Can long-lived species keep pace with climate change? Evidence of local persistence potential in a widespread conifer

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Abstract

Aim: Climate change poses significant challenges for tree species, which are slow to adapt and migrate. Insight into genetic and phenotypic variation under current landscape conditions can be used to gauge persistence potential to future conditions and determine conservation priorities, but landscape effects have been minimally tested in trees. Here, we use Pinus contorta, one of the most widely distributed conifers in North America, to evaluate the influence of landscape heterogeneity on genetic structure as well as the magnitude of local adaptation versus phenotypic plasticity in a widespread tree species.

Location: Western North America.

Methods: We paired landscape genetics with fully reciprocal in situ common gardens to evaluate landscape influence on neutral and adaptive variation across all subspecies of P. contorta.

Results: Landscape barriers alone play a minor role in limiting gene flow, creating marginal geographically-based structure. Local climate determines population performance, with survival highest at home but growth greatest in mild climates (e.g., warm, wet). Survival of two of the three populations tested was consistent with patterns of local adaptation documented for P. contorta, while growth was indicative of plasticity for populations grown under novel conditions and suggesting that some populations are not currently occupying their climatic optimum.

Main Conclusions: Our findings provide insight into the role of the landscape in shaping population genetic structure in a widespread tree species as well as the potential response of local populations to novel conditions, knowledge critical to understanding how widely distributed species may respond to climate change. Geographically based genetic structure and reduced survival under water-limited conditions may make some populations of widespread tree species more vulnerable to local maladaptation and extirpation. However, genetically diverse and phenotypically plastic populations of widespread trees, such as many of the P. contorta populations sampled and tested here, likely possess high persistence potential.
1 | INTRODUCTION

The velocity of anthropogenically driven climate change poses significant challenges for long-lived species, and the longevity of tree species makes them particularly vulnerable to local extirpation. Tree species persistence will depend on rapid adaptation to novel conditions, long-distance dispersal to track ecological niche requirements, or acclimation via plasticity (Aitken et al., 2008). However, rates of both evolutionary change (Etterson & Shaw, 2001) and migration (Davis & Shaw, 2001; de Lafontaine et al., 2018) for many tree species are expected to lag behind the pace of climate change, leaving individuals and ultimately populations, reliant upon plastic responses as they become mismatched with local conditions (Aitken et al., 2008; St Clair & Howe, 2007). Local persistence is most likely in phenotypically plastic and genetically variable populations, as these attributes provide the basis for response to change over both short (i.e., fate of individuals in one generation) and long (i.e., population persistence across generations) timeframes (Benito Garzón et al., 2011; Bontrager & Angert, 2019; Crispo, 2008). Thus, understanding the potential for long-lived tree species to persist through rapid climatic and local environmental change requires insight into the spatial distribution of phenotypic plasticity and genetic variation. This information will be critical to predicting how species distributions may shift with climate change and in determining conservation priorities for at-risk populations.

A species’ ability to respond to environmental change is strongly influenced by the landscape conditions where a given population occurs (Manel et al., 2003), and tree species distributed over heterogeneous landscapes likely consist of populations with highly differentiated responses. Heterogeneity in the distribution of abiotic and biotic factors has the potential to impede gene flow by creating geographic barriers or a matrix of unsuitable habitat across which dispersal cannot occur (Sork et al., 1999; Wang & Bradburd, 2014). On one hand, isolated populations may be able to adapt to local conditions more rapidly because non-adapted alleles no longer flow into the population (Lind et al., 2018). Such populations may also lack the genetic variation to respond to novel environmental selection, thus increasing the risks of local extirpation (Aitken et al., 2008). When landscape heterogeneity does not impede gene flow, selection might instead favour increased plasticity or a generalist phenotype. Species distributed across complex, climatically variable landscapes are, consequently, subjected to one of two divergent evolutionary pathways, resulting in either specialist populations that are highly locally adapted or the evolution of highly plastic generalists that tolerate a wide range of conditions (Frank et al., 2017).

Widespread tree species provide a natural experiment for evaluating population response to landscape heterogeneity and assessing persistence potential to rapidly changing conditions, but the effect of the landscape has been minimally tested in tree species (Bothwell et al., 2017). Evidence of pollen-mediated gene flow over broad spatial scales (e.g., ~100 km in Pinus sylvestris, Robledo-Arnuncio, 2011; up to 3,000 km in Pinus banksiana, Campbell et al., 1999) suggests that many widely dispersed, wind-pollinated tree species have the potential to overcome the landscape conditions known to limit gene flow in geographically-restricted plant species (Grossenbacher et al., 2014). Despite the potential for high connectivity, geographically based phenotypic variation is common in tree species (Savolainen et al., 2007). Spatially structured phenotypic variation in the face of high gene flow may reflect local adaptation in response to selection imposed by the environment (i.e., role of genetics, environment, and their interaction) or may be a product of high phenotypic plasticity with no heritable genetic basis (i.e., based on environment alone) (Benito Garzón et al., 2011; Kawecki & Ebert, 2004). While plasticity is likely to decrease extirpation risk under rapid climate change if it provides a mechanism by which individuals can phenotypically shift towards a new local optimum, it may also create vulnerability if the plastic response is suboptimal or lags behind local environmental change and reduces the probability for directional selection to support local persistence (Chevin et al., 2013; Chevin & Hoffmann, 2017; Ghalambor et al., 2007). Without insight into the influence of landscape complexity on genetic and phenotypic variability within and among populations, we lack the ability to determine the potential of tree species to evolve in response to ongoing, rapid climate change and thus the ability to identify conservation priorities for forest ecosystems.

Pinus contorta (Douglas Ex. Louden) is one of the most widely distributed tree species in North America, and its occurrence across a topographically and climatically heterogeneous landscape makes it a consummate species for quantifying the influence of landscape complexity on genetic and phenotypic variation. For this reason, P. contorta is one of the most well-studied conifers in biogeographical (e.g., Strong, 2010; Wheeler & Critchfield, 1985; Wheeler & Gurley, 1982a, 1982b), forest productivity (e.g., Chui et al., 2006; McLane et al., 2011; Rehfelt et al., 1999; Wang et al., 2010) and evolutionary (e.g., Fazekas & Yeh, 2006; Godbout et al., 2008; Liepe et al., 2016; Mahony et al., 2020; Yang & Yeh, 1995) research on forest tree species. However, little is known about the influence of climatically and topographically heterogeneous landscapes on range-wide population genetic structure and population response to novel landscape conditions in this and other widely distributed tree species—information critical to evaluating local population persistence under future conditions.

