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Pinyon Pine and People Progressing Simultaneously across the Great Basin: Coincidence? Causality?

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During the Holocene, singleleaf pinyon pine (Pinus monophylla) *spread across the mid-elevations of the central Great Basin to define the so-called pinyon curtain that marks the current northerly limit of pinyon woodlands. At the same time, Indigenous communities also dispersed across these landscapes, leaving behind their Paleoindian roots along the low-lying pluvial lake margins to populate the adjacent uplands. Here, we explore ecological and archaeological perspectives and offer new hypotheses on the co-arrivals of people and pinyon throughout the central Great Basin. We test several models of human migration and employ multiple projections from ideal free distribution theory as heuristics to document the correlations and understand causality.*

> While there is a certain intuitive appeal to the notion that people followed pinyon trees into the central Great Basin, candor compels us to admit…we know too little about the distribution of either people or pinyon (Thomas 1982:164).

One of us inadvertently set the tone for this paper four decades ago. Since then, we have learned much about the dispersion of both people and singleleaf pinyon pine (*Pinus monophylla*; hereafter "pinyon") across the Great Basin. Here, we pursue two parallel perspectives—ecological and archaeological—to develop testable hypotheses relating to the dispersions of pinyon pine and post-Paleoindian communities. We start with a revision of the Holocene spread of pinyon based on 43 new locations and recalibrated radiocarbon dates to develop two ecology-based hypotheses of pinyon's estimated times of arrival (ETAs) in the Great Basin. We outline alternative views of the sequential migrations of pinyon from one to multiple Late Pleistocene refugia, defining the so-called pinyon curtain that today marks the modern limits of pinyon woodlands. We also derive first-occupation estimates (ETAs) for 27 Great Basin archaeological sites dating from the Middle Holocene (9,000 years ago) through the onset of the Late Holocene Dry Period (LHDP; ca. 3,100 cal B.P.) (Mensing et al. 2023; Thomas 2024). We argue here that the independent archaeological record documents the spread of post-Paleoindian Indigenous communities as favorable wetlands habitats dried up. When this occurred, these communities abandoned their Late Pleistocene/Early Holocene lacustrine homelands to expand into the same upland landscapes being simultaneously populated by pinyon. We compare projections from ideal free distribution theory as heuristics to examine the relationships among these independent estimates of pinyon and people arrivals across the central Great Basin—investigating their correlations and exploring potential causality.

ECOLOGICAL PERSPECTIVES: HOLOCENE SPREAD OF PINYON PINE ACROSS THE GREAT BASIN

The transition from Late Pleistocene to Holocene climates triggered biogeographical upheavals worldwide. The Great Basin, with its hundreds of 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. Pinyon was unusual among Great Basin tree species for its long-haul Holocene

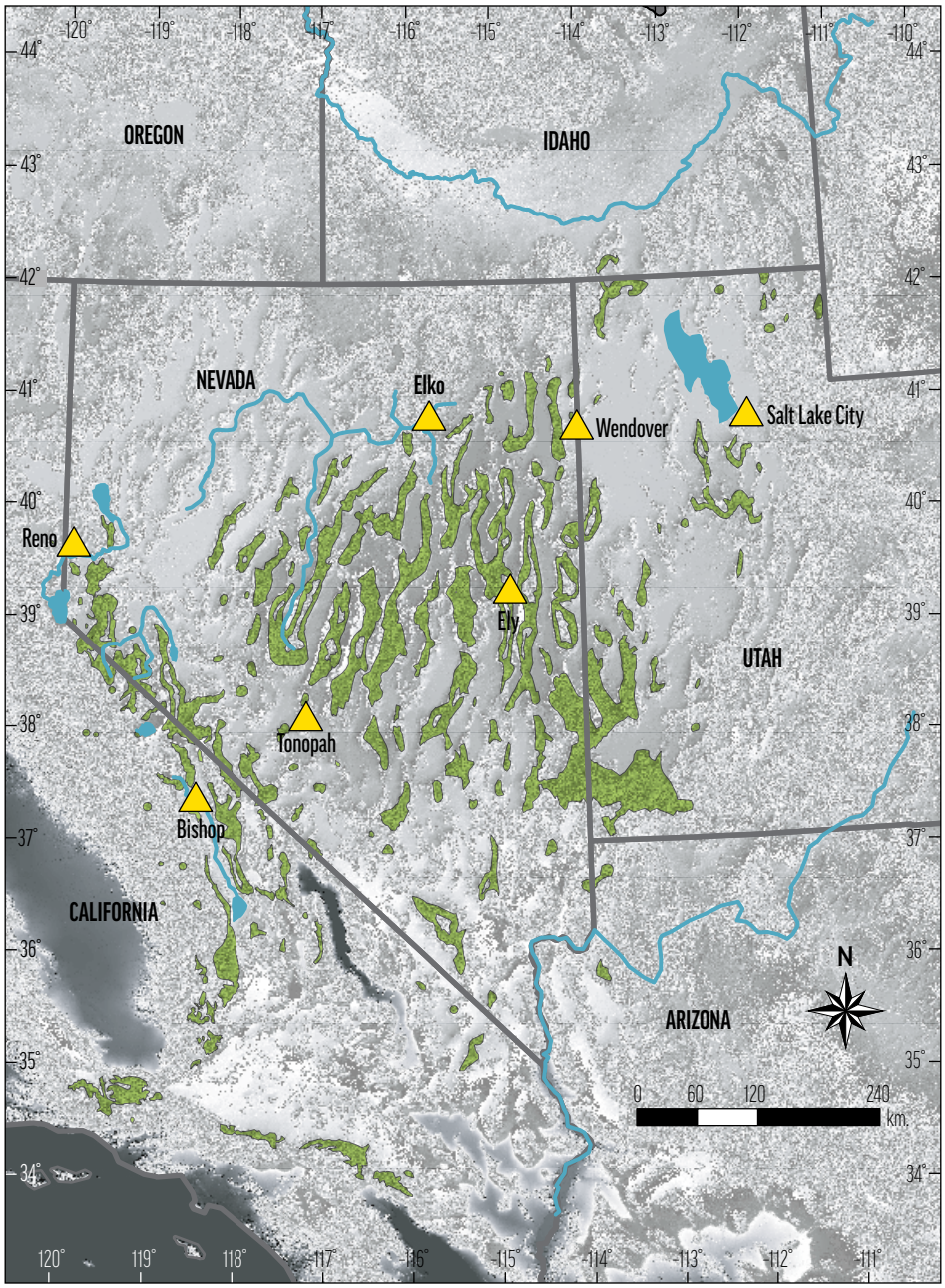

Figure 1. Current distribution of singleleaf pinyon pine in southwestern United States. Source: Data Basin, databasin.org, accessed September 5, 2023. Reported but undocumented pinyon stands in the Warner Mountains, northwest Great Basin, are not included.

migrations to its present widespread distribution (Fig. 1). We summarize here a revision of the Holocene migration of pinyon, with goals to: (1) reassess pinyon arrival dates using the most current radiocarbon calibrations; (2) add new locations; (3) analyze pinyon's migration processes and propose a new hypothesis for multiple mid-latitude Pleistocene pinyon refugia; and (4) provide background for assessment of human biogeography in the Great Basin. Details on the pinyon migration analyses are in Millar and Thomas (in press).

The path of pinyon's Holocene migration was reconstructed in prior studies primarily from woodrat (*Neotoma* spp.) midden evidence (Cole et al. 2012; Madsen 1986; Nowak et al. 1994a; Spaulding 1990; Thompson 1990; Van Devender 1977; Wigand 2017; Wigand and Nowak 1992; Wigand and Rhode 2002, see Millar and Thomas

in press for others). We also rely mostly on midden records, noting the following caveats: (1) woodrats have biases in their diets, and pinyon is not their preferred forage; (2) woodrats collect most vegetation within 20 m. of their middens (Cole et al. 2012), and thus many species are not included, especially when they are sparse; (3) woodrats shift in distribution with changing climates, and thus middens may be absent from broad regions during specific climate periods (Betancourt et al. 1990; Grayson 2011; Wigand and Rhode 2002). Our understanding of the historic range of woodrat middens is only as good as our ability to find and assess evidence (Grayson and Livingston 1993).

In addition to middens, we also use evidence from rockshelters and pollen to elucidate pinyon's migration path. Whether brought into rockshelters by humans or scavengers, pinyon remains have been identified and dated in time-series strata. With this evidence, however, there is uncertainty whether pinyon was growing near the site. Nut consumers can carry pinyon nuts considerable distances (e.g., Madsen and Rhode 1990). We use only two pollen records in our analyses. Pollen has limited value, as grains mostly cannot be resolved to species level and pollen can travel far distances. A few researchers (e.g., Woolfenden 2003) have taken the time and care to separate "pinyon-type" pollen successfully.

To reassess pinyon migration, we searched the literature for the oldest midden or pollen locations containing pinyon in the Great Basin. In cases where older strata in a midden or an older midden in the proximity lacked pinyon, we accepted these to be "arrival dates"; otherwise we assumed they represented the best available oldest date, which might or might not be an arrival date. A key part of our study, in addition to adding new locations, was to reassess dates. Many prior studies relied on conventional isotopic methods. Advances in radiocarbon dating, especially those assessed by Accelerator Mass Spectrometry, make dates more precise and require smaller sample sizes. We recalibrated radiocarbon dates from published studies based on the IntCal20 calibration curve (Reimer et al. 2020), using the CALIB revision 8 protocols with 95% probability time ranges (Stuiver and Reimer 1993).

Table 1 gives a comprehensive list of locations with updated dates for pinyon arrival in the Great Basin (see Millar and Thomas, in press, for details). Forty-three new locations are added beyond the most comprehensive recent list (Grayson 2011), and most dates are significantly

Table 1

PINYON PINE LATE PLEISTOCENE AND HOLOCENE DATES AND LOCATIONS ON FIGURES 3 AND 4

Location No.	Location	Mountain Range/Basin	RCYR	Error, +/- yrs.	Lab/Number	Cal B.P. range[a]	Midpoint of B.P. range	Latitude	Longitude	Elevation (m.)	References
Western Great Basin											
1	Painted Hills[b]	Virginia Mountains	—	—	—	—	250; 297	39.90302	-119.65086	1,616	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[b]	Virginia Range	400	100	Beta-26016	151-633	392	39.489946	-119.693355	1,632	Novak et al 1994b; Wigand and Novak 1992
3	Newton Creek[b]	Virginia Range	710	80	Beta-39750	541-775	658	39.370613[c]	-119.694450[c]	1,600[c]	Wigand 2002; Wigand and Novak 1992
4	Schurz	Walker Lake Valley	890	70	Beta-35816	685-921	803	38.933109[c]	-118.849724[c]	1,615	Novak et al 1994b; Wigand and Novak 1992
5	Silver City[b]	Virginia Range	1,030	90	Beta-29160	734-1,175	955	39.26248	-119.643598	1,585	Novak et al 1994b; Wigand and Novak 1992
6	Geiger Grade	Virginia Range	1,090	90	Beta-39755	792-1,244	1,018	39.388469[c]	-119.707067[c]	1,548[c]	P. Wigand personal communication 5/4/23
7	Navy/Army Depot	Wassuk Range	1,170	50	Beta-35803	958-1,244	1,101	38.543294[c]	-118.711146[c]	1,676	Novak et al 1994b; Wigand and Novak 1992

Table 1 *(Continued)*

PINYON PINE LATE PLEISTOCENE AND HOLOCENE DATES AND LOCATIONS ON FIGURES 3 AND 4

Location No.	Location	Mountain Range/Basin	RCYR	Error, +/- yrs.	Lab/Number	Cal B.P. range[a]	Midpoint of B.P. range	Latitude	Longitude	Elevation (m.)	References
Western Great Basin *(Continued)*											
8	Lead Lake, Carson Sink	Stillwater Range	1,250	60	Beta-47198	1,007-1,293	1,150	39.611546	-118.49808	1,161	Wigand and Nowak 1992; Wigand and Rhode 2002 (Lead Lake is a pollen record; Stillwater Range is a nearby midden record)
9	Wolf Creek	Zunnamed Range	1,490	90	Beta-29 155	1,189-1,548	1,369	38.625456	-119.720229	1,798	Nowak et al. 1994b
10	Little Valley	Sierra Nevada	1,500[c]	NA	NA	—	1,500[c]	39.196908[c]	-119.907713[c]	2,134	Wigand 2017; Wigand and Rhode 2002 (based on undifferentiated pine pollen)
11	Slinkard Valley[b]	Zunnamed Range	2,150	75	Beta-50521	1,945-2,336	2,140	38.633495	-119.571863	1,809	Novak et al 1994b; Wigand and Novak 1992
12	Chidago Flats[b]	White Mountains	3,040	60	Beta-53077	3,066-3,382	3,224	37.646354	-118.552408	2,075	Jennings 1995
13	Deep Springs Overlook	White Mountains	3,290	70	A-4979	3,373-3,690	3,532	37.358844	-118.155358	2,682	Jennings and Elliott-Fisk 1993
14	Rhyolite Ridge[b]	Silver Peak Range	3,490	70	Beta-65683	3,572-3,964	3,768	37.797489	-117.826316	1,957	Jennings 1995
15	Sherwin Summit[b]	Sierra Nevada	3,610	70	Beta-163829	3,812-4,144	3,978	37.535161	-118.614345	2,074	Wigand 2002
16	Wyman Canyon	White Mountains	4,510	90	A-4984	4,868-5,445	5,157	37.426362	-118.074386	2,560	Jennings and Elliott-Fisk 1993
17	Dry Lakes Plateau[b]	Bodie Mountains	4,980	80	Beta-106615	5,591-5,900	5,746	38.298635	-118.998543	2,382	Halford 1998a, 1998b
18	Silver Canyon	White Mountains	5,640	70	A-4982	6,295-6,620	6,458	37.40913	-118.195523	3,048	Jennings and Elliott-Fisk 1993
19	Papoose Flat	Inyo Mountains	7,880	60	Beta-86099	8,547-8,983	8,765	37.022685	-118.109189	2,609	Reynolds 1997
20	Falls Canyon	White Mountains	8,790	110	A-4981	9,550-10,159	9,854	37.738715	-118.379941	1,830	Jennings and Elliott-Fisk 1993
Central Great Basin											
21	Bronco Charlie	Ruby Mountains	3,050	150	A-2726	2,866-3,471	3,169	40.149941	-115.516982	1,886	Thompson 1984
22	Gatecliff Rockshelter[b]	Toquima Range	5,290	180	QC-289	5,654-6,404	6,029	39.003255	-116.782834	2,320	Thomas 1983b
23	Roberts Mountains[b]	Roberts Mountains	5,640	25	PSU-6417	6,318-6,489	6,404	39.81	-116.35	2,601[c]	D. Rhode personal communication 5/26/23
24	Cathedral Canyon[b]	White Pine Range	6,035	25	PSU-7091	6,794-6,489	6,642	39.146412[c]	-115.558408[c]	1,935[c]	D. Rhode personal communication 5/26/23
25	Pahranagat Range[b]	Pahranagat Range	9,230	50	Beta 86072	10,248-10,555	10,402	37.37[c]	-115.37[c]	2,187[c]	P. Wigand personal communication 5/4/23
26	Eleana Range[b]	Eleana Range	10,620	120	USGS-876	12,098-12,767	12,433	37.121593	-116.234205	1,805	Spaulding 1983, 1985
Eastern Great Basin											
27	Grouse Creek Junction	NW Bonneville Basin	2,400	30	Beta-351364	2,347-2,681	2,514	41.433	-113.832	1,466	Rhode 2013
28	Almo Cr A-1	City of Rocks	2,428	39	AA88-400	2,351-2,701	2,526	42.123	-113.673	1,600-2,700	Weppner et al. 2013
29	Collar and Elbow	Toano Range	3,040	30	Beta-351364	3,165-3,350	3,258	40.99	-114.32	2,122	D. Rhode, personal communication 5/26/23
30	Pilot Range	Pilot Range	3,430	30	Beta-340985	3,564-3,815	3,690	41.319	-113.988	1,607	Rhode 2013

