

# Douglas-fir plantations in Europe: a retrospective test of assisted migration to address climate change

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## Abstract

We evaluate genetic test plantations of North American Douglas-fir provenances in Europe to quantify how tree populations respond when subjected to climate regime shifts, and we examined whether bioclimate envelope models developed for North America to guide assisted migration under climate change can retrospectively predict the success of these provenance transfers to Europe. The meta-analysis is based on long-term growth data of 2800 provenances transferred to 120 European test sites. The model was generally well suited to predict the best performing provenances along north–south gradients in Western Europe, but failed to predict superior performance of coastal North American populations under continental climate conditions in Eastern Europe. However, model projections appear appropriate when considering additional information regarding adaptation of Douglas-fir provenances to withstand frost and drought, even though the model partially fails in a validation against growth traits alone. We conclude by applying the partially validated model to climate change scenarios for Europe, demonstrating that climate trends observed over the last three decades warrant changes to current use of Douglas-fir provenances in plantation forestry throughout Western and Central Europe.

**Keywords:** bioclimatic envelope models, exotic species, model validation, no-analogue climates, provenance trials, *Pseudotsuga menziesii*, species distribution models

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## Introduction

Climate change may pose a substantial risk to forest health and productivity by causing a mismatch with the environmental conditions to which individual tree populations are adapted (e.g. O'Neill *et al.*, 2008; Mckenney *et al.*, 2009; Rehfeldt & Jaquish, 2010). In western North America, climate change observed over the last several decades has already resulted in populations lagging behind their climatic optimum by an average of 130 km in latitude, or the equivalent of 60 m in elevation (Gray & Hamann, 2013). Although trees tend to have a high degree of plasticity, allowing them to physiologically or morphologically respond to changing environments, these abilities will eventually be exceeded, leading to reduced forest health and productivity, and eventually to losses of local populations (Aitken *et al.*, 2008; Allen *et al.*, 2010).

Human-aided movement of species populations in large-scale reforestation programmes could be an effective and cost-efficient climate change adaptation strategy (Ukrainetz & O'Neill, 2009; Gray *et al.*, 2011; Pedlar

*et al.*, 2011, 2012). Such large-scale management interventions, however, can entail risks of unintended consequences, especially when guided by imperfect models or incomplete ecological knowledge. Species distribution models could potentially guide assisted migration prescriptions, but they have rightly been criticized as too simplistic to infer growth, survival, migration or adaptation of species in response to climate change (e.g. Hampe, 2004). As a consequence, scientists and natural resource managers have been reluctant to recommend such imperfect tools for resource management and conservation applications. On the other hand, it has been argued that, compared to forecasting complex demographical processes, guiding assisted migration in a reforestation context is a much simpler task to which species distribution models are well suited (Gray *et al.*, 2011; Hamann & Aitken, 2013).

To investigate the realism of climate envelope model predictions, we use North American species introductions to Europe as a retrospective experiment on how trees respond when subjected to climate regime shifts. We can use growth data from these species introductions to assess how well bioclimate envelope models designed to guide assisted migration under climate change predict appropriate planting stock for a

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particular climate environment. Here, we evaluate a type of climate envelope model that projects locally adapted populations within a species range, rather than the species as a whole (Gray & Hamann, 2011; Gray *et al.*, 2011; Roberts & Hamann, 2012a). The underlying hypothesis is that closer climatic matches between the origin of the North American seed source and the European planting environment (as determined by climate envelope models) should be associated with better growth relative to provenances with poorly matched climates.

Species introductions are normally preceded by systematic provenance experiments, where seed sources from throughout the native species range are tested across a wide range of potential planting environments. Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] is arguably the most thoroughly tested and commercially important North American tree species planted in Europe (Kleinschmit & Bastien, 1992; Hermann & Laverder, 1999). Systematic provenance trials comparing different North American seed sources began across Europe as early as the 1910s (e.g. Schober, 1959; Stimm & Dong, 2001), often showing that provenances with superior growth originated from the coast of southern Washington or northern Oregon in the United States (e.g. Birot & Burzynski, 1981; Kenk & Thren, 1984; Kleinschmit & Bastien, 1992; Ballian *et al.*, 2002; Isajev & Lavadinovi, 2003; Perić *et al.*, 2009). However, a comprehensive compilation of Douglas-fir provenance trial results in Europe is lacking.

In this study, we developed a North American climate envelope model to test its capacity to predict suitable climate habitat for Douglas-fir provenances under potentially novel climate conditions in Europe. This also involves testing whether European climate conditions are analogous to North American conditions or whether they represent novel combinations of climate variables, potentially compromising model performance. Secondly, we compile and synthesize results from 120 provenance plantations of Douglas-fir across Europe for validation of climate envelope model projections. Third, given satisfactory predictive model performance, we aim to map suitable planting sites for Douglas-fir sources in Europe and derive guidelines for seed movement under projected climate change.

## Materials and methods

### *Provenance data and analysis*

Data from European Douglas-fir provenance trials were compiled from 39 journal publications and technical reports. We selected studies where provenance means were reported in the form of tables or charts that allowed for reliable data

