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Species distribution models may misdirect assisted migration: insights from the introduction of Douglas-fir to Europe

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Abstract. Species distribution models (SDMs), which statistically relate species occurrence to climatic variables, are widely used to identify areas suitable for species growth under future climates and to plan for assisted migration. When SDMs are projected across times or spaces, it is assumed that species climatic requirements remain constant. However, empirical evidence supporting this assumption is rare, and SDM predictions could be biased. Historical human-aided movements of tree species can shed light on the reliability of SDM predictions in planning for assisted migration. We used Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a North American conifer introduced into Europe during the mid-19th century, as a case-study to test niche conservatism. We combined transcontinental data sets of Douglas-fir occurrence and climatic predictors to compare the realized niches between native and introduced ranges. We calibrated a SDM in the native range and compared areas predicted to be climatically suitable with observed presences. The realized niches in the native and introduced ranges showed very limited overlap. The SDM calibrated in North America had very high predictive power in the native range, but failed to predict climatic suitability in Europe where Douglas-fir grows in climates that have no analogue in the native range. We review the ecological mechanisms and silvicultural practices that can trigger such shifts in realized niches. Retrospective analysis of tree species introduction revealed that the assumption of niche conservatism is erroneous. As a result, distributions predicted by SDM are importantly biased. There is a high risk that assisted migration programs may be misdirected and target inadequate species or introduction zones.

Key words: assisted migration; climate matching; niche conservatism; niche shifts; no-analog climate; *Pseudotsuga menziesii*; species distribution models; species range.

INTRODUCTION

Climate change predictions point toward more frequent and severe drought events, which are expected to threaten the biodiversity, resilience, and productivity of forest ecosystems in the coming decades (Lindner et al. 2010). Proactive management actions have been proposed to maintain forest ecosystem services. The assisted migration of tree species to areas newly suitable under future climates has been proposed as a strategy to anticipate climate change. Species distribution models (SDMs) that generate projections of species ranges under current and future climatic conditions are widely used for guiding assisted migration plans. Indeed, SDM predictions have been employed to target endangered species, to delimitate areas where they could potentially grow in the future and to assess the risk of invasion after introduction. (Gray et al. 2011, Araújo and Peterson 2012, Duvoneck and Scheller 2015, Hällfors et al. 2016a). The development of SDMs in the last few decades has been characterized by an increasingly mechanistic representation

of ecophysiological processes underlying species response to climate. However, the most frequently used SDMs are still correlative niche models that statistically relate observations of species occurrence with coarse-scale climatic variables; as they are easier to implement and less heavily parametrized than process-based models (Morin and Lechowicz 2008, Dormann et al. 2012). Many demonstrations of the high predictive power of correlative niche models when applied to current native ranges have been made (Elith et al. 2006). However, they rely on important ecological assumptions that have not been ascertained and the reliability of projections to new geographical areas or future climates is often questioned (Pearman et al. 2008, Araújo and Peterson 2012, Veloz et al. 2012).

Correlative SDMs are based on Hutchinson's niche theory, in which multiple environmental factors jointly define the potential geographical range of a given species (Hutchinson 1957). Hutchinson distinguishes the "fundamental niche" from the "realized niche" of a species. While the former is a conceptual hypervolume delimited by the combination of environmental conditions that permits survival, growth, and reproduction of individuals; the second is a subset of this hypervolume constrained by biotic interactions (Hutchinson 1957). This

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definition of the realized niche has since been extended to refer to any projection of the observed geographical distribution of a species in the environmental space, regardless of the particular mechanism that limits the species' fundamental niche (Colwell and Rangel 2009).

Niche models are calibrated on observed species presences. Therefore, what they actually represent is not the fundamental niche, but the realized niche (Morin and Lechowicz 2008). As a result, for model predictions to be accurate when projecting to new temporal or geographical frames, both the fundamental and the realized niches must be conserved (Pearman et al. 2008, Veloz et al. 2012).

However, conservatism of the fundamental niche, which states that the environmental requirements of a given species remain identical across space or time, may be unwarranted, first and foremost because of genetic adaptation (Hällfors et al. 2016b). Indeed, wide-ranging species have been shown to differentiate into multiple genetically distinct populations that are adapted to local environments; and evidence of rapid genetic adaptation under climate change has been reported (Hoffmann and Sgrò 2011). Conservatism of the realized niche seems even more dubious than conservatism of the fundamental niche, given that modifications in inter-specific competition and changes in dispersal dynamics as well as in phenotypic plasticity (the ability of individual genotypes to express different phenotypes in varying environments) have all been identified as important mechanisms allowing species to adjust to non-optimal conditions under rapid climate change (Aitken et al. 2008, Nicotra et al. 2010).

Moreover, projections of niche models are particularly problematic in the absence of climate analogues between the domain of calibration and the domain of projection. This is because it cannot be inferred from presence observations that a species occupies its whole niche: the fundamental niche might actually be larger than the full set of environmental conditions available in the current species range (Pearman et al. 2008, Veloz et al. 2012). Finally, land-use and management practices are highly variable across space and time and influence the biotic and abiotic constraints that define species' realized niches, which weakens correlations between species presence and climatic conditions (Aitken et al. 2008).

Theoretical criticisms of the assumptions underpinning correlative niche modeling have been abundantly reviewed in biogeography and ecology literature (Guisan and Thuiller 2005, Pearman et al. 2008, Hoffmann and Sgrò 2011, Araújo and Peterson 2012). They highlight the urgent need for empirical assessments of the bias and uncertainties associated with SDM predictions to inform the debate on assisted migration (McLachlan et al. 2007, Richardson et al. 2009). Evidence of misleading predictions from correlative SDMs have come from experiments in controlled conditions (Davis et al. 1998), retrospective modelling of species distribution during the late glacial period according to pollen fossils (Veloz et al.

