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Identifying potential provenances for climate-change adaptation using spatially variable coefficient models

Marieke Wesselkamp^{1*}, David R. Roberts^{1,2,3} and Carsten F. Dormann¹

Abstract

Background Selection of climate-change adapted ecotypes of commercially valuable species to date relies on DNA-assisted screening followed by growth trials. For trees, such trials can take decades, hence any approach that supports focussing on a likely set of candidates may save time and money. We use a non-stationary statistical analysis with spatially varying coefficients to identify ecotypes that indicate first regions of similarly adapted varieties of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) in North America. For over 70,000 plot-level presence-absences, spatial differences in the survival response to climatic conditions are identified.

Results The spatially-variable coefficient model fits the data substantially better than a stationary, i.e. constant-effect analysis (as measured by AIC to account for differences in model complexity). Also, clustering the model terms identifies several potential ecotypes that could not be derived from clustering climatic conditions itself. Comparing these six identified ecotypes to known genetically diverging regions shows some congruence, as well as some mismatches. However, comparing ecotypes among each other, we find clear differences in their climate niches.

Conclusion While our approach is data-demanding and computationally expensive, with the increasing availability of data on species distributions this may be a useful first screening step during the search for climate-change adapted varieties. With our unsupervised learning approach being explorative, finely resolved genotypic data would be helpful to improve its quantitative validation.

Keywords Climate-change adaptation, Douglas-fir, Ecotype, Genetic variation, Identifying ecotypes, Provenance tests, *Pseudotsuga menziesii*, Spatially variable coefficient models

Introduction

Local adaptation strategies to current environmental changes—be it climatic, with respect to atmospheric pollution with NO_x, CO₂ and SO_x, or to pests and

diseases—heavily rely on identifying species, breeds and lineages that are best suited for such conditions and hence maintain higher yields in forests, croplands and animal production [1–4]. Widespread species such as common forest trees live under differing climatic conditions throughout their range. These conditions exert selective pressure, often leading to specific local adaptation to habitat conditions [2, 5]. In trees, this may result in substantial variation in cold hardiness or drought resistance among populations of the same species [1, 6–9]. Adaptive differences may eventually become genetically encoded and analysis of such intra-specific variation thus

*Correspondence:

Marieke Wesselkamp
marieke.wesselkamp@biom.uni-freiburg.de

¹ Department of Biometry and Environmental System Analysis, University of Freiburg, Tennenbacher Straße 4, Freiburg 79106, Germany

² InnoTech Alberta, 3608 – 33 Street NW, Calgary, AB T2L 2A6, Canada

³ Alberta Biodiversity Monitoring Institute, 1-107 Centennial Centre for Interdisciplinary Studies (CCIS), University of Alberta, Edmonton, AB T6G 2E9, Canada



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can reveal geographic patterns that are related to external selective factors [1, 10].

Populations of a species descending from different provenances can be tested for climatic adaptation by their growth performance under new conditions [11–13]. However, such growth trials are extremely time consuming, and tree provenance trials initiated in the 20th century are now still analysing young trees [14–16]. Genetic investigations can aid the identification of climatically adapted populations by delimiting ecotypes, which are then subjected to experimental physiological investigations (e.g. [17]). Yet, there may be hundreds of seed sources to choose from and being able to pre-select regions from which to sample specimen for genetic and/or physiological investigations could save both time and money.

Douglas-fir (*Pseudotsuga menziesii*) is a wide-ranging tree species, known to be closely adapted to its environment [18]. Due to the high economic and ecological importance, its characteristics have been well analysed in many studies and data on its distribution and characteristics are available. Its habitat extends from the coast of British Columbia (Canada), through the Rocky Mountains and adjacent mountainous regions down to the Mexican mountains. Two varieties are recognized: *Pseudotsuga menziesii* var. *menziesii*, growing along the Pacific coast line from British Columbia into California and *Pseudotsuga menziesii* var. *glauca*, inhabiting the interior mountain ranges. Since it is highly adaptive and productive, Douglas-fir has also been introduced as a non-native species to European forests [19]. Long-term provenance trials have been carried out in order to monitor provenance performance [15, 16, 20, 21]. Data from these trials can be used to investigate adaptive and genetic variation among populations (e.g. [19, 22, 23]). Based on their genetic, morphological or physiological population characteristics, ecological adaptation models predict best performing provenances and thereby support the delineation of seed zones that are suitable for reforestation and restoration management [14, 24]. Different modelling approaches have been used for such purposes, including purely generic clustering [22, 25], climate envelope models (e.g. [14]), transfer functions (e.g. [26, 27]), genecological models [21] and regression trees [28].

Most studies focus on the performance of test provenances, while less attention has been paid to the pre-selection of provenance regions [29]. In the work of Rehfeldt et al. [30], the importance of a climate-based approach to provenance selection in the face of climatic changes is highlighted. Based on the findings of Wei et al. [22], the authors classified “climatypes” of Douglas-fir populations in North America. When local adaptation

occurs, optimal climatic habitat conditions for a population vary from those of other populations farther away [1]. So does a model that represents the varying relation between the climatic environment and a species' occurrence. The issue of spatial variability in modelled relations is referred to as (spatial) non-stationarity [31, 32]. Most common modelling approaches assume stationarity and represent the relation between model predictors and model response *globally*: the model estimates are constant throughout the complete spatial distribution. The assumption of stationarity, however, is not met when intra-specific variation occurs [31, 33]. In contrast, modelling this relation *locally*, model coefficients vary across space and thus represent the individual-environment linkage for each observation [31, 32]. If a priori genetic information is available, one can separately analyse sub-populations (e.g. [33–38]). Without such information, two methods commonly used to capture non-stationary model relations are spatially varying-coefficient models (SVCMS) and geographically weighted regression (GWR) (both approaches reviewed and compared in [39]).

In this study, we use a non-stationary modelling approach, specifically a SVCMS, to identify ecotypes of a wide-spread species based only on climatic distribution data. We do this for Douglas-fir, whose occurrence data are available for its entire North American range. Ecotypes, *sensu* Turesson [40], are varieties of a species which show genotypic similar responses to a specific habitat. Our analysis is based on the assumption that environmental adaptations can be an early stage of genetic differentiation (e.g. [21, 41]). Our aim is to demonstrate how this approach can aid identification of populations to be sampled for climate-tolerance related genetic profiling. The method is based on the assumption that ecotypic variations of Douglas-fir in responses to climate are reflected in the model coefficients. We hypothesize that clustering of these model coefficients yields tentative ecotypes from which provenance regions can be inferred. To test these emerging ecotypes, we compare their distribution to six DNA classes as delineated by Rehfeldt et al. [13].

Methods

Study distribution and data

Analysis was carried out with a dataset that contains the complete distribution of Douglas-fir throughout Canada, USA and Mexico in form of binary coded presence and absence observations (Fig. 3a). It consists of 73,932 records of which 18,601 are presences and 55,331 absences. The data set was assembled by the USDA Forest Service and supplied to us by G.E. Rehfeldt ([13], and pers. comm.). Presence-absence data were collated from a network of forest inventory and research ground

plots of Mexican, Canadian and US American organizations (CONAFOR, CFS, FIA, respectively). Non-forested areas have been presented by a random sample of data points, used in North American vegetation analysis [13, 42]. According to their geographic location, each presence observation in the data set has been assigned to one of six DNA classes, which correspond to genetics-based large-scale provenance regions (Fig. 3b; [13]). The assignment was done by Rehfeldt et al. [13] and is based on well-documented knowledge and supported by the genotypic classification of a preceding study carried out by Wei et al. [22]. The data provided along with [13] contains information on 44 populations from large-scale genotypic regions in Douglas-fir that were used to investigate the intervarietal phylogeographic history in the original study [22]. In [13] however, they were used to assign the 18,601 presences to six DNA classes and that we in this work use for qualitative comparison with our ecotypic regions.

