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ORIGINAL ARTICLE

Packrat middens and the Holocene palaeohistory of Colorado piñon (*Pinus edulis*) in western Colorado

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ABSTRACT

Aim Our aim was to determine the age and dispersal history of Colorado piñon (*Pinus edulis*) in western Colorado during the early to late Holocene using radiocarbon-dated needles and nutshells from packrat (*Neotoma* spp.) middens.

Location The Uncompahgre Plateau (UP) comprises more than 600,000 ha of public and private lands in west-central Colorado, USA. Elevations within UP range from 1400 to 3140 m and it is characterized by numerous deep canyons and flat-topped mesas. The Upper Gunnison Basin (UGB) encompasses a 243,000-ha area enclosed within the southern Rocky Mountains in south-western Colorado, USA. It spans 2200–4300 m in elevation, with no outlet apart from the Black Canyon of the Gunnison lower than 2650 m.

Methods Middens were sampled by breaking off small sections of solidified deposits located in caves and crevices that were then disaggregated in water with repeated rinsing to separate all the plant remains. Single conifer needles and nutshells from 28 middens were radiocarbon dated to determine the age and timing of dispersal into western Colorado.

Results Thirty-two midden samples were collected, of which 28 produced identifiable plant remains that were radiocarbon dated. Piñon needles and/or nutshells were identified and radiocarbon dated from 20 of these middens from seven localities in UP. The results indicated that piñon did not become established in UP until *c.* 6000 yr BP, which contrasts with the nearby UGB, where piñon charcoal has been identified from seven archaeological sites with dates ranging from 8000 to 3000 yr BP.

Main conclusions Our data are consistent with a model of late Pleistocene/early Holocene piñon migration into the Colorado Plateau from Arizona and New Mexico before becoming established in western Colorado. The timing of the piñon migration into south-central Colorado along the Rio Grande corridor from New Mexico remains uncertain. While piñon–juniper woodlands currently dominate the lower elevations of UP, piñon had disappeared from UGB by *c.* 3000 yr BP and remains absent there today except for a few isolated trees.

Keywords

Biogeographical reconstruction, climatic impacts, dispersal, Holocene vegetation history, migration history, piñon–juniper woodlands, radiocarbon dating, Uncompahgre Plateau, Upper Gunnison Basin.

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INTRODUCTION

Piñon–juniper woodlands are widespread in the American Southwest, covering approximately 24 million ha; they have been an important economic resource prehistorically, and still are (Floyd, 2003). The Colorado piñon pine (*Pinus edulis* Engelm.), hereafter referred to as piñon, is currently found throughout New Mexico, north-eastern Arizona and the Colorado Plateau through Utah and western Colorado (Fig. 1). The current distribution of this species probably originated from populations to the south and east in New Mexico, Arizona and Texas that migrated northwards during the early Holocene, not reaching the extreme limits of its current range to the north and east until the late Holocene (Betancourt *et al.*, 1991; Lanner & Van Devender, 1998; Anderson & Feiler, 2009). In western Colorado, piñon–juniper woodland comprises 40% of the vegetation landcover of the *c.* 600,000-ha Uncompahgre Plateau (UP), where piñon co-dominates with Utah juniper [*Juniperus osteosperma* (Torr.) Little] at elevations between 1830 and 2440 m.

Packrat (*Neotoma* spp.) middens are an excellent palaeoecological tool for investigating the past distributions of plant communities, including piñon–juniper woodland, in the American Southwest. These middens often contain abundant plant remains (leaves, needles, sticks, seeds and pollen) that have been preserved intact for thousands of years in the dry, arid climate, especially when deposited in caves and crevices (Betancourt *et al.*, 1990). The bushy-tailed packrat, *Neotoma cinerea* (Ord, 1815), is one of several packrat species to use and nest regularly within caves and cliffs; it also has the greatest distribution and elevational range of all *Neotoma* species (Vaughan, 1990). It is the only species found in the Upper Gunnison Basin (UGB) of Colorado today, although two other species, *Neotoma albigula* Hartley, 1894 and *Neotoma mexicana* Baird, 1855, also occur in UP (Armstrong *et al.*, 2011). As packrats tend to collect vegetation, bones and other objects from within *c.* 50 m of their nest sites (Vaughan, 1990), their middens provide a record of local vegetation through time. Packrat middens that are more than 50,000 years old have been documented (Webb & Betancourt, 1990). Moreover, previous studies on packrat middens from western North America have demonstrated their value in explaining a 1000-m elevational shift in juniper in Death Valley, California (Smith *et al.*, 2009), during the Pleistocene and early Holocene, and the presence of an extra-limital population of piñon in northern Colorado that became established there in the late Holocene (Betancourt *et al.*, 1991).

To understand better the past history and distribution of piñon–juniper woodlands in UP, in 2004 the Bureau of Land Management (BLM; Montrose, Colorado, USA) supported

