CHAPTER M3

HISTORICAL BIOGEOGRAPHY OF SINGLELEAF PIÑON IN THE GREAT BASIN

CONSTANCE I. MILLAR AND DAVID HURST THOMAS

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CHAPTER M3
HISTORICAL BIOGEOGRAHY OF SINGLELEAF PIÑON PINE IN THE GREAT BASIN

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The transition from Late Pleistocene to Holocene climates triggered biogeographical upheavals worldwide that included species' range shifts, changes in community composition and structure, altered disturbance regimes, and development of new ecological interactions.[1] The Great Basin, with its hundreds of high mountain ranges interspersed by broad basins, was a prominent stage on which such dynamics unfolded. Many plant and animal species remained scattered at low elevations throughout the Great Basin during the cold Late Pleistocene. Without significant displacements in latitude, they responded to Holocene warming by migrating upslope in elevation where they found favorable habitat. Singleleaf piñon pine (*Pinus monophylla,* hereafter "piñon") was unusual among Great Basin tree species for its long-haul Holocene migrations in the Great Basin. The story of piñon's progress, from its absence in much of the Great Basin to its current widespread dominance (fig. M3-1), is the focus of this chapter.

Others have outlined piñon's dramatic history (e.g., Lanner, 1983; Wigand and Nowak, 1992; Woolfenden, 1996; Lanner and Van Devender, 1998; Grayson, 2011; Cole et al., 2012; Wigand, 2017), so why a new summary? Our goals are fourfold: 1) to reassess published piñon migration dates using the most current radiocarbon calibrations, 2) to add locations newly recognized, 3) to reassess piñon's migration processes and propose a new hypothesis for multiple Pleistocene piñon refugia, and 4) to provide background for assessment of human biogeography

[1] We respectfully acknowledge the pioneering work of piñon scholars Ronald Lanner and Kenneth Cole (both deceased), who set the foundation and standards for subsequent analysis. We thank Dave Rhode and Peter Wigand for generously sharing information on piñon sites and Wally Woolfenden for consultation on discriminating piñon from pollen samples. David Charlet, Donald Grayson, Chrissy Howell, Lisbeth Louderback, Dave Rhode, and Bob Westfall provided critical reviews, which we greatly appreciate. We thank Lorann Pendleton and Diana Rosenthal-Roberson for editorial review of the manuscript and Tom Blaber, Anna Semon, and Kayla Younkin for rendering the figures.

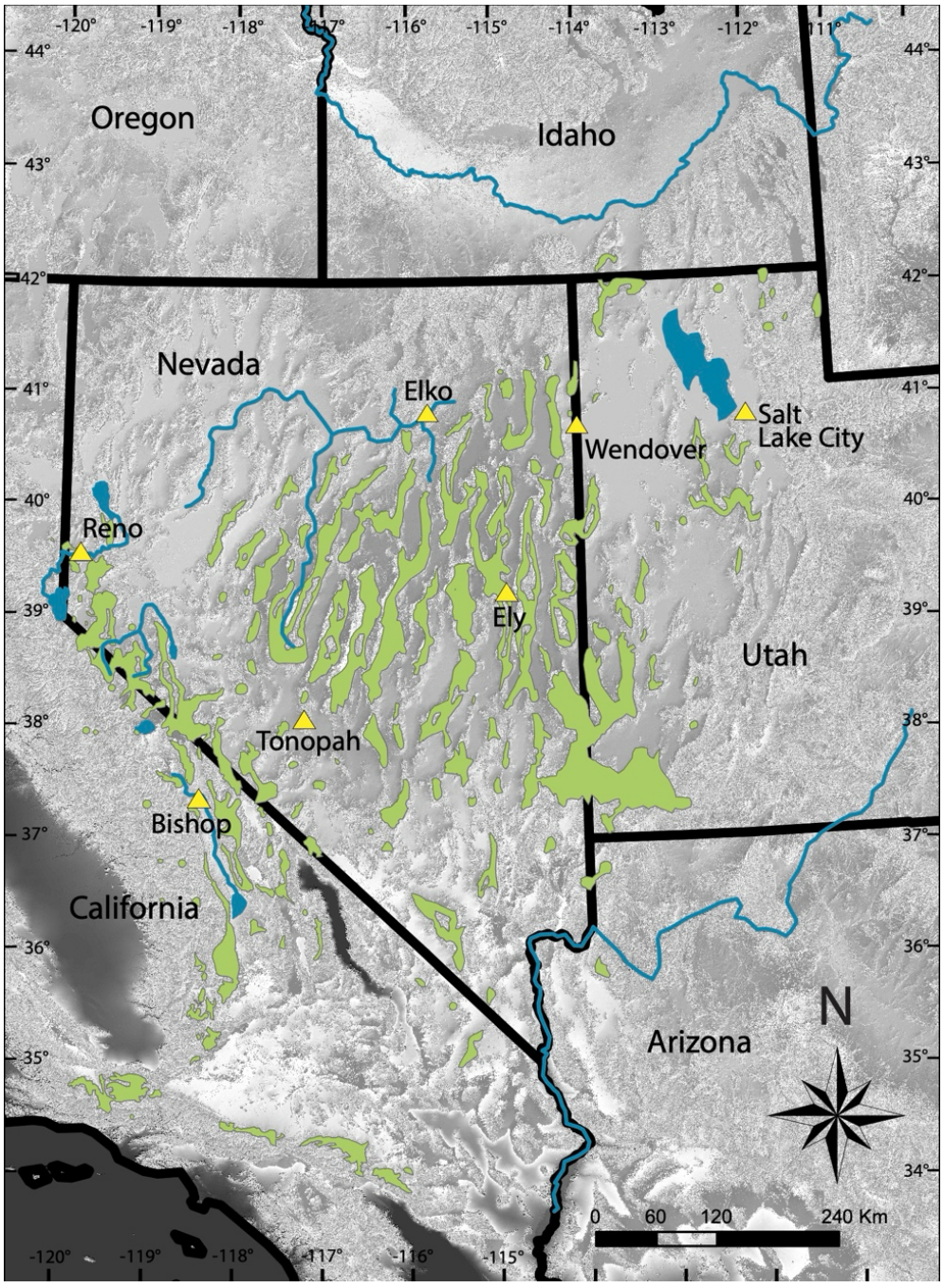

FIG. M3-1. Current known distribution of singleleaf piñon pine in southwestern United States. Source: Data Basin, databasin.org, accessed September 5, 2023. Reported but undocumented piñon stands in the Warner Mountains, northwest Great Basin, are not included.

in the Great Basin (chap. E). In so doing, we aim to illuminate the hand-and-glove relationship of people to piñon.

A TAXONOMIC DISCLAIMER: THE SYNGAMEON DILEMMA

Many pine species form occasional hybrid individuals among close relatives. The group of piñon species in the American Southwest (subsection *Cembroides*), however, is particularly promiscuous. Where species come into contact, they regularly form hybrid zones, and those hybrid populations can take off on their own evolutionary path as nascent new species. Until the molecular revolution brought methods to unveil these dynamics at the DNA level, studies of possible hybridization relied on morphological analysis. While informative, they were not definitive, as morphological analysis is confounded by a large amount of natural variation within the piñon species, variation that often mimics hybrid characteristics. Current studies of singleleaf piñon (*Pinus monophylla*) and its closest relatives in the American Southwest*, P. edulis, P. californiarum, P. quadrifolia, P. fallax*, and *P. juarezensis*, illuminate a complex maze of hybrid situations and emerging species within the group (Montes et al., 2022; Buck et al., 2023). This situation is referred to as a syngameon, denoting a multispecies interbreeding network having diverse evolutionary outcomes (Buck and Flores-Rentería, 2022; Buck et al. 2023)

Our focus in this chapter is on singleleaf piñon in the Great Basin. As part of the greater piñon syngameon, singleleaf piñon not only forms hybrid zones at its eastern overlap with *P. edulis* (Colorado piñon) and at its southern contact with *P. californiarum*, but individual trees show admixture in various singleleaf piñon core geographic regions with these and other taxa. The question arises: what species of piñon is in each of the 69 middens and one pollen sample we rely on for analysis below? In the midden studies, identification relied on morphology alone, and this was no doubt always made on number of needles/fascicle (note: other taxa than *P. monophylla* have single needles and "pure" *P. monophylla* populations naturally have about 2% two-needled fascicles). Fortunately genetic studies show most of the core range of singleleaf piñon in the central and northern Great Basin to be mostly "pure." At the eastern edge of its range, significant interbreeding with *P. edulis* comes into question. We deal with this in the pertinent section later. In the southern Great Basin, *P. monophylla* widely overlaps with *P. californiarum* and formed/forms admixed populations. This southern hybridization situation

likely has a long history among singleleaf and other piñon taxa as well. This Mojave desert region was, as we narrate below, a large, prolonged refugial area for *P. monophylla* and other piñons during the Late Pleistocene. No doubt it was a melting pot of interbreeding during that time. We (and others) admit defeat in trying to understand what genes might have been incorporated into *P. monophylla* during its stay in the Late Pleistocene southern refugium and then carried into the Great Basin in the Early Holocene; likely it was a genetic hodge-podge, mostly (but not all) sorted into pure singleleaf by now except at the range margins.

Recognizing this complexity, we accept the individual midden authors' determination of species from needle analysis, and use all middens that were identified as containing singleleaf piñon. We do, however, challenge identifications made from pollen in a northern Utah site, as described later.

METHODS USED TO IDENTIFY PIÑON MIGRATION: STRENGTHS AND WEAKNESSES

The path of piñon's Holocene migration has been reconstructed primarily from woodrat (*Neotoma* spp.) midden evidence. In that woodrats are common and abundant small mammals throughout the Great Basin (current and past), their middens are similarly widely distributed. Macrofossils of piñon (seeds, needles, wood) in middens can be securely identified and radiocarbon dated. The most reliable determinations come from directly dated piñon remains; lacking that, packrat scat or other associated foliage (often *Juniperus* spp.) has been used. Although radiocarbon dates previously processed by conventional methods can still be employed, ^{14}C dates produced by the Accelerator Mass Spectrometry method are more precise and require smaller sample sizes. Regardless of how derived, all radiocarbon dates must be calibrated using tree-ring or other controls to convert ages expressed in "radiocarbon years" to calendrical age estimates.

Although woodrats are considered to be cosmopolitan herbivores, meaning they forage on and cache a wide range of plant species, they do have dietary preferences. Piñon is not top on their list, and, thus, midden remains are not wholly unbiased samples of the surrounding landscape. Further, woodrats forage only short distances from their middens, with the estimate that vegetation within 20 m of the midden is incorporated in middens (given biases in diet), and vegetation beyond 50 m is not included (Cole et al., 2012). The short collection radius of

woodrats is a major limitation to understanding the historical biogeography of piñon. Especially under colonizing conditions, piñons may first appear in a new mountain range in a widely scattered distribution, and only decades or centuries later expand in density such that piñon material is incorporated in middens.

Another caveat about midden analysis is that woodrat populations, like piñon woodlands, shift in response to climates. In many cases, as climates changed, woodrats abandoned regions of the Great Basin, leaving no middens for analysis during the period of their absence (Betancourt et al., 1990; Wigand and Rhode, 2002; Grayson, 2011). A further caveat is common to assessments of species' historic ranges in general: our understanding of distributions is only as good as our ability to find and assess evidence (Grayson and Livingston, 1993).

In addition to middens, evidence from rockshelters has been used to elucidate piñon's migration path. Whether brought into caves by humans or scavengers, piñon remains have been identified and dated in time-series strata. A caveat about rockshelter evidence is that there is uncertainty whether piñon was growing in the close vicinity of the cave. Nut consumers, especially avian species and humans, can carry piñon nuts from some distance (e.g., Madsen and Rhode, 1990).

Pollen also has been used to track piñon's historic distribution in the Great Basin. This approach has limited value, however, as many pine species occur in the Great Basin and pollen is very difficult to identify to species, In addition, pine pollen is wind-dispersed and travels very far in great abundance. A few researchers (e.g., Woolfenden, 2003) have taken the time and care to separate "piñon-type" pollen successfully.[2] Otherwise, assigning identity to piñon is either a guessing game (that is, no other pine species would be near) or pollen is associated with piñon macrofossils. Importantly when piñon pollen can be identified, unlike midden remains, it can provide an advance indicator of the species occurring in the general region (Cole et al., 2012).

In our efforts to reassess piñon migration below, we searched the literature for the oldest midden or pollen locations by region containing piñon in the Great Basin. In cases where older strata in a midden—or an older midden in the proximity—lack piñon, we accept these to be

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[2] Although piñon-type pollen can be separated from other pine species, pollen grains of singleleaf piñon and Colorado piñon (*Pinus edulis*) cannot be distinguished morphologically, even by electron microscope. Species identity is inferred from associated macrofossils or from known prehistoric or modern distribution of each species (Bagnell, 1975; Jacobs, 1983, 1985; Cole et al., 2012).

"arrival dates;" otherwise, they represent the best available oldest date (maximum date), which might or might not be an arrival date.

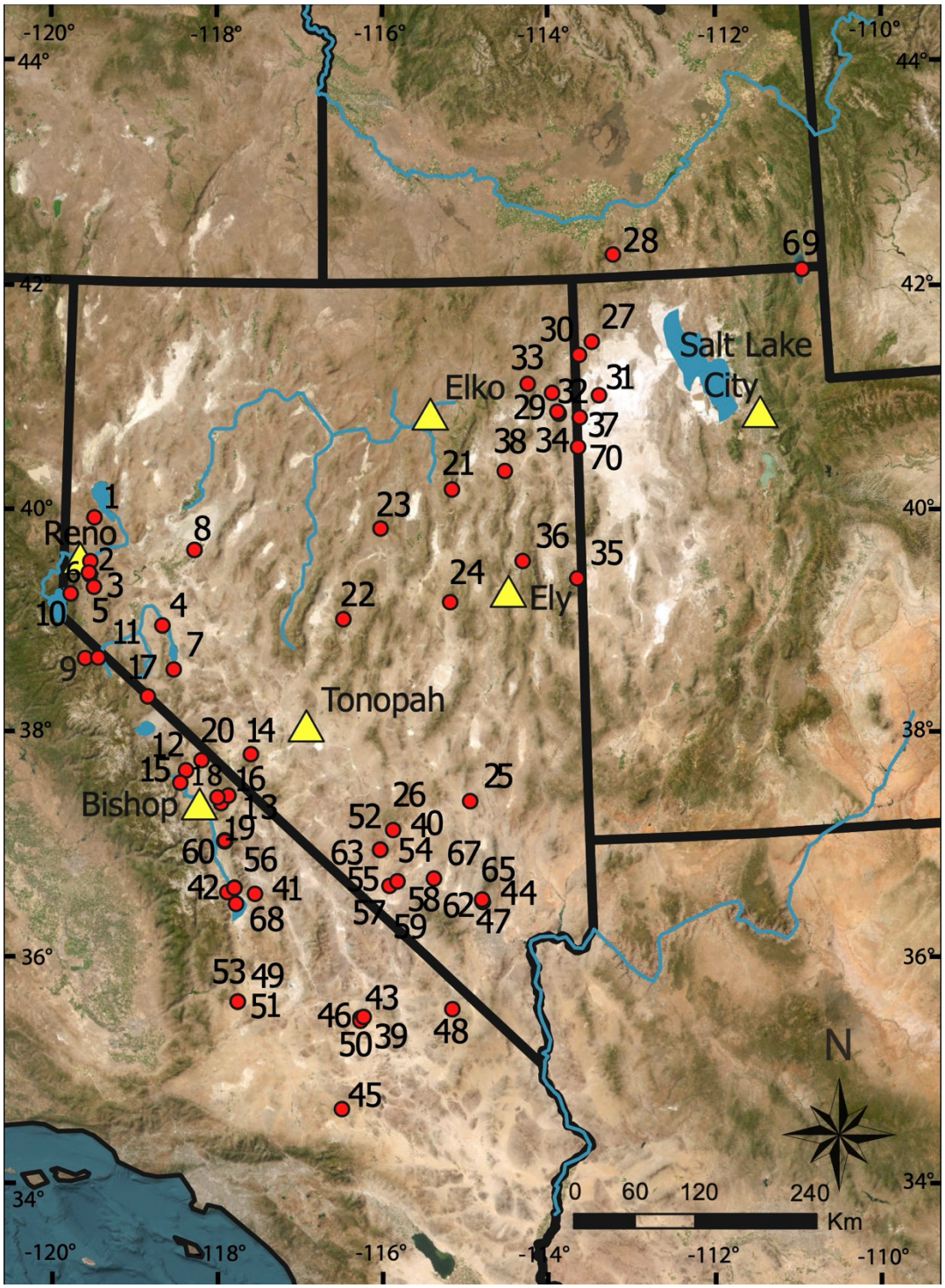

FIG. M3-2. Locations of Pleistocene- and Holocene-dated piñon in the Great Basin. Numbers refer to locations in table M3-1.