Climatic and bioclimatic variables were generated for each presence and absence location (reference period: 1961-1990) with the ClimateNA v5.10 software package, available at <http://tinyurl.com/ClimateNA>, based on the PRISM methodology described by Wang et al. [43].

Model selection

SVCMS are computationally expensive, which is why we fit the model using only three uncorrelated climate variables that have been identified before as being the main drivers for the climatic niche of Douglas-fir [18]. The spatially-varying coefficient Generalized Additive Model (GAM) was substantially more computer intensive than an ordinary Generalized Linear Model (GLM) (in our case by a factor of 10,000). Pre-selecting a manageable number of (uncorrelated) predictors thus is advisable also in situations where the ecological niche is less well known than in our study species. Climate predictors and their squares, e.g. temperature difference and squared temperature difference, were standardised to mean 0 and standard deviation 1 before being fit. The use of second polynomials in a regression model allows for non-linear effects of predictors on the response, as we would expect for climatic niches [44].

Spatially varying-coefficient model

We build a spatially varying-coefficient model (SVCMS) through a generalized additive model (GAM) [45, 46] as implemented in the *mgcv* package for the R programming environment [47]. The GAM was chosen due to its straightforward implementation of SVCMS [46]. Extending the class of GLMs by allowing specification of (semi-parametric) smooth-functions f_j that can be imposed

on a set of predictors x_1, \dots, x_k , a generalized additive model for logistic regression can be written as

$$g(E(Y)) = \beta_0 + \sum_{j=1}^p f_j(x_j), \quad (1)$$

with the expected value of the response variable $\mu = E(Y)$, transformed by the link function $g(p) = \ln(\frac{p}{1-p})$ for logistic regression, and an intercept β_0 [45]. To implement spatially variable coefficients, the smooth functions are specified as functions of equidistant longitude (x) and latitude (y) of each datum, $\{x_x, x_y\}$, in km. These were centered on the origin of the coordinate system for more robust estimation [48]. In the model setup, $\{x_x, x_y\}$ were multiplied by the covariates of interest [39, 49]. Thus, the SVCMS looked like this:

$$g(E(Y)) = f_{\beta_0}(x_x, x_y) + \sum_{j=1}^k f_j(x_x, x_y)x_j \quad (2)$$

We chose to represent climatic predictors as quadratic functions, with separate spatial smooths for the linear and the quadratic model terms. We thus have the following predictors with spatially variable parameters in the model: a spatial intercept, yearly mean temperature difference (TD), TD^2 , total summer (May to August) precipitation (PPT_sm), PPT_sm^2 , mean temperature of warmest month (MTWM) and $MTWM^2$. Gaussian-process splines with (initial) 100 base dimensions were chosen for each term to smooth estimates [50]. Model parameters were fit by maximum likelihood estimation. Predicting the model terms to the presence locations yielded a $18,601 \times 7$ matrix with individual model coefficients for each plot where Douglas-fir occurs.

We used two reference models to be able to gauge the effect of spatially variable coefficients: in direct analogy to the SVCMS we fit a (stationary) GLM with quadratic terms; just like the GAM fits linear and quadratic effects (where the splines refer only to how these parameters change through space: see eqn 2), so does the GLM. Secondly, we fit a GLM with additional pairwise interactions: if the spatial variation in the estimated coefficients of the SVCMS are due to statistical interactions of the climatic predictors, then this model would capture this effect. All models were compared by their Akaike Information Criterion.

Coefficient clustering

Ecotypes were defined as groups of populations with similar responses to environmental variables. The statistical model captures this similarities in its spatially-varying coefficients (SVCs) that are therefore implicitly assumed

to represent similar ecotypic traits. An unsupervised classification algorithm, namely a fast k -medoids clustering algorithm ([51], using R's cluster::pam) was applied to detect similar subsets in the SVC matrix of presence observations and subsequently assign these observations to ecotypic clusters based on the detected similarity (see Fig. 1 for a schematic overview of where this procedure is embedded in the analysis). In this matrix, estimates for MTWM and the intercept were relatively narrowly distributed, whereas estimates for the effect of TD and PPT_sm exhibited some extreme values. For visualisation, these were 96%-winsorised [52], i.e. extreme values reduced to the second or 98th percentile, resulting in Fig. 2. For clusters of environmental responses however, we omitted the spatial intercept (Fig. 2, panel g), as it only adjusts prevalence estimates. Thus, we used a SVC matrix of $18,601 \times 6$ model terms. Correspondence of the detected ecotypes with the six large-scale DNA regions was quantified by the Rand index, $R(C, C') = \frac{2(n_{11} + n_{00})}{n(n-1)}$, where n_{11} is the number of observations both in clusters C and C' , n_{00} those neither in C nor C' , and n the total number of observations [53].

Based on the observation that coefficients exhibit very different ranges, we decided to compare k -medoids on two different versions of the coefficient matrix: 1. directly on the terms as returned by the model, 2. on the standardised terms (i.e. the correlation matrix), which reduced domination by MTWM estimates. While standardization did not remove the effect of extremes completely, it at least mitigated it (SI, Fig. 1). The resulting clusters differed slightly between these two versions (see Fig. 3 and SI, Fig. 1), but we deem the first approach to be more appropriate for grouping environmental responses, as it keeps the model parameters' magnitudes, which are directly interpretable as strength of an effect [54].

In the unsupervised classification, we determined the optimal number of clusters using the GAP statistic [55] (SI, Fig. 2). While this indicated as a global optimum without any clusters, the gap statistics identifies a local maximum at ten clusters. We conducted our analysis towards two different ways for validation: (1) the SVC matrix was clustered into six ecotypes to quantify the proposed method with the

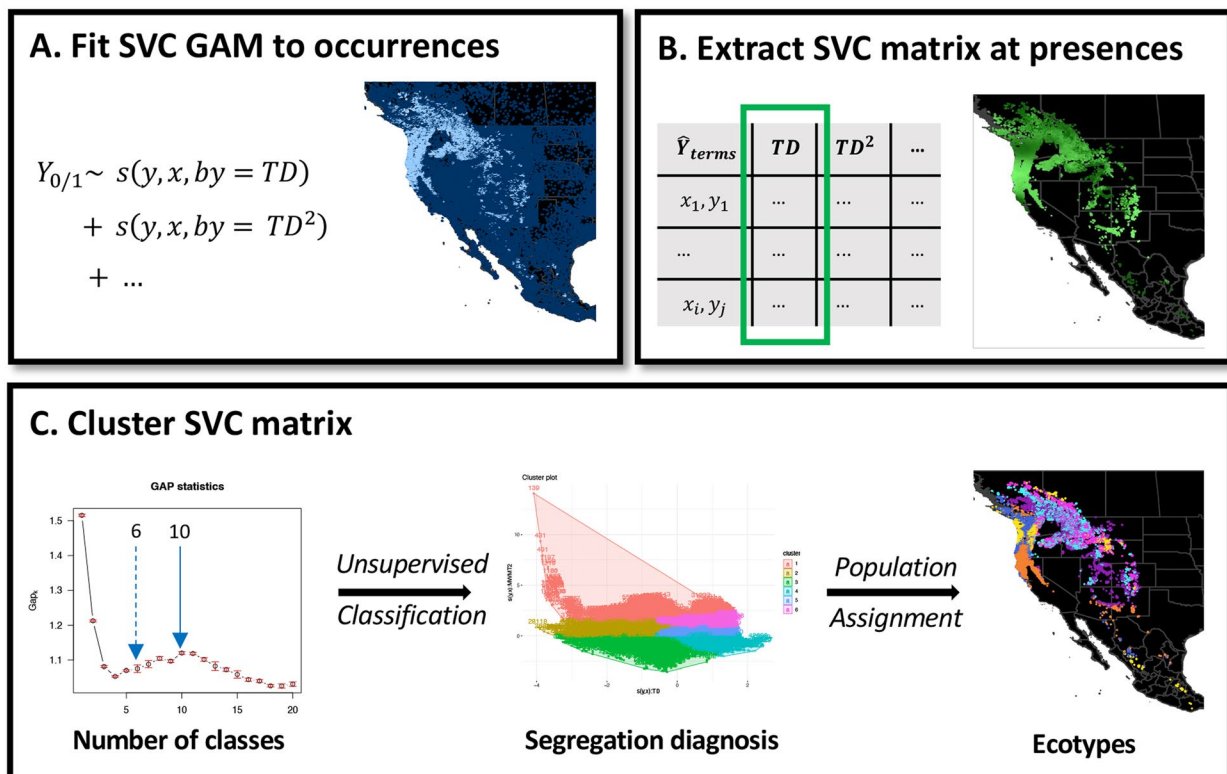


Fig. 1 Schematic outline of technical steps from fitting the spatially-varying coefficient (SVC) model to outlining ecotypic regions. A) We fit a GAM to Douglas-fir occurrence data, allowing the smooth terms to vary in space. B) This model predicts occurrences at present populations based on a SVC matrix. C) The coefficients in the SVC matrix are classified by an unsupervised classification algorithm and based on a choice of the optimal amount of clusters, populations are assigned to these ecotypic classes