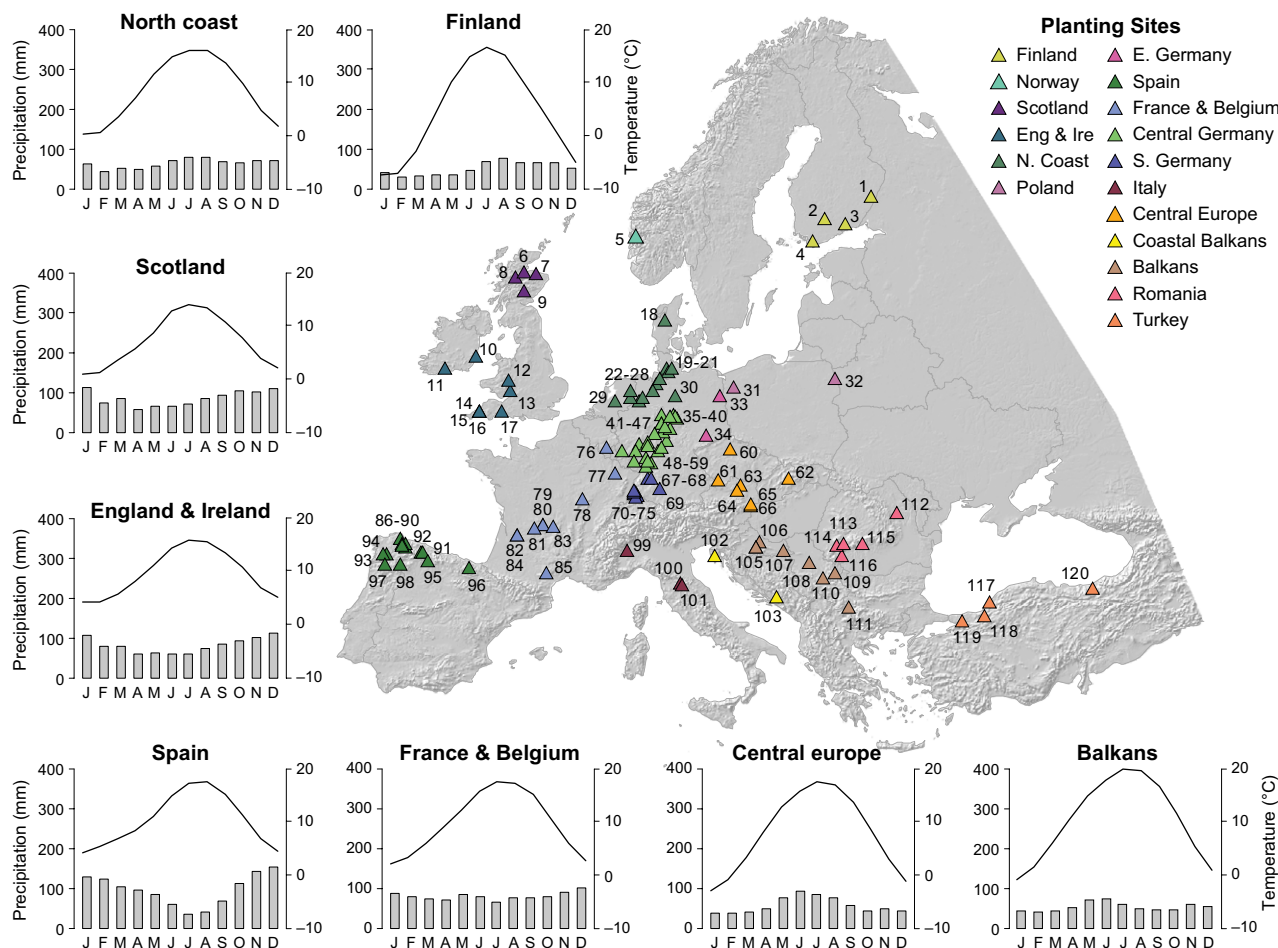
transcription. The resulting database has over 2800 entries (Appendix 1), representing 700 North American provenances tested at 120 European planting sites (Appendix 2). Height was used as a measure of performance as these data were consistently reported. All reported provenance and test site coordinates were cross-checked against their location descriptions and, if possible, linked and cross-checked with seed collection identifiers by the International Union of Forest Research Organization (IUFRO), which have been widely used in provenance trials. In case of significant discrepancies, data were removed unless unambiguous corrections could be made.

To allow for concise reporting of results, we grouped European test sites into 17 different regions that reflect different climatic regions and use national boundaries where possible (Fig. 1; Appendix 3). Likewise, all North American seed collection sites were assigned to 13 groups that represent similar climatic conditions but also genetic differences among populations (Fig. 2; Appendix 4). As an aid, we used multivariate regression tree analysis to cluster genotypes according to Hamann *et al.* (2011). This technique can only be applied to individual provenance trials or trial series with near-complete replication of genotypes, so that multiple results have to be interpreted jointly. While there is a clear distinction between the coastal and interior varieties of Douglas-fir, much of the species' genetic variation consists of latitudinal and altitudinal clines. For grouping across latitudinal clines, we used political boundaries for convenience and ease of communication. For east-to-west and altitudinal clines, distinguishing coastal, low elevation dry, and coast mountain groups, we use topographical and climatic data (for more details on the grouping see: Isaac-Renton, 2013).

Height data from provenance trials were normalized for each European planting site to account for different ages and various site factors unique to each provenance trial. Thus, provenance performance was evaluated strictly relative to other provenances at the same site, which applies to all analysis and interpretation in this article. To derive regional means of normalized provenance performance, an analysis of variance (ANOVA) was performed using a mixed model implemented by PROC MIXED of the SAS statistical software package (SAS Institute Inc., 2010, SAS 9.2 for Windows, Cary, NC, USA). North American source regions and European planting regions were specified as fixed effects. Planting sites within European regions and provenances within North American regions were specified as random effects. Regional means for fixed effects were estimated with the least squares means method, also implemented with PROC MIXED. Rank changes of provenances among regions were tested according to Gail & Simon (1985).

### *Climate data*

Climate data were generated using two custom software packages, ClimateWNA for western North America (Wang *et al.*, 2012; Hamann *et al.*, 2013) and ClimateEU, an equivalent, unpublished software package for Europe (<http://ualberta.ca/~ahamann/climate.html>). The ClimateWNA and ClimateEU are software front-ends for interpolated climate



**Fig. 1** European planting sites coloured by region, with selected regional climate diagrams displaying average monthly temperature (°C) and average monthly precipitation (mm). Complete location and growth data for individual planting sites are provided in Appendix 1 and 2. Complete regional climate and sample size statistics are shown in Appendix 3.

databases generated with the Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly *et al.*, 2008). The software was used to query climate data for all collection and planting locations used in this study, and to generate gridded climate surfaces for Europe at 1 km resolution in Albers Equal Area projection to be used for climate envelope model projections.