2012), manipulative displacement of species (Duncan et al. 2009), and analyses of invasive species spread (Broennimann et al. 2007).

In the present research, we studied the case of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to test the reliability of using correlative niche models for projections into exotic climatic conditions. Douglas-fir is native to the Western Coast of North America and was introduced in Europe during the mid-19th century, where it has since become one of the most important non-native timber species in terms of area planted and volume harvested (Hermann and Lavender 1999). However, important diebacks have been reported after the severe drought and heat wave that affected Western and Central Europe in 2003, revealing Douglas-fir's vulnerability to cumulated or severe soil water deficit (Sergent et al. 2014b). Commercial timber species are particularly targeted by assisted migration programs. Indeed, their long-generation time precludes rapid adaptation to climate change while reforestation provides the opportunity to establish stands composed of species and populations that are resilient to future climatic conditions. In this context, we examined niche conservatism for Douglas-fir by comparing the realized niches in the native and introduced ranges.

METHODS

Presence/absence data

For the North American native range, we assembled Douglas-fir occurrence data from forest inventories in British Columbia, Alberta, the United States, and Mexico (see Appendix S1). Absence data was compiled from vegetated areas where Douglas-fir was not observed. The presence and absence layers from the three countries were then merged to obtain a presence raster of 24599 cells and an absence raster of 47664 cells for the whole North American range, with a 2.5-arcminute resolution. Presence cells were classified as interior (*P. menziesii* var. *glauca*) or coastal (*P. menziesii* var. *menziesii*) based on the zonation presented in Snajberk and Zavarin (1976). The native presence/absence data set had a broad extent and a relatively coarse resolution. It was not only derived from herbaria records, but also from photo-interpreted data, and some of the plot coordinates had been fuzzed. Therefore, it cannot be excluded that isolated Douglas-fir trees, especially seedlings and saplings, were missed in this census, and that the occurrence of Douglas-fir stands rather than Douglas-fir trees was detected. As a consequence, our native model calibrated with this data set is not a species distribution model in the narrower sense. We nevertheless use the term "species distribution model (SDM)" hereafter because it is very commonly employed in literature to refer to niche models, including niche models calibrated on forest inventory data sets of species occurrence (Gibson et al. 2014, Henderson et al. 2014).

We used a European forest inventory database compiled as part of the FunDivEurope research project to validate the projections of the “native” Douglas-fir niche model in Europe (functional significance of forest diversity; UE collaborative project reference 265171, FP7-Environment). This database comprised national forest inventories from Finland, Sweden, Germany, Spain, Wallonia, France, and Romania (Appendix S1). Plot latitudes and longitudes were fuzzed up to 500 m. The data base contains 3788 plots where Douglas-fir is present for 227671 absence plots. The FunDiv data set is, to our knowledge, the most comprehensive data set merging national forest inventories at the European scale. However, several European countries where Douglas-fir is present are not covered by its extent. Therefore, we used growth data from Douglas-fir provenance trials that were set by the IUFRO in Europe (Kleinschmit and Bastien 1992) for a complementary visual validation of model predictions.

Our assumption was that native Douglas-fir populations show higher growth rates in sites of high habitat suitability where climate is optimal (Hirzel and Le Lay 2008). Therefore, we expected growth increment to be positively correlated with climatic suitability. The IUFRO database is composed of growth data from 108 plantations that were established in the late 1960s in 30 European countries where a total of 180 provenances were planted (Kleinschmit and Bastien 1992). The data base is characterized by an unbalanced design: not all native populations have been planted at all the trial sites, and measurements have been made at different ages. This is potentially problematic because the provenance can

impact growth performance independently of the climatic conditions at the sites of introduction. Indeed, for a similar level of climatic suitability, a site where many interior populations have been planted will show a lower average growth-rate than another one where coastal populations are more represented (Kleinschmit and Bastien 1992). We removed measurements taken before the age of seven years from the database and calculated the average annual growth for each site, based on the heights of the most represented and best performing provenances from Washington and Oregon. The seven-year filter threshold was chosen because tree height begins to increase linearly after age seven (J. C. Bastien, *personal communication*).

Climate data

We pre-selected an initial set of 23 climatic variables from the Worldclim climatic rasters version 1.4 (release 3) at a 2.5-arcminute resolution derived from 1950 to 2000 weather records (Hijmans et al. 2005). This initial set of 23 variables, which characterized regional climates, was used to test for niche conservatism (Table 1). As the source of climatic data may influence the result, we repeated the analysis with the same set of predictors derived from the CRU TS3.10 data set (Harris et al. 2014). Out of these 23 variables, only 13 predictors were included in the SDM of Douglas-fir (Table 1): the most correlated variables were identified by means of a principal components analysis (PCA) ordination plot and a Spearman correlation matrix. Whenever several variables were correlated, the least explanatory variables were eliminated: a preliminary Random Forest analysis was run to sort the variables in

TABLE 1. Bioclimatic variables used for testing niche conservatism and variable importance of predictors selected for species distribution models.

