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ARTICLE

Do low-elevation ravines provide climate refugia for subalpine limber pine (*Pinus flexilis*) in the Great Basin, USA?

Constance I. Millar, David A. Charlet, Robert D. Westfall, John C. King, Diane L. Delany, Alan L. Flint, and Lorraine E. Flint

Abstract: Climate refugia are locations where decoupled climate processes enable species to persist despite unfavorable climate changes in surrounding landscapes. Despite theoretic bases and paleo-ecological evidence, refugia have not been widely characterized under modern conditions in mountain regions. Conifers in the Great Basin, USA, provide an opportunity to evaluate the potential of low-elevation ravine and riparian (LERR) contexts to function as climate refugia. We provide evidence for significantly higher than expected occurrence of limber pine (*Pinus flexilis* E. James) in LERR contexts (mean 64%) across 43 mountain ranges. We document with observed and modeled data that LERR contexts are cooler and wetter than expected for their elevations, have low solar radiation, and produce larger (more positive) lapse rates relative to upland slopes. Together these findings suggest that LERR contexts generate decoupled microclimates that provide climate refugia for limber pine. In that refugia management has been promoted as a contemporary climate adaptation strategy, our findings suggest that LERR contexts be further evaluated for their conservation potential.

Key words: climate refugia, Great Basin, limber pine, microclimates, cold-air drainage.

Résumé : Les refuges climatiques sont des endroits où le découplage des processus climatiques permet que des espèces persistent malgré les changements climatiques défavorables dans les paysages environnants. Malgré des bases théoriques et des preuves paléoécologiques, les refuges n'ont pas été souvent caractérisés en région montagneuse dans les conditions modernes. Dans le grand Bassin, aux États-Unis, les conifères offrent une opportunité d'évaluer la possibilité que les milieux riverains dans les ravins situés à faible altitude (LERR) se comportent comme des refuges climatiques. Nous présentons des indices que l'occurrence du pin flexible (*Pinus flexilis* E. James) est significativement plus élevée qu'elle devrait l'être dans les LERR (moyenne de 64 %) parmi 43 chaînes de montagne. Avec des données observées et modélisées, nous documentons le fait que les LERR soient plus frais et humides qu'anticipé à leur altitude, qu'ils reçoivent un faible rayonnement solaire et qu'ils produisent de plus grands gradients adiabatiques (plus positifs) relativement aux endroits situés plus haut sur la pente. Ensemble, ces résultats indiquent que les LERR génèrent des microclimats découplés qui fournissent des refuges climatiques pour le pin flexible. Étant donné que l'aménagement des refuges a été mis de l'avant en tant que stratégie contemporaine d'adaptation au climat, nos résultats indiquent que les LERR devraient être davantage évalués pour leur potentiel de conservation. [Traduit par la Rédaction]

Mots-clés : refuges climatiques, grand Bassin, pin flexible, microclimat, drainage d'air frais.

Introduction

From a theoretic standpoint, tree species in mountain environments respond to thermal changes in predictable ways (Beniston 2003). As temperatures increase, isotherms rise in elevation, and montane species recruitment shifts upward, tracking suitable habitat. As climates cool, the opposite pattern emerges. Over long time spans and under naturally changing paleohistoric climates, these patterns have been widely documented (Huntley and Webb 1989). As tree species shifted in response to natural climate changes, former habitat was vacated, resulting in local and regional extirpations (Huntley and Birks 1983). Similarly, as anthropogenic warming accelerates, mountain tree species are expected to migrate upward, a pattern that has been documented in many regions (Baker and Moseley 2007; Beckage et al. 2008; Lenoir et al. 2008). As in the past, local and regional extirpations are predicted as species shift higher on mountains, eventually running out of space ("elevational squeeze"; Bell et al. 2014).

These expected patterns, however, are often violated (Lenoir et al. 2010; Crimmins et al. 2011). In exceptional paleohistoric cases, conifer populations appeared to persist in place through long periods of apparent climate unsuitability (Birks and Willis 2008). Whether identified or inferred, climate refugia have been invoked to explain such circumstances (Haffer 1982; Bennett and Provan 2008; Rull 2009). Refugia are disjunct locations where unique environmental conditions, together with decoupled climatic processes, allow species to survive broader climate change (adapted from Dobrowski 2011). Refugia have been identified at many scales, from large regions (e.g., Beringia, Brubaker et al. 2005) to small patches where microclimates confer stably favorable conditions (Rull 2009). Populations surviving in refugia, whether large or small, serve to maintain genetic diversity and

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C.I. Millar, R.D. Westfall, and D.L. Delany. Pacific Southwest Research Station, USDA Forest Service, 800 Buchanan St., Albany, CA 94710, USA.
D.A. Charlet. College of Southern Nevada, Department of Biology, 700 College Drive, Henderson, NV 89002, USA.
J.C. King. Lone Pine Research, 2604 Westridge Drive, Bozeman, MT 59715, USA.
A.L. Flint and L.E. Flint. California Water Science Center, U.S. Geological Survey, Placer Hall, 6000 J Street, Sacramento, CA 95819, USA.
Corresponding author: Constance I. Millar (email: cmillar@fs.fed.us).

Fig. 1. Map of the Great Basin showing overall distribution of limber pine, occurrence records of limber pine from the conifer atlas records, and limber pine reference sites used for modeled and observed climate and solar radiation analyses. PIFL, *Pinus flexilis*. Basemap: National Geographic Society et al. (2011).

