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RESEARCH ARTICLE

Ecological analysis of intraspecific variability of eastern white pine *(Pinus strobus)* under climate change by combining provenance and demographic data

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Abstract
Context Many forest tree species are composed of a gradient of populations adapted to different environmental segments, especially to temperature gradients. Therefore, populations are likely to respond differently to climate change compared to the entire species.
Objectives Using *Pinus strobus* as an example, we model geographic patterns of growth potential and habitat suitability to understand how intraspecific genetic variation affects its response under climate change, and facilitate management.
Methods We model populations' growth potential based on data from provenance tests and delineate three intraspecific regions: cold, middle, and warm. We predict climatic habitat suitability by modelling relative abundance for each of the intraspecific regions for current and future climates. Finally, we combine habitat suitability with growth potential and explore how combinations of these two can be used to match genotypes and climate.
Results Suitable combinations of habitat quality and growth potential shift from the US to Canada in the future, especially under the RCP 8.5 scenario, although the Northeast states retain desirable combinations of both. The main contributors to the future abundance and productivity are populations from the middle region, followed by those from the warm region. Future suitable habitats for populations in the cold region show the most decline, supporting the need for more management of these populations.
Conclusions By delineating homogeneous population groups into three intraspecific regions, and considering both habitat suitability and growth potential, our analysis evaluates potential future changes for eastern white pine, including assisted migration, to facilitate better management of this commercially and ecologically important species.

Keywords Eastern white pine provenances · Intraspecific regions · Homogeneous population groups · Growth potential · Habitat suitability · Climate change · Assisted migration

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Introduction

Elucidating the fate of wide-ranging tree species under a changing climate is challenging because it requires a thorough understanding of ecological genetics, or the spatial distribution of genetic attributes across a

species range. Most efforts that project suitable habitats under future climate scenarios treat tree species as homogenous units (McKenney et al. 2007; Iverson et al. 2008; Matthews et al. 2019) in spite of extensive work showing that most tree species consist of a continuous gradient of populations genetically attuned to portions of the species climatic range (Sluder and Dorman 1971; Rehfeldt et al. 2014; Garzón et al. 2019; Chardon et al. 2020). This is mainly because data required to account for intraspecific genetic variation are available for only a few commercially important tree species (mostly conifers). While predictions from species-wide models can be useful for management (Swanston et al. 2016; Iverson et al. 2019b), they do not convey whether the right genotype is aligned with the area's climate which is necessary for a more informed application of assisted migration of populations and seed zone delineation (Rehfeldt and Jaquish; 2010; Gray et al. 2011; Joyce and Rehfeldt, 2013; Rehfeldt et al. 2014; Pike et al. 2020).

Intraspecific genetic differences are a challenge to incorporate in climate projection models and require experimental data to delineate genetically homogenous groups (Rehfeldt and Jaquish, 2010; Joyce and Rehfeldt, 2013; Rehfeldt et al. 2014; Garzón et al. 2019). Provenance tests have provided the necessary information of baseline phenotypic and genetic variation across tree species' ranges albeit with limitations (e.g., Leites et al. 2012a). These studies have also revealed that genetic variation in forest trees is clinal, with species differing mainly in the steepness of the clines (e.g., Leites et al. 2019).

For several temperate species, provenance trials have also revealed that the climatic optimum differs among populations, and populations tend to reside in climates colder than their optimum (Namkoong, 1969; Thomson and Parker 2008; Rehfeldt et al. 2018). This discrepancy between the *physiological optimum*, the climate where the population potentially has the best growth rates but is usually excluded due to competition, and the *ecological optimum*, climates where a population is most competitive and hence frequently present, implies that populations are not necessarily matched to their geographic location. The *growth potential* (GP), the inherent capacity for growth at the physiological optimum (Rehfeldt et al. 2018), can be estimated from classical provenance test studies where natural populations are tested in common gardens.

To improve our understanding of species trajectories under a changing climate of these wide-ranging species with high intraspecific variability, we need to compare the response of tree species populations relative to the combined ecological and genetic factors affecting those responses (Matthews et al. 2019). Previous studies have mostly emphasized the ecological component (e.g., Prasad 2015; Iverson et al. 2019a and many others), or the ecological genetics component (e.g., Rehfeldt et al. 1999; Wang et al. 2006; Leites et al. 2012b; Eckert et al. 2013; Rehfeldt et al. 2018). However, combining genetic and ecological components to evaluate the effect of climate change on tree species provides richer insights (Rehfeldt and Jaquish 2010; Joyce and Rehfeldt 2013; Rehfeldt et al. 2014; Prasad and Potter 2017).

Using eastern white pine as a model species, our goal is to assess its potential intraspecific responses under a changing climate, by modelling and clustering growth potential using forestry provenance test data and combining these with climatic habitat suitability modelled from relative abundance calculated with forest inventory data. Eastern white pine is an ideal species because it is widely distributed in the eastern US and has multiple provenance test data sets available. It grows at elevations from sea level to 1200 m under a wide variety of soils and tolerates and even thrives under disturbance (Wendel and Smith 1990; Abrams, 2001). Also, this commercially and ecologically important tree species is currently facing multiple health threats (Costanza et al. 2018) that necessitates more careful management.

In this paper we assume that the relative importance value (also referred to as relative abundance), derived from forest inventory and analysis (FIA) data (Bechtold et al. 2005; O'Connell et al. 2017), represents the realized niche of eastern white pine, and that it correlates approximately with the ecological optimum (Wiens et al. 2009; Rehfeldt et al. 2018). We derive three separate intraspecific population regions, from unsupervised classification of modelled growth potential clines, and model habitat suitability from relative abundance within these regions. In doing so, we describe how these assumed *homogeneous population groups* are likely to respond differently under future climates and highlight which regions may warrant more attention from a management perspective (Garzón et al. 2019). Additionally, by combining habitat suitability with growth potential, we map and

evaluate regions that have desirable combinations of these two vital features under current and future climates in order to assess the suitability of assisted migration of eastern white pine.

Methods

Data

Provenance studies data

Data from range-wide provenance tests that measured total tree height were digitized for eastern white pine. The data comprised 138 natural populations tested in one or more of 28 test sites established between 1959–1968 and reported in seven publications (Fig. 1, Table 1). Test sites were designed as complete randomized block designs in most cases, with number of blocks ranging between 1 and 24, and plots ranging from 1- to 4-tree plots. Number of populations in common between studies varied. Measurement age from planting vary across tests between 5–14 years although most were around 10 years. To deal with age differences, total tree height was divided by age to obtain average annual growth rate (HG), which served as the variable of interest in subsequent analyses.

Demographic data

Forest Inventory and Analysis (FIA) data (Bechtold et al. 2005; O'Connell et al. 2017) collected during the periods 2000–2016 were used to calculate demographic variables for eastern white pine. There were 6940 plots with eastern white pine presence out of a total of > 100,000 plots in the eastern United States.

Relative importance value (RIV, also referred as relative abundance), a measure of abundance which incorporates the biotic influence, is calculated from the basal area and number of stems of the overstory and understory of the species (Iverson et al. 2008; Peters et al. 2019).

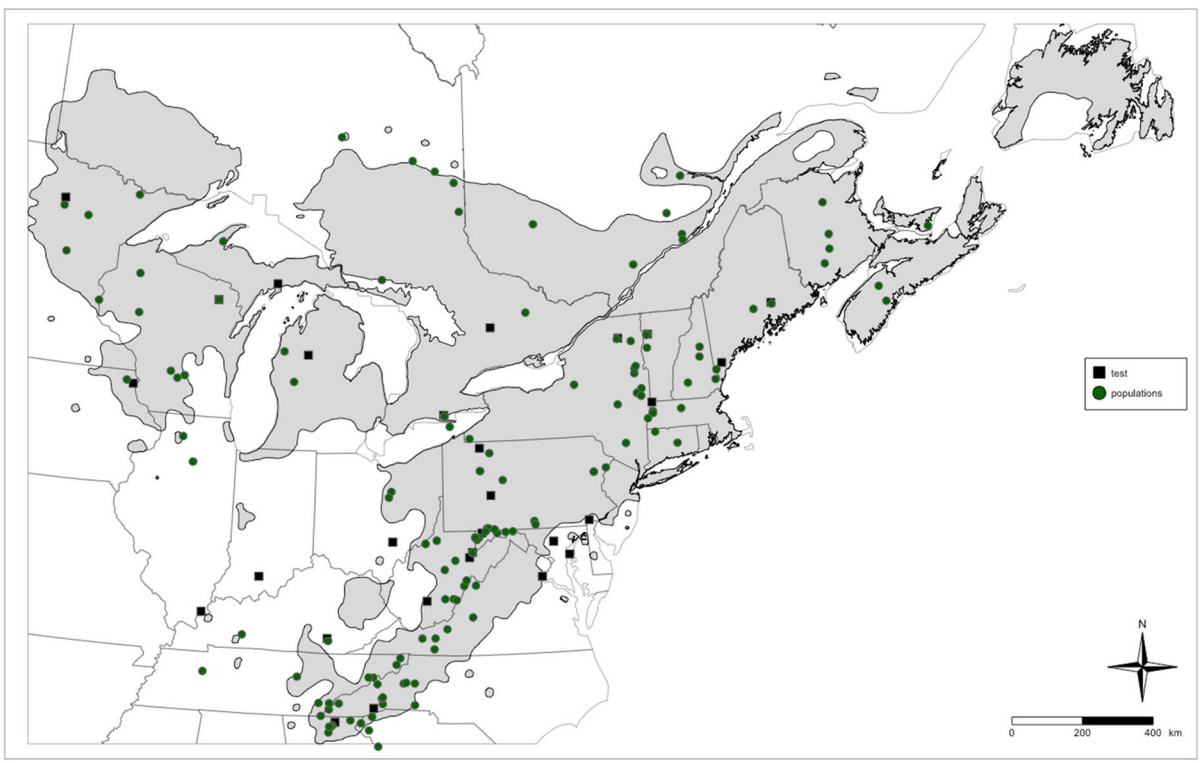


Fig. 1 Geographic range of eastern white pine according to Little 1971 (gray area), and location of populations (green circles) and tests (black squares) used in this study