Table 1 *(Continued)*

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Eastern Great Basin *(Continued)*											
31	Silver Island Canyon	Silver Island Range	4,410	90	Beta-70606	4,846–5,296	5,071	40.954	-113.77	1,765	Rhode 2000
32	Itchy Ban	Goshute Range	5,070	50	Beta-82952	5,661–5,921	5,791	40.802	-114.248	1,802	Rhode 2000
33	Icicle Cave ICD	Pequop Range	5,340	40	Beta-120585	5,998–6,272	6,135	41.076	-114.604	2,242	Rhode 2000
34	Marblehead Mine	Goshute Range	5,960	90	Beta-73389	6,557–7,152	6,855	40.821	-114.264	1,808	Rhode 2000; Rhode and Madsen 1995
35	Council Hall Cave	North Snake Range	6,120	80	WK-157	6,789–7,244	7,017	39.331446[c]	-114.095162[c]	2,041	Thompson 1979; Thompson and Hattori 1983
36	Valley View	Schell Creek Range	6,250	150	A-2430	6,785–7,429	7,107	39.499854	-114.716855	2,350	Thompson and Hattori 1983; Thompson 1984
37	Danger Cave[b]	Silver Island Range	6,710	70	Beta-43727	7,432–7,676	7,554	40.763148	-114.004811	1,314	Rhode 2000; Rhode and Madsen 1998
38	Cottonwood Canyon	Cherry Creek Range	7,690	70	Beta-79087	8,378–8,595	8,487	40.305	-114.8975	2,105	Rhode 2000
69	Bear Lake	Bear River Range	—	—	—	19,000–17,000; 15,000–present	—	41.982316	-111.294014	1,806	Doner 2009 (based on pollen differentiated as pinyon type)
70	Blue Lakes Marsh	Bonneville Basin	—	—	—	<8,000	—	40.5	-114.036	1,297	Louderback and Rhode 2009 (based on undifferentiated pine pollen)
Southern Great Basin											
39	No Name West	No Name Basin	9,910	90	Beta-65979	11,191–11,729	11,460	35.42267	-116.605641	1,220	Koehler et al. 2005
40	Forty Mile Canyon	Pinnacles Ridge	9,390	40	QL-4222	11,270–11,670	11,470	36.946498	-116.379364	1,250–1,310	Spaulding 1994
41	Inyo Cave 1, 2A	Inyo Mountains	11,150	80	OS-38897	12,842–13,180	13,011	36.55225	-117.767398	1,945	Cole et al. 2012
42	Alabama Hills	Owens Valley	11,450	80	Beta 168109	13,171–13,469	13,320	36.565018[c]	-118.073196[c]	1,327[c]	Wigand 2017
43	Granite Mountain	Granite Mountains	11,470	70	Beta-52489	13,180–13,475	13,328	35.445820[c]	-116.607224[c]	1,320	Koehler et al. 2005
44	Penthouse 2(2)	Sheep Range	11,550	150	A-1772	13,162–13,750	13,456	36.469961	-115.250092	1,580	Cole et al. 2012; Van Devender and Spaulding 1979
45	Mount Ord	Lucerne Valley	11,850	50	NA	13,529–13,796	13,663	34.634933	-116.8102	1,219	King 1976
46	No Name East	No Name Basin	11,910	90	Beta-65984	13,594–14,026	13,810	35.42267	-116.605641	1,220	Koehler et al. 2005
47	Penthouse 1(3)	Sheep Range	12,350	55	OS-35220	14,107–14,836	14,472	36.470287	-115.249973	1,600	Cole et al. 2012; Van Devender and Spaulding 1979
48	Clark Mountain	Clark Mountain	12,460	190	I-3690	14,040–15,282	14,661	35.518181[c]	-115.602443[c]	1,916	Mehringer and Ferguson 1969
49	Rober's Roost	Scodie Mountains	12,870	400	A-1762 RR#1D	14,031–16,503	15,267	35.590086[c]	-117.94669[c]	1,130	McCarten and Van Devender 1988; Van Devender and Spaulding 1979
50	No Name West	No Name Basin	12,780	100	Beta-65977	14,974–15,579	15,277	35.42267	-116.605641	1,290	Koehler et al. 2005
51	Rober's Roost	Scodie Mountains	12,960	270	A-1761 RR#2A	14,367–16,310	15,339	35.590086[c]	-117.94669[c]	1,130	McCarten and Van Devender 1988; Van Devender and Spaulding 1979
52	Forty Mile Canyon	Pinnacles Ridge	12,870	50	QL-4224	15,216–15,577	15,397	36.946498[c]	-116.379364[c]	1,250–1,310	Spaulding 1994
53	Rober's Roost	Scodie Moutains	13,300	360	A-1763 RR#1C	14,933–17,077	16,005	35.590086[c]	-117.94669[c]	1,130	McCarten and Van Devender 1988; Van Devender and Spaulding 1979
54	Forty Mile Canyon	Pinnacles Ridge	15,870	70	QL-4223	18,954–19,383	19,169	36.946498[c]	-116.379364[c]	1,250–1,310	Spaulding 1994
55	Forty Mile Canyon	Pinnacles Ridge	16,410	70	QL-4234	19,569–20,001	19,785	36.946498[c]	-116.379364[c]	1,250–1,310	Spaulding 1994

Table 1 *(Continued)*

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Location No.	Location	Mountain Range/Basin	RCYR	Error, +/- yrs.	Lab/Number	Cal B.P. range[a]	Midpoint of B.P. range	Latitude	Longitude	Elevation (m.)	References
Southern Great Basin *(Continued)*											
56	Haystack Mountain	Owens Valley	17,680	150	Beta-35503	20,954-21,902	21,428	36.603996[c]	-117.996219[c]	1,155	Koehler and Anderson 1995
57	Skeleton Hills	Skeleton Hills	17,900	600	NA	20,231-22,991	21,611	36.623823[c]	-116.279102[c]	925	Lanner and Van Devender 1998; Spaulding 1990
58	Specter Range-2	Specter Range	18,740	90	USGS-994	22,443-22,922	22,683	36.66329[c]	-116.190402[c]	1,190	Spaulding 1983, 1990
59	Specter Range-2	Specter Range	19,080	370	UW-638	22,976-24,743	23,860	36.66329[c]	-116.190402[c]	1,190	Spaulding 1983
60	Haystack Mountain	Owens Valley	20,960	240	Beta-34833	24,125-25,358	24,704	36.603996[c]	-117.996219[c]	1,155	Koehler and Anderson 1995
61	Haystack Mountain	Owens Valley	20,590	210	Beta-40000	24,191-25,283	24,737	36.603996[c]	-117.996219[c]	1,155	Koehler and Anderson 1995
62	South Crest SC4b	Sheep Range	21,700	500	LJ-2840	24,986-27,142	26,064	36.481339[c]	-115.254263[c]	1,980	Spaulding 1977
63	Forty Mile Canyon	Pinnacles Ridge	21,830	110	QL-4220	25,886-26,353	26,120	36.946498[c]	-116.379364[c]	1,250-1,310	Spaulding 1994
64	Haystack Mountain	Owens Valley	22,900	270	Beta-39273	26,463-27,702	27,083	36.603996[c]	-117.996219[c]	1,155	Koehler and Anderson 1995
65	Long Canyon	Sheep Range	30,400	1,500	A-1379	31,310-37,856	34,583	36.491242[c]	-115.256103[c]	1,800	Spaulding 1977
66	Forty Mile Canyon	Pinnacles Ridge	47,240	3,000	QL-4218	45,378-54,980[b]	49,179	36.946498[c]	-116.379364[c]	1,250-1,310	Spaulding 1994
67	Spotted Range-2	Spotted Range	>40,000	—	—	—	—	36.684897[c]	-115.785841[c]	1,184[c]	Wells and Jorgensen 1964
68	Owens Lake	Owens Valley	—	—	—	<126 kyrs	—	36.461768	-117.975848	1,084	Woolfenden 2003 (based on pollen differentiated as pinyon type)

[a]Original radiocarbon dates have been revised, and a midpoint calculated from the range for purposes of discussion only.
Divisions of Western, Central, and Eastern Great Basin follow the traditional three migration paths outlined by Lanner and Van Devender 1998.

[b]Dates likely to be arrival times, interpreted by lack of pinyon in older strata of the same or nearby midden.

[c]Coordinates and dates estimated from publication informaton.

changed. Three patterns emerge from this synthesis, outlined here, and interpreted subsequently:

1) The oldest evidence, dating to the Late Pleistocene, derives from the southern Great Basin in areas currently known as the Mojave Desert. All but one Great Basin pinyon location dating to the Late Pleistocene occur south of 37° N latitude.

2) Arrival dates in the Great Basin progress from older to younger in a south-to-north pattern; most arrival dates north of 37° N are younger than ca. 8,000 cal B.P., and many are younger than ca. 6,000 cal B.P. Four locations at latitudes north of 37° N have anomalously old dates, older than ca. 8,500 cal B.P.

3) Late Pleistocene pinyon locations, as well as the species' current known distribution limits, extend farther north in the eastern Great Basin than in the western and central Great Basin. This long-recognized asymmetry is, however, challenged by new evidence for pinyon populations at a high northern latitude in the western Great Basin, addressed in one of our hypotheses.

FACTORS INFLUENCING PINYON'S LATE PLEISTOCENE AND HOLOCENE BIOGEOGRAPHY

Climate is the overall arbiter of plant distribution in that only when the climate is or becomes favorable (i.e., within

a species' habitat envelope) can a species advance its range toward areas with the requisite climate (Woodward and Williams 1987). As climate becomes unfavorable, the opposite happens; that is, mortality occurs and the range retreats. Pinyon thrives under warmer and drier conditions than its upland relatives (reviewed in Miller et al. 2019). It tolerates warm summers, although it thrives with moderate summer precipitation and accommodates wet, cold winters (Thompson et al. 2015). For pinyon to emerge out of its Late Pleistocene range in the southern Great Basin, thus, depended on climate becoming favorable. During the Holocene, the combination of pinyon's favored climate conditions—described by factors of temperature and precipitation—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 (Cole et al. 2012; Grayson 2011; Miller et al. 2019; Wigand and Rhode 2002). Relative to the cold, wet Late Pleistocene, the Early Holocene (11,650–8,276 cal B.P.) was warmer and drier. Relative to modern conditions, however, the Early Holocene was cooler and wetter (Grayson 2011). The Middle Holocene (8,276–4,200 cal B.P.), by any comparison, was a period of maximum heat and extended (millennial) drought. The Late Holocene (after 4,200 cal B.P.) has been a rollercoaster of wet and dry periods, trending cooler, and heralding the Little Ice Age (ca. A.D. 1400–1920), which was the coolest period since the end of the Pleistocene.

Climate is not sufficient alone to define pinyon's migration (Cole et al. 2012; Lanner and Van Devender 1998). The spread of pinyon into the central Great Basin was far slower and in more complex geographic patterns than the appearance of favorable climates. Conditioning factors determine what plant geographers recognize as the realized distribution range versus the potential range of a species. Primary among mitigating factors are seed dispersal vectors. Pinyon could only migrate as far, as fast, and to locations that its dispersing agents could reach while within the limits of pinyon generation times. Dispersal involves short-distance, population-expansion processes ("diffusion"), and long-distance founding events. Pinyon seeds are large, heavy, unwinged, and dense with nutritive tissues (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 pinyon is legendary for its coevolution with corvid birds, in particular Pinyon Jays (*Gymnorhinus cyanocephalus*) and Clark's Nutcrackers (*Nucifraga columbiana*) (Miller et al. 2019). Both species are particularly effective because of their caching habits: the birds plant seeds at a soil depth optimal for germination. Pinyon Jays forage primarily on pinyon and disperse seeds in large quantities. Most seeds are cached less than 1 km. from collection, with rare long-distance (maximum 10 km.) dispersal observed (Vander Wall and Balda 1981). Clark's Nutcrackers are also particularly important pinyon seed dispersers, although whitebark pine (*Pinus albicaulis*) is their primary host. Clark's Nutcrackers similarly disperse enormous numbers of seeds: up to 17,900 pinyon seeds per bird in a season (Vander Wall 1988). Most pinyon seeds are cached within 1 km. of the harvested trees (Vander Wall 1988). Longer distances are achieved by Clark's Nutcrackers while caching. Vander Wall and Balda (1977, 1981) observed nutcrackers caching pinyon seeds 5 km. away; the maximum distance observed was 22 km. (Vander Wall and Balda 1977). This dispersal pattern, where the great majority of seeds are planted at short distances from collection trees and seed dispersal to far distances is extremely rare (a leptokurtic distribution; Clark et al. 1998), is common for many pine and other tree species (e.g., Burczyk et al. 1996; Nathan et al. 2001; Wenny 2001).

Humans have also been considered as seed dispersers (e.g., Betancourt et al. 1991; Madsen 1986; Mehringer 1986; Potter and Green 1964; Rhode and Madsen 1998; Simms 2008). Intentional pinyon planting seems highly improbable given its long regeneration time (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 where pinyon grows 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). Trading pine nuts with distant neighbors where pinyon does not grow might also introduce the species to novel landscapes, given the caveats below.

