluation

   The second objective of the study was to compare the predictions of the URFs with a climate envelope model (Appendix 7.1), validation of the URFs with independent data from provenance trials across Europe (Appendix 7.2) and to analyze the uncertainties of the model predictions under climate change scenarios (see paper II in Appendix 7.2 for details).

iii. Model application

   The third objective of the study was to apply the URFs for identifying adapted populations of Douglas-fir for Central Europe under climate change (Appendix 7.1, & 7.2), predict growth performance of the identified populations of Douglas-fir under current and future climate conditions (Appendix7.2)and to apply the URFs to predict distribution of Douglas-fir in Europe and North America (see paper III in Appendix 7.3 for details).

These objectives were accomplished by three papers (see Appendix 7) and are displayed in Figure 1.



Paper I

Model Development

Development of the URFs by integrating genetic and environmental drivers

Paper I & II

Model Evaluation

Model evaluation comprised of:

(i) *Model inter-comparison*: Predictions of the URFs were compared with Climate Envelope approach

(ii) *Model validation*:

Predictions of the URFs were validated against independent data from across Europe

(iii) Model sensitivity and uncertainty analysis

Paper II & III

Model application

(i) Recommending adapted populations of Douglas-fir for central Europe under climate change

(ii) Predicting growth performance of the recommended populations

(iii) Application of the URFs as species distribution model (SDM) in natural range of Douglas-fir in north America and Europe

(iv) Testing the effect of seed origin on distribution of Douglas-fir in north America and Europe

Fig. 1 Schematic diagram of the contribution of individual papers to the overall study

3 Materials and methods

3.1 Case study region

The case study region comprised of Austria and southern Germany (Fig. 2). The URFs were developed from provenance trial data from the case study region. The case study region was further employed in predicting suitable Douglas-fir populations under current climate and potential future climates.

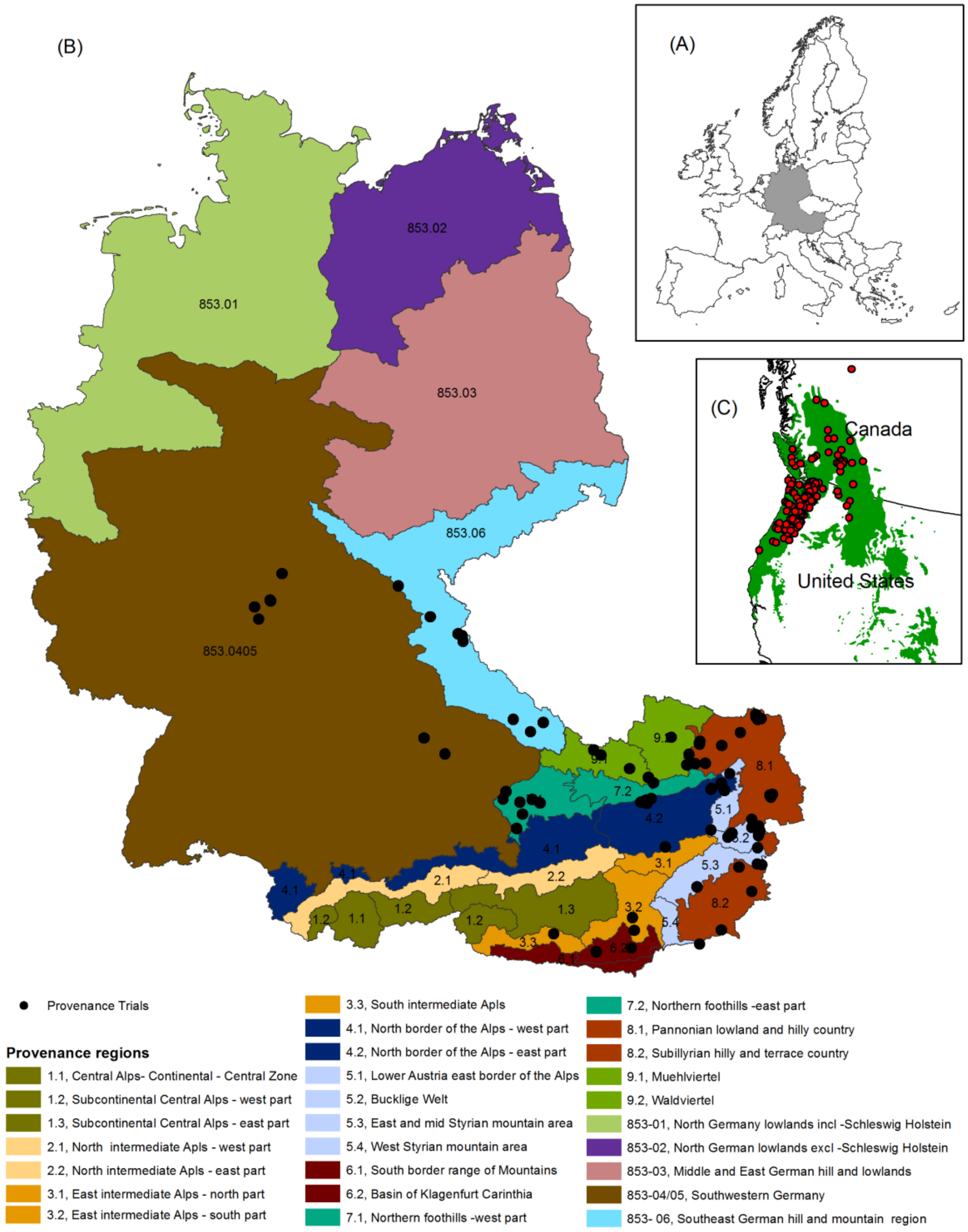


Fig. 2 A) Location of the study region in Europe highlighted in gray. B) Location of the provenance trials (black dots) in the case study region of Austria and Germany. The colored polygons represent the legally defined provenance regions. C) Locations of the seed origin of

Douglas-fir (red dots) in western North America which was planted in the provenance trials shown in (B). The natural distribution of Douglas-fir is shaded in green.

3.2 Provenance Trials

Data from 50 Douglas-fir provenance trials located in Austria and Germany (Fig. 2) in Central Europe were used in this study. These trials had been established between 1973 and 1993 by the Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), Vienna, Austria and the Bavarian Office for Forest Seeding and Planting (ASP), Teisendorf, Germany. In these trials 290 provenances of Douglas-fir originating from Northwest America (Fig. 2) were planted across a wide gradient of climatic conditions (see Appendix 7.1 for details). The provenance trials were designed as randomized blocks. Within each block (replication) three to four-year-old pre-cultivated seedlings of selected provenances were planted in plots of 20-100 individuals with a spacing of 2m x 2m.The provenance trials provided data on tree diameter at breast height (DBH) and tree height at tree age 24. From this data two indicators of growth performance were calculated: i) “dominant height of populations at age 24” (hereafter referred to as H24) and “basal area per hectare at age 24” of individual populations (hereafter referred to as BA24). H24 was computed as the 75 percentile of all tree heights of a given population at age 24 and BA24 was computed as the mean basal area across the number of replicates of individual provenance within the trial (see Appendix 7.1 for details).

3.3 Climate data

3.3.1 Climate data for model development

For trials in Austria daily climate data (mean temperature and precipitation sum), covering the period from installation of each trial until the most recent measurements were obtained from the Austrian network of weather stations maintained by the Central Institute of Meteorology and Geodynamics. For the same period gridded climate data for the greater Alpine region available from Haslinger et al. (2012) were obtained for trials in Germany. From this temperature and precipitation data, ten biologically relevant climate variables (see Appendix 7.1) were calculated for further analysis. For climate data of the population origin, mean values of the same ten climate variables (see Appendix 7.1) for "current climate" (average for the period 1950-2000) were generated for each population origin location using the high-resolution climate model Climate-WNA v4.72 (Wang et al. 2012).

3.3.2 Climate data for model application

For application of the model in the case study region (see Appendix 7.1) and at the scale of Europe and North America (see Appendix 7.2 and 7.3) the WorldClim database (Hijmans et al. 2005) was used. The ten climate variables used as independent variables were calculated at a 30 arc-sec resolution for "current climate" (average for the period 1960-1990) and two time slices of two transient climate change scenarios ("2050" as average for the period 2041-2060 and "2070" as average for the period 2061-2080) from the MPI-ESL-LR climate model (Block and Mauritsen 2013) under two Representative Concentration Pathways scenarios (RCPs 4.5 and RCP 8.5) (van Vuuren et al. 2011).

3.4 Development of the Universal Response Functions

Universal response functions (URFs) were developed by integrating the effects of climate of planting locations in Central Europe (i.e. environmental effects) and climate of population or seed origin in North America (i.e. genetic effects) on growth performance (H24 and BA24) of Douglas-fir populations into a multivariate regression model. Quadratic functions were chosen to develop the URFs because they fit the data well and have been used by earlier studies (e.g. Wang et al. 2010;

McLane et al. 2011; Yang et al. 2015).The URFs (eq. 1) predict H24 or BA24 as a function of climate of the trial locations and seed origin, respectively. Significant climate predictors were selected using a multimodel approach (Burnham and Anderson 2002; Dormann et al. 2013) from the set of ten climate variables of trial locations and seed origin, accounting for multicollinearity resulting in the following response model (eq. 1).

$$\mathrm{Y}_{sp} = b_o + b_1\mathrm{MAT_s} + b_2\mathrm{MAT_s}^2 + b_3\mathrm{SHM_s} + b_4\mathrm{SHM_s^2} + b_5\mathrm{MAT_p} + b_6\mathrm{MAT_p}^2 + b_7\mathrm{MAT_s} * \mathrm{MAT_p} + \mathrm{e_{sp}}$$

Here, Y_{sp} is the growth performance (either H24 or BA24) of the population *p* at the trial sites *s*. $\mathrm{MAT_s}$ and $\mathrm{SHM_s}$ are the mean annual temperature and the summer heat moisture index of trial sites and $\mathrm{MAT_p}$ is the mean annual temperature of population origin; b_0 to b_8 are the intercept and regression coefficients, and $\mathrm{e_{sp}}$ is the residual error. $\mathrm{SHM_s}$ is a drought index calculated as the ratio of mean temperature of summer months (June- September) and mean summer precipitation (see Appendix 7.1 for details).

3.5. Model Evaluation

3.5.1. Model intercomparison

The URFs can be optimized to identify the best performing populations or seed origin for a given planting site and optimal planting site for a given seed origin with respect to climate of seed origin or planting sites. For this study the URFs were optimized to calculate the value of the climate variable of population/seed origin (i.e. $\mathrm{MAT_p}$) which, when substituted in the URF model (eq.1), provides the highest growth performance with respect to H24 and BA24 at any given 30 arc sec grid cell of the case study area. This was done by calculating the first order partial derivative of the URFs with respect to MAT_p (seeAppendix7.1 for details). The population origin recommended by the URF approach was termed as *optimum* population.

Best performing populations were also identified with a climate envelope approach following Isaac-Renton et al.(2014). The climate envelope approach recommended population or seed origin based on similarity of climate between the seed origin in North America and planting locations in the case study region in Central Europe. Mahalanobis distance (Mahalanobis 1936) matrix between principal components of climate variables (see Appendix 7.1) of each grid point of the case study area and population origin in Northwestern North America was calculated according to Roberts & Hamann(2012).For each grid point of the case study area, the grid point with the lowest Mahalanobis distance in Northwestern North America was selected from the distance matrix and chosen as the origin of most suitable population (see Appendix 7.1 for details).The population origin identified by the climate envelope approach was termed as *envelope* populations. Thereafter, growth performance of both *optimum* and *envelope* populations were predicted with the URFs and compared.

3.5.2 Model validation

In a validation experiment the URFs were used to predict the height growth performance of 20 provenance trials across Europe obtained from Isaac-Renton et al. (2014). Tree age of each provenance trial was different and ranged from 13 to 34 years. For a comparison between predicted and observed tree height, Spearman's rank correlation and the hit-rate were used. The hit-rate was calculated as the percentage of the 25% tallest populations at the validation provenance trial site that were also predicted to be top-ranking by the URF model (see Appendix 7.2 for details).

3.5.3 Analysis of model sensitivity

Model parameter uncertainty or model sensitivity were estimated by analyzing the change in growth performance as response to changing the regression coefficient of one climate variable at a time while keeping others constant at their mean value. Model sensitivity was estimated for a range of climate conditions that are expected to occur in our study region today and in future (MAT_s2-12°C and SHM_s 20-100). The sensitivity of the individual regression coefficients was summed up and expressed as a percentage deviation from the predicted H24 or BA24 to describe the uncertainty of the full model. The uncertainty of the full model was estimated for each of the provenance regions of the study region in Central Europe. Furthermore, uncertainty due to the different climate change scenarios was estimated as the absolute percentage difference in growth performance between the URF predictions under RCP 8.5 and RCP 4.5 scenarios in 2070 compared to the mean of the growth performance of the two scenarios (see Appendix 7.2 for details).

3.6 Model application

3.6.1 Identification of best performing population of Douglas-fir

For practical recommendations, the URFs were optimized with the derivative free solver MIDACO (Schlueter and Munetomo 2013) to identify optimum population origin for each legally defined provenance region (Fig. 2) of the case study area. Each provenance region was divided into 500 m altitudinal subzones in order to account for the underlying climatic differences within the provenance regions(see Appendix 7.2). This optimization process calculated the MAT_p for each altitudinal sub zone of individual provenance regions of the case study area. The MIDACO solver was used because it was found to have higher accuracy (Körkel et al. 2005; Audet and Orban 2006; Rios and Sahinidis 2013) compared to optimization via partial derivative approaches for complex and non linear functions like the URFs (see Appendix 7.2 for details).

This procedure identified population/seed origin in terms of mean annual temperature (MAT_p) of populations in North America, whereas the OECD guidelines (OECD 2012) which is the basis of seed procurement and movement in several EU countries recommend that the origin of reproductive material for reforestation should be precisely identified with respect to geographic location. Therefore, in order to recommend seed origin for practical purposes, we identified altitudinal belts within seed zones of Douglas-fir in Northwest America having the MAT_p predicted by the URFs. For this purpose, a 30 arc-sec resolution digital elevation model of Northwest America was reclassified into altitudinal belts, each spanning across 500 meters. Zonal statistics for MAT_p were obtained for each of these altitudinal belts within the seed zones of British Columbia (BC), Washington (WA) and Oregon (OR) (see Appendix 7.2 for details).

3.6.2 Estimation of growth performance

The URFs were applied to estimate growth performance of *optimum* populations at each 30 arc sec grid point (see Appendix 7.1) and for each legally defined provenance region (see Appendix 7.2) of our case study region in Central Europe under current climate and climate change scenarios. The URFs were also used to predict growth performance of 40 seed stands from North America in the study area. These seed stands were selected as the source of seed materials of the category “selected” for plantations in Europe following the guidelines of (OECD), Organization of Economic Cooperation and Development (OECD 2012) (see Appendix 7.2 for details).

3.6.3 Application of URFs as species distribution models

The URFs can be used as species distribution models (SDMs) by converting the predicted growth performance to occurrence (presence or absence). The thresholds for occurrence of Douglas-fir were set to H24 ≥ 3m and BA24 ≥ $2m^2ha^{-1}$, respectively, as they represent the observed minima of dominant height and basal area in our data set (see Appendix 7.3 for details). The resulting SDMs were named as URF-SDMs. Presence/ absence information of Douglas-fir was obtained at 71182 inventory plots across North America from Coops et al. (2011) and Schroeder et al. (2010). The URF-SDMs were applied at each of these plots to predict presence or absence of Douglas-fir based on the thresholds defined above. As our main interest was to test the URFs for its usage with locally adapted provenances, the climate of the observed locations (MAT_s) was set equal to the climate of the population origin (MAT_p) at any particular location of the observed data set. Performance of the URFs in predicting presence or absence of Douglas-fir was estimated by statistics like accuracy, sensitivity and true skill statistics (TSS) (Allouche et al. 2006) (see Appendix 7.3 for details).

Based on the predicted presence/absence data, maps of the occurrence of Douglas-fir were developed at 30 arc sec resolution in Europe and North America under current and future climate with two seed origin scenarios (i.e. *local seed sources* where MAT_s was set equal to MAT_p) and (*optimum seed sources* identified by optimizing the URFs with respect to MAT_p). see Appendix 7.3 for details.

4 Results

4.1 URFs for Douglas-fir

Mean annual temperature (MAT_s) and summer heat moisture index (SHM_s, i.e. the ratio of mean temperature and precipitation of the summer months) at the trial locations and mean annual temperature of population origin (MAT_p) as well as the interaction of MAT_s and MAT_p were found to be significant predictors of dominant height and basal area growth performance (see Appendix 7.1). Climate variables of the trial locations were found to be stronger predictors of growth performance than climate variables of the population origin. Overall, the URFs explained more than 88% of variation in growth performance.

Model evaluation comprised of comparing the URFs with a climate envelope model, model validation with independent data from across Europe and estimation of the model uncertainties. Comparing the URFs with the climate envelope approach shows, that under both current climate and climate change, the population origin in terms of $MAT_{p,}$ identified by the URFs, differ significantly from those identified by the climate envelope approach (Fig. 3). Generally, the variation between the populations recommended by the climate envelope approach is considerably higher than the variation among populations recommended by the URF approach (Fig. 3), both within and among altitudinal zones and for all climate scenarios. Populations identified by the URF models show significantly higher estimated growth performance than population origins identified by the climate envelope approach under both current and climate change scenarios (Fig. 4) (see Appendix 7.1 for details).

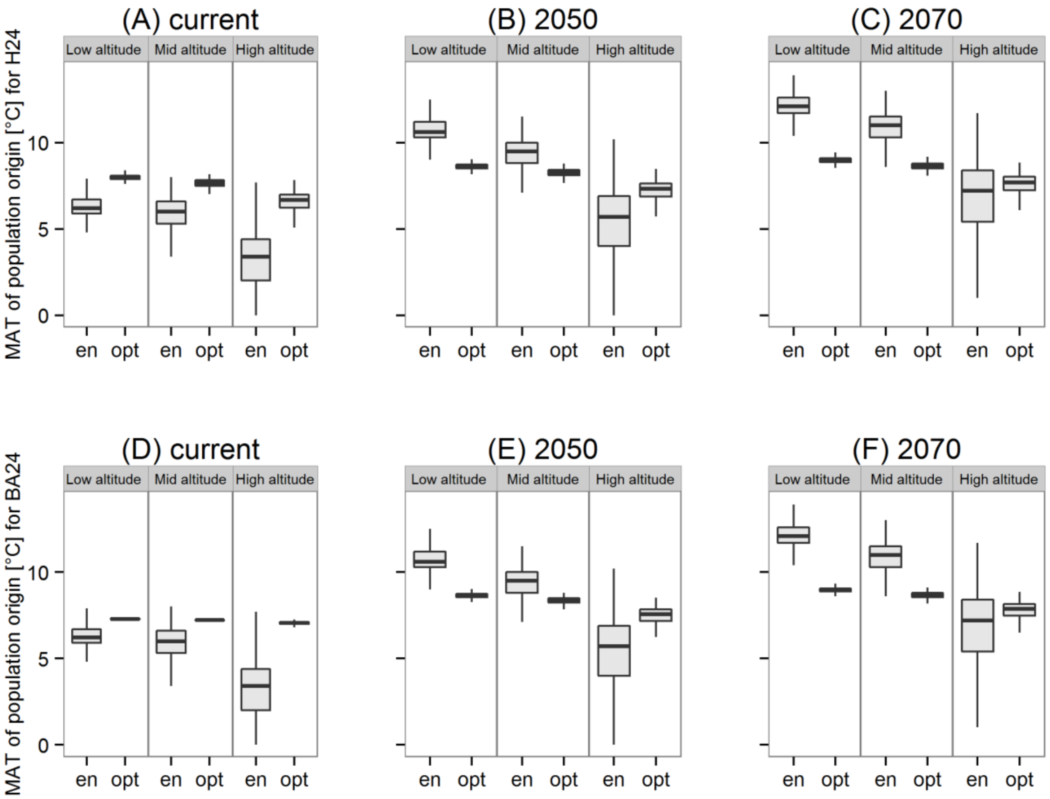


Fig. 3 Recommended climatic origin (as given by MAT of population origin) for H24 (A,B,C) and BA24 (D,E,F) under current climate (A,D) and two time slices of a transient climate change scenario (B,E) 2050 and (C, F) 2070. The populations to be planted were either selected to have optimum tree height (H24) or basal area (BA24) as drawn from the URF model (= 'opt' populations) or from the climate envelope approach which is based on similarity of climate between the study region and the natural distribution of Douglas-fir in Northwest America (= 'en' populations). For concise reporting, the recommended population origins were obtained for three altitudinal zones (Low: 0-500m;Mid: 500-1000m; High >1000m) of the case study region.

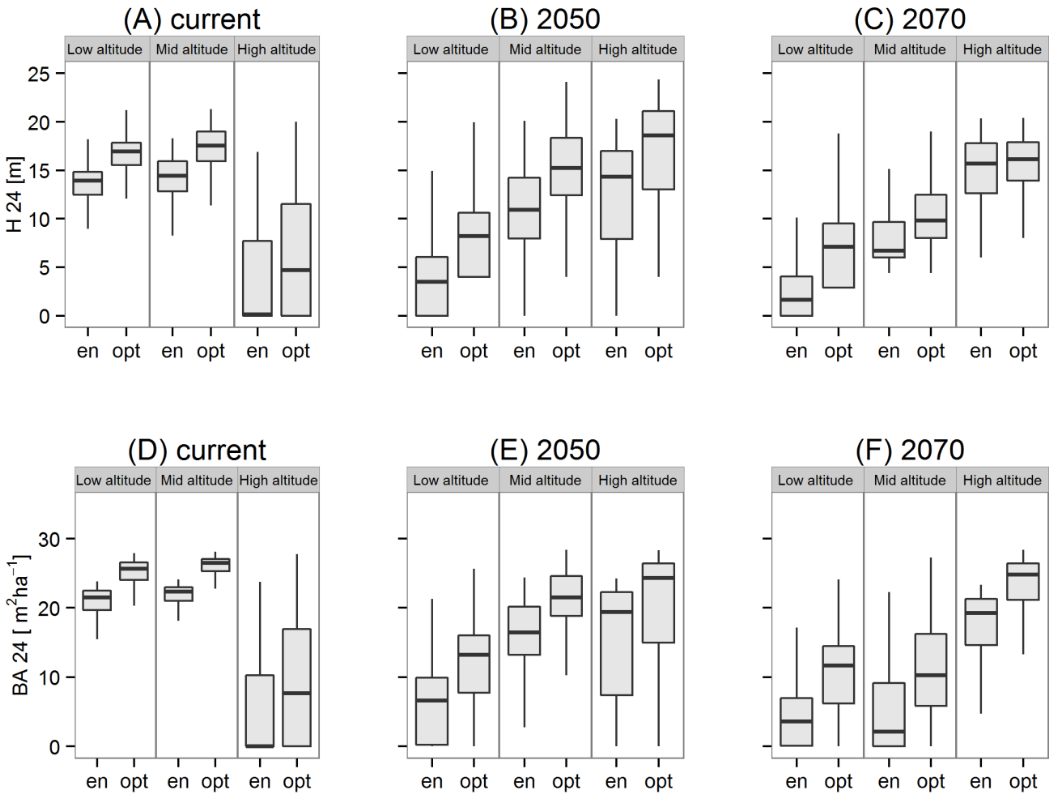


Fig. 4 Estimated growth performance (as given by dominant tree height H24 or mean basal area BA24) for populations to be planted at three altitudinal zones (Low: 0-500m; Mid: 500-1000m; High >1000m) of the case study region under current climate (A,D) and two time slices of a transient climate change scenario (B,E) 2050 and (C,F) 2070.The populations with optimum height and basal area respectively were either drawn from the URF model (= 'opt' populations) or drawn from the climate envelope approach which is based on similarity of climate between the study region and the natural distribution of Douglas-fir in Northwest America (= 'en' populations).

Model validation with independent provenance trial data from across Europe suggest that the URFs perform better in Central and Southeastern Europe compared to maritime Western Europe (Fig. 5).See Appendix 7.2 for details.

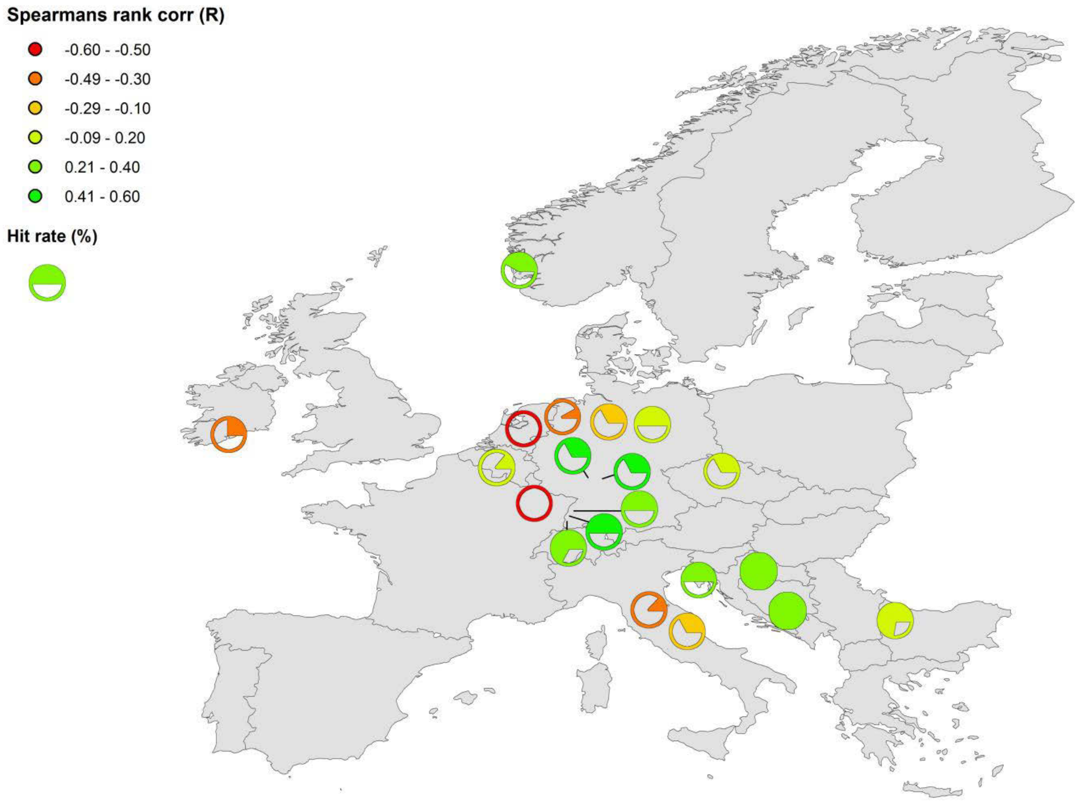


Fig. 5 Evaluation of the URF models with independent data from 20 provenance trials across Europe. The pie charts within each of these locations represent the Hit rate which is the percentage of top ranking population (top 25 %) in terms of height growth performance that were identified as top ranking by both URF and observed data. The colors of the pie charts represent the Spearman's rank correlation between URF predictions and observed data; red indicating low and green indicating high correlation.

From all the climate predictor variables in the URFs, the model predictions were most sensitive to changes in summer drought (SHM_s) and mean annual temperature of planting sites (MAT_s), and least sensitive to changes in (MAT_p) mean annual temperature of seed origin (see Appendix 7.2 for details). The sensitivities from the individual climate variables were summed up and expressed as a percentage deviation from the predicted H24 or BA24 to describe the uncertainty of the full model. The overall model uncertainty increased with mean annual temperature of the planting site (see Appendix 7.2 for details). Under current climate, uncertainty in the model predictions for the study area, expressed as percentage deviation from the predicted growth performance, ranges from 10 to 30 % in case of H24 (Fig. 6D), and from 20 to 40 % in case of BA24 (see Appendix 7.2). Under climate change the pannonian East of Austria and lower altitude regions of North and central Germany are predicted to have maximum model uncertainty amounting to 30 to 70 % of the predicted H24 (Fig. 6E, F) and 40–85 % of predicted BA24 (see Appendix 7.2 for details).

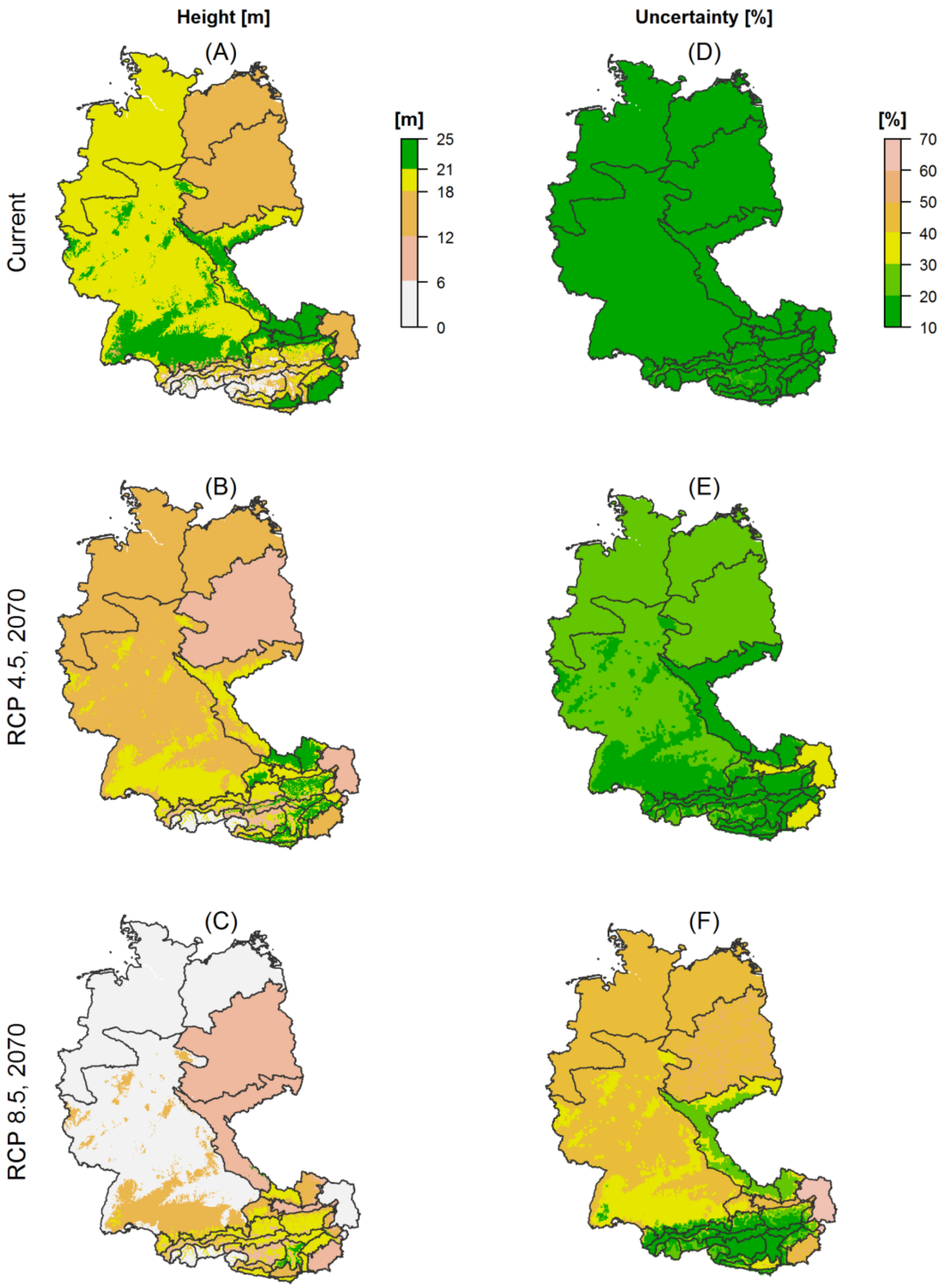


Fig. 6 Height growth performance of seed sources predicted to be optimum for the provenance regions of the study region under (A) current climate and (B, C) under two climate change scenarios RCP4.5 and RCP 8.5 in 2070. D, E, and F depict the uncertainty in the prediction of URFs indicated by the percentage deviation from the predicted H24 due to

changes in regression coefficients. For growth performance in terms of BA 24 (see Appendix 7.2).

4.2 Model application

Model application comprised of identifying optimum population origin for the case study area, predicting growth performances of the optimum population and demonstrating the use of the URFs as species distribution models (SDM).

Under both, current climate and climate change, populations originating from coastal British Columbia (BC), the western Cascade mountains and from coastal regions of Washington (WA) and Oregon (OR) with MAT_p ranging from 6-9.5 °C were predicted to be the most productive seed sources of Douglas-fir in terms of growth performance for the study region (Fig. 7B). Geographically, these optimum seed zones are located between30 – 50° N latitude and 121 – 127°W longitude (Fig. 7B). Current seed stands in North America, providing seed material for Europe under the legal framework of OECD also have similar growth performance and geographic origin as the optimum populations predicted by the URFs (see Appendix 7.2 for details).Those seed sources appear to be suitable under both current and future climates in the study region in Central Europe.

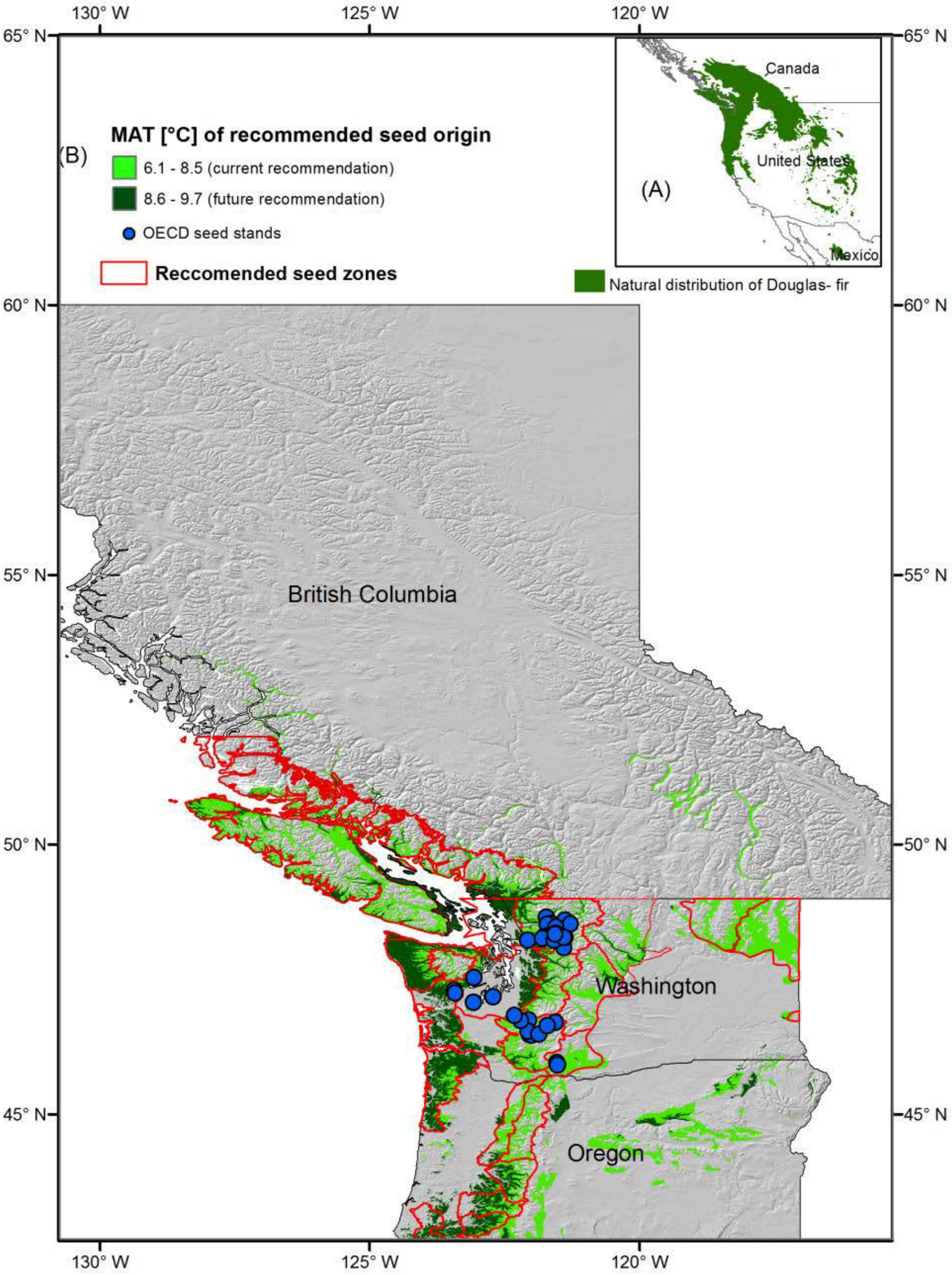


Fig. 7 (A) Natural distribution of Douglas-fir in NW America. (B) Seed origin of Douglas-fir shown by mean annual temperature [°C] in NW America, predicted to be optimum by the URF$_S$ in terms of height and basal area growth performance when planted in the study area under current climate and climate change scenarios. The location of the 40 seed stands

identified under OECD scheme are shown as blue dots. The red lines demarcate the recommended seed zones for obtaining planting materials for the study area.

