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ORIGINAL ARTICLE

Late Holocene expansion of ponderosa pine (*Pinus ponderosa*) in the Central Rocky Mountains, USA

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ABSTRACT

Aim Ponderosa pine (*Pinus ponderosa*) experienced one of the most extensive and rapid post-glacial plant migrations in western North America. We used plant macrofossils from woodrat (*Neotoma*) middens to reconstruct its spread in the Central Rocky Mountains, identify other vegetation changes coinciding with *P. ponderosa* expansion at the same sites, and relate *P. ponderosa* migrational history to both its modern phylogeography and to a parallel expansion by Utah juniper (*Juniperus osteosperma*).

Location Central Rocky Mountains, Wyoming and Montana, and Black Hills, Wyoming and South Dakota, USA.

Methods Plant macrofossils were analysed in 90 middens collected at 14 widely separated sites in the northern part of the range of *P. ponderosa* var. *scopulorum*. Middens with and without *P. ponderosa* were ^{14}C dated to pinpoint time of appearance at each site. Sensitivity experiments using a bioclimatic model were used to evaluate potential climatic drivers of late Holocene expansion.

Results *Pinus ponderosa* colonized the Black Hills region by at least 3850 yr BP (all ages given in calendar years before present). It expanded into the eastern Bighorn Mountains of northern Wyoming by 2630 yr BP, quickly spreading north in the western Bighorns from 1400 to 1000 yr BP. Concurrent with the latter expansion, *P. ponderosa* spread *c.* 350 km to the Little Belt and Big Belt Mountains in western Montana, establishing its northern limit and the modern introgression zone between var. *scopulorum* and var. *ponderosa*. Expansion in the Central Rockies of *P. ponderosa* involved two known haplotypes.

Main conclusions *Pinus ponderosa* expanded its range across large parts of northern Wyoming and central Montana during the late Holocene, probably in response to both northward and westward increases in summer temperature and rainfall. The underlying climatic driver may be the same as for the contemporaneous expansion of *J. osteosperma*, but will remain undetermined without focused development and integration of independent palaeoclimate records in the region.

Keywords
bioclimatic modelling, haplotype, Holocene, *Juniperus osteosperma*, migration, *Pinus ponderosa* var. *scopulorum*, plant macrofossils, woodrat middens

INTRODUCTION

Global climate change will force many species to adjust their geographical distributions in the near future, with important consequences for biodiversity, conservation biology and ecosystem services (Iverson & McKenzie, 2013). The rates and pathways of migrations will depend on many factors, including ecophysiology, life history, landscape structure, disturbance regimes, genetic and historical legacies and ecological interactions (Lyford *et al.*, 2003; Neilson *et al.*, 2005;

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Jackson & Sax, 2010). Although future climates and species migrations may lack precise analogues in the past (Williams & Jackson, 2007), important lessons can be drawn from the suite of northward migrations that followed the last deglaciation in the Northern Hemisphere. The late Holocene offers opportunities for understanding patterns and mechanisms of migrations because they occurred under climate change with boundary conditions similar to today; high-site densities associated with younger records provide good spatial and temporal coverage; and historical patterns can be linked directly to living populations via genetic, demographic and other ecological studies.

Palaeoecological studies provide informative details of tree migrational responses to changing climates during the past 4000 years. Notable examples include beech (*Fagus sylvatica*) and spruce (*Picea abies*) in southern Sweden (Björkman & Bradshaw, 1996), tamarack (*Larix laricina*) in north-western Québec (Peñalba & Payette, 1997), yellow birch (*Betula alleghaniensis*) (Jackson & Booth, 2002; Booth *et al.*, 2004), beech (*Fagus grandifolia*) (Woods & Davis, 1989; Reeves, 2006) and hemlock (*Tsuga canadensis*) (Davis, 1987; Davis *et al.*, 1998; Parshall, 2002) in the western Great Lakes, Utah juniper (*Juniperus osteosperma*) and Colorado pinyon (*Pinus edulis*) in the central Rocky Mountains (Lyford *et al.*, 2003; Jackson *et al.*, 2005; Gray *et al.*, 2006), and one-needle pinyon (*Pinus monophylla*) in the north-eastern Great Basin (Weppner *et al.*, 2013). These migrational histories indicate that range expansions frequently proceed episodically, with alternating rapid advances and prolonged pauses that often coincide with climatic changes. In some cases, broad synchrony of advance among species, even across different and widely separated biomes (e.g. Jackson & Booth, 2002; Lyford *et al.*, 2003; Jackson *et al.*, 2009), suggest a common climatic pacemaker. In others, the staggered migrational histories of two or more species in the same region could represent differential responses to multiple climatic events or to different variables (e.g. growing-season length, winter versus summer precipitation) within a directional trend. These different climatic drivers may act on range dynamics both directly through physiology and demography, and indirectly through disturbance, species interactions, and both slow and fast changes in ecosystem rates and properties. Sorting out these differences requires not just detailed migrational histories, but also robust and independent evidence for past climate variability and change that can specify, to the degree possible, shifts in temperature, precipitation, seasonality and variance in both space and time. Such regional 'master chronologies' of seasonal temperature and precipitation reconstructions, more often than not, are lacking even for the late Holocene.

Ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) underwent a post-glacial migration in the western North American interior comparable in magnitude with the well-documented migrations onto formerly glaciated terrain in eastern North America (Davis, 1981; Webb, 1988). This widespread conifer, comprising two morphologically, genetically and climatically well-defined varieties (Conkle & Critchfield, 1988; Norris *et al.*, 2006; Potter *et al.*, 2013, 2015), extends from the western Great Plains to the Pacific coast and from the Mexican border north to the Fraser River Valley in British Columbia (Fig. 1). The interior variety (*P. ponderosa* var. *scopulorum* Engelm.), occurs in the eastern half of the species' range, whereas var. *ponderosa* occurs in the western half (Fig. 1).

Wofford *et al.* (2014) tested for intraspecific variation in chloroplast simple sequence repeat (cpSSRs; microsatellites) loci in the *P. ponderosa* complex, and identified three operational taxonomic units (OTUs) within var. *ponderosa* and two OTUs within var. *scopulorum*. In a mitochondrial minisatellite DNA study of *P. ponderosa* across its geographical range, Potter *et al.* (2013) identified ten haplotypes among 104 populations (Fig. 1), consistent with Johansen & Latta (2003). In a follow-up study, based on highly polymorphic nuclear satellite and isozyme markers in these same populations, Potter *et al.* (2015) found pervasive inbreeding and complex phylogeographical patterns, suggesting that (1) *P. ponderosa* may be in the process of differentiating into distinct regional lineages, (2) the number of unique and rare alleles decreases with latitude, consistent with recent (post-glacial or Holocene) migration and (3) isolated refugia in the core of the modern distribution may have played a role in Holocene migration, as evidenced by exclusive occurrence of some genetic clusters far north of the known glacial refugia in southern Sierra Nevada and southern Arizona/New Mexico.