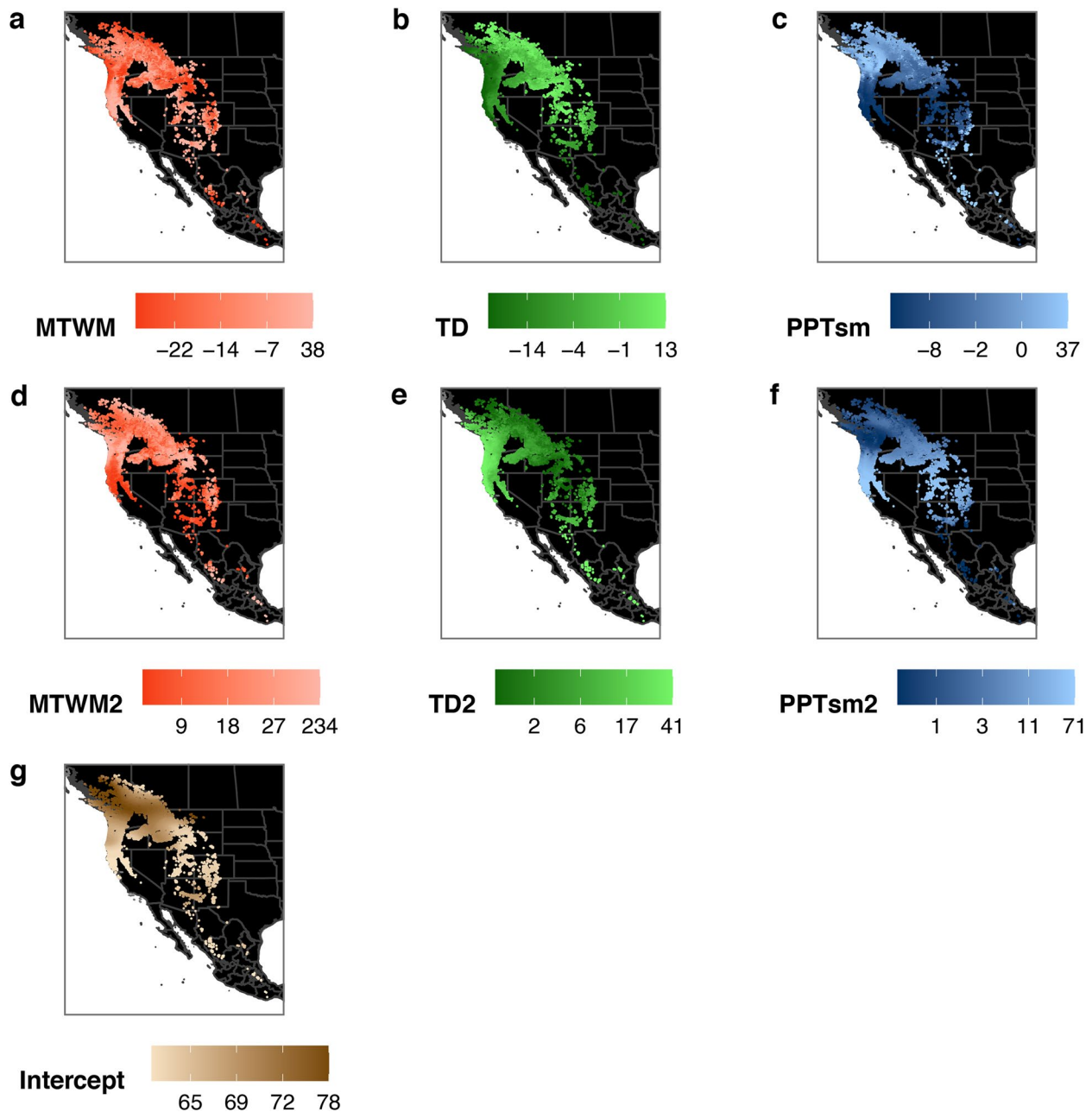


Fig. 2 Map of rounded estimates for the effect of the three climatic predictors (top row), their quadratic terms (second row) and the intercept (bottom row). Note that all predictors were standardized before the SVCM was fitted

available large-scale DNA classes.(2) We examined higher resolved ecotypes based on the suggested ten clusters to qualitatively validate these with recent evidence of smaller-scale DNA classes ([14, 25, 56], e.g.). We will discuss the results of the qualitative validation, while corresponding figures can be found in the supplementary information (SI, Qualitative validation of ten ecotypes).

Cluster differentiation

Variation within and among clusters were assessed by comparing predicted climate niches, depicting individual response norms in marginal conditional effect plots. The effect of a climate predictor on the predicted occurrence was calculated over a sequence from its smallest to its largest value with the other two predictors held constant at the cluster's mean value. This was done for each