Unintentional dispersal by seed loss is possible. Seeds lost at village sites, and especially from pinyon seed caches, might have served as sources for pine establishment. These situations, however, would occur in

locations where pinyon was already growing, and thus would have only assisted in local expansion of established woodlands. Foragers sometimes carried "trail food," including pinyon nuts, during residential and logistic moves (Basgall et al. 2003:360). Such trail food, including pinyon nut remains, has been identified from an alpine village in the White Mountains (Bettinger 1991; Scharf 2009). Unintentional long-distance transport of pinyon by loss of seeds from carrying bags during far-flung forager movements seems a low-probability means of pinyon dispersal. Beyond the value of pinyon seeds to travelers and their care to avoid loss, factors mitigate against pinyon being established by human sojourners. 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 seeds (Millar and Thomas in press). Even if seed viability were maintained in foragers' trail food, other factors would reduce the likelihood of lost nuts serving as planting sources. These factors include: (1) pinyon's seed germination, planting, and seedling-establishment requirements, which are unlikely to be met under random seed loss; (2) the small number of seeds that humans could carry; and (3) the short-term viability of pinyon seeds, with viability falling to less than 10% within 6–12 months of seed maturation (Meeuwig and Basset 1983).

Plant biogeographers commonly model migration dynamics as a diffusion process (Cousens et al. 2008). This assumes a wave front along the colonizing edge of the species' distribution that moves toward favorable habitat. Factors such as generation time, seed size and buoyancy, and seed dispersal vectors contribute to modeling the gradual movement into new environments. While short-distance diffusion occurs as a background beat enabling local expansion, a few far-flung events, as in rare long-distance dispersal by Clark's Nutcrackers, can give the migrating front a "jump start" forward. If climate refugia exist, they can give the appearance of long-distance transport by their location ahead of the main front (Pearson 2006). Refugia are small areas of favorable habitat that persist during otherwise inclement climate phases (e.g., ice ages) and serve as important sources of far-flung species expansions once climates ameliorate.

Great Basin topography, with its hundreds of mountain ranges and intervening basins, also played an important role in the geographic path of pinyon's Holocene spread (Charlet 2007). The tectonic processes of Basin and Range expansion and Walker Lane dynamics (Jayko and Burski 2011) resulted in fault-blocked, north-south trending ranges throughout the Great Basin. These ranges provided continuous habitat on their lower slopes for pinyon expansion, whereas broad and treeless intermountain basins were local restrictions.

INTERPRETING PINYON'S LATE PLEISTOCENE AND HOLOCENE MIGRATION IN THE GREAT BASIN

Using revised arrival and oldest-available dates, a comprehensive set of locations (Table 1), and recognizing the role of rare long-distance dispersal, we interpret the three patterns described above and introduce two hypotheses for pinyon's Holocene migration into the Great Basin. Here we summarize from Millar and Thomas (in press).

Late Glacial Refugia

The first pattern of Late Pleistocene pinyon locations clustered in the southern Great Basin has been widely interpreted as a large regional refugium for warm- and winter-wet-adapted pinyons (singleleaf pinyon and other species; (Cole et al. 2012; Grayson 2011; Lanner 1983; Lanner and Van Devender 1998; Reynolds 1996; Spaulding 1990; Van Devender and Spaulding 1979; Woolfenden 1996). Cold full-glacial climates at central and northern Great Basin latitudes were outside pinyon's climate tolerance, and pinyon was assumed to be absent from mid to north latitudes in the Late Pleistocene Great Basin. Instead, pinyon and its associates retreated into areas now dominated by Mojave Desert ecosystems in the southern Great Basin (and other southern locations), where low elevations provided glacial-age climates that were adequately warm yet winter-wet for pinyons (Grayson 2011; Madsen 1986; Miller et al. 2019; Van Devender 1977; Woolfenden 1996).

Holocene Migration out of Southern Refugia

Although full glacial conditions were waning across North America after ca. 12,000 cal B.P., modern circulation patterns favorable for pinyon emerged throughout much

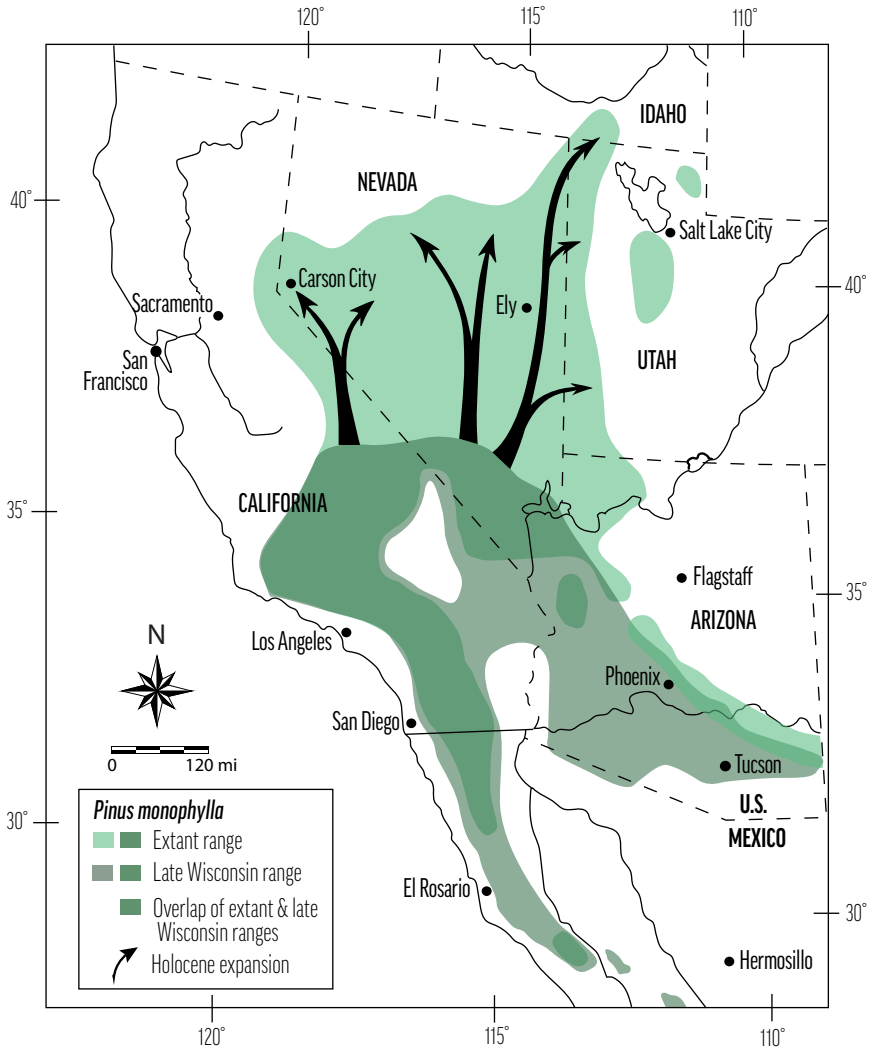

Figure 2. Late Pleistocene Mojave-region refugial locations of singleleaf pinyon pine and northward Holocene migration along three paths in the western, central, and eastern Great Basin. Adapted from Lanner and Van Devender (1998).

of the central Great Basin only after ca. 9,000–8,000 cal B.P. (Van Devender and Spaulding 1979). The pattern of pinyon arrival and oldest dates progressing more or less in sequence from south to north (Table 1) has been unanimously interpreted by Great Basin biogeographers (Fig. 2) to reflect northward migration by pinyon out of southern Great Basin glacial-age refugia (Cole et al. 2012; Grayson 2011; Lanner 1983; Halford 1998a; Lanner and Van Devender 1998; Madsen 1986; Miller et al. 2019; Nowak et al. 1994a; Spaulding 1990; Thompson 1990; Van Devender 1977; Wigand 2017; Wigand and Nowak 1992; Wigand and Rhode 2002; Woolfenden 1996). Pinyon dates younger than ca. 8,000–7,500 cal B.P. at low latitudes have been interpreted as reflecting persisting woodland conditions in the Mojave region refugia. Only after ca. 8,000 cal B.P. were very cold, continental winters and cold, arid summers ameliorating sufficiently to trigger pinyon's migration northward (Van Devender and Spaulding 1979).

Hypotheses for Holocene Pinyon Migration out of Southern Refugia

Prior interpretations of pinon's northward migration in a broad wavelike pattern in the central Great Basin are challenged by new dates and locations. These show several anomalously old pinyon records (older than 8,000 cal B.P., Table 1) at northerly latitudes that are difficult to explain by progressive movement of pinyon northward. We outline two hypotheses as possible migration scenarios.

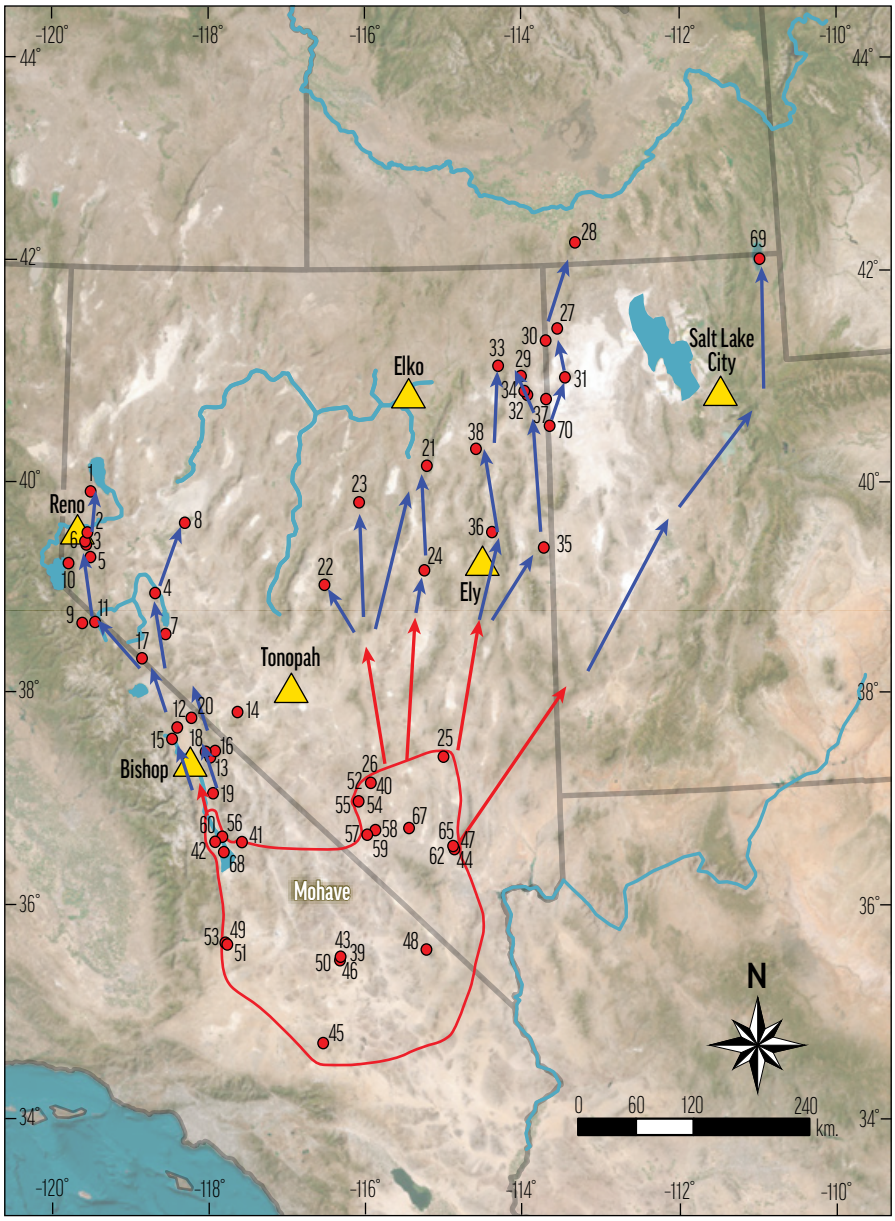

Figure 3. Hypothesis I: Migration of pinyon pine from a southern Pleistocene refugium, estimated from midden and pollen locations and radiocarbon dates in Table 1. The red polygon denotes the southern Late Pleistocene refugium, red arrows show movement out of that refugium during the Early Holocene, and blue arrows show subsequent movement. The southern Mojave refugium is labeled in white letters.

Northward Migration

Hypothesis I is the widely accepted scenario of previous pinyon studies (Figs. 2, 3), which assumes that pinyon did not occur at latitudes greater than about 37° N throughout the Late Pleistocene. From refugia located at less than about 37° N, pinyon tracked warming climates northward, starting ca. 8,000 cal B.P. and following distinct paths in the western, central, and eastern Great Basin (Fig. 2). Within each region, pinyon migration unfolded in a stepping-stone pattern northward, with the pace at the northern front varying as microclimate trends emerged. Migration was fastest in the eastern Great Basin and slowest in the west, resulting primarily from climate differences among the regions (Grayson 2011), and, as a result, pinyon reached its farthest northern latitude in the eastern Great Basin.

New locations and revised dates of several mid-latitude locations challenge this hypothesis by illuminating dates

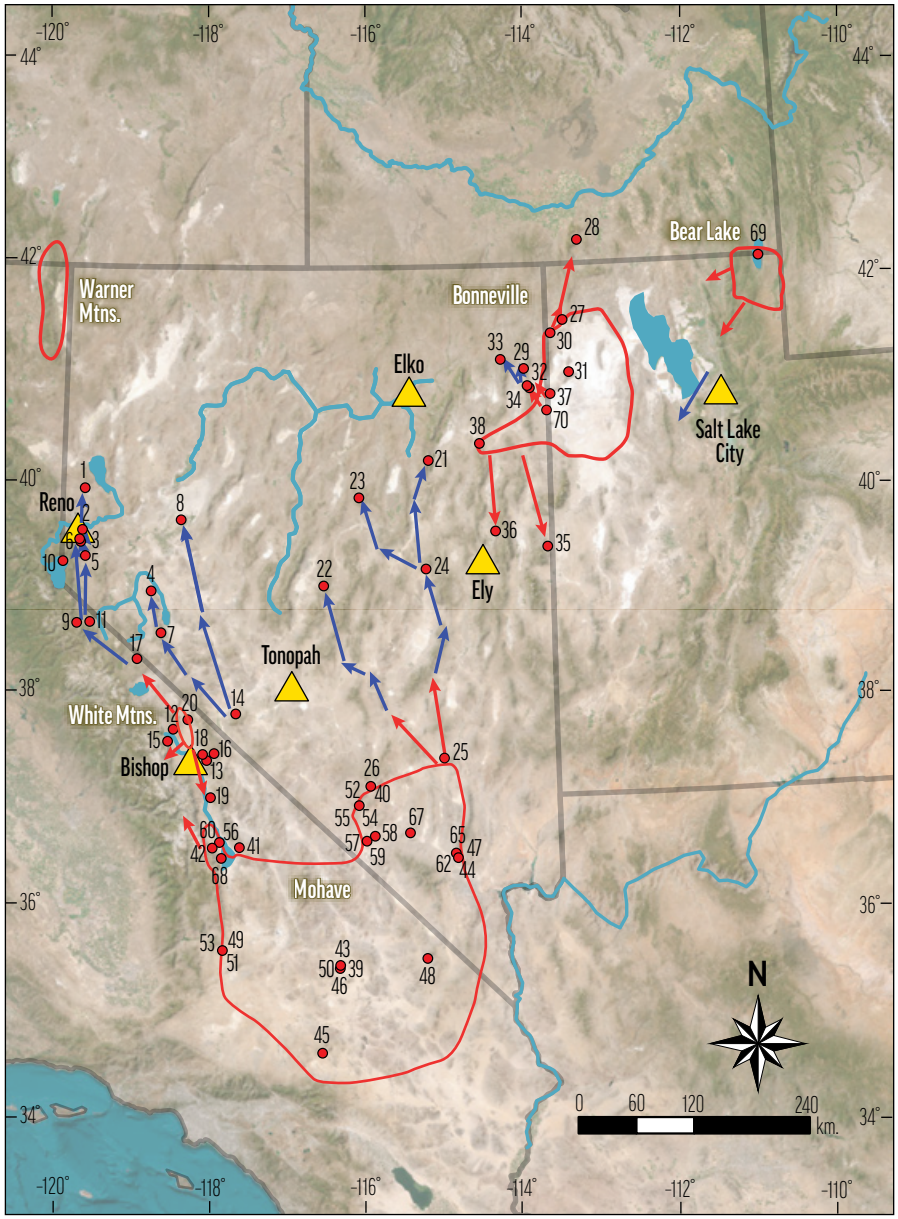

Figure 4. Hypothesis II: Northward migration of pinyon pine from the southern Pleistocene refugium and outward from four Pleistocene refugia at higher latitudes in the western and eastern Great Basin estimated from midden and pollen locations and radiocarbon dates in Table 1, and, for the Warner Mountains 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. The five refugia are labeled with white letters.

that are too old to be achieved by progressive northward migration, and the possibility that pinyon occurred equally far north in both the western and eastern Great Basin.