In contrast to its broad distribution today, there is no fossil evidence of *P. ponderosa* var. *scopulorum* north of 34°N during the Last Glacial Maximum (LGM). Despite extensive glacial-age macrofossil records at low- and mid-elevational sites across the western interior, *P. ponderosa* var. *scopulorum* is absent from all but two sites, respectively, in southern New Mexico and Arizona (Fig. 1). In contrast, many current associates, including Douglas-fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*), were widespread across the region (Betancourt, 1990; Cole, 1990; Jackson *et al.*, 2005). The limited glacial distribution of var. *scopulorum* implies that the Central and Southern Rockies and Colorado Plateau were either too cold or had insufficient growing-season precipitation to support extensive populations (Norris *et al.*, 2006). During the past 13,000 years, var. *scopulorum* has expanded to foothills, low mountains, and scarps of eastern Wyoming, western South Dakota and south-eastern and central Montana, up to 1600 km north of its recorded glacial distribution.

Holocene expansion is recorded at several sites in and near the Colorado Plateau region (Betancourt, 1990; Cole, 1990; Weng & Jackson, 1999; Jackson *et al.*, 2005), but few records exist from suitable elevations along the Rocky Mountain axis and adjacent Great Plains (Fig. 1). Consequently, the Holocene record of var. *scopulorum* in the northern two-thirds of its range consists of only a few, mostly incomplete, records (Fig. 1). At Owl Canyon in northern Colorado, Betancourt *et al.* (1991) found *P. ponderosa* macrofossils in the oldest

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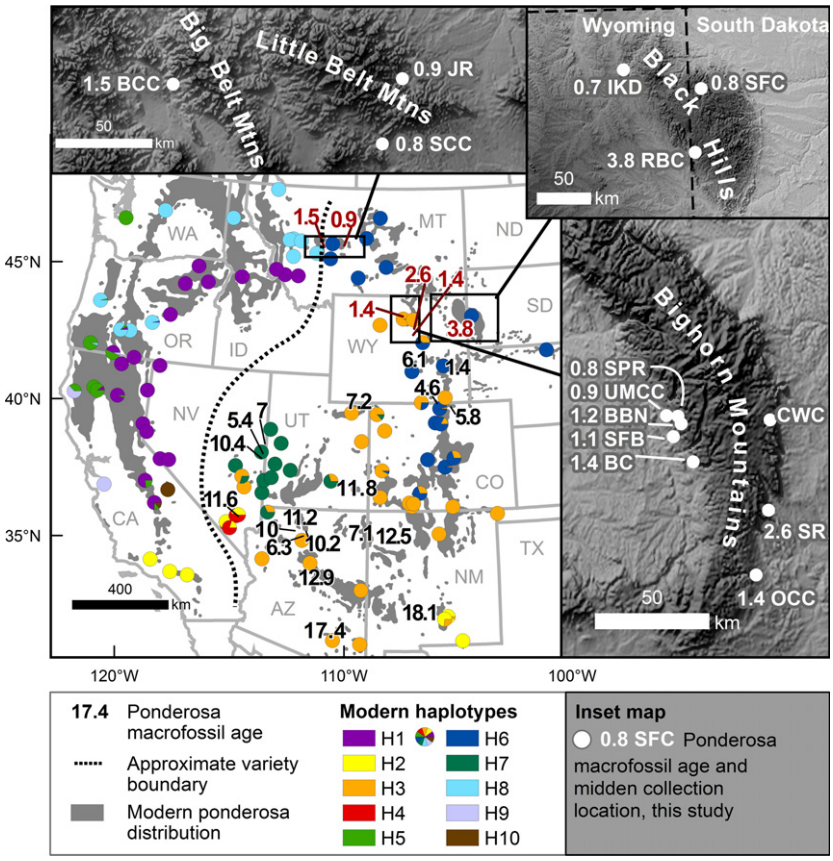

Figure 1 Map distribution of *Pinus ponderosa* (grey shading), location of modern haplotypes from Potter *et al.* (2013), and ages (kiloyear BP) of the earliest *P. ponderosa* macrofossil occurrence at a site during and since the last glacial (within the range of var. *scopulorum*). The state abbreviations include Arizona (AZ), California (CA), Colorado (CO), Idaho (ID), Montana (MT), New Mexico (NM), North Dakota (ND), Nevada (NV), Oregon (OR), Texas (TX), South Dakota (SD), Utah (UT) and Wyoming (WY). Site locations and sources of information are listed in Appendix S1, Table S1.1. The ages in red on the large map, and those in white on the inset maps, are from this study.

dated midden, providing a minimum establishment age of *c.* 5800 yr BP. Establishment is documented *c.* 6100 yr BP at Fremont Canyon in central Wyoming (S.T. Jackson & J.L. Betancourt, unpublished data). In south-eastern Wyoming, two middens provide minimum establishment dates for *P. ponderosa* in the Laramie Basin (4570 yr BP) and the Hartville Uplift (1430 yr BP) (Wells, 1970).

Here, we report on the late Holocene migrational history of *P. ponderosa* var. *scopulorum* in the northern part of its range in Wyoming, South Dakota and Montana. We assessed this history based on plant macrofossil analyses of 90 woodrat (*Neotoma sp.*) middens from 14 sites distributed across the region (Fig. 1). The midden records provide a framework for understanding the spatiotemporal patterns of *P. ponderosa* migration in the region. Although we did not identify genetic variants from macrofossils found in the middens, we used the survey of modern *P. ponderosa* haplotypes in the region (Potter *et al.*, 2013) to compare the timing of Holocene *P. ponderosa* expansion with the current distributions of dominant haplotypes regionally and near each site. Specific goals were to determine (1) whether *P. ponderosa* expansion generally proceeded as a 'front' driven by short-distance dispersal or through long-distance dispersal events followed by 'backfilling' by using our midden records and palaeorecords from other studies, (2) the degree to which our fossil evidence for *P. ponderosa* matches inferences about population history by using phylogeographical information from other studies, and (3) the extent to which *P. ponderosa* migration in the Central Rockies coincided with other biogeographical changes and independent evidence of palaeoclimatic changes. Specifically, we compare detailed migrational histories across the same region for *P. ponderosa* and *J. osteosperma*, which expanded into some of the same sites during the late Holocene despite having a very different climate niche than *P. ponderosa*. We marshalled evidence from our midden records, palaeorecords and models from other studies, and simulations with our own bioclimatic model to test how a specific set of climate changes would impact a modelled distribution of *P. ponderosa*. We use this comparative study to further explore plant migrational dynamics and their climatic triggers in the Central Rockies.

MATERIALS AND METHODS

Pinus ponderosa woodlands occur on rocky scarps and uplands of the Black Hills (WY, SD), Bighorn Mountains (WY), and Little Belt and Big Belt Mountains (MT) (Fig. 1). Sites vary in their elevation (Table 1) and proximity to local upper and lower limits of *P. ponderosa*. A commonality of the sites is that July is the warmest month while May is generally the wettest (see Appendix S1: Fig. 1.1 in Supporting Information).

