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Research

Genetic trials improve the transfer of Douglas-fir distribution models across continents

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Climate change is likely to result in novel conditions with no analogy to current climate. Therefore, the application of species distribution models (SDMs) based on the correlation between observed species' occurrence and their environment is questionable and calls for a better understanding of the traits that determine species occurrence. Here, we compared two intraspecific, trait-based SDMs with occurrence-based SDMs, all developed from European data, and analyzed their transferability to the native range of Douglas-fir in North America.

With data from 50 provenance trials of Douglas-fir in central Europe multivariate universal response functions (URFs) were developed for two functional traits (dominant tree height and basal area) which are good indicators of growth and vitality under given environmental conditions. These trials included 290 North American provenances of Douglas-fir. The URFs combine genetic effects i.e. the climate of provenance origin and environmental effects, i.e. the climate of planting locations into an integrated model to predict the respective functional trait from climate data. The URFs were applied as SDMs (URF-SDMs) by converting growth performances into occurrence. For comparison, an ensemble occurrence-based SDM was developed and block cross validated with the BIOMOD2 modeling platform utilizing the observed occurrence of Douglas-fir in Europe. The two trait based SDMs and the occurrence-based SDM, all calibrated with data from Europe, were applied to predict the known distribution of Douglas-fir in its introduced and native range in Europe and North America.

Both models performed well within their calibration range in Europe, but model transfer to its native range in North America was superior in case of the URF-SDMs showing similar predictive power as SDMs developed in North America itself. The high transferability of the URF-SDMs is a testimony of their applicability under novel climatic conditions highlighting the role of intraspecific trait variation for adaptation planning in climate change.

Keywords: climate change, species distribution model, transferability

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Introduction

Change in species composition and diversity due to unintended invasion and intended human aided transport of species beyond their native ranges is a major component of global environmental change. Particularly for long-living organisms such as forest trees, the rate of adaptation is likely to be slower compared to the rate of climate change leading to adaptation lags or even extinction (Aitken et al. 2008, Aitken and Bemmels 2015). As such, there has been considerable interest in developing models to aid our understanding of species distribution limits (Sykes et al. 1996, Zimmermann et al. 2010, Guisan et al. 2013). These models are generally termed as species distribution models (SDMs) or niche models and are applied to 1) develop and test hypotheses about species distribution limits (Kreyling et al. 2015); 2) reconstruct changes of species distributions in the past, 3) predict species range in the future, and the consequences thereof for natural and artificial ecosystems (Sykes et al. 1996, Thuiller et al. 2008); and 4) develop conservation and management strategies with regard to ongoing climate change (Guisan et al. 2013, Hamann and Aitken 2013).

SDMs are often classified into 1) occurrence-based SDMs, which are based on statistical relationships between appropriate climate variables and the occurrence of a species (Guisan et al. 2013), and 2) mechanistic or trait-based SDMs, where the occurrence of a species is modeled based on a functional understanding of its physiological, reproductive, or genetic limits (Higgins et al. 2012, Valladares et al. 2014, Gutiérrez et al. 2016). An in-depth review of major SDM approaches however found that the differences between the occurrence and trait-based SDMs are not strictly dichotomous and some approaches are more mechanistic than correlative and vice versa (Dormann et al. 2012). Moreover, the distinction between various model types is often rooted in the kind of niche estimated by the respective model rather than in technical or methodological differences (Pearson et al. 2006, Dormann et al. 2012, Peterson et al. 2015, Shabani et al. 2016). Principally, occurrence-based SDMs represent the realized niche including abiotic as well as biotic constraints, whereas trait-based SDMs preferentially describe the species' fundamental niche and might incorporate species interactions, dispersal limitations, or genetic variation if a functional understanding of these processes exists (Kearney and Porter 2009, Kearney et al. 2010, Peterson et al. 2015).

Occurrence-based SDMs statistically correlate observed species presence or presence/absence with environmental variables assuming that this correlation defines the causality of occurrence. In contrast, the trait-based SDMs indirectly formulate the causality of occurrence as mathematical functions defining the variation in the species' functional and life history traits (morphology, behavior, physiology, development, growth, reproduction) as a response to environmental factors (Dormann et al. 2012). Therefore, trait-based SDMs are closer to a mechanistic approach and can be applied to access the likelihood of species' occurrence although the underlying mathematical functions might be correlative in nature (Buckley et al. 2010, Dormann et al 2012).

The major advantage of occurrence-based SDMs is that they can be easily developed from species' presence or presence/absence data and high-resolution environmental data, which have become available in the last decades (Peterson et al. 2015). However, occurrence-based SDMs have been criticized for only focusing on the species' current distribution and thus realized niche, while under climate change SDMs are required to identify areas where a species could possibly occur (Wiens et al. 2009). Thus, their potential for applications under novel climates, or to be transferred to other region is limited (Randin et al. 2006, Kearney et al. 2010, Dormann et al. 2012). Modeling the potential distribution of a species in its introduced range poses additional challenges for occurrence-based SDMs, such as non-availability of reliable occurrence data (Brus et al. 2012) and lack of understanding of 'niche conservation' whereby species may or may not have similar niches in the native and introduced ranges (Broennimann et al. 2007, Camenen et al. 2016).

As trait-based SDMs incorporate the explicit relationships between environmental conditions and functional and life history traits, they are conceptually independent of currently observed species distributions (Kearney and Porter 2009, Buckley et al. 2010, Peterson et al. 2015). This offers a major advantage, in terms of the applicability of such SDMs to a novel environment (Buckley et al. 2010, Dormann et al. 2012, Peterson et al. 2015).

A limitation shared by most occurrence-based and trait-based SDMs is that they treat species as a homogenous unit in terms of intraspecific variations in distribution, functional and life history traits (Dormann et al. 2012, Peterson et al. 2015). Particularly, in the case of species with wide intraspecific variation in fitness-related traits such as morphology, physiology, development, growth, and reproduction, the cumulative niche of individual populations or subspecies is wider than that of a generic species (Pearman et al. 2010, Oney et al. 2013, Hällfors et al. 2016). These studies provide empirical evidence in favor of the assumption that intraspecific genetic variation can be used to potentially buffer effects of climate change on future tree species distributions. Practically, this implies that if appropriate provenances/seed material needs are identified, the effects of climate change induced migration lag of trees can be overcome to a certain extent (Benito Garzón et al. 2011, Aitken and Bemmels 2015). At present, the wide application of SDMs which account for intraspecific variation is limited by the availability of sufficient provenance trial data and by the difficulty to validate the models for regions where a species may be introduced. However, if in addition to intraspecific variation also the limited migration capacity of trees is being considered, the modeled species distributions in climate change may indicate an even more serious risk for species and populations (Valladares et al. 2014, Hällfors et al. 2016).