The URFs were applied to predict the growth performance of the optimum populations for each legally defined provenance region of the case study area (Fig. 6). Under current climate, the provenance regions of north Germany, northern lowlands, central and east Germany, and southwest Germany, and the Austrian provenance regions in the south, east, and north of the Alps including the eastern continental regions are predicted to have above-average growth performance with up to 37%higher dominant height (H24) and 45% higher basal area (BA24) compared to the provenance regions in the higher altitude Alpine regions (Fig. 6A &Appendix 7.2). Under climate change, the provenance regions which were predicted to have above-average growth performance under current climate were predicted to have 10–36 % reduction in dominant height and 12–40 % reduction in basal area by 2070 under RCP4.5 and RCP 8.5 scenarios, respectively (Fig 6B, C & Appendix 7.2). Under both climate change scenarios, the pannonian East of Austria and lower altitudinal regions (0–500 m) of north and central Germany are predicted to experience the strongest decline in growth performance compared to current climate (see Appendix 7.2 for details).

The URFs were used as species distribution models (URF-SDMs) by converting predicted growth performance to presence and absence. The URF-SDMs correctly predicted observed presence and absences in 55% (for H24) and 70% (for BA24) on more than 70000 inventory plots across North America (Table 1). The overall model performance estimated by the true skill statistic is 0.32 and 0.37, respectively (Table 1, Fig. 8).The 15% and 30% of the plots where Douglas-fir was observed but predicted as absent by the URFs (omissions) are mainly situated in southern California (Fig. 8). The true absences that were misclassified by the URF-SDMs as presences are located in the south and southeast of the Rocky Mountains (Fig. 8) and at the northern range limit of the species. Among the two models, URF-SDM for tree height has a lower omission rate but also a higher rate of false positives, while the rate of false positives is reasonably small in the URF-SDM for basal area at the expense of a higher omission rate (Table 1).

Table 1. Accuracy of the two URF-SDMs for predicting observed presence/absence at 71182 inventory plots in dataset in western North America.

	H24	BA24
Accuracy	0.55	0.70
Sensitivity	0.85	0.67
Specificity	0.48	0.70
True Skill statistics	0.32	0.37
H24 predicts absence but URF-BA24 predicts presence	0.00	
H24 predicts presence but URF-BA24 predicts absence	0.24	

Accuracy = the proportion of the presence and absence records correctly identified by the model
Sensitivity = the proportion of true presences correctly identified by the model
Specificity = the proportion of true absences correctly identified by the model
True Skill statistics = measure of model performance independent of prevalence. TSS value range from -1 to +1 where +1 indicate perfect agreement and values <=0 indicate a performance equivalent to random guess (Allouche et al. 2006).
URF-H24= URF for dominant height at age 24 and
URF- BA24= URF for basal area at age 24

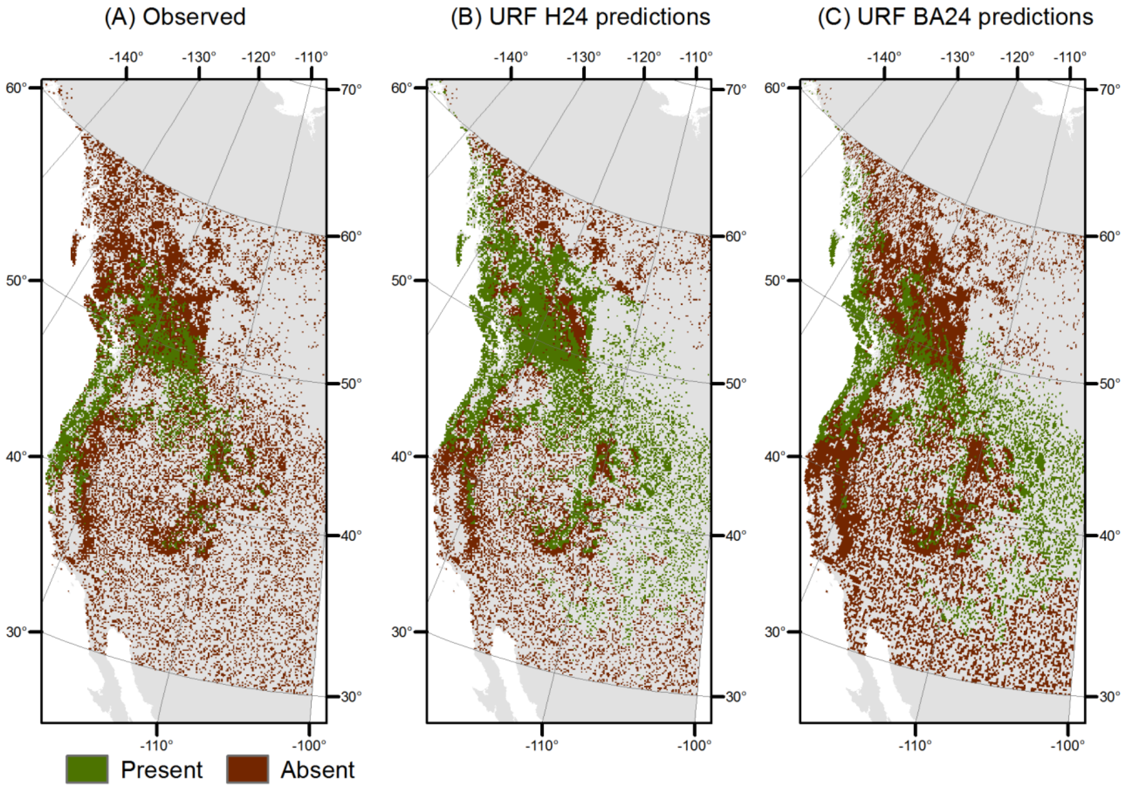


Fig. 8 (A) Observed distribution of Douglas-fir in at 71,182 locations in North America and (B, C) predicted distributions of Douglas-fir using the URF for dominant height (H24) and the URF for mean basal area (BA24), respectively, at age 24.

Applying the URF-SDMs to predict distribution of Douglas-fir in Europe reveals that under current climate 70% of the total geographic area of Europe is suitable for Douglas-fir if optimum seed sources are planted (Fig. 9). The suitable area reduces by 31% if local seeds are planted (see Appendix 7.3 for details). Under climate change, the difference in suitable areas strongly depends on the utilized seed sources, whereby suitable area for cultivation of optimum seed sources are significantly larger than local seed sources (Fig. 9 and Appendix 7.3).

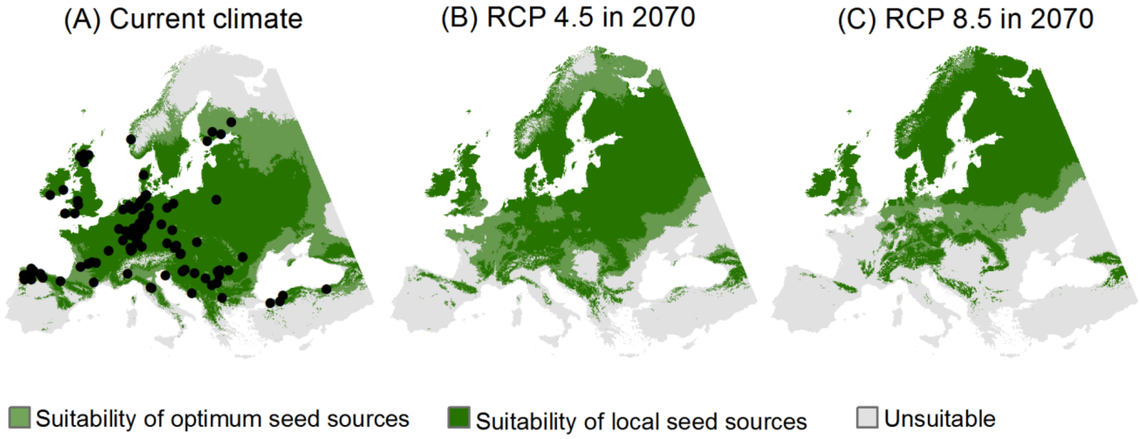


Fig. 9 Predicted potential distribution of Douglas-fir in Europe under current climate (A) and two climate change scenarios in 2070 (B, C). The suitable habitats shown in dark green represents *local seed sources* selected on the basis of similarity of climate between North America and Europe. Areas in light green represent the gain in suitable habitats if the *optimum seed sources* were identified by the URFs. Black dots in (A) mark the locations of successful provenance trials across Europe available from Issac-Renton et al (2014)

5 Discussion and conclusion

5.1 Methodological issues

A major aim of the study on which this thesis is based was to compare methods to identify populations of non-native Douglas-fir adapted for the expected future climatic conditions in Central Europe. Provenance trials of Douglas-fir established in Europe offers not only a unique opportunity to study the effects of climate change on growth and fitness of the provenances, but also generates valuable lessons for assisted migration. In this study, the *response functions* and *climate envelopes*, two major approaches for identifying populations for future climatic conditions were compared. The climate envelope approach is based on the concept of local adaptation which assumes that populations are adapted to and have maximum growth and fitness in their regions of current occurrence. The response functions on the other hand are based on climatic constraints of growth and fitness of populations.

URFs calibrated from empirical growth data recommended significantly different population origin than the climate envelope approach (Fig. 3). Also, the populations recommended by URFs had significantly higher growth performance (Fig. 4).This was confirmed by a recent meta-analysis by Isaac-Renton et al. (2014) who compared relative growth performance of Douglas-fir within provenance trials across Europe. They found that populations recommendation based on similarity of climate between population origin and planting locations does not always correlate with growth performance, especially in continental and Central Europe where the climate of population origin is significantly different from that of the planting locations (Isaac-Renton et al. 2014). A major limitation of the climate envelope approach is, that it ignores the actual environmental and genetic constraints of growth performance because it is based solely on the species presence and absence in its region of origin. Thus, climate envelope models might not contain those climatic variables to which local populations are adapted to, but instead are based on an approximation of a limited set of climate predictors that define the species' occurrence. Therefore, the application of climate envelope models to identify populations which are adapted to future climate may be error prone (Marris 2008; McKenney et al. 2009). However, the advantage of the climate envelope approach is, that it does not require extensive data on growth and fitness for its calibration and that it is easy to develop and elusively easy to interpret.

Major advantage of the response function approach such as the URFs is, that they are based on empirical relations between growth, fitness and their climatic drivers. The URFs are an advancement over the site specific *transfer functions* (Matyas 1994; Carter 1996; Andalo et al. 2005) and population specific *response functions* (Wang et al. 2006; Kapeller et al. 2012) because they integrate both genetic and environmental drivers of growth performance into a single model equation. Therefore, URFs can be used to identify growth performance of any population at any planting site and vice versa and are not limited to a specific site or provenance. Limitation of the URF approach is, that extensive data from provenance trials are needed for calibration. Moreover, such trials are often not established in extreme environments, and often provenances from the entire distribution range are not planted at all trial sites. In this study we have addressed this issue by developing anchor points (Wang et al. 2006). Gene-ecological functions were developed for the extreme (warm and cold) provenance trial sites. These functions were used to predict the growth performance of those provenances not planted in such extreme conditions, thereby balancing the provenance trials at both warm and cold extremes of the covered gradient (see Appendix 7.1 for details). This issue needs further investigation and refinement because for developing the anchor points, provenances from both leading and trailing ends of the natural range of the species needs to be planted at climatically extreme sites.

Another advantage of the URFs is, that they can be used as species distribution models (SDMs) by converting growth performance to occurrence/non-occurrence information. In spite of their popularity, the SDMs have been criticized for not accounting for intra-specific variations (ONeill et al. 2008; Aitken et al. 2008; Oney et al. 2013) and lack of mechanistic basis (Buckley et al. 2010; Kearney et al. 2010). Moreover, most SDMs are based on the *realized niche* of a species whereas to predict species distribution under climate change the SDMs should identify the *fundamental niche* of the species (Wiens et al. 2009). The URF approach overcomes the limitations of the conventional SDMs because (i) the URFs are mechanistically based on relation between climate and functional traits such as tree height and basal area, rather than correlation between observed current occurrence, and climate, and (ii) the URFs also include intra-specific variation enabling predictions of the species distribution at a population level.

The overall accuracy of the URF-SDMs in identifying presence and absence of Douglas-fir in North America was close to the accuracy level of recent studies based on dynamic process based models (e.g. Coops et al. 2011; Weiskittel et al. 2012), even though the URFs are simple empirical statistical models with few climate parameters. This demonstrates the parsimonic character of the URFs and reiterates the discussion on model simplicity/complexity vs model accuracy (Merow et al. 2014).However, the URF-SDM's predictions contradicts observed presence of Douglas-fir at the trailing edge in the coastal regions of southern California which is most likely a result of lack of provenances from that region in the dataset used for calibration of the URFs (see Appendix 7.3 for details). This is a known limitation of historic common garden trials where provenances from the entire natural range were not consistently tested and climatically extreme trial sites at or beyond the species range limits were not included (Matyas 1994; Leites et al. 2012b). While historic provenance trials of tree species were established mainly to guide foresters to select most productive planting stocks, future trial series should rather aim at developing a better understanding of the species specific climate constraints and the correlations between functional traits and the environmental conditions of test sites and seed sources. A further scope of improvement of the URFs would be to integrate additional functional traits such as wood characteristics, phenological observations and edaphic variables such as soil moisture, available nitrogen and soil Ph as predictors.

5.2 Applicability of the URFs under climate change

Model uncertainty and uncertainty of future climatic conditions together make recommendations based on models challenging. Moreover, legal requirements like international resolutions, country specific rules and regulations at regional scale makes it even more difficult to provide scientifically robust recommendations to forest managers and policy makers. Therefore, analysis of uncertainty in model results is advised (Lindner et al. 2014). The present study aimed at translating model predictions into practical recommendations for forest and seed managers while accounting for both model sensitivity and uncertainty and considering the legal framework for forest reproductive material at national and international levels.

Under current climate, model uncertainty was found to be significantly lower (Fig. 6) compared to potential future climates indicating confidence in the model for identifying suitable seed sources of Douglas-fir in the study region under the current climate. Under climate change, the predictions of the URFs have higher uncertainty in the pannonian East of Austria and north Germany lowlands, and lowest in southeast Germany (Fig. 6).Generally, model uncertainty was found to increase with MAT and SHM of the planting sites (see Appendix 7.2 for details), confirmed also by other recent studies such as Spadavecchia et al. (2011) and Albert et al. (2015).This implies that predictions of the URFs need to be cautiously interpreted at sites with complex soil moisture regime accompanied by warm summers.

Validation of the URFs with independent data from 20 Douglas-fir provenance trials across Europe indicated that under climatic conditions that are similar to the calibration data, the URFs worked well, for example in Central and continental Europe but performs poorly when applied to climatically and geographically more distant plantation sites located in northwestern maritime and Mediterranean Europe. Thus, the empirical relation between climate and growth response in the URFs might lack generality across Europe. Also, the growth response in the trials might be affected by non-climatic factors like soil or forest management, which differs across these 20 trials. The lack of generality of the URF models strongly indicate the need of further analysis of provenance trials across Europe.

However, the most crucial issue for our study was to determine the applicability of the URFs to predict growth performance of populations under conditions of climate change. The model validation suggests that the URFs performed well in the majority of the sites located in southeastern Europe (e.g. Bosnia and Croatia) where the present climate conditions corresponded to scenarios expected for 2050 and 2070 across the study region (see Appendix 7.2 for details). This indicates, that the URFs are suitable tools for estimating Douglas-fir growth performance in expected future climates in Central Europe.

5.3 Implications of the study

The findings of this thesis, that are relevant for a broader audience, can be structured as follows: (i) role of intra-specific variation in adaptive forest management under climate change, (ii) development of a decision making tool for identifying adapted populations and suitable site conditions for reforestation in the future.

The URFs predict that populations originating from the western Cascade Range and coastal regions of Washington and Oregon are the best performing populations for both current and future climate conditions in the study region in Central Europe. This result corroborates well several recent studies (e.g. König 2005; Rehfeldt et al. 2014a; Isaac-Renton et al. 2014). Therefore, substantial change in the planting material is not required for the study area under climate change. This is remarkable, given that the temperature in the study region under the most pessimistic climate change scenario (i.e. RCP 8.5) is expected to rise between 3°C and 4.5°C until the end of the century (Jacob et al. 2013). However, the population origin recommended by the URFs should be examined along with the uncertainty in model predictions under climate change especially in the eastern continental regions of Central Europe (see Appendix 7.2 for details).

Recommendation of populations or seed sources based only on growth performance can be error prone because the trade-off between growth and fitness is well known in Douglas-fir. To navigate this limitation, the URFs were based on both dominant height and basal area growth performance. Dominant height is a reliable indicator of growth performance whereas basal area is based on both diameter growth and survival rate and thus also affected by site-specific climate events. Since the optimum populations predicted by both URFs are highly correlated (Fig. 6, Appendix 7.1 and 7.2), they have not only superior growth performance but also reasonably good fitness.

The flexibility of the URFs as a decision making tool is remarkable. The model can be used as response function, transfer function or as a SDM to predict growth performance of particular provenance, site productivity or suitability of a site for planting a particular species or provenance. Model validation reveals lack of generality of the URFs which is a known problem of statistical models with respect to extrapolation. A process based modeling approach would be ideal in such a situation, however such a model comes at a higher cost of calibration and might lack accuracy at a local level (Gutiérrez et al. 2016).

Climate change is likely to result in a mismatch between the new environment expected in the future and the current environment a species is adapted to (Aitken et al. 2008). Assisted migration has been suggested as an option to facilitate the colonization of forest tree species in new habitats with suitable climate in the future because natural migration that would allow species to track up with the changing environment is far below the expected speed of climate change (Petit et al. 2008; Nathan et al. 2011). However, in the case of long-lived communities such as forests, assisted migration of species to new and favorable climate is most likely to take several decades. Therefore, lessons learned from artificial seed transfer to sites with different climatic conditions (e.g. provenance trials of Douglas-fir in Europe) generates valuable knowledge for the implementation of assisted migration programs.

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7 Appendix

7.1 Paper I

Chakraborty D, Wang T, Andre K, Konnert M, Lexer MJ, Matulla C, Schueler S (2015) Selecting Populations for Non-Analogous Climate Conditions Using Universal Response Functions: The Case of Douglas-Fir in Central Europe. PLoS ONE 10(8): e0136357

PLOS | ONE

RESEARCH ARTICLE

Selecting Populations for Non-Analogous Climate Conditions Using Universal Response Functions: The Case of Douglas-Fir in Central Europe

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Abstract

Identifying populations within tree species potentially adapted to future climatic conditions is an important requirement for reforestation and assisted migration programmes. Such populations can be identified either by empirical response functions based on correlations of quantitative traits with climate variables or by climate envelope models that compare the climate of seed sources and potential growing areas. In the present study, we analyzed the intraspecific variation in climate growth response of Douglas-fir planted within the non-analogous climate conditions of Central and continental Europe. With data from 50 common garden trials, we developed Universal Response Functions (URF) for tree height and mean basal area and compared the growth performance of the selected best performing populations with that of populations identified through a climate envelope approach. Climate variables of the trial location were found to be stronger predictors of growth performance than climate variables of the population origin. Although the precipitation regime of the population sources varied strongly none of the precipitation related climate variables of population origin was found to be significant within the models. Overall, the URFs explained more than 88% of variation in growth performance. Populations identified by the URF models originate from western Cascades and coastal areas of Washington and Oregon and show significantly higher growth performance than populations identified by the climate envelope approach under both current and climate change scenarios. The URFs predict decreasing growth performance at low and middle elevations of the case study area, but increasing growth performance on high elevation sites. Our analysis suggests that population recommendations based on empirical approaches should be preferred and population selections by climate envelope models without considering climatic constrains of growth performance

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should be carefully appraised before transferring populations to planting locations with novel or dissimilar climate.

Introduction

Climate change poses serious threats to the ability of forests to provide multiple ecosystem services [1]. In many forests, trees possibly will not be able to tolerate increasing climate stress (e.g. drought severity and frequency) and new disturbance factors may occur and result in increased and abrupt tree mortality [2, 3]. Although tree species are known to adjust physiologically and morphologically to changing environmental conditions [4–6], climate change is expected to result in a mismatch between the new environment and the environment to which a species is adapted to [7]. Natural migration that would allow species to track up with the changing environment is far below the expected speed of climate change according to combined fossil and DNA studies [8] and modelling analysis [9]. Thus, assisted migration has been suggested as an option to facilitate the colonization of forest tree species in new habitats with suitable climate in the future and thus improve the long-term prospects of trees and its related communities [10–12]. In order to implement assisted migration schemes it is crucial to identify those populations within species which are best suited for predicted future climate conditions at a given site or region. Similar challenges are being faced by forestry, where populations of productive tree species with desired characteristics (e.g. productivity, environmental stability) are being selected for plantations worldwide. Generally, tree species are known to exhibit wide intraspecific variation for many phenotypic traits as a result of the local adaptation of individual populations to specific climate conditions [13, 14]. These intraspecific variation within tree species needs to be considered in order to understand and predict future suitable niche space [15, 16] and to develop guidelines for reforestation in forest management and forest conservation practices [17–19].

Comparisons of current climate change to paleoclimatic variations indicate that new climates, substantially different from current conditions commonly referred to as non-analogous [20] might evolve in the future and give rise to new ecosystems [20, 21]. Non-native tree species often originate from climates non analogous to its region of introduction (S1 Fig). In the case of long living communities like forests, results from assisted migration of species to new and favorable climate is most likely to take several decades. Therefore lessons learned from artificial seed transfer to non-analogous climate in forestry can help us to understand the implications of assisted migration of species. One of the most prominent examples for such species is the North American Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco). Due to its superior growth, wood quality and market value [22] Douglas-fir has been introduced globally. In Europe, the intraspecific variation in growth performance of Douglas-fir was first recognized when growth of certain seed sources outperformed others across a wide range of planting sites [23]. At present, recommendations on provenance use for forest managers published from national authorities are based on empirical studies. Few attempts have been made to relate these recommendations to the climate conditions of the plantation area or to test for local adaptations and effects of a provenance transfer to non-analogous climate conditions.

To guide the identification of suitable populations for reforestation under particular climatic conditions two major conceptual approaches can be employed: first, the empirical response function approach, which identifies suitable populations on basis of correlations between quantitative traits and climatic parameters using climate-response functions [18, 24, 25], and second, the climate envelope approach that compares the climate conditions of the seed origin with the climate at putative planting locations [19, 26]. Conceptually the climate envelope approach aims at identifying geographical regions which have identical climatic condition as that of the planting area [19]. In this approach, for a given planting location, a climatically identical seed origin is identified by statistical approaches like regression trees, principal component analysis, canonical correlations, minimum distance etc.[26–28].The climate envelope approach has been criticized because the assumption of local being optimal may be invalid if climate of population origin and planting locations are not analogous which may be frequently the case in the future [20, 29]. Thus, their use may be irrelevant under climate change [11, 30]. The response function approach is based on measures of traits that are related to fitness components and thus may include any population genetic processes e.g. selection, demography, drift or gene flow that may have shaped the trait expression. A limitation of the response function approach is the availability of extensive data from common garden/ provenance trials to develop such response functions. In provenance trials, several populations of a species are planted in a particular climate or throughout an appropriate climatic gradient with the primary objective of identifying populations with desired growth characteristics and survival rates. Due to the increasing interest in climate change, such trials were revisited to understand the relation between growth performance and climate and to recommend suitable populations for future conditions [31, 32].

Two types of response functions have been widely used to characterize the intraspecific variation of the climate- growth relationship. A transfer function is based on correlation between growth performance of several populations and climate of a particular planting location [17, 33, 34], but such a transfer function is applicable only to the site for which it was developed. A response function on the other hand is based on the correlation between growth performance of a particular population and the climatic conditions across a range of planting sites [18, 24, 32] and is specific for the population for which it was developed. To address these limitations, Wang *et.al* [14] proposed to combine the transfer and response functions into an integrated model they referred to as Universal Response Function (URF). The URF therefore incorporates both genetic and environmental effects on growth response of populations.

In this study, we use the Universal Response Function (URF) approach to predict growth performance of Douglas-fir populations utilizing provenance trials across a wide climatic gradient in Central and continental Europe.

Our objectives were (i) to identify climatic factors that drive genetic and environmental variation in growth performance of Douglas-fir populations and to develop URFs from a network of provenance trials, (ii) to apply the URFs to recommend populations based on growth performance for the case study area under current and potential future climate conditions, and (iii) to compare projected growth performance of populations selected with URFs with populations selected with a climate envelope approach.

Materials and Methods

Provenance trials

We utilized data from 50 Douglas-fir provenance trials in central Europe (Fig 1) located in Austria and Germany, established between 1973 and 1993 by the Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), Vienna, Austria and the Bavarian Office for Forest Seeding and Planting (ASP), Teisendorf, Germany. These trials, including a selection of 290 populations of Douglas-fir originating from Northwest America (Fig 2) were established across a wide gradient of climatic conditions in Central Europe (Fig 3, S1 Fig). All trials were installed within multifunctional forests for which no restrictions in reforestation

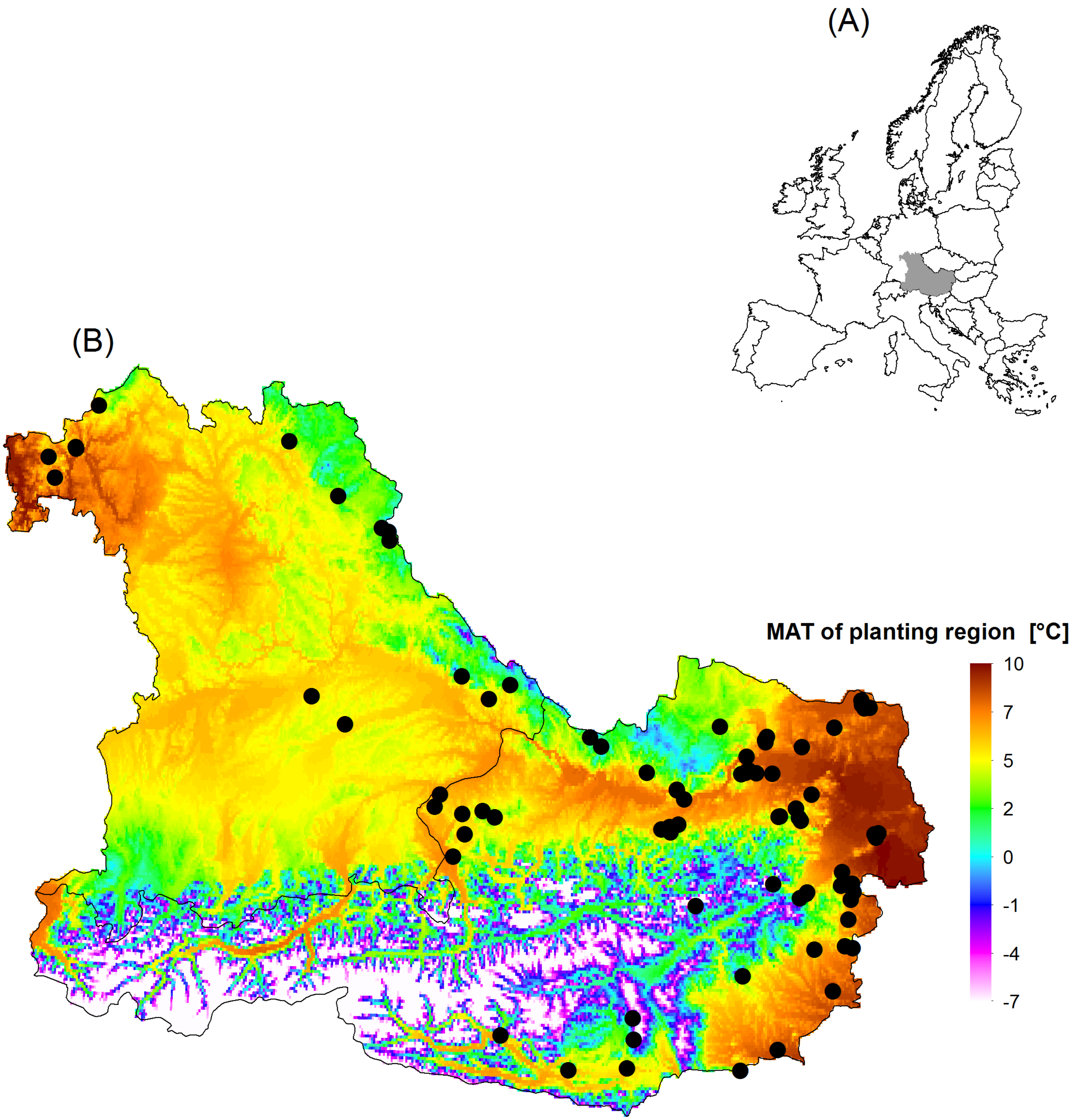

Fig 1. Location of the case study. A) Location of the study area in Europe highlighted in gray. **B**) Location of the provenance trials (black dots) in the case study region of Austria and southern Germany. Although, the study region is geographically small, it covers a wide climatic gradient as indicated by the mean annual temperature (MAT) because of its proximity to the Eastern Alps. The authors of the manuscript *"Selecting populations for non-analogous climate conditions using Universal Response functions*: *the case of Douglas-fir in Central Europe"* are the copyright holders of the Fig 1 and Fig 2 used in the manuscript. We, therefore permit the open-access journal PLOS ONE to publish Fig 1 and Fig 2 under the Creative Commons Attribution License (CCAL) CC BY 3.0 (http://creativecommons.org/licenses/by/3.0/us/).

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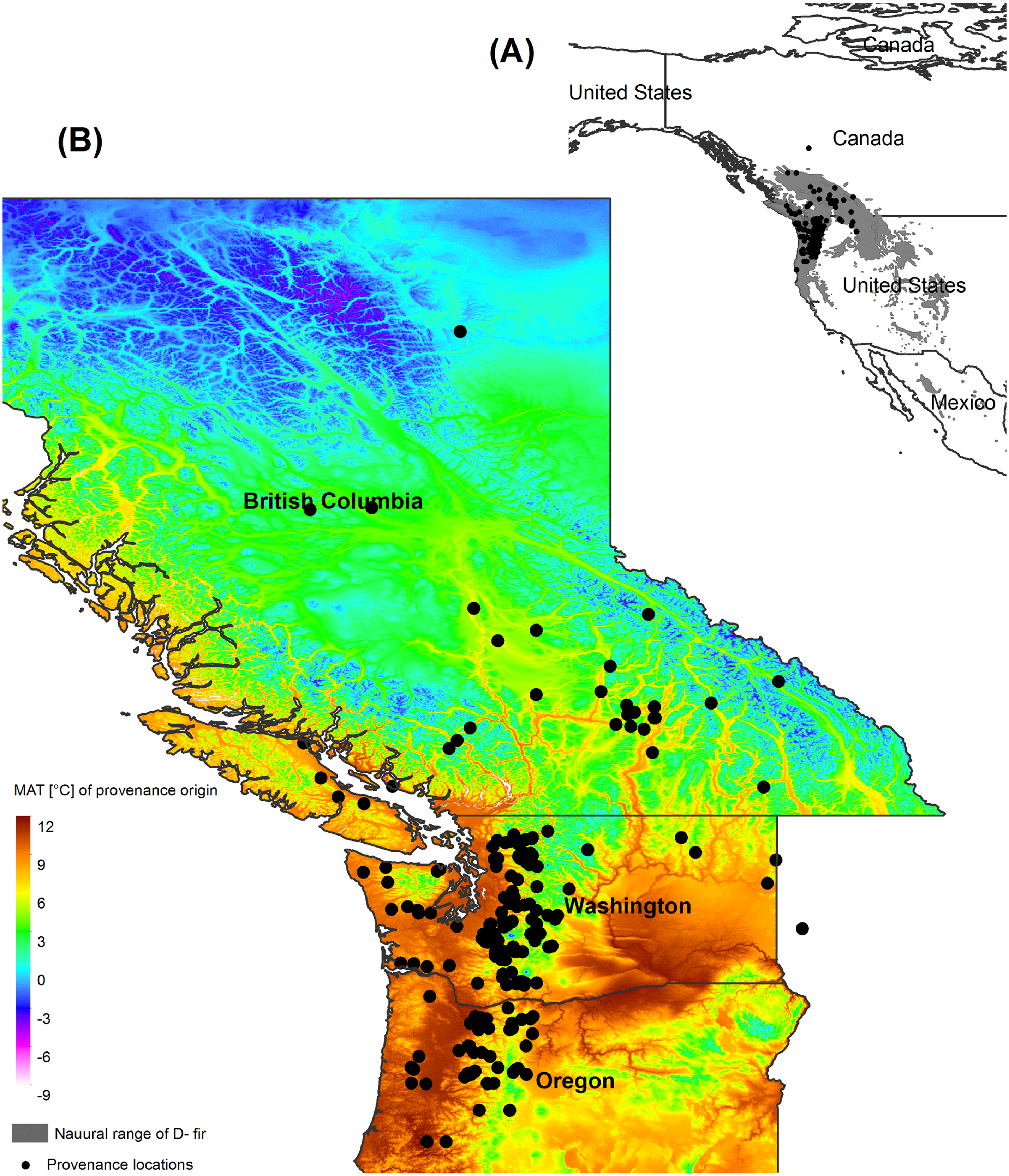
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● Provenance locations

Fig 2. Location of provenance origin in North America. A) Location of the origin of the Douglas-fir provenances planted in the study area and the natural distribution range of Douglas-fir (shaded in gray). **B)** Zoomed in location of provenance origin in British Columbia (BC), Washington (WA) and Oregon (OR) with respect to their mean annual temperature. The authors of the manuscript *"Selecting populations for non-analogous climate conditions using Universal Response functions*: *the case of Douglas-fir in Central Europe"* are the copyright holders of the Fig 1 and Fig 2 used in the manuscript. We, therefore permit the open-access journal PLOS ONE to publish Fig 1 and Fig 2 under the Creative Commons Attribution License (CCAL) CC BY 3.0 (http://creativecommons.org/licenses/by/3.0/us/).

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with Douglas-fir exist and for which no permission was and is required (Forest Act § 1a. Section {1}). Our study did not involve endangered or protected species and was carried out in strict accordance with the respective national (Act of Forest Reproductive Material §1 Section {3}) and international (OECD seed scheme) regulations of forest reproductive material.

The provenance trials were designed as randomized blocks. Within each block (replication) three to four year old pre-cultivated seedlings of selected provenances were planted in plots of 20–100 individuals with a spacing of 2m x 2m. After fifteen years, tree density was reduced to approximately ten trees per plot (i.e. 1000 trees per hectare) in order to have equal stem density across all trials. At various ages (between 10–35 years) diameter at breast height (DBH) were measured for each individual tree. In addition, at 35 trial sites tree heights were also measured for 50–100 randomly selected trees at age 24. In order to maximize the utilization of the dataset to as many trial sites and populations as possible, we used data of tree heights and DBH as two parallel response variables, where the DBH data were transformed into measures of the basal area per hectare. For trials in which DBH data were not available at tree age 24, we estimated DBH24 from the mean annual DBH increment between two successive measurements. The "basal area per hectare at age 24" of individual populations (hereafter referred to as BA24) was then computed as the mean value across the three to four replicates of that population within the trial. Since tree heights were not measured for each individual tree, site specific height-DBH models (S1 Table) were utilized to estimate individual tree heights. The resulting response variable "dominant height of populations age 24" (hereafter referred to as H24) was computed as the 75 percentile of all tree heights of a given population at age 24. The 75 percentile characterizes the potential height growth of dominant trees and is fairly insensitive to thinnings or strong intraspecific competition between trees [24].

Climate data

To develop the URFs, climate data representing the growing conditions for H24 and BA24 at each trial site were required. We used daily climate data from the Austrian network of weather stations maintained by the Central Institute of Meteorology and Geodynamics for trial in Austria, and gridded climate data for the greater Alpine region available from an earlier research project (reclip: century [35]) for trials in southern Germany. The climate of both data sets were used for interpolations to the coordinates of the trial sites resulting in time series data of daily mean temperature and precipitation covering the period from installation of each trial until the most recent measurements. For the interpolation to each trial, data of the four closest weather stations and the four closest grid cells, respectively, were first adjusted to the altitude of the trial sites and secondly interpolated to the trial coordinates by inverse distance weighted interpolation. From temperature and precipitation data, ten biologically relevant climate variables (Table 1) were calculated for further analysis.

For climate data of population origin, mean values of the same climate variables (Table 1) for "current" climate (average for 1950–2000) were generated for each population origin location using the high-resolution climate model Climate WNA v4.72 [36].