Northward Migration with High-Latitude Refugia

Hypothesis II also accepts the existence of a large Late Pleistocene pinyon refugium in the current Mojave Desert and northward migration in the Early Holocene out of this region. It differs by postulating additional regions of Late Pleistocene pinyon refugia at higher latitudes that were other sources for expansion once climates ameliorated (Fig. 4). Given that Utah juniper (*Juniperus osteosperma*) persisted throughout the Late Pleistocene in many central and northern Great Basin locations (Grayson 2011;

Nowak et al. 1994a, 1994b; Rhode 2000; Wigand 2017; Wigand and Nowak 1992; Wigand and Rhode 2002), it would be surprising if pinyon did not co-occur. Although Utah juniper and pinyon have different habitat/climate envelopes (Cole et al. 2012; Miller et al. 2019) and juniper cannot be considered a direct proxy for pinyon, their climate tolerances are highly overlapping (Thompson et al. 2015). If anything, more Pleistocene refugia might be expected for pinyon than for juniper, given pinyon's apparent tolerance of cooler temperatures.

Based on recalibrated dates and new midden locations, we propose four high-latitude Late Pleistocene refugia (Fig. 4). Three of these are old enough and far enough north to make migration from a southern Mojave-area refugia after 8,000 cal B.P. improbable in the time available; the fourth, although its age is unknown, is so far north and removed from the current distribution that it suggests ancient origins. A western refugium ("White Mountains refugium") we propose existed in a small region around the Falls Canyon midden along the northwestern base of the White Mountains, California. These pinyon middens date to 10,159–9,550 cal B.P., overlapping the Mojave-region refugia dates. Utah juniper occurs in the Falls Canyon midden and in surrounding older middens (Jennings 1995), corroborating conditions that could have supported pinyon in low abundance in the general region during the Late Pleistocene. This proposed refugium is further supported by anomalous modern occurrences nearby of other pine species that are highly disjunct from their main ranges. Elliott-Fisk and Peterson (1991) interpret those as Quaternary relicts persisting in isolated White Mountain refugia.

We propose a second refugium in the far northwestern Great Basin, in the region of the Warner Mountains, California ("Warner refugium," Fig. 4). This location is not included in Table 1 because it is neither a fossil (midden, pollen) site nor has pinyon been documented there at present. Diverse lines of evidence, including ethnographic (Kelly 1934; R. Hughes, personal communication 1977), a 1948-dated herbarium record for two mature pinyons (SOC 16444), and several other pieces of 20th-century evidence indicate four disjunct locations for pinyons in the north and south Warner Mountains (details in Millar and Thomas in press). These are 170–260 km. from the nearest known stands of pinyon near Reno. If validated, the Warner pinyon populations suggest that pinyon could have existed throughout the Holocene as far north in the western as in the eastern Great Basin. Alternately, as we develop below, a pinyon population in the Warner Mountains might have originated in the Holocene during a period when climate favored rapid spread along the western Great Basin into areas farther north than it currently exists. Subsequent changes in Holocene climate would have caused the extinction of any such former northern populations, leaving only tempting clues such as we have for the Warner Mountains. A third mid-latitude Pleistocene pinyon refugium we propose was a large region in the eastern Great Basin, Utah ("Bonneville refugium," Fig. 4), with westerly locations anchored by middens at Cottonwood Canyon, Nevada (Cherry Creek Range; 8,595–8,378 cal B.P.[1]) and archaeological remains at Danger Cave, Utah (Silver Island Range; 7,676–7,432 cal B.P.). These and other nearby pinyon locations with dates older than 7,000 cal B.P. suggest a potential pinyon refugium network in this area. Slightly younger pinyon middens in the region, including Valley View, Council Hall Cave, and Marblehead Mine, may also have been part of the refugium metapopulation, becoming incorporated in middens after local conditions ameliorated. Lake-effect Bonneville Basin climates could have contributed to maintaining conditions equable for pinyon growth (Eichenlaub 1987; Rhode 2000; Wigand and Rhode 2002).

We propose the low slopes around Bear Lake in far northern Utah as a fourth potential refugium ("Bear Lake refugium," Fig. 4). Pinyon pollen (identified as *Pinus monophylla* and *P. edulis*, Colorado pinyon) extracted from a sediment core in Bear Lake was separated from other pine species and occurred in strata at continuous low levels from 19,000 years ago to present (Doner 2009). While pine pollen can travel long distances, levels of pinyon in cores similar to that found by Doner (2009) have been interpreted to be local sources. The multi-millennial long Owens Lake core (Woolfenden 2003) is an example, where pinyon was interpreted to be growing in the local environment. While Colorado pinyon genes currently occur in an unusual and isolated hybrid population with singleleaf pinyon in the nearby Crawford Mountains, most of the pinyon currently in mountains around Bear Lake is singleleaf pinyon pine and the nearest pure Colorado pinyon pine is 170 km. distant. Accepting that some Colorado pinyon likely

grew in the greater Bear Lake region during the Late Pleistocene, we consider it highly likely that singleleaf pinyon also grew in the region (details in Millar and Thomas in press).

In the four high-latitude refugia, we speculate that pinyon occurred as small, isolated stands 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 the severe climates surrounding their refugia, and little opportunity to be incorporated into middens. As climates ameliorated after ca. 8,000 cal B.P., refugial populations became sources for local dispersal in multiple directions, producing the effect—from the vantage of the present—of previously unexplained rapid long-distance northward migration rates from the Mojave region.

A major challenge to the high-latitude refugia hypothesis is the lack of pinyon in Great Basin Late Pleistocene records other than the Bear Lake pollen core and the very early Holocene record at Falls Canyon. Many Great Basin conifer species occur in modern conditions as highly disjunct small stands, often only one to several trees (Charlet 1996, 2007), and we consider it possible that the refugia such as we propose could have existed without being incorporated in middens—an argument also advanced by Hamrick et al. (1994). The absence of pinyon from middens could result from biases of woodrat food selection, short distances from the midden that woodrats collect, and absence of woodrats from regions during unfavorable climate intervals. If palynologists had distinguished pinyon-type pollen from other Great Basin sediment cores, they may have found more evidence for pinyon during the Late Pleistocene than current evidence suggests.

Shifts in pinyon's distribution, especially at the margins of the range, should also be considered when evaluating refugia in millennia past. Pinyon does not currently grow at the locations or elevations of several Holocene pinyon sites near the north end of its modern range (Bear Lake, Danger Cave, Blue Lakes Marsh, Grouse Creek Junction, Table 1). Those locations range a few to 40 km. from, and 260 m. to 600 m. below, the nearest pinyon stands at present; pinyon occurred in middens at those sites as recently as 2,514 cal B.P. (Grouse Creek Junction). Lack of pinyon at present, thus, does not provide sufficient evidence that pinyon was not growing in an area in the recent— or distant—past.

To test these two hypotheses of pinyon migration, we developed a new model of probabilistic migration rates based on observed short- and long-distance seed dispersal distances by the primary vector, Clark's Nutcracker (developed in detail in Millar and Thomas in press). Prior analyses used step rates developed either from mean distances estimated from ages of fossil records at varying distances apart (Cole et al. 2012) or process-based rates from observations of bird dispersal and pinyon generation time (Lanner 1983). We used a process approach but differed from Lanner, who estimated a single "wave-front" dispersal (diffusion) rate range based on longest distances observed for nutcrackers to plant pinyon seeds. Instead, we developed two rates, one a diffusion rate of gradual spread beyond the edges of existing stands—documented as the most common behavior of Clark's Nutcrackers—and the other a long-distance founder-event rate, observed to be very rare.

From these process-based rates, we assessed step-by-step movements in chronosequence for pinyon migration in the western, central, and eastern Great Basin for pinyon Hypotheses I and II (details in Millar and Thomas in press). We considered the hypothesis that required fewer rare founding events and fewer "unexplainably" high rates (much greater even than distances likely under long-distance parameters) to be favored. Evaluating conditions this way indicated pinyon Hypothesis II (northward migration with four high-latitude refugia) over pinyon Hypothesis I (solely northward migration). Beyond the need to explain far northern records that have dates too old for pinyon to have arrived in the time available, Hypothesis I had many other very large step rates that required unknown dispersal mechanisms. While Hypothesis II was favored by the existing evidence, the comparisons depend on assumptions and existing arrival date evidence; both hypotheses have challenges that await further evaluation (Millar and Thomas in press).

As a third possibility, not yet reaching the level of a hypothesis, we offer the following new migration scenario, which resolves some of the problems summarized above (Millar and Thomas in press). This scenario proposes that pinyon migrated northward

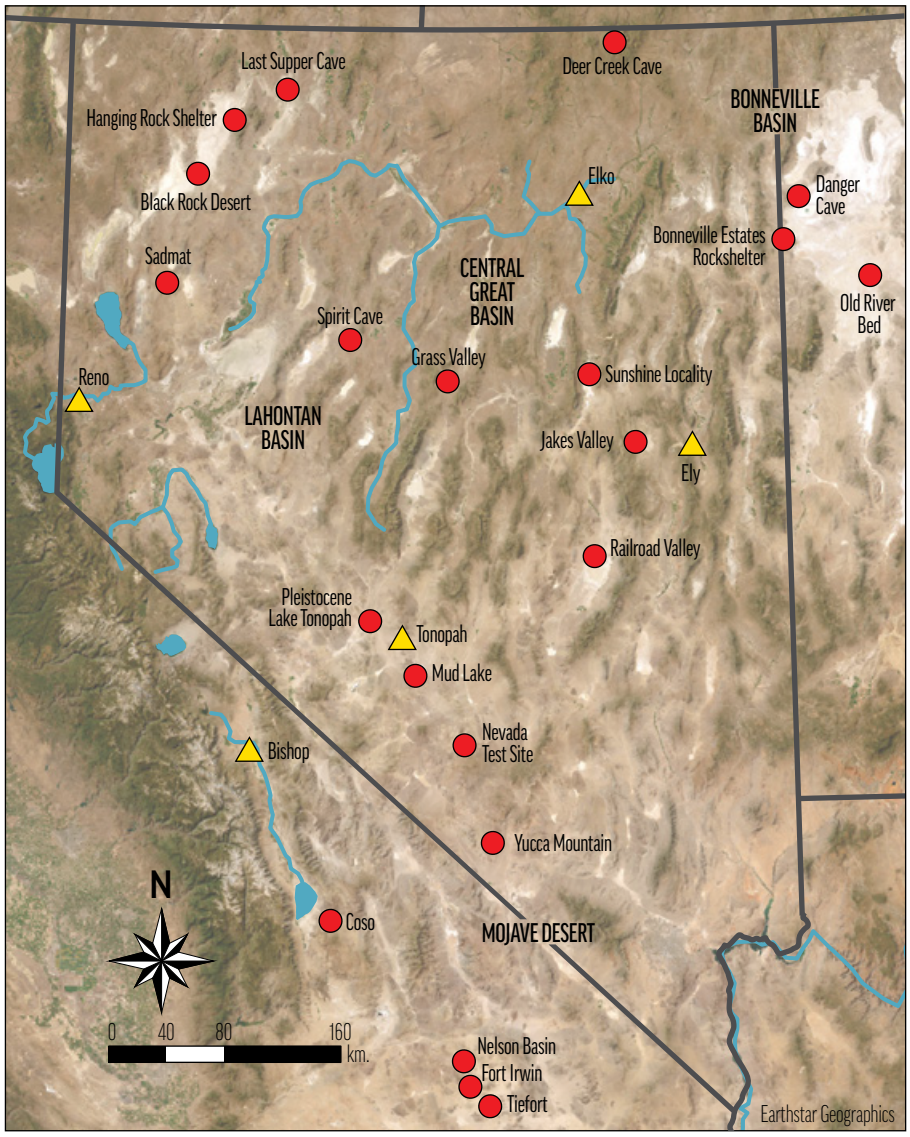

Figure 5. Distribution of significant Paleoindian occupations in the Great Basin.

in the late Early Holocene from a Mojave-region Pleistocene refugium. It differs from Hypotheses I and II in suggesting that during the Middle or Late Holocene pinyon not only reached middle latitudes (as evidenced from middens of Table 1) but expanded to latitudes farther in the Great Basin, potentially reaching beyond 42° N, the latitude of pinyon presently in southern Idaho, in some areas. Deteriorating climates of the Late Holocene—and century/millennial periods of oscillating climates within that time frame—caused eventual extinction of most northern-tier pinyon populations, except in the far east and potentially in the Warner Mountains in the far west.

ARCHAEOLOGICAL PERSPECTIVES: POST-PALEOINDIAN DISPERSAL FROM PALEOINDIAN HOMELANDS

We postulate that post-Paleoindian communities arose directly from Paleoindian homelands. As Early Holocene climates warmed, pluvial lakes desiccated, fostering the possible co-occurrence of pinyon and people spreading from isolated refugia into the central Great Basin uplands[2].