Variable	Definition	Variable importance (mean decrease in accuracy)
BIO1	annual mean temperature	
BIO2	mean diurnal range (mean of monthly [max temp – min temp])	0.120
BIO3	isothermality (BIO2/BIO7) ($\times 100$)	
BIO4	temperature seasonality (standard deviation $\times 100$)	0.147
BIO5	max temperature of warmest month	
BIO6	min temperature of coldest month	
BIO7	temperature annual range (BIO5 – BIO6)	
BIO8	mean temperature of wettest quarter	0.124
BIO9	mean temperature of driest quarter	
BIO10	mean temperature of warmest quarter	0.118
BIO11	mean temperature of coldest quarter	0.173
BIO12	annual precipitation	0.114
BIO13	precipitation of wettest month	
BIO14	precipitation of driest month	
BIO15	precipitation seasonality (coefficient of variation)	0.098
BIO16	precipitation of wettest quarter	
BIO17	precipitation of driest quarter	0.113
BIO18	precipitation of warmest quarter	
BIO19	precipitation of coldest quarter	
PETPGrSeas	April to September precipitation (growing season), Hargreaves' PET	0.171
Kc	Kira coldness index (Kira 1991)	
Kw	Kira warmness index (Kira 1991)	
CONc	Conrad's continentality index (Conrad 1946)	0.159

Note: PET, potential evapotranspiration.

order of importance, according to mean decrease in accuracy averaged across 20 forests.

Testing for realized niche conservatism

Following Broennimann et al. (2007), we ran a PCA on climatic variables to compare the distribution of native and introduced Douglas-fir in the resulting climatic space. All presence pixels from both the North American and European ranges were projected in the same climatic space. Because the North American data set contained a lot more presence plots than the European one, occurrences were weighted using argument `lw` of the `dudi.pca` function in package `ade4` to retain equal balance between North American and European presences. The circle of equilibrium contribution was represented in order to identify the climatic variables that contributed the most to the ordination. The radius of this circle equals the length of the vector representing a variable that would contribute equally to all the dimensions of the PCA space. Therefore, the variables that have vectors longer than this radius make a higher contribution than average (Borcard et al. 2011).

The magnitude and statistical significance of the climatic distance between the natural and introduced ranges were assessed with a between-class analysis (Dolédec and Chessel 1987). As in a classical analysis of variance, the variability (or inertia) associated with the first three PCA components was decomposed according to the partition between North American and European presences. We obtained a between-class inertia ratio, i.e., the percentage of inertia explained by the qualitative variable “continent,” which was further tested with 999 Monte Carlo permutations. We used the R packages `vegan` 2.3-0 (Oksanen et al. 2016) and `ade4` 1.7-2 (Dray and Dufour 2007).

Species distribution model

Presences/absences of Douglas-fir in the native range were related to the above-mentioned subset of 13 descriptors of the North American climate by means of a Random Forest algorithm. This unsupervised machine learning technique is constructed from multiple regression trees derived from bootstrap samples of the original data. Each node of each decision tree is obtained by splitting the data according to a randomly selected explanatory variable (Breiman 2001). This method has shown utility for mapping species distributions (Evans and Cushman 2009). We used the `RandomForest` 4.6-10 R package (Liaw and Wiener 2002). To prepare the presence/absence data set, we followed the sampling protocol from Worrall et al. (2013). Twenty data sets were constructed, each containing 100000 observations in order to build 20 “forests” of 500 trees. Each of the 20 forests was built using different randomly sampled training and testing data sets including 75% and 25% of observations, respectively. At each bootstrap iteration,

the tree grown with the training data set was used to predict presence/absence of the testing data set, also called the out-of-bag (OOB) sample. The misclassification error rates were thus calculated for each tree and averaged in order to obtain an out-of-bag estimate of error rate. The 20 forests were used to predict presence/absence probabilities for all of the North American and European ranges. The resulting 20 rasters of predicted probabilities were then averaged for mapping. We compared these predictions to observed occurrences of Douglas-fir in North America and Europe: AUC (area under the receiver operating curve; Swets 1988) and TSS (true skill statistics; Allouche et al. 2006) were computed and further averaged with the R package `ROCR` 1.0-7 (Sing et al. 2005). Average annual growth from the IUFRO trial sites was added for further visual validation of the model predictions in Europe.

RESULTS

Testing for realized niche conservatism

The PCA of the 23 bioclimatic variables for North American and European Douglas-fir presences revealed three significant axes, according to the broken stick model (De Vita 1979). Each of these three axes accounted for 41% (PC1), 27% (PC2), and 16% (PC3) of the correlations, respectively, adding up to more than 84% of correlations explained. Therefore, the reduced climatic space delimited by the first three components can be accepted as a good approximation of the realized climatic Douglas-fir niche.

Observations of presence locations in the PC1–PC2 reduced climatic space (accounting for >68% of the correlations) revealed that the realized Douglas-fir niche in North America and Europe were clearly distinct, with very limited overlap (Fig. 1A). PC1 discriminated native occurrences of *P. Menziesii* var. *glauca* in North America from occurrences of Douglas-fir in Europe. The circle of equilibrium contributions (Borcard et al. 2011) indicated that PC1 was related to continentality, more specifically to the range of temperatures between warm and cold season, while PC2, which sorted occurrences of *P. menziesii* var. *menziesii* in North America from those of the European Douglas-fir, was related to the distribution of precipitation across the year; and the total amount of precipitation during the wet season (Fig. 1B). PC3 (16% of the correlations) was positively correlated with mean annual precipitation and negatively correlated with warm temperatures in summer (Fig. 2). The European climatic niche overlapped with the North American native niche along this third climatic gradient. However, the European niche had a much reduced extent compared to the North American native niche.

Average temperature and precipitation encountered in the introduced range of Douglas-fir had analogues in a limited portion of the native range (Fig. 2).