Table M3-1. Piñon Pine Late Pleistocene and Holocene Dates and Locations

Original radiocarbon dates have been revised, and a midpoint was calculated from the range for purposes of discussion only. Dates likely to be arrival times are indicated by "*," which is interpreted by lack of piñon in older strata of the same or nearby midden. Coordinates and dates estimated from publication informaton are noted with "~~." Divisions of western, central, and eastern Great Basin follow the traditional three migration paths outlined by Lanner and Van Devender 1998.

Map #, see figure M3-2	Location	Mountain Range/Basin	RCYR	Error, +/- yrs	Lab/Number	Cal yr B.P. range (revised data)	Midpoint of cal yr B.P. range	Longitude	Latitude	Elevation (m)	Citation
1. Western Great Basin											
1	*Painted Hills	Virginia Mountains	–	–	–	–	250; 297	39.90302	-119.65086	1616	First date is estimated age of oldest living tree in the early 1990s (Robin Tausch, USFS; Wigand and Nowak, 1992); second date derives from re-coring the same tree by Millar, Dec. 2023. Georeference: Millar, unpub. field observations, Dec. 2023
2	*Hidden Valley	Virginia Range	400	100	Beta-26016	151–633	392	39.489946	-119.693355	1632	Wigand and Nowak, 1992; Nowak et al. 1994a
3	*Newton Creek	Virginia Range	710	80	Beta-39750	541–775	658	~~39.370613	~~-119.694450	~~1600	Wigand and Nowak, 1992; Wigand, 2002
4	Schurz	Walker Lake Valley	890	70	Beta-35816	685–921	803	~~38.933109	~~-118.849724	1615	Wigand and Nowak, 1992; Nowak et al., 1994b
5	*Silver City	Virginia Range	1030	90	Beta-29160	734–1175	955	39.26248	-119.643598	1585	Wigand and Nowak, 1992; Nowak et al., 1994b
6	Geiger Grade	Virginia Range	1090	90	Beta-39755	792–1244	1018	~~39.388469	~~-119.707067	~~1548	Peter Wigand, personal commun., 5/4/23
7	Navy/Army Depot	Wassuk Range	1170	50	Beta-35803	958–1244	1101	~~38.543294	~~-118.711146	1676	Wigand and Nowak, 1992; Nowak et al., 1994b
8	Lead Lake, Carson Sink	Stillwater Range	1250	60	Beta-47198	1007–1293	1150	39.611546	-118.49808	1161	Wigand and Nowak, 1992; Wigand and Rhode, 2002
9	Wolf Creek	Zunnamed Range	1490	90	Beta-29 155	1189–1548	1369	38.625456	-119.720229	1798	Nowak et al., 1994b
10	Little Valley	Sierra Nevada	~~1500	NA	NA	–	~~1500	~~39.196908	~~-119.907713	2134	Wigand and Rhode, 2002; Wigand, 2017 (based on undifferentiated pine pollen)
11	*Slinkard Valley	Zunnamed Range	2150	75	Beta-5052I	1945–2336	2140	38.633495	-119.571863	1809	Wigand and Nowak, 1992; Nowak et al., 1994b
12	*Chidago Flats	White Mountains	3040	60	Beta-53077	3066–3382	3224	37.646354	-118.552408	2075	Jennings, 1995
13	Deep Springs Overlook	White Mountains	3290	70	A-4979	3373–3690	3532	37.358844	-118.155358	2682	Jennings and Elliott-Fisk, 1993
14	*Rhyolite Ridge	Silver Peak Range	3490	70	Beta-65683	3572–3964	3768	37.797489	-117.826316	1957	Jennings, 1995
15	*Sherwin Summit	Sierra Nevada	3610	70	Beta-163829	3812–4144	3978	37.535161	-118.614345	2074	Wigand, 2002
16	Wyman Canyon	White Mountains	4510	90	A-4984	4868–5445	5157	37.426362	-118.074386	2560	Jennings and Elliott-Fisk, 1993
17	*Dry Lake Plateau	Bodie Mountains	4980	80	Beta-106615	5591–5900	5746	38.298635	-118.998543	2382	Halford, 1998
18	Silver Canyon	White Mountains	5640	70	A-4982	6295–6620	6458	37.40913	-118.195523	3048	Jennings and Elliott-Fisk, 1993
19	Papoose Flat	Inyo Mountains	7880	60	Beta-86099	8547–8983	8765	37.022685	-118.109189	2609	Reynolds, 1997
20	Falls Canyon	White Mountains	8790	110	A-4981	9550–10159	9854	37.738715	-118.379941	1830	Jennings and Elliott-Fisk, 1993
2. Central Great Basin											
21	Bronco Charlie	Ruby Mountains	3050	150	A-2726	2866–3471	3169	40.149941	-115.516982	1886	Thompson, 1984
22	*Gatecliff Rockshelter	Toquima Range	5290	180	QC-289	5654–6404	6029	39.003255	-116.782834	2320	Thomas, 1983
23	*Roberts Mountains	Roberts Mountains	5640	25	PSU-6417	6318–6489	6404	39.81	-116.35	~~2601	Dave Rhode, personal commun., 5/26/23
24	*Cathedral Canyon	White Pine Range	6035	25	PSU-7091	6794–6489	6642	~~39.146412	~~-115.558408	~~1935	Dave Rhode, personal commun., 5/26/23
25	*Pahranagat Range	Pahranagat Range	9230	50	Beta 86072	10,248–10,555	10402	~~37.37	~~-115.37	~~2187	5/4/23
26	*Eleana Range	Eleana Range	10620	120	USGS-876	12,098–12,767	12433	37.121593	-116.234205	1805	Spaulding, 1983, 1985
3. Eastern Great Basin											
27	Grouse Creek Junction	NW Bonneville Basin	2400	30	Beta-351364	2347–2681	2514	41.433	-113.832	1466	Rhode, 2013
28	Almo Cr A-1	City of Rocks	2428	39	AA88-400	2351–2701	2526	42.123	-113.673	1600–2700	Weppner et al., 2013
29	Collar and Elbow	Toano Range	3040	30	Beta-351364	3165–3350	3258	40.99	-114.32	2122	Dave Rhode, personal commun., 5/26/23
30	Pilot Range	Pilot Range	3430	30	Beta-340985	3564–3815	3690	41.319	-113.988	1607	Rhode, 2013
31	Silver Island Canyon	Silver Island Range	4410	90	Beta-70606	4846–5296	5071	40.954	-113.77	1765	Rhode, 2000
32	Itchy Ban	Goshute Range	5070	50	Beta-82952	5661–5921	5791	40.802	-114.248	1802	Rhode, 2000
33	Icicle Cave ICD	Pequop Range	5340	40	Beta-120585	5998–6272	6135	41.076	-114.604	2242	Rhode, 2000
34	Marblehead Mine	Goshute Range	5960	90	Beta-73389	6557–7152	6855	40.821	-114.264	1808	Rhode & Madsen 1995; Rhode 2000
35	Council Hall Cave	North Snake Range	6120	80	WK-157	6789–7244	7017	~~39.331446	~~-114.095162	2041	Thompson, 1979; Thompson and Hattori, 1983

36	Valley View	Schell Creek Range	6250	150	A-2430	6785–7429	7107	39.499854	-114.716855	2350	Thompson and Hattori, 1983; Thompson, 1984
37	*Danger Cave	Silver Island Range	6710	70	Beta-43727	7432–7676	7554	40.763148	-114.004811	1314	Rhode and Madsen, 1998; Rhode, 2000
38	Cottonwood Canyon	Cherry Creek Range	7690	70	Beta-79087	8378–8595	8487	40.305	-114.8975	2105	Rhode, 2000
69	Bear Lake	Bear River Range				19,000–17,000; 15,000–present		41.982316	-111.294014	1806	Doner, 2009 (based on pollen differentiated as piñon type)
70	Blue Lakes Marsh	Bonneville Basin				<8000		40.5	-114.036	1297	Louderback and Rhode, 2019 (based on undifferentiated pine pollen)
4. Southern Great Basin											
39	No Name West	No Name Basin	9910	90	Beta-65979	11,191–11,729	11460	35.42267	-116.605641	1220	Koehler et al., 2005
40	Forty Mile Canyon	Pinnacles Ridge	9390	40	QL-4222	11,270–11,670	11470	36.946498	-116.379364	1250–1310	Spaulding, 1994
41	Inyo Cave 1, 2A	Inyo Mountains	11,150	80	OS-38897	12,842–13,180	13011	36.55225	-117.767398	1945	Cole et al., 2012
42	Alabama Hills	Owens Valley	11,450	80	Beta 168109	13,171–13,469	13320	~~36.565018	~~-118.073196	~~1327	Wigand, 2017, 2023
43	Granite Mountain	Granite Mountains	11,470	70	Beta-52489	13,180–13,475	13328	~~35.445820	~~-116.607224	1320	Koehler et al., 2005
44	Penthouse 2(2)	Sheep Range	11,550	150	A-1772	13,162–13,750	13456	36.469961	-115.250092	1580	Van Devender and Spaulding, 1979; Cole
45	Mount Ord	Lucerne Valley	11,850	50	NA	13,529–13,796	13663	34.634933	-116.8102	1219	King, 1976
46	No Name East	No Name Basin	11,910	90	Beta-65984	13,594–14,026	13810	35.42267	-116.605641	1220	Koehler et al., 2005
47	Penthouse 1(3)	Sheep Range	12,350	55	OS-35220	14,107–14,836	14472	36.470287	-115.249973	1600	Van Devender and Spaulding, 1979; Cole et al., 2012
48	Clark Mountain	Clark Mountain	12,460	190	I-3690	14,040–15,282	14661	~~35.518181	~~-115.602443	1916	Mehringer and Ferguson, 1969
49	Robber's Roost	Scodie Mtns	12,870	400	A-1762 RR#1D	14,031–16,503	15267	~~35.590086	~~-117.94669	1130	Van Devender and Spaulding, 1979; McCarten and Van Devender, 1988
50	No Name West	No Name Basin	12,780	100	Beta-65977	14,974–15,579	15277	35.42267	-116.605641	1290	Koehler et al., 2005
51	Robber's Roost	Scodie Mountains	12,960	270	A-1761 RR#2A	14,367–16,310	15339	~~35.590086	~~-117.94669	1130	Van Devender and Spaulding, 1979; McCarten and Van Devender, 1988
52	Forty Mile Canyon	Pinnacles Ridge	12,870	50	QL-4224	15,216–15,577	15397	~~36.946498	~~-116.379364	1250–1310	Spaulding, 1994
53	Robber's Roost	Scodie Mountains	13,300	360	A-1763 RR#1C	14,933–17,077	16005	~~ 35.590086	~~-117.94669	1130	Van Devender and Spaulding, 1979; McCarten and Van Devender, 1988
54	Forty Mile Canyon	Pinnacles Ridge	15,870	70	QL-4223	18,954–19,383	19169	~~36.946498	~~-116.379364	1250–1310	Spaulding, 1994
55	Forty Mile Canyon	Pinnacles Ridge	16,410	70	QL-4234	19,569–20,001	19785	~~36.946498	~~-116.379364	1250–1310	Spaulding, 1994
56	Haystack Mountain	Owens Valley	17,680	150	Beta-35503	20,954–21,902	21428	~~36.603996	~~-117.996219	1155	Koehler and Anderson, 1995
57	Skeleton Hills	Skeleton Hills	17,900	600	NA	20,231–22,991	21611	~~36.623823	~~-116.279102	925	Spaulding, 1990; Lanner and Van Devender, 1998
58	Specter Range-2	Specter Range	18,740	90	USGS-994	22,443–22,922	22683	~~36.66329	~~-116.190402	1190	Spaulding, 1983, 1990
59	Specter Range-2	Specter Range	19,080	370	UW-638	22,976–24,743	23860	~~36.66329	~~-116.190402	1190	Spaulding, 1983
60	Haystack Mountain	Owens Valley	20,960	240	Beta-34833	24,125–25,358	24704	~~36.603996	~~-117.996219	1155	Koehler and Anderson, 1995
61	Haystack Mountain	Owens Valley	20,590	210	Bcta-40000	24,191–25,283	24737	~~36.603996	~~-117.996219	1155	Koehler and Anderson, 1995
62	South Crest SC4b	Sheep Range	21,700	500	LJ-2840	24,986–27,142	26064	~~36.481339	~~-115.254263	1980	Spaulding, 1977
63	Forty Mile Canyon	Pinnacles Ridge	21,830	110	QL-4220	25,886–26,353	26120	~~36.946498	~~-116.379364	1250–1310	Spaulding, 1994
64	Haystack Mountain	Owens Valley	22,900	270	Beta-39273	26,463–27,702	27083	~~36.603996	~~-117.996219	1155	Koehler and Anderson, 1995
65	Long Canyon	Sheep Range	30,400	1500	A-1379	31,310–37,856	34583	~~ 36.491242	~~-115.256103	1800	Spaulding, 1977
66	Forty Mile Canyon	Pinnacles Ridge	47,240	3000	QL-4218	45,378–54,980*	49179	~~36.946498	~~-116.379364	1250–1310	Spaulding, 1994
67	Spotted Range-2	Spotted Range	>40,000	–	–	–	–	~~36.684897	~~-115.785841	~~1184	Wells and Jorgensen, 1964
68	Owens Lake	Owens Valley	–	–	–	<126 kyrs	–	36.461768	-117.975848	1084	Woolfenden, 2003 (based on pollen differentiated as piñon type)

LATE PLEISTOCENE AND OLDEST HOLOCENE PIÑON DATES IN THE GREAT BASIN

The path of piñon's migration in the Great Basin is written in the patterns of Late Pleistocene dates and distribution, especially the arrival and oldest known Holocene dates throughout the Great Basin. Table M3-1 and figure M3-2 present the most comprehensive set of Holocene locations known to us (Late Pleistocene locations are also included, but not exhaustively, especially oldest middens), along with revised radiocarbon dates for all locations (table M3-1).

All radiocarbon dates in table M3-1 were calibrated according to the IntCal20 calibration curve (Reimer et al., 2020) using the CALIB revision 8 protocols (Stuiver and Reimer, 1993). Table M3-1 reports 95% probability time ranges from which the samples derive.[3]

Although calibrated radiocarbon dates were formerly reported as single-point estimates (using the so-called "intercept method"), table M3-1 follows current conventions that employ the "probability method" to compute the 95% time range from which the sample derives.[4]

Five patterns emerge from this new synthesis of piñon dates and locations in the Great Basin, outlined here and interpreted subsequently:

1) The oldest evidence, dating to the Late Pleistocene, occurs in the southern Great Basin, specifically the Mojave Desert or transitional Mojave ecosystems (Late Pleistocene-aged piñon has also been found west, south, and east of the Great Basin in Arizona, California, and Mexico [Lanner and Van Devender, 1998], areas we do not include in the present

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[3] We note that in this chapter (and chap. E), that it is appropriate in places to depart from convention and use a point estimator rather than the now-standard "probability method" for computing the 95% probability time range. A variety of point estimates has been previously employed in radiocarbon dating, including mode, median, average, the central point of the confidence intervals, and the local mode inside the confidence intervals. Table M3-1 reports the calibrated midpoint of the 95% probability range. In doing so, we recognize that because of the non-linear relationship between "radiocarbon ages" and "calibrated ages," the midpoint likely distorts the 95% probability density function to some degree (Telford et al., 2004; Michczyòski, 2007).

Our departure from convention is justified at times due to the "noisy" data involved in estimating arrival dates for piñon pine and human colonization. In both cases, we argue that despite a degree of bias, calibrated radiocarbon midpoints provide useful first-order heuristics for estimating first arrivals.

[4] Although previous chapters have employed the cal A.D./B.C. convention, here we employ cal B.P. to be consistent with the relevant paleoecological literature.

discussion). All but one piñon location dating to the Late Pleistocene/earliest Holocene (> 10,100 cal B.P.) are found south of ~37.5° N latitude.

2) Late Pleistocene/earliest Holocene piñon locations, as well as its current known distribution limit, extend farther north in the eastern Great Basin than in the western and central Great Basin; this long-recognized asymmetry is, however, challenged by potential pinyon populations at a similarly northern latitude in the western Great Basin, described below.

3) Oldest dates generally progress from older to younger in a south-to-north pattern, with important exceptions in the western and eastern Great Basin where locations dating older than 7600 cal B.P. challenge an orderly northward progression.

4) Older dates by latitude are in the central and eastern Great Basin compared to the western Great Basin, with exceptions.