In a recent study, we developed two universal response functions (URFs), that predict the intraspecific phenotypic variation of functional traits such as dominant tree height and basal area of the North American Douglas-fir *Pseudotsuga menziesii* for plantations in central Europe as a response to climatic drivers (Chakraborty et al. 2015, 2016). In URFs, the relationships between two functional traits (tree height and basal area) and the environmental variables are mathematically specified as causal relations allowing a mechanistic understanding of trait variation and species distribution although the model formulations are correlative and empirical in nature (Dormann et al. 2012). Functional traits such as dominant height are reliable indicators of the tree's competitive status within a stand, thus representing vitality and reproductive potential. Moreover, basal area combines both radial growth and stem density and thus also depends on initial survival as another important life history trait (Díaz et al. 2015).

Currently, Douglas-fir is considered as one of the most attractive non-native conifers in Europe, because of its excellent growth performance and superior wood quality (Hermann and Lavender 1999). However, comparisons of climatic conditions in the native range in North America with potential future climate conditions in central Europe indicated, that the species' future suitability might be questionable and cast doubts on the most appropriate seed sources (Isaac-Renton et al. 2014). In addition, recent occurrence based-SDMs (Boiffin et al. 2017) calibrated with presence/absence data in North America failed to predict the observed occurrence of Douglas-fir in Europe, thus questioning the validity of such traditional models when extrapolated. Our universal response functions (URFs) (Wang et al. 2010), are based on extensive provenance trial data from Austria and southern Germany and can be applied at any putative planting site in Europe (Chakraborty et al. 2015) to predict future growth performance and to identify the most suitable planting stock for stand establishment (Chakraborty et al. 2016). The URFs combine genetic effects, i.e. the climate of provenance origin and environmental effects, i.e. the climate of planting locations into an integrated model to predict the respective functional trait from climate data. The URFs were subjected to model evaluation to examine the effects of change in model coefficients (parameter uncertainty) and climate data (climate change uncertainty) on model performance. Moreover, model results were evaluated on independent trial data from across Europe. Although the models were calibrated within a relatively narrow geographic range in central Europe, the models were found to applicable under a wide range of environmental conditions and in particular for conditions of southeastern Europe which resemble the expected climate change (Chakraborty et al. 2016). This result prompted us to test if the URFs can be applied as SDMs in the sense of testing the suitable climate in which Douglas-fir can grow. This can be achieved by truncating the lower end of the estimated trait response curves, thereby converting the variation in functional traits to the climatic suitability of occurrence (Wang et al. 2010, Dormann et al. 2012). Mathematically, this requires thresholds for predicted functional trait values above which the species is known to grow and reproduce (Buckley 2008, Buckley et al. 2010, Stahl et al. 2014, Gutiérrez et al. 2016).

In order to determine the applicability of SDMs both in space and time, the concept of transferability (Thomas and Bovee 1993, Glozier et al. 1997) has been conceived and applied for a wide range of questions, including, for example, tracing the evolutionary history of species (Nogués-Bravo 2009), the assessment of species' invasive potential into new habitats (Peterson et al. 2001, Peterson 2003), or simply the sensitivity of SDMs to extrapolation (Randin et al. 2006, Barbosa et al. 2009). Transferability of the occurrence-based SDMs depends on two major criteria, 1) within the occurrence data used for model development species are in equilibrium with their environment, 2) and the analogy of climate between training and application area. SDMs developed with data on functional traits such as the URFs do not rely on the assumption of species being in equilibrium with their environment and climate analogy and therefore are assumed to have superior transferability (Vanreusel et al. 2007). However, comparison of transferability of occurrence-based and functional trait-based SDMs are rare (but see, Kearney et al. 2010) and do not exist for SDMs built on intraspecific trait variation.

The aim of this study is to examine the transferability of SDMs based on intraspecific trait variation and to compare them with occurrence-based SDMs when applied outside of their calibration ranges. The study does not aim to replace existing SDMs calibrated with data from a species natural range, but rather focuses on testing approaches of predicting climatic suitability for species for which reliable presence/absence data does not exist.

Material and methods

Trait-based URF-SDMs

The URFs for the current study were developed from tree growth data of 50 provenance trials in Austria and southern Germany that included 290 provenances of both the coastal and interior variety of Douglas-fir and 77 000 individual tree measurements (Supplementary material Appendix 1 Fig. A1). Although these trials are located across a relatively narrow geographic range (Supplementary material Appendix 1 Fig. A1), they cover a wide climatic spectrum (Fig. 1). The tested provenances originate from a wide range of climatic conditions in the native range of Douglas-fir in North America (Fig. 1) (see Chakraborty et al. 2015 for details).

All trials were established between 1973 and 1993 by the Austrian Research Centre for Forests BFW, Vienna, Austria and the Bavarian Office for Forest Seeding and Planting ASP, Teisendorf, Germany. 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

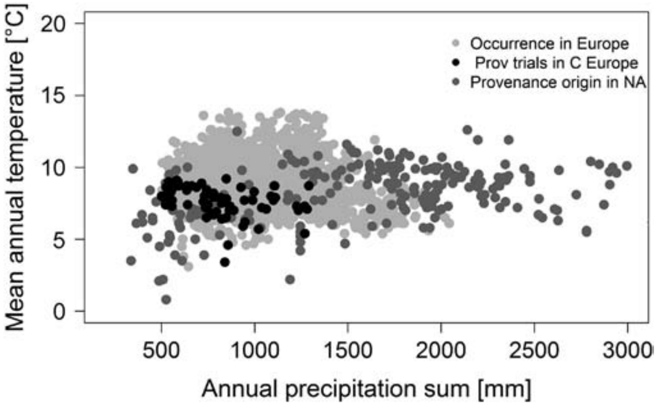

Figure 1. Distribution of the provenance trials in central Europe (black), provenance origin in North America (dark gray) used to calibrate the universal response functions (Chakraborty et al. 2015) and observed occurrences of Douglas-fir in Europe (Isaac-Renton et al. 2014, Mauri et al. 2017) (light gray) in a bioclimatic parameter space represented by mean annual temperature [°C] and annual precipitation sum [mm].

of 2 × 2 m. After fifteen years, tree density was reduced to approximately ten trees per plot (i.e.1000 trees ha^{-1}) in order to have equal stem density across all trials. At various ages (between 10–35 yr) diameter at breast height (DBH) of all trees and tree height of 50–100 randomly selected trees were measured at each trial. Mean tree survival across all the trials were generally high (~ 74%) and differences in survival between provenances small as revealed by preliminary analysis (see also Schultze and Raschka 2002). From this data, two functional traits, the dominant tree height at age 24 (H24) and the mean basal area per hectare (BA24) were used as response variables of the URFs (Chakraborty et al. 2015, 2016). The URFs are quadratic models (Eq. 1) relating one of these functional traits to the climate of the trial locations in central Europe and the climate of the seed origins in North America.

