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

Sarah M. Bisbing[1] | Alexandra K. Urza[1,2] | Brian J. Buma[3] | David J. Cooper[4] | Marjorie Matocq[1] | Amy L. Angert[5]

[1]Department of Natural Resources & Environmental Science, Program in Ecology, Evolution, & Conservation Biology, University of Nevada - Reno, Reno, NV, USA

[2]Rocky Mountain Research Station, USDA Forest Service, Reno, NV, USA

[3]Department of Integrative Biology, University of Colorado, Denver, CO, USA

[4]Department of Forest and Rangeland Stewardship & Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA

[5]Departments of Botany and Zoology, University of British Columbia, Vancouver, BC, Canada

Correspondence
Sarah M. Bisbing, Department of Natural Resources & Environmental Science, Program in Ecology, Evolution, & Conservation Biology, University of Nevada - Reno, 1664 N. Virginia St, Reno, NV, 89557, USA.
Email: sbisbing@unr.edu

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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.

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KEYWORDS
adaptational lag, common gardens, landscape genetics, local adaptation, lodgepole pine, microsatellites, persistence potential, phenotypic plasticity, *Pinus contorta*

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 & Guries, 1982a, 1982b), forest productivity (e.g., Chuine et al., 2006; McLane et al., 2011; Rehfeldt 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,