Here, we use P. contorta to evaluate—(a) the degree to which landscape heterogeneity influences range-wide genetic connectivity
and variability and (b) the magnitude of local adaptation versus phenotypic plasticity in climatically differentiated environments. We paired landscape genetics with a fully reciprocal in situ common garden study to ask: (a) what are the patterns of genetic differentiation across the topographically and climatically heterogeneous range of this widespread tree species? (b) is there evidence of local adaptation in fitness components such as survival and growth? and (c) what is the degree of phenotypic plasticity in fitness components? Our study provides a unique perspective by pairing a range-wide landscape genetics assessment with a fully reciprocal common garden trial to quantify the influence of landscape complexity on genetic and phenotypic variation in a widespread tree species. Additionally, rather than focusing on well-researched subspecies *latifolia*, the most widespread and economically important subspecies, we sampled and tested variation across the range of the species and including all subspecies. Our research provides insight into the role of the landscape in shaping population genetic structure in a widespread tree species as well as the potential response of local populations to novel environmental conditions, knowledge critical to understanding how widely distributed species may respond to rapid climate change.

2 | METHODS

2.1 | Study species

*Pinus contorta* occurs over 33 degrees of latitude from Baja California, Mexico, to the Yukon Territory, Canada, and from sea level along the Pacific to over 3,500 m in the Sierra Nevada of California, USA (Critchfield & Little, 1927; Wheeler & Critchfield, 1985; Wheeler & Guries, 1982; Figure 1). The species is divided into four subspecies (ssp. *bolanderi*, *contorta*, *latifolia*, *murrayana*; Critchfield, 1957, Figure 1). The most widespread subspecies (*contorta*, *latifolia*, *murrayana*) are isolated from one another by ice fields, deserts, and mountain ranges, while narrowly distributed *bolanderi* occurs only in the edaphically unique dwarf forest ecosystem of Mendocino, Mexico.
TABLE 1  Geographic descriptions of each *Pinus contorta* sampling location by subspecies and region

| Subspecies   | Region                        | Sampling Location          | Code   | Site Ownership                      | Location          | Samples (N = 508) | Latitude | Longitude | Average elevation (m) |
|--------------|-------------------------------|-----------------------------|--------|-------------------------------------|-------------------|-------------------|----------|-----------|----------------------|
| ssp. murrayana | Sierra Nevada               | Wellman’s Divide            | *murrayana* 1 | San Jacinto State Park             | California        | 10                | 33.7991 | -116.6746 | 2,956                             |
|              |                               | Hidden Lake Drive           | *murrayana* 2 | San Jacinto State Park             | California        | 10                | 33.8019 | -116.6422 | 2,651                             |
|              |                               | Onyx Peak                   | *murrayana* 3 | San Bernardino National Forest     | California        | 10                | 34.1953 | -116.7126 | 2,743                             |
|              |                               | Champion                    | *murrayana* 4 | San Bernardino National Forest     | California        | 10                | 34.2190 | -116.9732 | 2,307                             |
|              |                               | Dawson Saddle               | *murrayana* 5 | Angeles National Forest            | California        | 10                | 34.3678 | -117.8034 | 2,415                             |
|              |                               | Big Meadow                  | *murrayana* 6 | Sequoia National Forest            | California        | 10                | 35.8872 | -118.3429 | 2,372                             |
|              |                               | Horeshoe Meadows            | *murrayana* 7 | Inyo National Forest               | California        | 10                | 36.4486 | -118.1700 | 3,049                             |
|              |                               | Crooked Meadows             | *murrayana* 8 | Inyo National Forest               | California        | 10                | 37.8424 | -118.8626 | 2,656                             |
|              |                               | Tuolumne Meadows            | *murrayana* 9 | Yosemite National Park             | California        | 10                | 37.8715 | -119.3731 | 2,600                             |
|              |                               | Levitt Meadows              | *murrayana* 10 | Humboldt-Toiyabe National Forest  | California        | 10                | 38.3088 | -119.5870 | 2,523                             |
| ssp. bolanderi | Coastal California and Oregon | Luther Pass                 | *bolanderi* 11 | Tahoe National Forest             | California        | 10                | 38.7870 | -120.0019 | 2,212                             |
|              |                               | Russian Gulch              | *bolanderi* 1 | California SP                     | California        | 10                | 39.3111 | -123.7600 | 132                               |
|              |                               | Van Damme Pygmy            | *bolanderi* 2 | California SP                     | California        | 10                | 39.2631 | -123.7376 | 183                               |
|              |                               | Van Damme                  | *bolanderi* 3 | California SP                     | California        | 10                | 39.2658 | -123.7500 | 160                               |
| ssp. contorta | Southeast Alaska            | Spring Ranch                | *contorta* 1 | California SP                     | California        | 10                | 39.2857 | -123.7959 | 44                                |
|              |                               | Patrick’s Point            | *contorta* 2 | California SP                     | California        | 10                | 41.1397 | -124.1606 | 52                                |
|              |                               | Tolowa Dunes               | *contorta* 3 | California SP                     | California        | 10                | 41.7964 | -124.2232 | 28                                |
|              |                               | Port Oxford                | *contorta* 4 | Oregon SP                         | Oregon            | 10                | 42.7392 | -124.5107 | 151                               |
|              |                               | Sand Dunes                 | *contorta* 5 | Siuslaw NF                        | Oregon            | 10                | 44.0633 | -124.1198 | 7                                 |
|              |                               | Old Sitka                  | *contorta* 6 | Tongass NF                        | Alaska            | 10                | 57.1286 | -135.3687 | 45                                |
|              |                               | Blanket Bog                | *contorta* 7 | Tongass NF                        | Alaska            | 10                | 56.6387 | -132.6610 | 66                                |
|              |                               | Bay Bog                    | *contorta* 8 | Tongass NF                        | Alaska            | 10                | 58.0588 | -135.0962 | 21                                |
|              |                               | Jumbo Bog                  | *contorta* 9 | City and Borough of Juneau        | Alaska            | 10                | 58.2615 | -134.3864 | 203                               |
|              |                               | Sundown Bog                | *contorta* 10 | City and Borough of Juneau        | Alaska            | 15                | 58.3340 | -134.5941 | 23                                |
|              |                               | FAA Bog                    | *contorta* 11 | State of Alaska                   | Alaska            | 10                | 58.3358 | -134.5622 | 50                                |
|              |                               | Dundas Bay                 | *contorta* 12 | Glacier Bay National Park         | Alaska            | 5                 | 58.3253 | -136.2032 | 0                                 |
|              |                               | Dick’s Arm                 | *contorta* 13 | Glacier Bay National Park         | Alaska            | 10                | 58.2301 | -136.6287 | 0                                 |