Pinus ponderosa is dominant at all study sites in the Black Hills, co-occurring with Rocky Mountain juniper

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(*J. scopulorum*) at Redbird Canyon and white spruce (*Picea glauca*) at Spearfish Canyon (Table 1). Redbird Canyon, at the south-west edge of the Black Hills, is drier than higher elevational Black Hills uplands, while the deeply incised Spearfish Canyon includes moister local habitats than most of the Black Hills.

In Montana and north-central Wyoming, low-elevational study sites are occupied by *P. ponderosa –Juniperus* woodlands that occasionally include *P. flexilis*. *Pinus ponderosa* is dominant or co-dominant at all sites. It co-occurs with *J. scopulorum* and *P. flexilis* at low-elevational sites in Montana and the eastern Bighorn Mountains, and with *J. osteosperma* at low sites in the western Bighorns (Table 1, Appendix S1). *Pinus ponderosa* density increases at higher elevations, where it co-occurs with *Pseudotsuga menziesii* and *J. communis*. Scattered shrubs occur at all sites in all regions, particularly skunkbrush sumac (*Rhus trilobata*) and currant-bush (*Ribes* spp.). Curl-leaf mountain mahogany (*Cercocarpus ledifolius*) occurs in the eastern and western Bighorns and Big Belt Mountains.

We documented spatiotemporal patterns of *P. ponderosa* expansion based on 14 woodrat midden series across the northern, modern range of var. *scopulorum* (Fig. 1, Table 1). The bushy-tailed woodrat (*Neotoma cinerea*), the northernmost woodrat species, occurs throughout the region and is likely responsible for assembling all of the middens used in this study. Woodrat middens incorporate plant materials collected from surrounding vegetation and bushy-tailed woodrats show a predisposition to collecting conifers, including *P. ponderosa* (Lyford *et al.*, 2004). Because individual middens are point samples, representing a plant-collecting radius of 10^1–10^2 m, midden series are inefficient at detecting low-density populations, including colonizing populations (Lesser & Jackson, 2011). However, once populations reach density and dispersion sufficient to ensure proximity of trees to most or all midden sites, probability of occurrence in midden assemblages is very high, and thus midden chronologies can yield good records of expansion and infilling (Lyford *et al.*, 2004; Lesser & Jackson, 2011).

We targeted sites where *P. ponderosa* var. *scopulorum* grows today in settings suitable for Holocene midden preservation, primarily bedrock escarpments and cliffs. At each study site, overhangs and crevices were searched for fossil middens, which were extracted, examined and cleaned in the field. Middens were re-inspected and further cleaned in the laboratory before disaggregation in water, sieving (2 mm and 1 mm mesh), and air-drying. All material in the > 2-mm fraction was examined, sorted and identified. The finer fraction was scanned to identify any taxa not observed in the coarse fraction. Abundances of each taxon were assessed on a relative abundance scale of 1–5 (1 = single occurrence; 5 = dominant) (Spaulding *et al.*, 1990). We used accelerator mass spectrometry (AMS) to date 100 macrofossils from 90 middens, using *P. ponderosa* macrofossils (usually needles), whenever they occurred in the middens. In middens, where *P. ponderosa* was absent, macrofossils of other conifers were dated. In a few cases, both *P. ponderosa* and other species from the same midden were dated separately. After pre-treatment, graphite targets were prepared on vacuum lines at the University of Arizona Desert Laboratory and measured by a tandem accelerator mass spectrometer (TAMS) at the University of Arizona Accelerator Facility. Radiocarbon dates were converted to calendar years before present (scale origin 1950 AD) using the IntCal04 curve (Reimer *et al.*, 2004) within the CALIB 5.01 program (Stuiver *et al.*, 2005). Dates are reported as the median of calibrated radiocarbon age ranges and herein referred to as yr BP; radiocarbon dates and calibrated age ranges are reported in Appendix S2, Table S2.1.

Table 1 Summary of midden series location, age range and number of middens.

Site	Map ID	Latitude	Longitude	Elevational range (m)	Age range (yr BP)	No. middens
Big Belt Mountains						
Beaver Creek Canyon	BCC	46.790	−111.878	1146–1280	298–7872	6
Black Hills						
Inyan Kara Drainage	IKD	44.504	−104.757	1213–1268	156–711	2
Spearfish Canyon	SFC	44.229	−103.953	1689–1862	112–753	4
Redbird Canyon	RBC	43.798	−104.010	1457–1545	0–3849	7
East Bighorn Mountains						
Slip Road	SR	43.837	−106.886	1817–2103	1139–5668	8
Outlaw Cave Campground	OCC	43.580	−106.960	1713–2030	180–2781	7
Crazy Woman Canyon	CWC	44.188	−106.847	2070–2075	5642–8497	2
Little Belt Mountains						
Spring Creek Canyon	SCC	46.551	−110.449	1554–1641	430–2220	5
Judith River Sites	JR	46.845	−110.306	1539–1622	385–5826	8
West Bighorn Mountains						
Black Canyon	BC	44.027	−107.286	1835–2006	694–5850	7
Upper Military/Cottonwood Creeks	UMCC	44.202	−107.436	1737–1987	140–3050	11
Brokenback Narrows	BBN	44.173	−107.363	2109–2249	768–2472	7
South Fork Paintrock	SPR	44.199	−107.383	2097–2304	767–3217	6
South Fork Brokenback	SFB	44.127	−107.396	1554–1780	601–10944	9

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Plant macrofossils were identified by comparison with reference collections at the Quaternary Plant Ecology Laboratory and the Rocky Mountain Herbarium at the University of Wyoming. Most identifications were routine, but three differentiations required special attention: First, differentiation of *Pinus flexilis* and whitebark pine (*P. albicaulis*) needles is difficult (Harlow, 1947). Because most of the middens were late Holocene in age and limber pine occurs at many of the sites today, we report all needles deriving from 5-needle fascicles as limber pine. Whitebark pine occurs in our study area only in subalpine forests of the Little Belt and Big Belt Mountains. Second, needles of lodgepole pine (*Pinus contorta*) occur in fascicles of two, like many *P. ponderosa* needles, but are significantly shorter. We differentiated needle fragments based on position of vascular bundles in cross-section (Harlow, 1947). Third, both varieties of *P. ponderosa* occur near the Big Belt Mountains, hybridizing extensively in central Montana (Johansen & Latta, 2003; Latta & Mitton, 1999). Needles of var. *ponderosa* occur almost exclusively in fascicles of three or more, while those of var. *scopulorum* occur in fascicles of both two and three. At our Big Belt site, all middens contained both 3-needle and 2-needle *P. ponderosa* needles, so we assumed all needles were var. *scopulorum*. We cannot exclude the possibility that some represent var. *ponderosa* or hybrids.

We assessed the influence of Holocene climate change on *P. ponderosa* expansion using data and methods from an earlier modelling study (Norris *et al.*, 2006), in which we developed a classification tree model and variety-specific minimum volume ellipsoid (MVE) models to predict and understand the current distribution of *P. ponderosa*. We used the *P. ponderosa* climate spaces for each variety, defined using 1961–1990 climate averages in the MVE models, to test how *P. ponderosa* distribution might have differed in the past under different climatic conditions, and then compared the resulting modelled distributions to our midden record.