Predictor candidates for developing the URFs consisted of 20 biologically relevant climate variables at each of the trial locations in Austria and southern Germany and the seed origin locations in North America (Supplementary material Appendix 1 Table A1). Climate variables of trial locations covering the period from the installation of each trial until the most recent measurements were obtained from regional networks of weather stations and from Haslinger et al. (2012). For each provenance trial, the daily mean temperature and precipitation from the four closest weather stations of the national meteorological service ZAMG were used. These data were adjusted to the altitude of the trial sites and thereafter interpolated to the trial coordinates by inverse distance weighted interpolation (Chakraborty et al. 2015). For climate data of the provenance origin, mean values of the same climate variables as in Supplementary material Appendix 1 Table A1 were obtained for the period 1950–2000 for each provenance origin location using the high-resolution climate model Climate-WNA ver. 4.72 (Wang et al. 2012a).

Significant climate predictors for the URF model were selected using a multimodel approach, implemented with the R package 'leaps' (Lumley 2009) which performs an exhaustive search for the best subsets of the explanatory variables using an efficient branch-and-bound algorithm independent of the criterion such as AIC, BIC, etc used for penalizing models with redundant explanatory variables (Jørgensen 2004, Lumley 2009, Dormann et al. 2013) (Eq. 1):

$$\begin{aligned} \mathrm{Y}_{sp} &= b_o + b_1\mathrm{MAT}_\mathrm{s} + b_2\mathrm{MAT}_\mathrm{s}^2 + b_3\mathrm{SHM}_\mathrm{s} + b_4\mathrm{SHM}_\mathrm{s}^2 \\ &\quad + b_5\mathrm{MAT}_\mathrm{p} + b_6\mathrm{MAT}_\mathrm{p}^2 + b_7\mathrm{MAT}_\mathrm{s}{*}\mathrm{MAT}_\mathrm{p} + e_{sp} \end{aligned} \tag{1}$$

Here, Y_{sp} is the growth performance (either H24 or BA24) of the provenances p at the trial sites s; MAT_s and 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_7 are the intercept and regression coefficients, and e_{sp} is the residual error. The coefficients of the two URFs can be found in Table 1. The URFs explained ~ 89% of the variation in dominant height and basal area (Chakraborty et al. 2015, 2016). The URFs predict functional traits or growth performance which needed to be converted to the occurrence of the species or its climatic suitability. However, it is technically possible that the URFs can predict unrealistically small values of H24 and BA24 due to stochasticity in climate variables. Therefore, a minimum value of H24 and BA24 was needed which could define the threshold above which the climate was considered suitable for Douglas-fir to grow survive and reproduce. These thresholds were identified by examining the variation in true skill statistics (TSS) (Eq. 2) with a stepwise increase in thresholds for climatic suitability (2 to15 m, in case of H24) and (2 to15 m^2 ha^{-1} in case of BA24) following Gutiérrez et al. (2016).

$$TSS = \left(Sensitivity + Specificity - 1\right) \tag{2}$$

The value at which increase in H24 and BA24 caused no further change in TSS was selected as the threshold to convert growth performance to climatic suitability. This corresponded to thresholds ≥ 10 m for H24 and ≥ 3 m^2 ha^{-1} for BA24 (Supplementary material Appendix 1 Fig. A2). The selected thresholds are also close to the shortest tree height and lowest basal area values in our provenance trial data set. We named this approach as the trait-based, URF-SDMs.

Species occurrence data

Current occurrence (presence and absence) of Douglas-fir was obtained from 588 983 inventory plots in Europe available from the database of Mauri et al. (2017) as well as from 120 known locations of provenance trials of Douglas-fir in Europe (Isaac-Renton et al. 2014). Out of the total of 589 103 locations, Douglas-fir was present at 5357 locations. The database of Mauri et al. (2017) combined observed presence and absence of major European tree species from

Table 1. The universal response functions (URFs). Results of multiple regression analysis predicting dominant height at age 24 and basal area at age 24 of Douglas-fir populations from the site and seed origin climate as independent variables in an 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. For details see Chakraborty et al. (2015).

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
$MAT_s \times MAT_p$	0.068	0.002	0.064	0.071	< 0.001	0.004
Model R^2·adj				**0.87**		
URF for basal area (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^2·adj				**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.

the three existing datasets: the Forest Focus (Hiederer et al. 2011), Biosoil (Houston et al. 2011) and from national forest inventories (Vidal et al. 2016). The climatic extent of the observed occurrences across Europe is much higher than that of provenance trials sites and encompasses Douglas-fir seed introductions from the last 150 yr (Fig. 1). Though the exact origin of seeds planted at these presence locations is unclear, it certainly covers a wide spectrum of coastal and interior provenances, because past provenance recommendations in European countries were highly diverse and included also interior seed material (Giese 1985) and the admixture of the subspecies can still be identified today (Konnert and Ruetz 2006).

The current occurrence of Douglas-fir in Europe represents only artificial plantations and hence might not necessarily indicate locations of unsuitable habitat. To address this issue of unreliable absences we treated the observed absences as pseudoabsences by applying geographic and climatic constraints on occurrences according to Senay et al. (2013) in a three-step approach. With this approach we seek to identify absence locations which are both geographic as well as climatically different from the observed presence locations. This approach includes: specifying a geographical extent outside the observed presences; environmental profiling of the absences outside this geographic extent and k-means clustering of the environmental profiles and selecting random samples within each cluster. In our case, a 2-degree buffer was found to be optimum following Senay et al. (2013). The absence locations outside this geographic extent were classified into 15 environmentally dissimilar clusters according to k-means clustering algorithm. The number of pseudoabsence locations was further reduced by randomly selecting a sample of locations defined by the 95% confidence interval from each of the 15 clusters. The resultant dataset was used to calibrate an occurrence-based SDM.