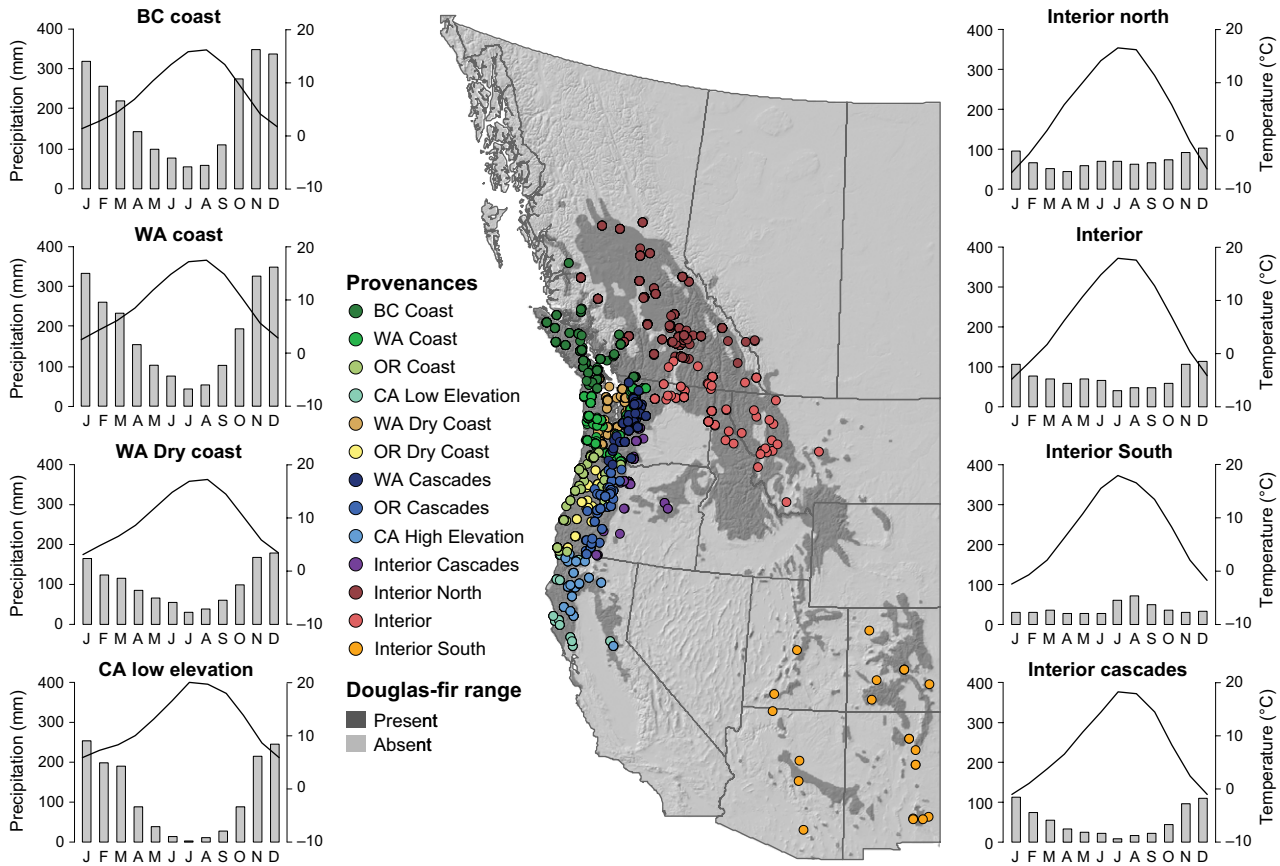
We use the 30 year climate normal period from 1961 to 1990 as a climate reference period, and a 15 year climate average from 1996 to 2009 to represent recent climate change. Eight biologically relevant climate variables were selected that account for most of the variance in climate data while avoiding multicollinearity: mean annual precipitation (MAP), mean summer precipitation (MSP), precipitation as snow (PAS), mean annual temperature (MAT), mean warmest month temperature (MWM), mean coldest month temperature (MCM), growing degree-days above 5 °C (GDD) and Hargreave's climatic moisture deficit (CMD). The variables are explained in detail in Wang *et al.* (2012).

To represent potential future climates, we use projections of the CMIP3 multimodel data set, corresponding to the fourth

IPCC assessment report (Meehl *et al.*, 2007). To limit the modelling effort, we work with an ensemble mean of all available model runs for the A2 emission scenario but, similar to Fordham *et al.* (2011), excluded poorly validated AOGCMs (MIROC3.2, MRI-CGCM2.3.2, MIROC3.2, IPSL-CM4, FGOALS-g1.0, GISS-ER, GISS-EH, and GISS-AOM). Model projections were added as anomalies to the 1 km resolution baseline data using the delta method and bilinear interpolation, also implemented with the ClimateEU and ClimateWNA software packages (Wang *et al.*, 2012; Hamann *et al.*, 2013).

### Species distribution modelling

We use the Random Forest ensemble classifier (Breiman, 2001), implemented with the *randomForest* v.4.6-6 package for the R programming environment (R Core Team, 2012) to predict which North American provenances best match European climate conditions. Random Forest was selected for its ability to output a class-based variable as well as for its predictive accuracy (e.g. Roberts & Hamann, 2012a). The model was



**Fig. 2** Western North American seed collection sites, coloured by regional groups of provenances. The Douglas-fir species range is shown in dark grey. Selected climate graphs indicate regional averages for provenance locations for the variables average monthly temperature (°C) and average monthly precipitation (mm). Complete regional climate and sample size statistics are provided in Appendix 4.

trained using North American climate data for provenance locations as predictor variables, and North American groups of provenances (Fig. 2) as a categorical response variable with 13 classes. Projections of North American provenance groups were then made for Europe from 1 km resolution climate surfaces for the 1961–1990 normals, the recent 1997–2009 average, and for ensemble projections for the 2020s, 2050s and 2080s. To reduce overpredictions (there were no absence values in the provenance data set), the provenance projections were clipped to the projected presence range of Douglas-fir in Europe using a second Random Forest run based on Douglas-fir presence–absence records from more than 50 000 forest inventory plots in the United States and Canada (see Roberts & Hamann, 2012a for complete methodology).

It has been demonstrated that ecological niche model projections into climate arrangements or extremes without analogues in the model training data can compromise model performance (Williams & Jackson, 2007; Roberts & Hamann, 2012b). To quantify the dissimilarity between North American climate conditions used for model training (1961–1990 normals) and European climate conditions for predictions (1961–1990, 2080), we use the multivariate Mahalanobis distance measure. The Mahalanobis metric is an Euclidian distance of principal components, and thus accounts for covariance among the original

climate variables. Distance calculations were performed from European grid cells to North American reference points with PROC PRINCOMP, SCORE and FASTCLUS according to SAS Knowledge Base Sample 30662 of the SAS statistical software package (SAS Institute Inc., 2010). Because it is not computationally feasible to create a complete distance matrix for every possible combination of 1 km grid cells among the North American and European climate data sets, we used 770 reference points representing average climate conditions at the finest level of western North American ecosystem delineations (see Roberts & Hamann, 2012b for complete methodology). The final no-analogue maps therefore represent the minimum climate distance of each European grid cell to any of 770 North American climate reference points.