Paleoindian Preludes

Great Basin Paleoindians (pre-9,000 cal B.P.) pursued lowland lifeways where long-term marshlands fringed the Great Basin (Fig. 5). The seemingly paradoxical archae-

ological record shows that foraging Paleoindian populations were technologically oriented toward large game procurement, yet simultaneously exploiting a diverse set of lower ranked resources, and practicing extremely high residential mobility, as reflected in expansive lithic conveyance zones (Elston and Zeanah 2002; Elston et al. 2014). These studies suggest that Paleoindians initially targeted wetlands with abundant and readily encountered large game. As encounter rates with large game declined due to overharvest, Paleoindians shifted to new locations, eventually moving to the nearest adjacent wetland, once again to target high-ranking artiodactyls. So viewed, Paleoindian success was predicated on low human population levels with ample unoccupied landscape and little competition for adjacent wetlands.

When the wetlands began to dry out toward the end of the Early Holocene and habitat for high-ranking game declined, this Paleoindian adaptive strategy reached a "tipping point" (Scheffer et al. 2012). The disappearance of wetlands was a critical factor in the transition from Paleoindian to post-Paleoindian subsistence systems. While hunters continued to pursue large game where they could be found at lower rates of return, collectors targeted lower-ranked resources such as bulrush, goosefoot, sedge, and cattail—each requiring higher handling costs, but with the distinct advantage of being abundant and closely spaced (Madsen 2002, 2007; Raven 1992:8; Zeanah 2004; Zeanah et al. 1995). Intensive seed grinding convincingly appeared only at the transition to the Middle Holocene, with a proliferation of seed grinding implements, signaling a shift in sexual division of labor among post-Paleoindian foragers (Elston et al. 2014).

Although most well-dated Paleoindian sites cluster near productive wetlands, others (including Last Supper Cave, Antelope Overhang, and Dirty Shame Rockshelter) are located along streams in volcanic uplands, suggesting that some groups expanded to new habitats during the Early Holocene (Smith and Barker 2017). Paleoindians clearly did not avoid occasional forays into the uplands to procure nonlocal toolstone and to hunt upland artiodactyls (Bradley et al. 2022; Estes 2009; Puckett 2023) and this Paleoindian use of uplands appears throughout much of western North America. Their broad-spectrum diet also included leporids (Smith 2022), fish, and waterfowl (Jenkins 2000). Great Basin Carved Abstract rock art panels (dating to the Terminal Pleistocene/Early Holocene) are in upland areas favorable for exploiting geophyte root crops (Cannon and Ricks 1986), leading Middleton et al. (2014) to conclude that Paleoindian communities utilized the uplands, where they collected root crops. Additional plant foods (such as chokecherries (*Prunus* spp.), elderberries (*Sambucus* spp.), currants (*Ribes* spp.), and others) were also likely very abundant during the Late Pleistocene in the uplands.

Two recent studies confirm projections from ideal free distribution (IFD) theory for Paleoindian communities in the Great Basin. McGuiness (2022) determined that two suitability proxies (caloric resource abundance and resource return rate estimates) were consistent with IFD expectations for Paleoindian settlement locations within the western Great Basin. When Allgaier and Codding (2023) evaluated IFD predictions for Paleoindians across the Great Basin, they found Basin-wide agreement that Paleoindians were significantly clustered around lakes. The Bonneville Basin was judged most suitable, with the lowest average distance to marsh habitats; these were the earliest occupied, consistent with IFD predictions.

Post-Paleoindian Upland Strategies

Post-Paleoindian communities were no longer tethered to the now-evaporated lakes and marshlands of their Paleoindian ancestors. Although logistic upland hunting sometimes required considerable mobility, in general they "mapped onto" upland resources that were patchy in time and space—in effect, often moving themselves to important resources and abandoning the marsh-tethered strategies of transporting resources to people. Despite increasing aridity, Simms (2008:149) appropriately downplayed the challenges of aridity to emphasize instead the emerging opportunities as reflected in the human landscapes of the Middle Holocene that proliferated across the Intermountain West (Louderback 2022; Rhode 2008).

Coincident with the disappearance of smaller marshland habitats, pinyon-juniper woodlands were expanding northward during the Middle Holocene and likely outward from higher-latitude refugia. Post-Paleoindian communities did the same, simultaneously migrating outward and up in elevation from their desiccating pluvial lake homelands. Increased frequencies of Northern Side-notched projectile points document increased use of the uplands with a continued lowland presence, primarily along creeks and springs, increasingly notably after 6,000–5,000 cal B.P.

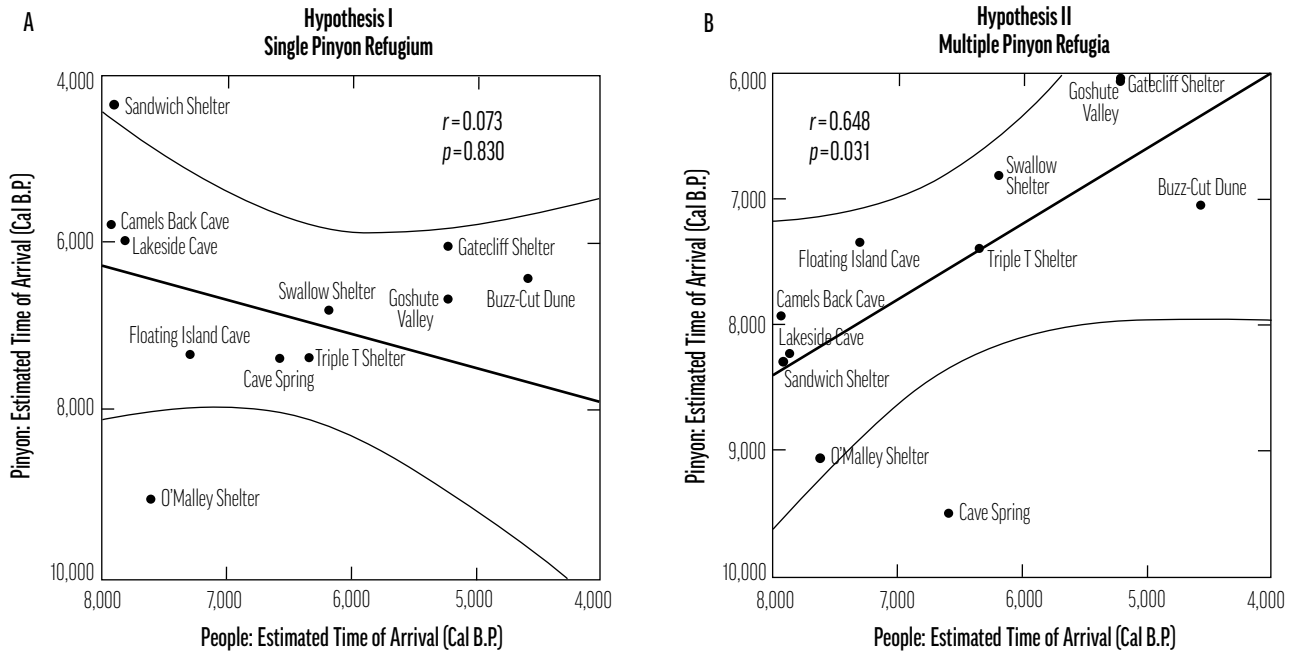

Figure 6. (A) Testing Hypothesis I, comparing the estimated times of arrival (ETA) based on the single pinyon refugium model (Y-axis) against ETAs for first significant occupations in the central Great Basin (X-axis). The correlation of $r=0.073$ is not statistically significant. (B) Testing Hypothesis II, comparing the estimated times of arrival (ETAs) based on the multiple pinyon refugia model (Y-axis) against ETAs for first significant occupations in the central Great Basin (X-axis). The correlation of $r=0.648$ is statistically significant.

These post-Paleoindian communities settled into their mountainous landscape with a resilience capable of adjusting group size and composition (Simms 2008:32–37; see also Madsen 2002:388). Post-Paleoindians alternated between winter villages, short-term camps near fish-driving spots, and short stays at various summer root places. They convened temporary large group events to stage pronghorn and jackrabbit drives, with associated fandangos that strengthened kinship ties and regional identities (Hockett et al. 2013; Thomas 1972).

TRACKING POST-PALEOINDIAN DISPERSALS

We hypothesize that post-Paleoindian dispersals were simultaneous with the Holocene expansion of pinyon pine, and we attempt to test that hypothesis. We track the first occupations of people within the central Great Basin starting in the Middle Holocene (shortly after 9,000 cal B.P.) through the onset of the Late Holocene Dry Period (ca. 3,100 cal B.P.). This comparison is grounded in a database of 4,613 cultural radiocarbon dates (Thomas 2024:Tables 2.3 and 2.4), summarized as median estimated time of arrival (ETA). These are based on datable first occupations from 27 archaeological sites spanning the Middle Holocene through the Late Holocene Dry Period (Table 2).[3]

Hypothesis Testing: Comparing ETAs for Pinyon Pine and People

Figure 6 compares ETAs for pinyon pine and people across the Great Basin, with the X-axis plotting first-arrival estimates for the archaeological sites detailed on Table 2. The Y-axis of Figure 6A plots ETAs of pinyon pine within the foraging range of each archaeological site based on the northward migration rates under pinyon Hypothesis I, the single refugium model developed in previous sections (transferred on a site-by-site basis in Table 2). The estimates of pinyon ETA at each site assume a maximum cumulative expansion rate of 57 m./yr. (for details on migration rates, see Millar and Thomas in press).[4]

For distances greater than about 100 km., we assumed that stochastic processes dominate, with the ETAs calculated at 50% long-distance events (142 m./yr.). At O'Malley Shelter, for instance, we project that (1) pinyon arrived at this site by 9,074 cal B.P. (based on ETAs computed under pinyon Hypothesis I assumptions)

Table 2

POST-PALEOINDIAN FIRST OCCUPATIONS AND CORRELATES[a]

Archaeological Site	ETA_{people} Range cal B.P.	ETA_{people} Median cal B.P.	ETA_{pinyon} Hyp. I cal B.P.	ETA_{pinyon} Hyp. II cal B.P.	NPP kg. C./m.^{2}	Basic Diet Breadth E/T	Distance to Nearest Paleoindian Homeland km.	References
Dust Devil	8,400–8,220	8,310	6,600	5,290	1,241	323	123	Stokes et al. 2003
Camels Back Cave	8,010–6,040	7,930	5,771	7,939	2,518	323	21	Schmitt and Madsen 2005:Table 3.1
Sandwich Shelter	8,400–7,420	7,910	4,336	8,296	2,635	323	100	Marwitt et al. 1971
Lakeside Cave	7,840–7,790	7,820	5,961	7,820	1,594	323	100	Madsen 2000; Madsen and Kirkman 1988:Fig. 2
O'Malley Shelter	7,840–7,420	7,610	9,074	9,074	2,591	420	30	Fowler et al. 1973
Floating Island	7,420–7,180	7,300	7,343	7,343	0	323	25	K. Jones, personal communication 2005[b]; Madsen 2000
South Fork Shelter[c]	6,750–6,320	6,535	—	—	3,905	572	110	Heizer et al. 1968; Spencer et al. 1987
Spotten Cave	6,670–6,120	6,395	4,307	4,923	4,200	229	132	Mock 1971
Cave Spring	6,660–6,500	6,580	7,384	9,509	1,508	537	45	M. Delacorte, personal communication 2003
Triple T Shelter	6,490–6,200	6,345	7,389	7,389	1,726	557	102	Thomas and Kelly 1988
Rose Spring	6,410–5,970	6,275	14,866	14,866	3,078	412	11	Yohe 1992
Swallow Shelter	6,310–6,010	6,190	6,808	6,808	2,420	189	102	Dalley 1976
Pie Creek Shelter[c]	5,890–5,470	5,680	—	—	1,516	155	159	McGuire et al. 2004
Corn Creek Dunes	5,570–5,460	5,510	13,386	13,386	1,602	314	140	Williams and Orlins 1963
Goshute Valley	5,390–5,050	5,220	6,665	6,043	1,319	156	42	Cunnar et al. 2019
Gatecliff Shelter	5,390–5,050	5,220	6,029	6,029	3,007	411	106	Thomas 1983b, 2020
Tosawihi Quarries[c]	4,850–4,300	4,575	—	—	2,161	163	—	Elston (2006); Elston and Drews 1992
Buzz-Cut Dune[b]	4,840–4,300	4,575	6,417	7,040	1,815	323	27	Madsen and Schmitt 2005
James Creek Shelter[c]	4,850–3,990	4,285	—	—	1,968	404	191	Elston and Budy 1990
Gypsum Cave	4,240–4,010	4,125	13,224	13,224	0	314	145	Gilreath (2009); Harrington 1933
Etna Cave	4,030	4,030	9,740	9,740	1,702	420	164	Fowler 1973
Coso	4,650–3,260	3,355	15,912	14,912	1,678	412	—	Gilreath and Hildebrandt 1993
Newberry Cave	4,140–3,690	3,915	13,523	13,523	1,482	314	56	Davis and Smith 1981; Davis et al. 1981
Alabama Gates	3,820–3,510	3,656	13,320	13,320	6,163	188	146	Delacorte 1999; Delacorte et al. 1994
Firebrand Cave	3,680–3,450	3,565	12,837	12,837	1,287	314	198	Blair and Winslow 2006
Dry Susie Creek[c]	3,140–2,860	3,000	—	—	2,097	560	175	Hockett 2003
Little Boulder Basin[c]	2,850–2,740	2,795	—	—	1,959	432	160	Schroedl 1996, 2001

[a]For specific site plots, see Thomas in press.

[b]Kevin Jones, Utah State Archaeologist.

[c]Beyond modern limit of pinyon pine.

and (2) people first arrived at O'Malley Shelter by 7,610 cal B.P., an estimate based on available radiocarbon evidence (although unexcavated deposits might exist at this site; Table 2, Figure 6A).

Comparing people ETAs to pinyon pine ETAs under the single pinyon refugium hypothesis for these 27 sites has correlation of $r=0.073$, which is not statistically significant ($p=0.830$). When lowland sites are excluded as outliers, the correlation coefficient still fails to reach statistical significance ($n=8$, $r=0.073$, $p=0.863$).