Utilizing the WorldClim database [37] the climate variables (Table 1) were also calculated for each grid point of a 30 arc-sec digital elevation model of the case study area for "current

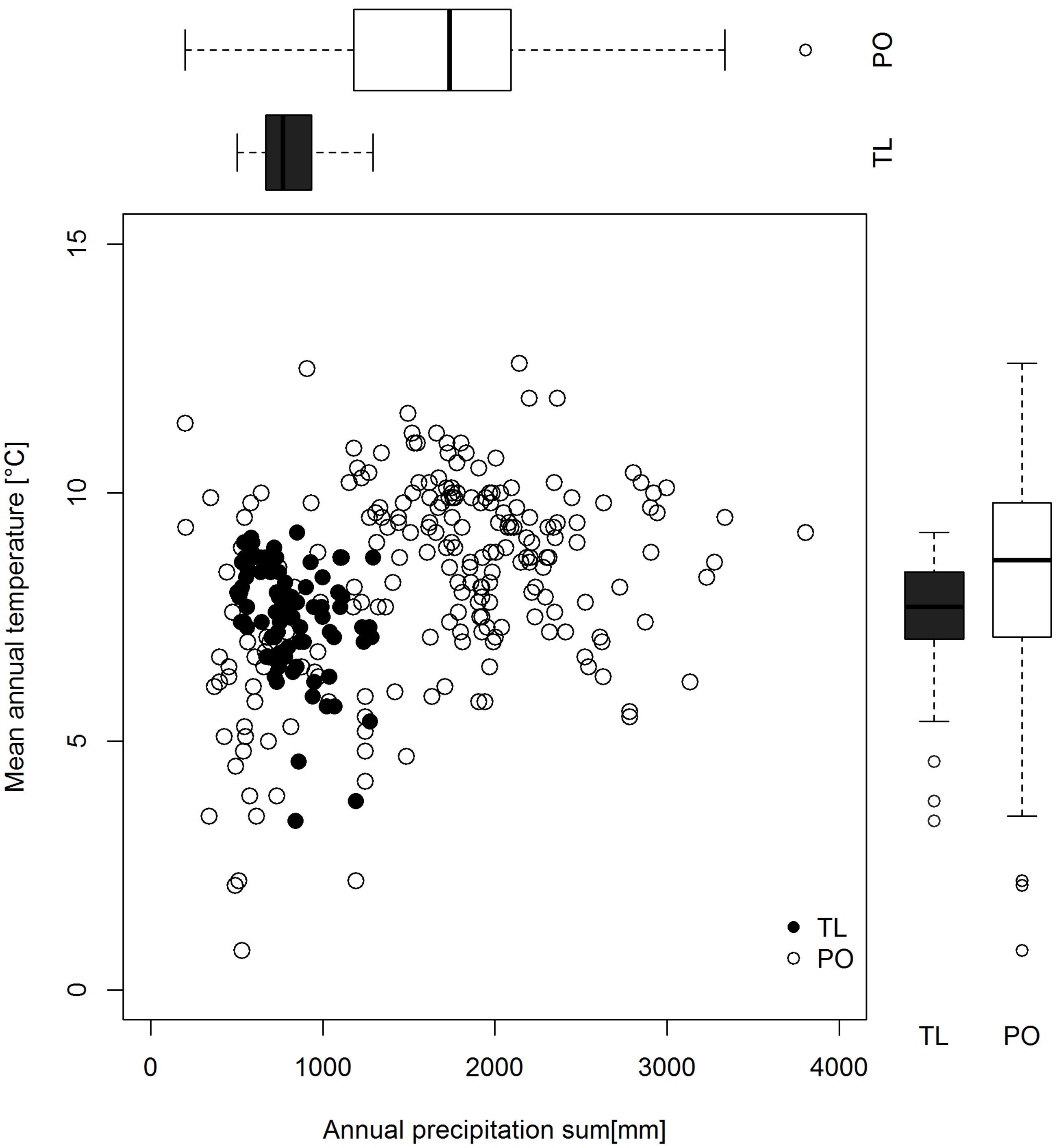

Fig 3. Climatic location of trials and the provenance origin. Distribution of trial locations (TL = black dots and boxplots) and population's origin (PO = white circles and boxplots) in a bioclimatic parameter space represented by mean annual temperature [°C] and annual precipitation sum [mm]. Although the trial locations fit well into the parameter space of the population origin for these two climate parameters, they show significant variation for other, more seasonal climate parameters, as shown by S1 Fig; indicating non analogy between climate of trial locations and population origin.

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climate" (average for 1950–2000) and two time slices of a transient climate change scenario ("2050" as average for the period 2041–2060 and "2070" as average for the period 2061–2080)

Table 1. Climate variables used to develop the Universal response functions. For trial sites (suffix "s") and the location of the population origin (suffix "p") the same set of predictor variables was tested for model building. TD = MWMT-MCMT; AHM = (MAT/10) / (MAP/1000); SHM = MWMT/ (MSP/1000).

Variable	Trial site	Population origin
Mean annual temperature	MAT_s	MAT_p
Mean coldest month temperature	$MCMT_s$	$MCMT_p$
Mean warmest month temperature	$MWMT_s$	$MWMT_p$
Continentality	TD_s	TD_p
Mean annual precipitation	MAP_s	MAP_p
Mean summer precipitation (June-Sep)	MSP_s	MSP_p
Annual heat moisture index	AHM_s	AHM_p
Summer heat moisture index	SHM_s	SHM_p
Degree days below 0°C	$DD{<}0_s$	$DD{<}0_p$
Degree days above 5°C	$DD{>}5_s$	$DD{>}5_p$

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from a run of the MPI-ESL-LR climate model [38] under a Representative Concentration Pathways (RCPs 8.5) scenario [39].

Development of the URFs

To understand the effect of climatic conditions at trial locations and at population origin on growth performance of Douglas-fir populations URFs according to Wang *et al.* [14] were developed for the two response variables H24 and BA24. URFs are quadratic functions (Eq 1) relating an indicator of growth performance to the climate of the trial locations in the case study area in central Europe and to the climate of the population origin in North America (see: Table 1):

$$Y_{sp} = b_o + b_1X_{1s} + b_2X_{1s}^2 + b_3X_{2p} + b_4X_{2p}^2 + b_5X_{1s} * X_{2p} + e_{sp} \qquad \text{(Eq 1)}$$

Here, Y_{sp} is the growth performance (H24 or BA24) of the population p at the sites; b's are the intercept and regression coefficients; X_{1s} and X_{2p} are climate variable of trial location and population origin respectively; $X_{1s}{}^*X_{2p}$ is the interaction between the trial climate X_{1s} and the source climate X_{2p} and e_{sp} is the residual. We selected the quadratic function to develop the URFs because it fits our data well and have been used by earlier response function studies (e.g. [14,40,41]).

To identify the most important climate variables and their interaction terms, univariate regression models were used to test for their contribution in explaining the variation in H24 and BA24 applying a multimodal approach [42, 43]. Here, climate variables with correlation coefficients $r > 0.7$ and variance inflation factors $VIF > 5$ were identified and the variable with the lower explanatory value according to the Akaike Information Criteria (AIC) [44] was excluded from further model development. The remaining uncorrelated climate variables including their quadratic and interaction terms were tested in an all subset multi model selection procedure [42, 43] implemented with the LEAPS package in R [45].The URF model with the lowest AIC value [44] was selected as the "best" model.

An important step in the URF development procedure was the extension of the calibration data set. Since the overall design of the provenance trial series was not balanced and not all populations were planted at every trial site, genecology functions following Wang *et al.* [18] were applied to determine anchor points which allow to estimate the growth performance of populations also at climatically extreme trials, where they had not been planted. Genecology functions map the observed growth performance of populations from a wide spectrum of population origins at extreme (cold, warm) trial sites (S2 Table).

All statistical analyses were carried out within the R environment for statistical computing and visualization [46].

Recommendation of suitable populations

The best performing populations for the each grid cell of the case study area under current and future climate conditions can be identified from the first order partial derivative of the URF models solved for the climate parameter of the population origin (for details see; Wang *et al.* [14]). This approach provides a value of the climate parameter of population origin which when used in the URF equation provides the highest growth performance with respect to H24 and BA24 at any given grid point of the case study area.

In addition, suitable populations for plantation in Europe were identified with a climate envelope approach following Isaac-Renton *et al.* [26]. This population recommendation is based on the similarity of climate between the population origin in North America and the case study region in Central Europe and was developed in the following way: i) a Mahalanobis distance [47] matrix between principal components of climate variables (see Table 1) of each grid point of the case study area and population origin in Northwestern North America was calculated according Roberts and Hamann [48]. The variables used for this comparison were five biologically relevant climate variables which account for most of the variance in climate data while avoiding multicollinearity: mean annual temperature (MAT), mean warmest month temperature (MWMT), mean summer precipitation (MSP), summer heat: moisture Index (SHM) and growing degree-days above 5°C (GDD $>$ 5°C) ii) For each grid point of the case study area, the grid point with the lowest Mahalanobis distance in Northwestern North America was selected from the distance matrix and chosen as the location of most suitable population.

Estimation of growth performance

The URFs were used to estimate growth performance (H24 and BA24) for each 30 arc sec grid cell of the case study area with: i) populations identified by the URF approach and ii) populations identified by climate envelope approach because the climate envelope model itself did not allow an estimate of growth performance. In this paper the populations recommended by the URFs are referred to as "optimum" populations and those recommended by the climate envelope approach as "envelope" populations. Comparisons between the selected optimum and envelope populations and their growth performance were made by Wilcoxon signed rank tests. Due to the high topographic heterogeneity in our case study region (compare Fig 1) these comparisons were made for three distinct altitudinal zones: 0–500m (low), 500–1000m (mid), and $>$1000m (high).

Results

Climate predictors of growth performance

From the ten climate variables (Table 1) tested, three variables of the trial location: a temperature variable (MAT_s), a moisture as well as temperature variable (SHM_s) and the continentality (TD_s), and one variable of the population origin (MAT_p) as well as the interaction of the trial location and population origin variables $MAT_s{}^* MAT_p$ were found to be significant predictors of H24 and BA24 (Table 2). The only significant climate variable of the population origin is the

Table 2. Results of multiple regression analysis predicting dominant height at age 24 (H24) and basal area at age 24 (BA24) of Douglas-fir populations from site and population origin climate as independent variables in a Universal response function (URF). For explanation of acronyms see Table 1. Partial R^2 refers to the change in the adjusted model R^2 when the respective variable is removed from the URF. The percent contribution of a particular explanatory variable is calculated as the percentage of its partial R^2 over the sum of partial R^2 of all explanatory variables.

	URF for H24 [m]						URF for BA24 [m^2ha^{-1}]					
Independent variables	**Parameter estimate**	**Confidence interval**		***p-value***	**Partial R^2**	**Contribution to sum of partial R^2[%]**	**Parameter estimate**	**Confidence interval**		***p-value***	**Partial R^2**	**Contribution to sum of partial R^2[%]**
		5%	**95%**					**5%**	**95%**			
Intercept	45.14						23.25					
MAT_s	5.973	5.92	6.03	<0.001	0.078	28.05	10.86	10.48	11.24	<0.001	0.099	37.73
MAT_s^2	-0.457	-0.461	-0.453	<0.001	0.089	32.09	-0.60	-0.63	-0.58	<0.001	0.056	21.27
TD_s	1.133	1.106	1.159	<0.001	0.013	4.86	-0.81	-0.93	-0.71	<0.001	0.007	2.55
SHM_s	0.529	0.519	0.539	<0.001	0.021	7.65	0.39	0.33	0.46	<0.001	0.004	1.66
SHM_s^2	-0.0053	-0.0054	-0.0052	<0.001	0.022	7.96	-0.005	-0.005	0.004	<0.001	0.008	3.09
MAT_p	1.494	1.459	1.527	<0.001	0.014	4.99	3.81	3.603	4.020	<0.001	0.040	15.47
MAT_p^2	-0.1318	-0.133	-0.1299	<0.001	0.035	12.77	-0.24	-0.25	-0.23	<0.001	0.047	18.08
MAT_s*MAT_p	0.0675	0.064	0.0702	<0.01	0.004	1.59	-0.02	-0.04	-0.01	<0.001	0.0003	0.11
				Model R^{2}·adj						Model R^{2}·adj		
Full model				0.88						0.89		

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mean annual temperature (MAT_p). All precipitation and moisture variables of the population origin were found to be not significant.

Linear and quadratic forms of MAT_s and MAT_p explained more variation (77% in case of H24 and 92% in case of BA24) than SHM_s and TD_s as indicated by the percent contribution of the variables to the sums of the partial R^2 given in Table 2. The effect sizes of climate variables shown by partial R^2 (Table 2) indicates that overall effects of climate variables were stronger in BA24 than H24.

To quantify the environmental and genetic effects of climate on H24 and BA24 two simplified functions (Table 3) from the first order partial derivatives of MAT_s and MAT_p were developed. These functions were developed by rebuilding the URFs with only the two most influential climate variables i.e. MATs and MAT_p which explained major amount of the variation in growth performance (77% in case of H24 and 92% in case of BA24). The interaction of MAT_s and MAT_p were not included in these simplified functions because they explain less than 1% of the variation in H24 and BA24. The environmental effects in both URFs are substantially stronger than the genetic effects shown by the regression slope of the functions (Table 3). The values of both environmental and genetic effects (Fig 4) were positive at mean annual temperatures lower than 8°C and become negative at mean annual temperatures higher than 8°C. Therefore sites colder than 8°C will increase their growth performance in a warmer climate, but sites warmer than 8°C are expected to show lower growth performance.

Table 3. Environmental and Genetic effects of mean annual temperature on growth performance of the two indicators of growth traits used (H24 and BA24). MAT, mean annual temperature (°C). The suffix "s" or "p" denote trial locations and population's origin respectively.

H24	Environmental effect	$\frac{\delta y}{\delta MATs} = 6.55 - 0.92 * MATs$
	Genetic effect	$\frac{\delta y}{\delta MATp} = 1.94 - 0.24 * MATp$
BA24	Environmental effect	$\frac{\delta y}{\delta MATs} = 10.62 - 1.20 * MATs$
	Genetic effect	$\frac{\delta y}{\delta MATp} = 3.66 - 0.48 * MATp$

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Comparison of population recommendation approaches

Under current climate (Fig 5) and for all three altitudinal zones of our case study region (low, mid and high) the populations drawn from the climate envelope approach originate from significantly (Wilcoxon signed rank test; $p < 0.01$) colder regions of northwestern North America (MAT 3–5°C) than the optimum populations inferred with the URF model (MAT 6–8°C) in terms of both H24 and BA24. Generally, the variation between the populations recommended by the climate envelope approach is considerably higher than the variation among populations recommended by the URF approach (Fig 5) both within and among altitudinal zones and for all climate scenarios.

Under climate change scenarios (2050 and 2070), the envelope populations originate from significantly warmer regions (MAT 8–14°C) in all altitudinal zones, while the recommendations of the URFs do not change significantly (Fig 5B, 5C, 5E and 5F). According to the recommendations of the UFR model, the optimum populations for future climate originate from regions in northwestern North America with MAT 7–9°C.Generally, the population recommendations of both URF models are highly correlated with respect to MAT_p (Pearson's correlation coefficient $r = 0.95$). Both the approaches however show some similar trend like: populations selected for higher altitude sites originate from colder locations in North America than those suitable for lower and mid altitudes of the study area (Fig 5).

Growth performance under current and future climate

Under current climate (Fig 6A and 6D), the growth performance (H24 and BA24) in the low and mid altitude zones is predicted to be higher than at high altitude areas for populations

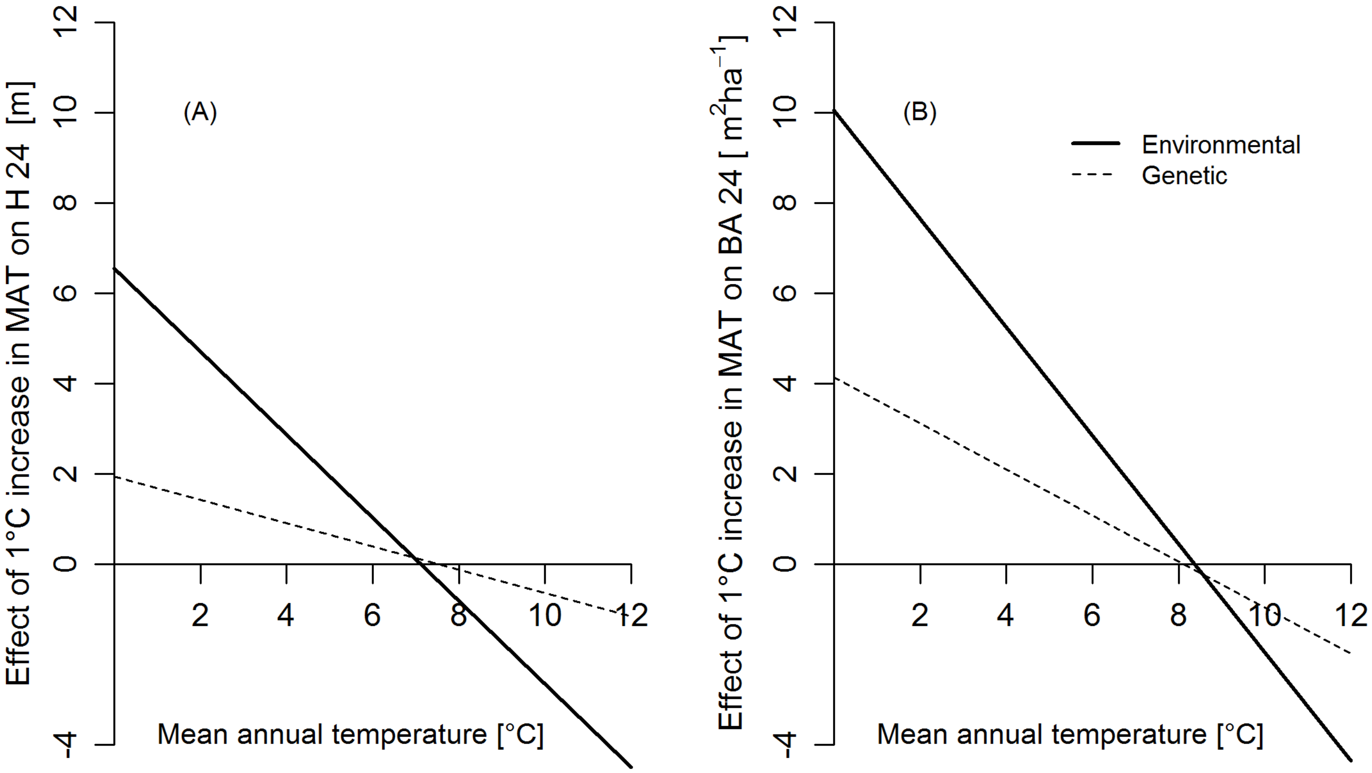

Fig 4. Environmental vs genetic effect. Change in **A)** H24 and **B)** BA24 associated with a 1°C change in MAT of trial sites (environmental effect) and at population origin (genetic effect). For example: in a trial site with (MAT = 0°C), an increase of 1°C in MAT will result in 6.5 m increase in H24 and a population originating from 1°C MAT will be 2m taller than a population originating from 0°C MAT.

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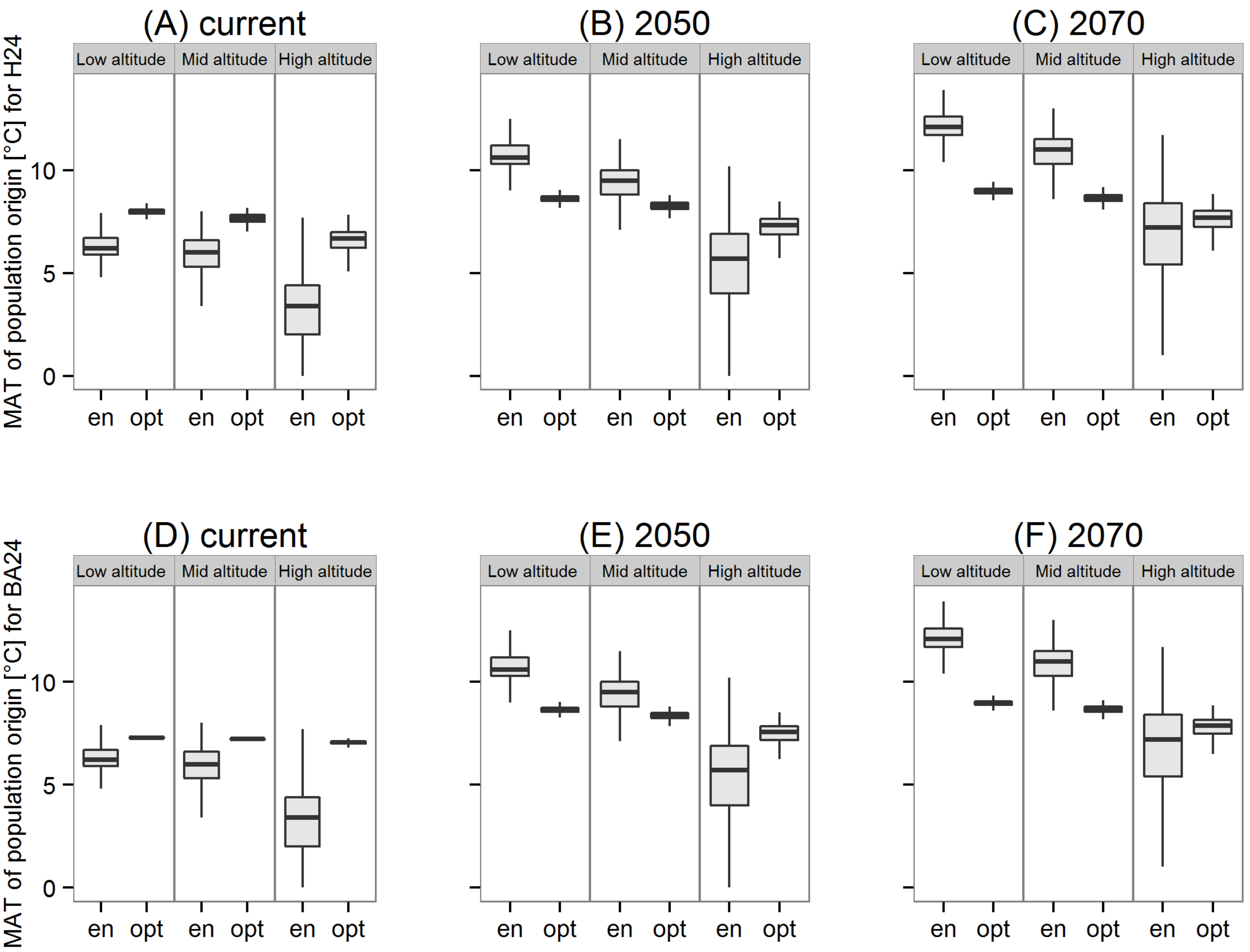

Fig 5. Recommended population origin. Recommended climatic origin (as given by MAT of population origin) for H24 (A, B, C) and BA24 (D, E, F). Populations to be planted at three altitudinal zones (Low: 0–500m; Mid: 500–1000m; and High > 1000m) of the case study region under current climate (A, D) and two time slices of a transient climate change scenario (B, E) 2050 and (C, F) 2070. The populations to be planted were either selected to have optimum tree height (H24) or basal area (BA24) as drawn from the URF model (= 'opt' populations) or drawn from the climate envelope approach which is based on similarity of climate between the study region and the natural distribution of Douglas-fir in Northwest America (= 'en' populations).

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selected by the URF and the climate envelope approach. Under climate change (Fig 6B, 6C, 6E and 6F) this trend reverses and growth performance declines in the low and mid altitude zones.

Under current climate and within both time slices of climate change (2050 and 2070) the growth performance of optimum populations selected by the URFs was estimated to be significantly higher (Wilcoxon signed rank test; $p < 0.01$) than the performance of populations selected by the climate envelope approach. Across all altitudinal zones, envelope populations were predicted to reach 55% lower tree heights and 47% lower basal area than optimum populations selected by the URFs (Fig 6A and 6D, Table 4) in current climate. Under future climate (2050 and 2070),envelope populations are predicted to reach 42% and 64% lower tree heights and 50% and 72% lower basal areas compared to the optimum populations (Fig 6B, 6C, 6E and 6F, Table 4).

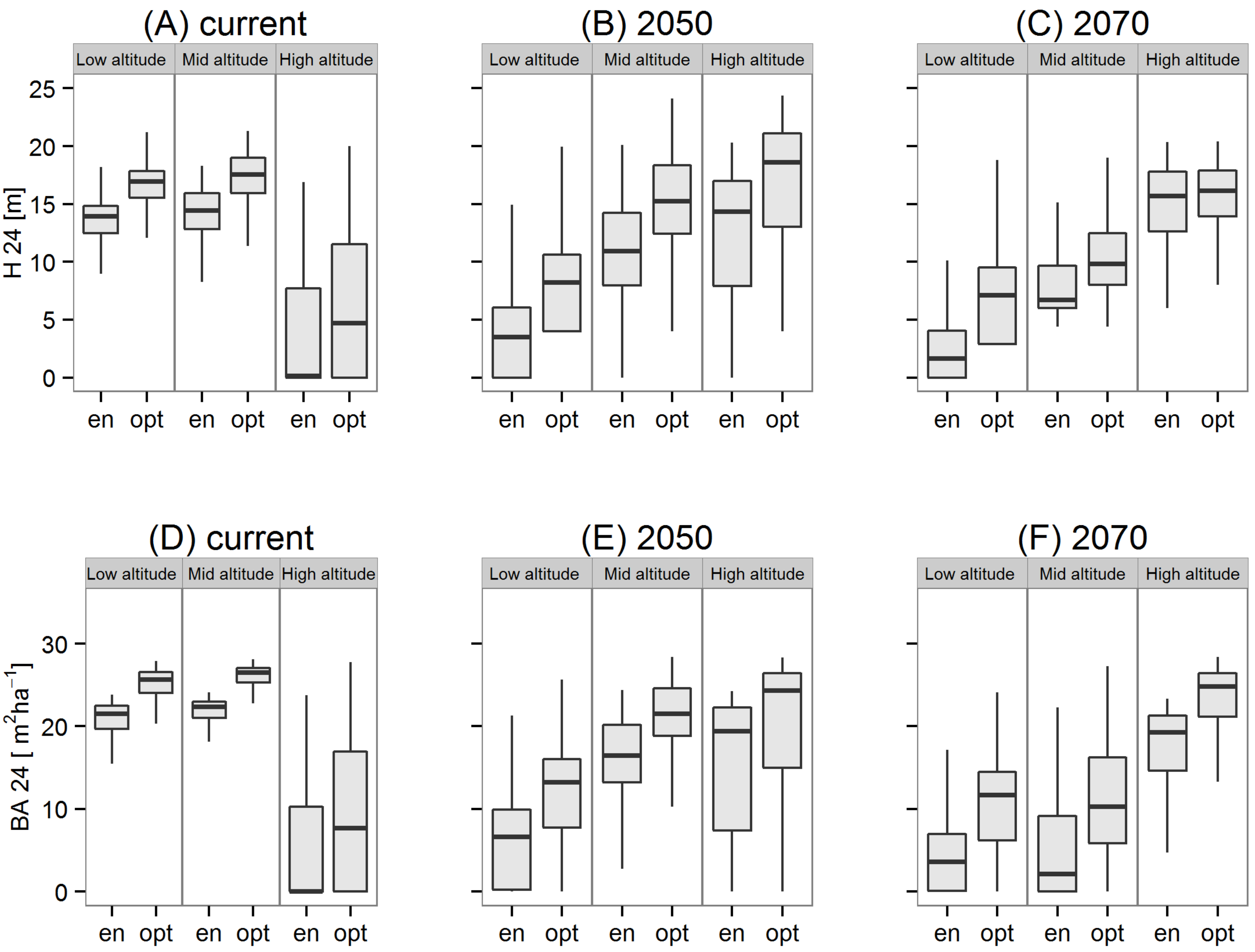

Fig 6. Estimated growth performance. Estimated growth performance (as given by dominant tree height H24 or basal area BA24) for populations to be planted at three altitudinal zones (Low: 0–500m; Mid: 500–1000m; and High >1000m) of the case study region under current climate (A, D) and two time slices of a transient climate change scenario (B, E) 2050 and (C, F) 2070.The populations with optimum height and basal area respectively were either drawn from the URF model (= 'opt' populations) or drawn from the climate envelope approach which is based on similarity of climate between the study region and the natural distribution of Douglas-fir in Northwest America (= 'en' populations).

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Under future warm and dry conditions of 2050 and 2070 growth performance of both optimum and envelope populations are predicted to decline in low (0–500 m) and mid (500–1000 m) altitudes of the case study area (Fig 6B, 6C, 6E and 6F, Table 4). The URFs also predict that the plantation of optimum populations suitable for future (2070) climate under current climatic condition result into an increase of 17% height growth and 21% basal area growth (Table 4) in comparison to optimum populations selected for current climate.

Discussion

Climate predictors in URFs

Among the various climate parameters of the trial sites tested, we found mean annual temperature, continentality and the moisture regime during summer (Table 2) to be the most important variables that influence growth performance of Douglas-fir in the study region. Generally,

Table 4. Tree height (H24) and basal area (BA24) growth performance of the optimum populations predicted by the URF model in comparison with populations recommended by climate envelope approach under three climate scenarios (current, 2050 and 2070) and two scenarios of population selection: first, populations were selected for current climate conditions and second, populations were selected for future climate conditions of 2070. For the comparison, growth performance of the URF "optimum" model under current climate conditions was set to 100% on which the changes in growth performance of different models and population selections were related.

		Optimum populations		**Envelope populations**	
	Climate scenario	**Population selection based on current climate**	**Population selection based on future climate (2070)**	**Population selection based on current climate**	**Population selection based on future climate (2070)**
H24 [m]	Current	100%	+17%	-55%	-10%
	2050	-36%	-13%	-42%	-31%
	2070	-51%	-22%	-64%	-59%
BA24 [m^2ha^{-1}]	Current	100%	+21%	-47%	-17%
	2050	-41%	-18%	-50%	-40%
	2070	-62%	-42%	-72%	-69%

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the temperature related variables were found to be stronger predictors of growth performance than precipitation related variables. Previous studies on North American trial sites that focused on climate transfer also found temperature variables to be more important, but identified mean and minimum temperature of the coldest month, and negative degree days to be the best predictors [25, 49]. In our analysis, temperatures of the coldest month of trial sites and population origin were found to have less impact than MAT_s and MAT_p and were therefore excluded from the final URFs following the multi-model approach [42, 43]. This discrepancy between the North American studies and our analysis could be due to differences in tree age, because the previous studies were either based on three year old seedlings [25] or comprised trees in ages between 2–10 years [49], while our study is based on measurements in ages of 24 years.

Among the ten climate variables of the population origin tested (Table 1); the mean annual temperature was the only parameter that was found to contribute considerably to the two URF models (Table 2). Given the significant difference in annual precipitation of the origin of the populations tested in our study (Fig 3, S1 Fig) this is remarkable, because it suggests that within the present collection of populations none has developed specific adaptations to water limited conditions. Even at the driest continental sites in eastern Austria (e.g. trial Poysbrunn: MAP_s = 540 mm, MSP_s = 292 mm) populations originating from the western Cascades ($MAP_p > 2000$ mm and $MSP_p \sim 500$ mm) revealed the best growth performance. This is in agreement with Leites *et al.*[25], where for 236 interior Douglas-fir populations also no significant effect of precipitation related variables of population origin were found, although the interior distribution area is more drought prone and thus more likely to develop respective local adaptations. Recent dendroclimatic studies [50] showed that during severe drought periods Douglas-fir decreased its annual growth and found significant variation in the intraspecific drought response [51]. Although our trials sites in continental Austria faced similar drought events [52], such isolated events seems to have little effects on the overall performance of the populations throughout the growing period of the 24 years analyzed here. Another reason for the limited effect of precipitation on growth performance could be that not only populations from warmer and drier climates reveal better drought performance, but also populations from cooler climates and higher elevations [53]. Thus, adaptations to both relatively cool winters and arid summers [53] might obscure clear regression across the wide range of population tested in the present study. Since MAT_p and any of the precipitation related climate variables of provenance origin show only little ($r < 0.7$), non-significant correlations (S3 Table), we can also exclude that precipitation variables of the provenance origin were removed due to collinearity between temperature and precipitation within the natural distribution area.

A comparison of the climate effect of the trial environment with the climate effect of the population origin (genetic effect) revealed a substantially stronger effect of the trial climate (Fig 4). Other studies on coniferous trees [14, 25] came to similar conclusions and reasoned that selection pressures of local climate regimes need to occur over long periods of time to cause genetic effects and might be counteracted by extensive gene flow [54]. Thus, the observed variation in growth performance is principally a results of phenotypic plasticity of populations planted in contrasting environments and to a smaller degree a result of genetic effects [14, 55]. Our study indicates that environmental and genetic effects in Douglas-fir are minimum if planting sites are located at MAT_s of 6–8°C and population originate from similar temperature range (Fig 4). This temperature range is the optimum predicted by the URFs for both height and basal area growth.

Overall, the two URFs (Table 2) explain 88% of the variation in H24 and 89% in case of BA24. BA24 seems to be more strictly influenced by climatic factors than H24 (Table 2, Table 3, Fig 4), probably because BA24 summarizes DBH growth and the tree survival rate, both of which are affected by climate parameters. Given that precise information of the initial tree mortality were not available for our dataset, the relationship between survival and BA24 is shown by the slightly higher correlations between BA24 and tree density than between BA24 and DBH (S4 Table). Thus, we can assume that tree mortality reduced tree density below the threshold of the first thinning regime and shaped the mean basal area of the populations. The URFs for both response measures (Table 2) are consistent in the sense that the same set of climate variables was found to constitute the best model. And finally, the two models result in similar population recommendations for height and basal area growth and can thus be considered as reliable for recommending optimum populations with high growth performance in the study area.

The empirical data from which the URFs were developed originate from trial sites established through a wide climatic gradient (Fig 1, Fig 2 and Fig 3) even though the provenance trials are located in a relatively narrow geographical range (Southern Germany and Austria). We are aware of the limitations of empirical modeling approach used in this study where biotic and abiotic factors like CO_2 concentration, soil conditions, and disturbances are not taken into account. Moreover, our dataset did not include trial locations colder than 3.4°C MAT and warmer than 10°C and this likely restrict the application of the URFs when estimating growth performance beyond this range and for climate scenario beyond 2070.

Implications for Douglas-fir management in Europe

Our study suggests that populations originating from regions with mean annual temperature ranging from 6–8°C (typical climate for western Cascade Range and coastal regions of Washington and Oregon) are the best performing populations for current climate conditions in the study region, but future plantations should make use of populations from slightly warmer climate of MAT_p between 7–9°C (Fig 5). Given that the temperature in the study region in the applied climate change scenario RCP 8.5 is expected to rise between 3°C and 4.5°C until the end of the century [56], this relatively small adjustment of population recommendation is remarkable. It can be explained by the relatively low interaction between MAT_p and MAT_s in the two URF models (Table 2) explaining only ~ 1% of the variation in H24 and BA performance. Overall, the optimum populations identified by the URF models (Fig 5) are in good agreement with former provenance studies[23, 26, 57] and with the current recommendations for seed transfer in many European countries.

The URFs predict that majority of the case study area except the higher elevation alpine zones provide favorable climatic condition for planting Douglas-fir (Fig 6A and 6D) under current climate. Under climate change scenarios (Fig 6B, 6C, 6E and 6F) there is a steady decline in growth performance in the currently productive lower elevation zones. These lower elevations of continental eastern Austria and northwestern Bavaria are already close to the warmer limit of MAT_s and SHM_s of our URFs and may thus not accommodate further increase in temperature and summer drought in the future. On the contrary, the mid and high elevation zones of the case study area are likely to experience increasing growth performance in climate change (Fig 6). Especially the mid elevation zone is likely a favorable climatic zone for Douglas-fir in the future. Although the high elevation zones (>1000m) are also predicted to show higher growth performance, recommendations for these region should be drawn with care, because practical experience of planting Douglas-fir at higher altitudes is limited and also from the present study only two sites are located above 1000 m. Thus, growth constrains imposed by other climate or soil descriptors typical for high alpine forests might occur and needs to be examined before broader plantations can be advised.

Comparison of URF and climate envelope approaches

Assisted migration, the translocation of populations and species to suitable habitats outside their present distribution range is being discussed as conservation concept for endangered populations and species in the light of climate change. Although Douglas-fir is not considered to be a vulnerable species in northwestern North America, the lessons learnt from its facilitated transfer to Europe and the consequences of its plantation within non-analogous climate conditions in continental Europe on growth and survival pattern will help to better understand effects of climate change on local populations and to develop translocations guidelines for other tree species and populations.