(Continues)
### TABLE 1 (Continued)

| Subspecies       | Region                      | Sampling Location | Code   | Site Ownership          | Location                        | Samples (N = 508) | Latitude  | Longitude | Average elevation (m) |
|------------------|-----------------------------|-------------------|--------|-------------------------|--------------------------------|-------------------|-----------|------------|----------------------|
| ssp. *latifolia* | Yukon to Central British Columbia | Alcan Highway     | *latifolia* 1 | Yukon Forest Management  | Yukon Territory                 | 15                | 60.8528   | -135.7060 | 670                  |
|                  |                             | Mt McIntyre*a     | *latifolia* 2 | Yukon Forest Management  | Yukon Territory                 | 10                | 60.6561   | -135.2151 | 1,213                |
|                  |                             | Canol Road*a      | *latifolia* 3 | Yukon Forest Management  | Yukon Territory                 | 20                | 60.5669   | -133.0992 | 1,351                |
|                  |                             | Pine Flats        | *latifolia* 4 | Yukon Forest Management  | Yukon Territory                 | 10                | 60.1398   | -130.2309 | 866                  |
|                  |                             | Edziza            | *latifolia* 5 | Ministry of Forests      | British Columbia                | 10                | 57.2055   | -130.2252 | 789                  |
|                  |                             | Smithers Community Forest | *latifolia* 6 | Ministry of Forests      | British Columbia                | 10                | 54.7370   | -127.2562 | 865                  |
|                  | Rocky Mountains             | Columbia Icefields| *latifolia* 7 | Jasper National Park     | Alberta                         | 10                | 52.3569   | -117.3489 | 1569                  |
|                  |                             | Glacier Lake      | *latifolia* 8 | Banff National Park      | Alberta                         | 10                | 51.9731   | -116.7596 | 1,456                |
|                  |                             | Kootenay          | *latifolia* 9 | Kootenay National Park   | Alberta                         | 10                | 50.8809   | -116.0481 | 1,182                |
|                  |                             | Flathead          | *latifolia* 10 | Flathead National Forest | Montana                        | 11                | 48.4572   | -113.6403 | 1,620                |
|                  |                             | Judith Basin      | *latifolia* 11 | Helena National Forest   | Montana                        | 10                | 46.3211   | -111.8512 | 2,215                |
|                  |                             | Lewis & Clark     | *latifolia* 12 | Lewis and Clark National Forest | Montana                   | 6                 | 46.8209   | -110.4757 | 1982                  |
|                  |                             | Lemhi            | *latifolia* 13 | Bitterroot National Forest | Idaho                      | 11                | 45.4771   | -113.8847 | 2040                  |
|                  |                             | Idaho            | *latifolia* 14 | Nez Perce National Forest | Idaho                      | 3                 | 45.2690   | -115.0195 | 1993                  |
|                  |                             | Custer           | *latifolia* 15 | Salmon-Challis National Forest | Idaho                     | 8                 | 44.4960   | -114.5536 | 2,640                |
|                  |                             | Valley           | *latifolia* 16 | Payette National Forest  | Idaho                          | 11                | 44.6545   | -115.8714 | 1,925                |
|                  |                             | Fremont          | *latifolia* 17 | Targhee National Forest  | Idaho                          | 6                 | 44.3423   | -111.6920 | 2,056                |
|                  |                             | Bunsen Peak      | *latifolia* 18 | Yellowstone National Park | Wyoming                     | 12                | 44.9218   | -110.7195 | 2,194                |
|                  |                             | Summit           | *latifolia* 19 | Wasatch National Forest  | Utah                           | 11                | 40.9192   | -110.6473 | 3,090                |
|                  |                             | Eagle            | *latifolia* 20 | White River National Forest | Colorado                 | 7                 | 39.6099   | -106.4021 | 2,868                |
|                  |                             | Gunnison         | *latifolia* 21 | Gunnison National Forest | Colorado                       | 5                 | 38.6162   | -106.5003 | 3,109                |
|                  |                             | Larimer          | *latifolia* 22 | Arapaho-Roosevelt National Forest | Colorado | 12                | 40.3772   | -105.3533 | 2,720                |
|                  | Black Hills                 | Tillson Creek    | *latifolia* 23 | Black Hills National Forest | South Dakota                | 10                | 44.1859   | -103.8353 | 1,965                |
|                  |                             | Nahant School    | *latifolia* 24 | Black Hills National Forest | South Dakota                | 10                | 44.1989   | -103.7740 | 1,786                |

Note: Bold rows indicate seed lots (i.e., populations) tested in common garden study.

*a*Subspecies further classified as var. *yukonensis* (Strong, 2010)

*b*Samples collected via the USFS Forest Inventory & Analysis Program.
2.2 | Population and landscape genetics

2.2.1 | Sampling and study design

Potential sampling locations were identified using occurrence data from U.S. Forest Service Forest Inventory & Analysis (FIA, Glenn Christensen and John D. Shaw, personal communication) and British Columbia Ministry of Forests Biogeoclimatic Ecosystem Classification (Will MacKenzie, personal communication) records. Sampling locations were stratified into six regions that represent major physiographic divisions of western North America based on landform and landscape features (Fenneman, 1917): (a) Sierra Nevada, California, (b) Coastal California and Oregon, (c) Southeast Alaska, (d) Yukon Territory to central British Columbia, (e) Rocky Mountains (Alberta to Colorado) and (f) Black Hills, South Dakota (Table 1).

Twenty sampling locations were randomly selected from occurrences in regions one through four. In region four, we included two sampling locations representing proposed variety yukonensis (Strong, 2010), and we avoided sampling across much of central and southern British Columbia where commercial plantations of *latifolia* are common. Some region five samples of *latifolia* were provided by the FIA program (n = 13, Table 1), with additional sampling locations selected to fill in gaps not sampled by FIA (n = 3). In region six, the two known populations were sampled. Ultimately, 51 locations (Table 1, Figure 1) were sampled. At each sampling location, one gram of current-year needles was collected from 10 individuals (>50 m apart) and preserved using silica gel desiccant. Additionally, we recorded the presence/absence of serotinous cones and tree form as one of four categories (1—short stature (<3 m height), twisted bole, 2—short stature, straight bole, 3—small tree (>3 m height), small diameter (<50 cm), or 4—tall tree, large diameter (>50 cm). Given the geographic scope of *P. contorta*’s distribution, we prioritized sampling a greater number of locations rather than more individuals per location, providing the power necessary to detect geographic patterns in genetic structure (Eckert et al., 2008).

2.2.2 | DNA extraction and microsatellite amplification

Total genomic DNA was extracted using DNeasy plant kits (Qiagen) at the U.S. Department of Agriculture National Forest Genetics Laboratory. Of 15 highly polymorphic SSR markers initially tested (Lesser et al., 2012), nine amplified across all samples (Appendix Table S1). Loci were amplified in multiplex under identical conditions, with locus-specific primers 5’-tailed with universal primer sequences (as described by Missiaggia & Grattapaglia, 2006, see Appendix S1 for details). PCR products were separated on a 3730xl Genetic Analyzer (Life Technologies), and peak sizes were determined using GeneMarker v2.2 (SoftGenetics LLC). Samples were scored three times to verify peaks and resolve conflicts.

