Uncertainty in the modelled mortality of two tree species (*Fraxinus*) under novel climatic regimes

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Abstract
Aim: Based upon species distribution models (SDMs), many studies have predicted that climate change will cause regional extinctions of tree species within the next 50–100 years. SDM-based predictions have been challenged on procedural and theoretical grounds, but for tree species they are largely beyond the practical reach of direct experimental validation. Here we report the experimental consequences of moving seedlings from ~50 natural populations of each of two ash (*Fraxinus*) species to experimental sites spanning a range of 10°C colder to 10°C warmer (mean annual temperature) than home environments.

Location: Eastern North America.

Methods: We measured population-by-test-site survival percentages and mean trunk diameters at an average age of 35 years. We then used linear, mixed-effect models to develop transfer functions for each species and predict survival and mean annual growth as functions of fixed and random effects including, especially, the climatic distance (CD) between test site and home environment.

Results: Survival and growth were highest at CD ≈ 0 and declined as populations were moved to warmer or colder environments, indicating that survival and growth were optimal when populations were in home-like climates. However, variance around the model fit was substantial, and we could not statistically detect, even at $\alpha = .50$, elevated mortality following displacements into environments 3.5°C (white ash) and 4.1°C (green ash) warmer in mean annual temperature. Survival rates of 80%–100% were common even within populations subjected to warming conditions greater than those predicted to cause meso-scale extinctions in this century. We show that within-population genetic variance, phenotypic plasticity and idiosyncratic aspects of the non-climatic environment and its interaction with genotype each likely contributed to these unexpected responses to climatic displacement.

Main conclusions: Results emphasize the uncertainty that underlies predictions of climate-induced extinctions of long-lived woody plants over time frames of 50 to perhaps 100 years into the future.
1 | INTRODUCTION

Projected changes in climate have led to numerous attempts to model the future distributions of plant and animal species under new climatic regimes. Predicted range shifts based on species distribution models (SDMs) vary depending upon modelling approach and assumptions, but forecasts of local and regional extinctions over the next century have typically been high even for long-lived tree species (Morin et al., 2008). For example, Morin and Thuiller (2009) used two modelling approaches to predict distributional shifts in the year 2,100 for 15 North American tree species under two future climatic scenarios. Even under the least-change scenario (an increase in global mean temperature of 1.0°C), species were projected to disappear from an average of 19%–31% of their currently occupied areas, and for many individual species, the projected losses were over 40%. It is an alarming prospect that species may completely disappear over large areas within the lifetimes of people now living. Other modelling studies have produced qualitatively similar results, some even predicting the widespread disappearance of trees and other plants by mid-century (Bakkenes et al., 2002; Cheaib et al., 2012; McKenney et al., 2007; Rogers et al., 2017; Thuiller, 2004).

Because it is virtually impossible to experimentally test range-shift responses to novel climates, SDM-based predictions of future extinctions have largely gone unchallenged except on procedural or theoretical grounds (Botkin et al., 2007; Davis et al., 1998; Hampe, 2004; Loehle & LeBlanc, 1996). Common objections include the unknowability of relationships among the species’ ill-defined fundamental niche and current and future realized niches (Guisan & Thuiller, 2005), uncertainty about the quantitative relationship between habitat loss and extinction likelihood (Thuiller et al., 2004), and the fact that time-explicit extinction events cannot be projected from SDMs that do not include recruitment and mortality inputs (Araújo & Peterson, 2012). SDM outcomes can be tested against other models (Bollinger et al., 2000; Iverson et al., 2017; Morin & Thuiller, 2009; Pearson et al., 2006; Thuiller, 2004), but with rare exceptions (Araújo et al., 2005) they are largely beyond the practical reach of experimental or observational validation.