**Results**

*Observed provenance performance*

The ANOVA of growth response among North American provenances in Europe shows that all fixed effects and their interaction were significant (Table 1) and that 7% of all rank changes are significant ( $\alpha = 0.05$ ), indicating

**Table 1** Type III sum of squares analysis of variance table with fixed effects being regional groups of planting sites in Europe (EU) as shown in Fig. 1 and regional groups of North American provenance collections (NA) as shown in Fig. 2. Planting sites within EU regions and provenances within NA regions were defined as random effects and therefore not tested for significance

Variable	MS	DF <sub>num</sub>	DF <sub>den</sub>	F	P
EU	0.64	16	104	4.34	<0.0001
NA	9.98	12	645	3.34	<0.0001
EU × NA	1.19	113	1896	2.24	<0.0001
Site (EU)	1.34	104	–	–	–
Prov (EU)	1.12	645	–	–	–
Residual	0.61	1896	–	–	–

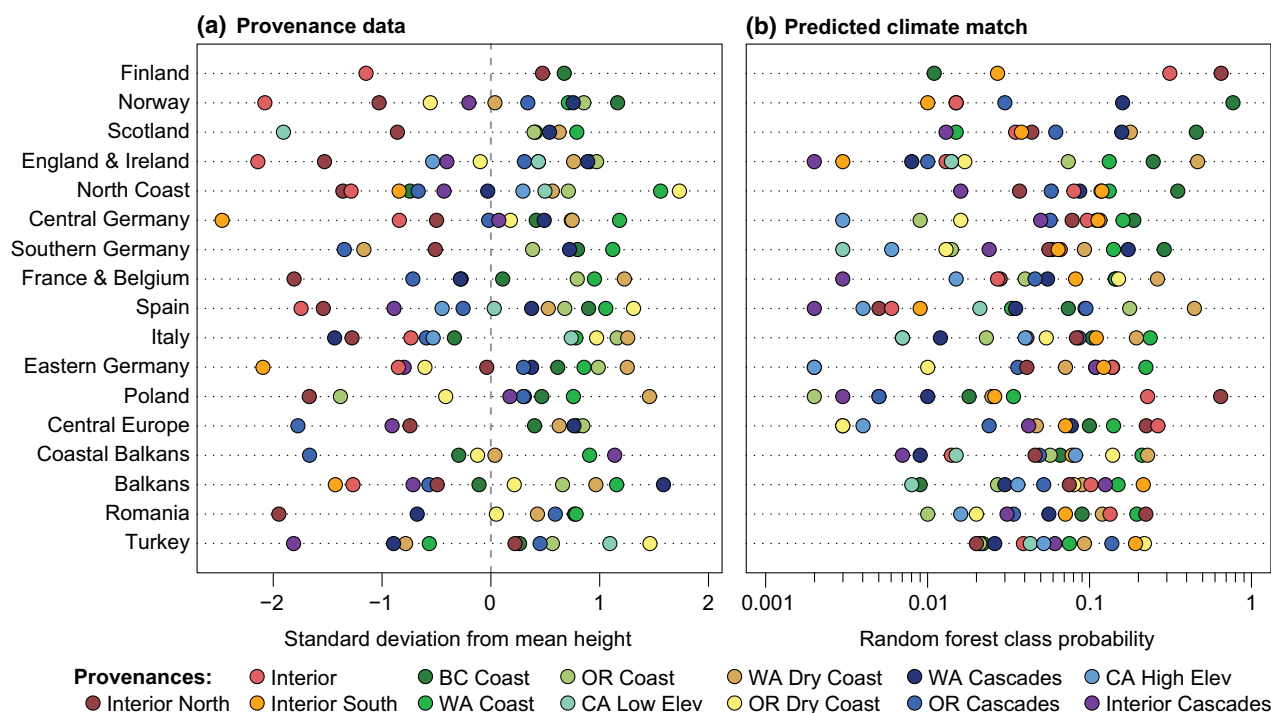
that different North American provenance groups are best suited to different European regions in a number of cases. Random effects were not tested as per definition. We explore the nature of the significant interaction by means of a dot plot (Fig. 3a). Additional statistics to complement the dot plot are provided in Table 2 (left panel), and include the number of European planting sites on which the dot-plot means are based, the total number of North American provenances on which the dot-plot means are based and the average standard

deviations of dot-plot means. A full table of means, sample sizes and standard deviations for each mean is provided in Appendix 5.

The data suggest that northern sources from Washington and British Columbia perform well in northern European sites such as Finland, Norway, Scotland, England and Ireland. Seed sources from the higher elevation regions of the Washington Cascades perform well in some areas of Northern Europe, Central Europe and interior regions in the Balkans. Across Western Europe, coastal Washington populations perform well, with dry coastal sources emerging as good performers in more eastern (i.e. Poland and Eastern Germany) and southern areas (i.e. Spain and Italy). All performance values are expressed as average standard deviations of height from the planting site means, and standard errors tended to be less than one half of one standard deviation, with the exception of the Coastal Balkans, Romania and Turkey, where lower confidence in means can be attributed to fewer provenances and test sites.

*Model statistics and no-analogue climates*

Cross-validation statistics for the presence–absence Random Forest model, based on withholding one-third of the data, was previously quantified with an Area



**Fig. 3** Observed performance of provenances at European test sites (a), and the climatic match between North American source locations and European planting sites according to a Random Forest climate envelope model (b). Note that not all provenances were planted within all European regions and that provenances predicted with probabilities below  $10^{-3}$  are not shown. Additional statistics corresponding to this Figure are shown in Table 2 and Appendix 5.