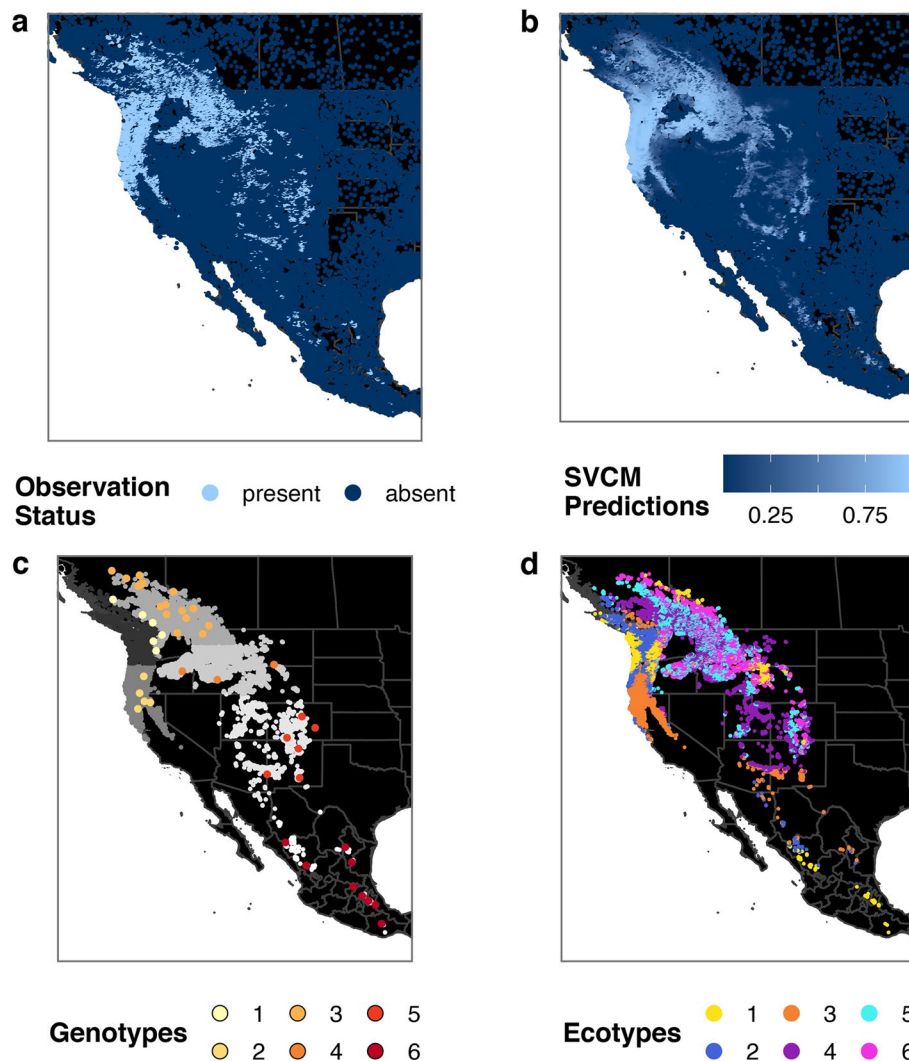


Fig. 3 Distribution of Douglas-fir and its deduced ecotypes. Panel **a** displays the presence and absence observations as contained in the data set. Panel **b** shows model predictions for probability of Douglas-fir occurrence, computed by the generalized additive model with spatially variable coefficients. In panel **c**, assignments of observed data points to provenance regions, provided within the data set are mapped in grey tones [13]. The coloured points represent the 44 populations which were genetically analysed and used as baseline for outlining the large scale genotypic regions [22]. Panel **d** shows the assignment of presence data points to one of six ecotypes derived from the model coefficients

observed environmental condition separately, and then averaged across all presence locations of a cluster (also referred to as partial dependence plot). Changes in model prediction for the observation then indicated an effect of the climatic factor on its occurrence.

In order to test for the importance of the Douglas-fir specific clusters, we pursued the cluster analysis also with a “neutral” model, i.e. we fitted the same model with spatially-varying coefficients to randomized presences and absences. Its model terms thus only represent the clustering of climatic predictors across space but carry no Douglas-fir specific information. Similarity of the results was compared with both, the genetic-based provenance regions and the ecotypes.

Results

The spatially-variable coefficient model (SVCM, Table 1) had a substantially better fit than the stationary GLM with the same structure or a GLM with additional pairwise interactions (Akaike Information Criterion ($AIC_{SVCM} = 23439$, $AIC_{GLM} = 38891$, $AIC_{GLM-I} = 34694$). It explained 72.4% of the deviance, indicating a very well-fitting model (see also Fig. 3a and b). All three predictors were contributing significantly to the model (see Table 1). Mean temperature of the warmest month (and its square) were the most important model parameters, with χ^2 -values at least four times higher than those of other model parameters (Table 1).

Table 1 Summary of the spatially variable-coefficient model. Edf and Ref.dof refer to two different ways to compute the numbers of degrees of freedom absorbed by the spatial spline for a model term. TD, PPT_sm and MTWM refer to temperature difference, summer precipitation and temperature of the warmest month. All χ^2 -values are significant at $p < 0.001$

	edf	Ref.dof	χ^2
s(y,x)	43.76	47.43	330.35
s(y,x):TD	3.00	3.00	127.58
s(y,x):TD2	3.00	3.00	125.35
s(y,x):PPT_sm	32.72	37.25	301.61
s(y,x):PPT_sm2	35.32	39.39	193.43
s(y,x):MWTM	41.68	45.75	1406.34
s(y,x):MWTM2	47.78	51.37	1345.66

The spatial variability of model parameter estimates is depicted in Fig. 2, the averages sizes of these coefficients per ecotype are given in the supplementary information. While in itself hardly interpretable, the result demonstrates clear spatial patterns, with smooth transitions between regions of high and low values. These patterns form the basis for the clustering analysis to identify ecotypes.

The “neutral” spatially-varying coefficient model reported a poor fit with a deviance explained of 0.02% and an AIC of 83431. The model summary can be found in the supplementary information (SI: Table 5).

Identification of ecotypes

The six ecotypes identified by *k*-medoids clustering based on the terms of the SVCM exhibit large overlap with the DNA classes (Table 2), but also suggest some deviations. A quantitative comparison of the clustering output to the DNA-classes yielded an agreement of over 75% (Rand index = 0.756, see also Table 2). Ecotypes differed from the genotypes in that, firstly, some are geographically disjunct (ecotypes 1 and 2) and that, secondly, specifically inland they range further than the homogeneous large-scale DNA classes (ecotypes 4 and 5) (Fig. 3, bottom panels).

With the exception of ecotype 3, clusters do not explicitly accord with only one DNA class (Table 2). In their upper ranges, cluster allocations reveal between 47% accordance (ecotype 6 with DNA class 3) and 86% accordance (ecotype 3 with DNA class 2). While ecotype 6 ranges across the two northern interior genotypic regions (DNA class 3 and 4) nearly equally strong, ecotype 3 covers much of the range of the southern coastal genotype (DNA class 2), with some disjunct but spatially close ecotypic populations in the southern interior region and the northern transition zones.

Another ecotype that is strongly disjunct is ecotype 1 with already two disjunct groups in the northern coastal genotypic region, ranging until the southern coast, and some visible group in the interior north and middle, as well as in Mexico. Ecotype 2 can mainly be found in the northern coastal regions but also ranging than the genotype in this area, namely further south along the coast and further towards the inland regions of DNA class 3. Ecotype 4 shows the largest spread in latitude, from British Columbia over Washington and into the central and southern Rocky Mountains. Overall, these findings show some clear contrasts to the large-scale genetic and taxonomic distinction of coastal and interior subspecies (Fig. 3 bottom left).

Quantifying the similarity of the “neutral” clusters with the DNA classes also yielded an accordance of over 76% (Rand index = 0.763), while they also correspond to over 77% with our ecotypes (Rand index = 0.77) (SI, Fig. 7). This essentially suggests that the SVCM-ecotypes indeed indicate climatic niches.

Response norms

Douglas-fir ecotypes respond to climatic conditions in a similar, yet separable way. The overall climate niche of Douglas-fir seems to be at a temperature optimum around 15°C, with a preference for 10–20°C temperature difference and low precipitation (< 400 mm) (Fig. 4). The signal of all three climatic predictors is an occurrence probability larger than 0.75, suggesting that the underlying ecotypes are well constrained by the predictors used.

Table 2 Confusion matrix of the 18,601 Douglas-fir presence classifications by DNA (columns) and by coefficient similarity (rows) (percentage of ecotypes assigned to each DNA class in brackets)

	DNA_1	DNA_2	DNA_3	DNA_4	DNA_5	DNA_6
Ecotype 1	1132 (52.8)	509 (23.8)	257 (12.0)	164 (7.7)	8 (0.4)	73 (3.4)
Ecotype 2	1405 (57.1)	986 (40.1)	4 (0.2)	5 (0.2)	9 (0.4)	53 (2.2)
Ecotype 3	135 (4.5)	2580 (86.8)	0 (0.0)	8 (0.3)	211 (7.1)	37 (1.3)
Ecotype 4	70 (1.9)	28 (0.7)	2351 (62.4)	796 (21.1)	520 (13.8)	0 (0)
Ecotype 5	64 (1.6)	29 (0.7)	2305 (57.1)	1500 (37.2)	137 (3.4)	0 (0)
Ecotype 6	61 (1.9)	42 (1.3)	1524 (47.3)	1515 (47.0)	83 (2.6)	0 (0)