To create hypothetical past climate conditions, we focused on variables likely to have changed during deglaciation, those to which *P. ponderosa* var. *scopulorum* is especially sensitive, and on potential middle Holocene solar insolation forcing. Five climate modifications relative to modern conditions were chosen: (1) reduced June precipitation, (2) reduced July precipitation, (3) lowered January temperature, (4) lowered January temperature combined with increased July temperature and (5) lowered July temperature (Table 2). We applied three levels of change to each variable: temperature variables were modified by 1°, 2° and 3°C relative to modern, and precipitation variables were modified by 20%, 40% or 60% relative to modern. These gradations are less than estimated amounts of temperature change modelled for the LGM (e.g. Schmittner *et al.*, 2011), or are reasonable to expect if seasonal moisture sources substantially changed during the Holocene.

RESULTS

Pinus ponderosa macrofossils are continuously present after their earliest occurrence in all midden records except one. These temporal patterns indicate that, once established near midden sites, *P. ponderosa* populations persisted and probably expanded. In most cases, the appearance of *P. ponderosa* was the most dramatic change in the midden series; the occurrence and abundance of other trees and shrubs were mostly stable throughout the late Holocene.

Midden Analyses

Black Hills

Pinus ponderosa populations have occurred in Redbird Canyon for at least the past 3850 years, and in the other two sites for at least the last 700–800 years (Fig. 2a). *Pinus ponderosa* macrofossils occur in the oldest middens at all three sites; the lack of older middens without ponderosa prevents us from specifying the time window for colonization. *J. scopulorum* occurs in most Redbird Canyon middens and *J. communis* occurs in nearly all Black Hills middens. *Picea glauca* is consistently present in Spearfish Canyon middens.

Table 2 Variables used to create distributional model and the direct or indirect modifications applied to each variable for each climate experiment. 'D' indicates that variable was directly affected and was recalculated, 'I' indicates variable was affected indirectly and was recalculated, '–' indicates no change to the variable.

	Modification				
Affected model variable	↓ June precipitation	↓ July precipitation	↓ Jan temperature	↓ Jan temperature ↑ July temperature	↓ July temperature
January temperature	–	–	D	D	–
April temperature	–	–	–	–	–
July temperature	–	–	–	D	D
January precipitation	–	–	–	–	–
June precipitation	D	–	–	–	–
July precipitation	–	D	–	–	–
Length of frost free period	–	–	–	–	I
Growing season precip (GSP)	I	I	–	–	I
GSP/Avg summer temperature	I	I	–	I	I
Roughness index	–	–	–	–	–

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East Flank, Bighorn Mountains

Middens from Crazy Woman Canyon and Slip Road document early to middle Holocene absence of *P. ponderosa*, which first appears 2630 yr BP at Slip Road (Fig. 2b). *Pinus ponderosa* occurs consistently in all younger middens, with two exceptions from Outlaw Cave. *Pinus flexilis* and *J. scopulorum* occur throughout the Holocene, and *C. ledifolius* occurs in almost all middens younger than 6000 yr BP.

West Flank, Bighorn Mountains

Pinus ponderosa is absent from all middens more than 1500 yr BP in age, and occurs in all middens < 1000 yr BP (Fig. 3). Earliest documented occurrences are at 1410 yr BP (Black Canyon) (Fig. 3b) and 1200 yr BP (Brokenback Narrows) (Fig. 3a). All middens at all sites contain macrofossils of *P. flexilis*, *J. scopulorum*, and, with one exception, *C. ledifolius* (Fig. 3). *Pseudotsuga menziesii* occurs in most high-elevational middens throughout the Holocene (Fig. 3a), and *J. osteosperma* is present at low elevations after 2460 yr BP (Fig. 3c).

Little Belt Mountains

Pinus ponderosa is absent from all middens older than 1000 yr BP, and present in all younger middens (Fig. 4a). *Pinus flexilis*, *P. menziesii*, *J. scopulorum* and *J. communis* have occurred at both Little Belt sites throughout the middle to late Holocene (Fig. 4a).

Big Belt Mountains

Temporal density in the Big Belt midden series is sparse (Fig. 4b). *Pinus ponderosa* first occurs 1460 yr BP, and is absent from the next-oldest midden at 4400 yr BP (Fig. 4b). *Pinus flexilis*, *P. menziesii*, and *J. scopulorum* occurred throughout the Holocene, while *C. ledifolius* was established in the late Holocene (Fig. 4b).

Bioclimatic Modelling

We ran sensitivity experiments to determine which climate variables might have contributed to the late Holocene expansion of *P. ponderosa* var. *scopulorum*. Of the five model experiments (Fig. 5), only two produced results consistent with the macrofossil record of this study: a decrease in July precipitation (Fig. 5b) and a decrease in July temperature (Fig. 5e). Under decreased July temperature, *P. ponderosa* var. *scopulorum* habitat largely disappears in central Montana and the Bighorn Mountains (Fig. 5e). Lower July temperature also excluded *P. ponderosa* from the cooler central part of the Black Hills, but not from the periphery, consistent with the macrofossil record of *P. ponderosa* presence in the Black Hills for the last 3850 years. The effect of July temperature change on *P. ponderosa* (Fig. 5e) can be interpreted as either a consequence of lower July temperature or of a shorter growing season and