**Table 2** Supplementary statistics for Fig. 3, showing the number of planting sites in each European region ( $N_{\text{sites}}$ ), the number of provenances tested in each region ( $N_{\text{prov}}$ ) and the average standard error of regional least squares means of provenances ( $\overline{SE}$ ). The right panel shows the predicted gain (in units of standard deviations from an overall mean of zero) if forest resource managers were to select the top three provenance groups predicted by the Random Forest model for reforestation (1st, 2nd, 3rd). The last column shows the Pearson correlation coefficient between observed provenance performance (Fig. 3a) and climate match predicted by the climate envelope model (Fig. 3b)

Region	Provenance data			Predicted gain			$r$
	$N_{\text{sites}}$	$N_{\text{prov}}$	$\overline{SE}$	1st	2nd	3rd	
Balkans	8	57	0.32	-1.43	1.16	-0.71	-0.41
Central Europe	7	69	0.37	-0.74	0.79	0.40	-0.01
Central Germany	25	177	0.17	0.42	1.18	0.75	0.04
Coastal Balkans	2	11	0.68	0.04	0.91	-0.12	0.20
Eastern Germany	2	58	0.48	0.86	0.38	-0.85	-0.09
England & Ireland	8	81	0.31	0.76	0.44	0.91	0.40
Finland	4	8	0.46	0.47	-1.15	0.67	-0.07
France & Belgium	10	89	0.30	1.23	-0.27	0.95	0.65
Italy	3	72	0.33	0.78	1.26	-0.34	0.34
North Coast	14	200	0.27	-0.74	1.56	-0.84	-0.25
Norway	1	48	0.52	1.16	0.76	0.34	0.46
Poland	2	27	0.50	-1.67	0.76	1.46	-0.59
Romania	5	10	0.64	-1.95	0.78	0.43	-0.38
Scotland	4	35	0.43	0.41	0.63	0.54	0.36
Southern Germany	9	18	0.35	0.80	0.72	1.12	0.54
Spain	13	121	0.20	0.53	0.68	-0.26	0.40
Turkey	4	31	0.60	1.46	0.45	-0.78	0.35

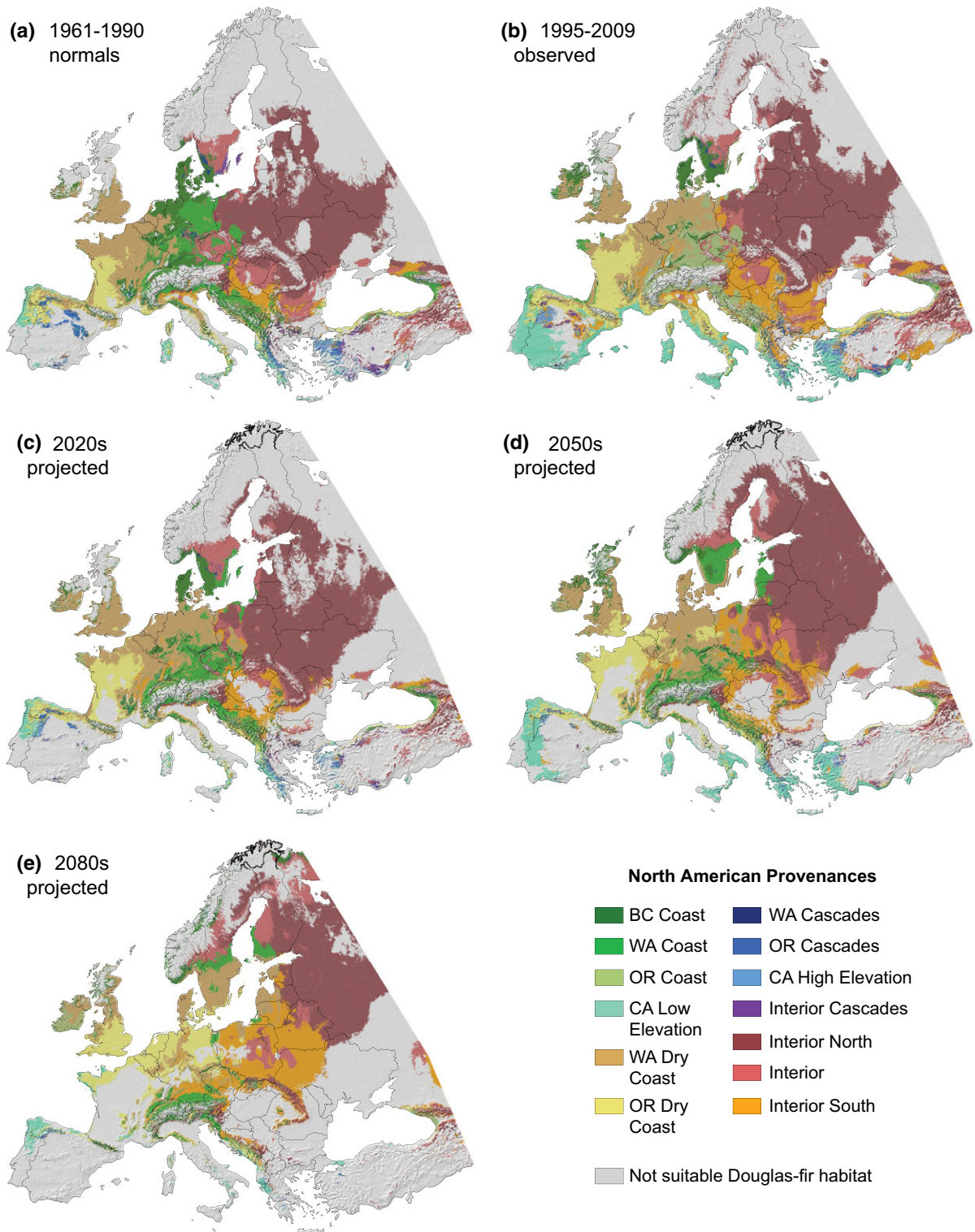
Under the receiver operating characteristic Curve (AUC) of 0.94 for Douglas-fir (Roberts & Hamann, 2012a). The multiprovenance Random Forest model developed for this study had an out-of-bag misclassification error rate of 3.25% and a Fleiss' Kappa statistic of 0.96. Random Forest importance values, ranking the variables according to how often they were used in regression tree splits across all trees are provided in Appendix 6. Annual moisture and winter temperature variables were most suited to distinguish among provenance groups, while summer temperature and other precipitation variables had lower importance values.