Table 1 Summary of provenance studies used to model genetic clines in growth potential

Study	No. populations	No. tests	Age
Fowler and Heimburger (1969)	12	2	7
Funk (1971)	16	3	10
Garret et al. (1973)	28	13	7–8
Genys (1987)	86	2	14
King and Nienstaedt (1969)	17	4	5
Sluder and Dorman (1971)	16	3	10
Wendel and Cech (1976)	28	1	6

$$RIV(x) = 50 \times \frac{BA(x)}{\sum BA(all\ species\ in\ plot)} + 50 \times \frac{NS(x)}{\sum NS(all\ species\ in\ plot)}$$

where x is the species, in this case, eastern white pine, in the plot, BA is the basal area, and NS is the number of stems (summed for overstory and understory trees). In monotypic stands, the RIV would reach a maximum of 100 percent. RIV is a surrogate for accumulated growth and survival and therefore provides a measure of where eastern white pine does best ecologically in its realized niche because it is measured relative to all the other species in the plot. Modelled relative abundance (Fig. 2a) is referred to as habitat suitability or habitat quality (HQ) to distinguish the raw FIA scores from the modelled ones because the latter quantifies habitat suitability rather than provide an accurate measure of relative abundance.

Percent mortality (PM) is the ratio of the count of the number of eastern white pine trees that are dead to the total number of eastern white pine trees in the plot, and seedling count (SC) is the number of seedlings $<$ 2.5 cm in diameter and at least 30.5 cm tall. This latter variable provides a measure of regeneration potential.

Values for all FIA plots that were not designated as plantations within 20 $\times$ 20 km cells were averaged to calculate the demographic variables. The number of

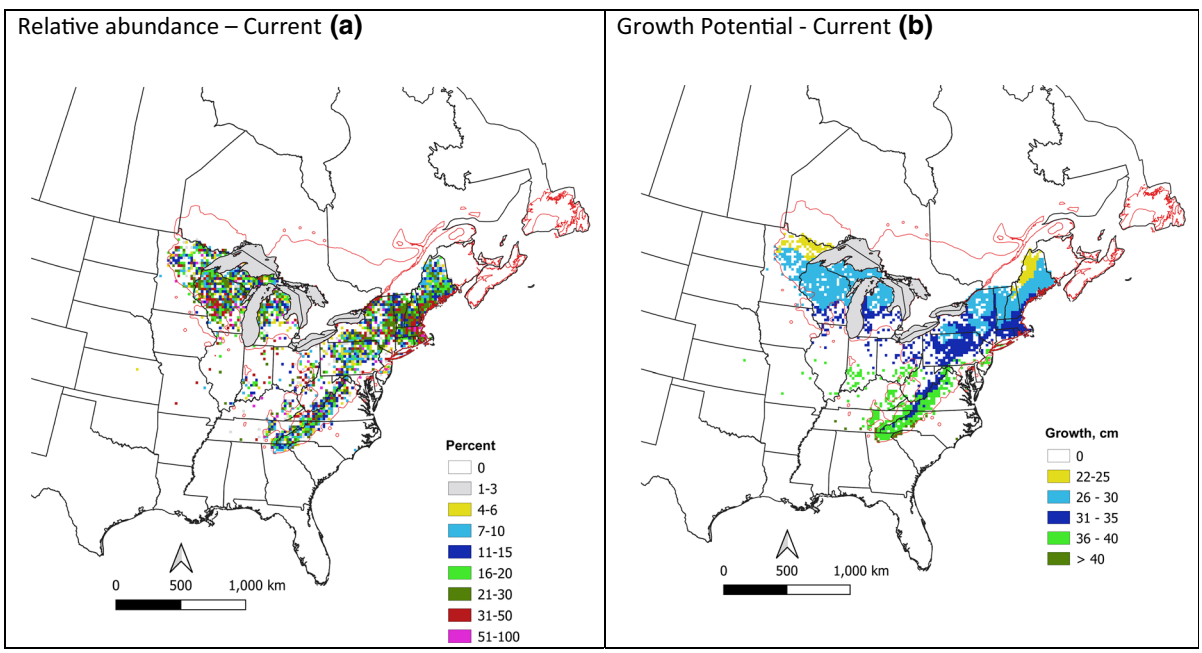


Fig. 2 Modelled current relative abundance (left, **a**) using multi-model ensemble, and growth potential measured in average annual growth rate in cm (right, **b**), as a function of population mean annual temperature. The red outline is Little's range boundary of eastern white pine

FIA plots per 20 × 20 cell varied, with a mean of 4 (sd = 3). Including all plots ensured a good coverage of the entire eastern white pine distribution without omissions. Even though we excluded all FIA plots designated as "plantations", there are some areas outside the traditional range of eastern white pine that FIA sampling captured due to naturalized populations, and/or populations that have migrated.

Current and future climates

Climate normals for 10 variables (Table 2) were screened from the AdaptWest database (AdaptWest Project 2015; Wang et al. 2016) for current (1981–2010) and, future (2071–2100) periods (the process is explained in the Modelling suitable ecological habitats section below). We used two future climate scenarios, RCP 4.5 (medium emission pathway) and RCP 8.5 (high emission pathway), to understand the future dynamics of eastern white pine (Wang et al. 2016). An ensemble of 15 General Circulation Models (AdaptWest Project 2015) was used for future projections by these two scenarios (IPCC 2013; USGCRP 2017). We aggregated the original data in GIS, from 1 × 1 km resolution to 20 × 20 km by calculating the mean of the climate values within the 20 × 20 cell in order to match the resolution of the aggregated FIA plot data.

Modelling genetic clines in growth potential

Genetic clines in growth potential were modelled using population average height growth of test sites. It is assumed that the inherent growth potential is more accurately exhibited in test site climates that are at least as warm as or warmer than the provenance climates (Leites et al. 2019). Therefore, only observations where populations were tested in sites with climate as mild or milder than the home climate were used, with mean annual temperature (mat.ss) as a measure of climate mildness. In total, 106 populations were represented across 1 or more of the 28 tests. Mean annual temperature has been documented as an important variable associated with intraspecific differentiation in several species (reviewed by Aitken and Bremmels 2016). To model clines in population average height growth we use a linear mixed effect model of the following form:

$$HG_{ij} = \beta_0 + u_j + u_i + \beta_1 mat.ss_i + \varepsilon_{ij} \quad (1)$$

$$\varepsilon_{ij} \sim \mathrm{N}\left(0, \sigma^2\right), u_i \sim \mathrm{N}\left(0, \sigma_i^2\right), u_j \sim \mathrm{N}\left(0, \sigma_j^2\right)$$

where HG is tree height growth in cm/year, mat.ss is the mean annual temperature at the population's seed origin, i is the population index, and j is the test site index, β_0 and β_1 are fixed effect parameters and u_j, u_i are population and test random effects, respectively (Table 3). The model was fit using the lme4 package (Bates et al. 2015) in R (R Core Team 2019).

Current and future geographic patterns of growth potential

In order to understand how growth potential varies spatially, we mapped the growth potential model's fixed-effect predictions across the entire range of eastern white pine for current as well as the future RCP 4.5 and RCP 8.5 scenarios. Projections of growth potential into the future incorporate 'optimistic' future

Table 2 Climate variables used as predictors in the habitat suitability (HQ - MME) model of eastern white pine

Abbreviation	Variable
mat	Mean annual temperature (°C)
mwmt	Mean temperature of the warmest month (°C)
mcmt	Mean temperature of the coldest month (°C)
map	Mean annual precipitation (mm)
msp	Mean summer (May to Sep) precipitation (mm)
dd0	Degree-days below 0 °C (chilling degree days)
dd5	Degree-days above 5 °C (growing degree days)
nffd	The number of frost-free days
pas	Precipitation as snow (mm)
emt	Extreme minimum temperature over 30 years

For more information, see: Wang et al. (2016)

Table 3 Statistical summary of the growth potential mixed-effect model (Eq. 1)

Parameter	Estimate	Std. error	p-value
Intercept	20.5	2.4	7.0e-12***
mat.ss	1.41	0.16	1.4e-13***
σ_{test}	10.3		***
$\sigma_{Population}$	4.1		***
$\sigma_{Residual}$	3.9		

Both the Intercept and mean annual temperature (mat.ss) effects are significant. σ_{test}, $\sigma_{Population}$, $\sigma_{Residual}$ are the standard deviations of the test site index, population index, and the residual respectively. *** indicates that it is statistically significant

conditions if assisted migration and seed transfer management guidelines are put in place to re-align genotypes and climate (Rehfeldt et al. 2018), because adaptation by natural selection occurs at a much slower pace than the future climate projections for 2071–2100. We therefore explore and suggest possible future outcomes which may be useful for managers seeking guidance for future landscapes.

Delineation of intraspecific regions based on growth potential clines

The modelled growth potential clines describe continuous variation across the mean annual temperature gradient (Fig. 2b). To further explore within species responses to climate, we group the continuous variation of modelled growth potential into regions using unsupervised cluster analysis. We used the *clara* algorithm (*pamk* function in the *fpc* package) in R (R Core Team 2019) for clustering which performs partitioning around medoids with the optimum number of clusters estimated by the average silhouette index (Rousseeuw 1987; Kaufman and Rousseeuw 1990). The average silhouette index measures how self-similar a cluster is compared to other clusters, with higher values indicating better cluster separation. The *clara* method is more robust because it minimizes the sum of dissimilarities instead of the sum of squared Euclidean distances (as in the k-means clustering algorithm), and can accommodate much larger datasets like ours (Reynolds et al. 1992).