However, it is possible to experimentally test the survival and growth of tree populations under alternative climates by moving them (or their offspring) to new locations, and this has been done many times in common garden tests. Although they do not replicate nature (cf. Aitken et al., 2008), such experiments offer the opportunity to test indirectly, but plausibly and rigorously, the consequences of changes in climate. Common garden provenance trials of autochthonous tree populations relocated to novel environments offer experimental analogues (space-for-time substitutions) to modelled predictions of the fate of in situ populations under alternative future climates (Aitken et al., 2008; Franks et al., 2014; Matyas, 1994). Provenance trials typically reveal high levels of adaptation to home environments based on (a) genetic differences among populations in fitness traits such as growth rate; (b) clinal patterns of genetic variation that correspond with environmental gradients; and (c) measurable interactions between genotype and environment resulting from differential adaptation (Alberto et al., 2013; Campbell, 1979; Howe et al., 2003; Morgenstern, 1996; Rehfeldt et al., 1999). Especially for species of temperate and boreal regions, the literature on this topic is so extensive that it is expected that any widely distributed tree species is a heterogeneous collection of locally adapted populations, assuming they have grown in place without human agency. As long as populations differ genetically ($Q_{st} > 0$), they will respond independently to climatic change according to their own requirements and tolerances, not the broader fundamental niche of the entire species (Aitken et al., 2008; Beaulieu et al., 2004; Benito-Garzón et al., 2011; Hampe, 2004; O’Neill et al., 2008; Pearson & Dawson, 2003; Rehfeldt et al., 1999; Savolainen et al., 2007; Valladares et al., 2014). Indeed, except for the potentially mitigating effects of immigrating seed or pollen, it is always the case that plant populations survive or fail on their own as the environment changes.

Numerous studies have modelled growth in provenance tests as a function of the climatic distance between provenance and plantation environments (Carter, 1996; Matyas & Yeatman, 1992; Rehfeldt et al., 1999; Schmidtling, 1994, and others). Their usual purpose has been to understand the effects of climatic change on forest productivity and how to mitigate those effects through deliberate population transfers. Our principal interest was to understand the effects of climatic change on population survival, and relatively few studies have modelled survival as a function of climatic displacement (Berlin et al., 2016; Kung & Clausen, 1984; Martínez-Berdeja et al., 2019; Rehfeldt et al., 1999, 2003; Reich & Oleksyn, 2008; Sáenz-Romero et al., 2017). With one exception discussed later, no study to our knowledge has modelled survival past age 20 years. Here, we analysed survival and growth in ~35-year-old provenance trials of green ash (Fraxinus pennsylvanica Marsh.) and white ash (F. americana L.) as a function of the climatic distance between population origins and novel test environments. Our investigation was invited by the generally healthy condition of these trials, especially because the trees had survived in novel environments for an interval corresponding roughly with the time frame of published predictions of local extinctions by mid-century. The objective was to measure the strength of the effect of novel climates on population survival and growth as a test of the deterministic limits of modelled responses to climatic change over a time frame of decades.
2 | METHODS

2.1 | Tree survival and growth

Our data were collected from plantations of green and white ash planted as part of provenance trials organized in the mid-1970s (Bey et al., 1976; Steiner, 1983). Green ash seeds were collected from trees in wild (autochthonous) populations (Figure 1), and their seedlings were distributed to test sites within the species’ range. Plantation designs were based on four-tree population plots randomized within four to eight complete field blocks. Family identities by mother tree were maintained for 36 populations in the Pennsylvania plantation by using family subplots within population plots. In a separate but approximately contemporaneous study, white ash seeds were similarly collected from trees in wild populations (Figure 2), and their seedlings were planted at test sites within the species’ range. The design of these plantations followed either of two formats: five-tree population plots with populations replicated across five field blocks, or five-tree family plots (similarly replicated), where a family comprised the progeny of one of the open-pollinated female parents collectively representing a population. In all cases, the population mean at a planting site was the data element of main interest.

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**FIGURE 1** Putative pre-Columbian distribution of green ash and locations of provenances and test plantations represented in this study (Little, 1971). From provenance to test site, population climatic displacements ranged from −7.8 to +10.1°C MAT

**FIGURE 2** Putative pre-Columbian distribution of white ash and locations of provenances and test plantations represented in this study (Little, 1971). From provenance to test site, population climatic displacements ranged from −9.7 to +7.4°C MAT
During the years 2008 to 2012, we measured survival and diameter at breast height (DBH, 1.37 m) for a total of 56 unique green ash populations and 46 unique white ash populations at eight test sites (five of green ash and three of white ash; Table 1, Figures 1 and 2). The mean tree age at time of measurement was 35 years (range 33–37). An invasive insect, the emerald ash borer, has since destroyed most plantations, but at the time of measurement it was either not present or present in such low numbers that its effect on survival and growth was negligible (Steiner et al., 2019). Data elements used in subsequent analyses were population mean percentage survival, by plantation, and population mean annual diameter growth (DBH divided by age, in mm/year), by plantation. The three Michigan plantations had been systematically (non-selectively) thinned by removing half of the trees in each plot by position. These trees and others removed because of incidental human activity (e.g. utility and road maintenance) were excluded in calculations of survival rates. In addition to these data, archival data for survival and height, taken periodically beginning at the end of the 3rd through the end of the 15th or 16th growing seasons, were available for the Maine and Pennsylvania plantations of green ash.