In a recent meta-analysis, Isaac-Renton *et al.*[26] compared relative growth performance of Douglas-fir within provenance trials across Europe and the recommended populations drawn from these trials with a climate envelope model based on similarity of climate between population origin and trial locations. They found that populations recommended by their climate envelope approach are correlated with the results of provenance tests in the Atlantic climate of Western Europe. However, in Central and southeastern Europe no correlation between empirical data and model result were found [26]. This latter result is in agreement with our study, because we found that the empirical trial data and the URFs calibrated from them resulted in significantly different population selections (Fig 5) than the climate envelope approach. Also, the modeled growth potential of populations selected by the URFs was significantly higher than the predicted growth performance of the envelope populations (Fig 6) across the complete case study area. This mismatch between the population selection based on URFs and population selection via climate envelope approach (Fig 5) also persists under conditions of climatic change indicating that population selection based on climate envelope may not be an appropriate approach if the climate of the planting location and the climate of the population origin differ as much as in our study (Fig 3, S1 Fig). There may be various reasons for this mismatch between envelope and optimum population selection: first, the climate envelope concept ignores the actual environmental and genetic constraints of growth performance because it is based solely on the species presence and absence. Thus, climate envelope models might not contain those climate variables to which local populations are adapted to, but based on an approximation of a limited set of climate predictors that define the species' occurrence.

Secondly, low correlations between the measured growth traits in our provenance trials with the trees' long-term survival and fitness [21, 58] could be responsible for the varying selection of populations. In particular, young provenance trials were suggested to be misleading [26] as they might not have experienced putative extreme climate events that drive climate-specific mortality. For Douglas-fir, it is also well known that a tradeoff exists between superior growth performance mainly of coastal populations and higher frost tolerance of interior populations [59–61]. However, we believe that the results of our study are not affected by missing extreme events in the juvenile phase of the trees in an otherwise more unfavorable environment, because our analysis is based on both height (H24) and basal area growth (BA24). H24 is a reliable indicator of growth performance and BA24 is based on both diameter growth and survival rate and thus also affected by site-specific climate events. Optimum populations predicted by both URFs (Fig 5) are highly correlated (Pearson's correlation coefficient r = 0.95) indicating that the populations recommended by the URFs are consistent and reasonably adapted to the trial site climate. Thus, we believe that the present URFs are valid enough to draw conclusion from our 24 year old trees to mature Douglas-fir plantations in the study area.

Direct implication of the use of potentially erroneous climate envelope models for assisted migration schemes may result in recommendation of populations which in practice have lower rates of survival, decreased fitness and productivity. Therefore, empirical approaches using common garden and population transfer trials in combination with sophisticated statistical models such as the URFs (Table 2) will likely provide better knowledge of the climatic and genetic constraints of species and a better basis for selecting populations for future climate conditions than climate envelope model that are based only on species occurrences.

Conclusion

We conclude that populations of Douglas- fir originating from the western Cascade Range and coastal regions of Washington and Oregon have optimum growth performance in the study area under both current and future climate conditions. Our study also provides evidence that if the population source and plantation climate differ substantially as in our study, assisted migration schemes may not realize their targets if populations are selected based on climate envelope approach. Thus, whenever data from genetic field trials exist, empirical approaches like the URFs should be preferred. The URFs allow to predict performance of any population across a wide range of climate conditions and thus overcomes the major limitation of single provenance trials that are limited to a specific environment.

Supporting Information

S1 Fig. Comparison of climate variables of trial locations in the case study area of central Europe (Austria and Southern Germany) with the climate variables of the population's origin in Northwest North America. The results of independent sample t-test comparing each climate variable between trial location and population's origin is also shown. Note: MAT = Mean annual temperature; MCMT = Mean coldest month temperature; MWMT = Mean warmest month temperature, TD = Continentality (i.e. MWMT-MCMT); MAP = Mean annual precipitation; MSP = Mean summer precipitation (June-Sep); AHM = Annual heat moisture index; SHM = Summer heat moisture index; DD < 0 = Degree days below °C; D > 5°C = Degree days above 5°C (See Table 1 for details of the climate variables).
(TIFF)

S1 Table. Models for estimating site specific heights from DBH. The quadratic forms are $y = a + bx^2 + cx$ and linear forms are $y = a + bx$: where a is intercept; b and c are parameters. y

refers to Height [m] and x refers to DBH [cm]. RMSE refers to root mean squared error.
(DOCX)

S2 Table. Models for developing anchor points. Column 1 shows the trial sites from which anchor points were developed. Figures within parentheses refer to mean annual temperature (MAT) of the respective trial sites (MAT_s).Here: x = MAT_p (MAT of population origin); Y = H24 [m] andY_1 = BA24 [m^2ha^{-1}].
(DOCX)

S3 Table. Correlation between mean annual temperature (MAT_p) and precipitation related climate variables of population origin in North America. For definition of the acronyms see Table 1.
(DOCX)

S4 Table. Correlations between the URF variable basal area [m^2] and the two factors for its computation: tree density [trees ha^{-1}], and DBH [cm]. The table gives the mean, median, maximal and minimal correlation coefficients of the individual trials as well as correlation across all trial sites, demonstrating the equal contributions of tree density and DBH to basal area.
(DOCX)

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Author Contributions

Conceived and designed the experiments: SS MJL. Performed the experiments: SS MK DC TW. Analyzed the data: DC TW SS. Contributed reagents/materials/analysis tools: SS MK KA CM. Wrote the paper: DC SS MJL TW.

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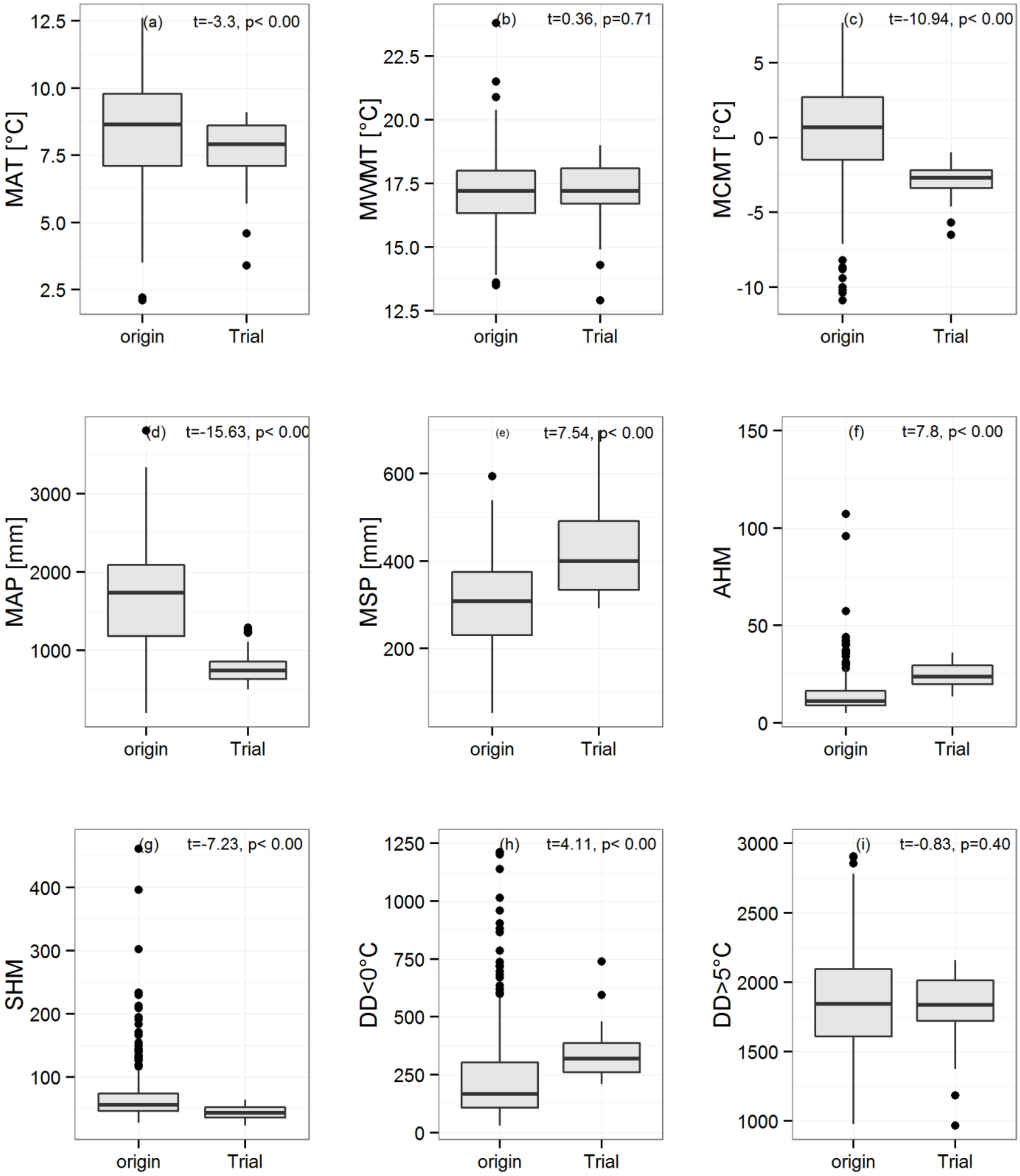
Supporting Information (S1)



S1 Fig Comparison of climate variables of trial locations in the case study area of Central and continental Europe (Austria and Southern Germany) with the climate variables of the population’s origin in Northwest America. The results of independent sample *t test* comparing each climate variable between trial location and population’s origin are also shown.

Note: MAT=Mean annual temperature; MCMT=Mean coldest month temperature; MWMT=Mean warmest month temperature, TD=Continentality (i.e. MWMT-MCMT); MAP=Mean annual precipitation; MSP= Mean summer precipitation (June-Sep);AHM=Annual heat moisture index; SHM=Summer heat moisture index; DD<0=Degree days below °C; D>5°C=Degree days above 5°C (See Table 1 for details of the climate variables)

Supporting Information (S2)

S2 Table. Models for estimating site specific heights from DBH. The quadratic forms are $y = a + bx^2 + cx$ and linear forms are $y = a + bx$: where a is intercept; b and c are parameters. y refers to Height [m] and x refers to DBH [cm]. RMSE refers to root mean squared error.

Trial	a	b	c	*p* value	R^2	RMSE [m]	Bias [%]	Functional form
Buchschachen	6.65	0.6379	-0.008	<0.001	0.75	0.96	0.00	quadratic
Drassmarkt	-0.15	1.3373	-0.0238	<0.001	0.73	0.93	0.00	quadratic
Eberstein	5.47	0.7109	-0.0117	<0.001	0.50	0.99	0.00	quadratic
Gansbach	5.9	0.7004	-0.0112	<0.001	0.65	0.74	0.00	quadratic
Goettweig_K_I	4.47	0.7226	-0.0106	<0.05	0.48	1.30	0.00	quadratic
Hassbach_I	2.57	1.0284	-0.0167	<0.001	0.77	0.92	0.00	quadratic
Hassbach_II	-3.17	1.4386	-0.0251	<0.001	0.82	0.92	0.00	quadratic
Hochstrass_78	-0.97	1.3296	-0.0232	<0.001	0.83	0.82	0.00	quadratic
Karlsbach	4.41	0.7949	-0.0088	<0.001	0.81	0.91	0.00	quadratic
Loelling	3.08	0.8190	-0.0138	<0.05	0.45	1.35	0.00	quadratic
Manhartsberg_I	2.13	1.1382	-0.0251	<0.005	0.62	1.02	0.00	quadratic
Mannersdorf_I	9.22	0.2388		<0.001	0.45	0.87	0.00	linear
Mattersburg	8.29	0.6148	-0.0079	<0.001	0.76	0.65	0.00	quadratic
Poyssbrunn_I	4.67	0.9260	-0.0137	<0.001	0.78	0.76	0.00	quadratic
Poyssbrunn_II	10.51	0.3616		<0.001	0.68	1.21	0.00	linear
Reidlingberg	2.87	0.9233	-0.0148	<0.001	0.74	0.89	0.00	quadratic
Ritzing	1.33	1.1410	-0.0171	<0.001	0.85	0.70	0.00	quadratic
Rohrbach	2.8	0.9857	-0.0127	<0.001	0.82	1.00	0.00	quadratic
Schlossberg_78	-0.23	1.3058	-0.0218	<0.001	0.63	1.70	0.00	quadratic
Somerrein	4.97	0.7235	-0.0121	<0.05	0.48	0.84	0.00	quadratic
St. Johann am W.	2.32	1.0536	-0.0179	<0.001	0.57	1.10	0.00	quadratic
Stollberg	-3.88	1.6899	-0.0335	<0.001	0.84	1.00	0.00	quadratic
Stronsdorf	1.68	1.1764	-0.0207	<0.001	0.53	1.27	0.00	quadratic
Traismauer	5.92	0.4493		<0.001	0.66	1.25	0.00	linear
Tullnerbach	3.15	0.9017	-0.0150	<0.001	0.86	0.71	0.00	quadratic
Ulmerfeld_I	6.53	0.5978	-0.0069	<0.001	0.56	1.20	0.00	quadratic
Waldhof_I	5.96	1.0696	-0.0177	<0.001	0.71	1.01	0.00	linear

Supporting Information (S3)

S3 Table.Models for developing anchor points. Column 1 shows the trial sites from which anchor points were developed. Figures within parentheses refer to mean annual temperature (MAT) of the respective trial sites (MAT_s). Here: x =MAT_p (MAT of population origin); Y = H24[m] and $Y_{1=}$ BA24 [m^2ha^{-1}]

Trials used to develop anchor points for H24	**Genecology function for anchor points**
Cold sites	
Lölling (MAT_s = 3.4 °C)	$Y= -0.1407x^2 + 1.9099x + 5.1875$
Eberstein (MAT_s = 4.8 °C)	$Y= -0.124x^2 + 1.75x + 7.99$
Thorndahl (MAT_s = 6.2 °C)	$Y= -0.1826x^2 + 1.9798x + 10.232$
Kirchberg am W. (MAT_s = 6.4 °C)	$Y= -0.1915x^2 + 2.5164x + 8.8469$
Warm sites	
Hochstrass/Bodenmais_titling (MAT_s = 7.5 °C)	$Y= -0.2112x^2 + 3.4629x + 5.272$
Stornsdorf (MAT_s = 8.5 °C)	$Y= -0.1129x^2 + 1.8313x + 9.1932$
Poysbrunn II (MAT_s = 9 °C)	$Y= -0.1473x^2 + 2.3196x + 6.1425$

Trials used to develop anchor points for BA24	**Genecology function for anchor points**
Cold sites	
Lölling (MAT_s = 3.4 °C)	$Y_1= -0.2606x^2 + 4.0457x - 5.976$
Eberstein (MAT_s = 4.8 °C)	$Y_1= -0.1567x^2 + 2.0633x + 5.6448$
Bodenmais Russel(MAT_s = 5.7 °C)	$Y_1= -0.24x^2 + 3.82x + 8.22$
Thorndahl(MAT_s = 6.2 °C)	$Y_1= -0.25x^2 + 4.09x + 8.2$
Warm sites	
Hochstrass/Bodenmais_titling (MAT_s = 7.5 °C)	$Y_1= -0.3651x^2 + 6.4086x + 1.546$
Stornsdorf (MAT_s = 8.5 °C)	$Y_1= -0.4247x^2 + 6.6797x - 1.3146$
PoyssbrunnII (MAT_s = 9 °C)	$Y_1= -0.2698x^2 + 3.8576x + 6.6439$

Supporting Information (S4)

S4 Table. Correlation between mean annual temperature (MAT_p) and precipitation related climate variables of population origin in North America. For definition of the acronyms see (Table 1).

Correlation of MAT_p with the following climate variables	**Pearson's correlation coefficient**	***p value***
MAP_p	0.31	0.054
MSP_p	0.15	0.073
AHM_p	-0.28	0.065
SHM_p	0.01	0.246

Supporting Information (S5)

S5 Table.Correlations between the URF variable basal area [m^2] and the two factors for its computation: tree density [trees ha^{-1}], and DBH [cm]. The table gives the mean, median, maximal and minimal correlation coefficients of the individual trials as well as correlation across all trial sites, demonstrating the equal contributions of tree density and DBH to basal area.

	Density vs. basal area	**DBH vs. basal area**
Mean	0.32	0.41
Median	0.37	0.41
Max	0.94	0.91
Min	-0.94	-0.35
Correlations across all trials	0.19	0.24
Number of trials with negative correlations	2	6
Number of trials with positive correlations	47	43

Appendix

7.2 Paper II

Chakraborty D, Wang T, Andre K, Konnert M, lexer MJL, Matulla C, Weißenbacher L, Schueler S (2016) Adapting Douglas-fir forestry in Central Europe: evaluation, application, and uncertainty analysis of a genetically based model. European Journal of Forest Research 135: 919-936

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ORIGINAL PAPER

Adapting Douglas-fir forestry in Central Europe: evaluation, application, and uncertainty analysis of a genetically based model

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Manfred J. Lexer[5] · **Christoph Matulla**[3] · **Lambert Weißenbacher**[1] ·
Silvio Schueler[1]

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Abstract Recommendations on suitable seed sources for reforestation are usually model based and include uncertainties arising from model assumptions, parameter estimation, and future climate scenarios. Due to the long-lived nature of forests, such uncertainties need to be considered when developing guidance for managers and policy makers. We evaluate the uncertainties and apply our recently developed genetically based models, Universal Response Functions (URFs) in Austria and Germany. The URFs predict growth performance (dominant height and basal area at age 24) of Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) populations, as a function of both environmental and genetic factors. We evaluated the URFs by comparing the predicted height growth performances with observations from independent provenance trial data across Europe. Also, the sensitivity of the URF variables and the overall model uncertainty were estimated and compared to the uncertainty due to climate change projections. Model evaluation suggests that the URFs perform better in Central and Southeastern Europe compared to maritime Western Europe. Summer drought and mean annual temperature of planting sites were the most sensitive variables of the models, whereas the mean annual temperature of seed origin was the least sensitive. Model uncertainty increased with mean annual temperature of the planting site. Uncertainty due to projected future climate was found to be higher than the model uncertainty. The URFs predicted that provenance regions of southwest Germany and southeast Austria below 1500 m altitude will be suitable, whereas Pannonian east of Austria will become less suitable for growing Douglas-fir in future. Current seed stands in North America providing planting materials for Europe under the legal framework of the Organization for Economic Cooperation and Development shall continue to provide the most suitable seed material also in the future.

Keywords Climate change · Douglas-fir · Provenance trials · Seed origin · Uncertainty

Introduction

Planting alternative tree species and provenances suited to probable future climates in Europe has been suggested as a vital strategy supporting the adaptation of European forests ecosystems to climate change (e.g., Wang et al. 2006; McLachlan et al. 2007; Marris 2008; Bolte et al. 2009; Temperli et al. 2012). This may also include the plantation of non-native species if they provide superior productivity,

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forest stability, and carbon storage under the expected climate change conditions across Europe (Bolte et al. 2009). The North American Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) is globally one of the most economically attractive conifers and has been introduced in over 30 countries, mainly due to its growth performance, excellent wood quality, and resistance against drought and insect attacks (St Clair et al. 2005). In Europe as well, these characteristics have made Douglas-fir one of the preferred non-native tree species and provenance trials have been established beginning in the early 1900s (Schober 1955).

Seed production from introduced Douglas-fir forests in Europe or past breeding activities cannot meet the increasing demand for appropriate reproductive material at present (Konnert and Ruetz 2006). With the increasing need to adapt to a changing climate, it has been questioned whether the genetic material introduced within the last 100 years will perform equally well under climate change conditions or whether alternative provenances from North America should be considered (Kölling 2008; Isaac-Renton et al. 2014).

A recent analysis of provenance trials in Austria and southern Germany by Chakraborty et al. (2015) suggests that only minor changes of provenance recommendations are required, even though the growing conditions in Central Europe are expected to change significantly under projected climate change. Chakraborty et al. (2015) employed the Universal Response Functions (URFs), a statistical modeling approach (Wang et al. 2010) to predict growth performance of provenances as a function of the climate of seed origin (genetic effects) and planting locations (environmental effects). Since the URFs combine both environmental and genetic effects on growth variation, they overcome the limitation of population-specific response functions (Wang et al. 2006; Kapeller et al. 2012) and site specific transfer functions (Matyas 1994; Carter 1996; Andalo et al. 2005; Eilmann et al. 2013) and has received wide attention for identifying provenances with optimum growth performance for future climate. The URFs can take any mathematical form; however, quadratic functions are mostly used because of their biological realism and simplicity (Wang et al. 2010; Yang et al. 2015; Chakraborty et al. 2015). In order to identify optimum seed origin for a given planting location or optimum planting location for a given seed source, the URFs are solved by the partial derivative of the model (Wang et al. 2010; Yang et al. 2015; Chakraborty et al. 2015). However, the increasing number of climate predictor variables results in models with higher complexity, non-linearity, and non-convexity, and thus, the partial derivative approach is not sufficient to solve the URFs for its optimal solution. An alternative approach for solving complex model functions is to view the URF model as an optimization problem, where a maximization of growth performance and/or survival within an allowed set of climate variables, i.e., across the range of predicted climate scenarios, is being targeted. Such an optimization problem can be solved by derivative-free optimization procedures mostly implemented through specialized software packages (Audet and Orban 2006; Karasözen 2007; Rios and Sahinidis 2013).

Matching seed sources with planting locations to identify the most suitable forest seed stock is mainly model based (Wang et al. 2006, 2010; Isaac-Renton et al. 2014; Chakraborty et al. 2015) and includes inherent uncertainties. These uncertainties can be attributed to (i) model assumptions, (ii) parameter selection, and (iii) future climate scenarios (Loehle and LeBlanc 1996; Lexer and Hönninger 2004; Pearson et al. 2006; Millar et al. 2007; Wang et al. 2012a; Lindner et al. 2014; Albert et al. 2015). Due to the long-lived nature of forests, such uncertainties need to be considered when developing guidance for policy makers and giving recommendations for forest managers (Spittlehouse and Stewart 2003; Lindner et al. 2014).

One of the best methods for assessing model uncertainties is through model evaluation (Hammonds et al. 1994), a process in which the model predictions are compared to independent data sets from the "real world." However, Loehle (1997) argued that such evaluation approaches might not always be as informative as expected because the independent data set might include other sources of uncertainty. Therefore, the full range of uncertainty including both uncertainties due to model parameters also called model sensitivity and uncertainty due to input variables needs to be understood (Lexer and Hönninger 2004). A standard approach for estimating model sensitivity is to test the effect of each parameter on the predictions by changing one parameter at a time, keeping other parameters constant (Hallgren and Pitman 2000; Lexer and Hönninger 2004). For estimating the uncertainty associated with imperfect knowledge about the input variables, approaches like the Monte Carlo techniques can be employed (Gardner et al. 1990).

Besides model uncertainty, adopting scientifically valid adaptive measures complying with the various international and national legal statutes is a challenge for both scientists and forest managers. In Europe, forest seed harvest, seedling production, and the transfer of reproductive material of any tree species involve elaborate national and international legal frameworks. Prominent among such legal regulations are the European Council Directive 1999/105/EC (Konnert et al. 2015) at the European Union level. The EU directive differentiates four different categories of forest reproductive material such as (i) source identified, (ii) selected, (iii) qualified, and (iv) tested. National legislations that are based on the EU directive make use of these categories, but might specify different minimum requirements for imports into the various countries and its usage in plantations: For example, Douglas-fir imports into Germany require at least the category “selected,” whereas imports into Austria and many other European countries are adequate if the less rigorous category “source identified” is being used. At the international level, marketing and transfer of forest reproductive material are controlled by the “Scheme for the Control of Forest Reproductive Material Moving in International Trade” of the Organization for Economic Cooperation and Development (OECD 2012). The OECD scheme is voluntary and also defines the same four categories of forest reproductive material as the Council Directive 1999/105/EC (European Union 2000; Konnert et al. 2015). Additionally, the EU directive and the OECD scheme recommend that forest reproductive material under any of these categories must be obtained from the basic materials, namely seed source, stand, and seed orchards (Konnert et al. 2015). Each EU and many OECD countries also have regulations regarding the movement and utilization of seeds within the country, often on the basis of legally defined provenance regions or seed zones (Fig. 1) which might be specifically defined for individual species (e.g., Germany) or equivalent to general ecoregions (e.g., in Austria). Thus, the implementation of climate change adaptation measures requires recommendations on the basis of the legal regulations and sound scientific knowledge.

In this study, we evaluate the recently developed URFs (Chakraborty et al. 2015) for Douglas-fir across Central Europe and apply them in our study region (Austria and Germany). The objectives of the study are (i) to analyze the uncertainties of the model predictions under future climate, (ii) to evaluate the URF models with independent trial data in order to test its applicability in Europe, and (iii) to transfer the model results into practical recommendations and guidelines for forest and nursery managers.

Materials and methods

Universal Response Functions (URFs)

Tree growth data for developing the URFs included 290 provenances of Douglas-fir planted in 50 provenance trials in Austria and Germany (Fig. 1). From these data, we calculated dominant tree height at age 24 (H24) and mean basal area (BA24) as indicators of growth performance which were then used as response variables in the URFs (for details, see Chakraborty et al. 2015). The URFs are quadratic functions (Eq. 1) relating indicators of growth performance to the climate of the trial locations in Central Europe as well as to the climate of the seed origin in North America. Applying a multi-model variable selection approach (Burnham and Anderson 2002; Lumley 2009; Dormann et al. 2013) to a set of 10 climate variables, the mean annual temperature ($\mathrm{MAT_s}$), summer heat moisture index ($\mathrm{SHM_s}$), and continentality ($\mathrm{TD_s}$) of the trial locations in Central Europe and the mean annual temperature ($\mathrm{MAT_p}$) of the seed origin in North America were found to be significant predictors of growth performance explaining up to 89 % of the observed variation:

$$\begin{aligned}\mathrm{Y_{sp}} = {} & \mathrm{b_o + b_1MAT_s + b_2MAT_s^2 + b_3SHM_s + b_4SHM_s^2} \\ & \mathrm{+ b_5TD_s + b_6MAT_p + b_7MAT_p^2 + b_8MAT_s} \\ & \mathrm{\times MAT_p + e_{sp}}\end{aligned} \tag{1}$$

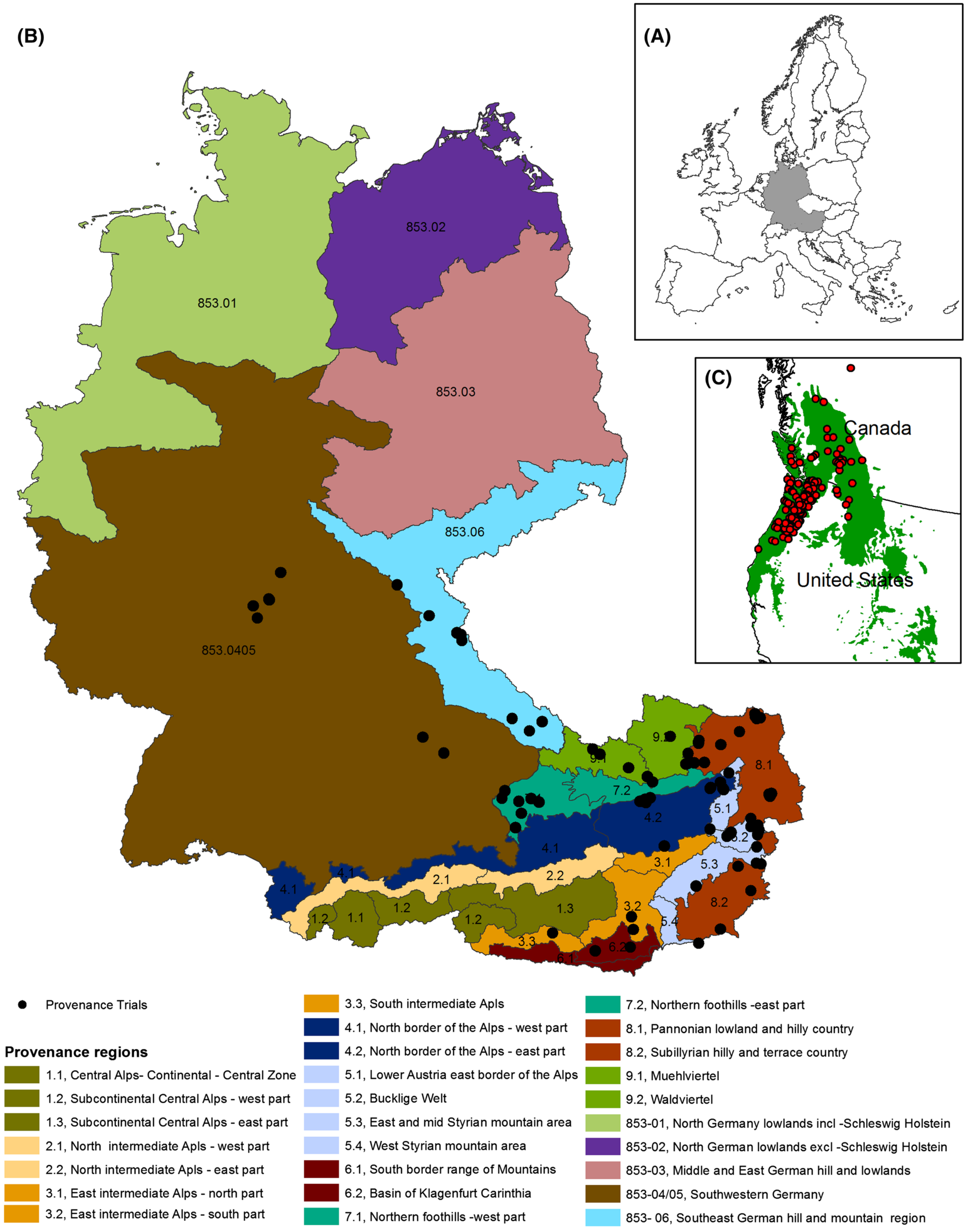
Here, Y_{sp} is the growth performance (either H24 or BA24) of the provenance p at the site s; b_0 to b_8 are the intercept and regression coefficients; and e_{sp} is the residual error. For the present analysis, the model of Chakraborty et al. (2015) was further simplified by removing continentality ($\mathrm{TD_s}$) because it contributed less than 5 % of the total explained variation in H24 and BA24 and had contrasting slopes for H24 and BA24 compared to the other predictors making model interpretation difficult.

The coefficients of the URFs for H24 and BA24 are shown in Table 1. The response surfaces of the two URFs are shown in Fig. 2 for the relations of growth performance to $\mathrm{MAT_s}$ and $\mathrm{MAT_p}$, while the other environmental predictors were kept constant at the mean value.

Uncertainty of model parameters

Model parameter uncertainty, i.e., model sensitivity, was estimated in the following way: the regression coefficient of each of the climate variables of the URFs was changed in three steps through its 95 % confidence interval (minimum, mean, and maximum) while keeping the regression coefficients of all other independent variables constant at the mean value. This allowed estimating the sensitivity of each climate variable’s individual regression coefficient for a range of climate conditions that are expected to occur in our study region today and in future ($\mathrm{MAT_s}$: 2–12 °C and $\mathrm{SHM_s}$ 20–100). The sensitivity of the individual regression coefficients was summed up and expressed as a percentage deviation from the predicted H24 or BA24 to describe the uncertainty of the full model.

The uncertainty of the full model was estimated for each of the provenance regions of the study region in Central Europe (Fig. 1). To account for differences within the provenance regions, each provenance region was divided into 500-m altitudinal subzones. The uncertainty of the full model was estimated under “current climate” (average for 1950–2000) and two time slices of a transient climate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● Provenance Trials
Provenance regions
1.1, Central Alps- Continental - Central Zone
1.2, Subcontinental Central Alps - west part
1.3, Subcontinental Central Alps - east part
2.1, North intermediate Apls - west part
2.2, North intermediate Apls - east part
3.1, East intermediate Alps - north part
3.2, East intermediate Alps - south part
3.3, South intermediate Apls
4.1, North border of the Alps - west part
4.2, North border of the Alps - east part
5.1, Lower Austria east border of the Alps
5.2, Bucklige Welt
5.3, East and mid Styrian mountain area
5.4, West Styrian mountain area
6.1, South border range of Mountains
6.2, Basin of Klagenfurt Carinthia
7.1, Northern foothills -west part
7.2, Northern foothills -east part
8.1, Pannonian lowland and hilly country
8.2, Subillyrian hilly and terrace country
9.1, Muehlviertel
9.2, Waldviertel
853-01, North Germany lowlands incl -Schleswig Holstein
853-02, North German lowlands excl -Schleswig Holstein
853-03, Middle and East German hill and lowlands
853-04/05, Southwestern Germany
853- 06, Southeast German hill and mountain region

◀**Fig. 1** **a** Location of the study region in Europe highlighted in gray. **b** Location of the provenance trials (*black dots*) in the case study region of Austria and Germany. The *colored polygons* represent the provenance regions. **c** Locations of the seed origin of Douglas-fir (*red dots*) in western North America which was planted in the provenance trials shown in (**b**). The natural distribution of Douglas-fir is shaded in *green*

change scenario ("2050" as average of the period 2041–2060 and "2070" as average of the period 2061–2080) from a run of the MPI-ESL-LR climate model (Block and Mauritsen 2013) under the Representative Concentration Pathways RCP 4.5 and RCP 8.5 scenarios (van Vuuren et al. 2011). Climate data for estimating the model uncertainty were obtained from WorldClim database (Hijmans et al. 2005). The WorldClim database provides GCM outputs which are downscaled and corrected for bias using WorldClim 1.4 (Hijmans et al. 2005).

Furthermore, uncertainty due to the different climate change scenarios was estimated as the absolute difference between the URF prediction under RCP 8.5 and RCP 4.5 scenarios in 2070, compared to the mean prediction of the two scenarios. This scenario uncertainty was calculated for each provenance region and altitudinal subzones.

Model evaluation

In order to test the applicability of the URFs, we performed a model evaluation against independent data. For this purpose, we selected 20 provenance trials (Table S1, in the supplementary materials) between 13 and 34 years of age located across Europe from the meta-analysis of Isaac-Renton et al. (2014). These evaluation data were selected because the ranks of the populations in terms of tree height do not change between age 13 and 34 years, as apparent from the data on which the URFs were developed. The evaluation data of Isaac-Renton et al. (2014) contain tree height data and thus allowed an evaluation of the URF for H24 but not for BA24. The climate variables at evaluation trial locations and for the places of provenance origin were determined with WorldClim (Hijmans et al. 2005) and Climate WNA v4.72 (Wang et al. 2012b), respectively. Finally, the URF model for H24 was used to predict the dominant height of populations at the evaluation trial sites. For a comparison between predicted and observed tree height, we used Spearman's rank correlation and the hit rate. The hit rate was calculated as the percentage of 25 % tallest populations at an evaluation trial site that was also predicted to be top ranking by the URF model. The

Table 1 Results of multiple regression analysis predicting dominant height at age 24 (H24) and basal area at age 24 (BA24) of Douglas-fir seed sources from site and seed origin climate as independent variables in a Universal Response Function (URF)

Independent variables	Parameter estimate	St error	95 % confidence interval		p value	Partial R^2
URF for H24 [m]						
Intercept	−19.280	0.163	−19.598	−18.959	<0.001	
MAT_s	6.204	0.037	6.131	6.277	<0.001	0.084
MAT_s^2	−0.443	0.003	−0.448	−0.438	<0.001	0.084
SHM_s	0.442	0.006	0.430	0.454	<0.001	0.015
SHM_s^2	−0.005	0.000	−0.005	−0.004	<0.001	0.017
MAT_p	1.517	0.022	1.474	1.561	<0.001	0.014
MAT_p^2	−0.133	0.001	−0.136	−0.131	<0.001	0.036
$MAT_s \times MAT_p$	0.068	0.002	0.064	0.071	<0.001	0.004
Model R^2adj				0.87		
URF for BA24 [$m^2\ ha^{-1}$]						
Intercept	−41.810	1.017	−43.80	−39.81	<0.001	
MAT_s	10.890	0.237	10.42	11.35	<0.001	0.0991
MAT_s^2	−0.636	0.017	−0.67	−0.60	<0.001	0.0627
SHM_s	0.547	0.039	0.47	0.62	<0.001	0.0093
SHM_s^2	−0.007	0.000	−0.008	−0.006	<0.001	0.0145
MAT_p	3.839	0.130	3.58	4.09	<0.001	0.0410
MAT_p^2	−0.241	0.008	−0.25	−0.22	<0.001	0.0479
$MAT_s \times MAT_p$	−0.028	0.011	−0.04	−0.007	<0.001	0.0003
Model R^2adj				0.88		

Partial R^2 refers to drop in R^2 of the full model when the climate variable is removed from the full URF model

MATs mean annual temperature of planting site, *SHMs* summer heat moisture index (mean temperature of warmest month/(mean summer temperature (May–Sep)/1000)), *MATp* mean annual temperature of seed origin

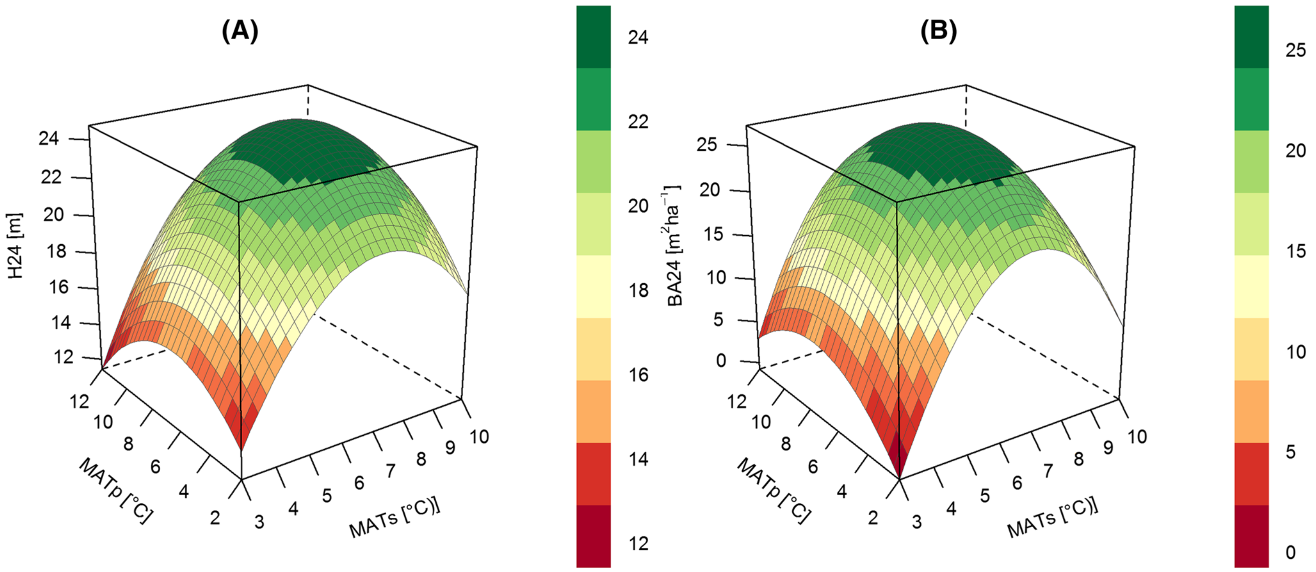


Fig. 2 Simplified response surfaces with URF models with only MAT_s and MAT_p keeping all other variables constant at their respective mean values for (**a**) height at age 24 and (**b**) basal area at age 24

evaluation trial data, given by Isaac-Renton et al. (2014), as well as the original publication on which they are based, do not allow to estimate statistical differences between provenances. Thus, small observed differences might result from random differences from the trial mean and bias our correlations with model predictions. However, it would be interesting to test whether the differences among the provenance mean in the evaluation trials and URF predictions result in similar variation among provenances. Therefore, we calculated the coefficient of variation of the observed tree heights from the evaluation dataset and compared it with the coefficient of variation across provenances, predicted by the URF model.