In order to determine the optimum number of clusters, we examined the mean annual temperature ranges within the clusters, in addition to the silhouette index. We chose mean annual temperature ranges of $\sim$ 3–4 °C, to ensure that the clusters were not too small as to be of no practical importance.

Comparing demography among intraspecific regions

The FIA plots for RIV and percent mortality were rasterized to 20 km cells by using the mean values/cell, and the mean cell statistics were computed (Table 4). For seedlings, which indicate regeneration potential, the total number of seedlings/plots was rasterized to 20 km cells and the average for the cell calculated. This average was multiplied by 74.97 to convert to seedlings/acre (the number of seedlings per acre that the seedling count theoretically represents based on sampling design; see Woudenberg et al. 2010).

Demography means among the delineated intraspecific regions were compared using ANOVA and Tukey's honest significance (Tukey HSD) test using an α level of 0.01 or lower in R (R Core Team 2019). To guard against potential spatial independence issues among the intraspecific regions, we also conducted a non-parametric analysis (Kruskal–Wallis rank sum test) along with pairwise comparisons using Wilcoxon rank sum test and verified that both parametric and non-parametric tests agreed.

Modelling suitable ecological habitats (HQ)

Climatic habitat suitability (HQ) based on the RIV derived from FIA data for current and future climate scenarios was predicted at a cell resolution of 20 $\times$ 20 km using a multi-model ensemble (MME) technique (Prasad, 2018). The HQ model was developed using current climate values and then projected into the future under the RCP 4.5 and 8.5 emissions scenarios for the entire range of eastern white pine. As noted earlier, we used 10 climate variables (Table 2) as the primary drivers. This was done after screening 27 bioclimatic climate variables available in the AdaptWest data base (AdaptWest 2015) using random forest and boosting (see MME below). The 10 climate variables were selected for the final HQ model by examining the variable importance that contributed substantially to the overall fit. Highly correlated variables (Pearson correlation coefficient $>$ 0.85)

Table 4 Variation of demography (mean *relative abundance, percent mortality and mean sum of seedlings)*, extreme minimum temperature (EMT) and mean annual temperature (MAT) with the three intraspecific zones

Intraspecific region	FIA plots	Extreme minimum temperature (EMT), °C	Mean ANNUAL temperature (MAT), °C	Relative abundance (RIV)	Percent mortality (PM)	Sum of mean seedlings/acre (SC)
Warm	1751	− 26.04	12.3	17.0a	18.8a	2500a
Middle	2747	− 31.94	8.1	21.0b	19.6a	3116a
Cold	2442	− 37.61	5.2	17.7a	21.0a	1430b

Number of FIA plots are also shown. Statistically significant differences are indicated with different lowercase letters ($\alpha = 0.01$)

were not selected—but this criterion was relaxed if including the variable resulted in a superior fit based on mean squared error (MSE).

The multi-model ensemble (MME) technique, used to model habitat suitability from relative importance values, stabilizes prediction uncertainty by averaging the consensus predictions (i.e., where all models predicted nonzero values) of five machine learning techniques: three versions of random forest (RF), and two versions of generalized gradient boosting methods (Jones and Cheung 2015; Martre et al. 2015; Zhang et al. 2015; Prasad 2018; Prasad et al. 2020). The MME used the *ranger* module for the three versions of RF, and the *gbm* and *Xgboost* modules for the two versions of boosting in R (R Core Team 2019).

Built-in validation methods, bootstrap sampling and cross-validation, in the five models ensure that the models do not overfit (Svetnik et al. 2003). To ensure that built-in validation was sufficient, and optimal model parameters were chosen, we used the package *caret* in R which does a stratified random split of the data into training and test sets to evaluate and choose the parameters for best model performance (Kuhn 2008). Finally, by averaging only the consensus predictions, we chose the dominant trend across the models, further boosting our confidence in the predicted outputs.

Results

Geographic patterns in growth potential

The model of growth potential as a function of population home climate had a statistically significant slope ($\alpha = 0.01$), which we interpret as evidence of intraspecific genetic differentiation in height growth (HG) driven by mean annual temperature (Table 3; Campbell and Sorensen 1978; Rehfeldt 1984; Davis et al. 2005). The slope is positive which indicates that populations from warmer origins attained higher HG than populations from colder climates when evaluated in the provenance studies (common gardens). Marginal and conditional R^2 for this model were 0.1 and 0.9 respectively.

Delineation of intraspecific regions

Clustering the mapped predictions of the growth potential model yielded three regions that we named as cold, middle, and warm regions (Fig. 3a). The number of clusters were chosen to ensure a temperature range within each cluster that was not too narrow for practical applications but still had high silhouette value (above the third quartile). The joint contour plot of the three clusters (Fig. 3b) with growth potential and habitat suitability (modelled RIV) as the axes, shows that the growth potential has minimum overlap among the regions (reflecting our choice of clusters), but the habitat suitability shows overlapping distributions, which indicates that within each cluster, there are large areas where the habitat suitability of eastern white pine is low to medium and smaller areas where it is higher (tails of the distribution in Fig. 3b). The area of high habitat suitability is larger in the middle region, although in each region, higher values of habitat suitability do not coincide with the higher values of growth potential. This implies that eastern white pine can occupy climatically suboptimal areas, most likely due to potential inter and intra specific interactions. We further explore this via maps resulting from modelled current and future climates.

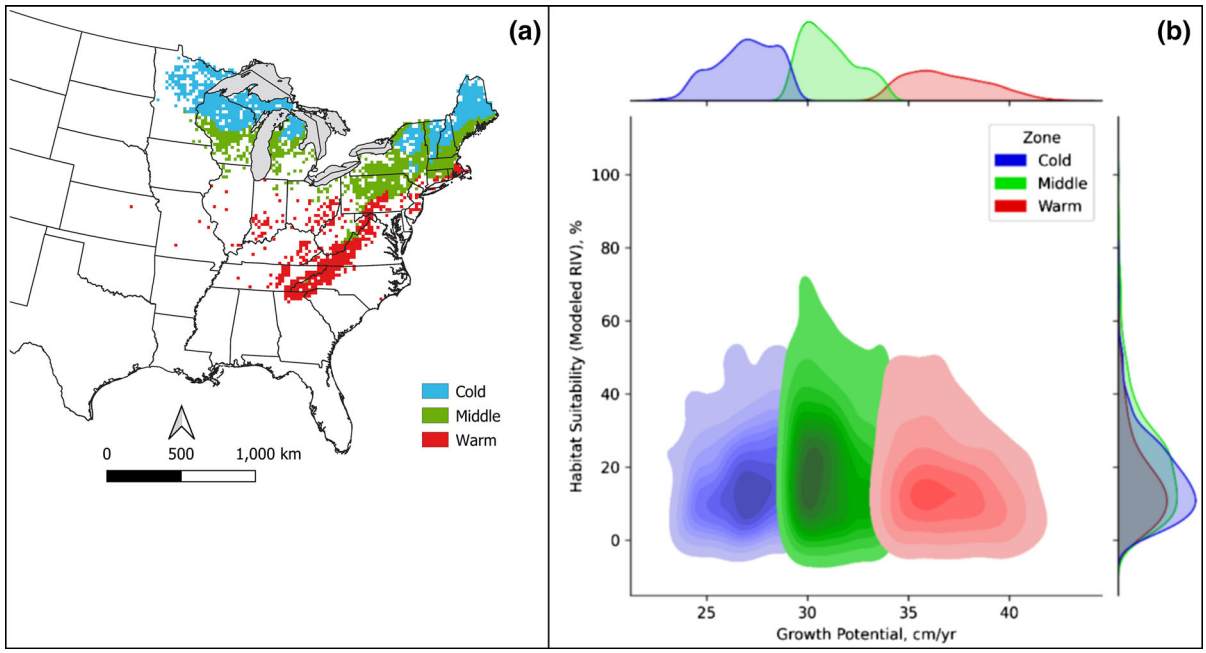


Fig. 3 Intraspecific zones (left, **a**) derived from clustering modelled growth potential—northern cluster is labelled the cold-zone, the middle cluster as the middle-zone and the southern cluster as the warm-zone. The joint contour plot (right, **b**) shows the three clusters plotted with growth potential and habitat suitability as the axes

Demographic differences among intraspecific regions

Statistical evaluation of demography via FIA-derived variables, RIV (relative importance value or relative abundance), PM (percent mortality) and SC (seedling count), helps us understand abundance, mortality, and regeneration differences among the intraspecific regions (Table 4). The RIV was significantly higher in the middle region compared to the other two regions ($\alpha = 0.01$). Percent mortality was not significantly different among the regions, which suggests that current changes in climate are affecting the populations similarly at this point. Seedlings/acre were highest in the middle region and significantly lower in the cold region, suggesting a lower regeneration potential for populations in colder zones. Comparing among the three demographic variables, the middle region seems to be better positioned from an ecological standpoint as it has higher relative abundance, similar mortality, but increased regeneration counts, compared with the cold and warm regions. On the other hand, the cold region has lower relative abundance, similar mortality, and lower regeneration counts—the latter of some concern for the populations occupying extreme conditions in the north, based on current climatic conditions.

Suitable habitats and growth potential—current and future

Predicting suitable habitats based on the MME technique yielded an average R^2 of 0.4. We modelled and mapped the predicted suitable climatic habitats under RCP 4.5 and RCP 8.5 scenarios for the (a) entire eastern white pine range in the eastern United States and, (b) each of the three intraspecific regions separately, in order to understand how the entire species and, the homogenous groups of populations were responding separately to climate change. Even though our observed abundance data was limited by the FIA locations in the US, we allowed the climatic data to extend into Canada, to enable the modelled future habitats of eastern white pine to occupy an extended range. Therefore, the climatic habitats based on the current RIV distribution in the US extend beyond the full range under RCP 4.5 and RCP 8.5 scenarios.