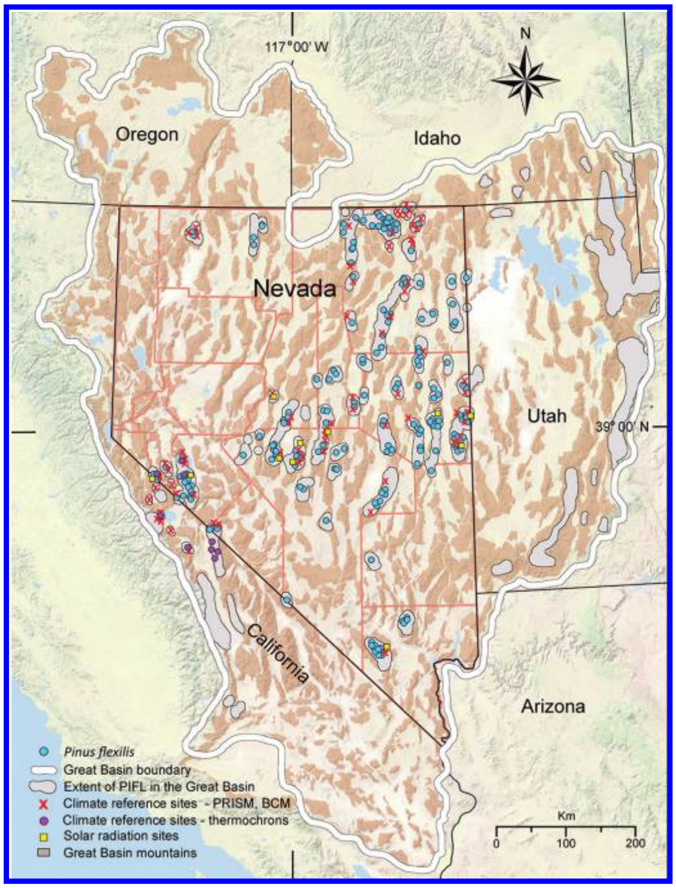
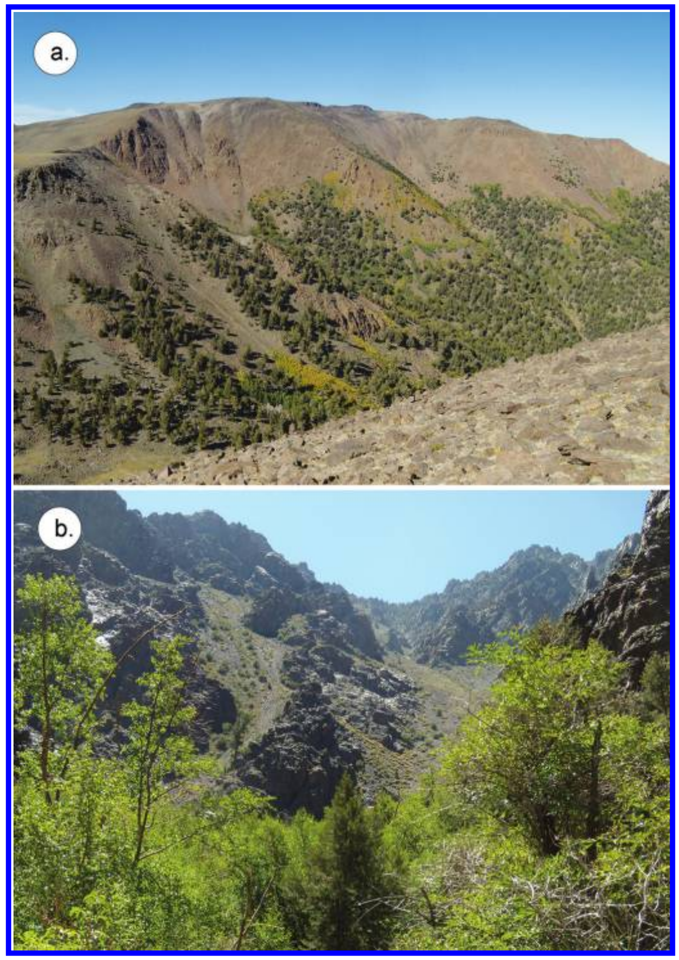


Fig. 2. Limber pine topographic contexts in the Great Basin mountains: (*a*) upland limber pine stands forming subalpine forest (Mt. Jefferson, Toquima Range, Nevada); (*b*) low-elevation ravine–riparian (LERR) limber pine below the main distribution of the species (North Twin River, Toiyabe Range, Nevada). Photos: C.I. Millar. [Colour online.]



become sources for species expansion when climates ameliorate. Mimicking these processes, a strategy of managing species in climate-adaptation refugia for contemporary climate change has emerged (Ashcroft 2010; Morelli et al. 2016), although this has been little implemented. Given the vulnerabilities of montane tree species under climate change (Bell et al. 2014), there is a need to better explore the role of climate refugia in mountain regions (Dobrowski 2011). Such information would help to elucidate historical biogeographic processes of mountain species, as well as provide input to climate adaptation and conservation planning.

The Great Basin (GB) of the American West provides an opportunity to investigate the ecological role of climate refugia across a natural experiment afforded by many mountain ranges (Fig. 1). The hydrographic GB defines a region of roughly 520 000 km^2 where waters drain into interior, evaporative basins. Contained within this region are 635 distinct mountain ranges (Charlet 1996), including at least 37 with summits that extend above 3050 m (Grayson 2011; unpublished data) The ranges are isolated by broad basin networks with floors that reach ~750–1800 m.

In conjunction with a semi-arid climate, the physiography of the current GB dictates a warm, dry landscape punctuated by isolated high, cool mountain ranges that provide suitable habitat for upland conifers. Woodland conifers grow in bands along the basin margins and on low foothills < 1500 m. The higher ranges, with montane, subalpine, and alpine environments that collectively amount to 7.5% of the area of the GB (Brussard et al. 1999), support 19 upland conifer species (Charlet 1996). Limber pine (*Pinus flexilis* E. James) is the widest ranging subalpine conifer in the GB and is known from 53 mountain ranges in Nevada (Charlet 1996; D.A. Charlet, unpublished data), six ranges in eastern California (Griffin and Critchfield 1976), and at least 15 ranges in the GB parts of Utah and Idaho (Burns and Honkala 1990). Limber pine is the sole high-elevation conifer in many GB mountain ranges, occurring above ~2700 m and regularly forming the upper tree line; the high record for Nevada is 3505 m (Charlet 1996). Limber pine often co-occurs with bristlecone pine (*Pinus longaeva* D.K. Bailey) in the southern and eastern GB, with whitebark pine (*Pinus albicaulis* Engelm.) in the northern and western GB, with Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in the eastern GB, and with a few other conifers in scattered locations. Beyond the GB, limber pine extends broadly through the Rocky Mountains and Interior Pacific Northwest. In the GB, limber pine is adapted to dry, continental climates, establishes on well-drained rocky substrates, and occurs on diverse soil types, although less commonly on carbonate or organic soils (Burns and Honkala 1990). Forests are often sparse yet extend across upland slopes, tending toward northern exposures (Fig. 2*a*).