5) With important exceptions, Holocene arrival and oldest dates at latitudes above ~ 37° N are younger than ~8000 cal B.P., and most are younger than ~6000 cal B.P.

FACTORS INFLUENCING PIÑON'S LATE PLEISTOCENE AND HOLOCENE BIOGEOGRAPHY

Here we discuss driving forces that influenced (and continue to affect) the migration of piñon in the Holocene Great Basin.

CLIMATE

"Climate is the primary driver of woodland dynamics, resulting in expansion, contraction, migration, and changes in woodland structure and species composition" (Miller et al., 2019: 83). The central role of climate has long been the primary tenet in the science of plant distributions (e.g., Woodward, 1987). Climate is the overall arbiter of distribution in that only when the climate is or becomes favorable (i.e., within the species' habitat envelope) will the species be able to advance its range toward the favorable climate. As climate becomes unfavorable, the opposite happens, that is, mortality occurs and the range retreats. Piñon is, among woody species, remarkably responsive to climate: when conditions are good, piñon gets going. The species can become established rapidly and spread across the landscape quickly. Similarly, as conditions deteriorate, piñon also responds quickly, as is the current case in many parts of the

Great Basin, where two decades of severe drought are causing widespread mortality (Shriver et al., 2022).

Much has been written about weather and climate conditions favorable for piñon, especially conditions sufficient for critical phases of seed production, germination, and seedling establishment (reviewed in Miller et al., 2019; precipitation and temperature tolerances are illustrated in supplemental fig. 1(more in Thompson et al., 2015). Relative to subalpine Great Basin tree species such as limber pine (*Pinus flexilis*), piñon thrives under warmer and drier conditions. It tolerates relatively warm summers, although it prefers some summer precipitation (which is especially important during the seedling establishment phase) and accommodates wet and cool—but not very cold or deeply snowy—winters (details in Thompson et al., 2015; supplemental fig. 1). Grayson (2011: 257–258) pointed out the "Goldilocks sweet spot" of piñon's climate envelope: winter is too cold and wet, so upland species (e.g., limber pine) outcompete; summer is too wet, so Colorado piñon pine (in far eastern regions where the species meet) takes over; summer is too hot and dry, so Utah juniper (*Juniperus osteosperma*) dominates.

In regard to piñon's Holocene migration, therefore, for piñon to emerge out of its Late Pleistocene range in the southern Great Basin depended on climate becoming favorable. During the Holocene, the combination of piñon's favored climate conditions—driven by factors of temperature and precipitation—appears to have unfolded in a ragged south to north wave across the Great Basin. These changes emerged in fits and starts and included major and minor trends and variability regionally and locally (Wigand and Rhode, 2002; Grayson, 2011; Cole et al., 2012; Miller et al., 2019). Relative to the cold, wet Late Pleistocene, the Early Holocene (11,650–8276 cal B.P.) was warmer and drier. Relative to modern conditions, however, the Early Holocene was cooler and wetter (Grayson, 2011). The Middle Holocene (8276–4200 cal B.P.), by any comparison, was a period of maximum heat and extended (millennial) drought. The Late Holocene (< 4200 cal B.P.) has been a rollercoaster of wet and dry periods, generally trending cooler, and heralding the Little Ice Age (~A.D. 1400–1920 [550–30 cal B.P.]), which was the coolest period since the end of the Pleistocene.

Although piñon responded to these large and small changes, climate—however primary a driver—is not sufficient alone to define piñon's migration (Lanner and Van Devender, 1998; Cole et al., 2012). The spread of piñon into the central Great Basin appears to have been far slower and in more complex geographic patterns than the appearance of favorable climates.

Conditioning factors outlined below determine what plant geographers recognize as the realized distribution range from the potential range of a species. In the discussions that follow, we assume that Holocene piñon migration out of refugia lagged behind the arrival of favorable climates.

Dispersal Vectors

If climate favorable for piñon had spread across the entire Great Basin instantaneously in the Early Holocene (which it did not), piñon could only migrate as far, as fast, and to locations that its dispersing agents could achieve within the limits of piñon generation times. The role of piñon dispersal and dispersing agents is, therefore, key to interpreting the species' Holocene migration patterns across the Great Basin. Dispersal involves short-distance, population-expansion processes, and long-distance founding events. The latter can involve migration across unfavorable gaps in habitat, such as low-elevation basins or large lakes, to colonize and establish in far-away places. The ecology and importance of piñon's dispersing agents greatly influenced its pattern and rate of spread.

Piñon seeds are large, heavy, unwinged, and dense with nutritive tissues (carbohydrates and fats; Botkin and Shires, 1948). Cones open at maturity and commonly face upward; seeds are loosely contained on the cone scales. These conditions favor avian dispersal and indeed piñon is legendary for its coevolution with corvid birds, in particular Pinyon Jays (*Gymnorhinus cyanocephalus*) and Clark's Nutcrackers (*Nucifraga columbiana*) (reviewed in Miller et al., 2019). Both corvid species are particularly effective because of their caching habits: birds plant seeds at a soil depth (3–5 cm) optimal for germination. Pinyon Jays forage primarily on piñon pine and disperse seeds in large quantities. Ligon (1978) estimated that an individual jay could cache up to 18,000 piñon seeds in a 5-month season. Most seeds are cached <1 km from collection, with distances up to 10 km the maximum seed-caching distance observed (Vander Wall and Balda, 1981).

Clark's Nutcrackers favor seeds of whitebark pine (*Pinus albicaulis*); limber pine is second in their diet preference. When those species are in low abundance, cone crops are poor, or unfavorable weather forces jays to lower elevations, nutcrackers forage on piñon nuts as well as other large-seeded lower-elevation pines such as Jeffrey pine (*Pinus jeffreyi*, Vander Wall, 1988) or Douglas fir (*Pseudotsuga menziesii*, Schaming, 2016). Clark's Nutcrackers forage on piñon late in fall, after they have depleted crops of higher elevation species. Clark's Nutcrackers also

disperse enormous numbers of seeds: an individual bird can disperse 17,900 piñon seeds in a season (Vander Wall, 1988). Most piñon seeds are cached within 1 km of the harvested trees (Vander Wall, 1988). Longer distances are also achieved by Clark's Nutcrackers while caching. Vander Wall and Balda (1977, 1981) observed nutcrackers caching piñon seeds 5 km and very occasionally 15 km from collection stands; the maximum distance that has been observed is 22 km (Vander Wall and Balda, 1977). This pattern of dispersal in both jay species, where the great majority are planted at short distances from collection trees and dispersal of seeds to far distances is very rare, defining a leptokurtic distribution (discussed in detail below), is widely documented for pine and other tree species (e.g., Burczyk et al., 1996; Nathan et al., 2001; Wenny, 2001).

Three other jay species also disperse piñon seeds (Vander Wall and Balda, 1981; Lanner, 1983). Steller's Jay (*Cyanocitta stelleri*), and Western Scrub Jay (*Aphelocoma californica*) occur only in the western Great Basin, while Woodhouse's Scrub Jay (*Aphelocoma woodhouseii*) occurs only in the central and eastern Great Basin (Thomas and Millar, 2023). These jays do not specialize on piñon seeds. When they do harvest piñon, they disperse seeds <3 km from collection trees.

Rodents, including ground squirrels and chipmunks, are also important short-distance dispersal vectors; the number of piñon-foraging species is much larger in the western Great Basin than in the central and eastern Great Basin (Thomas and Millar, 2023). Although rodents do not disperse nuts long distances, they do plant seeds in microsites under shrubs more often than birds. These microsites are more favorable for piñon seedling establishment (Miller et al., 2019). Jays, by contrast, plant nuts in inter-shrub spaces, where piñon seedling and sapling survival is lower.

Humans have also been considered for their role in seed dispersal, including piñon and other pine species (e.g., Potter and Green, 1964; Madsen, 1986; Mehringer, 1986; Betancourt et al., 1991; Rhode and Madsen, 1998; Simms, 2008). Intentional planting seems highly improbable given the long regeneration time of piñon (Krugman and Jenkinson, 1974), with the implication that seeds would not be available for useful harvest for one to several human generations after planting. An exception might be in situations where people traveled seasonally or annually from a homeland with piñon to an area lacking the species; intentional planting in the latter area would ensure pine nut crops for visits in a distant future (Davis-King and Snyder,

2010). Unintentional dispersal by loss of seeds is possible. Seeds lost at village sites, and especially from piñon seed caches, conceivably might have served as sources for pine establishment. These situations, however, would occur in locations where piñon was already growing, and thus would have assisted in local expansion of extant woodlands.

Foragers sometimes carried "trail food," including piñon nuts, during long-distance residential and logistical moves (Basgall et al., 2003: 360). Such trail food, including piñon nut remains, has been identified at Midway, an alpine hunting camp in the White Mountains above the piñon zone (Scharf, 2009). Unintentional long-distance transport of piñon by loss of seeds from carrying bags during far-flung forager movements seems a low-probability means of piñon dispersal (but see a later section). Beyond the value of piñon seeds to travelers and their likely care to avoid loss, a number of factors mitigate against piñon being established by human sojourners. A primary concern is viability of nuts carried by foragers. Several widely used prehistoric nut collection and processing practices would diminish seed viability or kill seeds outright. These include collecting unripe (green) cones whose seeds may not be mature enough to germinate; after-ripening immature cones over fire, which would lower viability or kill seeds; and roasting nuts, which would kill them (Thomas and Millar, 2023; Thomas and Millar in press). Due to ecological factors that cause variation in cone morphology in different parts of the Great Basin, processing by heat was more likely in the western and eastern Great Basin (Thomas and Millar, 2023).

Even if seed viability was maintained in foragers' trail food, other factors would reduce the likelihood of lost nuts serving as planting sources. These include piñon's seed germination, planting, and seedling-establishment requirements, which are unlikely met under random seed loss; the low number of seeds that humans would carry, further reducing the probability of nuts becoming established and the short-term viability of piñon seeds, with viability falling to <10% within 6–12 months of seed-maturation (Meeuwig and Basset, 1983). These factors combine to reduce the probability that piñon nuts—carried long distances by humans and subsequently lost from human carrying bags—would successfully become established as founding colonists.

Topography and Seed-Dispersal Corridors

The topography of the Great Basin, with its hundreds of mountain ranges and intervening basins, no doubt played a significant role in the patterns of piñon's Holocene spread (Charlet, 2007). Effective corridors for dispersal would occur where favorable habitats were continuous, such as along mid-elevation contours of mountain ranges—higher or lower depending on climate.

By contrast, barriers to long-distance dispersal would be imposed by unfavorable environments, such as elevations above treeline in mountains and low elevation basins or large water bodies. The tectonic processes of Basin and Range expansion and Walker Lane dynamics (Jayko and Bursik, 2011) resulted in fault-blocked, north-south trending ranges throughout the Great Basin. Several of these are hundreds of kilometers long, the largest being the Sierra Nevada and White-Inyo Ranges in the western Great Basin, the Schell Creek Range of the central Great Basin, and the Wasatch Range of the eastern Great Basin. These and scores of smaller ranges would have provided continuous habitat on their lower slopes for piñon expansion. In addition to intermountain basins as local restrictions, the large, broad region of the Carson-Lahontan Sink and Walker Lane lowlands in western Nevada likely was a significant barrier to piñon dispersal.

Reid's Paradox and the Importance of Fat Tails

Plant biogeographers interested in the response of species to changing climate have long modeled migration dynamics as a diffusion process (Cousens et al., 2008). This assumes a wave front along the colonizing edge of the main species' distribution that moves toward favorable habitat. Factors such as generation time, seed size and buoyancy, and seed and pollen dispersal vectors contribute to modeling the gradual movement into new environments. Rates of migration by diffusion can then be used to calculate the predicted time that would have been needed for the species to move a certain distance, and these can be compared with micro- and macrofossil evidence of observed arrival times and actual distances traveled.

Diffusion models used to predict geographic shifts by tree species, especially in Europe and eastern North America, during the Late Pleistocene-Holocene transition quickly illuminated a serious problem: distances traveled by trees far exceeded the rates and times predicted by diffusion. This is referred to as "Reid's Paradox" for the Victorian botanist, Clement Reid, who

estimated that for post-glacial oaks in England to have diffused as far as they did (~600 mi) in a matter of a few thousand years (from dated fossil evidence) would take "something like a million years" (Reid, 1899). Reid's paradox now broadly refers to the mismatch between theoretical estimates of migration based on plant diffusion models and observed rates of migration, particularly in postglacial movements northward (Powell and Zimmerman, 2004; Lesser and Jackson, 2013).

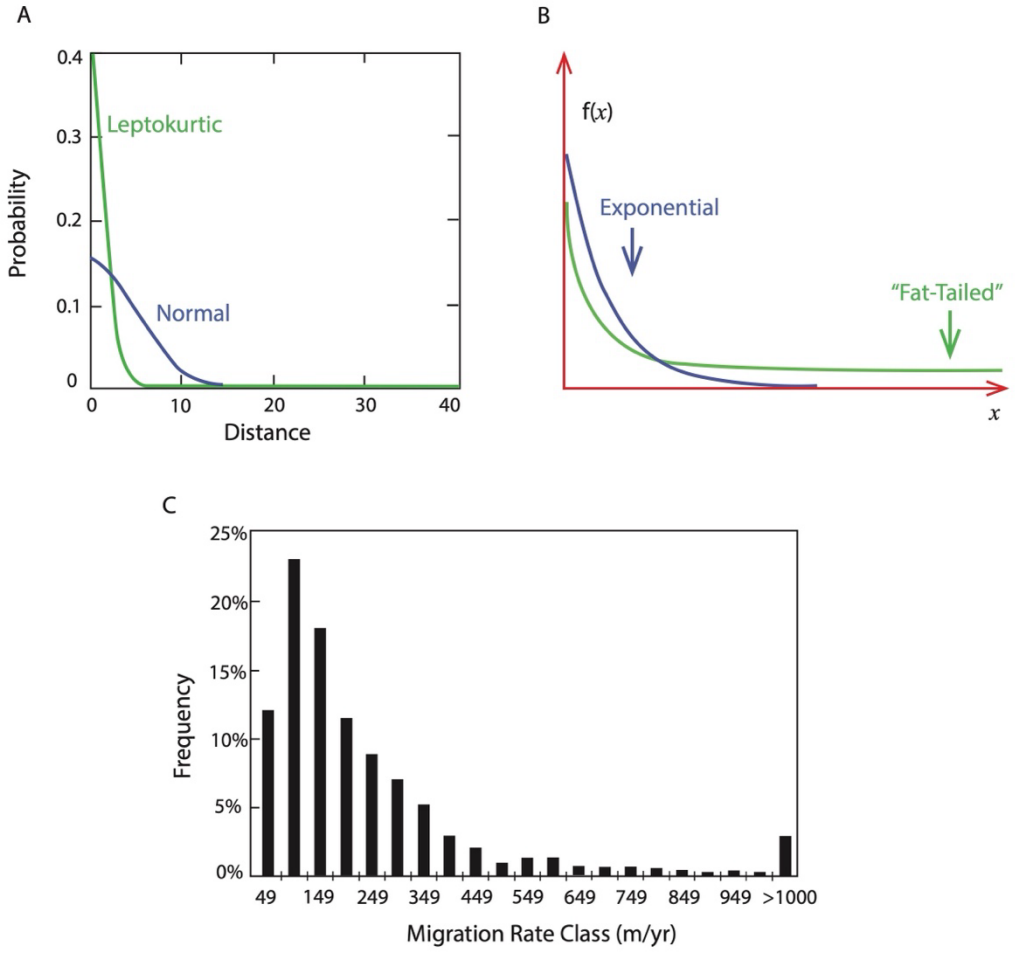

FIG. M3-3. Examples of leptokurtic distributions. **A.** A leptokurtic dispersal curve (green line) with a normal distribution curve (blue line) for comparison. Both curves have equal variance, $v = 5$ (Ibrahim et al., 1996). **B.** A leptokurtic dispersal curve with a "fat tail," where there are greater chances (higher probability) of extremely long-distance dispersal events than for the leptokurtic curve shown in panel A ("Statistics How To" https://www.statisticshowto.com/heavy-tailed-distribution/). **C.** Case example of a leptokurtic distribution in estimated migration rates of spruce (*Picea*) in eastern North America during the Holocene. The mean and median rates are 220 m/year and 140 m/year, respectively. In this case, the tail is also "fat." (Clark et al., 1998).