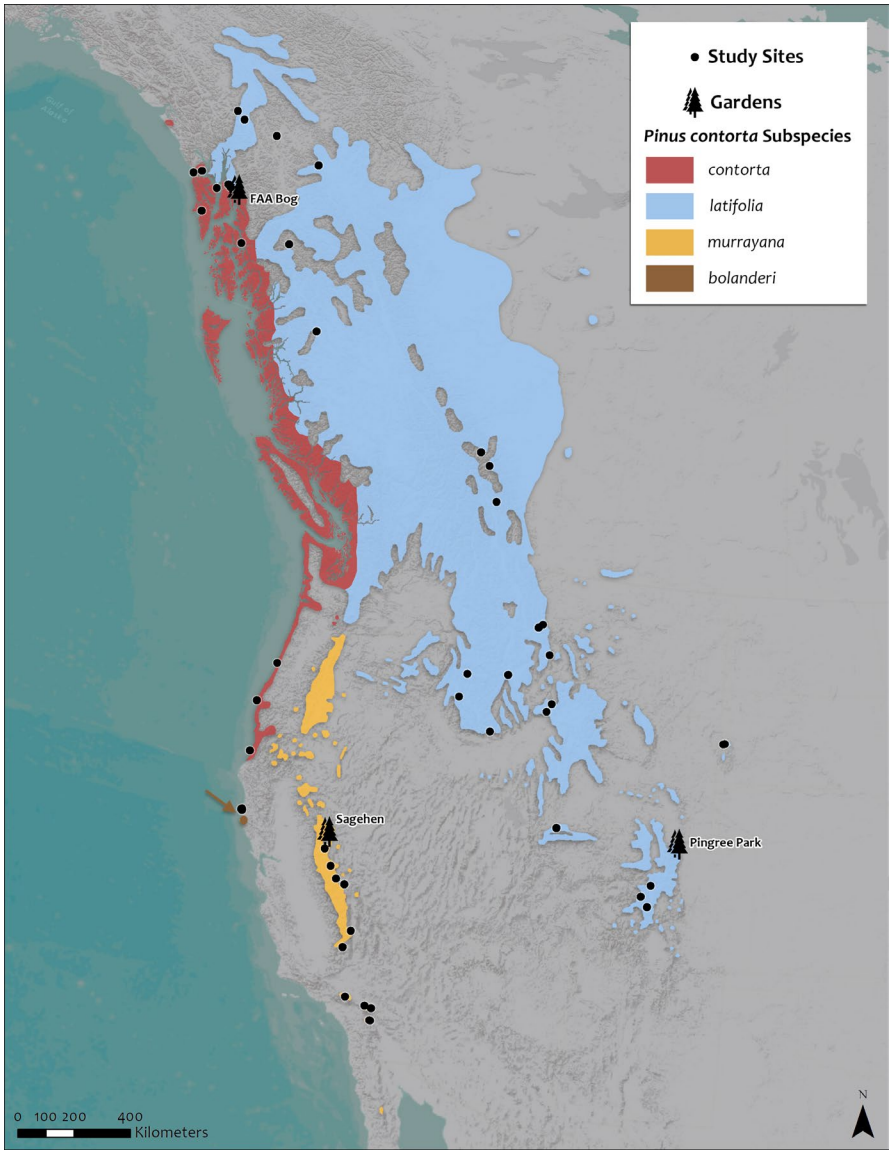


FIGURE 1 Natural distribution of the four subspecies of *Pinus contorta* and sampling locations of this study across western North America. Closed black circles = sampling locations, black trees = common garden locations, blue = ssp. *latifolia*, red = ssp. *contorta*, yellow = ssp. *murrayana*, brown = ssp. *bolanderi*. Subspecies *bolanderi* is endemic to Mendocino county, California, and barely visible on this range-wide map; a brown arrow indicates its distribution. Subspecies mapped delineations were digitized over Little's *Pinus contorta* map (1971) based on best available information from the 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, as individuals shapefiles do not exist for each subspecies. Map projection is a USA Contiguous Albers Equal Area Conic

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
		Luther Pass	***murrayana* 11**	**Tahoe National Forest**	**California**	**10**	**38.7870**	**−120.0019**	**2,212**
ssp. *bolanderi*	Coastal California and Oregon	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	*conotorta* 1	California SP	California	10	39.2857	−123.7959	44
		Patrick's Point	*conotorta* 2	California SP	California	10	41.1397	−124.1606	52
		Tolowa Dunes	*conotorta* 3	California SP	California	10	41.7964	−124.2232	28
		Port Oxford	*conotorta* 4	Oregon SP	Oregon	10	42.7392	−124.5107	151
		Sand Dunes	*conotorta* 5	Siuslaw NF	Oregon	10	44.0633	−124.1198	7
		Old Sitka	*conotorta* 6	Tongass NF	Alaska	10	57.1286	−135.3687	45
		Blanket Bog	*conotorta* 7	Tongass NF	Alaska	10	56.6387	−132.6610	66
		Bay Bog	*conotorta* 8	Tongass NF	Alaska	10	58.0588	−135.0962	21
		Jumbo Bog	*conotorta* 9	City and Borough of Juneau	Alaska	10	58.2615	−134.3864	203
		Sundown Bog	*conotorta* 10	City and Borough of Juneau	Alaska	15	58.3340	−134.5941	23
		FAA Bog	***conotorta* 11**	**State of Alaska**	**Alaska**	**10**	**58.3358**	**−134.5622**	**50**
		Dundas Bay	*conotorta* 12	Glacier Bay National Park	Alaska	5	58.3253	−136.2032	0
		Dick's Arm	*conotorta* 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 Britsh 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
		Windermere Kootenay	*latifolia 9*	Kootenay National Park	Alberta	10	50.8809	−116.0481	1,182
		Flathead[b]	*latifolia 10*	Flathead National Forest	Montana	11	48.4572	−113.6403	1,620
		Judith Basin[b]	*latifolia 11*	Helena National Forest	Montana	10	46.3211	−111.8512	2,215
		Lewis & Clark[b]	*latifolia 12*	Lewis and Clark National Forest	Montana	6	46.8209	−110.4757	1982
		Lemhi[b]	*latifolia 13*	Bitterroot National Forest	Idaho	11	45.4771	−113.8847	2040
		Idaho[b]	*latifolia 14*	Nez Perce National Forest	Idaho	3	45.2690	−115.0195	1993
		Custer[b]	*latifolia 15*	Salmon-Challis National Forest	Idaho	8	44.4960	−114.5536	2,640
		Valley[b]	*latifolia 16*	Payette National Forest	Idaho	11	44.6545	−115.8714	1,925
		Fremont[b]	*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[b]	*latifolia 19*	Wasatch National Forest	Utah	11	40.9192	−110.6473	3,090
		Eagle[b]	*latifolia 20*	White River National Forest	Colorado	7	39.6099	−106.4021	2,868
		Gunnison[b]	*latifolia 21*	Gunnison National Forest	Colorado	5	38.6162	−106.5003	3,109
		Larimer[b]	***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]Subepcies further classifed as var. *yukonensis* (Strong, 2010)