Occurrence-based SDM

Utilizing this species occurrence (presence/absence) dataset, an SDM, based on the correlation between the current occurrence of Douglas-fir in Europe and its climate was developed. Climate was represented by 20 biologically relevant climate variables (Supplementary material Appendix 1 Table A1) obtained from 'Climate-EU: historical and projected climate data for Europe' (Wang et al. 2012a) for the average of the time period 1961–1990. The most influential variables explaining the current occurrence of Douglas-fir in Europe were identified by the recursive feature elimination (RFE) approach, accounting for multicollinearity ($r \geq 0.7$) and implemented with the 'party' package (Strobl et al. 2009) of R. The relative importance of the most influential climate variables can be found in Supplementary material Appendix 1 Table A2.

To calibrate the occurrence-based SDM an ensemble distribution modeling approach, BIOMOD2 (Thuiller et al. 2013) was implemented in R programming environment (R Core Team).

BIOMOD2 offers a computational platform for multi-method modelling that generates the probability of presence outputs for each of the modeling approach as well as a variety of ensemble projections (Thuiller et al. 2013). Hence, BIOMOD2 attempts to combine the strengths of multiple modeling algorithms while accounting for their uncertainties. In this study we used all the 10 available algorithms of BIOMOD2 such as GLM (generalized linear models), GAM (generalized additive models), GBM (generalized boosted regression models), CTA (classification tree analysis), ANN (artificial neural networks), SRE (surface range envelop or BIOCLIM), FDA (flexible discriminant analysis), MARS (multivariate adaptive regression spline), RF (random forest for classification and regression), and MAXENT.Tsuruoka.

To avoid overfitting (Lever et al. 2016) of the models resulting from the likelihood of dependence in the training data, we performed a cross-validation by clustering the species occurrence data into 3 blocks based on climatic characteristics (Burman et al. 1994, Fielding and Bell 1997, Vaughan and Ormerod 2005, Lieske and Bender 2011, Roberts et al. 2017). A principal component analysis with the 20 bioclimatic variables (Supplementary material Appendix 1 Table A1) suggested that the first three components accounted for 97% of the total variation in climate. Utilizing these three principal components the species occurrence dataset was partitioned into 3 blocks each with a relatively homogeneous climate following the partitioning around medoids routine. This method allowed us specifying the number of clusters and ensuring that each block had enough presence and absence values as suggested by Roberts et al. (2017). The 'k-fold' approach (Burman et al. 1994, Fielding and Bell 1997, Roberts et al. 2017) was adopted for cross validation whereby three model clusters M1, M2, and M3 (Supplementary material Appendix 1 Fig. A3) were developed, each withholding a block for model validation and two for model calibration.

Predicted probabilities from the individual models of the BIOMOD2 within each model cluster were ensembled as a consensus model which combined the median probability over the selected models with TSS > 0.7. The median was chosen because it is known to be less sensitive to outliers than the mean. Predicted probability of occurrence of Douglas-fir from the ensemble model was converted to presence and absence with the maximizing TSS approach (Thuiller et al. 2013). This maximizing TSS approach was found to be one of the most reliable approaches for choosing a reclassification threshold by a large number of studies (Liu et al. 2005, Freeman and Moisen 2008, Nenzén and Araújo 2011). All the three ensemble model clusters were then applied to predict the distribution of Douglas-fir in Europe and North America.

The ensembled predictions of the tree model clusters were then combined into a single final model which represented the median predictions of the three ensemble model clusters and plotted as maps (see Supplementary material Appendix 1 Fig. A2 for details). This final ensembled model was referred to as 'occurrence-based SDM'.

Transferability of the SDMs

The two trait-based URF-SDMs and the occurrence-based SDM were applied to predict the observed occurrence of Douglas-fir in both its introduced range in Europe and native range in North America. This included the 589 103 locations in Europe (Isaac-Renton et al. 2014, Mauri et al. 2017) and 71 182 inventory plots in North America (Schroeder et al. 2010, Coops et al. 2011). Climate of trial location was set to be equal to climate of provenance origin ($MAT_s = MAT_p$ in Eq. 1) for applying the URF-SDMs in both Europe and North America.

The performance of the three SDMs was quantified by model sensitivity, specificity, true skill statistics (*TSS*) and transferability index (T_{TSS}). Sensitivity is the proportion of true presences correctly identified by the model, and specificity the proportion of true absences correctly identified. *TSS* (Eq. 2), also known as Hansen Knuipers discriminant (Allouche et al. 2006) is independent of the size of the dataset and the prevalence of the species and accounts for both commission and omission errors (Allouche et al. 2006). *TSS* values range from –1 to +1 where +1 indicate perfect agreement and values ≤ 0 indicate a performance equivalent to a random guess (Allouche et al. 2006).

Transferability index T_{TSS} is the ratio of *TSS* in the extrapolated region (TSS_{ex}) and *TSS* in the model calibration region (TSS_{in}) as given in Eq. 3.

$$T_{TSS} = \frac{Tss_{ex}}{TSS_{in}} \qquad (3)$$

In this study, the true skill statistics (*TSS*) and transferability index (T_{TSS}) (Heikkinen et al. 2012) were adopted as a measure of transferability of the models from its calibration range to application area.

Data deposition

Data available from Figshare Digital Repository: <http://dx.doi.org/10.6084/m9.figshare.1468400> (Schueler 2015).

Results

Performance and transferability of SDMs in the native and introduced range of Douglas-fir

Cross-validation reveals that all the model clusters performed equally well in predicting the evaluation data with TSS ranging from 0.43–0.99 with an average of 0.80 (Supplementary material Appendix 1 Table A3). However, significant differences existed in performances of the individual model algorithm (Supplementary material Appendix 1 Table A3).

When applied in their calibration range in Europe, the occurrence-based SDM (median of the three ensembled model clusters) obtained a model sensitivity and specificity of 0.99 and thus a remarkable *TSS* of 0.98 (Table 2,

Table 2. Performance and transferability of SDMs. The performance of the three SDMs for predicting observed presence/absence of Douglas-fir in its introduced range in Europe (EU) and its native range in North America (NA). Performances of SDMs in recently published literature in NA and EU are reported in cells highlighted in gray.