Figures 4, 5 and 6 show the dynamics of both HQ (suitable habitats/habitat quality, left columns) and GP

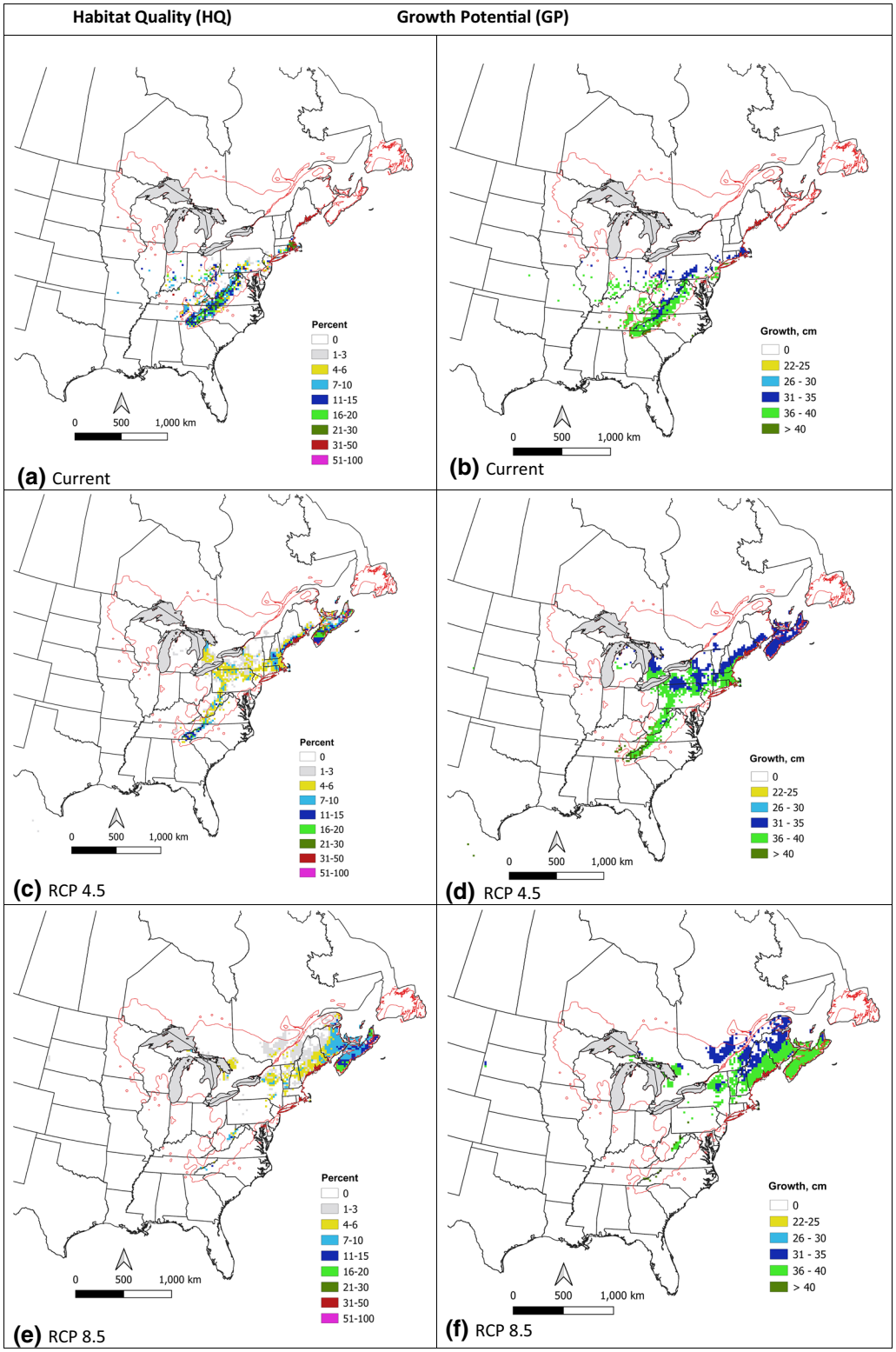
(growth potential, right column) for current and future conditions for the warm, middle, and cold regions respectively. We interpret HQ maps as indicative of ecological conditions for each intraspecific region, and the GP maps as indicative of the conditions related to the physiological potential for each intraspecific region (ecological and physiological optimums sensu Rehfeldt et al. 2018). Comparing the HQ in the three figures (left columns) reveal that suitable ecological habitats will move northwards for all three intraspecific regions under future climates. This is especially so under the RCP 8.5 conditions (Figs. 4e, 5e, 6e), reflecting greater movement under warmer conditions. For the warm region (Fig. 4), even under relatively milder RCP 4.5 (Fig. 4c), there is a decrease in the areas of most suitable habitats in the US (lower predicted RIV of remaining habitats), with the primary habitat gains in the Canadian province of Nova Scotia. Under RCP 8.5, this movement is even stronger (Fig. 4e). The middle region (Fig. 5) also shows a strong push towards the north but tend to retain areas of suitable habitats in the northeastern US, especially under RCP 4.5 (Fig. 5c). Populations in the cold region in the US, however, tend to lose most of their habitats as suitable habitat moves into Canada (Fig. 6), especially under the RCP 8.5 (Fig. 6e). The habitat quality of the potentially gained habitats in the north also are of a lower relative abundance (RIV), which could indicate a degradation of habitat quality even within ecologically suitable habitat. This is cause for concern and would not have been highlighted if the species was modelled a whole, without the intraspecific delineation of populations groups.

The same three figures (Figs. 4, 5 and 6) also show where geographically current populations will be best aligned with future climate (b, d, f on all three figures). This is under assisted migration and management practices that actively match genotypes and climate, i.e., where current populations would be matched to future climates (see section '*Current and future geographic patterns of growth potential*'). The trends among the three regions, as expected, show agreement with the changes in habitat quality but also indicate a uniformly increasing growth potential within the geographic areas where current populations will be aligned with future climate (b, d, f on all three figures). Because the modeled GP is a function of mean annual temperature, the future growth potential reflects changes in mean annual temperature. However, because the northern regions are predicted to warm faster (USGCRP 2017), we are likely to see increasing mismatches northward, especially in Canada between the HQ and GP scenarios in the future. This will be more pronounced under RCP 8.5 which predicts larger future increases in temperature (for example, Figs. 6e, f). Therefore, the combination of HQ and GP can yield important insights on possible future trajectories because it allows us to identify ecologically suitable areas (HQ) within areas where current populations will be aligned with climate (GP). This information will be crucial for the active management of eastern white pine via assisted migration (Pedlar et al. 2012; Pedlar and McKenney, 2017; Young et al. 2020).

Combining HQ and GP

By combining HQ and GP, we can assess suitable combinations of both ecological habitat and genetic growth potential (HQ;GP, Fig. 7) and identify areas of highest potential abundance and productivity under assisted migration practices. To do this, we first reclassified HQ (1–5; 5–10; > 10%) and GP (22–28; 28–34; > 34, cm) into three classes—low, medium, and high—after examining their distributions and summary statistics. Next, to incorporate the variations stemming from the three intraspecific regions, we combined the three regions separately and mosaicked them together by averaging the overlapping regions (Fig. 7), instead of using the entire distribution of the species which would have masked the underlying differences among the three regions. The resulting combined HQ;GP maps allow the visualization of potential future landscapes where suitable combinations of HQ and GP are likely to be, and hence enable better understanding to prioritize management accordingly. The four most suitable combinations among the nine possible are HQhi;GPhi, HQmed;GPhi, and HQhi;GPmed, HQmed;GPmed. We see movement of these suitable combinations to the north, from current (Fig. 7a) to RCP 4.5 and RCP 8.5 (Fig. 7b, c). At the northern end of eastern white pine's range, there are fewer desirable combinations, but the much higher warming potential of RCP 8.5 (Fig. 7c) facilitates improved growth under more suitable conditions compared to RCP 4.5 (Fig. 7b). Along the southern margins of the distribution, northern Michigan and Wisconsin are poised to lose almost all of their

Warm Zone:


Habitat Quality (HQ)
Growth Potential (GP)
Percent
0
1-3
4-6
7-10
11-15
16-20
21-30
31-50
51-100
Growth, cm
0
22-25
26 - 30
31 - 35
36 - 40
> 40
0 500 1,000 km
(a) Current
(b) Current
(c) RCP 4.5
(d) RCP 4.5
(e) RCP 8.5
(f) RCP 8.5

◀**Fig. 4** Warm zone: The left column shows the habitat quality (HQ) maps and the right column the growth potential (GP) maps. The first row is the current modelled distribution, the middle row is the RCP 4.5 and the last row is the RCP 8.5. The modelled future GP (**d** and **f**) show idealized conditions because the growth potential has been extrapolated to match future HQ habitats

suitable combinations under RCP 8.5, although areas of suitable HQ;GP are retained under RCP 4.5.

Another important insight when HQ;GP maps are evaluated together with the maps of the separate regions (Figs. 4, 5 and 6) is that the main contributors to desirable HQ:GP combinations in the future are populations from the middle and warmer regions (see Figs. 5 and 4). The cold region (Fig. 6) is characterized by lower HQ values in the future in spite of increases in GP for these populations (Figs. 6b, d, f). Therefore, the lower GP values relative to those of the other two regions suggest they would contribute less to overall abundance and productivity under assisted migration.

Table 5 shows the changes between current and future climates by quantifying area-wise changes for all combinations of HQ and GP shown in Fig. 7, thus providing an indication of changes in eastern white pine abundance and productivity if all genotypes are matched to future climate via assisted migration. The most optimal combination, HQhi;GPhi decreases compared to the current from 84.8 to 26.8 km^2*1000 under RCP 4.5 and to 55.6 under RCP 8.5. Even the next best HQhi;GPmed shows a big decrease under RCP 8.5 (from the current 229.2 to 70.8), but RCP 4.5 registers an increase to 289.2, showing that, according to this modelling approach, a moderate increase in future temperatures is favorable for this combination. The largest gain in suitable combinations is HQmed;GPmed (from the current 94.0 to 292.4 under RCP 4.5 and 633.6 under RCP 8.5) followed by HQmed;GPhi (from the current 50.0 to 96.0 under RCP 4.5 and 213.6 under RCP 8.5). Figure 7 highlights that even under assisted migration, losses in eastern white pine abundance and productivity could be expected. It also highlights the regions where these changes are happening – with a clear movement of favorable conditions to the north, and from the US to Canada.