Selection of best seed source and estimation of growth performance

The optimum seed sources for the region can be identified by calculating the value of MAT_p which when substituted in the URF model yield highest growth performance. In our earlier paper (Chakraborty et al. 2015), we estimated the optimum MAT_p values with the partial derivative method. In the current analysis, we used an optimizing solver called MIDACO (Schlueter and Munetomo 2013) which is a derivative-free solver for general optimization problems. MIDACO implements a meta-heuristic algorithm based on a mixed integer extension of the "ant colony optimization" that uses multi-kernel gaussian probability density functions to sample stochastically solution candidates for the optimization problem. In short, MIDACO is able to find the optimum value of a variable in complex functions involving several continuous or integer variables, their orders, and interactions.

We used MIDACO for each of the legally defined provenance regions (Fig. 1) of Austria and Germany further divided into 500-m altitudinal subzones in order to account for the underlying climatic differences within the provenance regions. The MIDACO solver was used to calculate the optimum MAT_p in the following way:

(i) For each altitudinal subzones, minimum, maximum, and mean values of climate variables (MAT_s and SHM_s) were calculated from the 30 arc sec resolution raster of the WorldClim database (Hijmans et al. 2005) for "current climate," "2050" and "2070" under RCP 4.5, and RCP 8.5 scenarios (van Vuuren et al. 2011).

(ii) The MIDACO solver then uses the minimum, mean, and the maximum value of MAT_s and SHM_s to identify the respective optimum MAT_p employing a heuristic algorithm. For the optimization, the following MIDACO parameters were applied: max time: 60; max eval: 50000; accuracy: 0.0000001; random seed: 1; qstart: 0; autostop: 0; oracle: 0; focus: 0; ants: 100; kernel: 20; character: 0.

The above optimization process identifies seed origin in terms of mean annual temperature (MAT_p) of populations in North America, whereas the OECD guidelines (OECD 2012) recommend that origin of reproductive material for reforestation should be precise with respect to geographic locations. Therefore, in order to recommend seed origin for practical purposes, we identified altitudinal belts within seed zones of Douglas-fir in Northwest America where the optimum MAT_p predicted by the URFs occur. For this purpose, a 30 arc sec resolution digital elevation model of Northwest America was reclassified into altitudinal belts, each spanning across 500 meters. Zonal statistics for MAT_p were obtained for each of these altitudinal belts within the seed zones of British Columbia (BC), Washington (WA), and Oregon (OR).

After identifying the optimum seed origin, the URFs (Table 1) were used to predict growth performance (H24 and BA24) for each altitudinal subzone of the provenance regions (Fig. 1) of Austria and Germany. The predicted growth performances were plotted as maps for both current climate and the climate change scenarios described above. The URFs were also used to predict growth performance of 40 seed stands (Table S2 in the supplementary materials) in North America identified as the source of seed materials of the category "selected" for plantations in Europe following the OECD guideline (OECD 2012). For concise reporting of the recommendations, these seed stands were grouped into six clusters according to the MAT_p (Table S2).

All statistical analyses and figures were developed with the R environment for statistical computing and visualization (R Core Team 2013).

Results

Model sensitivity and uncertainty

The parameter sensitivity of the two URFs (H24 and BA24) was analyzed by calculating the effects of the change in the regression coefficients within their 95 % confidence limits on the model prediction. The overall model uncertainty was represented by summing up individual parameter sensitivity and expressed as a percentage deviation from the predicted H24 or BA24. Among the climate variables, the URFs for both dominant height and basal area growth performance had the highest sensitivity for summer heat moisture index SHM_s (Fig. 3, Fig. S1 in the supplementary materials) followed by MAT_s. The sensitivity contributed by MAT_p and the interaction of MAT_s and MAT_p were comparably low for both H24 and BA24 (Fig. 3, Fig. S1). For all regression coefficients, the sensitivity increased with increasing mean annual temperature of the plantation site, in particular if interpolations were made beyond the range of trial locations from which the models have been developed (Fig. 3, Fig. S1). The overall model uncertainty of predicted height growth performance calculated by summing up the sensitivities of individual regression coefficients ranged from 0.8 m (20 %) at MAT_s of 2 °C and up to 5 m (55 %) at MAT_s of 12 °C (Fig. 4a). The model uncertainty of the URF for the basal area (BA24) was higher and ranged from 5 $m^2\ ha^{-1}$ (43 %) at MAT_s of 2 °C up to 17 $m^2\ ha^{-1}$ (80 %) at MAT_s of 12 °C (Fig. 4b). Uncertainty due to the two climate change scenario expressed as the difference in predicted growth performance between RCP 4.5 and RCP 8.5 scenarios in 2070, compared to the mean of the prediction between the two scenarios, ranged from 0 to 100 % for both H24 and BA24 (Fig. 5).

Model evaluation

Model evaluation with independent data revealed the highest hit rates (Table 2; Fig. 6) at trial sites located in Southeastern Europe (up to 100 %) and Central Europe (14–59 %), whereas lower hit rates were obtained for trials at the Apennine Peninsula (13–33 %) and at maritime Western European sites (0–33 %). Spearman's rank correlation between predicted and observed population height provided a similar picture (Table 2; Fig. 6) with positive correlations ($0.18 < r < 0.59$) for trials located in Belgium, Bosnia, Bulgaria, Croatia, Norway, and Germany. Negative correlations (Table 2) were observed for trials in Ireland, Netherlands, Italy, and France ($0.07 < r < -0.63$).

The observed coefficient of variation among provenances is (0.02–0.26) and for the majority of trials very similar to the coefficient of variation predicted by the URF (range: 0.05–0.14; Table 2, Fig. S2 in the supplementary material). The absolute differences between observed and predicted tree heights varied strongly for many trials, mainly due to differences in tree age between model predictions (age 24) and observations (age 13–34).

Optimum seed sources

We found that under both current climate and climate change, seeds originating from coastal British Columbia (BC), the Western Cascade Mountains and from coastal regions of Washington (WA) and Oregon (OR) with MAT_p ranging from 6 to 9.5 °C will be the most productive seed sources of Douglas-fir in terms of growth performance for the study region (Fig. 7b, Tables S3, S4 in the supplementary materials). Some isolated low altitude locations in southeast BC, WA, and OR were also recommended by the URFs to be optimum seed sources for our study region in terms of MAT_p (Fig. 7b, Tables S3, S4).Geographically, these optimum seed zones are located between 30 and 50° N latitude and 121 and 127°W longitude (Fig. 7b). Generally, seed should originate from altitudes below 1500 m within these seed zones (Table S5 in the supplementary materials). The OECD seed stands are predicted to be suitable for obtaining seed of Douglas-fir for the study region in Central Europe under both current and future climate conditions (Fig. 7b). Out of the 40 OECD stands,

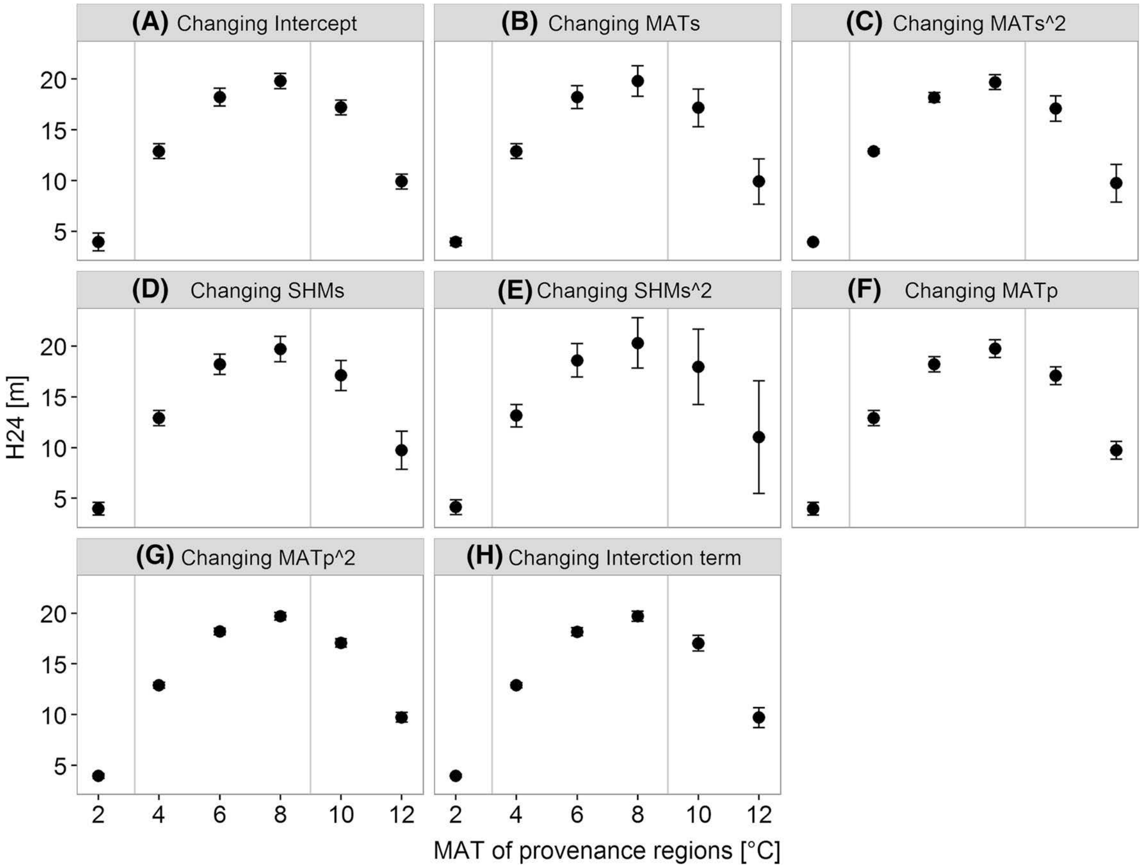


Fig. 3 Uncertainty in the prediction of URF for H24 [m] with a change in regression coefficients of climate variables. The *black dots* represent the predicted H24 [m] and the *error bars* represent the 95 % confidence interval. The *x-axis* shows MAT of provenance regions in Austria and Germany. The range of MAT enclosed within the *gray vertical lines* represents the MAT of trial locations used to calibrate the URF$_s$

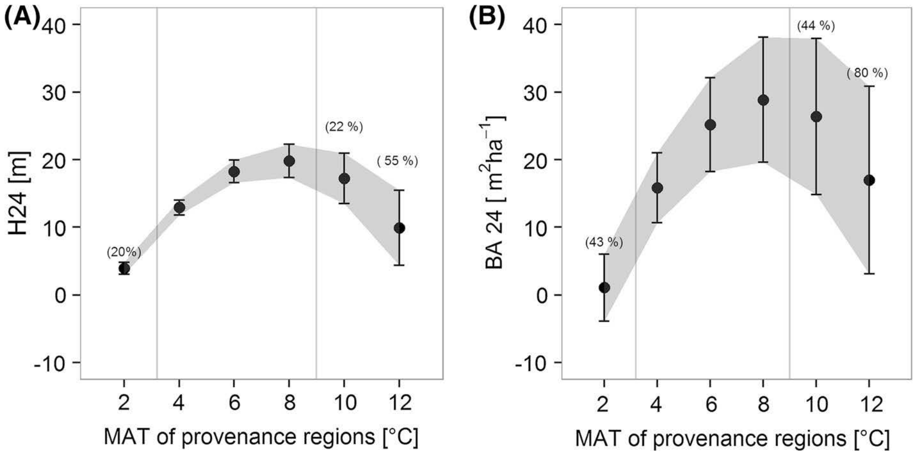


Fig. 4 Overall uncertainty in URFs prediction for (**a**) H24 (**b**) BA24. The *black dots* depict predicted value and the *error bars* represent the respective 95 % confidence intervals. The confidence intervals shown as *gray band* indicate the maximum width of the 95 % confidence intervals resulting from a change in the regression coefficients of climate variables. The *x-axis* shows MAT of the provenance regions in Austria and Germany. The range of MAT enclosed within the *gray vertical lines* represents the MAT of trial locations used to calibrate the URF$_s$. The *figures* in *brackets* represent the percentage deviation of the 95 % confidence interval from predicted value at MAT of 2, 10, and 12 °C

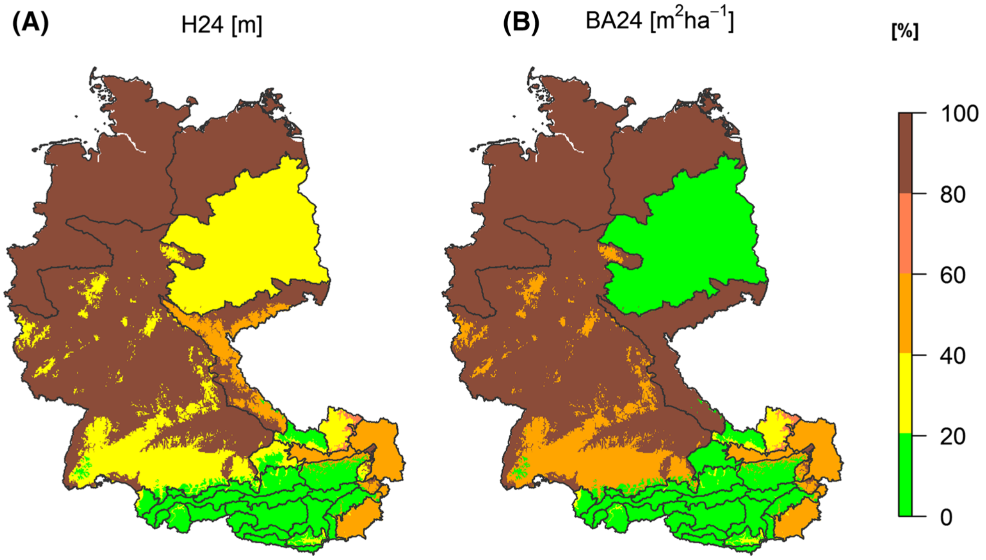


Fig. 5 Uncertainty in model predictions for H24 (**a**) and BA24 (**b**) due to climate change scenarios. The *figures* show the difference between the predictions for the scenarios RCP 8.5 and RCP 4.5 in 2070 given in percentage of the mean of the two scenarios

clusters CL1 and CL2 are predicted to be consistently top performers in terms of H24 and BA24 under both current climate and climate change conditions (Table 3, Table S6 in the supplementary material). These clusters comprise of seed stands such as *Cowlitz Randle (Cispus River), Trout Lake, Carlton Creek–Cowlitz River, Ashford Elbe, Darrington, Skate Creek, Packwood 2.5 (FRD 52), Randle (Cowlitz River area), Trout Lake and Baker Lake* (Table S2).

Growth performance under current and future climate

The average of the predicted dominant height (H24) and basal area (BA24) across all provenance regions of the study region is 17 m and 22 m^2ha^{-1}, respectively (Table 3, Table S6). Under current climate, the German provenance regions, North Germany, Northern lowlands, Middle and East Germany, and southwest Germany, and the Austrian provenance regions in the south, east, and north of the Alps including the eastern continental regions are predicted to have above-average growth performance with up to 37 % higher height and 45 % higher basal area than the provenance regions in higher altitude Alpine regions (Table 3, Table S6). Growth performance also varies within provenance region: For example, in the regions southwest and southeast Germany, the intermediate and high altitudinal areas above 500 m (e.g., the Black forest, Schwäbische Alb, Erzgebirge, Bayerische Wald) have around 40 % higher growth performance than the sites at lower altitudes <500 m (Fig. 8a, Fig. S3A in the supplementary materials) located in the same provenance regions. Under current climate, model uncertainty ranges from 10 to 30 % of the predicted H24 and from 20 to 40 % of the predicted BA24 (Fig. 8d, Fig. S3D).

Under climate change, provenance regions with low growth performance at present (e.g., mainly intermediate and high elevation sites in the Alps) are predicted to undergo a 53 % increase in height growth under RCP 4.5 scenario and 39 % under RCP 8.5 scenario by 2070 on average (Table 3; Fig. 8). A similar trend is also observed for basal area growth performance where the current provenance regions with below-average growth performance are predicted to have 81–93 % increase in basal area under RCP 4.5 and RCP 8.5 scenarios, respectively, by 2070 (Table S6, Fig. S3, Table S4). However, the current provenance regions with above-average growth performance are predicted to have 10–36 % reduction in height and 12–40 % reduction in basal area by 2070 under RCP 4.5 and RCP 8.5 scenarios, respectively.

Under both climate change scenarios, the Pannonian east of Austria and lower altitudinal regions (0–500 m) of the North and Middle Germany are predicted to experience the strongest decline in growth performance compared to current climate. (Table 3, Table S6; Fig. 8, Fig. S3).

The Pannonian east of Austria and lower altitude regions of North and Middle Germany also have maximum model uncertainty under climate change. The model uncertainty varies from 30 to 70 % of the predicted H24 and 40–85 % of predicted BA24 in these regions (Fig. 8, Fig. S3). The higher altitude alpine regions have lower model uncertainty under climate change (Fig. 8, Fig. S3).

Uncertainty due to climate change scenarios is higher (40–100 %) in North Germany, and low altitude regions of

Table 2 Evaluation of the URF for H24 with independent data from provenance trials across Europe

Reference	Country	Trial	Age	N	MAT_p min	MAT_p mean	MAT_p max	Lat	Long	Alt	MAT_s	SHM_s	R	Hit rate	CV-Obs	CV-URF
Nanson (1978)	Belgium	Freux	22	31	8.6	10.1	11.4	49.97	5.45	460	7.9	35.6	0.18	14	0.07	0.05
Ballian et al. (2002)	Bosnia	Blinge	32	4	8.5	9.0	10.0	43.08	18.05	951	9.5	48.6	0.4	100	0.03	0.07
Petkova (2011)	Bulgaria	Petrohan	24	54	3.9	7.4	10.2	43.23	23.15	600	9.1	62.4	0.2	72	0.2	0.11
Perić et al. (2005)	Croatia	Kutina	34	4	10.3	10.7	11.0	45.55	16.72	145	10.4	49.4	0.4	100	0.02	0.09
Perić et al. (2009)	Croatia	Kontija-Istria	24	7	6.5	9.6	11.1	45.13	13.9	337	12.6	48.8	0.29	50	0.06	0.11
Sika and Pav (1990)	Czech.Rep	Jizbice	20	12	5.7	8.0	9.5	50.26	14.99	600	6.3	48.4	−0.02	33	0.11	0.07
Aussenac (1980)	France	Arboretum	16	10	8.0	9.6	11.3	48.74	6.35	227	9.4	52.6	−0.63	0	0.06	0.09
Schober (1955)	Germany	Braunlage	24	8	3.6	7.7	11.4	51.72	10.61	569	6.2	33.6	0.06	50	0.03	0.08
Schober (1955)	Germany	Gahrenberg	24	9	1.5	7.7	11.0	51.42	9.58	170	8.8	46.5	−0.05	33	0.03	0.14
Kenk and Thren (1958)	Germany	Kirchzarten	23	6	4.2	7.8	11.4	47.96	7.96	394	9.5	36.4	0.35	50	0.04	0.07
Kenk and Thren (1958)	Germany	Schauinsland	22	9	2.2	7.5	9.5	47.91	7.89	1159	5.1	20.4	0.58	67	0.06	0.09
Kenk and Thren (1958)	Germany	Schopfheim	22	5	2.2	6.9	8.8	47.72	8	940	6.3	24.3	0.3	50	0.08	0.06
Kenk and Thren (1958)	Germany	Sindelfingen	22	9	2.3	7.1	9.5	48.71	9.01	590	7.8	43	0.59	33	0.08	0.11
Kenk and Thren (1958)	Germany	Wiesloch	22	9	2.3	7.1	9.5	49.25	8.64	105	10.3	56.9	0.59	33	0.1	0.06
Lally and Thomson (1998)	Ireland	Rathdrum	24	15	8.4	9.7	11.5	51.98	−8.22	65	9.8	38	−0.25	25	0.03	0.06
Ducci and Tocci (1987)	Italy	Faltona	16	11	5.8	9.5	11.5	43.62	11.76	754	10.4	61.4	−0.17	33	0.09	0.07
Ducci and Tocci (1987)	Italy	Vallombrosa	16	34	5.1	9.2	11.6	43.73	11.56	965	9.2	46.1	−0.36	13	0.13	0.13
Kranenborg and De Vries (1995)	Netherlands	Sleenerzand	20	50	5.7	9.0	10.6	52.8	6.81	18	8.7	45.5	−0.38	8	0.06	0.06
Kranenborg and De Vries (1995)	Netherlands	Sprielderbos	20	44	5.7	8.9	10.8	52.25	5.66	55	8.8	45.8	−0.54	0	0.07	0.06
Magnesen (1986)	Norway	Moberglien	13	46	1.6	6.7	10.5	60.17	5.45	100	7.1	17.6	0.41	42	0.26	0.07

Hit rate refers to percentage of populations which the URFs ranked correctly among the top 25 % at the validation trial sites. For reference of the data source, see Table S1

N number of population in a particular trial, *Lat* latitude [°N], *Lon* longitude [°W], *Alt* altitude[m], *MATs* mean annual temperature [°C] of trial location, *SHMs* summer heat: moisture index of trial locations, MAT_p mean annual temperature [°C] of provenance origin, *R* Spearman's rank correlation coefficients between observed and predicted heights, *CV-Obs* coefficients of variation between provenances observed in the validation trials, *CV-URF* coefficient of variations between provenances predicted by the URF for H24

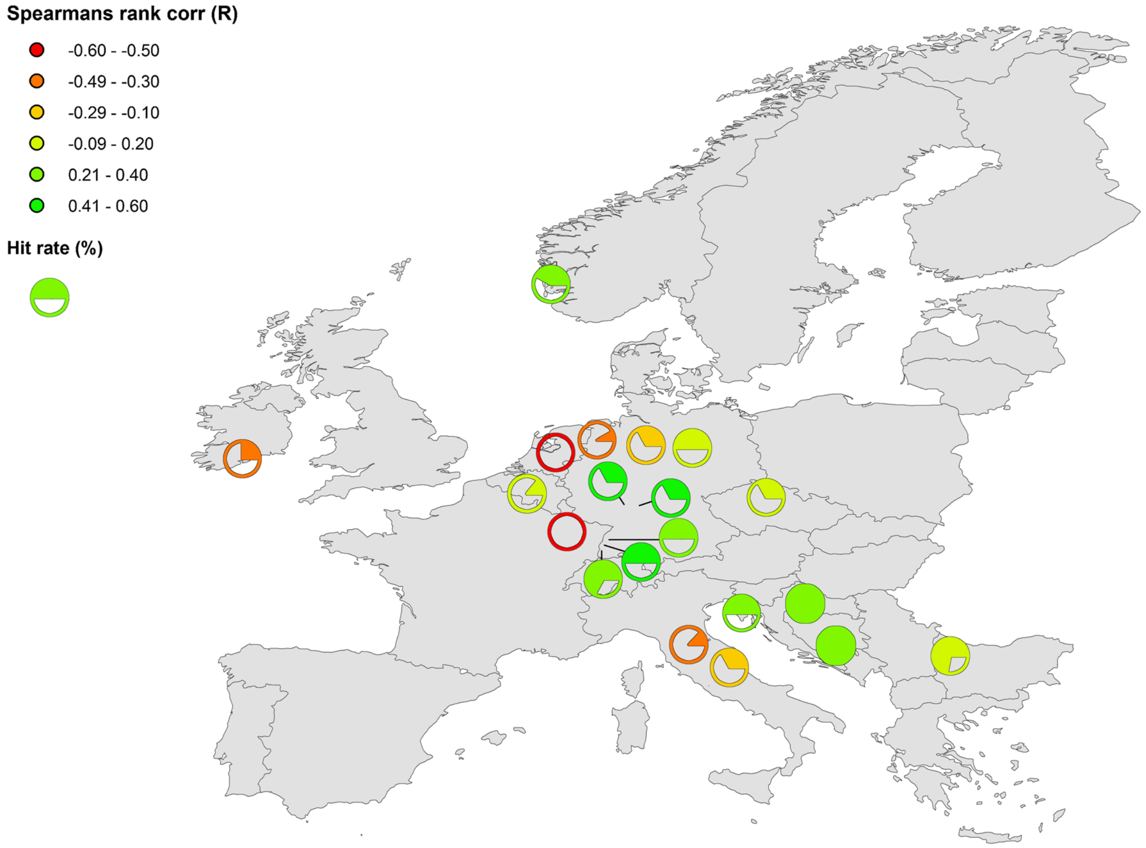


Fig. 6 Evaluation of the URF model with independent data from 20 provenance trials across Europe. The *pie charts* within each of these locations represent the *hit rate* which is the percentage of top ranking population (top 25 %) in terms of height growth performance that were identified as top ranking by both URF and observed data. The *colors* of the *pie charts* represent the Spearman's rank correlation between URF predictions and observed data, *red* indicating low and *green* indicating high correlation

southwest and southeast Germany, and in the Pannonian east of Austria (Fig. 5), whereas uncertainty due to climate change scenario is lower in the Alpine regions and Mid- and East German lowlands corresponding to 0–40 % (Fig. 5). Uncertainty due to the two climate change scenarios RCP 8.5 and RCP 4.5 (Fig. 5) is higher than the model uncertainty (Figs. 4, 8, Fig. S3).

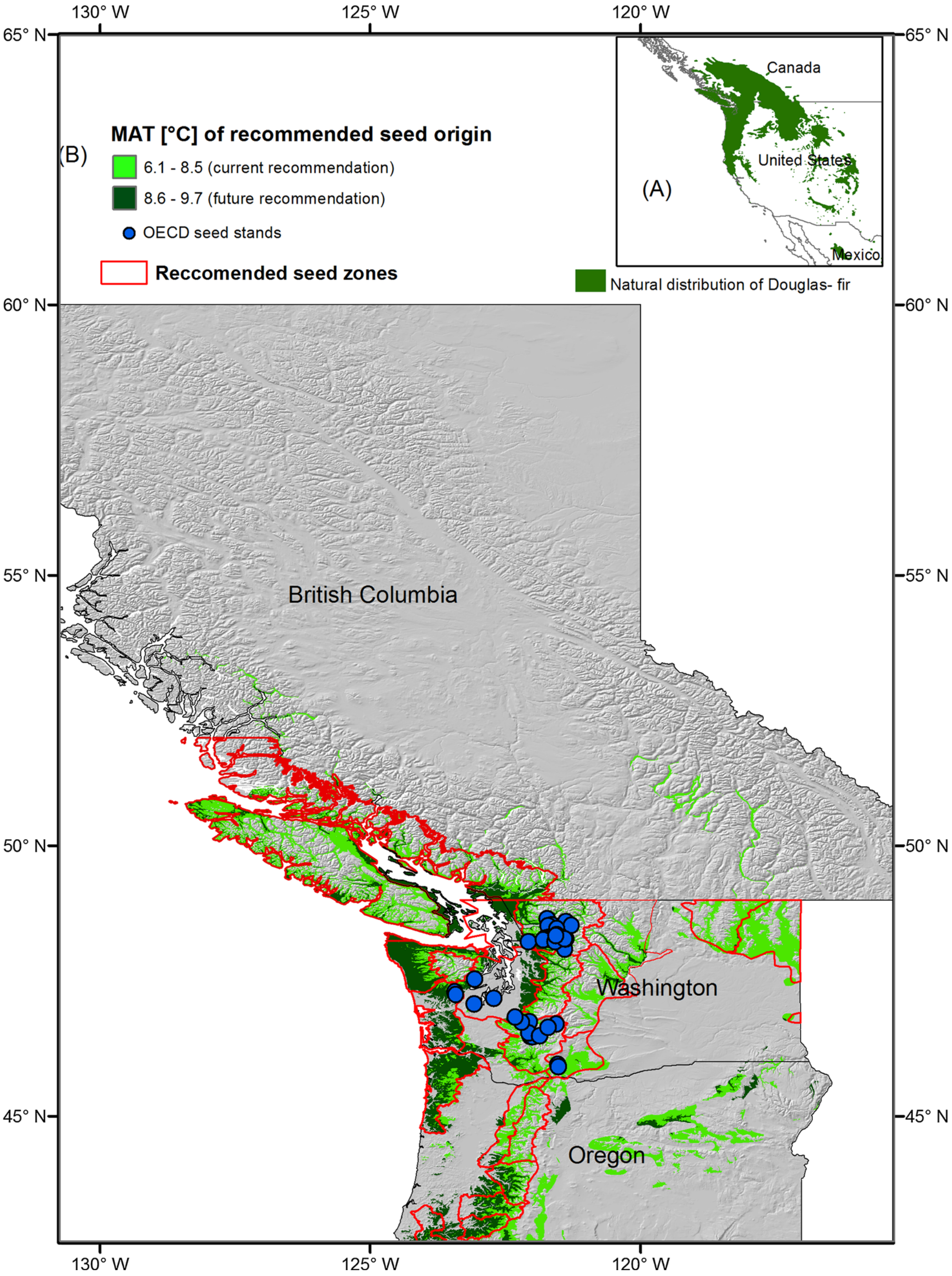
Discussion

Translating scientific knowledge on climate change adaptation into concrete strategies and management guidelines is a challenging task. Typical problems are a lack of understanding of the effects of uncertainty of climate change scenarios, model uncertainty, and the uncertainty due to extrapolation of model results beyond the calibration range, given that most of our predictions are model based. Moreover, legal requirements such as international resolutions, country-specific rules and regulations at the regional scale need to be considered when developing guidance for managers and policy makers. Within the present study, we aimed at translating model predictions, which integrates both genetic and environmental effects of climate, into practical recommendations for forest and seed managers while considering the legal framework for forest reproductive material on national and international levels. Meanwhile, we also report the effects of uncertainties arising from the model parametrization and uncertain future climates.

Prediction uncertainties

Recent studies (Wang et al. 2012a; Lindner et al. 2014) discussed various sources of uncertainties in the prediction of forest models and approaches for quantifying and reporting them. Predictions based on multiple climate scenarios and estimating the variation in model output due to change in parameter values are robust approaches for quantifying and communicating uncertainty of forest models under unknown future conditions (Wang et al. 2012a; Lindner et al. 2014). In the present study, we focused on uncertainty in model predictions arising from model parameter estimates due to contrasting climate

Fig. 7 **a** Natural distribution of Douglas-fir in NW America. **b** Seed origin of Douglas-fir shown by mean annual temperature [°C] in NW America, predicted to be optimum by the URF$_s$ in terms of height and basal area growth performance when planted in the study area under current and climate change scenarios. The location of the seed stands identified under OECD scheme is shown as *blue dots*. The *red lines* demarcate the recommended seed zones



change scenarios. Model uncertainty under current climate is fairly uniform across the study region indicating confidence in the model for identifying suitable seed sources of Douglas-fir in the study region with optimum growth performance under the current climate. Under climate change, the highest model uncertainties (70 % for H24 and 85 % for BA24) can be observed for the Pannonian east of Austria and North Germany lowlands, whereas it is only around 10 % in southeast Germany (Fig. 8, Fig. S3).