LEPTOKURTIC DISPERSAL: Previously, we mentioned the leptokurtic distribution of piñon seed dispersal by corvid jays, whereby most caching flights occur close to the collection trees, but rare flights can occur at long distances. Distributions with leptokurtic behavior differ from the more familiar normal and exponential distributions (fig. M3-3). For instance, in figure M3-3A, both curves have the same variance, but the tail in the leptokurtic curve is much longer, meaning not only that most dispersal events are at shorter distances than in a normal distribution but that some dispersal events occur at far greater distance in the leptokurtic case. While the probability of very distant dispersal (like fig. M3-3A) is extremely low, a so-called "fat-tailed" leptokurtic curve (fig. M3-3B; Powell and Zimmerman, 2004) has a larger, if still small, probability at great distance. Figure M3-3C illustrates a real example in spruce (*Picea*) for its Holocene migration in eastern North America. Most events occurred with low migration rates (less than 220 m/year), whereas there was 2% probability of events that occurred >1000 m/year.

The key element of Reid's Paradox is that "dispersal theory embraces 'fat tails'" (Clark et al., 1998: 15). That is, in their many forms, rare but long-distance—even highly improbable—dispersal events are seen as explaining many observed migration histories and essential to understanding migration processes. While diffusion continues to occur as the background beat enabling local expansion, a few far-flung events can catalyze important distant colonizations.

Extra long-distance dispersal processes are thought to occur in several low-probability ways. Transport vectors include avian travelers, far-wandering frugivorous mammals, large wind events (hurricanes, tornadoes, and wind blowing seeds across snow), and rivers (Clark et al., 1998). The *potential* of these ecological and abiotic agents for long-distance transport, however, often does not translate to *effective* dispersal due to problems such as mismatch of plant phenology and seasonality, lack of adequate planting, or damage to seeds during transport.

Another important situation recognized for long-distance colonization is the role of climate refugia (Pearson, 2006). Species persisting in isolated, small pockets of favorable habitat during otherwise inclement climate phases (e.g., ice ages) served as important sources of far-flung species expansions once climates ameliorated. Over time, these once-refugial populations coalesced with each other and with the advancing wave fronts from the main species distribution, leaving the appearance of continuous migration.

We embrace this resolution of Reid's paradox by rare long-distance and improbable events in considering post-glacial migration of both piñon pine and human foragers. We also

recognize, as plant geographers underscore, that fat-tailed distributions are annoyingly difficult to characterize directly. Thus, the rare extra-long-distance piñon seed dispersal by Clark's Nutcrackers, the seemingly improbable planting of seeds by wandering humans, or the hither-to undiscovered Pleistocene refugial piñon populations, may in fact underlie critical elements of piñon's migration into the Great Basin. We attempt to use these factors in reassessing piñon's Holocene migration into the Great Basin.

PUTTING IT TOGETHER: INTERPRETING PIÑON'S MIGRATION IN THE GREAT BASIN

Using revised arrival and oldest-available dates, a comprehensive set of locations (table M3-1, fig. M3-2), and recognizing the importance of leptokurtic dispersal and fat tails, we attempt to interpret the patterns described above of piñon's Holocene migration into the Great Basin. In the sections below, we propose and test two hypotheses, one traditional and one new, regarding piñon's distribution of dates and locations.

Late Glacial Refugia

The first pattern of Late Pleistocene piñon locations clustered in the southern Great Basin has been widely and confidently interpreted as a large regional refugium for warm- and winter-wet adapted piñons (singleleaf piñon and other species) during the Late Wisconsin (Van Devender and Spaulding, 1979; Lanner, 1983; Cole et al., 2012; Spaulding, 1990; Woolfenden, 1996; Lanner and Van Devender, 1998; Grayson, 2011). Although we have no evidence to understand how piñon may have ranged in the Great Basin during warm intervals prior to the Last Glacial Maximum, cold full-glacial climates at central and northern Great Basin latitudes were outside piñon's climate tolerances. Rather, they favored cold-adapted limber pine, bristlecone pine (*Pinus longaeva*), whitebark pine, and diverse species of sagebrush (*Artemisia* spp.) at lower elevations than current (P.V. Wells, 1983; Thompson, 1990; Wigand and Nowak, 1992). Late Pleistocene piñon woodlands and piñon associates, by contrast, retreated into areas now dominated by Mojave Desert ecosystems in the southern Great Basin.

Low elevations and low latitudes provided glacial-age climates that were adequately warm yet winter-wet for piñons (Van Devender, 1977; Madsen, 1986; Woolfenden, 1996;

Grayson, 2011; Miller et al., 2019). During the full-glacial period, the temperature gradient between the equator and continental ice caps in North America was steeper than at present, causing southward displacement of the subtropical Pacific high anticyclone. Piñon locations during the Late Pleistocene occurred almost exclusively at elevations below ~1300 m, conditions that extended across much of the current Mojave Desert. The intensification of the Aleutian low cyclone at these latitudes and elevations brought heavy winter precipitation, yet mild temperatures, to the American Southwest that continued into the Early Holocene, favoring stable persistence of piñon in this region for many millennia of the Late Glacial (Van Devender and Spaulding, 1979).

Holocene Migration out of Southern Refugia

Although full-glacial conditions were waning across North America after ~13 ka, slow melting of the high-latitude ice cap glaciers continued to displace the polar jet stream and winter storm tracks southward. The Cordilleran ice sheet took millennia to shrink, and only by ~9–8 ka did it fragment and shrink significantly enough to trigger major changes in hemispheric circulation (Van Devender and Spaulding, 1979). These were catalyzed by exposure of high-latitude land masses and emergence of Arctic ocean water, with resulting changes in albedo and energy. These changes led to development of the present general circulation patterns. Thus, while warming, post-glacial conditions were starting to spread across middle latitudes after ~9–8 ka, including south/central Great Basin latitudes. The Early Holocene conditions in areas now considered the Mojave, Sonoran, and Chihuahuan deserts remained winter-wet and mild enough to support piñon-juniper woodlands (Van Devender and Spaulding, 1979). The persistence of these woodlands (with associated species now not present in the dry desert) at low latitudes until ~8 ka testifies to these lingering conditions (Van Devender, 1977; Van Devender and Spaulding, 1979).

The pattern of piñon arrival and oldest dates progressing more-or-less in time from south to north (table M3-1) has been unanimously interpreted by Great Basin biogeographers to reflect northward migration by piñon out of southern Great Basin glacial-age refugia (Van Devender, 1977; Lanner, 1983; Madsen, 1986; Spaulding, 1990; Thompson, 1990; Wigand and Nowak, 1992; Nowak et al., 1994a; Woolfenden, 1996; Lanner and Van Devender, 1998; Wigand and Rhode, 2002; Grayson, 2011; Cole et al., 2012; Wigand, 2017; Miller et al., 2019). The pattern of

dates in central Great Basin latitudes being younger than ~8–7.5 ka has further been interpreted to reflect persisting woodland conditions in the regions now considered Mojave Desert combined with eventual development of favorable climates in the Early and Middle Holocene. Only after ~8 ka were very cold, continental winters and cold, arid summers ameliorating sufficiently for piñon to migrate northward toward favorable Great Basin habitats, and to become extirpated at southern latitudes. This transition appears to have happened rapidly and synchronously, triggering extirpation of southern woodlands and migration out of southern, Mojave-regional refugia (Van Devender and Spaulding, 1979). Emergence of much warmer and drier climates in the Middle Holocene after 8 ka influenced northward expansions of piñon.

As introduced above, piñon's northward Holocene migration was influenced by basin and range topography as well as emerging favorable climates, a pattern also widely acknowledged (Lanner, 1983; Madsen, 1986; Thompson, 1990; Wigand and Nowak, 1992; Lanner and Van Devender, 1998; Wigand and Rhode, 2002; Grayson, 2011; Wigand, 2017). The north-south-trending mountain ranges of the Great Basin served to funnel piñon northward along what have been proposed as three primary migration paths. These were in the western, central, and eastern Great Basin (Lanner and Van Devender, 1998; fig. M3-4), although they may have overlapped, especially in the central and western regions. The broad fans and lower slopes of mountain ranges that extend along their long north-south fronts provided diverse habitat options (i.e., multiple elevations) for northward-expanding piñons to find optimal conditions. While this topography presented more-or-less continuous northward corridors along many ranges, the high elevations of the ranges, by contrast, served to facilitate significant migration west- or eastward. Lower passes might have been dispersal corridors (Charlet, 2007).

Low, broad basins, with alkaline soils left in the now-playa lake beds were additional barriers to east-west movement (Wigand and Nowak, 1992; Wigand and Rhode, 2002; Grayson, 2011). These barriers were likely most effective where inter-mountain basins or low-elevation areas were large, such as the Carson Sink and Walker Lane areas of the west-central Great Basin.

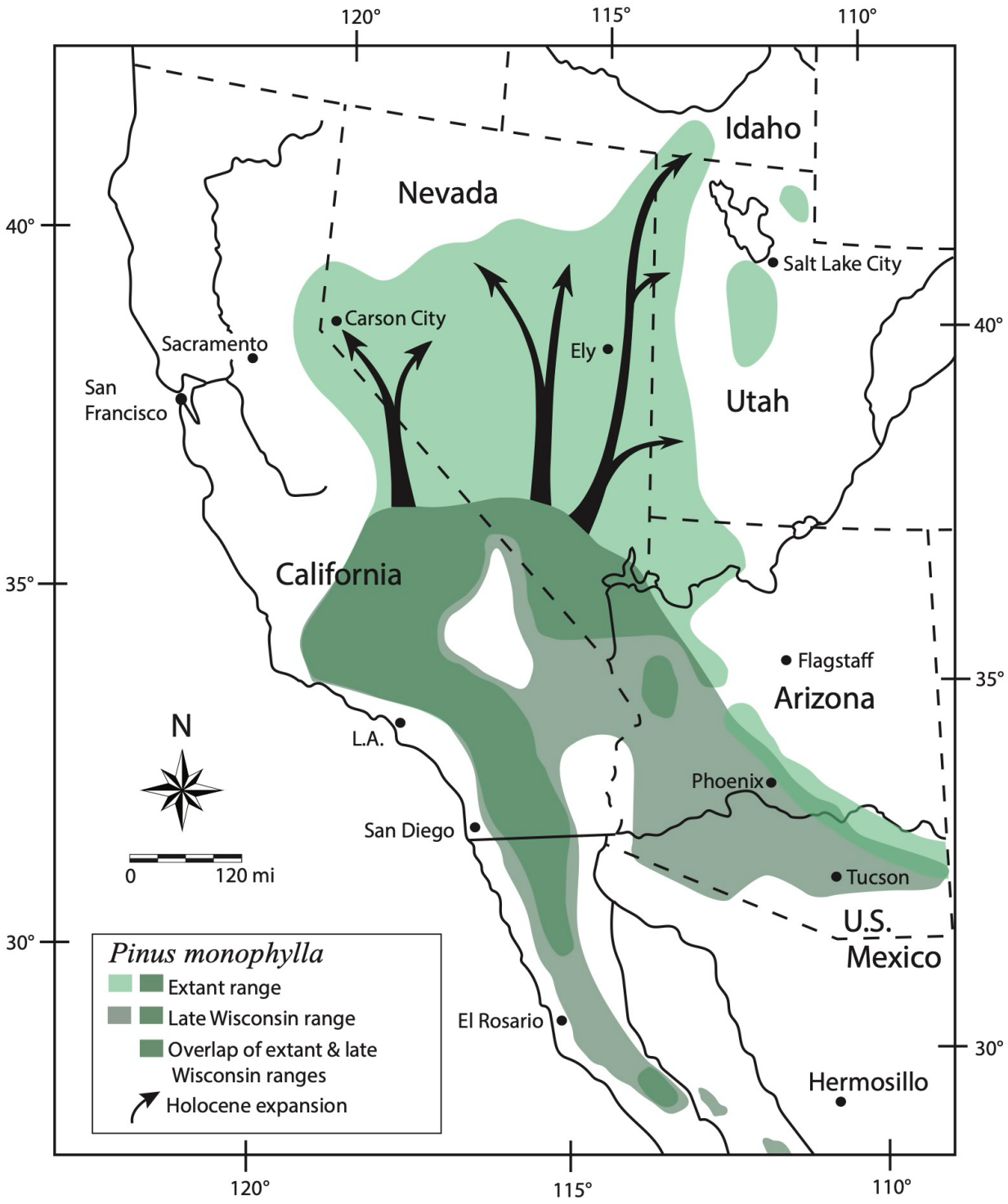

FIG. M3-4. Late Pleistocene Mojave-region refugial locations of singleleaf piñon pine and northward Holocene migration along three paths in the western, central, and eastern Great Basin. Adapted from Lanner and Van Devender (1998).

Piñon migration along three north-south corridors is supported by differences in multivariate patterns of monoterpene compositions (reflecting genetic diversity), whereby western populations from Mammoth Lakes, CA differed from central NV populations, and those differed from populations in the Ely, Nevada area (Smith and Preisler, 1988). These mid-latitude populations had similar genetic distance to a southern population of the species. Resolution in this study, however, was not adequate to test the hypotheses we present below.

Hypotheses for Holocene Piñon Migration out of Southern Refugia

We come to several pressing questions in piñon's mid-late Holocene migration patterns: (1) Anomalous occurrence of very old piñon dates at northerly latitudes and other exceptions to an orderly progression of arrival dates northward; (2) Different apparent rates of migration among the western-, central-, and eastern migration paths; and (3) Differences in the northernmost extents of piñon migration among these regions, although we introduce an alternative of symmetry in northern extents between the western and eastern Great Basin. We take up the issue of old dates and dates that are out of south-north order first as the basis for introducing a new migration hypothesis alongside the traditional version.

Northward Migration (Hypothesis 1): The first hypothesis we consider is the widely accepted scenario outlined here (fig. M3-5): From Late Pleistocene refugia at latitudes south of ~36° N latitude, piñon began to migrate northward following warming climates after ~8 ka. Piñon followed three general migration paths in the western, central, and eastern Great Basin (fig. M3-4; after Lanner and Van Devender, 1998). Within each region, piñon migration unfolded in a stepping-stone pattern northward, with the pace at the northern front (the "piñon curtain") varying as minor climate trends emerged. Migration was fastest in the eastern Great Basin and slowest in the west, resulting primarily from climate differences among the regions, and as a result, piñon reached its farthest northern latitude in the eastern Great Basin. A major challenge to this hypothesis is the existence of very old midden and pollen dates containing piñon at relatively high latitudes, which is difficult to explain by migration after ~8 ka from Mojave-area refugia.

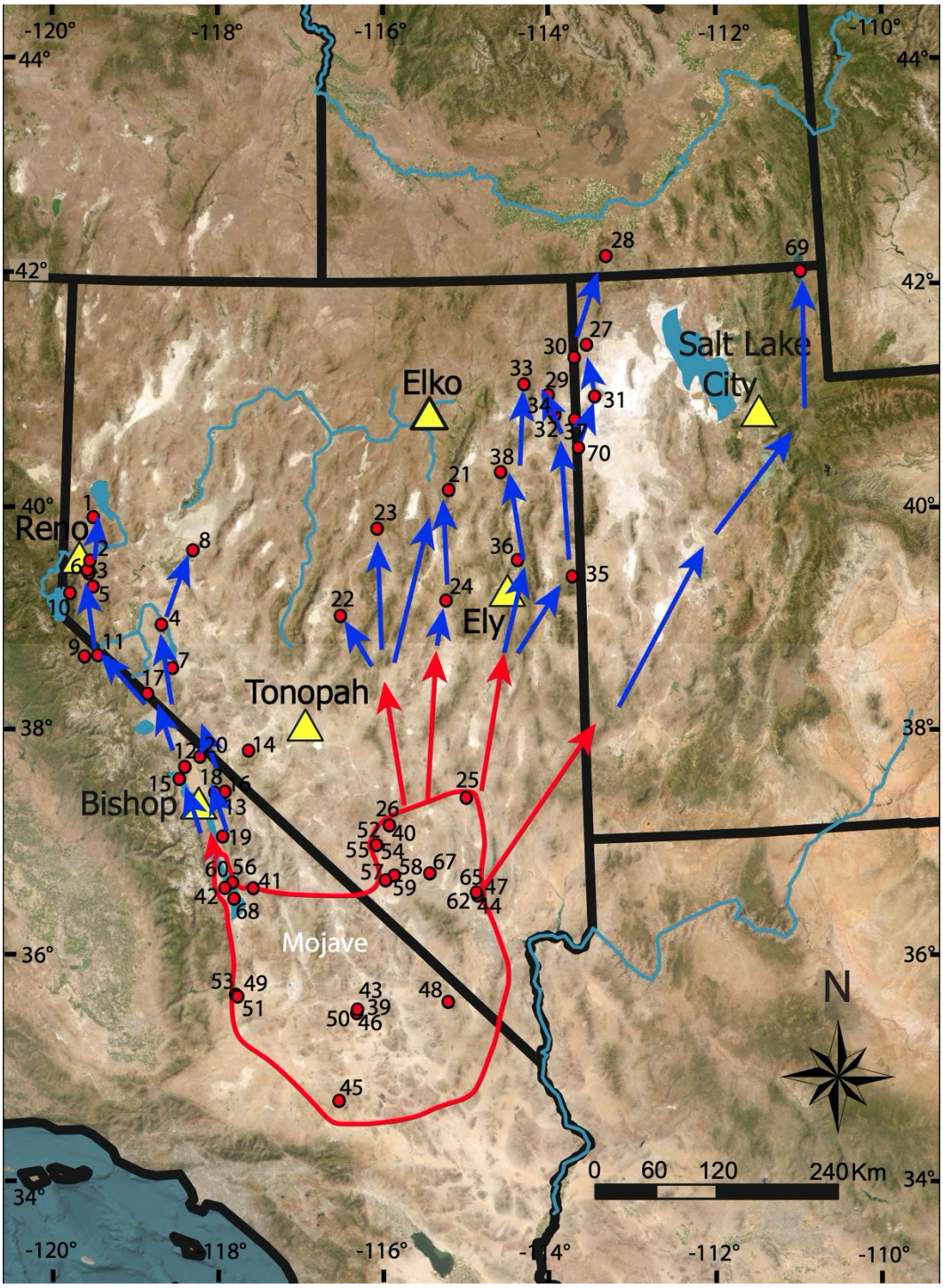

FIG. M3-5. Hypothesis 1: Migration of piñon pine from a southern Pleistocene refugium, estimated from midden locations and radiocarbon dates in table M3-1. The red polygon denotes the southern Late Pleistocene refugium, red arrows show movement out of that refugium during the Early Holocene, and blue arrows show subsequent movement.