### 2.2 | Climatic data

Climatic data were gathered from National Climatic Data Center (U.S.) and Environment Canada for stations nearest to provenance and plantation locations, at distances that averaged 18 km for provenances and 10 km for test sites. We gathered yearly data for 26 temperature and precipitation variables (see Table S1) and calculated normals (long-term means) based on the interval 1900–1975 for provenances (historical climate at population origins up to the time of seed collection) and the interval 1975–2010 for test sites (growth conditions during the study period). Mean annual temperature (MAT) was estimated as the mean of normal mean temperatures for January, April, July and October. For analysis, each climatic variable was scaled by subtracting the mean and dividing by the standard deviation of all provenance and test site values for a species.

Depending upon species and performance variable, 18–23 climatic variables were significant predictors of population survival or growth in preliminary analyses using test site as a random effect on the intercept and both linear and quadratic forms of each climatic variable in turn. To reduce climatic data to a smaller number of uncorrelated composite variables, principal component analyses (PCA) were performed using provenance + test site climatic data for those variables identified as significant predictors (Table S1). PCA was performed separately for each combination of species and response variable because green and white ash occupy different distributions with different climates, and because we had no reason to believe that climate would have the same relationship with survival as with growth rate. For the four analyses, the first principal component accounted for 72%–76% of the variation in the multivariate data set, and the second principal component accounted for 9%–20%. As a measure of displacement between the original and novel climates, climatic distance (CD) on the first principal component (PC1) was calculated as the difference between the principal component score for the provenance and that for the test site. A second climatic distance (CD2) was similarly calculated using PC2. For CD1, a negative value signified a move to a warmer and wetter climate (Table S1), and a positive value a move to a colder/drier climate. However, temperature was the dominant variable category for PC1, especially in white ash, so for convenience we will refer to the axis of CD1 values as signifying population displacements to "warmer" (negative) or "colder" (positive) environments. In all four analyses, CD1 was highly correlated with MAT ($r^2 = .86–.99$). As might be expected, PC2 discriminated between warm/dry versus cold/wet environments. Climatic distances based on PC2 proved to have little explanatory power and were not used in final models (see below).

### 2.3 | Modelling and data analysis

Survival and growth data were then analysed using mixed-effects linear regression models (Leites et al., 2012) with CD1, CD2, PrClim (the PC2 score for provenance climate) and PrClimCD1 as fixed effects, and the class variables provenance and test site as

| State          | Longitude (°W) | Number of populations | Tree age at measurement (years) |
|----------------|---------------|-----------------------|---------------------------------|
| Green ash      |               |                       |                                 |
| Pennsylvania   | 40.8          | 56                    | 37                              |
| Maine          | 44.3          | 29                    | 34                              |
| Michigan #1    | 42.4          | 36                    | 34                              |
| Vermont        | 44.3          | 25                    | 33                              |
| Michigan #2    | 42.2          | 37                    | 34                              |
| White ash      |               |                       |                                 |
| Kentucky       | 38.3          | 22                    | 36                              |
| Kansas         | 39.3          | 27                    | 36                              |
| Michigan       | 42.4          | 35                    | 35                              |

**TABLE 1** Summary information for test plantations included in the study

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1 Or population, in this context. The terms provenance and population are often used interchangeably when it is assumed that an autochthonous population has a unique genetic identity that reflects the nature of its environment.
random effects on the intercept. Including PrClim and its interaction with CD allowed us to account for the possibility that responses to climatic displacement were population-specific in a manner related to the home environment (Leites et al., 2012; Rehfeldt et al., 1999). This modelling approach to provenance test data produces a general transfer function in which population responses to climatic distance are generalized by accounting for test site main effects unrelated to climate (Carter, 1996; Leites et al., 2012; Matyas & Yeatman, 1992; O’Neill & Nigh, 2011; Rehfeldt et al., 1999; Schmidtting, 1994).