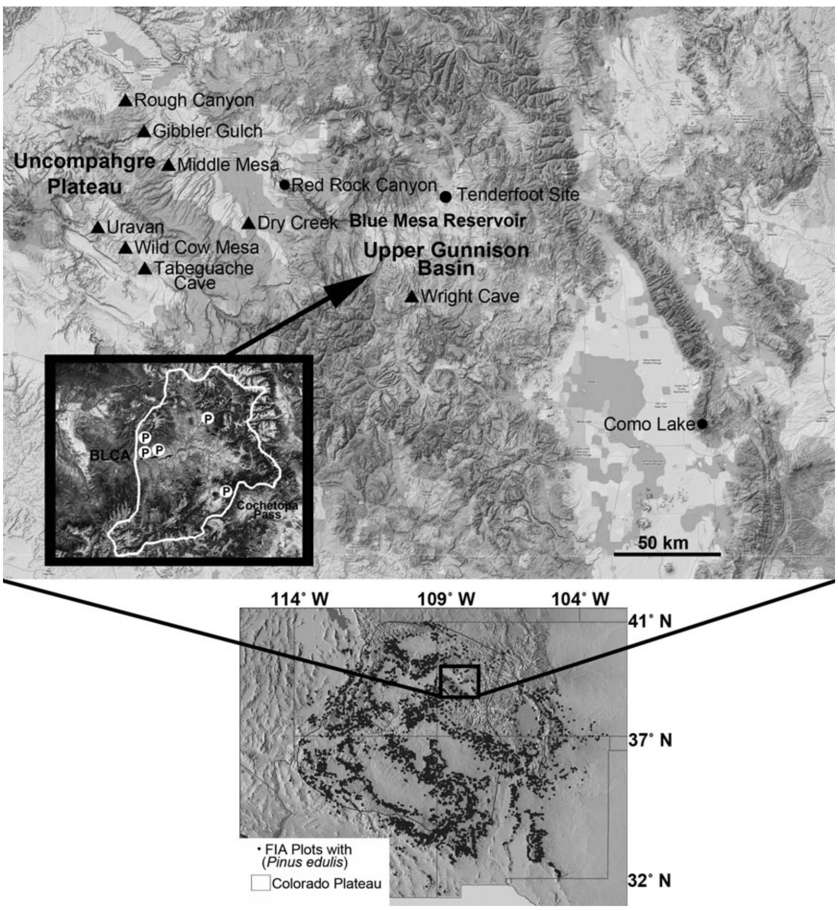

Figure 1 A map of the packrat (*Neotoma* spp.) midden sites (triangles) on the Uncompahgre Plateau and Upper Gunnison Basin (UGB), Colorado, USA. The inset shows the boundary of UGB (white line) and the location of isolated trees or small stands of piñon (P; *Pinus edulis*) extant in the basin today (BLCA, Black Canyon of the Gunnison). The boundary of the Colorado Plateau in the four-corners region (Utah, Colorado, New Mexico and Arizona) is shown on the lower map (dark line) with the current distribution of piñon in this region, including Forest Inventory and Analysis data (FIA; produced by the US Geological Survey and the US Department of Agriculture, available at http://perceval.bio.nau.edu/MPCER_OLD/pjwin/pjmaps.htm).

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an investigation of ancient packrat middens for evidence of the age and distribution of piñon–juniper woodlands in the region. This research supplemented previous work on packrat middens from UGB, south-central Colorado (Emslie *et al.*, 2005), from where archaeological evidence suggests that piñon may have been present from 8000 to 3000 yr BP (Stiger, 2001), even though it is essentially absent today. For the current study, 29 packrat midden samples from UP were collected and analysed, along with three additional samples from UGB, to help reconstruct past forested ecosystems in western Colorado.

Study area

UP is a large, uplifted region, described as a mountain range (Marshall, 2006) or domed upland (UP Partners, 2003), that comprises more than 600,000 ha of public and private lands in west-central Colorado (Fig. 1). It is bordered by the Dolores and San Miguel rivers to the west and south, and the Gunnison and Uncompahgre rivers to the north-east and east. Elevations on the plateau range from 1400 to 3140 m and the plateau is characterized by numerous deep canyons and flat-topped mesas. It is within these canyons that the dry climate has preserved packrat middens within crevices, rock shelters and shallow caves, for hundreds to thousands of years. The current vegetation on the plateau is dominated by piñon–juniper woodland, sagebrush (*Artemisia* spp.), riparian vegetation in canyon bottoms, and aspen (*Populus tremuloides* Michx.), ponderosa pine (*Pinus ponderosa* ex. C. Lawson) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) at higher elevations.

UGB encompasses 243,000 ha enclosed completely within the southern Rocky Mountains in south-western Colorado. The northern Colorado and Uncompahgre plateaus border the basin to the west, while mountain parks and the upper drainages of the Rio Grande are located to the east and south-east (Fig. 1). UGB spans 2200–4300 m in elevation, with no outlet lower than 2650 m, except through the narrow gorge of the Black Canyon of the Gunnison (BLCA) to the west. This canyon, which includes a 20-km section that is more than 700 m deep and only 400 m wide at its narrowest point, may act as a filter or complicate the movement of species in and out of the basin (Armstrong *et al.*, 2011). This geographical isolation of UGB helps explain its unique floral assemblage, including the absence of some species that should occur there but do not [e.g. piñon, ash (*Fraxinus* spp.) and groundcherry (*Physalis* spp.); Barrell, 1969; Stiger, 2001; Emslie *et al.*, 2005]. Historical records indicate that the interior basin habitats have remained relatively unchanged and undisturbed since the area was first explored and surveyed by the US government in 1853 (Beckwith, 1854). Plant communities in UGB are dominated by sagebrush at lower elevations, with Utah juniper, Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* Douglas), aspen and ponderosa pine at higher elevations. Subalpine forests are dominated by Engelmann spruce, with alpine vegetation above 4200 m (Barrell, 1969). As already noted, piñon does not currently occur within UGB (Barrell, 1969; Stiger, 2001), except for a few isolated trees and small stands (Emslie *et al.*, 2005), but it is present within the extensive piñon–juniper woodlands located on the rim of BLCA.

MATERIALS AND METHODS

The surveys for packrat middens in the UP and UGB regions were concentrated along exposed cliffs with dry caves and crevices where long-term preservation was most likely. We also investigated sites reported by the BLM and US Forest Service (USFS; Gunnison, Colorado, USA). UP in particular is vast and, while we made a concerted effort to sample within all quadrants of the region, there were geographical gaps in the sampling that could not be rectified.