Discussion

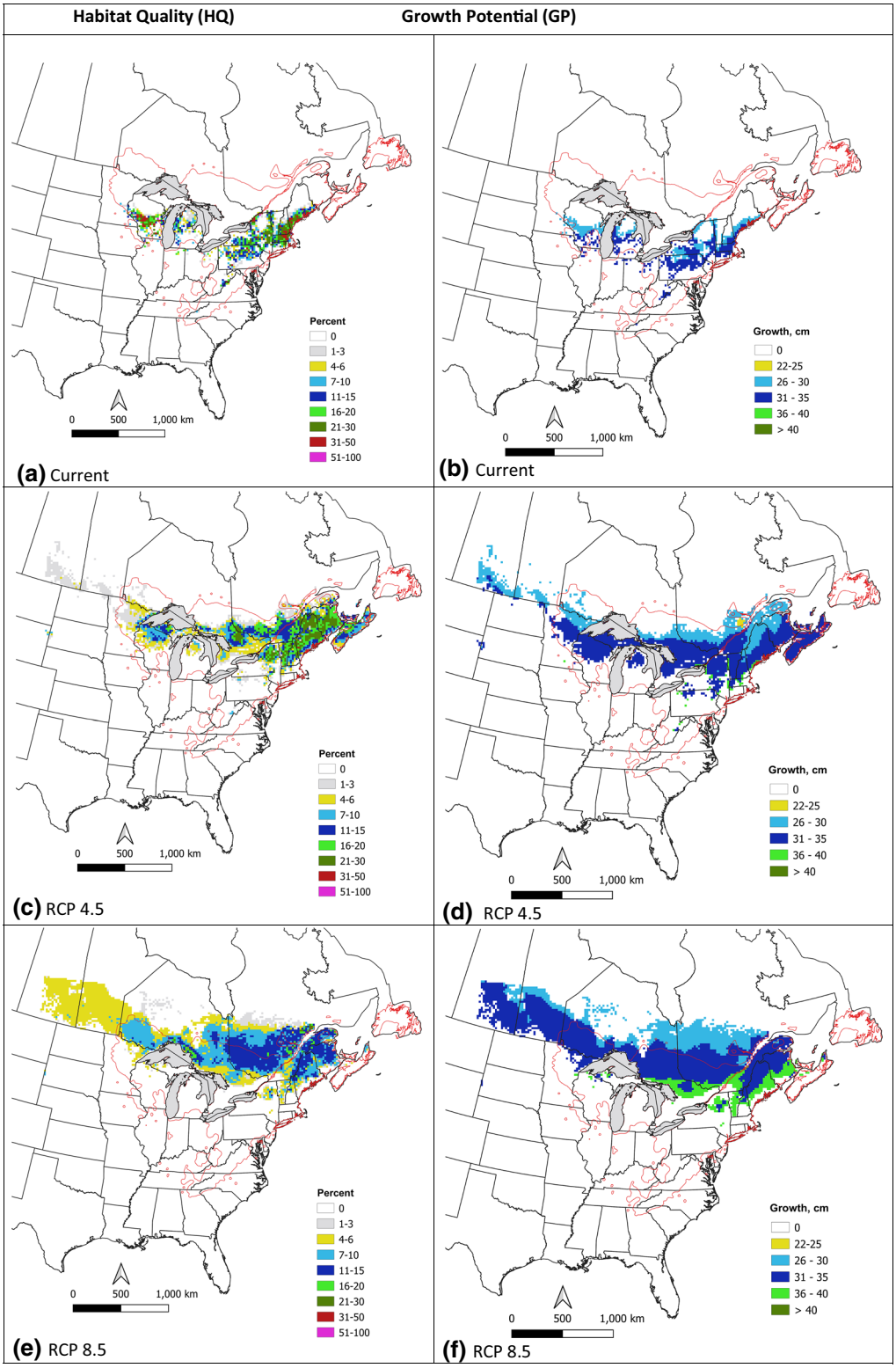
Forest species that inhabit a wide range like eastern white pine (Little, 1971) are composed of populations which tend to be locally adapted to a portion of the environmental gradients, especially temperature (Morgenstern 1996; Loehle 1998; Matthews et al. 2019). Therefore, responses to climate change will likely be population specific instead of species specific (Aitken and Bemmels 2016; Rehfeldt et al. 2018). In this study, we aimed to evaluate intraspecific variation in response to climate change by combining models of geographic patterns in growth potential derived from provenance tests data and models of geographic patterns in habitat suitability derived from FIA inventory data. We assume that the former models relate to the climate conditions related to populations' physiological optimum and the latter to conditions related to populations' ecological optimum (sensu Rehfeldt et al. 2018).

The innovative aspects of our analysis consisted of (a) delineating homogenous population groups as three intraspecific regions by unsupervised clustering of growth potential patterns; (b) modelling climatic habitat suitability separately for each of the intraspecific regions to understand how ecological conditions for each region respond under future climates; and, (c) combining the modelled patterns in growth potential with the habitat suitability modelled from relative abundance data to map and explore how assisted migration aimed to realign genotypes and climate (geographic changes in GP) combine with future ecologically suitable areas (HQ), to better understand the fate of eastern white pine.

Growth potential

The mixed-effects GP model shows positive slope with the fixed-effect component, mat.ss (mean annual temperature), matching previously detected genetic clines in studies of eastern white pine and other conifers (Joyce and Rehfeldt 2013; Aitken and Bemmels 2016). The changes in the geographic location of current GP regions (cold, middle, and warm) that we project for future temperatures (Figs. 4, 5, 6) illustrate regions where current population groups (intraspecific regions) are likely to find habitats aligned with their physiological optimum in the future. These maps can inform assisted migration and seed-zone matching to

Middle Zone:


Habitat Quality (HQ)
Growth Potential (GP)
Percent
0
1-3
4-6
7-10
11-15
16-20
21-30
31-50
51-100
Growth, cm
0
22-25
26 - 30
31 - 35
36 - 40
> 40
0 500 1,000 km
(a) Current
(b) Current
(c) RCP 4.5
(d) RCP 4.5
(e) RCP 8.5
(f) RCP 8.5

◀**Fig. 5** Middle zone: The left column shows the habitat quality (HQ) maps and the right column the growth potential (GP) maps. The first row is the current modelled distribution, the middle row is the RCP 4.5 and the last row is the RCP 8.5. The modelled future GP (**d** and **f**) show idealized conditions because the growth potential has been extrapolated to match future HQ habitats

help realign genotypes and climate, but are not a projection of potential migration because evolutionary adaptive traits are not likely to keep pace with rapid climate change, although adaptive plasticity (Rehfeldt et al. 2001; Peterson et al. 2018; David et al. 2019; Fréjaville et al. 2019; Bisbing et al. 2020) is likely to play some role in alleviating mismatches. Our models indicate that for the three intraspecific regions, current populations will be aligned with future climate in geographic areas north and northeast of current geographic areas under different climate change scenarios. They also indicate that within an intraspecific region, current populations in future geographic areas will be those of higher GP and that is more accentuated in the cold intraspecific region (Fig. 6b, d, f). This agrees with studies that indicate that populations adapted to cold climates are likely to increase growth with moderate warming (Rehfeldt et al. 1999; Wang et al. 2006; Leites et al. 2012a, b).