Although much remains enigmatic about the distribution of conifers in the GB ranges, paleoecological evaluation (Wells 1983; Thompson 1988, 1990; Grayson 2011) and analyses of modern distributions (Charlet 2007) suggest that upland conifers, including limber pine, were much more widespread across GB ranges during the Late Pleistocene than at present. Cooler and wetter climates of pluvial periods forced montane-adapted species such as limber pine downslope and into basins, allowing them to expand into new ranges (Thompson 1990). Stochastic factors, as well as deterministic elements, influenced what species reached which ranges, as well as extirpations in small ranges. Warming of the early Holocene, accompanied by higher precipitation than present, promoted upslope migration and vigorous growth, with limber pine forests likely attaining their greatest Holocene densities and widest elevation spans (Tausch et al. 2004). Increasing warmth and aridity of the middle Holocene millennia and subsequent periods such as the Late Holocene Dry Period (Mensing et al. 2013) and the Medieval Climate Anomaly (Stine 1994) created inhospitable conditions for conifers in the foothills and basins, severely reducing intermountain migration of cool-adapted conifers. These dry, hot intervals appear to have forced species, including limber pine, upslope by as much as 300–500 m, reducing population densities and driving local extirpations (Thompson 1988; Grayson 2011).

Compared with this historical scenario, the modern phenomenon of limber pine scattered across GB mountain ranges presents a conundrum. If hot, dry intervals of the middle Holocene and subsequent dry intervals drove upslope migration, forcing elevational squeeze and range extirpations, and if recolonizations from adjacent ranges were unlikely, why is limber pine present in so many ranges? Further, why do many apparently relict stands of limber pine — often the only occurrence of the species in a range — occur at low elevations (Fig. 2*b*)? Using the GB as a case study, we hypothesize that unique environments exist, which, owing to their topographic and microclimatic conditions, maintain relatively cooler and wetter conditions compared with adjacent contexts during warm and dry intervals. These locations might be favored as refugia for cool-adapted GB conifers such as limber pine. We further hypothesize that refugial environments are characterized by low-elevation ravine and riparian (canyon bottom) environments (hereafter, LERR) that experience cold-air drainage (CAD). In this study, we test predictions using new data on limber pine distribution and climatic relationships:

1. the percentages of limber pine stands occurring in LERR contexts are greater than expected based on the geographic representation (proportion) of these environments in GB mountains;
2. climatic conditions, including atmopheric lapse rates and soil-moisture conditions, of LERR contexts provide conditions similar to, or more favorable than, upland slopes of typical subalpine contexts.

Materials and methods

Geographic representation

Vegetation maps or GIS layers that would allow the geographic distribution of limber pine to be evaluated do not exist for the GB at the resolution needed. To estimate the distribution of limber pine occurrences in LERR locations relative to other contexts, we used a database of modern occurrence records developed for the *Atlas of Nevada Conifers* (Charlet 1996) and additional records from a second edition (D.A. Charlet, unpublished). Occurrence records derive from all mountain ranges with suitable habitat for limber pine in Nevada and specify individual, georeferenced, native trees, indexed by local site within mountain range. Records derive from experienced botanists and were sourced from published literature, verified field observations, or herbarium records; 95% of all occurrence records are verified with herbarium voucher specimens.

Each limber pine record included information on environmental context, based on six categories: ravine–riparian, which we tentatively categorized as LERR; rock–cliff; hydrothermally altered soils; upland slopes; nivation slopes (concave); and pass. We confirmed the location of each LERR record with ArcGIS (Environmental Systems Research Institute (ESRI) 2015) and Google Earth Pro (vs. 7.3.0; google.com/earth). In that we were interested in potential low-elevation refugial occurrences, where limber pine distribution was widespread in a range (i.e., records spanned >300 m elevation), we evaluated only records that occurred in the lowest quartile of the elevation span for that range. Where limber pine had unusually restricted elevation spans in a range (≤300 m), we used all records available in the assumption that these occurrences represent relict populations. In both cases, records were tallied by range to estimate the percentage of the total number that was located in LERR contexts.

Canyon and ravine bottoms account for a very small proportion of area relative to the total surface area of GB montane landscapes. To evaluate whether limber pine is overrepresented in LERR environments, we assessed the mean proportion of LERR landforms relative to the five other categories in the limber pine atlas database. An assessed value of 1% was derived from a range given as 1%–3% for GB riparian ecosystems (Jewett et al. 2004) and estimations that we made for a set of 10 watersheds across the distribution of limber pine in Nevada. From the latter exercise, a value of 1% is likely much greater than the actual proportion.

Climate and ecohydrology

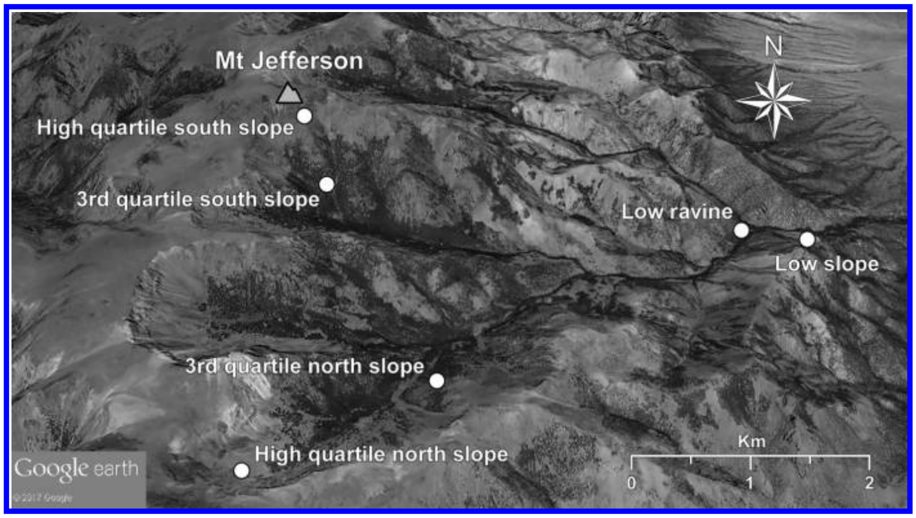
We used two approaches to assess environmental conditions for limber pine LERR locations relative to upland sites. In the first approach, we modeled climate values for a dataset that included observed occurrences (LERR sites) and remotely detected occurrences (upland locations). For LERR reference sites, we selected 77 field-observed records of limber pine (Supplementary Table S1[1]). We chose records that were disjunct from one another and occurred at low elevations relative to the distribution of limber pine in the corresponding mountain range; cumulatively, these sites represented the geographic spread of limber pine across mountain ranges in the GB. Lowland slopes adjacent to the LERR trees were typically vegetated with pinyon–juniper or mountain-mahogany woodlands and (or) sagebrush shrublands.