Generally, model uncertainty increases with MAT and SHM of the planting sites (Fig. 4). Recent studies with process-based forest models like Albert et al. (2015) found that effects of drought on forest growth vary strongly between different sites, species, and climate projections. Spadavecchia et al. (2011), however, found that temperature-related variables are the major contributor to uncertainty in the predictions of forest models. This implies that predictions of our models need to be cautiously interpreted at sites with complex soil moisture regime accompanied by warm summers. The model uncertainty is larger for predictions of basal area compared to height growth performance (Fig. 4). This is because the basal area is more

Table 3 Growth performance (mean of the altitudinal subzones within provenance regions) predicted by the URFs for H24 for the provenance regions of Austria and Germany

Country	Provenance region number	Provenance regions	H24 [m]		Change from current H24 [%]				
			Current	Top seed stands under current climate	RCP 4.5		RCP 8.5		Top seed stands under RCP 8.5 in 2070
					2050	2070	2050	2070	
AU	1.3	Subcontinental Central Alps—east part	11.6	CL1	59.9	80.6	95.7	70.2	CL1
AU	2.2	North intermediate Apls—east part	11.7	CL1	62.1	82.1	96.5	72.6	CL1
AU	1.2	Subcontinental Central Alps—west part	13.3	CL1	40.8	53.6	65.2	41.4	CL1
AU	1.1	Central Alps- Continental—Central zone	13.8	CL1, CL2	34.8	44.2	54.3	29.1	CL1
AU	2.1	North intermediate Apls—west part	13.9	CL1	40.8	52.2	61.6	42.8	CL1
AU	3.1	East intermediate Alps—north part	14.2	CL1,	56.9	71.4	84.2	56.7	CL1, CL2
AU	3.2	East intermediate Alps—south part	14.3	CL1	52.9	68.1	80.1	55.8	CL1, CL2
AU	4.2	North border of the Alps—east part	14.8	CL1, CL2	37.7	46.2	56.5	33.7	CL1, CL2, CL3
AU	5.3	East and mid-Styrian mountain area	14.8	CL1, CL2	59.7	69.4	85.2	51.3	CL1, CL2
AU	5.1	Lower Austria east border of the Alps	14.9	CL1, CL2	40.1	48.4	69.2	29.3	CL1, CL2
AU	5.4	West Styrian mountain area	15.1	CL1	43.1	54.2	61.5	44.1	CL1, CL2
AU	4.1	North border of the Alps—west part	15.2	CL1, CL2	26.3	33.7	37.6	27.4	CL1, CL2
AU	3.3	South intermediate Apls	15.6	CL1	25.9	35.3	37.5	22.3	CL1, CL2
AU	5.2	Bucklige Welt	15.8	CL1	34.7	38.7	43.5	19.2	CL1, CL2, CL3
GE	853-04/05	Southwestern Germany	16.6	CL1	15.2	17.6	19	−0.4	CL1, CL2, CL3
AU	6.1	South border range of mountains	16.7	CL1	20.1	25.8	27.1	18	CL1, CL2
GE	853-02	North German lowlands excl—Schleswig–Holstein	17.4	CL1, CL2	−20.4	−18.7	−52.8	−67.1	CL2, CL3
AU	8.1	Pannonian lowland and hilly country	17.7	CL1, CL2, CL3	−35.1	−58.7	−61.9	−75.8	CL2, CL3, CL4
GE	853-03	Middle and East German hill and lowlands	18.6	CL1, CL2	−19.8	−31.6	−41.7	−69	CL1, CL2, CL3, CL4
GE	853-06	Southeastern Germany	19.1	CL1	4.4	0.6	2.3	−24.8	CL1, CL2, CL3, CL4
AU	9.1	Muehlviertel	19.8	CL1	5.5	5.9	5.4	−3.8	CL2
GE	853-01	North German lowlands incl—Schleswig–Holstein	20.4	CL1, CL2	−14	−16.4	−33.2	−76.9	CL1, CL2, CL3, CL4
AU	6.2	Basin of Klagenfurt Carinthia	20.9	CL1, CL2	1.2	1	−1.4	−12.3	CL2, CL3
AU	7.1	Northern foothills—west part	21.1	CL1, CL2	−3.3	−3	−7.1	−18.1	CL1, CL2, CL3
AU	9.2	Waldviertel	21.7	CL1, CL2	−3.6	−8.2	−9.5	−39.4	CL1, CL2, CL3
AU	8.2	Subillyrian hilly and terrace country	21.7	CL1, CL2, CL3	−7.4	−11.7	−14.9	−39.4	CL2, CL3, CL4
AU	7.2	Northern foothills—east part	21.7	CL1, CL2, CL3	−6.2	−9.4	−13.3	−33.9	CL2, CL3

The change in growth performance is calculated as change in percentage from the current climate. Top seed stands are cluster of those OECD seed stands which are predicted to yield maximum H24 in the respective provenance regions. For explanation of the clusters (CL1, CL2, CL3, CL4), see Table S2

AU Austria, *GE* Germany

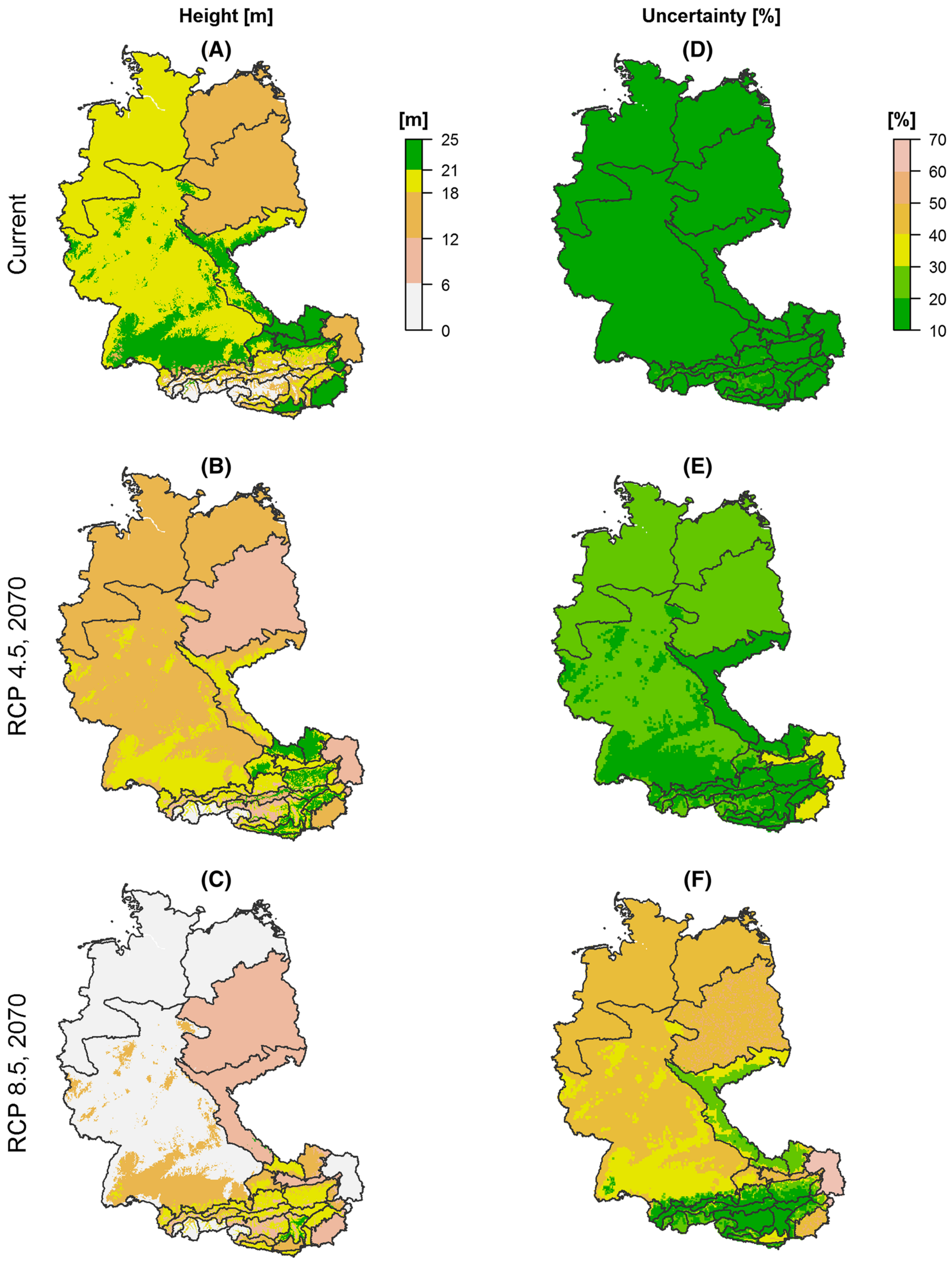


Fig. 8 Height growth performance of seed sources predicted to be optimum for the provenance regions of the study region under (**a**) current climate and (**b**, **c**) under two climate change scenarios RCP 4.5 and RCP 8.5 in 2070. **d**, **e**, and **f** depict the uncertainty in the prediction of URFs indicated by the percentage deviation from the predicted H24 due to change in regression coefficients

strictly influenced by climatic factors as it summarizes diameter growth and the tree survival rate, both of which are driven by climate conditions (Chakraborty et al. 2015).

Uncertainty due to climate change scenarios was estimated from the difference between the predictions for the scenarios RCP 8.5 and RCP 4.5 in 2070 given in percentage of the mean of the predictions of the two scenarios. Uncertainty due to climate change scenarios was found to be highest in North, southwest, and southeast Germany and in the Pannonian east of Austria (Fig. 5), and lowest in the high and intermediate altitude provenance regions of the Alps and Mid-German lowlands. This might have resulted from an approximately 2 °C difference in temperature between RCP 4.5 and RCP 8.5 scenarios making the higher and mid-altitude Alpine regions climatically suitable and the east of Austria and North Germany less suitable for planting Douglas-fir in future. We found that uncertainty due to climate change scenarios (Fig. 5) was higher than the model uncertainty (Fig. 8, Fig. S3). Studies on understanding uncertainty due to model parameters and uncertainty due to climate change scenario independently are scarce. Reyer (2013) attempted to separate the effects of uncertainty due to model parameters and uncertainty due to a combination of model parameters and climate scenarios on net primary productivity and found that the uncertainty due to the combination of climate change and parameter uncertainty is substantially higher than uncertainty due to climate scenarios alone. However, studies on forest growth like Albert et al. (2015) and species distribution Pearson et al. (2006) point toward the general conclusion that uncertainty due to extrapolation of the model to unknown condition (for example, different climate change scenarios in our study) is the major source of overall uncertainty on forest development. However, in our study, quadratic response surfaces curve down within the range of the climate of the test sites, which make it relatively safe for extrapolation (Fig. 2).

To evaluate the performance and the general applicability of the URFs, we performed a model evaluation with observed growth data from 20 Douglas-fir provenance trials across Europe (Table S1). Under climatic conditions that are similar to the calibration data, the URFs worked well; for example, in Central and Continental Europe, rank correlations up to $r = 0.59$ and hit rates up to 100 % were found (Table 2; Fig. 6). The most crucial issue for this comparison is whether the URFs can be applied to predict growth performance of populations under conditions of climate change. In our evaluation, the majority of sites for which the models were validated successfully are located in Southeastern Europe (e.g., Bosnia and Croatia), where the present climate conditions corresponded to scenarios expected for 2050 and 2070 across the study regions. This indicates that the URFs are suitable tools for estimating Douglas-fir growth performance in future climates. However, when applied to climatically and geographically more distant plantation sites (e.g., France, Netherlands, Ireland and Italy) the URFs show rather low performance (Table 2; Fig. 6). The most likely explanation for this discrepancy is that our URFs were developed with trial data from more continental trials, whereas sites in Western Europe experience maritime, more humid climate. Thus, our empirical relation between climate and growth response in the URFs might lack generality across Europe. Also, the growth response in the trials might be affected by non-climatic factors such as soil or forest management, which differs across European countries. The lack of generality of our models strongly calls for a further common analysis of provenance trials across Europe.

Another aspect of the model evaluation exercise was that in the observed data obtained from Isaac-Renton et al. (2014), the statistical significance of the ranks in the provenances was not available. Thus, many observed differences might, in fact, be a product of random variation and such variation cannot be judged by the URF models. If it would be possible to group the provenances in the evaluation trials into statistically different classes, the discrepancies between observed and predicted growth performances might have been lower. Interestingly the predicted coefficient of variation between growth performances of provenances is in the same range as observed in many evaluation trials (Table 2), suggesting that although the URFs were not successful for Western European trials (Table 2, Fig. 6), the predicted variation in growth performances of the provenances is similar to the observed variation (Fig. S2).

Model recommendations for Douglas-fir in Central Europe

Both the URFs predict that North Germany and the Pannonian east of Austria will become less suitable for growing Douglas-fir under future climate (Fig. 8, Fig. S3). These regions are already close to the warmer and drier limit with respect to $\mathrm{MAT_s}$ and $\mathrm{SHM_s}$ of our URFs and thus may not accommodate a further increase in temperature and summer drought in the future. Provenance regions of southwest Germany and southeast Austria are suitable for growing Douglas-fir in future in terms of growth performance in particular at altitudinal ranges of 500–1500 m (Fig. 8, Fig. S3; Table 3) because these regions have higher growth performance as well as comparatively low model uncertainties. However, practical experience of growing Douglas-fir above 1000 m a.s.l is limited, and thus, any plantation at such elevations should take special care of suitable site conditions and being aware of abiotic risks (Chakraborty et al. 2015). If Douglas-fir plantations might be extended beyond that altitudinal range, we strongly suggest further experiments in order to improve prediction accuracy and confidence.

The derivative-free optimizing approach (Schlueter and Munetomo 2013) used in the current study provides high confidence in the identified populations, because such an approach was found to have higher accuracy (Körkel et al. 2005; Rios and Sahinidis 2013), compared to the partial derivative approach used in earlier studies such as Wang et al. (2010) and Chakraborty et al. (2015). Also, the optimization approach is able to identify the most suitable population across a range of climate conditions as characterized by a parameter space of several climate factors. Thus, it can not only be applied on a spatial scale throughout heterogeneous environments, i.e., provenance regions or seed zones but on time scales to identify the best seed source for the next two tree generations, where traditional approaches allowed recommendations only for distinct time periods (Chakraborty et al. 2015).

We found that populations originating from the Western Cascades and coastal regions of WA, OR, and BC having MAT of 6–9.5 °C would yield maximum growth performance in terms of both dominant height and basal area when planted in majority of our study region under both current and future climate conditions (Fig. 7; Tables S3, S4). This result is in good agreement with several studies that indicate the superiority of growth performance of coastal and Cascade populations of Douglas-fir under a wide range of climatic conditions in both Europe and North America (Isaac-Renton et al. 2014; Bansal et al. 2014; Montwé et al. 2015). Although we found that some isolated low altitude locations in the interior distribution range of Douglas-fir in North America also have the predicted optimum MAT_p (Fig. 7b, Table S5), we have limited evidence to support the suitability of provenances originating from this region for our study area. The predicted growth performance of the certified seed stands under OECD guidelines (Table 3, Table S6; Fig. 7) is an important contribution of the URFs and will be useful for forest and seed managers for obtaining planting material of Douglas-fir for our study region. Our results indicate that the OECD stands will continue to be sources of the most productive provenances also in the future (Table 3, Table S6; Fig. 7) supporting our previous finding that very little adjustments in terms of the already planted materials have to be done in majority of the study region (Chakraborty et al. 2015). Beside seed stands already certified today, our analysis allows the identification of further seed stands for future certification as “selected stands” and suitable provenances of the category “source identified,” where the latter might be imported into Austria or other European countries (Tables S2, S5).

Conclusions

Model-based recommendations on developing adaptation measures for biological systems under likely future climate require an understanding of the modeled processes and uncertainty of the future conditions. Our URF models are based on a large dataset of growth performance (model for H24) and the combined effects of growth performance and initial mortality (BA24) throughout a wide range of climatic conditions (Chakraborty et al. 2015). Thus, our models allow reliable predictions for suitable seed sources and future productivity with respect to intraspecific variation. This provides a strong advantage compared to (1) climate envelope models (e.g., Kölling 2008; Isaac-Renton et al. 2014) that only evaluate general climate suitability or the suitability of provenances, and (2) forest growth models which do not account for provenance variation and often require detailed information on future soil and climate information (e.g., Eckhart et al. 2014). Generally, a more explicit dealing with certain environmental risk for cultivation would be desirable, i.e., dealing with drought and frost resistance. However, incorporating such effects will ultimately increase the prediction uncertainty because climate change models do not allow a reasonable prediction of specific climate extremes on regional and local levels, so far. Our models resulted in a considerable model uncertainty, which is, however, still below the uncertainty of different climate change scenarios. Moreover, model evaluation across Europe suggests that our URFs are more suitable for expected conditions of climate change in Central Europe than for a more maritime climate and might thus be a valuable tool in adaptation management in Central Europe.

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Supplementary materials: Figures

Adapting Douglas-fir forestry in Central Europe: evaluation, application, and uncertainty analysis of a genetically based model

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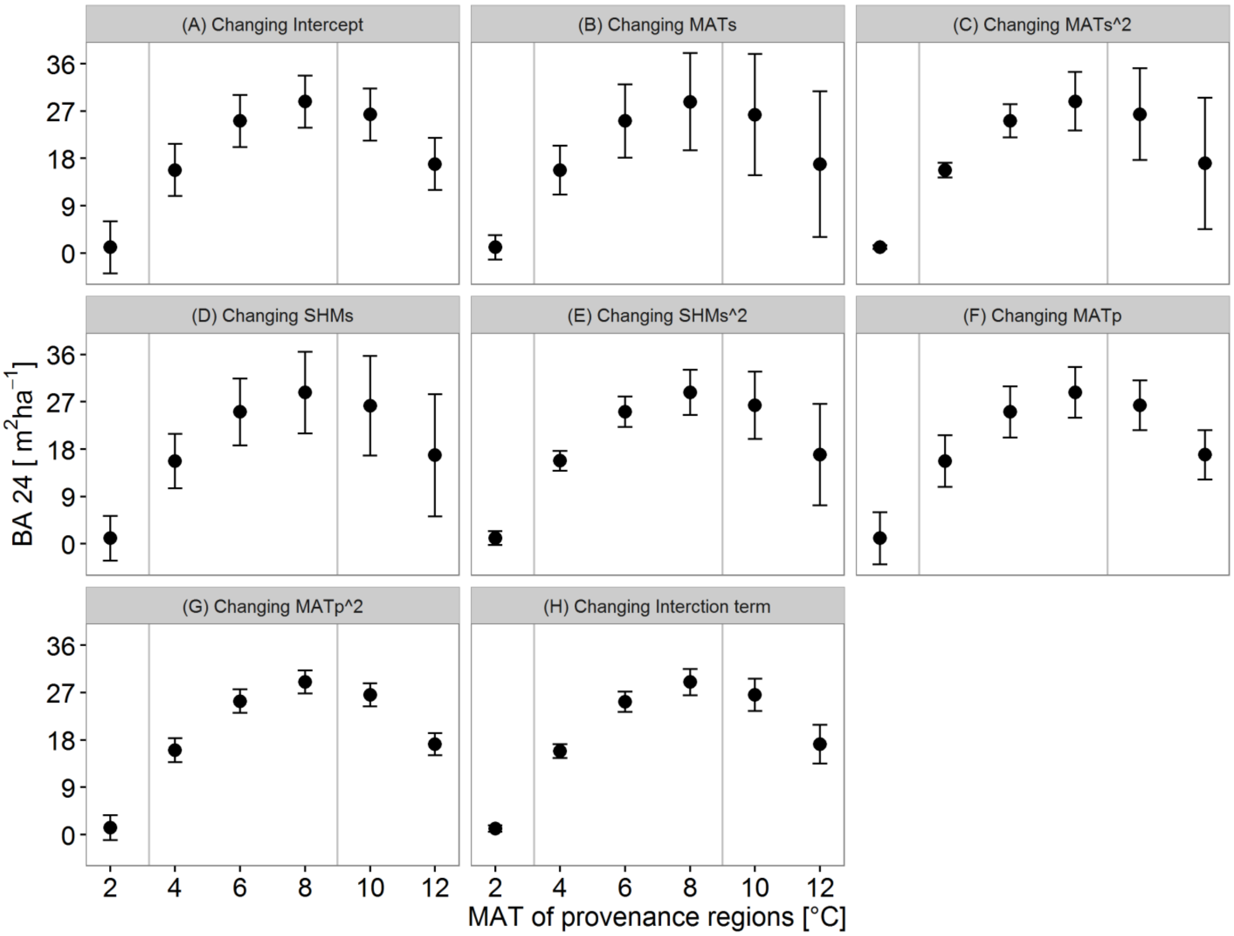
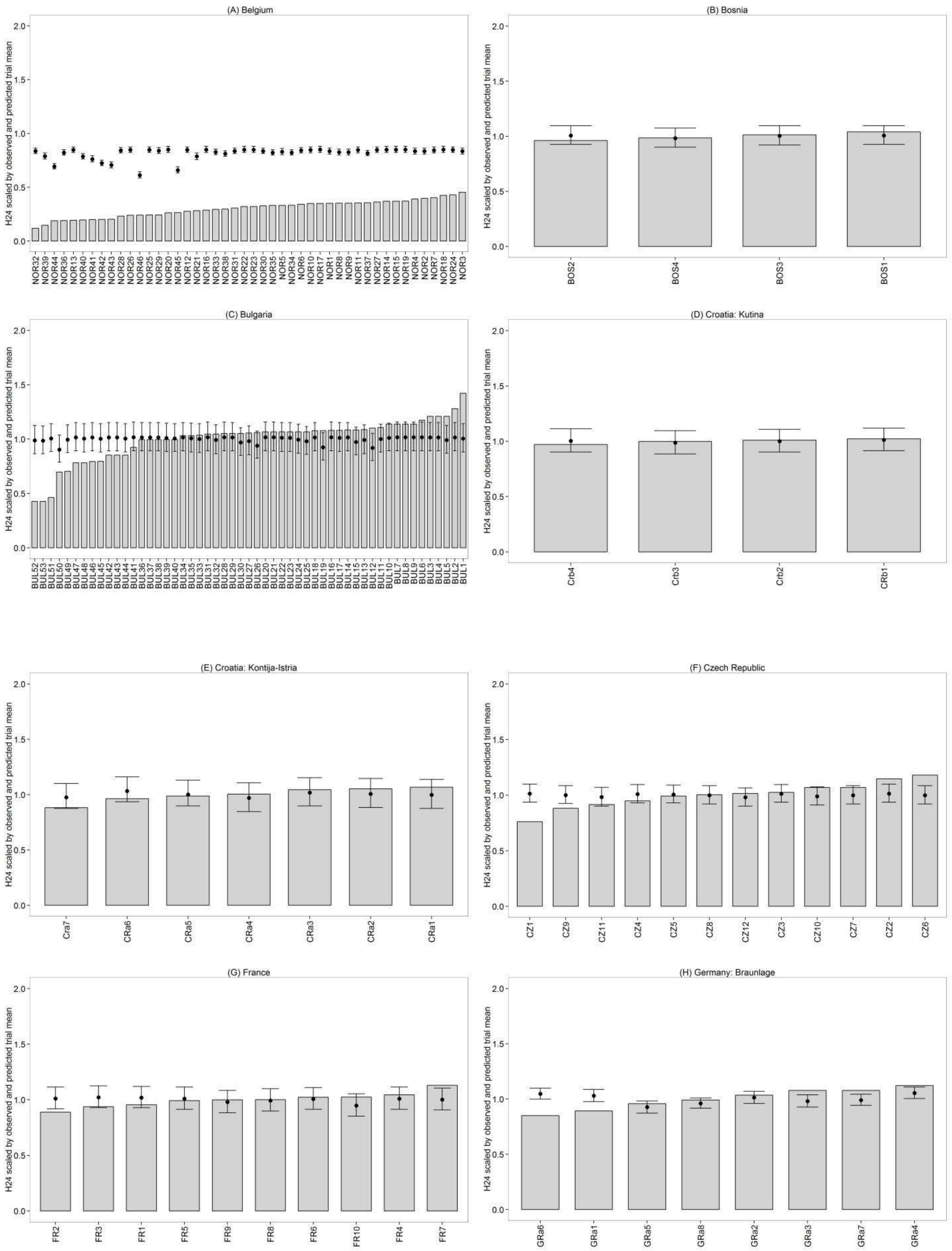
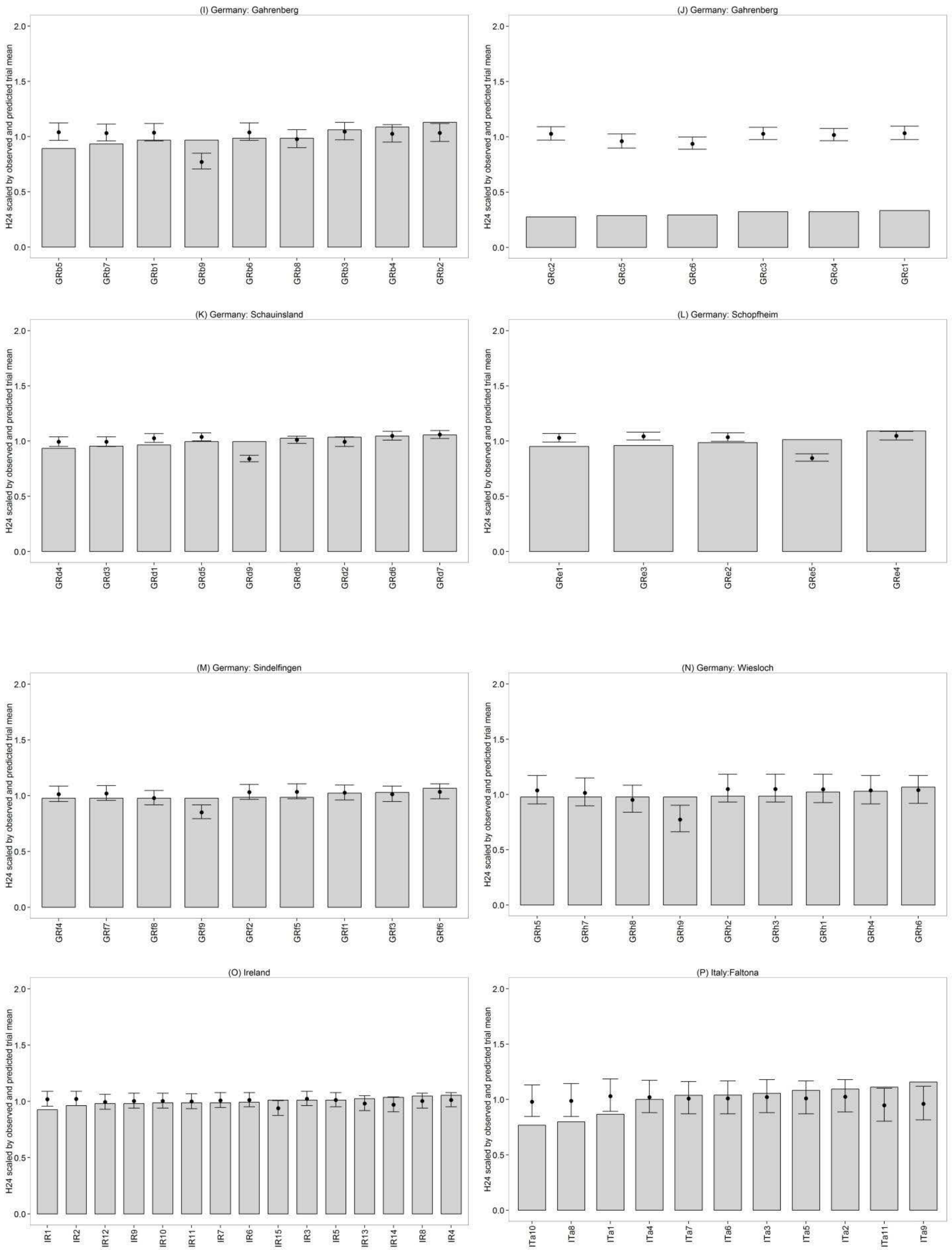
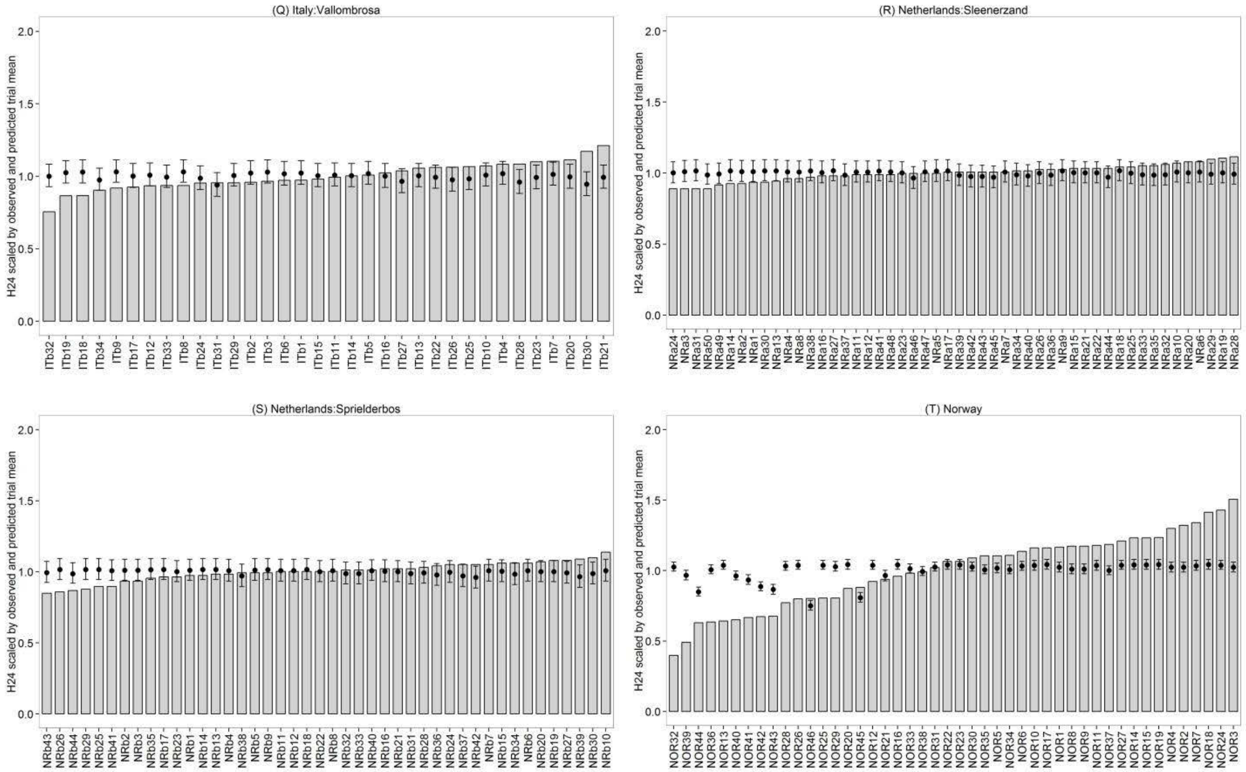


Fig S1 Uncertainty in the predictions of URF for BA24 [m^2ha^{-1}] with a change in regression coefficients of climate variables. The black dots represent predicted BA24 [m^2ha^{-1}] and the error bars represent the 95% confidence interval. The x-axis shows MAT of provenance regions in Austria and Germany. The range of MAT enclosed by the gray vertical lines represents the MAT of trial locations used to calibrate the URF$_s$


(A) Belgium
H24 scaled by observed and predicted trial mean
2.0
1.5
1.0
0.5
0.0
NOR32 NOR39 NOR44 NOR36 NOR13 NOR40 NOR41 NOR42 NOR43 NOR28 NOR26 NOR46 NOR25 NOR29 NOR20 NOR45 NOR12 NOR21 NOR16 NOR33 NOR38 NOR31 NOR22 NOR23 NOR30 NOR35 NOR5 NOR34 NOR6 NOR10 NOR17 NOR1 NOR8 NOR9 NOR11 NOR37 NOR27 NOR14 NOR15 NOR19 NOR4 NOR2 NOR7 NOR18 NOR24 NOR3
(B) Bosnia
H24 scaled by observed and predicted trial mean
2.0
1.5
1.0
0.5
0.0
BOS2 BOS4 BOS3 BOS1
(C) Bulgaria
H24 scaled by observed and predicted trial mean
2.0
1.5
1.0
0.5
0.0
BUL52 BUL53 BUL51 BUL50 BUL49 BUL47 BUL48 BUL46 BUL45 BUL42 BUL43 BUL44 BUL41 BUL36 BUL37 BUL38 BUL39 BUL40 BUL34 BUL35 BUL33 BUL31 BUL32 BUL28 BUL29 BUL30 BUL27 BUL26 BUL20 BUL21 BUL22 BUL23 BUL24 BUL25 BUL18 BUL19 BUL16 BUL17 BUL14 BUL15 BUL13 BUL12 BUL11 BUL10 BUL7 BUL8 BUL9 BUL6 BUL3 BUL4 BUL5 BUL2 BUL1
(D) Croatia: Kutina
H24 scaled by observed and predicted trial mean
2.0
1.5
1.0
0.5
0.0
Crb4 Crb3 Crb2 CRb1
(E) Croatia: Kontija-Istria
H24 scaled by observed and predicted trial mean
2.0
1.5
1.0
0.5
0.0
Cra7 CRa6 CRa5 CRa4 CRa3 CRa2 CRa1
(F) Czech Republic
H24 scaled by observed and predicted trial mean
2.0
1.5
1.0
0.5
0.0
CZ1 CZ9 CZ11 CZ4 CZ5 CZ8 CZ12 CZ3 CZ10 CZ7 CZ2 CZ6
(G) France
H24 scaled by observed and predicted trial mean
2.0
1.5
1.0
0.5
0.0
FR2 FR3 FR1 FR5 FR9 FR8 FR6 FR10 FR4 FR7
(H) Germany: Braunlage
H24 scaled by observed and predicted trial mean
2.0
1.5
1.0
0.5
0.0
GRa6 GRa1 GRa5 GRa8 GRa2 GRa3 GRa7 GRa4


(I) Germany: Gahrenberg
H24 scaled by observed and predicted trial mean
0.0
0.5
1.0
1.5
2.0
GRb5
GRb7
GRb1
GRb9
GRb6
GRb8
GRb3
GRb4
GRb2
(J) Germany: Gahrenberg
GRc2
GRc5
GRc6
GRc3
GRc4
GRc1
(K) Germany: Schauinsland
GRd4
GRd3
GRd1
GRd5
GRd9
GRd8
GRd2
GRd6
GRd7
(L) Germany: Schopfheim
GRe1
GRe3
GRe2
GRe5
GRe4
(M) Germany: Sindelfingen
GRf4
GRf7
GRf8
GRf9
GRf2
GRf5
GRf1
GRf3
GRf6
(N) Germany: Wiesloch
GRh5
GRh7
GRh8
GRh9
GRh2
GRh3
GRh1
GRh4
GRh6
(O) Ireland
IR1
IR2
IR12
IR9
IR10
IR11
IR7
IR6
IR15
IR3
IR5
IR13
IR14
IR8
IR4
(P) Italy:Faltona
ITa10
ITa8
ITa1
ITa4
ITa7
ITa6
ITa3
ITa5
ITa2
ITa11
ITa9



FigS2(A) to (T), Observed height (bars), vs predicted height (dots) and its 95% confidence interval due to change in regression coefficients. The observed heights are scaled to respective observed trial means and predicted heights are scaled to predicted trial means. The x- axis of each plot represents the provenances.

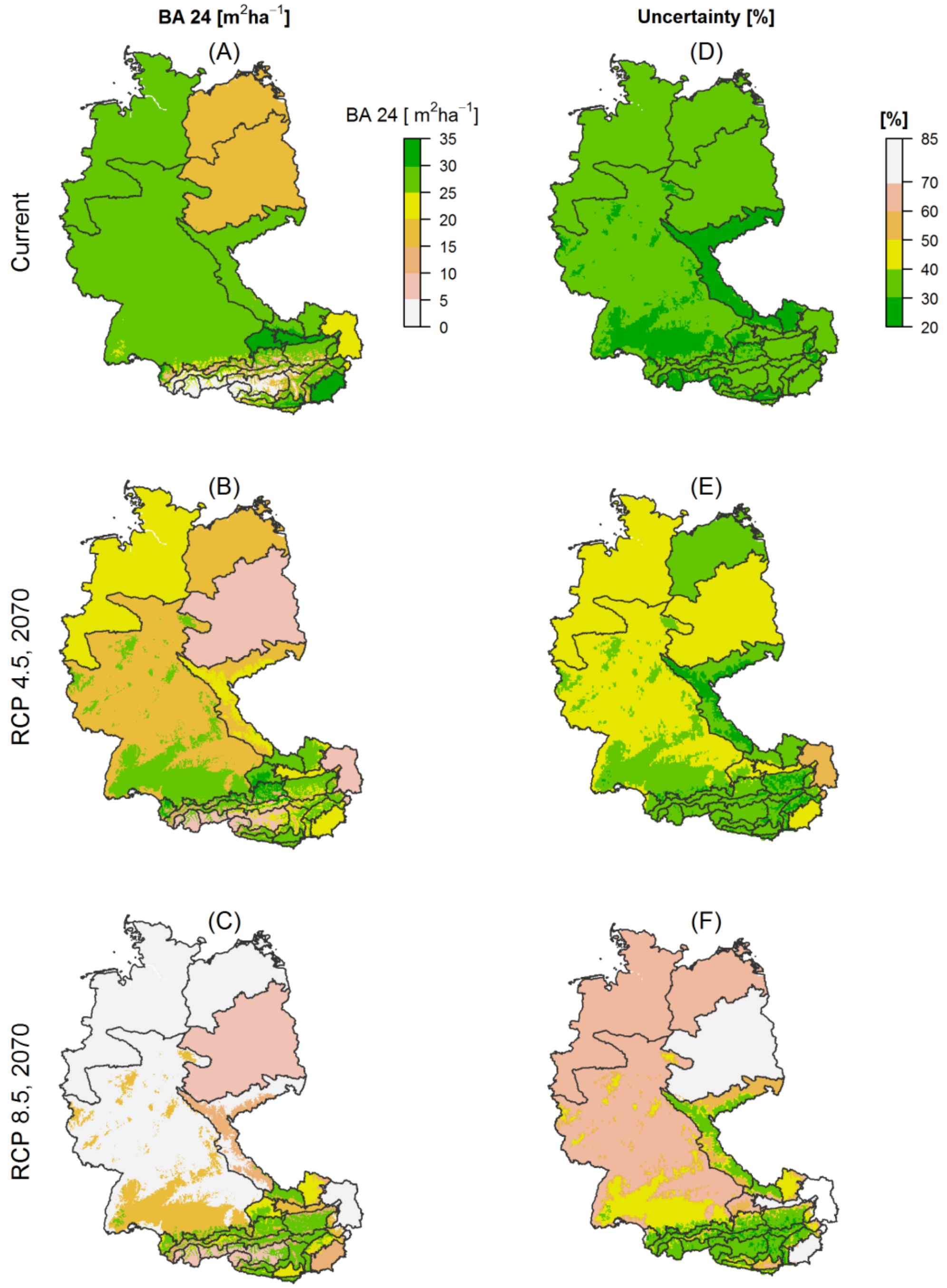


Fig S3 Basal area growth performance of seed sources predicted to be optimum for the provenance regions of Austria and Germany under A) current climate and (B, C) under two climate change scenarios RCP4.5 and RCP 8.5 at 2070. D, E, and F depict the uncertainty in the prediction of URF_s indicated by the percentage deviation from the predicted BA24 due to change in regression coefficients

Supplementary materials: Tables

Adapting Douglas-fir forestry in Central Europe: evaluation, application, and uncertainty analysis of a genetically based model

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Table S1 References of data sources for model evaluation.

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Table S2 Details of 40 seed stands in Washington identified according to OECD guidelines to acquire seed materials to be planted in Austria and Germany.If the seed stand number is missing (*) the stand is not yet included in the National list for USA and seed cannot be introduced into Europe, but should be added to the list due to its proven suitability for present and future conditions.