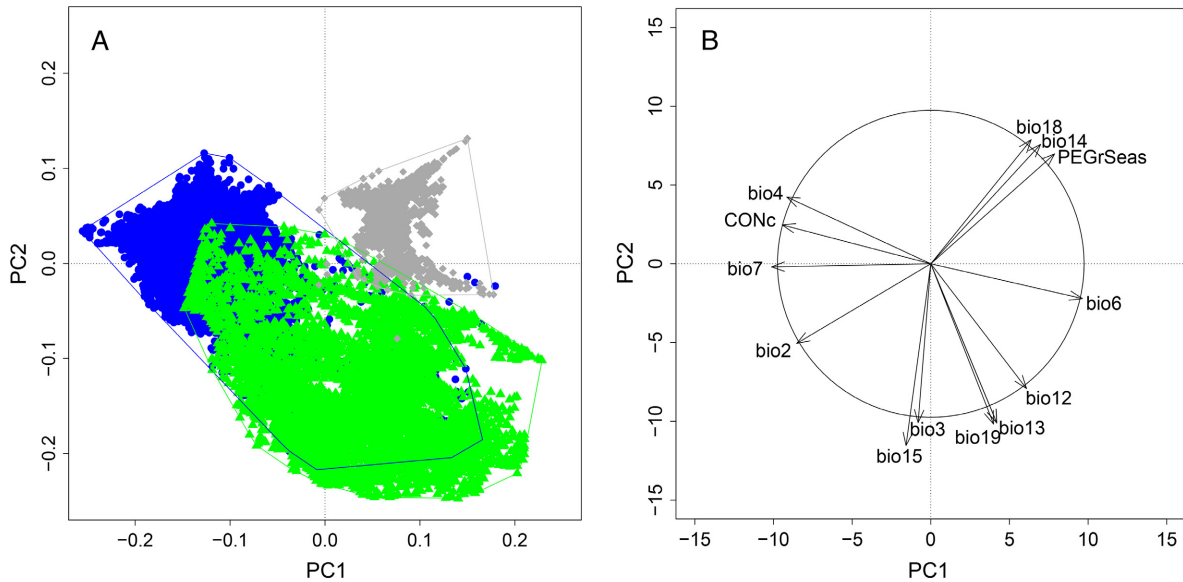


FIG. 1. (A) Bioclimatic space PC1–PC2 showing niche shift. Occurrences from the native range are represented by blue dots for *P. mienziesii* var. *glauca*, by green triangles for *P. mienziesii* var. *mienziesii*, and by gray diamonds for *P. mienziesii* introduced in Europe. Convex hulls that exclude outliers are represented around each population. (B) Circle of equilibrium contribution indicating the bioclimatic variables significantly contributing to ordination in the PC1–PC2 space. Refer to Table 1 for climatic variable definitions. (Color figure can be viewed at wileyonlinelibrary.com.)

However, the seasonal variability of temperature and the distribution of precipitation differed completely from the native to the introduced range. Very limited overlap between the native and introduced niches was similarly observed when the analysis was repeated with

the CRU TS3.10 data set (Appendix S2). The inertia percentage between the North American and European ranges reached 36% and was highly significant, consistent with the visual observation of climatic niche shift.

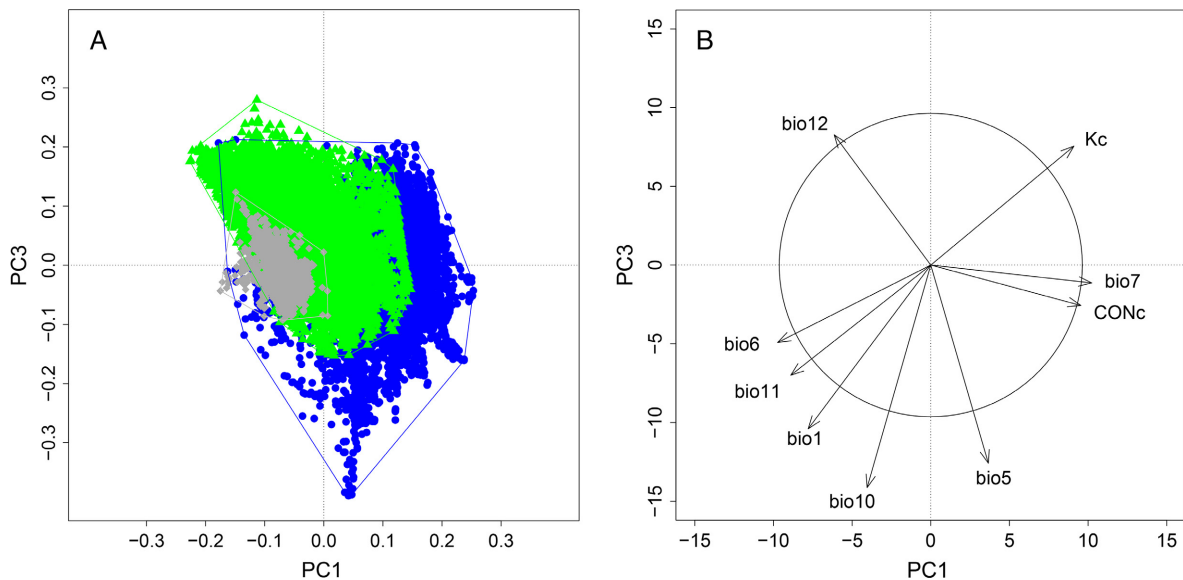


FIG. 2. (A) Bioclimatic space PC1–PC3 with partial niche overlap. Occurrences from the native range are represented by blue dots for *P. mienziesii* var. *glauca*, by green triangles for *P. mienziesii* var. *mienziesii*, and by gray diamonds for *P. mienziesii* introduced in Europe. Convex hulls are represented around each population. (B) Circle of equilibrium contribution indicating the bioclimatic variables significantly contributing to ordination in the PC1–PC3 space. Refer to Table 1 for climatic variable definitions.

SDM predictions in the native range

The Random Forest model of Douglas-fir occurrence driven by the 13 climatic descriptors showed very high predictive power in North America. The overall mean AUC and TSS reached 0.99 and 0.83 (Fig. 3). The average out-of-bag error rate of the model was 4% with near equality between commission and omission error proportions (3.3% and 4.3%, respectively). When variable importance was assessed, the three most explicative climatic descriptors of Douglas-fir presence were mean temperature of coldest quarter, precipitation during the growing season, and Conrad’s index of continentality (Table 1).