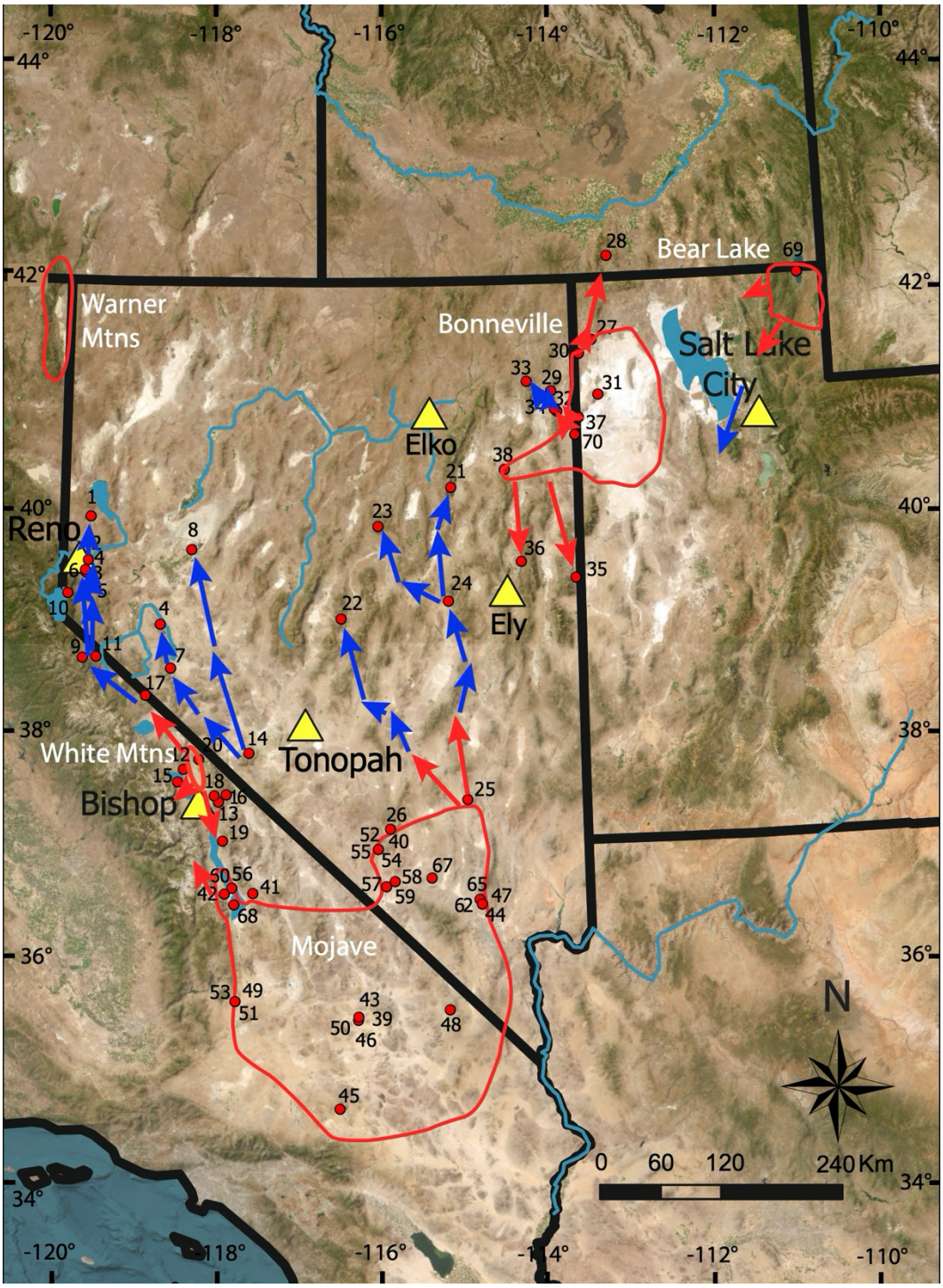

FIG. M3-6. Hypothesis 2: Northward migration of piñon pine from the southern Pleistocene refugium and outward from four Pleistocene refugia at higher latitudes in the western and eastern Great Basin, estimated from midden locations and radiocarbon dates in table M3-2 and, for the northeast California refugium, from ethnographic evidence and herbarium records. The red polygons denote five Late Pleistocene refugia, red arrows show movement out of the refugia during the Early Holocene, and blue arrows show subsequent movement.

NORTHWARD MIGRATION WITH HIGH-LATITUDE REFUGIA (HYPOTHESIS 2): Our alternate hypothesis, like the first, accepts the existence of a large Late-Pleistocene piñon refugium near the current Mojave region, and that Early Holocene migration occurred northward out of this region. It differs from the traditional hypothesis in postulating regions of Late Pleistocene piñon refugia at higher latitudes that became additional sources for emigration once climates ameliorated (fig. M3-6). The existence of refugia at middle latitudes in the Great Basin has been considered previously (Lanner, 1983; Grayson, 2011), but in a general manner and without explicit geo-reference. Quoting Grayson (2011: 257), "It is also possible that piñon pine actually existed in undetected isolated pockets in the central, but not the western, Great Basin during the late Pleistocene and then expanded outward when conditions more amenable to their existence returned." Given that juniper persisted throughout the Late Pleistocene in many locations of the central and northern Great Basin (Wigand and Nowak, 1992; Nowak et al., 1994b; Rhode, 2000; Wigand and Rhode, 2002; Grayson, 2011; Wigand, 2017), and that most of these were Utah juniper (*Juniperus osteosperma*), it would be surprising if piñon refugia did not also occur. Although Utah juniper and singleleaf piñon have different habitat/climate envelopes (Cole et al., 2012; Miller et al., 2019), they are highly overlapping. Piñon-juniper woodlands are modern as well as ancient associations (supplemental figs. 1, 2). If anything, more Pleistocene refugia might be expected for piñon than for juniper, given piñon's apparent tolerance of cooler temperatures.

We propose that, in addition to the Mojave region, four regions of high-latitude Late Pleistocene refugia occurred (fig. M3-6). Three regions are old enough and far enough north to make migration post-8 ka from southern Mojave-area populations improbable in the time available (discussed in depth in the section on migration); the fourth, although its age is unknown, is so far removed from the current distribution as to suggest ancient origins. We speculate two western refugia: one occurring over a broad mountain area and one that contained few and very small piñon stands in a local area. Two eastern refugia we propose comprised networks of scattered sites. For all of these, we speculate that piñon hunkered down in compatible microsites that were buffered from Late Pleistocene and Early Holocene climate extremes by vagaries of topography and microclimate variability. Under such conditions, the stands would have had no/little expansion capacity due to challenging climates in and surrounding the refugia. As climates ameliorated after ~8 ka, refugial stands would become sources for local dispersal outward in multiple directions, producing the effect—from the

vantage of the present—of very rapid long-distance rates under an assumption of northward migration from the Mojave region.

From newly calibrated dates, we propose that one far western refugium was a low-elevation region at and below the Falls Canyon midden, California, which we call the White Mountain refugium (fig. M3-6). A small refugial environment might have occurred along the base of the west slope of the White Mountains in northern Chalfant/Benton Valleys. Piñon in the Falls Canyon midden dates to 9550–10159 cal B.P., which overlaps time ranges of piñon's southern, Mojave-region refugia (table M3-1). Utah juniper occurs in the Falls Canyon midden, as well as in middens of older ages surrounding it (Volcanic Tablelands, Redrock Canyon, Chidago Flats; Jennings, 1995), corroborating conditions that could have supported piñon during the Late Pleistocene in the valleys and low slopes of the northwestern White Mountains.

Adding evidence to this area as a conifer refugium is the modern occurrence of the only Jeffrey pine and ponderosa pine (*Pinus ponderosa*) stands in the White/Inyo Mountains, which exist in tiny, low-elevation, isolated stands in Jeffrey Mine and Lone Pine Canyons, near Falls Canyon. Ponderosa pine is especially unusual here, being highly disjunct from its closest main distribution on the western slopes of the Sierra Nevada. Similarly, lodgepole pine (*P. contorta*) grows as the only occurrence of the species in the White/Inyo Mountains in a highly disjunct population on nearby Chiatovich Flats. Elliott-Fisk and Peterson (1991) interpreted the occurrence of these species as relicts of ancient, widespread forests persisting through the Quaternary. A species-wide genetic study of ponderosa pine found unique alleles occurring in one of the disjunct stands in the region of Falls Canyon, further suggesting ancient origins (Potter et al., 2015). That these species, in particular warm-adapted ponderosa pine, appear to have persisted through cold Wisconsin climates in this area adds support to our proposal that piñon was able to persist at low, protected elevations near Falls Canyon during the Late Pleistocene and Early Holocene.

The second refugium we propose was in the far northwestern Great Basin in the region of the Warner Mountains, California, Oregon, and possibly northwest Nevada. This location is not included in our tables of locations and migrations because it is neither a fossil (midden, pollen) site nor has piñon been documented there at present (yet!). The strong likelihood of the species in the Warner Mountains comes from multiple sources that indicate four distinct and widely separated locations. Ethnographic reports indicate two areas of piñon stands, one on the eastside

of the north Warner Mountains and one in the south Warner Mountains; these reports detail pine-nut collection, processing, and use from these areas (Kelly, 1934; see relevant unpublished interview by Hughes[5]). Modern evidence for two additional locations comes from 20th-century sources. Most importantly, a definitive herbarium collection of piñon, now housed in the Southern Oregon University Herbarium, represents specimens collected by a respected botanist in 1948. The voucher describes two large, old-growth piñon trees growing on rocky cliffs on the westside of the north Warner Mountains in Oregon (latitude 42.07°N). These trees have not been verified in recent decades; the locations are accessed through private land and permission to survey has not yet been obtained by the authors. Another piñon location in the north Warner Mountains, near the CA-OR state line, was reported to an experienced botanist by agency staff performing bighorn sheep surveys in the late 1980s (Frank Callahan, Pete Figuera, personal commun.).

Although currently undocumented, the existence of piñon in the Warner Mountains in the past centuries at least seems likely from the various reports. Piñons in this region, as in far northern Utah (described later), may occur as single trees, widely scattered (corroborated in ethnography of Kelly, 1934), and remain unobserved by modern explorers of the range. The great distance (170–260 km) to the nearest recognized modern (and recent) occurrence of piñon near Reno (and these are only a small number of trees) makes the likelihood that the Warner piñons originated from existing southern stands extremely low. The alternative we propose is that piñons have grown in the Warner Mountains for millennia and represent a Pleistocene refugium. Their occurrence, if proven, documents piñon to have existed in the Holocene as far north in the western Great Basin as in the eastern Great Basin.

A third mid-latitude Pleistocene piñon refugium we propose was a larger region in the eastern Great Basin, centered around the greater Bonneville Basin (fig. M3-6), with westerly locations suggested by piñon in middens at Cottonwood Canyon, NV (Cherry Creek Range; 8378–8595 cal B.P.[6]) and Danger Cave, UT (Silver Island Range; 7432–7676 cal B.P.); we call this the Bonneville refugium. These and other nearby piñon locations with date ranges >7000 cal

[5] The 1977 interview with a Hammawi consultant was conducted by Richard Hughes. It is in possession of the author.

[6] This date derives from a needle of *Pinus flexilis* and is the oldest possible date from this sample. Piñon also occurs in the midden (a younger date derived from a piñon needle).

B.P. (table M3.1) corroborate the possibility of a regional piñon refugium located here. In this area, we imagine a network of scattered small populations growing in favorable microsites above the Bonneville Lake levels as they varied through time, with no expansion and marginal persistence during cold periods, as in the western Great Basin. Similarly, these stands would have served as subsequent sources for piñon expansion radiating in multiple directions to the younger piñon middens that occur in the region. We consider it possible that other slightly younger piñon middens in the region, such as Valley View, Council Hall Cave, and Marblehead Mine, may have been part of the refugium metapopulation and were only incorporated in middens after conditions allowed local expansion. Lake-effect climates of the Bonneville Basin (Rhode, 2000; Wigand and Rhode, 2002) may have contributed to maintaining a piñon network refugium in this region. Usually considered to result in higher precipitation downwind from the water body (presumably east in this case), large lakes also influence air temperature by creating more equable conditions year-round, being warmer in winter and cooler in summer (Eichenlaub, 1987).

We propose a fourth refugium for the lowlands south of Bear Lake in far northern Utah, which we call the Bear Lake refugium (fig. M3-6; Doner, 2009). Piñon pollen extracted from a sediment core in Bear Lake was separated by the analyst from other pine species and occurred in strata at continuous if low levels from 19,000 years ago to present. While pine pollen in general can travel long distances, levels of piñon in cores like that found by Doner (2009) have been interpreted to derive from local sources, as in the multimillennial-long Owens Lake core (Woolfenden, 2003), and we accept the conclusion that piñon grew in the region of Bear Lake. Although Doner (2009) separated singleleaf piñon from Colorado piñon grains in the sediment cores, we do not believe these pollen species can be discriminated from each other, especially under light microscopy (Bagnell, 1975; Jacobs, 1983, 1985). Thus, we consider the combined percents of both species graphed in the Doner (2009) diagram to represent cumulative "piñon-type pollen."

Piñon at present in this part of Utah occurs in scattered distributions, isolated from each other and from the core species range to the west and south. Unlike most of its range where piñon grows in large, extensive populations, in this region piñons grow as widely scattered individuals in dense woodland communities dominated by junipers (*Juniperus osteosperma* and *J. scopulorum*). Lanner (1971) first described many of these occurrences, and Lanner and

Hutchinson (1972) interpreted the disjunct populations in central Utah to be ancient relicts persisting from periods of different climate when piñon was more widespread. Further scattered individuals of piñon have subsequently been described in the Bear River Mountains/northern Wasatch Range (Weiss, 1999).

Some of these populations, notably in the Crawford Mountains just south and east of Bear Lake, were described as containing hybrid individuals between singleleaf and Colorado piñon (two leaves/fascicle; Lanner and Hutchinson, 1972). Millar visited the Crawford Mountains in 2023 and concurred that the morphologic expression of the piñon trees was mostly intermediate between the two species. Interestingly, she observed few if any trees that were morphologically "pure singleleaf" or "pure Colorado" piñon; rather trees that she inspected showed intermediate characteristics (based on needle number, number of stomatal rows, and number of resin canals). We speculate that the population in the Crawford Mountains represents a stable, ancient hybridization event that became isolated from the parent species long ago. In general, hybrids of singleleaf x Colorado piñon occur only in a narrow zone of contact along their border at the eastern edge of the Great Basin (Lanner, 1974; Buck et al., 2023). In that pure Colorado piñon currently does not occur in the vicinity of northern Utah (~170 km to the nearest large pure population), it appears to have been extirpated at some time in the past. If both parent species had persisted, they would most likely have overwhelmed the hybrids in the Crawford population, reverting the stand to whichever species was dominant, a situation documented by artificial crossing studies and modern molecular analyses (Lanner, 1974; Buck et al., 2023). We propose that the apparent stability of the admixed stand in the Crawford Mountains represents a hybrid fitness advantage, combining the xeric adaptations of singleleaf piñon with slightly colder and summer-wet adaptations of Colorado piñon. These may have contributed to the persistence of piñons in the Crawford Mountains for millennia.