[b]Samples collected via the USFS Forest Inventory & Analysis Program.

California. Subspecies differ in crown shape, tree form, and cone traits (*latifolia* populations are predominantly serotinous; Benkman & Siepielski, 2004) and are hypothesized to be adapted to local climate and environmental conditions (Rehfeldt et al., 1999; Ying & Liang, 1994).

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—tall 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_{ST} (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_A), number of effective alleles (N_E), expected heterozygosity (H_E), unbiased expected heterozygosity (uH_E) and inbreeding levels (F_{IS}). 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

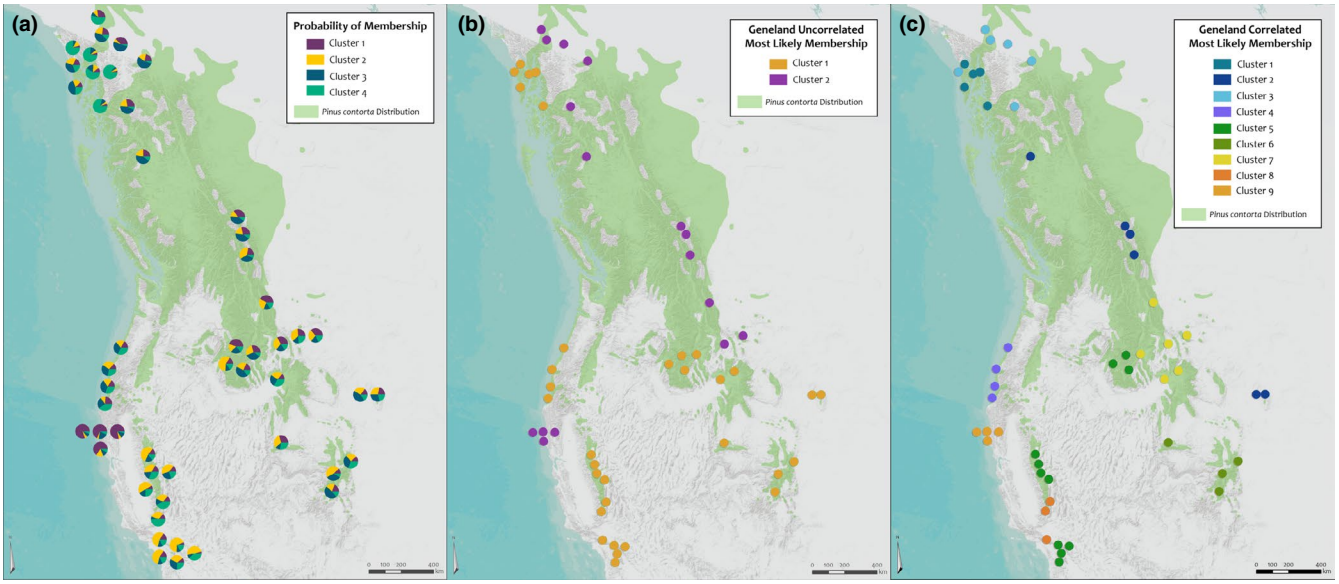


FIGURE 2 Population structure of *Pinus contorta*, as identified by replicated (a) STRUCTURE analysis and merged using CLUMPP, as compared to (b) uncorrelated and (c) correlated runs in GENELAND. (a) Probability of membership to each genetic cluster ($K = 4$) is represented by a population-level pie chart, indicating four genetic clusters with admixture across all sampling locations. (b) GENELAND assignments of sampling locations to each identified genetic cluster for uncorrelated runs ($K = 2$), using genetic, geographic, and phenotypic data and assuming allele frequencies are similar across populations (Guillot et al., 2012). (c) GENELAND assignments of sampling locations to each identified genetic cluster for correlated runs ($K = 9$), using genetic, geographic, and phenotypic data and accounting for the abundance of rare alleles in genetic data (Guillot et al., 2012). Map projection is a USA Contiguous Albers Equal Area Conic