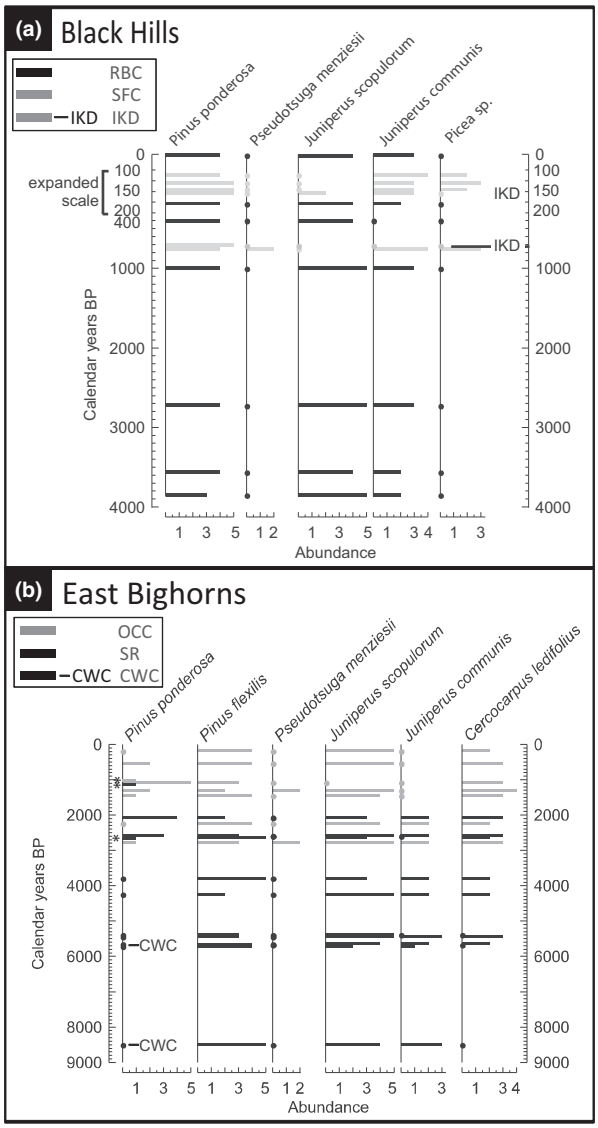

Figure 2 Macrofossil relative abundance data for (a) Black Hills sites. Redbird canyon middens shown with black symbols, Spearfish Canyon middens shown with grey symbols, Inyan Kara Drainage middens also shown in grey, but marked with 'IKD' and (b) Macrofossil relative abundance data for East Bighorns sites. Outlaw Cave Campground middens shown with grey symbols, Slip Road middens shown with black symbols, Crazy Woman Canyon middens also shown in black but marked with CWC. In both diagrams, filled circles designate absence. (*) indicates a radiocarbon date from a single ponderosa macrofossil found in a midden that contained no other ponderosa macrofossils.

reduced growing-season precipitation, both of which may be correlated with reduced July temperature.

Under decreased July precipitation, *P. ponderosa* var. *scopulorum* is excluded from most of central Montana and the Bighorn Mountains (Fig. 5b) but retained in the Black Hills. Because growing-season precipitation in the Bighorns and central Montana is dominated by May and June precipitation (see Appendix S1, Fig. S1.2), a 20% reduction in July precip-

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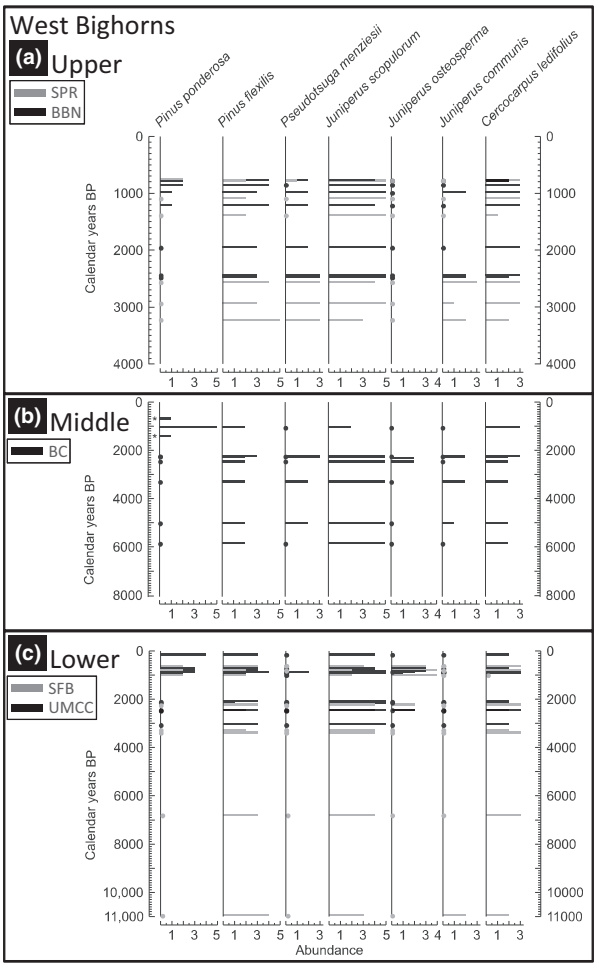

Figure 3 Macrofossil relative abundance data for sites on the west slope of the Bighorn. Mountains. (a) upper elevational sites: South Fork Paintrock (grey symbols) and Brokenback Narrows (black symbols) (b) middle elevation Black Canyon site (c) lower elevational sites: South Fork Brokenback (grey symbols) and Upper Military/Cottonwood/Creeks (black). Symbols as in Fig. 2.

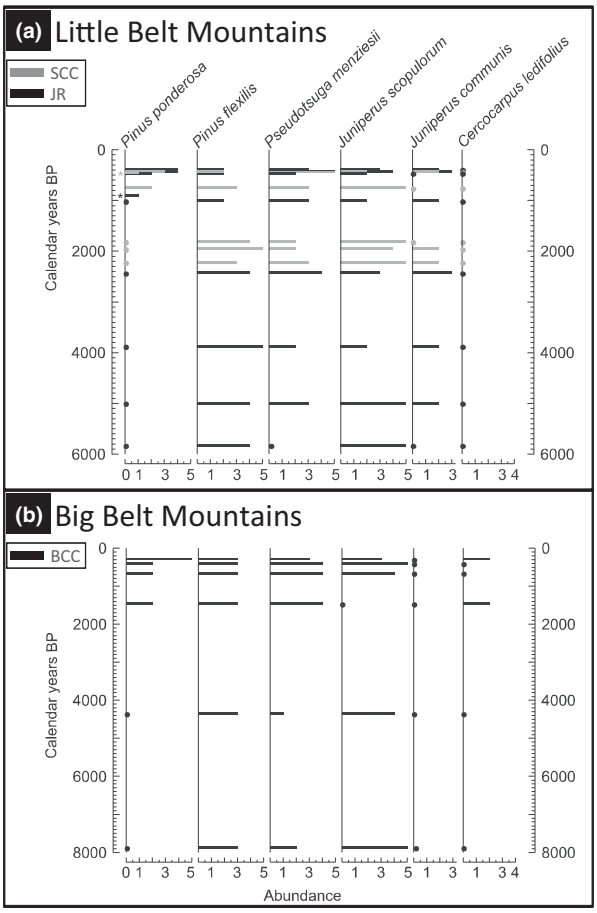

Figure 4 Macrofossil relative abundance data for the Little and Big Belt Mountains. (a) Little Belt Mountains sites: Spring Creek Canyon (grey symbols) and Judith River (black symbols). (b) Big Belt Mountains, Beaver Creek Canyon site. Symbols as in Fig. 2.

itation represents a relatively small decrease in growing-season precipitation and highlights the sensitivity of var. *scopulorum* populations there to late summer precipitation. This is not an unexpected outcome, as periods of moisture stress and moisture recharge are known to drive the growth of ponderosa and other western montane species (e.g. Williams *et al.*, 2013).

DISCUSSION

Ponderosa Pine Migration in the Central Rockies and Great Plains

The fossil record of *P. ponderosa* migration in western North America is incomplete and fragmentary (Fig. 1). The most complete records are from the Colorado Plateau region, which shows rapid northward expansion during the late-glacial and early Holocene (Fig. 1). In less than 5000 years, it expanded *c.* 500 km from the Arizona/Utah border to the Utah/Wyoming border at the north-eastern end of the Colorado Plateau (Fig. 1). Migration in the Southern Rocky Mountains and adjacent plains is poorly documented, but populations reached the CO/WY border no later than 5800 yr BP and likely earlier.