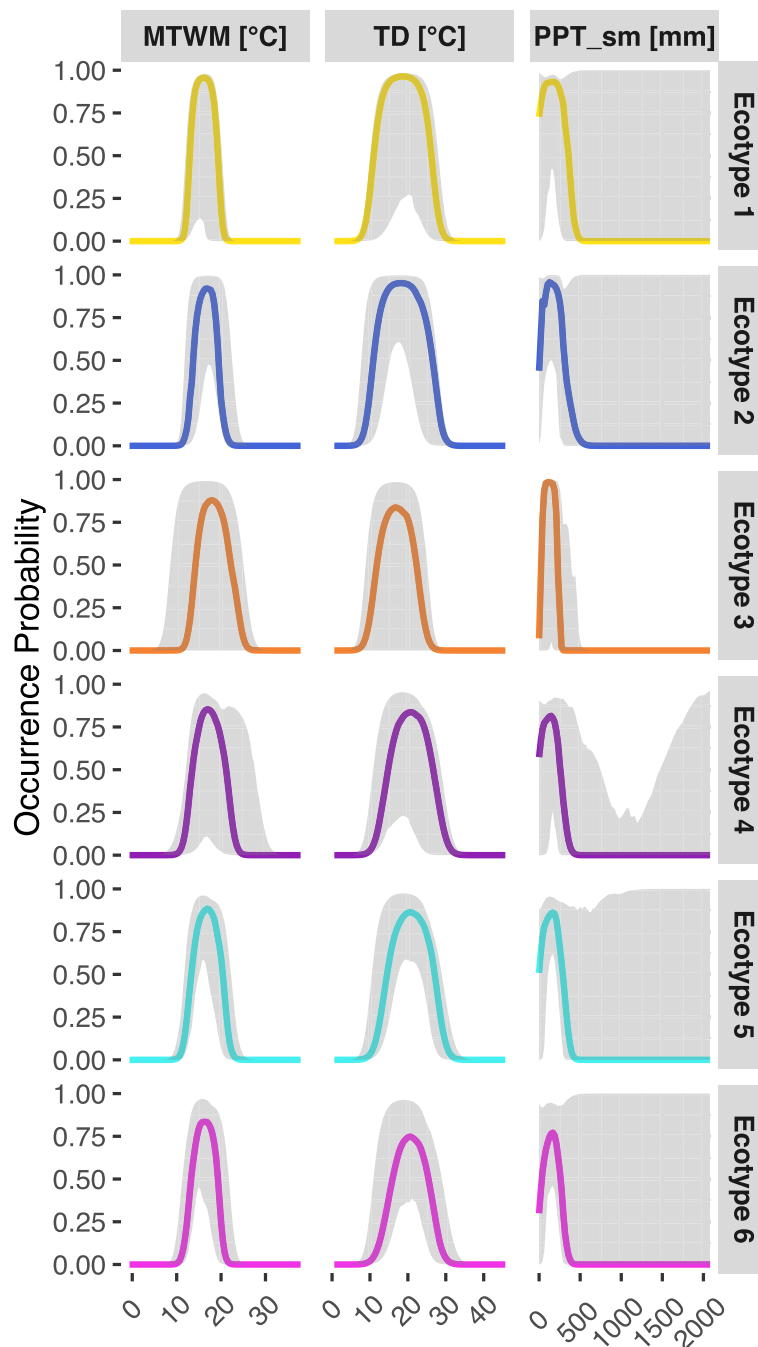


Fig. 4 Climate niches of the six clusters identified from model coefficients. Plots are effects of changing the focal predictor while holding the other two at their mean value, for each presence location of that cluster. The median effect (with grey smooth defined by 0.05 and 95% quantiles) is displayed in the ecotypes' colours. A reduced total size of response indicates a climatic niche with small effect of this predictor on Douglas-fir occurrence

Douglas-fir ecotypes are distinguishable, firstly, by the signal of the climatic predictors, secondly by the variation in that signal and thirdly by its range, i.e. peakedness of the effect curve.

Ecotypes 1 and 2, both mainly found in the northern and southern coastal regions, show a very strong

(Table 3) and sharp signal (Fig. 4) over all climatic predictors. The variation in their response to precipitation, however, is large. Not so for the ecotype 3, found mainly in southern coastal regions that specifically for precipitation shows the highest, sharpest and most robust signal. In contrast, the ecotypic responses to MTWM and TD

Table 3 Maximum conditional median effect size of each predictor on ecotypes, corresponding to the median largest occurrence probability in Fig. 4. The closer the value to 1, the narrower the niche with respect to this variable

	Ecotype 1	Ecotype 2	Ecotype 3	Ecotype 4	Ecotype 5	Ecotype 6
MTWM	0.96	0.92	0.88	0.85	0.88	0.83
PPT_sm	0.93	0.96	0.98	0.81	0.86	0.77
TD	0.96	0.95	0.84	0.84	0.86	0.75

are clearly wider and more variable than their northern coastal friends.

The niche positions of the mainly interior distributed ecotypes are very similar but with a slightly less signal. Further, the variations of their responses have a left (e.g. TD, ecotypes 5 and 6) or right (MTWM, ecotype 4) tendency. Their response to precipitation is poorly constrained by the data. In part, the poorer definition of ecotypes 3 and 6 may be explained by their lower number of records over the larger geographic range (Table 2).

In direct comparison with the map of ecotypes (Fig. 3) it becomes apparent that even disjunct ecotypes of the northern and southern regions (ecotype 4, 5) or eastern and western (ecotypes 1, 2) exhibit rather similar climatic niches with respect to the three predictors under consideration.

Discussion

Data on the geographic distribution of a species may hold information allowing us to identify groups of populations with similar responses to the environment, as shown here for Douglas-fir and climate. Based on the assumption that trait adaptations to environmental variables are a component of genetic differentiation, we interpret these groups as tentative ecotypes of Douglas-fir [41]. Assigning Douglas-fir populations in their distribution area in North America to six different response groups, ecotypes exhibit different responses characteristics to climate effects, presumably having different climate optima. Quantification of the geographic distribution of the identified ecotypes showed overlap with available large-scale DNA regions to some degree, while qualitative comparison with finer resolved and genetically analysed provenance regions implies ecotypic and genotypic similarities [14, 25, 56]. The results suggest that ecologically induced intra-specific variation in (unobserved) occurrence-related traits, as well as an increased intra-variety differentiation, potentially hybrids, found in transition zones ([57, 58], p. 38) can be detected in a first screening step with a climate-based, local modelling approach to provenance outlining. With this being an explorative approach, the resulting model hypothesises ecotypes which are not validated until compared with genetic information.

Identified provenance regions

The two main varieties of Douglas-fir, *Pseudotsuga menziesii* var. *menziesii* and *Pseudotsuga menziesii* var. *glauca*, consist of sub-specific populations adapted to certain environments [18]. In allozyme studies it has been shown that beyond variation among varieties, there are also intra-variety allozymic differences as well as clinal variations in both, the coastal and Rocky Mountains subspecies [58, 59]. As such, multiple studies on the genetic differentiation of these two varieties linked genotypes to large-scale regions (e.g. [23, 25, 59, 60]). Allozyme and fossil pollen surveys detected two population sources for the coastal variety, var. *menziesii*, and suggest two to four sources for the Rocky Mountains variety, var. *glauca* [23, 59]. The Mexican populations are mostly treated separately and have even been suggested as an own variety [61]. Although belonging to the subspecies of *Pseudotsuga menziesii* var. *glauca*, particularly the central Mexican populations morphologically and physiologically differ from this variety [61, 62].

Based on the genetic literature, we grouped Douglas-fir populations first into six classes to quantitatively compare deduced ecotypes with available data on large-scale DNA regions [13, 22, 63]. Then we also grouped Douglas-fir populations into ten classes to qualitatively assess their similarities with recent smaller-scale DNA regions [14, 25, 56]. Clustering of the spatially-varying coefficient (SVC) matrix partly reproduced the six DNA class regions without using the DNA-data: we identified spatially well separated, latitudinally arranged, yet disjoint mainly coastal (ecotypes 1, 2 and 3) and interior ecotypes (ecotypes 4, 5, 6). A Mexican ecotype is only indicated but has not been classified as a standalone group. Comparing these ecotypes to the available large-scale DNA classes (Fig. 3c) yields up to a maximum of 86% accordance for the southern coastal variety. Overall, identified ecotypes show much larger ranges, transition into each other and are more fragmented than the strictly outlined DNA class regions, even within the two varieties of *Pseudotsuga menziesii*.

