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POSSIBILITIES AND LIMITATIONS OF USING HISTORIC PROVENANCE TESTS TO INFER FOREST SPECIES GROWTH RESPONSES TO CLIMATE CHANGE

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ABSTRACT. Under projected changes in global climate, the growth and survival of existing forests will depend on their ability to adjust physiologically in response to environmental change. Quantifying their capacity to adjust and whether the response is species- or population-specific is important to guide forest management strategies. New analyses of historic

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provenance tests data are yielding relevant insights about these responses. Yet, differences between the objectives used to design the experiments and current objectives impose limitations to what can be learned from them. Our objectives are (i) to discuss the possibilities and limitations of using such data to quantify growth responses to changes in climate and (ii) to present a modeling approach that creates a species- and population-specific model. We illustrate the modeling approach for *Larix occidentalis* Nutt. We conclude that the reanalysis of historic provenance tests data can lead to the identification of species that have population-specific growth responses to changes in climate, provide estimates of optimum transfer distance for populations and species, and provide estimates of growth changes under different climate change scenarios. Using mixed-effects modeling techniques is a sound statistical approach to overcome some of the limitations of the data.

KEY WORDS: Climate-change response functions, provenance tests, genotype by environment interaction, provenance transfer functions, *Larix occidentalis* Nutt, linear mixed-effects models.

1. Introduction. The long history of provenance testing in forestry has shown that native populations of forest trees are reasonably well adapted; i.e., physiologically attuned to the environments they inhabit (see Morgenstern [1996]). Associations between growth traits and climate gradients, which have been interpreted as signals of genetic adaptation, have been studied for centuries (see Langlet [1971]). In forestry, knowledge about these associations has been used extensively to guide reforestation efforts (see Johnson et al. [2004]). Seed can be transferred and planted only so far from the place of origin, i.e., the seed-source environment and the planting environment can differ only within certain limits, before growth and survival rates are depressed and damage levels increase.

Under projected changes in global climate, the growth and survival of existing forests will depend on the forest's ability to adjust phenotypically, because substantial changes are projected to occur during their lifetime (Matyas [1996]). Quantifying forests' capacity to adjust is critical both for developing science-based adaptive management strategies and for projecting future growth under different scenarios. Modeling the growth responses of forest species to changes in climate can be

used to quantify this capacity by estimating the magnitude and direction by which growth is affected given certain changes in climate.

Early work on the effects of spatial environmental changes on the growth of forest species and populations provides a base for current modeling efforts. Pioneering studies such as Campbell's [1974] examined the response of phenology to changes in geographic variables, which were used as surrogates for climate, and developed approaches to predict populations' performance given seed-source geographical characteristics. Later, studies such as Matyas and Yeatman [1992] described populations' performance using measures of the similarity between the environment where the seed was collected and that of the test location.

Data for these studies originated in provenance tests that were designed to evaluate, in a common environment, the growth and survival characteristics of many populations of a given geographic area. Their objectives were to identify populations that had the highest growth potential for the test geographic area, to construct seed transfer guidelines and seed zones for reforestation (e.g., Campbell and Sorensen [1978], Raymond and Lindgren [1990]), and to describe species-specific clines in genetic variation (e.g., Rehfeldt [1982, 1989]).

In the early 1990s, provenance tests were "rediscovered" as experiments in spatial climate change with the potential to yield significant insights regarding forest species responses to global climate change (Matyas [1994], Schmidtling [1994], Carter [1996], Matyas [1996], Rehfeldt et al. [1999, 2001, 2002]). Because the climate at the seed source differed from that of the test location, the population has been subjected to a spatial climate change. Such a change has been termed *climate transfer distance* (e.g., Rehfeldt et al. [2003]). If a population has been tested at several locations, then the growth response to these spatial changes in climate can be quantified.

New analyses of provenance tests data are yielding relevant and useful insights (e.g., Rehfeldt et al. [2001], Wang et al. [2006]). Yet, differences between the objectives used to design the experiments and current objectives impose limitations as to what can be learned from them. Specifically, the selection of planting locations and of seed sources to be tested at a planting location focused on the original objectives but may not be optimal for the current purposes. Tests were generally located in areas of relatively good productivity and rarely in harsh climates

where survival and growth could be compromised. Additionally, tests were intended to evaluate "the performance of populations originating from ecologically reasonable distances" (Matyas and Yeatman [1992]). At the population level, these tests emphasized observations around the optimum performance instead of observations of populations that were moved to extreme environments. The latter would have provided information about "maladapted provenances of little practical interest" (Raymond and Lindgren [1990]) at that time. The result is that, in most cases, only narrow ranges of climatic transfer distances are available for tested locations and tested populations.

For current objectives, which are focused on describing broad-scale responses of species and populations to large changes in climate, maladapted provenances provide essential information. A study design that was aligned with current information needs would test populations from a species' entire geographic distribution, especially from the xeric and thermal margins, and include many test sites located throughout the entire geographical distribution to ensure a wide range of climate transfer distances.

To fully take advantage of the insights that new analyses of provenance tests can provide, the modeling approaches need to specifically address and account for these limitations.

2. Modeling approach. Leites et al. [2012] proposed merging species- and population-level responses into one model using mixed-effects modeling techniques. This approach overcomes as much as possible the major limitations imposed by the lack of test sites in harsh locations and by relatively small population transfer distances. Here, we illustrate and discuss this modeling approach using western larch (*Larix occidentalis* Nutt) provenance tests data.