2.2.3 | Genetic diversity and differentiation

After screening and adjusting for null alleles, genotyping errors, and deviations from Hardy–Weinberg Equilibrium (see Appendix S2 for details), we calculated pairwise *F*<sub>ST</sub> (i.e., the inbreeding coefficient or proportion of genetic variance contained within a subpopulation relative to total genetic variance) and the following parameters, averaged across loci, for each sampling location using GenAlEx (Peakall & Smouse, 2012): percent polymorphic loci (PPL), allelic richness (*N*<sub>A</sub>), number of effective alleles (*N*<sub>E</sub>), expected heterozygosity (*H*<sub>E</sub>), unbiased expected heterozygosity (*uH*<sub>E</sub>) and inbreeding levels (*F*<sub>IS</sub>). We used the “pegas” package in R (Paradis, 2010; R Core Team, 2019) to quantify population differentiation within and among sampling locations and subspecies using a hierarchical analysis of molecular variance (AMOVA).

2.2.4 | Population clustering

We estimated the number of population genetic clusters (*K*) across the range of *P. contorta* using two approaches: (a) clustering based on genetic information alone and (b) integrating genetic, geographic and phenotypic information to incorporate characteristics typically used in subspecies delineations. We first used *Structure* 2.3.2 (Falush et al., 2007; Pritchard et al., 2000) to assign individuals to genetic clusters without grouping them a priori based on geographic location or phenotype; model parameters were set according to updated model run and publishing guidelines (Gilbert et al., 2012; Janes et al., 2017; See Appendix S3 for details). Then, we assessed the role of geographic location (i.e., latitude, longitude) and phenotypic variation (i.e., field-collected data, detailed above) in determining population structure using both uncorrelated and correlated models in “Geneland” 4.0.6 (Guillot et al., 2005, 2012). Uncorrelated models assume allele frequencies vary among populations. Correlated models, conversely, assume allele frequencies are similar among populations (e.g., rare alleles in certain populations are also rare in others), which can be more powerful in identifying subtle genetic divisions. See Appendix S3 for methodologies on population assignment and selection of *K*.

2.2.5 | Landscape genetics

Pairwise genetic distances among sampling locations were calculated using conditional genetic distance (cGD), where genetic distances
are based on genetic covariance and estimated from graph distances as the shortest path connecting pairs via population graph topology (Dyer et al., 2010). Pairwise cGD is more sensitive than traditional metrics (e.g., $F_{ST}$), accounting for both direct and indirect connectivity (Dyer et al., 2010). We estimated cGD using the "GStudio" package in R (Dyer, 2016).

We tested for range-wide genetic connectivity by comparing pairwise cGD to pairwise spatial and environmental distances, testing hypotheses of isolation by distance (IBD), barrier (IBB), resistance (IBR) and environment (IBE). For tests of IBD, we calculated pairwise Euclidean geographic distance (km) using Vincenty ellipsoid distance in the "geosphere" package in R (Hijmans et al., 2017). For IBB, we created a binary matrix representing hypothesized barriers to gene flow: Central Valley of California separating coastal and mountain populations, Juneau Icefield and Coast Mountain Range separating coastal Alaska and interior Yukon and British Columbia populations, and Great Basin-Intermountain West separating Sierra Nevada and Rocky Mountain populations. Tests of IBR were performed using a resistance map derived from habitat suitability modelling, representing landscape resistance to movement among populations (Appendix Figure S1). IBE was evaluated using among-population climate dissimilarities irrespective of spatial connectivity, calculated as pairwise Euclidean distances based on the first three principal components from an analysis of seven bioclimatic variables ("prcomp" function in R). See Appendix S4 for detailed methodologies.

We used multiple approaches to evaluate which hypotheses (IBD, IBB, IBR, IBE) best describe observed patterns of genetic distance. First, we used Mantel and partial Mantel tests in the R package "vegan" (Oksanen et al., 2018) under a reciprocal causal modelling framework (Cushman et al., 2013) to evaluate relative support as the difference between reciprocal partial Mantel tests for each hypothesis. Because Mantel and partial Mantel tests are criticized for their tendencies towards inflated type I error rates (Guillot & Rousset, 2013), we also implemented multiple matrix regression with randomization (MMRR, Wang, 2013) in the R package "ecodist" (Goslee & Urban, 2007) to test for consistency of results, comparing all possible combinations of hypotheses to identify the models with the greatest support.

### 2.3 Common gardens

Cones from 10 mature (>30 cm diameter-at-breast-height) individuals at each of nine sampling locations were opportunistically collected in Fall 2010, but seed viability limited testable populations to only three sources (bolded locations in Table 1). Fortunately, one collection was viable from each of the three main contrasting climates across which $P. contorta$ is distributed: warm and wet ($contorta\,11$, coastal southeast Alaska), cold and dry ($latifolia\,22$, southern Rocky Mountains of Colorado), and warm and dry ($murrayana\,11$, central Sierra Nevada Mountains of California) (Figure 3a,b; climate details in Appendix S5).

Seeds were sown in May 2011, and seedlings were grown under non-limiting greenhouse conditions and winter-hardened prior to planting (See Appendix S6 for details). In June 2012, seedlings were transferred to three field common garden locations (Figure 1), and
FIGURE 3 Climate and plant performance from Pinus contorta reciprocal common garden transplant experiment using subspecies contorta (home environment = Alaska; green squares), latifolia (home environment = Colorado; purple triangles), and murrayana (home environment = California; orange circles). Subspecies’ responses suggest phenotypic plasticity and local adaptation. (a) Annual precipitation and mean annual temperature (1985–2017). Data are shown as mean ± 1 SE for each garden location. (b) Annual cumulative climatic water deficit from 1985–2017 for each garden location. Dashed vertical line at year 2012 represents the timing of garden installation. (a, b) Climate data are from TerraClimate (Abatzoglou et al. 2018). (c–e) Fitness components for seedlings from three source populations planted in 2012 into three reciprocal common gardens. (c) Per cent of seedlings alive in 2016, explained by garden (E, p < .001), seed source (G, p = .01), and a garden-by-source interaction (GxE, p < .001). (d) Seedling basal diameter growth (mm) from 2012 to 2016, which had a significant effect of G (p < .001). (e) Seedling height growth (cm) from 2012 to 2016, which was affected by E (p < .001) and GxE (p = .03). (d, e) Data are shown as population-level means (±1 SE). For panels (c)–(e), support for local adaptation is indicated when there is greater performance of a local genotype compared to a foreign genotype within a single site or greater performance of a genotype at home compared to its performance when planted away (G), while plasticity is indicated when genotypes perform differently across environments (i.e., lines are not flat, E & GxE). Crossing of reaction norm lines indicates that performance of a genotype depends on the environment.