Solidified middens were sampled by first cleaning the exposed surface and then removing a small (*c.* 1-kg) interior portion with a rock hammer and chisel; GPS positions were recorded to within a *c.* 10-m radius. Most of the 32 midden samples collected were from 12 sites at seven major localities in UP (Fig. 1); one site at one location in UGB was also sampled (Table 1). The locations and samples are described in Appendix S1.

After collection, all midden samples were transported to the University of North Carolina Wilmington (UNCW, Wilmington, NC, USA), where they were processed in the laboratory. Each midden was disaggregated in plain tap water until all the plant remains were freed from the matrix. The water was then strained out of the remaining mixture using a #20 (0.84-mm) mesh. This mixture was then dried and sorted to recover all plant remains. Macrofossil remains (needles, leaves and seeds) were identified from 28 of the 32 middens by comparison with modern specimens using the collections at the University of Utah Records of Environment and Disturbance (RED) laboratory (Salt Lake City, UT, USA). Selected specimens of conifer needles and nutshells, and non-conifer seeds and other plant parts, especially from extra-limital species, from 28 of the 32 midden samples were submitted for radiocarbon analysis to Beta Analytic Inc. (Miami, FL, USA), the University of Georgia Center for Applied Isotope Studies (Athens, GA, USA) and the University of California Irvine Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory (Livermore, CA, USA) (Table 1). A total of 41 radiocarbon dates was completed, of which 20 were from piñon from 20 midden samples, 18 were from other conifer species, and three were from non-conifer species. All dates were corrected for isotopic fractionation of $\delta^{13}C$ and are reported here in radiocarbon years before present (yr BP).

RESULTS

Twenty-eight of the 32 midden samples produced identifiable plant remains, from which eight species of conifers were

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Table 1 Packrat (*Neotoma* spp.) midden localities in the Uncompahgre Plateau and Upper Gunnison Basin regions, Colorado, USA, sampled during 2004–2008, with the names and acronyms of major localities, site numbers, midden sample numbers, sampling dates and GPS locations, and identification of radiocarbon samples by weight, laboratory number and ^{13}C-corrected ^{14}C age ± standard deviation. All dates are from the University of California Irvine Keck Carbon Cycle Accelerator Mass Spectrometry Facility, except those from the University of Georgia Center for Applied Isotope Studies (R), and Beta Analytic Inc. (Beta), as indicated.

Major localities, site numbers and acronyms	Sample no.	GPS location	Elevation (m)	Sampling date	Sample description	Weight (g)	Lab. no.	Corrected ^{14}C age (yr BP)
Uncompahgre Plateau								
Rough Canyon 1 (RC 1)	S1	38°58′19.8″ N, 108°36′24.6″ W	1740	4 August 2004	*Pinus edulis* needle	0.024	Beta 206434	340 ± 40
	S3			4 August 2004	*Pinus ponderosa* needle	0.038	Beta 206435	6300 ± 40
	S3			4 August 2004	*Pinus edulis* needle	0.0027	R 01309	6035 ± 50
	S3			4 August 2004	*Pinus flexilis* needle	0.0021	R 01310	12443 ± 79
	S3			4 August 2004	*Pseudotsuga menziesii* needle	0.0019	R 01311	12076 ± 68
RC 1, Unit 1 (U1)	S4			2 August 2005	*Pinus edulis* needle	0.0085	R 01314	5805 ± 53
	S5			2 August 2005	*Pinus edulis* needle	0.0094	R 01313	5828 ± 49
RC 1, Unit 2 (U2)	S6			2 August 2005	*Pinus edulis* needle	0.0118	R 01312	5177 ± 47
Gibbler Gulch 2 (GG 2)	S2	38°48′35.1″ N, 108°30′48.5″ W	2020	4 August 2004	*Pinus flexilis* needle	0.021	Beta 206433	12440 ± 40
	S3			2 August 2005	*Pinus edulis* needle	0.0231	R 01305	1875 ± 42
	S4			2 August 2005	*Picea engelmannii* needle	0.0075	R 01306	12234 ± 64
	S4			2 August 2005	*Pinus flexilis* needle	0.0160	01307	12001 ± 63
	S4			2 August 2005	*Pseudotsuga menziesii* needle	0.0059	R 01308	10373 ± 60
	S5			2 August 2005	*Pinus flexilis* needle	0.0149	R 01303	12059 ± 61
	S5			2 August 2005	*Celtis reticulata* seed	0.0406	R 01304	8716 ± 80
Gibbler Gulch 3 (GG 3)	S1	38°49′20.4″ N, 108°29′33.1″ W	1970	2 August 2005	*Pinus edulis* needle	0.0050	R 01302	682 ± 44
Dry Creek 1 (DC 1)	S1	38°29′06.1″ N, 108°03′22.4″ W	1830	2 August 2005	*Pinus edulis* needle	0.0108	R 01318	5840 ± 51
	S2			2 August 2005	*Pinus edulis* needle	0.0121	R 01315	4559 ± 49
Dry Creek 2 (DC 2)	S1	38°30′53.3″ N, 108°03′17.9″ W	1840	2 August 2005	*Yucca* sp. leaf tip	0.0265	R 01316	3475 ± 51
	S2			2 August 2005	*Pinus edulis* needle	0.0144	R 01317	1570 ± 42
Middle Mesa Site 1 (MM 1)	S1	38°44′10.4″ N, 108°28′57.8″ W	2390	31 July 2006	*Pinus edulis* needle	0.0138	35114	4090 ± 25
Middle Mesa Site 2 (MM 2)	S1	38°44′07.7″ N, 108°27′55.6″ W	2290	31 July 2006	*Pinus edulis* needle	0.0031	35116	5450 ± 25
	S2				*Pinus edulis* needle	0.0291	35115	6005 ± 25
Wild Cow Mesa Site 1 (WCM 1)	S1	38°23′02.74″ N, 108°38′5.21″ W	1790	5 August 2007	*Pinus edulis* needle	0.0136	44732	4465 ± 20
Uravan Site 1 (UR 1)	S1	38°24′03.6″ N, 108°44′30.7″ W	1575	2 August 2006	*Pinus edulis* needle	0.0074	35104	5740 ± 25
	S2			2 August 2006	*Pseudotsuga menziesii* needle	0.0035	35106	9915 ± 45
	S2			2 August 2006	*Pinus* needle, indeterminate	0.0006	35107	9950 ± 45
	S3			2 August 2006	*Pinus edulis* nutshell	0.0654	35105	2495 ± 25
UR1 resample	S2R			6 August 2008	*Pinus edulis* needle	0.0102	56850	2265 ± 20
	S2R			6 August 2008	*Juniperus communis* needle	0.0024	56851	9695 ± 30
Uravan Site 3 (UR 3)	S3A	38°24′02.4″ N, 108°44′31.9″ W	1585	6 August 2008	*Pinus edulis* needle	0.0182	56852	1765 ± 15
	S3B			6 August 2008	*Pinus edulis* needle	0.0035	56853	6410 ± 20
	S3B			6 August 2008	*Juniperus scopulorum* twig	0.0275	56854	6140 ± 20
Tabequache Cave II (TCII)	S1	38°22′30.39″ N, 108°26′41.66″ W	2200	9 August 2007	*Pinus edulis* needle	0.0108	44733	1220 ± 20
	S1				*Picea engelmannii* needle	0.0050	44735	1515 ± 20