Type of SDM	Developed in	Applied in	Sensitivity	Specificity	TSS	T_{Tss}
URF-SDM for H24	EU	EU	0.98	0.55	0.53	
		NA	0.66	0.72	0.38	0.71
URF-SDM for BA24	EU	EU	0.99	0.54	0.53	
		NA	0.67	0.70	0.37	0.68
Occurrence-based SDM	EU	EU	0.99*	0.99*	0.98*	
		NA	0.12*	0.92*	0.05*	0.05
Boiffin et al. 2017	NA	NA	–	–	0.83	
		EU	–	–	0.03	0.04
Coops et al. 2011	NA	NA	0.76	0.7	0.46	
Rehfeldt et al. 2014	NA	NA	0.99	0.95	0.93	
Weiskittel et al. 2012	NA	NA	0.9	0.79	0.69	

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 a random guess.
T_{Tss} = transferability index (Heikkinen et al. 2012). $T_{TSS} < 1$ provides higher predictive accuracy in interpolative forecasting than in extrapolation, and vice versa.
*Median sensitivity, specificity and TSS and T_{Tss} of the three ensemble model clusters (see Supplementary material Appendix 1 Fig. A2 for details).

Fig. 2, Supplementary material Appendix 1 Table A4). The machine learning algorithms such as RF, GBM, ANN performed consistently better in all the three model clusters whereas SRE performed consistently poorer in comparison (Supplementary material Appendix 1 Table A4).

The performance of the two URF-SDMs to predict the species' presence, i.e. its sensitivity is similarly high (0.98 for H24 and 0.99 for BA24) but the performance to correctly predict absences (specificity) is comparatively lower (0.55 for H24 and 0.55 for BA24) resulting in TSS of 0.53 for both URF-SDMs (Table 2). Sites where the URF-SDMs failed to predict observed absences lie mainly in the Scandinavia and eastern Europe (Fig. 2C, D).

When applied in the native range of Douglas-fir in North America, the sensitivity of the URF-SDMs to correctly predict observed presences was 0.66 and 0.67 and thus significantly higher than the occurrence-based SDM with a sensitivity of only 0.12 (Table 2). In contrast, the performance of the occurrence-based SDM in predicting the observed absences in NA (i.e. median specificity = 0.92) was higher compared to the URF-SDMs which has a sensitivity ranging from (0.70–0.72, Table 2). In particular, the URF-SDMs have a lower ability to predict the absence of Douglas-fir in the south and southeast of the Rocky Mountains (Fig. 3C, D) and at the northern range limit of the species.The URF-SDMs performed well to predict the observed occurrence of Douglas-fir at the north and center of its distribution in North America, whereas failed partly to predict observed occurrences at the south of the coastal range in California and southern Oregon (Fig. 3C, D). The occurrence-based SDM performed particularly well in predicting the observed occurrences of Douglas-fir in the coastal range of North America (Fig. 3B) whereas it failed completely to predict observed occurrences in the interior range of Douglas-fir (Fig. 3B). Overall, the URF-SDMs have better performance in North America than the occurrence-based SDM in terms of *TSS* (0.37–0.38 vs 0.05).

When transferred to North America the *TSS* of the URF-SDMs declined by 28% in case of the URF-SDM for H24 and by 30% in case of URF-SDM for BA24 (Table 2). In contrast, the *TSS* of the occurrence-based declined strongly by 96% (Table 2). The transferability of the trait-based URF-SDMs were superior ($T_{TSS} = 0.68–0.71$) compared to the occurrence-based SDMs not only for the final ensemble model ($T_{TSS} = 0.04$) but also for all model cluster and individual models within the model cluster (Supplementary material Appendix 1 Table A4).

The URF-SDMs did not differ significantly in their performance irrespective of being applied in the introduced or native range of Douglas-fir. Whereas the transferability of the SDM based on the correlation between observed occurrence and current climate declined significantly when applied in a climate outside its calibration range.

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 model evaluation and application to the novel or non-analogous climate regimes outside of the species' current environment. Present climates will at least partly disappear and future conditions will constitute new combinations of annual and seasonal climate factors (Ohlemüller et al. 2006, Williams and Jackson 2007).

In the present study, we compared two intraspecific, trait-based SDMs with a occurrence-based SDM, all developed