40 seedlings of each subspecies (N = 120 per garden, 360 total) were planted in a fully reciprocal, randomized design in home and foreign locations. From 2012 to 2016, we tracked survival and sampled basal diameter (mm) and height (cm). We calculated growth as the 2012–2016 difference in height or basal diameter. We used generalized linear models to assess genetic (G), environment (E) and genetic-by-environment interaction (GxE) effects on survival and growth. We modelled fitness components (survival through 2016, diameter growth and height growth) as a function of height at time of planting, E (garden, fixed effect), G (seed source = subspecies, fixed effect) and GxE interaction using the glm function in R. We based our interpretation of performance responses on the definition of local adaptation outlined in Kawecki and Ebert (2004) in which local versus foreign patterns are best indicative of local adaptation. Here, model support for local adaptation is indicated by a GxE interaction such that there is greater performance of a local genotype compared to a foreign genotype within a single site or greater performance of a genotype at home compared to its performance when planted away. Plasticity is indicated by performance response due to a garden effect, in our case the influence of E alone as well as the GxE interaction. We specifically included starting height in our analysis to account for any influence of greenhouse conditions and initial growth on in situ growth and survival. We additionally fit alternative models that included climate transfer distances, calculated as the difference
### TABLE 2
Mean (±standard error) sampling location and subspecies descriptive statistics at nine microsatellite loci for 51 *Pinus contorta* sampling locations from California, USA to the Yukon Territory, Canada

| Subspecies          | Sampling Location       | N  | PPL   | N_s | N_e | H_e    | uH_e  | F Index |
|---------------------|-------------------------|----|-------|-----|-----|--------|-------|---------|
| **Within murrayana**|                         |    |       |     |     |        |       |         |
| ssp. murrayana      | Wellman's Divide        | 10 | 100   | 4.1 | 2.9 | 0.50   | 0.53  | 0.19    |
|                     | Hidden Lake Drive       | 10 | 90    | 4.2 | 2.7 | 0.45   | 0.47  | 0.05    |
|                     | Onyx Peak               | 10 | 100   | 4.4 | 2.9 | 0.51   | 0.54  | 0.06    |
|                     | Champion                | 10 | 90    | 5.1 | 3.3 | 0.54   | 0.57  | 0.14    |
|                     | Dawson Saddle           | 10 | 100   | 5.0 | 2.8 | 0.58   | 0.62  | 0.28    |
|                     | Big Meadow              | 10 | 100   | 3.9 | 2.0 | 0.41   | 0.43  | 0.14    |
|                     | Horeshoe Meadows        | 10 | 100   | 4.7 | 2.7 | 0.57   | 0.60  | 0.05    |
|                     | Crooked Meadows         | 10 | 100   | 5.3 | 3.5 | 0.55   | 0.58  | 0.02    |
|                     | Tuolumne Meadows        | 10 | 100   | 4.6 | 3.2 | 0.49   | 0.51  | 0.11    |
|                     | Levitt Meadows          | 10 | 100   | 4.7 | 3.1 | 0.55   | 0.58  | 0.12    |
|                     | Luther Pass             | 10 | 100   | 4.1 | 2.5 | 0.54   | 0.58  | 0.03    |
| **Within bolanderi**|                         | 30 | 93±4  | 4.1 | 2.6 | 0.46   | 0.49  | 0.02    |
| ssp. bolanderi      | Russian Gulch           | 10 | 80    | 3.9 | 2.5 | 0.45   | 0.47  | 0.00    |
|                     | Van Damme Pygmy         | 10 | 90    | 4.1 | 2.7 | 0.45   | 0.48  | 0.11    |
|                     | Van Damme               | 10 | 90    | 4.2 | 2.6 | 0.48   | 0.51  | 0.05    |
| **Within contorta** |                         | 130| 92±2  | 4.2 | 2.7 | 0.51   | 0.54  | 0.03    |
| ssp. contorta       | Alcan Highway           | 15 | 90    | 4.8 | 2.7 | 0.46   | 0.48  | 0.20    |
|                     | Mt McIntyre             | 10 | 100   | 5.2 | 3.3 | 0.58   | 0.62  | 0.17    |
|                     | Canol Road              | 20 | 100   | 4.3 | 2.8 | 0.55   | 0.58  | 0.21    |
|                     | Pine Flats              | 10 | 90    | 5.4 | 3.9 | 0.58   | 0.62  | 0.22    |
|                     | Edziza                  | 10 | 100   | 4.9 | 3.2 | 0.58   | 0.61  | 0.02    |
|                     | Smithers Community Forest| 10  | 100  | 5.3 | 3.8 | 0.60   | 0.64  | 0.06    |
|                     | Columbia Icefields      | 10 | 100   | 3.9 | 2.1 | 0.46   | 0.50  | 0.04    |
|                     | Glacier Lake            | 10 | 100   | 5.8 | 3.4 | 0.56   | 0.60  | 0.07    |
|                     | Windermere Kootenay     | 10 | 100   | 5.3 | 3.7 | 0.58   | 0.61  | 0.04    |
|                     | Flathead                | 11 | 90    | 4.9 | 3.5 | 0.59   | 0.63  | 0.29    |
|                     | Judith Basin            | 10 | 100   | 4.2 | 2.6 | 0.54   | 0.57  | 0.14    |
|                     | Lewis & Clark           | 6  | 70    | 3.4 | 2.3 | 0.40   | 0.44  | 0.15    |
|                     | Lemhi                   | 11 | 100   | 5.4 | 4.1 | 0.59   | 0.62  | 0.16    |
|                     | Idaho                   | 3  | 70    | 2.4 | 2.0 | 0.40   | 0.47  | 0.03    |
|                     | Custer                  | 8  | 90    | 4.1 | 2.7 | 0.50   | 0.54  | 0.08    |

(Continues)
between climate in the garden location and climate in the seed source location (mean annual precipitation, mean annual temperature, mean annual climatic water deficit), as predictors. We used AIC for model comparison. The survival model used a binomial distribution (logit link), and the growth models used a Gaussian distribution (identity link). Statistical significance ($p < 0.05$) was calculated using ANOVA with chi-squared (survival) and $F$-statistics (growth), and pseudo-$R^2$ values were estimated using the variance-function method in R package "rsq" (Zhang, 2018).

### 3 RESULTS

#### 3.1 Population genetic variation and variance partitioning

Nine markers successfully amplified across samples from 50 sampling locations and were highly polymorphic (mean = 95% ± 1 standard error (SE), Table 2). The mean inbreeding estimate ($F_{st}$) was 0.08 (±0.02 SE, Table 2), which is in line with estimates of high within-population genetic diversity estimates in other conifer species (see Hamrick, 2004). A total of 150 alleles were identified across the nine loci, with $N_A$ per locus ranging from 7 (PIC04 & PIC07) to 27 (locus PIC077) and $N_s$ per sampling location ranging from 2.4 to 5.8 (Table 2). Mean $uH_e$ was 0.55 (±0.01 SE) within sampling locations and 0.56 (±0.04 SE) among subspecies. Pairwise $F_{st}$ ranged from 0.042 to 0.191 (excluding uniquely high contorta 9 pairwise comparisons), with the contorta 12, latifolia 12 and murrayana 11 sampling locations driving the highest pairwise values (Appendix Table S2).