National Seed Stand number	County	Seed stand	Lat [°N]	Long [°W]	Alt zone	Alt [m]	MAT_p[°C]	Seed stand cluster
430/31	King	Cowlitz Randle (Cispus River)	46.47431	-121.998	4	1125	7.0	CL1
430/31	King	Cowlitz Randle (Cispus River)	46.47867	-121.993	3.5	975	7.6	CL1
652/10	Klickitat	Trout Lake	45.96259	-121.534	3	825	7.7	CL1
430/40	Lewis	Carlton Creek - Cowlitz River	46.70827	-121.559	2.5	675	8.0	CL1
422/31	Pierce	Ashford Elbe	46.75163	-122.048	2	525	8.0	CL1
430/31	King	Cowlitz Randle (Cispus River)	46.4722	-122.017	3	825	8.2	CL2
*	Snohomish	(Darrington)	48.21868	-121.529	2.5	675	8.2	CL2
430/11	Lewis	Skate Creek, Packwood 2.5 (FRD 52)	46.64869	-121.715	2.5	675	8.2	CL2
*	Lewis	Randle (Cowlitz River area)	46.48931	-121.865	3	825	8.2	CL2
653/10	Klickitat	Trout Lake	45.92074	-121.523	2.5	675	8.3	CL2
402/20	Skagit, Whatcom	Baker Lake	48.64999	-121.727	1.5	375	8.4	CL2
430/31	King	Cowlitz Randle (Cispus River)	46.48236	-122.042	2.5	675	8.7	CL3
030/81	Mason	Matlock	47.30277	-123.43	1.5	375	8.8	CL3
*	Skagit	Concrete Jackmann Creek	48.54336	-121.647	2.5	675	8.8	CL3
403/91	Snohomish	Bedal Creek Campground	48.09402	-121.398	1.5	375	8.9	CL3
*	Snohomish	DarringtonSuiattle River	48.27842	-121.386	2.5	675	8.9	CL3
422/20	Lewis	Mineral	46.73618	-122.194	2	525	8.9	CL3
*	Snohomish	DarringtonSuiattle River	48.28973	-121.397	2	525	9.2	CL4
403/13	Skagit	Texas Pond	48.34133	-121.563	1.5	375	9.2	CL4
403/11	Skagit, Snohomish	Darrington Round Mountain	48.30631	-121.714	1.5	375	9.4	CL4
403/50	Skagit	Sauk Prairie Flats	48.35863	-121.547	1	225	9.4	CL4
403/41	Snohomish	Sauk River (Darrington)	48.22946	-121.58	1.5	375	9.4	CL4
403/71	Skagit	DarringtonTenas Creek	48.31978	-121.423	1.5	375	9.5	CL4

402/10	Skagit	Bacon Point	48.60271	-121.382	1.5	375	9.5	CL4
403/12	Skagit, Snohomish	Darrington Round Mountain foothill	48.29163	-121.776	1	225	9.6	CL5
*	Snohomish	DarringtonSuiattle River 5	48.28363	-121.397	1.5	375	9.7	CL5
403/14	Snohomish	French Point, White Horse	48.26306	-121.798	1	225	9.7	CL5
222/10	Mason	Lake Cushman	47.53656	-123.071	1	225	9.7	CL5
430/10	Lewis	Cowlitz River Area	46.54331	-122.066	1.5	375	9.8	CL5
030/12	Mason	Matlock	47.24761	-123.42	0.5	75	9.9	CL5
403/10	Snohomish	Darrington Flats	48.27479	-121.754	1	225	9.9	CL5
403/61	Snohomish	Suiattle River Flats (Darrington)	48.27816	-121.402	1	225	10.0	CL5
402/31	Skagit	Marble CreekCampground	48.5354	-121.28	1.5	375	10.0	CL5
403/51	Skagit	Central Sauk Prairie	48.33906	-121.547	0.5	75	10.0	CL5
422/10	Pierce	Pack Forest	46.83844	-122.321	1.5	375	10.1	CL6
402/40	Skagit	Marblemount -	48.46683	-121.544	0.5	75	10.2	CL6
202/20	Snohomish	Arlington	48.22615	-122.073	0.5	75	10.2	CL6
241-12	Mason, Grays Harbor	McCleary	47.08003	-123.076	0.5	75	10.4	CL6
402/50	Skagit	Concrete-Rockport	48.52335	-121.707	0.5	75	10.6	CL6
232/10	Thurston	Yelm	47.18217	-122.714	0.5	75	10.6	CL6

Lat= Latitude [°N]

Long= Longitude [°W]

Alt.zone= Altitudinal zones (0.5 = 0 – 150 m; 1.0 = 150 – 300 m; 1.5 = 300 -450 m; 2.0 = 450 -600m; 2.5 = 600 -750m; 3.0 = 750 – 900m; 3.5 = 900 – 1050m; 4.0 = 1050 – 1200m)

Alt= Mean altitude of the respective altitudinal zones

MAT_p= Mean annual temperature of the seed stand

Table S3 MAT of seed origin recommended to be optimum by the URF for H24 [m] growth performance for each altitudinal sub zone in provenance regions of Austria and Germany

Zone ID	**Zone name**	**Zone altitude [m]**	**Recommended MAT of seed origin [°C]**		
			current	**RCP 4.5 in 2070**	**RCP 8.5 in 2070**
1.1	Central Alps- Continental - Central Zone	500 - 1000	7.5	7.9	8.2
1.1	Central Alps- Continental - Central Zone	1000 - 1500	7.0	7.4	7.7
1.1	Central Alps- Continental - Central Zone	> 1500	5.6	5.9	6.3
1.2	Subcontinental Central Alps - west part	500 - 1000	7.5	7.9	8.3
1.2	Subcontinental Central Alps - west part	1000 - 1500	6.9	7.3	7.7
1.2	Subcontinental Central Alps - west part	> 1500	5.7	6.1	6.4
1.3	Subcontinental Central Alps - east part	500 - 1000	7.2	7.6	8.0
1.3	Subcontinental Central Alps - east part	1000 - 1500	6.7	7.1	7.5
1.3	Subcontinental Central Alps - east part	> 1500	5.9	6.3	6.6
2.1	North intermediate Apls - west part	500 - 1000	7.6	8.0	8.3
2.1	North intermediate Apls - west part	1000 - 1500	6.9	7.3	7.6
2.1	North intermediate Apls - west part	> 1500	6.1	6.5	6.8
2.2	North intermediate Apls - east part	500 - 1000	7.3	7.6	8.0
2.2	North intermediate Apls - east part	1000 - 1500	6.7	7.1	7.5
2.2	North intermediate Apls - east part	> 1500	6.1	6.4	6.8
3.1	East intermediate Alps - north part	0 - 500	7.5	7.9	8.3
3.1	East intermediate Alps - north part	500 - 1000	7.2	7.6	7.9
3.1	East intermediate Alps - north part	1000 - 1500	6.7	7.0	7.4
3.1	East intermediate Alps - north part	> 1500	6.1	6.5	6.8
3.2	East intermediate Alps - south part	0 - 500	7.6	8.0	8.4
3.2	East intermediate Alps - south part	500 - 1000	7.2	7.5	7.9
3.2	East intermediate Alps - south part	1000 - 1500	6.7	7.1	7.4
3.2	East intermediate Alps - south part	> 1500	6.1	6.5	6.8
3.3	South intermediate Apls	0 - 500	7.9	8.2	8.7
3.3	South intermediate Apls	500 - 1000	7.6	7.9	8.3

3.3	South intermediate Apls	1000 - 1500	6.9	7.3	7.7
3.3	South intermediate Apls	> 1500	6.1	6.5	6.8
4.1	North border of the Alps - west part	0 - 500	7.9	8.3	8.6
4.1	North border of the Alps - west part	500 - 1000	7.4	7.8	8.1
4.1	North border of the Alps - west part	1000 - 1500	6.9	7.2	7.6
4.1	North border of the Alps - west part	> 1500	6.2	6.6	6.9
4.2	North border of the Alps - east part	0 - 500	7.7	8.1	8.5
4.2	North border of the Alps - east part	500 - 1000	7.3	7.6	8.0
4.2	North border of the Alps - east part	1000 - 1500	6.7	7.0	7.4
4.2	North border of the Alps - east part	> 1500	6.2	6.5	6.9
5.1	Lower Austria east border of the Alps	0 - 500	7.9	8.2	8.6
5.1	Lower Austria east border of the Alps	500 - 1000	7.4	7.8	8.2
5.1	Lower Austria east border of the Alps	1000 - 1500	6.7	7.1	7.5
5.1	Lower Austria east border of the Alps	> 1500	6.0	6.4	6.8
5.2	Bucklige Welt	0 - 500	7.8	8.2	8.6
5.2	Bucklige Welt	500 - 1000	7.5	7.8	8.2
5.2	Bucklige Welt	1000 - 1500	6.7	7.1	7.5
5.2	Bucklige Welt	> 1500	6.2	6.6	7.0
5.3	East and mid Styrian mountain area	0 - 500	7.7	8.1	8.5
5.3	East and mid Styrian mountain area	500 - 1000	7.3	7.7	8.1
5.3	East and mid Styrian mountain area	1000 - 1500	6.7	7.1	7.5
5.3	East and mid Styrian mountain area	> 1500	6.1	6.5	6.9
5.4	West Styrian mountain area	0 - 500	7.7	8.1	8.5
5.4	West Styrian mountain area	500 - 1000	7.3	7.7	8.1
5.4	West Styrian mountain area	1000 - 1500	6.7	7.1	7.5
5.4	West Styrian mountain area	> 1500	6.2	6.6	7.0
6.1	South border range of Mountains	0 - 500	7.7	8.1	8.5
6.1	South border range of Mountains	500 - 1000	7.5	7.9	8.3
6.1	South border range of Mountains	1000 - 1500	6.9	7.3	7.7
6.1	South border range of Mountains	> 1500	6.4	6.8	7.1
6.2	Basin of Klagenfurt Carinthia	0 - 500	7.7	8.1	8.5

6.2	Basin of Klagenfurt Carinthia	500 - 1000	7.5	7.9	8.3
6.2	Basin of Klagenfurt Carinthia	1000 - 1500	7.2	7.7	7.9
7.1	Northern foothills -west part	0 - 500	7.8	8.2	8.5
7.1	Northern foothills -west part	500 - 1000	7.6	8.0	8.4
7.2	Northern foothills -east part	0 - 500	7.9	8.3	8.7
7.2	Northern foothills -east part	500 - 1000	7.6	8.0	8.4
8.1	Pannonian lowland and hilly country	0 - 500	8.1	8.4	8.9
8.2	Subillyrian hilly and terrace country	0 - 500	7.9	8.3	8.7
8.2	Subillyrian hilly and terrace country	500 - 1000	7.6	8.0	8.4
9.1	Muehlviertel	0 - 500	7.8	8.1	8.5
9.1	Muehlviertel	500 - 1000	7.4	7.7	8.1
9.1	Muehlviertel	1000 - 1500	6.9	7.2	7.6
9.2	Waldviertel	0 - 500	7.7	8.0	8.5
9.2	Waldviertel	500 - 1000	7.4	7.8	8.1
853.01	North Germany lowlands incl -Schleswig Holstein	0 - 500	7.9	8.2	8.5
853.02	North German lowlands excl -Schleswig Holstein	0 - 500	7.8	8.1	8.5
853.03	Middle and East German hill and lowlands	0 - 500	7.9	8.2	8.6
853.03	Middle and East German hill and lowlands	500 - 1000	7.5	7.7	8.2
853.0405	Southwestern Germany	0 - 500	7.9	8.2	8.5
853.0405	Southwestern Germany	500 - 1000	7.6	7.9	8.3
853.0405	Southwestern Germany	1000 - 1500	7.0	7.4	7.7
853.0405	Southwestern Germany	> 1500	6.4	6.7	7.1
853.06	Southeast German hill and mountain region	0 - 500	7.6	8.0	8.3
853.06	Southeast German hill and mountain region	500 - 1000	7.3	7.7	8.0
853.06	Southeast German hill and mountain region	1000 - 1500	6.7	7.1	7.4

Table S4 MAT of seed origin recommended to be optimum by the URF for BA24 [m^2 ha^{-1}] growth performance for each altitudinal sub zone in provenance regionsof Austria and Germany

Zone ID	Zone name	Zone altitude [m]	Recommended MAT of seed origin [°C]		
			current	RCP 4.5 in 2070	RCP 8.5 in 2070
1.1	Central Alps- Continental - Central Zone	500 - 1000	7.04	7.06	7.08
1.1	Central Alps- Continental - Central Zone	1000 - 1500	7.01	7.03	7.06
1.1	Central Alps- Continental - Central Zone	> 1500	6.93	6.95	6.97
1.2	Subcontinental Central Alps - west part	500 - 1000	7.04	7.07	7.09
1.2	Subcontinental Central Alps - west part	1000 - 1500	7.01	7.03	7.05
1.2	Subcontinental Central Alps - west part	> 1500	6.94	6.96	6.98
1.3	Subcontinental Central Alps - east part	500 - 1000	7.03	7.05	7.07
1.3	Subcontinental Central Alps - east part	1000 - 1500	7.00	7.02	7.04
1.3	Subcontinental Central Alps - east part	> 1500	6.95	6.97	6.99
2.1	North intermediate Apls - west part	500 - 1000	7.05	7.07	7.09
2.1	North intermediate Apls - west part	1000 - 1500	7.01	7.03	7.05
2.1	North intermediate Apls - west part	> 1500	6.96	6.98	7.00
2.2	North intermediate Apls - east part	500 - 1000	7.03	7.05	7.07
2.2	North intermediate Apls - east part	1000 - 1500	7.00	7.02	7.04
2.2	North intermediate Apls - east part	> 1500	6.96	6.98	7.00
3.1	East intermediate Alps - north part	0 - 500	7.04	7.06	7.09
3.1	East intermediate Alps - north part	500 - 1000	7.02	7.04	7.07
3.1	East intermediate Alps - north part	1000 - 1500	6.99	7.01	7.04
3.1	East intermediate Alps - north part	> 1500	6.96	6.98	7.00
3.2	East intermediate Alps - south part	0 - 500	7.05	7.07	7.09
3.2	East intermediate Alps - south part	500 - 1000	7.02	7.04	7.07
3.2	East intermediate Alps - south part	1000 - 1500	6.99	7.02	7.04

3.2	East intermediate Alps - south part	> 1500	6.96	6.98	7.00
3.3	South intermediate Apls	0 - 500	7.06	7.08	7.11
3.3	South intermediate Apls	500 - 1000	7.05	7.07	7.09
3.3	South intermediate Apls	1000 - 1500	7.01	7.03	7.05
3.3	South intermediate Apls	> 1500	6.96	6.98	7.00
4.1	North border of the Alps - west part	0 - 500	7.06	7.09	7.11
4.1	North border of the Alps - west part	500 - 1000	7.04	7.06	7.08
4.1	North border of the Alps - west part	1000 - 1500	7.01	7.03	7.05
4.1	North border of the Alps - west part	> 1500	6.97	6.99	7.01
4.2	North border of the Alps - east part	0 - 500	7.06	7.08	7.10
4.2	North border of the Alps - east part	500 - 1000	7.03	7.05	7.07
4.2	North border of the Alps - east part	1000 - 1500	6.99	7.02	7.04
4.2	North border of the Alps - east part	> 1500	6.96	6.99	7.01
5.1	Lower Austria east border of the Alps	0 - 500	7.06	7.08	7.11
5.1	Lower Austria east border of the Alps	500 - 1000	7.04	7.06	7.08
5.1	Lower Austria east border of the Alps	1000 - 1500	7.00	7.02	7.04
5.1	Lower Austria east border of the Alps	> 1500	6.95	6.98	7.00
5.2	Bucklige Welt	0 - 500	7.06	7.08	7.10
5.2	Bucklige Welt	500 - 1000	7.04	7.06	7.08
5.2	Bucklige Welt	1000 - 1500	7.00	7.02	7.04
5.2	Bucklige Welt	> 1500	6.97	6.99	7.01
5.3	East and mid Styrian mountain area	0 - 500	7.06	7.08	7.10
5.3	East and mid Styrian mountain area	500 - 1000	7.03	7.05	7.07
5.3	East and mid Styrian mountain area	1000 - 1500	7.00	7.02	7.04
5.3	East and mid Styrian mountain area	> 1500	6.96	6.98	7.01
5.4	West Styrian mountain area	0 - 500	7.06	7.08	7.10
5.4	West Styrian mountain area	500 - 1000	7.03	7.05	7.07
5.4	West Styrian mountain area	1000 - 1500	7.00	7.02	7.04
5.4	West Styrian mountain area	> 1500	6.97	6.99	7.01
6.1	South border range of Mountains	0 - 500	7.05	7.08	7.10
6.1	South border range of Mountains	500 - 1000	7.04	7.06	7.09

6.1	South border range of Mountains	1000 - 1500	7.01	7.03	7.05
6.1	South border range of Mountains	> 1500	6.98	7.00	7.02
6.2	Basin of Klagenfurt Carinthia	0 - 500	7.05	7.08	7.10
6.2	Basin of Klagenfurt Carinthia	500 - 1000	7.04	7.07	7.09
6.2	Basin of Klagenfurt Carinthia	1000 - 1500	7.03	7.05	7.07
7.1	Northern foothills -west part	0 - 500	7.06	7.08	7.10
7.1	Northern foothills -west part	500 - 1000	7.05	7.07	7.09
7.2	Northern foothills -east part	0 - 500	7.07	7.09	7.11
7.2	Northern foothills -east part	500 - 1000	7.05	7.07	7.09
8.1	Pannonian lowland and hilly country	0 - 500	7.08	7.10	7.12
8.2	Subillyrian hilly and terrace country	0 - 500	7.07	7.09	7.11
8.2	Subillyrian hilly and terrace country	500 - 1000	7.05	7.07	7.09
9.1	Muehlviertel	0 - 500	7.06	7.08	7.10
9.1	Muehlviertel	500 - 1000	7.04	7.06	7.08
9.1	Muehlviertel	1000 - 1500	7.01	7.03	7.05
9.2	Waldviertel	0 - 500	7.05	7.07	7.10
9.2	Waldviertel	500 - 1000	7.04	7.06	7.08
853.01	North Germany lowlands incl -Schleswig Holstein	0 - 500	7.07	7.08	7.10
853.02	North German lowlands excl -Schleswig Holstein	0 - 500	7.06	7.08	7.10
853.03	Middle and East German hill and lowlands	0 - 500	7.07	7.08	7.11
853.03	Middle and East German hill and lowlands	500 - 1000	7.04	7.06	7.08
853.0405	Southwestern Germany	0 - 500	7.06	7.08	7.10
853.0405	Southwestern Germany	500 - 1000	7.05	7.07	7.09
853.0405	Southwestern Germany	1000 - 1500	7.01	7.03	7.06
853.0405	Southwestern Germany	> 1500	6.97	7.00	7.02
853.06	Southeast German hill and mountain region	0 - 500	7.05	7.07	7.09
853.06	Southeast German hill and mountain region	500 - 1000	7.03	7.05	7.07
853.06	Southeast German hill and mountain region	1000 - 1500	7.00	7.02	7.04

Table S5 Seed zones of North America, recommended by the URFs for acquiring planting material for the provenance regions of Austria and Germany. Within each seed zone recommended MAT_p (°C) are given for different altitudinal zones (0-500m; 500-100m, and 1000-1500m). Cells shaded in light gray represent recommended seed zone and altitudinal zone for current climate and cells with dark gray shade represent recommended seed zone under future condition. BC, WA and OR stands for British Columbia, Washington and Oregon respectively. The figures within brackets in the Seed-zones represents the old seed zone number which were merged to form the current seed zone.

		Altitudinal belts (m)		
Seed zone	**State**	**0-500**	**500-1000**	**1000-1500**
M	BC	8.06	7.47	
QNL	BC	6.26	4.5	2.21
GL	BC	9.31		
NE	BC	7.09	5.67	3.3
QL	BC	5.89	3.59	1.83
SM	BC	7.13	4.96	2.67
2 (072,081,082,090,512)	OR	9.32	7.78	5.9
3 (512, 511,321)	OR	11.05	8.91	6.93
4 (061,062,071)	OR	10.77	8.78	6.6
5 (051,052,053)	OR	10.28	8.1	6.34
6 (251,252)	OR	10.23	8.23	6.04
7 (270)	OR	9.84	7.84	5.75
8 (261,262,481)	OR	10.39	8.93	6.03
9 (461,471)	OR		7.28	5.32
10 (491)	OR	10.51	8.58	6.16
11(492)	OR	11.42	9.5	7.5
12 (451,452,462,472)	OR	11.29	9	6.79

13 (463,473,483)	OR	10.85	9.06	7.27
14 (482, 472)	OR		9.18	6.92
15 (493, 501)	OR	10.61	9.01	7.1
16 (502)	OR	11.39	9.54	7.13
CHELAN (600,621)	WA	9.61	6.71	3.79
ELWHA (011,012,221,222)	WA	8.2	6.47	4.36
GRANDE RONDE (852,851)	WA	11.02	8.04	5.29
HOH ((011,012)	WA	8.83	6.79	4.96
ISLANDS (201,202,211,221)	WA	9.15	6.9	4.61
KETTLE (614,801,802,803)	WA	8.42	6.77	4.72
KITSAP (222,231,232,421,422,412,411)	WA	9.86	7.24	4.87
LOWER COLUMBIA(041,042 ,240, 430)	WA	9.83	7.98	5.99
PEND OREILLE (804,813,812,811,822,821,830)	WA	8.42	7.27	5.12
PULLMAN	WA		8.12	6.7
SKAGIT (401,402,403,202,201)	WA	8.82	6.42	3.81
SNOQUALMIE(411,412,421)	WA	8.86	6.78	4.18
TOUTLE (422,430,440)	WA	9.41	7.44	5.09
TWIN HARBORS (030,041)	WA	9.23	7.36	5.24
WHITE SALMON(651, 652, 653,642)	WA	9.53	7.48	5.09
YAKIMA (232,641,631,622)	WA	9.4	6.52	4.15

Table S6 Growth performance (mean of altitudinal sub zones within provenance regions)predicted by the URF for BA24 for the provenance regions of Austria and Germany. The change in growth performance is calculated as change in percentage from the current climate. Top seed stands are cluster of those OECD seed stands which are predicted to yield maximum BA24 in the respective provenance regions.

Country	**Provenance region number**	**Provenance regions**	**BA 24 $[m^2\ ha^{-1}]$**		**Change from current BA24 [%]**				
			Current	**Top seed stands under current climate**	**RCP8.5**		**RCP8.5**		**Top seed stands under RCP 8.5 in 2070**
					2050	**2070**	**2050**	**2070**	
AU	1.3	Subcontinental Central Alps - east part	14.8	CL1, CL2	81.7	107.7	136.5	130.4	CL1, CL2
AU	2.2	North intermediate Apls - east part	15.1	CL1, CL2	89.3	115.7	148	143.2	CL1, CL2
AU	1.2	Subcontinental Central Alps - west part	17.6	CL1, CL2	50.2	63	81.8	69.7	CL1, CL2
AU	1.1	Central Alps-Continental - Central Zone	18.1	CL1, CL2	41.4	49.7	64.9	46.6	CL1, CL2
AU	2.1	North intermediate Apls - west part	18.3	CL1	53	65.2	82.5	74.8	CL1, CL2
AU	3.1	East intermediate Alps - north part	18.3	CL1	94.9	117.6	151.3	136.9	CL1, CL2

AU	3.2	East intermediate Alps - south part	18.5	CL1	89.6	113.1	145.2	134.6	CL1, CL2
AU	4.2	North border of the Alps - east part	19.0	CL1	55	65.8	88.3	74.7	CL1, CL2
AU	5.3	East and mid Styrian mountain area	18.8	CL1	165.8	190.6	258.7	228.8	CL1, CL2
AU	5.1	Lower Austria east border of the Alps	18.9	CL1	51.6	55.1	98.4	73.2	CL1, CL2
AU	5.4	West Styrian mountain area	19.5	CL1	81.5	99.6	123.9	117.5	CL1, CL2
AU	4.1	North border of the Alps - west part	20.9	CL1	35.3	43	52.4	49.6	CL1, CL2
AU	3.3	South intermediate Apls	21.4	CL1	36.5	45.6	55.5	47.9	CL1, CL2
AU	5.2	Bucklige Welt	19.8	CL1, CL2	64.4	69.7	84.8	68.5	CL1, CL2
GE	853-06	Southeast German hill and mountain region	21.7	CL1	20.1	21.2	26.9	8.3	CL1, CL2
AU	6.1	South border range of Mountains	22.4	CL1	29.3	34.3	41.3	35.9	CL1, CL2
GE	853-02	North German lowlands excl -Schleswig Holstein	19.7	CL1	-24.9	-22	-67.7	-82.2	CL1, CL2
AU	8.1	Pannonian lowland and hilly country	22.2	CL1	-42.1	-72.3	-69.9	-82.7	CL1, CL2
GE	853-03	Middle and East German hill and lowlands	21.8	CL1	-25.9	-43.4	-49.4	-80.8	CL1, CL2
GE	853-04/05	Southwestern Germany	23.8	CL1	7.5	-0.3	5.5	-31	CL1, CL2
AU	9.1	Muehlviertel	26.7	CL1	9.3	7.7	10.5	-1.3	CL1, CL2
GE	853-01	North Germany lowlands incl -Schleswig Holstein	26.7	CL1	-14.9	-18.5	-39.9	-93.1	CL1, CL2
AU	6.2	Basin of Klagenfurt Carinthia	29.1	CL1	4.0	2.5	2.8	-11.3	CL1, CL2

AU	7.1	Northern foothills -west part	30.7	CL1	-0.6	-1.9	-3.4	-15.8	CL1, CL2
AU	9.2	Waldviertel	28.9	CL1	-2.2	-10.2	-8.5	-47.2	CL1, CL2
AU	8.2	Subillyrian hilly and terrace country	30.3	CL1	-5.9	-13.4	-13.3	-42	CL1, CL2
AU	7.2	Northern foothills -east part	30.4	CL1, CL2	-4.3	-10.1	-11.1	-35.3	CL1, CL2

AU= Austria and GE= Germany. For explanation of the clusters (CL1, CL2, CL3, CL4) see Table S2.

7.3 Paper III

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[#] Contributed equally

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Title: There and back again: genetic trials enable the transfer of Douglas-fir distribution models across continents

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Abstract

Species distribution models (SDMs) have been widely used to assess the impact of climate change on forest trees and ecosystems services. However, the application of SDMs to novel climate regimes remains a critical challenge. We utilized genotype-specific trait variation of Douglas-fir, introduced as seeds from North America and grown on various sites in Central Europe, to build SDMs for two functional traits (tree height and basal area) and applied them in western North America and Europe. Surprisingly, the accuracy of our models is comparable to the SDMs developed in North America based on presence/absence data or process-based models. Furthermore, our SDMs integrate both environmental and genetic effects and can be used as seed selection and regeneration tools. The models can be applied to identify the best-performing planting stock for any location under current and future climate and to map the most appropriate future habitat for a given seed provenance. Using the optimal seed sources, areas suitable for planting Douglas-fir could increase by 47% for current and 79 - 131% for future climates in Europe, and 59% for current and 42-45% for future climates in North America. Our results suggest that integrating genetic variation of functional traits into SDMs will considerably broaden SDM applications from climate change impact studies to decision-making in forest and conservation management. We recommend establishing more medium and long-term trials for forest tree and endangered plant species to facilitate the integration of intraspecific variation into SDMs.

Keywords: climate change, *Pseudotsuga menziesii*, provenance trial, species distribution model, universal response function

Introduction

Identifying species distribution limits has attracted much attention recently (1–3). Observed past and present changes in species distributions gave rise to questions on causes of range expansions and reductions (4), on potential impacts of climate change on future distribution ranges (5–8), and to discuss consequences of such changes for evolution and biodiversity (9–11). Species distribution models (SDMs) have played a central role in improving our knowledge of distribution limits and interrelations between species and their environment more recently (12, 13). The most important objectives of SDMs are: i) to develop hypotheses about species distribution limits (14); ii) to model changes of distributions in the past and future and its consequences for natural and artificial ecosystems (1, 13); and iii) to develop conservation and management strategies with regard to ongoing global change (2, 15).

SDMs can be roughly classified into i) correlative SDMs, which are based on statistical relationships between appropriate climate variables and the presence/absence of a species, and ii) mechanistic SDMs, where the occurrence of a species is being modeled based on a functional understanding of its physiological, reproductive, or genetic limits (16–18). The underlying concepts define their usability: correlative SDMs model the realized niche including biotic as well as abiotic constraints, whereas mechanistic SDMs are able to describe basically the species' fundamental niche and might be extended by incorporating species interactions, dispersal limitations, or genetic variation if a functional understanding of these processes exists. The major advantage of correlative SDMs is that they can be easily developed from species' presence/absence data and high-resolution environmental data, which have become available in the last decades. However, correlative SDMs have been criticized for being only focusing on the species' current distribution, while under climate change, SDMs are required to identify areas where a species could possibly occur (8). Thus, their potential to be transferred to other regions (19) and applications under novel climates is limited (20). As mechanistic SDMs incorporate the explicit relationships between environmental conditions and selected fitness-related traits, they are independent of currently observed species distributions (21).

In forest tree species, mechanistic SDMs were applied to predict the distribution of single species (18), communities and ecosystems (22, 23), and beyond that, the distribution of continent-wide tree flora (24). Furthermore, the genetic variation of functional traits available from provenance tests and common garden experiments was used to predict the future occurrence and growth performance of tree species (25–28). These studies revealed that accounting for intraspecific genetic variation could potentially buffer effects of climate change on future tree species distributions (27, 29). This is because the cumulative niche of several individual populations or subspecies is wider than that of a generic species (29). However, if in addition to intraspecific variation also the limited migration capacity of trees is being considered, the modeled species distributions in climate change indicate an even more serious risk of species and populations (16). Practically, this implies that the appropriate seed material needs to be selected and transferred within and across current species ranges to overcome the migration lag of trees (30, 31). Such management measures not only require the identification of the climatic constraints on species distributions but a deeper understanding of the environmental drivers for local adaptation (32, 33) in order to avoid maladaptation (34). At present, the wide application of such intraspecific SDMs is limited by the availability of sufficient common garden data and by the difficulty to validate the models for other regions and novel climate regimes.

In a recent study, we developed and evaluated (35, 36) two models for predicting the functional variation of tree height and basal area of the North American Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) for plantations in Central Europe in dependence of climatic drivers. At present, Douglas-fir is considered as one of the most attractive non-native conifers in Europe because it has superior growth performance and excellent wood quality (37). However, climate comparisons suggested that future climate condition in Central Europe might be less suitable for this species and cast doubts on the most appropriate seed sources (38). Our models, the Universal Response Functions (URFs) (26), are based on extensive provenance trial data from Austria and Southern Germany and can be applied at any putative planting site in Europe (36) to predict future growth performance and to identify the most suitable planting stock for reforestation (35). The

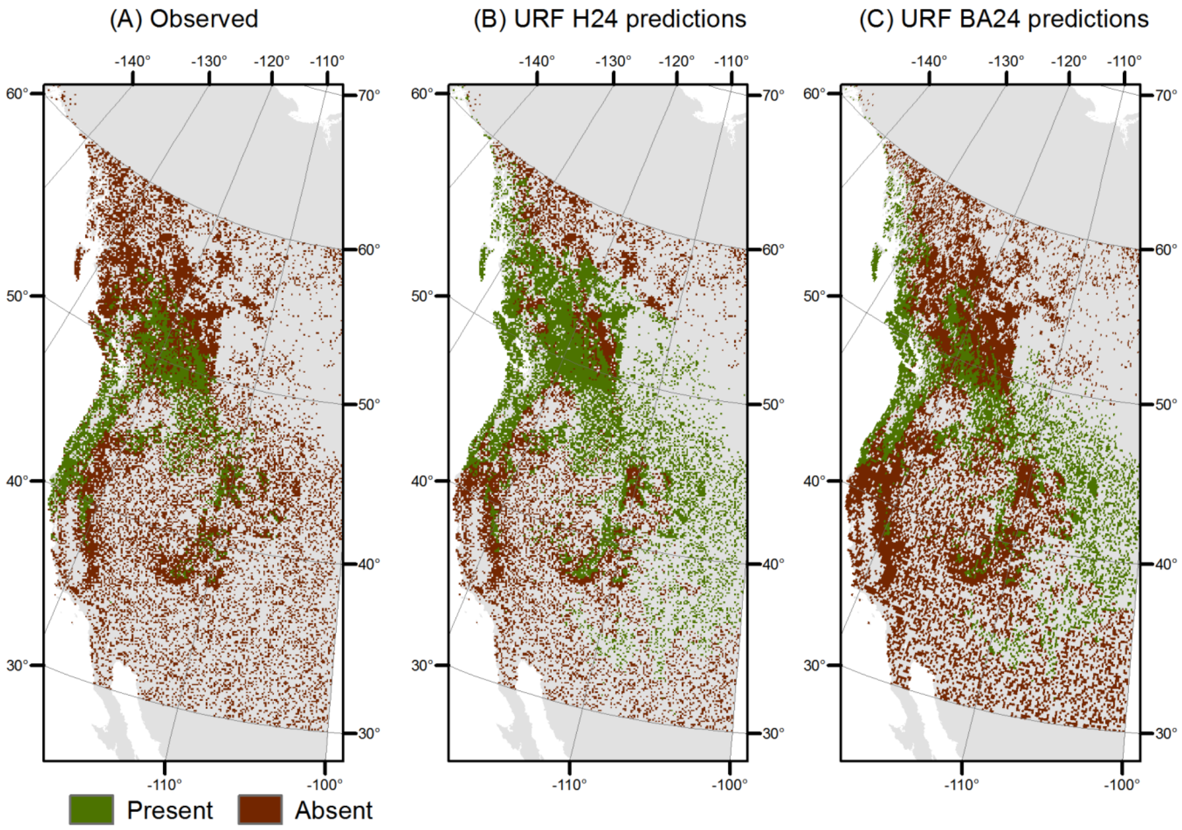
URFs combine the climate of provenance origin (genetic effects) and the climate of planting locations (environmental effects) into an integrated model to predict the respective functional trait from historic and current climate data. By truncating the lower end of the estimated trait response curves, the URFs can be also be used as SDMs to predict the potential distribution of species under climatic change (26).

In this study, we address the following questions: (1) are URF-SDMs developed for Douglas-fir in Europe suitable to predict the distribution of Douglas-fir in its native range in western North America. (2) what is the potential effect of climate change on the natural distribution of Douglas-fir in North America and on the range of suitable plantation sites in Europe? (3) can reforestations with appropriate seed sources help to stabilize potentially eroding distributions in climate change?

Results

Performance of URF-SDMs as distribution model in North America

When we applied our URF-SDMs to predict the occurrence of Douglas-fir at 71,182 inventory plots in western North America, where the species occurred on 12,469 plots, our URF-SDMs predicted the presence of the species at the plots at high accuracies, 85% using the model for tree height and 67% using the model for basal area (Table 1). The plots where Douglas-fir was observed but predicted to be absent (omissions) are mainly located at the trailing edge of the coastal range in California and southern Oregon (Fig. 1). The proportion of observed absences correctly identified by the URFs is 48% and 70% using the URFs for tree height and basal area, respectively (Table 1). The true absences that were misclassified by the models as presences are located in the south and southeast of the Rocky mountains (Fig. 1) and at the northern range limit of the species. Overall, the accuracy of the two SDMs to correctly predict observed presence and absences is 55% (H24) and 70% (BA24) and the model performance represented by the true skill statistics is 0.32 and 0.37, respectively (Table 1). Between the two SDMs, the URF for dominant tree height has lower omission rate but also a higher rate of false positives, while the rate of false positives is reasonable small with the URF for the basal area at the expense of higher omission rate. For all further analysis, we used a combined prediction of presences of both models.



(A) Observed

(B) URF H24 predictions

(C) URF BA24 predictions

Fig. 1 Observed distribution of Douglas-fir in at 71,182 locations (A) and predicted distributions of Douglas-fir using the URF-SDMs for dominant height (H24) and for mean basal area (BA24) in North America.

Table 1. Accuracy of the two URF-SDMs for predicting observed presence/absence at 71182 inventory plots in dataset in western North America.

	H24	**BA24**
Accuracy	0.55	0.70
Sensitivity	0.85	0.67
Specificity	0.48	0.70
True Skill Statistics	0.32	0.37
URF-H24 predicts absent but URF-BA24 predicts present	0.00	
URF-H24 predicts present but URF-BA24 predicts absent	0.24	

Accuracy = the proportion of the presence and absence records correctly identified by the model
Sensitivity = the proportion of true presences correctly identified by the model
Specificity = the proportion of true absences correctly identified by the model
True Skill statistics = measure of model performance independent of prevalence. TSS value range from -1 to +1 where +1 indicate perfect agreement and values <=0 indicate a performance equivalent to random guess (57).

Modeled distribution of Douglas-fir in western North America

When we applied our model to western North America, 1.75 M km² are predicted to be suitable plantation area under current climate if local seed sources are being utilized (Table 2). In climate change, the suitable area for Douglas-fir increases up to 22 % mainly due to improved growing conditions at the Northern edge of the distribution (Fig. 2). Across the various biogeographic regions, the highest increase is predicted for the prairie, the subarctic and the warm continental mountains (Table S1 in Supporting Information). On the other hand, suitable area in the coastal and western cascade range of Oregon and Washington which is the most important production area of Douglas-fir in North America is predicted to decline up to 74% under the RCP 8.5 scenario if local provenances are being planted. This decline of Douglas-fir could be mitigated by planting trees from alternative provenances. In Oregon and Washington approximately 30 000 km² of Douglas-fir forests could be sustained if alternative provenances are selected as seed sources using our optimum height model (Fig. 2 D-F, Table S2 in Supporting Information). Across western North America, optimum seed selection would gain 45% and 42% land area under the RCP4.5 and RCP8.5 scenario, respectively, in comparison to local seed deployment schemes (Table 2).