Western larch is a western North America species that has a relatively small natural distribution in southeastern British Columbia, Canada, and the USA Inland northwest (Figure 1). Within its natural range, western larch is ecologically and commercially important. It is an important species for reforestation, and tree breeding programs to improve growth traits are currently in place in both jurisdictions (Jaquish et al. [1993], Rehfeldt and Jaquish [2010]).

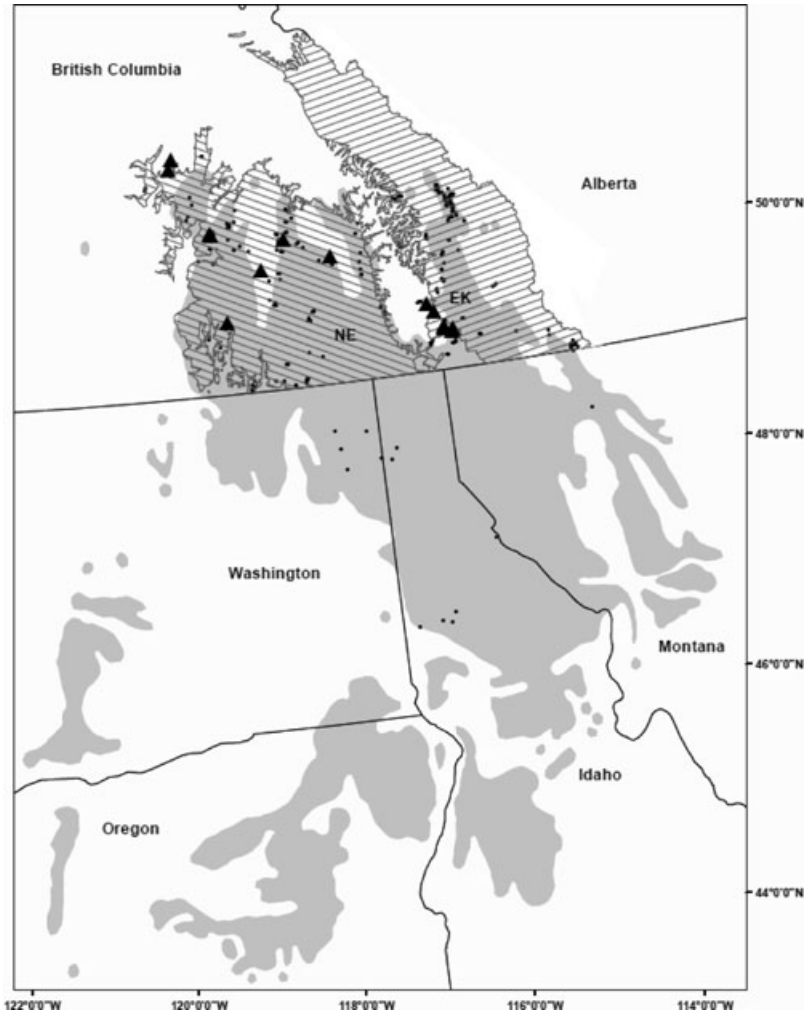

FIGURE 1. Geographic location of populations' origin (circles), test site locations (triangles) and B.C. western larch seed zones (EK = East Kootenay; NE = Nelson) superimposed on Little's [1971] western larch geographic distribution.

In this example, our specific objective was to model the 10-year height (HT10, cm) response to changes in climate of western larch populations growing in provenance tests in British Columbia.

2.1. Data. Open-pollinated seed was collected from individual wild-stand parent trees from the Nelson and East Kootenay seed planning zones in southern British Columbia (Jaquish et al. [1993], Figure 1). A total of 666 half-sib families were tested. Since some of the parent trees inhabited the same geographic area, we identified all families with the same latitude and longitude of origin and within an elevation range of 100 m (i.e., same provenance) as belonging to one single population. These defined populations became our modeling unit. Two hundred and fifty-two populations were tested in four test series. Test series were defined by design; i.e., because of practical limits to the testing program, sets of populations were tested in different test series. Each test series also comprised different test locations. To link the test series and test location, 22 families were planted in all test series and test locations. The number of test locations within each test series was three or four. Within each test location, families were planted in 8–10 replicate blocks in row-plots of four trees. Population HT10 (i.e., the average height of all families identified as one population) by block and test location was used in this analysis. The geographic location of populations and test locations is presented in Figure 1. The distribution of latitude, longitude, and elevation represented by these populations are presented in Figure 2. A description of the tests is provided in Table 1.