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Table 1 Continued

Major localities, site numbers and acronyms	Sample no.	GPS location	Elevation (m)	Sampling date	Sample description	Weight (g)	Lab. no.	Corrected ^{14}C age (yr BP)
Upper Gunnison Basin								
Wright Cave (WC)	S1	38°5′28.98″ N, 107°1′34.63″ W	2865	30 July 2006	*Pinus contorta* needle	0.0218	35108	4940 ± 25
	S1			30 July 2006	*Pinus ponderosa* fascicle	0.0212	35109	4935 ± 25
	S1			30 July 2006	*Picea engelmannii* needle	0.0029	35110	4935 ± 30
	S2			30 July 2006	*Pseudotsuga menziesii* needle	0.0048	35111	230 ± 25
	S3	38°5′28.98″ N, 107°1′35.98″ W		30 July 2006	*Pseudotsuga menziesii* needle	0.0028	35112	630 ± 25
	S3			30 July 2006	*Picea engelmannii* needle	0.0034	35113	2895 ± 25

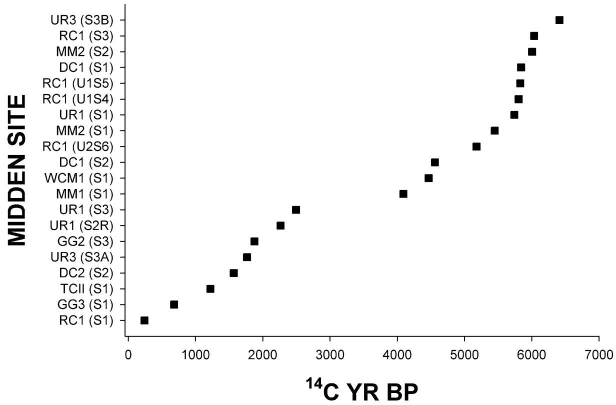

Figure 2 A graph of 20 radiocarbon dates from piñon (*Pinus edulis*) needles and nutshells from packrat (*Neotoma* spp.) middens from the Uncompahgre Plateau, Colorado, USA. Each date has been corrected for the ^{13}C isotopic fractionation and has a standard deviation ranging from 20 to 80 years. For site codes, see Table 1.

identified: *J. scopulorum*, *J. osteosperma*, *Pinus edulis*, limber pine (*Pinus flexilis* E. James), *Pinus ponderosa*, *Pinus contorta*, *Picea engelmannii* and *Pseudotsuga menziesii*; direct radiocarbon dates were obtained from all of these except *J. osteosperma*, which occurred in most UP midden samples and is common across UP today (Table 1). *Pinus flexilis* needles were recovered from GG 2 (S2, S4, and S5) and RC 1 (S3) (Table 1) and the three radiocarbon dates from these needles ranged from 12,000 to 12,440 yr BP (Table 1). Both sites have piñon–juniper woodland surrounding them today. *Pinus contorta* and *Pinus ponderosa* were identified from only one midden sample (WC S1) in UGB. Piñon needles and/or nutshells were identified and radiocarbon dated from 20 midden samples from all seven localities in UP (Table 1); no evidence for piñon was found in the midden from UGB. Six of the oldest piñon dates clustered around 5740–6035 yr BP, with one slightly older date of 6410 yr BP (Fig. 2).