SDM predictions in the introduced range

Annual temperature range and precipitation seasonality defined the climatic gradient that best sorted occurrences of the North American Douglas-fir from those of the European Douglas-fir. These two climatic gradients were in large part captured by variations in two of the climatic descriptors we had selected: Conrad’s continentality index and precipitation-potential evapotranspiration during the growing season, which were also the most explanative predictors of the distribution of Douglas-fir in North America.

For this reason, model performance plunged in the European introduced range, in the absence of analogues in continentality and precipitation-PET during the growing season. TSS and AUC value reached 0.032 and 0.55, respectively. Predictions are considered random when AUC does not differ from 0.5 and poor when it ranges between 0.5 and 0.7 (Swets 1988).

The probabilities of Douglas-fir presence in Europe as predicted by the SDM were generally low compared to those predicted in North America, with probabilities greater than 0.6 in very restricted areas of eastern Galicia and northern Portugal and probabilities greater than 0.5 limited to northern Spain and Portugal, to the Loire, Centre, and Normandy regions in France and to a narrow strip in eastern England. In Scotland, Ireland, Wales, Germany, and all of central and Eastern Europe, probabilities did not exceed 0.5, except for the shores of the Black Sea (Fig. 4A).

Neither the FunDiv presence/absence data nor ingrowth measurements from the IUFRO trial sites were in agreement with these predictions. Indeed, the SDM failed to predict important stands of Douglas-fir in the French Massif Central or in southwestern Germany (Fig. 4B). The highest growth rates in Europe were measured in Scotland, Ireland, Wales, and southwestern England where the model predicted very low suitability

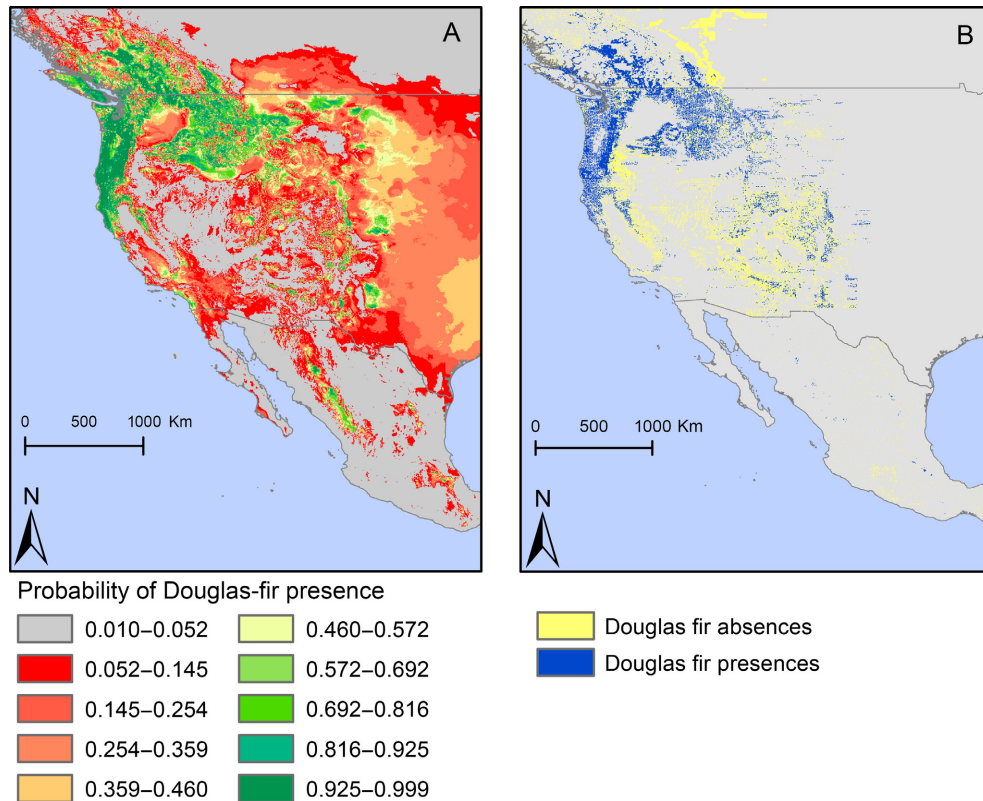


FIG. 3. (A) Probabilities for Douglas-fir presence predicted by the Random Forest algorithm, 20 forests with 500 trees and 13 climatic descriptors, and (B) observed presences/absences in the native North American range.