Figure 6B makes similar comparisons when projecting pinyon ETAs under the multiple pinyon refugia hypothesis.[5] The result ($r=0.648$, $p=0.031$) demonstrates a statistically significant relationship. We conclude that the spread of pinyon from multiple Pleistocene refugia (pinyon Hypothesis II) is significantly correlated with the

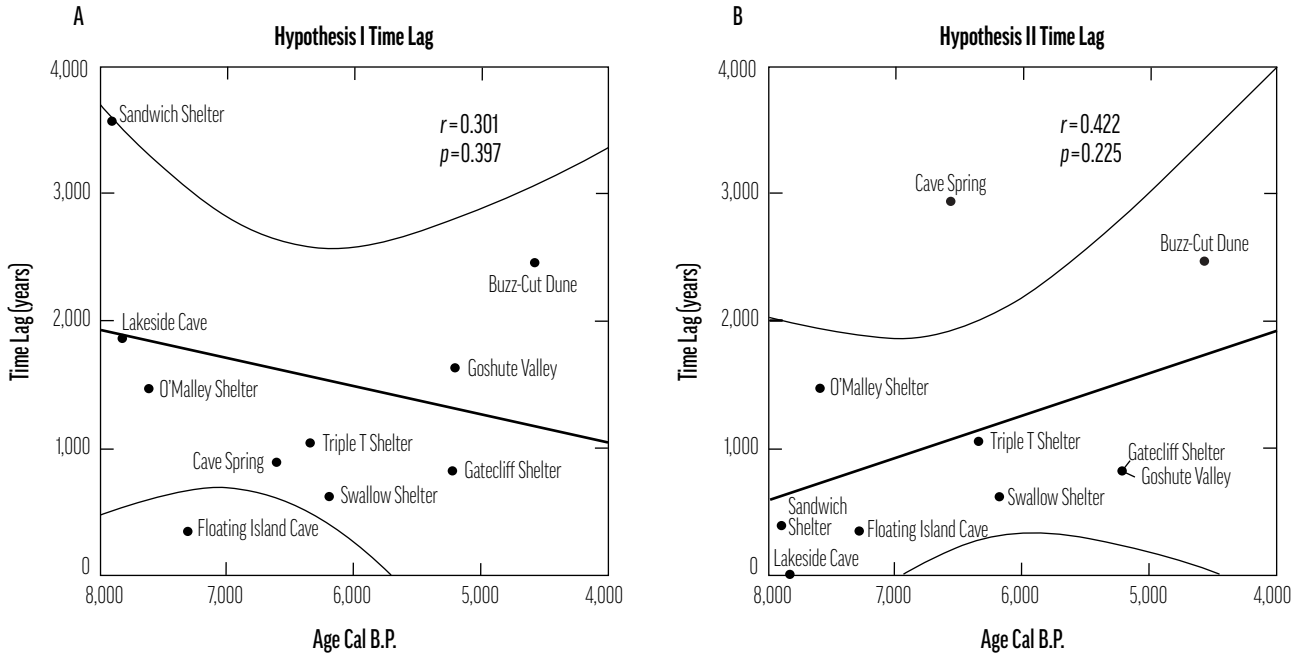

Figure 7. (A) Comparison of the time lag between pinyon arrival and first post-Paleoindian settlement at 12 archaeological sites based on the single pinyon refugium model (Hypothesis I). The correlation of $r=0.301$ is not statistically significant. (B) Comparison of the time lag between pinyon arrival and first post-Paleoindian settlement at 12 archaeological sites based on the single pinyon refugium model (Hypothesis II). The correlation of $r=0.422$ is not statistically significant.

simultaneous spread of post-Paleoindian communities across the central Great Basin.

Modeling Time Lags:
The Single Southern Pinyon Refugium Hypothesis

People Dispersing before Pinyon Arrival. Table 2 documents that people first occupied six sites before the arrival of pinyon within the foraging radius (as projected by pinyon Hypothesis I): Dust Devil, Camels Back Cave, Sandwich Shelter, Lakeside Cave, Floating Island, and Spotten Cave. The mean time lag between pinyon arrival and first occupations ranges between 43 and 3,570 years, with a mean of 1,898±1,129 years.

People Occupying the Southern Pinyon Refugium. Despite the long-term presence of pinyon pine in the southern Great Basin (pre-9,000 cal B.P.), a considerable time lapse transpired before significant archaeological occupations in the region appeared at Rose Spring, Corn Creek Dunes, Gypsum Cave, Coso, Newberry Cave, Alabama Gates, and Firebrand Cave. The mean time lag between pinyon arrival and first occupations in the southern pinyon refugium area ranges between 11,557 and 7,876 years, with a mean of 8,690±2,400 years.

Pinyon-free First Occupations. Table 2 shows that significant first post-Paleoindian occupations appeared at six archaeological sites established beyond the northern limit of the pinyon curtain (Figure 1)—places where pinyon did not grow during the post-Paleoindian period: South Fork Shelter (6,535 cal B.P.), Pie Creek Shelter (5,680 cal B.P.), Tosawihi Quarries (4,575 cal B.P.), James Creek Shelter (4,285 cal B.P.), Dry Susie Creek (3,000 cal B.P.), and the Little Boulder Basin (2,795 cal B.P.). Pinyon grew far to the south when each of these settlements was occupied—well beyond the presumed foraging range. Pinyon continued to be notably absent through the ethnohistoric interval.

People Arriving Shortly after Pinyon. Figure 7A plots the time lags between pinyon arrival and 10 post-Paleoindian occupations. Time lags range from 43 years at Floating Island Cave to 3,574 years at Sandwich Shelter using Hypothesis I estimated times of pinyon arrival (Table 2). Figure 7A shows that overall, the time lag between when pinyon was established, and first post-Paleoindian settlement decreases through time. The correlation coefficient is $r=0.301$), but this relationship is not statistically significant at $p=0.397$.

Modeling Time Lags:
The Multiple High-latitude Refugia Hypothesis

Table 2 also summarizes ETAs for pinyon pine under Hypothesis II, that the northward migration of pinyon pine from the southern Pleistocene refugium was augmented by dispersions from four Pleistocene refugia at higher latitudes in the western and eastern Great Basin (Figure 4 and Table 1).

People Dispersing before Pinyon Arrived. Table 2 documents that only three sites (Dust Devil, Spotten Cave, and Camels Back Cave) were occupied before the projected arrival of pinyon under Hypothesis II. The time lags between first pinyon and initial post-Paleoindian occupations are estimated to have been 3,020, 1,472, and 9 years, respectively. These results differ notably from Hypothesis I results because Hypothesis II allows for the possibility of more local arrivals originating in the high-latitude Great Basin refugia.

Pinyon-free First Occupations. Hypotheses I and II project that the same six archeological sites were established beyond the northern limit of the pinyon curtain (Figure 1)—places where pinyon did not grow during the post-Paleoindian period (and does not grow today).

People Arriving Shortly after Pinyon. Figure 7B plots the time lags between 10 post-Paleoindian occupations and first pinyon arrival under pinyon Hypothesis II. Time lags range from a simultaneous estimated arrival within the foraging radius of Lakeside Cave to 1,464 years at O'Malley Shelter, with a mean lag of 1,102±900 years (nearly four centuries less than under pinyon Hypothesis I, but this difference is not statistically significant). Figure 7B also shows that (unlike the Hypothesis I result) the time lag between pinyon progressing from multiple refugia and first post-Paleoindian settlement increased slightly through time; the correlation coefficient of $r=0.422$, defining a weak linear relationship that is not statistically significant ($p=0.225$).

Modeling Distance to Paleoindian Homelands

Our hypothesis that post-Paleoindian dispersions emanated directly from Paleoindian homelands is supported by genetic evidence from the Lahontan Basin that shows a linkage between ancestral Paleoindian through modern Numic populations without a total population replacement (Moreno-Mayar et al. 2018). Figure 8 expresses this hypothesis as a simple nearest-neighbor model for post-Paleoindian dispersals, comparing the raw distance of post-9,000 cal B.P. upland sites (Table 2) against the nearest known Paleoindian center (Fig. 5).

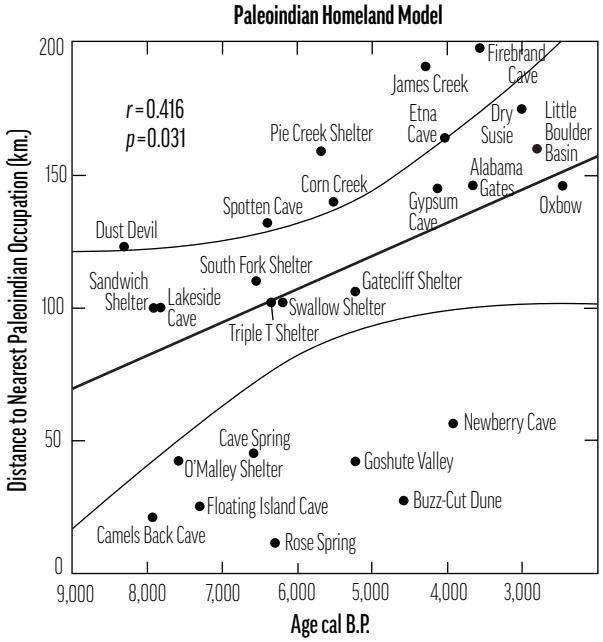

Figure 8. Testing the Nearest Paleoindian Neighbor model by comparing the distance to nearest Paleoindian occupation against ETAs for first significant occupations in the upland central Great Basin (X-axis). The correlation of $r=0.416$ is statistically significant.

Measuring Distance to Paleoindian Homeland. Figure 8 operationalizes the hypothesis of direct geographical and time-sequenced linkages between ancestral Paleoindians and their post-Paleoindian descendants by specifically estimating the dispersions from deteriorating Paleoindian marshlands (beginning in the Middle Holocene) into upland desert-mountain landscapes of the central Great Basin.[6]

Testing the Nearest Paleoindian Neighbor Model. Table 2 demonstrates that the average distance from Middle Holocene occupations (older than 6,000 cal B.P.) and the nearest-neighbor (abandoned) Paleoindian site is 72.5±43.7 km. The comparable average nearest-neighbor distance for the earliest post-Paleoindians (often termed Early Archaic [6,000–3,500 cal B.P.]) increases to 138.3±47.9. This difference is statistically significant ($p=0.0009$; $t=3.72$, $df=25$; Table 2).

Figure 8 plots nearest-Paleoindian-neighbor regression of distance between ETAs for initial post-Paleoindian

occupations (9,000–3,500 cal B.P.) and the closest well-documented Paleoindian site (older than 9,000 cal B.P., based on radiocarbon dates). This linear trend is statistically significant (r=0.416, p=0.031).

Implications of the Nearest Paleoindian Neighbor Model. Although linking specific Paleoindian and post-Paleoindian sites remains difficult, these results confirm the application of the generic nearest-neighbor model. As successive generations spread out across the central Great Basin, post-Paleoindian frontiers moved increasingly farther away from Paleoindian homelands. Between ca. 8,400 and 6,000 cal B.P., virtually all Early Holocene settlements clustered within two days' walk (60 mi., 90 km.) of the closest Paleoindian sites. After this—between 6,000 cal B.P. to the onset of the LHDP (3,100 cal B.P.)—the distance from Paleoindian homelands increased to more than 80 mi. (132 km.).

WERE POST-PALEOINDIAN DISPERSALS IDEAL AND FREE?

To help understand how human populations distribute themselves across the landscape, several archaeologists have turned to the theoretically informed predictions and explanations of the ideal free distribution model (as summarized in Codding and Bird 2015; Weitzel and Codding 2022). In a landmark paper setting out this approach, Fretwell and Lucas (1969) defined the ideal free distribution (IFD) model with negative density dependence, and two variants, the IFD with Allee effects (positive density dependence), and the IFD with ideal dominance distribution (also known as the ideal despotic distribution). The dual IFD models and the Allee variant are relevant here.

The IFD with negative dependence assumes that environments vary in suitability, and, as populations increased either by in-migration or in situ growth (Fretwell 1972; Fretwell and Lucas 1969), higher-ranking habitats should be populated first and continue to be occupied as lower-ranking habitats subsequently are occupied (Kennett et al. 2006:270; Sutherland 1983:1–14), assuming density effects on suitability are constant across habitats (Codding and Bird 2015:15). Dual baseline predictions emerge: (1) that individuals should always settle in the most suitable habitat first, which was previously unoccupied, and (2) that people should eventually move to lower-ranking habitats because the first highest suitable habitat is now equal to the next suitable habitat due to the IFD model being negative density dependent. Across an environment, populations may eventually reach an equilibrium point at which all individuals have the same opportunity for success. Paleoindian settlement patterns in the Great Basin and elsewhere have been shown to be consistent with IFD model predictions with negative density dependence (Allgaier and Codding 2023; McGuinness 2022; Miller and Carmody 2022). This is important because it provides a way to test whether the hypotheses match with the predictions of the IFD model. If people were simultaneously occupying habitats across the Great Basin, this may indicate that people were moving to lower-ranked habitats over time.

We can apply these baseline IFD model predictions to the post-Paleoindian dispersions from Paleoindian homelands: Did post-Paleoindian communities initially occupy higher-ranking habitats (i.e., those with the highest "suitability" for survivability and reproduction) and only later occupy lower-ranking habitats?

Defining Suitability

Critical to IFD modeling is the key assumption that individuals seek to maximize "suitability"—the potential for a habitat to positively impact an individual's evolutionary fitness. So defined, habitat suitability declines with the addition of each new individual to a habitat due to competition for resources and eventually resources declining. Applied intuitively to the archaeological record, assumptions of the IFD model suggest that the "most suitable" locations are those providing ready access to key resources, water, shelter, and so forth. The operational question becomes how best to define "suitability" in a quantitative, replicable manner. To address post-Paleoindian occupations, we first define suitability using Net Primary Productivity (NPP) and energetic return rate proxies based on diet breadth modeling.

Modeling Net Primary Productivity (NPP)

Codding and Jones (2013) used NPP as a baseline proxy of habitat suitability in demonstrating that ethnohistoric population densities in ancient California follow IFD predictions, with higher population densities occurring

in more suitable habitats. Morgan et al. (2020:138–140) expanded NPP proxies to estimate an environment's ability to produce plant biomass and thereby assessed the energetic efficiency of alpine village life in California's White Mountains. Weitzel and Codding (2022) tasked NPP with tracking the distribution of food production in eastern North America. For other applications of NPP in archaeology, see Currie and Mace (2012), Yaworsky et al. (2020), Hanna and Giovas (2022), and Vernon et al. (2022).

Measuring NPP. Over the past three decades, the Earth Observing System within the U.S. National Aeronautics and Space Administration has generated estimates for the earth's terrestrial surface, measuring daily primary biomass production by photosynthesizing plants, gross primary productivity (GPP), and annual summaries of NPP, defined as the sum of gross primary productivity minus the cost of growth and maintenance of living cells in permanent woody tissue. Modifying the procedures outlined by Morgan et al. (2020), we derived terrestrial NPP measures from MODIS satellite data (Running and Zhao 2021) and assigned specific single pixel estimates (based on a 0.5-km. grid scale) to each of the 27 post-Paleoindian occupations documented on Table 2.