Climate data for the test locations and populations' seed sources were estimated using Rehfeldt's [2006] climate model for North America. These data are available at http://forest.moscowfsl.wsu.edu/climate/. By using the climate normals from 1961 to 1990, we assumed that they represent the climate inhabited by the parent generation from which the seed were collected. Note, however, that all test series were planted after 1991. Even though the climate has been warming, we expect that the climate normals for the 1961–1990 period would underrepresent the site means by only a few tenths of a degree. Climate transfer distances were calculated as the difference between a given climate variable at test site and the climate variable at the geographic location of seed collection (hereafter climate at seed source). Supporting Information

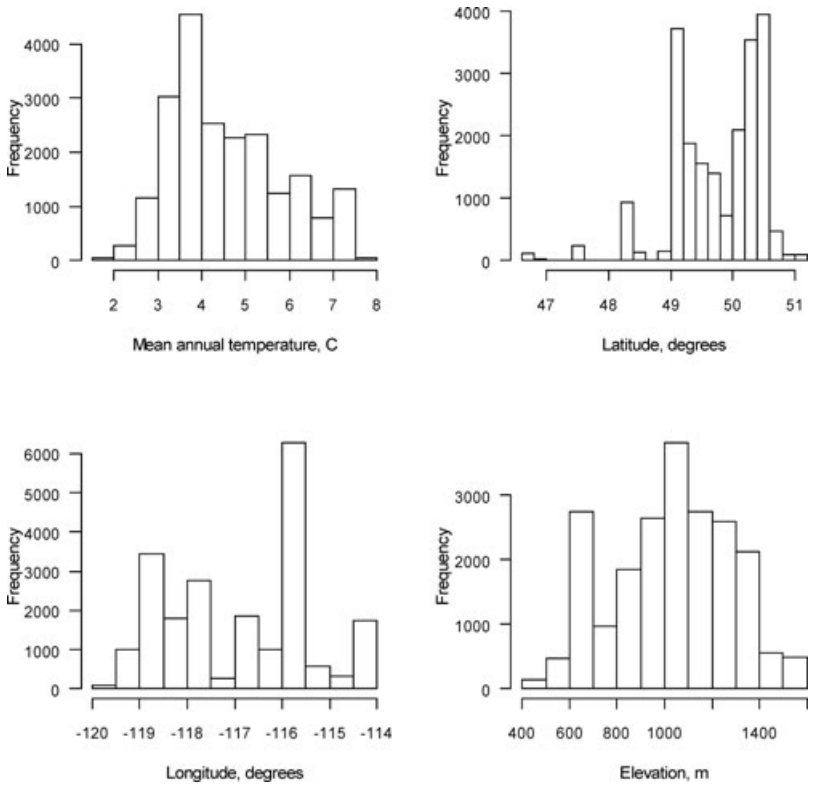

FIGURE 2. Distribution of mean annual temperature, latitude, longitude, and elevation represented by the populations included in this study.

Appendix S1 presents a summary of the climate variables used in this analysis.

2.2. Methodology. The modeling approach was based on a conceptual model (Figure 3, outward diagram) which describes the assumed relationship between long-term environment, seed-source genetics, and short-term environment. The model describes the population's realized growth as a function of (i) its genetics, (ii) the similarity of the experienced short-term climate to the long-term climate that

TABLE 1. Description of the western larch provenance test series used in this study.

Test series	Location (Lat. and long in degrees, elev. in m)	No. populations	No. blocks	Ten-year height (cm)	
				Mean	SD
EKS2	ANGU (49.60/−116.15/1140)	70	8	469.3	37.9
EKS2	LLAM (49.35/−115.85/1035)	70	8	400.6	37.3
EKS2	SEM2 (49.39/−115.97/1430)	70	8	470.9	39.2
EKS2	ULAM (49.33/−115.87/1145)	70	8	385.4	33.4
EKS1	LAMB (49.35/−115.85/1035)	86	10	376.0	41.0
EKS1	SAWM (49.52/−116.07/1470)	86	10	358.7	34.2
EKS1	SEM1 (49.39/−115.96/1370)	86	10	340.6	39.4
NE1	BEAV (49.64/−118.86/1250)	103	8	303.5	43.8
NE1	WILS (50.13/−117.37/950)	103	8	299.7	79.8
NE1	CROS (51.12/−119.42/1070)	103	8	467.6	63.8
NE1	MIR1 (50.43/−118.98/830)	103	8	414.0	81.4
NE2	CAMR (50.32/−117.98/950)	80	8	379.3	71.5
NE2	MIR2 (50.42/−118.97/850)	80	8	440.9	60.2
NE2	SPRK (51.03/−119.47/820)	80	8	534.2	71.4

has partly shaped the genetic makeup of the population, and (iii) the interaction of genetics and climate. It also includes long-term climate as a factor shaping genetic differences among populations. This conceptual model guided the definition of the statistical model (Figure 3, inward diagram). We model the response with a quadratic model form because it has been previously used to approximate the height response to changes in the environment (Morgenstern and Mullin [1990], Matyas and Yeatman [1992], Carter [1996], Rehfeldt et al. [1999, 2002]).

The modeling proceeded as follows, and is summarized in Figure 4. Based on the conceptual model (Figure 3), we needed to identify the climate variable that was most important in determining the effects of *climate transfer distance* on the response variable, HT10. Due to

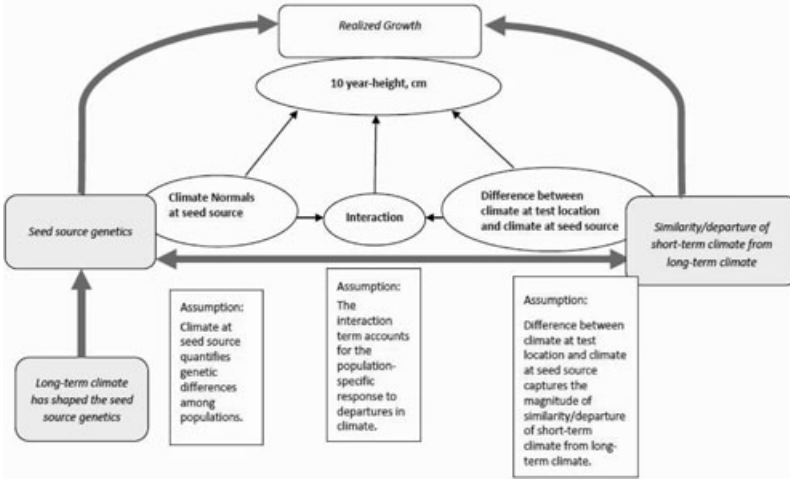

FIGURE 3. Conceptual model.