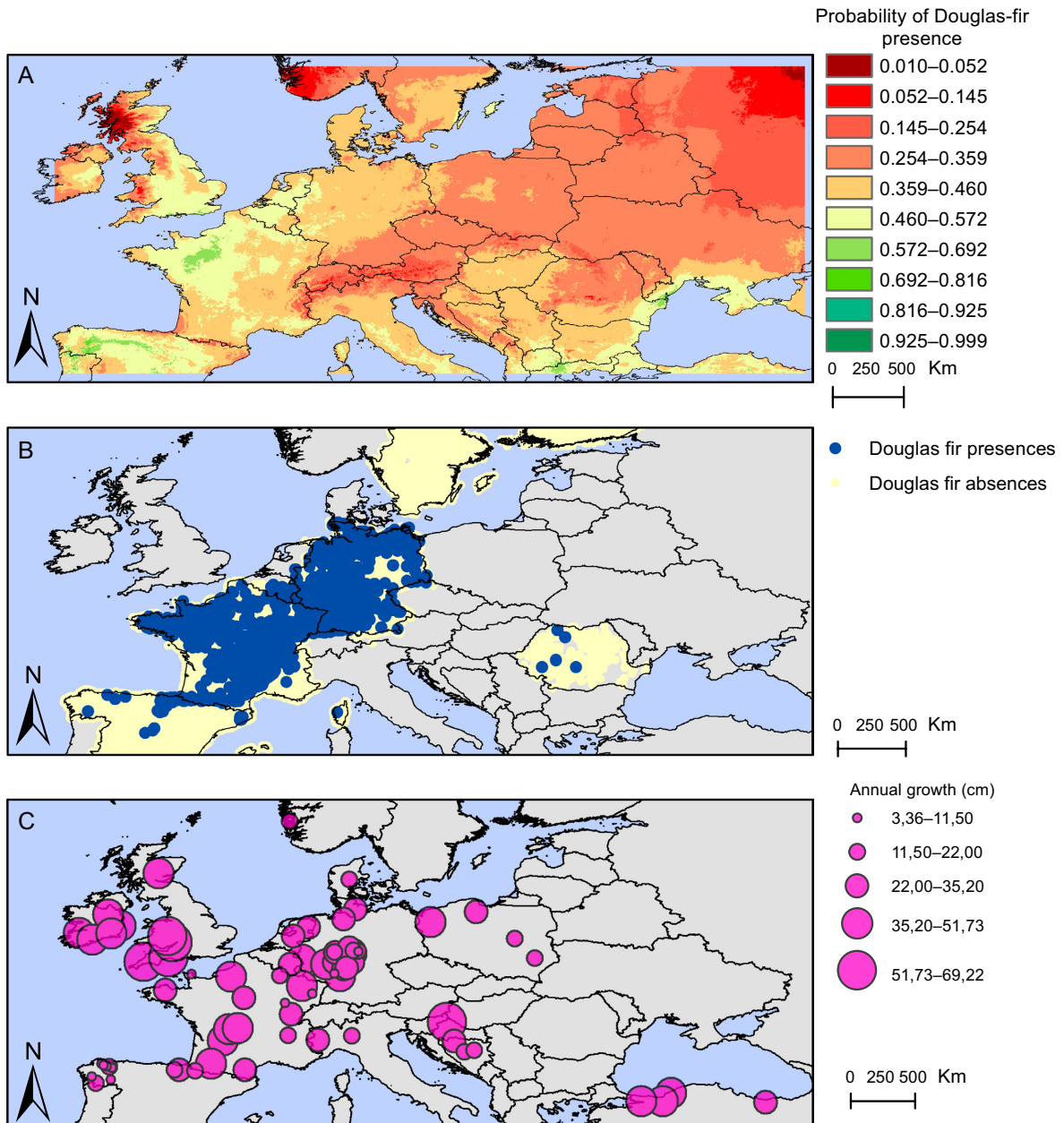


FIG. 4. (A) Predictions of probabilities for Douglas-fir presence in the introduced range from the Random Forest model calibrated in the native range. (B) Observed presence/absence of Douglas-fir in Europe from the FunDiv data set. (C) Annual growth (cm) of Washington and Oregon provenances of Douglas-fir as measured in IUFRO European trial sites. Symbol size represents annual growth classes.

of climate for Douglas-fir. The best (though nevertheless low) climatic suitability was predicted in eastern Galicia where ingrowth was low compared to other IUFRO trial sites (Fig. 4C).

DISCUSSION

Our results clearly demonstrate that Douglas-fir occupies distinct realized niches in its native and introduced ranges. We propose two non-mutually exclusive

hypotheses to explain the lack of overlap between the realized niches in Europe and in North America: (1) the fundamental niche has changed as a result of changes in genotypes (under natural or human-driven selection) and (2) the constraints defining the realized niche have changed.

Change in the fundamental niche

Important shifts in bioclimatic niches similar to those observed for Douglas-fir have been previously reported

for invasive species. In these studies, rapid genetic adaptation after invasion, sometimes occurring within less than 20 years, was identified as the dominant mechanism underlying the invader's range expansion (Broennimann et al. 2007, Whitney and Gabler 2008). It could be argued that rapid genetic adaptation has occurred since Douglas-fir was introduced in Europe in 1827, if the species is seen as an invasive in Europe (Carrillo-Gavilán and Vilà 2010). Moreover, evidence of natural genetic adaptation to local climates has been reported in Douglas-fir's native range where genetic clines in growth (Leites et al. 2012), phenology (Gould et al. 2011), resistance to cold, and resistance to drought (Bansal et al. 2015) have been related to latitudinal and elevational gradients.

On the other hand, a large proportion of the European Douglas-fir forests recorded in the FundivEurope data set were planted and subjected to silvicultural management intended to ensure productive stands. Due to these silvicultural practices, the opportunities for natural selection that occur during germination and establishment were circumvented (Aitken et al. 2008). Therefore, it is unlikely that rapid genetic adaptation of Douglas-fir under natural selection would suffice to explain the niche shift observed in the introduced range. However, genetic improvement and selection for vigor, shape and flushing lateness could have played an important role in widening the range of environmental conditions suitable for Douglas-fir. For example, in France, most of the Douglas-fir seeds planted originate from the La Luzette seed orchard (Souceyrac, Lot, France), planted more than 30 years ago with 40 American populations and 20 second-generation French populations. Douglas-fir trees from La Luzette are recommended for plantations in very diverse environmental conditions and have shown to grow 12% taller (height at 6 yr) and to flush 4 days later than controls from a Washington population (Bastien et al. 2013).

Change in the realized niche

No-analog climates and compensating factors.—The SDM calibrated on observed presences and North American climates captured the realized niches of Douglas-fir in its native range. Low suitability was predicted for most parts of Europe because of the absence of analogues, yet Douglas-fir was able to survive and grow in this new set of environmental conditions: introduction to Europe opened portions of the fundamental niche that were inaccessible in North America.