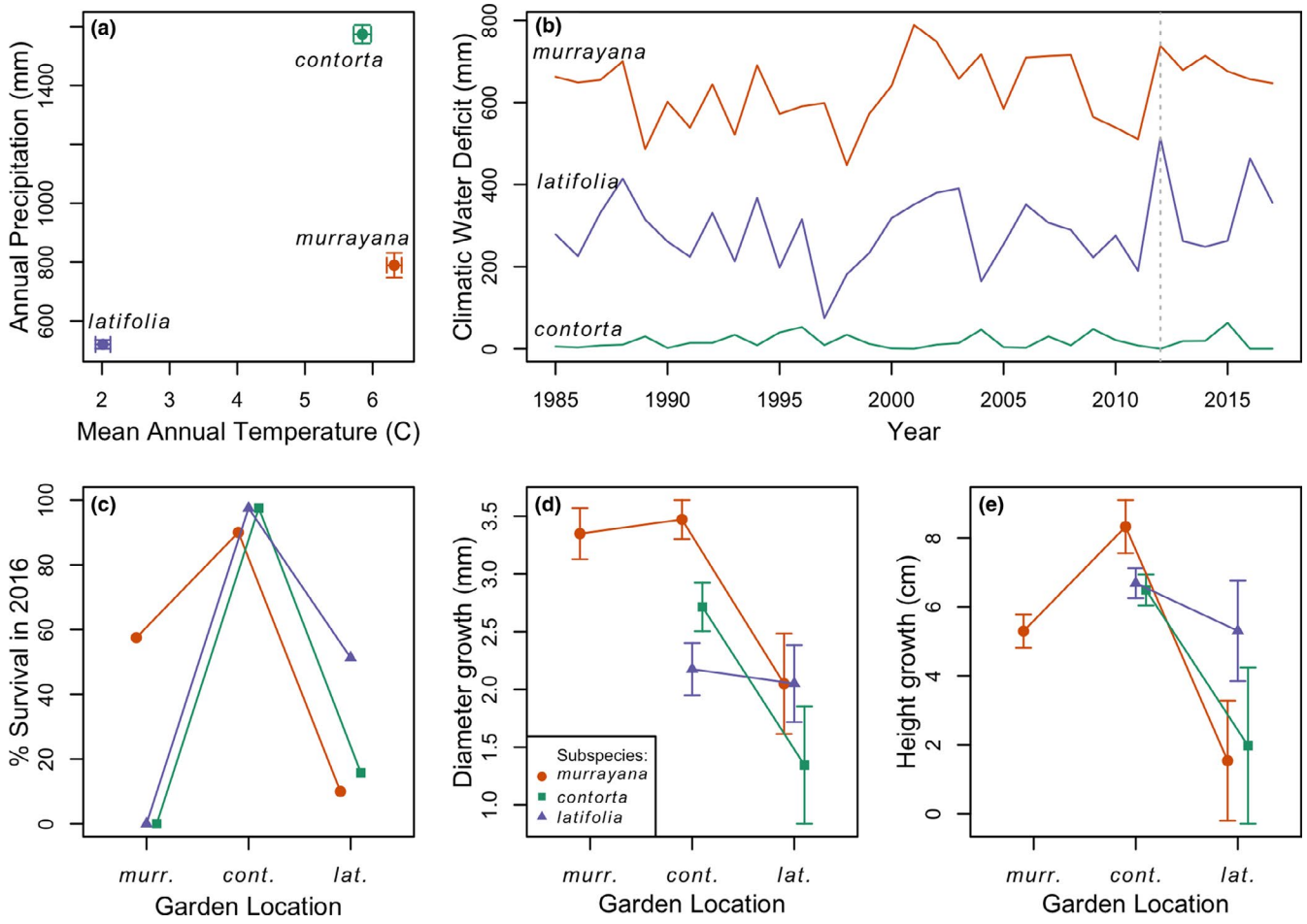


FIGURE 3 Climate and plant performance from *Pinus contorta* reciprocal common garden transplant experiment using subspecies *contorta* (home environment = Alaska; green squares), *latifolia* (home environment = Colorado; purple triangles), and *murrayana* (home environment = California; orange circles). 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_A	N_E	H_E	uH_E	F *Index*
ssp. *murrayana*	Wellman's Divide	10	100	4.1 ± 0.8	2.9 ± 0.7	0.50 ± 0.09	0.53 ± 0.10	0.19 ± 0.10
	Hidden Lake Drive	10	90	4.2 ± 0.9	2.7 ± 0.6	0.45 ± 0.11	0.47 ± 0.12	0.05 ± 0.06
	Onyx Peak	10	100	4.4 ± 0.7	2.9 ± 0.7	0.51 ± 0.09	0.54 ± 0.09	0.06 ± 0.09
	Champion	10	90	5.1 ± 0.9	3.3 ± 0.8	0.54 ± 0.09	0.57 ± 0.10	0.14 ± 0.08
	Dawson Saddle	10	100	5.0 ± 0.7	2.8 ± 0.4	0.58 ± 0.06	0.62 ± 0.07	0.28 ± 0.12
	Big Meadow	10	100	3.9 ± 0.7	2.0 ± 0.4	0.41 ± 0.07	0.43 ± 0.08	0.14 ± 0.08
	Horeshoe Meadows	10	100	4.7 ± 0.7	2.7 ± 0.4	0.57 ± 0.06	0.60 ± 0.06	0.05 ± 0.12
	Crooked Meadows	10	100	5.3 ± 1.0	3.5 ± 0.9	0.55 ± 0.08	0.58 ± 0.09	−0.02 ± 0.11
	Tuolumne Meadows	10	100	4.6 ± 1.0	3.2 ± 0.9	0.49 ± 0.10	0.51 ± 0.10	0.11 ± 0.09
	Levitt Meadows	10	100	4.7 ± 0.9	3.1 ± 0.8	0.55 ± 0.08	0.58 ± 0.08	0.12 ± 0.16
	Luther Pass	10	100	4.1 ± 0.7	2.5 ± 0.3	0.54 ± 0.07	0.58 ± 0.07	−0.03 ± 0.12