We began with the following model to test the importance of both measures of climatic distance and their quadratic terms:

\[ y_i = b_0 + u_{ij} + u_{ij} + b_1 CD_{ij} + b_2 CD^2_{ij} + b_3 \text{PrClim}_1 + b_4 \text{PrClim}_2 + b_5 CD_{ij} + b_6 CD^2_{ij} + e_{ij} \]

where \( y \) = percentage survival or mean growth rate for the \( i \)th population at the \( j \)th test site of green ash or white ash; \( CD_{ij} \) and \( CD^2_{ij} \) are the climatic distances between the \( i \)th provenance and \( j \)th test site measured on the first and second principal component axes, respectively; \( u_{ij} \) and \( u_{ij} \) are random effects of provenance and test site, respectively; and \( b_1 \)–\( b_6 \) are fixed-effect parameters. This model was reduced by examining one variable at a time using a bootstrapped likelihood ratio test with 5,000 simulations to determine if the model was significantly less explanatory without the variable (\( p < .05 \)), testing first each fixed-effect variable by fitting models using maximum likelihood estimation and then each random-effect variable by using restricted maximum likelihood estimation. Removing \( CD_{ij} \), \( CD^2_{ij} \) and \( u_{ij} \) did not significantly reduce likelihood in any model, and each made negligible contributions to explained variance (\( -0.3\% \) on average). Accordingly, these variables were discarded, and we concluded that the PC2 expression of climate and its derivatives had little or no explanatory potential for our purposes. References below to climatic variables (CD and PrClim) should be understood to mean CD and PrClim (i.e. climate described by the first principal component).

We then examined the following model by removing variables and testing as described above:

\[ y_i = b_0 + u_{ij} + (b_1 + u_{ij})CD_{ij} + (b_2 + u_{ij})CD^2_{ij} + b_3 \text{PrClim}_1 + b_4 \text{PrClim}_2 \cdot CD_{ij} + e_{ij} \]

where \( y \) = percentage survival or mean growth rate for the \( i \)th population at the \( j \)th test site of green ash or white ash; \( CD_{ij} \) is the climatic distance between the \( i \)th provenance and \( j \)th test site; \( \text{PrClim} \) is the climate of the \( i \)th provenance; \( u_{ij} \) and \( u_{ij} \) are random effects; and \( b_0 \)–\( b_4 \) are fixed-effect parameters. All random effects in this model measure whether responses to climatic displacement were idiosyncratically affected by test sites. The only exception to the earlier procedure was that we tested the random effects \( u_{ij} \) and \( u_{ij} \) on CD and \( CD^2 \), respectively, by using a single reduced model (both terms removed together) because the fixed (main) effects of both variables had already been shown to be significant. Because of the small number of test sites for white ash, it was not possible to fit a random test site effect on slopes \( u_{ij} \) and \( u_{ij} \) in that species so only intercept effects \( (u_{ij}) \) were estimated. Otherwise, if a variable contributed significantly to one model it was retained in all models. This facilitated comparisons, and it had the virtue for our purposes (see below) of erring towards a stronger model fit if there was any evidence a variable was important. Only the removal of PrClim·CD failed to significantly reduce likelihood in all models and was eliminated. Finally, \( R^2 \) values for models and model variables were calculated using the method of Nakagawa and Schielzeth (2013) to separate explained variance into marginal \( R^2 (R^2_m \) the proportion of total variance explained by fixed effects) and conditional \( R^2 (R^2_c \) the proportion of total variance explained by all model variables including the random effects) (Vonesh et al., 1996).

The designs of the Pennsylvania plantation of green ash and Kansas plantation of white ash permitted robust tests of family-within-population as a source of variation in performance variables. In the white ash case, we analysed mean annual diameter growth using linear regression with restricted maximum likelihood to estimate population and family random effects and their variance components (\( \sigma^2_p \) and \( \sigma^2_f \), respectively). Survival was modelled as a binomial using generalized linear regression and the Laplace approximation, and the significance of family effects was computed using a parametric bootstrapped likelihood ratio test of 5,000 simulations comparing the full model (population, family-within-population, error) to one without family as a random variable. For green ash, family variation in mean annual diameter growth was analysed in separate ANOVAs for each population, sums of squares and degrees of freedom were pooled across populations for a combined test of within-population genetic variation, and the variance components \( \sigma^2_p \) and \( \sigma^2_f \) were calculated as for white ash. Family survival rates in green ash were not analysed because of low sample sizes. The proportion of species-wide quantitative trait genetic variance contained within the average population (\( Q_{ST} \)) was estimated as \( 1 - Q_{ST} \), where \( Q_{ST} = \sigma^2_p/(\sigma^2_p + 8 \sigma^2_f) \) (Spitze, 1993; Wright, 1949) based upon the assumption that each open-pollinated family was composed of half-sibling offspring (Falconer, 1960).