Other trees and shrubs identified from the UP middens included Rocky Mountain maple (*Acer glabrum* Torr.), common juniper (*Juniperus communis* L.), netleaf hackberry (*Celtis reticulata* Torr.), single-leaf ash (*Fraxinus anomala* Torr. Ex. S. Wats.), four-winged saltbush (*Atriplex canescens* (Pursh) Nutt.) and skunkbrush (*Rhus trilobata* Nutt.) (see Appendix S2 for a complete list of the plant macrofossils identified from all the middens). Of these taxa, only netleaf hackberry and common juniper were directly radiocarbon dated, the former to 8716 ± 80 yr BP (from GG 2) and the latter to 9695 ± 30 yr BP (from UR 1) (Table 1). Netleaf hackberry is found on dry hillsides or ravines with sandy soils, similar to the environment at GG 2 today, but is currently extra-limital from the site by around 40 km (Little, 1976).

DISCUSSION

The presence of *Pinus flexilis* at two sites from UP in the late Pleistocene reflects the late glacial conditions that

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characterized south-western palaeoenvironments at that time (Van Devender & Spaulding, 1979). Limber pine needles are common components of Pleistocene middens across the Colorado Plateau, but these are the first records of this conifer from UP. It retracted from its broad distribution across the Colorado Plateau after *c.* 12,000 yr BP and currently occurs at elevations of 1500–3350 m in Colorado, Utah and the northern Rocky Mountains (Little, 1971; Carter, 1988). Warming trends in the early Holocene eventually resulted in the mixed conifer forests that dominate the higher elevations of UP today, with Engelmann spruce and fir occurring above 2440 m, ponderosa pine and Gambel oak (*Quercus gambelii* Nutt.) above 2300 m and piñon–juniper woodland at *c.* 1830–2440 m (UP Partners, 2003). Radiocarbon dates of piñon from middens at the south and north ends of UP indicate that this species was well established across the plateau by *c.* 6000 yr BP. In contrast, midden samples that pre-dated the appearance of piñon (at RC 1, GG 2 and UR 1) all had species that currently occur at higher elevations and in cooler, moister climates than found in the vicinity of those sites today, including Engelmann spruce, limber pine and common juniper. Common juniper presently occurs at elevations ranging from 1500 to 2300 m in Colorado (Carter, 1988) but is now extra-limital from UR 1 by at least 95 km (Little, 1976).

Holocene palaeohistory of piñon in Colorado

The apparent establishment of piñon on UP by *c.* 6000 yr BP is consistent with a model of late Pleistocene/early Holocene migration from northern and central Arizona and southern New Mexican glacial refugia (Cole *et al.*, 2013). It was present in the Verde Valley and western Grand Canyon near the end of the Last Glacial Maximum, *c.* 16,000 yr BP, and had migrated to Navajo Mountain on the Arizona/Utah border and into Chaco Canyon (New Mexico) by *c.* 8000 yr BP (Fig. 3; Betancourt, 1990; Cole *et al.*, 2013). Over the next 2000 years, piñon became established in south-east Utah (McVickar, 1991), Colorado National Monument (Cole *et al.*, 2013) and UP. Piñon continued to expand across the northern Colorado Plateau, and reached most of its current distribution between 4000 and 2000 yr BP (Betancourt, 1990; Sharpe, 1991; Cole *et al.*, 1997; Coats *et al.*, 2008; Madsen *et al.*, 2009), although it only reached its most northern and eastern locales during the past 1000 to a few hundred years (Betancourt *et al.*, 1991; Jackson *et al.*, 2005; Anderson & Feiler, 2009).

Unlike UP, the history of piñon in UGB is more complex. Isolated trees and small stands of piñon are so far known from five disparate locations in UGB today, but they probably represent recent incursions rather than relict populations

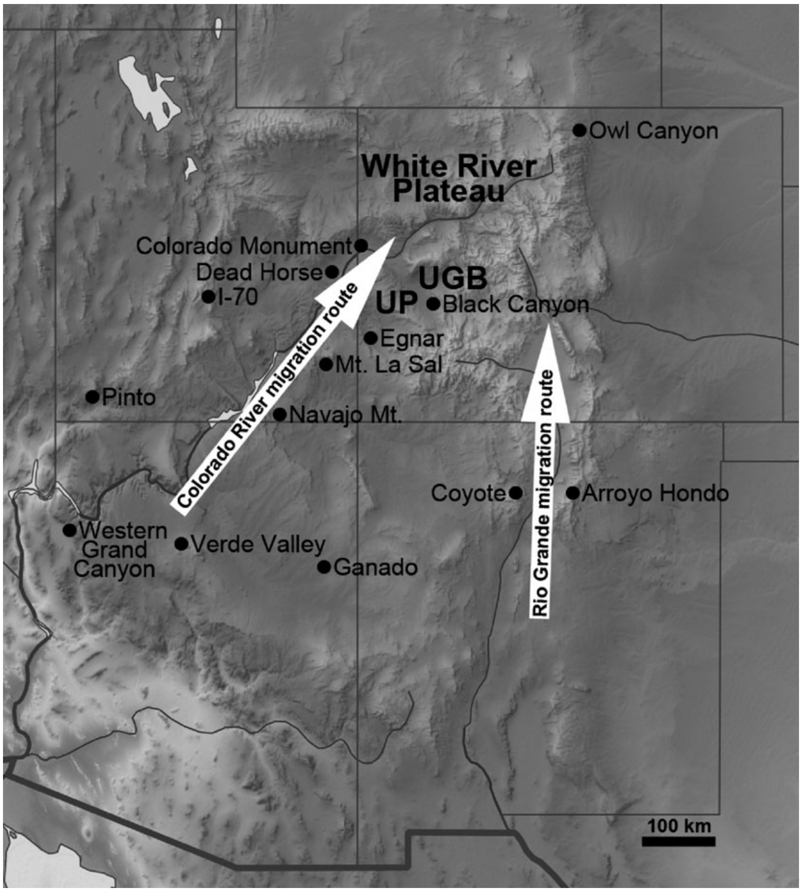

Figure 3 A map of the Colorado Plateau, USA (top), depicting the hypothesized migration routes of piñon populations from Pleistocene refugia in Texas, southern New Mexico and south-central Arizona (Lanner & Van Devender, 1998). UP, Uncompahgre Plateau; UGB, Upper Gunnison Basin.