Clustering of the SVC matrix into six groups only approximated the spatial pattern of genetic variation [13]. By allowing for more clusters, which would also be the approach if no DNA-based clusters were previously

identified (e.g. [55]), a wider range of ecotypic clusters emerged (see supplementary information), in line with European provenance trials of Douglas-fir and studies on intra-varietal genetic structures [14, 56]. Such a larger number of clusters leads to more spatial compactness in the southern coastal ecotypes and points out an inter-varietal small-scale differentiation in the north (SI, Fig. 5 and SI Tab. 4). An experiment on clustering the SVC matrix separately for the coastal, interior and Mexican varieties suggested a fragmentation of the coastal variety into six ecotypes (SI, Fig. 6), which does not fully match a current evidence of four coastal genetic cluster with additional admixed populations [56], but supports its known small-scale differentiation [25]. Douglas-fir is known for its strong local diversity in association to environmental forcing variables [58], of which we only considered three. This might also lead to finer resolved ecotypic regions than considered in our qualitative comparison. In a future work, more predictors could be considered and by dimensional reduction techniques still used in this computationally demanding approach. Dependencies might remain partially incomplete, as selective forces are not restricted to climatic conditions, but also to soil [64], fire [65], pests and so forth [19]. Still, the high spatial coherence of the clusters suggests that the approach as such may have potential that warrants further testing.

Differentiation of ecotypes

Our ecotypic classification is determined by the interplay of three climatic factors throughout the range of Douglas-fir that might have been responsible for part of the genotypic adaptations in its biogeographic history [66]. These predictors constrain ecotype identification by prior knowledge that is taken from the literature [13]. Douglas-fir, as a highly adaptable species, responds strongly to temperature- and moisture-related changes in its environment ([67], Fig. 4). Gen-ecological studies repeatedly confirmed that intra-specific variation is mainly driven by temperature, specifically winter cold, and by drought, related to summer precipitation [6, 13, 67]. In our analysis, winter temperature was substituted by the highly correlated proxy 'yearly temperature difference' (i.e. continentality), while summer temperature and precipitation were directly included in the model. Traits which report adaptation to summer temperature and precipitation change from north to south throughout the distribution of coastal Douglas-fir [60]. Cold hardiness-related traits typically characterize populations of higher elevations and with greater distance to the Pacific ocean, i.e. interior populations [67]. Variation in these traits appears along latitude and elevation [57, 68].

The growth responses of the interior variety, *Pseudotsuga menziesii* var. *glauca*, to climate change scenarios,

have been shown to remarkably differ between central and southern interior populations [63]. Our analysis does indeed differentiate within this subspecies, since the three large-scale DNA-regions (Fig. 3c) were also in our analysis subdivided into overall three population clusters, with some fragmented disjunct populations that were assigned to the mainly coastal ecotypes. Increasing elevation of growth sites towards lower latitudes is reflected in rather subtle changes of responses to the temperature related predictors [57]. That might be the reason why climate niches of *Pseudotsuga menziesii* var. *menziesii* ecotypes differ only slightly from those of *Pseudotsuga menziesii* var. *glauca*, i.e. in the strength of the signal and its variation. As known beforehand, precipitation vagary (PPT_sm) and continentality (TD), which characterize the habitat of the coastal and interior varieties respectively [63], reveal large-scale clinal patterns in space (Fig. 2). The effect of summer temperature (MTWM), seems to be the strongest and sharpest for northern coastal ecotypes (1 and 2) and together with a contrasting high variation in precipitation vagary distinguishes them clearly from the southern coastal ecotype 3 (Fig. 4). Southern populations of this variety (corresponding to ecotype 3) are known to suffer from both heavier summer drought and winter precipitation [63] and are also more resistant to drought, while northern populations (corresponding to ecotypes 1 and 2) are more productive [69].

The most glaring difference between botanical knowledge and genetics on one side, and the statistically identified ecotypes on the other, is the disjunct distribution of some subgroups of ecotypes, which cover areas in both coastal and interior range. Also the wide latitudinal range of ecotypes that mainly cover the interior distribution (Fig. 3) is not in line with this knowledge. The subdivision into ecotypes that belong to both, the coastal and interior variety of *Pseudotsuga menziesii* on a small range, such as in British Columbia where we find populations of all ecotypes, indeed happens in a transition zone where we can expect a lot of substructure in populations [57, 66]. This becomes evident when allowing for more clusters in SI, Fig. 4 where the fragmented populations of each variety belong to an own ecotype. Even though local adaptation diversity is known to be very high in Douglas-fir [58], in this area however, it was shown that neutral genetic processes shape the differentiation. The wide ranging distributions of our interior ecotypes (4, 5 and 6) do not overlap much with genotypic regions that were classified in other studies [25, 56]. Yet, the disjunct ecotypic subgroup of ecotype 3, of which we find populations in Arizona and New Mexico might point out some of the intra-varietal diversity [25]. However, when applying the cluster algorithm to the coastal and

interior varieties separately (see supplementary information), we find strong similarities with the hierarchical genotypic clusters from [25]. While some ecotypes seem to represent higher levels and cover the whole interior distribution, the resolution of ecotypic differentiation in the Canadian states as well as in Montana, Wyoming and Idaho is denser and higher (SI, Fig. 7).

The approach used here only identifies ecotypes *with respect to climate*, and is ignorant of other environmental drivers (soil, fire, pests). It is conceivable that the two varieties differentiated by soil preferences overlap substantially in their survival response to climate. Since we analyse occurrence data, and not growth as e.g. Rehfeldt et al. [30], only survival responses matter for the results presented here. Lab research in Douglas-fir seedlings of coastal vs interior provenance found differences in some phenotypic traits, such as growth rates [66], but failed to find difference in others, such as twig water potential response to drought, in CO₂ assimilation or stomatal conductance, despite differences in root and leaf terpene concentrations [17]. The classification of Douglas-fir populations into six ecotypes by similar responses is somewhat a simplification, as intra-specific variation in adaptation is continuous [13]. Allowing for more ecotypes, for example ten (see supplementary information) did reduce the disjunction of both the coastal and interior variety, but is still limited in representing known interior provenances (SI, Fig. 4).

Conclusion

Modelling the distribution of a species allowing for spatially variable responses to model predictors allows us to suggest populations that are more similar to another in their response to climate. Since genetic variation is moulded by climate [8], it could prove helpful to pre-select populations for provenance testing by their ecotype-climate niches.

The resulting ecotypes are tentative hypotheses and simultaneously require independent validation, ideally by a combination of genetic and common garden experiments on survival and growth [25]. We propose to use existing occurrence information to inform such sampling as a first screening method (see also [70]).

Ideally, we could follow up on our analysis with sampling of sites with different environmental conditions within ecotypic regions to test for within-cluster homogeneity. In regions with overlap of ecotypes, sampling may need to be more intense (e.g. in Alberta, Canada; Idaho, Wyoming, Arizona, New Mexico, USA; and Durango, Mexico). At the large scale of our analysis, transition zones and overlaps may also be statistical artefacts of the smooth representation of

environmental effects. The strictness of ecotype boundaries cannot be estimated from our data and would require genetic analyses.

Statistical ecotype proposals are likely to improve with the number of data points and finer grain of distribution data. Also, a good prior knowledge of the species' main environmental constraints helps reducing computational burden. In addition to our example of a commercially interesting tree species, the suitability of this approach can be further investigated at widespread species that are known for sub-specific genetic and morphological differentiation, such as red deer (*Cervus elaphus*) [71], wolf (*Canis lupus*) [72] or barn owl (*Tyto alba*) [73].