Within murrayana		110	98 ± 1	4.6 ± 0.2	2.9 ± 0.2	0.52 ± 0.02	0.55 ± 0.02	0.10 ± 0.03
ssp. *bolanderi*	Russian Gulch	10	80	3.9 ± 0.8	2.5 ± 0.6	0.45 ± 0.10	0.47 ± 0.10	0.00 ± 0.09
	Van Damme Pygmy	10	90	4.1 ± 0.8	2.7 ± 0.7	0.45 ± 0.10	0.48 ± 0.11	0.11 ± 0.10
	Van Damme	10	90	4.2 ± 0.6	2.6 ± 0.5	0.48 ± 0.09	0.51 ± 0.10	−0.05 ± 0.07
Within bolanderi		30	93 ± 4	4.1 ± 0.4	2.6 ± 0.3	0.46 ± 0.05	0.49 ± 0.06	0.02 ± 0.05
ssp. *contorta*	Spring Ranch	10	80	3.6 ± 0.5	2.5 ± 0.4	0.48 ± 0.09	0.51 ± 0.10	−0.01 ± 0.13
	Patrick's Point	10	90	3.7 ± 0.7	2.8 ± 0.5	0.52 ± 0.10	0.56 ± 0.10	0.10 ± 0.13
	Tolowa Dunes	10	100	4.8 ± 0.9	2.9 ± 0.8	0.50 ± 0.08	0.52 ± 0.09	−0.06 ± 0.12
	Port Oxford	10	90	4.1 ± 0.8	2.7 ± 0.5	0.53 ± 0.08	0.56 ± 0.09	0.03 ± 0.10
	Sand Dunes	10	90	4.9 ± 1.0	2.8 ± 0.7	0.47 ± 0.10	0.49 ± 0.11	−0.02 ± 0.08
	Old Sitka	10	100	4.6 ± 0.9	2.9 ± 0.7	0.51 ± 0.08	0.54 ± 0.09	0.05 ± 0.09
	Blanket Bog	10	100	3.9 ± 0.6	2.5 ± 0.5	0.51 ± 0.07	0.54 ± 0.07	−0.05 ± 0.14
	Bay Bog	10	100	4.2 ± 0.6	2.4 ± 0.4	0.51 ± 0.06	0.54 ± 0.07	0.04 ± 0.08
	Jumbo Bog	10	70	4.9 ± 1.4	3.1 ± 0.9	0.53 ± 0.11	0.56 ± 0.11	0.05 ± 0.09
	Sundown Bog	15	100	4.3 ± 0.7	2.5 ± 0.5	0.52 ± 0.06	0.54 ± 0.07	−0.10 ± 0.11
	FAA Bog	10	100	4.2 ± 0.9	2.6 ± 0.5	0.51 ± 0.08	0.55 ± 0.08	0.22 ± 0.12
	Dundas Bay	5	80	2.7 ± 0.5	2.1 ± 0.4	0.41 ± 0.10	0.46 ± 0.11	0.01 ± 0.14