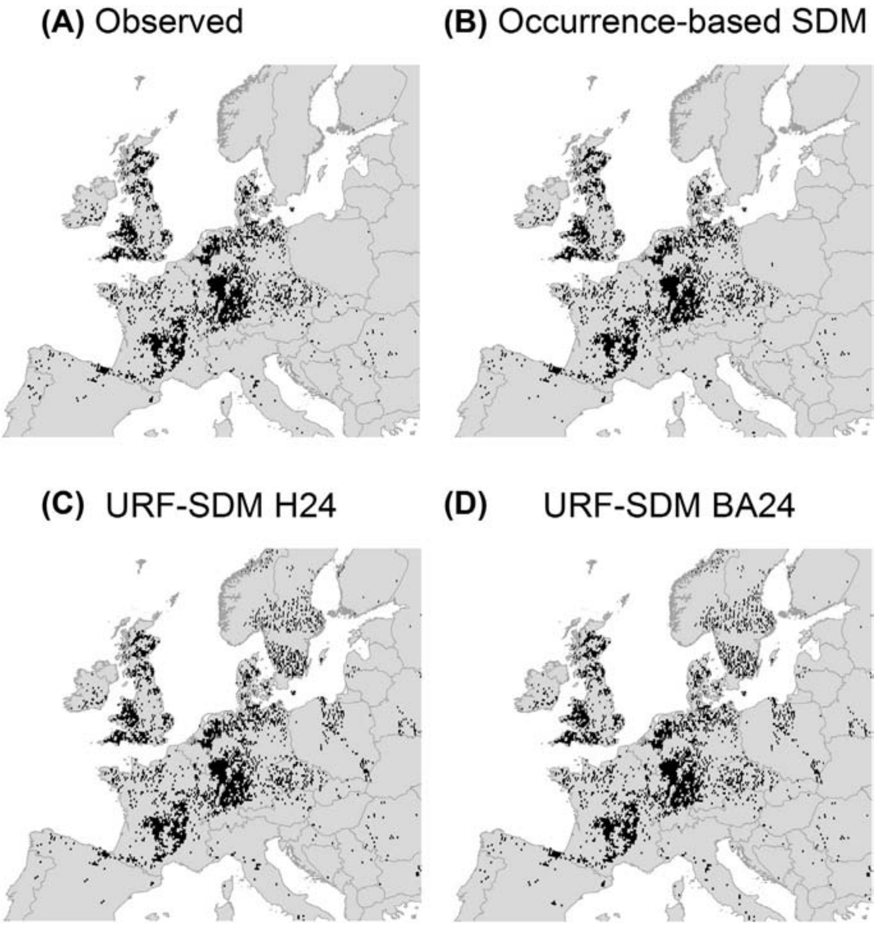

Figure 2. Observed and predicted distribution of Douglas-fir in Europe. (A) The observed distribution of Douglas-fir in 588 983 inventory plots in Europe. The predicted distributions with: (B) occurrence-based SDM calibrated in Europe; (C) the trait-based URF-SDM for dominant height and (D) the trait-based URF-SDM for mean basal area. Black represent areas predicted by the models to have climate suitable for Douglas-fir whereas gray area represents climatically unsuitable areas.

from European data, and analyzed their transferability to the native range of Douglas-fir in North America as a testimony for their application in novel climate. The non-analogy of climate between Europe and North America has been demonstrated by recent studies (Isaac-Renton et al. 2014, Chakraborty et al. 2015, Boiffin et al. 2017). We found that the occurrence-based SDM, based on presence/absence data across Europe, had very low transferability and largely failed to predict the species natural distribution. In contrast, the trait-based URF-SDMs showed significantly higher transferability despite the fact that the geographic and climatic range of the test sites in Europe was comparatively smaller than the climatic range of occurrences for the occurrence-based SDMs (Fig. 1). On the other hand, the precipitation gradient from which the provenances originate in North America was wider than the precipitation gradient of the European occurrence locations (Fig. 1), while the thermal gradient depicted by MAT was similar for provenance origin and European occurrences. Within the trait-based URF-SDMs the temperature was found the dominant drivers of height and basal area growth, whereas precipitation of provenance origin was not found to effect the observed trait variation (Chakraborty et al. 2015). Overall, our trait-based URF-SDMs show predictive power (Table 2) comparable to occurrence-based SDMs developed in North America itself (Weiskittel et al. 2012, Rehfeldt et al. 2014) or physiological process-based growth models (Coops et al. 2011, Gutiérrez et al. 2016).

The occurrence-based SDM showed an excellent performance in Europe (Fig. 2) and also a high accuracy to predict the absence of Douglas-fir in North America (Fig. 3). However, the occurrence-based SDM was unable to predict the presence of the species within the species interior native range (Fig. 3B). This imbalance between sensitivity and specificity of the occurrence-based SDM (Table 2) can also be interpreted as its inferior transferability or lack of generality (Qiao et al. 2017, Yen et al. 2017).

The superior transferability of the trait-based SDMs in North America may also be argued to driven by the data used to calibrate the two types of models. Provenances from both coastal and interior Douglas-fir were used to calibrate our trait-based SDMs (Chakraborty et al. 2015, 2016), whereas the exact information on the provenance origin of