### Results

Parameter estimates and 95% bootstrap confidence intervals for the four final models are shown in Table 2. Fixed-effect variables (CD, \( CD^2 \) and PrClim) explained 21%–43% of variance in survival and diameter growth, depending on species, and the random effects of test site on intercepts and slopes added 23%–46% to explained variance in each case. Provenance climate (PrClim) had a significant effect (\( p \leq .05 \)) only in the model for green ash mean annual diameter growth. Test site significantly affected the intercept in all models and slope coefficients in green ash models. Modelled maximum survival rates were 83% and 73% for green and white ash, respectively, and modelled maximum mean annual diameter growth rates were 5.0 mm for both species. Within the limits of modelling error, maximum survival and growth occurred at CD values close to 0 (i.e. little difference between provenance and test site climates), and rates declined as test sites were either colder or...
warmer than home environments (Figure 3). However, response curves were highly variable among test sites for green ash, reflecting the significant effect of test site on slope coefficients for CD and CD^2. This is graphically illustrated only for growth in Figure 3, but test site had significant effects on slope coefficients for survival, also.

As shown in the upper panels of Figure 3, the statistical uncertainty surrounding modelled survival maxima in optimal climates (i.e. at or near CD = 0) can be projected onto the domain of CD values to identify the range of climates over which modelled survival was not significantly reduced by climatic displacement. For this purpose, we chose an α level of .50 to reduce Type II error and conservatively minimize the estimated range of putatively safe climatic displacements. The graphically determined intervals were climatic distances of −3.4 to +3.7 for white ash and −5.7 to +3.2 for green ash. Based on relationships between CD and MAT, these correspond to climatic distances of +3.5°C (white ash) and +5.6°C (green ash) over which populations were displaced to warmer environments with no statistically detectable increase in mortality. The asymmetry around zero in green ash reflects the fact that estimated optimum survival occurred in an environment 1.5 units of CD warmer than the null transfer distance. As mentioned, this difference is not significantly different from zero. If optimum survival in green ash had been estimated at CD = 0, which is perhaps realistic, the apparently safe maximum displacement for each species would be +3.5 (white ash) and 4.1°C (green ash).

Relative heights from ages 3 through 15 or 16 years in the Pennsylvania and Maine plantations of green ash are diagrammed in Figure 4 based on a division of populations into three approximately equal-sized groups: those moved to a warmer environment (CD < −2.0) (Group 1 in Figure 4), those moved to a colder environment (CD > +2.0) (Group 2) and those native to climates like the test sites (−2.0 ≤ CD ≤ +2.0). Group 1 populations were initially the shortest in both plantations but gained in relative height with time, and Group 2 populations were initially the tallest but gradually lost in relative height. By year 7, the near-local populations were tallest in both plantations, and they remained the tallest afterwards. Patterns of change or adjustment were qualitatively identical for both plantations but more exaggerated in the colder Maine plantation, where Group 1 populations eventually became nearly (97%) as large as near-local populations and Group 2 populations declined to 78% relative height. Mortality in all groups in both plantations was statistically independent of size during the period depicted in Figure 4, so the changes in relative height were not caused by group differences in selective mortality. Relative size differences among groups at the time of the last height measurements at age 15 or 16 (Figure 4) remained virtually unchanged through age −35, as measured then by DBH, except that Group 2 populations in Maine appeared to recover to 87% relative size, at least in part through selective mortality.

Variation among open-pollinated families within populations was significant for diameter growth (p < .0001) and survival (p < .001).
FIGURE 3  Survival and mean annual diameter growth at 35 years average age of green ash and white ash populations plotted against climatic distance (CD). Negative CD values represent population displacements from colder to warmer environments and positive CD values the opposite. Data points are adjusted for test site effects and constrained to ≤100% survival. Solid black lines represent fitted fixed-effects curves with respect to CD only. Labelled lines in the lower left panel illustrate the random effects of the Michigan #2, Vermont, Pennsylvania, Michigan #1, and Maine test sites (from top to bottom) on slope coefficients $b_1$ and $b_2$. Heavy dashed lines demark the 50% confidence limits for fitted random and fixed effects. Green dashed lines in the two upper figures are explained in the text. The algorithm for CD differed according to species and performance variable, so CD is not comparable between panels.