	Dick's Arm	10	90	4.3 ± 0.8	3.1 ± 0.6	0.56 ± 0.09	0.60 ± 0.09	0.14 ± 0.08
Within contorta		130	92 ± 2	4.2 ± 0.2	2.7 ± 0.2	0.51 ± 0.02	0.54 ± 0.02	0.03 ± 0.03
ssp. *latifolia*	Alcan Highway	15	90	4.8 ± 0.9	2.7 ± 0.7	0.46 ± 0.09	0.48 ± 0.10	0.20 ± 0.11
	Mt McIntyre	10	100	5.2 ± 0.8	3.3 ± 0.7	0.58 ± 0.07	0.62 ± 0.08	0.17 ± 0.08
	Canol Road	20	100	4.3 ± 0.8	2.8 ± 0.5	0.55 ± 0.07	0.58 ± 0.08	0.21 ± 0.13
	Pine Flats	10	90	5.4 ± 1.0	3.9 ± 0.9	0.58 ± 0.10	0.62 ± 0.11	0.22 ± 0.12
	Edziza	10	100	4.9 ± 0.7	3.2 ± 0.6	0.58 ± 0.08	0.61 ± 0.09	−0.02 ± 0.11
	Smithers Community Forest	10	100	5.3 ± 1.0	3.8 ± 0.8	0.60 ± 0.09	0.64 ± 0.10	0.06 ± 0.10
	Columbia Icefields	10	100	3.9 ± 0.3	2.1 ± 0.3	0.46 ± 0.06	0.50 ± 0.07	0.04 ± 0.08
	Glacier Lake	10	100	5.8 ± 1.2	3.4 ± 0.8	0.56 ± 0.09	0.60 ± 0.09	−0.07 ± 0.09
	Windermere Kootenay	10	100	5.3 ± 0.9	3.7 ± 0.8	0.58 ± 0.10	0.61 ± 0.10	0.04 ± 0.10
	Flathead	11	90	4.9 ± 0.9	3.5 ± 0.7	0.59 ± 0.08	0.63 ± 0.08	0.29 ± 0.10
	Judith Basin	10	100	4.2 ± 0.6	2.6 ± 0.5	0.54 ± 0.06	0.57 ± 0.07	0.14 ± 0.08
	Lewis & Clark	6	70	3.4 ± 0.7	2.3 ± 0.5	0.40 ± 0.10	0.44 ± 0.11	0.15 ± 0.10
	Lemhi	11	100	5.4 ± 1.1	4.1 ± 1.0	0.59 ± 0.09	0.62 ± 0.10	0.16 ± 0.07
	Idaho	3	70	2.4 ± 0.4	2.0 ± 0.3	0.40 ± 0.09	0.47 ± 0.11	−0.03 ± 0.19
	Custer	8	90	4.1 ± 1.0	2.7 ± 0.6	0.50 ± 0.09	0.54 ± 0.09	0.08 ± 0.12