To compare conditions of LERR reference trees with limber pine stands on upland slopes, we used Google Earth imagery to identify high-elevation locations of limber pine above each of the 77 LERR trees. Limber pine can be distinguished in most mountain ranges because it is the only subalpine conifer species present. Where it is sympatric with other conifers, pines can be readily distinguished from non-pines by crown shape and crown density. Limber pine can be distinguished with high confidence from bristlecone pine where these species co-occur by crown form and by color and density of foliage on branches. Most of our selected locations are known by us to be valid from field surveys.

For each LERR tree, we selected a maximum of four points located in typical upland slope limber pine forests, including two points centered within the uppermost elevation quartile for the species in the range, one each on north and south aspects, and two points centered within the third highest quartile, one each on north and south aspects (Fig. 3). We selected points only when limber pine forests occurred on these slopes, thus not every LERR tree had four upland points associated with it. A fifth point was selected at a similar low elevation to each LERR tree on a north slope adjacent to the ravine, but out of the ravine base. In total, the locations, including the LERR reference tree and slope locations, summed to 361 points across 33 mountain ranges. For each

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2017-0374.

Fig. 3. Example of locations for limber pine climatic and ecohydrologic analysis. “Low ravine” is the field-observed reference limber pine site at the low-elevation, riparian–ravine (LERR) context; “low slope” is an adjacent slope site at the same elevation as the LERR site but not in the ravine; 3rd quartile and high-quartile north and south slopes are centers of limber pine stands at 3rd highest and highest quartiles on north and south aspect slopes, respectively. In cases where limber pine stands did not occur on the upper north or south slopes, a sample was not included. Image of Pine Creek Canyon, Toquima Range, Nevada; Google Earth, ©2017 Google.



point, we compiled latitude, longitude, elevation, and aspect data in ArcGIS (Environmental Systems Research Institute (ESRI) 2015).

For these points, we evaluated recent (1981–2010) climatic conditions using 3-arcsec (90 m grid) PRISM temperature data supplied by Chris Daly (downscaled for position, slope, and solar loading; Oregon State University), extracting data for annual, July, August, and September minimum and maximum temperatures (Tmin and Tmax, respectively). We also extracted annual precipitation and July minimum and maximum vapor pressure deficit (VPD) data from the 30-arcsec (~800 m grid) PRISM model (1981–2010 normals; Daly et al. 1994). We intersected these data with locations of the 361 limber pine reference points.

Atmospheric lapse rates were calculated as the differences in temperatures, standardized to 1000 m intervals, between the low ravine and low slope locations, respectively, to upper slope points. Under standard atmospheric conditions, temperature decreases with increases in elevation and, thus, lapse rates are negative. The standard lapse rate for our region is approximately −6.5 °C per 1000 m (Maurer et al. 2002). Under certain atmospheric conditions (e.g., inversions or cold-air pooling) and in highly localized environmental contexts, temperatures can warm with increasing elevation and lapse rates become positive. Where lapse rates differ from standard rates, local microclimatic processes are likely to be decoupled from free atmospheric conditions (Daly et al. 2010). We used the combined July–August–September (summer) Tmin and Tmax for each range to estimate lapse rates.

To evaluate soil-water relationships, we modeled climatic water deficit (CWD) for the 361 limber pine points using the 270 m Basin Characterization Model (BCM, 1981–2010 normals; Flint et al. 2013) and following the approach of Millar et al. (2015). CWD is a measure of moisture availability to plants as indicated by evaporative demand that exceeds available water; values range from zero, when soils are fully saturated, to positive with no upper limit. In other GB studies, CWD correlated better with limber pine growth than did climatic variables (Millar et al. 2012). Differences in temperature, precipitation, VPD, and CWD were assessed among ranges, topographic position, and aspect by a factorial model ANOVA but excluding interactions because of imbalances. Errors (residuals) in the models were normally distributed for temperatures and CWD and nearly normal in precipitation. Differences in topographic position were assessed by paired tests. To examine changes in temperature and CWD over the 1940–2015 period of record, we also conducted a mixed-model ANOVA of annual data, with the position × year interaction to test heterogeneity of the regression slopes by the four positions.

In the second approach to assessing conditions at LERR locations relative to upland sites, we directly measured field temperatures. At a subset of limber pine sites, we deployed thermochrons (Maxim iButtons, programmed and deployed as in Millar et al. 2015) along elevational transects that spanned seven mountain ranges containing limber pine in eastern California and Nevada. Each transect included at least one LERR limber pine, as well as mid- to upper-slope and high-slope locations, the latter two within typical upland limber pine forests. Thermochrons were deployed in different years, depending on the mountain range, starting in 2006. Data were last downloaded in autumn 2016. The 22 thermochron locations included 2–9 years ($\bar{x} = 6$) of data. For analysis, we used summer values and evaluated mean annual, daily, and 4 h periodic Tmin and Tmax. Lapse rates were calculated as above. Differences in observed temperatures and lapse rates were assessed among ranges, locations in ranges, and topographic position by a factorial model ANOVA with interactions.

We calculated total daily solar radiation using the solar radiation tool in ArcMap (Fu and Rich 1999) for a sample of limber pine watersheds. The solar analyst tool uses aspect and slope from a 30 m digital elevation model (DEM) to derive a measure of total daily clear-sky radiation (diffuse and direct). We selected the single-day period of 15 August to represent total solar radiation during peak summer heat and drought, a date used for similar reasons in other GB analyses (Van Gunst et al. 2016; Jeffress et al. 2017). We selected 11 watersheds for analysis from the records used for climate analysis (Fig. 1) and calculated solar loading for ravine bottoms at LERR sites and their respective highest elevation quartile north- and south-aspect limber pine stands. Differences in solar radiation sums among positions and aspects were assessed with a factorial ANOVA.

Results

From the newly compiled conifer atlas, we extracted 252 limber pine records spanning 43 mountain ranges to analyze topographic position (Table 1). For 11 mountain ranges with limber pine records limited to ≤300 m elevation distribution, 45% of the total records occurred in LERR contexts. For ranges where limber

Table 1. Occurrence (%) records for limber pine in low-elevation riparian–ravine (LERR) contexts.