AMOVAs revealed that 88% of genetic diversity is attributable to variation within sampling locations (Appendix Table S3). A moderate, but significant ($p < .001$), portion of population structure resided among sampling locations (12%), and hierarchical analyses indicated that more variation resided among sampling locations (10%) than among subspecies (2%) or regions (2%). All test strata were significant at $p < .001$. Regional analyses were consistently similar to subspecies-level analyses so were not considered further.

#### 3.2 Population clustering

Through Structure analyses, we identified four genetic clusters ($K = 4$) as the most likely division of population structure (Figure 2a & Appendix Figures S2–S3). Admixture was high among sampling locations, and this was reflected in cluster assignment. However, geographic structuring of clusters was apparent among subspecies (Figure 2a). We explored the possibility of hierarchical clustering beyond the four clusters, but there was no further geographically coherent substructure (Figures S4–S5). All bolanderi and the adjacent contorta sampling locations ($n = 4$) clustered together, with >65% probability of membership to a single cluster (Cluster 1, Figure 2a). Only one sampling location from murrayana was dominated by a single cluster (Cluster 2, >65%, Figure 2a), while three locations had the highest probability of membership to this same cluster (Cluster 2, >50%). Coastal California and Oregon contorta contained mixed membership across all clusters, but Alaska contorta were dominated by a single cluster (Cluster 4, 50% of locations with >65% probability of membership, Figure 2a). Widely distributed latifolia showed marked admixture, with strong contribution from Cluster 3 in some sampling locations but no cluster dominating membership (Figure 2a). The conspicuous lack of genetic clustering suggests widespread gene flow across the contiguous portions of P. contorta’s distribution but also indication of barriers to connectivity for the coastal portions of the range (bolanderi and contorta sampling locations, Figure 2a) and some isolation at the southern extent of murrayana.
TABLE 3 Relative support matrix from reciprocal causal modelling optimization testing potential landscape influence against Pinus contorta genetic distances, following Bothwell et al., 2017

|       | IBB | IBE | IBD | IBR |
|-------|-----|-----|-----|-----|
| IBB   | 0   | 0.18| 0.34| 0.16|
| IBE   | -0.18| 0  | 0.23| 0.00|
| IBD   | -0.34| -0.23| 0 | -0.18|
| IBR   | -0.16| 0.00| 0.18| 0 |

No <del author="Sarah M Bising" command="Delete" timestamp="1604959680386" title="Deleted by Sarah M Bising on 11/9/2020, 2:08:00 PM" class="reU3">t</del>e: In reciprocal causal modelling, relative support represents the difference between reciprocal partial Mantel coefficients for all pairs of hypothesized landscape influences. Specifically, each cell is calculated as: (genetic distance - row model) - (genetic distance - column model) | row model). IBB = isolation by barrier, IBE = isolation by environment, IBR = isolation by distance, and IBD = isolation by resistance. In our analysis, IBB was fully supported (bolded values) independent of all other hypotheses, which is indicated by the IBB row containing all positive values and the IBB column containing all negative values. IBD exhibited no independent partialling out the effects of landscape heterogeneity. See Appendix Table S5 for detailed Mantel and Partial Mantel results.

**GEneLAnd** yielded different clustering under both uncorrelated (K = 2, Figure 2b) and correlated (K = 9, Figure 2c) allele frequency models. Uncorrelated clusters (K = 2, Figure 2b) roughly divide the species’ range by the Canadian & US Northern Rocky Mountains in which all murrayana, southern latifolia and contorta clustered as Cluster 1 (Figure 2b). In this model, groupings of bolanderi and contorta in Mendocino, CA, clustered with northern latifolia, which corresponds with sampling locations possessing a higher probability of membership to **STRUCTURE** Cluster 1 (Figure 2a,b). Pairwise FST, for the two clusters was 0.02, indicating high admixture and low between-cluster differentiation. Correlated model clusters (K = 9, Figure 2c) generally match ecoregions of western North America, with, for example, the Great Continental Divide splitting sampling locations into western versus eastern clusters in Idaho and Montana (Figure 2c). This model also identified subclusters within each subspecies, where latifolia was divided into six genetic clusters (Figure 2c). Pairwise FST among clusters ranged from a low of 0.01 between clusters 1 and 6 to a high of 0.09 between clusters 1 and 3. GEneLAnd results also suggest high gene flow with geographic substructure for the correlated model alone. **STRUCTURE** cluster assignment and correlated GEneLAnd models indicate that populations tested in the common garden trial have a high probability of assignment to different clusters (or cluster dominance), while the uncorrelated GEneLAnd model assigns these three sources to a single cluster (Figures 2a–c).

### 3.3 | Landscape genetics

All analyses using pairwise cGD (Appendix Table S4) identified isolation by barrier (IBB) as the strongest predictor of genetic differentiation (Appendix Table S5). The relative support matrix (Table 3), calculated from reciprocal partial Mantel coefficients, shows that IBB was supported independently of all alternative hypotheses (positive values across IBB row), while no other hypotheses were supported after accounting for IBB (negative values across IBB column). The strongest single predictor of genetic variation was IBB (Mantel’s r = 0.268, p < .001) even after accounting for isolation by resistance (IBR, Mantel’s r = 0.207, p < .001), environment (IBD, Mantel’s r = 0.200, p < .001) and distance (IBD, Mantel’s r = 0.273, p < .001). Although IBE and IBR explained genetic variation when considered alone (IBE: Mantel’s r = 0.183, p < .001; IBR: Mantel’s r = 0.180, p = .01), these landscape characteristics were no longer significant after accounting for IBB (p > .05). There was no support for IBD (Mantel’s r = 0.041, p > .16).

Results from complementary MMR models (Appendix Table S6) also identified IBB as the strongest predictor of genetic variation (R² = 0.07, p < .001), followed by IBR (R² = 0.03, p < .001) and IBE (R² = 0.03, p = .01), while IBD was non-significant (R² = 0.002, p > .34). Adding additional predictors to the IBB model resulted in slight increases in explanatory power (from R² = 0.07 to R² = 0.08), but IBB was the only significant predictor in all models in which it was included.