Between *c.* 6000 and 3000 years, the expansion stalled in the northern parts of its range in Wyoming and Montana. There, *P. ponderosa* first appeared at most sites between 1600 and 840 yr BP (Fig. 6). The combination of long delay in establishment followed by rapid expansion across a large area suggests expansion driven by climate rather than limitation by dispersal. Understanding this process requires examining our records in the context of the modern phylogeographical distribution of ponderosa pine and the Holocene expansion of *J. osteosperma* in the same area.

Comparison with phylogeographical records

Comparison of palaeoecological records with phylogeographical patterns enriches understanding of biogeographical

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history (Betancourt *et al.*, 1991; Jackson *et al.*, 2005; Magri *et al.*, 2006). Like many conifers, *P. ponderosa* phylogeography can be examined in detail thanks to paternal (pollen) inheritance of chloroplast DNA and maternal (seed) inheritance of mitochondrial DNA (mtDNA). According to Potter *et al.* (2013), three mtDNA haplotypes of *P. ponderosa* occur in our study region (Fig 1): H3, extending from south-eastern Arizona to the Bighorn Mountains, H6, occurring in the west-central Great Plains and Black Hills westwards to the Rocky Mountain fronts of Colorado, Wyoming, and Montana, and H8, ranging from the southern Cascades into Idaho and western Montana. Chloroplast and nuclear marker data suggest that the two varieties of *P. ponderosa* (var. *scopulorum* and var. *ponderosa*, respectively, represented by H6 and H8) hybridize (Latta & Mitton, 1999). Nevertheless, the two mtDNA haplotypes are clearly delineated in the introgression zone (Potter *et al.*, 2013).

Our midden sequences record movement of two haplotypes, H3 (Bighorns) and H6 (Bighorns, Black Hills and Montana). Mitochondrial DNA haplotype maps suggest a two-pronged, anastomosing migration of H3 and H6 (Fig 1).

The pattern of H3 expansion appears to be north and east in the Colorado/Green River drainage, potentially from glacial refuges in Arizona and New Mexico (Fig. 1). Haplotype 3 populations along the eastern front of the Rockies in Colorado and Wyoming may have been established by east-trending chains of long-distance dispersal colonization; isolated populations of *P. ponderosa* occur on the flanks of the Green and Seminoe Ranges of south-central Wyoming and the Park and western Front Ranges of northern Colorado (www.rmh.uwyo.edu). *Pinus ponderosa* is capable of population establishment and maintenance via long-distance dispersal events spanning 75–100 km (Lesser & Jackson, 2012, 2013). H3 established populations on the eastern slopes of the central Rockies from central Colorado to the Bighorns (Fig. 1) and is dominant in sampled populations from the Bighorns.

The pattern of H6 expansion appears to be northward east of the Rocky Mountain crest. Our records from the Black Hills show that *P. ponderosa* (today H6) was established by 3850 yr BP and probably much earlier. The central Great Plains and Black Hills might have served as source populations for Holocene spread of H6, but glacial-age occurrence of *P. ponderosa* in those regions is unlikely given colder conditions. A more likely scenario is post-glacial northward spread of H6 along the Rocky Mountain front from glacial-age sources in foothills of the Southern High Plains and the highlands of the Middle Rio Grande Basin (NM, TX, NE Mexico). H6 populations could have then spread north-westwards into Montana up the Yellowstone, Powder, and Missouri River valleys, which today support closely spaced populations along escarpments extending from north-eastern Wyoming all the way to the Big and Little Belt Mountains.

Our data imply either migration covering 300–350 km (direct distance) in 1000–1500 years (Fig. 6), or climate driven expansion from rare local populations established earlier by long-distance dispersal. The central Montana introgression zone between var. *scopulorum* and var. *ponderosa* (Latta & Mitton, 1999; Johansen & Latta, 2003) was established within the last 1500 years with the expansion of H6 (var. *scopulorum*) into the region. The recent establishment of the hybrid zone is consistent with molecular evidence (Latta & Mitton, 1999; Johansen & Latta, 2003).

Analysis of ancient DNA from macrofossils preserved in these and other middens might yield further details on the sequence and pattern of migration in the region, particularly if the haplotypes could be matched. Molecular studies with higher sampling density and perhaps different markers would be required to define the modern distribution within this region. Without this information, the migrational history remains speculative and the dominance of a haplotype in an area could result from either earlier establishment or higher suitability for local conditions.

The Parallel Expansions of *P. ponderosa* and *J. osteosperma*

Species migrations emerge from multiple processes, including propagule dispersal, population growth, species interactions, episodic disturbance and environmental heterogeneity in space and variability in time (Jackson *et al.*, 2009; Lesser & Jackson, 2012). These processes, particularly for woody plants, require years to centuries to unfold, which may obscure the ultimate causes. Timing of regional colonization events and subsequent infilling may lag onset of favourable climate by decades to centuries or more. In theory, lags can be identified by comparing migrational histories with independent palaeoclimatic reconstructions. This is frequently impossible, however, given a lack of 'master' palaeoclimate chronologies for most regions, incongruity among proxies and among sites within a region, age-model uncertainties for individual records, and differential sensitivity of palaeoclimate proxies and species ranges. The interior of western North America has numerous palaeoclimate records of various kinds, but they currently comprise a hodgepodge of often conflicting interpretations (see Cumming *et al.*, 2002). On the other hand, the migration of *P. ponderosa* in the region coincided with other migrations, other ecological transitions and climatic changes documented at other sites (Lyford *et al.*, 2002, 2003; Shuman *et al.*, 2009). We examine *J. osteosperma* in detail because it has an extensive Holocene midden record at or near many of the same sites we examined for *P. ponderosa*.

Juniperus osteosperma is a woodland species with climatic tolerances that only partly overlap those of *P. ponderosa* (Lyford *et al.*, 2003; Norris *et al.*, 2006) and a geographical range centred on the Great Basin, a region where *P. ponderosa* is conspicuously rare or absent (Fig 1). Both species migrated rapidly through Utah, reaching the Wyoming border in the early Holocene (9490 yr BP for *J. osteosperma* and 7250 yr BP for *P. ponderosa*) (Jackson *et al.*, 2005), and both expanded north in Wyoming via long-distance dispersal