Testing the NPP Model. For Middle Holocene-age initial settlements (older than 7,000 cal B.P.), NPP estimates range between 4,200 kg. C./m.² at Spotten Cave and 0 kg. C./m.² at Floating Island Cave averaging 1,431.2± 1,440.9 kg. C./m.² (Fig. 9, Table 2). For subsequent Early Archaic occupations (6,000–3,500 cal B.P.), first-occupations average 2,213.1±1,286.3 kg. C./m.², ranging from 6,163 kg. C./m.² at Alabama Gates (in Owens Valley) to 0 at Gypsum Cave. The correlation between first-arrival times of post-Paleoindians and net primary productivity through time is $r=0.006$ and does not differ significantly from zero ($t=-0.030$, $p=0.976$).[7]

NPP and Ideal Free Distribution Implications

IFD modeling holds that "best locations" should be occupied before lower-ranking habitats. When operationally defining "habitat suitability" as net primary productivity, a high-ranking habitat should have high levels of NPP, and with lower levels having lower NPP measures. Our data show no support for IFD model predictions for the post-Paleoindian period.

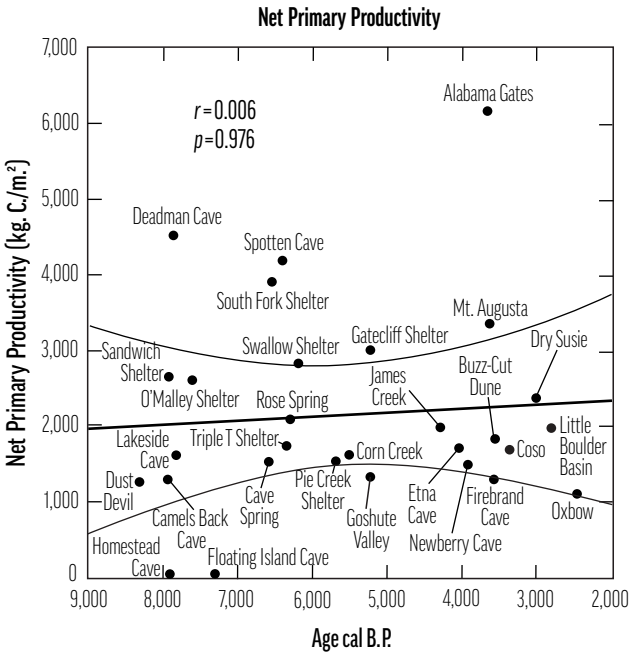

Figure 9. Testing Net Primary Productivity (NPP) against ETAs for first significant occupations of the upland central Great Basin (X-axis). The correlation of $r=0.006$ is not statistically significant.

Larger issues undermine the potential of NPP proxies for deep Great Basin history. Figure 10 compares the distribution of NPP measures across California and the floristic zones of the Intermountain West. The distribution of NPP measures across the Great Basin shows remarkably little variability—less than 20% of the range evidenced across neighboring California (cf. Codding and Jones 2013; Morgan et al. 2020:Table 1, Figure 2)—the obvious question is whether variability in NPP values is sufficient in the Great Basin to condition meaningful human responses or for NPP values to be a useful indicator of habitat suitability.

More significant problems arise with NPP proxies due to the pivotal assumption made by the MODIS model, holding that these biome-specific parameters are constant across time and space (Running and Zhao 2021). Most IFD studies in archaeology make the simplifying assumption that suitability remains constant over time, empowering static proxies extracted from modern environmental measurements. This assumption has led to useful findings and may be particularly appropriate for assessments of suitability based on predominantly abiotic or geographically fixed features of the environment

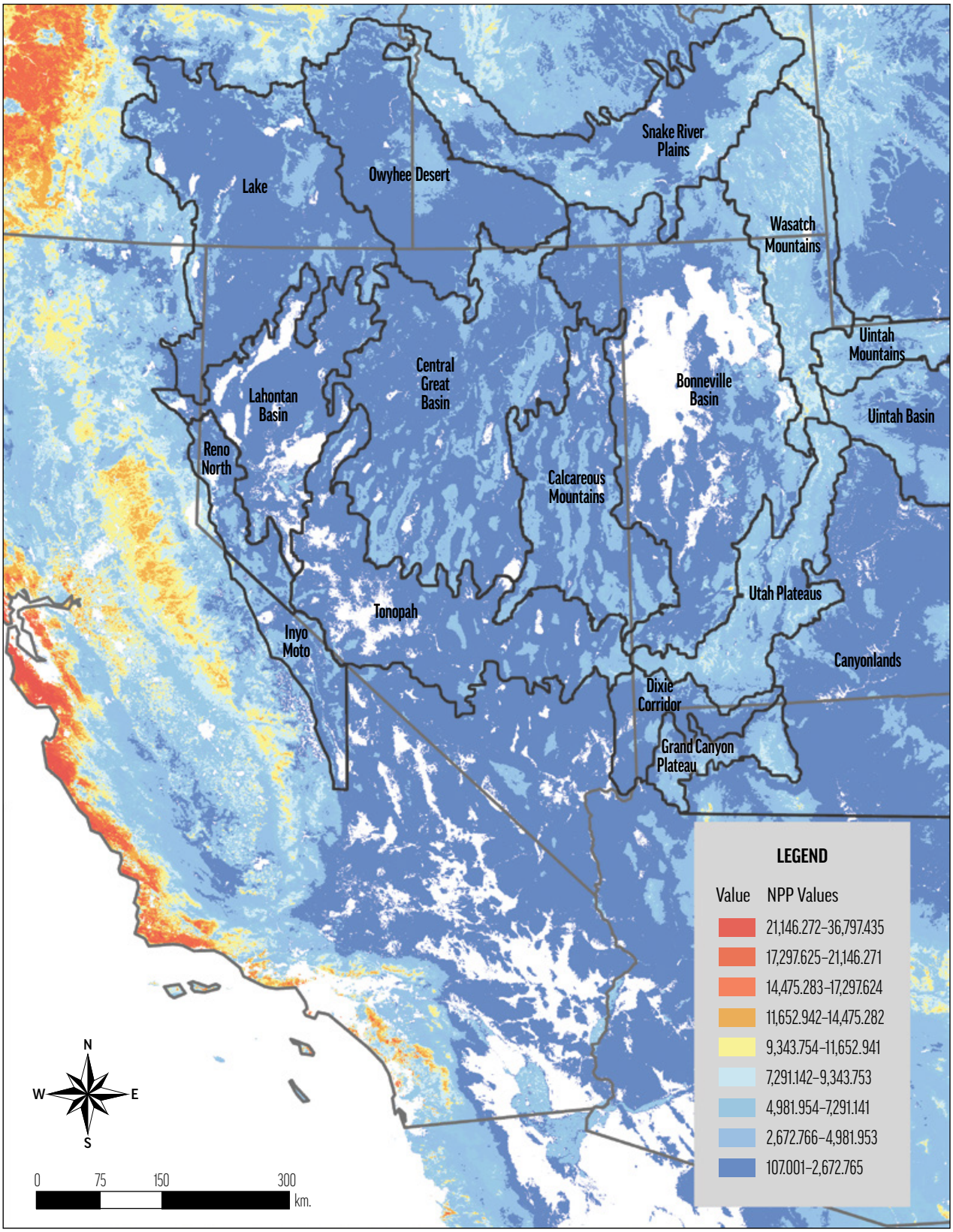

Figure 10. Distribution of Net Primary Productivity (NPP) across California and the Great Basin (cf. Codding and Jones 2013) based on terrestrial NPP measures from MODIS satellite data (Running and Zhao 2021).

(Winterhalder et al. 2010). But in fact, suitability, especially if measured by NPP, changes dramatically over time for a variety of reasons that can impact the dynamics of IFD (Kennett and Winterhalder 2008; McClure et al. 2006; Miller and Carmody 2022; Vernon et al. 2022).

Archaeologists and ecologists familiar with the Intermountain West during the Holocene are abundantly aware of the remarkable climatic changes that characterized the region, even within the recent past (Mensing et al. 2023; Thomas et al. 2023). One is compelled to ask: How can NPP values derived from data over the past three decades even remotely be expected to reflect the well-documented climatic variability within the Holocene Great Basin?

Modeling Multi-Scalar Prey Choice Models

"Habitat suitability" can also be operationally defined based on energetic return rate estimates realized by foragers working the same landscapes. Magargal et al. (2017) developed several spatially explicit, multi-scalar prey choice models that ranked foraging return rates computed for potential prey items within a patch, the distribution of those patches, and algebraic expressions approximating the outcomes of different subsistence strategies. These investigators then projected experimental data on resource profitability and abundance onto the historical distribution of Great Basin vegetation communities to compute several diet-breadth return rate estimates for ethnohistoric Numic-speaking groups.

The Basic Prey Choice Model. This baseline construct models whether a forager should pursue a plant or animal prey item on encounter or to continue searching for more profitable resources within that same patch (Magargal et al. 2017). The basic prey choice model is grounded in a scenario of a forager optimally taking any prey item upon encounter if it increases the aggregate return rate within the forager's collection range within a specific patch. Additional resource types are added relative to their rank order of expected post-encounter profitability, from which Magargal et al. (2017) calculated the overall within-patch return rate and projected the average expected returns achieved by individuals in proportion to the proportional area of each patch within each range. The aggregated overall return (E/T) takes E as equal to the total energetic return from a patch relative to the total search and handling time (T) within that patch.

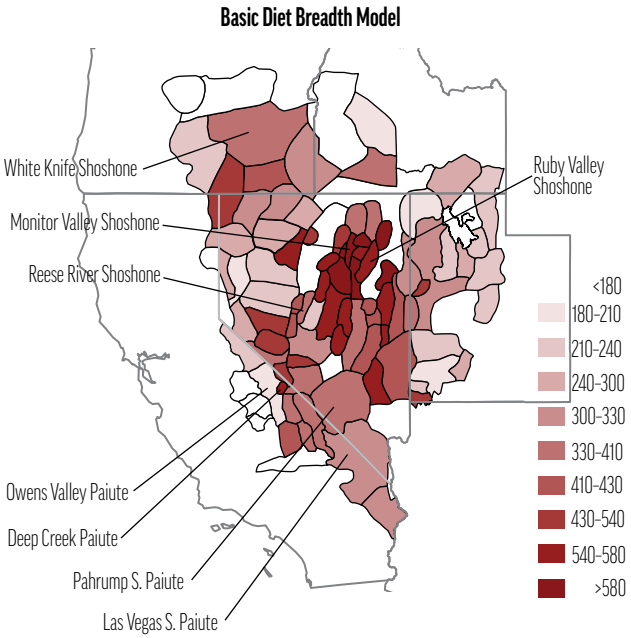

Figure 11. Basic Diet Breadth model as derived by Magargal et al. (2017), plotting E/T (the aggregated overall return rate) for 94 ethnohistoric Numic-speaking groups (reproduced with permission).

Testing the Basic Prey Choice Model. Figure 11 arrays E/T return rates for 94 ethnohistoric Numic-speaking groups. The Western Shoshone of Ruby Valley registered the highest basic return-rate (575.2 kcal/hr.), followed closely by the Monitor Valley Shoshone (557.8 kcal/hr.) and the Northern Paiute of Deep Creek Valley (567.8 kcal/hr.). The Goshute Valley Shoshone (155.9 kcal/hr.), White Knife Shoshone (163.7 kcal/hr.), and the Northern Paiute of Owens Valley (188.2 kcal/hr.) have the three lowest-ranking return rates for the basic E/T model. Magargal et al. (2017:6) caution that "while the absolute values from these studies may be imprecise… they are likely accurate on a relative scale reflecting the true ordinal ranking of different prey-types."

Table 2 assigns these basic diet breath estimates (expressed as E/T) to radiocarbon-dated people ETAs for post-Paleoindian sites in the central Great Basin. Figure 12 plots the regression between post-Paleoindian ETA and estimated return rates. This is clearly not a linear relationship ($r=0.0829$, $p=0.6775$).

These same data can be partitioned temporally, producing mixed results. The 14 Middle Holocene sites have an average E/T estimate of 382.5 kcal/hr., ranging from 557–572 kcal/hr. at South Fork Shelter and

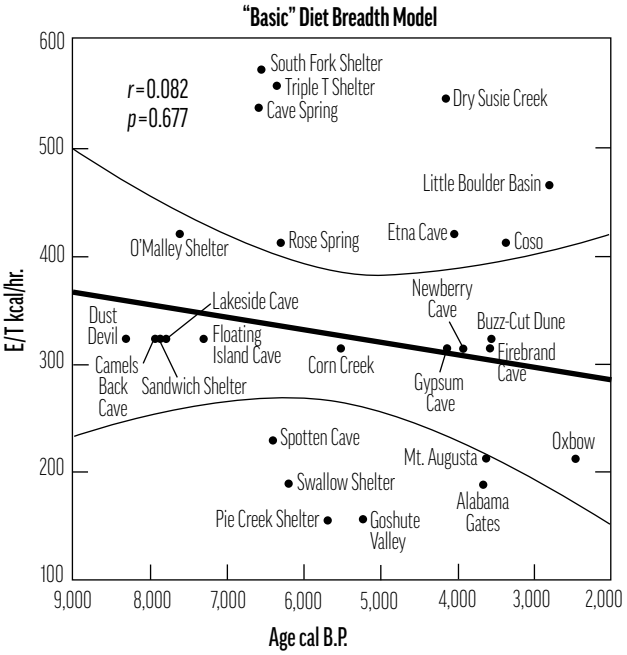

Figure 12. Testing basic diet breadth return rates (E/T) (after Magargal et al. 2017) against ETAs for first significant occupations of the upland central Great Basin (X-axis). The correlation of $r=0.082$ is not statistically significant.

Triple T Shelter to 229–323 kcal/hr. at multiple sites in the Bonneville Basin (including Spotten Cave, Camels Back Cave, and Lakeside Cave). The subsequent 15 Early Archaic occupations (6,000–3,500 cal B.P.), such as Gatecliff Shelter, have E/T = 382.5 ± 129.5 kcal/hr. These nearly identical average values for E/T contrast with IFD predictions of decreased return rates through time.

Diet Breadth and Ideal Free Implications

We also operationally projected IFD assumptions of habitat "suitability" using all additional diet breadth models derived by Magargal et al. (2017:e23000)[8]. In all cases, IFD models predict that higher-ranked habitats should show higher estimated return rates and habitats with lower-ranking habitats should have lower return rates. None of these IFD models show a statistically significant trend for post-Paleoindian populations to seek out higher-ranking habitats during their migration from the Paleoindian homelands or during in situ expansion. We conclude that the range of prey choice models derived by Magargal et al. (2017) fails to correlate with the archaeological record of initial post-Paleoindian occupations in the central Great Basin.

So, the question becomes: Why do Paleoindian occupational sequences in the Great Basin (and elsewhere) seem to follow basic IFD predictions with negative density dependence, yet post-Paleoindian dispersals do not? We believe that the second variant of the ideal free distribution model (Fretwell and Lucas 1969)—the IFD with Allee effects (positive density dependence)—accounts for this difference.

Allee Effects

In its basic form, the IFD model is negative density dependent, meaning that additional individuals entering a habitat decreases suitability. While it is unlikely that individuals had perfect knowledge of all suitable habitats or enjoyed unconstrained abilities to move from one habitat to another, multiple studies have demonstrated the IFD is useful as a null model (Robinson et al. 2019:68).