European climate dissimilarity maps for the 1961–1990 period and the 2080s period are provided in Appendix 7. Multivariate distance measurements between modern 1961–1990 North American climates and European climates for the modern 1961–1990 and future periods show generally low dissimilarity, lacking no-analogue climates that have been shown to compromise model performance (cf. Roberts & Hamann, 2012b). Some localized exceptions of higher dissimilarity appear in both the 1961–1990 and future climates in Georgia, bordering the Black Sea, at the southern base of the Alps in Italy, Slovakia, and Croatia, and at the northern base of the Alps in Northern Switzerland, Southern Germany and Austria. For the 2080s climate projection, dissimilarity increases to moderate levels

through the northern Baltic area and through the Carpathian Mountains.

#### *Provenance predictions*

The correlation between observed provenance performance (Fig. 3a) and climate match predicted by the climate envelope model (Fig. 3b) is positive for Western Europe (median Pearson correlation coefficient of 0.40) with the best correlations for France & Belgium and Southern Germany (Table 2). For Eastern Europe, correlations were negative (median  $r = -0.13$ ) with the strongest negative correlations for Poland and the Balkans. In addition, we report the productivity gain if a forester was to use any of the top three provenances recommended by the bioclimate envelope model. Performance of the top three provenances would be on average 0.34 standard deviations above the average of all tested provenances. Poor Random Forest predictions are particularly apparent for central and eastern European regions with continental climate conditions, including the Balkans, Romania, Eastern Germany, Central Europe, Poland and Finland. Here, the top three Random Forest predictions show field performance that is on average not better than the zero site mean ( $-0.05$ ). For the remaining western European regions, Random Forest-based provenance



**Fig. 4** Random Forest predictions of suitable North American Douglas-fir provenances for Europe under 1961–1990 climate normal conditions, a recent 15 year climate average from 1995 to 2009, and ensemble projections for the 2020s, 2050s and 2080s under the A2 emission scenario.

selections would yield a growth improvement of 0.50 standard deviations above the average of all tested provenances.

When Random Forest projections are expanded to all of Europe, rather than just the provenance test sites, it is apparent that coastal Douglas-fir populations are the top-ranked seed source in Western Europe under 1961–1990 climate (Fig. 4). In contrast, populations from the interior distribution of Douglas-fir in North America are predicted to match climate conditions in Eastern and Southern Europe the best (Fig. 4). Provenance predictions under the observed 1995–2009 climate period are similar in direction and magnitude to model predictions under the 2020s climate change scenarios, showing a trend of southerly and dry provenances shifting northward throughout Europe. For example, provenances from dry coastal Washington replace provenances from the wetter Washington and British Columbia coast throughout Northern Germany, while habitat for provenances from the dry southern interior of North America expand in the southeast. By the 2050s, Oregon dry coast provenances currently best suited to Southwestern France may be suitable for plantations in Belgium, the Netherlands, Northern Germany, and the southern United Kingdom.

## Discussion

### *Climate match vs. provenance performance*

Different growth responses of North American populations in different European planting regions highlight the importance of selecting planting stock that is genetically adapted to suitable environmental conditions. Interactions among provenance groups and climate regions also imply that climate change is likely to reduce forest health and productivity throughout the species range, not just at a species' southern and low elevation range limits. This is because all locally adapted populations experience a mismatch between new climate conditions and their individual climate niches to which they are adapted. For Douglas-fir in North America, locally adapted populations in the north may actually be more vulnerable to climate change than those in the south (Chen *et al.*, 2010).

Similar principles apply for introduced species. Introduced provenances that have proven superior for a particular region in the past, may no longer be the best choice for reforestation under changing climates. The meta-analysis of 120 European provenance trials revealed north–south clines in optimal performance in western European sites that mirror north–south clines of provenance differentiation in the native range of the

coastal variety. The Random Forest model was generally well suited to predict the best performing provenances based on a multivariate climate match along those north–south clines. However, the multivariate climate match was not a good indicator to predict optimal growth performance for the interior variety of Douglas-fir: the model systematically failed to predict superior provenance performance of coastal North American provenances under continental climate conditions of Eastern Europe.

There are a number of potential reasons for such discrepancies that could include methodological, experimental or biological causes. The first issue is that we extrapolate geographically beyond model training data, and therefore the model may simply fail in Eastern Europe by encountering no-analogue climate conditions. We could exclude this explanation because climate dissimilarity to North American model training data is not apparently different among Eastern and Western Europe (Appendix 7), and not at a magnitude where it has been shown to compromise model accuracy (Roberts & Hamann, 2012b). An alternate explanation lies with the provenance trials themselves: young provenance trials could be misleading if they were as yet untested by extreme weather events typical of the region, thereby allowing more poorly adapted, but faster-growing, populations to temporarily outperform more suitable genotypes. Some eastern planting sites have indeed been evaluated below age 10, but important counterexamples exist as well: provenance trials in Finland and Croatia are several decades old.

### *Capacity adaptation vs. survival adaptation*

The distribution of temperate tree species is typically restricted by a trade-off between their ability to survive extreme environmental events and their growth capacity to compete with other species for light (Leinonen & Hanninen, 2002). Experimental test plantations reliably reveal the capacity for growth among different species or among different genotypes of the same species. However, they can only reveal survival adaptations if an extreme event occurs at the test site and the life stage of the tree where it is vulnerable. For example, an extreme drought event may reveal different survival among genotypes at the sapling stage when root systems are relatively small, but a comparable drought event may not have any effect in the same plantation at age 30. Therefore, results from provenance field trials should be supplemented by physiological tests before making confident choices of seed transfers to new locations.

In the case of Douglas-fir, it has long been known, based on physiological tests in provenance trials, that



interior provenances have less growth potential but are also far more drought tolerant and drought resistant than the coastal variety (Ferrell & Woodard, 1966; Pharis & Ferrell, 1966; Kavanagh *et al.*, 1999). Similarly, cold tolerance of the interior variety is far higher, and the coastal variety can sustain very high mortality and frost damage when planted under continental climates (e.g. Rehfeldt, 1977). Thus, when combining the meta-analysis of differential provenance performance across 120 test sites with additional physiological knowledge of the coastal vs. interior varieties, the Random Forest projections that are based on a climate matching approach between North American sources and European target environments appear to be largely sensible guidelines for seed use. Where recommendations for seed use shown in Fig. 3a vs. 3b significantly diverge, the Random Forest model always errs on the side of safer choices with respect to survival adaptation. For continental climates in Finland, Central and Eastern Europe, the interior varieties are likely to be more appropriate and safer choices for reforestation, even though provenance trials demonstrate that the coastal variety can have higher productivity.