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(Fig. 1). As noted above, piñon is present along and just below the rim of BLCA, and unpublished data from packrat middens collected in the southern tributary Red Rock Canyon (Fig. 1) reveal abundant piñon needles in middens dating between 4000 and 5100 yr BP (J.I. Mead, East Tennessee State University, Johnson City, TN, USA, pers. comm.), suggesting that piñon arrived at BLCA around the same time as it appeared at UP. Archaeological investigations suggest that piñon was present and common enough for use as firewood in Archaic hearths at Tenderfoot Site (Fig. 1), as well as from six other Archaic sites in UGB, from *c.* 8000 to 3000 yr BP based on archaeological charcoal (Stiger, 2001; M. Stiger, Western State Colorado University, Gunnison, CO, USA, pers. comm.). Identification of the piñon charcoal, easily distinguished from other *Pinus* species by its distinct resin duct morphology (Minnis, 1987), was confirmed by six independent analysts using identification manuals and charred comparative material (Stiger, 2001; M. Stiger, pers. comm.). Moreover, Markgraf & Scott (1981) found pollen evidence for a downwards expansion of pine forests in the basin from 10,000 to 4000 yr BP, with a spike in piñon pollen shortly before 4000 yr BP, further verifying the presence of this species in UGB during the Holocene. In contrast to these data, an earlier analysis of 17 packrat middens from UGB, ranging in age from 3450 to 160 yr BP, lacked any evidence of piñon (Emslie *et al.*, 2005), as did one midden sample (WC S1) collected for this study dating to 4935 yr BP (Table 1). This sample, however, was taken at an elevation above that of most piñon today (2845 m) and included needles of three other pine species with which piñon is not usually associated. The conclusion from all these data is that piñon had entered UGB by 8000 yr BP and was locally extirpated sometime between 4000 and 3000 yr BP. Older middens at lower elevations in UGB are needed to provide a higher resolution for the timing for these arrival and extirpation events.

Other early evidence for piñon in Colorado includes pollen in lake sediment collected from Como Lake in the Sangre de Cristo Range, south-east of UGB and adjacent to the Rio Grande River stretch of the San Luis Valley (Shafer, 1989; Fig. 1). Piñon pollen had appeared in the sediment core by 9500 yr BP, with its highest abundance being in sediments deposited between 7000 and 3500 yr BP. Piñon pollen, however, may be an unreliable indicator of the nearby presence of piñon trees, because Madsen *et al.* (2009) have reported small percentages of piñon pollen from sediment cores collected from Grizzly Lake on the White River Plateau in central Colorado throughout the entire 11,990 cal. yr BP record, and no other evidence exists for piñon this early further north than central New Mexico and Arizona. Thus, at least in this case, it is likely that the pollen was deposited over long distances far removed from where the species actually occurred.

Piñon migration routes into Colorado

The early appearance and subsequent disappearance of piñon in UGB is difficult to explain. Post-glacial piñon migration from southern refugia has been proposed as simultaneously occurring along the Colorado and Rio Grande River corridors (Lanner & Van Devender, 1998). Unfortunately, while data from packrat middens along the Colorado River route are robust, the midden data from the Rio Grande River corridor in New Mexico are poor, with middens too young to record the critical middle Holocene expansion. A study by Spaulding (1992) in Sandia Canyon near Los Alamos located middens no older than 2500 yr BP, although the two oldest middens, SCa-3 and SCa-5(1), were dominated by piñon macrofossils, and a single midden collected from Frijoles Canyon in Bandelier National Monument dating to 3195 $\pm$ 85 yr BP also contained abundant piñon remains (Betancourt & Turner, 1988). Until a collection of middens is made along the Rio Grande corridor that date to the early to mid-Holocene, the migration history here will remain obscure.

It is possible that piñon was able to migrate more quickly up the Rio Grande drainage into central-eastern Colorado (Fig. 3), and then into UGB, than it was along the Colorado River into Utah and western Colorado. It is notable that small piñon stands occur at the west and east entrances to the basin (the west end of the Blue Mesa Reservoir and just below North Pass, respectively; Fig. 1) that could reflect ancient routes for piñon migration into UGB. These routes could also have been accessed via animal dispersion, such as via pinyon jays (*Gymnorhinus cyanocephalus*) and Clark's nutcrackers (*Nucifraga columbiana*), which carry and cache piñon nuts over large areas (Vander Wall & Balda, 1977; Betancourt *et al.*, 1991). Possible reasons for the difference in migration rates require additional investigation, and may relate to differences in land form and soil characteristics suitable for piñon growth. This species requires dry, rocky slopes and mesa tops with moisture of 200–400 mm year^{-1}, and most piñon–juniper woodlands in Colorado occur at an elevational range of 1680–2440 m (Armstrong *et al.*, 2011). Although the high elevation barrier that divides UGB from the Rio Grande corridor (North and Cochetopa passes, *c.* 3100 m elevation; Fig. 1) could limit access to the basin, piñon is known to occur up to 3200 m in the San Francisco Mountains (northern Arizona), perhaps assisted by avian dispersal (Vander Wall & Balda, 1977).