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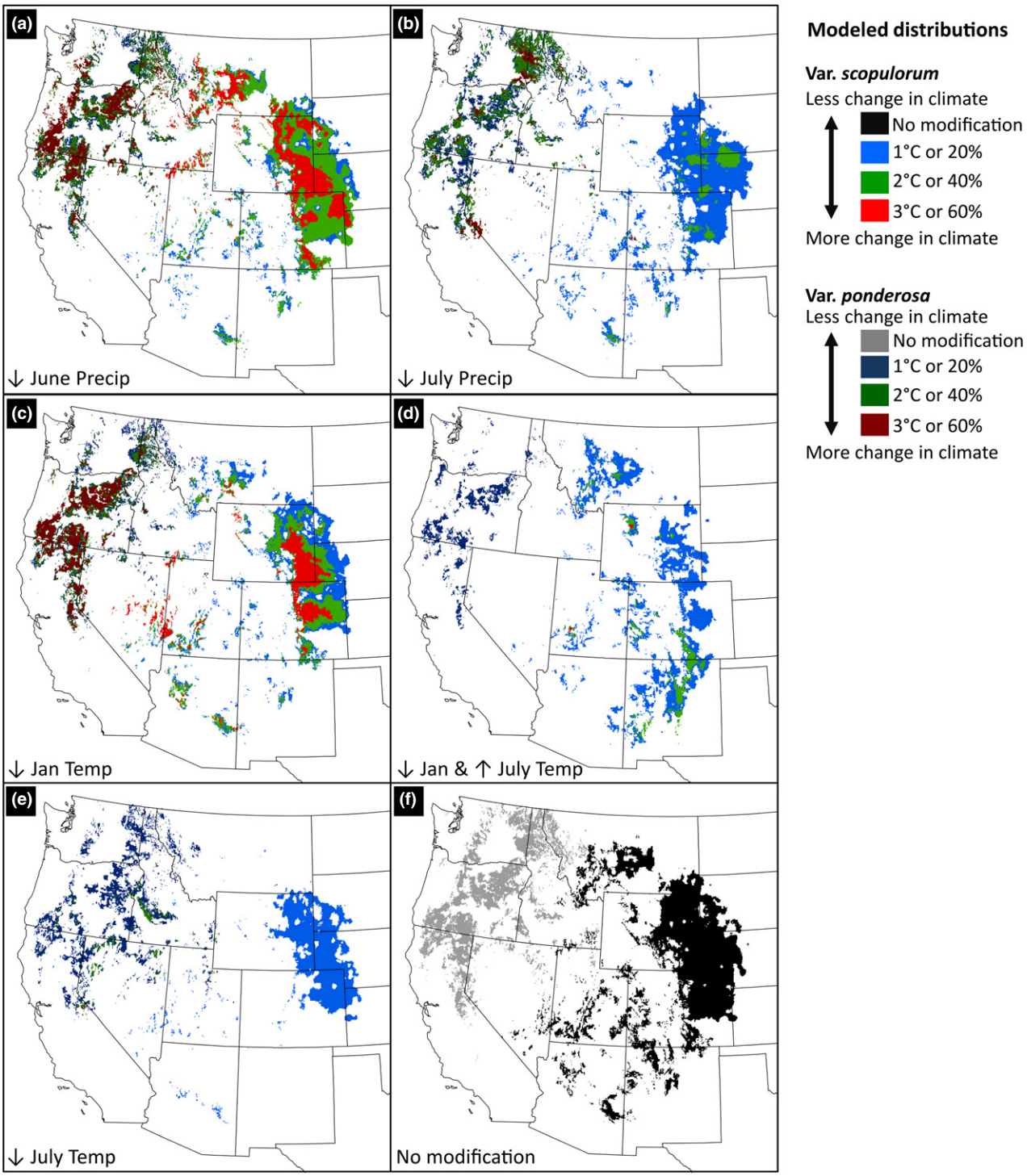

Figure 5 Predicted *P. ponderosa* habitat under varying climate conditions. Climate modifications as follows: (a) ↓ June Precipitation, (b) ↓ July Precipitation, (c) ↓ January Temperature, (d) ↓ January Temperature and ↑ July Temperature, (e) ↓ July Temperature, f) No temperature modification. Three levels of modification were applied: **blue** = 1° temperature change or 20% precipitation change; **green** = 2° temperature change or 40% precipitation change; **red** = 3° temperature change or 60% precipitation change. **Bright hues** show predicted habitat using model for var. *scopulorum*; **dark hues** show predicted habitat using model for var. *ponderosa*.

events in the early to middle Holocene. The latter pattern is best documented for *J. osteosperma*, which was established at both Mahogany Butte (WY) and East Pryor Mountain (MT) by 5400 yr BP (Fig. 6). The record for *P. ponderosa* is sparser, but its colonization at Fremont Canyon 6100 yr BP overlaps with the period of *J. osteosperma* migration. The northward migration during the early and middle Holocene (until *c.* 6,000 BP) is consistent with a pattern of higher

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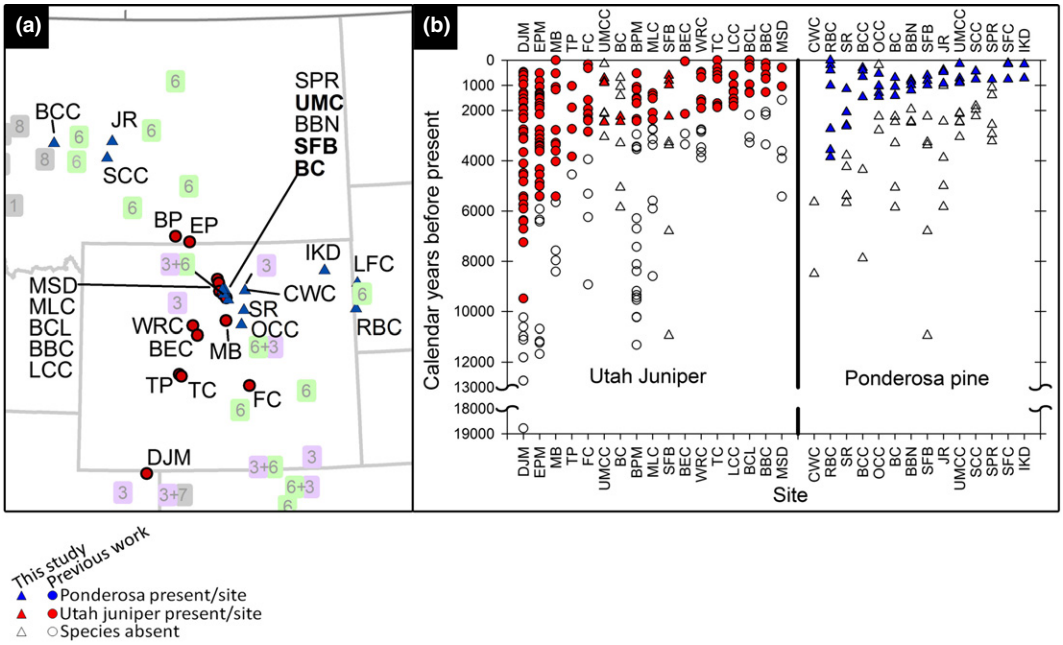

Figure 6 (a) Map showing location of midden series developed to reconstruct the migrational histories of *Juniperus osteosperma* (red circles; from Lyford *et al.*, 2003) and *P. ponderosa* (blue triangles; this study). Bold font denotes sites with records for both species. Modern haplotype populations (H1, H3, H6, H7, H8) plotted from Potter *et al.* (2013); (b) Record of *P. ponderosa* and *J. osteosperma* presence–absence from each site, filled symbols indicate presence, open symbols indicate absence.

temperatures during this time, as discussed for *J. osteosperma* by Lyford *et al.* (2002, 2003). Significantly, both migrations stalled between *c.* 6000–3000 yr BP. *Juniperus osteosperma* expansion resumed after 2800 yr BP (Fig. 6), colonizing and backfilling other sites in the eastern Bighorn Basin until *c.* 1000 yr BP (Lyford *et al.*, 2003). Resumption of *P. ponderosa* migration is first recorded 2600 yr BP with an establishment in the eastern Bighorns, and appearing at the other northern Wyoming and Montana locations between 1600 and 840 yr BP (Fig. 6). Although late Holocene *J. osteosperma* expansion in the Central Rockies may have commenced before that of *P. ponderosa*, the entire period of documented *P. ponderosa* expansion overlapped with that of *J. osteosperma* expansion, in some cases at the same sites (Fig. 6).