Intraspecific analysis of HQ

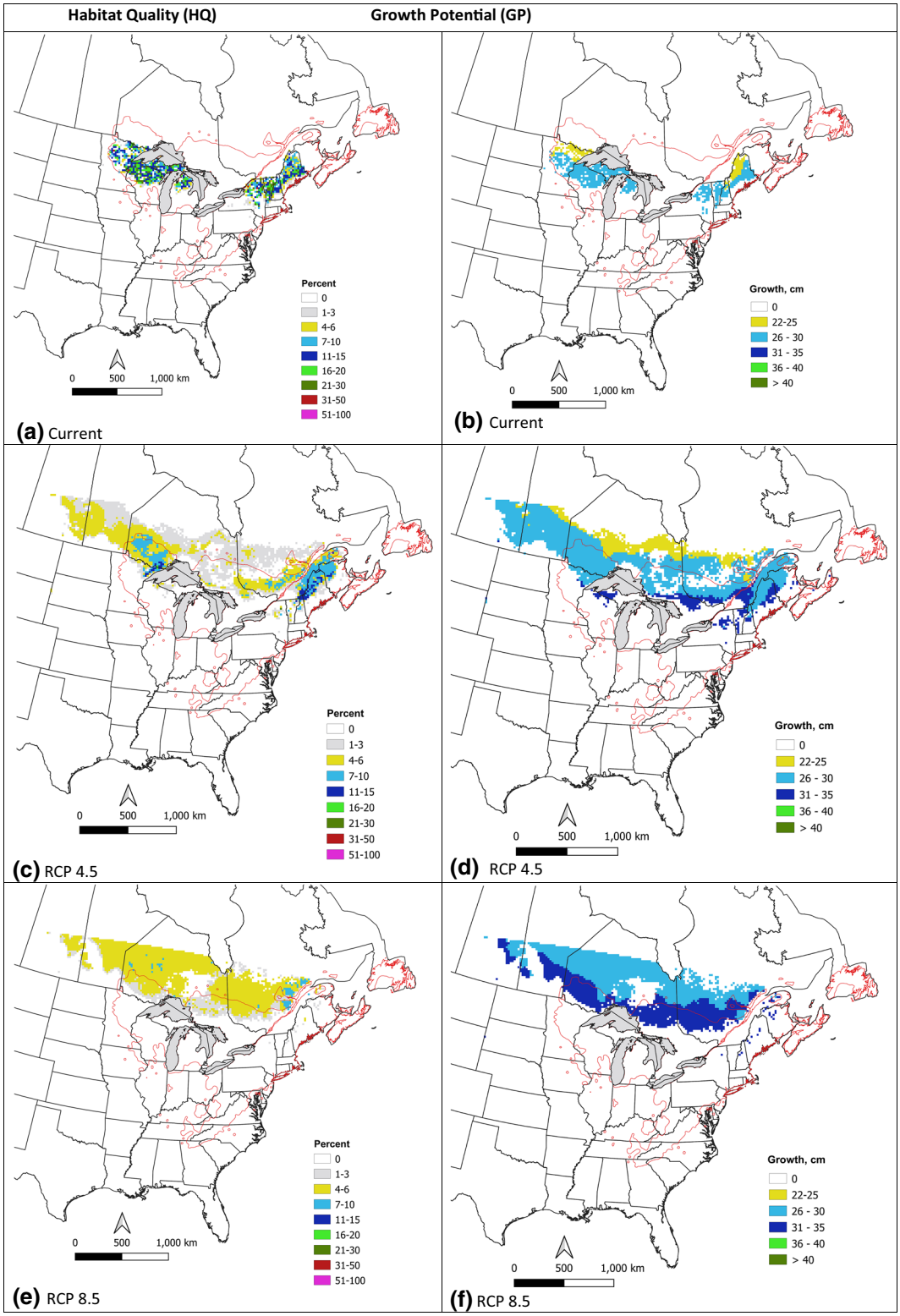
We have restricted the current HQ to the United States because equivalent demographic data were not available in Canada—however, we have projected future HQ to encompass relevant parts of Canada by including climate beyond the current range of eastern white pine (Figs. 4, 5, 6). While RCP 4.5 shows habitats moving north, there is still viable habitat in the northeastern US, compared to RCP 8.5, which shows almost all HQ moving into Canada. It would not have been clear from the current FIA distribution whether some population groups are more affected than others. By using intraspecific regions, we identify groups of populations that are more vulnerable to losing suitable habitats from an ecological standpoint. Under an assisted migration strategy that realigns genotypes and climate, the populations of the cold region (Fig. 6a, c, e) will not contribute as much to the future eastern white pine abundance and productivity because current populations do not have the highest growth potential and the ecologically suitable areas are projected to decrease as well. Notably, the HQ of southern populations, which are mainly in the southern Appalachians, are projected to move north and east, but not north and west. Even though moisture variables along with the temperature variables figured among the top in our MME, it is difficult to gauge from our analysis whether this trend is linked to increased incidences of drought westward. However, with our more nuanced intraspecific analysis we are able to show that HQ areas for populations of the middle region are the areas that may contribute the most area to future ecologically suitable habitats for the species in the United States (Figs. 5a, c, e). It also highlights that in addition to the concern about the vulnerability of southern populations to novel climates under warming scenarios (Kremer et al. 2012; Aitken and Bemmels 2016; Pedlar and McKenney 2017), populations in the cold region (region of putative cryptic refugia as inferred by Nadeau et al. 2015) may also need additional attention for genetic conservation. This is also highlighted by the significantly lower seedling counts in the cold region indicating lower regeneration potential. A compensating factor for populations in the warm region is that studies point to greater phenotypic plasticity in these populations compared to populations from the cold region (Cooper et al. 2019).

A novel aspect of our study was combining HQ with GP to map and assess suitable combinations of these two features for laying the groundwork for managing this important species under future conditions, assuming current populations are moved to geographic locations where genotypes and climate are aligned. The maps of HQ + GP combinations (Figs. 7a, b, c) show that regions of high potential are pushed mainly to Canada, although the US state of Maine in the northeast retains some good combinations. Also, HQ + GP combinations disappear in the Midwest (Wisconsin and Michigan) under RCP 8.5 (Fig. 7).

Management implications under climate change

To manage wide-ranging species with high intraspecific variability under future climates, we need to focus on modelling populations' responses instead of species as a whole. We do that by including population

Cold Zone:


Habitat Quality (HQ)
Growth Potential (GP)
Percent
0
1-3
4-6
7-10
11-15
16-20
21-30
31-50
51-100
Growth, cm
0
22-25
26 - 30
31 - 35
36 - 40
> 40
0 500 1,000 km
(a) Current
(b) Current
(c) RCP 4.5
(d) RCP 4.5
(e) RCP 8.5
(f) RCP 8.5

◀**Fig. 6** Cold zone: The left column shows the habitat quality (HQ) maps and the right column the growth potential (GP) maps. The first row is the current modelled distribution, the middle row is the RCP 4.5 and the last row is the RCP 8.5. The modelled future GP (**d** and **f**) show idealized conditions because the growth potential has been extrapolated to match future HQ habitats

groups represented by the three intraspecific regions, and considering both demographic and growth potential, enabling more meaningful management interventions. The projected movement of eastern white pine habitat under future climate scenarios support the need for more intensive management of this commercially, aesthetically, and ecologically important tree species throughout its range, with special attention in those areas deemed vulnerable. Managers planning for future climate changes seek spatially helpful products to guide management wisely across landscapes, and this guidance needs to consider both ecological and genetic aspects (Swanston et al. 2016; Janowiak et al. 2018). Our combined HQ + GP maps, along with separate HQ projections across intraspecific population groups, will aid in planning for such scenarios. By combining ecological aspects via the RIV (a surrogate for ecological optimum, Rehfeldt et al. 2018), with physiological optimum aspects via modelled GP, we can map these two features across the range of eastern white pine as well as provide guidance for promoting forest conservation and adaptation under climate change via assisted migration and gene conservation practices (Pedlar et al. 2012; Pedlar and McKenney 2017; Young et al. 2020). For example, areas identified as optimal because of good combinations of HQ and GP (Figs. 7b, c), can be potential planting sites to test the performance of assisted migration of eastern white pine when assessed with the relevant local factors. When considering assisted migration, the tradeoffs between survival and cold hardiness become important, which can limit the effectiveness of long-distance transfers (Sebastian-Azcona et al. 2018; Leites et al. 2019). The combined HQ + GP maps can also be used in conjunction with Figs. 4, 5 and 6 to plan for assisted gene flow for population groups threatened by rapid climate change. The same maps can also be used in conjunction with seed-zones to manage stocks under current and future climate scenarios (Bucharova et al. 2019; Pike et al. 2020). The northward movement of suitable combinations in the future also point to the value of sustained cooperation via joint projects between the US and Canada for addressing climate change effects on forests (Prasad et al. 2020).

Post glacial migration

In addition to the above factors, it is helpful to incorporate historical information of tree species migration to better manage future forests. Cyclical glaciation, especially during the Pleistocene, was one of the principal agents in shaping the population structure of many species by historically influencing gene flow (Massatti et al. 2018; Edelaar and Bolnick 2019). Studies of historical migration pathways that shaped the postglacial phylogeography of eastern white pine are typically based on neutral genetic markers (Nadeau et al. 2015; Zinck and Rajora 2016). While these studies cannot determine if the geographic patterns of population structure are adaptive, it does shed light on contemporary population genetic structure based on historical migration pathways. Zinck and Rajora (2016) used 12 nuclear and 3 chloroplast microsatellite DNA markers to reveal one southern refugium, two recolonization routes, and three ancestral lineages in eastern white pine. Similarly, the study using SNP markers by Nadeau et al. (2015) identified putative cryptic northern refugia in the northern US Midwest and distinct northern and southern groups and subgroups. Naturally, one cannot expect one-to-one similarity among groups derived from non-adaptive historical genetic studies and population clusters derived from current growth potential– however, combining information from both approaches can aid genetic conservation programs by prioritizing areas that may be at risk in several dimensions. For example, the refugia, historical trajectories, and genetic diversity indices derived from post glacial migration studies can be assessed for overlap with areas of suitable habitats and growth potential to prioritize management under future climates. This illustrates the value of incorporating diverse studies, based on both current and historical ecological and genetic components, when managing future forested landscapes.