FIGURE 4  Mean tree heights, with standard errors, from age 3 to age 15 or 16 years in the Maine and Pennsylvania plantations of green ash for populations moved from colder to warmer environments (Group 1, CD < −2.0) and warmer to colder environments (Group 2, CD > 2.0). Heights are expressed as proportions of the mean for near-local populations (−2.0 ≤ CD ≤ +2.0), shown as horizontal green lines. The climates of Maine and Pennsylvania differ (Maine is colder), so groups do not contain identical sets of populations between test sites. Trend lines are smoothed.
in the Kansas plantation of white ash and for diameter growth ($p < .001$) in the Pennsylvania plantation of green ash. The family variance component ($\sigma^2_f$) accounted for 74.7% of total measured genetic variance ($\sigma^2_p + \sigma^2_f$) in growth rate in white ash and 31.0% in green ash. $Q_{IS}$ was 0.959 and 0.782 for mean annual diameter growth in white ash and green ash, respectively, and 0.642 for survival in white ash.

4 | DISCUSSION

Modelled survival and growth were greatest under near-local conditions (CD values near zero) and declined as populations were moved to climates increasingly different from home environments. This confirms the expectation that green and white ash populations are best adapted to where they occur autochthonously and is consistent with the known presence of ecoclinical relationships with climate in these two species (Alexander et al., 1984; Clausen, 1984; Clausen et al., 1981; Roberds et al., 1990; Shumway et al., 1991; Steiner et al., 1988; Williams, 1984).

Model fits in the current study (55% to 77% of the variance in population-by-test-site means) compare favourably with other transfer functions, which sometimes account for test site effects in mixed model analyses, as here, and sometimes by standardizing population means as percentages of test site means (Andalo et al., 2005; Carter, 1996; Leites et al., 2012; Matyas & Yeatman, 1992; O’Neill & Nigh, 2011; Rehfeldt et al., 2003; Rehfeldt et al., 1999; Sáenz-Romero et al., 2017; Schmidtlng, 1994; St. Clair et al., 2020; Thomson et al., 2009). As stated earlier, the focus of interest in such studies has usually been the models themselves and what they imply about the opportunity to increase forest productivity by planting non-local seedlings or the potential to mitigate climatic change through assisted migration. Here, instead, we wish to draw attention to the seemingly unpredictable component of tree response (i.e. modelled random effects and unmodelled variation) as something of equal scientific interest, especially when expectations of future distributions can be informed by a multi-decade record of experimental data.

As is common in provenance tests, much of the variance in population means arose from test site main effects that were apparently unrelated to climate. All test sites were under different management control and usually different ownership, so it is to be expected that differences in plantation management and care likely affected tree growth and survival in addition to non-climatic characteristics of the local natural environment (Allen et al., 2010; Davis et al., 1998; Sáenz-Romero et al., 2017; Thuiller et al., 2005). However, even after accounting for test site effects, and with a highly relaxed criterion of $p < .50$ for significance, we could detect no increase in mortality at displacements as great as $+3.5$ and $+4.1°C$ MAT in white and green ash, respectively. Survival rates were 80 to 100% in nearly half of the instances of populations moved to climates $\geq 3.0°C$ warmer than home environments, although there were no instances of high survival in white ash beyond $-5°C$ warmer (Figure 5). We believe it is significant that many trees survived, even thrived, for 35 years following warming levels that are expected to cause meso-scale losses of suitable habitat in this century for dozens of tree species in the region of our study (McKenney et al., 2011). This does not mean there were no harmful effects of elevated temperatures, but at a minimum it means that the effects were small enough in many instances to be negated or obscured by the presence of other factors. In the following paragraphs, we discuss the evidence for three such factors: within-population genetic variation, genotype x environment (G x E) interaction and phenotypic adjustment.

4.1 | Within-population genetic variation

The average population of green and white ash contained a large fraction of total species-wide genetic variance ($Q_{IS}$) in the two quantitative traits measured here: 0.78 and 0.96 for growth of green and white ash, respectively, and 0.64 for survival of white ash. These may even be slight underestimates considering possible causes of bias, especially “drift” effects on population means caused by the limited number of seed parents. Other tree species in temperate climates have similarly high $Q_{IS}$ values (or correspondingly low $Q_{ST}$ values) for traits that affect growth rate and temperature acclimation (Alberto et al., 2013; George et al., 2019; Howe et al., 2003). The presence of high levels of within-population genetic variance means that some trees should fare well in climates that are suboptimal for their population relatives, and a population exposed to climatic change could be reasonably well adapted to the new climate after the removal of some fraction of individuals through natural mortality. A remnant but highly variable population would be a foundation for further adaptation in subsequent generations through recombination and natural selection (Davis et al., 2005).
4.2 | Genotype × Environment interaction