Piñons in the other region near Bear Lake and the Bear River Mountains also occur as scattered individuals and small stands dominated by other species. These have been reported as singleleaf piñon (Lanner and Hutchinson, 1972; Ryan Buck, personal commun.; Millar, personal observations, 2023). Taken together, we consider the piñon-type pollen documented over the past 19,000 years in the Bear Lake core (Doner, 2009) to represent primarily singleleaf piñon. We conclude that singleleaf piñon was dominant in the region although Colorado piñon was likely present, and the region served as a Late Pleistocene-Holocene refugium for singleleaf

piñon. Potential support for Pleistocene climates being milder in the Bear River Mountains—and thus appropriate as a piñon refugium—comes from the observation that Pleistocene glaciation was not as extensive as in neighboring ranges (Reheis et al., 2009). Current annual precipitation in the Bear River Range is high (mean, 125 cm; Reheis et al., 2009), and likely was higher in the Pleistocene, further providing climate adequate to harbor piñons in scattered refugia. Piñon in a Bear Lake refugium would have served as sources for expansion outward as climates allowed.

A challenge to the high-latitude refugia hypothesis is the lack of piñon in Great Basin Late Pleistocene/earliest Holocene records other than the Falls Canyon midden and the Bear Lake pollen core. In that Great Basin conifers commonly occur in modern conditions as highly disjunct stands and often contain only one to several trees (Charlet, 1996, 2007). We consider it feasible that small refugia such as we propose could have existed and would readily go undetected in paleo-studies. We speculate that piñon may have persisted in such small stands as not to have been incorporated in middens known or analyzed to date. This argument was advanced by Hamrick et al. (1994: 290) to explain high genetic diversity of piñon; "it is also possible that populations of supposedly Holocene-immigrant species were present during the most recent glacial period in small, isolated refugia, readily missed by localized macrofossil samples." The minor and occasional occurrences of piñon within the extensive juniper woodlands of northern Utah provide a model for our speculative refugium conditions—and a reason for piñon's absence from middens.

Further lack of piñon in middens comes from the caveats pointed out in an early section, including the bias of woodrats in their diets, the short distance from the midden that woodrats collect from, and the potential absence of woodrats from a region during unfavorable climate periods. Regarding pollen, if more pollen researchers had been able to separate pine pollen and identified piñon from Great Basin sediment cores, we might have found that the species was more widespread in the Late Pleistocene than midden evidence suggests.

Shifts in piñon's distribution, especially at the margins of the range, should also be considered when evaluating refugia in millennia past. Piñon does not currently grow in the locations or elevations of six Holocene piñon records near the north end of its modern range (Bear Lake, Silver Island Canyon, Danger Cave, Blue Lakes Marsh, Grouse Creek Junction, and Lead Lake; see table M-1). Those locations range 12–26 km from the nearest piñon stands at present; they also range from 260–600 m below present piñon stands. Piñon was growing near

those sites as recently as 1150 cal B.P. (Lead Lake) and 2514 cal B.P. (Grouse Creek Junction). Lack of piñon at present, thus, does not provide sufficient evidence that piñon wasn't growing in an area in the recent—or distant—past.

Additional support for high-latitude refugia comes from comparison of current annual temperatures and precipitation, which indicates the areas of our proposed refugia to have similar modern values to Late Pleistocene southern refugia. For example, using the PRISM Explorer model based on monthly and annual normals for the period 1991–2020 (https://prism.oregonstate.edu/explorer/; Daly et al. 1994), mean annual precipitation at three southern Late Pleistocene refugial locations was 20 cm (Eleana Range, 21 cm; Inyo Caves, 24 cm; Alabama Hills, 15 cm), and mean annual temperature was 12°C (Eleana Range, 12°C; Inyo Caves, 10°C; Alabama Hills, 14°C). For the two high-latitude refugia, mean annual precipitation was 16 cm (Falls Canyon, 18 cm; Danger Cave, 13 cm) and mean annual temperature was 11°C (Falls Canyon, 11°C; Danger Cave, 11°C).

Migration Rates

Rates for Diffusion and Long-distance Dispersal: One way to test the two hypotheses is to calculate step-wise migration rates between midden locations and evaluate whether one scenario generates more reasonable rates than the other. Several Great Basin biogeographers have estimated piñon's Holocene mean migration rates. Cole et al. (2012) estimated migration rates of 21–60 m/year from arithmetic distance between known distant midden/pollen locations (based on latitude) divided by the time difference in piñon arrival dates between locations. Lanner (1983) took a process approach to dispersal. He estimated the generation time needed for a seed to germinate, mature, reproduce, and a new crop of seedlings to establish and produce a significant mature cone crop, as well as dispersal vectors. Based on a diffusion model and using 13 km as an annual dispersal distance of Clark's Nutcrackers, Lanner (1983) estimated a process-based rate of 130 m/year. Using a more liberal generation time (80 years) and greater dispersal distance (19 km), Lanner also considered a diffusion migration rate of 240 m/year to be feasible.

We calculated rates of piñon migration based on what we consider to be more reasonable values for a diffusion model, and separately evaluated the role of long-distance dispersal and "fat

tails." For the diffusion model, we estimated the time to produce a new, self-reproducing stand from effective colonists (i.e., viable seeds that successfully germinate, establish, and produce viable seeds) in a formerly piñon-less area that is adjacent to an existing population. Piñon trees reach sexual maturity in ~25–35 years but do not produce significant seed crops until trees are ~75–100 years old (Krugman and Jenkinson, 1974; Meeuwig et al., 1990); we use 88 years as an average value. The proximity of the existing main population benefits expansion by diffusion. Cone-crop irregularity aside (masting, etc.), trees in the main population serve as regular sources of large amounts of seeds toward the expanding front. Large main populations attract abundant Clark's Nutcrackers as well as Pinyon Jays, which serve as vectors for local planting. An abundant flow of seeds from the main population would provide a cone-producing stand along the advancing front in one generation's time (88 years).

We differ from Lanner (1983), however, who developed his wave-front (diffusion model) migration rates by assuming an annual dispersal distance by Clark's Nutcrackers of 13–19 km. Given the leptokurtic distribution of seeds by nutcrackers—and that piñon pines are at least third in species' priority for nutcrackers' diet—we do not feel these to be reasonable distances for routine dispersal. By far most seeds of both Clark's Nutcrackers and Pinyon Jays are cached within 1 km of collection trees, with 3–5 km also being observed. Using 1 km and 5 km as a reasonable range for annual dispersal, we calculate diffusion rates from an existing population into a naive landscape as ~11–57 m/year.

Accepting "fat tails"—i.e., long-distance dispersal is possible if rare—we also estimated rates based on maximum likely dispersal distances by nutcrackers. We assume these events would occur as "jumps" across gaps of unfavorable terrains, such as low, broad basins between mountain ranges. Time to maturity/full cone crop in this case remains 88 years, but dispersal is 22 km, the maximum observed for Clark's Nutcrackers. Long-distance dispersal most likely is accomplished by a single or few nutcrackers who ferry a small number of seeds (a single pouch-full) into the new habitat, creating a founder event. Considering the many factors that limit seedling survival, this long-distance dispersal event would translate at best into establishment of a single or few colonist pines.[7] Even once this tree/trees began to produce mature cone crops, and

[7] An anecdotal and putative example of such a long-distance dispersal event is the tiny stand of whitebark pines (fewer than 10 trees) that occurs high in the cirque of Middle Creek Canyon, eastern White Mountains, CA. The only occurrence of the species known in the White-Inyo

assuming nutcrackers had reason to be in the vicinity based on presence of other host species (e.g., limber pine), the founder piñon was unlikely to be an effective source for further long-distance colonization. As described before, nutcrackers are not drawn to stands of a single or few trees that produce only a small number of cones (Christensen et al., 1991). In the very small likelihood, however, that nutcrackers did subsequently disperse seeds another 22 km to naive territory from the initial single/few colonists once they were mature (88 years), this would yield a long-distance dispersal rate of 250 m/year.

More likely, subsequent long-distance dispersal events would require development of a larger cone-producing stand, with individuals comprising offspring from the colonist(s). This would require another 88 years. Such a stand might then be adequate to attract nutcrackers (cumulative 176 years) and become a source for a second rare long-dispersal event (i.e., another 22 km jump). At an annual rate, this becomes 125 m/year. These rates are close to what Lanner (1983) calculated, but he considered this a diffusion model. We believe rates this large represent very low probability events that are unlikely to occur in sequence. The reliance on repeat inflow of seeds from distant large populations before the remote colonists can multiply to become self-sustaining stands has been documented for ponderosa pine (Allee effects, Lesser and Jackson, 2013).

Because of long-distance nutcracker dispersal being rare, estimated annual rates over long time periods would remain only somewhat larger than the diffusion rates of 11–57 m/year. To generate a mean rate of ~80 m/year over 2000 years, for example, would require an unlikely 50% of annual migration steps to be 125 m/year with the other 50% of the years at a moderate diffusion rate of 30 m/year. This assumes a 250 m/year rate requires 25% of the annual steps to be long-distance. To attain rates larger than 100 m/year over 2000 years requires the low

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Mountains, botanist Dean Taylor found and vouchered this single cluster of whitebark pines growing amid subalpine forests comprising bristlecone and limber pines in 1986 (Taylor, personal commun.). The trees are mature but not old, and appear most likely to be from a founder event and not relictual of a past broader distribution. The location lies in leeward direction of a broad pass of the range crest where winds, moisture, and perhaps nutcrackers fly through. Notably, the nearest whitebark pine occurrence (extensive forests) is 25 km to the west in the Glass Mountains; the terrain in between is inhospitable low basins. Despite decades of earnest searching by botanists, no other occurrence of the species has been found in the range. A rare long-distance dispersal by one Clark's Nutcracker carrying a pouch of seeds could explain this stand's origin, with no apparent further founding events or diffusion happening yet.

likelihood of long-distance dispersal occurring ~50–90% of the years, depending on the expansion and long-distance rates used. In sum, we consider rates larger than ~80 m/year over time periods of a millennium or more to be difficult to explain within the metrics currently known for piñon dispersal.

VERY-VERY LONG-DISTANCE MIGRATION: While the science of nutcracker dispersal does not support mean dispersal rates at millennial scales to be larger than ~80 m/year, we embrace Reid's paradox in the case of unexpectedly larger rates and look for other head-scratching solutions. One such solution would be very long dispersal events by nutcrackers, i.e., successful planting flights greater than 22 km. According to Grayson (2011: 257), "if we are really desperate, we could even invoke the history of the cattle egret…and wonder whether a flock of Clark's Nutcrackers was blown off course 7000 years ago…" Reid himself (1899)—in desperation—offered birds blown off course by hurricane winds as a solution to his dilemma.

Very long-distance dispersal for any species is infamously difficult to estimate. For vectors such as birds it is almost impossible to assess, even when birds are tagged and successfully recaptured at great distances or GPS collars track their movements. Where tagging has been done with Clark's Nutcrackers, birds that flew out of the study area (i.e., emigrated long distances) were lost and did not contribute to dispersal calculations (Lorenz and Sullivan, 2009; Schaming, 2016). Despite these challenges, there have been qualitative observations of long-distance flights made by ornithologists and bird observers of so-called irruptions of Clark's Nutcrackers. Irruptions occur when large numbers of birds appear in locations far from their known ranges (Newton, 2007). These differ from regular seasonal migrations, and occur at irregular, rare intervals. Irruptions have been documented for Clark's Nutcrackers since the late 1800s. For instance, nutcrackers were observed in large numbers in autumns of 1898, 1919, 1935, 1950, 1955, and 1961 along the California coast, more than 200 km from their closest native range in the western Sierra Nevada (Davis and Williams, 1957, 1964). Other irruptive events have occurred in the American Southwest, where Clark's Nutcrackers were observed more than 170 km from their native range (Taylor and Voorhies, 1936). In the Siberian nutcracker (*Nucifraga columbiana macrorhychos*), irruptive events were documented to involve flights as great as 7000 km (Newton, 2007)! In all these cases, the birds flew into ecosystems that do not support their preferred nut forage; rather, the birds foraged on insects, plants, and

even carcasses of dead animals. These events occurred in late autumn and were highly correlated with low-no cone crops of forage tree species in the nutcrackers' native range. Super long-distance flights are interpreted as the birds searching for food of any kind far beyond their homelands. Irruption flights are more likely in species/regions where tree species mast, as with piñon in the western Great Basin (Thomas and Millar, 2023), which forces the birds to fly far to find food during years with no cone crops.

Importantly for our context, irruptive long-distance flights are not known to occur as nut-caching events. Instead, the opposite is true; birds are in search of food. Nonetheless, like others who faced Reid's paradox, we accept that irruptive events might have occurred in the Holocene Great Basin, causing nutcrackers to fly hundreds to thousands of kilometers. The very low probability of seeds being carried a very long distance by a few birds in these irruptive flights multiplied by very long times may be just the "fat tail" events that could solve a problem of one or more very large migration rates.

OBSERVED RATES UNDER TWO MIGRATION HYPOTHESES: To test our two hypotheses for piñon migration, we estimated stepwise migration rates along western-, central-, and eastern Great Basin paths using the two hypotheses as guides for most likely geographic steps. We excluded analysis of migration to the potential Warner Mountains refugium; its great isolation from other parts of the species range made analysis unnecessary. We differ from previous scholars who estimated migration rates generally based on time for an apparent piñon front to reach increasingly northerly latitudes. Our approach, fraught with problems as it is, attempts to be more precise, using the actual midden data—locations and times—to estimate step-by-step migration rates. This requires that we select specific paths for the steps, and assume that migration progress actually occurred as the relative difference in the midden dates. This approach is challenged by uncertainty about the existing midden record: does it represent what occurred or are there important missing data (e.g., Grayson and Livingston, 1993)? We feel that specificity of our approach is worth an analytic attempt.

Tables M3-2 and M3-3 give our estimated migration rates using recalibrated dates and the latest location information and following step-by-step progress of piñon in the three general corridors of figure M3-4 (Lanner and Van Devender, 1998). In the first case, we calculated rates based on Hypothesis 1, the traditional scenario of gradual migration northward along each

latitudinal corridor. We estimated rates between locations in approximate chronological order from oldest to youngest (table M3-2). We assumed Holocene migration starting (i.e., initial movement northward) from southern Pleistocene refugia in the current Mojave region under an assumption that piñon did not start migrating out of southern refugia until 9 ka (Van Devender, 1977; Van Devender and Spaulding, 1979). In one situation (Falls Canyon), the midden date was older than 9000 cal B.P., and we used 10 ka as the emigration date from the south. There is no logical way to suggest a south-to-north migration to the ~19,000-year-old piñon recorded in the Bear Lake core, so we ignored migration and migration rates involving this location.

In the second case (table M3-3), we estimated rates based on Hypothesis 2, calculating steps between locations along similar south-to-north paths out of Late Pleistocene southern, Mojave-area refugia, but also considering emigration outward from high-latitude refugia (western and eastern Great Basin), as well. In this scenario, we used 9 ka as the initial emigration date for all steps, and we considered an interior western Great Basin path as well as a far-west corridor (along the eastern Sierra Nevada). Further, in the vicinity of the high-latitude refugia, we allowed some local longitudinal movements (e.g., west-east; east-west) as well as some locally southward migration.

Many step rates under both hypotheses were within our diffusion range (11–57 m/year). A reasonable number (5–7 for each hypothesis) were greater than 57 m/year and less than 90 m/year, which (as we argued above) could include routine diffusion plus a small number of long-distance nutcracker dispersals accepting unusual circumstances (fat tails). The mean rate overall under Hypothesis 1 was 135.9 m/year; excluding events greater than 100 m/year yielded a mean rate of 43.9 m/year. Under Hypothesis 2, the overall mean rate was 72.8 m/year; excluding events greater than 100 m/year yielded a mean rate of 41.7 m/year. By this measure, the scenario including high-latitude refugia (Hypothesis 2) produced more reasonable migration step rates than Hypothesis 1.

What especially separated the two hypotheses, however, were differences in numbers of migration steps with rates greater than 100 m/year and rates that were extremely high. Hypothesis 1 had 13 steps with rates >100 m/year whereas Hypothesis 2 had three such steps. Hypothesis 1 had five steps with rates greater than 250 m/year, including rates of 420 and 979 m/year. Hypothesis 2 had three steps with rates >100 m/year, and these were lower than in Hypothesis 1 (117, 309, and 412 m/year).

Table M3-2. Hypothesis One: Northward Migration from Southern Refugium

Observed rates for western, central, and eastern Great Basin piñon migration, calculated as distance/time between points, giving priority to south-to-north migration and to dispersal steps in relative chronosequence. 9 ka is used as a conservative date for dispersal out of southern Mojave Pleistocene refugium, except where a midden had an older date. Green highlights are rates >100 m/yr, which are highly improbable over the time periods indicated (see text).