Molecular studies on ancient and modern piñon needles in the American Southwest have revealed the presence of four haplotypes in Utah and western Colorado today that may be derived from ancestral populations from Arizona as well as southern New Mexico and Texas (Duran *et al.*, 2012). Limited genetic analysis indicates that two south-western Colorado populations of piñon (Egnar and Black Canyon) share a common chloroplast haplotype with New Mexican populations, for instance the Arroyo Hondo and Coyote populations (Fig. 3; Duran *et al.*, 2012). However, the genetic data alone do not solve this migration question, as one population in far south-western Utah (Pinto) also shares this haplotype (Duran *et al.*, 2012). Without additional genetic data, tracing the migration route of piñon with these haplotypes remains uncertain. Finally, even if an early migration of piñon into

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UGB did occur, the question remains why only isolated trees survive there today, while all nearby populations apparently recovered from mid- to late Holocene climate events. Additional genetic analyses are warranted to address the ancestry of fossil and modern piñon populations in UP and UGB. Establishing the haplotypes of isolated piñon trees and stands now present in UGB may also help reveal the migration routes into UGB, past and present.

CONCLUSIONS

Packrat middens have proven to be a powerful tool in the reconstruction of the biogeographical history of a variety of important species across the American West (Lyford *et al.*, 2003). Macrofossils of junipers and pines are so commonly collected by packrats that the presence or absence of these species in middens from particular time periods and geographical regions are the best tools that can be used to infer the migration history and climatic impacts on these prevalent species. The late glacial distribution of Colorado piñon is known to be well south of its modern distribution, across western Texas and central New Mexico, in the western Grand Canyon and along the Mogollon Rim in Arizona (Phillips, 1977; Van Devender & Spaulding, 1979; Van Devender, 1986; Cinnamon & Hevly, 1988; Pendall *et al.*, 1999; Betancourt *et al.*, 2001).

Although the arrival of piñon at its most northern and eastern modern distributions is known to have occurred only in the past 1000 years (Betancourt *et al.*, 1991; Cole *et al.*, 1997, 2013; Jackson *et al.*, 2005; Gray *et al.*, 2006), the pattern of migration across the Colorado Plateau to reach its modern distribution is still not well understood. The data presented here regarding UP and UGB have added important insights into the intermediate stages of the northwards migration of piñon since the early Holocene. We believe that our data indicate piñon expanded its range during the Holocene by following a path along the Colorado River drainage, moving from the south-west to the north-west, and reaching UP by the mid-Holocene. However, the history of piñon migration along the Rio Grande River drainage remains elusive, with no midden data available that support a hypothesis of rapid migration into Colorado and UGB, countering the pollen and charcoal data that suggest otherwise. A worthwhile contribution to piñon migration history could be made with a focused effort to collect late Pleistocene and Holocene middens along the northern Rio Grande River corridor.

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REFERENCES

Anderson, R.S. & Feiler, E. (2009) Holocene vegetation and climate change on the Colorado Great Plains, USA, and the invasion of Colorado piñon (*Pinus edulis*). *Journal of Biogeography*, **36**, 2279–2289.

Armstrong, D.M., Fitzgerald, J.P. & Meaney, C.A. (2011) *Mammals of Colorado*. University Press of Colorado, Boulder, CO.

Barrell, J. (1969) *Flora of the Gunnison Basin*. Natural Land Institute, Rockford, IL.

Beckwith, E.G. (1854) *Report of explorations for a route for the Pacific railroad*. Report to War Department, US Government, Washington, DC.

Betancourt, J.L. (1990) Late Quaternary biogeography of the Colorado Plateau. *Packrat middens: the last 40,000 years of biotic change* (ed. by J.L. Betancourt, T.R. Van Devender and P.S. Martin), pp. 259–292. University of Arizona Press, Tucson, AZ.

Betancourt, J.L. & Turner, R.M. (1988) *Potential for packrat midden studies in the area of Bandelier National Monument*. Unpublished report. Bandelier National Monument, Los Alamos, NM.

Betancourt, J.L., Van Devender, T.R. & Martin, P.S. (1990) *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson, AZ.

Betancourt, J.L., Schuster, W.S., Mitton, J.B. & Anderson, R.S. (1991) Fossil and genetic history of a pinyon pine (*Pinus edulis*) isolate. *Ecology*, **72**, 1685–1697.

Betancourt, J.L., Rylander, K.A., Peñalba, C. & McVickar, J.L. (2001) Late Quaternary vegetation history of Rough Canyon, south-central New Mexico, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **165**, 71–95.

Carter, J.L. (1988) *Trees and shrubs of Colorado*. Johnson Books, Boulder, CO.

Cinnamon, S.K. & Hevly, R.H. (1988) Late Wisconsin macroscopic remains of pinyon pine on the southern Colorado Plateau, Arizona. *Current Research in the Pleistocene*, **5**, 47–48.

Coats, L., Cole, K.L. & Mead, J.I. (2008) 50,000 years of vegetation and climate history on the Colorado Plateau, Utah and Arizona, USA. *Quaternary Research*, **70**, 322–338.

Cole, K.L., Henderson, N. & Shafer, D.S. (1997) Holocene vegetation and historic grazing impacts at Capitol Reef National Park reconstructed using packrat middens. *Great Basin Naturalist*, **57**, 315–326.

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Cole, K.L., Fisher, J.F., Ironside, K., Mead, J.I. & Koehler, P. (2013) The biogeographic histories of *Pinus edulis* and *Pinus monophylla* over the last 50,000 yrs. *Quaternary International*, **310**, 96–110.

Duran, K.L., Pardo, A. & Mitton, J.B. (2012) From middens to molecules: phylogeography of the piñon pine, *Pinus edulis*. *Journal of Biogeography*, **39**, 1536–1544.

Emslie, S.D., Stiger, M. & Wambach, E. (2005) Packrat middens and late Holocene environmental change in southwestern Colorado. *Southwestern Naturalist*, **50**, 209–215.