G × E interaction is present when the relative performance of genotypes (populations in this case) differs according to environment. General transfer functions (Figure 3) illustrate G × E interaction directly because any two populations modelled on the function are always the same distance apart on the x-axis at whatever test site they are grown, but they change in relative performance on the y-axis according to test site climate if the function is nonlinear, as here. In this case, the source of the interaction is known, and it can be modelled as a fixed, predictable effect. A second, confounding, source of G × E interaction is demonstrated by the presence of test site effects on the slope and intercept parameters for CD and CD²—creating a sort of contingent phenotypic plasticity (see below) in which phenotypic response to a climatic displacement is modulated by local site effects in unknown ways. This category of G × E interactions, which cannot be predicted at our current level of understanding, accounted for a substantial portion of variance in all models. For interactions of unknown cause, the effect of habitat on genotypic response to climate cannot be anticipated, and expectations of survival or growth in a modified climate are necessarily uncertain.

4.3 | Phenotypic adjustment

Data from the early years of the Pennsylvania and Maine plantations of green ash show that cold-climate populations were initially the slowest growing and warm-climate populations the fastest. This is often the case in provenance tests, and it is believed to arise from metabolic or phenological constraints imposed by cold tolerance on growth potential in cold climates, and the presumed advantage of faster growth in warm climates (Howe et al., 2003; Leites et al., 2019). These distinctions did not persist, however, and cold- and warm-climate groups both underwent large phenotypic changes in relative growth rate during the first decade or so after planting. With time, those moved from colder environments partially overcame initial disadvantages in growth rate, and those moved from warmer environments lost their growth rate advantage and were eventually surpassed in size by near-local populations. Except for warm-climate populations in Maine (Group 2), which continued to decline in relative height to age 16, group means at each location converged to within a 10% range. At least initially, the change was always in the direction of the mean for near-local populations. For populations moved from warmer to colder environments, the initial loss of relative height can be partly explained by shoot dieback from winter injury to some of the trees following the 3rd, 4th and 5th growing seasons at one or both test sites, but especially Maine (Steiner et al., 1988; Williams, 1984). The gradual loss of relative height in populations moved to colder climates could be interpreted as maladaptation, even where it continued past the last record of winter injury. However, the increasingly better relative height of trees moved to warmer climates, converging towards greater similarity with near-local populations, seems to be clearly a case of adaptive phenotypic adjustment. This continued into the fourth decade if diameter is taken as equivalent to height as a measure of relative size.

A similar convergence of growth rates towards a local norm appears to have occurred in a reciprocal transplant test of Abies sachalinensis populations collected and planted at six locations along an elevational gradient (Ishizuka & Goto, 2012). Despite significant home-site advantages, especially at high elevations, the ratio of the population to test site variance components for height decreased from 4.5 at age five years to 0.1 at age 36 as population means converged at each location. Phenotypic adjustments are consistent with an emerging understanding of phenotypic plasticity as an essential attribute of long-lived, sessile organisms that occupy changeable environments (Benito-Garzón et al., 2019; Franks et al., 2014; Loehle & LeBlanc, 1996; Nicotra et al., 2010; Reich et al., 2016). Some evidence suggests that phenotypic plasticity may play a larger role than genetic variation in the response of tree populations to climatic change (Benito-Garzón et al., 2019; Franks et al., 2014), although even the capacity for plasticity and the adjustments themselves are now understood to be potentially heritable through epigenetic control systems (Bossdorf et al., 2008; Grant-Downton & Dickinson, 2005, 2006; Richards et al., 2010; Zhang et al., 2013; Yang et al., 2020). This is an active area of research, and much remains to be learned.