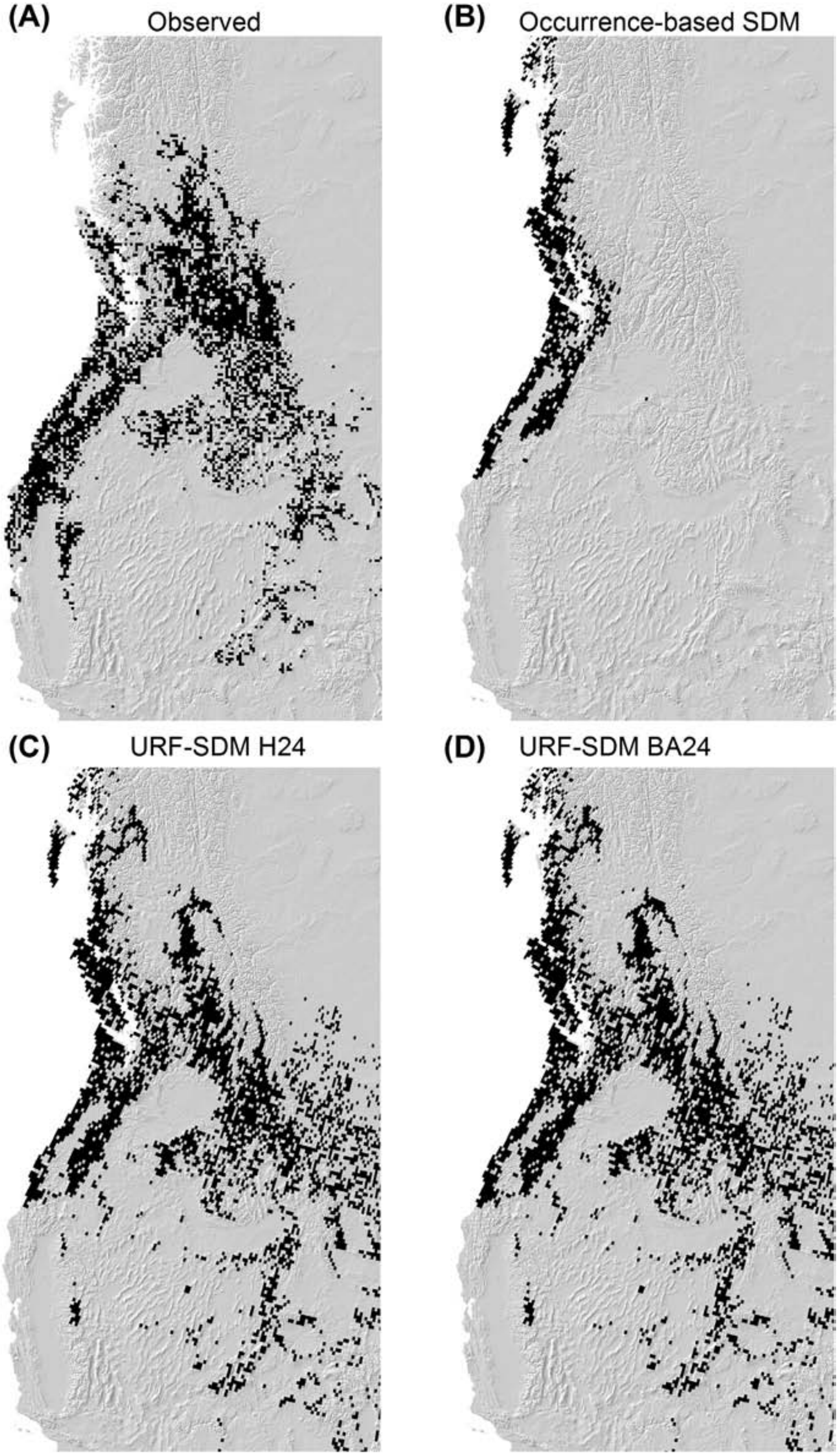

Figure 3. Observed and predicted distribution of Douglas-fir in North America. (A) The observed distribution of Douglas-fir in 71 182 inventory plots in North America. The predicted distributions with: (B) occurrence-based SDM calibrated in Europe; (C) the trait-based URF-SDM for dominant height and (D) the trait-based URF-SDM for mean basal area. Black represent areas predicted by the models to have climate suitable for Douglas-fir whereas gray area represents climatically unsuitable areas.

the occurrence dataset for calibrating the occurrence-based SDM is unknown. Nevertheless, the occurrence dataset likely consists of both coastal and interior Douglas-fir. This is because there have been several introductions of Douglas-fir in Europe during the last 150 yr and initially no genetic preference of the planting material was involved, whereby both coastal and interior provenances were planted. Therefore, stands older than 50 yr in the inventory are likely to have a fair share of interior provenances or being admixed of various provenances and varieties (Konnert and Ruetz 2006, Hintsteiner et al. 2018). It was only later that results from IUFRO coordinated provenance trials revealed the advantages of planting coastal Douglas-fir which might have been implemented in younger plantations. In addition, until recently, interior provenances were recommended for plantations under more continental site conditions because of their frost tolerance and survival rates (Kohl and Nather 1976, Giese 1985). However, it should be noted that the occurrence-based SDMs cannot utilize information on provenance differentiation since it is based on the correlation between occurrence and local climate.

Nevertheless, we tested if a constrained dataset for the calibration of the URF will compromise its transferability. Therefore, we developed URFs with only coastal provenances and applied them as URF-SDMs by converting height and basal area predictions to presence/absence with the same thresholds as the URF-SDMs calibrated with both interior and coastal Douglas-fir. These trait-based URF-SDMs calibrated with coastal provenances and the occurrence-based SDM were applied to predict presence/absence of 1) full occurrence dataset with both coastal and interior areas, and 2) coastal only occurrences of Douglas-fir in North America. The occurrence locations in North America were delimited to the coastal and interior Douglas-fir distribution according to Rehfeldt et al. (2014), whereby the crest of the Coastal Mountains of British Columbia separated the var. *menziesii* (coastal Douglas-fir) in the west from var. *glauca* (interior Douglas-fir) populations in the east. We found that the URFs with only coastal provenances have very similar model coefficients as the URFs with both coastal and interior provenances (Supplementary material Appendix 1 Table A5). Hence, the URF-SDMs on the basis of coastal only Douglas-fir had similar transferability as the URF-SDMs on basis of both coastal and interior provenances (Supplementary material Appendix 1 Table A6). The transferability of the occurrence-based SDMs remained inferior compared to the trait-based URF-SDMs when predicting the coastal Douglas-fir. This result supports the supposition that SDMs based on functional traits are rather independent of specific climate-occurrence correlations and thus closer to a mechanistic approach.

The choice of modeling method which is known to influence the transferability of SDMs (Heikkinen et al. 2012, Lever et al. 2016, Werkowska et al. 2017) is not likely to affect our findings since low transferability of the occurrence-based SDMs were consistent across a wide range of models and their ensembles (Supplementary material Appendix 1 Table A4). A similar low transferability was recently reported by Boiffin et al. (2017) for an occurrence-based SDM of Douglas-fir developed in North America and transferred to Europe, confirming the low performance of such SDMs if transferred to non-analogous climate of another continent. Thus, our occurrence-based SDM seems to suffer mainly from the non-analogy between European climate at the interior range for Douglas-fir, where cold continental climate conditions prevail (Boiffin et al. 2017). Moreover, Douglas-fir in Europe might have never been planted at such climatically extreme sites, and thus presence data for fitting a better occurrence-based SDM are not available.

In this study, the uncertainties due to modeling algorithms were accounted for with an ensemble modeling approach, BIOMOD2. The ensemble approach which obtains model consensus by combining predictions across a range of model algorithms (such as the median predictions of all models used in this study), were found to provide higher accuracies in predictions compared to single models (Araújo and New 2007, Coetzee et al. 2009, Buisson et al. 2010, Thuiller et al. 2013). Uncertainties due to the choice of thresholds to convert predicted probability to binary presence and absence was accounted with the maximizing TSS approach whereby several thresholds are tested and the one which results in maximum sensitivity and specificity and therefore maximum TSS is selected. In absence of reliable independent data for model validation, the commonly used cross-validation approach by randomly splitting training data was found to violate the assumption of independence of the training dataset resulting in overfitted models (Burman et al. 1994, Vaughan and Ormerod 2005, Roberts et al. 2017). Although a cross-validation was not required in our case because the independent occurrence dataset in North America was available for validation of the occurrence-based SDMs, the possibility of overfitting due to spatial dependence in our data still existed. Therefore we adopting a block cross-validation approach whereby dependency in the training data is broken by clustering the occurrence dataset into blocks of similar entities (climatically similar blocks in our case); an approach which was found to be effective for avoiding overfitting of models (Burman et al. 1994, Heikkinen et al. 2012, Wenger and Olden 2012, Bahn and McGill 2013, Radosavljevic and Anderson 2014, Fithian et al. 2015, Roberts et al. 2017). Although the provenance trials used to build the models cover only a part of the climate conditions of the observed distribution of Douglas-fir in Europe (Fig. 1), the URF-SDMs demonstrate superior performance in its native as well as the introduced ranges (Table 2).