(A) Mountain ranges with elevation spans of limber pine ≤300 m

No. of mountain ranges	Mean minimum elevation (m)	Mean maximum elevation (m)	Elevation span (m)	Total no. of records	% LERR mean
10	2390	2491	101	20	45

(B) Mountain ranges with elevation spans of limber pine >300 m

No. of mountain ranges	Mean minimum elevation (m)	Mean maximum elevation (m)	Elevation span (m)	No. of records: Total	No. of records: Low quartile	% LERR low quartile mean
33	2251	2907	656	232	70	69

Note: (A) Records limited to an elevation span of ≤300 m within a mountain range. Percent LERR evaluates all records for those ranges. Mountain ranges: Antelope, Bodie, Buck Creek, Butte, Copper, Grapevine, Kern, Pine Grove, Piñon, Tuscarora. (B) Records with an elevation span of >300 m within a mountain range. Percent LERR evaluates only records from the lower quartile of the elevation span for that range. Mountain ranges: Anchorite, Cherry Creek, Duck Creek, East Humboldt, Egan, Fish Creek, Fox Creek, Goshute, Grant, Groom, Hot Creek, Independence, Jarbidge, Mary's River, Mahoghanies, Monitor, Pequop, Pine Forest, Quinn Canyon, Roberts, Ruby, Santa Rosa, Schell Creek, Sheep, Shoshone, Snake Range, Spring, Sweetwater, Toiyabe, Toquima, Wassuk, White, White Pine. In both cases, the range of % LERR across the mountain ranges was 0%–100%.

pine records extended >300 m in elevation, 69% of the lowest elevation quartile records were in LERR contexts. These percentages were so large relative to the estimated proportion of landscape area in LERR contexts that statistical analysis to test excess representation was unnecessary.

Of the 361 reference points used for climatic analysis, the 77 LERR tree locations had mean elevation of 2236 m, and the highest slopes supporting limber pine had mean elevation of 3112 m (Table 2). PRISM-modeled climate data estimated the 77 limber pine LERR sites to be warmer in minimum and maximum summer temperatures and drier in annual precipitation than respective upper-elevation limber pine slopes ($p < 0.01$). By contrast, the LERR sites were cooler and wetter than the respective low-elevation north-slope locations ($p < 0.001$). LERR sites had significantly higher maximum July VPD values than the highest north-aspect sites only ($p = 0.0102$); VPD values were not significantly different for LERR sites relative to third-quartile north- and south-aspect slopes and for LERR sites relative to the highest south-aspect sites (Table 2). CWD means were significantly higher for the LERR context than for the upper slope positions ($p < 0.0001$), although significantly lower than for the adjacent low-slope locations ($p < 0.0005$). CWD means were significantly higher on upper south aspects than on upper north aspects ($p < 0.01$).

Mean lapse rates based on PRISM data were significantly larger (less negative; $p < 0.0001$) when calculated between LERR contexts and the highest quartile slope positions ($\bar{x}$ = −3.2 °C per 1000 m for Tmin; −6.7 °C per 1000 m for Tmax) than mean lapse rates calculated between the third-highest quartile and highest elevation slopes ($\bar{x}$ = −6.1 °C per 1000 m for Tmin; −8.4 °C per 1000 m for Tmax; Table 2). The Tmin lapse rate for the LERR context had significantly greater values — including large positive values — than the regional standard rate ($p < 0.0001$) and values nearly equal to the standard rate in Tmax. By contrast, the high slopes had Tmin lapse rates nearly equal to the standard value and Tmax lapse rates were smaller (more negative) than the regional standard. Expected mean Tmax based on elevation differences and observed upper slope lapse rates for LERR Tmin would be 11.0 °C and 25.7 °C, which is 2.7 °C and 1.4 °C warmer than the Tmin and Tmax values estimated by PRISM for the LERR locations, respectively. Plotting all PRISM-extracted summer precipitation and summer Tmin values together for the LERR and upper slope limber pine locations revealed that many LERR locations were cooler and wetter than upland slopes supporting limber pine stands (Fig. 4). In many cases, LERR values overlapped those of the upper slope in one or both climate variables.

Thermochron-derived temperatures observed along elevation transects in seven GB mountain ranges corroborated that LERR positions were cooler than expected based on their low elevations (Table 3). In some locations, and at certain times of the day, summer Tmin and Tmax and mean temperatures at the low reference location were lower than or similar to temperatures at locations on mid- and high-elevation slopes (Fig. 5). Differences in summer hourly temperatures between LERR and upland sites were smallest at night and in the mornings (Tmin) and highest at midday to early evening (Tmax). Summer Tmin lapse rates further documented the relative coolness of the LERR contexts. Rates calculated by time of day indicated the diurnal cooling effect. At the Wassuk Range sites (Fig. 5*a*), for example, mean lapse rate at 0400 h was −0.2 °C per 1000 m (range, 0.2 to −0.5 °C), while at 1600 h, the mean rate was −6.9 °C per 1000 m (range, −6.1 to −7.5 °C). Considering overall summer rates based on LERR locations relative to successively higher points along elevational transects, all lapse rates were significantly larger (more positive; $p < 0.001$) than the regional standard lapse rate and ranged from −4.9 to 17.5 °C per 1000 m ($\bar{x}$ = 0.1 °C per 1000 m) (Table 3).

Solar radiation values were significantly different among aspects, with south-aspect slopes receiving 50% more radiation than north-aspect slopes and LERR sites ($p = 0.013$), whereas elevation differences for the same aspects were not significant. Solar radiation at the LERR sites (2947 $W{\cdot}m^{-2}$) was significantly lower than on the highest south-aspect slopes (3759 $W{\cdot}m^{-2}$) and non-significantly different from that on the highest north-aspect slopes (2525 $W{\cdot}m^{-2}$). A plot of 30 m solar radiation values for a low ravine with limber pine illustrates low radiation along the canyon bottom and north aspect and a sharp gradient to high loading on the opposite slope (Fig. 6).

Discussion

Several types of data provide evidence that LERR environments support refugial conditions for limber pine in the GB. The finding of 64% of limber pine occurrence records across 43 mountain ranges in LERR contexts documents a much higher proportion in LERR locations than expected on the basis of proportionate representation among contexts. Although detailed information does not exist on the proportion of topographic conditions constituting the GB mountains, by far, most mountain area capable of supporting conifers comprises slope landforms. From a physiographic standpoint, ravine bottoms and riparian areas contribute little land area to mountain regions (Jewett et al. 2004), making the observed occurrence of limber pines in these sites strikingly high. This is even more disproportionate in that the LERR records were often located considerably below the primary elevation distributions of the species. That this finding might pertain to other montane conifers in the GB is suggested by the high proportions

Table 2. Climate and hydroecologic conditions and lapse rates for limber pine in low-elevation riparian–ravine (LERR) contexts compared with slope contexts in 33 Great Basin mountain ranges.