When *P. ponderosa* and *J. osteosperma* expanded their ranges to 40°N in the middle Holocene they also crossed a north–south dipole in regional precipitation (and snowpack) responses to Pacific climate variability that has existed for at least the last millennium (Dettinger *et al.*, 1998; Pederson *et al.*, 2011) and possibly longer (Mensing *et al.*, 2013; Shuman *et al.*, 2014). Lyford *et al.* (2003) suggested that *J. osteosperma* expanded across central Wyoming owing to warmer summers and perhaps winter drying. Warmer growing seasons may have triggered *P. ponderosa* expansion on the western slope of the Bighorns. Increases in summer precipitation may have aided the west and/or north-westward expansion of *P. ponderosa* into Montana.

Juniperus osteosperma and *P. ponderosa* were not alone in their northward migration during this time: Both *P. edulis* and *P. monophylla* expanded to their northernmost outposts on either side of the Rockies and north-eastern Great Basin, respectively, at the same time (Betancourt *et al.*, 1991; Gray *et al.*, 2006; Weppner *et al.*, 2013). *Ephedra* also colonized one of its northernmost sites today at Dutch John Mountain, coincident with colonization by *P. edulis*, another species displaced to the south during the late Pleistocene (Jackson *et al.*, 2005).

The northward expansion of multiple tree species despite different life histories, precipitation sensitivities, source populations, dispersal vectors and vagaries of midden occurrence and sampling is consistent with a rise in temperature. For individual species this may be mediated by changes in precipitation amount, seasonality, or frequency. Taken together, model results for *P. ponderosa* (Fig. 5) and *J. osteosperma* (Lyford *et al.*, 2003) and the migration history of both species suggest that a relatively small change in average climate (Fig. 5), or in its variance, can result in a large change in distribution of individual species (*P. ponderosa* and *J. osteosperma*), while resulting in few other changes in local vegetation composition (as evidenced by our midden records), a pronounced individualistic response and perhaps a lesson for the future.

Given the similarity in timing and direction for these migrations, and the likely role of increasing growing-season temperatures (or growing-season length), why is an obvious climatic trigger not clearly identified in other regional glacial, lacustrine and alluvial records? We suggest that this discordance is common across the regional amalgam of middle to late Holocene palaeoclimatic records. Until it is resolved, independent

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evidence of the climatic changes that modulated rapid advances and prolonged stillstands may remain elusive, not only in the Central Rockies, but elsewhere in North America.

Ongoing natural invasions: where are they going?

Late Holocene natural invasions of *P. ponderosa*, *J. osteosperma,* and other species are clearly ongoing, raising the question of where they might go in a rapidly changing world. Since 1850, roughly the end of the Little Ice Age, demographic and other evidence shows expansion and infilling of *P. ponderosa* across the forest-grassland ecotone in the Black Hills, the western Great Plains, and the Colorado Front Range (Steinauer & Bragg, 1987; Mast *et al.*, 1997; Brown & Sieg, 1999; Kaye *et al.*, 2010), and *J. osteosperma* has undergone widespread population infilling and territorial expansion at many individual sites (Lyford *et al.*, 2003). On the other hand, colonizing *P. ponderosa* populations stopped expanding in the Bighorn Basin in the same interval (Lesser & Jackson, 2012). The extent that these patterns can be attributed to climate or historic land use is undetermined.

Future changes in the distribution of ponderosa pine will depend in large part on the nature and pace of climate change in the region (principally warming) and on the successful dispersal of adapted haplotypes. Rehfeldt *et al.* (2014) applied a multimodel ensemble to climatic envelopes of both *P. ponderosa* varieties for representative concentration pathway (RCP) 6.0 (one of four greenhouse gas concentration trajectories adopted by the Intergovernmental Panel on Climate Change; in RCP 6.0, concentrations peak around 2080, then decline). By 2060, projected losses in niche space at lower elevations for var. *ponderosa* will be balanced by gains at higher elevations and to the north (Fig. 5 in Rehfeldt *et al.*, 2014). However, var. *scopulorum* is projected to lose half of its niche space. In the central Rockies, the largest losses of niche space are in the scarp woodlands of the Greater Platte River Basin, the lower elevations of the Black Hills and the across the hills and tablelands of south-eastern and central Montana, including the modern var. *ponderosa* × var. *scopulorum* introgression zone. The main areas for projected expansion of var. *scopulorum* include the western slopes of the Bighorn Mountains in Wyoming, and the foothills of the Canadian Rockies east of Banff, Alberta.

This study demonstrates that late Holocene expansion in the Central Rockies has been slow on a human time-scale, taking millennia regionally and centuries locally. If expansion to newly available climatic niches is to be realized within modern management timeframes (the next century), its translocation could be assisted by deliberate planting of suitable genotypes of var. *scopulorum*. Similarly, in other parts of the range of *P. ponderosa*, revegetation with genotypes adapted for the future climate (Rehfeldt *et al.*, 2014) may be justified, given the rapid pace of expected climate change in comparison to the species' dispersal capabilities.

Finally, the early signs of ongoing and future migration may be structural changes in woodlands and forests, for example densification of *P. ponderosa* where it is was present but less common before. Current and future land use, cheatgrass (*Bromus tectorum*) invasion and novel fire dynamics may now interact with climatically driven *P. ponderosa* migration, affecting both fragmentation and dispersal modes and pathways for *P. ponderosa* in the central and northern Rockies.

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SUPPORTING INFORMATION

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

Appendix S1 Table S1.1. Locations and sources for earliest records of *P. ponderosa* mapped in Fig. 1; Table S1.2. Modern abundances of major taxa present at midden sites; Figure S1.1. Modified Walter-Lieth climate diagrams; Figure S1.2. Map of western North America showing per cent of annual average precipitation falling in the summer months (April–September).

Appendix S2 Table S2.1. Radiocarbon ages and plant macrofossil abundances for all middens in this study.

BIOSKETCHES

Jodi Norris is broadly interested in the biogeography and conservation biology of plants and animals, particularly as they relate to protected areas in western North America. She began this study as part of her doctoral dissertation in the Jackson Lab at the University of Wyoming.

Julio Betancourt studies patterns, sources and impacts of climate variability on ecological, geomorphic and hydrological systems at scales critical for understanding natural processes and informing resource management.

Stephen T. Jackson studies ecological responses to environmental change and variability, and their implications for natural-resource management.

Author contributions: J.R.N., J.L.B. and S.T.J. designed the study, and J.R.N. performed much of the initial research. J.R.N., J.L.B. and S.T.J. contributed equally to the writing.

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