the limitation of these data in terms of the range of observed transfer distances, we screened the variables to find those climate transfer distance variables for which the range was such that the quadratic response of HT10 on transfer distance was statistically detectable. For this screening process, we fit a quadratic linear model between HT10 and each of the 17 variables describing climate transfer distance. The variables corresponding to models with a nonsignificant quadratic term (t-test, alpha = 0.01) were excluded from further consideration, on the grounds that the observed range of the variable was likely too short to provide statistical power. Of those with a statistically significant negative quadratic term (t-test, alpha = 0.01), seven were selected based on the level of significance of the quadratic term and on the model's coefficient of determination (R^2). This screening step identified seven candidate climate transfer distance variables.

The conceptual model also required the selection of a *climate at seed-source* variable that best described the differences among populations' genetics, i.e., a variable that was best correlated to the populations' performance across sites. Spearman's rank correlation (ρ) was calculated between HT10 and each of the 17 variables that represented the

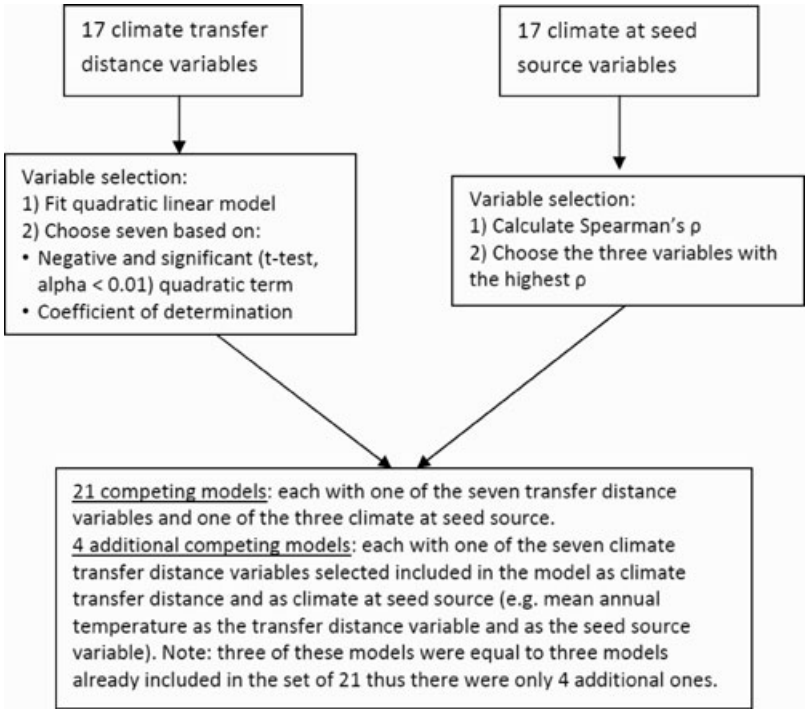

FIGURE 4. Diagram illustrating the variable selection process and the resulting competing models.

climate at seed source. The three with the highest ρ were selected to be included in the candidate models. The climate at seed-source variables with the highest ρ were the same climate variables selected as climate transfer distance, except in one case.

Each competing model included one climate transfer distance variable both as a linear and quadratic fixed effect, a climate at seed-source variable as a linear fixed effect and an interaction between climate transfer distance and climate at seed-source fixed effect. Twenty-one candidate models were evaluated. Each model included one of the seven selected climate transfer distance variables and one of the three selected climate at seed-source variables.

Additionally, we evaluated models including one of the seven selected climate transfer distances and the same climate variable as seed-source climate (e.g., mean annual temperature as the transfer distance variable and as the seed-source variable). This resulted in four additional competing models.

The inclusion of the random effects attended to the structure of the data and to the conceptual model. To account for within-group correlation the following random effects were assumed to affect the model's intercept: a population random effect crossed with a test-series random effect, a test location random effect nested within test series, and a block random effect nested within test location within test series.

To address the conceptual model, a population random effect was included to modify the linear term of the climate at seed source, and similarly one was included to modify the linear term of the climate transfer distance. We hypothesized that a single climate variable may account for part of the genetic differences. The inclusion of these random effects served to account for any remaining genetic effects while providing a measure of the model's population-level unexplained variation. Akaike's Information Criterion (AIC, Akaike [1973]) was used to select the model that best fitted the data. The model had the following form:

$$\begin{aligned} y_{i(j(k(ln)))} &= \left(b_0 + u_{1n} + u_{2j(k(l))} + u_{3k(l)} + u_{4l}\right) + (b_1 + u_{5n})x_{1nk} \\ &\quad + b_2 x_{1nk}^2 + (b_3 + u_{6n})x_{2n} + b_4\left(x_{1nk} \times x_{2n}\right) \\ &\quad + \epsilon_{i(j(k(ln)))}. \end{aligned} \tag{1}$$

where y = 10-yr height for the ith observation in the jth block in the kth test location in the lth test series and the nth population; x_1 = climate transfer distance for the nth population at the kth test location; x_2 = climate at seed source for the nth population; j = block index; k = test location index; l = test series index; n = population index; b_0–b_4 are fixed-effects parameters; u_1–u_6 are random effects.