(A) Climate and ecohydrology

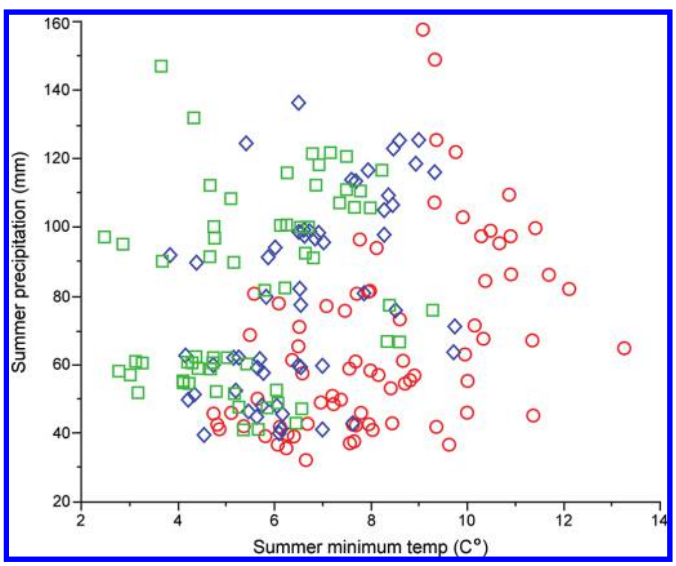
			Summer temperature (°C)								July VPD (kPa)			
	Elevation (m)		Tmin		Tmax		Annual precip. (mm)		Annual CWD (mm)		Maximum		Minimum	
Topographic position	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
LERR	2236	169	8.5	2.3	24.9	1.6	473	150	712	156	29.8	3.3	7.1	2.1
Low slope (non-LERR)	2234	169	8.7	2.2	27.0	1.6	446	143	733	134	31.3	3.6	7.2	2.3
3rd highest quartile slope (north)	2818	189	6.4	1.3	20.8	1.1	606	137	436	109	23.8	2.7	6.6	1.4
3rd highest quartile slope (south)	2939	121	6.3	1.1	20.2	1.1	659	145	582	99	22.9	2.2	7.2	1.0
Highest quartile slope (north)	3031	204	4.9	1.0	18.7	1.1	733	209	393	138	20.2	2.5	5.6	1.3
Highest quartile slope (south)	3192	149	4.3	1.3	18.1	1.2	717	160	514	121	20.5	2.8	6.2	1.1

(B) Lapse rates

	Lapse rate (°C per 1000 m)	
Relative positions	Tmin	Tmax
LERR : highest quartile north	−3.6	−6.9
LERR : highest quartile south	−2.8	−6.1
Low slope : highest quartile north	−3.9	−7.7
Low slope : highest quartile south	−3.1	−6.2
3rd highest quartile north : highest quartile north	−5.9	−8.3
3rd highest quartile south : highest quartile south	−6.2	−8.5

Note: Mean and standard deviation (SD) from 77 reference LERR limber pine records, with 361 records in total, in California and Nevada. Refer to Materials and methods for explanation of locations and record numbers. (A) Summer (July–August–September) minimum and maximum temperatures (Tmin, Tmax), annual precipitation (precip.), annual climatic water deficit (CWD), and July minimum and maximum vapor pressure deficits (VPD). Temperature data are from 3-arcsec 1981–2000 historic normals, PRISM model (from Chris Daly, Oregon State University); precipitation and CWD values were developed with the Basin Characterization Model (Flint et al. 2013), and VPD values are from the 30-arcsec PRISM model (Daly et al. 1994). (B) Lapse rates among topographic positions, based on summer minimum and maximum temperatures (Tmin and Tmax, respectively) from 3-arcsec PRISM.

Fig. 4. Scatter diagram showing summer precipitation and summer minimum temperatures (temp) for low-elevation riparian–ravine (LERR) limber pine reference trees and corrresponding limber pine locations on upland slopes. Circles represent LERR trees, diamonds are third-quartile upland slope locations, and squares are fourth-quartile (highest) upland slope locations. [Colour online.]



of LERR occurrences found for 14 other species (mean 61%, range 37%–89%; unpublished atlas data).

A caveat for these results lies with the data used. Being non-randomly sampled occurrence records, the database might not accurately represent the distribution of the species and be biased toward accessible locations. These were not, however, “convenience samples”, and the experienced botanists who recorded the observations sought to document representative and distributed occurrences, including unexpected habitats and elevations, as well as common settings. The total number of records, and representations across many mountain ranges, provide large sample sizes and redundancy.

Climate modeling for limber pine in LERR contexts added supporting evidence for the refugial nature of LERR contexts. The 84 reference trees used for PRISM and BCM estimations and direct thermal measurements were selected to represent limber pines in LERR environments, while the upland sites represent the typical species distributions (Elliott-Fisk and Peterson 1991). While we found that the disjunct, low outliers lie in generally warmer and drier climate zones than respective stands on upland slopes of the same watershed, when all points were considered together (a climate envelope estimate), LERR sites greatly overlapped climate space of upland sites. A considerable proportion of LERR sites had cooler and (or) wetter conditions than upland slope forests. Values of minimum VPD were not significantly greater for LERR than upland slopes, corroborating expected moist atmospheric conditions in ravine bases relative to their elevations. Further, from PRISM, BCM, and observed data, the LERR locations had cooler and wetter conditions and moister soils, than non-limber pine slope locations at similar elevations.

Especially important in evaluating the LERR environments are the differences in lapse rates of the LERR sites to high slope positions from rates calculated along gradients of the upper slope forests. Using the latter rates would imply much warmer temperatures for LERR positions than observed. Further, the occurrence of lapse rates significantly different from the standard regional atmospheric value, including small negative values and positive rates, provides evidence for decoupled microclimates in LERR environments. Decoupling appears to promote stably cooler conditions at LERR sites than expected for their elevations and likely partly results from CAD occurring during the nights, with cool air pooling in canyon bases and forming inversion conditions (Daly et al. 2007). Shading, as expected in narrow canyon bases and corroborated by low solar radiation, would further decouple these

Table 3. Thermochron-observed temperatures and lapse rates for limber pine in low-elevation riparian–ravine (LERR) contexts and slope location of limber pine sites.