Abbreviations

AIC	Akaike Information Criterion
GAM	Generalized Additive Model
GLM	Generalized Linear Model
GWR	Geographically weighted regression
MTWM	mean temperature of warmest month
PPT	sm total summer (May to August) precipitation
SVCM	Spatially varying-coefficient model
TD	yearly mean temperature difference

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12862-024-02260-z>.

Supplementary Material 1.

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Authors' contributions

DRR and CFD planned and designed the research and initiated the analysis. MW performed the analysis. MW and CFD and DRR wrote the manuscript.

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request. The code for the analysis can be found here: <https://github.com/MWesselkamp/Spatially-varying-coefficient-model>.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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References

- Savolainen O, Pyhäjärvi T, Knürr T. Gene flow and local adaptation in trees. *Ann Rev Ecol Syst.* 2007;38:595–619.
- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol Appl.* 2008;1:95–111.
- Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, et al. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For Ecol Manag.* 2010;259(4):698–709.
- Reich PB, Sendall KM, Rice K, Rich RL, Stefanski A, Hobbie SE, et al. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. *Nat Clim Chang.* 2015;5(2):148.
- Fournier-Level A, Korte A, Cooper MD, Nordborg M, Schmitt J, Wilczek AM. A map of local adaptation in *Arabidopsis thaliana*. *Science.* 2011;334(6052):86–9. <https://doi.org/10.1126/science.1209271>.
- Bansal S, Harrington CA, Gould PJ, St Clair JB. Climate-related genetic variation in drought-resistance of Douglas-fir (*Pseudotsuga menziesii*). *Glob Chang Biol.* 2015;21:947–58.
- Amburgey SM, Miller DAW, Grant EHC, Rittenhouse TAG, Benard MF, Richardson JL, et al. Range position and climate sensitivity: The structure of among-population demographic responses to climatic variation. *Global Change Biol.* 2018;24(1):439–54. <https://doi.org/10.1111/gcb.13817>.
- Rehfeldt GE, Leites LP, Joyce DG, Weiskittel AR. Role of population genetics in guiding ecological responses to climate. *Global Change Biol.* 2018;24(2):858–68.
- Bisbing SM, Urza AK, Buma BJ, Cooper DJ, Matocq M, Angert AL. Can long-lived species keep pace with climate change? Evidence of local persistence potential in a widespread conifer. *Divers Distrib.* 2021;27(2):296–312.
- Emery NJ, Henwood MJ, Offord CA, Wardle GM. Actinotus helianthi Populations across a Wide Geographic Range Exhibit Different Climatic Envelopes and Complex Relationships with Plant Traits. *Int J Plant Sci.* 2015;176(8):739–50. <https://doi.org/10.1086/682336>.
- Matyas C. Climatic adaptation of trees: rediscovering provenance tests. *Euphytica.* 1996;92(1–2):45–54.
- Benito Garzón M, Alía R, Robson TM, Zavala MA. Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Glob Ecol Biogeogr.* 2011;20(5):766–78. <https://doi.org/10.1111/j.1466-8238.2010.00646.x>.
- Rehfeldt GE, Leites LP, St Clair JB, Jaquish BC, Sáenz-Romero C, López-Upton J, et al. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Realized climate niches. *Forest Ecol Manag.* 2014;324:126–37.
- Isaac-Renton MG, Roberts DR, Hamann A, Spiecker H. Douglas-fir plantations in Europe: a retrospective test of assisted migration to address climate change. *Global Change Biol.* 2014;20(8):2607–17.
- Petkova K, Georgieva M, Uzunov M, et al. Investigation of Douglas-fir provenance test in North-Western Bulgaria at the age of 24 years. *J For Sci.* 2014;60(7):288–96.
- Weller A, Jansen M. Internationale Douglasien-Provenienzversuchsserie von 1961: Vergleich ausgewählter Herkünfte auf Basis von Oberhöhenleistung und Rangveränderungen bis Alter 58 Jahre. *Forstarchiv.* 2017;88:3–16.
- Kleiber A, Duan Q, Jansen K, Verena Junker L, Kammerer B, Rennenberg H, et al. Drought effects on root and needle terpenoid content of a coastal and an interior Douglas fir provenance. *Tree Physiol.* 2017;37(12):1648–58.
- Rehfeldt GE. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): a synthesis. *Forest Ecol Manag.* 1989;28(3–4):203–15.
- Eckhart T, Walcher S, Hasenauer H, van Loo M. Genetic diversity and adaptive traits of European versus American Douglas-fir seedlings. *Eur J For Res.* 2017;136(5):811–25.
- Ballian D, Mikić T, Pintarić K, et al. Provenance trials with Douglas fir (*Pseudotsuga menziesii* Mirb. Franco) at Blinje site near Kreševo. *Radovi Šumarskog Fakulteta Univerziteta u Sarajevu.* 2002;32:9–18.
- St Clair JB, Howe GT. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. *Global Change Biol.* 2007;13(7):1441–54.
- Wei XX, Beaulieu J, Khasa DP, Vargas-Hernández J, López-Upton J, Jaquish B, et al. Range-wide chloroplast and mitochondrial DNA imprints reveal multiple lineages and complex biogeographic history for Douglas-fir. *Tree Genet Genomes.* 2011;7(5):1025–40.
- Gugger PF, Sugita S, Cavender-Bares J. Phylogeography of Douglas-fir based on mitochondrial and chloroplast DNA sequences: testing hypotheses from the fossil record. *Mol Ecol.* 2010;19(9):1877–97.
- Chakraborty D, Wang T, Andre K, Konner M, Lexer MJ, Matulla C, et al. Adapting Douglas-fir forestry in Central Europe: evaluation, application, and uncertainty analysis of a genetically based model. *Eur J For Res.* 2016;135(5):919–36.
- Hintsteiner WJ, Van Loo M, Neophytou C, Schueler S, Hasenauer H. The geographic origin of old Douglas-fir stands growing in Central Europe. *Eur J For Res.* 2018;137(4):447–61. <https://doi.org/10.1007/s10342-018-1115-2>.
- Leites LP, Robinson AP, Rehfeldt GE, Marshall JD, Crookston NL. Height-growth response to climatic changes differs among populations of Douglas-fir: a novel analysis of historic data. *Ecol Appl.* 2012;22(1):154–65.
- Chakraborty D, Wang T, Andre K, Konner M, Lexer MJ, Matulla C, et al. Selecting populations for non-analogous climate conditions using universal response functions: The case of Douglas-fir in Central Europe. *PLoS ONE.* 2015;10(8):e0136357.
- Hamann A, Gylander T, Chen PY. Developing seed zones and transfer guidelines with multivariate regression trees. *Tree Genet Genomes.* 2011;7(2):399–408.
- Booth TH, Searle SD, Boland DJ. Bioclimatic analysis to assist provenance selection for trials. *New For.* 1989;3:225–34.
- Rehfeldt GE, Leites LP, St Clair JB, Jaquish BC, Sáenz-Romero C, López-Upton J, et al. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Clines in growth potential. *For Ecol Manag.* 2014;324:138–46.
- Osborne PE, Foody GM, Suárez-Seoane S. Non-stationarity and local approaches to modelling the distributions of wildlife. *Divers Distrib.* 2007;13(3):313–23.
- Thorson JT, Barnes CL, Friedman ST, Morano JL, Siple MC. Spatially varying coefficients can improve parsimony and descriptive power for species distribution models. *Ecography.* 2023;e06510. <https://doi.org/10.1111/ecog.06510>.
- Chardon NI, Pironon S, Peterson ML, Doak DF. Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. *Ecography.* 2020;43(1):60–74.
- Hällfors MH, Liao J, Dzurisins J, Grundel R, Hyvärinen M, Towle K, et al. Addressing potential local adaptation in species distribution models: implications for conservation under climate change. *Ecol Appl.* 2016;26(4):1154–69. <https://doi.org/10.1890/15-0926>.
- Ikeda DH, Max TL, Allan GJ, Lau MK, Shuster SM, Whitham TG. Genetically informed ecological niche models improve climate change predictions. *Global Change Biol.* 2016;164–76. <https://doi.org/10.1111/gcb.13470>.
- Hu XG, Wang T, Liu SS, Jiao SQ, Jia KH, Zhou SS, et al. Predicting future seed sourcing of *Platykladus orientalis* (L.) for future climates using climate niche models. *Forests.* 2017;8(12):471. <https://doi.org/10.3390/f8120471>.
- Meynard CN, Gay PE, Lecoq M, Foucart A, Piou C, Chapuis MP. Climate-driven geographic distribution of the desert locust during recession periods: Subspecies' niche differentiation and relative risks under scenarios of climate change. *Global Change Biol.* 2017;23(11):4739–49. <https://doi.org/10.1111/gcb.13739>.
- Theodoridis S, Patsiou TS, Randin C, Conti E. Forecasting range shifts of a cold-adapted species under climate change: are genomic and ecological diversity within species crucial for future resilience? *Ecography.* 2018;41(8):1357–69. <https://doi.org/10.1111/ecog.03346>.
- Finley AO. Comparing spatially-varying coefficients models for analysis of ecological data with non-stationary and anisotropic residual dependence. *Methods Ecol Evol.* 2011;2(2):143–54.
- Turesson G. The species and the variety as ecological units. *Hereditas.* 1922;3(1):100–13.
- Lowry DB. Ecotypes and the controversy over stages in the formation of new species. *Biol J Linn Soc.* 2012;106(2):241–57.
- Rehfeldt GE, Crookston NL, Sáenz-Romero C, Campbell EM. North American vegetation model for land-use planning in a changing climate: a solution to large classification problems. *Ecol Appl.* 2012;22(1):119–41.