Even though Douglas-fir copes relatively well with drought, annual growth and survival are highly dependent upon water availability during the growing season (Littell et al. 2008, Sergent et al. 2014a, b). Therefore, the generally higher levels of April–September precipitation-PET that prevail in Europe are favorable conditions for Douglas-fir. In Scotland, on the western coasts of the UK, in the southwestern part of Germany, and on the mid-altitude slopes of the French Massif Central where

abundant presence and very high growth rates have been recorded, very low suitability for Douglas-fir was erroneously predicted by the SDM because of high precipitation-PET during the growing season. Even though annual precipitation is generally higher in British Columbia, Washington, and Oregon than in Europe, it is less evenly distributed across the year, being much more abundant in winter compared to most of Europe. Moreover, in the Pacific Northwest, Douglas-fir might be excluded from areas with the highest April–September precipitation-PET (such as the western coast of British Columbia above 49° N latitude) because of cold temperatures at high-elevation sites and the high frequency of severe frosts. This correlation between growing season precipitation-PET and high elevation/cold temperatures has no analog in Europe, where the higher winter temperatures could actually favor Douglas-fir, especially through winter photosynthesis (Choisnel et al. 1990). Indeed, common garden experiments in North America have revealed that several interior Douglas-fir populations occupied suboptimal climates. Seedlings sampled from these populations reached their growth optima at plantation sites where mean winter temperatures were several degrees higher than in their provenance region (Leites et al. 2012).

Bias in SDM predictions can also be caused by local compensating factors that remain undetected because of the coarse resolution at which SDMs are calibrated (Randin et al. 2009). The niche model calibrated in the native range predicted the highest climatic suitability in Europe to be on the southern slopes of the Cantabrian Cordillera. The particular climatic conditions in this area match those in the Pacific coast and interior valleys of the Cascades very closely with mild temperatures, high levels of precipitation, and marked seasonality. However, the annual growth measured at the 10 IUFRO provenance tests in northern Spain was low compared to that measured at other European trial sites, presumably because of low to moderate site fertility, shallow soils, and steep slopes (Zas Arregui et al. 2003). At the regional scale, soil nutrient status and water-holding capacity rather than climatic variables are the main drivers of stand productivity; important decreases in site index occur on the dry and nutrient-depleted soils (Curt et al. 2001). Low nutrient availability can also impede growth recovery after extreme drought events in Douglas-fir stands (Sergent et al. 2014b).

In France and Wallonia, recommendations to forest managers are mainly based on climate. Indeed, foresters are advised to refrain from planting Douglas-fir on sites where annual rainfall is less than 700 mm, and where summer precipitation is less than 250 mm (de Champs et al. 1997). Such advice ignores climatic conditions in the native range, where summers are usually drier (Broennimann et al. 2007), and does not account for PET and local compensating factors like soil extractable water, though these factors exert a dominant influence on productivity.

If local factors can explain poor Douglas-fir performance in areas of suitable climate, they could also explain

enhanced performance where climate suitability is lower. For example, former land-use in plantations has a strong influence on Douglas-fir growth (Curt et al. 2001). In France, Douglas-fir stands were often planted on former cultivated lands (de Champs et al. 1997) that have been subjected to repeated fertilization with presumably long-lasting legacies on site fertility. Our native model calibrated with coarse-scale climatic variables may have been too simplistic as it did not include such local factors that may be important in defining the niche hypervolume. However, the large difference between the high in North America and low predictive powers in Europe suggests that the combinations of regional and local environmental factors that permit the positive growth of Douglas-fir differ between the two continents.

Silvicultural practices.—Differences in biotic agents, disturbance regimes and management between the native and the introduced ranges could have caused the realized niche in Europe to diverge from the realized niche in North America, even if the climatic requirements of the species remained identical on both continents.

In Europe, Douglas-fir forests are more intensively managed and monitored than in North America; this results in very different age-class frequencies, regeneration success, and growth rates between the native and introduced ranges. Indeed, in Europe, most Douglas-fir stands are planted with two- to three-year-old seedlings that have been grown and selected in nurseries beforehand (de Champs et al. 1997). Planting is commonly preceded by site preparation such as stump removal or tillage. Seedlings are planted with local inputs of fertilizers and most seedlings benefit from ectomycorrhizal inoculation in the nursery, which stimulates initial growth after out-planting (Garbaye 1994). Subsequent weed control, brushing, and protection from browsing are frequently implemented to ensure the initiation of a productive stand. Successive commercial thinnings are performed every 5–10 years, and the final harvest generally occurs between 40 and 60 years (de Champs et al. 1997). As a result, European Douglas-fir forests are younger and more productive than those in the native range.

In the native range, most forest lands were managed in order to maximize timber harvest, with extensive clearcutting until the 1990s. Then, under public pressure, laws and guidelines were implemented to promote conservation and alternative management strategies (Thomas et al. 2006). Even though initial management practices considerably reduced the proportion of natural old-growth forests, the mean age of Douglas-fir forests in Canada and in the Pacific Northwest is higher than the usual rotation time in Europe (95 yr in British Columbia, 101 yr in Alberta, 78 yr in Oregon, 79 yr in Washington, and 73 yr in Idaho (Pan et al. 2012). Generally speaking, younger stands are less susceptible to infestation by biotic agents or damage from extreme climatic events (Bréda and Peiffer 2014). Therefore, the realized niche of Douglas-fir could have been artificially widened in Europe due to an age effect.