Location; topographic position	Elevation (m)	Temperature (°C) Annual Tmax	Annual Tmin	Annual Tmean	Summer Tmax	Summer Tmin	Summer Tmean	Lapse rate (°C per 1000 m)
Sierra Nevada								
Lundy; mid slope	2902	11.0	1.7	5.6	18.5	8.9	12.8	
Lundy; high slope	2958	10.5	1.7	5.3	17.9	9.0	12.5	1.4
Glass and White Mountains								
Owens Gorge; LERR	2045	14.3	−0.9	6.1	25.2	7.2	15.6	
Owens Gorge; top slope	2144	15.0	−0.2	6.4	26.6	8.7	16.8	15.5
Cell Phone Ravine; LERR	3058	8.3	−0.7	3.2	17.5	7.4	11.6	0.2
Schulman; mid slope	3100	6.7	−0.3	2.9	16.7	8.2	11.8	0.9
Relay Ridge; mid slope	3204	7.4	−1.0	2.6	17.5	7.5	11.7	0.3
Patriarch; high slope	3547	3.5	−2.9	0.2	12.8	5.8	9.1	−0.9
Bighorn Peak; high slope	3556	4.2	−2.8	0.3	13.7	5.7	9.0	−1.0
White Mountains								
Cell Phone Ravine; LERR	3058	8.3	−0.7	3.2	17.5	7.4	11.6	
Schulman; mid slope	3100	6.7	−0.3	2.9	16.7	8.2	11.8	17.5
Relay Ridge; mid slope	3204	7.4	−1.0	2.6	17.5	7.5	11.7	0.4
Patriarch; high slope	3547	3.5	−2.9	0.2	12.8	5.8	9.1	−3.3
Bighorn Peak; high slope	3556	4.2	−2.8	0.3	13.7	5.7	9.0	−3.6
Sweetwater Mountains								
Sweetwater Cyn; LERR	2326	13.0	1.1	6.5	21.6	8.6	14.5	
Sweetwater Cyn; high slope	3011	8.3	0.5	3.7	16.1	7.6	11.0	−1.4
Wassuk Range								
Corey Cyn; LERR	2099	12.6	1.5	6.8	23.2	9.6	15.9	
Big Indian Mountain; high slope	2968	6.6	0.2	3.3	16.8	10.1	12.8	0.6
Toquima Range								
Pine Creek; LERR	2408	11.1	1.1	5.8	22.7	11.2	16.5	
Pine Creek Cirque; high slope	3263	4.8	−1.4	1.5	15.3	8.4	11.6	−3.3
Pine Creek treeline; high slope	3436	4.6	−2.6	0.6	15.0	7.4	10.6	−3.7
Snake Range								
Pole Cyn; LERR	2109	14.1	2.3	7.4	27.3	13.3	19.1	
Lower Lehman; LERR	2249	12.4	2.6	7.1	24.4	13.2	18.2	−0.4
Wheeler Road; mid slope	2930	6.9	−0.1	3.4	17.8	10.2	13.9	−3.7
Brown Lake; mid slope	3016	6.3	−1.6	2.1	18.1	8.9	12.8	−4.8
Bald Mountain; high slope	3210	6.2	−2.4	1.5	17.1	7.9	11.9	−4.9
Mt. Wheeler treeline; high slope	3407	3.1	−2.9	−0.2	14.5	7.3	10.3	−4.6
Means								
LERR	2501	11.6	0.7	5.6	21.7	9.2	14.7	
High slope	3322	5.3	−1.8	1.4	15.2	7.5	10.8	
Lapse rate								0.1

Note: Annual and summer (July–August–September) maximum, minimum, and mean temperatures (Tmax, Tmin, Tmean, respectively). Lapse rates were based on summer minimum temperatures and represent comparisons of low-reference trees with respectively higher slope limber pine locations.

sites from warmer and drier conditions otherwise experienced at these elevations.

Caveats regarding the climate data relate to the capacity of thermochrons and models to faithfully represent conditions for localized and specific habitats such as narrow ravine bases. These topographic features have very small area with steep relief, and, thus, model tile elevations do not accurately resolve the specific ravine bases. Processes such as shading and CAD further confound modeling accuracy. Relative to thermochron values, PRISM estimated warmer summer Tmax temperatures and cooler summer Tmin temperatures; these differences were mostly smallest for the LERR locations and greater at upslope positions.

Implications for LERR environments as refugial contexts

Dobrowski (2011) outlined a theoretic framework for terrain-based climate refugia in temperate mountain landscapes, emphasizing that for refugia to exist and persist, their microclimatic processes must be decoupled from regional trends, otherwise they would be short-lived (see also Hampe and Jump 2011). Our analyses corroborate reports wherein terrain influences appear to promote decoupling in canyon bottoms (Dobrowski 2011; Hampe and Jump 2011; Gentili et al. 2015). Decoupling is promoted via greater topographic shade, lower solar loads, and CAD processes, resulting in larger lapse rates (greater positive values) than expected and collectively leading to locally cool, moist conditions (Lundquist et al. 2008; Curtis et al. 2014). The association of these factors with lower winds (Dobrowski 2011), greater slope drainage from uplands (Jewett et al. 2004), shading from riparian vegetation (Birks and Willis 2008), and thermal stability as a result of higher humidity (Caissie 2006; Hampe and Jump 2011) would be expected to lead to lower evaporative stress and to maintain high soil-water availability in canyon bottoms relative to adjacent slopes (Curtis et al. 2014). Thus, despite the relatively warmer

Fig. 5. Representative hourly summer temperatures averaged over the period of record at low-elevation ravine–riparian (LERR) limber pine sites versus adjacent upland pine stands: (*a*) Wassuk Range, Nevada: Corey Canyon (low ravine; 2099 m) and Big Indian Mountain (high montane slope; 2968 m); (*b*) volcanic tablelands and White Mountains, California: Owens Gorge (extramarginal low ravine; 2045 m); Cell Phone Ravine (low ravine; 3058 m); Schulman Grove (high montane slope, 3098 m).