For the selected model, the statistical significance of the random effects was assessed using likelihood ratio tests. The statistical significance of the fixed effects was assessed by calculating 95% nonparametric bootstrap confidence intervals for the parameter estimates using 1000 bootstrap replications. The bootstrap intervals were based on resampling the populations, rather than the plots. All analyses

were performed in the statistical environment R (R Development Core Team [2008]) and the models were fit using the lmer function of the lme4 package.

2.3. Results. The model with the lowest AIC had minimum temperature of the coldest month (MIN) as the climate transfer distance variable and as the seed-source climate variable. In this model, the interaction between the climate transfer distance and the climate at seed source was statistically significant (i.e., confidence interval for this parameter entirely below zero, $\alpha < 0.05$) which suggests a population-specific response to changes in climate. The estimates of the fixed effects suggest that populations from geographic areas with the warmest winters have (i) their optimum at warmer temperatures, (ii) benefit from a short negative transfer distance (i.e., moved to colder winters), and (iii) are negatively affected by transfers into warmer winters. Populations from colder climates have their optimum HT10 at colder temperatures and benefit when transfer distance is positive by several degrees. An illustration of the fixed-effects predictions for three hypothetical populations is presented in Figure 5.

In addition, fixed-effects predictions indicate that, even though at transfer distance zero populations did not differ largely in HT10, populations seem to inhabit different degrees of suboptimal climates. Populations from geographic areas with warmer winters have optimum growth when transfer distance is negative but close to zero, whereas populations from colder climates expressed optimum growth at winters several degrees warmer than their inhabited climate (i.e., positive transfer distances). Evidence of populations inhabiting suboptimal climates exist for several forest species (e.g., Namkoong [1969]). This phenomenon has been explained as the result of either an adaptational lag (Matyas [1996]) or an interaction between populations' adaptation to the environment and interspecific competition (e.g., Rehfeldt et al. [2004]).

The likelihood ratio tests indicated that the inclusion of the test series random effect did not improved the model. All other random effects did improve the model fit according to our criterion (lower AIC). The estimates of the variance components for the random effects suggest that there is a large amount of variation at all group levels. These

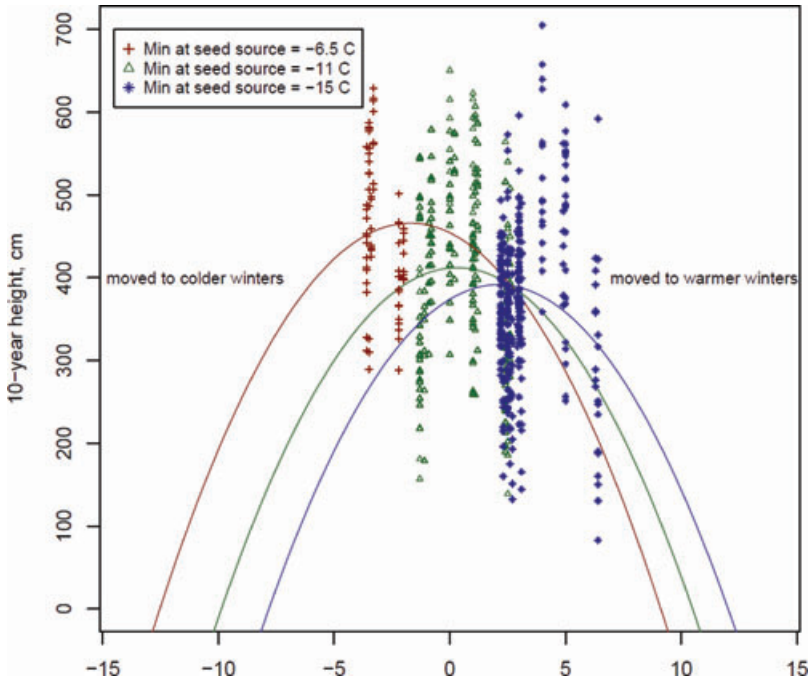

FIGURE 5. Illustration of the fixed-effects predictions (selected model, Table 2) for three hypothetic populations originating in places with minimum temperature of the coldest month (MIN) of –6.5, –11, and –15°C. Observations correspond to those from all populations with MIN equal to the chosen magnitudes and they include observations for different test locations and blocks.

sources of variations remain unexplained from the point of view of the model's predictive ability. In terms of understanding climate change effects on growth, the test location random effect and the population random effects are of particular interest. The population and test location random effects on the intercept (u_1 and u_5, Table 2) had the largest standard deviation. This indicates a limited usefulness of the mean species HT10 as an indicator because the variation of populations' mean HT10 or test-sites' mean HT10 is large. It also indicates that for predictive purposes, the model may benefit from additional population and test-location fixed effects.

TABLE 2. Parameter estimates and bootstrap 95% confidence intervals for the selected model.