Floyd, L. (2003) *Ancient piñon–juniper woodlands*. University Press of Colorado, Boulder, CO.

Gray, S.T., Betancourt, J.L., Jackson, S.T. & Eddy, R.G. (2006) Role of multidecadal climate variability in a range expansion of pinyon pine. *Ecology*, **87**, 1124–1130.

Jackson, S.T., Betancourt, J.L., Lyford, M.E., Gray, S.T. & Rylander, K.A. (2005) A 40,000-year woodrat-midden record of vegetational and biogeographical dynamics in north-eastern Utah, USA. *Journal of Biogeography*, **32**, 1085–1106.

Lanner, R.M. & Van Devender, T.R. (1998) The recent history of pinyon pines in the American Southwest. *Ecology and biogeography of pine* (ed. by D.M. Richardson), pp. 171–182. Cambridge University Press, Cambridge, UK.

Little, E.L., Jr (1971) *Atlas of United States trees, Vol. 1, Conifers and important hardwoods*. Miscellaneous Publication 1146, United States Department of Agriculture, Washington, DC.

Little, E.L., Jr (1976) *Atlas of United States trees, Vol. 3, Minor western hardwoods*. Miscellaneous Publication 1314, United States Department of Agriculture, Washington, DC.

Lyford, M.E., Jackson, S.T., Betancourt, J.L. & Gray, S.T. (2003) The influence of landscape structure and climate variability on a late Holocene plant migration. *Ecological Monographs*, **73**, 567–583.

Madsen, D.B., Rhode, D., Louderback, L.A. & Metcalf, M. (2009) *Packrats, pollen, and pine along the El Paso-Piceance pipeline*. Unpublished report submitted to Alpine Archaeology, Montrose, CO.

Markgraf, V. & Scott, L. (1981) Lower timberline in central Colorado during the past 15,000 yr. *Geology*, **9**, 231–234.

Marshall, M. (2006) *Uncompahgre*. Western Reflections Publications Co., Montrose, CO.

McVickar, J. (1991) *Holocene vegetation change at Cowboy Cave, southeastern Utah, and its effect upon human subsistence*. MSc Thesis, Northern Arizona University, Flagstaff, AZ.

Minnis, P.E. (1987) Identification of wood from archaeological sites in the American Southwest. I. Keys for gymnosperms. *Journal of Archaeological Science*, **14**, 121–131.

Pendall, E., Betancourt, J.L. & Leavitt, S.W. (1999) Paleoclimatic significance of δD and δ^{13}C values in pinyon pine needles from packrat middens spanning the last 40,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **147**, 53–72.

Phillips, A.M., III (1977) *Packrats, plants, and the Pleistocene in the lower Grand Canyon*. PhD Thesis, University of Arizona, Tucson, AZ.

Shafer, D. (1989) *The timing of late monsoon precipitation in the southwestern United States*. PhD Thesis, University of Arizona, Tucson, AZ.

Sharpe, S.E. (1991) *Late-Pleistocene and Holocene vegetation change in Arches National Park, Grand County, Utah and Dinosaur National Monument, Moffat County, Colorado*. MSc Thesis, Northern Arizona University, Flagstaff, AZ.

Smith, F.A., Crawford, D.L., Harding, L.E., Lease, H.M., Murray, I.W., Raniszewski, A. & Youberg, K.M. (2009) A tale of two species: extirpation and range expansion during the late Quaternary in an extreme environment. *Global and Planetary Change*, **65**, 122–133.

Spaulding, W.G. (1992) *Late Quaternary paleoclimates and sources of paleoenvironmental data in the vicinity of Los Alamos National Laboratory*. Unpublished report, Bandelier National Monument, Los Alamos, NM.

Stiger, M. (2001) *Hunter-gatherer archaeology of the Colorado high country*. University Press of Colorado, Boulder, CO.

UP Partners (2003) *Uncompahgre Plateau Project (UP) plan*. Available at: http://upartnership.org/ (accessed 22 September 2014).

Van Devender, T.R. (1986) Late Quaternary history of pinyon–juniper–oak woodlands dominated by *Pinus remota* and *Pinus edulis*. *Proceedings of the Pinyon–Juniper Conference, Intermountain Research Station* (ed. by R.L. Everett), pp. 99–103. United States Department of Agriculture, Ogden, UT.

Van Devender, T.R. & Spaulding, W.G. (1979) The development of climate and vegetation in the southwestern United States. *Science*, **204**, 701–710.

Vander Wall, S.B. & Balda, R.P. (1977) Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs*, **47**, 89–111.

Vaughan, T.A. (1990) Ecology of living packrats. *Packrat middens: the last 40,000 years of biotic change* (ed. by J.L. Betancourt, T.R. Van Devender and P.S. Martin), pp. 14–27. University of Arizona Press, Tucson, AZ.

Webb, R.H. & Betancourt, J.L. (1990) The spatial and temporal distribution of radiocarbon ages from packrat middens. *Packrat middens: the last 40,000 years of biotic change* (ed. by J.L. Betancourt, T.R. Van Devender and P.S. Martin), pp. 85–102. University of Arizona Press, Tucson, AZ.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 A description of the sampled Colorado packrat midden sites.

Appendix S2 Plant macrofossil identifications from Colorado packrat middens.

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BIOSKETCHES

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Author contributions: S.E. initiated the project, conducted fieldwork, processed middens, prepared the initial manuscript and completed all revisions; L.C. identified the plant macrofossils, assisted with some fieldwork and contributed extensively to the manuscript; E.O. helped process the midden material and sorted plant material before analysis by L.C.

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