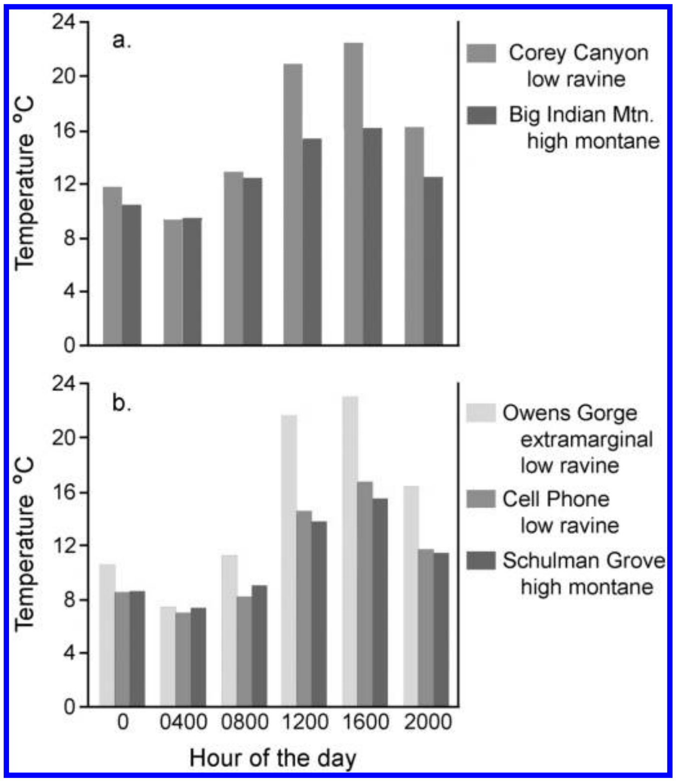
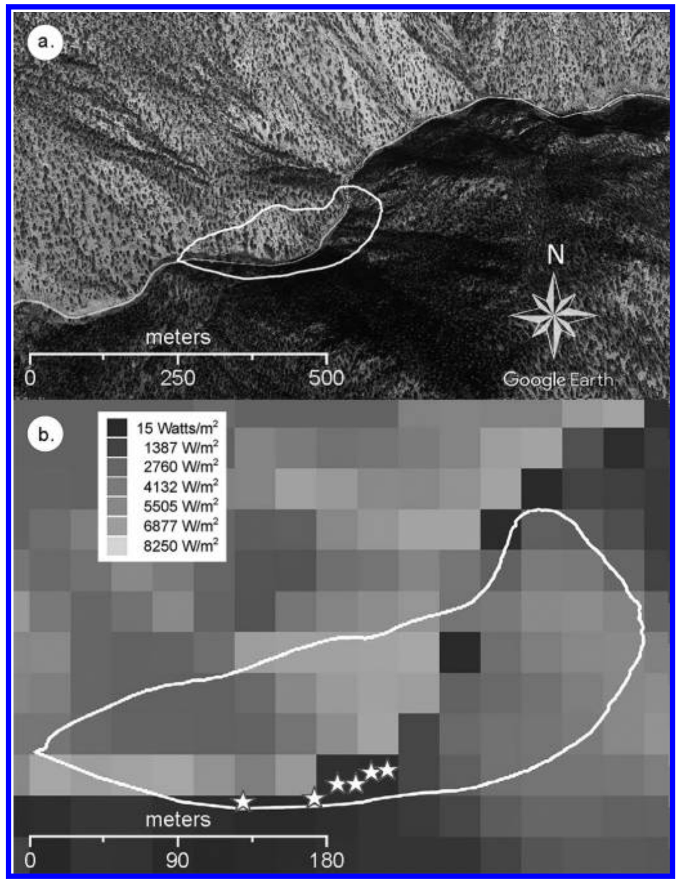


Fig. 6. Solar loading along a low-elevation ravine, Corey Canyon, Wassuk Range, Nevada, showing a polygon that contains limber pines growing in the narrow riparian zone: (*a*) Google Earth image (©Google 2017) showing ravine base (scattered limber pines) and adjacent slopes supporting woodland conifers (*Pinus monophylla* – *Juniperus osteosperma*); (*b*) solar radiation plot for 15 August, from ArcMap. Squares are 30 m DEM tiles; shading indicates solar radiation loads (expressed in watts per square metre), with darker shades indicating lower solar loads and white indicating the highest load. Stars indicate low-elevation ravine limber pine trees.



temperatures and higher CWD values that we found in LERR sites relative to high-elevation conifer slopes, canyon bottoms generally appear to afford cool sites relative to uplands, and these should provide persistently lower water-stress conditions for conifers.

Water stress is an especially important limiting factor for upland conifers in semi-arid regions such as the GB (Crimmins et al. 2011; Dobrowski 2011). Notably, although pines generally require well-drained mineral soils for germination, seedlings of several upland species, including limber pine, are establishing in organic soils under dense low-canyon riparian forests of water birch (*Betula occidentalis* Hook.) and willow (*Salix* spp.) and persisting in these location into mature trees that emerge above hardwood canopies. These young pines witness the capacity of upland conifers to establish in humic soils and the importance of shaded, wet conditions. During hot, dry climate intervals, desiccating winds, high drainage, and evaporative stress on uplands slopes may reach critical thresholds limiting conifer growth, whereas we expect that low canyon bases would accumulate moisture and retain cool conditions adequate for trees to establish and persist.

Decoupled microclimates of canyon bottoms might provide refugia for GB conifers during cold intervals, as well as during warm periods. During late Holocene cold centuries such as the Little Ice Age (LIA, ~1450–1925 CE), temperatures at high elevations on upland slopes likely became limiting for conifer reproduction. Warmer temperatures and sheltered locations of canyon bottoms would then serve as refugia, as they apparently did for mountain conifers in Pleistocene cold periods (Birks and Willis 2008; Dobrowski 2011). Relict populations may have persisted from the LIA in GB mountains and continued to occupy these locations as late 20th-century climates warmed and dried. Thus, these contexts might serve as thermal refugia in cold periods and moisture-mediating refugia in dry intervals. If LERR environments do serve as refugial sites during both cold and dry periods, then limber pine occurrence should exhibit greater temporal persistence at such locations.

In sum, LERR limber pine sites are small-scale locations where decoupled microclimate factors enable more stable population processes over time compared with the rest of the range. Despite a strong theoretic basis for terrain-based warm-period refugia in mountain environments, evidence has been sparse to test hypotheses (Birks and Willis 2008; Dobrowski 2011). Our studies provide preliminary evidence that low-elevation ravine–riparian bottoms have characteristics to sustain limber pine and likely other conifers during warm, dry intervals, thus serving as climate refugia. For conservation planning, these environments, especially locations where conifers grow at present in otherwise sparsely populated GB ranges and mountains beyond this region, deserve priority for further delineation, monitoring, and protection.

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