4.4 | Synthesis

Long-standing concerns about the effects of warming climates on tree distributions have been substantiated in some species by evidence of contemporary range shifts, or incipient shifts, at range margins (Elliott, 2012; Fei et al., 2017; Hickling et al., 2006), while other species have exhibited no changes or even shifts in the unexpected direction (Parmesan & Yohe, 2003; Rabasa et al., 2013; Zhu et al., 2012). On a larger scale, there appears to be scant evidence yet to support SDM-based predictions made 30+ years ago of range shifts on the scale of hundreds of km that were to occur over the following century (Smith & Tirpak, 1989). In an early analysis of SDMs for trees, Loehle and LeBlanc (1996) argued that models were forecasting biologically implausible scenarios of forest dieback and range shrinkages. Similarly, Botkin et al. (2007) and Schwartz (2012) presented a series of first-principle arguments against the methodology and biological assumptions of SDMs, with the conclusion that most models were inherently biased in the direction of predicting extinctions. Research in the past decade has substantiated some of the reasons for those criticisms by showing that models which incorporate additional biological parameters such as phenotypic plasticity and local adaptation tend to predict range shifts that are less alarming than conventional SDMs (reviewed by Benito-Garzón et al., 2019). Because of uncertainties like these, some authors of SDMs have cautioned that modelled projections of climate-induced distributional shifts and local extinctions should not be regarded as actual predictions (Benito-Garzón et al., 2011; Cheaib et al., 2012; Hamann & Wang, 2006; Morin & Thuiller, 2009).
Our results tend to validate those cautions, at least for time horizons over which populations can persist as living individuals capable of enduring or adjusting to new climate conditions. Those time horizons may be decades, as addressed in this paper, or much longer, as in the case of bristlecone pine trees that have withstood climatic changes for millennia near the elevational limits of tree growth (LaMarche, 1969). Of course, the indefinite persistence of a population requires successful reproduction and recruitment of progeny cohorts, which cannot be predicted from our data. However, the same factors that appear to have contributed to survival in this study may also contribute to the indefinite persistence of a population and its descendants following climatic change: within-population genetic variation as a necessary condition for adaptive selection, random components of G × E interaction as evidence for unexplained variation in local fitness and phenotypic adjustment as a potentially heritable adaptation.

A key finding of our study is that at the level of the individual population (test site effects removed, Figure 3), and especially at the level of population-by-test-site combinations (Figure 5), such a small portion of variation in response to climate was explained by adaptive norms that any a priori predictions of mortality or growth rate would have been, in most cases, wildly inaccurate. Although the duration of our tests was only ~35 years, it is reasonable to conclude that the results are qualitatively valid for 50+ years as there was little evidence of imminent mortality at the time of measurement. To our knowledge, the only longer study in which survival was modelled as a function of climatic displacement is a 100-year test of Douglas-fir populations moved to several test sites in the Pacific Northwest of North America (St. Clair et al., 2020). In that study, displacements (~2.2°C to +5.6°C MAT) accounted for no more than ~6% mortality over study-wide background levels. As in the current study, climatic displacement caused marginal increases in mortality, but all populations survived in reduced numbers. These studies provide experimental evidence that trees are much more capable of enduring 50–100 years of novel climates than is assumed in many SDM-based predictions.

Assisted migration of populations is sometimes advocated on the expectation that the climate may change faster than populations can migrate or adapt (Aitken & Bemmels, 2016). Planting forest trees is expensive, especially if done with no expectation of cost recovery through future timber harvests, so the uncertainties of assisted migration must be weighed carefully (Gray et al., 2011; Park & Talbot, 2012; Williams & Dumroese, 2013). For green and white ash, we could not reliably detect elevated mortality under warmer environments would be different than the models show. A more complete understanding of species’ response to climatic displacement would have been possible if we had tested sites that were near or beyond the warm and cold limits of species’ distributions. In green ash, for example, no populations from south of Pennsylvania were displaced to warmer test sites, and none of those from north of Vermont were moved to colder sites. It is possible, for example, that the survival of southern populations moved to even warmer environments would be different than the models show. Such a difference would show up as a PrClim × CD effect, which had negligible explanatory power in the models reported here.

4.5 | Limitations

Model precision would have been enhanced if all populations were represented at all test sites, but because of logistical constraints this is a refinement that is often missing from multi-site provenance tests. A more complete understanding of species’ response to climatic displacement would have been possible if we had test sites that were near or beyond the warm and cold limits of species’ distributions. In green ash, for example, no populations from south of Pennsylvania were displaced to warmer test sites, and none of those from north of Vermont were moved to colder sites. It is possible, for example, that the survival of southern populations moved to even warmer environments would be different than the models show. Such a difference would show up as a PrClim × CD effect, which had negligible explanatory power in the models reported here.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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**BIOSKETCH**

The authors are interested in the ecology, genetics and biogeography of forest trees and how knowledge of these topics can inform an understanding of responses to climatic change. Together, their research has encompassed North American, European and Asian species, but their focus in recent years has been hardwood (angiosperm) trees of the eastern United States and adjacent Canada.

Author contributions: K.C.S., J.L.B, and L.P.L conceived and designed the study. J.L.B, K.C.S, and S.F performed data acquisition. Statistical analyses and their interpretation were performed by L.E.G, K.C.S, and J.L.B. The original manuscript was written and its figures drafted by K.C.S, and L.E.G, S.F, and L.P.L contributed to revisions.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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