Source location or refugium	Map #	Source date or date of refugium	Arrival location	Map #	Arrival date	Step time difference (yrs)	Step distance (km)	Observed migration rate (m/yr)	Notes
1. Western Migration Path–Far west corridor									
Inyo Caves	41	13011	–	–	–	–	–	–	Pleistocene refugium
Inyo Caves	41	13011	Falls Canyon	20	9854	146	143	979	Rate calculated as leaving Inyo Caves @ 10 ka
Inyo Caves	41	13011	Papoose Flat	19	8765	235	60	255	Rate calculated as leaving Inyo Caves @ 9 ka
Papoose Flat	19	8765	Silver Canyon	18	6458	2307	45	20	
Papoose Flat	19	8765	Wyman Canyon	16	5157	3608	45	12	
Papoose Flat	19	8765	Deep Springs Overlook	13	3532	1625	38	23	
Silver Canyon	18	6458	Bodie Mountains	17	5746	712	122	171	
Silver Canyon	18	6458	Sherwin Summit	15	3978	2480	40	16	
Wyman Canyon	16	5157	Rhyolite Ridge	14	3768	1389	47	34	
Sherwin Summit	15	3978	Chidago Flats	12	3224	754	16	21	
Rhyolite Ridge	14	3768	Navy Army Depot	7	1101	2667	112	42	
Rhyolite Ridge	14	3768	Lead Lake	8	1150	2618	210	80	
Chidago Flats	12	3224	Slinkard Valley	11	2140	1084	141	130	
Slinkard Valley	11	2140	Wolf Creek	9	1369	771	13	17	
Wolf Creek	9	1369	Geiger Grade	6	1018	351	83	236	
Lead Lake	8	1150	Painted Hills	1	250	900	104	116	
Geiger Grade	6	1018	Silver City	5	955	63	15	238	
Silver City	5	955	Newton Creek	3	658	297	13	44	
Newton Creek	3	658	Hidden Valley	2	392	266	13	49	
Hidden Valley	2	392	Painted Hills	1	250	142	44	309	
Mean								**146.9**	
Mean excluding rates >100 m/yr								**32.5**	
2. Central Migration Path									
Eleana Range	26	12433	–	–	–	–	–	–	Pleistocene refugium
Pahranagat Range	25	10402	–	–	–	–	–	–	Pleistocene refugium
Pahranagat Range	25	10402	Cathedral Canyon	24	6642	2358	200	85	Rate calculated as leaving Pahranagat @ 9 ka
Pahranagat Range	25	10402	Gatecliff Shelter	22	6029	2971	218	74	Rate calculated as leaving Pahranagat @ 9 ka
Cathedral Canyon	24	6642	Roberts Mountain	23	6404	238	100	420	
Cathedral Canyon	24	6642	Bronco Charlie	21	3169	3473	112	32	
Mean								**152.8**	
Mean excluding								**63.7**	
3. Eastern Migration Path									
Pahranagat Range	25	10402	–	–	–	–	–	–	Pleistocene refugium
Pahranagat Range	25	10402	Cottonwood Canyon	38	8487	513	336	655	Rate calculated as leaving Pahranagat @ 9 ka
Pahranagat Range	25	10402	Valley View	36	7107	1893	245	129	Rate calculated as leaving Pahranagat @ 9 ka
Pahranagat Range	25	10402	Council Hall Cave	35	7017	1983	247	125	Rate calculated as leaving Pahranagat @ 9 ka
Cottonwood Canyon	38	8487	Danger Cave	37	7554	933	95	102	
Danger Cave	37	7554	Marblehead Mine	34	6855	699	23	33	
Marblehead Mine	34	6855	Icicle Cave	33	6135	720	40	56	
Marblehead Mine	34	6855	Itchy Ban	32	5791	1064	3	3	
Itchy Ban	32	5791	Collar and Elbow	29	3258	2533	22	9	
Itchy Ban	32	5791	Silver Island Canyon	31	5071	720	44	61	
Silver Island Canyon	31	5071	Pilot Range	30	3690	1381	44	32	
Pilot Range	30	3690	Alamo Creek	28	2526	1164	87	75	
Pilot Range	30	3690	Grouse Creek Junction	27	2514	1176	18	15	
Uplands around Bear Lake	–	–	Bear Lake	–	–	–	–	–	
Mean								**107.9**	
Mean excluding rates >100 m/yr								**35.5**	

Table M3-3. Hypothesis Two: Northward Migration with High-latitude Refugia

Observed rates for western, central, and eastern Great Basin pinyon migration, calculated as distance/time between points following topographic paths and including migration out of Pleistocene refugia in the southern Great Basin as well as out of higher-latitude refugia. 9 ka is used as a conservative date for dispersal out of southern-Mojave Pleistocene refugium. Green highlights are rates >100 m/yr, which are highly improbable over the time periods indicated (see text).

Source location or refugium	Map #	Source date or date of refugium	Arrival location	Map #	Arrival date	Step time difference (yrs)	Step distance (km)	Observed migration rate (m/yr)	Notes
1a. Western Migration Path–Far west corridor									
Alabama Hills	42	13320	–	–	–	–	–	–	Pleistocene refugium
Inyo Caves	41	13011	–	–	–	–	–	–	Pleistocene refugium
Falls Canyon	20	9854	–	–	–	–	–	–	Pleistocene refugium
Falls Canyon	20	9854	Papoose Flat	19	8765	1089	83	76	
Papoose Flat	19	8765	Silver Canyon	18	6458	2307	45	19	
Falls Canyon	20	9854	Bodie Mountains	17	5746	4108	83	20	
Falls Canyon	20	9854	Sherwin Summit	15	3978	5876	31	5	
Sherwin Summit	15	3978	Chidago Flats	12	3224	754	16	21	
Bodie Mountains	17	5746	Slinkard Valley	11	2140	3606	62	17	
Slinkard Valley	11	2140	Wolf Creek	9	1369	771	12	16	
Slinkard Valley	11	2140	Silver City	5	955	1185	68	57	
Silver City	5	955	Newton Creek	3	658	297	12	40	
Slinkard Valley	11	2140	Geiger Grade	6	1018	1122	82	73	
Newton Creek	3	658	Hidden Valley	2	392	266	14	52	
Hidden Valley	2	392	Painted Hills	1	250	142	44	309	
Mean								**58.8**	
Mean excluding Hidden Valley to Painted Hills								**36.0**	
1b. Western Migration Path–Fish Lake Valley–Excelsior Mountains corridor–Wassuk/Carson Sink									
Papoose Flat	19	8765	Wyman Canyon	16	5157	3608	45	12	
Wyman Canyon	16	5157	Deep Springs Overlook	13	3532	1625	10	6	
Wyman Canyon	16	5157	Rhyolite Ridge	11	3768	1389	47	34	
Rhyolite Ridge	14	3768	Navy Army Depot	7	1101	2667	113	42	
Rhyolite Ridge	14	3768	Lead Lake	8	1150	2618	120	46	
Lead Lake	8	1150	Painted Hills	1	250	900	105	117	Alternate path
Mean								**42.8**	
Mean excluding Lead Lake to Painted Hills								**28.0**	
2. Central Migration Path									
Eleana Range	26	12433	–	–	–	–	–	–	Pleistocene refugium
Pahranagat Range	25	10402	–	–	–	–	–	–	Pleistocene refugium
Pahranagat Range	25	10402	Cathedral Canyon	24	6642	2358	196	83	Rate calculated as leaving Pahranagat @ 9 ka
Pahranagat Range	25	10402	Gatecliff Shelter	22	6029	2971	219	74	Rate calculated as leaving Pahranagat @ 9 ka
Cathedral Canyon	24	6642	Roberts Mountain	23	6404	238	98	412	
Cathedral Canyon	24	6642	Bronco Charlie	21	3169	3235	114	35	
Mean								**151.0**	
Mean excluding Cathedral Canyon to Bronco Charlie								**64.0**	
3. Eastern Migration Path									
Bear Lake	69	Late Pleistocene	–	–	–	–	–	–	Pleistocene refugium
Cottonwood (CCR)	38	8487	–	–	–	–	–	–	Pleistocene refugium
Danger Cave	37	7554	–	–	–	–	–	–	Pleistocene refugium
Cottonwood	38	8487	Valley View	36	7107	1380	89	64	
Cottonwood	38	8487	Council Hall Cave	35	7017	1470	126	86	
Danger Cave	37	7554	Marblehead Mine	34	6855	699	22	31	
Marblehead Mine	34	6855	Itchy Ban	32	5791	1064	2	2	
Danger Cave	37	7554	Silver Island Canyon	31	5071	2483	29	12	
Marblehead Mine	34	6855	Icicle Cave	33	6135	720	40	56	
Silver Island Canyon	31	5071	Pilot Range	30	3690	1381	45	33	
Marblehead Mine	34	6855	Collar and Elbow	29	3258	3597	19	5	
Pilot Range	30	3690	Grouse Creek Junction	27	2514	744	18	24	
Pilot Range	30	3690	Alamo Creek	28	2526	1164	86	73	
Mean								**38.6**	

By these comparisons, Hypothesis 2 overall and stepwise produces more reasonable migration rates than Hypothesis 1. In each scenario, nonetheless, there are one to several "impossibly" large step rates. How could those occur? The most likely explanation is the step paths we chose were not the paths of actual piñon migration, and our results were affected by missing data, as described above. For instance, under Hypothesis 2, we selected a step migration as Cathedral Canyon to Roberts Mountain, which resulted in the unreasonably high rate of 412 m/year. If we had assumed, instead, that step to be from Cottonwood Canyon to Roberts Mountain, the rate would be a very reasonable 40 m/year. We did not prioritize the latter route, however, because it required a tortuous topographic, east-to-west pass over and around seven mountain ranges that we felt less likely than the path we chose. If we had a greater distribution of middens and arrival dates, the paths might have become clearer, and the two scenarios may have resulted in very different outcomes.

Putting these aside and accepting the conundrum of extremely high rates (more than 250 m/year and especially >400 and >900 m/year) in both scenarios, we consider alternative explanations, per resolutions to Reid's paradox generally. A possibility we are forced to consider is that nutcrackers indeed successfully transported and planted piñon seeds extremely long distances in the Holocene Great Basin. This might have occurred as a result of very long flights observed in the modern era as irruptive events, though they have never been documented to be seed-dispersing. Further, it may be that current ecological understanding of the maximum distance that nutcrackers can fly to cache/plant seeds is underestimated, and that nutcrackers may, on occasion, disperse seeds much greater distances than the maximum 22 km reported. Finally, with Grayson (2011), and with no documentation, we might in desperation invoke large wind events to blow birds far off course.

We argued that far-flung piñon stands established via human assistance would be highly unlikely. As in nutcrackers, however, we must also consider dispersal by humans as a possible resolution to the dilemmas of Reid's paradox for piñon. Especially for the relatively large distance (44 km) and very short time (142 years) between Hidden Valley and Painted Hills arrival dates in the far western Great Basin (= migration rate of 309 m/year, table M3-3), we propose that piñon might have been introduced to the Painted Hills, the current northernmost distribution in the western Great Basin, via human agency. Colonization at Painted Hills by nutcrackers seems less likely; the total time between arrival dates at these sites is less than

adequate for two generations of piñon to produce adequate crops for bird transport (176 years) to Hidden Valley. Lack of forage species (e.g., whitebark, limber, or ponderosa pines) in the Painted Hills further reduces the chance that nutcrackers would fly to virgin territory with piñon seeds on an irruptive flight and that they would cache seeds. Importantly, however, the current four piñon trees known from Painted Hills are in remote areas and steep slopes. Three occur together and one of these is likely the parent of the younger two; the fourth Painted Hills piñon is 2.5 km away. These four piñons are in locations highly likely to be planted by humans; if humans were involved in establishing the species in this range, we assume there was (is?) an older stand somewhere in the range in a more likely environmental context of value to humans, and the known four trees were planted by birds from that stand. Fire or other factors may have eliminated a once-human-planted stand from the range.

As a line of reasoning for human planting in this range, we point out first that the piñon arrival dates for Painted Hills (estimated from tree ring counts to be ~300 years old in 2023) and Hidden Valley (with a radiocarbon two-sigma range of 151–633 cal B.P.) overlap and are not statistically significant. If piñon arrived at Painted Hills and Hidden Valley around the same time, the migration rate would be even larger. Even supposing a simultaneous arrival date, the 44 km distance invites the possibility of human involvement.

The Hidden Valley-Painted Hills area lies on the northeastern margin of Washoe tribal territory, adjacent to prime pine harvesting areas used during ethnohistoric times (D'Azevedo, 1986: fig. 1). The Washoe speak a Hokan language and are considered to have lived in this general area for millennia. It seems entirely feasible that Washoe foragers, perhaps carrying basket-loads of pine nuts, could have spread piñon across a 44 km distance (a 27 mi walk).

Immediately to the east is the Pyramid Lake catchment, inhabited during this interval by the Numic-speaking Numa (Northern Paiute) who likely arrived sometime after 1000 cal B.P. (Fowler and Liljeblad, 1986)—and perhaps considerably later. The first arrival of piñon in Northern Paiute territory is estimated at 1007–1293 cal B.P. To reach Hidden Valley and the Painted Hills requires travel of more than 75 km, crossing the Carson Sink and skirting Pyramid Lake—not a likely scenario.

A third (far-fetched) possibility involves John C. Frémont who became "almost obsessed" with piñon pine during his wintertime traverse of the Sierra Nevada in January 1844.[8] Somewhere along the way, he purchased a few pounds of pine nuts from a local tribe, finding that "when roasted, their pleasant flavor made them an agreeable addition to our now scanty store of provisions" (Frémont et al., 1845, quoted in Lanner, 1981: 95, 107). After naming Pyramid Lake, Frémont's route took him along Truckee River south to the Wadsworth area and continued south to the Carson River. Because Frémont was traveling southward from Oregon, he first entered the piñon-juniper woodland somewhere in the vicinity of Painted Hills, Hidden Valley, and Pyramid Lake, raising the possibility of commerce in pine nuts as a potential mechanism of seed-dispersal during the mid-19th century.[9]

We find evidence in migration rates that support the Hypothesis 2 northward Early Holocene migration from Mojave refugia plus emigration radiating locally from four high-latitude refugia. Rates for Hypothesis 2 confer with a dominant diffusion model with rare long-distance dispersal events, as expected. Hypothesis 1, in contrast, has more very large step rates that require unknown dispersal mechanisms. To the extent that those high rates are real (given biases of the data), very, very large distance/short time dispersal events (making extremely long leptokurtic tails) require us to invoke bird irruption events, dispersal by humans, or undocumented extreme events. Hypothesis 1 is challenged by locations that are far north (including the Warner Mountain refugium) and have very old dates, which is difficult or impossible (in the case of the Bear Lake record) to explain by migration from the Mojave region.

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[8] Frémont soon would bring piñon pine to the attention of the scientific community, formally recording the name *Pinus monophylla* in his journal (Cronquist et al., 1972: 47).

[9] This suggestion can be amplified for the ethnohistoric era. Writing about the Owens Valley Paiute, Steward (1933: 71) noted that "trading was done across the Sierra Nevada by Owens Valley Indians with Western Mono, Mono Lake with Miwok … Muir in 1870 saw women in a party, traveling barefoot, carrying the loads … Mono Lake traded pinenuts, piuiga, cuza'vi, baskets, red paint, pijapi, white paint, ivi, and salt for bead money, acorns, manzanita berries, apo'sogwa, sow berry, tama, and elderberries, hubu'xia. They often wintered in Yosemite, especially when pinenuts were scarce." Steward (1941: 428) added that the Northern Paiute brought piñon nuts to Burns in the old days to trade. I think the distance would prohibit such a thing before the horse was introduced." Several 19th-century accounts from the *Reese River Reveille* newspaper show extensive commerce in piñon nut trade by the 19th-century Western Shoshone (H.V. Wells, 1983).

All said, we do not find definitive evidence strongly favoring one or the other hypothesis—or another that we have not considered—and leave open the possibility of either.

REGIONAL DIFFERENCES IN MIGRATION RATES: Most piñon scholars have concluded from older piñon dates in the central and eastern Great Basin that migration rates were greater in those regions (Lanner, 1983; Grayson, 2011; Cole et al., 2012; Miller et al., 2019). These conclusions were made under assumptions of dominantly south-to-north migration from Mojave-area refugia along three corridors, i.e., Hypothesis 1. Considering the possibility of high latitude Late Pleistocene piñon refugial areas, however, and their role in local expansion after ~8 ka, we find a different result about regional rates (table M3-3). Mean rate overall for the western corridor (far west and slightly interior paths) was 49.7 m/year; for the central corridor, mean rate was 64.0 m/year (excluding one anomalous rate); and for the eastern region, the mean rate was 38.6 m/year. Thus, with the presence of four refugial areas—and assuming emigration from these regions in the mid-Holocene—migration rates in the eastern region were lower than the other areas. Having no (obvious) refugia in the central Great Basin, that region may have relied on south-to-north migration, resulting in the largest mean migration rate.