Parameter	Parameter estimate	Bootstrap confidence intervals (α = 0.95) lower	upper
b_0 (intercept)	515.79	483.2	540.2
b_1 (min.trds)	−36.77	−51.47	−19.57
b_2 (min.trds^2)	−3.98	−4.94	−3.09
b_3 (min)	9.45	6.42	11.55
b_4 (min.trds*min)	−3.57	−4.73	−2.18
SD (u_1, pop intercept)	192.88		
SD (u_2, pop linear min)	15.52		
SD (u_3, pop linear min.trds)	15.74		
SD(u_5, test location)	63.62		
SD(u_6, block)	27.56		
SD (ϵ)	54.59		
Cor(u_1, u_2)	0.897		
Cor(u_2, u_3)	0.914		
Cor(u_1, u_3)	0.992		

Note: Given the selection of a fixed number of the possible variables at each of the two stages of model development, not all possible models resulting from all possible variable combinations were evaluated. This may potentially result in the true confidence intervals for the parameter estimates having less coverage than the nominal 0.95. *min.trds= minimum temperature of the coldest month transfer distance in °C, min = minimum temperature at seed-source location in °C.

The standard deviation of the population-level random effect affecting the climate at seed-source variable (u_2, Table 2) is very high, which indicates that most of the among-population differences are not reflected by differences in the seed-source MIN. The positive correlation among the population random effects on the intercept, the MIN linear term, and the MIN transfer distance linear term (u_1, u_2, u_3, Table 2)

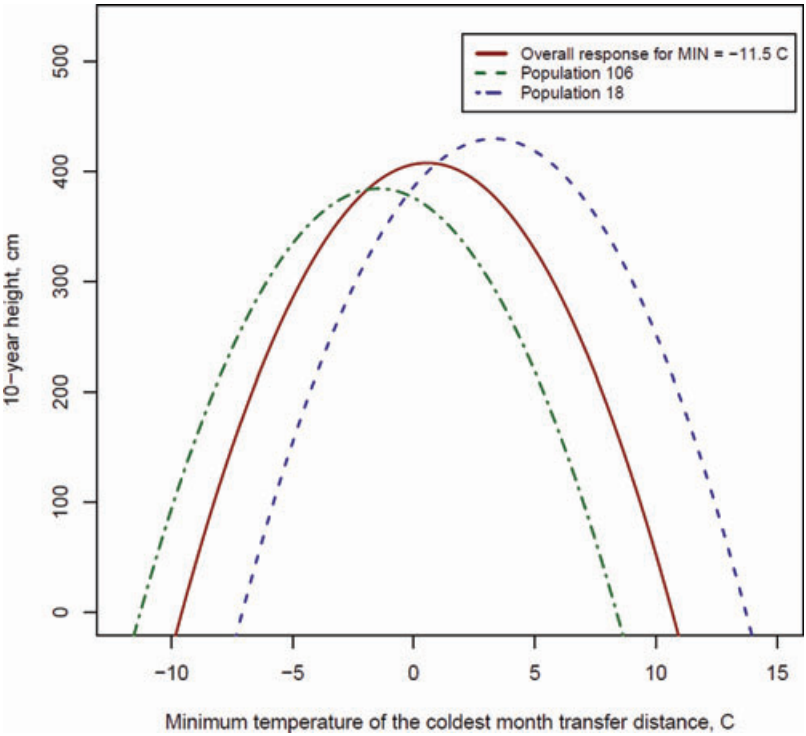

FIGURE 6. Illustration of the population-level HT10 response to changes in minimum temperature of the coldest month for two populations originating in places with minimum temperature of the coldest month (MIN) equal to –11.5°C (fixed effects have been modified by the population-specific random effects but the test location and block random effects have been assumed to be zero) and the fixed-effects response for populations originating at MIN –11.5°C (overall response). These two populations originated in places with the same MIN but differ in their geographic coordinates: population 18 originated at longitude –118.6, latitude 49.02, and elevation 1300 m, whereas population 55 originated at longitude –115.19, latitude 49.27, and elevation 1067 m.

results in populations originating at the same MIN having predicted optimum HT10 at different transfer distances. An illustration of two populations' responses with the same MIN but with extremely different random effects is presented in Figure 6. These responses show the population-level responses assuming the mean random effect for

test location, and block (i.e., zero). The magnitude of the population random effects was mildly associated with the seed-source longitude (Spearman's correlation coefficient of 0.14 and 0.13 for u_2 and u_3, respectively). Within the inhabited geographic region, the western and eastern edges are dry whereas the middle region is relatively wet. The western edge is warm and dry, whereas the eastern edge is cool and dry. Maps of western larch genetic variation reveal that tree growth potential is highest in the warm, moist middle region and declines in the dry peripheral regions to the east and west (Rehfeldt and Jaquish [2010]). These differences could partially explain this large variation of the population-level random effects. Other explanations may reside in the data and the model form and its assumptions. In terms of the latter there are two issues: (i) a quadratic model enforces a symmetry around maximum HT10 that may not properly represent the response to changes in climate for all the populations: e.g., those from warmer climates may by affected more abruptly by transfers to warmer climates than a symmetric equation allows; (ii) we are assuming the within-population random effects variance to be equal. Due to the data structure, the model includes crossed and nested random effects. Modeling the within-population variance would greatly increase the model complexity. The diagnostic plots do not show any major issues (Figures S1–S3, Appendix S2); however, if the within-population variance is not constant then the estimated among-population variance could be inflated.