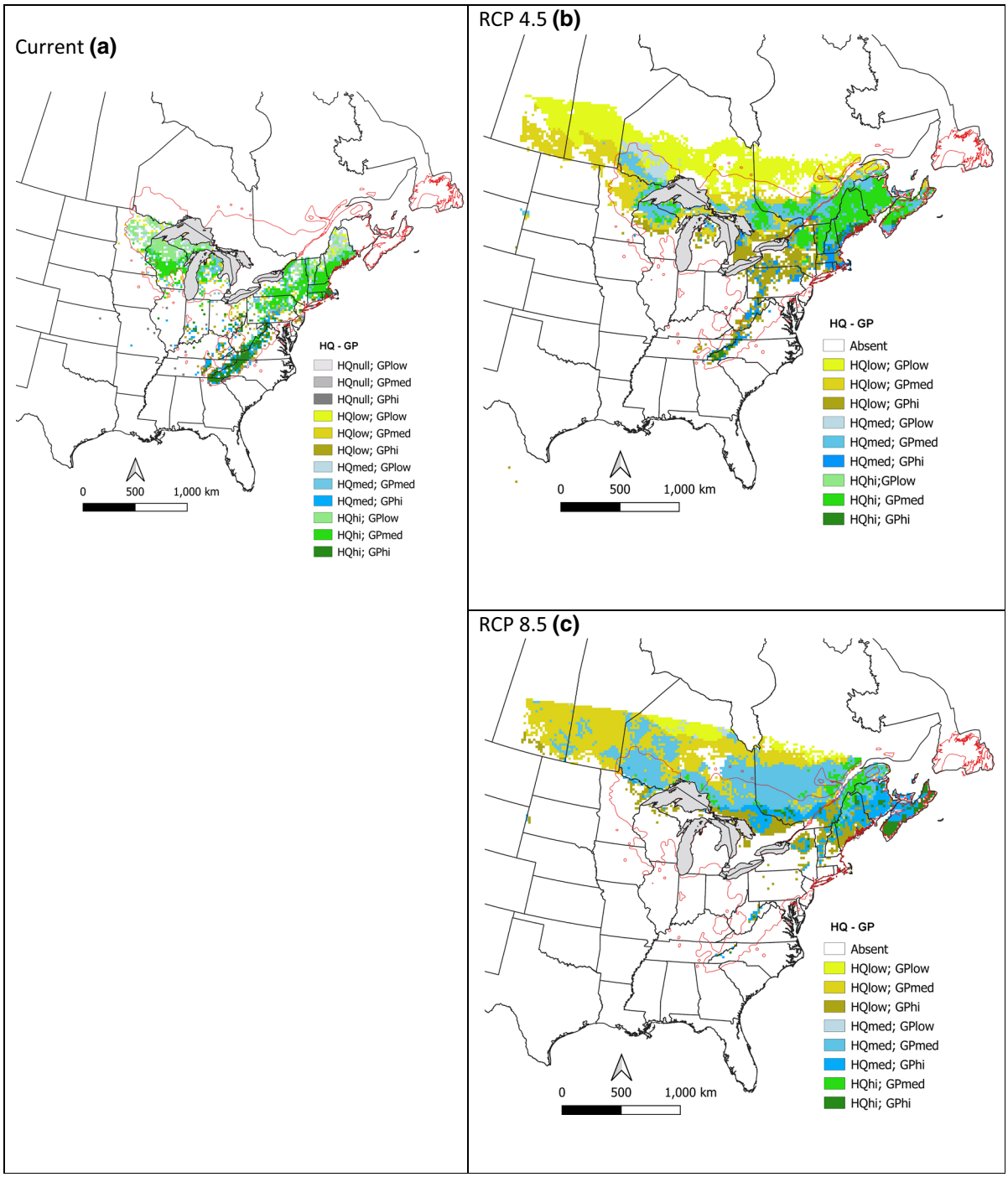


Fig. 7 Combined habitat suitability (HQ) and growth potential (GP) to assess management potential of white pine under current and future climate (RCP 4.5 and RCP 8.5) conditions. The three intraspecific zones (cold, middle and warm) were combined separately by averaging the overlapping areas

Table 5 Geographic area in habitat quality (HQ) and growth potential (GP) combinations for current and future climates—milder (RCP 4.5) and harsher RCP 8.5

HQ + GP	Current (km^2 * 1000)	RCP 4.5 (km^2*1000)	RCP 8.5 (km^2*1000)
HQlow; GPlow	21.6	631.6	97.6
HQlow; GPmed	42.8	435.2	622.0
HQlow; GPhi	37.6	260.0	234.0
HQmed; GPlow	69.6	59.6	10.8
HQmed; GPmed	94.0	292.4	633.6
HQmed; GPhi	50.0	96.0	213.6
HQhi; GPlow	109.6	2.80	0
HQhi; GPmed	229.2	289.2	70.8
HQhi; GPhi	84.8	26.8	55.6
TOTAL	739.2	2093.6	1938

This table should be used in conjunction with Fig. 7

Limitations

In our current analysis, we have not considered the natural migration potential of eastern white pine to match the future suitable habitats. However, another study (Prasad et al. 2020) show that the migration potential of eastern white pine decreases quite rapidly from the current range boundary in $\sim$ 100 years and that combinations of high HQ and colonization likelihoods are scarce. In the absence of assisted migration, potential migration is therefore another factor that should be considered to ensure favorable projected combinations in the landscape.

We have also not included the role of disturbance, both natural (e.g., drought and diseases) and anthropogenic (land-use changes, etc.). These changes are difficult to incorporate into the modelling framework due to their uncertainty and the paucity of data. By focusing the analysis to climate related changes, we delegate these other factors as regional and local management challenges that are best evaluated on a case-by-case basis.

In addition, we have not assessed the potential effects of phenotypic plasticity in our analysis, although phenotypic plasticity may ameliorate the effects of climate change (Hendry 2016).

We acknowledge that the population groups represented by the three broad intraspecific regions encompass many populations. We confined our analysis to three regions to highlight the main trends and keep good climatic separation among the regions. This grouping of populations into large regions shows broad, but important trends and are practical for managers to incorporate when considering climate-change related issues in their management plans.

Finally, it is possible that eastern white pine may be adapted to factors other than temperature, like moisture availability and soils, but these patterns were not observable from available provenance data (Walthert et al. 2017; Gibson et al. 2019). However, edaphic factors are generally more regional and local in scope and rarely lead to macro-scale emergent distributions compared to climate (Pederson et al. 2015; Aitken and Bemmel 2016). Therefore, these features need to be evaluated separately with more local studies and are beyond the scope of the present analysis.

In summary, our analysis, and products, which incorporate eco-evolutionary and genetic principles, can be used as a guide for more diversified understanding and management of eastern white pine under future conditions. However, it is important to state that this study is not intended to be a substitute for, but rather to complement, well-designed field experiments, which alone can test and assess if model predictions are accurate enough to be useful. While the study is focused on eastern white pine, the methods and approaches presented are generalizable to tree species that occupy large ranges for which provenance and demographic data are available.

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Data availability Upon request.

Declarations

Conflicts of interest We declare no conflict of interest or competing interests.

Ethical approval Has been internally reviewed by the Northern Research Station, USDA Forest Service.

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References

Abrams MD (2001) Eastern white pine versatility in the pre-settlement forest. Bioscience 51:967

AdaptWest Project (2015) Gridded current and projected climate data for North America at 1km resolution, interpolated using the ClimateNA v5.10 software (T. Wang et al. 2015). Available at https://adaptwest.databasin.org. Accessed 13 Jul 2018

Aitken SN, Bemmels JB (2016) Time to get moving: assisted gene flow of forest trees. Evol Appl 9:271–290

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Soft 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Bechtold WA, Patterson PL (2005) The enhanced forest inventory and analysis program—national sampling design and estimation procedures. Southern Research Station, Asheville, p 85

Bisbing SM, Urza AK, Buma BJ et al (2020) Can long-lived species keep pace with climate change? Evidence of local persistence potential in a widespread conifer. Diver Distrib. https://doi.org/10.1111/ddi.13191

Bucharova A, Bossdorf O, Hölzel N et al (2019) Mix and match: regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. Conserv Genet 20:7–17

Campbell RK, Sorensen FC (1978) Effect of test environment on expression of clines and on delimitation of seed zones in Douglas-fir. Theor Appl Genet 51:233–246

Chardon NI, Pironon S, Peterson ML, Doak DF (2020) Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. Ecography 43:60–74

Chen T, Guestrin C (2016) XGBoost: reliable large-scale tree boosting system. Preprint at https://arxiv.org/pdf/1603.02754v1

Cooper HF, Grady KC, Cowan JA et al (2019) Genotypic variation in phenological plasticity: reciprocal common gardens reveal adaptive responses to warmer springs but not to fall frost. Glob Change Biol 25:187–200

Costanza KKL, Whitney TD, McIntire CD et al (2018) A synthesis of emerging health issues of eastern white pine (*Pinus strobus*) in eastern North America. For Ecol Manage 423:3–17

Cutler DR, Edwards TC, Beard KH et al (2007) Random forests for classification in ecology. Ecology 88:2783–2792

DavidF W, Potts LJ, Sasser KL, Shaffer JD (2019) Causes and consequences of phenotypic plasticity in complex environments. Trends Ecol Evol 34:555–568

Davis MB, Shaw RG, Etterson JR (2005) Evolutionary responses to changing climate. Ecology 86:1704–1714

Eckert AJ, Wegrzyn JL, Liechty JD et al (2013) The evolutionary genetics of the genes underlying phenotypic associations for loblolly pine (*Pinus taeda*, Pinaceae). Genetics 195:1353–1372

Edelaar P, Bolnick DI (2019) Appreciating the multiple processes increasing individual or population fitness. Trends Ecol Evol 34:435–446

Fowler DP, Heimburger C (1969) Geographic variation in eastern white pine, 7-year results in Ontario. Silvae Genetica 18:97–144

Fréjaville T, Fady B, Kremer A et al (2019) Inferring phenotypic plasticity and population responses to climate across tree species ranges using forest inventory data. Glob Ecol Biogeogr. https://doi.org/10.1111/geb.12930

Funk D (1971) Eastern white pine seed source trials: ten-year results from three Midwestern plantations in the U.S. U.S. Forest Service Research Note NC-113

Garret PW, Schreiner EJ, Kettlewood H (1973) Geographic variation in eastern white pine in the Northeast. USDA, Washington

Garzón MB, Robson TM, Hampe A (2019) ΔTrait SDMs: species distribution models that account for local adaptation and phenotypic plasticity. New Phytol 222:1757–1765

Genys JB (1987) Provenance variation among different populations of *Pinus strobus* from Canada and the United States. Can J Res 17:228–235

Gibson A, Nelson CR, Rinehart S et al (2019) Importance of considering soils in seed transfer zone development: evidence from a study of the native *Bromus marginatus*. Ecol Appl. https://doi.org/10.1002/eap.1835

Gray LK, Gylander T, Mbogga MS et al (2011) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. Ecol Appl 21:1591–1603

Hendry AP (2016) Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. JHERED 107:25–41

IPCC (2013) Climate change 2013: the physical science basis. In: Stoker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Naules A, Xia Y, Bex V, Midgley PM (eds) Contribution of working group I to the Fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, p 1535

Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern US tree species

under six climate scenarios. Forest Ecol Manage 254:390–406
Iverson L, Peters M, Prasad A, Matthews S (2019a) Analysis of climate change impacts on tree species of the Eastern US: results of DISTRIB-II modeling. Forests 10:302
Iverson LR, Prasad AM, Peters MP, Matthews SN (2019b) Facilitating adaptive forest management under climate change: a spatially specific synthesis of 125 species for habitat changes and assisted migration over the eastern United States. Forests 10:989
Janowiak MK, DAmato AW, Swanston CW, et al (2018) New England and northern New York forest ecosystem vulnerability assessment and synthesis: a report from the New England climate change response framework project. Northern Research Station, Newtown Square
Jones MC, Cheung WWL (2015) Multi-model ensemble projections of climate change effects on global marine biodiversity. ICES J Mar Sci 72:741–752
Joyce DG, Rehfeldt GE (2013) Climatic niche, ecological genetics, and impact of climate change on eastern white pine (*Pinus strobus* L.): guidelines for land managers. For Ecol Manage 295:173–192
Kaufman L, Rousseeuw PJ (1990) Finding groups in data: an introduction to cluster analysis. Wiley, New York
King JP, Nienstaedt H (1969) Variation in eastern white pine seed sources planted in the lake States. Silvae Genet 18:83–86
Kremer A, Ronce O, Robledo-Arnuncio JJ et al (2012) Long-distance gene flow and adaptation of forest trees to rapid climate change. Ecol Lett 15:378–392
Kuhn M (2008) Building predictive models in R using the caret package. J Stat Soft. https://doi.org/10.18637/jss.v028.i05
Leites LP, Rehfeldt GE, Robinson AP et al (2012a) Possibilities and limitations of using historic provenance tests to infer forest species growth responses to climate change: growth-climate responses. Nat Resour Model 25:409–433
Leites LP, Robinson AP, Rehfeldt GE et al (2012b) Height-growth response to climatic changes differs among populations of Douglas-fir: a novel analysis of historic data. Ecol Appl 22:154–165
Leites LP, Rehfeldt GE, Steiner KC (2019) Adaptation to climate in five eastern North America broadleaf deciduous species: growth clines and evidence of the growth-cold tolerance trade-off. Perspect Plant Ecol, Evol Syst 37:64–72
Little EL (1971) Atlas of United States trees. Conifers and important hardwoods. Miscellaneous Publication, Washington
Loehle C (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. J Biogeogr 25:735–742
Martre P, Wallach D, Asseng S et al (2015) Multimodel ensembles of wheat growth: many models are better than one. Glob Change Biol 21:911–925
Massatti R, Prendeville HR, Larson S et al (2018) Population history provides foundational knowledge for utilizing and developing native plant restoration materials. Evol Appl 11:2025–2039
Matthews TJ, Sadler JP, Kubota Y et al (2019) Systematic variation in North American tree species abundance distributions along macroecological climatic gradients. Glob Ecol Biogeogr 28:601–611
McKenney DW, Pedlar JH, Lawrence K et al (2007) Potential impacts of climate change on the distribution of North American trees. Bioscience 57:939–948
Morgenstern EK (1996) Geographic variation in forest trees. UBC Press, Vancouver
Nadeau S, Godbout J, Lamothe M et al (2015) Contrasting patterns of genetic diversity across the ranges of *Pinus monticola* and *P. strobus*: a comparison between eastern and western North American postglacial colonization histories. Am J Bot 102:1342–1355
Namkoong G (1969) Nonoptimality of local races. In: Proceedings of the 10th Southern Forest Tree Improvement Conference. Texas Forest Service, Texas A&M University Press, College Station, Texas, USA, pp 149–153
O'Connell BM, Conkling BL, Wilson AM, Burrill EA, Turner JA, Pugh SA et al (2017) The forest inventory and analysis database: database description and user guide version 7.0 for Phase 2. U.S. Department of Agriculture, Forest Service, p 830
Pederson N, D'Amato AW, Dyer JM et al (2015) Climate remains an important driver of post-European vegetation change in the eastern United States. Glob Change Biol 21:2105–2110
Pedlar JH, McKenney DW (2017) Assessing the anticipated growth response of northern conifer populations to a warming climate. Sci Rep. https://doi.org/10.1038/srep43881
Pedlar JH, McKenney DW, Aubin I et al (2012) Placing forestry in the assisted migration debate. Bioscience 62:835–842
Peters MP, Iverson LR, Prasad AM, Matthews SN (2019) Utilizing the density of inventory samples to define a hybrid lattice for species distribution models: DISTRIB-II for 135 eastern U.S. trees. Ecol Evol. https://doi.org/10.1002/ece3.5445
Peterson ML, Doak DF, Morris WF (2018) Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. Glob Change Biol 24:1614–1625
Pike C, Potter KM, Berrang P et al (2020) New seed-collection zones for the eastern United States: the eastern seed zone forum. J Forest. https://doi.org/10.1093/jofore/fvaa013
Prasad AM (2015) Macroscale intraspecific variation and environmental heterogeneity: analysis of cold and warm zone abundance, mortality, and regeneration distributions of four eastern US tree species. Ecol Evol 5:5033–5048
Prasad AM (2018) Machine learning for macroscale ecological Niche modeling—a multi-model, multi-response ensemble technique for tree species management under climate change. In: Humphries G, Magness DR, Huettmann F (eds) Machine learning for ecology and sustainable natural resource management. Springer Nature, Switzerland
Prasad AM, Potter KM (2017) Macro-scale assessment of demographic and environmental variation within genetically derived evolutionary lineages of eastern hemlock (*Tsuga canadensis*), an imperiled conifer of the eastern United States. Biodivers Conserv 26:2223–2249
Prasad A, Pedlar J, Peters M et al (2020) Combining US and Canadian forest inventories to assess habitat suitability and

migration potential of 25 tree species under climate change. Divers Distrib. https://doi.org/10.1111/ddi.13078
R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Rehfeldt GE, Jaquish BC (2010) Ecological impacts and management strategies for western larch in the face of climate-change. Mitig Adapt Strateg Glob Change 15:283–306. https://doi.org/10.1007/s11027-010-9217-2
Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA (1999) Genetic responses to climate in pinus contorta: niche breadth, climate change, and reforestation. Ecol Monogr 69:33
Rehfeldt GE, Wykoff WR, Ying CC (2001) Physiologic plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. Clim Change 50:355–376
Rehfeldt GE, Leites LP, Bradley St Clair J et al (2014) Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Clines in growth potential. Forest Ecol Manage 324:138–146
Rehfeldt GE, Leites LP, Joyce DG, Weiskittel AR (2018) Role of population genetics in guiding ecological responses to climate. Glob Change Biol 24:858–868
Rehfeldt GE (1984) Microevolution of conifers in the northern Rocky mountains: a view from common gardens. In: Lanner RM (ed) Proceedings, 8th North American Forest Biology Workshop, 30 July-1 Aug. 1984, Utah State Univ., Logan, Utah, pp 132–146.
Reynolds A, Richards G, de la Iglesia B, Rayward-Smith V (1992) Clustering rules: a comparison of partitioning and hierarchical clustering algorithms. J Math Model Algoritm 5:475–504
Rousseeuw PJ (1987) Silhouettes: a Graphical Aid to the Interpretation and Validation of Cluster Analysis. Computational and Applied Mathematics 20:53–65. https://doi.org/10.1016/0377-0427(87)90125-7
Sebastian-Azcona J, Hacke UG, Hamann A (2018) Adaptations of white spruce to climate: strong intraspecific differences in cold hardiness linked to survival. Ecol Evol 8:1758–1768
Sluder ER, Dorman KW (1971) Performance in the southern Appalachians of eastern white pine seedlings from different provenances. Southeastern Forest Experiment Station, Asheville
Svetnik V, Liaw A, Tong C et al (2003) Random forest: a classification and regression tool for compound classification and QSAR modeling. J Chem Inf Comput Sci 43:1947–1958
Swanston CW, Janowiak MK, Brandt LA et al (2016) Forest Adaptation resources: climate change tools and approaches for land managers, 2nd edn. Northern Research Station, Newtown Square
Thomson A, Parker WH (2008) Boreal forest provenance tests used to predict optimal growth and response to climate change. 1. Jack Pine. Can J for Res 38:157–170
USGCRP (2017) Climate science special report: fourth national climate assessment. In: Wuebbles DJ, Fahey DW, Hibbard KA, Dokken DJ, Stewart BC, Maycock TK (eds) U.S. global change research program, vol 1. IOWA State University, Washington, p 470
Walthert L, Meier ES (2017) Tree species distribution in temperate forests is more influenced by soil than by climate. Ecol Evol 7:9473–9484
Wang T, Hamann A, Yanchuk A et al (2006) Use of response functions in selecting lodgepole pine populations for future climates: lodgepole pine populations for future climates. Glob Change Biol 12:2404–2416
Wang T, Hamann A, Spittlehouse D, Carroll C (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11:e0156720
Wendel GW, Cech F (1976) Six-year results of a white pine seed-source test in West Virginia. USDA, Washington
Wendel GW, Smith HC (1990) *Pinus strobus* L. Eastern white pine. In: Burns RM, Honkala BH (eds) Silvics of North America, vol 1. USDA, Washington
Wiens JA, Stralberg D, Jongsomjit D et al (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. Proc Natl Acad Sci 106:19729–19736
Woudenberg SW, Conkling BL, O'Connell BM, LaPoint EB, Turner JA, Waddell KL (2010) The forest inventory and analysis database: database description and user's manual version 4.0 for Phase 2. Rocky Mountain Research Station, Fort Collins
Young DJN, Blush TD, Landram M et al (2020) Assisted gene flow in the context of large-scale forest management in California, USA. Ecosphere. https://doi.org/10.1002/ecs2.3001
Zhang L, Liu S, Sun P et al (2015) Consensus forecasting of species distributions: the effects of niche model performance and niche properties. PLoS ONE 10:e0120056
Zinck JWR, Rajora OP (2016) Post-glacial phylogeography and evolution of a wide-ranging highly-exploited keystone forest tree, eastern white pine (*Pinus strobus*) in North America: single refugium, multiple routes. BMC Evol Biol. https://doi.org/10.1186/s12862-016-0624-1