Interventionist silvicultural practices such as broad-scale genetic amelioration, fertilization, and sustained monitoring of competition have recently been implemented too recently to translate into significant regional growth benefits in the native range of Douglas-fir and are mostly restricted to the most accessible territories owned by wood products industries in Washington and Oregon (Hermann and Lavender 1999, Talbert and Marshall 2005). These areas represent 20.9%, 19%, and 14% of the forest lands in Washington, Oregon, and California, respectively, and tend to be concentrated in the coastal zone of the Douglas-fir native range. The use of interventionist silvicultural techniques is increasing but remains infrequent in British Columbia. Of the 52 million ha of provincial or state forests in British Columbia, 22 million ha are considered suitable for timber harvesting. Between 1976 and 2007, 260000 ha (1.2%) were subjected to fertilization, 605000 ha (2.8%) were subjected to planting of selected seeds, 55000 ha (0.3%) were subjected to pruning, and 667000 ha (3.0%) to spacing (British Columbia Ministry of Forests Mines and Lands 2010). Interventionist management like the silvicultural techniques implemented in Europe can potentially make up for imperfect climatic suitability at a given site; thereby contributing to maintaining Douglas-fir presence outside of its native climatic niche, or to artificially flattening response curves to several climatic variables in the introduced range (Aitken et al. 2008).

Nevertheless, jumping to the conclusion that genetic selection and intensive forestry would allow foresters to neglect climatic suitability before planting would be erroneous. Indeed, important diebacks of Douglas-fir stands have occurred after severe and repeated soil water deficits in the last decades (Sergent et al. 2014b), and the frequency and magnitude of such events is expected to increase in coming years. Important crown reddening frequently occurs in young Douglas-fir plantations in Europe; late-winter or early-spring weather conditions are involved in this phenomenon (Goudet 2009). The important diebacks in Douglas-fir stands reported after the 2003 drought and heat wave in Europe generated a strong demand for SDM predictions from forest managers who want to avoid the negative effects of such events. However, correlative niche models are generally calibrated with long-term climate means, which smooth short-term variability in the climate (Zimmermann et al. 2009). Therefore, the effects of weather hazards on species growth and survival are poorly represented, even more so because correlative models mostly include coarse-scale variables and ignore local factors that promote resilience at the stand scale (Zimmermann et al. 2009, Sergent et al. 2014b).

Implications for assisted migration

Assisted migration is proposed as a strategy to prevent tree species from becoming maladapted to future climates, with associated decreases in forest health and

productivity. Candidates for assisted migration are species predicted to experience important range contractions for which large areas of suitable climates will become available beyond the boundaries of their current range (Hällfors et al. 2016a). A major argument against assisted migration is the uncertainty associated with such predictions of future species ranges. On the other hand, proponents of assisted migration argue that the pace of climate change is such that conservation plans must be promptly implemented, despite the incomplete information (McLachlan et al. 2007).

We have analyzed historical human-aided movement of tree species to evaluate the bias in SDM predictions and the potential implications for assisted migration (Isaac-Renton et al. 2014). Our results demonstrate that the discrepancy between predictions and observations can be large, even for long-lived species and for recent introductions. Suitability of the introduced range was importantly underestimated. Schwartz (2012) proposed that correlative SDMs inherently underestimate climatically suitable areas, partly because projections to non-analog climates lead to omission errors. In the present study, high climatic suitability was also predicted in areas where productivity was low, presumably because local non-climatic factors had not been included in our model. It is impossible for modelers to measure all the environmental variables defining the boundaries of the fundamental niche hypervolume, even though a small subset of the most relevant descriptors can be identified by trial and errors (Booth et al. 1988). SDMs represent valuable tools that should be dedicated to this purpose.

Hutchinson's representation of the fundamental niche and the resulting species distribution modelling fail to account for the combination of environmental variables that are unrealized in the geographic space at a particular time. Large portions of the conceptual hypervolume are unfilled because environmental factors covary, and because physical constraints (topography, deposits) prevent the realization of all favorable environment in the real world. With temporal change, or when moving to new continents, correlations between variables change, and vacant parts of the hypervolume are filled (Jackson and Overpeck 2000, Colwell and Rangel 2009, Veloz et al. 2012). Omission errors arise from the fact that SDMs assume that the whole hypervolume is filled and that the observed presences are a good approximation of the fundamental niche, while in fact our knowledge of the fundamental niche is necessarily very limited.

We addressed the mechanisms susceptible to cause a niche shift in light of Douglas-fir ecology. However, compensating factors at broad and local scales as well as genetic adaptation, changes in disturbance regimes and silvicultural practices are relevant to virtually any tree species. Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Loblolly pine (*Pinus taeda* L.), or Monterey pine (*Pinus radiata* D. Don) are other examples of timber species that have successfully been introduced and intensively managed in new continents (Schultz 1997, Lavery and

Mead 1998). The introduction of Douglas-fir into a new geographical zone can also be interpreted as a space-for-time substitution (Isaac-Renton et al. 2014), the present conclusions therefore apply to predictions of future species distribution under rapid climate change. We conclude that planning assisted migration of tree species on the basis solely of predictions from correlative niche models is hazardous. SDMs can nevertheless be useful from a management and conservation perspective since they identify areas where climates remain similar and are known to be suitable (though not necessarily optimal) for species growth. They also provide valuable indications of the ecological mechanisms and management practices causing shifts in the realized niche. Outputs from niche models can serve as a basis for the implementation of complementary field and numerical experiments. Transplantation experiments and remote sensing of forest productivity have been identified as valuable information for guiding assisted migration plans (Gray et al. 2011, McLane and Aitken 2012). Predictions from correlative SDMs should also be combined as much as possible with those from process-based models, for a more explicit simulation of species interactions, silvicultural scenarios, eco-physiological responses to climate and weather hazards, local soil properties, and disturbances (Morin and Lechowicz 2008, Zimmermann et al. 2009, Duveneck and Scheller 2015, González-Moreno et al. 2015).

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