We therefore propose that the North America-trained bioclimate envelope model appears to provide appropriate guidelines for seed transfer to Europe when considering additional qualitative information on survival adaptation, even though the model partially fails in the strictly quantitative validation against growth data as shown in Fig 3. By implication, bioclimate envelope models should be useful tools to guide seed transfer under climate change, both in Europe and within its native range. Because of the conceptual shortcomings of provenance tests to reliably detect important survival adaptations, we propose that climate envelope model projections should always be considered as well before making seed transfer decisions to address climate change.

#### *Climate-based seed transfer*

Model projections for Europe under 1961–1990 reference climate conditions, representing a climate period without a strong anthropogenic warming signal, and also representing a period where most of the provenance trials included in this study were grown and evaluated, generally conformed to previously published conclusions from provenance data. For example, coastal Washington sources from both high precipitation areas adjacent to the coast and from relatively drier areas further inland have been top performers across Western Europe (Fig. 4a). In addition, our meta-analysis of provenance data showed that dry coastal sources were more successful in southern and eastern European

planting sites and seed sources from more northern locations have performed well in northern European planting locations.

Under the observed 1995–2009 climate period, representing approximately a 30 year warming trend relative to the 1961–1990 baseline (mid-point 2002 minus mid-point 1975), the Random Forest model suggests that the climate envelope of more southerly and dry populations shifted northward (Fig. 4b). Those projections driven by observed climate trends very closely resemble multimodel ensemble future projections for the 2020s (Fig. 4c), which present a strong argument for making changes to the reforestation stock when establishing new Douglas-fir plantations in Europe. While we provide corresponding projections for the 2050s and 2080s, it is generally well known that projections further into the future come with large uncertainties, which we do not quantify in this study.

That said, it has been argued that implementation of climate change adaptation strategies in forestry should rely on observed trends and short term projections with a 10–20 year planning horizon (Gray *et al.*, 2011). Reforestation stock must survive current climate environments, and given that seedlings are most vulnerable to suboptimal climates, we cannot plant for 2050s or 2080s projections that have yet to materialize. With a shorter planning horizon, genotypes will only be well adapted during establishment and the first part of the rotation length. While this may be an imperfect solution, it is an improvement over the status quo of management based on historical climates that already appear to have shifted substantially.

#### **Acknowledgements**

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#### **References**

- Aitken SN, Yeaman S, Holliday JA, Wang TL, Curtis-Mclane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.
- Allen CD, Macalady AK, Chenchouni H *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Ballian D, Mikic T, Pintaric K (2002) Provenance trials with douglas fir (*Pseudotsuga menziesii* Mirb. Franco) at Blinje site near Kresevo. *Works of the Faculty of Forestry, University of Sarajevo*, **1**, 9–18.
- Biro Y, Burzynski G (1981) Analyse comparée d'un test de provenances de Douglas installé en France et en Pologne [Comparative analysis of a provenance trial of Douglas fir set up in France and Poland]. *Revue Forestière Française*, **33**, 116–126.