3. Discussion.

3.1. Modeling approach.

3.1.1. *Narrow transfer distance range and few observations per population.* A major challenge of using data from provenance tests for forest growth responses to changes in climate is centered on the lack of a wide range of transfer distances. A range that includes extreme transfers, for which maladaptation effects result in widespread mortality, is commonly unavailable. Having such information would allow more reliable modeling of the hypothesized quadratic response, but without it, the estimated y-intercepts may have no biological meaning;

in fact, the quadratic response may be fit as upwardly concave which is biologically unrealistic.

Another challenge is that in many cases only a few height-climate transfer distance observations are available for each population. We address both challenges by merging species- and population-level responses using a mixed-effects models framework. By using all populations, the climate transfer distance range is sufficiently wide to allow for the modeling of a mean species-level response. Any group-level effects are accounted for by introducing random effects. The departures of populations from the species-level response can then be quantified by incorporating population-level fixed and random effects into the model. In such a model, populations with insufficient information will have responses closer to the species-level response, i.e., they will be shrunk toward the mean response. As the western larch example shows, even with few test locations, and thus few height-climate transfer distance observations per population, this approach allows for the modeling of the HT10 growth response to changes in climate. We note that Wang et al. [2010] addressed these challenges by merging population response functions and transfer models into a single equation (referred as "universal transfer function"). Even though both approaches combine population- and species-level information into a single equation, there are important differences in the statistical methodology. For example, Wang et al. [2006, 2010] use "anchor points" to address the narrowness of the range of observations available for a single population. We, for reasons explained earlier, find the use of a mixed-effects model to be a better statistical alternative to address this issue as well as to address the issues of data structure that are discussed later.

3.1.2. *Data structure and model specification.* Provenance test data commonly include several test locations. At each test location, the experiments are invariably laid out in a valid experimental design, usually a randomized complete block. In addition, due to time differences in seed collections, physical space issues, or seed transfer considerations, and because of differences in the scope and objectives of disparate studies, groups of test sites evaluated different sets of populations (in our example these are called test series). They sometimes included a small set of populations that were evaluated in all sites and could serve as a link between the "test series." This generates a structure

in the data which, in our case, included crossed and nested levels as well as potential autocorrelation at a given level (e.g., among observations within a given population). Previous statistical analyses using provenance test data to model height-growth response to climate have ignored these elements of the experimental design. This omission could lead to underestimating the residual variance which in turn affects confidence intervals and hypothesis testing. In addition, if the model is not properly specified, then important effects may be confounded or not detected (Wood [2006, pp. 277–282]). Mixed-effects models are able to accommodate the data structure through the selection of fixed and random effects. Although we argue that mixed-effects models improve on previous efforts, we acknowledge that further improvements may be possible. For example, our modeling exercise required a simple covariance model that assumed constant variance as a function of the response variable, and conditional independence of the residuals and random effects. We accommodated these assumptions by being more conservative in our conclusions. Modeling the variance and/or autocorrelation in a model with crossed and nested effects is theoretically possible but computationally challenging, and beyond the scope of the current project.

Quadratic equations have been used successfully as a model form that approximates the height response to changes in climate (Morgenstern and Mullin [1990], Matyas and Yeatman [1992], Carter [1996], Rehfeldt et al. [1999, 2002]). An advantage of this model form is its linearity in terms of how the parameters enter the model. Incorporating the required crossed and nested random effects to such model is less complex than doing so when using nonlinear model forms. A disadvantage, however, is that quadratic equations impose symmetry around the optimum. A model form that was not constrained by this symmetry may describe better the response of growth to environmental variables such as those related to temperature. Rehfeldt et al. [2003] used a Weibull probability density function that had been modified for the use of nonlinear regression techniques. In such a case, the climate transfer distances need to be modified to have a positive value. Even though this model form is a good alternative to represent skewed distributions, it is computationally complex if crossed and nested random effects are to be incorporated. In addition, the lack of observations at extreme transfer distances (common in these data

sets) may preclude the model from approaching zero asymptotically at large transfer distances. Cauchy functions have also been used (e.g., Raymond and Lindgren [1990], Thomson and Parker [2008], Thomson et al. [2009]). However, this model form does not provide an advantage over the quadratic equation in terms of providing flexibility for responses that may be asymmetrical about the optimum height. The trade-off between model form and model complexity for the analysis of these data makes the quadratic equation a reasonable approximation for our purposes.

3.2. The conceptual model. As our example illustrates, climate changes, as measured by changes in the minimum temperature of the coldest month, were associated with height growth. Populations showed a maximum height at certain transfer distance and growth declined as transfer distances departed from that optimum. In the process of selecting a model, it became apparent that the models that fitted the data better in terms of AIC used temperature-related climate variables as predictors. Even though species distributions are determined largely by the balance of temperature and moisture variables (e.g., Stephenson [1990], Rehfeldt et al. [2006]), intraspecific differences have been found to be more temperature related (e.g., Matyas [1996]). Provenance tests were located within the geographic range of the species under evaluation, so it should be kept in mind that the analyses of these data and their results are contingent on precipitation having been adequate for the growth of the species under evaluation.