43. Wang T, Hamann A, Spittlehouse D, Carroll C. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE*. 2016;11(6):e0156720.
44. Austin MP. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol Model*. 2007;200:1–19.
45. Hastie TJ, Tibshirani RJ. *Generalized Additive Models*. London: Chapman & Hall; 1990.
46. Wood SN. *Generalized Additive Models: An Introduction with R*. 2nd ed. London: Chapman and Hall/CRC; 2017.
47. R Core Team. *R Foundation for Statistical Computing. R: A Language and Environment for Statistical Computing*. 2019. <https://www.R-project.org/>. Accessed 16 Jan 2024.
48. Dambon JA, Sigrist F, Furrer R. Maximum likelihood estimation of spatially varying coefficient models for large data with an application to real estate price prediction. *Spat Stat*. 2021;41:100470.
49. Hastie T, Tibshirani R. Varying-coefficient models. *J R Stat Soc Ser B (Stat Methodol)*. 1993;55:757–96.
50. Comber A, Harris P, Brunsdon C. Spatially Varying Coefficient Regression with GAM Gaussian Process splines: GAM(e)-on. *AGILE GIScience Ser*. 2022;3:1–6. <https://doi.org/10.5194/agile-giss-3-31-2022>.
51. Schubert E, Rousseeuw PJ. Fast and eager k-medoids clustering: O(k) runtime improvement of the PAM, CLARA, and CLARANS algorithms. *Inf Syst*. 2021;101:101804. <https://doi.org/10.1016/j.is.2021.101804>.
52. Dixon WJ. Simplified estimation from censored normal samples. *Ann Math Stat*. 1960;31(2):385–91. <https://doi.org/10.1214/aoms/1177705900>. Zbl: 0093.15802.
53. Rand WM. Objective Criteria for the Evaluation of Clustering Methods. *J Am Stat Assoc*. 1971;66(336):846–50. <https://doi.org/10.1080/01621459.1971.10482356>.
54. Hastie T, Tibshirani RJ, Friedman JH. *The Elements of Statistical Learning: Data Mining, Inference, and Prediction*. 2nd ed. Berlin: Springer; 2009.
55. Tibshirani R, Walther G, Hastie T. Estimating the number of clusters in a data set via the gap statistic. *J R Stat Soc Ser B (Stat Methodol)*. 2001;63(2):411–23.
56. Van Loo M, Hintsteiner W, Pötzelsberger E, Schüler S, Hasenauer H. Inter-varietal and intravarietal genetic structure in Douglas-fir: nuclear SSRs bring novel insights into past population demographic processes, phylogeography, and intervarietal hybridization. *Ecol Evol*. 2015;5(9):1802–17.
57. Lavender DP, Hermann RK. *Douglas-fir: the genus Pseudotsuga*. Corvallis: Forest Research Publications Office, Oregon State University; 2014.
58. Randall WK, Berrang P. Washington tree seed transfer zones. Washington State Department of Natural Resources; 2002. https://www.dnr.wa.gov/publications/lm_wfn_seedzone_book.pdf. Accessed 06 Feb 2024.
59. Li P, Adams W. Range-wide patterns of allozyme variation in Douglas-fir (*Pseudotsuga menziesii*). *Can J For Res*. 1989;19(2):149–61.
60. St Clair JB, Mandel NL, Vance-Borland KW. Geneecology of Douglas fir in western Oregon and Washington. *Ann Bot*. 2005;96(7):1199–214.
61. Reyes-Hernandez VJ, Vargas-Hernandez JJ, Lopez-Upton J, Vaquera-Huerta H. Phenotypic similarity among Mexican populations of *Pseudotsuga* Carr. *Agrociencia*. 2006;40(4):545–56.
62. Gugger PF, González-Rodríguez A, Rodríguez-Correa H, Sugita S, Cavender-Bares J. Southward Pleistocene migration of Douglas-fir into Mexico: phylogeography, ecological niche modeling, and conservation of 'rear edge' populations. *New Phytol*. 2011;189(4):1185–99.
63. Chen PY, Welsh C, Hamann A. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. *Global Change Biol*. 2010;16(12):3374–85.
64. Campbell RK. Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in southwestern Oregon. *For Sci*. 1991;37(4):973–86.
65. Hermann RK, Lavender DP. *Pseudotsuga menziesii* (Mirb.) franco Douglas-fir. *Silvics N Am*. 1990;1:527–40.
66. George J, Schueler S, Grabner M, Karanitsch-Ackerl S, Mayer K, Stierschneider M, et al. Looking for the needle in a downsized haystack: Whole-exome sequencing unravels genomic signals of climatic adaptation in Douglas-fir (*Pseudotsuga menziesii*). *Ecol Evol*. 2021;11(12):8238–53.
67. Howe GT, Jayawickrama K, Cherry M, Johnson G, Wheeler NC. Breeding Douglas-fir. *Plant Breed Rev*. 2006;27:245.
68. Rehfeldt GE. Genetic differentiation of Douglas-fir populations from the northern Rocky Mountains. *Ecology*. 1978;59(6):1264–70.
69. Eilmann B, de Vries SM, den Ouden J, Mohren GM, Sauren P, Sass-Klaassen U. Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) provenances. *For Ecol Manag*. 2013;302:133–43.
70. Guisan A, Broennimann O, Engler R, Vust M, Yoccoz NG, Lehmann A, et al. Using niche-based models to improve the sampling of rare species. *Conserv Biol*. 2006;20:501–11.
71. Skog A, Zachos FE, Rueness EK, Feulner PGD, Myrsterud A, Langvatn R, et al. Phylogeography of red deer (*Cervus elaphus*) in Europe. *J Biogeogr*. 2009;36(1):66–77. <https://doi.org/10.1111/j.1365-2699.2008.01986.x>.
72. Vilà C, Amorim IR, Leonard JA, Posada D, Castroviejo J, Petrucci-Fonseca F, et al. Mitochondrial DNA phylogeography and population history of the grey wolf *Canis lupus*. *Mol Ecol*. 1999;8(12):2089–103. <https://doi.org/10.1046/j.1365-294x.1999.00825.x>.
73. Roulin A. *Barn Owls: Evolution and Ecology*. Cambridge: Cambridge University Press; 2020.

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