In some cases, however, the opposite can be true, in which adding individuals becomes beneficial due to cooperative behaviors that enhance habitat suitability. The variant of the IFD with an Allee effect applies when individual levels of fitness are correlated with population size (Allee 1931, 1938, 1949; Jazwa et al. 2013; Stephens et al. 1999).

This seems particularly true for cases of human range expansion in which positive density dependence arises through social organization and shared technologies that generate "economies of scale in the capture, defense, and use of resources" (Codding and Bird 2015; Winterhalder et al. 2015:473). Allee effects could also arise from habitation modification, capital improvement, or economies of scale—including help in clearing woodlands (to make cultivation easier), burning habitats (keeping tree cover in an earlier successional stage or encouraging cone production), or helping to facilitate technology (as with irrigation projects; see Kennett et al. 2006:Figure 12.3B).

Post-Paleoindian Transitions

Analyzing post-Paleoindian transitions in the Tennessee River drainage system, Miller and Carmody (2022) found that colonizing Paleoindians preferentially settled into the most suitable (higher ranking) sub-drainages consistent with IFD predictions of negative density dependence. But these same predictions failed to account for the distribution of post-Paleoindians because increasing population

densities and shifting subsistence strategies undermined underlying assumptions of the standard IFD. Throughout the Mid-South, Middle Holocene conditions transformed household economies due to reduced residential mobility resulting from intensified use of predictable and storable food resources such as oak and hickory. Adding new individuals became beneficial due to the increased availability of oak and hickory mast and the first appearance of widespread food-storing strategies (e.g., Gardner 1997). Miller and Carmody (2022) concluded that whereas Paleoindian patterning was consistent with negative density dependent predictions of the IFD, when post-Paleoindian communities expanded to upland areas, positive density dependence (Allee effects) came into play due to the broader distribution of oak-hickory forests and initial IFD predictions no longer held.

Our analysis suggests that parallel processes operated in the Great Basin, where Paleoindian settlement patterning was consistent with negative density dependent predictions from the IFD model. Paleoindian lacustrine practices necessitated that people hunted and gathered resources from marshland habitats that were highly ranked, thus occupied first. This pattern changed dramatically when Middle Holocene aridity dried the pluvial lakes and marshlands, encouraging post-Paleoindians to move away from wetland habitats. Communities no longer aggregated around high-ranking resources restricted to the lakesides and marshes. With less concentrated population densities, smaller settlements budded off and competition for prime lacustrine real estate diminished. Less suitable habitats with lower-ranking resources were diversified geographically, and people shifted to upland desert/mountain mosaics. This suggests why negative density dependent IFD model predictions became less relevant during the post-Paleoindian period. Neighbors were welcomed as suitability increased with population growth, aided by options for more communal food procurement. Allee effects would pertain until population densities became high enough that resource depletion and excess competition occurred. Post-Paleoindian behaviors, however, involved family hamlets that were never large enough to incur the high-population side of the density curve. Increasing population densities raised individual fitness levels from the onset of Middle Holocene aridity until the LHDP shifted habitat suitability once again (Mensing et al. 2023; Thomas et al. 2023). The simultaneous migration of pinyon pine into upland habitats was a boon to post-Paleoindians deserting lacustrine homelands in several ways.

Pinyon Directly Facilitated Post-Paleoindian Dispersals

Julian Steward recorded the ubiquity of pine nut use by ethnohistoric Great Basin Shoshoneans, but he also classically warned that the notoriously unpredictable nature of pinyon harvests seriously constrained their overarching importance and prevented the participation in the settled village life of other hunter-gatherer "bands" (Steward 1933:24, 1938:27, 65, 70, 88).

We have previously taken exception to Steward's assumption that boom-and-bust pinyon reproductive cycles were universal across the Great Basin, arguing instead that evolutionary processes generated significant regional variability in cone production and seed production (Thomas and Millar 2023). These regional differences included the number of cone and seed predators, which affects the evolution of masting (i.e., occasional heavy crop years interspersed with low to no cone crop years) and morphological characteristics related to cone-scale thickness and serotiny (where cone scales stay closed on maturity)—all likely rendering pinyon procurement in the central Great Basin far superior to that further west. We have subsequently extended our analysis to assess seed availability and predators, cone traits, and cone masting to the eastern Great Basin (Millar and Thomas in press). We now believe that pine nuts in eastern Nevada and western Utah share similar foraging limitations as those of the western Great Basin.

If so, then Holocene-age pinyon migrating into the central Great Basin provided a predictable, low-cost, easily available, and readily stored resource that directly facilitated post-Paleoindian dispersals in multiple ways.

Pinyon Helped Buffer Extinction Risks

Allee (1938) emphasized cases of increasing population densities having positive influences on fitness among human populations, helping to strengthen social structure especially at the lowest population densities (Allee 1949; Sutherland 1983, 1994). Low-density human populations risk extinction because of group size effects on fertility and survivorship (including stochastic loss of the entire group), such as unbalanced sex ratios, inbreeding

depression, and reduced cooperative foraging (Steele 2009:126–127). Such risks can be minimized when low-density foragers split into semi-autonomous groups of different sizes, with these groups occasionally joining together. These occasional group congregations would enhance the average number of potential partners available to each reproductively fertile individual, as well as providing numerous other benefits.

When Robinson et al. (2019) compared population growth and decline throughout Holocene Wyoming, they found that Allee-like benefits to aggregation—rather than IFD negative density dependence—helped explain settlement decisions in response to growing populations. Codding et al. (2019) similarly concluded that incorporating Allee's principles may help to explain the emergence of territorial behaviors, in which individual benefits gained from aggregation making in-group cooperation worthwhile. We see similar processes characterizing the post-Paleoindian transition in the central Great Basin.

Pinyon Helped Underwrite Costs of Supra-Villages

Allee effects suggest that habitual cooperation and coordinated labor events specifically facilitated underwriting the costs of supra-village events involving the coordinated labor and habitual cooperation evident in fandangos, festivals, sweat house gatherings, large-scale hunting features, and warfare (Robinson and Thomas 2024; Thomas 2024). Such supra-village events provided not just the mechanisms for social networking and strengthening kinship ties and group solidarity, but also expanded the local gene pool, thus enhancing individual and group fitness (Dobson and Lyles 1989; Freeman et al. 2019; McDonald and Hewlett 1999).

Pinyon Helped Enable Mass Capture Technologies

Harvesting and storing pine nuts also helped hunters get more game. When local conditions warranted, post-Paleoindian communities cooperated to gather large amounts of food in pinyon harvests, communal jackrabbit drives, and communal antelope drives. Some resources were consumed immediately to support fandangos and other supra-village gatherings, while surpluses were cached for the winter.

Figure 13 plots nearly 100 large-scale trapping structures against the distribution of pinyon throughout

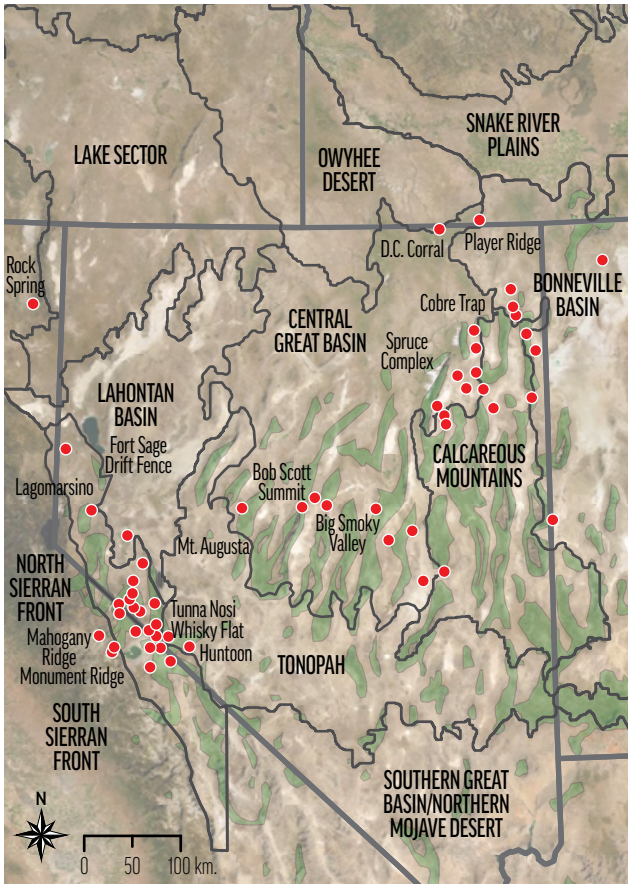

Figure 13. Spatial relationship of large-scale hunting features and the modern distribution of the pinyon-juniper woodland (after Hockett et al. 2013:Figure 4).

the Great Basin, the earliest dating back to the Middle Holocene and continuing for millennia. Consistent with zooarchaeological evidence from Bonneville Estates Rockshelter (Hockett 2007, 2015), this archaeological evidence demonstrates that post-Paleoindian diet breadth broadened to include large-scale communal hunts involving construction of corrals and a continuation of individual or family-based hunts from Paleoindian times. We agree with Hockett and Dillingham (2023) that the widespread distribution of large-scale communal artiodactyl hunting was deliberately positioned in exactly those places where the pinyon-juniper woodland was spreading (Hockett et al. 2013:77; Hockett and Dillingham 2023:124).

The availability of stored pinyon nuts doubtless also supported long-range logistic forays from more permanent residential base camps (Hildebrandt and McGuire 2002; Hildebrandt et al. 2016; McGuire et al. 2018; Thomas 1983a:35; Thomas et al. 2023). This logistic radius

extended the zone exploited by hunters, who stayed away from the residential camp overnight, for weeks or longer. The absence of hunters during their forays cut down the number of daily providers in the base camp, further privileging cached food supplies (particularly pine nuts).

CO-DISPERSING PINYON PINE AND PEOPLE: CORRELATION? CAUSALITY?

Multiple proxies document the estimated times of arrival for pinyon pine and initial post-Paleoindian occupation across the central Great Basin (Tables 1 and 2). The paleoecological reconstructions are based on 70 calibrated radiocarbon dates on pinyon fossils from woodrat middens and on pollen evidence. We frame two hypotheses charting Middle Holocene and later pinyon migrations, one where pinyon migrated strictly from southern Great Basin refugia and the other positing four additional high-latitude refugia. Archaeological trajectories were based on clusters of radiocarbon dates from 27 post-Paleoindian occupations simultaneously migrating into these same habitats.

Correlations?

These comparisons reveal notable correlations between the pinyon and post-Paleoindian dispersal estimates (Figures 6 and 7).

- While the correlation under pinyon Hypothesis I lacks statistical significance, pinyon Hypothesis II generated a significant linear relationship through time that began in the Bonneville Basin and extended westward within the emerging pinyon woodland.
- Charting the estimated time lapses between pinyon arrival and first post-Paleoindian occupations (Figure 7), pinyon Hypothesis I predicts that people arrived at a dozen localities an average of ~1,600 years later than pinyon. For pinyon Hypothesis II estimates, this time lag decreased to ~1,100 years at the same sites.
- Assuming that Paleoindians were directly ancestral to post-Paleoindians in the same region, we found that nearest-neighbor distances from Paleoindian homelands increased significantly through time, from an average of approximately 90 km. in the Middle Holocene to more than 130 km. for the 6,000–3,500 cal B.P. interval.

These results confirm correlations between pinyon pine and post-Paleoindian migrations across the central Great Basin.

Causality?

Did pinyon pine migration from Late Pleistocene refugia cause the simultaneous expansion of people away from lacustrine Paleoindian homelands into the neighboring pinyon uplands?

The answer is clearly "no." Despite the obvious correlations, Table 2 documents considerable variability in post-Paleoindian expansion strategies. For one thing, several post-Paleoindian sites within the expansion zone were inhabited well before pinyon arrived. Six more sites were occupied at the same time in the pinyon-free zone north of the pinyon curtain (where pinyon did not grow at the time and is not present now). In the southern Pleistocene refugium, post-Paleoindian archaeological sites did not appear for thousands of years, even though pinyon pine had flourished there continuously since the Late Pleistocene,

Correlations between pinyon and people migrations? Yes. Causality? No.

FACILITATIVE ROLES OF PINYON PINE

We conclude that instead of a direct causal relationship, post-Pleistocene arrival of pinyon pine helped facilitate simultaneous post-Pleistocene dispersals by helping to buffer extinction risks, underwriting costs of supra-village and mass capture events, and enabling logistic hunting strategies. At first facultative, pinyon nut procurement would eventually become a driving force defining Central Mountains Archaic lifeways that would persist—with key survival adjustments during the Late Holocene Dry Period—for nine millennia through the ethnohistoric period in the Great Basin.

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NOTES

[1]This date derives from a needle of *Pinus flexilis*. Pinyon also occurs in the midden; a younger date derived from a pinyon needle, but undated pinyon also occurs, so we consider the oldest date as possible for pinyon.

[2]Thomas (2024:Chap. 5) provides the paleoecological, archaeological, and theoretical background for this section. Important references include Duke 2011, Duke and King 2014, Duke and Young 2007, Louderback and Rhode 2009, Madsen et al. 2015, Oviatt et al. 2003, Rhode et al. 2005, and Thompson 1992).

[3]For each archaeological site, we estimated first-arrival dates for the earliest cluster of radiocarbon dates. These initial clusters ranged from two to five dates, for which a pooled mean and standard error were computed. The median of that pool date is used in all subsequent statistical comparisons. All raw dates and computed pooled estimates are listed in Thomas (in press).

[4]Estimates for lowland sites are based on pinyon pine growing within a reasonable foraging radius at places like Lakeside Cave (Madsen 2000:64), Floating Island Cave (Lupo et al. 2021:12), Camels Back Cave (Schmitt and Madsen (2005:7) and Buzz-Cut Dune (Madsen and Schmitt, 2005:7); see also Madsen and Rhode (1990).

[5]Two single outliers (Dust Devil and Spotten Cave) were removed from this figure.

[6]Rather than attempt to model exact topography, Table 2 employs the linear distance estimates (in km.) from the nearest Paleoindian homeland (as estimated in Millar and Thomas in press; see also Duke and King 2014; Duke and Young 2018).

[7]Elsewhere, this same NPP proxy was also projected against an independent sample of 70 first post-Paleoindian occupations dated by Great Basin projectile point chronologies (Thomas in press). The average NPP for Middle Holocene first occupations (>6,000 cal B.P.) is 2,311 kg. C./m.², with the mean NPP value for subsequent Early Archaic sites (6,000—3,500 cal B.P.) increases slightly to 2,443 kg. C./m.². This sequence, although not statistically significant ($t = 0.6857$, $df = 51$, $p = 0.4960$), reversing IFD projections of decreasing NPP through time (with increasing NPP through time).

[8]Data presented in Thomas (in press).

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