### 3.4 | Common gardens

We found significant variation in fitness components (survival, basal diameter, and height), with populations displaying responses indicative of local adaptation for some genotypes and phenotypic plasticity across all genotypes in the three climatically differentiated garden (Figures 3c–e). Models including garden and seed source location as categorical predictors performed better than models that included continuous climate transfer distances (ΔAIC > 4), so climate models were not considered further. Seedling survival was driven by E (DF = 2, Chi² = 168.7; p < .001), G (DF = 2, Chi² = 10.3; p = .01) and a GxE interaction (DF = 4; Chi² = 75.8; p < .001), with an estimated pseudo-R² of 63.3%, and was not predicted by starting height (DF = 1; Chi² = 1.4; p = .24). Each seed source had the highest survival at its local site (consistent with the local-foreign criterion for local adaptation) and highest absolute survival in the contorta garden (inconsistent with the home-away criterion for local adaptation but showing strong plasticity) (Figure 3c), where 98% of contorta and latifolia and 90% of murrayana survived to 2016 in the murrayana garden, which had the highest climate water deficit over the sampling period (Figure 3b), only local murrayana trees survived to 2016.

Seedling basal diameter growth differed by G (pseudo-R² = 0.17; DF = 2, F = 8.9, p < .001), indicating genetic differentiation, yet there was no evidence of local adaptation or plasticity (no strong GxE interaction, DF = 2, F = 2.4, p = .10) nor effect of E (DF = 2, F = 1.7, p = .19) or starting height (DF = 1, F = 1.8, p = .18). Seedling height growth (pseudo-R² = 0.11) differed by E (DF = 2, F = 9.1, p < .001), and there was a GxE interaction (DF = 2, F = 3.5, p = .03), with
non-significant effects of G (Df = 2, F = 0.8, p = .45) and starting height (Df = 1, F = 2.0, p = .16). The GxE interaction suggests widespread plasticity, as all subspecies reached the largest basal diameters and heights in the contorta garden, and also lends some support for local adaptation of the latifolia source, which had the highest relative diameter and height growth at home compared to foreign sources (Figure 3d,e). Both latifolia and murrayana grew taller than contorta in its home site, suggesting that the warm, wet environment provided a release from the moisture stress common to their respective home environments.

4 | DISCUSSION

The fate of tree species under rapid climate change will hinge on a match between genotypes and environments (Aitken & Bemmels, 2016; Aitken et al., 2008), and insight into genetic and phenotypic variation under current landscape conditions can be used to gauge persistence potential to future conditions and determine conservation priorities. For widely distributed P. contorta, populations have remained connected via gene flow over large geographic and environmental distances, with landscape barriers producing some population substructure for geographically-isolated portions of the species’ range. Landscape conditions do, nonetheless, shape phenotypic responses of P. contorta populations. In our climatically differentiated gardens, survival was highest for local populations of two of the three populations tested here, while growth for all populations was highest under mild climate conditions (e.g., warm, wet). These findings are consistent with patterns of local adaptation and plasticity documented for P. contorta but also suggest that some populations have the plasticity for higher survival under more favourable conditions and are not currently occupying their climatic optimum. Collectively, our findings indicate that, despite generally high connectivity, reduced survival under water-limited conditions may make some populations of P. contorta more vulnerable to local maladaptation and extirpation, and these populations should be prioritized in conservation efforts. However, our findings also suggest that widespread tree species possess genetically diverse and phenotypically plastic populations likely to have high persistence potential under rapid climate change.

4.1 | How do heterogeneous landscapes influence genetic connectivity?

Genetic connectivity is a well-documented phenomenon in widely distributed, wind-pollinated tree species (Hamrick, 2004; Kremer et al., 2012), and the limited population genetic structure identified here provides another data point supporting genetic connectivity across the nearly continuous distribution of P. contorta (Fazekas & Yeh, 2006; Wheeler & Guries, 1982a, 1982b; Yang & Yeh, 1995). Greater structure or landscape influence may have been more apparent had we utilized a greater number of neutral markers or identified areas of the genome undergoing selection. However, despite this limitation, our sampling across the species’ range allowed us to identify subtle landscape constraints to gene flow, which limited connectivity to isolated or narrowly distributed populations and created geographic substructure (Figure 2a). The presence of persistent geographical barriers drove substructure and was the only measurable landscape effect on gene flow (Table 3), in contrast to the strong influence of distance and the environment in many other plant species (Sexton et al., 2014). Notably, the geographic-genetic structure quantified using the markers tested here does not overlay subspecies delineations but does match expectations of high gene flow over large distances for widespread conifers (Hamrick, 2004; Kremer et al., 2012) while also mapping geographic substructure for isolated regions of the species’ range.

Genetic structure in widespread tree species, such as P. contorta, may be further influenced by the now-obscured landscape and climate conditions present when seedlings of long-lived species established (Yeaman & Jarvis, 2006) or even much older historic processes that influenced colonization and migration (e.g., Pleistocene glaciers, Ortego et al., 2015), but historic climate datasets of sufficient resolution do not exist to test these hypotheses. Moreover, the fact that environmental conditions did not structure genetic variation in P. contorta suggests that population genetic structure of long-lived tree species may not yet reflect contemporary patterns of gene flow as mediated by current landscape conditions, revealing a potential lag in the response of widespread tree species to climate change (Gugger et al., 2013; Ortego et al., 2015).

4.2 | Local adaptation despite gene flow?

While gene flow can maintain connectivity between populations distributed across complex landscapes, climatically- or spatially-varying selection can be strong enough to overcome the homogenizing effects of gene flow (Kawecki & Ebert, 2004). In our climatically-differentiated gardens, we observed some patterns of survival consistent with local adaptation despite gene flow across the range of P. contorta. This finding, combined with outcomes from the Illingworth provenance trials in British Columbia (e.g., Rehfelt et al., 1999, 2001; Ying & Liang, 1994), supports the notion that P. contorta populations are locally adapted to somewhat narrower ranges of climatic conditions than are present across its entire range. Cold-tolerance, for example, may have affected survival in our study, a characteristic observed to strongly affect P. contorta survival and growth (Liepe et al., 2016; Mahony et al., 2020; Rehfelt et al., 1999, 2001; Wang et al., 2010). In our experiment, murrayana and contorta populations had strikingly low survival in the cooler latifolia garden (Figure 3c), suggesting maladaptation to the extreme winter temperatures of this intermountain climate. Warming winter temperatures predicted across the range of P. contorta (Mahony et al., 2017) may relieve maladapted populations of this limitation. Climate change is, however, simultaneously generating novel springtime freezing events and increasing growing-season minimum temperatures, which are
documented to drive declines in Pinus contorta (Mulvey & Bisbing, 2016; Sullivan et al., 2015) and co-occurring species (Buma et al., 2017) and may lead to regeneration failures in temperature-constrained populations.

Water availability is also documented to drive local adaptation in Pinus contorta (Mahony et al., 2020), and, in our gardens, reciprocal transfers between wet and dry environments had the most profound impact on survival. Specifically, the exclusive survival of murrayana but complete mortality of other populations in the drought-impacted murrayana garden (2012–2016 California drought, Lund et al., 2018) is consistent with greater drought tolerance of populations with a history of exposure to aridity (Figure 3b, Kolb et al., 2016). At the other extreme, transfer to the wet, maritime climate of the contorta garden led to the highest absolute survival for all populations, and water availability appears to be a significant driver of Pinus contorta success. Local declines are likely in portions of the species’ distribution where, despite predicted increases in precipitation (Mahony et al., 2017), concurrent temperature increases will change the timing and type of precipitation (e.g., from snow- to rain-dominated precipitation; Buma et al., 2019) and thus growing-season water availability. Given that drought is expected to become increasingly common across its range (Coops & Waring, 2011; Mahony et al., 2020), drought adaptation may be key to local Pinus contorta population persistence.