We have as much difficulty explaining these new rate differences as previous authors had. Climate has been invoked as having remained harsher and less favorable for piñon expansion longer in the western region (Grayson, 2011; Miller et al., 2019). We accept climate differences as likely to be important, but unlikely to be harsher in the eastern Great Basin where rates were lowest.

We consider two conditions not previously described that might contribute to the regional rate differences we estimated. The first combines topography, tree species diversity, and behavior of Clark's Nutcrackers. In the far west, in particular along the eastern Sierra Nevada escarpment and adjacent regions, high-ranking (for nutcrackers) whitebark pine and limber pine forests were widely distributed throughout the Late Pleistocene (Wigand and Nowak, 1992; Nowak et al., 1994a; Rhode, 2000; Wigand and Rhode, 2002; Wigand, 2017), including along the mid-elevation eastern slopes of the long north-trending Sierra Nevada. Similarly, other nutcracker forage species such as Jeffrey and ponderosa pines existed in mixed conifer forests of this region. The presence of these species, whitebark pine in particular, would sustain year-round resident nutcracker populations in high abundance (Powell and Zimmerman, 2004). Nutcrackers would include piñon in their diet less often given their options than in regions (central/eastern

Great Basin) where species diversity was lower, making fewer opportunities for piñon dispersal. The diversity and continuity of forage species would further reduce the need for long-distance flights and lower the possibility of irruptive events taking birds far afield. The abundance of high-ranking whitebark pine along continuous elevations would induce competition among adjacent nutcracker populations, with the likely effect of reducing migration flight distances. Combined, we see these factors leading to more diffusion migration occurring in the western corridor than in the central region.

In the eastern Great Basin, we consider low rates to primarily result from a network of small, scattered refugial stands at relatively high latitudes, which, after ~8 ka, expanded locally and served as sources for new colonization in the surrounding region. Further, Pleistocene southern Mojave-area refugial populations, in the Eleana Range (37.1°N) and Pahranagat Range (37.4°N) middens, were at higher latitude than Pleistocene sites in the far west (Haystack Mountain and Inyo Cave, 36.6°N, Alabama Hills, 36.5°N), giving the eastern region a leg-up on northward expansion, which results in lower calculated step rates.

High rates in the central corridor may relate to the spatial pattern of mountain ranges and basins combined with low diversity of nutcracker forage species. Between the southern Pleistocene refugia and the large region of central Nevada high ranges (Shoshone, Toiyabe, Toquima, Monitor, and Hot Creek ranges), topography includes large, low-elevation basins with scattered small ranges. Thus range-hopping (across basins) would be necessary for piñon nuts to be transported northward. With limber pine being the only nutcracker forage species in this region before piñon's arrival (thus, no Pinyon Jays), crop failure and small population sizes would encourage nutcrackers to fly far afield to search for food. Nutcrackers are observed to undertake long-distance flights only to locations where they will find food, thus they would be encouraged to fly to distant mountain ranges if limber pine grew there. If piñon nuts had been picked up in their sublingual pouches at southern locations, then colonization to a formerly piñon-less range would be possible. Such dispersal patterns would result in larger migration step rates than conditions in the western and eastern regions.

We interpreted this scenario for a modern colonization, where one of us (Millar) found piñon seedlings established north of the species' known modern northern range limit. In the Snake Mountains (41.5°N), north of the Humboldt River, she found two widely separated piñon seedlings (~5 years old) growing within the sparse limber pine populations of the range. In this

region, mountain ranges are small and scattered. We speculate that nutcrackers fly to the Snake Mountains to forage on limber pine, and when they fly from closest limber/piñon populations more southerly, colonist piñons could have been established.

A final pattern that others have observed, and one we challenge, is an asymmetry in the northernmost extent piñon has reached to the present, ostensibly having migrated much farther north in the eastern Great Basin (42.1°N) than in the western (39.9°N). If the Warner Mountains refugium (42.2°N) is accurate, however, piñon would have persisted during the Holocene (and still does?) at equally far northern latitudes in the west as in the east. Climate constraints seem as imminent in the east as the west at northerly latitudes, and topography/bird conditions do not suggest reasons that would limit piñon at these latitudes on either side of the Great Basin.

Adding to early emigration from the area we propose as the eastern piñon refugia, we corroborate a role for humans assisting piñon's migration there also. The work of Rhode and Madsen (1995, 1998) elegantly documents a sequence in midden strata of Danger Cave, whereby limber pine transitions to piñon pine rather rapidly ~7500 cal B.P. Very small stands, potentially remote from human habitation areas, might well have been overlooked (undiscovered) until they started to expand as climates and bird-dispersal allowed, as suggested elsewhere (Kelly, 1934). Once on their radar, the importance of piñon nuts to Middle Archaic foragers' diets suggests that humans would seek out and carry nuts routinely as trail food, returning them to their residential sites. If Danger Cave were in the region of expanding piñon stands from scattered refugial populations, it is reasonable that humans would discover such stands and return piñon nuts to their rockshelter residence. We agree with Rhode and Madsen (1998) that if this occurred around the Danger Cave area or otherwise around refugial stands, these were likely short-distance transports, given the short longevity of pine nuts and the simultaneous availability—diminishing with time—of limber pine seeds. We propose that humans started using piñon once stands had expanded from smaller, older, and more distant relictual stands in the region.

EAST-WEST MIGRATION: In the discussions above, and as authors before us have done, we propose that the primary direction of piñon's Holocene migrations has been south to north, following climate amelioration through the Holocene, with additional local expansions around high-latitude refugia. Given the ages of the middens and their latitudes, however, one might interpret long-distance migration as having been primarily east to west. We interpret that long distance east-to-west migration is a spurious effect of the differences and existence/latitudes of

refugial populations among the regions. This is not to say that local east-west migration did not occur. Migrations in other directions than south-to-north appear likely over short distances. Nutcrackers flying over a mountain crest during seed-caching flights no doubt occurred, as these are boreal-adapted species. Further, the attraction of limber pine stands in locations to the west or east across a basin may well have attracted nutcracker colonization flights in those directions. However, conditions favoring northward movement were likely to establish colonists in previously piñon-less terrain before seeds coming over barriers from the east. Thus, although east to west migration may have occurred, it would likely have lagged relative to northward movement, and unlikely served to provide novel long-distance colonization of piñon to a region.

SUMMARY AND CONCLUSIONS

In this chapter, we compile a comprehensive, up-to-date list of piñon occurrences in the Great Basin, some of which are confident migration-arrival dates while others are the oldest known date for piñon in the area. We have reevaluated these legacy dates and recalibrated their probability distributions using the most recent (IntCal20) calibration curve. From the locations and new dates, patterns emerged about Holocene migration of piñon into the Great Basin, several of which corroborate interpretations by earlier scholars. These include (1) evidence for retreat of piñon from much of central-northern latitudes during the cold last glacial period; (2) persistence of piñon woodlands for multi-millennia of the Pleistocene and Early Holocene in low-elevation regions of the southern Great Basin (now Mojave Desert); (3) migration northward from these southern Late Pleistocene refugia beginning ca. 9–8 ka; and (4) migration basically northward along three latitudinal corridors (western, central, and eastern). Together, these constitute a widely accepted “traditional” scenario, which we refer to as Hypothesis 1.

The new data, in addition, suggest several new patterns, including some locations with very old dates at relatively high latitudes and occurrence of piñon far north of its current known range limit, which indicates alternative processes. We propose a second scenario, Hypothesis 2, in which four high-latitude Late Pleistocene refugia occurred in addition to the large southern Pleistocene refugia in small areas that retained favorable microclimates for piñon. One high-latitude refugium is a small area in northern Chalfant Valley, western Great Basin (the White Mountains refugium), a second in the far northwestern Great Basin (the Warner Mountains refugium), a third in the eastern Great Basin as a larger complex of stands in the greater

Bonneville region above the Pleistocene lake levels (the Bonneville refugium), and a fourth in the lowlands around Bear Lake, northeastern Great Basin (Bear Lake refugium). During the Late Pleistocene, cold climates would restrict expansion of the stand areas at these locations. Under Hypothesis 2, we assume migration not only northward into the three latitudinal corridors from the southern Mojave region but also emigration outward in multiple directions from the high-latitude refugia after ca. 9–8 ka.

Analysis of differences in migration rates between steps allowed us to test these hypotheses. Differing from past scholars, we recognized the importance of leptokurtic dispersal based on corvid bird ecology, wherein most dispersal is short-distance (diffusion) with rare long-distance events. Given factors of bird and piñon ecology, we estimated piñon diffusion rates to be 11–57 m/year and long-distance rates to be 125–250 m/year. We generated observed step rates between specific midden locations under both hypotheses and found Hypothesis 2 to result in a greater number of reasonable rates than Hypothesis 1. Differences in mean rates between the latitudinal corridors differed from past analyses, with highest mean rate in the central Great Basin and lowest mean rate in the eastern Great Basin. Differences in climate, topography, history of conifer forests, and role of humans are possible explanations for these rate differences.

Each hypothesis, despite points in its favor, has serious challenges given assumptions we have made. For Hypothesis 1, the newly calibrated, very old dates at high latitudes in the western and eastern Great Basin are very difficult to explain by migration from southern, Mojave-region refugia starting 9–8 ka. For Hypothesis 2, the lack of more than two known piñon locations dating to the Pleistocene/earliest Holocene challenges our proposal that small stands persisted through the Late Pleistocene Great Basin, although the occurrence of *Juniperus osteosperma*, with its similar climate tolerances to piñon, in many central-northern Great Basin middens supports piñon persistence. Further, the potential occurrence of piñon in the Warner Mountains, far disjunct from its current range, suggests an ancient and persistent presence of the species there. Both hypotheses result in a few (Hypothesis 1) to many (Hypothesis 2) inter-step migration rates that require us to invoke undocumented dispersal mechanisms.

As a third possibility, not yet reaching the level of a hypothesis, we offer the following new migration scenario, which resolves some of the conundrums summarized above. This scenario proposes that piñon migrated northward in the late Early Holocene from a Mojave-region Pleistocene refugium. It differs from Hypotheses 1 and 2 in suggesting that, during the

Middle Holocene, piñon had both reached middle latitudes (as evidenced from middens of table M3-1) and expanded to latitudes even farther north across the west-east extent of the Great Basin, potentially reaching >42°N, the latitude of piñon presently in southern Idaho. Deteriorating climates of the Late Holocene—and century/millennial periods of oscillating climates within that timeframe—caused eventual extinction of most northern-tier piñon populations, except in the far east and potentially in the Warner Mountains in the far west.

Indirect evidence exists for such Holocene migration north of the contemporary piñon curtain in addition to the existence of the high-latitude Idaho and possible Warner Mountains populations. Several piñon scholars have stressed that fluctuating climates of the Middle and Late Holocene would have caused piñon expansion and contraction (extinction) events that would obscure the true chronological pattern of migration; they point to locations where this might have happened (Cole et al., 2012; Wigand, 2017). Further evidence comes from the six midden locations mentioned above that occur at the northernmost margins of what we consider the modern piñon curtain. Those middens contained piñon but the species does not grow at the midden locations now. This suggests that piñon populations that might have existed at higher latitudes did not get included in analyzed middens, and subsequently were extirpated.

Finally, direct evidence exists for extreme northward migration (>41°N) of Colorado piñon, which had a Late Quaternary pattern very similar to singleleaf piñon (Cole et al., 2012). Locations up to 250 km north of the current distribution of Colorado piñon have been interpreted to represent migrations to the area starting 8000 years ago and disappearing by 3000 years ago (Betancourt, 1986; Emslie et al., 2015). The unusual existence of a hybrid population between singleleaf and Colorado piñons in the Crawford Mountains (northern UT), where Colorado piñon is presently more than 150 km distant, is another hint of early northern migration followed by extirpation (Lanner and Hutchinson, 1992).

We address this scenario in greater detail and provide further analysis of Hypotheses 1 and 2 in an evolving study (Thomas and Millar, in prep.). We also leave evaluation to future piñon scholars to test our assumptions and hypotheses, most fruitfully accomplished through discovery and analysis of new woodrat middens, pollen cores, and other evidence.

These hypotheses provide a theoretical baseline from which to compare the empirical distribution of archaeological sites, in an attempt to seek potential relationships between people and piñon pine moving simultaneously across the Holocene Great Basin.

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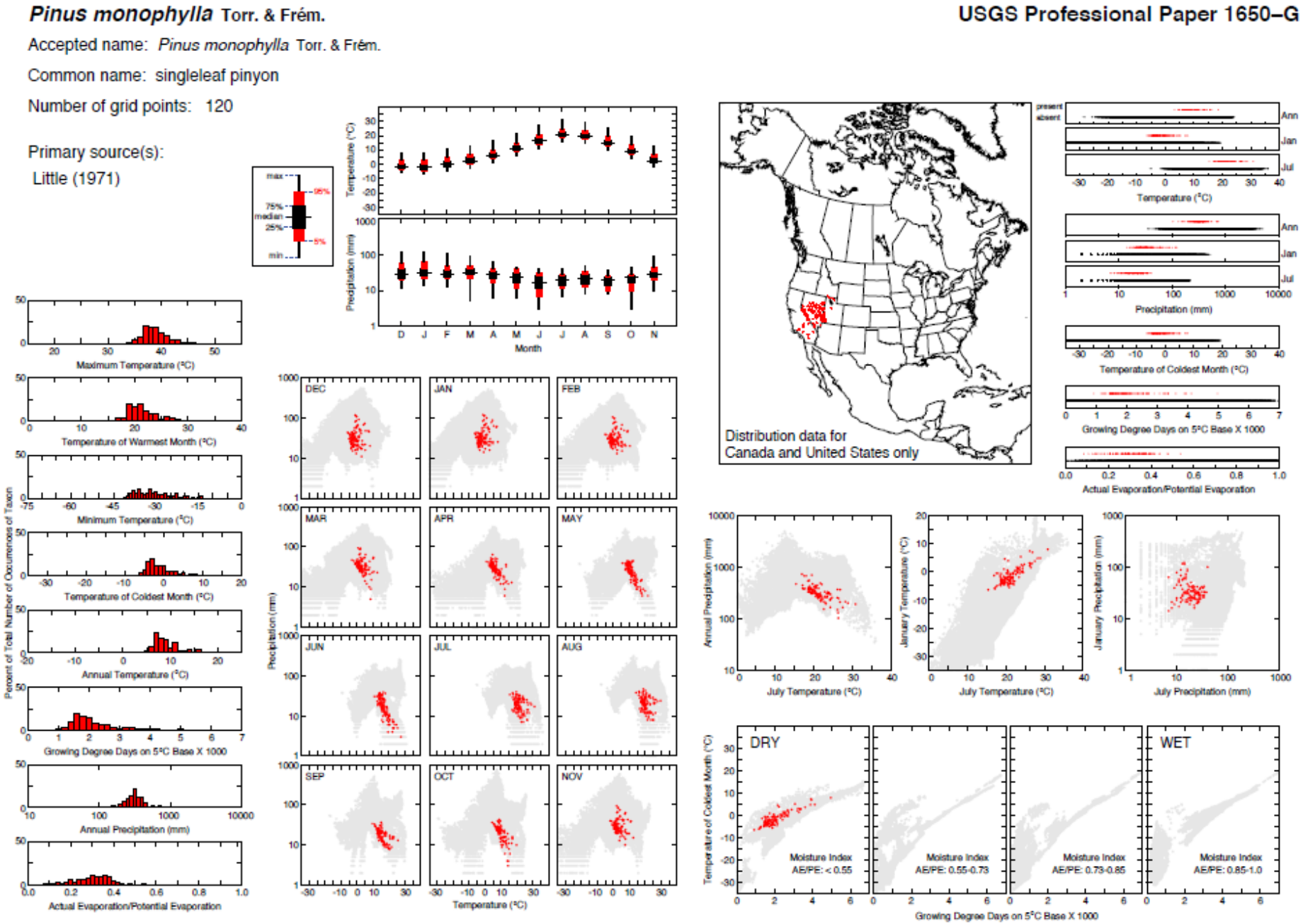
Supplemental Figure 1: Climate tolerances for Pinus monophylla. From Thompson et al., 2015.



Supplemental Figure 2: Climate tolerances for Juniperus osteosperma. From Thompson et al., 2015.