The choice of threshold for converting variations in functional traits to species occurrence is very crucial. In this study, the choice of threshold is unlikely to cause serious bias in our results since the selected threshold (Supplementary material Appendix 1 Fig. A2) does not change model performance with a change in threshold value. Moreover, our choice of threshold (Supplementary material Appendix 1 Fig. A2) also corresponds to the smallest observed tree height and basal area in our dataset. A comparable method of selecting thresholds for process-based SDMs was also reported by Gutiérrez et al. (2016).

The result of this study can be considered as a successful test case for model application in climate change. Hence, the URF-SDMs can be used to identify present and future climate suitability of Douglas-fir in Europe, North America or in other plantation areas worldwide (Hermann and Lavender 1999). 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 and on the analogy between the present and future climate regimes (Wang et al. 2010). The superiority in transferability of the trait-based URF-SDMs supports previous studies that proposed functional, fitness-related traits as a basis for developing SDMs (Violle and Jiang 2009, Stahl et al. 2014, Funk et al. 2016). Dominant height and basal area are two such functional traits incorporated in our URF-SDMs. The dominant height is closely related to a tree's competitive fitness for capturing available light and basal area incorporates both initial tree mortality and diameter growth (Chakraborty et al. 2015). Tree size and density related traits were found to represent two-thirds of the total variation in plant functional traits critical for growth and survival (Díaz et al. 2015), further supporting the need of SDMs based on such functional traits. While H24 and BA24 may well represent traits critical for growth and survival, reproduction is not as well characterized. Therefore, future URFs may also integrate additional functional traits (seed characteristics, wood characteristics, phenological observations, etc.) to allow more specific risk-benefit analysis of assisted migration or assisted gene flow management (Aitken and Bemmels 2015).

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 (Fig. 3C, D) is likely caused by missing provenances from California and northern BC in the European trial sites. This highlights the fact that despite the reliability of predictions of the URF-SDMs, they are not totally free from limitations when extrapolated (Kearney et al. 2010, Peterson et al. 2015). 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 (Thompson et al. 1999, Coops et al. 2011). Within Europe, the trait-based URF-SDMs show relative low accuracy in correctly predicting absences (specificity) in Scandinavia and eastern Europe, where observed absences were predicted as presences (Fig. 2C, D). This may arise from the micro scale effects of soil and moisture regimes not characterized by the 20 climate variables screened in this study. This may also indicate that the observed absences may not necessarily indicate unsuitable sites for Douglas-fir in the introduced regions. Instead, it may simply indicate that in these areas Douglas fir was not planted as a preferred alternative tree species to domestic conifers such as Norway spruce.

Therefore we identified those locations which are both climatically and geographically distant from the observed presence locations with a three step approach according to Senay et al. (2013) assuming such locations as unsuitable for Douglas-fir. Traditionally when reliable absences or no absence locations are available pseudoabsences are selected randomly or based on geographic or climate alone profiling (Barbet-Massin et al. 2012, Iturbide et al. 2015). In general, the random selection of pseudoabsence was found to be the most error prone strategy (Barbet-Massin et al. 2012, Senay et al. 2013, Iturbide et al. 2015). Conceptually, climatic alone or geographic alone strategies for defining absence are not sufficient because climate and geographic features do not influence species occurrence in isolation but interact with each other (Barbet-Massin et al. 2012). The geo-climatic profiling of the absence data allowed obtaining a clearer data structure with lower uncertainty and the k-means clustering ensured that geo-climatically dissimilar absences points are selected. Therefore, the three step profiling of pseudoabsence based on both climate and geographic constraints is likely to generate reliable absence locations which is crucial requirement when the species being studied is a non-native one such as Douglas-fir in Europe.

Conceptually, the trait-based URF-SDMs seek to approximate the fundamental niche which is larger than the observed current distribution of the species in Europe (Soberon and Peterson 2005) and is therefore closer to a mechanistic approach (Dormann et al. 2012, Peterson et al. 2015, Shabani et al. 2016). Missing trials at climatically extreme sites underpin known limitations of historical common garden trials, where provenances from the entire natural range were not consistently tested at the species range limits (Matyas 1994, Leites et al. 2012). 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 fewer trial sites without affecting the prediction accuracy of the models (Wang et al. 2010). For forest tree species, new trials will be able to provide meaningful data within 15 to 20 yr. Also, for endangered annual and smaller perennial plants, such trials can deliver data for building URF-SDMs in a few years (Bradley St Clair et al. 2013, Wilczek et al. 2014).

More important than the accuracy of any SDM is the potential application in climate change adaptation. Occurrence-based SDMs based on presence/absence data allow to identify putative retraction areas at species trailing edges and expansion areas at the species leading edges (Thuiller et al. 2008) and thus may be used to identify vulnerable populations, species or ecosystems and potential new habitats (Wang et al. 2012b, Schueler et al. 2014). However, for concrete recommendations of seed transfer either into novel climates or within the species current range, occurrence-based SDMs are rather unsuitable. To a certain extent, the same is also true for other mechanistic SDMs as they rarely address the intraspecific variation of the underlying physiological principles and come at higher costs of calibration (Gutiérrez et al. 2016). In contrast, URFs explicitly consider genetic variations and are able to predict the future performance of individual populations or seed sources. This advantage can be used in two directions (Wang et al. 2010): 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. Since forest trees are often dominant 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 a new habitat for endangered local populations.

Species distribution models are likely to guide a wide range of decisions in forest management and conservation. Our findings indicate that using occurrence-based SDMs for such decisions may be error-prone, especially if the environmental conditions of the application and calibration range are not analogous. The non-analogy of site conditions is very common in Europe because many local tree species have been planted outside their natural distribution. Under such condition, the existing presence/absence data is likely to violate the assumption of the equilibrium between the current occurrence of a species and its environment.

The URF-SDMs have the potential to overcome this problem, but they require data from provenance trials. Provenance trials are probably the greatest contribution of forest science to evolutionary biology (Aitken and Bemmels 2015) and constitute a valuable source of data for developing SDMs based on ecophysiological constraints of species distribution. Our study can be regarded as a case study of incorporating genetic variation in functional traits to model species distribution ranges; however, a multi species-multi-model comparison is likely to further improve the generalization of the results. Our analysis strongly suggests that such field experiments should be established not only for forest trees but also for other wild plants species, as they can provide crucial information on the species adaptive capacity and their potential distribution in a changing environment. However practical challenges exist in establishing and maintaining such long-term trial series.

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Supplementary material (Appendix ECOG-03888 at <www.ecography.org/appendix/ecog-03888>). Appendix 1.