Table 2. Climatically suitable area for Douglas-fir forests in western North America and Europe under current climate and for two climate change scenarios (RCP 4.5 & RCP 8.5) as predicted by the URF-SDM for tree height. Two seed provenance selection schemes are being applied and the gains of plantation area by using optimum seed source selection are shown. See TableS1, S2 and S3 for specific regions.

	Seed selection scheme*	**Current climate**	**RCP 4.5**	**RCP 8.5**
North America	Local seed sources	1.75 M km^2	2.04 M km^2 (+16.4%)	2.14 M km^2 (+22.3%)
	Optimum seed sources	2.78 M km^2	2.95 M km^2 (+6.3%)	3.04 M km^2 (+9,5%)
	Gains of area	58.7 %	44.9 %	42.1 %
Europe	Analogous	4.20 M km^2	3.28 M km^2 (-10%)	2.45 M km^2 (-11%)
	Optimum seed sources	6.15 M km^2	5.85 M km^2 (-3%)	5.64 M km^2 (-6%)
	Gains of area	46.6 %	78.5 %	130.8 %

* Local seed sources in North America and analogous seed sources in Europe refer to provenances that originate from climatically identical locations as the intended planting sites. Optimum seed sources yield the maximum growth performance at the particular site and were identified by solving the partial derivate of the URF function for MAT_p.

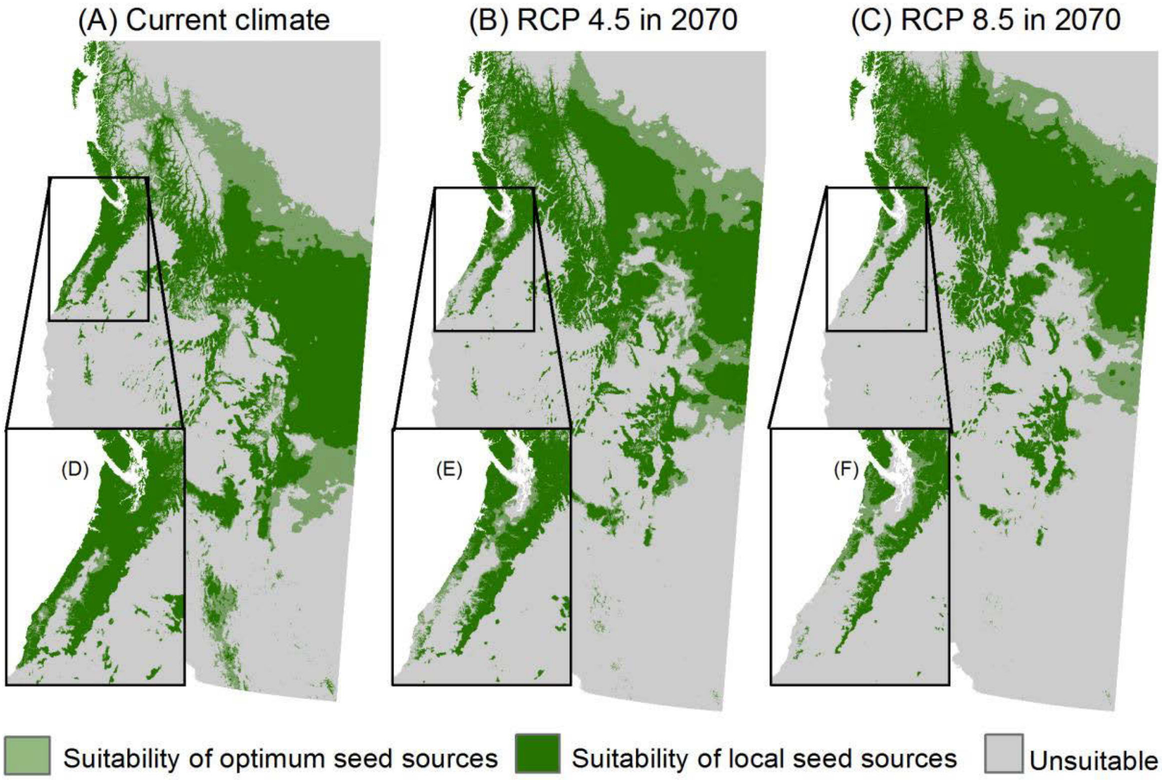


Fig. 2 Predicted distribution of Douglas-fir in Western North America under current climate (A) and two climate change scenarios in 2070 (B, C). The suitable habitats shown in dark green represent the areas where climates match the climates of local seed sources. Areas in light green represent the gain in suitable habitats if the optimum seed sources were identified by the URF-SDMs. Details of the trailing edge in its coastal range are shown in D, E, F.

Suitable plantation areas in Europe

At present, 70% of the total geographic area of Europe is predicted to be climatically suitable for Douglas-fir if optimum seed sources are to be used (Fig. 3, Table 2, Table S3 in Supporting Information). This area also comprises the locations of continent-wide provenance trials (38). Among different biogeographic regions, the area suitable for Douglas-fir plantations ranges from 17 % in Anatolian to 100% in the Pannonian region (Fig. 3, Table S3 in Supporting Information). Under climate change, the suitable area is expected to decrease by up to 11% (Table 2). The highest losses of suitable area are predicted for the Steppic region (by up to –90%) and the Mediterranean region (by up to

–78%) while huge parts of the Boreal (by up to +51%) and Alpine region (+44%) will become more suitable for Douglas-fir cultivation until 2070 (Table S3).

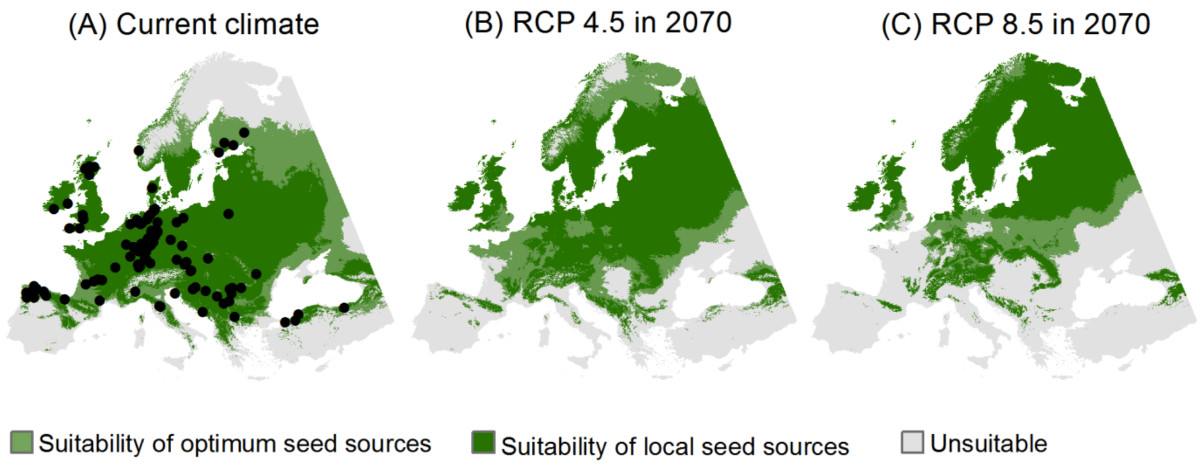


Fig. 3 Predicted potential distribution of Douglas-fir in Europe under current climate (A) and two climate change scenarios in 2070 (B, C). The suitable habitats shown in dark green represents seed sources selected on the basis of similarity of climate between North America and Europe. Areas in light green represent the gain in suitable habitats if the optimum seed sources were identified by the URF-SDMs. Black dots in (A) mark the locations of successful provenance trials across Europe (38)

Areas suitable for plantations of this species for present and future would strongly depend on the selection of seed sources. If European plantations are to be established with seeds originating from climatically analogous regions in North America, only 48% of the total geographic area of Europe is predicted to be suitable for Douglas-fir at present. This area is 31% smaller compared to the scenario when optimum seed sources are planted (Fig. 4, Table 2). In climate change, the suitable area with climatically analogous provenances would be about 57% smaller than that with optimum seed sources to be used. In particular, almost no suitable areas would be available for planting this species in the Mediterranean, the Pannonic and the Steppic region if consider using climatically analogous seed sources instead of selecting the best-performing ones.

Discussion

Predicting species distributions is crucial for understanding the impacts of climate change on ecosystems and for developing effective adaptation strategies. One of the major challenges of distribution modeling is the model evaluation and application to novel, non-analogous climate regimes outside of the species present environment. Present climates will at least partly disappear and future condition will constitute new combinations of annual and seasonal climate factors (39, 40). Our study, to our best knowledge, is the first successful application of SDMs across continents and to non-analogous climate. Developed based on genotype-specific growth data of the non-native Douglas-fir in Central Europe, our URF-SDMs show a surprisingly high accuracy, comparable to the SDMs developed in North America based on range-wide presence/absence data (28, 41) or physiological process-based growth models (23). The overall accuracy of our models to correctly identify presence and absence of Douglas-fir in North America ranged from 54 to 68 percent and is close to the accuracy level of 73% found by (23) or 86% of (41), where the latter studies require a higher number of climate predictors (n=16 in case of (23) and n=8 in case of (41)) than our prediction of functional traits with an environmental-genetic model (n=3). The accuracy of our model is also higher than a recent attempt to predict distribution of Douglas-fir with a dynamic process-based ecosystem model (17) reiterating the discussion on whether model complexity leads to prediction accuracy (42). The URF's success rate for predicting presence is higher than that of absence indicating the usefulness of the URFs in identifying the climatic suitability of Douglas-fir growing in its natural range in North America and elsewhere. Hence, the URFs can also be used to identify present and future climate suitability of Douglas-fir in Europe or in other plantation areas worldwide (37).

The high accuracy of our URFs in predicting its native range in North America, even though the models were developed with data from Europe, is probably a result of its underlying fundamental niche approach. The URF approach integrates both genetic and environmental effects into a single function to predict the effect of climate on the performance of populations originated from and planted at various climate conditions (26) . When it is used to develop a SDM, it predicts fundamental niche of a species. Due to the integrated use of climate variables from both seed sources and planting sites, the URF model has considerably reduced its dependence on a large sample size (26). The high accuracy of our URF models indicate that the observed data from the provenance trials in Austria and southern Germany alone have trained our URF models to well reflect the fundamental niche of this species in both North America and Europe, and probably some other part of the world as well. The present limitations of our URFs to predict the coastal range of Douglas-fir in California and to match observed absences at the species northern limit is likely caused by missing seed provenances from California and northern BC in the European trial sites. Also, none of the European test sites experienced similar cold conditions as occurring in northern BC and this might result in an overestimation of the species growth potential at the northern limits were absolute temperature minimum and frost restricts the species occurrence (23, 43). These restrictions underpin known limitations of historic common garden trials where provenances from the entire natural range were not consistently tested and climatically extreme trial sites at or beyond the species range limits were not established (44, 45). While current provenance trials were established for foresters to select the most productive planting stock, future trial series should rather aim at achieving a better understanding of the species specific climate constraints and the correlations between functional trait variation and the environmental conditions of test sites and seed sources. Such trials should be carefully designed with provenances from the entire climatic range and test sites established including locations outside of the species range. Thanks to the availability of gridded climate data and the URF approach, such trial series can be achieved with fewer provenances planted on less trial sites without affecting the prediction accuracy of the models (26). For forest trees, new trials will be able to provide meaningful data within 15 to 20 years. Also, for endangered annual and smaller perennial plants, such trials can deliver data for building URF-SDMs in a few years (46, 47). If such URFs also integrate additional functional traits (wood characteristics, phenological observations, etc.) they will certainly allow more specific risk-benefit analysis of assisted migration and gene flow measures (30), which is strongly required to transfer scientific knowledge into practical management. Moreover, new trials and sophisticated models will improve our understanding of the genetic basis of adaptive capacity of populations and species (48, 49)

More important than the definitive accuracy of any SDM are its potential application in climate change adaptation. Correlative SDMs based on presence/absence data allow to identify putative retraction areas at species trailing edges and expansion areas at the species leading edges (13) and thus may be used to identify vulnerable populations, species or ecosystems and potential new habitats (26, 50). However, for concrete recommendations of seed transfer either into novel climates or within the species current range, correlative SDMs are rather unsuitable. The same is true for mechanistic SDMs as they rarely address the intraspecific variation of the underlying physiological principles and come at a higher cost of calibration (17). In contrast, URFs explicitly consider genetic variations and are able to predict the future performance of single populations. This advantage can be used in two directions (26): first, to identify the best-performing provenance planting stock for any given planting site under current climate and any climate change scenario; and second, to identify the most appropriate future habitat for a given seed provenance. The first option is important for forest and restoration managers, as they are interested in increasing productivity of future forests or the stability and long-term persistence of the managed ecosystems. Forest trees are often foundation species for a specific ecosystem, a change to better adapted genetic materials of the same species might be favored against a complete change in species composition that may result in cascading changes of the forest communities. The second option is the perspective of a genetic conservation manager, searching for new habitat for endangered local populations. If we apply the URFs for western North America, in searching for the optimum planting stock, we would be able to gain 59% potential habitat for Douglas-fir under present conditions and up to 45% in climate change if we compare it to local seed deployment schemes (Table 2). A similar result was obtained for Europe, where provenance selection via URFs would result in 6.2 M km² suitable sites while provenance selection according to climate analogy allows only 4.2 M km² to be utilized. This difference is projected to be even greater in future climates because the areas suitable for planting this species would decline within the most ecotypes of Europe, which is in contrast to western North America. With optimal provenance selection, this decline can be limited to 5-8 %, whereas reforestations with climatically-analogous populations would result in a loss of 22-42% of the suitable land area.

To our knowledge only few studies till date attempts to estimate the utilization and potential distribution of Douglas-fir in Europe (17, 38, 51). Brus et al. (2012) used a limited number of Douglas-fir presence/absence in Europe and predicted substantially smaller distribution than that predicted by the URFs, likely because the small number of presence locations did not capture the physiological limits of the species. On the other hand, Isaac-Renton et al. (2014) applied a Random Forest ensemble classifier trained with climate data of North American provenance groups and obtained a similar potential distribution in Europe as our URF-SDM. However, when compared to provenance plot data, the Random forest model (38) failed to predict the optimal provenances for Eastern Europe and would result in erroneous seed recommendation. This is in contrast to our URFs, which were found to show a reasonable performance in particular if being applied within a warmer and drier climate (35), further highlighting the potential of URFs as tools for conservation and ecosystem management in climate change.

Materials and Methods

Universal response functions as SDMs

Universal response functions (URFs) were developed from tree growth data of 50 provenance trials in Austria and southern Germany that included 290 provenances of Douglas-fir and measurements from in total 77,000 trees. From these trials, two functional traits, the dominant tree height at age 24 (H24) and the mean basal area per ha (BA24) were used as response variables of the URFs (35, 36). URFs are quadratic models (eq. 1) relating each one of these functional traits to the climate of the trial locations in Central Europe and the climate of the seed origin in North America. Significant climate predictors were selected using a multimodel approach (52–54) on a set of 10 climate variables from both the trial locations and the seed origin resulting into the following response model:

$$\mathrm{Y}_{sp} = b_o + b_1\mathrm{MAT_s} + b_2\mathrm{MAT_s}^2 + b_3\mathrm{SHM_s} + b_4\mathrm{SHM_s}^2 + b_5\mathrm{MAT_p} + b_6\mathrm{MAT_p}^2 + b_7\mathrm{MAT_s} * \mathrm{MAT_p} + e_{sp}$$

Here, Y_{sp} is the growth performance (either H24 or BA24) of the provenances p at the trial sites s; $\mathrm{MAT_s}$ and $\mathrm{SHM_s}$ are the mean annual temperature and the summer heat moisture index of trial locations; MAT_p is the mean annual temperature of provenance origin; b_0 to b_8 are the intercept and regression coefficients, and e_{sp} is the residual error. The coefficients of the two URFs which can be found in (Table 3).

Growth estimates were converted to occurrence (presence/absence) by truncating the URFs with various growth thresholds ranging from 2 to 15 m in the case of H24 and from 2 to 15m^2ha^{-1} for BA24. These thresholds were tested for their effect on the obtained model sensitivity, specificity, accuracy and true skill statistics (TSS). Finally, we selected thresholds of ≥ 3m for H24 and ≥ 2m^2ha^{-1} for BA24 as they represent the observed minima of dominant height and basal area in our data set and were found to result in reasonable sensitivity values and are located within the optimum range of TSS (Fig. S1 in supporting information). The resultant SDMs were named as URF-SDMs

Table 3. Results of multiple regression analysis predicting dominant height at age 24 and basal area at age 24 of Douglas-fir populations from site and seed origin climate as independent variables in a Universal Response Function (URF). Partial R^2 refers to drop in R^2 of the full model when the climate variable is removed from the full URF model.

Independent variables	**Parameter estimate**	**St error**	**95% Confidence interval**		***p-value***	**Partial R^2**
URF for dominant tree height (H24) [m]						
Intercept	-19.280	0.163	-19.598	-18.959	<0.001	
MAT_s	6.204	0.037	6.131	6.277	<0.001	0.084
$MAT_s{}^2$	-0.443	0.003	-0.448	-0.438	<0.001	0.084
SHM_s	0.442	0.006	0.430	0.454	<0.001	0.015
SHM_s^2	-0.005	0.000	-0.005	-0.004	<0.001	0.017
MAT_p	1.517	0.022	1.474	1.561	<0.001	0.014
MAT_p^2	-0.133	0.001	-0.136	-0.131	<0.001	0.036
MAT_s*MAT_p	0.068	0.002	0.064	0.071	<0.001	0.004
Model R^2adj				0.87		
URF for basal area (BA24) [m²ha^{-1}]						
Intercept	-41.810	1.017	-43.80	-39.81	<0.001	
MAT_s	10.890	0.237	10.42	11.35	<0.001	0.0991
$MAT_s{}^2$	-0.636	0.017	-0.67	-0.60	<0.001	0.0627
SHM_s	0.547	0.039	0.47	0.62	<0.001	0.0093
SHM_s^2	-0.007	0.000	-0.008	-0.006	<0.001	0.0145
MAT_p	3.839	0.130	3.58	4.09	<0.001	0.0410
MAT_p^2	-0.241	0.008	-0.25	-0.22	<0.001	0.0479
MAT_s*MAT_p	-0.028	0.011	-0.04	-0.007	<0.001	0.0003
Model R^2adj				0.88		

MAT_s = Mean annual temperature of planting site
SHM_s = Summer heat moisture Index (Mean temperature of Warmest month/ (Mean summer temperature (May-Sep)/1000))
MAT_p = mean annual temperature of seed origin

Model evaluation in North America

We obtained occurrence data (presence and absence) of Douglas-fir at 71,182 inventory plots (Fig1. A), across North America from (23, 55). Out of the 71,182 plots Douglas - fir's presence was observed in 12,469 plots and absence in 58,713 plots. In order to evaluate the URF-SDMs for H24 and BA24 in North America, we applied them at each of the 71,182 locations of the mapped species occurrence data. Climate data for these applications were obtained from ClimateWNA (56). As our main interest was to test the URFs for its usage with locally adapted provenances, the climate of the presence/absence locations (MAT_s) was set equal to the climate of the putatively stocking provenances (MAT_p) at any particular location of the occurrence data set. Model performance was quantified by *sensitivity* which is the proportion of true presences correctly identified by the model, and *specificity* the proportion of true absences correctly identified by the model. The overall model performance was quantified with True skill statistics (TSS) also known as Hansen Knuipers discriminant (57) and the *accuracy*, which is the proportion of the presence and absence records correctly identified by the model. TSS is independent of the size of the data and the prevalence of the species and accounts for both commission and omission errors (57).

Predicting distributions in North America and Europe under climate change

Although Douglas-fir is the most successful tree introduction into Europe, it is being discussed whether present plantation areas might still be suitable in global warming and to where future plantation might be expanded. Also, the species' natural distribution in western North America is predicted to be altered in climate change. Thus, the two URFs were applied both in western North America and across Europe for each grid cell of a 30 arc-sec climate projection obtained from the WorldClim database (58). Climate data were obtained for –current climate" (average for 1950–2000) and two time slices of a transient climate change scenario (–2050" as average for the period 2041–2060 and –2070" as average for the period 2061–2080) from a run of the MPI-ESL-LR climate model (59) under Representative Concentration Pathways RCPs 8.5 and RCP 4.5 (60). Douglas-fir was considered to be suitable if both URF-SDMs for H24 and BA24 predict presence according to the thresholds defined above. As the model for H24 includes also all predictions for presences of the model for BA24, the combined model is equal to the predictions of URF-SDM for BA24 and was thus used for further analysis.

Effects of intraspecific variation on species distribution in future climate

In order to demonstrate the capacity of the URFs to account for intraspecific variation in the species distribution, we estimated Douglas-fir distributions in Europe and North America with two scenarios of seed origin: i) with local seed sources, and ii) with optimum seed sources planted in each grid-cell. Local seed sources refer to provenances that originate from climatically identical locations as the intended planting sites (i.e. by substituting $MAT_p = MAT_s$ in the URF equation as in the validation analysis). Optimum seed sources are those provenances that yield the maximum growth performance when planted at a particular site (i.e. grid cell). Optimum seed sources were identified by solving the partial derivate of the URF function for MAT_p (for details see (36). For concise reporting, climate suitability of Douglas-fir was obtained for each biogeographic region of Europe and North America (Fig. S2 and S3 in Supporting Information).

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Supporting Information

There and back again: genetic trials enable the transfer of Douglas-fir distribution models across continents

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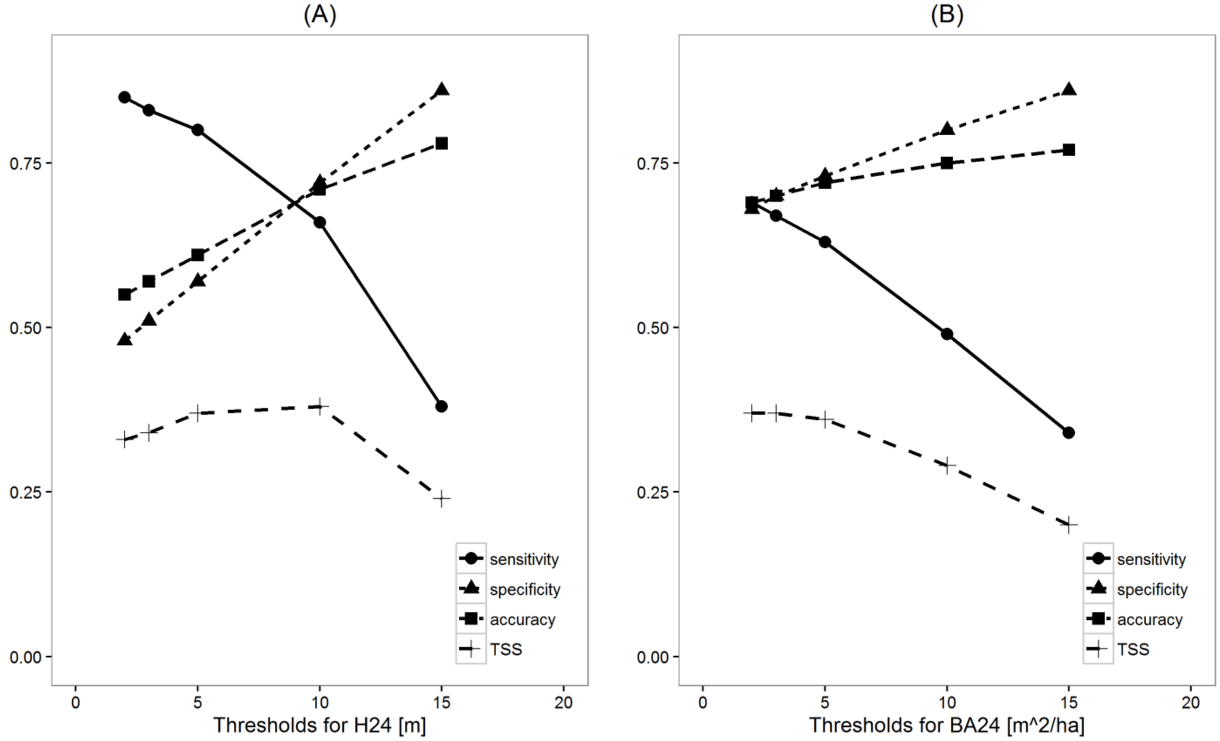

Fig. S1. Change in model accuracy due to selection of different thresholds for converting growth response to occurrence.

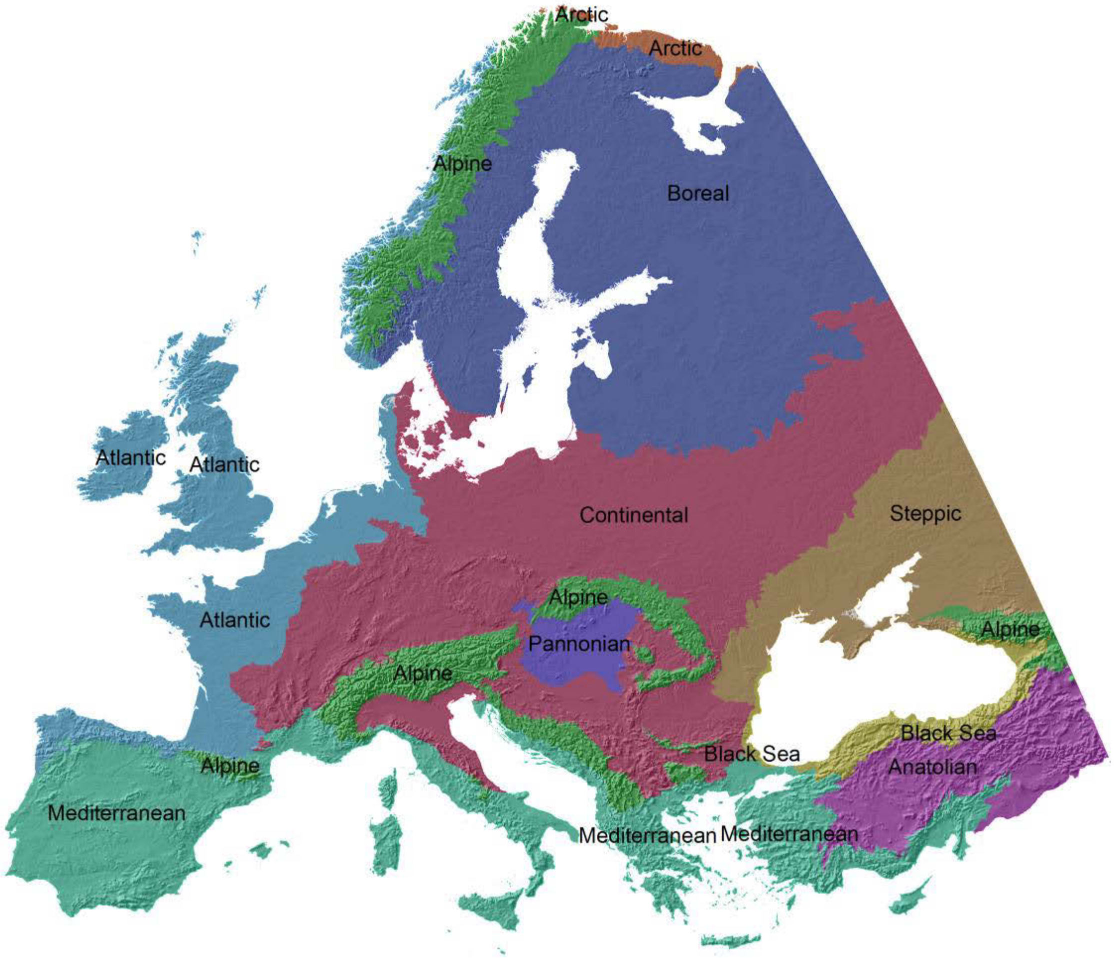

Fig. S2. Biogeographic regions of Europe according to European Environment Agency. Source: http://www.eea.europa.eu/data-and-maps/data/digital-map-of-european-ecological-regions

Fig. S3. Biogeographic regions of North America according to USPEA. Source: https://archive.epa.gov/wed/ecoregions/web/html/na_eco.html#LevelI

Table S1. Climate suitability of Douglas-fir in each of the biogeographic regions of North America (See Fig. S2) predicted by the URF-SDMs under two seed origin scenarios (optimum and local seed origin) and two climate change scenarios (RCP 4.5 and RCP 8.5).

		Area climatically suitable for Douglas-fir [Km^2]			**Percentage of the total geographic area of the region, climatically suitable for Douglas-fir[%]**			**Change of suitable area from current climate [%]**	
	Region	**Current**	**RCP 4.5 in 2070**	**RCP 8.5 in 2070**	**Current**	**RCP 4.5 in 2070**	**RCP 8.5 in 2070**	**RCP 4.5 in 2070**	**RCP 8.5 in 2071**
Optimum seed sources	Marine Division	39655	26750	16669	88.7	59.8	37.3	-32.5	-58.0
	Marine Mountains	294113	328592	335794	59.2	66.1	67.6	11.7	14.2
	Mediterranean Division	1509	275	0	1.3	0.2	0.0	-81.8	-100.0
	Mediterranean Mountains	25025	11394	3141	8.0	3.7	1.0	-54.5	-87.4
	Prairie Division	49407	129241	129241	38.2	100.0	100.0	161.6	161.6
	Savanna Division	0	0	0	0.0	0.0	0.0	0.0	0.0
	Savanna Mountains	24273	1436	148	31.8	1.9	0.2	-94.1	-99.4
	Subarctic Division	73020	429321	627764	3.8	22.1	32.4	0.0	0.0
	Subarctic Mountains	11124	73972	181707	1.0	6.4	15.8	565.0	1533.5
	Temperate Desert Division	66504	33019	18735	8.9	4.4	2.5	-50.4	-71.8
	Temperate Desert Mountains	29779	20719	11201	23.7	16.5	8.9	-30.4	-62.4
	Temperate Steppe Division	1071810	813559	614054	93.5	71.0	53.6	-24.1	-42.7
	Temperate Steppe Mountains	564411	630018	595549	65.6	73.3	69.3	11.6	5.5
	Tropical/Subtropical Desert Division	48618	3911	1524	4.0	0.3	0.1	-92.0	-96.9
	Tropical/Subtropical Desert Mountains	44596	5173	789	25.7	3.0	0.5	-88.4	-98.2
	Tropical/Subtropical Steppe Division	114335	13225	3321	21.3	2.5	0.6	-88.4	-97.1
	Tropical/Subtropical Steppe Mountains	114614	63904	29513	64.0	35.7	16.5	-44.2	-74.3
	Tundra Division	19738	60870	132515	2.7	8.4	18.3	208.4	571.4
	Tundra Mountains	30614	56087	73550	7.5	13.7	18.0	83.2	140.2
	Warm Continental Mountains	152108	248573	263111	49.7	81.2	86.0	63.4	73.0
	Total	**2775253**	**2950039**	**3038326**	**25.8**	**27.4**	**28.2**	**6.3**	**9.5**

Analogous/ Local seed sources	Marine Division	34068	15654	7422	76.2	35.0	16.6	-54.1	-78.2
	Marine Mountains	223795	274654	278185	45.0	55.3	56.0	22.7	24.3
	Mediterranean Division	1130	1	0	0.9	0.0	0.0	-99.9	-100.0
	Mediterranean Mountains	16913	5812	1370	5.4	1.9	0.4	-65.6	-91.9
	Prairie Division	2450	98130	129233	1.9	75.9	100.0	3905.3	5174.8
	Savanna Division	0	0	0	0.0	0.0	0.0	0.0	0.0
	Savanna Mountains	4354	30	2	5.7	0.0	0.0	-99.3	-100.0
	Subarctic Division	0	161652	369588	0.0	8.3	19.1	0.0	0.0
	Subarctic Mountains	1368	29935	67535	0.1	2.6	5.9	2088.2	4836.8
	Temperate Desert Division	47188	23316	12970	6.3	3.1	1.7	-50.6	-72.5
	Temperate Desert Mountains	20747	15970	8315	16.5	12.7	6.6	-23.0	-59.9
	Temperate Steppe Division	806484	576280	409496	70.3	50.3	35.7	-28.5	-49.2
	Temperate Steppe Mountains	388099	517168	499213	45.1	60.1	58.1	33.3	28.6
	Tropical/Subtropical Desert Division	10687	1365	626	0.9	0.1	0.1	-87.2	-94.1
	Tropical/Subtropical Desert Mountains	17307	318	21	10.0	0.2	0.0	-98.2	-99.9
	Tropical/Subtropical Steppe Division	24415	4257	1543	4.6	0.8	0.3	-82.6	-93.7
	Tropical/Subtropical Steppe Mountains	86894	34241	14184	48.5	19.1	7.9	-60.6	-83.7
	Tundra Division	4777	51494	62580	0.7	7.1	8.7	978.0	1210.0
	Tundra Mountains	13416	37809	56592	3.3	9.2	13.8	181.8	321.8
	Warm Continental Mountains	44705	187729	219228	14.6	61.3	71.6	319.9	390.4
	Total	**1748797**	**2035815**	**2138103**	**16.2**	**18.9**	**19.9**	**16.4**	**22.3**

Table S2. Climate suitability of Douglas-fir in the coastal region (Washington and Oregon predicted by the URF-SDMs under two seed origin scenarios (optimum and local /analogous seed origin) and two climate change scenarios (RCP 4.5 and RCP 8.5).

		Area climatically suitable for Douglas-fir [Km^2]			**Percentage of the total geographic area [%] climatically suitable for Douglas-fir**			**Change of suitable area from current climate [%]**	
	States	Current	RCP 4.5 in 2070	RCP 8.5 in 2071	Current	RCP 4.5 in 2070	RCP 8.5 in 2070	RCP 4.5 in 2070	RCP 8.5 in 2070
Optimum	Oregon	94978	55974	32233	36.0	21.2	12.2	-41.1	-66.1
	Washington	93008	79808	64008	52.8	45.3	36.4	-14.2	-31.2
	Total	187986	135782	96241	42.8	30.9	21.9	-27.8	-48.8
Analogous	Oregon	76463	37580	20215	29.02	14.26	7.67	-50.85	-73.56
	Washington	83781	64485	45504	47.60	36.64	25.85	-23.03	-45.69
	Total	160244	102065	65719	36.46	23.22	14.95	-36.31	-58.99

Table S3. Climate suitability of Douglas-fir in within each biogeographic region of Europe (see Fig. S1) predicted by the URF-SDMs under two seed origin scenarios (optimum and local seed origin) and two climate change scenarios (RCP 4.5 and RCP 8.5).

		Area climatically suitable for Douglas-fir [km^2]			**Percentage of the total geographic area [%] climatically suitable for Douglas-fir**			**Change of suitable area from current climate [%]**	
	Region	current	RCP 4.5 in 2070	RCP. 8.5 in 2070	current	RCP 4.5 in 2070	RCP. 8.5 in 2070	RCP 4.5 in2070	RCP. 8.5in 2070
Optimum seed sources	Alpine	424489	601783	609954	55.46	78.62	79.69	41.77	43.69
	Anatolian	73184	34463	32500	16.77	7.90	7.45	-52.91	-55.59
	Atlantic	856850	696898	664294	98.24	79.90	76.16	-18.67	-22.47
	Black Sea	113542	41912	37349	78.40	28.94	25.79	-63.09	-67.11
	Boreal	1406769	2115471	2121457	66.00	99.24	99.52	50.38	50.80
	Continental	2321826	2082477	2011354	99.24	89.01	85.97	-10.31	-13.37
	Mediterranean	281190	75199	62498	22.99	6.15	5.11	-73.26	-77.77
	Pannonian	134167	67802	50180	100.00	50.54	37.40	-49.46	-62.60
	Steppic	538116	133601	54639	82.92	20.59	8.42	-75.17	-89.85
	Total	6150131	5849604	5644223	71	67	65	-4.88	-8.22
Analogous/Local seed sources	Alpine	296836	355934	493818	38.78	46.50	64.51	19.91	66.36
	Anatolian	9926	1466	1127	2.27	0.34	0.26	-85.23	-88.65
	Atlantic	689540	410885	340054	79.06	47.11	38.99	-40.41	-50.68
	Black Sea	54288	11720	8164	37.48	8.09	5.64	-78.41	-84.96
	Boreal	636090	1037437	1019403	29.84	48.67	47.82	63.10	60.26
	Continental	2073890	1433751	575049	88.64	61.28	24.58	-30.87	-72.27
	Mediterranean	122746	18740	4498	10.04	1.53	0.37	-84.73	-96.34
	Pannonian	131996	1710	247	98.38	1.27	0.18	-98.70	-99.81
	Steppic	180050	5311	2997	27.74	0.82	0.46	-97.05	-98.34
	Total	4195360	3276951	2445356	48	38	28	-21.89	-41.71