Our common garden interpretations do, however, need to be made with caution given several limitations. Testing one population per subspecies (due to limited seed viability) did not allow us to determine whether or not there are clear breaks among subspecies or rather continuous variation across the species’ range. Future work should include more populations per subspecies as well as test sites covering the range of current and predicted future Pinus contorta habitat conditions. Moreover, short-term experiments for long-lived tree species may not provide definitive evidence for local adaptation (e.g., Pinus ponderosa, Wright, 2007), and long-term tracking of individuals will be required to validate findings. Finally, trait responses may be controlled by many genes, and populations may harbour a vast reservoir of adaptive variation to facilitate rapid evolutionary responses (Barghi et al., 2019). Despite these limitations, our conclusions remain consistent with findings of local adaptation in Pinus contorta and other widespread conifers (Rehfeldt et al., 2001, 2002, 2014, 2018; Wright, 2007), and we hypothesize that patterns of local adaptation will become more apparent over time (Germino et al., 2019).

4.4 | Is persistence potential enough?

Although plasticity may provide populations time to adapt, it is concerning that many populations of Pinus contorta and other conifers of western North America already lag behind their climatic optimum (Gray & Hamann, 2013; Johnstone & Chapin, 2003). Climate change projections indicate a decline in Pinus contorta suitable habitat across much of the species range by 2080 (Coops & Waring, 2011; Oney et al., 2013), and productivity and growth are expected to decline at lower latitudes and elevations in the near future (Rehfeldt et al., 2001; Wang et al., 2006). Populations occurring at lower elevations, particularly at southern latitudes, are at particular risk of local extirpation due to compounding warming and drying (Coops & Waring, 2011; Mahony et al., 2017; Rehfeldt et al., 2001). The pace of evolutionary change for long-lived tree species is expected to be slow, and habitat suitability (Gray & Hamann, 2013), provenance testing (Rehfeldt et al., 2001), and growth chamber (Liepe et al., 2016) studies of Pinus contorta corroborate our findings that some populations already lag substantially behind their climatic optima.

Similar mismatches to contemporary climate were recently identified in Pinus ponderosa (Martinez-Berdeja et al., 2019) and Quercus lobata (Browne et al., 2019) and interpreted as evidence of environmental change that exceeds the pace of evolutionary change (i.e., adaptational lag; Mátyás, 1994). In these species, populations from warmer, drier climates had the highest growth potential when grown in cooler or wetter conditions, suggesting a mismatch to current climate and high vulnerability to ongoing warming and drying. Consistent with these findings, maximum survival and growth of latifolia and murrayana populations tested here occurred under the mild climate of our contorta garden, providing additional evidence for a lag between Pinus contorta occurrence and its climatic optimum. Populations growing under extreme local conditions may still possess adaptations (e.g., drought tolerance) making them optimally suited for the home environment but be diminished in growth and survival due to the climatic lag between local and optimal conditions, which may be best explained by adaptation to historic colder, wetter climates.
Prior research on *P. contorta* historical migrations and contemporary invasions into meadows (*latifolia*; Jakubos & Romrer, 1993; *murrayana*; Helms, 1987; Anderson, 1996; Lubetkin et al., 2017) provides support for an adaptational lag across much of its current distribution. Slow, progressive warming and drying during the early Holocene are the likely origin of *P. contorta*'s adaptational lag, which led to extirpation of *murrayana* from lower elevations and forced populations to track cooler, wetter climates by migrating to higher elevation (Anderson, 1996). Warmer growing seasons since the end of the Little Ice Age (ca. 1.870) have led to further moisture stress for *latifolia* and *murrayana*, and montane meadows provide a local source of relief and opportunity for establishment (Helms, 1987; Jakubos & Romrer, 1993; Lubetkin et al., 2017). For long-lived tree species, such as *P. contorta*, persistence through climate fluctuations over geologic time may mean that maladaptation to contemporary climate is common (Gray & Hamann, 2013), populations are instead adapted to historic climates (Browne et al., 2019), and projected climate conditions will only exacerbate adaptational lags and perpetuate growth under suboptimal conditions.

5 | CONCLUSIONS

Our findings suggest that *P. contorta* populations likely have high persistence potential via phenotypic plasticity and high genetic variability. However, geographically-based genetic substructure in some portions of the species’ range as well as complete mortality of non-local populations in our most water-limited garden also indicate that some populations may be vulnerable to local maladaptation and extinction with rapid climate change. Management of conifers is already incorporating assisted migration as part of a conservation strategy for maintaining viable populations of these long-lived species (e.g., O’Neill et al., 2008; Young et al., 2020), and our results suggest that such efforts may be warranted for vulnerable populations, complementing the natural processes of high gene flow and local adaptation within widespread conifers.

ACKNOWLEDGEMENTS

Research was supported by The Wilderness Society’s Gloria Barron Fellowship (to SB) and National Park Service’s George Melendez Wright Climate Change Fellowship (to SB) as well as the US Army Corps of Engineers Cold Regions Research and Engineering Laboratory (to DC). Elizabeth Leger reviewed earlier manuscript drafts and provided invaluable insights for refinement. The authors thank Helen Bothwell, Danny Nielsen, and Jason Sexton for advice on analysis as well as Becky Chong, David D’Amore, Toni DeSanto, Paul Hennon, Valerie Hipkins, Andy Krohn, Jill Larson, John Paul, Kristen Pelz, Conor Phelan, Doug Rischbieter, and Dan Wickes for field and laboratory support. John Shaw and Glenn Christensen of the USFS and Will McKenzie of BC’s Ministry of Forests were instrumental to identifying sampling locations and obtaining additional needle samples.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13191.

DATA AVAILABILITY STATEMENT

All data generated for this study are available through the Dryad Digital Repository: https://doi.org/10.5061/dryad.nvx0k6dqv (Bisbing, 2021)

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**BIOSKETCH**

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Author contributions: S.B., A.A., & D.C. conceived of the idea; S.B. collected the data. S.B. & A.U. analyzed the data. S.B. led writing.

**SUPPORTING INFORMATION**

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

**How to cite this article:** Bisbing SM, Urza AK, Buma BJ, Cooper DJ, Matocq M, Angert AL. Can long-lived species keep pace with climate change? Evidence of local persistence potential in a widespread conifer. *Divers Distrib*. 2021;27:296–312.

[https://doi.org/10.1111/ddi.13191](https://doi.org/10.1111/ddi.13191)