(Continues)

TABLE 2 (Continued)

Subspecies	Sampling Location	N	PPL	N_A	N_E	H_E	uH_E	F *Index*
	Valley	11	100	4.8 ± 1.1	3.5 ± 1.0	0.53 ± 0.09	0.57 ± 0.10	0.20 ± 0.13
	Fremont	6	90	3.8 ± 0.8	2.9 ± 0.7	0.48 ± 0.09	0.54 ± 0.11	0.08 ± 0.13
	Bunsen Peak	12	100	5.4 ± 0.8	3.2 ± 0.7	0.57 ± 0.08	0.61 ± 0.08	0.22 ± 0.08
	Summit	11	100	4.1 ± 0.7	3.0 ± 0.6	0.53 ± 0.08	0.57 ± 0.09	0.07 ± 0.11
	Eagle	7	90	3.9 ± 0.7	3.0 ± 0.6	0.55 ± 0.09	0.59 ± 0.10	0.19 ± 0.12
	Gunnison	5	80	3.4 ± 0.8	2.9 ± 0.6	0.45 ± 0.12	0.50 ± 0.13	−0.05 ± 0.11
	Larimer	12	100	4.8 ± 1.0	3.4 ± 0.8	0.57 ± 0.09	0.60 ± 0.09	0.11 ± 0.07
	Tillson Creek	10	100	5.0 ± 0.8	3.1 ± 0.7	0.54 ± 0.09	0.57 ± 0.09	0.08 ± 0.08
	Nahant School	10	100	4.7 ± 0.8	2.9 ± 0.7	0.49 ± 0.09	0.52 ± 0.09	0.06 ± 0.11
Within latifolia		238	95 ± 2	4.6 ± 0.2	3.1 ± 0.1	0.53 ± 0.02	0.57 ± 0.02	0.10 ± 0.02
Among subspecies		508	99 ± 1	11.0 ± 1.1	3.8 ± 0.6	0.56 ± 0.04	0.56 ± 0.04	0.14 ± 0.03
Across all locations		508	95 ± 1	4.4 ± 0.1	2.9 ± 0.1	0.52 ± 0.01	0.55 ± 0.01	0.08 ± 0.02

Note: PPL, percent polymorphic loci; N_A, mean number of different alleles; N_E, mean number of effective alleles; H_E, expected heterozygosity; uH_E, unbiased expected heterozygosity; *F* Index, Fis.