- Breiman L (2001) Random forests. *Machine Learning*, **45**, 5–32.
- Chen PY, Welsh C, Hamann A (2010) Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. *Global Change Biology*, **16**, 3374–3385.
- Daly C, Halbleib M, Smith JI *et al.* (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, **28**, 2031–2064.
- Ferrell WK, Woodard ES (1966) Effects of seed origin on drought resistance of Douglas-Fir (*Pseudotsuga Menziesii*) (Mirb) Franco. *Ecology*, **47**, 499–503.
- Fordham DA, Wigley TML, Brook BW (2011) Multi-model climate projections for biodiversity risk assessments. *Ecological Applications*, **21**, 3317–3331.
- Gail M, Simon R (1985) Testing for qualitative interactions between treatment effects and patient subsets. *Biometrics*, **41**, 361–372.
- Gray LK, Hamann A (2011) Strategies for reforestation under uncertain future climates: guidelines for Alberta, Canada. *PLoS ONE*, **6**, e22977.
- Gray LK, Hamann A (2013) Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change*, **117**, 289–303.
- Gray LK, Gylander T, Mbogga MS, Chen PY, Hamann A (2011) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecological Applications*, **21**, 1591–1603.
- Hamann A, Aitken SN (2013) Conservation planning under climate change: accounting for adaptive potential and migration capacity in species distribution models. *Diversity and Distributions*, **19**, 268–280.
- Hamann A, Gylander T, Chen PY (2011) Developing seed zones and transfer guidelines with multivariate regression trees. *Tree Genetics & Genomes*, **7**, 399–408.
- Hamann A, Wang TL, Spittlehouse DL, Murdock TQ (2013) A comprehensive, high-resolution database of historical and projected climate surfaces for western North America. *Bulletin of the American Meteorological Society*, **94**, 1307–1309.
- Hampe A (2004) Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, **13**, 469–471.
- Hermann RK, Lavender DP (1999) Douglas-fir planted forests. *New Forests*, **17**, 53–70.
- Isaac-Renton M (2013) Guiding Douglas-fir seed selection in Europe under changing climates: bioclimatic envelope model predictions vs. growth observed in provenance trials. MSc Thesis, University of Alberta, Edmonton, AB, Canada.
- Isajev V, Lavadinovi V (2003) Douglas-fir provenance tests in Serbia. In: *Conifers Network, Report of the Fourth Meeting*. (eds Koskela J, Samuel CJA, Matyas C, Fady B), pp. 61–65. Biodiversity International, Rome, Italy.
- Kavanagh KL, Bond BJ, Aitken SN, Gartner BL, Knowe S (1999) Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. *Tree Physiology*, **19**, 31–37.
- Kenk G, Thren M (1984) Ergebnisse verschiedener Douglasienprovenienzversuche in Baden-Württemberg. Teil I. Der Internationale Douglasien-Provenienzversuch 1958 [Results of different Douglas-fir provenance trials in Baden-Württemberg. Part I: The International Douglas-fir Provenance Trial 1958]. *Allgemeine Forst und Jagdzeitung*, **155**, 1658–1184.
- Kleinschmit J, Bastien JC (1992) IUFRO's role in Douglas-fir [*Pseudotsuga Menziesii* (Mirb.) Franco] tree improvement. *Silvae Genetica*, **41**, 161–173.
- Leinonen I, Hanninen H (2002) Adaptation of the timing of bud burst of Norway spruce to temperate and boreal climates. *Silva Fennica*, **36**, 695–701.
- Mckenney D, Pedlar J, O'Neill G (2009) Climate change and forest seed zones: past trends, future prospects and challenges to ponder. *Forestry Chronicle*, **85**, 258–266.
- Meehl GA, Stocker TF, Collins WD *et al.* (2007) Global climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), pp. 747–845. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- O'Neill GA, Hamann A, Wang TL (2008) Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology*, **45**, 1040–1049.
- Pedlar JH, Mckenney DW, Beaulieu J, Colombo SJ, McLachlan JS, O'Neill GA (2011) The implementation of assisted migration in Canadian forests. *Forestry Chronicle*, **87**, 766–777.
- Pedlar JH, Mckenney DW, Aubin I *et al.* (2012) Placing forestry in the assisted migration debate. *BioScience*, **62**, 835–842.
- Perić S, Jazbec A, Tijardović M, Margaletić J, Ivanković M, Pilaš I, Medak J (2009) Provenance studies of Douglas fir in the locality of 'Kontija' (Istria). *Periodicum Biologorum*, **111**, 487–493.
- Pharis RP, Ferrell WK (1966) Differences in drought resistance between coastal and inland sources of Douglas fir. *Canadian Journal of Botany*, **44**, 1651–1659.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, Available at: <http://www.R-project.org>. (accessed 12 September 2012).
- Rehfeldt GE (1977) Growth and cold hardiness of intervarietal hybrids of Douglas-Fir. *Theoretical and Applied Genetics*, **50**, 3–15.
- Rehfeldt GE, Jaquish BC (2010) Ecological impacts and management strategies for western larch in the face of climate-change. *Mitigation and Adaptation Strategies for Global Change*, **15**, 283–306.
- Roberts DR, Hamann A (2012a) Method selection for species distribution modelling: are temporally or spatially independent evaluations necessary? *Ecography*, **35**, 792–802.
- Roberts DR, Hamann A (2012b) Predicting potential climate change impacts with bioclimate envelope models: a palaeoecological perspective. *Global Ecology and Biogeography*, **21**, 121–133.
- Schober R (1959) Ergebnisse von Douglasien-Provenienzversuchen in Deutschland, Holland und Dänemark. *Allgemeine Forst- und Jagdzeitung*, **14**, 145–152.
- Stimm B, Dong PH (2001) Der Douglasien-Herkunftsversuch Kaiserslautern nach neun Jahrzehnten Beobachtung [The Kaiserlautern Douglas fir provenance trial after nine decades of observation]. *Forstwissenschaftliches Centralblatt vereinigt mit Tharandter forstliches Jahrbuch*, **120**, 173–186.
- Ukrainetz NK, O'Neill GA (2009) Adapting to adaptation: assisted migration addresses climate change. *Association of BC Forest Professionals*, **16**, 16–17.
- Wang TL, Hamann A, Spittlehouse DL, Murdock TQ (2012) ClimateWNA: high-resolution spatial climate data for western North America. *Journal of Applied Meteorology and Climatology*, **51**, 16–29.
- Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix 1.** Database of North American provenance performance at European planting sites. Variables include the provenance name or ID as reported in the original publication (Provenance name), the Canadian province or US state of origin (State), the provenance source location in latitude (Lat) and longitude (Long) in decimal degrees, and elevation in metres (Elev), an ID assigned by the International Union of Forest Research Organizations (IUFRO ID, where available), planting site names (Site name) and number (Site no.) used in this study and corresponding to Fig. 1 and Appendix 2, mean height of provenances in metres (Height, m), and in standard deviations from the planting site mean (Height, StDev).

**Appendix 2.** List of European planting sites by country with the associated study reference. For each planting site, the site name (Site name), site number as in Fig. 1 and Appendix 1 (Site no.), and the site latitude (Lat) and longitude (Long) in decimal degrees, and site elevation in metres (Elev) is given. Further, we report the age of the plantation in years (Age), the average tree height at this age in metres (Height), and the European region into which the site was grouped for analysis (Region).

**Appendix 3.** Sample size and climate statistics for European regions, indicating the number of test sites that represent the group ( $N_{\text{sites}}$ ), how many of 13 North American provenance regions were tested at these sites ( $N_{\text{NA}}$ ), and the total number of individual provenances tested ( $N_{\text{prov}}$ ). Climatic characterization of the test sites include regional averages of mean annual precipitation (MAP), mean summer precipitation (MSP), precipitation as snow (PAS), mean annual temperature (MAT), mean warmest month temperature (MWM), mean coldest month temperature (MCMT), growing degree-days above 5 °C (DD5) and Hargreaves climatic moisture deficit (CMD).

**Appendix 4.** Sample size and climate statistics for North American groups of provenances, indicating the total number of provenances that represent each group ( $N_{\text{prov}}$ ), and at how many of the 17 European planting regions these seed sources were planted ( $N_{\text{EU}}$ ). Climatic characterization of the provenance source locations include regional averages of mean annual precipitation (MAP), mean summer precipitation (MSP), precipitation as snow (PAS), mean annual temperature (MAT), mean warmest month temperature (MWM), mean coldest month temperature (MCMT), growing degree-days above 5 °C (DD5) and Hargreaves climatic moisture deficit (CMD).

**Appendix 5.** Least squares means of height (Height) with standard errors (SE) in units of standard deviations from the overall site mean by North American source region (NA region) and European planting region (underlined). Sample size statistics include the number of sites ( $N_{\text{sites}}$ ) which contained a provenance from the associated North American source region and the number of provenances ( $N_{\text{prov}}$ ) from that source region. This table corresponds to height data shown in Fig. 3a.

**Appendix 6.** Random Forest importance values for climate predictor variables. Importance values are based on an out-of-bag evaluation and represent the count of votes cast for the correct class. To evaluate the importance of predictor variables, each variable receives a random permutation of its values, and its importance value is then calculated as the original number of votes for the correct class minus the number of votes for the correct class after random permutation, averaged across all trees.

**Appendix 7.** Map showing the minimal dissimilarity between 770 selected North American climate reference points and European climate conditions for (a) the 1961–1990 normal period and (b) the projected climate for the 2080s period under the A2 scenario. Dissimilarity is measured as a multivariate Mahalanobis distance based on eight climate variables.