The fixed-effect interaction between climate transfer distance and population's MIN was statistically significant. This outcome indicates that, for our example, growth responses to climate may be population-specific. It also highlights the importance of including this interaction in the model when evaluating different species, because this information is crucial for planning adaptation management strategies.

We now distinguish between two collections of the models evaluated: those including the same climate variable for the effects of seed-source climate and climate transfer distance, and those for which the climate variable used for the seed-source climate varied from that used for the climate transfer distance. The former collection best fit the data. The important difference between these two collections of models can

be shown by decomposition: the former includes the actual magnitude of the climate at test location, whereas the latter only includes relative information about the test location climate. In terms of our conceptual model, the former collection specifies not only the difference between short-term and long-term climate but the actual short-term climate. This is because in such a case, the original specification of the model

$$HT10_i = b_0 + b_1 x_1 + b_2 x_2 + b_3 x_2^2 + b_4 x_1 x_2 + e_i,$$

where x_1 is climate at seed source (e.g., mean annual temperature) and x_2 is climate transfer distance calculated as the difference between climate at test site and climate at seed source $(x_{2t} - x_{2s})$, but using a climate variable different than the one used to characterize seed-source climate x_1 (e.g. difference in frost-free days between test location and seed source) becomes:

$$HT10_i = b_0 + b_1 x_{1s} + b_2(x_{1t} - x_{1s}) + b_3(x_{1t} - x_{1s})^2 + b_4 x_{1s}(x_{1t} - x_{1s}) + e_i,$$

where x_1 is a given climate variable either at seed source (x_{1s}) or at test location (x_{1t}). If we rearrange algebraically, we can readily observe how the actual short-term climate information is specified in the former collection of models:

$$HT10_i = b_0 + (b_1 - b_2)\ x_{1s} + (b_3 - b_4)\, x_{1s}^2 + b_2 x_{1t} + b_3 x_{1t}^2 - 2b_3 b_4 x_{1t} x_{1s} + e_i.$$

This last formulation shows that in the former collection short-term climate has direct effects on HT10 whereas the same effects in the latter collection appear as only a component of transfer distance. This difference between the collections of models highlights the relevance of the short-term climate that is experienced by the populations as much as the difference between short- and long-term climates in explaining the population's observed height growth. For some species, it may be necessary to modify the conceptual model to include additional experienced short-term climate information.

Our results are consistent with previous work on the genetic structure of western larch. Genetic variability within and among populations tends to be abundant (Rehfeldt [1992]), but clines relating genetic variability to climatic gradients tend to be of low slope (Rehfeldt [1982], [1995], Rehfeldt and Jaquish [2010]). That is, climate accounts for relatively low proportions of the variance among populations. As a consequence, genotype-by-environment interactions expressed in climate transfer distances are real but nonetheless tend to have small effects. Nonetheless, populations will respond differently to changes in climate. This study, as well as the previous, point to winter temperatures as being the primary factor controlling genetic differences in growth potential of western larch populations (Rehfeldt and Jaquish [2010]).

Our example illustrates that population-level information is key to detecting differences in responses of populations. The inclusion of seed-source MIN facilitated detection of population-specific responses. Yet, the population-level random effects estimates indicate that MIN was not enough to capture a large portion of the differences among populations. This could be explained by western larch's high intrapopulation variability (Rehfeldt [1992]) coupled with clines of low slope (Rehfeldt [1982], [1995]). It may also be necessary to incorporate in the model more than one variable to represent climate at seed source. In such a case, gains due to the inclusion of multiple seed-source variables in the model will have to be weighed against the increase in the model complexity. Variables that reflect climate inter- and intraannual variability also could be relevant to explain population differences and these should be evaluated when estimates become available.

4. Conclusions. New analyses of historic provenance tests present an opportunity to increase our understanding of species' response to changes in climate using already available data. Identification of species that will likely have population-specific responses, approximations to estimates of optimum transfer distance for populations and species, and approximations to estimates of growth changes under different climate change scenarios are useful potential outputs of direct relevance to natural resource managers.

Results of these analyses, however, need to be interpreted in the light of the limitations imposed by the data. Lack of information on edges of

the geographic distribution, which results in a short range of transfer distances available for analysis, may preclude the statistical detection of important climate variables that affect growth responses. This lack of information can be somewhat overcome by combining all populations in a single model using mixed-effects models as demonstrated here.

Analyses of provenance tests data to model growth responses to changes in climate need to account for the experimental design effects to provide defensible conclusions. In our example, these design effects were accounted for by random effects. Even if these random effects remain as unexplained sources of variation from a predictive standpoint, they provide important insights about these responses. The magnitude of unexplained variation is a source of information as valuable as those that we are able to explain as they can provide directions for improvement and a realistic context for the use of the model predictions.

An accounting of experimental design effects has to be balanced with the chosen model form (e.g., linear versus nonlinear models) to ensure that the resulting model is not overly complex. This is true for historic provenance tests as well as any future tests as there are practical limits to the size of a provenance test.

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SUPPORTING INFORMATION

The following additional supporting information may be found in the online version of this article:

Appendix S1. Climate variables calculated by Rehfeldt's [2006] climate model

Appendix S2. Model diagnostic plots for the selected western larch model (Table 2).

FIGURE S1. Graphical summary of model fit (equation 1, Table 2)

FIGURE S2. Graphical summary of model fit (equation 1, Table 2).

FIGURE S3. Graphical summary of model fit (equation 1, Table 2).