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 ($\alpha = 0.05$) 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_{IS}) 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 (PICO4 & PICO7) to 27 (locus PICO77) and N_a 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 Bisbing" command="Delete" timestamp="1604959680386" title="Deleted by Sarah M Bisbing on 11/9/2020, 2:08:00 PM" class="reU3">te</del>: 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 | column model) − (genetic distance ~ column model | row model). IBB = isolation by barrier, IBE = isolation by environment, IBD = isolation by distance, IBR = 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 support after 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 F_{ST} 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 subdivisions within each subspecies, where *latifolia* was divided into six genetic clusters (Figure 2c). Pairwise F_{ST} 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 (IBE, 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 MMRR analyses (Appendix Table S6) also identified IBB as the strongest predictor of genetic variation ($R^2 = 0.07$, $p < .001$), followed by IBE ($R^2 = 0.03$, $p < .001$) and IBR ($R^2 = 0.03$, $p = .01$), while IBD was non-significant ($R^2 = 0.002$, $p > .34$). Adding additional predictors to the IBB model resulted in slight increases in explanatory power (from $R^2 = 0.07$ to $R^2 = 0.08$), 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 (surival, 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 ($\Delta AIC > 4$), so climate models were not considered further. Seedling survival was driven by E (DF = 2; Chisq = 168.7; $p < .001$), G (DF = 2; Chisq = 10.3; $p = .01$) and a GxE interaction (DF = 4; Chisq = 75.8; $p < .001$), with an estimated pseudo-R^2 of 63.3%, and was not predicted by starting height (DF = 1; Chisq = 1.4; $p = .24$). Each seed source had the highest relative 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-$R^2 = 0.17$; 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-$R^2 = 0.11$) 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 glaciations, 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., Rehfeldt 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; Rehfeldt 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 *P. 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 *P. 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 *P. 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 *P. 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 *P. 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 *P. 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).

4.3 | Persistence potential via phenotypic plasticity?

We also observed evidence of high phenotypic plasticity in all populations, and this response, despite local adaptation, is likely to promote local population persistence in *P. contorta* and other widely distributed tree species (Alberto et al., 2013). With an estimated 12 generations required for *Pinus* species to adapt to projected future conditions (Rehfeldt et al., 2001, 2002), evolutionary change is unlikely to match the pace of climate change, and phenotypic plasticity may allow population persistence under a wide range of future local conditions. Previous work found that plasticity in *P. contorta* growth potential was highest for populations from warmer environments, whereas cold-hardy populations were limited in growth plasticity but exhibited higher survival in colder environments (Rehfeldt et al., 2018). Population response in our gardens was consistent with these expectations: *murrayana* from the warm, dry Sierra Nevada had low survival in the cold, dry *latifolia* garden but exceptional growth rates across all environments, while *latifolia* had high survival at home and a limited growth response elsewhere. This ability of *P. contorta* genotypes to be plastic in their response to environmental heterogeneity may provide the foundation for persistence potential by buffering local populations from negative selection and giving this long-lived, slow-to-migrate tree species more time to adapt to novel local conditions (Alberto et al., 2013; Crispo, 2008).

4.4 | Is persistence potential enough?

Although plasticity may provide populations time to adapt, it is concerning that many populations of *P. 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 *P. 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 *P. 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* (Martínez-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 *P. 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 & Rommer, 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 & Rommer, 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 extirpation 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.

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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)

ORCID

Sarah M. Bisbing https://orcid.org/0000-0002-5534-9352
Alexandra K. Urza https://orcid.org/0000-0001-9795-6735
Brian J. Buma https://orcid.org/0000-0003-2402-7737
David J. Cooper https://orcid.org/0000-0003-3391-3538
Marjorie Matocq https://orcid.org/0000-0003-4829-3749
Amy L. Angert https://orcid.org/0000-0003-3082-0133

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BIOSKETCH

Sarah Bisbing is an Assistant Professor of Forest Ecosystem Science at the University of Nevada – Reno studying the effects of climate change and altered disturbance regimes on tree regeneration, growth and survival. Collectively, the authors are working to quantify the effects of climate change on natural ecosystem dynamics and the mechanisms driving species success across western North America.

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SUPPORTING INFORMATION

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

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